Durham University

Durham E-Theses

Phytosociological studies on rich fen systems in England and Wales

Bryan D. Wheeler

How to cite:

Wheeler, Bryan D. (1975) Phytosociological studies on rich fen systems in England and Wales. Doctoral thesis, Durham University.

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a https://etheses.durham.ac.uk/id/eprint/10390/ is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the full Durham E-Theses policy for further details.

Academic Support Office, The Palatine Centre, Durham University, Stockton Road, Durham, DH1 3LE
e-mail: e-theses.admin@durham.ac.uk Tel: +44 0191 334 6107
https://etheses.durham.ac.uk

The copyright of this thesis rests with the author. No quotation from it should be published without his prior written consent and information derived from it should be acknowledged.

PHYTOSOCIOLOGICAL STUDIES ON RICH FEN SYSTEMS IN ENGLAND AND WALES

BY

Bryan D. Wheeler (B.Sc. Dunelm)

A Thesis

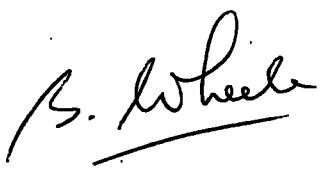
submitted for the degree

of Doctor of Philosophy

in the University of Durham.

Department of Botany. August, 1975.

Except for text references to publications, the content of this thesis is entirely my own work. It has not previously been submitted for any degree or diploma



Bryan D. Wheeler.

August 1975.

CONTENTS

Volume 1

Abstract i

Conventions and terms iii

Acknowledgments vi

PART I. The Context

Chapter 1: Introduction 1

1.1. Introduction 1
1.2. The aim of the project 8
1.3. The concepts of phytosociology 10
1.4. The concept of rich fen 17
1.5. Work on rich fen plant communities in England and Wales 24

Chapter 2: Syntaxonomic categories of rich fen vegetation 30

2.1. Phragmitetea 31
2.2. Parvocaricetea 37
2.3. Scheuchzerietea 41
2.4. Molinio-Arrhenatheretea 43
2.5. Franguletea 49
2.6. Alnetea glutinosae 50

Part II. The Methods

Chapter 3: Some methodological approaches to a phytosociological survey 52

3.1. Introduction 52
3.2. Sampling procedures 55
3.3. The extraction of units of vegetation 62
3.4. Units of vegetation 83

Chapter 4: The methods used 88

4.1. The sites examined 88
4.2. Sampling strategy 89
4.3. Computer-based classificatory procedures 94
4.4. A comparison of clustering strategies 99
4.5. The strategy for extracting vegetation units 105
4.6. Syntaxonomic work 108

Part III. The Vegetation

Chapter 5: Rich fen systems in England and Wales 111

5.1. Morphological categories of rich fen 111
5.2. Norfolk and Suffolk 112
5.3. Cambridgeshire and Huntingdonshire 120
5.4. The South Midlands 121
5.5. Southern England 123
5.6. S.W. England and S. Wales 125
5.7. Central England 126
5.8. North Wales 128
5.9. Northern England 130
5.10. Southern Scotland 134

Chapter 6: The plant communities of rich fen 136

6.1. Group 1. Sedge swamp communities 138
6.2. Group 2. Cladium-Phragmites vegetation 169
6.3. Group 3. Species-poor tall fen communities 210
6.4. Group 4. Communities of calcareous mires 222
6.5. Group 5. Carex diandra-lasiocarpa-rostrata communities 293
6.6. Group 6. Rich fen meadow communities 324
6.7. Group 7. Molinia caerulea communities 370
6.8. Group 8. Epilobium hirsutum - Filipendula ulmaria tall herb fen communities 396
6.9. Group 9. Mire forest communities 402

Chapter 7: The rich fen circle of vegetation 441

Discussion 441
Summary 470

References 478

Appendix 1. The syntaxonomy of the higher vegetation units of rich fen and related wetland types.

Volume 2

Phytosociological tables

List of text figures

Fig. 4.I.	p.91
Fig. 4.II.	p.91
Fig. 4.III.	p.94
Fig. 4.IV.	p.104
Fig. 5.I.	p.113
Fig. 6.1.I.	p.146
Fig. 6.2.I.	p.173
Fig. 6.2.II	p.173
Fig. 6.4.I.	p.223
Fig. 6.4.II.	p.259
Fig. 6.5.I.	p.293
Fig. 6.6.I.	p.431
Fig. 6.6.II.	p.326
Fig. 6.6.III	p.336
Fig. 6.6.IV.	p.338
Fig. 6.7.I.	p.376
Fig. 6.9.I.	p.402
Fig. 7.I.	p.440
Fig. 7.II.	p.455

Tables

Tab. 4.1.	p.101
Tab. 4.2.	p.102

"In earthly mire, philosophy may slip".

Sir Walter Scott: 'The Poacher'

ABSTRACT

The thesis presents an attempt to detect, define and characterise, on the basis of their floristic composition, the principal types of rich fen vegetation in lowland England and Wales.

Some 1,000 samples were taken from a wide variety of rich fen systems throughout England and Wales and from one area in S. Scotland, by a subjective procedure based upon stand selection. A computer-based system was developed to handle these data combining both numerical and traditional (Zürich-Montpellier) methods of analysis. The data were processed by normal and inverse Information Analysis in conjunction with a computer-assisted hand-sorting routine leading to the production of structured species-sample tables.

One hundred and eight noda were identified and described and compared with related units recognised from Britain and N.W. Europe. Sixty eight were arranged into 11 Associations of which 4 represent new syntaxa. The remainder were placed into sociations or left as noda of uncertain status. The communities were all classified into higher syntaxa essentially following the scheme advocated by WESTHOFF & DEN HELD (1969). The Classes and Alliances used to contain the communities are:

Phragmitetea	Phragmition reedswamp communities
	Magnocaricion tall growing sedge and reed fen vegetation of topogenous mire
Parvocaricetea	Caricion davallianae low-growing sedge vegetation of calcareous mire
Molinio-Arrhenatheretea	Calthion palustris fen meadow vegetation
	Molinion caerulea Molinia-dominated fen grassland
	Filipendulion species-poor, tall herbaceous vegetation of eutrophic mires
Franguletea	Salicion cinereae fen scrub communities
Alnetea glutinosae	Alnion glutinosae alder carr vegetation

The new Associations described are the Peucedano-Calamagrostietum canescentis of the Magnocaricion; the Schoeneto-Juncetum subnodulosi of the Caricion davallianae; and the Crepido-Salicetum pentandrae and the Betulo-Dryopteridetum cristatae, both of the Franguletea.

A short account of the occurrence of rich fen systems in lowland England and Wales is given.

A brief discussion of the rich fen circle of vegetation in lowland England and Wales is also given.

Reference:

WESTHOFF, V. & A. J.DEN HELD (1969). Plantengemeenschappen in Nederland. Zutphen.

CONVENTIONS AND TERMS

Species nomenclature

Unless otherwise indicated species nomenclature has following these authorities:

Phanerogams: DANDY, J. E. (1958). *List of British Vascular Plants*. Br. Mus. Nat. Hist., London.

DONY, J. G., C. M. ROB & F. H. PERRING (1974). *English names of Wild Flowers*. London.

Gymnadenia conopsea var. *densiflora* is abbreviated to *Gymnadenia densiflora*; *Galium palustre* ssp. *palustre* is referred to as *Galium palustre* and ssp. *elongatum* as *Galium elongatum*.

Mosses: WARBURG, E. F. (1963). *Census Catalogue of British Mosses* (3rd ed.). Brit. Bryol. Soc., Ipswich.

Liverworts: PATON, J. A. (1965). *Census Catalogue of British Hepatics* (4th ed.). Brit. Bryol. Soc., Ipswich.

Lichens: JAMES, P. W. (1967). *A New Check-list of British Lichens*. The Lichenologist 3, 95-153.

Phytosociological tables.

In the phytosociological tables in Volume 2 the species names have been abbreviated. Each has been given a reference number and in case of confusion or ambiguity there is a listing of the full names of the species, together with their reference numbers, which should be consulted.

In the releve tables the characters displayed refer to cover-abundance values; in the synoptic tables they represent presence classes. Here, if more than 5 releves contribute to a particular synoptic list the presence values are printed in Roman numerals. An exception to this is in the full synoptic data table (Table A) where Roman numerals are not used at all.

In the text, Associations, sociations and other comparable syntaxa are underlined with a single dashed line; higher order units (Alliances and above) are underlined with a double dashed line.

Wetland terminology and conventions

The following definitions have been used:

bog - ombrotrophic peatland (sensu DU RIETZ, 1949; 1954).

carr - fen woodland.

fen - minerotrophic wetland (sensu DU RIETZ, 1949; 1954), with a summer water-table at, or below, the surface.

fen grassland - relatively dry, grass-dominated areas associated with fen systems.

fen meadow - fen areas that are grazed or mown wet to damp, rush or sedge-dominated with a good representation of grassland (Molinio-Arrhenatheretea) species.

marsh - a general term for semi-terrestrial waterlogged areas.

mire - a general term for semi-terrestrial waterlogged areas.

moss - ombrotrophic peatland.

rich fen - see 1.4. (more or less sensu DU RIETZ, 1949; 1954).

swamp - wetland with a summer water-table constantly above the surface of the substratum.

wetland - a general term for wet areas, including swamp.

eutrophic; oligotrophic - refer to the nutrient richness of the substrate.

Note also this convention: when dealing with zonations around pools, mires etc. inner zones are developed towards the aquatic side, whilst outer zones are the more terrestrial.

ACKNOWLEDGEMENTS

I am deeply indebted to many people for help given during the period of the research that is recorded in this thesis. In particular, many thanks are due to Dr. and Mrs. E. A. Ellis of Wheatfen, for much help and hospitality and for fruitful discussions on the vegetation of broadland; to Dr. D. Gunton for introducing me to the gentle art of writing computer programs; and to the staff of the Durham Computer Unit for elucidating why they would not work! To the Reverend G. G. Graham for assisting in the determination of some of the bryophytes; to the staff of Durham University Library for their diligence in tracing diverse obscure journals; to Professor D. Boulter for providing the facilities for the research; to the University of Durham for a Research Studentship and for contributing towards the travelling expenses; to Miss M. Berryman for her co-operation and perseverance in typing the thesis; and to the botanists too numerous to mention, who provided detailed information concerning the location of rich fen systems.

Thanks are due also to Mr. R. Maycock of Bletchley for many enjoyable days in the field; to Mr. and Mrs. R. Burgess of Chester for much hospitality; and to all colleagues and friends in Durham for their forebearance and help.

Finally, particular thanks are due to Dr. D. J. Bellamy for his enthusiasm and encouragement throughout the work; and also to my parents, without whom the project would never have been started.

PART I: THE CONTEXT

Chapter 1.

Introduction.

1. Introduction

1.1. Introduction

In post-glacial times the wetland habitat has played a prominent part in the physiographical evolution of the landscape of lowland England and Wales. 'Indeed we may picture the flatter lowlands of post-glacial Britain as studded with lakes and meres bordered by wide stretches of swamp, marsh and fen' (TANSLEY, 1939). And, elsewhere also, wetland was extensively developed wherever circumstances led to waterlogging of the ground, especially along badly-drained valleys and in glacial hollows.

WILCOX (1933) has compiled a tentative map to illustrate the distribution of marshlands in prehistoric England. She shows extensive wetlands developed along the lower reaches of many river valleys, especially near to the estuaries, as with the River Mersey or the Solway Firth. But the largest areas shown are those associated with the flat alluvial plains of eastern England that are only a few feet above the level of the sea. Most notable of these is the Fenland basin of East Anglia - a vast area of some 1,500 square miles, developed around the lower reaches of the Rivers Witham, Welland, Nene and Ouse, as they drain down to the Wash. There are many other areas too - the river valleys of east Norfolk, the eastern margins of Lincolnshire, parts of south

DURHAM UNIVERSITY
20 JAN 1975
SCIENCE LIBRARY

Yorkshire around the Humber estuary - that are similarly flat and low-lying and have supported an extensive wetland habitat.

In the early post-glacial period, however, some of the largest areas of wetland were most probably outside of the present coastline of England and Wales. Deposits of peat trawled from the floor of the southern North Sea have been shown to have formed in the pre-boreal and early boreal periods, some 10,000 years ago (GODWIN & GODWIN, 1934). It would seem likely that at that time the present floor of this part of the North Sea was a swampy region of forests (birch and pine) and fens developed around the estuaries and deltas of the Rhine and the rivers of eastern England. As, however, the work of GODWIN & CLIFFORD (1938) and GODWIN (1941a) has indicated, by contrast the Fenland basin of East Englia at that time was probably still relatively dry - an area of pine and birch forest developed on the Jurassic clays and Gault that constitute the bedrock of the basin, or on the boulder clays and gravels that had been deposited over them. Areas of wetland were then largely confined to river channels and depressions. The same appears to have been the case for the river valleys of East Norfolk. At some stage, most probably between 7,000 and 5,500 B.C., the wetlands of the southern North Sea were submerged by a rapidly-rising sea-level. However, the Fenland basin seems to have remained relatively well drained, until about 3,000 B.C. when the continuing rise of the level of the sea relative to the land

(most probably a result of isostatic downwarping of the land rather than a eustatic rise in sea level (WILLIS, 1961)), caused deterioration of the drainage of the basin and the establishment of wet conditions over large areas. Thus, during Neolithic times gradual waterlogging of the surface led to the accumulation of fen peat and the destruction of the woodlands. Soon, however, much of this lower fen peat itself came to be inundated by the continuing marine transgression and this caused all but the margins of the basin to be covered with a deposit of fen clay. A contemporaneous deposit of marine clay occupies the lower reaches of the east Norfolk rivers. But with the eventual regression of the sea, in the early Bronze Age fens and fen-woods re-established themselves and, in some places at least, subsequently gave way to the development of acidic raised bogs on top of the fen- and brushwood-peats. However, near the coastal margins of the basin this also came to be terminated in Romano-British times by a further marine transgression, probably of eustatic origin (WILLIS, 1961), which deposited an extensive band of silts around the Wash (and which, further inland, led to a swamping of the peat surface). Similarly, in the valleys of East Norfolk, there is an extensive deposit of upper clay, representing this same transgression.

In these vicissitudes of the Fenland mention has already been made of the development of acidic peat in certain places. This has also occurred in many other wetland areas too, where,

very often, the occurrence of basiphilous vegetation has only been as a precursor to the development of extensive cupolas of acidic peat. GODWIN (1941b; 1948) has shown this for part of the Somerset levels (a flat plain just above sea level bordering the Severn estuary). Here, at about 3,500 B.C., peat started to accumulate upon the waterlogged surface of the marine clays that filled the valleys. This was fen peat, derived from vegetation of sedges and reeds and, in places, from fen woodland. However, this basiphilous vegetation subsequently came to be replaced by the development of acidic wetland types leading to the formation of extensive areas of acidic raised bog on top of the fen peat (though as it happened, subsequent floodings of the bog surfaces by calcareous water (see CLAPHAM & GODWIN, 1948) did, in fact, permit the transient re-establishment of basiphilous wetland vegetation, at least in some places). This replacement of fen vegetation by that of acid bog has occurred in many wetland systems and seems to represent the natural ontogenesis of mires (WEBER, 1908) - at least in suitable climatic regions (BULOW, 1929; BELLAMY, 1972). Thus, many former areas of fen have developed into raised bog, though fen has sometimes been able to persist, as part of a dynamic developmental complex, in peripheral areas or as "fen windows" within the mire.

However, in addition to purely natural factors determining the extent and nature of the mirelands, one influence that has had enormous effects has been that of man. Returning to the

Fenland basin of East Anglia, it is evident that here Mesolithic and Neolithic man was present in the forests prior to the onset of peat-formation. Subsequently, however, the development of a waterlogged environment proved to be inhospitable. Again, towards the end of the Bronze Age, when the peat surface became much drier and forest re-established, numerous artefacts indicate that man was once more active in the area. This, however, does not appear to have been true of the Iron Age cultures, even though the Fenland waterways provided the routes for their entry into Britain. Presumably, by this time the peat fens were once again too wet.

The deposition of silts around the Wash during the Romano-British marine transgression provided a favourable environment for agriculture and during Roman times the area became quite thickly populated. It is still only becoming apparent just how extensive the Roman influence actually was, but it most certainly extended well into the peat fens where it is evident that drains were cut - probably for transport as well as for drainage (see SALWAY et al., 1966). However, it was not until the seventeenth century that the Company of Adventurers was formed and the systematic reclamation of the fens began under the influence of the Earl of Bedford and the Dutch engineer, Vermuyden (see DARBY, 1956). The last meres were drained in the mid-nineteenth century.

This reclamation of vast tracts of fen for agricultural land is paralleled in most of the other large wetland areas of lowland England. Thus, the marshy expanses which once occupied the floor of the Vale of Pickering no longer exist. The flat levels of Holderness support agricultural land. An important exception, however, is to be found in the river valleys of East Norfolk. Most certainly here large areas of former wetland have been embanked and drained and converted into extensive grazing levels, especially in the lower reaches of the valleys. But there also remain considerable areas of undrained, unembanked, sodden fens.

Apart from the Norfolk Broads area, however, the most extensive remnants of fen today persist in what were once some of the smallest sites: in small valleys, in shallow fen basins. They sometimes represent "Poor's fens" - areas of Common land or Lammas ground, left unreclaimed perhaps because they were particularly inimical to drainage. Nonetheless, these unreclaimed areas still have had a long history of exploitation. The deep basins of the Norfolk broads have been shown to be the fruits of a vast medieval peat industry (see LAMBERT et al., 1960), and, as well as these, it would seem likely that shallower peat cuts have also been made over nearly all of the surface of these fens. Similarly, elsewhere there are very few extant peat fens that have not been used for turbary at some time. The fens have been used

in other ways too: as mowing marshes providing thatch, litter and hay; as a source of osiers; or as rough grazing for cattle and other stock. These various activities have clearly had a profound effect upon the vegetation of the fens. Mowing and grazing have served to maintain herbaceous fen communities in areas that otherwise would be fen carr; peat cutting has helped to maintain open habitats and has provided areas of free water to serve as a template for renewed hydroseral development.

It is evident that in at least some of the sites that remain there have been considerable changes in the vegetation cover during recent times, mainly towards a diminution in floristic diversity. In some places this has been due to the depredations of man, such as attempted drainage schemes etc. though in others it seems to have been more as a result of the curtailment of human activity. The establishment of fen carr vegetation on abandoned mowing marshes is a clear example of this, but others may also be cited. Thus, the present rarity of plants such as the fen violet (Viola stagnina) or the fen orchid (Liparis loeselii) may perhaps be attributed to a lack of disturbance, in particular the cessation of peat working (WALTERS, 1965). Because of the absence of detailed descriptive material it is difficult to assess the extent to which present-day vegetation of fen systems has changed from, say, seventy years ago. However, a number of the species given by PALLIS (1911) as being characteristic

of the east Norfolk fens most certainly are not so now. And comparisons of earlier records from sites (as in local Floras etc.) with current ones points to the loss of a number of species from many places, even though the cause of extirpation is often by no means obvious.

Currently, the extent of fen vegetation in lowland England and Wales continues to diminish as even further sites are reclaimed so that in some areas it is now represented only by a few square metres of waterlogged ground around a calcareous spring. And, although a number of fen systems have been incorporated into nature reserves and in some sense conserved, nonetheless many, if not all, still remain subject to some more insidious threats - the possibility of a general reduction in the height of the water-table; the inflow of agricultural chemicals into the systems; and, by no means least, the economics of maintaining the requisite strategy of management.

1.2. The aim of the project.

In the light of the continuing destruction and modification of fenland areas in Britain and the consequent affects upon both the individual plant species and the vegetation as a whole; and also in the absence of any comprehensive description of fen vegetation from England and Wales, it was felt that the time was opportune for a descriptive survey to

be made.

The precise aim of the survey may be formulated as follows: to detect, define and characterise, on the basis of floristic composition, the principal types of rich fen vegetation in lowland England and Wales.

It was recognised at the outset that it might be useful if the results of this survey could be related to those obtained from similar work on rich fen vegetation elsewhere in Western Europe. It was also recognised that the results could be useful in a variety of contexts. In particular, such a survey might be able to provide:

(a) a basis upon which the extracted vegetation-types could be further described by criteria other than floristic composition;

(b) an assessment of the sociological amplitude of the species of rich fen;

(c) a context within which further phytosociological and ecological studies on rich fen vegetation and plants could be made;

(d) a means of entry into the wider eco-sociological problems of rich fen vegetation;

but such objectives were to be purely derivative from the primary aim of the project.

In particular, this survey was <u>not</u> designed to fulfil

some of the objectives that are sometimes associated with "phytosociological surveys", namely:

(a) the description of the entire vegetation cover of individual sites;

(b) a description of the vegetation-types in terms of plant material parameters such as species abundance or performance, structure, physiognomy, phenology etc., or in terms of their syndynamics;

(c) a characterisation of the vegetation-types in terms of environmental parameters.

It was felt that these more detailed studies could more appropriately be performed subsequent to an initial descriptive survey aimed at extracting the main vegetation units.

1.3. The concepts of phytosociology

Plants only occasionally grow as isolated individuals. More usually they are found in some degree of spatial association with other plants - either of the same or of different species. The corporate growth of plant material over the earth's surface constitutes vegetation. Phytosociology (or phytocoenology) may be regarded as a "science of vegetation" concerned with the social organisation of plants. In its widest sense therefore it encompasses the whole range of vegetational phenomena: structure, morphology and dynamics, as well as

inter-relationships with the associated environment. Frequently, however, the term is just used to refer to some form of description of vegetation. This may be an intensive study of a restricted area aimed at describing the organisation, interactions and dynamics of a particular vegetational system. Or, it may take the form of an extensive study aimed at examining the inter-relations between different samples of vegetation. This approach is often associated with the attempt to define and delimit different types of vegetation for the purpose of characterisation and systematisation and corresponds with the aim of the present work.

1.3.1. The nature of vegetation: the plant community.

The nature of vegetation is defined by its component plant material. The basic unit of plant material is the species and vegetation may be usefully regarded as an interacting system of species-populations. The distribution of species-populations is a function both of their availability and their ecological amplitude. The first is determined by historical and geographical factors; the second by their genetically determined response to the environment (which includes both the abiotic status of the site, together with the biotic influence of other organisms).

Within a particular landscape the species-population are usually not distributed either uniformly or randomly but

instead are restricted to certain sites. This imparts a pattern to the vegetation which tends to be expressed by the recurrence of particular combinations of species in association with one another and hence by the differentiation of the vegetation cover into a patchwork of vegetational types which can be identified by their floristic composition and appearance. This patterning has led to the concept of the plant community.

The plant community (Pflanzengesellschaft Germ.) is a fundamental concept of plant sociology but disagreement as to the precise meaning of the term has engendered both controversy and confusion. It has been used in two very different ways. Sometimes it has been used to refer to a particular portion of vegetation occupying real space. This is the "real" or "concrete" community - the chorological unit of the plant cover - and related concepts are those of the stand and the phytocoenose (WESTHOFF, 1951). Alternatively, the term may be used to denote some unit of vegetation that has been abstracted from samples of "real" vegetation. This is the "abstract" community - a phytosociological concept - and it is related to the terms community-type (WHITTAKER, 1962), nodum (sensu POORE, 1956) and phytocoenon (WESTHOFF, 1951). Often authors have used the expression in an ambiguous way or as a general term referring both the chorological and phytosociological entities.

1.3.2. The chorological plant-community: the stand.

Some attention has been given to the way by which vegetation varies spatially. TANSLEY (1939) represented many other European ecologists in suggesting that "fundamentally the vegetation of the world is a mosaic of plant communities, whose distribution is determined by a corresponding mosaic of habitats" (p.216). Various workers have pointed towards the occurrence of relatively homogeneous areas of vegetation (stands) separated by relatively narrow transitional zones (boundaries) (e.g. GLEASON, 1939; DU RIETZ, 1921; POORE, 1955b; DAHL, 1957). The concept of homogeneity within a stand has been examined by DAHL & HADAC (1949), GOODALL (1954b), DAHL (1957), BARKMAN (1968). DAHL & HADAC define homogeneity as being when the individuals used for the characterisation of a community are homogeneously distributed - i.e. when the possibility of finding them is the same throughout the sample areas. They feel, however, that plant communities are never fully homogeneous.

There is much evidence to indicate that the distribution of plant species within a stand is not random: though as has often been recognised (SKELLAM, 1952; POORE, 1962) the pattern of species' distribution depends upon the scale at which it is being examined. CLAPHAM (1936) and DAHL (1957) have both recognised normal-, under- and over-dispersion of species in a wide range of vegetation types and with the

development of the technique of pattern analysis (GREIG-SMITH, 1952; KERSHAW, 1957) it has become evident that various types of pattern can be detected within vegetation.

Related to this is the phenomenon of mosaics. ROUSSINE & GOUNOT (1957) define a mosaic as "... a more or less regular alternation of components of restricted dimensions and different floristics". Such mosaics seem to be quite common in natural vegetation and examples have been given by WATT (1947), POORE (1955b) and BARKMAN (1968).

Thus, within the stand patchiness of various kinds can often be discerned. It is evident that true homogeneity rarely occurs but nonetheless, as POORE (1962) points out it often seems possible to recognise relatively homogeneous stands of vegetation in which the internal variation is small compared to that between stands. Such vegetation may be described as uniform.

The concept of uniform stands implies the occurrence of transitional zones and boundaries. DU RIETZ (1921) observed that "boundaries are, as a rule, astonishingly sharp and distinct .... diffuse boundaries .... of sites with continuous change in environmental factors - have not yet been found in any exactly analysed case ..." . TANSLEY (1939) also recognised ecotones bounding stands but points out that there is considerable variation in the sharpness by which they are delimited. The occurrence of sharp boundaries has been

widely recognised by others (e.g. WHITTAKER, 1956; DAHL, 1957). However, boundaries are not always sharp and the transition between stands may be gradual. For these situations the term ecocline (MAAREL & WESTHOFF, 1964) seems to be appropriate.

In contrast to these viewpoints various workers (e.g. GLEASON, 1917; GOODALL, 1954b; WHITTAKER, 1956; CURTIS, 1959) have emphasised the essential continuity of stands of vegetation. Whilst recognising that uniform stands with some sort of boundary can occur, WHITTAKER (1956) has demonstrated a gradual transition between stands along a continuous environmental gradient. He concluded that both continuity and discontinuity could be observed in vegetation. It is uncertain as to which represents the most "natural" situation. Both TANSLEY (1939) and DAUBENMIRE (1966) suggest that undisturbed vegetation is more distinctly discontinuous than disturbed. But WHITTAKER (1970) recognises continuous variation between intergradation between undisturbed stands and both GOODALL (1954b) and ANDERSON (1965) relate clear differentiation of stands to disturbance.

1.3.3. The phytosociological community: the phytocoenon.

Various analogies have been used to express the type of variation that may be observed between a set of stand samples. WEBB (1954) expressed it as an intergrading "spectrum".

POORE (1956) suggested a multidimensional "net" of variation, in which each community-type is represented by a knot connected to the others by strings. GOODALL (1954b; 1963) has proposed a geometric model in which samples may be represented as points in a multidimensional hyperspace in which the axes represent the variables specifying the stands (e.g. the species recorded). This abstract space has been termed vegetational space. The distribution of the cloud of points within this will depend upon the nature of the samples. Thus, samples with recurring species combinations will form a cloud of high density; samples with rare combinations of species will occupy peripheral areas of lower density. GOODALL (1963) relates various possible distributions of points in vegetational space to different ideas as to the inter-relationships between stand samples. A continuous, asymmetric cloud, representing a continuously changing vegetation may be referred to as a continuum. Pronounced discontinuity may be expressed as a series of clusters which, if they are fairly homogeneous, will be hyperspherical or isodiametric.

The question as to whether abstract vegetational data form a continuum or discrete units has long been debated. On the one hand, continua have often been recognised (e.g. WHITTAKER, 1956) and, although POORE (1955c) recognised community-types, he also found that some types formed a floristic series and felt it more logical that all community-types could be thus

arranged. McVEAN & RATCLIFFE (1962) also suggest that "variation in Highland vegetation is virtually continuous". In contrast, the widespread recognition of community-types by European phytosociologists implies discrete vegetation units. Yet WHITTAKER (1962) suggests that many phytosociological tables show a continuous change of populations through a series of Associations and the recognition of variants and facies transitional to other community-types tends to confirm this. Furthermore, SCHWICKERATH (1942) and DUVIGNEAUD (1946) have emphasised variation within the vegetational units and TÜXEN (1955) has recognised "types" as foci in a field of variation. Thus, some mitigation between the two viewpoints may be possible and indeed, the difference seems largely one of emphasis. Clusters may well be recognisable within a continuous cloud of variation: the real difficulty lies in what constitutes clustering (see WILLIAMS, 1971). In any case, the distribution of points in vegetational space may reflect little more than the sampling technique used or the frequency of a particular environmental type within the sample area (GOODALL, 1963; DAUBENMIRE, 1966; McINTOSH, 1967).

1.4. The Concept of Rich Fen.

1.4.1. On the nomenclature and classification of wetlands.

Vernacular English contains a rich diversity of words to

refer to areas of land that are waterlogged for at least part of the year - which here are brought together under the one broad head of wetland. Marsh and bog are perhaps the most generally used, but in some regions (especially in East Anglia), fen predominates. Other words in widespread use are swamp, mire and moor and in Northern England ing and moss also regularly occur. Much less frequent are marish, moor-fen and morass. Regional usage may apply the same word to very different habitats and vegetation. Thus, carr in East Anglia refers to mire forest; in Yorkshire, to open marshy areas.

In the attempt to classify wetlands many of the above terms have been used in rather specific ways, although there are, of course, obvious disadvantages in giving words a precision which, in ordinary usage, they rarely possess. Furthermore, the use of some of these terms in rather different ways by different workers has not enhanced their utility. The word 'fen' is an instructive example. TANSLEY (1911; see also 1939) used 'fen' to refer to areas of peat with an alkaline to neutral reaction, choosing the term as this was the word applied to such areas in East Anglia where (in Britain) they are most extensively developed. The term thus refers primarily to a habitat-type, though clearly the vegetation naturally occupying this habitat formed part of the concept as well.

However, in addition to this, the word has also taken

on certain seral connotations. It has (for example, see TANSLEY, 1939), received wide usage to refer to a particular phase of the hydrosere, that is to say the phase composed of herbaceous plants growing on a more or less terrestrial substratum interpolated between the preceding phase of swamp and the succeeding phase of carr. It may be noted that here the use of 'fen' is restricted to encompass a herbaceous vegetation-type. It may further be noted that it refers to a topogenous type of wetland (i.e. one where the high water-table is determined by the topography of the landscape). This much closer to the usage of SPENCE (1964), who regards 'fen' as a vegetational concept, to refer to topogenous wetland vegetation. He does not just incorporate communities of alkaline peat, but also includes those developed on acidic or mineral substrata.

Compared with this, however, 'fen' has been used in a much wider sense by some Scandinavian workers. Thus, DU RIETZ (1949; 1954) recognised two main categories of mire vegetation: on the one hand, the vegetation of the bog formation (i.e. that of ombrotrophic mires - those which receive their water and nutrient supply directly, and exclusively, from the rainfall) and, on the other, the vegetation of the fen formation (i.e. that of minerotrophic mires - those which receive water that has been in contact with the mineral ground). This separation, based upon the "fen plant limit" (SJORS, 1948) (the "Niedermoorpflanzengrenze" or "Mineralboden-

wasserzeigergrenze"), i.e. the presence or absence of plant species regarded as indicative of minerotrophic water, thus corresponds with the "mineral soil water limit" ("mineral-bodenwassergrenze") (THUNMARK, 1942) with a calcium level of about 1 mg/l or slightly lower (WITTING, 1948). Thus, delimited, the category of bog corresponds closely with the "Hochmoore" of WEBER (1908).

As far as the fen formation is concerned a second main division has also been recognised, the "calciphyte plant limit". This separates rich fen vegetation (that is, fen vegetation rich in calciphyte species) from poor fen vegetation (that is, fen vegetation in which calciphytes are poorly represented or completely absent). This again is fundamentally a floristic distinction based upon the presence or absence of rich fen indicator species. It does not refer specifically either to the total number of species present or to the habitat conditions (see SJÖRS, 1948; MALMER, 1962). Nonetheless, the division does correspond well with the "calcareous water limit" (WITTING, 1948), so that rich fen vegetation is irrigated by more alkaline water (above about pH 6.5), which is also richer in calcium (above 18 mg/litre). It also usually supports greater species totals (PERSSON, 1962).

This division of fen vegetation corresponds with other schemes that have been put forward. Poor fen corresponds broadly with the "Uebergangsmoore" of WEBER (1908) and the

"Zwischenmoore" of POTONIE (1908); rich fen, with the "Niedermoore" and "Flachmoore" of these two authors.

Although DU RIETZ has distinguished the 'fen-plant limit' and the 'exclusive fen plant limit' as the major boundaries in the Swedish mire vegetation, nonetheless, recognising their wide compass and variation he has given a further subdivision: poor fen is divided into extreme poor fen and transitional poor fen. Similarly, rich fen has been divided into extreme rich fen and transitional rich fen. This is in keeping with the approach of SJÖRS (1950), who, emphasising the gradual nature of variation within mire vegetation, has recognised six classes of fen (cf. also BELLAMY, 1967; 1968).

It may be noted that the three main categories established by DU RIETZ do not correspond well with those set out by TANSLEY (1939). TANSLEY used the category of 'bog' to contain the vegetation developed upon peat with an acidic reaction. This concept, which is comparable with that of FRÜH & SCHROTER (1904), and may be referred to as 'bog' sensu lato, includes not only the vegetation of ombrotrophic mires, but also acid mires developed under the influence of nutrient-poor minerotrophic water. It thus includes much of the 'poor fen' of DU RIETZ. Conversely, the 'fen' of DU RIETZ is a broader concept than the 'fen' of TANSLEY with which, in fact, the category of 'rich fen' has much greater parity. The correspondence is not exact, however. For example, TANSLEY restricted the concept of fen to peatlands: the term marsh

was used to refer to waterlogged areas on an inorganic (mineral) substratum. Yet in Swedish usage, the concept of fen is broader than that of peatlands. As well as including some of the mire expanse communities developed over peat, it also encompasses mire margin communities which may or may not be on peat (see SJÖRS, 1948; RUUHIJÄRVI, 1960). These latter include the categories of fen meadow and spring.

The concept of fen (sensu DU RIETZ) thus includes not only topogenous wetlands (e.g. those developed in basins etc. where there is relatively stagnant ground water) but also soligenous types. These are developed under the influence of laterally moving ground water, as below seepage lines, along water courses etc. RATCLIFFE (1964), however, has preferred to use the term mire to refer to such soligenous wetland. But this term has also been widely used by many ecologists in a much more general sense. Thus, MOORE & BELLAMY (1974) define mire as 'all wetland systems where peat accumulates'. And, it has often been used in an even wider sense than this, as a broader concept than peatland (SJÖRS, 1948; DU RIETZ, 1954; SINKER, 1960). Thus, MÖRNSJÖ (1971) points out that 'all mire lands do not form peat but other types of humus or the strata may be of tufa'. In the present account the term is used in this latter, more general sense.

As might be expected, as a vegetational category, rich fen contains a rather wide range of plant communities. DU RIETZ (1949) gives some indication of its compass by observing that his category of extreme rich fen contains both

the communities of the Magnocaricion elatae Koch 26 - tall sedge communities normally of topogenous fens - and the Caricion davallianae Klika 34 - small sedge communities of (frequently) soligenous mires (see Chapter 2).

1.4.2. The concept of rich fen.

The concept of rich fen (sensu DU RIETZ, 1949; 1954) has been used as a convenient, broadly defined unit to contain the range of plant communities considered in the present survey. It has not been used in any precise way to contain communities with "calciphytes", as it is not evident which species come into this category; nor has it been used to refer to a precise habitat-type. Rather, here the conception of rich fen has been as a rather general category to contain a series of plant communities which, developed in wetland areas irrigated by minerotrophic water of neutral to alkaline pH and of fairly high base status, possess a certain coherence. It is thought of as a joint vegetation-habitat category. As such it includes both topogenous and soligenous types of mire, developed either on peat or on mineral ground, supporting either herbaceous or wooded vegetation (thus in terms of the hydrosere it incorporates both the 'fen' phase and the 'carr' phase). It also encompasses the category of fen meadow. These vegetation-types form the kernel of rich fen, but also, included peripherally, are certain swamp and

fen grassland types that have floristic and ontogenetic links with more typical rich fen vegetation.

This conception of rich fen, though not formally defined, would seem to correspond more or less with that of DU RIETZ (1949).

The term 'rich fen system' is a geographical concept and refers to wetland complexes that are predominantly composed of rich fen vegetation-types.

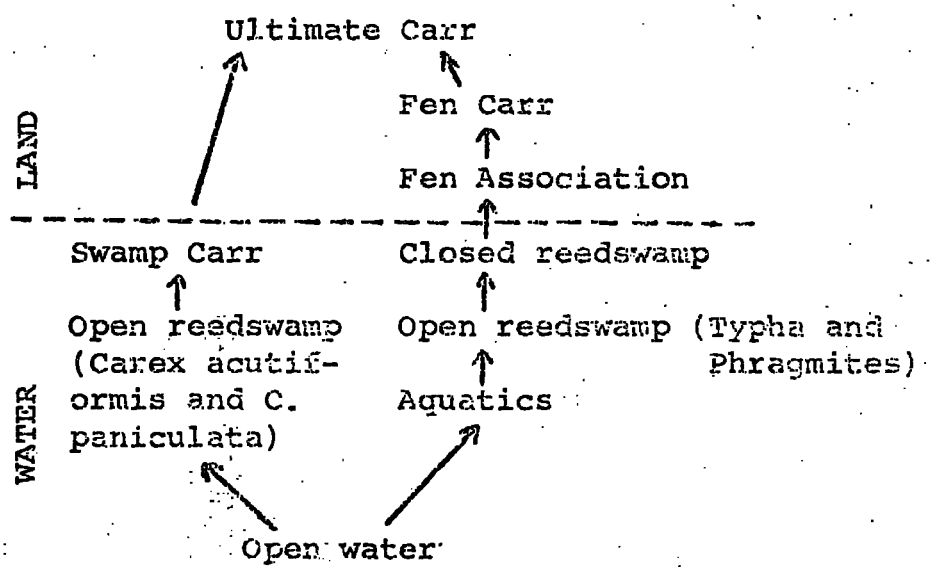
1.5. Work on rich fen plant communities in England and Wales

There has only been rather limited interest shown in the vegetation of the lowland fens of England and Wales by British ecologists. Most of this has been directed towards an understanding of the hydrosere rather than to the systematic description of the plant communities.

The early work is drawn together in TANSLEY (1939). Much of it comprises studies of fen systems in East Anglia. The first major studies were those of PALLIS (1911) in the fens associated with the Norfolk Broads. She distinguished two types of open fen and two types of carr, viz.:

FEN FORMATION	Fen Ass.	Bure valley fen	'a dense growth of grasses and sedges .. comparatively unrelieved by dicotylenous plants'
		Yare valley fen	'a rich flowery water-meadow, bright with forget-me-not.. ragged robin, valerian, flag, yellow meadow rue, etc.'
	Carr Ass.	Fen carr	
		Swamp carr	

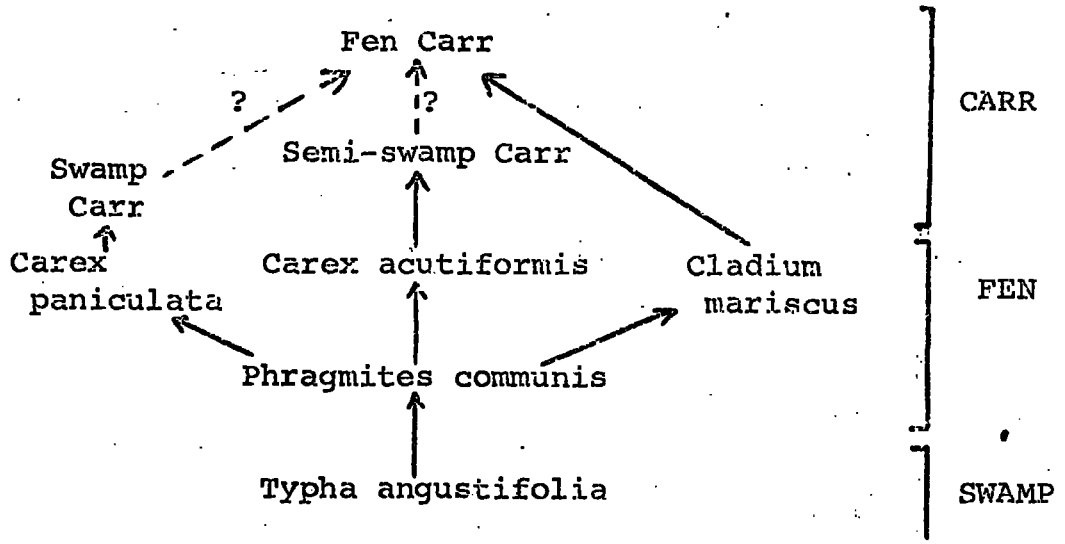
From the work of PALLIS, the following successional scheme may be given:



Subsequently there has been further work in broadland. ELLIS (1934) gave some account of the vegetation of Wheatfen in the Yare valley. But the main studies have been those of LAMBERT (1946; 1948; 1951). LAMBERT has distinguished two main series of communities: the communities of the primary succession where vegetation is actively encroaching upon open

water; and the secondary communities of older, more consolidated peats comprised either of sub-climax (climax ?) fen carr or the plagioclimax of mowing marsh. LAMBERT (1946) has given some description of the primary and secondary fen communities of the undrained fenland in the area of the Rockland and Surlingham Broads of the Yare valley. The initial reedswamp is composed of either an anchored fringe of Phragmites communis or a floating raft of Glyceria maxima. This leads into 'hover fen' - a rather species-poor, quaking mat of Glyceria - which is subsequently replaced by a Phragmites-dominated fen (see BUTTERY & LAMBERT, 1965a; 1965b). This then developed into carr communities, pioneered by the invasion of Salix cinerea, followed by Alnus. In the secondary fen, she recognises three main communities dominated by Glyceria maxima, Phragmites and Juncus subnodulosus, respectively.

LAMBERT (1951) has similarly described some communities from parts of the Bure valley. Hydrarchal development is particularly interesting here in that the type of fen carr that develops is determined by earlier communities of the prisere. Her scheme is:



Phragmites communis forms an initial primary fen, developing as a semi-floating raft upon a loose peat of Typha angustifolia. Unless artificially maintained as a reedbed, this is subsequently invaded by sedges. When Carex paniculata comes in as a prominent species to give "tussock-fen", the precocious establishment of Salix cinerea and Alnus on the tussock tops leads to a carr community that is effectively too heavy to be supported by the fen raft and subsidence occurs to produce a swamp carr. When the sedges are Carex acutiformis or Cladium mariscus, however, the establishment of tree seedlings is delayed until the fen surface is sufficiently raised above the water level by which time a greater thickness of peat has accumulated and a more stable fen mat produced. This is particularly the case with Cladium mariscus (which, incidentally, may directly encroach upon Typha swamp without an intervening Phragmites phase) as the thick leaf-mattresses

produced by the sedge are inimical to the establishment of seedlings and the establishment of carr following Cladium fen may require to be preceded by the interpolation of a Phragmites-dominated community. Thus, here a thick accumulation of fen peat is able to develop so that the subsequent growth of carr causes only a limited amount of subsidence. The succession involving Carex acutiformis is intermediate between these and gives rise to a semi-swamp carr.

LAMBERT also cites a number of secondary fen communities of the Bure valley, defined by their dominant species.

The second main site in East Anglia to be the subject of some work is Wicken Fen in Cambridgeshire. GODWIN & TANSLEY (1929) described the vegetation and distinguished the following herbaceous communities:

(a) Cladietum ('pure sedge') - Cladium-dominated areas in the lowest, wettest parts of the fen. Regarded as part of the prisere.

(b) Cladio-Molinietum ('mixed sedge') - Cladium and Molinia-dominated areas of fen that are mown every 4 years.

(c) Molinietum ('litter') - Molinia-dominated areas that are mown annually.

(d) 'Mixed fen' - herbaceous community resulting from the clearance of carr.

Particular attention has been given to long-term observation of the colonisation of the fen by bushes (GODWIN & TANSLEY, 1929; GODWIN, 1936; GODWIN et al., 1974).

In addition to these major works, there have also been a number of descriptive accounts (of varying nature) of

individual rich fen systems. (These will not be mentioned here, but will be referred to when relevant. References to specific sites are given in Chapter 5). Some account has also been given of the communities of the Breck fens (HASLAM, 1965). However, no broadly based survey of the vegetations of rich fen systems throughout lowland England and Wales has hitherto been published.

Chapter 2.

Syntaxonomic categories of rich fen vegetation.

2. Syntaxonomic categories of rich fen vegetation

In contrast to the limited degree of interest shown by British ecologists in vegetation systematics, Continental phytociologists have endeavoured to formulate a comprehensive syntaxonomic scheme in which to order and classify plant communities. A hierarchical classification has been adopted with the basic units of vegetation (Associations) being grouped into higher order syntaxa which, in ascending sequence, are referred to as Alliances, Orders and Classes. These categories, as well as representing floristically defined units, also tend to correspond to distinct structural and physiognomic types and often refer to specific types of habitat conditions, as well. It may, however, be recognised that these higher units do not always constitute clearly defined vegetational categories and, indeed, there has been widespread difference of opinion amongst phytosociologists as to which units constitute the most useful syntaxa. Hence, rather different syntaxonomic schemes have been drawn up and the precise compass and status of certain syntaxa have been variously interpreted.

Here a brief account will be given of the higher syntaxa that are relevant to the present survey and to which subsequent reference will be made. The categories used mainly correspond to those adopted by WESTHOFF & DEN HELD (1969) in their recent classification of the plant communities of Holland. It must be pointed out, however, that the evolution of these categories

has often been long and complex.

2.1. Class: PHRAGMITETEA Tx. et Prsg. 42

Synon: Phragmiteto-Magnocaricetea Klika 44

The Phragmitetea contains a whole range of plant communities characterised by the dominance of tall-growing telmatic grasses and sedges. It includes the species-poor pioneer vegetation of swamps encroaching upon the open water of lakes and streams etc., but also it accommodates the richer communities with a higher degree of organisation which follow on from these in hydrarchal development. Thus, on the one hand, placed here are swamp communities where the water level is generally above the substratum and which can be quite deep. On the other, there are the communities of fen vegetation where the water level is at or below the ground level for much of the year, except for periodic inundations.

The Class is frequently, but not exclusively, associated with nutrient-rich waters of lowland regions. It is a very widespread vegetation-type with a holarctic distribution pattern.

The higher units of the Phragmitetea are not well-defined floristically with species tending to be optimally rather than specifically developed in particular syntaxa. This, together with a general species-poverty and different ideas

as to the precise status and contents of the units, has led to a variety of character species being applied, so that within the literature there are many examples of the same species regarded as diagnostic for different units, even within the same geographical region. In this account of the syntaxa an attempt has been made to identify, from the literature, the most frequently cited character species of the Atlantic regions of N.W. Europe. This information has largely been derived from the works of TÜXEN (1937), VLIEGER (1937), BOER (1942), VAN DONSELAAR (1961), KRAUSCH (1964) and WESTHOFF & DEN HELD (1969). In general the lists of character-species extracted correspond well with those suggested by WESTHOFF & DEN HELD.

For the Phragmitetea the following character-species have been suggested:

Equisetum fluviatile	Rumex hydrolapathum
Alisma plantago-aquatica	Berula erecta
Iris pseudacorus	Sparganium erectum ssp. microcarpum

Within the Phragmitetea three Orders have been distinguished by many authors. These are the Phragmitetalia Koch 26 em. Pignatti 53, the Magnocaricetalia Pignatti 53 and the Nasturtio-Glycerietalia Pignatii 53.

2.1.1. Order: PHRAGMITETALIA Koch 26 em. Pignatti 53 denuo em. Segal et Westhoff 69

This Order is composed of species-poor communities of tall helophytes which often grow to form monotypic stands. These

develop in stagnant or slightly flowing nutrient-rich water of up to 2-3 m deep. The Order is characteristic of the lowland areas of Europe and is not well represented at altitudes above 150 m.

Character species are:

Phragmites communis	Sparganium erectum ssp. erectum
Typha latifolia	Iris pseudacorus

Various Alliances have been placed within the Phragmitetalia. They include the Oenanthion aquaticae Hejny 48 which contains certain herbaceous, sub-littoral communities which develop around the muddy, drying-up margins of pools. But, more relevant to the present survey is the Phragmition.

2.1.1.1. Alliance: PHRAGMITION (COMMUNIS) Koch 26 em. Balatova-Tulackova 63

This Alliance contains the characteristic tall-growing vegetations of reedswamps. It is developed throughout Europe in nutrient rich, fresh to slightly saline waters, around lakes, alongside canals and other waterways.

The following have been suggested as character species:

Acorus calamus	Scirpus lacustris
Butomus umbellatus	Typha angustifolia
Ranunculus lingua	

2.1.2. Order: MAGNOCARICETALIA Pignatti 53

This Order contains the 'Großseggengesellschaften' that are developed around the margins of lakes and pools or alongside

water-ways, occurring often as a zone in the shallower water behind the reedswamps of the Phragmition. The Order is also represented by communities in the wetter parts of nutrient-rich, rheotrophic mires. It may be referred to the category of rich fen in the scheme of DU RIETZ (1949). The communities will grow in the shallow water at the edge of swamps but also in drier conditions where the water-table is at or slightly below the surface for much of the year in areas subject to only occasional inundations. In the hydroseral sequence the vegetations of this Order are often preceded by Phragmition communities, although sometimes they can act as the primary invaders of open water. Under natural conditions the great-sedge phase is probably often only transient as the communities are rapidly colonised by woody plants and develop into fen woodland. Frequently, as a result of periodic mowing, however, this succession has been deflected, leading to the stabilisation of the Magnocaricetalia communities or to their development into other types of fen vegetation.

The Order is distributed throughout Europe (including the Mediterranean) and has representative communities in montane regions as well as in the lowlands.

Various attempts have been made to subdivide the Magnocaricetalia but in general one Alliance has been recognised, the Magnocaricion.

2.1.2.1. Alliance: MAGNOCARICION (ELATAE) Koch 26

For details of this, see the Magnocaricetalia.

The following character species have been given for the Alliance and Order:

Carex acuta	Peucedanum palustre
Galium palustre ssp. elongatum	Poa palustris
Lysimachia thyrisiflora	Scutellaria galericulata
	Carex elata

WESTHOFF & DEN HELD (1969) also suggest the following sedges:

Carex vesicaria	Carex acutiformis
C. paniculata	C. aquatilis

2.1.3. Order: NASTURTIO-GLYCERIETALIA Pignatti 53 em. Segal 69

This Order contains a number of community-types typically developed at the interface between water and land. It includes communities developed in and alongside brooks and streams together with certain types of the margins of lakes and pools. The Order occurs throughout Europe.

Many authors bring only one Alliance into this Order - The Glycerio-Sparganion Br.-Bl. et Siss. apud Boer 42. However, WESTHOFF & DEN HELD (1969) have included two others as well - the Apion nodiflori Segal 69 and the Cicution virosae Hejny 60 em. Segal. With these contents, these authors suggest the following as character-species:

Nasturtium microphyllum	Glyceria fluitans
Sparganium erectum ssp. neglectum	Myosotis scorpioides
Glyceria plicata	Veronica beccabunga

The Glycerio-Sparganion Br.-Bl. et Siss. 42 apud Boer 42 contains "Reedswamp" communities of shallow, muddy margins of lakes, ponds, small streams and ditches, typically with Glyceria spp., Veronica beccabunga, Rorippa nasturtium aquaticum, Sparganium erectum, S. emersum etc.' (BIRKS, 1973). The Apion nodiflori Segal 69 contains communities of clear, flowing water in brooks and springs characteristically with Apium nodiflorum, Rorippa nasturtium aquaticum and species of Callitriche. Neither of these are the concern of the present project. The third Alliance, the Cicution virosae, has more relevance though.

2.1.3.1. Alliance: CICUTION VIROSAE Hejny 60 em. Segal. 69

Synon: Carici-Rumicion hydrolapathi Passarge 64

Here are placed certain types of swamp vegetation which occur either as loose, free-floating mats, or as a more or less attached zone between open water and the surrounding swamps and marshes. In particular, the Cicuto-Caricetum pseudocyperi Boer et Siss. 42 is included here. This Association (see BOER, 1942) is composed of unstable floating rafts in which Carex pseudocyperus, Cicuta virosa and Calla palustris are important and characteristic species together with certain aquatics such as Hydrocharis morsus-ranae and Stratiotes aloides. Another Association is the Calletum palustris characterised by loose floating rafts of Calla.

WESTHOFF & DEN HELD (1969) suggest the following character species:

Carex pseudocyperus Sium latifolium
Cicuta virosa

The Alliance has mainly been described from Holland but it has also been recognised in adjoining areas and it may be quite widely distributed in Europe (WESTHOFF & DEN HELD, loc. cit.).

2.2. Class: PARVOCARICETEA Den Held & Westhoff 69

Synon: Scheuchzerio-Caricetea fuscae (Nordh. 36.) Tx. 37 p.p.; Caricetea nigrae Tx. 71

This Class contains plant communities which, until recently, were joined together with the communities of the Scheuchzerietea Den Held, Barkman et Westhoff 69 (see below) as members of a single Class, the Scheuchzerio-Caricetea fuscae (Nordh. 36) Tx. 37. (see Appendix).

The Class essentially comprises the vegetation of mires in which the herb layer is composed of low-growing paludal graminoids (viz. grasses, sedges and rushes) and where the bryophyte layer is extensively developed with either sphagnaceous or hypnaceous mosses predominating. An important feature of the habitat is the high, constant water-table which remains at, or just below, the ground-level throughout most of the year. The irrigating water may be oligotrophic to eutrophic; base-poor to base-rich. It is, however, always minerotrophic and normally contains only very low levels of nitrogen and

phosphorus. The communities can be found in a variety of situations; both topogenous and soligenous; associated with springs and areas of water seepage; in flat, expansive peaty fens ('Flachmoor'); in the "lagg" zone of ombrotrophic mires; in dune-slacks etc. The substratum is often peat but the communities can also be found on mineral ground.

The Class occurs throughout the euro-siberian regions, but its main distribution is in the north, where it may be found at all altitudes. In the south it mainly occurs in montane areas.

WESTHOFF & DEN HELD (1969) suggest as character species:

Pedicularis palustris	Potentilla palustris
Stellaria palustris	Hydrocotyle vulgaris
Calamagrostis neglecta	Riccardia pinguis
Epilobium palustre	Acrocladium cordifolium
Carex diandra	Drepanocladus exannulatus
Carex lasiocarpa	D. sendtneri
Carex demissa	

They also list five species which they consider differentiate the Parvocaricetea together with the Scheuchzerietea from all other Classes. These are:

Agrostis canina var. fascicularis	Sphagnum teres
Hammarbya paludosa	Carex rostrata
	Menyanthes trifoliata

Within the Class two Orders have been distinguished: the Tofieldietalia Prsg. apud Oberd. 49 and the Caricetalia nigrae Koch 26 em. Nordh. 36 denuo em. Tx. 37.

2.2.1. Order: TOFIELDIETALIA Prsg. apud Oberd. 49

Synon: Caricetalia davallianae Br.-Bl. 49

Placed here are communities of rich fen (sensu DU RIETZ, 1949) from mires of relatively high nutrient and base status. Hypnaceous mosses usually predominate in the bryophyte layer and Sphagna are infrequent. The range of Order is from sea level to montane/alpine.

As WESTHOFF & DEN HELD (1969) are only concerned with one of the Alliances of the Order, they give a joint list of Order and Alliance character species. However, from OBERDORFER (1957), SHIMWELL (1968) and JONES (1973) the following have been suggested for the Order:

Carex flava	Equisetum variegatum
Carex dioica	Campylium stellatum
Bartsia alpina	C. chrysophyllum
Juncus alpinoarticulatus	Drepanocladus revolvens
Eleocharis quinqueflora	Scorpidium scorpioides

2.2.1.1. Alliance: CARICION DAVALLIANAE Klika 34

Synon: Schoenion ferruginei Nordh. 36
Eriophorion latifolii Br.-Bl. et Tx. 43
Epipacto-Schoenion ferruginei Duvign. 49

Natural or semi-natural species-rich communities of moist to wet habitats of neutral to alkaline character. The herb layer is normally dominated by low-growing species of Carex; The moss layer normally has an extensive development of pleurocarpous mosses. With these there is often an abundance of

associated species - both herbaceous angiosperms and bryophytes. The substratum is normally an oozing peat, irrigated by calcareous ground water which is often constantly at a high level throughout the year. This is not always the case, however, and in dune-slacks in particular the water-table can show strong variations in height.

The following species cited by WESTHOFF & DEN HELD (1969) and OBERDORFER (1957) have been regarded as character species of the Alliance:

Carex lepidocarpa
Taraxacum limnanthes
Dactylorhiza incarnata
Eriophorum latifolium
Epipactis palustris
Liparis loeselii
Parnassia palustris
Acrocladium giganteum
Drepanocladus lycopodioides
D. vernicosus
Catascopium nigritum
Riccardia multifida
R. sinuata
Campylium elodes
C. polygamum
Fissidens osundioides
Camptothecium nitens
Bryum pseudotriquetrum
Mnium rugicum
Mnium seligeri
Mnium pseudopunctatum
Mnium cinclidioides
Cinclidium stygium
Pellia endiviifolia
P. neesiana
Sphagnum contortum
S. platyphyllum

The Alliance comprises lowland to montane communities. In the subarctic and subalpine-alpine zones it is replaced by vicariants.

2.2.2. Order: CARICETALIA NIGRAE Koch 26 em. Nordh. 36 denuo em. Tx. 37

Contained in this Order are the communities of poor fens (sensu DU RIETZ, 1949) which are characterised by the prominence of low-growing sedge species. One Alliance is usually recognised, the Caricion curto-nigrae Koch 26 em. Nordh. 36.

2.2.2.1. Alliance: CARICION CURTO-NIGRAE Koch 26 em. Nordh. 36

(sub nom. Caricion canescentis-Goodenowii)

Synon: Parvocaricion canescentis-fuscae Duvign. et Vanden Berghen 45

Small-sedge communities of oligotrophic to mesotrophic sites growing in nutrient-poor wet ground where the water-table is close to the surface for much of the year. The Alliance contains fairly species-rich communities with a relatively well developed bryophyte layer in which species of Sphagna may be prominent. These can be found in soligenous mires, alongside streams, in the "lagg" zone of ombrotrophic bogs and in dune-slacks where there are low levels of calcium.

WESTHOFF & DEN HELD (1969) suggest the following character species for the Order and the Alliance:

Carex nigra	Viola palustris
Carex curta	Juncus filiformis
Carex echinata	Epilobium palustre
Ranunculus flammula	Sphagnum recurvum ssp. amblyphyllum

The distribution of the Alliance follows that of the Class except that it is absent from alpine regions.

2.3. Class: SCHEUCHZERIETEA Den Held, Barkmann et Westhoff 69

This Class was created to accommodate one Order, the Scheuchzerietalia palustris Nordh. 36. It contains communities of hollows and pools in wet bogs and fens where the stagnant or slowly moving water forms a constantly high water-table.

WESTHOFF & DEN HELD (1969) placed only one Alliance in the Order. This was the Rhyncosporion albae Koch 26, a widely distributed Alliance containing the communities of wet depressions in ombrotrophic mires and poor fens. These characteristically have an impoverished and poorly-developed herb layer but there is normally a well-developed bryophyte layer in which Sphagna, especially Sphagnum cuspidatum, are prominent. Other species, particularly characteristic of this Alliance, are Rhynchospora alba, Scheuchzeria palustris, Carex limosa and Cladopodiella fluitans.

Some authors have placed a second Alliance within the Scheuchzerietalia. This is the Caricion lasiocarpae Vanden Berghen 49 (more or less synonymous with the Eriophorion gracile Prsg. apud Oberd. 57). This shows many parallels with the Rhyncosporion, occurring in wet hollows within mires, but, in contrast, it is found in association with more mesotrophic water often of higher base status. The communities of the Alliance often develop as floating mats of vegetation, encroaching upon areas of open water. The herb layer is often species-rich with a predominance of cyperaceous plants. The moss layer can also be well developed with pleurocarpous species such as Scorpidium scorpioides and Acrocladium giganteum, or with various species of Sphagna. The Alliance contains both acidophilous and basiphilous community-types and in this respect cuts across some of the established floristic boundaries along the base-poor to base-rich gradient.

The following species have been given as characteristic:

Carex rostrata	Menyanthes trifoliata
Carex lasiocarpa	Potentilla palustris
Eriophorum gracile	Equisetum fluviatile

The Caricion lasiocarpae has a predominantly northern distribution within the Euro-Siberian region.

It may be noted that WESTHOFF & DEN HELD (1969) do not recognise this Order as a valid syntaxon but instead consider that the community-types normally included within it can be satisfactorily partitioned between the Rhynchosporion, Caricion curto-nigrae and Caricion davallianae Alliances.

2.4. Class: MOLINIO-ARRHENATHERETEA Tx. 37

This Class contains many of the lowland grassland communities of Western Europe, together with certain semi-natural communities of mires and river banks. The vegetation is essentially man-made, having been created by the clearance of deciduous forest and maintained as a plagioclimax by mowing and grazing. It consists of a rather low-growing sward in which grasses (or grasses and rushes) are the main components. In some types, however, tall-growing herbs predominate. Characteristically, mosses are poorly developed.

The Class occurs on soils ranging from moist to wet; fairly nutrient-rich to highly nutrient-rich; mildly acidic to basic; unmanured to manured. It occurs throughout Europe wherever the ground is sufficiently moist, viz. in the Euro-

Siberian region and in northern parts of the Mediterranean.

In Britain the Class has been examined by O'SULLIVAN (1965; 1968a) and SHIMWELL (1968). These have suggested the following as character species:

Alopecurus pratensis	Ophioglossum vulgatum
Cardamine pratensis*	Plantago lanceolata*
Cerastium holosteoides*	Poa pratensis
Festuca pratensis	Poa trivialis
Festuca rubra	Ranunculus acris
Helictotrichon pubescens	Rumex acetosa*
Holcus lanatus*	Trifolium pratense*
Lathyrus pratensis	Vicia cracca*

The species marked * are also recognised as character species in Holland by WESTHOFF & DEN HELD (1969). These further suggest:

Centaurea pratensis	Fritillaria meleagris
Climacium dendroides	Prunella vulgaris
Colchicum autumnale	Rhytidiadelphus squarrosus

At least three Orders have been recognised in the Class, including the Holoschoenetalia of the northern Mediterranean. For western Europe the two main Orders are the Arrhenatheretalia Pawlowski 28 - which includes the fertile anthropogenic grasslands on moist, but well aerated, nutrient-rich, manured soils - and the Molinietalia Koch 26 containing a variety of communities of wetter conditions.

2.4.1. Order: MOLINIETALIA Koch 26

This Order encompasses a rather wide-range of community-types developed on a substratum which can be nutrient-poor to nutrient-rich, unmanured or manured, but which is

characteristically wet (at least periodically). O'SULLIVAN (1965) suggests that such wet conditions may be maintained either by a high water-table, turf or clay soils, or a regular high rainfall. He also suggests that the communities of the Order are less subject to the influence of man than those of the Arrhenatheretalia and that they can be considered semi-natural.

The following character-species have been proposed (O'SULLIVAN, 1965; SHIMWELL, 1968):

Cirsium palustre*	Lotus uliginosus
Angelica sylvestris*	Filipendula ulmaria
Deschampsia cespitosa*	Juncus acutiflorus
Achillea ptarmica*	Juncus conglomeratus
Equisetum palustre*	Myosotis caespitosa
Galium uliginosum*	Lychnis flos-cuculi
Juncus effusus	Hypericum tetrapterum

Those marked * have also been proposed by WESTHOFF & DEN HELD (1969). These further suggest:

Lathyrus palustris	Ophioglossum vulgatum
Cirsium oleraceum	Rhinanthus glaber
Dactylorhiza praetermissa	Sanguisorba officinalis
Lathyrus palustris	Thalictrum flavum (transgr.)
Lysimachia vulgaris	Valeriana dioica
Hieracium caespitosum	

The distribution of this Order follows that of the Class except that it is absent from the Mediterranean area, where the Holoschoenetalia Br.-Bl. 31 occurs.

Various Alliances have been assigned to this Order, including the Deschampsion caespitosae Horvatic 30, the Alopecurion pratensis Passarge 64 and the Cnidion venosi Balatova-Tulackova 65 - all of which contain communities of periodically flooded grassland. However, the three main

Alliances to be considered here are the Junco (subuliflori)-Molinion, the Calthion palustris and the Filipendulion.

2.4.1.1. Alliance: JUNCO (SUBULIFLORI)-MOLINION Westhoff 69

This Alliance contains communities of unmanured wet meadows and mires in which the purple moor grass, Molinia caerulea, is usually an important component. These may be developed on peats, clays or alluvial material. The Alliance is confined to the western, Atlantic parts of Europe, where it is often developed in base-poor, relatively acidic places. In Central Europe it is replaced by the Molinion coeruleae Koch 26 which in general contains communities that are much more species-rich and which are often developed in relatively base-rich, calcareous conditions.

WESTHOFF & DEN HELD (1969) have indicated that the Alliance is poorly characterised floristically, mainly by the absence of character species of other Alliances. They do, however, suggest the following characters:

Succisa pratensis	Juncus conglomeratus
Viola stagnina	Potentilla anglica

As differentials against the Calthion and Filipendulion they further suggest:

Molinia caerulea (optimally developed)	Sieglingia decumbens
Parnassia palustris	Platanthera bifolia
Gentiana pneumonanthe	

2.4.1.2. Alliance: CALTHION PALUSTRIS Tx. 37

Within this Alliance are communities of nutrient-rich nitrogenous meadows that are constantly, or at least periodically, wet. They may be developed both upon clays and peats. Included here are wet meadows that are artificially manured as well as areas developed under the influence of laterally moving, nutrient rich water - as can occur in certain spring mires and also along the edge of streams and brooks. In the first case, the communities are irrigated by water that is at a fairly high level throughout most of the year. In the second, the inundation may only be periodic.

O'SULLIVAN (1965) and SHIMWELL (1968) suggest the following as character species:

Caltha palustris*	Myosotis scorpioides
Crepis paludosa*	Polygonum bistorta
Senecio aquaticus	Bromus racemosus

Those denoted * are also recognised by WESTHOFF & DEN HELD (1969). These further suggest:

Carex disticha	Lychnis flos-cuculi
Lotus uliginosus	Scirpus sylvaticus
Luzula multiflora	Taraxacum hollandicum

O'SULLIVAN (1965; 1968b) has pointed out that, whereas in Central Europe there is little difficult in distinguishing Calthion and Molinion communities, this is not so in Ireland, where only Senecio aquaticus and Myosotis scorpioides occur as common character species of the Calthion.

2.4.1.3. Alliance: FILIPENDULION (Duvign. 46 p.p.) Segal 66

Communities belonging to this Alliance are found along the banks of brooks and rivers and upon alluvial flood plains. Such areas are rich in nutrients, especially nitrogen and phosphorus. The water-table is variable. For certain periods of the year it is often high and, indeed, the areas may be inundated by flood-water. At other times the substratum is relatively dry. Such areas are not mown or grazed and support tall growing herbaceous vegetations, in which Epilobium hirsutum and Filipendula ulmaria are usually prominent and which are often very species-poor.

SHIMWELL (1968) and O'SULLIVAN (1965) suggest as character species (for the Filipendulo-Petasition Br.-Bl. 47):

Epilobium hirsutum*	Stachys palustris
Eupatorium cannabinum*	Valeriana officinalis
Epilobium parviflorum*	

Those marked * are regarded by WESTHOFF & DEN HELD (1969) as differential species for the Filipendulion against other Molinietalia Alliances. As further differentials they suggest:

Calamagrostis canescens	Sonchus palustris
Euphorbia palustris	Symphytum officinale
Phalaris arundinacea	

They proposed as character-species:

Hypericum tetrapterum	Stachys palustris
Lythrum salicaria	

The Alliance occurs throughout West and Central Europe.

2.5. Class: FRANGULETEA Doing 62 em. Westhoff 68
Synon: Salici-Franguletea Jurko 64

This Class contains certain wetland communities dominated by shrubs, of about 1-5 m tall. It contains one Order and one Alliance. Further details will be given under the Alliance.

2.5.1. Order: SALICETALIA AURITAE Doing 62 em. Westhoff 68

2.5.1.1. Alliance: SALICION CINEREAE Mull. et Gors 58

Within this Alliance are placed shrub communities of wetlands developed upon a substratum of peat or mineral ground which has a continually high water level throughout the year, ranging from acid to neutral, from nutrient-poor to moderately nutrient-rich. The communities can be up to about 5 m high (but frequently are much lower), with a completely closed canopy or, in less well developed examples, with openings between some of the shrubs. Herbs are often not very well developed, but there may be many ferns and graminaceous plants and a rich carpet of bryophytes, either hypnaceous or sphagnaceous.

Often the communities of this Alliance form a zone around the edge of alder forests.

WESTHOFF & DEN HELD (1969) suggest as character species for the Alliance, Order and Class:

Frangula alnus
Salix aurita
Salix cinerea
Salix aurita x cinerea
Myrica gale

As differentials against other Classes of shrub communities they suggest:

Dryopteris cristata
Dryopteris carthusiana x cristata
Sphagnum squarrosum
other Alnion species

A lowland to montane, azonal community of the Euro-Siberian region, particularly towards the northern parts (to S. Sweden and the Baltic area).

2.6. Class: ALNETEA GLUTINOSAE Br.-Bl. et Tx 43 em. Müll. et Görs 58

This Class contains mire forest vegetation dominated by Alnus glutinosa. Note that not all alder forests are included here. Some, such as those developed on nutrient-rich, periodically-flooded, mineral ground alongside rivers, belong to another Class (the Querco-Fagetea Br.-Bl. et Vl. 37).

The Alnetea is an azonal syntaxon occurring throughout the Euro-Siberian region on the lowlands and in valley.

It contains one Order and one Alliance.

2.6.1. Order: ALNETALIA GLUTINOSAE Vl. 37 em. Müll. et Görs 58

2.6.1.1. Alliance: ALNION GLUTINOSAE (Malcuit 29) Meijer Drees 36 em. Müll. et Görs 58

The Alnion contains the climax (?) alder forest communities of mires. It represents the culmination of hydrarchal development in nutrient-rich, stagnant or slightly flowing waters, but may also be developed upon spring slopes. It is composed of mature, well-developed stands of woodland; with or without a shrub-layer; with a herb layer that is often poor in species; and with a bryophyte layer that varies from being fragmentary to richly developed. The substratum is usually peat and this may be very deep. It can be acidic or neutral, mesotrophic or eutrophic (sometimes oligotrophic) and is normally highly charged with water.

WESTHOFF & DEN HELD (1969) give as character species for the Alliance, Order and Class:

Alnus glutinosa	Dryopteris cristata
Thelypteris palustris	Sphagnum squarrosum

Additionally, they cite the following as differential species against other Classes of woodland:

Calamagrostis canescens	Salix cinerea
Solanum dulcamara	Salix aurita
Peucedanum palustre	Salix pentandra
Lycopus europaeus	Viola palustris
Scutellaria galericulata	Cirsium palustre
Carex paniculata	Iris pseudacorus

PART II: THE METHODS

Chapter 3.

Some methodological approaches to a phytosociological survey.

3. Some methodological approaches to a phytosociological survey

In this chapter a discussion is given concerning certain aspects of phytosociological methodology with specific reference to the techniques that have been used in this project. This is to provide a background to Chapter 4, in which the precise strategies that have been adopted are outlined.

3.1. Introduction

There are various possible methodological approaches to the type of phytosociological survey that is the concern of this project, that is to say a descriptive survey which aims at detecting and describing different types of vegetation on the basis of the species of plants that they contain. This diversity of approach reflects the long-standing interest that there has been in the description of vegetation in various parts of the world and the consequent development of rather different concepts and modes of study by different workers. Accounts of some of these have been given by WHITTAKER (1962), SHIMWELL (1971) and in various articles in the "Handbook of Vegetation Science" (WHITTAKER, 1973). It is sufficient here to observe that these variations in approach reflect not only the differing opinions of their exponents but are also a product of the particular natures of the

vegetations with which they have been concerned - what WHITTAKER (1962) refers to as 'the ecology of ecological traditions'.

One of the most fully-developed schools of phytosociological research within Europe, is that associated with the name of Professor J. Braun-Blanquet and which is sometimes referred to as the Braun-Blanquet School or the Zürich-Montpellier (ZM) school. Essentially this is 'ein pflanzensoziologische System auf floristiche Grundlage'. Its foundations were firmly laid by BRAUN-BLANQUET (1921, 1928) and since then it has expanded and developed into a comprehensive system of plant sociology that has been applied throughout much of Europe and indeed also in many non-European countries as well. For a long time, however, the system found little favour with British ecologists (see TANSLEY & ADAMSON, 1926). But more recently, with a rewakening of interest in vegetation description, it has been successfully adopted in Britain by O'SULLIVAN (1965), IVIMEY-COOK & PROCTOR (1966), SHIMWELL (1968), BRIDGEWATER (1970), BIRKS (1973) and JONES (1973) amongst others. Details of the principles and practises of the school are given by ELLENBERG (1956), BECKING (1957), MOORE (1962), WHITTAKER (1962), BRAUN-BLANQUET (1964), SHIMWELL (1971), WESTHOFF & MAAREL (1973) etc. Some criticisms have been expounded by EGLER (1954) and POORE (1955a, b; 1956a).

In recent years also, there has been the development of

what may loosely be referred to as the 'numerical approach'. Numerical estimates of similarity between plant community samples have, in fact, been in use for a long time (e.g. JACCARD, 1912), but the main development of numerical phytosociology has been within the last twenty years, encouraged by the availability of digital computers and the growth of the parallel science of numerical taxonomy. Two main approaches have evolved. One, emphasising the recognition of discrete units of vegetation, has led to the development of various procedures for classification, i.e. the arrangement of samples into groups with certain common properties. The other, seeing vegetation more as a phenomenon showing continuous variation in composition, has produced procedures for ordination, i.e. the arrangement of the samples along axes in which their properties determine their positions. There has been some antipathy between these two points of view. Both, however, are attempting to simplify and organise complex sets of data, albeit in rather different ways, and more recently the potentially complementary nature of the techniques has been recognised. For example, ordination could be of value in the detection of classes of vegetation (BRISSE & GRANDJOUAN, 1971).

SNEATH & SOKAL (1973) have given a comprehensive account of the 'numerical approach' which is relevant to plant sociology. ORLOCI (1973) has provided some details of ordination procedures and numerical procedures for classification

have recently been reviewed by WILLIAMS (1971) and GOODALL (1973b).

In a descriptive phytosiological survey the following stages may be recognised:

(a) selection of the vegetational parameters that are to be used for description.

(b) sampling of vegetation.

(c) comparison of samples.

(d) extraction of vegetation units.

(e) characterisation and systematisation of the units.

These will now be considered seriatim.

3.2. Sampling procedures.

Fundamental to a phytosociological survey is the taking of samples to represent the development of vegetation at a particular site. The nature of the samples made will determine the results of the survey and hence sampling is one of the most important components of phytosociological work. As it is also one of the most time-consuming, it is important that the sampling strategy should be efficient: i.e. it should allow the data required to be collected as rapidly as possible and should be commensurate with the aim of the project.

3.2.1. The attributes to be recorded.

For a floristically-based survey the essential attributes to be recorded as the species present. The species is a useful recording unit as it is clearly defined by reference to current taxonomic opinion. Potential problems are that (i) identification can sometimes be difficult (particularly at certain times of the year), and (ii) in some circumstances the occurrence of a number of rare species can lead to a markedly asymmetric species-sample matrix in which absences far outweigh presences. This may create problems in any subsequent application of numerical analytical techniques (LAMBERT, 1972).

The floristic data collected can either be binary (i.e. presence/absence) or some quantitative estimate of "abundance". GREIG-SMITH (1964) regarded the comparison of samples just in terms of binary characteristics to be crude and insensitive. However, in large-scale work using numerical analytical techniques, qualitative differences between samples may easily outweigh quantitative ones (WILLIAMS & DALE, 1962) and, with heterogenous data sets at least, binary data may be adequate or even preferable (LAMBERT & DALE, 1964; ORLOCI, 1968; NOY-MEIR et al., 1970; GREIG-SMITH, 1971). Indeed, some numerical strategies are only compatible with binary data and in any case the recording of quantitative measures requires extra time and is more appropriate for more detailed

studies of particular vegetations. For large-scale surveys subjective estimates of the relative quantities of species may be all that is needed. Various "cover-abundance" scales have been proposed for this purpose (e.g. the "Braun-Blanquet scale" (BRAUN-BLANQUET, 1928) and, although these are imprecise and open to substantial operator bias in their assessment, nonetheless, they can be used with only a small increase in total sampling time and can provide a useful adjunct to help describe vegetation classes established upon binary data for little extra effort. In the same way there is some value in recording other easily assessed properties of the vegetation cover (e.g. layering, "sociability" of species etc.) as is the case with the sampling techniques of the Zürich-Montpellier school of phytosociology. Here the standard sampling unit is the Aufnahme (German) or releve (French). It consists of a list of the species present in a sample annotated with observations on the characteristics of the vegetation and habitat (see ELLENBERG, 1956; BRAUN-BLANQUET, 1964; WESTHOFF & MAAREL, 1973).

3.2.2. Sampling strategies.

There are two basic approaches to the sampling of vegetation. First of all there are "objective" techniques in which samples are taken from points arranged with the minimum of selective bias (e.g. randomly or in some form of

systematic pattern). The advantages of this approach are that the position of the samples is largely free from user bias; that it can give consistent and repeatable results to which statistical treatment may be applied; and that it does not assume that the vegetation cover is differentiated into discernable stands. Potential disadvantages are that rare vegetation-types may miss being sampled; that random co-ordinates may be difficult to locate in the field (MOORE et al., 1970); and that the procedure is often very time-consuming. Nonetheless, the applicability of this type of sampling strategy to large-scale vegetation surveys has been suggested (e.g. LAMBERT, 1972). In contrast to this approach is the "subjective" approach in which the operator actually selects in the field the stand of vegetation to be described. The community is then sampled, only one sample being needed for a given stand. With this sort of method there is always the chance that the samples so selected may reflect nothing more than the prejudices of the operator. Nonetheless, there is also the possibility of what MUELLER-DUMBOIS & ELLENBERG (1973) refer to as "subjective sampling without preconceived bias", in which the samples made may be considered to accurately represent the nature of the vegetation at a given site. This approach has been widely used in many large-scale vegetation surveys, most certain by the ZM school and may be one of the reasons for the success of this system (BECKING, 1957).

Nonetheless, if the method is to avoid the attendent problems of inconsistency and irreproducibility, criteria for the selection of sample plots need to be enunciated.

3.2.3. Criteria for stand selection.

Accounts of ZM methodology usually give little information as to how sample plots are to be selected. However, from TÜXEN & PREISING (1942), ELLENBERG (1956), BECKING (1957), GOUNOT (1961) and KÜCHLER (1967) three criteria emerge: representativity, adequate size and uniformity.

3.2.3.1. Representativity. ELLENBERG (1956) in particular stresses the need for a thorough reconnaisance of the area being investigated in order to choose samples that will be representative of different developments of the vegetation. It may be noted, however, that such a procedure is often both difficult and time-consuming.

3.2.3.2. Minimal area. It is obviously important that all of the species that regularly occur in a phytocoenose should be present in any sample made to represent it. The concept of minimal area refers to the size of the sample that is required to effectively express the composition of a stand. For the determination of minimal area see BRAUN-BLANQUET (1964). Essentially it may be regarded as the sample size at which

there are only a few new species recorded with further increment of area (i.e. where the species-area curve becomes more or less horizontal). In practise, however, it seems that often species-area curves are not asymptotic (see HOPKINS, 1955) and there are substantial problems in an exact determination of the "minimal area" of a stand. Nonetheless, as an empirical tool for roughly assessing the magnitude of sample size required in a given vegetation type, the concept seems quite useful.

3.2.3.3. Uniformity. Subjective sampling strategies depend upon the recognition of "uniform" stands of vegetation. Hopefully, most field ecologists recognise that, in a given region, there are stands which are more uniform than others and their choice of stand is confined to these "more uniform" areas ' (POORE, 1962). Primarily, uniformity refers to floristic uniformity, e.g. the absence of well marked community-boundaries, though as POORE (1955a) points out uniformity is usually assessed using all of the observable properties of the vegetation and habitat. Note, however, that structural uniformity need not correspond with floristic uniformity: a uniform distribution of a dominant species could give a false impression of total floristic uniformity (GOUNOT, 1961).

In reality total uniformity is probably foreign to vegetation, and thus additional criteria are necessary to establish what constitutes a "uniform" stand. Thus, POORE (1955a)

recommends that purely quantitative variation among species within a stand can be accommodated within the uniform area. WESTHOFF & MAAREL (1973) suggest that where the growth form or aggregation of a species causes local heterogeneity, this may be regarded as part of the uniform area unless there are additional species exclusively associated with that plant in the stand. Clearly, however, there are various 'shades' of this phenomenon. Related to it are the sampling problems presented by vegetational mosaics.

As both POORE (1955b) and ROUSSINE & GOUNOT (1957) point out, the basic problem presented by mosaics is whether the different components should be sampled together or independently. BARKMAN (1968) restates the problem in terms of homogeneity; given that in a community different levels of homogeneity exist what is the smallest scale (finest pattern) that is to be regarded as heterogenous? POORE (1955b, 1962) suggests one potential criterion: that if the elements of the mosaic occur independently associated with different elements to form different mosaics in different places, then they could usefully be sampled separately. BARKMAN (1968) points out that, in the traditional ZM understanding of the problem, if the mosaic pattern is caused by primary abiotic factors then independent sampling is appropriate. This is not so if the pattern is created by biotic factors within the community. (nonetheless, it may be noted that the "hummocks" and "hollows" of ombrotrophic mire systems are usually sampled as

independent units). The difficulty of separating the elements of a mosaic may also be noted.

3.3. The extraction of units of vegetation.

Next attention will be given to methods that are available for the comparison of stands and the detection and extraction of units of vegetation.

3.3.1. On Classification. Classification consists of two distinct processes: (i) the creation of classes that are in some sense meaningful, and (ii) the allocation of individuals to these classes. The class concept essentially requires that individuals assigned to any one class are more similar one to another (on the basis of some defined parameter of resemblance) than they are to individuals in other classes.

A monothetic class is one which is defined by a unique set of attributes, i.e. all members possess all of the attributes that have been used to define the class. In a polythetic class no single attribute is essential for group membership but individuals possessing the greatest number of shared attributes constitute the class. A fully polythetic class is one where no attribute is common to all class members. Monothetic classes are thus created by an assigned definition; polythetic classes are self-structuring. Classes may be produced by the subdivision of a set of

individuals into a number of smaller sub-units (divisive approach) or by the fusion of the individuals themselves to form groupings (agglomerative approach). The first approach can be either monothetic or polythetic; the second is only polythetic. A 'natural' classification is one in which class members possess a large number of common characteristics (GILMOUR, 1964) so that within-class resemblance is maximised over many attributes and between class-resemblance is similarly minimised. Such classes are usually polythetic and may serve for a wide variety of purposes.

The problem of erecting a 'natural' classification of samples of vegetation on the basis of their overall floristic resemblances is one that is not easily solved. There are no pre-existing categories to which the samples can be allocated but instead the classes have to be generated de novo from the samples themselves. The problem thus becomes that of deciding what represents the most meaningful grouping into classes and, closely linked with this, determining how many classes are required.

The classification of a cloud of sample points arranged in vegetation space (see 1.3.3.1.) need not be dependent upon their distribution. Even a continuum may be arbitrarily divided into cells which could serve as classificatory units (CURTIS, 1959; GOODALL, 1963; LAMBERT & DALE, 1964). However, if clusters of points exist, the most 'natural' classification would be by hyperplanes partitioning the

vegetation space around the cluster centroids (i.e. their 'centres of gravity'). Even here, however, unless the clusters are completely discrete, arbitrary decisions are likely to be required as to the precise points at which adjoining clusters should be separated.

Cluster analysis may be used as a general term to refer to techniques aimed at identifying and extracting such clusters as may be inherent within a set of vegetational data. A 'natural' partitioning of vegetation space could possibly be achieved by monothetic procedures if the defining attributes have a consistently high level of correlation with the other features of the samples. Thus, dominant species, or species assessed to be important in some other way (see Association Analysis, 3.3.5.), may circumscribe 'natural' groupings. But generally a polythetic approach will be more likely to generate such classes and from this point of view a polythetic procedure is to be preferred. It must, however, be recognised that monothetic procedures have a very real advantage in that, by definition, the resultant monothetic classes have a defining set of attributes which permits them to be easily delimited and which makes the allocation of new samples a simple matter. In contrast polythetic classes may present substantial problems of diagnosis in that the only constant defining feature of the members of a cluster may be that they are all within a certain distance of the cluster centroid. A wide

variety of strategies for cluster analysis are available (see below). These methods have different conceptual bases and accordingly are of different propensities and so can produce rather different classifications of the same data set. It is thus important to recognise that any vegetation units extracted by the application of classificatory techniques may be a product of the clustering strategy used as well as of the underlying structure of the data set. (GOODALL (1973b) thus points to the desirability of ordination as a prelude to classification to give information on the spatial distribution, number and shape of the clusters of sample points arranged in vegetation space.) Moreover, even if it is possible to identify the clusters it remains an open question as to what extent these represent 'natural' units of vegetation. It is always possible that such clusters as there are, or at least some of them, may be an incidental product of the particular sample set available and do not reflect any natural reality. It must thus be emphasised that the establishment of a scheme of classes of vegetation is a primary survey as described here, is not to be regarded as an inviolate *fait accompli*. Rather it represents a hypothesis to be tested.

3.3.2. The Primary Matrix

Raw data may be incorporated into a *primary matrix* (or *raw table*), in which the columns represent *n* individuals

(samples; releves), and the rows represent p attributes (species) which define them. The intersections contain information (qualitative or quantitative) relating to the occurrence of each species in a given sample. The percentage occurrence of a given species in the set of samples represents its degree of presence; this is referred to as constancy if the samples are of equivalent size. This may be given as an exact percentage or in terms of percentage classes:

Class	Percentage range
I	1-20
II	21-40
III	41-60
IV	61-80
V	81-100

The primary matrix can be used for classificatory routines in two ways: (i) in its own right, as a means for revealing species-sample groupings; and (ii) as a source for secondary matrices upon which numerical strategies can be used.

3.3.3. Classification by tabular re-arrangement

Within the Zürich-Montpellier tradition clustering is by a process of rearrangement of the primary matrix. This approach is the empirical one of re-ordering the positions of the rows and columns to reveal "blocks" of correlated species records which can then be used to differentiate the set of samples into discrete classes. The procedure is subjective in nature and the technique is perhaps best learned from an

experienced phytosociologist (MOORE, 1962), but fairly explicit directions have been given by ELLENBERG (1956), SHIMWELL (1971) andWESTHOFF & MAAREL (1973). Essentially it represents a visual attempt to clarify the structure inherent within the matrix by the recognition of pattern. This may be achieved in a variety of way but a systematic approach involves the recognition of mutually exclusive sets of differential species followed by tabular re-ordering based upon these. As species with very high or low constancies are likely to be of little value in differentiating the table, differential species are usually those of less extreme presence. ELLENBERG (1956) suggests that differential species must have at least a 50% constancy in the groups for which they are differential and must occur only sporadically in other groups which they differentiate against.

The process thus achieves a simultaneous classification of both the samples and the species. MOORE et al. (1970) describe the technique as a "polythetic subdivisive classification of releves followed by their linear ordination". In a sense, however, it is also agglomerative in that it is often necessary to initially specify those samples that are sufficiently similar to one another to be included within the same raw table. For usually when relatively large numbers of samples are to be examined it is impractical to consider them all together in one matrix. In any case an initial agglomerative

sorting of stands into groups of supposed similarity often expedites subsequent divisive manipulations. The end-product of the sorting process is a differentiated table, in which the contained vegetation units are displayed together with their characterising species.

As MOORE et al. (1970) point out, one of the most useful features of this technique is the way the floristic data themselves are used to display the classification. It readily shows the degree of variation (intensity of clustering) within a group, the distinctness of its boundaries and its relationships to the other groups. The species data indicate the composition of the groups and permit the extraction of floristic criteria by which the classes may be defined.

The major disadvantages of the technique are (i) that the method is time-consuming and that the re-ordering of the matrix by re-writing it is an error-prone process; (ii) that the process is sufficiently imprecise for different workers to produce different groupings (at least when the groups are rather ill-defined); and (iii) that the upper limit to the number of samples that can be conveniently handled in any one analysis is rather low. (SHIMWELL (1971) suggests 40 as a manageable number, though this seems a rather conservative estimate). In the case of large data sets showing complex inter-relationships between vegetation units, it can accordingly be problematic to decide which samples should be analysed

together and with this there is the distinct possibility of the creation of anomalous vegetation units.

To reduce time and error various mechanical models have been devised to perform the tabular re-arrangements (DE SILVA, 1954; WILLMANS, 1959; ELLENBERG & CRISTOFOLINI, 1964). In particular, the electronic computer has been used for this purpose by MOORE (1971), DALE & ANDERSON (1972), HOLZNER & STOCKINGER (1973) and DALE & QUADRACCIA (1973).

Computer-based strategies to simulate the technique have also been devised. MOORE (1971) developed a semi-automatic monothetic divisive approach using mutually exclusive pairs of species as the basis for subdividing the set of samples. CESKA & ROEMER (1971) (CESKA, 1973) describe an iterative procedure for recognising groups of differential species which rearranges the order of samples on the basis of these.

3.3.4. Synoptic tables.

In the system of the ZM school, after a vegetation unit has been extracted it may then be condensed to form a single synoptic list in which is indicated the degree of presence of the species composing the unit. A number of such lists can then be incorporated into a synoptic table (WESTHOFF & MAAREL, 1973; equals the 'übersichtstabelle' of ELLENBERG, 1956). This is useful for the comparison of large numbers of community-types and can be of particular value in the characterisation of a vegetation unit.

3.3.5. Numerical clustering procedures.

Various numerical techniques have been used for the purpose of clustering individual objects into classes of some kind. Analyses based upon them may be generally referred to as "cluster analyses". The development of these techniques has received much impetus from the development of the digital computer and some rather sophisticated analytical strategies are currently available. Some account of the different types of clustering procedures is given by LAMBERT & DALE (1964), WILLIAMS (1971), SNEATH & SOKAL (1973) and GOODALL (1973b). The main methods refer to the so-called hierarchical strategies. These may be divisive, i.e. they progressively subdivide a complete population into sub-groups and finally into individuals; or they may be agglomerative and progressively fuse together individuals into sub-groups and ultimately into one group representing the complete population. Clusters are thus defined at each level of the hierarchy of fissions/ fusions and some criterion is required for assessing which hierarchical level represents a useful clustering of the individuals (this is the problem of how many classes are to be recognised within a given data set). It may be noted, however, that at any level the individuals are not necessarily optimally clustered. The aim of hierarchical strategies is to find the optimum route of fission or fusion within a population and this may mean that some clusters created are

not of optimal homogeneity (LANCE & WILLIAMS, 1966). The optimisation of the contents of the clusters is more the province of non-hierarchical strategies. These have been discussed by LANCE & WILLIAMS (1968) and seem potentially very appropriate for the classification of phytosociological data but they are at present much less well developed than the hierarchical kind.

3.3.6. Divisive method.

Most of the divisive strategies to receive widespread use have been monthetic: i.e. the subdivision of the population of samples has been into classes based upon the presence or absence of a particular attribute. These constitute the derived structuring methods of WILLIAMS & DALE (1965), in which it is the inter-relationships between the attributes (as established from the individuals in which they occur) that are used to classify the individuals themselves.

Association analysis. This technique, described by GOODALL (1953a) and subsequently developed by WILLIAMS & LAMBERT (1959; 1960), is based upon the idea that in a homogeneous community-type there are no significant associations between the species. The technique thus aims at so subdividing a population of samples as to produce groups in which significant associations are absent. This is achieved by selecting the species showing the maximum degree of association with all of the

others and then subdividing the populations into two classes based upon the presence or absence of this. Various measures of association have been used but IVIMEY-COOK (1972) reports that those based upon χ^2 have been the most effective. Most frequently the species showing the maximum value of $\Sigma\chi^2/n$ or $\Sigma\sqrt{\chi^2}/n$ has been used to sub-divide the population. After the first division is made the matrix of association coefficients is re-calculated for each of the sub-groups and the procedure iterates until suitably homogenous groupings are obtained (for the "stopping rules" of the process see WILLIAMS & LAMBERT, 1959).

3.3.7. Agglomerative methods.

These start off with individual samples and progressively fuse them to form groups of decreasing internal similarity until ultimately there is a single group which contains all of the individuals. The grouping process is based upon some measure of resemblance between the individuals so that those which are most similar are grouped together first (i.e. it is a direct-structuring method (WILLIAMS & DALE, 1965)).

There are a wide variety of agglomerative strategies available. As these are capable of producing rather different classifications of the same data set the choice as to which are to be used has to be exercised with care. In particular, different sorting strategies and different measures of resemblance can often have a profound effect on the form of

the classification (LANCE & WILLIAMS, 1966; WILLIAMS et al., 1966; FRENKEL & HARRISON, 1973).

3.3.7.1. Sorting strategies. The sorting strategy is the precise mechanism by which fusion of individuals and (later) groups proceeds. A variety of strategies are available (see SNEATH & SOKAL, 1973) but here only two will be mentioned.

Nearest-neighbour sorting represents the simplest strategy. Similarity coefficients are calculated for all pairs of individuals and then arranged into a linear order starting with the most similar pair. All the coefficients are then examined in a decreasing order of similarity. If neither individual of a coefficient is already in a group they form a new group; if one is in an existing group the other is added to it; if both are in different groups, the groups are fused. The technique is rapid as, for a group of n individuals, $(\frac{1}{2}n(n-1))$ coefficients are computed initially and then no further calculation is required. However, it often leads to rather weak clustering and frequently displays the phenomenon of chaining - the growth of a group by the successive addition of individuals or small groups rather than by the fusion of groups of comparable size.

Centroid sorting also involves the initial computation of $(\frac{1}{2}n(n-1))$ similarity coefficients. The most similar pair of individuals are then fused to form a new synthetic "individual".

A new set of coefficients is then calculated between this individual and all of the others and the process iterates. Apart from the number of calculations required a potential problem here is that of reversals, i.e. when similarity coefficients calculated in the later phases of the fusion process are greater than some of those calculated previously.

3.3.7.2. Similarity measures.

A very wide range of similarity (or dissimilarity) coefficients are available (see DAGNELIE, 1960; GOODALL, 1973a; SNEATH & SOKAL, 1973). Some operate on binary data, others with continuous data and some may be used with both data types. Some are symmetric and consider the absences of attributes as well as the presences in the estimate of similarity, whilst others are asymmetric and consider only presences. The matter as to whether the joint absence of an attribute should be regarded as contributing to the similarity of a pair of samples is contentious. If joint absences are to be considered then it is clearly only sensible in the context of a defined attribute list, i.e. where, in a given data set, every attribute has at least one occurrence. But even in this context problems can arise, relating particularly to the those data sets in which a number of individuals are defined by only a small proportion of the total attribute population. In plant sociology such situations can arise not only when

dealing with species-poor samples but also in highly species-rich communities, where the probability of the occurrence of most species in any one sample is low. It is then possible for the analysis to be dominated by the joint absence of the attributes (see FIELD, 1969; WEBB et al., 1967) so that samples that are quite dissimilar are brought together. On the other hand, when samples which are not too disparate are being examined, a consideration of joint absences may well provide a useful contribution to a clear-cut classification.

LANCE & WILLIAMS (1967) distinguished three types of similarity measure when considering the relationships between groups of individuals. Their notation, which represents a slight modification of that of WILLIAMS et al. (1966) is used here.

Consider two groups I and J which fuse to form group K. The measures that may be distinguished are:

(i)-measures that are solely concerned with a single group: normally some estimate of its degree of homogeneity.

(i,j)-measures that express the relationship between the two groups.

(i,j,k)-measures that express the degree of difference between the two original groups I and J, considered together, and their fusion product K.

When (i,j)-measures are used in a fusion strategy the two groups which are most similar one to another, are fused together. However, when (i,j,k)-measures are used then the most efficient fusion is obtained by uniting the two groups that produce the smallest change in the level of the coefficient

when fused together. In plant sociology the most widely used (i,j,k)-measure has been the information statistic (I).

3.3.7.3. The Information Statistic.

Given a group of n individuals characterised by p attributes with a_j individuals possessing the j^{th} attribute a statistic may be defined for the total information content of the system (I):

$$I = pn \log n - \sum_{j=1}^{p} \left[a_j \log a_j + (n-a_j) \log(n-a_j) \right]$$

This statistic, which is symmetric for presences and absences, arises from the concept of entropy. The term "Information" does not refer to "knowledge", but rather is a measure of disorder. It is a dissimilarity measure: the information level of a single individual, or a group of identical individuals, is zero. Increasing dissimilarity within a group is reflected as an increase in the total information level. The statistic has found wide usage in phytosiology (see ORLOCI, 1968).

One of the most remarkable properties of the statistic is that it is completely additive so that:

$$I(i) + I(j) + \Delta I(i,j,k) = I(k)$$

In terms of the notation used above, the Information gain I is an (i,j,k)-measure. The Information content, I, is an (i)-measure and can be used for assessing the homogeneity

of the group. The statistic can also be used as an (i,j)-measure, but in this case it degenerates into a multiple of Squared Euclidean distance. Thus, although it can be used in nearest neighbour sorting, the measures obtained are simply those of Euclidean distance. However, centroid sorting is appropriate for the statistic and when used with this in agglomerative procedures, WILLIAMS et al. (1966) reported that it produced a clear-cut hierarchy, free from both reversals and chaining, in which most of the individuals were rapidly fused into higher order groups and where the groupings at a given hierarchical level were roughly of a comparable size.

WILLIAMS et al. gave the name Information Analysis to refer to the use of the Information statistic in conjunction with a centroid sorting routine in agglomerative strategies. The numerical process involved is outlined by SNEATH & SOKAL (1973, p.241 ff.). Essentially the basis of fusion is to minimise the Information gain. There are various possibilities for determining at which hierarchical level the analysis should terminate (LAMBERT & WILLIAMS, 1966).

One problem which the strategy presents is that of group-size dependence. This means that, as a group increases in size, it becomes progressively more difficult for other individuals to join it. Hence, in situations where similar individuals form large and homogeneous groupings in the early stages of fusion, slightly aberrant individuals may not join

their parent clusters but instead may be placed together into a heterogenous "dustbin" group in which none of the members need have any particular affinity for one another. Providing such groups can be recognised this is in some respects a useful feature as it may serve to clarify the central pattern by removing anomalous individuals.

The early versions of Information analysis were restricted to binary data. DALE, LANCE & ALBRECHT (1971) have proposed two extensions of the method which permit some types of quantitative data to be used and DALE & ANDERSON (1972), using species-poor data, have attempted to compare the qualitative and quantitative versions. Their results suggested that the quantitative versions were more informative than the qualitative, though this efficacy may partly be related to the species-poverty of the data.

3.3.7.4. The Incremental Sum of Squares.

The Sum of Squares may be defined for a group containing n individuals, as the sum of the n Squared Euclidean distances between the n points of the cluter and their centroid. The use of the statistic as an (i,j,k)-measure in conjunction with a centroid sorting routine has been referred to as Ward's method. The statistic can be used with either binary or numeric data. Some of the properties of the measure have been examined by BURR (1970) and WILLIAMS et al. (1971). It

appears to generate classifications closely comparable with Information Analysis (see 3.3.9.).

3.3.8. Re-allocation strategies.

As has often been pointed out, one of the problems of all hierarchical strategies is the possibility of misclassification of some of the individuals. In agglomerative procedures individuals that fuse into a particular group in the early stages of the process can sometimes migrate in their affinities towards a completely different group as higher order groups come to be produced. Also, ambiguities are possible in the initial stages of fusion when an individual may have the same degree of similarity with a number of other individuals. Similarly, in monothetic divisive strategies the chance presence or absence of a division attribute can cause an individual to be grouped with others with which it is otherwise quite dissimilar.

As LANCE & WILLIAMS (1968) observe, the concept of re-allocation provides some solution to this problem. Having extracted a series of groups at a given level in a hierarchical strategy each individual can then be examined in turn to see if it would be better classified with one of the other groups. If it would, then it is re-allocated to this other group. The process requires to be iterative so that if one individual is re-allocated the others can then be examined for their affinities to the new groups.

3.3.9. Inverse Analysis.

The above discussion has all referred to Normal Analysis, i.e. the classification of stand-samples in terms of the species they contain. However, the same techniques are also applicable for Inverse Analysis, i.e. the classification of species in terms of the samples in which they occur.

3.3.10. Choice of clustering strategy.

As WILLIAMS (1971) points out, the choice of a numerical clustering strategy is often primarily determined by the computer programs that are available to the user. Apart from this constraint, however, various factors seem important in choosing a suitable method.

LAMBERT & DALE (1964) note that there are theoretical advantages to divisive methods: (i) that they operate on the information provided by the entire population, whereas agglomerative techniques operate on single units of minimal information; and (ii) they permit the analysis to be terminated in the upper or middle levels of the hierarchy without having to compute all of the lower-order groupings. However, for large data sets, only monothetic strategies are at present feasible due to the large computer time and storage demands of the polythetic divisive methods. And, although LAMBERT & WILLIAMS (1966) have pointed to the "substantial comparability of results for Association analysis and Information analysis", at least when classifying stand samples, nonetheless,

Association analysis is subject to the misclassification problems of a monothetic method and Information analysis would seem to be a more rigorous and satisfactory technique. However, monothetic divisive methods normally make less computational demands than polythetic agglomerative ones and might thus be regarded the most suitable technique for a large-scale primary survey (LAMBERT & WILLIAMS, loc. cit.). NOY-MEIR et al. (1970) suggest that Association analysis is likely to be more effective in classifying species-rich than species-poor vegetation.

Various polythetic agglomerative strategies were compared by WILLIAMS et al. (1966), who considered that most clear-cut and ecologically acceptable classification was produced by Information analysis. Other procedures involving centroid sorting were susceptible to reversals, whilst methods based upon a nearest-neighbour strategy gave only weak clustering with much chaining. Similar observations were made by FRENKEL & HARRISON (1973). The Information statistic itself is not very effective for dealing with continuous data but it is particularly suitable for binary matrices even with highly-skewed data - i.e. where a particular attribute is lacked by most of the population. However, the strategies using the Incremental Sum of Squares statistic have been shown to generate classifications very similar to those of the Information statistic (e.g. LAMBERT, 1972). It is able to accommodate both binary and continuous data and furthermore,

seems to be free from the tendency to produce non-conformist "dustbin" groups of samples to which Information analysis is prone (WILLIAMS et al., 1971). These authors consider that it is likely to replace the Information statistic, although they still commend the use of the latter in cases where the data are largely binary. BURR (1970) has indicated, however, that even here the Sum of Squares strategy may be preferred, at least in some circumstances. A more thorough assessment of the two techniques would seem to be in order.

Some comparisons have also been drawn between various numerical techniques and the traditional methods of tabular sorting. PROCTOR & IVIMEY-COOK (1966) made a favourable comparison between Association analysis and traditional phytosociology. Both MOORE et al. (1970) and DALE & ANDERSON (1972) make some comparison of numerical and traditional approaches. But although MOORE et al. conclude that the BRAUN-BLANQUET method was the most "efficient" for a general ecological survey, this conclusion was contested by DALE & ANDERSON. In particular, however, MOORE et al. stress the clarity of the BRAUN-BLANQUET tables for displaying the final classification as opposed to dendrograms, which give no indication of the nature of the floristic data involved.

On balance it would seem that numerical procedures have certain advantages over traditional methods, including those of speed and consistency, even if at present these advantages are 'more in potential than performance' (GOODALL, 1973b).

However, it is instructive to note the comments of WILLIAMS (1971): 'The special merit of these strategies is evidently that they simulate rather closely the mental processes of the professional taxonomist or ecologist. It ensures that, given an intractably extensive set of data, the computer can provide a solution that will reasonably approximate that which the professional would obtain intuitively, if he had sufficient time to study the data closely; ....'. Most certainly, numerical methods such as these can be powerful tools - even for traditional phytosociologists.

3.4. Units of Vegetation.

3.4.1. The floristic characterisation of vegetation units.

Having extracted vegetation units it then becomes necessary to define them in terms of their floristic composition that they may be suitably described. Within the ZM system three types of species have been commended for the purpose of diagnosis: constant companions, differential species and character species. Together these form the characteristic species combination of a syntaxon.

Constant species: are those which occur in 81-100% (i.e. constancy class V) of the samples of a given vegetation unit.

Differential species: ('Differentialart'; 'Trennart'). These are species of pronounced affinities to certain vegetation units and which may be used for differentiating between them.

Character species: ('Charakterart'; 'Kennart'). These are a special case of the differential species and they consist of those species of narrow sociological amplitude, which are more or less restricted to specific vegetation units. Three categories of character species can be recognised according to their degree of faithfulness to a particular syntaxon (BRAUN-BLANQUET, 1964):

Exclusive taxa ('treue'): Fidelity 5; Completely, or almost completely restricted to one vegetation unit.

Selective taxa ('fest'): Fidelity 4; Distinct preference for one vegetation unit but occurring also with a low degree of presence in others.

Preferential taxa ('holde'): Fidelity 3; in several vegetation units but optimally developed in one.

The faithfulness of a given species to a community-type can only be assessed when data relating to all, or most, of the vegetation of a given area are available. It may be possible to apply numerical techniques to extract them (cf. GOODALL, 1953b). Character species have formed an important part of the ZM methodology although it seems likely that absolute character species are practically non-existent (MUELLER-DUMBOIS & ELLENBERG, 1973) - occurring only as highly specialised plants of extreme habitats or as endemics or rare species of low presence within their vegetation unit, and thus of limited diagnostic value. There has, in fact, been a certain disenchantment with the character-species concept and ELLENBERG (1954) referred to the "crisis" within the doctrine.

This is largely because such species may lose their specificity to a given community-type when considered outside of the area for which they were originally defined. Most certainly many species have different sociological affinities in different geographical regions and attempts to accommodate this have been made by the erection of geographical categories of character-species (MEIJER DREES, 1951; BECKING, 1957).

Other possibilities for the floristic characterisation of vegetation units have also been explored. WESTHOFF & DEN HELD (1969) gave the concept of the character-combination (Dutch 'kencombinatie') in which a particular combination of species is regarded as being exclusive to a vegetation unit, though none of the individual species need be. Another approach has been by the recognition of sociological species groups (SCAMONI & PASSARGE, 1959; DOING, 1962). Vegetation units can then be defined by their particular combination of species-groups.

The use of the dominant species to characterise vegetation units has only limited commendation in a floristically based survey, unless it is also a character species. It may be noted, however, that the use of character species of Fidelity 3 to define a syntaxon could be tantamount to defining it on the dominant species.

3.4.2. Types of units.

Various vegetation units of vegetation have been proposed. The following usages have been made in this survey:

Nodum - following POORE (1955a) this is used to refer to an abstract unit of unspecified rank.

Sociation - following DU RIETZ (1936) this is used to refer to vegetation units defined by dominance in the different layers. Sociations with a common dominant in one of the layers but not in the others are united into consociations.

Association - this term has been used in a wide variety of ways (see WHITTAKER, 1962; SHIMWELL, 1972), but here it is recognised as an abstract floristic unit defined by its characteristic species combination. In the ZM school the presence of a character species has usually been a prerequisite to the recognition of an Association (e.g. BRAUN-BLANQUET, 1921) though WESTHOFF & DEN HELD (1969) describe Associations defined only by the character-combination concept.

Within the ZM system Associations are, on the one hand, fused into higher unit and, on the other, subdivided into lower categories. The rank of a unit is denoted by the suffix attached to its name as in the following scheme:

Class	-	etea
Order	-	etalia
Alliance	-	ion
Association	-	etum
Sub-Association	-	etosum
Variant	)	no ending
Sub-variant	)	
Facies	)	

Of these units those above the Association are all defined by character species and in general they usually do possess character species of high fidelity (WESTHOFF & MAAREL, 1973) and normally correspond to well-defined ecological categories. The Alliance would seem to be a particularly useful unit. According to MUELLER-DUMBOIS & ELLENBERG (1973, p.260) these are '.... as a rule structurally and physiognomically distinct ... well separated floristically .... more or less natural units' and they seem to 'correspond approximately to earlier Association concept of the Braun-Blanquet school'.

Below the Association the sub-units are distinguished by differential species except for the facies which is characterised by the dominance of a particular species. Some authors (e.g. DUVIGNEAUD, 1946; MEIJER DREES, 1951) have used the different sub-units of the Association to refer specifically to variations induced by particular environmental factors. The expression 'typicum' or 'typical' is often used to designate lower-order units, frequently to refer to species-poor groups which have no differential species of their own. WESTHOFF & DEN HELD (1969), however, have used the expression 'inops' (= having a shortage of) to refer to species-poor groupings.

4. The methods used.

Essentially an eclectic approach has been adopted, particularly combining concepts and methods of the Zürich-Montpellier tradition with some of the more recent numerical procedures. Although the work has broadly followed the pattern of a "traditional" phytosociological survey, an attempt has been made to develop an approach in which the decisions and criteria have been made explicit rather than implicit and which had, at least, some measure of consistency. In particular, attention has been given to the use of the digital computer and numerical classification techniques to handle the data collected in the survey. Because the approach does not conform to that of a particular phytosociological tradition, it has been considered necessary to set out the details of the precise methods that have been used.

4.1. The sites examined.

Fig. 5.1 shows the distribution of the sites that were examined. They are widely distributed throughout England and Wales and include most of the well-known rich fen systems, together with a large number of minor sites. The locations of appropriate sites were largely obtained from information kindly supplied by many local botanists and, in an attempt to be as comprehensive as possible, most of these were visited in

the survey. Where the map shows large areas with no sites this is due either to the absence of suitable areas or, more usually, to the lack of information. Particular attention was paid to sites in Norfolk, especially to the extensive mires of the river valleys in the east of the county (the broads area), as this region supports the best developed residuum of rich fen vegetation in England and Wales. Even here, however, it is necessary to emphasise the primary character of this survey as there are large areas, most certainly in broadland, that demand much more thorough examination.

The sites were visited during the months of June-September of 1972-1974. Most areas were only examined once.

4.2. Sampling strategy.

It was decided to adopt a sampling strategy based upon the subjective selection of stands to be described. Despite the many problems inherent in this approach it was considered to be the only feasible strategy commensurate with the particular constraints of this survey, viz. a large number of sites to be examined in a period of three years.

4.2.1. Stand selection. A total of about 1,000 samples were collected. In order to impart some measure of consistency and reproducibility the following criteria were observed in the selection of an appropriate sample site:

(a) the stand is to be recognised by its floristic and physiognomic features.

(b) the stand is to be selected after an initial reconnaisance of the whole area, whenever this is practicable.

(c) the stand area must be greater than 100 sq. m. Only exceptionally can smaller, fragmentary areas be sampled. In the case of large stands the sample must be situated towards the middle.

(d) the stand must represent the main (i.e. most extensive) developments of vegetation in a given site, although samples of less well developed extensive communities may also be additionally made if required.

(e) the stand must be free from obvious structural or floristic boundaries; strongly heterogenous areas are not to be sampled.

(f) vegetation showing purely quantitative changes in the floristic content can be regarded as forming a single stand.

(g) aggregations of a particular species forming patches of local dominance (etc.) need not be sampled independently unless, (i) there are additional species exclusively associated with them; or (ii) they are associated with a markedly different primary abiotic environment.

(h) the components of small-scale mosaic communities should be sampled together as joint members of a composite stand

though with annotation as to which species occupy which components of the mosaic.

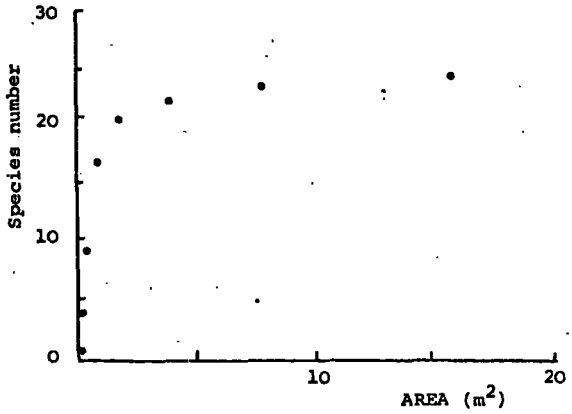
It was found that the application of these criteria led generally to consistent selection of stands which, in the case of a test experiment, was essentially reproduced by a second worker applying the same criteria at the same site.

4.2.2. Sample size. Fig. 4.I gives three examples of species-area curves made from calcareous mire, fen meadow and alder carr types of vegetation. These suggest a minimal area of about 50 square metres for herbaceous fen vegetation and about 200 square metres for carr. Thus, for herbaceous vegetation a standard sample size of 100 sq. m. was adopted and one of 400 sq. m. for carr. This was usually arranged as a square or rectangular quadrat.

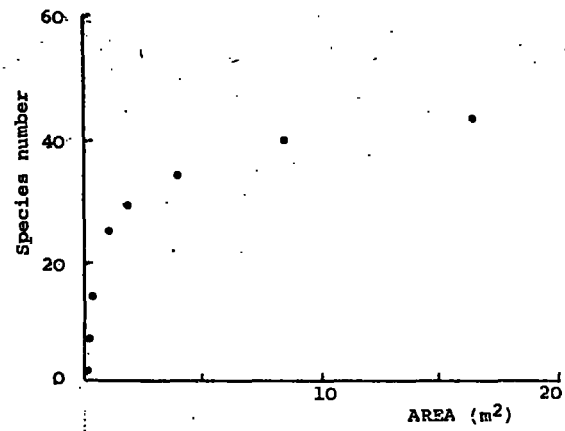
4.2.3. Sample records. The sample records were made on record cards printed specifically for this survey. A completed example is shown in Fig. 4.II.

4.2.3.1. Species present. After the delimitation of the sample plot area the stands were carefully examined to record the plant species. All of the phanerogams and bryophytes present were recorded, although species epiphytic upon trees were omitted. Identification presented few problems but certain

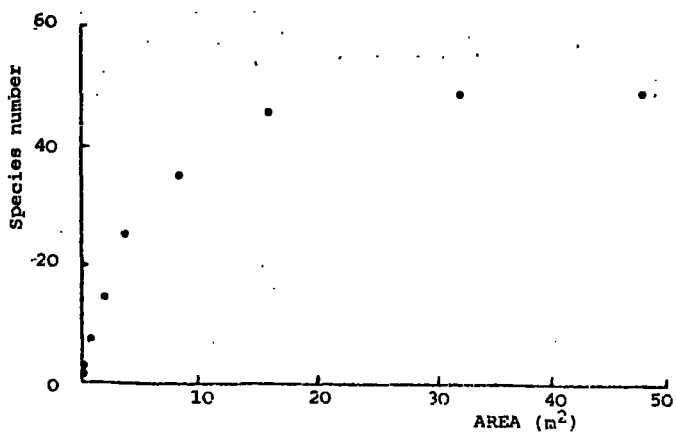
Fig. 4.I. Species-area curves.



(1.) Fen meadow. Drayton Parslow, Bucks.

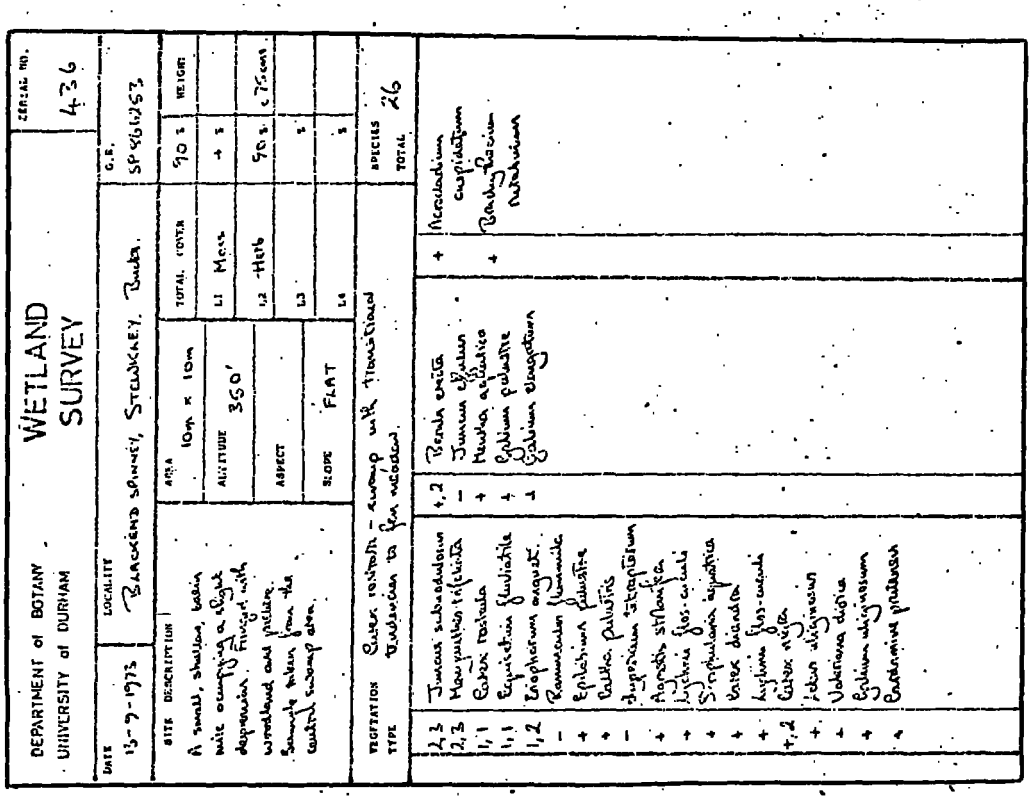


(2.) Schoenus nigricans mire. Cothill, Berks.

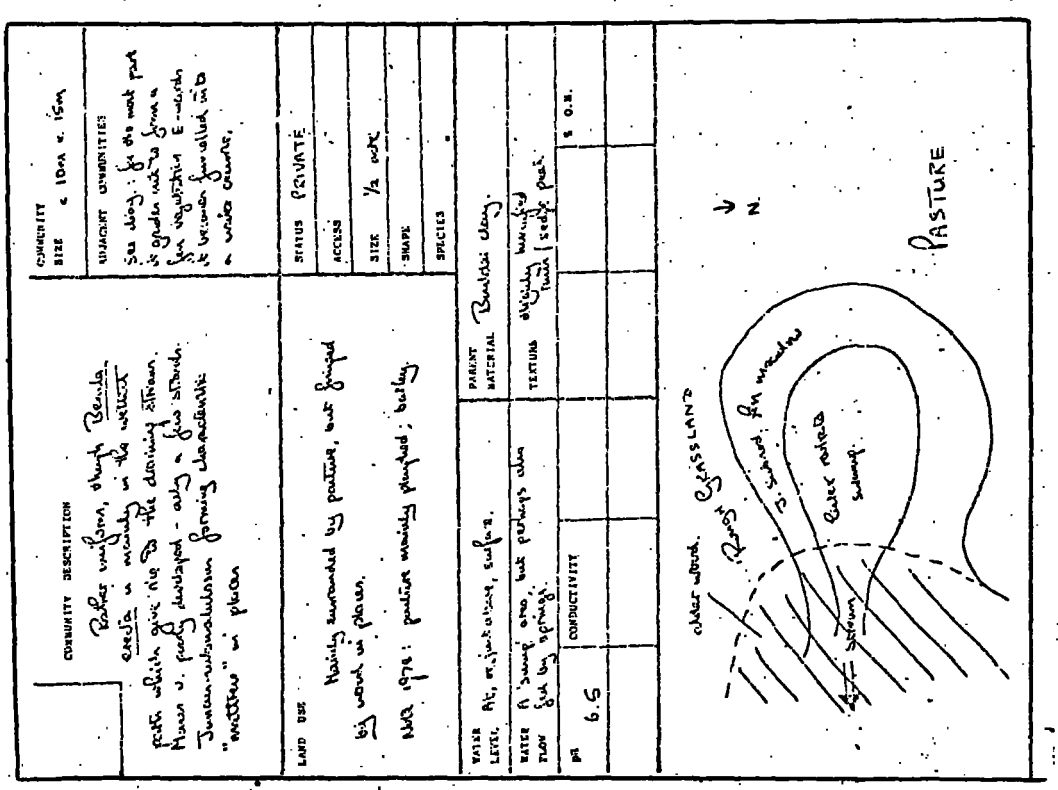


(3.) Alder carr. Barton Broad, Norfolk.

Fig. 4.II. Example of recording card (reduced)



a) front



b) reverse

species, in particular some bryophytes, were collected for subsequent determination. Many of the taxa could be satisfactorily identified from their vegetative growth, but this was quite impossible for some. Non-flowering examples of Dactylorchids were problematic and could only be referred to the genus - indeed these plants, even when in flower, presented some difficulties. The keys and descriptions of HESLOP-HARRISON (1953) were used for their determination. Individuals that seemed to be hybrids were ignored. Similarly, non-flowering Utricularia species have not been identified below the generic level. No attempt has been made to determine Taraxacum species nor to recognise species within the Rosa canina and Rubus fruticosus aggregates. Amongst the willows Salix atrocinerea has not been distinguished from S. cinerea. The two water forget-me-nots, Myosotis caespitosa and M. scorpioides have been separated by the criteria suggested by PERRING (1962), rather than those of CLAPHAM et al. (1962).

Amongst the bryophytes no attempt has been made to distinguish the subspecies bimum and pseudotriquetrum of Bryum pseudotriquetrum. Most of the Drepanocladus revolvens recorded is probably referable to the var. intermedius but not all specimens can be confidently assigned to this. In the liverworts it proved very difficult to separate vegetative Lophocolea bidentata from L. cuspidata and all of the records have been assigned to L. bidentata, to which, in fact, most of them probably refer. Calypogeia fissa and C. trichomanis have been

separated according to the suggestions of PATON (1962).

Fortunately nearly all of the angiosperms of rich fen are perennials and can usually be found at least as vegetative shoots. Moreover most of them are aestival. There are, however, a few vernal species. In particular, Ranunculus ficaria is often frequent in some rich fen communities, especially fen meadow, but as it usually dies back completely before the summer months, it has hardly ever been recorded in this survey. The same applies to a lesser degree to Anemone nemorosa in some types of fen woodland. The saprophytic orchid, Corallorhiza trifida, could also have been missed. With these exceptions, however, it is considered that the plant lists from each sample are both accurate and comprehensive, though the possibility that some species have been overlooked cannot be discounted.

4.2.3.2. Cover and other vegetational records. Within each sample plot brief notes were made on the structure of the vegetation, in particular on such layering as occurred. The total cover also provided by each layer was estimated and the cover of each species. This was according to the following scale:

Cover values used

-	less than 5% cover; species v. rare
+	less than 5% cover; frequent individuals
1	5-20% cover
2	20-40% cover
3	40-60% cover
4	60-80% cover
5	80-100% cover

This simple scale was easy to use and provides a rough indication of the relative proportions of the species in the stands.

An estimate was also made of the sociability of the species using the scale of Braun-Blanquet (BRAUN-BLANQUET, 1964, p.41).

4.2.3.3. Environmental information. The collection of detailed environmental information was incommensurate with the aims of the survey and was not carried out to any extent. However, to assist in describing the vegetation types, casual observations were recorded concerning exposition, slope, nature of the substratum, water depth, water flow and water, pH, together with notes on the topography and use of the surrounding land. These were not in any way to be used for defining the vegetational categories.

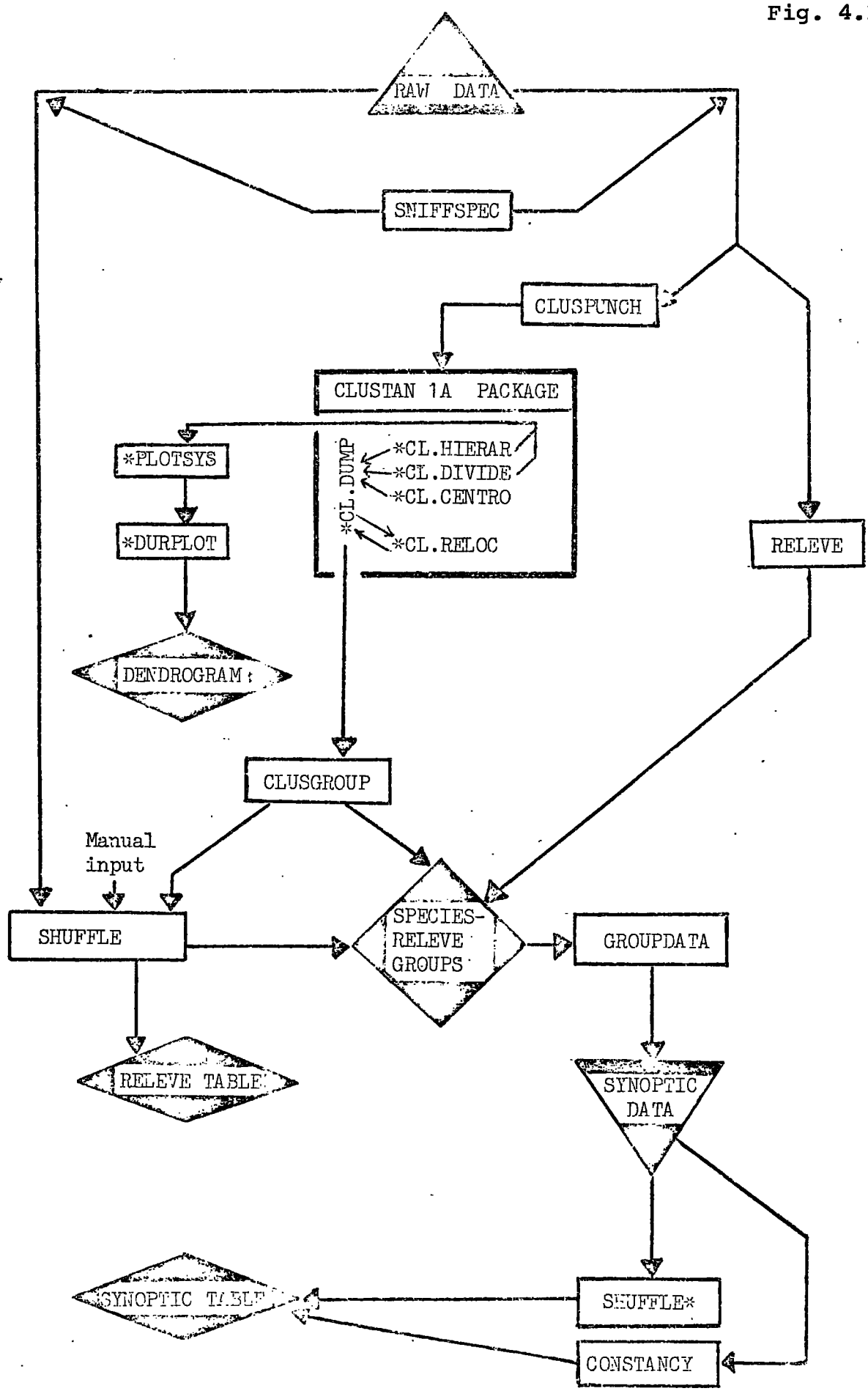
4.2.3.4. Outside of the sample. After the recording of the sample plot was complete a brief examination was made of the plant community outside of the area to ascertain if any additional species could be recorded. These are denoted by brackets surrounding the cover value.

4.3. Computer-based classificatory procedure.

It was recognised that the digital computer could be an important tool in classifying the samples. In particular, it

AVAILABLE COMPUTING PRCCEDURES FOR PHYTOSOCIOLOGICAL ANALYSIS

Fig. 4.III.



offered considerable possibilities for the mechanisation of the Braun-Blanquet table-sorting procedures by providing facilities for the rapid and error free re-writing of the primary matrix. Also, it presented the possibility of using numerical clustering strategies. An attempt was, therefore, made to develop a computer-based system that would permit the data to be processed by most of the classificatory procedures currently used by plant sociologists.

4.3.1. The system. Fig. 4.III. shows the computer-based system that was developed. (Note that triangles refer to data, diamonds to major output and rectangles to programs). This incorporated a number of existing programs but also several new ones had to be devised. These were all written in the FORTRAN IV (G-level) programming language. The system was designed to be used on the Northern Universities Multiple Access Computer installation with an IBM 360/67 computer.

4.3.2. Organisation of the data. Basically, sample data is arranged according to the so-called "Dublin"-format (MOORE, 1971) using the same format as specified by CESKA AND ROEMER (1971). (Only the cover-values of species can be recorded in this). The system is devised so that all

of the samples collected can be stored on magnetic disk on the computer. From this store it is then possible to access such individual samples as are required for a particular analysis.

4.3.3. Braun-Blanquet Table Method. Program SHUFFLE was written to provide a rapid and error-free means of re-ordering and re-writing the species-sample matrix. Essentially, it just represents a mechanisation of the processes involved, using the computer as an automatic typewriter. As well as its use for ZM-type sorting procedures another important use of the program is that it may be used to express, in tabular form, the results of numerical classifications.

"Automatic" Braun-Blanquet-type analysis can be performed using program RELEVE - which is the program originally designed by CESKA AND ROEMER (1971) (updated, CESKA, 1973) suitably modified for use in the system developed here.

4.3.4. Numerical clustering methods. The programs for numerical clustering strategies are all provided by the CLUSTAN 1A package (for details see WISHART, 1969). Of the various programs available here, DIVIDE can be used for Association Analysis (WILLIAMS AND LAMBERT, 1959) and Group Analysis (CRAWFORD AND WISHART, 1967); CENTRO for Information Analysis (WILLIAMS et al., 1966); and HIERAR for Ward's Method (WARD, 1963).

Facilities for the re-allocation of samples within the context of a hierarchical fusion strategy are provided by program RELOC.

The use of the CLUSTAN 1A package is facilitated by ancillary programs that were specifically written for the purpose. As these have been devised to interface with the particular operating systems of the N.U.M.A.C. installations they will not be described in detail. Program CLUSPUNCH converts the arrangement of data in the standard data file into a format that is appropriate for input into the CLUSTAN package. Options permit the data to be inputted either for normal or inverse analysis. In default operation the cover-abundance values of the samples are all reduced to binary (presence/absence) data for use in the CLUSTAN routines. However, there is an option which permits the cover values to be used as quantitative data by using the transformation of the suggested by MOORE et al. (1970). The program also provides facilities for rare attributes to be excluded from the subsequent clustering routines, if required. All attributes occurring less than a specified number of times (which may not be more than 6) are masked.

The numerical analyses are performed by the programs of the CLUSTAN package mentioned above. Of these, three (DIVIDE, CENTRO and HIERAR) generate dendrograms. *PLOTSYS and *DURPLOT are two system programs available to plot these directly on the graph-plotters.

The classification generated by the programs may be directly inputted into program SHUFFLE, so that it is expressed in tabular form. This is achieved by program CLUSGROUP, written specifically for this purpose. As input it is able to use either the sequence in which individuals are arranged in the dendrogram produced by the CLUSTAN routines or, alternatively, it can operate on information concerning the contents of the classes established at any one (predetermined) level of the hierarchy. These data are generated by the CLUSTAN programs themselves and can be used as direct input into program CLUSGROUP and thence to Program SHUFFLE.

All of the programs described above have been linked together to form a continuous system so that, having selected which samples are to be included within a particular run, it is possible to perform the numerical analysis required and to obtain a plot of the dendrogram together with a species-sample table ordered according to the classification produced. The system has also been arranged so that normal and inverse analyses of the same data set can be performed sequentially so that in the final table output both the species and the samples have been clustered.

Synoptic data. After the sample groupings have been formed (irrespective of the process), these can then be examined by program GROUPDATA. These produce some simple group diagnostics (e.g. average species total per sample; estimates of

homotoneity etc.). In particular, it also fuses all of the releve data for a particular group to produce a composite synoptic list, in which the degree of presence of each species is indicated. The list produced is punched onto computer cards in the same format as the original sample data. A number of such lists can then be incorporated into a synoptic data store and processed in just the same way as the original raw data to produce synoptic tables. However, instead of program SHUFFLE, program SHUFFLE* has to be used. Also, the "constancy" version of CESKA AND ROEMER's (1971) program (here denoted as program CONSTANCY) is required rather than the "releve" version.

4.4. A comparison of clustering strategies.

A pilot invesgitation was made to examine the clustering propensities of a number of different numerical strategies with a view to assessing which might serve as suitable methods for classifying the data collected in this survey.

A standard data set of 49 samples was collated from samples collected from parts of East Anglia. These were specifically chosen to produce a matrix which contained at least some very distinct groups of samples but which also had one diffuse group of somewhat "blurred" limits. The data were additionally selected so that at least one group would exist which could only be characterised negatively (i.e. by the absence of

differential species) rather than positively (i.e. by the presence of differentials). Thus, a variety of analytical situations were represented by the data and these provided a basis by which the different methods could be compared and evaluated.

Initially the data were examined by the Braun-Blanquet table method. Three stages of this process (raw table, partially sorted table and final table) are displayed in Tables X.1, X.2 and X.3. This readily revealed the eight clusters that had been envisaged in the creation of the data set, but also indicated that one of these (the ill-defined one) might usefully be sub-divided. Thus, 9 clusters were used as the standard for evaluation. It was considered that any strategy appropriate for processing the data collected in this survey should be able to identify these.

The clustering procedures used were:

1: "Braun-Blanquet table method" using the computer to aid table rearrangement.

2: Association analysis using $\sum X^2/n$ to select the division species.

3: Association analysis using $\sum \sqrt{X^2/n}$ to select the division species.

4: Group analysis using the Crawford-Wishart Interaction statistic.

5: Monothetic division to maximise Information fall.

6: Information analysis: centroid sorting to minimise Information gain.

7: Re-allocation strategy to optimise the Information statistic on the 9-cluster stage from (6).

8: Ward's method: centroid sorting to minimise increment of the Sum of Squares.

9: Re-allocation strategy to optimise the Sum of Squares on the 9-cluster stage from (8).

10: Ward's method: using quantitative data (viz. the transformation of the cover values suggested by MOORE et al. (1970).

11: Ward's method: using a different program to (8).

12: Polythetic fusion: centroid sorting using Squared Euclidean distance.

13: Polythetic fusion: nearest-neighbour sorting using Squared Euclidean distance.

14: Polythetic fusion: centroid sorting using a non-metric coefficient.

15: Polythetic fusion: nearest-neighbour sorting using a non-metric coefficient.

In Table 4.1. the contents of the clusters at the 9-cluster level are compared for all of the strategies. Samples belonging to the same cluster have been denoted by giving them the same

DURHAM UNIVERSITY SCIENCE 20 JAN 1976 LIBRARY

Sample	Clustering strategy														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
251	a	a	a	a	a	a	a	a	a	a	a	a	x	x	x
252	a	a	a	a	a	a	a	a	a	a	a	a	x	x	x
253	a	a	a	a	a	a	a	a	a	a	a	a	x	x	x
250	a	a	a	a	a	a	a	a	a	a	a	a	x	x	x
708	d	d	a	f	a	d	d	d	d	d	d	hh	x	x	x
282	d	d	b	k	b	d	d	d	d	d	d	hh	x	x	x
710	d	d	b	b	b	d	d	d	d	d	d	hh	x	x	x
243	d	d	b	b	b	b	d	b	d	d	b	hh	x	x	x
244	d	b	b	b	b	b	d	b	d	d	b	hh	x	x	x
247	b	b	b	b	b	b	b	b	b	d	b	hh	x	x	x
248	b	b	b	b	b	b	b	b	b	d	b	hh	x	x	x
260	b	b	b	b	b	b	b	b	b	d	b	hh	x	x	x
271	b	b	b	k	b	b	b	b	b	d	b	hh	x	x	x
272	b	b	b	l	b	b	b	b	b	d	b	l	l	x	x
273	b	b	b	b	b	b	b	b	b	d	b	hh	mm	x	x
705	b	b	d	q	d	b	j	b	j	d	b	hh	x	x	x
731	b	b	b	k	b	b	b	b	b	d	b	hh	x	x	x
147	c	c	c	r	c	c	c	c	c	c	c	c	c	x	x
146	c	c	c	q	c	c	c	c	c	c	c	c	c	x	x
140	c	c	c	r	c	c	c	c	c	c	c	c	c	x	x
141	c	c	c	q	c	c	c	c	c	c	c	c	c	x	x
144	c	c	c	r	c	c	c	c	c	c	c	c	c	x	x
145	c	c	c	q	c	c	c	c	c	c	c	c	c	x	x
182	e	e	e	l	e	j	j	j	j	d	j	ii	ii	y	y
774	j	d	d	q	d	j	j	j	j	d	j	hh	x	x	x
773	j	d	d	q	d	j	j	j	j	d	j	hh	x	x	x
714	j	b	b	a	b	j	j	j	j	d	j	jj	x	x	x
788	j	d	d	k	d	j	j	j	j	d	j	hh	x	x	x
789	j	d	d	k	d	j	j	j	j	d	j	hh	x	x	x
706	j	m	m	r	n	n	j	b	j	d	b	hh	x	x	x
754	n	n	n	l	n	n	n	n	n	m	n	kk	x	z	x
279	m	m	m	s	m	m	m	m	m	m	m	kk	x	aa	aa
256	n	n	n	s	n	n	n	n	n	n	n	kk	x	bb	bb
257	n	n	n	s	n	n	n	n	n	n	n	kk	x	bb	bb
269	m	m	n	s	m	m	m	m	m	m	m	kk	x	cc	cc
762	m	m	n	s	m	m	m	m	m	m	m	kk	x	dd	dd
181	h	h	h	s	h	h	h	h	h	**	h	kk	ff	ee	ee
177	h	h	h	s	h	h	h	h	h	h	h	kk	ff	ff	ff
180	h	h	h	s	h	h	h	h	h	h	h	kk	ff	ff	ff
188	h	h	h	s	h	h	h	h	h	**	h	kk	ff	ff	ff
276	i	i	i	f	i	i	i	i	i	i	i	i	i	x	x
201	i	i	i	g	i	i	i	i	i	i	i	i	i	x	x
277	i	i	i	g	i	i	i	i	i	i	i	i	i	x	x
280	i	i	i	f	i	i	i	i	i	i	i	i	i	x	x
285	i	i	i	b	i	i	i	i	i	i	i	gg	gg	x	gg
701	i	i	i	g	i	i	u	u	u	u	u	i	i	x	x
702	i	i	i	b	i	i	u	u	u	u	u	i	i	x	x
703	i	i	i	f	i	i	u	u	u	u	u	i	i	x	x
734	i	i	i	b	i	i	u	u	u	*	u	i	i	x	x
	ZM	monothetic divisive				polythetic agglomerative (ij,k)-measures						polythetic agglomerative (i,j)-measures			

Table 4.1. For explanation, see text.

alphameric character; where the same basic clusters have been recognised by different strategies the same alphameric character is used for the cluster in each case, so as to facilitate comparison. A table of this nature is of limited value as different strategies, even whilst identifying fundamentally the same clusters, need not necessarily do so at precisely the same level in the hierarchy. Nonetheless, the table emphasises that some of the strategies form virtually identical clusters to those of the Braun-Blanquet table at the 9-cluster stage. In particular, all of the polythetic agglomerative (i,j,k)-measures - with the exception of the quantitative version of Ward's method (strategy 10) - have produced clusters with a content virtually identical to those in the Braun-Blanquet tables. To a lesser extent the same applies to the monothetic divisive procedures (except for Group analysis). In the polythetic agglomerative (i,j)-measure strategies, however, the contents of the clusters are very different.

In Table 4.2. an attempt is made to assess the extent to which the different polythetic techniques have produced the same clustering of the samples, irrespective of the hierarchical level simply by establishing, from the dendrograms, which samples have been brought together and by comparing them with the initial groupings of the Braun-Blanquet classification grouped together in the dendrogram. The method of assessment has been (i) to indicate the extent to which samples placed together in the original Braun-Blanquet classification have

Table 4.2. Comparison of clustering strategies (2).

Group.	Clustering strategy.									
	1	6	7	8	9	11	12	13	14	15
1	4	4	4	4	4	4	4	4	4	4
2	5	3	5	3	5	3	3	3	4	4
3	9	8	8	9	8	9	7	8	8	8
4	6	6	6	6	6	6	5	5	5	5
5	6	5	6	5	6	5	5	5	5	5
6	3	3	3	3	3	3	3	3	3	3
7	3	3	3	3	3	3	3	3	2	3
8	4	4	4	4	4	4	4	4	4	4
9	9	9	9	9	9	9	9	9	9	8
Total misclassed		4	1	3	1	3	5	4	4	4

For explanations see text. The clustering strategies are those referred to in the text (above). The 9 groups are the groups of samples as arranged by a subjective sorting procedure and the figures below strategy 1 represent the number of samples assigned to each group by this procedure. The figures in the other columns refer to the number of samples, out of the original complement of samples assigned to a particular group, that have continued to be grouped together by the various numerical strategies. Below this is indicated the total number of samples that have not been placed with the other members of the original groups.

also been placed together by numerical techniques, and (ii) to sum the number of samples that have been placed differently.

The results indicate that all of the techniques have produced the same basic classification. All strategies have recognised Clusters 1, 6 and 8 with precisely the same contents as in the Braun-Blanquet sort. With the other groups there is a small degree of misclassification, but this involves only the same small number of samples. These are releve numbers 243, 244, 272, 705, 182 and 279. It may be noted from examination of Table X.3 that these are either of dubious floristic affiliation to any of the groups (e.g. 182) or in some way transitional between groups (e.g. 244; 705). Interestingly, S.182 was misclassified by all of the techniques using (i,j)-measures (also by Association Analysis) and is clearly an anomalous member of this set of samples. This would not have been made clear by the (i,j,k)-measure strategies. Nonetheless, overall these latter procedures performed best. The results of Ward's method and Information Analysis were closely comparable. In particular, when the samples were re-allocated at the 9-cluster stage (strategies 7 and 9) there was only one misclassification, in each case due to S.705. Both procedures re-allocated this from Cluster 3 to Cluster 5. Re-examination of Table X.3. suggests that this sample should probably not have been initially allocated to Group 3.

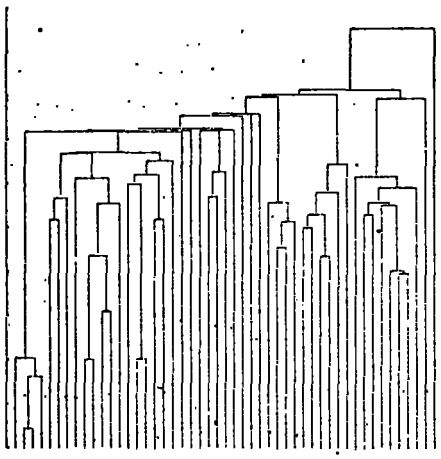
These results point to the value of numerical techniques for classifying phytosociological data, although it is important

to recognise that in this test only a small data matrix with relatively distinct groups was involved. However, with more complex matrices it becomes increasingly difficult to provide a reliable classification as a standard for the evaluation of the other techniques.

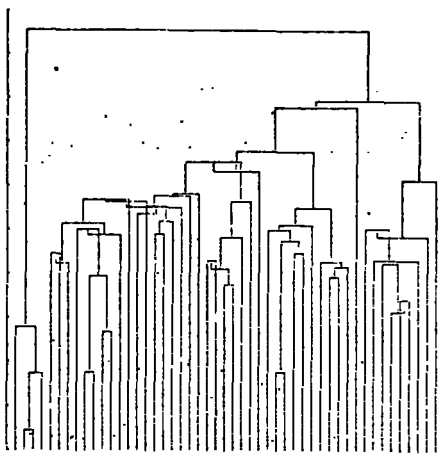
Another point of comparison between the polythetic methods is in the dendrograms produced. The five dendrograms derived from the techniques are shown in Fig. 4.IV. (The dendrogram for Ward's method is virtually the same as for Information Analysis and is not given). From these it is evident that Information Analysis has produced a well-structured, balanced dendrogram, in which the individual samples have been rapidly fused into higher order groups and which clearly shows the groupings that have been established. The same is not true for the other techniques where the dendrograms are poorly structured, crowded and confused, showing some degree of chaining. Those produced using the non-metric coefficient are more satisfactory than with Squared Euclidean distance as the similarity measure. In both cases, however, with centroid sorting routines, reversals are a prominent feature.

The results of this investigation suggest either Information Analysis or Ward's method as the most satisfactory of the available procedures, for the purposes of clustering phyto-sociological data, especially in combination with re-allocation strategies. It was thus decided to use Information analysis as the basis for the processing of the data of this survey.

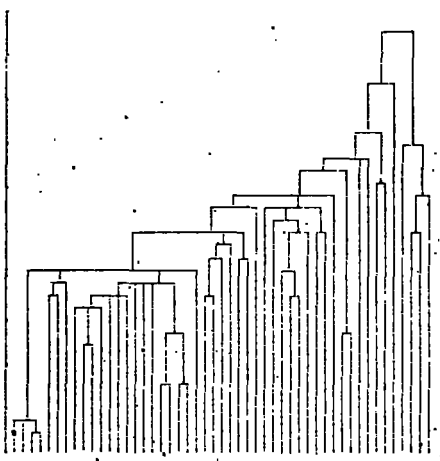
Fig. 4.IV. : Comparison of dendrograms of 5 agglomerative clustering procedures



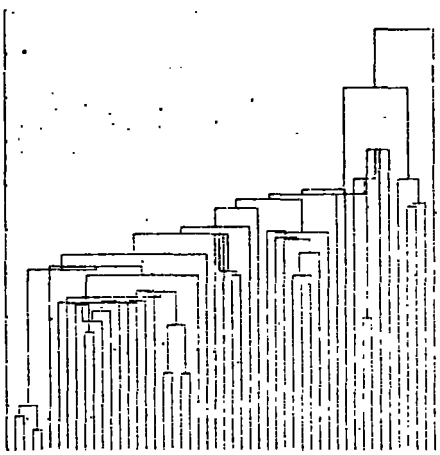
nearest-neighbour sort; euclidean distance



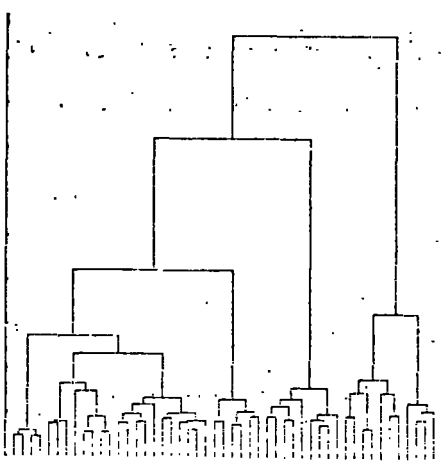
centroid sort; euclidean distance



nearest-neighbour sort; non-metric coefficient



centroid sort; non-metric coefficient



centroid sort; information statistic

4.5. The strategy for extracting vegetation units

It was decided to adopt a clustering strategy based upon numerical procedures using the Information statistic followed by the production of a species-sample table. It was considered that the Information analysis would provide a rapid and consistent clustering technique giving results largely commensurate with the traditional hand-sorting approach and that the subsequent production of a structured table would provide a clear display of the vegetation units extracted.

Unfortunately the data set could not be processed in one run, due to the excessive demands upon computer processing time, and storage made by the large number of samples. It was thus necessary to subdivide the data. It was apparent that these could be readily partitioned into 9 categories which were fairly well defined by physiognomic-ecological and floristic criteria. These were:

Group 1: swamp vegetation types.

Group 2: species-rich tall herbaceous fen communities dominated by *Cladium mariscus* and/or *Phragmites communis*.

Group 3: species-poor tall herbaceous fen communities dominated by *Glyceria maxima* or *Phragmites communis*.

Group 4: calcareous mire communities.

Group 5: topogenous mire communities with much *Carex diandra*, *C. lasiocarpa* and *C. rostrata*.

Group 6: rich fen meadow communities.

Group 7: fen grassland dominated by *Molinia caerulea*.

Group 8: species-poor tall-herb fen communities dominated by *Epilobium hirsutum* and/or *Filipendula ulmaria*.

Group 9: fen carr communities.

Fuller details of each group's content are recorded in the introduction to each group in Chapter 6. There were only a few ambiguities in initially assigning the samples to the groups. Where this was the case the sample was usually omitted from the analysis and then later subjectively allocated to the vegetation-unit with which it had greatest affinity.

It was still not possible to analyse some of the data sets on the N.U.M.A.C. IMB 360/67 installation because of their excessive size. However, access to the CLUSTAN routines on the IMB 370/168 at Cambridge obviated the need for any further subdivision.

Groups 1 and 8 were both analysed just using the Braun-Blanquet table method. This seemed the most appropriate strategy for these data sets which were species-poor, floristically heterogenous and contained only a small number of samples. All of the other groups were processed as follows:

(i) Both samples and species were grouped by normal and inverse Information analysis using program CENTRO of the CLUSTAN 1A package. Attributes occurring in less than 4 samples were excluded from the analysis. This was partly to reduce the size of the data matrix to expedite processing but also to help prevent the analyses becoming dominated by the joint absences of attributes.

(ii) On examination of the dendrograms and the ordered species-sample table produced by the above processes, a decision was made as to the hierarchical level representing the most "useful" partitioning of the data set. This was a subjective decision based upon the requirement for the units (i) to make ecological-sociological "sense", and (ii) to be well defined floristically. This latter constraint was introduced as it was considered that, for a primary classification, the most usable units are those which can be characterised by a few well defined floristic criteria.

(iii) When an appropriate hierarchical level was selected (normally at an Information level of 80-100) the groups were examined for the possibility of re-allocation of the samples (to redress misclassifications), using program RELOC.

(iv) The species-sample matrix was re-examined and occasional subjective re-allocation of selected stands was made to optimise the contents of the groups if this was considered appropriate.

(v) The main vegetational groups were extracted from the table, again selecting those which appeared to be usable categories according to the criteria above. The final units selected did not necessarily all form at the same level in the Information analysis hierarchy. Indeed, the restriction of the units recognised to those formed at one selected level would have obscured some very real floristic and ecological distinctions (cf. DALE & ANDERSON, 1972).

With the species-groupings re-ordering was also performed. Species that had no, or very limited, diagnostic value were placed at the bottom of the tables. No attempt was made to produce Association Tables (sensu the ZM school), where the species characteristic of the higher syntaxa are identified. Apart from the lack of knowledge as to the relevant species it was considered that any strong deviation from the species-groups established in the analyses would be more likely to obscure the structuring in the tables than to enhance it.

This analytical strategy did not produce a good classification of Group 3 and Group 6 data. Here, additional use was made of Ward's method using quantitative data derived by a transformation of the cover values of the samples (see 6.3. and 6.6.1.7.).

(vi) Each vegetation-unit was designated as a nodum and given a temporary name based upon the most prominent, constant or diagnostic species. These form the basic descriptive units of Chapter 6. An attempt has been made to extract easily-defined floristic criteria so as to characterise each nodum. However, as they represent polythetic classes, this has not always been possible.

4.6. Syntaxonomic work.

There are some distinct advantages to be gained from

naming units of vegetation. As it is even more advantageous if the same name used by different authors refers to the same type of vegetation, in considering potential names for the noda of this survey reference has been made to the work of British and Continental phytosociologists to ascertain whether they (the noda) can be satisfactorily relegated to any pre-existing units. This has meant tracing the (often complex) history of some of the names through the phytosociological literature.

When a nodum obviously fits into an established unit then this unit has been employed. When it does not clearly belong to any known unit, or where potential existing units seem unsatisfactory for other reasons, a new unit has been established. This has only been done in cases where it is considered that the vegetation-type in question has become adequately circumscribed for this to be possible. In those cases where it has obvious floristic connections with vegetation-types not yet described it was considered premature to establish definitive phytocoena. Noda falling into this category have just been given ad hoc names to serve as temporary labels until their sociological status can be better defined. It is considered that the establishment of Associations or other major vegetation categories can only be performed satisfactorily as a divisive procedure based upon an overall conspectus of a particular community-type in conjunction with related types. The proliferation of "Associations" as agglomera-

tively-derived units resulting from local, or otherwise inadequate, studies is not to be commended.

No attempt has been made to use fidelity as a basis for characterising the Associations, due to inadequate information concerning the sociological affinities of species for British vegetation as a whole. For some Associations, however, potential character species have been suggested. Generally, Associations have been characterised by the other elements of the characteristic species combination of the syntaxa, especially constant differential species.

The hierarchical subdivision of Associations has normally reflected the hierarchical relationships between the noda established by Information analysis. In some cases, however, through considerations of the nomenclature, characterisation and utility of the sub-groupings, it has been convenient to establish a rather different system of subdivisions on the basis of personal opinion and judgement. It is indicated where this has been done.

The arrangement of Associations into higher order syntaxa essentially follows the schemes of OBERDORFER et al. (1967) and WESTHOFF & DEN HELD (1969).

PART III: THE VEGETATION

Chapter 5.

Rich fen systems in England and Wales.

5. Rich fen systems in England and Wales

This chapter presents a general sketch of the occurrence of rich fen systems within England and Wales, as revealed in the present survey. In particular, it affords a brief introduction to the sites that are named in Chapter 6.

5.1. Morphological categories of rich fen

For the purposes of description certain categories of mires have been adopted. These are:

(a) spring mires - developed on the slopes of valleys and hillsides etc., in association with springs and areas of water seepage. These are always small in extent, often with little accumulated peat.

(b) valley mires - developed along the slopes and floors of valleys and may be quite extensive. Irrigated by springs and seepage areas with only a limited influence of through-flowing water.

(c) basin mires - developed in hollows (often of glacial origin), which may be completely peat-filled or have some open water. The slopes may support springs and associated mires but in the central basin area the water is topogenously determined. Often developed over deep peat.

(d) headwater mires - used as a general term for mire systems developed at the headwaters of streams and rivers. Irrigated by springs and seepage. May incorporate any of the

three above-named categories.

(e) flood-plain mires - developed on badly-drained flood-plains alongside rivers. Flat areas often with deep accumulations of peat. May be fed by springs along the landward margin but the main irrigation is from the river, which maintains high water-levels within the systems sometimes with occasional flooding.

(f) inundation mires - belong to the same category as (e) but do not have constantly a high water-table and are dry for much of the year except for certain periods when they may become flooded.

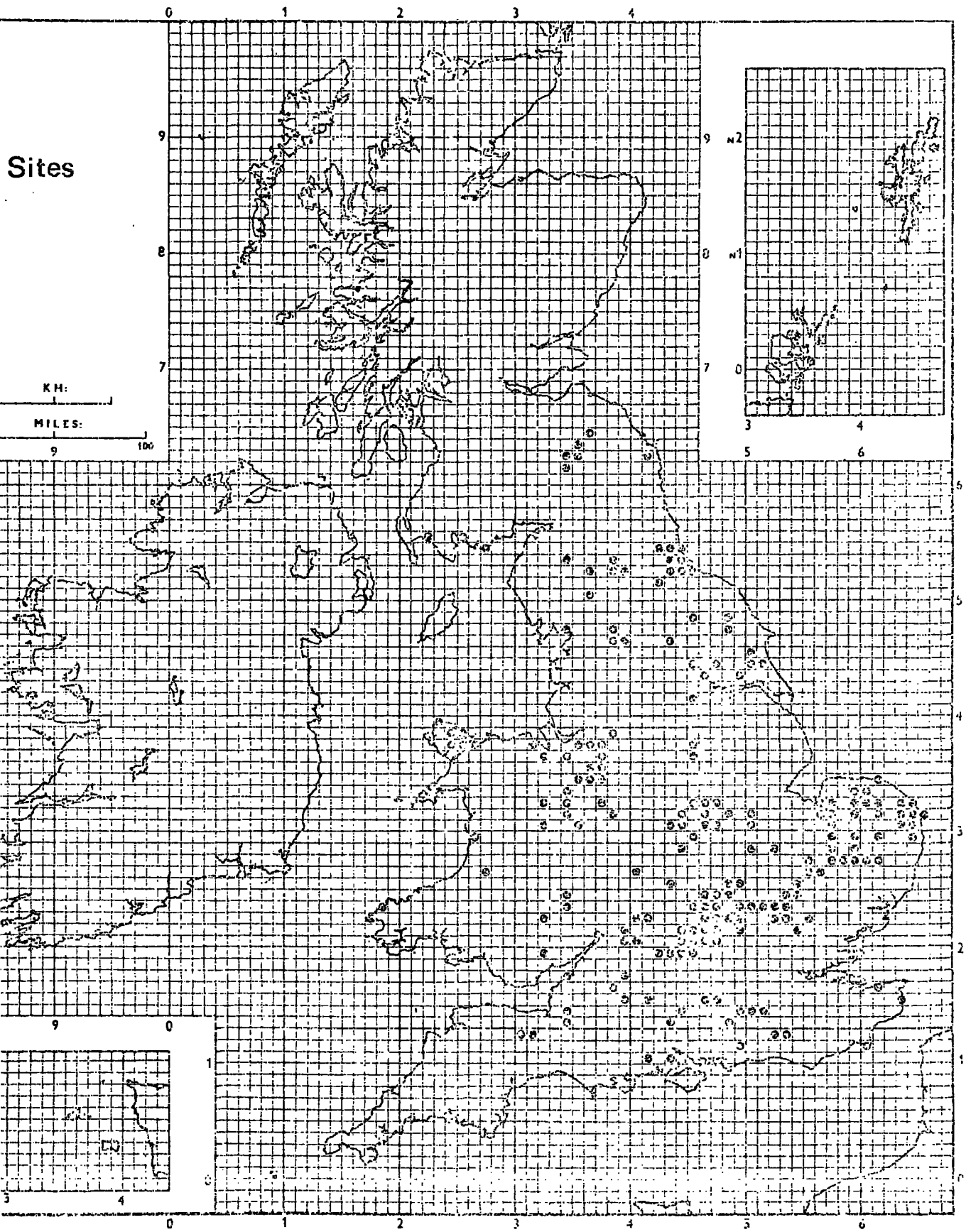
(g) lacustrine mires - developed on the flat, badly drained margins of lakes and pools upon which they are often encroaching by hydroseral development. There may be a small amount of irrigation by peripheral springs but the main water-supply is from the lake itself. When the water of the lake is derived entirely from springs around the edge then this constitutes the same category as basin mires (c).

A given rich fen system may contain one or several of these different types of mire.

Distribution of rich fen systems.

The distribution of the fen systems examined in this survey is shown in Fig. 5.I. These will be considered on a regional basis:

Fig. 5.I.



BASED UPON BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

5.2. Norfolk and Suffolk

These two counties, especially Norfolk, represent the most important area for rich fen in England and Wales, both in terms of the number of extant mires and also the diversity of plant communities represented. It is convenient to recognise two areas:

5.2.1. West Norfolk and North West Suffolk.

In West Norfolk and parts of N.W. Suffolk most of the rich fen systems are associated with the rivers flowing west into the Fens. These include the Lark, Little Ouse, Wissey, Nar and Gaywood rivers. In this slightly undulating area, mainly composed of glacial drift deposits capping a Chalk bedrock many areas of fen occur. These were once much more extensive, flanking long stretches of many of the rivers, but there has been much drainage and reclamation. Nonetheless, this area still supports of wide diversity of rich fen sites.

Most of the extant fen systems fall into the categories of valley mire, headwater mire and basin mire and are especially characteristic of the upper reaches of some of the rivers. Of particular interest is the complex of wetland developed along the Norfolk-Suffolk border between Thetford and Diss, where a number of rich fen sites occur. The extensive fen basin a few miles west of Diss, which is occupied by the Redgrave and Lopham fens, forms the source both of the R.

Waveney draining to the east and the R. Little Ouse draining to the west. In this same neighbourhood there are a number of other smaller fen systems, some developed on the shallow slopes between the river and the surrounding upland, other occupying small fen basins. These mires have been described in detail by BELLAMY & ROSE (1961). North of the R. Little Ouse there are a number of additional fen sites, especially associated with the upper reaches of the River Thet. Some of these, such as Old Buckenham Fen near Attleborough, are rather extensive. Others include Kenninghall Fen and Swangey Fen.

In the area between the Waveney-Ouse fens and King's Lynn there are some fen systems of a rather different character. These are well developed at Thompson Common and at East Walton Common. In both places there are extensive areas of dry, rough grassland containing numerous small, water-filled depressions. These depressions, which may represent solution hollows in the underlying chalk, are in varying stages of hydroseral development, some containing a large amount of open water, others being largely closed-over by fen communities (see 6.1.2.2.). A variety of fen communities are represented at these two sites but they are of particular interest in that they support several community-types of mesotrophic topogenous fen which otherwise are of very restricted distribution. Between Thompson and East Walton Commons is the Foulden Common-Gooderstone Common rich fen system. This also contains a number of depressions similar to those mentioned above, but

in addition it is also a headwater-fen complex and, in places it contains some highly species-rich vegetations developed under the influence of irrigation by calcareous springs.

In the region immediately east and south east of King's Lynn many of the wetland areas associated with the Nar and Gaywood rivers (see PETCH, 1947) have largely dried out. One site that retains much of its former interest, however, is Roydon Common. This is an extensive area developed over the Sandringham Sands of the Lower Greensand and mainly consists of dry heath. But there is also a shallow valley mire showing an interesting zonation of communities from wet heath along the margins to calcareous fen along the central drainage axis (see ROSE, 1953; DANIELS & PEARSON, 1974). Alongside this drainage axis are areas of mixed mire where the rich fen vegetation is intermixed with acidophilic species. Similar areas to this occur elsewhere in Norfolk, particularly at Buxton Heath just north of Norwich, and at Holt Lowes near the Norfolk coast. In both of these areas, however, the mires are developed in association with acidic glacial sands and gravels.

Much of central north Norfolk is drained by the R. Wensum which flows eastwards to Norwich to join the R. Yare. There are some areas of wetland associated with the Wensum itself, such as Sculthorpe Moor developed over the flat plain alongside the river near Fakenham, but of particular note are some rather small valley fens near the headwaters of some of the

tributaries. These include Scarning Fen near East Dereham and Booton Common near Reepham. The slopes of both of these fens are irrigated by highly calcareous water and support some very rich plant communities. Other examples in the area include Kettlestone Fen, near Kettlestone and Whitwell Common, near Reepham.

5.2.2. East Norfolk river valleys

Some of the most extensive and important areas of rich fen remaining in England and Wales occupy stretches of wide alluvial plains of the five main rivers that flow through East Norfolk to empty into the North Sea at Great Yarmouth. These rivers are the Waveney, the Yare, the Bure and the two tributaries of the Bure, the Ant and Thurne. The areas of fen to be considered here are all developed to the east of Norwich and constitute the region known as "broadland". Here the rivers occupy wide, shallow valleys cut into the surrounding upland - which consists of a gently undulating landscape of glacial clays and gravels overlying shelly Pleistocene Crag, reaching up to 150-200 ft. O.D. The flat valley floors, however, are but a few feet above sea level and the sluggish rivers flow with a negligible gradient down to the sea. The valleys themselves are filled with extensive accumulations of peat intercalated with bands of estuarine clay. These clays have been deposited during periods of marine transgression and

are most extensively developed in the lower reaches of the rivers; further upstream they are less thick and become increasingly confined to the river channel. In areas not influenced by these deposits there are continuous peats.

Over large areas of the valleys the rivers have been embanked and the surrounding marshes drained. This has particularly occurred in the lower reaches where the alluvial plains, here largely covered by the estuarine clays, have been reclaimed to produce extensive grazing levels. Similar reclamation has also been attempted further upstream, but with less success.

However, in the middle reaches of the valleys there remain substantial areas of undrained, unembanked peat fens. These have long been exploited by man as sources of peat and of litter, fodder and thatch and they have a long and complex history of peat cutting and of mowing. Extending through them - usually in direct connection with the river and providing some degree of water circulation - is an extensive system of dykes, which were cut for the purposes of access and transportation. In recent years, however, many of these have become derelict and overgrown as a result of the diminishing economic interest in the marshes.

Within the undrained fens are the broads - rather shallow bodies of water, which were shown by LAMBERT et al. (1960) to be the relicts of former deep peat excavations. These occur

with varying degrees of colonisation by swamp and fen communities as part of the hydroseral successional sequence so that some (e.g. Decoy Broad in the Bure valley) remain as large, open stretches of water, whilst others (e.g. Surlingham broad in the Yare valley), have largely closed over and represent only vestiges of their former extent. Some former broads (e.g. Sutton Broad in the Ant valley) have become almost completely overgrown, so that there is little, on the surface, to indicate their earlier occurrence. JENNINGS & LAMBERT (1951) refer to two categories of broad. There are side-valley broads, which occur in subsidiary valleys and form part of the drinage axis of the stream. The others, which occur in the main river valleys, are called by-passed broads and occupy the valley floor to either side of the river. (One apparent exception to this is Barton Broad in the Ant valley, as here the river flows directly through it. This, however, has been the result of a diversion of the river as, formerly, it flowed past the broad on the eastern side). Although these broads are "by-passed" and occur away from the central drainage axis of the valleys, nonetheless, most of them have open connections with the rivers through dykes and waterways so that there is some degree of water-circulation, though in some of the more land-locked broads this may only be slight. This connection has not always been retained, however, and, in particular, Upton Broad, which is in the lower reaches of the Bure valley and set well back from the

river, separated by drained grazing levels, is completely disconnected.

An important factor influencing the extent of water movement in the broads and dykes is the degree to which they are 'exposed' to tidal influences. The rivers Yare and Waveney are the most tidal and the broads are subject to considerable rhythmic tidal water movements. The Bure, in contrast, is subject to a much reduced degree of tidal rise and fall, and the Ant and the Thurne are hardly influenced by the tides at all. Here the degree of water-movement in the dykes and broads is very much reduced and in some isolated parts may be minimal.

Further details and descriptions of the individual broads are given by LAMBERT & JENNINGS (1951) (for the Bure valley only) and in LAMBERT et al. (1960) and ELLIS (1965). The vegetation of the fens has received some description by PALLIS (1911), NICHOLSON (1909), ELLIS (1934) and LAMBERT (1946, 1948, 1951, 1965).

These mires all fall into the category of flood-plain mires. In the Ant valley, however, above the main flood-plain mire complex small lateral valleys near Smallburgh and East Ruston support rich valley mires. Another small valley-mire, unfortunately now partly drained, in E. Norfolk, is at Flordon Common, S.E. of Norwich (BURRELL & CLARKE, 1910).

5.3. Cambridgeshire and Huntingdonshire

Wicken Fen, about 10 miles N.E. of Cambridge, represents one of the few remnants of the peat fens that once filled the Fenland basin of East Anglia. The mire is developed at the S.E. margin of this basin and has been preserved as a flood catchment area. It is a flood-plain mire with the water level in the dykes maintained artificially high by sluice gates at Upware. The peat is 3-4 m deep and in the past the area has been much used for peat cutting. The fen has also been widely used for the mowing of sedge (Cladium mariscus) and litter (Molinia caerulea) and has a complex management history which is expressed by the present-day patterns of the vegetation cover. Much of the present vegetation is composed of fen carr, but attempts are being made to maintain some areas as open fen. Descriptions of the vegetation have been given by YAPP (1909) and GODWIN & TANSLEY (1929).

The other major remnant of the Fenlands lies close to the S.W. margin of the basin. This is Woodwalton Fen, a rectangular block of flood-plain mire, which has been enormously influenced by man (see POORE, 1956b; DUFFEY, 1971). This was once an area of acidophilous raised bog, but, during the last 100 years, it has been extensively worked for peat and this has served to remove most of the upper acidic layers to expose the fen peat underneath. The area has been drained and reclaimed and at one time certain parts were used for grazing and even for cultivation. Now the area is designated as a

National Nature Reserve and a high water-level is maintained in the fen by means of the dyke system.

The second main rich fen system in Cambridgeshire is Chippenham Fen. This is a mire of some 230 acres developed in a shallow, spring-fed basin over a bedrock of Chalk, close to the edge of the Fenland. The fen has been extensively used for peat-cutting and many parts show a pattern of parallel trenches and ridges. Much of the N.E. part of the fen, as well as several other areas, consists of planted woodland dating from the end of the 18th Century.

Elsewhere in Cambridgeshire there are only a few marshy places. To the south of Cambridge, associated with the chalk, there remain some rather small, damp peaty areas associated with calcareous springs and seepage which support types of fen meadow vegetation. They include the Thriplow meadows, described by CROMPTON (1972), where there is a fairly rich fen meadow flora and which are of interest both because of the management experiments reported by CROMPTON & HEPBURN (1972), and also because it has been shown that a large part of the area was once under cultivation (CROMPTON, 1972).

5.4. The South Midlands

With one main exception, the South Midlands have not been noted for their wetland vegetation. The exception is the fen basins of the Cothill area of Berkshire where, irrigated by

calcareous water derived from the Corallian limestone, shallow peat-filled basins support well-developed examples of rich fen vegetation (TANSLEY, 1939; CLAPHAM, 1940). The best known example is at Cothill itself, a valley fen filled with calcareous peat up to 14 ft deep (CLAPHAM & CLAPHAM, 1939), but there are also other sites. Further small valley fens and spring fens occur in this area and also in adjoining parts of Oxfordshire.

Elsewhere in the South Midlands there are a number of small areas of rich fen, generally developed as spring mires and supporting a fen meadow type of vegetation. A number of such sites have been found in parts of North Buckinghamshire. These are particularly associated with deposits of glacial material - outwash sands and gravels together with chalky boulder clay - laid upon a Jurassic bedrock of Oxford Clay. This area, close to the towns of Bletchley and Buckingham, has a gently undulating landscape between 300-400 ft O.D. It forms a watershed drained by numerous small streams, and associated with springs at or near the headwaters of these are a number of small spring and valley mires (see Fig. 6.6.IV). Similar small spring fens also occur in places on the Great Oolite and Cornbrash exposures further north both in Buckinghamshire and N. Bedfordshire. In Hertfordshire they occur in similar situations on the deposits of boulder clay S.E. of the Chalk scarp. The Chalk itself has few associated fens but in some

places, where the Lower Chalk has washed down onto the Gault to form the Chalk Marl, small spring mires have developed.

In Bedfordshire and in the adjoining part of North Bucks., north west of the Chalk and Gault deposits, the Cretaceous system continues as a prominent exposure of Lower Greensand. This supports only limited wetland vegetation which in any case is often too acidophilic to be regarded as rich fen. However, in some small, sharply incised peaty-valleys there is limited development of fen woodland beneath springs and lines of water-seepage. Such areas were, in fact, previously more widespread but have largely been lost through drainage. Also in Bedfordshire, still on the Lower Greensand, is an area known as Flitwick Moor (see DONY, 1953). This site - a remnant of a once larger area - is part of a shallow peat-filled trough immediately S.E. of Ampthill. It was formerly much wetter but still supports an extensive cover of mesotrophic fen and carr. In places it is still cut for peat.

5.5. Southern England

Rich fen is not extensively developed in Southern England and only a small number of sites were located in this survey. Near Sandwick in East Kent, in a hollow in the Chalk, there remain fragments of the East Kent valley fens (ROSE, 1950) and much further west, along the north edge of the North Dows near Basingstoke, there are also some small mires associated

with calcareous springs draining the chalk. The most extensive of these is Greywell Fen, a valley mire extending for almost a mile along the headwaters of the R. Whitewater. There is also a small, but rich, spring mire at the headwaters of the Lyde River, near Basingstoke.

In Hampshire there are some extensive remnants of flood-plain mire developed over the narrow alluvial plains of the R. Test, where it flows through the Chalk. One important site is the grazed expanse of Bransbury Common, S.E. of Andover but south of this there are also some extensive marshes in the neighbourhood of Stockbridge where areas of tangled fen have been conserved by trout-fishing interests.

There is little wetland associated with the chalk in Wiltshire. In the Vale of Pewsey, on a floor of Gault which has been exposed by erosion of the Chalk, some small flood-plain mires occur on the river flats as relicts of a once more extensive marshy area.

The numerous valley mires of the New Forest have not figured prominently in this survey. In a few places, however, along the valley bottoms and on terraced seepage slopes above the streams, relatively base-rich conditions support mire communities with strong affinities to rich-fen types, e.g. near Ringwood at Stones Moor and Cranes Moor (NEWBOULD, 1960).

5.6. South-west England and South Wales

There is very little rich fen remaining upon the extensive peat moors of the Somerset levels. However, one important area of flood-plain mire still persists at Catcott Heath on the moors between the Polden Hills and the Wedmore Ridge. This is in a small dyke-surrounded fen compartment which supports a vegetation akin to some of the flood-plain mires of broadland (see WILLIS, 1967).

A second important rich fen system in Somerset is the Gordano Valley. This area (see WILLIS & JEFFRIES, 1959; JEFFRIES et al., 1968), close to the coast, is a wedge-shaped valley containing peat and alluvium enclosed between two ridges at a height of just a few feet above sea level. The peat deposits are over 3 m deep in places. They are dissected by a network of drains but nonetheless, remain wet and support various types of fen and fen-meadow vegetations.

In S. Somerset there are a few examples of spring mires which support rich fen communities. These are developed at about 300 ft O.D. in the neighbourhood of Wiveliscombe at the headwaters of some small streams draining down into the R. Tone. They include Holme Moor, Clean Moor and Slape Moor and, irrigated by base-rich, calcareous ground-water, support some rather rich calcareous mire communities.

In South Wales there are occasional areas of rich fen. In a few places base-rich springs have produced some small

spring mires. A good example in Monmouthshire is near Henllys just west of Cwmbran where the slopes of a small valley cut back into the Old Red Sandstone support a small spring mire. Also in Monmouthshire a more extensive area supporting both soligenous and topogenous types of mesotrophic fen is developed at Pont-y-spig along the bottom of a narrow, but deeply incised, valley beneath the rising slopes of Coatpit Hill, Fforest, a new miles north of Abergavenny.

Mention may also be made of Maendewi Pool near St. David's in Pembrokeshire. This is at Dowrog Common - an open area of moor with peat upon boulder clay at about 300 ft O.D. Much of the area is wet and marshy and, until recently, there was a pool with open water. In recent years, however, this has largely become overgrown by fen vegetation and currently supports some unusual examples of mesotrophic topogenous fen (see SEDDON & DAVIES, 1966).

5.7. Central England.

Over much of Central England there are very few areas of rich fen. In some places, however, small spring mires occur. In N.E. Northamptonshire such areas are associated with the Great Oolite in the vicinity of Peterborough and Stamford. In Leicestershire there are a number of small marshy places developed to the east of Leicester, mainly associated with glacial deposits over the Lower Lias. These show many

similarities with comparable sites in North Buckinghamshire (see above). They are small spring mires developed at 400-500 ft on valley-slopes, near the headwaters of some of the small streams that drain the area. Similar areas also occur over the Keuper Marl, not only in Leicestershire but also in Warwickshire and in Staffordshire and Cheshire. Small spring mires are also found on the Magnesian Limestone of Nottinghamshire and Derbyshire.

In the north west of Central England some of the most important areas of fen are provided by the glacial hollows of Cheshire-Shropshire plain. These hollows tend to occur in clusters and a number are developed around Ellesmere in North Shropshire; others in a shallow valley near Baschurch. They have in some cases become completely infilled by peat; in others they contain open water bordered by topogenous fen. The surrounding glacial deposits are of varying character, composed of two main structural types: boulder clay and sands and gravels. GORHAM (1957) has pointed out that, of the meres around Ellesmere, the three with marshy shores - Cole Mere, Crose Mere and Sweat Mere - are all contained within the sands and gravels. He has further noted that these three also have the richest water; they are all located over a Keuper Marl bedrock and, as well as receiving inflowing water from the immediately surrounding land (along drainage ditches; by seepage etc.), they may also be supplied with base-rich water percolating up from this deposit. SINKER (1962) has given some account of the

vegetation.

The landscape of the Cheshire plain is similarly dotted with many meres and mosses. North of Whitchurch there are the Norbury and Quoisley meres - both with a good fringe of topogenous fen. In North Cheshire there are many such areas too. They are mainly concentrated in areas of glacial sands and gravels rather than boulder clay and, whilst some of them may occupy glacial hollows, others may represent subsidence hollows created by solution processed within underlying saliferous beds in the Keuper deposits (TALLIS, 1973). Topogenous fen is well developed around one pool - Hatchmere - which occupies a basin in the glacial sands of the Delamere Forest region to the west of Northwich (see LIND, 1950).

5.8. North Wales.

Anglesey is particularly rich in rich fen systems - developed mainly in the eastern parts of the island in shallow depressions associated with the Carboniferous limestone, irrigated by calcareous ground water. The sites comprise a complex of habitats: the slopes of the basins are usually occupied by soligenous mires and flushes which drain down into the topogenous fen beneath. Many of the areas represent sites of former turbary; in some of them wide drainage ditches have been cut; some are used as rough pasture; and in places the vegetation is periodically mown.

Cors Erddreiniog (together with Cors Nantisaf to the north) is an extensive valley mire complex over 2 miles long about 3 miles N.N.E. of Llangefni. It seems to have developed over a shallow post-glacial lake and the present peat, which is up to 1½ m deep, overlies Chara marl. The east side of the mire is bordered by an outcrop of Carboniferous limestone. Cors Goch, immediately east of Cors Erddreiniog, occupies a long (1½ mile) hollow in the Carboniferous Limestone which is almost divided into two by a transverse limestone ridge. This too was once a shallow lake and areas of open water still occur, together with very wet areas of fen.

N.E. of Llangefni there are two further mire basins. Cors y Farl occupies a small, shallow, saucer-shaped depression in the limestone and comprises a central area of swamp and wet fen, which grades out to drier margins. The nearby Cors Bodelio is a more complex area occupying a shallow peat-filled valley about ¾ mile long. The present vegetation cover has been much influenced by past and present management, especially by drainage.

In the Lleyn peninsula the main area of rich fen is the long complex of Cors Geirch a few miles N.W. of Pwllheli. This area, which is not associated with Carboniferous Limestone, occupies the floor of a narrow valley on the site of a post-glacial lake and supports a diversity of wetland habitats including some extensive areas of calcareous fen. Elsewhere

in Lleyn (as in Anglesey) there are also idolated spring mires supporting basiphilic communities. Rich fen vegetation is additionally represented in a small, spring fed basin in glacial drift at 100 ft O.D. near Hirdre Uchaf between Tudweiliog and Edern.

5.9. Northern England.

In lowland East Yorkshire the flat levels of Holderness, only a few feet above the sea and drained by the R. Hull, still support some areas of fen as vestiges of the extensive meres and swampy marshes which once covered much of the area. To the N.E. of Beverley is a small flood-plain mire known as Pulfin Bog developed within a meander of the River Hull. Further north, near Great Driffield, at the northern margin of the levels where they begin to steepen into the uplands of the Yorkshire Wolds, there are some further fenny places. In particular, there are some well developed areas of grazed fen meadow in between the R. Hull and the Driffield canal towards Wansford to the east of Driffield. To the west, Kellythorpe marsh occupies a small wet depression.

On the alluvial flats on the west side ofthe Wolds there are some further wet areas. Alongside the Pocklington Canal, between Market Weighton and York, is a rich area of fen meadow. And near York itself, is the Askham Bog complex occupying a mile long elongate depression to the S.E. of the city

at about 50 ft O.D.

The Wolds themselves support a few calcareous spring mires.

On the north side of the Vale of Pickering some base-rich spring mires are associated with calcareous water derived from Jurassic strata of the Cleveland Hills. A number of such sites occur in various places along the slopes and floors of the narrow, incised valleys at 300-400 ft O.D., but some of the best developed occur at Ashberry Pastures, in a small valley to the N.W. of Helmsley, and at Dalby - some 20 miles further east - along the bottom of Thornton Dale to N.E. of Pickering.

In lowland parts of County Durham there are a few, small spring mires, mainly located in shallow valleys on the Magnesian limestone.

One of the best developed examples of lowland rich fen in Northern England is at Newham Bog in north Northumberland. This is a small basin mire developed at about 150 ft O.D. in a shallow glacial hollow, a few miles south of Bamburgh. Irrigated by calcareous water, it supports a vegetation cover with strong floristic affiliations to some of the calcareous mires of S.E. England.

A rich fen system with some similarities to Newham occurs in a hollow in the glacial drift of the Eden valley to the west of Penrith in Cumberland. This is Newton Reigny Moss, a peat-filled, calcareous basin mire at 600 ft O.D. This site

has been extensively cut for peat in the past and the surface is accordingly patterned. Parts of the mire have dried out in recent years after a drainage ditch was cut through the middle, but the peat cuts still support areas of very wet fen. South-east of Penrith at Temple Sowerby, there is also a shallow basin containing rich fen, though the vegetation here is almost exclusively fen carr.

In north-west and north-central England the Carboniferous Limestone provides water suitably calcareous for the development of rich fen in appropriate areas. In some places there are calcareous lakes with bordering topogenous fens, as at Cunswick Tarn below Cunswick Scar to the west of Keswick and at Hawes Water to the west of Carnforth in North Lancashire. In Westmorland a more upland (900 ft O.D.) example is Sunbiggin Tarn between Orton and Kirkby Stephen. Here too the shallow water is derived from the neighbouring Limestone fells and the tarn supports an extensive marginal development of topogenous fen (HOLDGATE, 1955b). This site represents the highest known locality for Cladium mariscus (WILSON, 1956). Adjoining Sunbiggin Tarn is Tarn Moor. This contains a shallow peaty valley of complex drainage irrigated on the one hand, by the outflow stream from the tarn and, on the other, directly supplied with calcareous water from numerous springs and seepage zones which drain the Limestone. It supports a complex development of rich fen vegetation (HOLDGATE, 1955a), ranging from open skeletal flushes on the steeper peripheral slopes

to areas of deep peat in the flatter parts. Peat has, in fact, been worked in some places and in parts of the valley floor old cuts have become overgrown by topogenous fen.

The Carboniferous Limestone of the Craven district of West Yorkshire supports numerous base-rich flushes and in some places more extensive spring mires also occur. However, the most notable development of calcareous mire in Craven is the complex area of wetland in the vicinity of Malham Tarn at about 1,250 ft O.D. (SINKER, 1960; PROCTOR, 1960, 1974; ADAM et al., 1975). The tarn itself occupies a depression in the surface of drift-covered Silurian shales beneath an escarpment of the Great Scar Limestone and is fed mainly by springs draining the limestone. The main water inflow is along a stream which enters the tarn on the N.W. side. South of this is a large area of raised bog (Tarn Moss) but to the North, between the stream and the upland, is a complex broad belt of fen which constitutes the 'North Tarn Fens'. This presents a complex vegetation cover including wet topogenous types of rich fen, drier fen meadow, fen carr etc. There are extensive areas of old peat cuts.

To the east of the Tarn are extensive areas of grazed soligenous mire. These - Ha Mire and Great Close Mire - are composed of open flushes and runnels draining the Limestone on the steeper slope, together with a more closed mire surface in the flatter parts where peat has been able to accumulate.

A further area of soligenous rich fen in the northern

Pennines is that developed in Upper Teesdale in County Durham. Such mires occur in various places in the dale, including some of the lower reaches, but of particular importance is the area known as Widdybank Pastures. This site, immediately north of the R. Tees, constitutes an extensive complex of grassland and mire developed over the east-facing slopes of Widdybank Fell between about 1,250 ft and 1,400 ft O.D. upon calcareous drift deposits. Numerous springs and seepage zones give rise to flushed grassland and calcareous marsh (see PIGOTT, 1956), especially on the steeper slopes and mire communities are also developed in flatter areas along the wet bottoms of the small shallow valleys that drain the area.

5.10. Southern Scotland.

The main area to be mentioned here consists of a number of mires developed in close proximity to one another amid pasture-land, along the Selkirk-Roxburgh border just to the east of Selkirk. These mires constitute the Whitlaw Mosses. They occur, at a height of about 800-900 ft O.D., in a series of small basins and shallow valleys in the glacial drift which overlies the Silurian bedrock of this region. They are fed by base-rich ground-water coming from springs and seepage areas on the sides of the basins. These slopes may support various soligenous wetland communities, but the main mire areas, which can be very wet, support topogenous fen.

The mires included here are Beanrigg Moss (DANIELS, 1973) - a very small but remarkably rich basin-mire containing a range of open swamp, fen and fen-meadow communities, together with a small amount of carr; Blackpool Moss, adjoining Beanrigg, mainly composed of carr; Murder Moss, the largest of the sites, with an extensive range of open swamp and fen community types. These three sites are the most base-rich of the mosses. A fourth site, Nether Whitlaw Moss, developed along a shallow valley, is more mesotrophic and shows an interesting transition to more acidophilous types of mire. Together these sites constitute the Whitlaw Mosses N.N.R. There are, however, other base-rich mires in the same neighbourhood. A particularly good example occupies a small, but quite deep basin, at Selkirk race-course and contains an interesting area of floating topogenous fen. There is also Over Whitlaw Moss - rather drier and more disturbed than the other sites.

Another basin mire containing rich fen vegetation - in many respects rather similar to the Whitlaw Mosses - is found in a shallow glacial hollow in the Stewartry. This is Newlaw Moss, just a few miles east of Kirkudbright.

Chapter 6.

The plant communities of rich fen.

6. The plant communities of rich fen.

In this Chapter an account is given of the different plant community-types of rich fen that have been distinguished in this survey. It is subdivided into 9 sections concordant with the 9 groups into which the samples were initially divided for analysis. These are: of page 105

6.1. Sedge swamp communities
6.2. Cladium-Phragmites vegetation
6.3. Species-poor tall fen communities
6.4. Communities of calcareous mires
6.5. Carex diandra-lasiocarpa-rostrata communities
6.6. Rich fen meadow communities
6.7. Molinia caerulea communities
6.8. Epilobium hirsutum-Filipendula ulmaria tall fen vegetation
6.9. Mire forest communities

Each section is introduced by a brief account of its compass, i.e. the types of vegetation that are included within it. A section may contain one or more major categories of vegetation (that is to say those which have subsequently become regarded as Associations or the equivalent). Each major category is treated in the same way. First a general account is given of its physiognomy, composition, distribution etc. Then comes a description of the various noda that have been recognised within it, together with their characterising species. This is followed by a consideration of the syntaxonomy of the vegetation-type and concluded by a synopsis of the proposed classification of the noda. The nodum included within a particular syntaxon is indicated by its paragraph number placed in parentheses after the syntaxon name.

When more than one Association is represented in a section, the section is concluded by a synopsis of all of the noda included within it. A summary of all the main syntaxa recognised is at the end of Chapter 7.

6.1. Group 1. Sedge swamp communities.

This group contains various sedge-dominated stands of vegetation growing in swamp conditions (i.e. with a summer water table usually above the level of the substratum). In general, swamp vegetation has not been included in this survey but samples have been taken from selected sedge-swamp types firstly because of their close floristic and developmental connections to fen, and secondly because they occupy the transition between deep water (reed)—swamp vegetation and more terrestrial community-types.

There is a strong tendency for stands of this type of vegetation to possess a low and variable complement of species. Thus, no attempt has been made to allocate the samples to vegetational units on the basis of overall floristic similarity but instead classes have been created based upon the dominant taxa. This would seem to be an efficient way of resolving the classificatory problems presented by the material and has the additional advantage of being compatible with the approach of many continental phytosociologists.

The communities considered here are:

6.1.1. Cladium mariscus swamp (Table 1A).

6.1.2. Carex elata swamp (Table 1A).

6.1.3. Carex paniculata swamp (Table 1B - in text).

6.1.4. Carex appropinquata swamp.

6.1.5. Juncus subnodulosus swamp (Table 1C - in text).

6.1.1. Cladium mariscus swamp communities - Table 1A.

Characterising species: Cladium mariscus (as dominant).

Description: Swamp vegetation dominated by the Great fen-sedge Cladium mariscus can sometimes be found in the wetter parts of fen systems, in old peat workings, shallow pools, and around the margins of some lakes in water depths of up to 70 cms. In such situations the Cladium plants show great vigour growing up to 2 m, flowering prolifically and often forming dense sedge beds in which the growth of associated species tends to be suppressed.

Cladium-swamp is therefore characteristically species poor and monotypic stands sometimes occur, though usually Phragmites communis can also be found growing up with the sedge. Certain other associates are sometimes found and these provide the basis for the recognition of sub-communities:

6.1.1.1. Typical ("inops") nodum. This comprises species poor stands of vegetation dominated by Cladium. Phragmites can also be abundant but there are few other associates and occasionally (e.g. S.485) only these two species occur. The community develops in a water-depth of 10-70 cms with a pH range of 6.0-8.0. It is of restricted occurrence in England and Wales. It occupies some of the deeper depressions of some commons in West Norfolk (especially Foulden Common). In the Broads it is occasionally found as primary swamp-fringing open water (as at Upton Broad, S.766) or occupying

"pulk-holes" - shallow areas of open water which may in part represent vestigial remnants of earlier peat cuts (but see also LAMBERT (1951), p.167). Here "broadland species" such as Cicuta virosa and Sium latifolium can be found. It is not, however, a frequent community.

The community is also occasionally developed as a swamp fringing small pools in N. England as in Yorkshire at Shirley Pool, Askern, at Eelmire Pool, Jervaulx, and at Hell Kettles, Co. Durham (WHEELER & WHITTON, 1971).

A Menyanthes variety of the community can be distinguished in which Menyanthes trifoliata is abundant often forming a loose-floating raft. With it are some additional associates notably Eupatorium cannabinum and Juncus subnodulosus, both of which are constant. This has been recorded from E. Walton, Foulden and Thompson Commons in W. Norfolk, and from a few very wet areas in the N. Wales fens. A Carex elata variety may also be recognised with the tussock sedge prominent in the lower levels of the vegetation (S.488; S.496).

Additionally it also seems possible to distinguish between situations of extreme Cladium dominance and those in which Phragmites is more significant with Cladium, showing reduced vitality and playing a less important role. This occurs mainly in the deeper water where the vegetation forms a fairly open reedswamp. In such circumstances Cladium often forms small polycormous patches associated with other reedswamp

species. A good example of this is at Hawes Water, Silverdale, where a narrow band of reedswamp has the following composition:

S.934 Hawes Water, Silverdale, Lancs. SD 479767

Phragmites communis ..	2,3	Total cover = 60%
Scirpus lacustris	2,3	
Cladium mariscus	1,2	
Nuphar lutea	1,1	
Solanum dulcamara	+	

Another example can be found in parts of the fringing swamp of Sunbiggin Tarn in Westmorland (HOLDGATE, 1955b).

6.1.1.2. Carex lasiocarpa nodum. Cladium is still the dominant species but with a reduced vitality, so that the sedge beds are often only 75 cms to 1 m tall. Phragmites communis is usually a sub-dominant species. Beneath these are extensive stands of Carex lasiocarpa (40-60 cms tall) often with C. rostrata. Menyanthes is also important. The water level ranges from a few centimeters to 40 cms but C. lasiocarpa is only prominent in the shallower parts and in the deepest water Cladium asserts strong dominance. In the free water Scorpidium scorpioides and Utricularia species occur as constants (U. intermedia, U. minor and U. neglecta have all been recorded). Other aquatics include Potamogeton coloratus and P. polygonifolium. Ranunculus lingua occurs at some sites and in shallower water Carex elata, Juncus subnodulosus and Schoenus nigricans can sometimes be found.

The nodum has mainly been recorded from the Anglesey fens. It occupies the wettest portions of Cors Goch and is

developed over an extensive area in the centre of the Cors y Farl basin. It is also developed at Thompson Common, Norfolk, in fragmentary form and in shallow water around part of Sunbiggin Tarn (S.989 and HOLDGATE, 1955b), and around pools on Anabaglish Moss, Wigtownshire (S.944 and SPENCE, 1964).

6.1.1.3. Other Cladium swamps in Britain.

A species-poor Cladium swamp has been recognised from Ireland by BRAUN-BLANQUET & TÜXEN (1952). Cladium stands are also frequent around some loughs of the Burren and IVIMEY-COOK & PROCTOR (1966) have established a Cladium mariscus-Utricularia intermedia nodum from these, but at least some of their lists may be assigned to the categories established here.

In parts of Connemara a rather different type of Cladium swamp may be found surrounding some of the loughs. This has received very little attention but two lists from swamp vegetation fringing two small pools in the Lough Cloonagat area, are of interest:

List number:	128	129
Cover:	50	60 %
Cladium mariscus	3,3	2,3
Phragmites communis		1,1
Eriocaulon septangulare	1,3	1,2
Nuphar lutea		2,3
Menyanthes trifoliata	+	+
Potamogeton polygonifolium .	+	
Utricularia sp.	+	+
Myriophyllum verticillatum .	+	

Both stands were growing in about 40 cms of water on a soft detritus mud.

6.1.1.4. Synecology. Swamp conditions provide the optimal habitat for Cladium mariscus (CONWAY, 1936; JESCHKE, 1959) and it is of interest that in northern parts of Britain the species only occurs in this type of community and not in drier fen. This may possibly be related to the protection given by a water layer to the growing point which is damaged by winter temperatures of less than $-2^{o}C$ (CONWAY, 1938). The plant is particularly characteristic of calcareous waters with a pH of around 7.0. Nonetheless, some stands may well support the opinion of BAUMANNS (1911) that "Cladium mariscus scheint den kalkhaltigen Schlammboden nicht besonders zu lieben". This matter, together with POELT's (1955) emphasis on the oligotrophic nature of the water (with respect to low levels of KNP), could usefully be clarified.

6.1.1.5. Synsystematics. For the synsystematic problems of Cladium-dominated vegetation see 6.1.1.6.

On the basis of the organisation, physiognomy and edaphic situation of Cladium-swamp vegetation the communities are probably best placed within the Phragmition alliance of the Phragmitetea, despite poor floristic characterisation. On the same criteria open reedswamp stands with much Phragmites and some Cladium may be best regarded as a Cladium facies of the Scirpo-Phragmitetum. However, dense stands of Cladium of shallower water may be united to form a Cladietum marisci sensu stricto following the conception of PFEIFFER (1961), which is equivalent to parts of the typical sub-association of KRAUSCH (1964) and the phragmitetosum subassociation of Westhoff & Segal (WESTHOFF & DEN HELD, 1969). It may, however, prove to be of little value to attempt to maintain the distinction between these two types in which case they are best united into the Cladietum marisci.

6.1.1.6. Synsystematics of Cladium-dominated vegetation. Initially, samples of vegetation containing large amounts of Cladium mariscus were categorised into subunits of other, better defined, community-types, e.g. the Schoenetum mariscosum serrati by KOCH (1926); the Scirpeto-Phragmitetum cladietosum by MESSIKOMMER (1928); or the Caricetum elatae cladietosum by LIBBERT (1932). However, ZOBRIST (1935) created an independent Association, the Mariscetum serrati (= Cladietum marisci), containing species-poor stands of vegetation

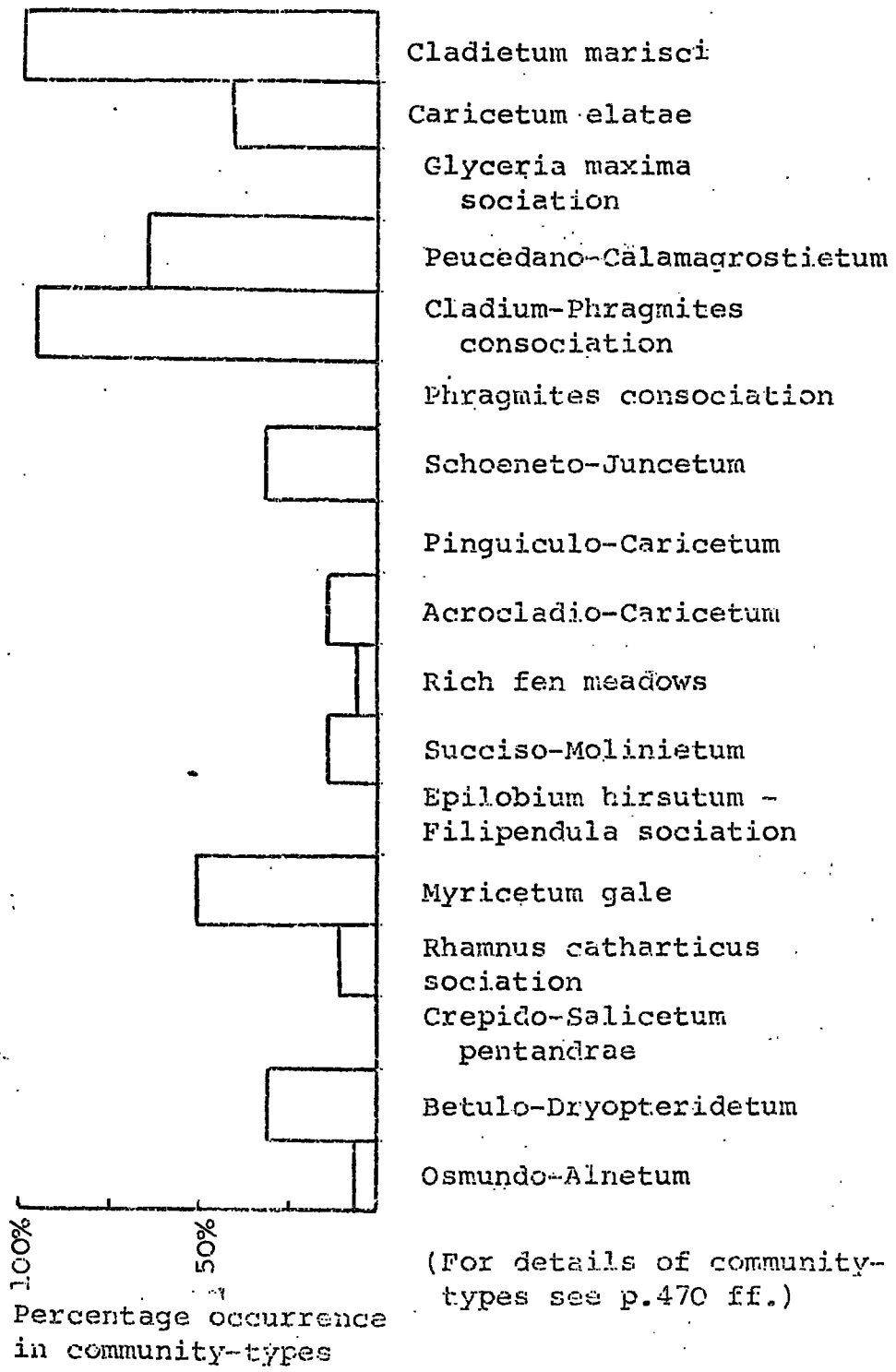
dominated by Cladium. Subsequently, the Association has been recognised by various workers (VOLLMAR, 1947; DUVIGNEAUD, 1949; LEBRUN et al., 1949; BRAUN-BLANQUET & TUXEN, 1952; TUXEN, 1955; OBERDORFER, 1957; WESTHOFF & DEN HELD, 1969; etc.) and this has led to certain questions concerning its precise identity and synsystematic placement.

Cladium occurs with a variety of accompanying species in various edaphic situations. This is reflected by the sociological amplitude of the species within the communities recognised within this survey (Fig. 6.1.I). On the European mainland too, apart from occasional occurrences within fen woodland (e.g. in the Alnetum glutinosae-Cardaminetosum amarae, CHRISTIANSEN, 1955), which may perhaps be best regarded as isolated events, it is clearly a component of rather different community-types. This is shown well by JESCHKE (1959) and KRAUSCH (1964), who distinguish a series of community-types, all dominated by Cladium, ranging from swamp stands with aquatic plants through less wet phases with various paludal species to the driest types containing species characteristic of base-rich mire. Physiognomically these communities are all similar though they have very different floristic complements.

As OBERDORFER et al. (1967) point out, it is possible to retain the Cladietum marisci sensu lato as an intact unit with a number of floristic variants. Alternatively, however, where appropriate, the material could be partitioned

Fig. 6.1.I.

Sociological amplitude of Cladium mariscus



(For details of community-types see p.470 ff.)

to other existing, well-defined Associations, perhaps with the retention of a Cladietum marisci in a more narrowly defined sense. KRAUSCH (1964) adopts the first view and has sub-divided the Association into two subassociations:

(a) typical subass. species-poor swamp community with a water-table of 5-70 cms.

(b) Carex elata subass. of drier sites with a sub-surface summer water level characterised by species such as Calamagrostis cānescens, Galium palustre, Lycopus europaeus, Lysimachia vulgaris, Lythrum salicaria, Pseucedanum palustre, Potentilla palustris, Thelypteris palustris and Carex elata.

Both sub-associations contain several variants.

WESTHOFF & DEN HELD (1969) adopt a similar approach recognising:

(a) phragmitetosum - a species-poor swamp community.

(b) thelypteridosum with Thelypteris palustris, Berula erecta and Galium elongatum, apparently related to the Thelypteris-variant of KRAUSCH's typical sub-association.

(c) scorpidietosum - containing species of the Tofieldietalia and transitional to it.

On the other hand, PFEIFFER (1961), in a monograph on the community, suggested that the Association could not be regarded as a coherent unit but that it should be split so that species-

poor pioneer stands of swamps should be regarded as sub-groups of other swamp Associations such as the Scirpo-Phragmitetum and that forms with mire species should be assigned to the appropriate mire communities. He retained the Cladietum in a more restricted sense to refer to dense Cladium stands formed by the optimal development of the species in shallow water. This corresponds to what KRAUSCH (loc. cit.) regarded as the kernel of his Cladietum where the sedge attains its greatest height and fecundity.

In choosing between these approaches the following points seem to be important:-

(i) The Cladietum marisci s.l. is only defined by the occurrence of Cladium mariscus - Scirpus tabernaemontanae has been suggested as a diagnostic species (VOLLMAR, 1947; OBERDORFER, 1957), but this has not been generally accepted. However, the results of some of the analyses recorded here indicate very strong floristic affinities between certain stands irrespective of the presence of Cladium (see Section 6.2.16. and Table 2). Nonetheless, any subdivision of the Association also requires a satisfactory reallocation of the subunits to other community-types.

(ii) Acceptance of the Cladietum s.l. creates additional problems concerning its synsystematic position. This has always been contentious, the community having been variously assigned to the Magnocaricion and Phragmition Alliances.

The problem has been exacerbated by the floristic poverty of the stands and the concomitant absence of character species. KRAUSCH (1964) suggests that the drier forms which usually have a greater number of characterising species, have generally been placed into the Magnocaricion. In contrast, authors describing wetter versions of the community-type (BRAUN BLANQUET & TUXEN, 1952; PIGNATTI, 1957; PASSARGE, 1964; IVIMEY-COOK & PROCTOR, 1966) have placed them in the Phragmition. JESCHKE (1959), recognising optimal development of the sedge in the species-poor Cladium-Phragmites swamp, together with floristic, organisational, ecological and physiognomic criteria also selected the Phragmition. KRAUSCH (1964) did the same even though his Carex elata-subassociation is largely characterised by Magnocaricion species.

(iii) The subunits of the Cladietum s.l. have different distributions. The Carex elata subassociation of KRAUSCH has a southern distribution. At the northern limit of the range of Cladium however, only the swamp form occurs as in the examples given by NORDHAGEN (1940), JALAS & OKKO (1951) and MÖRNSJÖ (1969).

These considerations commend the subdivision of the Association along the lines suggested by PFEIFFER (1961) with the recognition of a more narrowly defined Cladietum marisci as a community dominated by Cladium mariscus forming dense stands in relatively shallow water. This approach is

commensurate with that adopted for other large-sedge community-types (see, for example, the Caricetum elatae). It seems likely, however, that it may be difficult to clearly distinguish between this community-type and Cladium-facies of the Scirpo-Phragmitetum.

The status of Cladium stands that seem referable to KRAUSCH's Carex elata subassociation will be further discussed in 6.2.16.

6.1.1.7. Synopsis of Caldium swamp communities

PHRAGMITETEA Tx et Prsg. 42
PHRAGMITETALIA Koch 26
PHRAGMITION (COMMUNIS) Koch 26 em. Balatova-Tulackova 63

Scirpo-Phragmitetum Koch 26

Cladium facies

Cladietum marisci Zobrist 35 em. Pfeiffer 61

(Synon: Mariscus serrati Zobrist 35 p.p.
Caricetum elatae cladietosum Libbert 32 p.p.
Cladietum marisci phragmitetosum Segal et Westhoff 69)

typicum (6.1.1.1.)

monotypic Cladium stands
Cladium-Phragmites stands (typical variant)
Carex elata variant
Menyanthes trifoliata variant

caricetosum lasiocarpae (6.1.1.2.)

6.1.2. Carex elata swamp communities

Characterising species: Carex elata (as dominant).

6.1.2.1. Description. Carex elata (= C. hudsonii A. Benn.) sometimes occurs as the dominant species of a very characteristic but rather localised swamp community of shallow pools and derelict fen ditches. The plant grows as robust tussocks with a 'trunk' diameter of 30-40 cms and a similar height, though the height varies with the depth of water and in the deepest parts specimens up to 60 cms have been recorded. The tussocks tend to be set fairly close together and in an area of 10 m^2 up to 60 tussocks have been counted. Between the tussocks are interspaces which contain open water throughout the year except in the shallowest areas. The tussocks may grow directly from the mineral substratum of the swamp basins but more usually they are rather loosely attached to an often unconsolidated organic substratum which thinly covers the mineral ground. The identity and origin of this material has not been fully investigated but extensive remains of Phragmites communis can normally be found within it. In other situations, particularly in association with deeper water, a semi-floating raft may be formed with the tussocks loosely cohering through lateral roots growing out just below the water surface. However, in such circumstances the tussocks are highly unstable and it is doubtful if truly floating rafts occur to any extent.

The elevated tussocks and aquatic interspace provide a mosaic of habitats which is clearly shown by the distribution of the associated species of the community. In some of the areas of open water true aquatics may be found and Hydrocharis morsus-ranae, Hottonia palustris, Lemna minor, L. trisulca, Potamogeton natans and, occasionally, Nymphaea alba have all been recorded. In two localities (Thompson Common, Norfolk, and Llyn yr Wyth-Eidion, Anglesey), Sparganium minimum also occurs. In shallower water Menyanthes trifoliata, Potentilla palustris and, occasionally, Berula erecta often occur, sometimes in profusion. Most tussocks except for the most vigorous support some epiphytic species and on the tussock-tops Cardamine pratensis, Epilobium palustre and Hydrocotyle vulgaris can be frequent, especially on more moribund individuals. Saplings of Alnus glutinosa and Salix cinerea also occur. In general, mosses are rare or even completely absent from the community but scattered strands of Acrocladium cuspidatum can sometimes be found on the tussock-tops. The remaining complement of plants is composed of paludal species growing rather sparsely in association with the tussocks often being rooted in the peaty stock at or just below the water level. Eupatorium cannabinum, Lythrum salicaria, Lycopus europaeus and Ranunculus linqua regularly grow in this situation with Solanum dulcamara and Galium palustre. These last two species can sometimes form quite dense mats

scrambling over the tussocks. Both sub-species of the Galium have been recorded but G. palustre ssp. elongatum is perhaps the most important. At Thompson Common Calamagrostis stricta is sometimes abundant in this community.

The above description refers to the most species-rich version of Carex elata swamp. As Table 1A indicates floristically impoverished stands also occur. These are stands, often in slightly deeper water, composed of Carex elata tussocks with a sparse cover of Phragmites communis and/or Cladium mariscus. A few associates, such as Eupatorium cannabinum, may occur but most species, including all of the aquatics, of the richer community are absent.

6.1.2.2. Distribution and synecology. Carex elata swamp is of restricted occurrence within England and Wales. It is found developed around the edges of pools or, in a fragmentary form, in derelict fen ditches. The best examples of the community are found in West Norfolk at East Walton Common, Foulden Common and, especially, Thompson Common. Here the bedrock is chalk covered in places by a thin deposit of glacial gravels. A distinctive feature of these commons is the presence of numerous small water-filled hollows which

appear to be the product of solution processes within the chalk. These hollows provide some good examples of hydroseral development and some have become completely colonised by swamp and fen vegetation. Carex elata swamp forms a zone around the edge of several of the pools and in a few cases occupies the entire depression. The water depth ranges from +5 cms at the edge to +30 cms in the deepest parts. The pH range is 5.5-6.5. On the inside of the Carex elata is either open water or, more rarely, a Cladium-Phragmites reedswamp. On the outside there is usually rapid transition to a narrow band of grazed "fen-meadow" vegetation with much Juncus subnodulosus (see 6.6.8.2.) which then grades into drier calcareous grassland but in some of the steeper-sided basins this intermediate zone may be missing. The Carex elata swamp may well be playing an important part in the hydrosere within the pools, but at present it only seems to form this sublittoral swamp community and there is no distinct hydroseral gradient with the development of drier phases of Carex elata-dominated vegetation such as have been represented in the successional schemes of KOCH (1926) and VOLLMAR (1947). The peripheral Juncus subnodulosus fen meadow vegetation cannot be implicated as part of the hydrosere as, for the most part, it is growing on the wet lower slopes of the swamp basins.

Examples of C. elata-dominated vegetation which may also

be relegated to this community-type have also been recognised at Sunbiggin Tarn (HOLDGATE, 1955) and Esthwaithe North Fen (PEARSALL, 1918).

6.1.2.3. Syntaxonomy. Carex elata is a widespread species of the European continent, though with sub-oceanic/sub-mediterranean distributional tendencies. Wetland vegetation dominated by the plant is similarly of widespread distribution and has been described by many workers. KOCH (1926) gave a detailed account of stands dominated by the tussock sedge and united them into an association, the Caricetum elatae. Subsequently the same community has been recognised by many workers from different regions (LIBBERT, 1932; TUXEN, 1937; VLIEGER, 1937; BOER, 1942; VOLLMAR, 1947; OBERDORFER, 1957; NEUHÄUSL, 1959; JESCHKE, 1959; PASSARGE, 1964; KRAUSCH, 1964; WESTHOFF & DEN HELD, 1969; MÖRNSJÖ, 1969, etc.) and this stability of the community-type through the phytosociological literature is indicative of its distinctiveness and utility as a vegetational category. Both KOCH and VOLLMAR, however, recognised a number of facies typifying different phases of the development and degeneration of the community along the hydroseral gradient. These range from initial phases containing species relict from the preceding aquatic and reedswamp communities to terminal phases with species characteristic of Eriophorion latifolii vegetation. Clearly this conception of the Association encompasses a greater

range of community-types than is shown by the Carex elata stands considered here. These must, therefore, be assigned to the initial phases of the Association and regarded as a sublittoral variant.

VAN DONSELAAR (1961) recognised two sub-associations within the Caricetum elatae:

(i) typical sub-association with Senecio paludosus, Phalaris arundinacea, and Valeriana officinalis as differential species. This community corresponds more closely to the original description of KOCH (1926).

(ii) comaretosum sub-association differentiated by Lysimachia thyrisiflora, Calamagrostis canescens and the characteristic species of the Class Scheuchzerio-Caricetea such as Potentilla palustris and Epilobium palustre.

This sub-division, which has been adopted by WESTHOFF & DEN HELD (1969) is concordant with the recognition of a typical sub-ass. of richer sites and a Comarum sub-ass. of poorer sites by PASSARGE (1964). A similar sub-division seems to have been recognised by JESCHKE (1959). Clearly, the material described here falls into the Comaretosum sub-association, although Lysimachia thyrisiflora does not occur.

The species-poor Carex elata swamps with Phragmites communis have evident resemblances to the Caricetum elatae phragmitosum of both KOCH (1926) and VOLLMAR (1947), and this would seem a suitable denomination for this type of vegetation.

LIBBERT (1932) described a Caricetum elatae cladietosum. Here, however, Cladium is the dominant species and only some of the samples contain Carex elata and then often only in small amounts. It would seem more appropriate to regard such a community as a Carex elata sub-association of the Cladietum marisci (see 6.1.1.1.).

Character species

KOCH (1926) initially suggested Carex elata, Senecio paludosus and Scutellaria galericulata as character species for the Caricetum elatae. These species have been confirmed by LIBBERT (1932), VOLLMAR (1947) and OBERDORFER (1957) and others such as Teucrium scordium and Lathyrus palustris have sometimes also been suggested. None of these are suitable, however, for the characterisation of the British material all being absent from Carex elata swamp. Senecio paludosus is very rare, occurring only in one fenland ditch (WALTERS, 1974) and, despite being formerly more widespread (BENNETT, 1899), most probably was not a character species of this community. VAN DONSELAAR (1961) points out that in Holland the species has its optimal development outside of the Caricetum elatae. The same comments apply to Teucrium scordium. Nor is Carex elata itself restricted to this community-type but is frequently an important component of other vegetation units, especially within the Magnocaricion, although these fairly open swamp situations may provide it with an optimal

autenvironment (NEUHAUSL, 1959). This lack of character species means that the community has to be defined mainly on physiognomic and edaphic criteria, viz. the dominance of Carex elata in a swamp environment. Nonetheless, the community-type so defined corresponds well with the Caricetum elatae of continental phytosociologists, who, themselves, have sometimes used the dominant species as the main criterion for distinguishing between tussock-forming sedge communities (especially see KUHN, 1961).

6.1.3. Carex paniculata swamp - Table 1B.

Characterising species: Carex paniculata (as dominant).

6.1.3.1. Description: The greater tussock sedge, Carex paniculata, is sometimes found as the major component of certain areas of swamp bordering upon open water. Some of the best examples of this come from the margins of some of the broads in the East Norfolk valley fens, from which the community has already been described as "tussock-fen" by LAMBERT (1951; 1965).

The physiognomy of the community is completely determined by the enormous upstanding tussocks of Carex paniculata, which can attain heights of up to 1.5 m. These, according to the observations of LAMBERT, usually develop upon a fairly firm but semi-floating raft of Phragmites which, as the tussocks increase in size, consequently becomes depressed with the formation of pools between the stools. In these inter-tussock spaces the main species to be found are shoots of the reed, Phragmites communis, Carex riparia, Typha angustifolia and Sparganium erectum, together with the floating Lemna minor. Often, however, the pools may be almost completely devoid of higher plants.

The chief substratum for the associated species of the community is provided by the sedge tussocks themselves, and these can support a rich epiphytic flora with species such as Eupatorium cannabinum, Epilobium hirsutum, Lysimachia vulgaris,

Lythrum salicaria, Impatiens capensis, Peucedanum palustre and Thelypteris palustris. There is, however, considerable variation in the composition of the stands from place to place and some areas may be impoverished in associates.

An important feature of the tussocks is that they provide a suitable basis for the establishment of seedlings of Alnus glutinosa and Salix cinerea and in many of the stands various stages in the development of woody vegetation can be seen. This process has been described by LAMBERT (1951), who has shown that the progressive establishment of trees on the Carex paniculata tussocks leads to the formation of a swamp carr community.

In this survey Carex paniculata swamp has only been encountered occasionally. It occurs around various of the broads in East Norfolk (e.g. Wheatfen, Alderfen, Hoveton) but has often been found only as isolated fragments. The community is, however, well developed around parts of Barton Broad. Outside of the Norfolk Broads area examples of this type of vegetation have been recorded from Thompson Common in West Norfolk and Sweat Mere in Shropshire (see TANSLEY, 1939; SINKER, 1962). In these, however, broadland species such as Peucedanum palustre are absent.

In other places impoverished stands of Carex paniculata are sometimes found occupying swampy hollows. These are often only fragmentarily developed and may support a variety of associated species.

TABLE 1B. Carex paniculata swamp

	355	659	690	1067	704	799
Alnus glutinosa	+		+	+	2,3	1,1
Salix cinerea	1,1	3,3		+	+	2,3
Carex paniculata	3,3	3,3	3,3	3,3	3,3	2,3
Epilobium hirsutum	+		+	+	+	
Lythrum salicaria	+		+	+	+	+
Solanum dulcamara	+	+	+	+	+	+
Acrocladium cuspidatum		+		+	+	
Phragmites communis			+	1,1	+	1,2
Carex acutiformis			+	+		
Eupatorium cannabinum			+	+	+	+
Impatiens capensis				+	+	+
Galium palustre			+	+	+	+
Peucedanum palustre				+	+	+
Thelypteris palustris			+	1,1	1,2	
Lysimachia vulgaris				+	+	
Scutellaria galericulata				+	+	
Carex riparia						+
Carex pseudocyperus	+			+		
Cardamine pratensis						+
Equisetum fluviatile		+				
Filipendula ulmaria					+	
Galium uliginosum	+					
Iris pseudacorus	-			+	+	
Lycopus europaeus						+
Mentha aquatica				+		
Menyanthes trifoliata		1,3				
Myosotis scorpioides			+		+	
Ranunculus lingua	+	+				
Scrophularia aquatica					+	+
Sparganium erectum	+		+	+		
Typha angustifolia	1,1			-		
Urtica dioica					+	
Lemna minor	+	+		+	+	

Releve sites:

355: Sweat Mere, Cockshutt, Salop. SJ 438305.
659: Small pool on Thompson Common, Thompson, Norfolk, TL 934966.
690: West margin of Alderfen Broad, Neatishead, Norfolk, TG 353198.
1067: West side of Barton Broad, Barton Turf, Norfolk, TG 358215.
704: Herons Carr, Barton Broad, Barton Turf, Norfolk, TG 359209.
799: Wheatfen Broad, Surlingham, Norfolk, TG 329057.

6.1.3.2. Synsystematics: WESTHOFF & DEN HELD (1969) place stands of sedge swamp, which seem to be very similar to the floating mats of Carex paniculata from broadland, into the Caricetum paniculatae Wangerin 16. Not all phyto-sociologists have used this Association, however. In particular, there has been a Caricetum acutiformo-paniculatae Ul. et Van Zinderen Bakker 42 (see BOER, 1942; VAN DONSELAAR, 1961), which also encompasses closely related vegetation with Carex acutiformis or C. riparia as dominants with or without (usually without) a small amount of C. paniculata. Due to the strong floristic similarities between these communities irrespective of the dominant, this would appear to be a useful vegetational category, but the current trend (OBERDORFER, 1957, 1962; KRAUSCH, 1964; OBERDORFER et al., 1967; WESTHOFF & DEN HELD, 1969) seems to be towards recognising an independent Caricetum paniculatae and this will be followed here.

The Association has no good character species. Carex paniculata itself is widespread in various rich fen communities though usually not as abundant as in these sedge swamps. Therefore, like the other sedge swamp communities considered here, the Caricetum paniculatae is regarded as a dominance-type characterised by the occurrence of large amounts of C. paniculata.

6.1.4. Carex appropinquata swamp.

Characterising species: Carex appropinquata (as dominant).

6.1.4.1. Description: SEDDON & DAVIES (1966) reported the discovery of a large population of Carex appropinquata in a large shallow pool near Maendewi Farm, Dowrog Common, Pembrokeshire. This plant is an uncommon species in the British flora mainly occurring in fens in East Anglia and East Yorkshire, though with an important outlier at Malham Tarn, W.Yorks., and with earlier records from the Colne valley, N.W. of London, from which it has subsequently been lost (DRUCE, 1926; KENT & LOUSLEY, 1956).

The Pembrokeshire site is of particular interest as here the sedge is growing in a community rather different from those at its other known English localities. In the wettest parts of the site, encroaching onto open water, C. appropinquata is the dominant plant forming fairly small (30 cms) tussocks in association with a few larger tussocks of C. paniculata. The plants are sometimes rather sparsely distributed and the large interspaces are filled with floating mats of Menyanthes trifoliata together with Potentilla palustris. A complete floristic list is given below:

S.561 Maendewi Pool, Dowrog Common, St. Davids, Pembs. SM 769268

Sample size: 100 m^2

Cover: 70%

Carex appropinquata	3,3	Juncus articulatus	+
		Mentha aquatica	+
Agrostis canina	+	Menyanthes trifoliata	1,2
Baldellia ranunculoides	+	Rorippa nasturtium-aquaticum	+
Carex paniculata	+		
C. rostrata	+	Ranunculus flammula	+
Eleocharis palustris	+	Potentilla palustris	1,2
Eriophorum angustifolium	+	Sparganium erectum	--
Equisetum fluviatile	+	Typha latifolia	+
Galium palustre	+	Lemna minor	+
Hydrocotyle vulgaris	+		
Iris pseudacorus	+	Acrocladium cuspidatum	+

In slightly drier areas a related community occurs with reduced amounts of C. appropinquata and with a variety of additional species such as Cardamine pratensis, Holcus lanatus, Juncus acutiflorus and Molinia caerulea. This stand has clear floristic affinities with areas of relatively dry fen containing C. appropinquata at Malham Tarn (see 6.7.6.) though lacking many of the species of this site.

6.1.4.2. Syntaxonomy: ASZOD (1936) created an independent Association - the Caricetum paradoxae - to contain stands with much Carex appropinquata (= C. paradoxa Willd.). Stands with both Carex appropinquata and Carex paniculata have been referred to a Caricetum paradoxae-paniculatae Soo 47 and complexes with Menyanthes trifoliata have been put into a Cariceto-Menyanthetum caricetosum appropinquatae Soo 55. KOCH (1926) placed stands with quite large amounts of Carex elata into a Caricetum elatae caricetosum paradoxae (see also VOLLMAR, 1947).

More recently, communities with the name of Caricetum

appropinquatae have been described by OBERDORFER (1957), JESCHKE (1963), KRAUSCH (1964), WESTHOFF & DEN HELD (1969) and BALATOVA-TULACKOVA (1972). Such communities seem generally to be rare in Europe and are often developed only in fragmented form (WESTHOFF & DEN HELD, 1969). They have a predominantly northern distribution according to OBERDORFER (1957) but are largely absent from Atlantic regions (BALATOVA-TULACKOVA, 1972).

It would, however, seem as if rather different vegetational types have been brought together under the head of this Association. Thus, BALATOVA-TULACKOVA (1972) indicates the similarities of her communities to the Caricetum diandrae Jonas 33 and points out that the Association has relationships with the Caricion davallianae, the Caricion canescentis fuscae and the Molinietalia grassland (see also ASZOD, 1936), although, in fact, she places it within the Magnocarietalia (cf. SOO, 1957, who places a Caricetum appropinquatae-echinatae into the Eriophorion latifolii sensu Soo 47). However, in contrast, KUHN (1961) shows the floristic similarities of the Caricetum appropinquatae to the Caricetum elatae.

It is clear that the Carex appropinquata swamp community described here does not correspond to the drier Caricetum appropinquatae of BALATOVA-TULACKOVA. Stands dominated by C. appropinquata that could be referred to this development

of the Association have been recognised from some of the valley fens of East Norfolk (e.g. S.756, see Table 2) and from parts of Tarn Fen at Malham. These, however, may be satisfactorily accommodated within the Peucedano-Juncetum subnodulosi (see 6.2.14), the Scorpidio-Caricetum diandrae (see 6.5.5.) and the Carex nigra-Molinia caerulea community (see 6.7.6.), and there seems no need to allocate them to an independent Association. On the other hand, however, the Carex appropinquata swamp does show affinities to some of the stands included in the Association by OBERDORFER (1957) and KUHN (1961). Nonetheless, it is felt that, due to the small amount of material available together with uncertainties as to the precise compass of the Caricetum appropinquatae, this community will be just referred to as a 'Carex appropinquata-community'. It may be placed within the Magnocaricion - though lacking in character species, on physiognomic-ecological grounds.

6.1.5. Juncus subnodulosus swamp.

Characterising species: Juncus subnodulosus (as dominant).

6.1.5.1. Description: Juncus subnodulosus can sometimes be found forming populations within shallow swamps. The stands are usually only fragmentarily developed and there are only a few associated species. Examples have mainly been recorded from the edge of pools in fen systems.

TABLE 1C. Juncus subnodulosus swamp

	508	834	490	1093
Juncus subnodulosus	3,4	4,4	4,5	3,2
Phragmites communis		+	+	1,1
Carex panicea	-			
Carex paniculata	-			
Carex rostrata	1,1			
Schoenus nigricans	-			
Pedicularis palustris	+			
Carex lasiocarpa		+		
Cladium mariscus		+		+
Berula erecta			+	
Mentha aquatica			+	
Veronica beccabunga			+	
Carex elata				+
Schoenoplectus tabernaemontanae				+

Releve sites:

508: Ruskin Reserve, Cothill, Berks. SU459997.
834: Cors Goch, Llanfair-mathafarn-Eithaf, Ang. SH 501813.
490: Foulden Common, Foulden, Norfolk. TF 758000.
1093: Martham Broad, Martham, Norfolk.

6.1.5.2. Synsystematics: KRAUSCH (1964) described Juncus subnodulosus-swamp and placed it within the Phragmition Alliance. Clearly the community does not belong to the

Juncetum subnodulosi Koch 26 (see 6.6.16.), though JESCHKE (1959) has regarded similar communities as an initial-phase of this Association.

6.1.6. Synopsis of sedge swamp community-types

PHRAGMITETEA Tx. et Preising 42

PHRAGMITETALIA Koch 26

PHRAGMITION (COMMUNIS) Koch 26 em. Balatova-Tulackova 63

Scirpo-Phragmitetum Koch 26

Cladium facies

Cladietum marisci Zobrist 35 em. Pfeiffer 61

(Synon: Mariscus serrati Zobrist 35 p.p.
Caricetum elatae cladietosum Libbert 32 p.p.
Cladietum marisci phragmitetosum Segal & Westhoff 69)

typicum (6.1.1.1.)

monotypic Cladium stands
Cladium-Phragmites stands (typical variant)
Carex elata variant
Menyanthes trifoliata variant

caricetosum lasiocarpae (6.1.1.2.)

Juncus subnodulosus swamp stands (6.1.5.)

MAGNOCARICION (ELATAE) Koch 26

Caricetum elatae Koch 26 (6.1.2.)

typical facies
Phragmites facies (= phragmitosum Koch 26)

Caricetum paniculatae Wangerin 16 (6.1.3.)

Carex appropinquata community (6.1.4.)

6.2. Group 2. Cladium-Phragmites vegetation - Table 2.

Included within this group are stands of tall fen vegetation usually dominated either by Cladium mariscus or Phragmites communis. In contrast to the physiognomically similar vegetation included in Group 3, this vegetation is relatively rich in associated species. It incorporates most of the open fen vegetation of the East Norfolk flood-plain mires and will be referred to as Cladium-Phragmites vegetation. As this represents an important component of rich-fen vegetation in England and Wales a detailed account will be given.

6.2.1. Introduction

The group encompasses wetland vegetation of characteristic appearance and structure. The predominant components are tall-growing monocots - graminaceous and cyperaceous helophytes particularly Cladium mariscus and Phragmites communis and, to a lesser degree, Calamagrostis canescens. These grow in varying densities forming stands with a height of between 1-1.5 m and of rather uniform appearance. In parts of East Norfolk these can occupy extensive areas of marshland covering the flat valley floors with large tracts of rather dull and apparently uniform vegetation, often relieved only by the intricate network of dykes.

In the summer months the reedbeds have a subdued glaucous coloration until later in the year they are overtopped by the purple plumes of the flowering heads of the

Phragmites. Then in winter the plants die back and the inert haulms form straw-coloured expanses until new aerial shoots grow up from the rhizomes in late spring. By contrast, the sedge beds tend to remain a dull brown throughout the year with the dead tips of the mature leaves effectively masking the lower evergreen parts and also covering the new leaves that are growing up from the stock. Thus, Wicken Fen "appears during most seasons of the year as a brown waste dotted with bushes" (WALLIS, 1904) and indeed bushes - of Alnus glutinosa, Betula pubescens, Myrica gale, Salix cinerea and, to a lesser extent, Rhamnus catharticus - can often be prominent in the vegetation. With the bright green leaves of Calamagrostis canescens and the flowering heads of some of the taller herbaceous dicots - such as Angelica sylvestris, Eupatorium cannabinum, Filipendula ulmaria, Iris pseudacorus, Peucedanum palustre and Valeriana officinalis - they can contribute to alleviating the rather monotonous appearance of the marshes for at least part of the year.

Beneath this upper stratum three subordinate layers can also be recognised (cf. YAPP, 1909; GODWIN & TANSLEY, 1929). There is normally a "rush layer" of 60-80 cms height composed of Juncus subnodulosus and various sedges and herbs of medium height. Beneath this there is often a "small herb layer" of 10-40 cms with plants such as Mentha aquatica and Lycopus europaeus. In some of the less rich sites (for example, as

when Cladium forms dense stands) this layer may be very reduced or even absent. In some of the richest sites on the other hand many of the additional plants belong to this stratum. The lowest layer is the moss layer which is often very poorly developed.

There are a number of species that may sometimes be found climbing up through these stratal types. This is shown to a certain extent by Galium palustre but especially by plants such as Solanum dulcamara, Stellaria palustris and the rare Lathyrus palustris. Calystegia sepium can sometimes form dense lianas binding together the sedge and reed.

Some of the most extensive and best-developed examples of this type of vegetation occur in the mires of East Norfolk (i.e. the "broads" area). A brief account of this area has already been given (see Chapter 5). Essentially it is composed of four river valley systems containing large areas of undrained fen penetrated by an extensive network of irrigating dykes which are normally in open connection with the rivers. Some account of the vegetation has already been given by LAMBERT (1946, 1951, 1965). LAMBERT & JENNINGS (1951) and LAMBERT (1951) have made a major distinction between primary fens, i.e. those developed by the encroachment of fen vegetation upon the open water of the broads as part of a primary hydrarchal succession, and secondary fens, i.e. those developed upon deep solid peat outside the basins of the broads. Here

most attention has been given to the latter.

The present nature of the vegetation owes much to the activities of man - especially the secondary fens, which have been widely used as mowing marshes. Until recent years large areas were maintained in an open condition through annual mowing for hay and litter. Reed beds also have been harvested during the winter months for thatching. More recently, however, these activities have declined leading to large areas becoming overgrown. Concomitant with this has been the dereliction of many of the dykes extending through the marshes with a corresponding decrease in the degree of water circulation. Another factor that has been important in recent years is the influence of the coypu (Myocastor coypus) (see ELLIS, 1965, p.227). These herbivorous rodents attained high population levels in the broads in the years leading up to 1963 and caused widespread destruction of much of the fen vegetation as this provided them with an abundant source of food. Primary fen was affected particularly severely both in terms of the extensive disintegration of the mats of vegetation and also by the near-elimination of certain species such as Cicuta virosa , in particular areas. There was also an affect upon secondary fen vegetation with the creation of expansive muddy hollows by the removal of the vegetation cover. The animal may also have been instrumental in reducing bush colonisation on the marshes by preventing the growth of

sallows, in some places.

Areas of Cladium-Phragmites vegetation are known also from sites other than in broadland. In particular, Wicken Fen, which persists as a remnant of flood-plain mire in the Fenland of Cambridgeshire, supports such communities. Indeed, wetland vegetation of this kind may once have been widely distributed in the Fens but most areas have for a long time been drained and put to the plough. Similarly, on the peat moors of the Somerset levels, Cladium-Phragmites fen persists only in a small, isolated area.

Other examples of this vegetation type which will be considered here, have been collected from some of the valley fens of East Anglia and Anglesey. The distribution of sample sites is shown in Fig. 6.2.II.

6.2.2. Types of Cladium-Phragmites fen

Fig. 6.2.1. gives the dendrogram produced by Information Analysis on the set of samples of Cladium-Phragmites vegetation. The subsequent application of re-allocation procedures produced little change in the contents of the clusters except for the two groups 6.2.12 and 6.2.15 where there was some interchange of releves.

The final groups are quite well characterised floristically, though not all of them can be easily defined by a few monothetic criteria. Trends of variation can be detected within some

Fig. 6.2.I.

INFORMATION ANALYSIS OF CLADIUM-PHRAGMITES VEGETATION

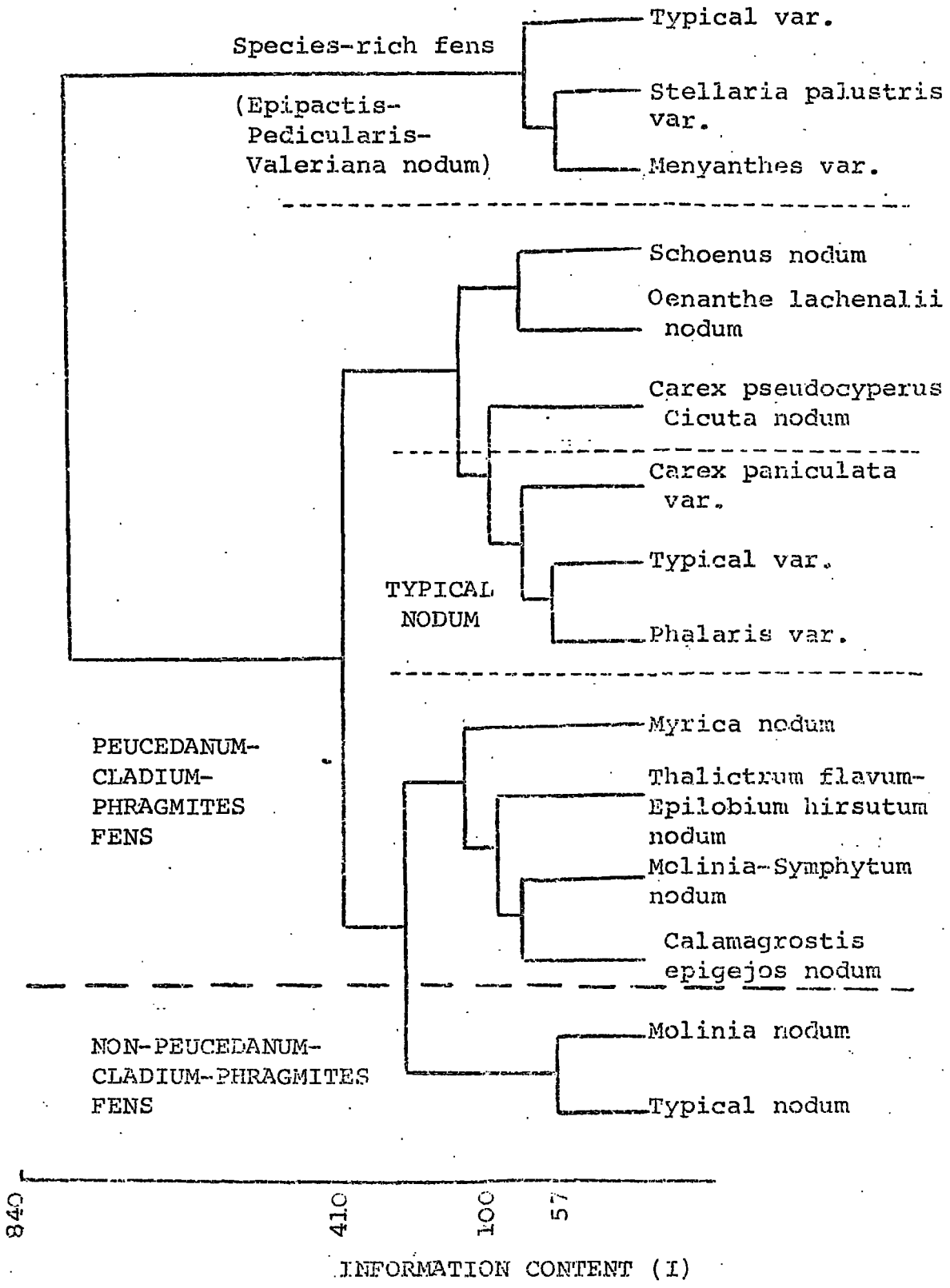
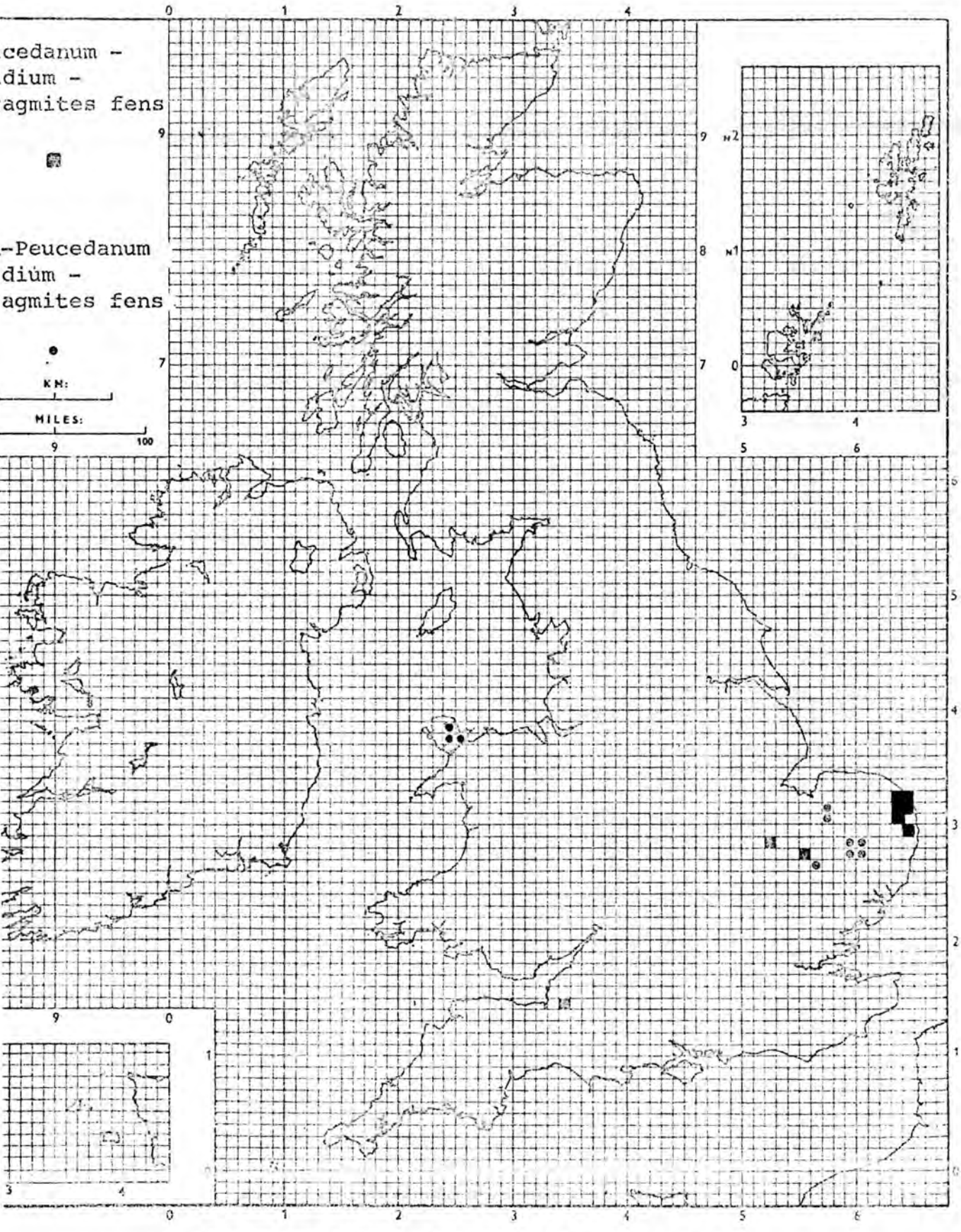


Fig. 6.2.II.



BASED UPON BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

of them and there are various samples that are clearly intermediate between certain units.

Primarily, the samples are arranged into two major groups: those without Peucedanum palustre, Lysimachia vulgaris and Galium palustre, and those containing this species-group. This division largely reflects a geographical partitioning of the stands: the group without these species is composed mainly of samples collected outside of broadland.

It will be convenient to treat these as two independent series of community-types. These will be referred to as

(i) non-Peucedanum Cladium-Phragmites fen; and

(ii) Peucedanum-Cladium-Phragmites fen.

6.2.3. Non-Peucedanum-Cladium-Phragmites fen.

Characterisation: May be distinguished from Peucedanum-Cladium-Phragmites fen by the absence of the Galium palustre, Lysimachia vulgaris and Peucedanum palustre species group.

Description: In the community types brought together in this series Cladium is constant and normally dominant. Phragmites is usually a subordinate species. The Cladium plants can sometimes form a very dense sward in which associates tend only to occur as scattered individuals. The following groups can be recognised:

6.2.4. Molinia nodum

Characterising species-group: Molinia caerulea, Potentilla erecta.

Description: This is defined by the constant occurrence of Molinia caerulea and Potentilla erecta. The former can reach high cover values (40%) and in these situations the Cladium cover is reduced to produce a "mixed fen" community. This group occurs in two well-defined situations:

(a) in the Anglesey fens it occupies quite large areas on flat peat-filled valley bottoms (Cors Erddreiniog and Cors Bodelio), where it represents the typical (i.e. most extensive) development of Cladium fen. The sedge forms dense stands with scattered bushes of Myrica. Beneath these Molinia forms large irregular tussocks, often with standing water between them. Schoenus nigricans tussocks occur

sporadically. The nature of the vegetation excludes many low-growing plants but species such as Carex panicea, Erica tetralix, Narthecium ossifragum and Serratula tinctoria may be found on the tussock-tops. The community shows a close relationship to Molinia-Myrica stands (6.7.4.3.) to which it may be developing.

(b) in parts of East Anglia a rather different community occurs composed of stands associated with a dry substratum in the summer months which, in some places at least, may have been induced by a general reduction in the height of the water-table. Cladium is generally dominant but sometimes it is usurped by Phragmites or is even completely absent. This is a mixed fen community with substantial amounts of Molinia and Schoenus. Some of the samples are characterised by Cirsium dissectum, Succisa pratensis and Valeriana dioica, which are absent from the Anglesey Cladieta. Mosses are generally missing but the rather dry conditions permit the occasional occurrence of plants of species such as Carex pulicaris, Centaurea nigra, Leontodon hispidus and L. taraxacoides and, in one place, Selinum carvifolia. These stands are often in contact with grassland dominated by Molinia caerulea. Localities include parts of Foulden Common, Chippenham Fen, parts of the marshland surrounding Hicking Broad and some of the Waveney valley fens. A list by BELLAMY & ROSE (1961) from Weston Fen may also belong here.

6.2.5. Typical nodum

A small heterogenous group composed of species-poor Cladium stands from East Anglia and Anglesey. It cannot be regarded as a viable syntaxon but serves as a useful "dump" for impoverished stands until their status has been better defined.

Related to these is the occasional development of dense stands of Cladium on very dry peat. Often the Cladium - of reduced vigour and fecundity - is persisting in sites that have been drained. There are very few associates except for certain ruderals. Two examples demonstrate this type of vegetation:

S.620 Marham Fen, Norfolk. Cover: 80%

Cladium mariscus	3,3	Galium uliginosum	+
Phragmites communis	1,1	Lycopus europaeus	+
Cirsium arvense	1,1	Mentha aquatica	+
Angelica sylvestris	+	Solanum dulcamara	+
Calamagrostis canescens	+	Sonchus oleraceus	+
Cirsium palustre	+	Arrhenatherum elatius	+
Eupatorium cannabinum	+		
Frangula alnus	+		

S10 Hickling Broad, Norfolk. Cover: 90%

Cladium mariscus	3,3	Cirsium arvense	+
Phragmites communis	1,1	Oenanthe lachenalii	+
Juncus subnodulosus	1,1	Rubus fruticosus	+
Angelica sylvestris	+		
Anthoxanthum odoratum	+		
Calystegia sepium	1,2		
Carex panicea	+		

6.2.6. Peucedanum series

Characterising species-group: Galium palustre, Lysimachia vulgaris, Peucedanum palustre.

Description: Included here are all of the Cladium-Phragmites vegetation types, for which the above species form a diagnostic group. It incorporates most of the fen vegetation found at Wicken and much of the vegetation of the marshes associated with the Norfolk broads. The milk parsley, Peucedanum palustre, although by no means present in all samples, is a characteristic component of this type of vegetation to which it shows quite strong fidelity. It can, however, also be found in related community-types in particular in some forms of fen carr (the Peucedanum var. of the Osmundo-Alnetum lycopetosum; see 6.9.1.4.). The plant, though formerly more widespread (BENNETT, 1903) is still abundant in the broads and at Wicken Fen with an important outlier at Catcott Heath on the Somerset peat moors.

The following species are constant:

Cladium mariscus	Lysimachia vulgaris
Eupatorium cannabinum	Mentha aquatica
Galium palustre	Phragmites communis
Juncus subnodulosus	Peucedanum palustre

The following are constant or frequent in many community-types:

Calamagrostis canescens	Potentilla palustris
Carex elata	Rumex hydrolapathum
Calystegia sepium	Scutellaria galericulata
Filipendula ulmaria	Valeriana officinalis
Hydrocotyle vulgaris	
Iris pseudacorus	Acrocladium cuspidatum
Lycopus europaeus	Campylium stellatum
Lythrum salicaria	

Within this series a number of community-types have been recognised. Interestingly, these have a striking geographical basis. Within broadland, not only is the Yare valley fen distinquished as a discrete type (as by PALLIS, 1911), but also the other valley systems tend to have characteristic communities too. Furthermore, individual fen complexes within the valleys tend to support particular types of vegetation. This most probably reflects the vegetational history of the sites as well as their edaphic status. Similarly, stands sampled from Wicken fen have also conjoined to form an independent community-type. The same also applies to samples from Woodwalton Fen.

6.2.7. Molinia-Symphytum nodum

Characterising species-group: Molinia caerulea, Symphytum officinale, Carex disticha, C. panicea, Lathyrus palustris, Thalictrum flavum, Brachythecium rutabulum.

Description: This distinct group has been created from the samples taken at Wicken Fen. The community is dominated either by Cladium or Phragmites.

These present different physiognomies but, from the samples taken, there are no obvious distinctions in the complement of associated species. These include Calamagrostis canescens and Juncus subnodulosus as important components as also is Molinia caerulea, especially in the absence of Cladium. The moss layer is poorly developed but Acrocladium cuspidatum and Campylium stellatum occur as constant species. Smaller herbaceous species such as Hydrocotyle and

Dactylorhiza incarnata can also frequently be found in the lowest strata. Although an unorthodox component of this type of vegetation elsewhere in East Anglia, Galium uliginosum is frequent at Wicken. On the other hand, Thelypteris palustris is curiously absent from large areas of the fen where it might have been expected. Shrubs are frequent, particularly Frangula alnus, Rubus fruticosus, Salix cinerea and S. repens var. fusca. Myrica, however, is absent being of very restricted distribution on the fen.

Much of the present fen area has been reclaimed from carr and is maintained in an open condition by periodic mowing.

The fen has long been reported as drying out (e.g. YAPP, 1908) and GODWIN (1931) recorded summer water-table levels of less than -30 cms. The vegetation cover most probably represents one of the driest versions of Cladium-Phragmites fen communities.

This community-type has been described in detail by YAPP (1908) and GODWIN & TANSLEY (1929). It is readily susceptible to bush colonisation (GODWIN, 1936) in which Frangula alnus plays a prominent primary part.

6.2.8. Calamagrostis epigejos nodum

Characterising species: Calamagrostis epigejos, Stachys palustris; also absence of many common fen species such as Juncus subnodulosus.

Description: This community-type is characterised by the

occurrence of Calamagrostis epigejos in large quantities, sometimes as the dominant species. Dissimilar to any other fen community, it is known only from Woodwalton Fen, Hunts., where it occupies a large area. It has been described from this site by POORE (1956b) and his lists give some indication of the range of floristic variation. There is a patchwork of dominant species over the fen: in some cases Phragmites communis is particularly prominent; in others, Phalaris arundinacea; in others, C. epigejos or C. canescens. These facies are illustrated by the samples made in this survey.

A number of common herbaceous fen species are frequent: Angelica sylvestris, Calamagrostis canescens, Eupatorium cannabinum, Epilobium hirsutum, Filipendula ulmaria, Lysimachia vulgaris, Lythrum salicaria, Thalictrum flavum etc. (see Table 2), but a number of species (e.g. Juncus subnodulosus) characteristic of rich fen in East Anglia are absent or very localised. Peucedanum palustre and Sonchus palustris occur in places, but these are introductions (DUFFEY, 1971). POORE (1956b) suggests that this poor flora is a product of the management history of the fen, in particular the unavailability of appropriate fen species to colonise the fen peat that was exposed by peat digging.

As well as the C. epigejos some other species help to characterise this community. In particular, Symphytum officinale and Stachys palustris are frequent. Also, on the rather dry peat, plants of Cirsium arvense and Urtica

dioica can often be found.

Mosses are rare. Brachythecium rutabulum is occasional.

6.2.9. Thalictrum flavum - Epilobium hirsutum - Carex riparia nodum

Characterisation: No simple monthetic criteria can be applied to characterise this nodum. It is, perhaps, best defined by two overlapping groups of species (see Table 2) viz.:

(i) Lathyrus palustris, Thalictrum flavum, Solanum dulcamara

(ii) Carex paniculata, C. riparia, Epilobium hirsutum.

Description: This is a distinct nodum composed chiefly of samples of secondary fen from the middle Yare valley - mainly from the Wheatfen complex - together with 2 releves made at Stanley Carrs in the lower Waveney valley and one from Catcott Heath, Somerset. Some description of this type of vegetation in the Yare valley has already been given by LAMBERT (1946). WILLIS (1967) has described the community at Catcott Heath.

The dominant plant of the community is Phragmites communis. With it there is often Carex riparia. Glyceria maxima occurs in some samples and can be abundant; and Phalaris arundinacea is occasional, often forming societies within Phragmites fen. In many places the large tussocks of Carex paniculata are prominent and of particular note is that the tussock-tops often provide a suitable substratum for the growth of certain

herbaceous dicots such as Peucedanum palustre and Lysimachia vulgaris. In contrast, Cladium mariscus is absent from most samples: indeed, this must be regarded as a rare species within the Yare fens (PALLIS, 1911).

A wide variety of dicotyledonous species contribute to the floristic diversity of this community. Fairly constant species include Angelica sylvestris, Caltha palustris, Eupatorium cannabinum, Filipendula ulmaria, Galium palustre, Iris pseudacorus, Lysimachia vulgaris, Peucedanum palustre and Valeriana officinalis. Other frequent species are Lycopus europaeus, Lythrum salicaria, Rumex hydrolapathum and Scutellaria galericulata.

It is clear that there is considerable variation within the nodum and more data are needed to clarify the situation. However, the following sub-groupings are tentatively suggested:

6.2.9.1. Carex appropinquata variant. Tussocks of Carex appropinquata are frequent in the rush layer. With them are quite large quantities of Juncus subnodulosus. Phragmites is dominant with Glyceria maxima rare or absent. In some places, however, Filipendula ulmaria can also reach high cover values. Additional species are Cardamine pratensis, Equisetum fluviatile, Epilobium parviflorum, Holcus lanatus, Poa trivialis and Rumex conglomeratus. Dactylorhiza praetermissa can often be found growing on the C. appropinquata tussocks.

At Wheatfen this community is found along the western margin of the complex in one place grading into a Juncus subnodulosus-dominated community (see 6.6.7.3.); in another, into carr. The map of ELLIS (1934) showed these areas as Juncus subnodulosus-fen and, in accordance with the scheme suggested by LAMBERT (1946), the present community most probably represents a phase in the encroachment of Phragmites into the Juncus-fen following the cessation of mowing.

The vegetation of the Catcott site seems to belong to this variant.

6.2.9.2. "Typical" variant. This is the "typical" development of the fen with Phragmites dominant and much Carex paniculata and Epilobium hirsutum. Some stands contain Juncus subnodulosus; others, Glyceria maxima; and there seems to be an inverse relationship between the occurrence of the two. There is a tendency for the stands with Juncus to be located towards the middles of the fen compartments. Those with Glyceria are nearer the bounding dykes and, close to some of the dykes, Glyceria can be especially important. This has been well described by LAMBERT (1946), who relates the prominence of Glyceria to the influence of moving tidal water within the dyke system - possibly associated with mineral enrichment effects. At Catcott Heath, Glyceria is similarly most abundant in association with the dykes. Carex acutiformis

occurs frequently in both types. Urtica dioica, however, seems mainly confined to stands with Glyceria. Occasional stands of Phalaris can sometimes be found. The other associated species of this variant are similar to those given by LAMBERT (loc. cit.) for Phragmites-dominated secondary fen.

6.2.9.3. Glyceria maxima variant. Only two samples are available to characterise this variant of the Yare fens. Glyceria maxima is the dominant species and Phragmites communis is relatively unimportant. There are fewer associates than in the other variants but these include species such as Eupatorium cannabinum, Lythrum salicaria, Rumex hydrolapathum, Peucedanum palustre and Thalictrum flavum.

The Glyceria characteristically occurs with its shoots for the most part prostrated along the ground with only the flowering heads and growing apices arising vertically. This would appear to be a response to exposure. As a result quite a thick "mattress" of Glyceria shoots and litter is produced. This matter has been discussed by LAMBERT (1946), who has ascribed the low species total of the stands to the mechanical influence of such "mattresses". This affect is likely to be least in maintained mowing marshes where the litter is cleared or burnt.

LAMBERT (loc. cit.) described a Glycerietum from the

mowing marshes of the Yare valley, which would appear to correspond to this variant. It seems to have been a widespread community. In this survey, however, it has only been encountered occasionally and tends to occur only as fragments bordering some of the dykes. This is presumably related to the spread of Phragmites fen following the cessation of regular mowing and the dereliction of some of the dykes. (Note also that most of the Glycerieta recorded from the Yare marshes has been referred to the Glycerietum maximae (6.3.1.) rather than to this community-complex. These contain even fewer species than this Glyceria-variant though the distinction is rather poor and somewhat arbitrary).

6.2.10. Myrica gale nodum. This community is largely characterised negatively by the absence of differential species. However, the constant occurrence of Myrica gale and Thelypteris palustris as major components of the vegetation, is particularly characteristic (though both species can be similarly important in other community-types).

Phragmites, Cladium and Calamagrostis canescens are the predominant species. All can achieve dominance at different localities, thus permitting the recognition of three facies of this community-type. Interspersed among these are numerous old "leggy" bushes of Myrica together with other shrubs, typically Betula pubescens, Salix cinerea, Salix repens and, to a lesser extent, Alnus glutinosa and Rubus fruticosus.

The yellow green fronds of Thelypteris palustris are abundant in the herb layer, but in general herbaceous plants are rare. Common species, such as Eupatorium cannabinum, Iris, Mentha aquatica and Valeriana officinalis, are frequently absent. Juncus subnodulosus is usually present, but often in very small amounts. Mosses may be completely absent and only Acrocladium cuspidatum and Campylium stellatum are usually found. In a few places Lathyrus palustris may be found scrambling through the vegetation, often with Stellaria palustris.

This community-type has been recorded mainly from various sites in the Ant valley, but it also occurs in the Upton and Woodbastwick fen complexes. It is normally of small extent and it is characteristic of derelict mowing marsh, isolated corners of fen compartments and of small open areas amongst fen carr, i.e. those areas that are being allowed to develop into scrub. Developmentally, it may be anticipated that Myrica will increase in the vegetation perhaps to become the dominant species of a transient community (see 6.9.5.) which will then pass into some form of carr.

6.2.11. "Typical" nodum.

Characterisation: Absence of differentials for other groups.

Description: Basically a reed fen community in which Cladium and Calamagrostis canescens, although occasionally present, are usually sub-ordinate species. Growing up with the

Phragmites are the common tall herbs of the marshes - Eupatorium cannabinum, Filipendula ulmaria, Lythrum salicaria, Peucedanum palustre, Valeriana officinalis and, to a lesser extent, Angelica sylvestris, Cirsium palustre and Lysimachia vulgaris. Juncus subnodulosus usually occurs and Carex elata is occasional. Frequent smaller herbs are Lycopus europaeus and Potentilla palustris and Thelypteris palustris can be abundant.

Within this group further sub-groupings can be recognised, though these not clearly defined and more data are required to clarify the situations:

6.2.11.1. "Typical" variant. This is a widespread community of mowing marsh on secondary fen with a rather low complement of general marshland species (average = 21 sp./10 m^2). It has been recorded from a number of sites in the middle Ant valley and, for example, most of the vegetation of the Reedham marshes would appear to belong to this community-type.

6.2.11.2. Phalaris variant. A community of the margins of certain Broads, recorded from Barton, Calthorpe and Hoveton. Phragmites is the dominant, but with it there is some Phalaris arundinacea, together with Epilobium hirsutum and Urtica dioica. Calamagrostis canescens can either be abundant or almost completely absent. There are some of the common species of the marshes - Eupatorium cannabinum, Iris pseudacorus,

Peucedanum palustre, Scutellaria galericulata and Valeriana officinalis - but the lists are variable and a number of species - Filipendula ulmaria, Lysimachia vulgaris, Lythrum salicaria and Rumex hydrolapathum - seem largely absent. However, more samples are required to confirm this.

6.2.11.3. Carex paniculata variant. Three samples constitute this group, all made from areas of primary fen in parts of the Upton Broad complex. They are characterised by the occurrence of Carex paniculata, usually in small quantities. Phragmites is the dominant plant but from two of the samples Cladium mariscus is also important. In all places the vegetation is developed on a swinging, though firm, raft of Phragmites rhizomes.

Primary fen has not been recorded often in this survey and more work is required to ascertain its phytosociological position. However, LAMBERT (1951), describing types of hydrarchal succession in the Bure valley broads, has recognised certain communities within the seres. In particular, she describes a primary uncut Phragmites fen with a number of "broadland" species, which contains Carex acutiformis, C. paniculata and C. riparia. This may be tentatively referred to this sub-group, though it seems likely that certain stands will have to be placed in the Carex riparia variant of the Carex pseudocyperus-Cicuta virosa nodum (6.2.12.3.). In her lists though Carex acutiformis is more constant than C. paniculata. It may, therefore, be more appropriate to consider

this a Carex acutiformis variant which contains a sub-varietal form with C. paniculata. LAMBERT's table also contains lists from mown primary Phragmites fen, distinguished from the uncut version by the absence of C. paniculata and C. riparia and by the addition of certain other species. Such a community is very similar to certain types of mown secondary fen and, in the scheme presented here must be referred to the typical sub-group (6.2.11.1.) above.

LAMBERT (1951) also recognised a Cladium-dominated primary fen, characterised by the thorough dominance of Cladium with few associated species. The floristic composition of her list suggests that this community cannot be placed within the Peucedanum series of Group 2 vegetation and instead it is considered as part of the non-Peucedanum series (6.2.5.). Clearly, on the basis of floristic composition, the two Cladium containing samples of primary fen mentioned above, do not belong to LAMBERT's Cladium-dominated primary fen, and instead must be regarded as a Cladium-facies of the Phragmites primary fen.

6.2.12. Carex pseudocyperus - Cicuta virosa nodum

The defining species of this community are the cowbane, Cicuta virosa, and the cyperus sedge, Carex pseudocyperus, together with Berula erecta and the Phragmition species Ranunculus lingua, Sium latifolium and Typha angustifolia. However, several stands that are clearly transitional between

this community-type and the last have been recorded and indeed the group itself is rather variable with the releves showing a gradual change in composition. Nonetheless, it seems possible to discern two sub-units whilst recognising the occurrence of intermediates.

6.2.12.1. "Typical" variant. A sub-unit of stands growing on fairly firm, consolidated peat, with a summer water-table depth of at least -20 cms. Phragmites is most commonly the dominant but Cladium is constant and, although generally infrequent, in some places it is sufficiently plentiful to form quite thick sedge beds. Growing up with these are scattered plants of the diagnostic species sometimes with Calamagrostis canescens and Rumex hydrolapathum. In the "rush layer" Juncus subnodulosus and Carex elata are both usually plentiful with smaller amounts of C. pseudocyperus. Herbaceous species are relatively abundant and include Berula erecta, Lycopus europaeus, Oenanthe fistulosa, Potentilla palustris, Thelypteris palustris and, less often plants such as Cardamine pratensis, Epilobium palustre, Lychnis flos-cuculi and Myosotis caespitosa. Straggling through the vegetation there is Galium palustre and often also the marsh stitchwort, Stellaria palustris. The moss layer, however, remains poorly developed, composed mainly of Acrocladium cuspidatum and Campylium stellatum. Bushes of Myrica, Salix cinerea and S. repens are occasional.

The community has been recorded mainly from the mowing marshes on either side of Barton Broad, but examples have also been found in the Woodbastwick complex.

6.2.12.2. Pedicularis - Menyanthes - Carex lasiocarpa variant.

This is a community of wetter places than is the case with the "typical" variant. It characteristically occupies depressions within areas of drier mire which have become closed over by the development of a semi-floating raft of living fen. This fen mat can be up to 1 m thick with the interlacing roots and rhizomes forming a firm substratum but frequently it is thinner.

There are several major contributors to the vegetation cover, though Phragmites is usually the most conspicuous along with Typha angustifolia. Cladium is often completely absent. Tall umbellifers are prominent with numerous plants of Cicuta, Peucedanum and Sium and Ranunculus lingua also occurs. However, many of the taller herbs of drier fen - Calamagrostis canescens, Filipendula ulmaria, Lysimachia vulgaris and Valeriana officinalis - tend to be absent. Beneath this upper stratum Juncus subnodulosus, Carex elata and C. pseudocyperus are abundant. Carex lasiocarpa also grows in many sites and it can completely dominate the "rush layer". Tussocks of Carex appropinquata are frequent, C. rostrata is occasional and at one place C. limosa occurs.

Beneath this canopy is a rich development of small herbs, often dominated by Menyanthes trifoliata, which can form local societies, or by Potentilla palustris. Caltha palustris, Mentha aquatica and Oenanthe fistulosa are frequently abundant and in some places Pedicularis palustris occurs. The moss layer, studded with Hydrocotyle vulgaris, is relatively well developed. As well as mats of Acrocladium cuspidatum, A. giganteum, Campylium stellatum and Scorpidium can also be found and on the oozing peat there is sometimes Alisma plantago-aquatica, Baldellia ranunculoides or Nymphaea alba.

This community-type has only been recorded from the middle Ant valley in the neighbourhood of Barton and Sutton Broads.

6.2.12.3. Carex riparia sub-unit. A distinct unit, although only composed of two stands both made from fragmentary areas of semi-floating fen at the margin of Filby Broad. With the dominant Cladium there is also Phragmites, Carex riparia, C. paniculata and Epilobium hirsutum. Ranunculus lingua, Sium latifolia and Typha angustifolia are all absent.

6.2.13. Oenanthe lachenalii nodum.

This rather well-defined group is composed of 14 releves made in the sedge fens of the Thurne valley, mainly from around Hickling broad but also from Martham and Horsey. It consists of comparatively species-poor (average = 22 plants/10 m^2) mowing marsh dominated in the main by Cladium but with Phragmites

also present in large quantities. These sedge beds are often rather shorter than is often the case (c. 80-100 cms) and they are frequently matted together by copious lianas of Calystegia sepium. The normal tall herbs of these fens occur though the constancy of Iris pseudacorus is notable. However, Filipendula ulmaria is largely absent and Valeriana officinalis and Calamagrostis canescens are both rare. In the rush layer Juncus subnodulosus is plentiful, often with Carex elata and usually with abundant Schoenus nigricans. There are normally numerous specimens of one of the most characteristic plants of these marshes, Oenanthe lachenalii. Oe. fistulosa also occurs, but not so regularly. The short herb layer is not well developed. Mentha aquatica is constant and in slightly wetter places Ranunculus flammula and Berula erecta can be found. Careful searching usually locates an occasional plant of Samolus valerandii. Mosses are poorly developed - mainly A. cuspidatum and Campylium stellatum - and with them there is usually Hydrocotyle vulgaris.

6.2.14. Schoenus nigricans nodum.

This community-type is rather similar to the preceding and transitional stands that can be found. The main features of distinction are:

(i) Calystegia sepium, Iris pseudacorus, Oenanthe lachenalii and Samolus valerandii are generally absent.

(ii) Salix repens occurs occasionally.

(iii) Pedicularis palustris is occasional and Lychnis flos-cuculi constant.

(iv) Schoenus nigricans is abundant in the rush layer.

The community has been recorded from mowing marshes in various parts of the middle Ant valley. Often richer areas with species such as Pedicularis palustris occur as small islands within a less diverse vegetation. In one stand that has been assigned to this group Carex appropinquata is dominant (S.756).

6.2.15. Species-rich Cladium-Phragmites fens (Epipactis palustris-Pedicularis palustris-Valeriana dioica nodum)

Characterising species-group: Epipactis palustris, Pedicularis palustris, Valeriana dioica. Also, Caltha palustris, Carex diandra, C. lasiocarpa, C. appropinquata, Cirsium dissectum, Acrocladium giganteum, Bryum pseudotriquetrum, Riccardia pinguis. Distinguish from 6.2.12 by absence or rarity of Berula erecta, Carex pseudocyperus, Cicuta virosa, Ranunculus lingua, Sium latifolium and Typha angustifolia.

Description: Under this heading is brought together a number of releves from regularly mown fen containing a large species complement. These samples represent a variety of community-types but nonetheless together they form a fairly coherent group. This is one of the most interesting groups of the East Norfolk fens. It shows clear affinities with the Schoenetum nigricantis cladietosum (6.4.3.2.) and the Scorpidio-Caricetum diandrae schoenetosum (6.5.7.) and provides the locus

for the occurrence of some of the rarest species of British rich fen.

As Table 2 shows the nodum contains several rather distinct community-types, though a number of constant species impart coherence (especially those in parentheses above). The vegetation is best regarded as "mixed fen" in which no species is exclusively dominant. Both Phragmites and Cladium occur in variable quantity. With them are many of the typical tall herbs: Lysimachia vulgaris, Filipendula ulmaria, Valeriana officinalis, Peucedanum etc. but some, in particular Eupatorium cannabinum, Iris pseudacorus and Rumex hydrolapathum, are largely absent. In the "rush layer" Juncus subnodulosus is abundant, with Carex elata often co-dominant and other cyperaceous species, especially Schoenus nigricans and Carex lasiocarpa, are important too. There is a rich small herb layer usually containing Cardamine pratensis, Carex panicea, Epipactis palustris, Pedicularis palustris and Valeriana dioica. Normally the moss layer is well developed too: Acrocladium cuspidatum and Campylium stellatum are constant and abundant and various additional species occur.

Within this basic framework a series of variants occur:

6.2.15.1. Stellaria palustris-Lotus uliginosus sub-group

A rather ill-defined and relatively species-poor variant (average = 40 spp.) with the stands showing clear affinities to some of the Schoenus-group samples. The four component

releves were all made in the same mire system - Broad Fen, Dilham - and they may be readily distinguished from others of this community-complex by the rarity of shrubs (especially Myrica) and by Agrostis stolonifera, Lotus uliginosus and Stellaria palustris growing as differential species. The "rush layer" usually contains much Schoenus nigricans and often Carex appropinquata, C. diandra and C. lasiocarpa can also be found. In the herb layer Thelypteris palustris is abundant with Cirsium dissectum, Mentha aquatica and Potentilla palustris as constants. The moss layer is quite well developed with Acrocladium giganteum, Chiloscyphus polyanthos, Mnium punctatum, Lophocolea bidentata, Riccardia pinquis etc.

6.2.15.2. "Typical" sub-group. Rather like the preceding and similarly somewhat ill-defined. However, Stellaria palustris and Lotus uliginosus are absent, Molinia caerulea is constant, shrubs are well developed and some samples contain Bryum pseudotriquetrum, Carex lepidocarpa, Fissidens adianthoides, Mnium seligeri and Succisa pratensis. Recorded from the Upton and Woodbastwick mire complexes.

6.2.15.3. Carex sub-group.

Characterised both by the prominence of sedge species within the rush layer, notably Carex appropinquata, C. diandra, C. elata and C. lasiocarpa all of which have quite high cover values, and also by the occurrence of additional species of

which Dactylorhiza incarnata, D. praetermissa, Equisetum fluviatile, Eriophorum angustifolium and Menyanthes trifoliata are constant and diagnostic. The samples brought together here are rather variable and it is possible to recognise three distinct variants. Two are wetter versions of the sub-group and contain Ranunculus lingua and Acrocladium cordifolium as differentials from the third.

6.2.15.3a. Ranunculus lingua variant-group. Recorded from the north side of the Sutton Broad basin and from an area near Catfield in the vicinity of Barton Broad. The community at Sutton occurs as part of a well-defined zone as flanking the alder carr which backs onto the upland. It is thus located well away from the central channel, separated by open Phragmites-fen and swamp. The community has clear spatial and floristic connections with certain samples of the Carex lasiocarpa-subsection of the Carex pseudocyperus-Cicuta virosa group, which replaces this community along much of the zone. S.735 is clearly intermediate (see Table 2).

The uppermost layer of the vegetation is poorly developed constituting only 20-30% of the total vegetation cover. The major components are species of the rush layer: Carex appropinquata predominates with large quantities of the thin wiry leaves of C. lasiocarpa and many small tufts of C. diandra and in one place there are a few plants of Carex limosa. Carex elata and Juncus subnodulosus are both abundant, but

Schoenus seems generally absent from the Sutton area. The small herb layer is well developed with Caltha palustris, Carex nigra, Epipactis palustris, Pedicularis palustris, Mentha aquatica and mosses are also abundant: Acrocladium cuspidatum, A. cordifolium, A. giganteum, Campylium stellatum, Fissidens adianthoides, Pellia endiviifolia, Riccardia pinguis etc. The stands are thus species rich (average = 50 spp./10 m^2).

On the east side of Barton Broad a related community occurs developed over 2-3 acres of wet mowing marsh. Here Cladium mariscus is much more strongly dominant, but the other sedges remain important components of the "rush layer". All of the species of the Sutton site occur with many others, some favoured by the wetter conditions and indicative of the close relationship with the Carex pseudocyperus-Cicuta virosa nodum, which can be found occupying wetter depressions within this community. Cicuta is frequent with the Cladium and scattered plants of Osmunda regalis occur (not normally cut by the mowers). Carex pseudocyperus, C. rostrata and Schoenus grow in the rush layer with a little C. limosa and beneath these are many smaller herbs: Carex lepidocarpa and, of particular note, scattered plants of Pyrola rotundifolia together with large quantities of the fen orchid, Liparis loeselii. Mosses are abundant and in addition to those above are Campylium elodes, Drepanocladus intermedius, D. vernicosus,

Mnium pseudopunctatum, Mn. seligeri, Scorpidium scorpiodes and Cinclidium stygium. With them are the trailing shoots of Anagallis tenella, Hydrocotyle vulgaris and a few plants of Hypericum elodes. PALLIS (1911) includes this last species as being occasional in the fen association in all the East Norfolk marshes, but this is the only record made during this survey.

Small fen pools contain Baldellia ranunculoides, Chara vulgaris, Hottonia palustris, Potamogeton coloratus, Utricularia cf. intermedia and U. minor. The resulting stands are very rich in species with up to 60/10 m^2.

6.2.15.3b. "Typical" variant. A drier version of this Carex sub-group demonstrated by a small area of sedge on the south side of the site of Sutton Broad. Phragmites and Cladium are both relatively sparse and séges of the rush layer contribute most to the vegetation. The wet fen species of the Barton complex (e.g. Ranunculus lingua, Cicuta virosa) are absent here and in the drier conditions Molinia caerulea becomes more important with Cirsium dissectum and Succisa pratensis. The small herb layer remains richly developed with a large colony of Liparis loeselii and occasional plants of Platanthera bifolia. The moss layer, though dessicated during the summer is quite rich with Campylium elodes and Scorpidium. Fen pools contain Utricularia minor.

This community-complex appears to be largely confined to the Ant valley, with remnants in some of the Bure marshes.

The examples given by PALLIS (1911) and TANSLEY (1939) indicate that this type of vegetation was once well developed in the Bure marshes, but much of this area has subsequently become overgrown with carr and currently these communities are only well developed in the mowing marshes of the weakly tidal Ant, where the absence of strong water movement may be important (LAMBERT, 1965).

6.2.16. Synsystematics of Cladium-Phragmites fen.

In evaluating the systematic location of these community-types the following observations are relevant:

(a) some of the noda which are well-defined on the basis of their total floristic content contain stands dominated by different species (usually either Phragmites or Cladium in varying proportions).

(b) some noda tend to be dominated by Phragmites with Cladium reduced or completely absent. These, however, have strong floristic affinities with those noda not so dominated and in the hierarchy of fusions produced by Information analysis the two types of grouping have often been placed together in some of the middle-order classes (see Table 2), i.e. there is no tendency to segregate those groups mainly dominated by the reed into one higher-order class.

(c) classification of the groupings (using the synoptic lists) with the other synoptic lists available by means of

Information analysis reveals no tendency for any of these groupings to be classified away from one another. This is a reflection both of the internal homogeneity of the Group 2 community-complex and also of its external heterogeneity (i.e. its dissimilarity with other community-types, created by a number of species being largely restricted to this Group, though this is, of course, partly a function of the proportion of samples made in different communities).

These observations suggest (a) that the community-types considered here form a coherent unit, and (b) that a primary sub-division on the basis of the dominant species would be incommensurate with the groupings established on a floristic basis. Accordingly, this precludes any synsystematic arrangement which would place the groupings of this complex into fundamentally different syntaxa.

The most satisfactory location for these communities would seem to be the Magnocaricion. Physiognomically, the sedge beds clearly belong here; this is not so for the reed beds which have a greater superficial resemblance to Phragmition communities. However, as from the above argumentation, they must both be placed within the same higher syntaxon, clearly this must be the Magnocaricion (a) on ecological groups: the water level is essentially sub-surface; (b) the floristic complement points to this Alliance: as well as the occurrence of various "Großseggen", Peucedanum palustre, which is

frequent within this community and largely restricted to it, has often been given as a Magnocaricion species (e.g. KOCH, 1926; TUXEN, 1937; OBERDORFER, 1957; 1962; KUHN, 1961). Calamagrostis canescens, with similar fiducial limits in British fen community-types, has also been given this status by KORNECK (1963), although OBERDORFER (1962) regards it primarily as a character species of the Alnion. KORNECK also considers Lathyrus palustris a Magnocaricion. In contrast, Phragmition-species such as Ranunculus lingua and Typha angustifolia and Cicution virosae-species such as Carex pseudocyperus, Cicuta virosa and Sium latifolium, are generally absent from this community-complex, only occurring as differential species for certain sub-community types.

In the past, stands dominated by Cladium mariscus have largely been placed within the Cladietum marisci and descriptions of this show clear resemblances to some of the British material (e.g. the Mariscetum of OBERDORFER (1957); the Cladietum marisci scorpidietosum of WESTHOFF & DEN HELD (1969)). In particular, the Carex elata sub-association of the Cladietum as recognised by KRAUSCH (1964) shows strong affinities. The species KRAUSCH gives to distinguish this from the typical sub-association include Thelypteris palustris, Carex elata, Galium palustre, Calamagrostis canescens, Lycopus europaeus, Lysimachia vulgaris, Lythrum salicaria and Peucedanum palustre - all characteristic species of the communities being considered. However, the previous decision

(6.1.1.6.) to confine the Cladietum marisci s.s. to Cladium-swamps of the Phragmition, means that the synsystematic position of this sub-association is not clear. In any case this sub-association does not resolve the placement of the Phragmites fens which could not be included here. The precise location of these communities is rather obscure from the literature. Some stands (e.g. S.697) with a reduced Phragmites cover and a strong development of Carex elata could be placed within the Caricetum elatae (comaretosum sub-ass. of VAN DONSELAAR, 1961) (cf. LIBBERT, 1932; "Ausbildungsform III" of JESCHKE, 1957). KRAUSCH (1964; 1965) has placed some stands very similar to some of mine into the Thelypteris palustris-variant of his Solanum dulcamara-sub-ass. of the Scirpo-Phragmitetum Koch 26 (= Thelypterido-Phragmitetum Kuiper 57). This is placed within the Phragmition, although some stands have more Magnocaricion-species than they do Phragmition. The Solanetosum sub-association itself (corresponding to BOER's (1942) "endphase" of the Scirpo-Phragmitetum and representing the driest development), might also contain some of the stands. Similarly, KORNECK (1963) has recognised a Calamagrostis canescens-sub-association with much C. canescens and Carex acutiformis and, less frequently, Peucedanum palustre and Lathyrus palustre. Another potential placement for some stands could be within the Cicuto-Caricetum pseudocyperi Boer et Siss. 42 of the Cicution virosae.

Clearly, apart from the uncertainties involved, such a

partitioning of the community-types is contrary to the enuciations made above and appears unsatisfactory, especially when the relevant Associations are themselves of debated status and uncertain limit (at least for England). However, KORNECK (1963) described a Junco subnodulosi - Calamagrostietum canescentis as an Association of the Magnocaricion with Calamagrostis canescens as a character species and Juncus subnodulosus as a differential. Some of the varieties of this have a species complement similar to some sub-communities recognised here. A Cladium sub-association contains stands of the Great fen sedge; a typical sub-association has Phragmites as dominant. The community differs from the Group 2 complex in that certain species, e.g. Carex elata, Rumex hydrolapathum, appear to be completely absent and that others, e.g. Cladium, Eupatorium, Potentilla palustris, have a more restricted sociological amplitude within the variants. Also, some community-types (e.g. versions with Schoenus nigricans) are missing. Nonetheless, the idea of a single Association to embrace all of this species-rich Cladium-Phragmites vegetation would seem a satisfactory solution for the Group 2 material. It, therefore, seems appropriate to create a new Association in which to include it all - perhaps a vicariant of the Junco-Calamagrostietum. This could be the Peucedano-Calamagrostietum canescentis with Peucedanum palustre and C. canescens as character species. The limits of such an

Association are not entirely clear. It could, for example, incorporate at least some of the Thelypterido-Phragmitetum Kuiper 57 as a Thelypteris sub-unit (perhaps also including some Thelypteris-rich Cladietea) or some of the Caricetum elatae Koch 26.

It may, however, be noted that some of the communities discussed in this section show pronounced affinities to other Associations that have been described. Thus, the Carex pseudocyperus-Cicuta virosa-nodum (6.2.12.) has some semblance of the Cicuto-Caricetum pseudocyperi Boer et Sissingh 42. This community (described by BOER, 1942; VAN DIJK & WESTHOFF, 1955; VAN DONSELAAR, 1961) has Cicuta virosa and Carex pseudocyperus as character species, sometimes as the dominants, and occurs usually as floating mats of vegetation. Typha angustifolia, Mentha aquatica and Lycopus europaeus are often prominent but Phragmites usually has a subordinate role. The nodum cannot be referred to this Association, but there are affinities. Similarly, the "species-rich"-nodum (6.2.15.) has strong similarities to certain Scorpidio-Caricetum diandrae communities (6.5.7.) and a case could be made for classifying it with these.

There remains, however, the non-Peucedanum series of Cladium-Phragmites communities. These clearly cannot be contained within the Peucedano-Calamagrostietum. Thus, instead of this Association, it would be possible to create

a larger single Association - a Cladio-Phragmitetum - in which the two series of communities could be brought together as sub-associations. Such a unit has little commendation: it would be rather large and have only a very weak floristic characterisation. Thus, it is preferred to retain the Peucedano-Calamagrostietum and regard the non-Peucedanum communities as belonging to an independent unit. This seems best referred to as a Cladium-Phragmites-consociation within which various sociations can be distinguished.

6.2.17. Synopsis of Cladium-Phragmites fen community-types.

Although the various community-types discussed above are quite well-defined, there are inevitably questions concerning their comparative ranks and hierarchical arrangement. The following syntaxonomic scheme is inevitably both subjective and arbitrary to some extent. It is, however, based upon the rankings suggested by the Information Analysis dendrogram in conjunction with utilitarian considerations.

The following scheme is proposed:

PHRAGMITETEA Tx. et Preising 42

MAGNOCARICETALIA Pignatti 53

MAGNOCARICION Koch 26

Peucedano-Calamagrostietum canescentis ass.nov.

Typicum

Molinia-Symphytum var. (6.2.7.)

Calamagrostis epigejos var. (6.2.8.)

Carex appropinquata var. (6.2.9.1.)

Myrica gale var. (6.2.10.)

Typical var. (6.2.11.)

Typical sub-var. (6.2.11.1.)

Phalaris sub-var. (6.2.11.2.)

Carex acutiformis sub-var. (6.2.11.3.)

Glycerietosum (6.2.9.)

Carex appropinquata var. (6.2.9.1.)

Typical var. (6.2.9.2.)

Juncus subnodulosus facies

Glyceria maxima facies

Glyceria maxima var.

Schoenetosum

typical var. (6.2.14.)

Oenanthe lachenalii var. (6.2.13.)

Cicutetosum (virosae) (6.2.12.)

typical var. (6.2.12.1.)

Carex riparia var. (6.2.12.3.)

Carex lasiocarpa var. (6.2.12.2.)

Caricetosum (diandro-lasiocarpae) (6.2.15.)

Menyanthes var.

Ranunculus lingua sub-var. (6.2.15.3a.)

Molinia sub-var. (6.2.15.3b.)

Stellaria palustris var. (6.2.15.1.)

Typical var. (6.2.15.2.)

Cladium-Phragmites consociation

Cladium sociation (6.2.5.)

Cladium-Molinia communities (6.2.4.)

6.3. Group 3. Species-poor tall fen communities - Table 3.

Into this group have been placed examples of tall herbaceous fen vegetation, all of which are characterised by a general species poverty. The dominant species are either Glyceria maxima or Phragmites communis with Carex paniculata important in some samples.

The application of Information Analysis to the data set produced results that were unsatisfactory as the groups established lacked any clear floristic characterisation. A quantitative version of Ward's method (using the transformation of the cover-abundance values suggested by MOORE et al., 1970) was also tried. This effectively segregated the data into dominance-types containing some floristic sub-groupings. It was decided to use this classification, though it is evident that the units defined by dominance colligate some rather different stands of vegetation.

The following units may thus be recognised:

(a) Glyceria maxima swamp and fen

(b) Phragmites fen

(c) Phragmites-Juncus subnodulosus fen

(d) Phragmites-Carex paniculata fen

6.3.1. Glyceria maxima swamp and fen.

Characterising species: Glyceria maxima (as dominant).

Stands of vegetation dominated by the Reed Sweet grass, Glyceria maxima are infrequent in rich fen systems. The plant

is much more characteristic of wet areas on mineral soil - by rivers and pools and on alluvial floodplains - than it is of peat, and as such it has not been prominent in this survey. It does, however, occur in some rich fens and samples from these, together with additional lists made in other habitats, permit an initial description of the communities.

Glyceria maxima can occur in a wide range of water-depths: from reedswamp (+60 to +80 cms) to dry fen (-50 to -60 cms) (LAMBERT, 1947a) and this provides the basis for the recognition of various types of Glyceria-dominated vegetation.

6.3.1.1. Glyceria swamp. A species-poor community of pools, reservoirs and sluggish rivers. Glyceria can form pure stands but usually there are some associates such as Polygonum amphibium and Solanum dulcamara. This type of swamp is widely distributed throughout lowland Britain. SPENCE (1964) has described a similar Glyceria maxima-society from Scotland. In these swamps the Glyceria is firmly anchored in the substratum and can form tall stands of 1.5 to 2 m height. LAMBERT (1946; 1947b) however, has also described a floating type of Glyceria swamp, which is particularly characteristic of the tidal Broads in the R. Yare valley, Norfolk. The community is formed from a floating raft composed of the intertwined rhizomes and recumbent aerial shoots of the plant and is well adapted to invading the open water of these old peat workings where the deep unconsolidated organic ooze and the

20-30 cm tidal fluctuation in water level is inimical to the development of the attached form of the community. The mat, however, is prone to disintegration - to form free-floating rafts or "hover" - and can only persist in areas with little tidal scour. A few associates can sometimes be found on the rafts, e.g. Impatiens capensis, Solanum dulcamara.

6.3.1.2. Glyceria maxima fen.

This encompasses a rather diverse assemblage of stands brought together through the dominance of Glyceria maxima. This plant typically forms quite tall (1.5 m) bright green stands, although the aerial shoots are often at least partially prostrated along the ground. Associates are few, but variable and the available data do not admit of any further satisfactory sub-division. The most constant species for the group are Epilobium hirsutum, Filipendula ulmaria, Solanum dulcamara and Urtica dioica. Some stands contain species such as Rumex hydrolapathum, Lysimachia vulgaris and Valeriana officinalis and have clear affinities with the Glyceria maxima variant of the Peucedano-Calamagrostietum canescentis (6.2.9.3.).

In the hydroseral successional sequence of the Yare valley broads following on from the floating Glyceria swamp, is a more consolidated mat of semi-floating "hover fen" (LAMBERT, 1946), which appears to be referable to this community (S.214).

Elsewhere on these fens species-poor stands of Glyceria can be found on the old mowing marshes, normally associated with the dykes.

6.3.1.3. Synsystematics

ALLORGE (1922) described an "Association à Scirpus lacustris et Glyceria aquatica" - a swamp community in which Glyceria maxima (= G. aquatica (L.) Wahlberg) could form extensive facies. Within the systematic scheme advanced by KOCH (1926) such facies were treated as variants of the reedswamp Association viz. Scirpeto-Phragmitetum glyceriosum aquaticae. This status was retained by many subsequent workers who regarded such Glyceria stands as either facies or variants of this Association (e.g. TUXEN, 1937; LEBRUN et al., 1949; BOER, 1942; KUHN, 1961; VAN DONSELAAR, 1961). However, the community has also been given the rank of an independent Association, the Glycerietum maximae Hueck 31, though in the past this has been interpreted rather broadly. Thus, JONAS (1933) included within it, in addition to Glyceria-swamp, stands dominated by Typha latifolia and Scirpus lacustris as variants of the Association. In a more restricted sense, however, the Association was later adopted by BRAUN-BLANQUET & TÜXEN (1952) and has been maintained by TÜXEN (1954; 1955), OBERDORFER (1957; 1962), JESCHKE (1959), GEHU (1961), KORNECK (1961) and PASSARGE (1964), as part of a general trend towards the upgrading of some of the facies

of the Scirpo-Phragmitetum. All of these placed the Association into the Phragmition Alliance except for PASSARGE (1964), who put it into his new Phalarido-Glycerion.

HUECK's (1931) description was of a species-rich community growing on nutrient-rich decomposing detritus in shallow water of fluctuating depth where the habitat may become periodically dry. The same sort of conditions have been recognised by the other workers but often a more species-poor community has been described (e.g. JESCHKE, 1959). However, one of the reasons why VAN DONSELAAR (1961) did not allocate his Glyceria-stands to this Association was because, as a shallow water Association, it seemed inappropriate for his deep water facies of the plant - and, indeed, NEUHÄUSL (1965, p.83 ff.) has shown that G. maxima produces societies of different structure in different hydrological and developmental contexts.

An interesting approach has been adopted by KRAUSCH (1964; 1965), who recognises both Glyceria maxima-variants of the Scirpo-Phragmitetum and also an independent Glycerietum maximae growing in rather more shallow conditions. The distinction between these is that in the first Glyceria it has a relatively low cover occurring intermixed with the dominants of the Scirpo-Phragmitetum, whereas in the Glycerietum the Glyceria is strongly dominant, Scirpo-Phragmitetum species are reduced or even absent and there is a greater smattering of Magnocaricion species. Whilst this

does not of necessity solve the problem expressed by VAN DONSELAAR (1961), nonetheless, it seems a useful distinction. This conception of the Association is clearly more restricted than some of the earlier ideas.

It raises also the question of the precise status of the community-type as, with the recognition of the plant as a well developed member of other Phragmitetea Associations, it can no longer be designated as a character species of the Glycerietum. This is recognised by WESTHOFF & DEN HELD (1969), who refer to a Glyceria maxima-sociation characterised by Glyceria as the dominant species. This would seem to be an appropriate denomination for the community-type considered here - and although this encompasses both Glyceria-swamp and fen there do not seem to be adequate floristic grounds for the assignation of these two types to different syntaxa.

6.3.2. Phragmites communis community-types.

The vegetation units grouped together here represent one of the most widespread and frequent types of fen vegetation. In most stands Phragmites communis is the exclusively dominant plant but in some Carex paniculata is also important. Generally, the stands are poor in associated species but Angelica sylvestris, Epilobium hirsutum, Eupatorium cannabinum, Filipendula ulmaria and, to a lesser extent, Cirsium palustre and Iris pseudacorus are characteristic and conspicuous

components. Galium aparine, Solanum dulcamara and Urtica dioica are also often found.

This type of vegetation is found in fen systems in many parts of England and Wales, though frequently it is only of limited extent. It may also be found beside rivers on alluvial flood plains and at the edges of lakes and reservoirs. Because of the disjunct and diverse nature of the sites and the impoverished and rather variable floristic complement, and the fact that only a relatively small number of samples are available the following classification, based both on dominance and floristic content of the stands, is only tentatively offered. However, the units distinguished do seem to have substantial utility.

6.3.2.1. Phragmites communis nodum.

In this community-type Phragmites communis is the dominant species forming dense tall (1-2 m) stands in which other species are infrequent or, occasionally, even completely excluded.

Pure stands of Phragmites are not common in fen systems. They tend to be rather small and often occupy the wetter parts - shallow depression, wet spring areas, etc. The reed can attain a height of 2 m+ and a density of about 250 culms/m^2 has been recorded. Similar pure stands of the reed can sometimes be found in reedswamp areas and the allocation of the above stands tofen is only based on the relative level

of the summer water-table.

Usually, however, there are at least some other species associated with the reed, especially Epilobium hirsutum, Solanum dulcamara and Urtica dioica. Some stands contain more typical "fen" species such as Angelica sylvestris, Eupatorium cannabinum, Thalictrum flavum and Juncus subnodulosus, but these are sporadic and the species total is generally low (average = 5-10/m^2).

The abiotic conditions of these sites are variable. Most are on fen peat, but some are developed in wet fen areas (e.g. S.053) whereas others (e.g. S.225; S.484) are on a completely dry substratum. In these situations ruderals such as Sonchus arvensis can occur.

Clearly this group cannot be regarded as a coherent unit. Rather it serves as a "dump" for species-poor Phragmites stands.

6.3.2.2. Phragmites communis - Juncus subnodulosus nodum.

This community-type is defined by the occurrence of a group of species including Juncus subnodulosus, Equisetum palustre, Galium uliginosum, Lathyrus pratensis, Lotus uliginosus and Vicia cracca. Phragmites remains dominant with some of the taller dicots especially Angelica sylvestris, Cirsium palustre, Epilobium hirsutum and Filipendula ulmaria. Mosses are rare. Occasionally there is Acrocladium cuspidatum and Brachythecium

rutabulum.

The defining species are characteristic of certain types of fen meadow and in some places at least this Phragmites-Juncus community may be the result of overgrowth of fen meadow by Phragmites following the cessation of grazing.

6.3.2.3. Phragmites-Carex paniculata nodum. A fairly well defined community-type of characteristic physiognomy. Phragmites communis retains a high level of cover but with it Carex paniculata often forming enormous tussocks of over 1.5 m high. Growing up with these are a number of herbaceous dicots: Angelica sylvestris, Cirsium palustre, Epilobium hirsutum, Eupatorium cannabinum, Filipendula ulmaria, Iris pseudacorus, Lythrum salicaria, Scrophularia aquatica and Symphytum officinale and, occasionally, Lysimachia vulgaris and Valeriana officinalis. Lower growing species such as Caltha palustris and Mentha aquatica can sometimes also be found. Mosses tend to be absent, though Acrocladium cuspidatum occasionally occurs.

This type of community is particularly characteristic of wet areas alongside chalk streams in parts of Hampshire, but it also occurs in fen systems elsewhere in S.E. England.

6.3.3. Synsystematics. The synsystematic placement of these communities is not clear. The Phragmites-dominated stands have

an obvious physiognomic resemblance to the reedswamp Association the Scirpo-Phragmitetum Koch 26. and indeed may well correspond, at least in part, to one of the driest communities included within this, viz. Scirpo-Phragmitetum solanetosum (see KRAUSCH, 1964; WESTHOFF & DEN HELD, 1969). This corresponds to the "endphase" of the Association that was recognised by BOER (1942), and WESTHOFF & DEN HELD give Solanum dulcamara, Galium palustre ssp. elongatum and Carex paniculata as species differential against other sub-associations. However, consequent upon the argumentation of 6.2.16., it would be inconsistent to place these community-types within the Phragmition despite the physiognomic similarities. Indeed with the weak floristic characterisation and heterogenous composition it is not clear what systematic location is appropriate. The occurrence of species such as Epilobium hirsutum, Eupatorium cannabinum and Filipendula ulmaria point to at least some affinity to the Filipendulo-Petasition Br.-Bl. 47 (and it is of interest that VAN DONSELAAR (1961) placed a Phragmites-consociation within this Alliance). However, some of the stands most certainly to not belong here.

It would, therefore, seem most appropriate to follow the procedure adopted for the Glyceria-stands and to unite the samples into a Phragmites-sociation. The synsystematic placement remains obscure but the Magnocaricion may serve as a suitable location.

The Phragmites-Carex paniculata nodum presents some

similar problems. Such stands with dominant Carex paniculata could be placed within the Caricetum paniculatae Wangerin 16 (see 6.1.3.2.), but here it is preferred to restrict this to the sedge swamp community, partly because C. paniculata need not be dominant in these Phragmites-C. paniculata fens. Instead it would seem more appropriate to regard this community-type as a sociation (related to the Carex paniculata-Angelica-sociation that has been recognised by SPENCE (1964)).

6.3.3. Synopsis of species-poor Glyceria and Phragmites dominated vegetation

PHRAGMITETEA Tx. et Preising 42

PHRAGMITETALIA Koch 26

PHRAGMITION (COMMUNIS) Koch 26 em. Balatova-Tulackova 63

Glyceria maxima sociation (6.3.1.)

(Synon: Association a Scirpus lacustris et Glyceria aquatica Allorge 22
Scirpeto-Phragmitetum glyceriosum aquaticae Koch 26
Glycerietum maximae Hueck 31

MAGNOCARICETALIA Pignatti 53

MAGNOCARICION Koch 26

Phragmites communis consociation

Phragmites communis sociation (6.3.2.1.)
(Synon: Scirpo-Phragmitetum solanetosum Krausch 64 p.p. ?)

Phragmites communis-Juncus subnodulosus sociation (6.3.2.2.)

Phragmites communis-Carex paniculata sociation (6.3.2.3.)

6.4. Group 4. Communities of calcareous mires - Table 4.

Introduction: Included in this group are stands of herbaceous vegetation in which relatively low-growing graminoid monocotyledons are the predominant components. In the main these are cyperaceous species: Schoenus nigricans and the smaller carices - Carex dioica, C. hostiana, C. lepidocarpa and C. panicea; juncaceous species, especially Juncus subnodulosus; and graminaceous plants - especially Molinia caerulea. With these there is usually a rich and characteristic assemblage of herbaceous dicotyledons and a well developed carpet of pleurocarpous mosses.

This type of vegetation occurs in moist to wet habitats which are irrigated by highly calcareous water of geogenous origin. It can thus be found in open flushes, on spring mires, and in certain peat basins. Related vegetation-types occupy dune-slacks, but these are not considered in this survey. The substratum is variable: skeletal clays, muds and gravels, peaty gleys, or deep peat. The water-table is usually fairly constant; normally just below the surface for most of the year. This habitat will be referred to as "calcareous mire".

The plant communities described here thus largely conform to the categories of "rich fen" and "extreme rich fen" in the system of DU RIETZ (1949) and they were examined in detail as they form a major component of the rich fen vegetation of England and Wales.

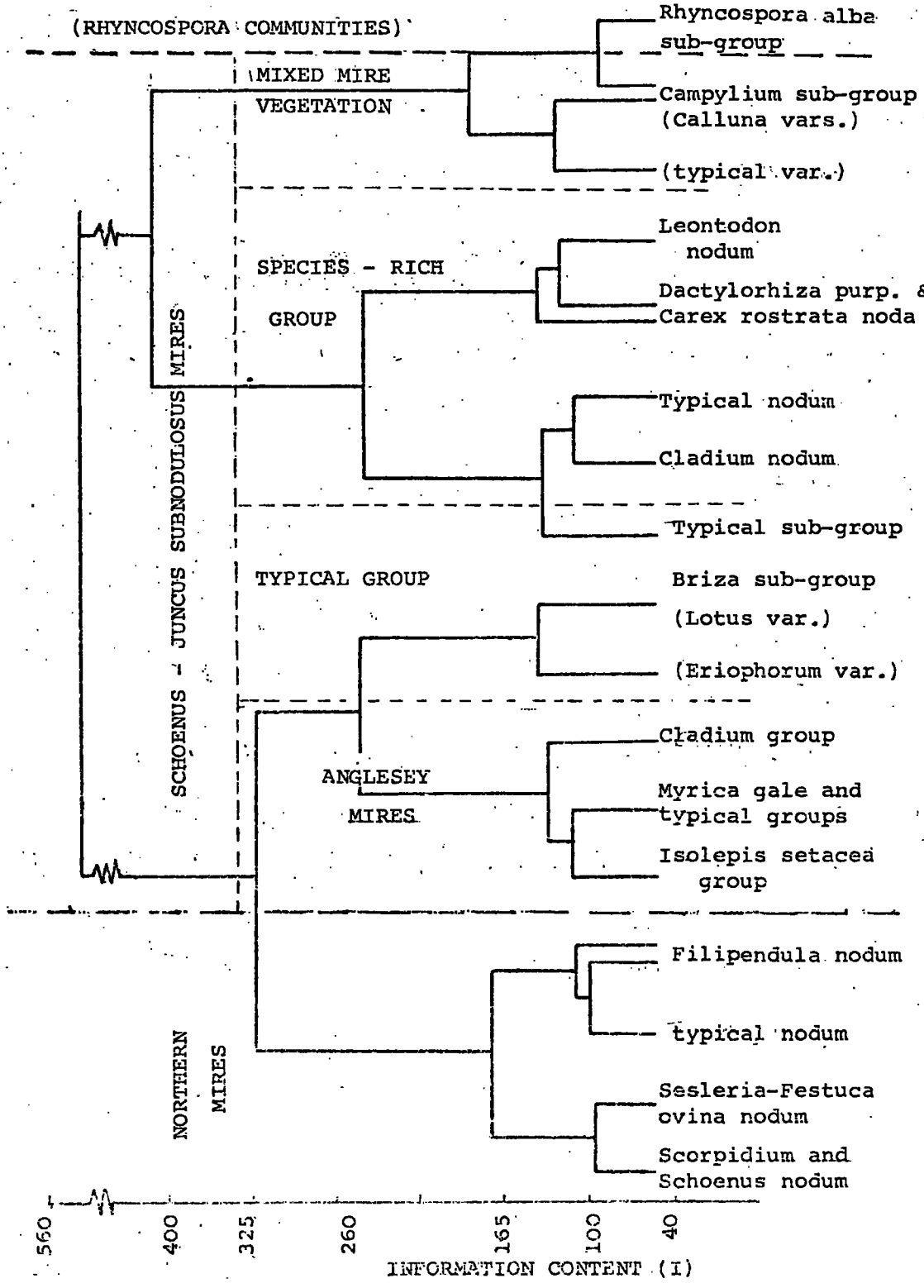
The samples included here come from various parts of the country. In keeping with the aim of the survey they are predominantly lowland - from S.E. England (especially East Anglia) and Anglesey. Some samples were also made in lowland parts of N. England and S. Scotland. In addition, examples of upland calcareous mires were examined in parts of the North Pennines. This was mainly as a preliminary attempt to clarify the relationships between the lowland community-types and such upland community-types as have been recognised by other workers and to place them within their wider context, especially for the purpose of delimitation. No attempt has been made to produce a systematic description and classification of the upland mires. Thus, whilst a large number of lowland mires have been examined only a small proportion of the upland types have been incorporated into this survey.

The results of Information Analysis on this set of releves are displayed in Fig. 6.4.I., showing the terminal groups which form the basis of the units recognised here. These groups were well-defined in the initial analysis and subsequent re-allocation strategies produced little change in the contents.

For descriptive purposes it is convenient to recognise five major groupings which correspond quite well with the four main divisions of the Information Analysis dendrogram (see Fig. 6.4.I.). These have been provisionally designated:

Fig. 6.4.I.

INFORMATION ANALYSIS OF THE VEGETATION OF CALCAREOUS MIRES.



(a) mixed mire nodum: composed of stands where there is an admixture of the typical species of calcareous mire and various acidophilic and ericetal species.

(b) species-rich nodum: containing a variety of well-defined community-types, all of which are relatively rich in species.

(c) typical nodum: a largely negatively defined group, not well characterised floristically and with a rather variable content. This initially contained a small "dustbin" group of 6 samples but this has not been included in the following description.

(d) Anglesey mires: a geographical grouping containing samples from mires in Anglesey.

(e) Northern mires: a geographical grouping containing most of the samples made from Northern Britain - both upland and lowland.

For descriptive purposes it will be convenient first to discuss groups (a) to (d), which will be given the collective title of Schoenus-Juncus subnodulosus mire. Then group (e) will be examined independently. Consideration will also be given here to some samples of calcareous mire made in Upper Teesdale which were not included in the initial computer analysis.

6.4.1. Schoenus nigricans - Juncus subnodulosus communities.

General description: This type of vegetation is composed of stands of rich fen vegetation in which the Black bog rush, Schoenus nigricans, is normally a characteristic and important component. With it Juncus subnodulosus and, to a lesser extent, J. articulatus and Molinia caerulea, are often prominent species. These plants typically produce a rather short (50-80 cms) herbaceous vegetation which, superficially, has the appearance of rough grassland.

Schoenus nigricans is usually the dominant species and when it is present in large amounts the community takes on a rather dull grey-green coloration throughout the year. In some cases, however, it is only present in small quantity or is even completely absent. In this situation in spring there may instead be a very distinct facies produced by the predominance of the dive-green leaves of Juncus subnodulosus. This gradually browns towards high summer as the leaves mature and the tawny flowering heads appear. In winter such stands turn to a subdued reddish brown.

In some localities the community takes on a rather different appearance as a result of the occurrence of tall-growing helophytes - notably Phragmites communis or Cladium mariscus. These form an upper stratum to the vegetation, but the plants are usually of reduced vigour and this layer is often only weakly developed, i.e. only c. 1 m tall with the plants distributed sparsely, sometimes just forming local

patches. This layer is normally only developed in isolated mires where there is no grazing. In such situations scattered shrubs of Alnus glutinosa, Betula pubescens and Salix cinerea and, occasionally, S. repens can also be found and during the summer months the flowering heads of some tall growing herbaceous species (e.g. Angelica sylvestris, Cirsium palustre and Eupatorium cannabinum) can be conspicuous. Even in these examples, however, it is the species of medium stature that are the major components of the community forming a "rush layer" between 50-80 cms tall. And even in thin layer the dominant species often contributes only 50-60% of the total vegetation cover for normally associated with it is a rich diversity of other species. Hemicryptophytes predominate with some helophytes and geophytes. Some of these contribute to the "rush layer" (e.g. Eriophorum angustifolium, Succisa pratensis), but mainly they are smaller plants forming a "small herb" layer of some 10-30 cms tall. Of these, small sedges such as Carex lepidocarpa, C. hostiana, C. panicea and C. nigra are frequent and often abundant either as scattered individuals or, occasionally, forming a low growing turf. With them are various herbaceous species of which Equisetum palustre, Epipactis palustris, Pedicularis palustris, Potentilla erecta and Valeriana dioica, are characteristic examples.

The degree of moss cover is variable, but in the optimal development of this type of vegetation bryophytes are abundant and can form an almost continuous carpet, contributing up to 70% of the total vegetation.

Community structure: The main structural component is normally Schoenus nigricans, which tends to impart a characteristic pattern to the community as a result of its growth form. A caespitose hemicryptophyte, it can grow to produce short, dense tufts of shoots, arising from a substantially sub-surface stock. These tufts are slightly elevated above the general ground-level. Alternatively, it can produce tussocks where the stock is raised well above ground level on a fibrous, peaty stool. There is a range of intermediates between these two forms.

Where Schoenus forms tussocks the community has a characteristic physiognomy with a regular alternation between the elevated tussocks and the inter-tussock depressions. The tussocks themselves can be of variable size: typical values are 40 cms height and 110 cms girth, though much larger specimens can be found up to 60 cms tall. Within a mature community there seems, however, a tendency for the tussocks to be of equivalent dimensions. This is partly an expression of the asymptotic increase in tussock-size with increasing age measured by DAWKINS (1939) but also a reflection of the infrequency of very young Schoenus tussocks within the

vegetation.

DAWKINS (1939) related the formation of tussocks in Schoenus nigricans to the erosion of the peat between Schoenus tufts by the action of moving water, aided by the influence of firing. A tussocky Schoenetum is thus characteristic of fen slopes rather than flat areas. This is not universally true, however, and in this survey tussocky communities have been found on flat, wet valley bottoms where erosion by moving water may not be important. The tussocky habit may partly be due to the growth form of the plant. It also seems to be prominent in grazed fens where it may be accentuated by trampling. It is of interest that on slopes where the substratum is a skeletal mineral soil rather than an organic deposit tufted plants of Schoenus tend to occur.

The growth of Schoenus is clearly related to the distribution of other species within the community. This is true both for the tufted and tussocked varieties but is emphasised particularly with the latter. The development of tussocks above the calcareous ground water produces a range of microhabitats along the wet-dry gradient sometimes with associated acidification in the elevated parts. A detailed analysis of the distribution of plant species within this mosaic remains in abeyance but some general observations may be recorded.

On the tops of some of the largest Schoenus tussocks species more characteristic of dry and often more acid conditions are established. They include Molinia caerulea,

Potentilla erecta, Polygala vulgaris, Euphrasia nemorosa, Linum catharticum, occasionally Drosera rotundifolia, and, in Anglesey especially, Calluna vulgaris, Erica cinerea, E. tetralix, Selaginella selaginoides, and Narthecium ossifragum. Mosses in particular show a distinct zonation (cf. CLAPHAM, 1940) with Brachythecium rutabulum, Ctenidium molluscum and Pseudoschleropodium purum growing in the most elevated parts.

The vegetation developed between the tussocks is at least partly dependent upon the tussock density. With high densities (e.g. 8-10 tussocks/m^2) the tussocks are almost coalescent and there are few intervening species. More usual tussock densities are 4-5 tussocks/m^2 in a well-developed stand and lower densities are common. Few data are available concerning tussock dispersion. DAWKINS (1939) reported over-dispersion in a well-developed Schoenus stand at Cothill, Berks. but casual observations elsewhere suggest that this is by no means always the case.

At high tussock densities there are few species in the interstices and the associated flora is impoverished. At lower levels there is a richer development of associates and then the hydrological conditions seem to be at least partly determinative of the precise composition of the assemblage. In sites with a marked sub-surface summer water-table with pronounced superficial dessication, the inter-tussock space is often filled with a sward of grasses and small sedges.

Mosses are often infrequent, though Ctenidium molluscum can be abundant. However, frequently when the summer water-level is only a few centimeters below the surface, a very rich community develops with a rather loose cover of small sedges and various herbaceous dicots. Mosses cover large areas, either as expansive carpets or as swelling mounds. Acrocladium cuspidatum and Campylium stellatum are usually the most important constituent species but other hypnoid species such as Drepanocladus revolvens can be abundant. Acrocarps also occur: Bryum pseudotriquetrum and Fissidens adianthoides are particularly frequent. Elongate thalli of Riccardia pinguis can usually be found with the mosses and, less regularly, other Riccardia species also occur. This rich development of bryophytes provides a substratum conducive to the germination and growth of seeds of higher plants and also accommodates the roots of certain small herbs including some of the rarer species (e.g. Dactylorhiza traunsteineri (cf. SUMMERHAYES, 1968, p.xvii), Drosera anglica). CLAPHAM (1940) has pointed to the possible involvement of these moss mats in permitting the colonisation of acidophilic species.

In sloping fens the interspaces often contain small runnels with moving surface water for at least part of the year. These support a generally sparse vegetation cover composed mainly of loose moss aggregates with species such as Cratoneuron commutatum, Drepanocladus revolvens, Scorpidium

scorpioides and Riccardia pinquis. Higher plants may be scarce though Juncus articulatus, Eleocharis quinqueflora, Carex lepidocarpa, Triglochin palustris and sometimes Menyanthes trifoliata are rather characteristic of such flushed areas. Away from the main influence of the moving water there is the development of a more closed vegetation and moss mats become more prominent.

In flat areas in some wet fen systems (e.g. in derelict peat workings) pools of open water occur between the tussocks. These contain hydrophytes such as Potamogeton coloratus, Utricularia spp. and Chara spp., sometimes with Scorpidium scorpioides and, occasionally, Drepanocladus lycopodioides.

In the absence of Schoenus nigricans irregularities in the fen surface are less pronounced. Molinia caerulea can form substantial tussocks, but these do not support so rich an epiphytic flora as Schoenus. Nonetheless, local variations in height associated with the base of shrubs, with slightly tufted species or with moss pillows serve to provide a complex mosaic of micro-habitats.

Constant species: Species occurring constantly in the community-types considered here are as follows:

Anagallis tenella
Carex panicea
Equisetum palustre
Juncus subnodulosus
Molinia caerulea
Potentilla erecta
Schoenus nigricans
Succisa pratensis
Valeriana dioica

Acrocladium cuspidatum
Campylium stellatum

Species constant except in the species-poor groups:

Carex lepidocarpa
Pedicularis palustris

Bryum pseudotriquetrum

Cratoneuron commutatum
Drepanocladus revolvens (mainly ssp. intermedius)
Riccardia pinguis

Species constant except in some of the mixed mire stands:

Angelica sylvestris
Cirsium palustre
Eupatorium cannabinum
Epipactis palustris

Galium uliginosum
Hydrocotyle vulgaris
Mentha aquatica

Differential species: Schoenus nigricans-Juncus subnodulosus mires can be separated from those of the Northern mires group by the occurrence (preferably together) of Anagallis tenella, Juncus subnodulosus and Schoenus nigricans and, with less certainty, by the scarcity of Carex dioica and Eleocharis quinqueflora.

6.4.2. Mixed mire vegetation (Drosera-Calluna nodum)

Characterising species: Aulacomnium palustre, Calluna vulgaris, Drosera rotundifolia, Erica tetralix, Myrica gale.

Community description: In this nodum have been placed examples of "mixed mire" vegetation in which species typical of base-rich mire occur in juxtaposition with acidophilic and ericetal species. Schoenus nigricans is a constant component of this community with Carex panicea, Drosera rotundifolia, Molinia caerulea and Myrica gale. There is a variety of both calcicolous and acidophilic species, but these vary in different developments of the community. As Table 4 shows this community-type shows a change from stands containing almost exclusively rich fen species to those with a preponderance of poor fen and wet heath plants. This forms the basis for a floristic sub-division and two major sub-groups may be recognised, of which the first can be further divided:

6.4.2.1. Sub-group of Campylium stellatum. A number of species are diagnostic for this group including Anagallis tenella, Juncus subnodulosus, Succisa pratensis and the mosses Acrocladium cuspidatum, Campylium stellatum and Scorpidium scorpioides. The last two species can often be abundant. This may then be further divided into three groups:

6.4.2.1a. Typical variety: This may largely be separated negatively from the other two groups by the absence of

Aulacomnium palustre, Calluna vulgaris and Erica tetralix. Rich fen species are well represented and include Carex lepidocarpa, Cirsium dissectum, and Epipactis palustris. The stands have a well-developed moss layer with much Acrocladium cuspidatum, Campylium stellatum, Bryum pseudotriquetrum, Drepanocladus revolvens, Riccardia pinguis, R. sinuata and Scorpidium scorpioides. Juncus bulbosus, Pedicularis sylvatica, Pinguicula lusitanica occur and in one of the samples Priessia quadrata was found; recorded only from Stones Moor, Hants., pH range 6.5-7.0.

6.4.2.1b. Variety of Calluna and Carex lepidocarpa. This represents the best development of "mixed mire". On the one hand, there is a good representation of rich fen species with the same types occurring as in the Carex lepidocarpa variety (above) (with the addition of Eleocharis quinqueflora and Carex dioica). The acidiophilic element is also prominent with the characterising species of mixed mire (see above) all being constant and abundant, together with the occasional occurrence of Carex echinata, Pedicularis sylvatica and Vaccinium oxycoccus. Sphagna are prominent, especially S. plumulosum, but S. palustre, S. recurvum and S. subsecundum also appear.

This variety has been recorded from parts of Roydon Common and Buxton Heath, Norfolk, where it grows close to the

central drainage axis, presumably receiving a high proportion of calcareous affluent. Drosera anglica and Mnium pseudo-punctatum can be found here and Cladium can also occur. The other example is from Tarn Moor, Orton, Westmorland.

Here the community is very well developed with large hummocks of Sphagnum fuscum and S. rubellum (see BELLAMY & REILEY, 1967) and the northern species Primula farinosa and Selaginella selaginoides. pH range 6.5-7.0.

Variety of Calluna vulgaris. Here Carex lepidocarpa and Riccardia pinguis etc. are largely absent and there is a general reduction in the number of rich fen species. Otherwise, very similar to the Calluna-Carex lepidocarpa variant. Recorded from Cors Goch, Anglesey and Holt Lowes, Norfolk, but zones corresponding to this have also been noted at Roydon Common, distal to the main drainage axis. pH range 6.0-7.0.

6.4.2.2. Sub-group of Rhyncospora alba. Characterised by the constant occurrence of Juncus acutiflorus, Narthecium ossifragum and Rhyncospora alba with the bryophytes Calypogeia muellerana, Cephalozia bicuspidata, Hypnum cupressiforme, Lepidozia setacea and Odontoschisma sphagni. Sphagna are very important: S. papillosum and S. plumulosum tend to be predominant but S. recurvum and S. subsecundum also occur. The community is poor in species - most of the rich fen plants being absent. Schoenus and Molinia are dominant with much

Myrica gale, Calluna and Erica tetralix. Pinguicula lusitanica sometimes occurs and also Drosera intermedia and Leucobryum glaucum.

This community has been recorded from the Cranes Moor area of the New Forest. It is clearly very distinct from the other Schoenus communities, but a related community occurs below the wet heath at Roydon Common. pH range at Cranes Moor, 4.5-5.5.

The growth of acidophilic species within base-rich ground water is of some interest. A partial explanation may be in the elevation of the substratum above the main influence of the water flow, together with the blanketing of the influence of mobile ions. CLAPHAM (1940) has pointed to the role of hypnoid mosses in permitting the establishment of acidophilic species by selective ion adsorption. BELLAMY & REILEY (1967) also point to the growth of Sphagnum fuscum hummocks on swelling tufts of Campylium stellatum and Cratoneuron commutatum in the rich fen at Tarn Moor. They have shown a clear discontinuity in cation content between 4-8 cms above the base of the hummock.

6.4.3. Species-rich Schoenus fen.

Characterising species-group: A rather nebulous group with Caltha palustris, Dactylorhiza incarnata, D. praetermissa, Lophocolea bidentata, Mnium seligeri, Pseudoschleropodium purum, Riccardia multifida.

This contains five community-types notable for their high

species-diversity and includes examples of the richest development of Schoenus fen in England. They have been brought together into a single major cluster by Information analysis. Schoenus nigricans is present in most of the samples and often dominant. With it both Juncus subnodulosus and Phragmites communis occur constantly, sometimes in large quantity.

Communities 6.4.3.3., 6.4.3.4. and 6.4.3.5. may be distinguished from 6.4.3.1. and 6.4.3.2. by the occurrence of a group of species including Eriophorum latifolium, Parnassia palustris, Ctenidium molluscum, Fissidens adianthoides and, with rather lower presence, Carex flacca and Pinguicula vulgaris. Many of these also occur in the moss-rich facies of 6.4.3.2.

6.4.3.1. Typical nodum.

Characterisation: Absence of differential species.

Description: This is the least species-rich group of the five communities and must largely be identified by the absence of differential species. There is also a reduction in the occurrence of certain other species which are otherwise of quite general occurrence in Schoenus-fen. Thus, Carex lepidocarpa and Pedicularis palustris are only of occasional occurrence. Mosses tend to be rather restricted too: Cratoneuron commutatum, Bryum pseudotriquetrum, Drepanocladus

revolvens and Riccardia pinguis only occur in a few samples. The chief mosses are just Acrocladium cuspidatum and Campylium stellatum, though Pseudoschleropodium purum is also constant. Species totals remain relatively high, however (c. 40 spp./10 m^2).

6.4.3.2. Cladium nodum.

Characterising species: Cladium mariscus; plus absence of other differentials.

Description: A distinct group characterised by the occurrence of Cladium mariscus. This can grow in large quantities to form rather open sedge beds of c. 1 m height. Also, diagnostic, though of lower constancy, are Carex elata and Galium palustre. Two rather distinct developments of the community can be distinguished. One is characterised by a well-developed moss carpet containing, in addition to Acrocladium cuspidatum and Campylium stellatum, other species such as Bryum pseudotriquetrum, Cratoneuron commutatum, C. falcatum, Ctenidium molluscum, Fissidens adianthoides, Drepanocladus revolvens. With these there is also Moerkia flotoviana, Riccardia pinguis, R. multifida and R. sinuata and occasionally other species such as Rhytidiadelphus squarrosa, Cephalozia bicuspidata and, rarely, Priessia quadrata. Associated with this moss carpet is some lower growing phanaerogams including Carex dioica, Parnassia palustris, Pinguicula vulgaris and Drosera anglica. This variant is very localised, being restricted to some wet fens bordering the headwaters of the R. Waveney and R. Ouse in

Suffolk. It is well documented by BELLAMY & ROSE (1961).

In the other development of the nodum mosses are much less important and of more sporadic occurrence. Filipendula ulmaria, Lotus uliginosus and Vicia cracca appear more characteristic of this variant. This variant is more widely distributed than the first, but again it is best developed in the Waveney-Ouse valley fens.

6.4.3.3. Dactylorhiza purpurella nodum.

Characterising species: Dactylorhiza purpurella.

Description: This group is composed of only three samples, all made in Northern England, from Dalby Bog, Yorks. and Newham Fen, Northumberland. Both of these represent rich developments of Schoenus vegetation with 68 species recorded from a 10 m^2 quadrat at Newham and 69 from Dalby. The diagnostic species is Dactylorhiza purpurella which replaces D. praetermissa in these northern sites. Otherwise, however, the affinities of both samples are clearly with the species-rich Schoenus mires of S.E. England rather than with other calcareous mire communities of northern parts. Juncus subnodulosus, predominantly a species of S.E. Britain (PERRING & WALTERS, 1962), is almost at its northern limit at Dalby. It is absent from Newham. Here, however, Epipactis palustris is growing close to the northernmost extension of its range. Both of the sites are characterised by an extensive growth of mosses, which may form

a thick carpet. At Newham in particular these include some uncommon species such as Moerkia flotoviana and Camptothecium nitens.

Schoenus tends to occur as local patches rather than dominating the whole area, and other species can be locally important: Carex flacca, C. lepidocarpa, C. panicea. At Dalby Juncus subnodulosus predominates over large area; at Newham, Carex diandra and C. paniculata.

6.4.3.4. Carex rostrata nodum.

Characterising species: Carex rostrata (Menyanthes trifoliata, Potamogeton coloratus, Utricularia sp.)

Description: A community-type of wet fens, best characterised by the occurrence of Carex rostrata, this includes some of the richest types of Schoenus-fen with up to 65 species being recorded in a relevé. These include a wide variety of herbaceous species and a rich development of mosses. Characteristic of these stands is the occurrence of very wet conditions between the Schoenus tussocks. This may either be as runnels or soaks on the sloping fens or as shallow pools in the flatter areas. Two rather different, but overlapping, varieties may be noted. The first, from the slopes of Scarning and Smallburgh fens in Norfolk, has Scorpidium scorpioides, Carex dioica, Menyanthes trifoliata and Drosera anglica. The other, from the fens of the Cothill basin in Berkshire, has Potamogeton coloratus and Utricularia neglecta.

The two types are found together on Gooderstone Common, Norfolk, where Drepanocladus lycopodioides also occurs. Amongst the lower plants, Chara vulgaris is a constant component of this community and C. hispida also grows in some fen pools at Cothill. (C. contraria has also been recorded from this site (BOWEN, 1968)).

6.4.3.5. Leontodon taraxacoides nodum.

Characterising species: Anthoxanthum odoratum, Centaurea nigra, Gymnadenia densiflora, Leontodon taraxacoides, Luzula multiflora, Polygala vulgaris.

Description: A well-defined nodum growing in relatively drier areas of Schoenus mire. The above species are all constant and frequent in the community and Leontodon taraxacoides is rather specific to it. These are all plants with affinities to Molinia-dominated vegetation and Molinia also is a constant and often abundant. Other drier grassland species include Briza media, Carex pulicaris, Cirsium dissectum and the mosses Ctenidium molluscum and Pseudoscleropodium purum (both of which can be plentiful). However, the other species of wetter fens still remain in this community and one sample (from Scarning Fen) contains both elements of this group and the Carex rostrata group. Another sample from Scarning contained Leiocolea rutheana.

6.4.4. Typical nodum.

Characterisation: Absence of differential species.

This group contains some of the least well-developed examples of Schoenus-Juncus subnodulosus fen. It is rather heterogenous and distinct sub-groups can be recognised:

6.4.4.1. Typical sub-group. This is not a well-defined group, composed in the main of samples that do not obviously belong elsewhere. It includes some of the least well developed stands of Schoenus fen, such as those occurring just as isolated fragments. The species totals are rather low (average = 24 spp./sample) and many of the commoner species are missing.

Either Schoenus or Juncus subnodulosus predominate, often with large amounts of Molinia caerulea. Other fairly constant species are Angelica sylvestris, Cirsium palustre, Carex panicea, Eupatorium cannabinum, Equisetum palustre, Galium uliginosum, Mentha aquatica, Phragmites communis, Potentilla erecta and Valeriana dioica. Anagallis tenella is completely absent. Mosses are not well developed - only Acrocladium cuspidatum and Campylium stellatum are frequent.

Many of the stands included here are rather dry with a closed vegetation cover. Related to these are highly impoverished stands from drained sites where, by the insurrection of Molinia caerulea, there is a trend towards Molinieta,

but Schoenus is able to persist for a while. The following list, from Roydon Fen (near Diss), Norfolk, illustrates this type of vegetation:

Roydon Fen, Roydon, Norfolk. TM 102797

Salix atrocinerea ..	+	Cladium mariscus	+
		Epipactis palustris ...	+
Molinia caerulea ...	3,3	Eupatorium cannabinum .	+
Schoenus nigricans .	2,3	Galium uliginosum	+
Phragmites communis.	1,1	Juncus subnodulosus ...	+
Angelica sylvestris.	+	Potentilla erecta	+
Carex pulicaris	+	Valeriana dioica	+
Cirsium palustre ...	+		
C. dissectum	+	Campylium stellatum ...	+

6.4.4.2. Briza media sub-group

Characterising species: None. Differentials from 6.4.4.1. are Briza media, Carex flacca and Anagallis tenella, together with the more sporadic occurrence of plants such as Carex lepidocarpa and Pedicularis palustris.

Contains the vegetation of various small, disjunct, sloping fens. These tend to be impoverished in some of the characteristic Schoentum species and the floristics are often strongly influenced by the intussusception of species from the contiguous communities. This results in a rather ill-defined vegetation-type.

The available data suggest that this grouping may be sub-divided:

(a) Variety with Lotus uliginosus

Species-group differential to Eriophorum latifolium var.:

Dactylorhiza fuchsii, Festuca rubra, Holcus lanatus, Lotus uliginosus, Ranunculus acris, Vicia cracca. Acrocladium cuspidatum and Equisetum palustre are also more frequent.

Schoenus is absent from some stands when Juncus subnodulosus and Molinia caerulea become more prominent. Other frequent species include Angelica sylvestris, Cirsium palustre, Eupatorium cannabinum, Galium uliginosum and Mentha aquatica.

(b) Variety with Eriophorum latifolium. A rather poorly defined variant with Carex hostiana, Eriophorum latifolium, E. angustifolium and Epipactis palustris as weak differentials against the Lotus uliginosus-variety. Schoenus nigricans is largely absent and Juncus subnodulosus occurs only in a few stands. This encompasses a variety of disjunct spring fens of lowland southern Britain, but it has marked affinities with the vegetation of calcareous mires in Northern Britain (6.4.10.) differing mainly in species such as Anagallis tenella, Epipactis palustris and Eupatorium cannabinum.

6.4.5. Anglesey fens.

Characterisation: Presence of Dactylorhiza purpurella, Gymnadenia densiflora, Linum catharticum, Serratula tinctoria, Sieglingia decumbens. Absence of Cirsium dissectum, Galium uliginosum, Valeriana dioica.

Description: This group is composed exclusively of samples collected from wetland areas in Anglesey. Rich fen is well developed over some eastern parts of the island where there are shallow calcareous basins associated with the Carboniferous Limestone bedrock. These were most probably occupied by post-glacial lakes but have subsequently become filled with fen peat and have been extensively used for turbary. There is no detailed documentation of the vegetation of these sites but incidental descriptions have been given by LACEY & ROBERTS (1958) and ROBERTS (1959).

In most of these areas Schoenus fen is widespread. It occupies two rather different habitats: (i) as a fringing zone of vegetation on the gentle slopes around the margins of the peat basins where it is associated with flushes and areas of water seepage; and (ii) on flatter wet areas over deeper peat (2-3 m) on the floors of the fen hollows. Even here, however, it is only developed in the proximity of calcareous ground water derived from the limestone. Thus, at Cors Nantisaf Schoenus-fen is found along the bottom of the slopes of the limestone scarp that borders the east margin of the mire and on the deeper peat of the fen basin immediately below this. Further from the edge, however,

Schoenus-vegetation is replaced by other types in which Molinia is prominent. pH measurements of groundwater from Schoenus areas gave values of between 7.0-8.0.

Floristically, this vegetation can be characterised by the absence of Cirsium dissectum, Galium uliginosum and Valeriana dioica. These are all either very rare or absent in Anglesey (GRIFFITH, 1895; PERRING & WALTERS, 1962). In contrast, Dactylorhiza purpurella, Serratula tinctoria, Gymnadenia densiflora, Linum catharticum and Sieglingia decumbens are well developed in the Anglesey Schoeneta and form a diagnostic species group. In addition, there are some other species of local occurrence which are particularly characteristic of these communities: Hypericum pulchrum, Ophrys insectifera and Plantago maritima.

Phytogeographically there is a mixture of southern and northern floristic elements. To the former belong Cladium mariscus, Epipactis palustris and Serratula tinctoria; to the latter, Carex hostiana, Dactylorhiza purpurella, and Selaginella selaginoides.

These communities are rich in species. In addition to the normal constants of Schoenus-Juncus subnodulosus communities (see 6.4.1.), the following are also constant or very frequent:

Graminoid monocots	Herbaceous dicots
Briza media	Centaurea nigra
Carex flacca	Linum catharticum
C. hostiana	Mentha aquatica
Juncus articulatus	Oenanthe lachenalii
J. subnodulosus	Parnassia palustris
Sieglingia decumbens	Pinguicula vulgaris
	Polygala vulgaris
Herbaceous monocots	Potentilla erecta
	Prunella vulgaris
Dactylorhiza fuchsii	Ranunculus flammula
D. incarnata	Serratula tinctoria
D. purpurella	Trifolium pratense
Gymnadenia densiflora	

Community-types: The samples of the Anglesey Schoeneta may be segregated into four community-types. The first three to be considered have the following species differential against the fourth: Anthoxanthum odoratum, Carex pulicaris, Centaurea nigra, Euphrasia nemorosa, Polygala vulgaris and Trifolium pratense. This is reflected in that the joining of the fourth group to the other three represents the last fusion made within the Anglesey community-group in the Information Analysis procedures (see Fig. 6.4.I.). The other three groups, however, are more similar to one another. They display intergradations and although useful monothetic criteria have been found which readily separate them into discrete units, nonetheless, additional data are required to confirm their validity.

6.4.5.1. Isolepis setacea group. This vegetation type is developed on flushed slopes marginal to the fen complex. Particularly characteristic is the occurrence of the bristle club-rush, Isolepis setacea, together with Triglochin palustris

and often quite large amounts of Juncus articulatus. Sagina nodosa and S. procumbens may also occur. Juncus subnodulosus is abundant in all of these stands, but the contribution of Schoenus is variable. In some places it is dominant and produces a tussocky vegetation with open runnels between the Schoenus plants, but in others it is relatively infrequent and here a low growing open turf dominated by Carex panicea is usually developed. Molinia is unimportant in this community-type and may be absent. In general, mosses are not well developed with Acrocladium cuspidatum, Campylium stellatum and Cratoneuron commutatum as the main species, but there is considerable variation in associates. Pellia endiviifolia occurs in some places.

This community has been recorded from flushes alongside Cors Bodelio, Cors Erdrreiniog and Cors Nantisaf.

6.4.5.2. Typical group: This community-type cannot be easily defined by any single species and is best recognised by the absence of differentials. It contains species-rich stands of vegetation: 63 species were found in one particularly rich sample but 50 is the average. Schoenus nigricans predominates with much Molinia caerulea, but Juncus subnodulosus often tends to be rather sparse. Bryophytes are quite well developed and include Acrocladium cuspidatum, Campylium stellatum, Drepanocladus revolvens, Fissidens adianthoides,

Riccardia pinguis, Pellia endiviifolia, Bryum pseudotriquetrum and Ctenidium molluscum.

Two rather different, though intergrading, variants may be noted. In one Angelica sylvestris, Eupatorium cannabinum and Filipendula ulmaria are prominent with Agrostis stolonifera and Holcus lanatus. In the second these species tend to be absent but Plantago maritima and Calluna vulgaris occur instead.

6.4.5.3. Myrica gale group: In places around the margins of the Cors Bodelio basin the fringing areas of Schoenus fen contain substantial amounts of Myrica gale and Molinia caerulea with some Erica tetralix. A similar community is developed on the slopes below the limestone scarp bounding the southern edge of Cors Goch. Apart from these species the vegetation type has a floristic composition similar to that of the typical group (6.4.5.2.). At Cors Bodelio in particular there is a rich assemblage of herbaceous plants and orchidaceous species are sometimes very well represented. At one place the following were recorded: Coeloglossum viride, Dactylorhiza maculata ssp. ericetorum, D. fuchsii, D. incarnata, D. purpurella, D. traunsteineri, Epipactis palustris, Gymnadenia conopsea ssp. densiflora, Ophrys insectifera and Platanthera bifolia.

6.4.5.4. Cladium group: Very distinct from the three groups above is a development of Schoenus fen along the bottom of the Cors Nantisaf basin. Cladium mariscus and Phragmites communis

with occasional plants of Myrica gale, contribute a rather sparse upper layer to the vegetation. Beneath them Schoenus tussocks predominate with a rich associated flora. The whole area is very wet with open water between many of the tussocks. In such pools and wet depressions Carex rostrata, Eriophorum angustifolium, Menyanthes trifoliata and Chara vulgaris may be found. By contrast, the tussocks of Schoenus nigricans and, to a lesser extent, Molinia caerulea provide elevated nuclei for the establishment of oxyphilous plants. This is especially noticeable where the tussocks have coalesced. Species growing on such places include Calluna vulgaris, Erica cinerea, E. tetralix, Drosera rotundifolia, Genista anglica, Hypericum pulchrum, Narthecium ossifragum, Polygala serpyifolia and Selaginella selaginoides, Sieglingia decumbens and Sphagnum plumulosum. The bryophyte layer is quite well developed between some of the tussocks and Campylium elodes occurred in one place. Smaller herbaceous species are frequent. Ophrys insectifera is frequent, normally on tussocks away from the wettest parts. ROBERTS (1959) has discussed the occurrence of this plant in Anglesey as these fens provide the only wetland localities for the plant in the United Kingdom. It does, however, occur in some fens in Eire (PRAEGER, 1934; HESLOP-HARRISON, 1953). Similarly, it grows in extreme rich fen in Scandinavia (DU RIETZ, 1950; MALMER, 1965) and also in Central Europe. OBERDORFER (1962) cites it as a species of the Molinion alliance. It may yet be discovered elsewhere in British fens.

With it there is Dactylorhiza traunsteineri.

Adjoining this Schoenus vegetation is Molinia-Myrica mire (6.7.4.3.) and patches of this seem to be forming within the Schoenetum where Schoenus and Molinia tussocks are forming an elevated substratum.

This community-type has also been recorded from parts of Cors Erddreiniog.

6.4.6. Distribution and syntaxonomy of Schoenus nigricans mires.

Calcareous mire communities with Schoenus nigricans as an important component are widely distributed throughout much of Europe from the Eu-Atlantic sectors to the Circum-Boreal and Central regions. Communities of this type have been recognised and described - often under the name Schoenetum nigricantis - from Ireland (BRAUN-BLANQUET & TÜXEN, 1952), France (ALLORGE, 1922; LEMEE, 1937); Belgium (DUVIGNEAUD & VANDEN BERGHEN, 1945; VANDEN BERGHEN, 1952), the Dutch coast (WESTHOFF & DEN HELD, 1969), N.W. Germany (TÜXEN, 1937), and N.E. Germany (KLOSS, 1965). The eastern limit appears to be in Czechslovakia where the community was recognised by KLIKA (1929). At this eastern limit, however, the community is rare and LIBBERT (1932) describing a Schoenetum from Neumark (N.E. Germany - also on the eastern limit) points out that it occurs more as a wet version of Molinia caerulea grassland than in its typical form. The community is particularly characteristic of the European lowlands but in parts of southern central Europe it is also

montane attaining up to 2,000 ft. It occurs in the pre-alpine regions of S. Germany (VOLLMAR, 1947; OBERDORFER, 1957; KORNECK, 1963) and in some of the warmer alpine valleys (KOCH, 1926), although in the higher montane areas it is replaced by Schoenus ferrugineus-communities.

The syntaxonomy of Schoenus nigricans have been discussed by GÖRS (1963), KLOSS (1965) and WESTHOFF & DEN HELD (1969). Essentially KOCH (1926) first introduced the Schoenetum nigricantis as an Association to contain Schoenus nigricans vegetation. However, reflecting the widespread distribution of this type of vetetation, phytogeographical considerations have led to the recognition of several geographical races (see KOCH, 1926; DUVIGNEAUD, 1949), although, as DUVIGNEAUD (loc. cit.) points out, these are not always easy to distinguish. Since then most of them have been upgraded to the status of vicariant Associations: the original community described by KOCH (1926) from Central Europe - the Schoenetum nigricantis helveticum - is synonymous with OBERDORFER's (1957) Orchido-Schoenetum nigricantis, which itself has come to be further subdivided into geographical races (GÖRS, 1964). Similarly, the Schoenetum nigricantis metuonense Westhoff 47 from dune slacks along the Dutch coast has become the Junco baltici-Schoenetum nigricantis Westhoff (43) 69.

From Atlantic regions of Europe various Schoeneta have been described. ALLORGE (1922) records various examples from Central France and KOCH (1926) referred to this as the

Schoenetum nigricantis parisiense characterised by the occurrence of the Atlantic Anagallis tenella, Cirsium dissectum and Oenanthe lachenalii. A similar community was described by LEMEE (1937). These communities, however, also contain more characteristically continental species including Orchis palustre and Selinum carvifolia. However, BRAUN-BLANQUET & TÜXEN (1952) have described a Eu-Atlantic community - which has come to be known as the Cirsio-Schoenetum nigricantis - from Ireland. This is only weakly characterised in a positive sense by the occurrence of A. tenella and C. dissectum, but the absence of continental and alpine species provides useful negative characteristics.

Thus, the concept of the "Schoenetum nigricantis" is best seen in terms of an Association-group which contains a number of vicariant Associations. As used here it in no sense corresponds to the Schoenetum nigricantis sensu TANSLEY (1939) who used it for the Schoenus-dominated blanket mires of Western Ireland. BRAUN-BLANQUET & TÜXEN (1952) (see also MOORE, 1968) refer this vegetation to the Pleurozia purpurea-Erica tetralix Association within the Oxycocco-Sphagnetea.

Both ALLORGE (1922) and LEMEE (1937) have pointed to the close relationship between communities containing Schoenus nigricans and those which are dominated by the fen rush, Juncus subnodulosus, but without any Schoenus. The latter community is found especially in small, peaty spring fens. KOCH (1926) created an independent Association - the Juncetum subnodulosi - into which such vegetation could be placed. This Association has been the centre of some considerable debate essentially because its floristic characterisation is very poor. Effectively, as SEGAL (1968) pointed out, it is defined only by the dominance of Juncus subnodulosus which, in fact, is a species of very wide sociological amplitude. It is evident that, although some communities referred to under this head are very different to the Schoenetum nigricantis, others are

very similar, something which was, in fact, recognised by KOCH. This has also been appreciated by many other workers (e.g. VOLLMAR, 1947; KLOSS, 1965) and indeed KORNECK (1963) has described an Epipactis palustris sub-association of the Juncetum subnodulosi, which contains not only typical species of the Schoenetum nigricantis, but also Schoenus nigricans itself. OBERDORFER et al. (1967), reflecting on the unsatisfactory nature of the Juncetum subnodulosi, look to the possibility of reallocating Juncus subnodulosus-dominated stands to other, better defined Associations.

Thus, some stands dominated by the fen rush could easily be referred to the Schoenetum nigricantis. This, in fact, was the approach of both ALLORGE (1922) and LEMEE (1937), who nominate a Schaeneto-Juncetum obtusiflori for this type of vegetation.

6.4.7. Syntaxonomy of the Schoenus-Juncus subnodulosus community-types

The following observations seem relevant:

(i) The constant occurrence of Juncus subnodulosus within the community-types together with the absence of any segregation of those stands containing Schoenus and those without it as the basis of group-formation in Information analysis, suggests that the stands must all be placed into the same syntaxon irrespective of dominance.

(ii) The name "Schoenetum nigricantis" is inappropriate for the taxon and its usage by SHIMWELL (1968) must be disallowed. Instead it must be designated as a vicariant of the "Schoenetum nigricantis" association-group. Following BRAUN-BLANQUET & TÜXEN (1952), Cirsium dissectum could be used to define a British vicariant but Anagallis tenella is more constant and would seem more appropriate.

(iii) A floristic unit created on this basis does not, of necessity, contain all stands with Schoenus as the dominant taxon.

It is, therefore, proposed to unite most of the community-types described here into a single Association. For this the title Schoeneto-Juncetum subnodulosi would seem appropriate but, to emphasise the Atlantic nature of the community a name such as Anagallo-Schoenetum nigricantis might be preferable.

It is felt, however, that the Rhyncospora alba communities of the mixed mire group (6.4.2.2.) cannot be satisfactorily placed in such an Association. These are, therefore, not included here.

6.4.8. Character species. A variety of character species have been given for this Association by Continental authors. Some of those given by KOCH (1926) (e.g. Primula farinosa, Tofieldia calyculata) subsequently came to be regarded as

character species for higher syntaxa (cf. OBERDORFER, 1957) and in any case largely referred to the Schoenus ferrugineus communities that have come to be placed into the Primulo-Schoenetum (Koch 26) Oberd.62. OBERDORFER (1962) suggests Orchis palustris as a character species for his Orchido-Schoenetum Oberd.57., but even this occurs in some other wetland community-types, and anyway is absent from Britain. From Belgium DUVIGNEAUD & VANDEN BERGHEN (1945) suggested Schoenus nigricans, Juncus subnodulosus and Liparis loeselii. But Juncus subnodulosus has a widespread sociological amplitude (cf. OBERDORFER, 1962) and Liparis can also occur in other communities. In Britain Liparis was once a fairly widespread species of mossy fens (BENNETT, 1902), but now it is confined to three or four localities (although a dune slack form (var. ovata) occurs in a number of places (see for example, WILLIS, 1967b). It still occurs in an area of Schoenus-mire at the headwaters of the R. Little Ouse in Suffolk but in its other localities it is in Cladium-fen (see 6.2.15.3.). Thus, depending upon the [syntaxonomic status of the] latter community, at most it can only be regarded as a local character species for the Caricion davallianae (cf. WESTHOFF & DEN HELD, 1969).

This leaves Schoenus nigricans itself. This, however, has a wide sociological amplitude (v. ALLORGE, 1937; GÖRS, 1964). The communities of calcareous mire are usually placed into the Caricion davallianae (see below), but it also occurs

on blanket bog in W. Ireland (placed into the Oxycocco-Sphagnetea by BRAUN-BLANQUET & TUXEN, 1952) and in transition mire in various places in western Britain - most probably belonging to the Rhynchosporion albae Koch 26. From Mediterranean areas it seems to have its sociological optimum in the Molinio-Holoschoenion Br.-Bl.47 (an Alliance which is largely vicariant for the Central and N.W. European Agropyro-Rumicion crispae Nord.40) but also occurs on the Rosmarinus heaths (ZWILLENBERG & DE WIT, 1952) of the Ononido-Rosmarinetea Br.-Bl.47. This wide amplitude reflects the wide distribution of the plant which is from Scotland and S. Norway to the Mediterranean regions of Europe and Africa. Thus, Schoenus could only be used as a regional character species and this is difficult in parts of Britain where it simultaneously occurs in different vegetation-types.

In this survey the only species found to be reasonably faithful to the Schoeneto-Juncetum subnodulosi is Dactylorhiza traunsteineri. Most of the localities of this plant are in Schoenus mire, though in parts of Anglesey the communities involved are transitional to Carex diandra-lasiocarpa vegetation. Interestingly, a new locality for the species in Argyll (KENNETH, 1971) was also associated with Schoenus. It is, however, a rare plant and could only be regarded as a local character species.

It would appear that there are no good character-species

for this community. It may, however, be defined floristically by the occurrence (preferably together) of Schoenus nigricans, Juncus subnodulosus and Anagallis tenella in association with the constant species of calcareous mire: Carex panicea, Molinia caerulea, Succia pratensis, Acrocladium cuspidatum and Campylium stellatum, and, less constantly, Carex lepidocarpa, Pedicularis palustris, Bryum pseudotriquetrum, Cratoneuron commutatum, Drepanocladus revolvens and Riccardia pinguis.

Sociological placement. After the recognition of the Caricion davallianae Schoenus nigricans vegetation of calcareous mires has always been placed here and, on the basis of its floristic composition, the Schoeneto-Juncetum subnodulosi clearly belongs here.

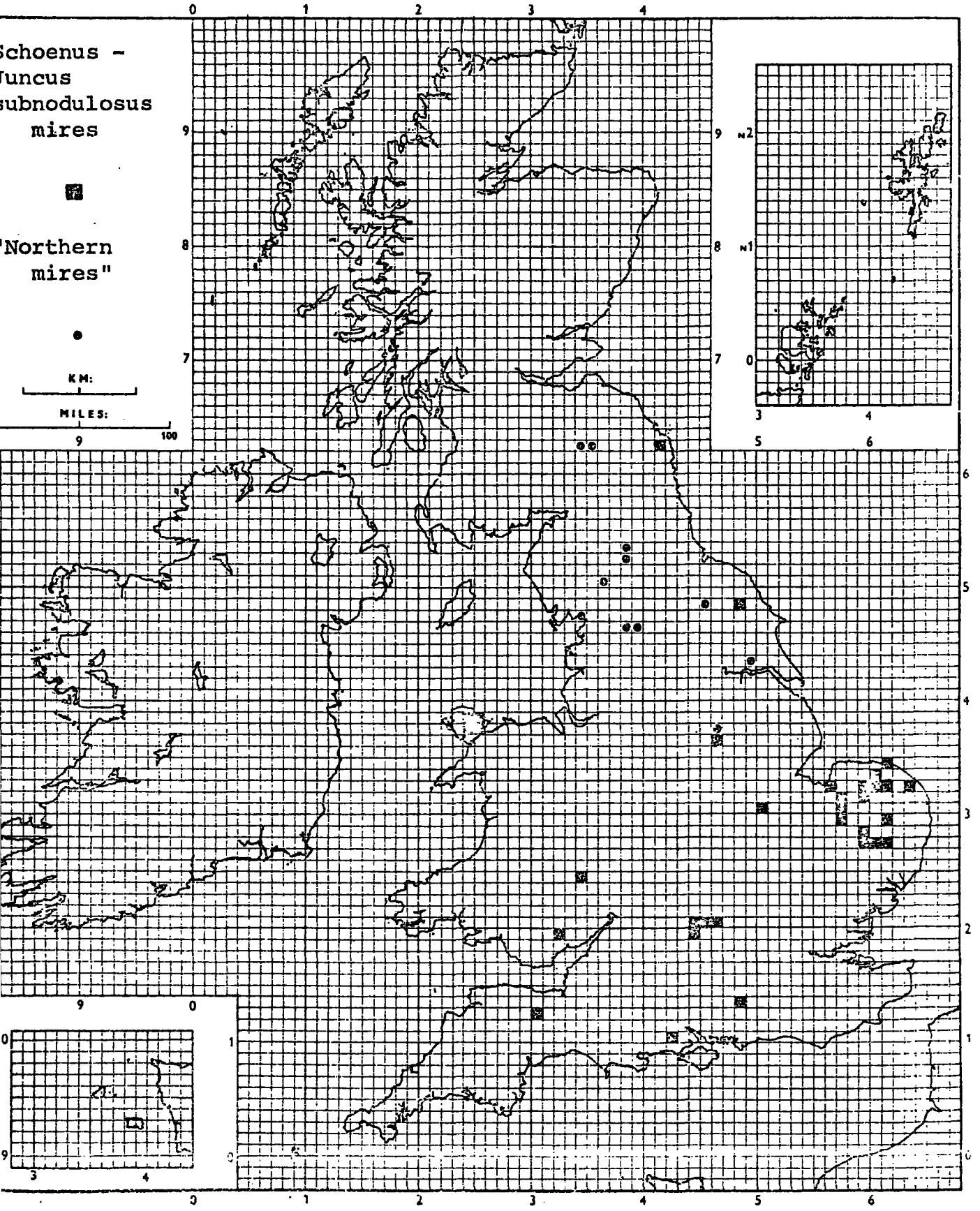
6.4.9. Occurrence and distribution.

This vegetation type is almost exclusively developed in areas irrigated by calcareous ground water, with a pH range of 6.5-8.0. It is typically developed beneath springs and lines of water seepage. Such sites have often accumulated a shallow layer of peat, though the community can also develop in skeletal situations where the underlying mineral material is exposed. Elsewhere Schoenus fen is developed in shallow, peat-filled basins supplied by water from calcareous strata. Here it is frequently associated with old peat workings, although the best development of the community is often on

the shallower peat on sloping ground along the margins of the mires. It would appear that irrigation by the inflow of geogenous water is necessary for the development of this community. Thus, it is absent from the flood-plain mires of East Norfolk where irrigation is largely by means of the throughflowing rivers and associated dykes. However, in the R. Ant system there are spring-fed valley fens occupying lateral valleys just above the main flood-plain mire complex and the community can be found in these. In the rather different context of the Breck Fens HASLAM (1965, 1966) has also shown that spring fed "headwater fens" contain Schoenus nigricans communities, whilst this species is absent from "valley fens" lower down the river which are, or have been, subject to winter flooding and which, in the absence of springs, have a fluctuating water-table. This may be caused by a difference in nutrient status with available nitrate and phosphate levels being low in the "headwater" situation.

Schoenus-Juncus subnodulosus mires are of infrequent occurrence in England and Wales. The main areas where they are found (see Fig. 6.4.II) are on the Chalk and calcareous boulder-clay in Norfolk; in association with Coralline Limestone in the Cothill basin, Berks.; and with Carboniferous Limestone in Anglesey. Other scattered localities are on the Oolites in Northants. and on the Magnesian Limestone in Notts. etc. The community was formerly more widespread.

Fig. 6.4.II.



BASED UPON BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

Schoenus has disappeared from many former localities. Thus, DRUCE (1926) mentions a Schoenus fen in North Bucks., which is no longer extant and many other examples can be found within local Floras, e.g. GIBBONS (1975). Even in Norfolk, where the community is still tolerably widespread, sites have been lost or modified by drainage or a general reduction in the height of the water-table; for example, the once rich Schoenus mires of Flordon Common (v. BURRELL & CLARKE, 1910) have become much impoverished through drainage.

6.4.10. Conservation.

Schoenus-Juncus subnodulosus mires have received a strong conservational commendation on account of Schoenus itself and many of the species characteristically associated with it. Many of these are of local, if not national, rarity and include plants such as Anagallis tenella, Carex dioica, Eriophorum latifolium, Epipactis palustris, Parnassia palustris, Pinguicula vulgaris and Pedicularis palustris. Even species such as Carex lepidocarpa, C. hostiana, Juncus subnodulosus and Menyanthes trifoliata are regarded as uncommon plants in much of S.E. England. These, together with national rarities such as Dactylorhiza traunsteineri, have meant that many examples of Schoenus-Juncus subnodulosus fens have been incorporated into Local Nature Reserves.

6.4.10. Northern mires.

General Description: The compass of this group is to contain stands of vegetation developed in association with calcareous mires and flushes in various parts of Northern England. The vegetation cover ranges from very open (c. 30% cover) to closed. The main components are small sedges, particularly Carex hostiana, C. lepidocarpa and C. panicea, which tend to produce a low-growing sward of some 10-20 cms. tall. With them Molinia caerulea sometimes shares dominance and Juncus articulatus can be important. Other low-growing monocots that are constant are Carex dioica and Eleocharis quinqueflora. However, in some lowland localities taller species such as Angelica sylvestris, Cirsium palustre and Filipendula ulmaria grow in the community giving a rather different physiognomy. Mosses are often well developed, especially Bryum pseudotriquetrum, Campylium stellatum, Cratoneuron commutatum, Drepanocladus revolvens and, in somewhat drier places, Ctenidium molluscum.

The corporate growth of these species can produce a continuous, rather uniform vegetation cover. In some marsh complexes, however, this may become dissundered into turfy hummocks separated by open, muddy depressions and runnels. This will be further discussed in the relevant sections.

The stands incorporated into this group have all been described from spring and seepage slopes flushed with base-

rich water. This may be largely sub-surface but in many places trickling surface water is found. The substratum is often skeletal, but in some places thin peaty-gleys have formed. The slope varies from almost flat to very steep (up to 50°). Such areas are often small and localised, concentred around springs but sometimes quite extensive flushed slopes occur.

In limestone areas of N. Britain this kind of habitat is rather widespread and the community-types can frequently be found, though often as rather small, disjunct areas which only support a impoverished vegetation cover. These sites have not been examined extensively in this survey and attention has largely been paid to flushed slopes peripheral to more complex mire systems. The main areas have been Great Close Mire, Malham Moor, West Yorks.; Tarn Moor, Orton, Westmorland; Widdybank Pastures, Upper Teesdale; and the Whitlaw Mosses on the Selkirk/Roxburgh border.

Constant species. The following species are of constant occurrence in all community-types:

Carex panicea
Carex lepidocarpa
Juncus articulatus
Pinguicula vulgaris
Triglochin palustris
Eleocharis quinqueflora
Bryum pseudotriquetrum
Campylium stellatum
Cratoneuron commutatum
Drepanocladus revolvens
Riccardia pinguis

The following are constant in all community-types except those of the most open flushed habitats:

Briza media	Succia pratensis
Carex dioica	Valeriana dioica
C. hostiana	
C. pulicaris	Acrocladium cuspidatum
Equisetum palustre	
Molinia caerulea	
Potentilla erecta	

Differential species: The Northern mires group can be separated from the Schoenus-Juncus subnodulosus mires by the occurrence of Carex dioica and Eleocharis quinqueflora and the absence of Anagallis tenella, Juncus subnodulosus and Schoenus nigricans.

From these Northern mires seven community-types have been distinguished. However, it must be emphasised that as only 39 lists have been made from this type of vegetation, and in the light of their wide floristic variation, the community-types can only be regarded as tentative.

The noda recognised are:

(a) Scorpidium nodum and the Schoenus-Scorpidium nodum.

(b) Sesleria-Festuca ovina nodum.

(c) "inops" nodum.

(d) Schoenus-nigricans-dominated stands.

(e) Filipendula ulmaria nodum.

(f) Chara vulgaris - Saxifraga aizoides nodum } From Upper Teesdale

(g) Bartsia alpina }

6.4.11. Scorpidium and Schoenus-Scorpidium noda.

Characterising species: Scorpidium scorpioides.

Description: A community of open flushes on gentle slopes irrigated by calcareous water (pH 6.5-8.0). The substratum is skeletal: sometimes a primitive peaty gley but more usually open stony clays and calcareous muds with the accumulation of organic matter being restricted to areas away from the main water flow. Such sites can be small and localised or they can form large complexes with open flushes and runnels intercalated between "islands" of peats and rocks.

Characteristic of the group is the open nature of the vegetation (cover = 20-60%) and a variable number of species (which is related to the degree of cover). In the open runnels bryophytes are prevalent with Scorpidium scorpioides, Cratoneuron commutatum, Drepanocladus revolvens and Riccardia pinguis. Bryum pseudotriquetrum, Campylium stellatum and Philonotis calcarea also occur and in the flushes above Great Close mire, Malham, Moerkia flotoviana and Priessia quadrata were recorded. Chara vulgaris can sometimes be abundant.

Angiosperms are not always well developed. Carex lepidocarpa and Juncus articulatus tend to predominate and Carex flacca and C. panicea are common. Other species can include Eriophorum latifolium, Parnassia palustris, Pinguicula vulgaris, Sagina nodosa and Triglochin palustris. Primula farinosa grows in the sites in N. England and Equisetum variegatum was also found in some of these.

In the flushes fringing the Tarn Moor wetland complex in Westmorland (see HOLDGATE, 1955a) Schoenus nigricans is an

important component of the vegetation. In the open runnels between the tussocks Eleocharis quinqueflora is frequently abundant. Schoenus, however, shows a marked tendency to be absent from the wettest parts where Carex lepidocarpa usually predominates. In drier parts it is more frequent and the firm, low tufts form a series of hummocks, separated by muddy hollows. In these latter, Scorpidium, Eleocharis etc. persist, and on the peaty hummocks plants such as Carex dioica, C. nigra, Calluna, Drosera rotundifolia, Mclinia caerulea, Potentilla erecta and Valeriana dioica are able to come in. Stands such as this constitute the Schoenus-Scorpidium community-type.

6.4.12. Sesleria-Festuca ovina nodum.

Characterising species-group: Sesleria caerulea, Festuca ovina, Leontodon autumnalis, Campanula rotundifolia.

6.4.12.1. The habitat: 'calcareous marshes'. This community-type was recorded from areas of "calcareous marsh" in the Craven district of West Yorkshire particularly from parts associated with the Great Close Mire and Ha Mire complexes near Malham. These are rather extensive mire basins developed over glacial drift at about 1,250 ft. Irrigated with highly calcareous water (pH 7.5-8.0) they contain various types of wetland vegetation (see SINKER, 1960). In particular, however, there is extensive development of 'calcareous marsh', especially on the gently sloping areas where flushes and

springs maintain wet conditions throughout the year. It is composed of hummocks of stony clay separated by an intricate network of runnels and wet depressions. Similar areas have been described from Upper Teesdale as "turfy marshes" (PIGOTT, 1956), produced where springs are cutting back into the glacial drift. The open nature and hummocky structure appears to be related mainly to the influence of cattle trampling causing the disintegration of an otherwise continuous turf. Thus, the ontogeny of the hummocks does not seem to be by accretion within the marshes but rather they represent residual portions of turf.

On a smaller scale similar flushed areas occur locally on the slopes of some small stream valleys. There are examples of this from the Malham area - by Thoragill Beck north of the Tarn on a steep (10^{o}-40^{o}) slope at 1,150 ft; and by Gordale Beck south-east of the Tarn on a 40^{o} slope at 1,200 ft. Here there is not the pronounced hummocks of the more typical calcareous marsh, but instead solifluction effects, probably accentuated by trampling, produce ridges across the slope, which present a similar range of micro-habitats.

6.4.12.2. Description: The community may be readily resolved into the two main components of runnel and hummock but there is much intergradation between the two. In the wetter areas, Carex lepidocarpa predominates with large amounts of Juncus

articulatus and some Eleocharis quinqueflora and Triglochin palustre. Mosses are abundant: especially Cratoneuron commutatum (mainly var. falcatum) and Drepanocladus revolvens. On the slightly elevated areas, around the bases and on the sides of the hummocks, there are many other species such as Bryum pseudotriquetrum, Campylium stellatum, Fissidens adianthoides and Riccardia pinquis. Others include Cratoneuron filicinum, Moerkia flotoviana, Priessia quadrata and Solenostoma triste.

The hummocks, in contrast, support a flora more reminiscent of calcareous grassland. Tufts of Festuca ovina can sometimes form an almost closed turf with other grasses such as Molinia caerulea, Briza media and, less frequently, Agrostis stolonifera and Sesleria caerulea. With these is a rich associated flora of sedges and herbaceous dicots. Carex dioica, C. flacca, C. hostiana, C. panicea are all abundant. Carex pulicaris is somewhat less frequent. The herbs include species of grassland - Campanula rotundifolia, Euphrasia nemorosa, Linum catharticum, Leontodon autumnalis, L. taraxacoides - as well as wetland plants like Parnassia palustris and Pinguicula vulgaris. The moss Ctenidium molluscum is often abundant in these situations.

There is a wide variety of additional species. These include two of the cotton grasses, Eriophorum angustifolium and E. latifolium. Primula farinosa is often abundant and Selaginella selaginoides is regularly found. Further in

the Malham area Bartsia alpina, Equisetum variegatum and Rhinanthus sphadiceus have been recorded in this community.

In one of the sites by Thoragill Beck there are a few tufts of Schoenus nigricans. These are rather stunted and sheep grazed but, nonetheless, seem to fruit successfully. At 1,150 ft. this must represent one of the highest localities for this species. The plant is generally restricted to sites below 600 ft (SPARLING, 1968), but it grows abundantly at 900 ft on Tarn Moor near Orton, Westmorland.

The rich floristics of these stands seem to be related to their open nature of the habitat with factors such as water erosion, solifluction, frost action and trampling, helping to conserve a dynamic instability.

6.4.13. typical nodum.

Characterising species: None. Distinguished from the other communities by the absence of differential species.

This group is represented by only two samples both from flushed slopes in different parts of the Whitlaw mosses, and because of its largely negative characterisation, must only be regarded as a tentative unit.

Although this is nominated as an "inops" group both the stands included here are rich in species, with more than 40 species in each. They show close similarities both to the turfy marshes of group 6.4.12. and to the Filipendula ulmaria group of 6.4.14 and to the other community-types in this Northern

calcareous mires Group. However, Eriophorum latifolium and Parnassia palustris are both missing and Ctenidium molluscum, abundant in some of the other groups, is only sparsely represented. From the turfy marshes of Northern England it is additionally distinguished by the absence of species such as Sesleria caerulea and Primula farinosa; from the Filipendula ulmaria group of 6.4.14. it is distinguished by the absence of the appropriate differential species.

It is essentially a community of flushed muddy slopes. The vegetation cover amounts to c. 80% with areas of bare mud and small runnels. Mosses, particularly Cratoneuron commutatum and Drepanocladus revolvens are abundant and Chara vulgaris also occurs. The phanerogam cover is essentially a low growing (25 cm) sward dominated by sedges with much Carex lepidocarpa, C. flacca, C. panicea, C. hostiana and Eleocharis quinqueflora.

6.4.14. Filipendula ulmaria nodum.

Differential species: Filipendula ulmaria, Anthoxanthum odoratum, Lotus uliginosus, Luzula multiflora, Mnium longirostrum.

Description: A species-rich community of flushed peaty-gleys which, on the basis of floristic composition and abiotic status, seems to be transitional between calcareous mire and wet grassland. This transition is reflected within the stands themselves where undulations in the surface produce a

differential representation of the species present.

The vegetation cover is more or less continuous. Grasses and sedges predominate with an abundance of associated herbs. Molinia caerulea, Carex hostiana, C. lepidocarpa and Juncus articulatus are all major components of the rather short turf. Other sedges include C. flacca, C. nigra, C. panicea and C. pulicaris; other grasses are Anthoxanthum odoratum, Agrostis stolonifera, Briza media, Holcus lanatus and, occasionally, Sieglingia decumbens and Festuca ovina.

The associates include species found generally in wet areas - Angelica sylvestris, Cardamine pratensis, Cirsium palustre, Cerastium holosteoides, Filipendula ulmaria, Lotus uliginosus and Luzula multiflora - together with more characteristically mire species - Eriophorum angustifolium, E. latifolium, Menyanthes, Parnassia palustris, Pedicularis palustris and Pinguicula vulgaris. Mosses are well developed: Ctenidium molluscum tends to predominate but with it there are Acrocladium cuspidatum, Bryum pseudotriquetrum, Campylium stellatum, Cratoneuron commutatum, Drepanocladus revolvens, Fissidens adianthoides and Riccardia pinguis.

This community-type is frequently represented on the slopes surrounding the mire basins of some of the Whitlaw Mosses in S. Scotland. Here various additional species have been recorded: Euphrasia nemorosa, Selaginella selaginoides and Salix repens with more acidophilic plants (e.g. Carex echinata,

Juncus acutiflorus, Erica tetralix). In one flushed area Camptothecium nitens is abundant.

A rather different community has been recorded from a small peaty spring mire near Grassington, W. Yorks. This is on drift associated with the Carboniferous limestone and, although it has the characterising species of this group, it represents a rather different development with species such as Schoenus nigricans, Gymnadenia densiflora, Polygala vulgaris and Primula farinosa. Equisetum variegatum also occurs.

6.4.15. "Turfy marshes" of Widdybank Pasture, Upper Teesdale.

The community-types considered here are composed of samples that were all taken from areas of calcareous marsh on the eastern slopes of Widdybank Fell, Upper Teesdale. This area - known as Widdybank pastures (see BRADSHAW & CLARK, 1965) - is an extensive tract of grassland developed over calcareous drift at an altitude of between 1,250 ft and 1,400 ft. There are many springs and areas of water seepage and this has given rise to a variety of types of wet habitats, ranging from slightly flushed grassy slopes, through open flushes and calcareous marsh (also on the slopes) to wet valley bottom areas in the lower parts of the Pastures, where there is restricted water throughflow and the accumulation of modest deposits of peat.

Here attention will be given to the areas of open calcareous marsh. PIGOTT (1956) has described in detail

one such area from the Pastures using the name "turfy marsh". Like the "calcareous marshes" from Great Close Mire in the Craven (see 6.4.12.) this "consists of a patchwork of hummocks scattered over a more or less smooth sloping expanse of sparsely turf-covered calcareous, muddy gravel" (PIGOTT, loc. cit.) created largely by trampling around the springs and seepage areas. Similar "turfy marshes" occur in places on the top of the fell where the vegetation has been described by JONES (1973), but they are more widespread in the Pastures. Here they form the locus for many species that are rare or absent from the surrounding grassland, in particular Bartsia alpina, Juncus alpinoarticulatus, Kobresia simpliciuscula, Saxifraga aizoides and Tofieldia pusilla.

Vegetation. In many respects the vegetation of these sites parallels that of similar calcareous marshes elsewhere in Northern Britain. They are distinguished mainly by the presence of some of the plants of the "Teesdale assemblage" (see BRADSHAW, 1970), together with the absence of certain lowland species.

Species constant for the marshes are:

Carex lepidocarpa	Pedicularis palustris
C. panicea	Pinguicula vulgaris
Equisetum palustre	Triglochin palustris
Eleocharis quinqueflora	
Eriophorum latifolium	Bryum pseudotriquetrum
Juncus articulatus	Cratoneuron commutatum

Two basic vegetation units have been recognised. These have been established through re-arrangement of the species-

relevé matrix by hand and numerical techniques have not been involved but there seems no reason to doubt that this has produced a satisfactory sub-division.

6.4.15.1. Chara vulgaris group. This is composed of samples made from the most open flushed areas of the marshes. In the majority of sites the open gravelly slopes form a complex mosaic with the hummocks and the two have then been included within the same sample. In places, however, the open areas are quite extensive and it has been possible to describe them independently. This group is, therefore, mainly distinguished by the absence of the hummock species but, additionally, Chara vulgaris can be abundant. Some of these flushed muds and gravels have very few plants at all and sometimes just isolated tufts of Carex lepidocarpa and spikes of Triglochin palustris can only be found. The samples included here, however, all had a richer flora with the constants listed above all fairly well represented. The most abundant species is usually Carex lepidocarpa, but Juncus articulatus can be locally frequent and, occasionally, in muddier location, Carex rostrata. The plants of the nearby hummocks are usually absent but occasional specimens can occur where there is a slight accumulation of mud etc. and Primula farinosa has sometimes been found in this context.

Clearly, this community is very similar to the open

flushes of the calcareous marshes of Great Close Mire etc. and the floristic affinities with the Scorpidium nodum established from these areas (6.4.11.) are substantial. The main points of distinction appear to be the occurrence of Saxifraga aizoides within the Widdybank flushes, together with the relative rarity of Scorpidium scorpioides.

6.4.15.2. Bartsia alpina group. This is the group of the "turfy marshes" proper and is readily distinguished from the Chara-group by a large number of differential species:

Briza media
Carex dioica
C. flacca
C. hostiana
C. nigra
C. panicea
C. pulicaris
Dactylorhiza incarnata
Eriophorum angustifolium
Festuca ovina
Molinia caerulea
Linum catharticum
Potentilla erecta
Primula farinosa
Selaginella selaginoides
Succisa pratensis
Sesleria caerulea
Valeriana dioica

Acrocladium cuspidatum
Campylium stellatum
Cratoneuron filicinum
Fissidens adianthoides
Leiocolea muelleri
Riccardia sinuata

Also, the following species occur:

Bartsia alpina
Carex capillaris
Kobresia simpliciuscula
Tofieldia pusilla

These are largely restricted to the "turfy marshes" in the Pastures. With them occur a variety of other species.

This community shows an obvious division into the components of muddy hummock and gravelly flushes. In the latter the species of the Chara-group occur, sometimes with Equisetum variegatum. The vegetation of the hummocks depends

upon their size and stability. Some of the largest hummocks near the edges of the marshes may support a grass turf very similar to that of the surrounding grassland with much Festuca ovina and Sesleria caerulea but nearer the centre, where the hummocks are often less distinct, more trampled and wet a variety of plants can be found. Both Festuca ovina and Sesleria can still occur but often Carex lepidocarpa predominates. Other species present here in abundance are Molinia caerulea, Carex panicea, Carex hostiana and, sometimes, C. nigra. Eriophorum latifolium is also sometimes plentiful. These rather open hummocks of mud, elevated above the main scour of flowing water, also provide the main locale for Bartsia alpina, Carex capillaris, Tofieldia and Kobresia. Other plants also present here include Parnassia palustris with Juncus alpinoarticulatus and J. kochii. Sometimes Gentiana verna and Galium boreale can also be found.

The moss of the driest hummocks - and also of some of the damper hollows - is Ctenidium molluscum. Elsewhere, especially on the slightly lower muds and gravels, a variety of other species can grow. These include the constant Acrocladium cuspidatum, Campylium stellatum, Cratoneuron commutatum, Drepanocladus revolvens with the acrocarpous Bryum pseudotriquetrum and the hepatics Riccardia pinguis and R. sinuata. In addition, a number of other species occur occasionally: Mnium pseudopunctatum, M. seligeri, Moerkia flotoviana, Pellia endiviifolia, Philonotis calcarea, Preissia quadrata, Soenostoma triste. On the driest hummocks, and sometimes on

large boulders, Rhacomitrium languinosum can appear.

Thus, despite the relatively low cover (with mosses contributing 10-30% and phanerogams up to 80%, but often only about 50%) these stands are species-rich. Many of the marshes have in excess of 50 different species.

This community is not only confined to the "turfy marshes". At least one area of hillside is known (S.1909) with very similar floristics but where the vegetation cover is not disintegrated into hummocks. This is a strongly flushed area which actually adjoins a turfy marsh. As well as the characteristic "turfy marsh" species it contains others such as Juncus acutiflorus, J. squarrosus and Luzula multiflora, which are more typical of the surrounding less flushed grassland. Carex hostiana is the dominant, and the vegetation cover was estimated at 95%. Sphagnum palustre occurs, mainly along the edges of a small stream which flanks the area.

These "turfy marshes" of Widdybank Pastures are not well represented elsewhere on the fell. There are only a few comparable examples on the west-draining slopes above Cow Green and some of the most characteristic plants - Bartsia alpina, Eriophorum latifolium, Parnassia palustris and Pedicularis palustris - appear to be largely absent here.

Interestingly, Schoenus nigricans is absent from these marshes which are perhaps above the altitudinal limit of the plant. However, near Orton in Westmorland, a small mire supports a community which is in some respect intermediate

between these sites and lower-level Schoenus flushes. Here (see WILSON, 1938) there is Bartsia alpina, Carex capillaris and Polygala amara growing with Schoenus nigricans and Epipactis palustris.

6.4.16. Schoenus nigricans-dominated stands.

A rather distinct group composed of only two releves both made from small spring mires associated with Coral ragstone near Rievaulx in the North York moors. Schoenus nigricans predominates with Juncus acutiflorus and Molinia caerulea. There are various of the smaller sedges: Carex dioica, C. lepidocarpa, C. nigra, C. panicea and C. pulicaris. Mosses are quite well developed with much Cratoneuron commutatum and Acrocladium cuspidatum. Primula farinosa occurs and also Pinguicula vulgaris and Parnassia palustris.

There are a number of small spring areas of similar type near Rievaulx, but many of them do not contain Schoenus but tend to be dominated by Juncus acutiflorus alone.

Of particular interest is the different nature of these Schoenus communities to those at Dalby Bog (see 6.4.3.3.), which is also associated with Coralline deposits 20 miles further east.

6.4.17. Syntaxonomy.

There have been a variety of Associations described by Continental phytosociologists to contain the rather variable

vegetation of calcareous flush communities. These include the Parnassio-Caricetum pulicaris (Oberd.57.) Görs 63 - a lowland Association with much Carex demissa and C. pulicaris; the Juncetum alpino-articulati Philippi 60 - which WESTHOFF & DEN HELD (1969) describe as a pioneer community of wet areas in clay-pits with Juncus alpino-articulatus ssp. arthrophyllus as a character species and an optimal development of Equisetum variegatum. From montane regions the Caricetum davallianae Koch 28 has often been described. This essentially contains spring-fen communities dominated by Carex davalliana. Floristically, such a unit is heterogeneous and recently MORAVEC (1966) has attempted to sub-divide it into a number of more uniform Associations. Communities with much Eleocharis quinqueflora have been placed into a Scirpetum pauciflorae Issler 33 (see 6.4.6.) or as a sub-association of the Schoenetum nigricantis KOCH 26, which itself can be developed in calcareous flushes.

Within the British Islands some of the upland and northern examples of calcareous mires and flushes have been relatively well described (that is, compared with material from lowland England and Wales). From Scotland both McVEAN & RATCLIFFE (1962) (also RATCLIFFE, 1964) and BIRKS (1969, 1973) have described a Carex panicea— Campylium stellatum community and a species poor mire vegetation dominated by Schoenus nigricans. McVEAN & RATCLIFFE also distinguished a Cariceto-Saxifragetum

aizoides of open calcareous flushes, but this was later split by BIRKS (1969) into a low altitude Eriophorum latifolium-Carex hostiana Ass. and a montane Carex-Saxifraga aizoides nodum.

SHIMWELL (1968), with rather meagre data, united flush communities dominated by Carex lepidocarpa, C. hostiana or C. dioica into a new Association, the Caricetum lepidocarpae-hostianae Shimwell 68, giving C. lepidocarpa and C. hostiana the status of character species, though they probably are not - as they have a wide sociological amplitude within rich fen vegetation. Such a unit would, nonetheless, seem to be of some utility for accommodating a number of calcareous flush vegetation types.

However, a more interesting approach was adopted by JONES (1973), who decided to combine a large proportion of the described "Associations" of calcareous flushes and mires into one rather large Association, the Pinguiculo-Caricetum dioicae Jones 73. This included not only her own vegetation-units from Widdybank Fell in Upper Teesdale, but also SHIMWELL's Caricetum lepidocarpae-hostianae and some community-types recognised from Scotland by McVEAN & RATCLIFFE (1962) and BIRKS (1969).

The basic elements of JONES' Association are as follows:

Association PINGUICULO-CARICETUM DIOICAE Jones 73.

Sub-ass. molinietosum (= Caricetum lepidocarpae-hostianae molinietosum Shimwell 68)

from flushes on the Carboniferous limestone in N. England; one of the lowest level sub-communities.

Sub-ass. equisetosum variegati

only from Widdybank Fell; diff.sp. = Equisetum variegatum

Sub-ass. thalictro-saxifragetosum (= Carex-Saxifraga aizoides nodum Birks 69)

montane community; diff.spp. = Thalictrum alpinum with Juncus triglumis, Saxifraga aizoides etc.

Sub-ass. eleocharetosum

Diff.spp.: Carex nigra, C. demissa, Eleocharis quinqueflora, Equisetum palustre, Eriophorum angustifolium, Juncus kochii.

Wide-ranging in floristics and habitat; from sea level to 2,650 ft.; contains several sub-communities into which stands from Carex panicea-Campylium stellatum McVean & Ratcliffe 62 and Eriophorum latifolium-Carex hostiana-Ass.Birks 69, have been re-located.

6.4.18. Characterising species. JONES suggests the following plants to characterise the Association: Carex dioica, C. lepidocarpa, Kobresia simpliciuscula, Tofieldia pusilla and Triglochin palustris as character species. And Carex pulicaris and Plantago maritima as differentials. Some comments seem appurtenant: the Kobresia and Tofieldia can probably be maintained as character species though in Britain both - but

especially the former - are only of local diagnostic value. However, Triglochin palustris can in no sense be given this status as it is widespread in many wetland types from rich fen to wet meadow. Similarly, Carex lepidocarpa is widespread in other types of calcareous mire. Carex dioica is a more tenable character species. Although it most certainly occurs in lowland examples of rich fen, it is not very frequent (though partly due to extinction); it is, however, still a frequent component of some of the mixed mire types (6.4.2.). Carex pulicaris cannot be regarded as a good differential being present in lowland community-types, particularly in the Schoenus mires of Anglesey. Similarly, Plantago maritima also occurs in the Anglesey sites. Thus, concertant with many other wetland community-types there seems a lack of good diagnostic species for this Association.

There are, however, a number of species constant in the unit and, although many of these are diagnostic species for higher syntaxa within the Parvocaricetea, a case can be made for regarding the Pinguiculo-Caricetum dioicae as a coherent unit. It would, in fact, seem likely that this community-type will ultimately have to be divided into a number of more precisely defined Associations, if only on utilitarian grounds. But for the present it would seem reasonable to leave it as a single unit until additional data are available to provide a comprehensive basis for segregation into better defined floristic types.

6.4.19. Syntaxonomy of the noda.

The colligation of the samples from the Northern mires into a single major group of the Information Analysis hierarchy points both to their similarities one with the other and also their fundamental distinctness from the other types of calcareous mire. The group contains both lowland (300 ft) and upland (1,250 ft) examples, though these are readily distinguished as the internal divisions. Clearly these communities do not belong to the Schoeneto-Juncetum subnodulosi in the sense recognised above (6.4.8.). On the other hand, however, most of the communities show close similarities with some parts of the Pinguiculo-Caricetum dioicae Jones 73 and most stands contain many of the diagnostic species of that group.

It seems possible to allocate most of the community-types to this Association. A possible exception, however, may be in the open flush communities of the Scorpidium nodum and the Chara vulgaris-Saxifraga aizoides nodum. These are species-poor groups where many stands lack the characteristic species of the Association, though most certainly showing strong spatial and floristic connections with it. They could, thus, be classed as a species-poor version of the Association; or they could be referred to another syntaxon - perhaps related to the Scirpetum pauciflorae Issler 33. However, with the small amount of material available, their placement has not

been resolved and they will be left as nodal groups of uncertain status.

Another problem is posed by the Schoenus-dominated stands of 6.4.16., which lack a number of species shared by the other communities described here such as Eriophorum latifolium, Pedicularis palustris, Drepanocladus revolvens, Riccardia pinguis etc. These could be regarded as Schoenus-sociations, characterised by the dominance of Schoenus nigricans, or as a species-poor version of the Pinguiculo-Caricetum. Because a number of species of the Association, including Pinguicula vulgaris and Carex dioica do occur in at least some stands of the nodum, the latter course is preferred, but clearly more data are required to clarify the situation.

The Filipendula-nodum presents a third problem, in that it contains a whole series of wet grassland species not found in the other noda, nor, indeed, in JONES' Association (e.g. Filipendula ulmaria, Anthoxanthum odoratum, Cerastium holosteoides, Prunella vulgaris etc.). Nonetheless, there is also a full complement of Caricion davallianae species and strong floristic affiliations to the Pinguiculo-Caricetum. In the absence of data to clarify the relationships between base-rich mires and flushed grasslands, the status of this nodum is not evident, but if it is to be placed into the Pinguiculo-Caricetum then clearly it must be as an independent sub-association, the filipenduletosum. For convenience, this course is adopted here. The subassociation thus constitutes

a lowland representative of the Pinguiculo-Caricetum with a complement of Molinio-Arrhenatheretea species and, because of this, with an enhanced affinity to some of other lowland representatives of base-rich mire (see Chapter 7).

The remaining noda have greater parity with the communities included by JONES in her Association. However, in attempting to allocate them to her several subassociations etc. various difficulties are met. Particular problems are created by a group of three species, Molinia caerulea, Eriophorum latifolium and Succisa pratensis. These are constant species of the molinietosum subass. but they also occur within the eleocharetosum. Here, however, they define a Succisa subvariant of a Saxifrago-Scorpidium variant of the subassociation; this variant being defined by Scorpidium scorpioides, Saxifraga aizoides, Blindia acuta, Erica tetralix and Carex echinata. However, the noda considered here contain both the species of the eleocharetosum subass. and of the Succisa subvariant, but not of the intervening Saxifrago-Scorpidium variant, (i.e. the communities show good floristic relationships to both the molinietosum and the eleocharetosum). Thus, to accommodate them some modification or addition to JONES' scheme is required. A variety of alternatives are possible. However, it has been noted that in some communities of the Succisa sub-var. some of the Saxifraga-Scorpidium differentials are not well represented. It is also evident that the eleocharetosum is a unit of wide floristic

compass with a diverse range of community-types. Thus, it is considered appropriate to remove the communities with Molinia, Succisa and Eriophorum latifolium from the eleocharetosum and to place them into the molinietosum, where these species also occur. Here they may be regarded as forming an Eleocharis variant to distinguish them from the rather species-poor community (typical variant) originally included in this subassociation by JONES. By this scheme the molinietosum is defined by Molinia caerulea, Succisa pratensis and Eriophorum latifolium on differentials. Eleocharis quinqueflora, Carex nigra, Eriophorum angustifolium and Carex demissa may or may not occur. They are, however, constant species of the eleocharetosum - which does not have specific differentials other than the species of its sub-communities. Clearly, the re-arrangement is partly a matter of personal preference, but it is considered that its merits are, (a) that it gives greater parity to the eleocharetosum and molinietosum in terms of the number of different community-types that they contain - which clearly makes for syntaxonomic simplicity and convenience; and (b) that it gives expression to the prominence of Molinia caerulea as a very widespread and abundant component of calcareous mires belonging to the Pinguiculo-Caricetum in Northern England. Further work is required, however, and it seems probable that, with the acquisition of more data, it will prove profitable to recognise more than one Association.

For the present, however, it is proposed just to expand the compass of the Pinguiculo-Caricetum dioicae to incorporate a wider variety of vegetation types, and also to re-organise its internal structure. The following scheme is presented:

PARVOCARICETEA Den Held & Westhoff 69
TOFIELDIETALIA Prsg. apud Oberd. 49
CARICION DAVALLIANAE Klika 34

Pinguiculo-Caricetum dioicae Jones 73 em.

molinietosum (Shimwell 68) Jones 73 em.

typical var. (inc. Caricetum lepidocarpae-hostianae molinietosum Shimwell 68)

Schoenus sub-var. (6.4.16.)

Eleocharis var.

Schoenus sub-var. (6.4.11. p.p.)
Sesleria sub-var. (6.4.12.)
(= ' calcareous marshes' Sinker 60)
Bartsia alpina sub-var. (6.4.15.2.)
(= 'turfy marshes' Pigott 56 p.p.)
typical sub-var. (6.4.13.)

eleocharetosum Jones 73 em.

typical var.
Saxifraga-Scorpidium var. em.

equisetosum variegati Jones 73

thalictro-saxifragetosum Jones 73

filipenduletosum subass. nov. (6.4.14.)

This Association thus encompasses both lowland and upland examples of calcareous mire in Northern Britain. It might also be possible to place some communities from southern Britain here as well, including perhaps those of the Eriophorum

latifolium variant of the typical subassociation of the Schoeneto-Juncetum subnodulosi.

6.4.20. Related community-types.

Related community-types have been described from Ireland. BRAUN-BLANQUET & TÜXEN (1952) recognised a Schoenus nigricans-Cirsium dissectum Association, which shows considerable floristic affinities to some of the Schoeneto-Juncetum subnodulosi communities. From the Burren, IVIMEY-COOK &

PROCTOR (1966) described a community with the same name but rather different floristics. They also mention Schoenus-flushes with much Schoenus nigricans and Molinia caerulea and some Sesleria caerulea.

A very different community also with Schoenus nigricans and Sesleria has been seen on the Burren during this survey:

6.4.20.1. Schoenus nigricans-Sesleria caerulea community

Included under this head are some rather curious stands of vegetation containing Schoenus nigricans recorded from the Burren in Co. Clare.

The locality was a series of south-facing eroding calcareous banks at about 200 ft alongside the R. Caher. On the steep (70^{o}), dry slopes there has developed a more or less closed vegetation cover composed of dense populations of Schoenus nigricans. Sesleria caerulea and Molinia caerulea are also abundant, but there are few other species: Thymus drucei, Rosa pimpinellifolia, Rubia peregrina, Geranium sanguineum and occasional plants of Arctostaphylos uva-ursi. There are a few bryophytes, mainly Tortella tortuosa and Fissidens crispus.

At the top of the slope the community grades into a heavily grazed Sesleria-dominated community. The grazed transition zone also contains Schoenus, of about 20% cover, with a fascinating assemblage of plants. The Molinia,

Rubia and Rosa pimpinellifolia of the slopes are largely absent and instead the turf is composed mainly of Sesleria caerulea with much Carex flacca and Dryas octopetala. Thymus druce and Antennaria dioica are both abundant. Other members of this assemblage include Gentiana verna, Hypericum pulchrum, Lotus corniculatus, Plantago lanceolata, Orchis mascula and, less frequently, Carex pulicaris, Calluna vulgaris, Hieracium pilosella and Arctostaphylos. The main mosses are Hypnum cupressiforme and Pseudoschleropodium purum.

Clearly this cannot be regarded as a wetland community but it is included here because of its intrinsic interest. The growth of Schoenus in such relatively dry conditions is concordant with the observations of ALLORGE (1937) and ZWILLENBERG & DE WIT (1952).

From Scotland McVEAN & RATCLIFFE (1962) and BIRKS (1973) have described a mire community strongly dominated by Schoenus nigricans. This has similarities with the Eriophorum latifolium-Carex hostiana Association Birks 69, which itself contains plentiful Schoenus. Here, however, Schoenus predominates and the stands are floristically poorer. The diagnostic species for the Pinguiculo-Caricetum dioicae are absent from many of the stands and there is a greater preponderance of more acidophilic species, e.g. Carex curta, C. demissa, Narthecium ossifragum, Potamogeton polygonifolius and, on Skye, Rhyncospora alba. In the moss layer Campylium stellatum

and Scorpidium scorpioides are constant often with Sphagnum subsecundum. These mires usually have a pH of greater than pH 6.5 and can be as high as pH 8. JONES (1973) did not include them within the Pinguiculo-Caricetum and, although perhaps those richer examples with the greatest similarities to the Eriophorum latifolium-Carex hostiana-Ass could be thus placed, it does seem best to leave them as an independent unit. Their phytosociological placement remains to be established. Also, their relationship to the Schoenus-Rhyncospora stands of S.W. England could be usefully clarified.

SPENCE (1970) has described a Schoenus nigricans-Molinia caerulea sociation from the Shetland Islands with Plantago maritima and Armeria maritima. HILLIAM and LEWIS (pers. comm.) have reported a similar community from a sub-maritime location on Unst.

Calcareous mire with Schoenus can develop in coastal dune-slacks (RANWELL, 1961). There is often a rich variety of associated species - both mire and maritime. A stand at Gupton Burrows, Pembrokeshire, has Schoenus growing with Anagallis tenella, Carex hostiana, C. lepidocarpa, C. pulicaris, Dactylorhiza spp., Epipactis palustris and Juncus subnodulosus. Similar stands occur elsewhere around the Welsh coast.

The following stand was also recorded from a maritime location:

6.4.20.2. Schoenus nigricans-Triglochin maritima stand.

A curious example of a stand with Schoenus has been noted from beneath the sea-cliffs along the coast of Kircudbright. Here a small, peaty flush is developed just above the shingle beach. The upper parts are largely dominated by Juncus subnodulosus but at the junction with the shingle a rather open community is developed with much Juncus subnodulosus and Molinia caerulea and with some Schoenus. There is an unusual assemblage of associates including the rare grass, Hierachloë odorata, mire species such as Anagallis tenella, and coastal plants like Triglochin maritima. The lower edge of the mire is only just above the level of spring tides and strands of (dead!) Fucus vesiculosus occur scattered within it.

The releve made is listed below:

Ravenshall Point, Kirkmabreck, Kirkcuds. NX 525522

Altitude: sea level

Cover: moss: 10% herb: 70% Total: 70%

Juncus subnodulosus	2,3	Juncus articulatus	+
Molinia caerulea	2,3	Lotus corniculatus	-
Schoenus nigricans	1,1	Plantago maritima	+
		Potentilla anserina	+
Anagallis tenella	+	P. erecta	+
Angelica sylvestris	+	Primula veris	+
Armeria maritima	+	Oenanthe lachenalii	+
Carex distans	+	Rhinanthus minor	+
C. flacca	1,1	Samolus valerandii	+
C. panicea	+	Succisa pratensis	+
Centaurium eryhtrae	+	Taraxacum sp.	-
Crithmum maritimum	+	Triglochin maritima	+
Cochlearia sp.	+	Vicia cracca	+
Festuca rubra	+	Acrocladium cuspidatum	+
Galium palustre	+	Bryum (pseudotriq ?)	+
G. verum	+	Ctenidium molluscum	1,1
Hierachloe odorata	+	Riccardia pinguis	+
Hydrocotyle vulgaris	+		

6.4.21. Synopsis of the communities of calcareous mires

PARVOCARICETEA Den Held & Westhoff 69

TOFIELDIETALIA Prsg. apud Oberd. 49

CARICION DAVALLIANAE Klika 34

Schoeneto-Juncetum subnodulosi ass. nov. (6.4.1.-6.4.9.)

- callunetosum (6.4.2.)
- cladietosum (6.4.3.2.)
- caricetosum rostratae (6.4.3.4.)
- leontodetosum (6.4.3.5.)
- typicum
  - Caltha var. (6.4.3.1.)
  - Typical var. (6.4.4.1.)
  - Briza media var. (6.4.4.2.)
- serratuletosum (6.4.5.)
  - Isolepis setacea var. (6.4.5.1.)
  - typical var. (6.4.5.2.)
  - Myrica gale var. (6.4.5.3.)
  - Cladium var. (6.4.5.4.)
- Dactylorhiza purpurella nodum (6.4.3.3.)

Pinguiculo-Caricetum dioicae Jones 73 em. (6.4.10.-6.4.19.

- molinietosum (Shimwell 68) Jones 73 em.
  - typical var. (inc. Caricetum lepidocarpae-hostianae Shimwell 68)
    - Schoenus sub-var. (6.4.16.)
  - eleocharis var.
    - Schoenus sub-var. (6.4.11. p.p.)
    - Sesleria sub-var. (6.4.12.)
      (= 'calcareous marshes' Sinker 60)
    - Bartsia alpina var. (6.4.15.2.)
      (= 'turfy marshes' Pigott 56 p.p.)
    - typical sub-var. (6.4.13.)
- filipenduletosum subass. nov. (6.4.14.)

Scorpidium nodum (6.4.11. p.p.)

Saxifraga aizoides-Chara nodum (6.4.15.1.)

6.5. Group 5. Carex diandra-lasiocarpa-rostrata communities - Table 5.

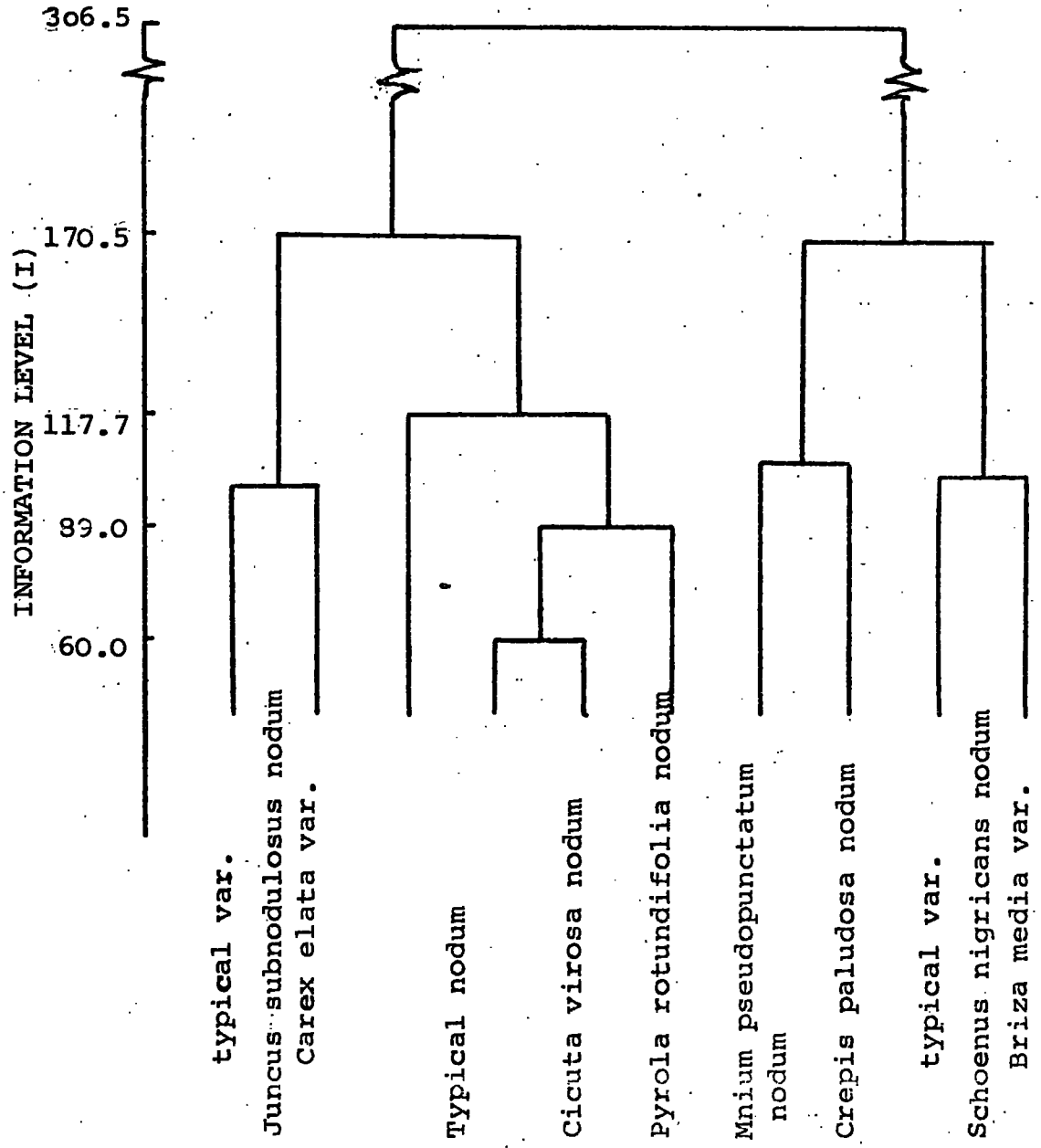
Included in this group are samples of vegetation in which the sedges Carex diandra, C. lasiocarpa and C. rostrata are important components. They were collected mainly from swampy areas of topogenous fen in small mire basins in various parts of the lowlands of N.W. England and S. Scotland.

The samples discussed here only include the richest developments of this type of mire and they most probably fall into the category of transitional rich fen in the scheme of DU RIETZ (1949; 1954). They are especially important in that they represent the main examples of topogenous rich fen in Northern Britain. In this area poor fen and transitional poor fen with Carex lasiocarpa and, especially, C. rostrata also occur, but these constitute a different series of community-types and have not been investigated here being outside the scope of the survey. However, until more information concerning these is available it will be difficult to confidentially delimit the richer types, or to establish their sociological placement.

The application of Information Analysis to the samples has led to the erection of seven well-defined groups. The contents of these remained stable when examined for the possibility of re-allocation of the stands. No "dustbin" groups were created but one sample was not a satisfactory member of any group and has been omitted from further

Fig. 6.5.I.

INFORMATION ANLYSIS OF CAREX DIANDRA-LASIOCARPA-ROSTRATA VEGETATION.



description.

The Information Analysis dendrogram is given on Fig. 6.5.1. Although the individual units are well defined floristically this does not apply to the higher order groupings. The seven "working units" will, therefore, be described for the most part without reference to their further hierarchical grouping but in a way that is most convenient for economy of description.

6.5.1. Carex diandra-lasiocarpa-rostrata communities

Introduction

The plant community-types detailed here are characterised by the prominence of cyperaceous species of medium height, viz. 40-80 cms. The main species are the lesser tussock-sedge, Carex diandra, the slender sedge, C. lasiocarpa and the bottle sedge, C. rostrata, though they may be present in varying proportions and C. diandra, in particular, may sometimes be completely absent. With these plants there is often much Eriophorum angustifolium and in some circumstances Schoenus nigricans can occur.

This preponderance of ~~of~~ graminoid monocots produces a rather drab, uniform vegetation of about 75 cms height. From a distance it can look rather like a grey-green expanse of low-lying grassland but on closer examination it is given a characteristic appearance by the long slender "hairs" of "die Fadensegge", the loose tufts of Carex diandra, the more

robust, glaucous shoots of Carex rostrata, and the glossy green leaves of Eriophorum angustifolium. Growing up with these there may be numerous spikes of Equisetum fluviatile. Rushes are not generally prominent except in certain community-types where Juncus subnodulosus is plentiful. In other circumstances J. articulatus and J. acutiflorus may occur but usually not in any abundance.

With the sedges various herbaceous dicots can be found. Caltha palustris, Cardamine pratensis and Lychnis flos-cuculi are fairly constant and Angelica sylvestris, Epilobium palustre and Valeriana officinalis are frequent as well. But particularly characteristic of this community-type is the constant - and often prolific - growth of Menyanthes trifoliata and Potentilla palustris. These can both form a dense ground layer,especially in the wetter parts, and in places may produce local societies.

Also rather characteristic of this type of vegetation is the development of an extensive moss carpet. This can often reach high cover values (50% +), but need not be rich in species. The genus Acrocladium is particularly represented. A. cuspidatum or A. giganteum are frequently the dominant species with occasional occurrences of A. cordifolium or even A. stramineum. Acrocladium giganteum seems to be especially typical of this type of fen.

In the wettest areas bushes are usually absent, but

elsewhere they can often be found - particularly Betula pubescens, Salix cinerea and S. pentandra (Alnus glutinosa has only been noted very occasionally) - and in places former herbaceous fen is passing into scrub.

This type of vegetation is well developed in some of the peat-filled basin mires of N.W. England and parts of S. Scotland. Irrigated by mesotrophic water (pH range 5.6-7.0) from springs and seepage areas these are sometimes very wet and swampy with shallow standing water in parts even during the summer. In such morasses this community-type can sometimes cover large areas. At drier sites similar conditions have sometimes become re-established in derelict peat-cuts and the community may be found there, but on a more localised scale.

In these very wet situations this type of vegetation often seems to develop as a mat floating, or semi-floating, over oozes of muds or re-deposited peat or even over open water. The process of raft-formation needs to be examined more thoroughly but it may well often commence with the development of a thin, but strong, raft composed of the interlocking rhizomes of Menyanthes trifoliata and sometimes the intertwined stems of Potentilla palustris. On this buoyant mat other species seem able to establish themselves. Carex rostrata gets a foothold, sometimes with swamp species such as Ranunculus lingua, but particularly characteristic

is the development of thick carpets of Acrocladium giganteum covering the rhizomes and stems, even when these remain immersed in shallow water throughout the year. Here, the moss can form loose, floating mats. Scorpidium scorpioides can also occur in similar situations, but has been observed only rarely.

With the accretion of the peat raft so that the surface is at or just above the water-level a number of additional species gradually become established, particularly on the moss carpet, including small herbaceous dicots like Epilobium palustre, Cardamine pratensis, Galium palustre, Myosotis scorpioides and Pedicularis palustris. This phase is the earliest in which Carex diandra has been observed, though C. lasiocarpa seems able to establish in more swampy conditions. In the moss carpet itself other species can also be found - Acrocladium cordifolium, Bryum pseudotriquetrum and Marchantia polymorpha.. Acrocladium cuspidatum also appears and on some of the more elevated rafts can become the dominant moss.

When the (now thick) floating raft is developed above the normal water level, this seems to represent the optimal stage for the Carex diandra-lasiocarpa community with both C. diandra and C. lasiocarpa abundant and a rich herbaceous flora. Mosses are still plentiful but in addition to the Acrocladia there can be others like Climacium dendroides,

Hylocomium splendens and Mnium affine.

The community does not always develop by means of a Menyanthes raft. In some peat cuts the initial stage would seem to be presented by stands of Equisetum fluviatile growing directly in the shallow water. This species is capable of growing even on unconsolidated oozes and the network of spreading rhizomes provide a base for Carex rostrata to establish itself. Here, however, it is not evident merely on casual inspection what the developmental sequence might be. In some cases the two types occur together. Menyanthes forms a raft floating on the water's surface; Equisetum fluviatile grows with it but is actually rooted in the substratum below.

In spring-fed kettle holes there is a tendency for the Carex diandra-lasiocarpa community to occur upon relatively thick peat in the central areas. Surrounding this is a very wet "lagg" which receives the inflowing water. This may be composed of various swamp types, with Menyanthes or Carex rostrata or Equisetum fluviatile as the dominant taxa. In the central parts, however, with the elevation of the substratum above the main influence of the minerotrophic water of the mire basin (except for occasional inundations), acidophilic species can come in. This may be observed at Nether Whitlaw moss, Selkirk. The centre of mire is separated from the sides of the basin by a narrow "lagg" of deep Carex rostrata swamp, which in places is floating. In

the central parts there are (treacherous) floating mats of wet Carex rostrata fen with Carex lasiocarpa and C. diandra, Menyanthes, Potentilla palustris etc. (and also the swamp species Cicuta virosa and Ranunculus lingua). In places, however, these give way to firmer mats of more acid peat which still have C. rostrata, C. diandra and C. lasiocarpa, but species such as Cicuta, Ranunculus lingua, and Hippuris vulgaris have gone and instead there is much Molinia caerulea and Carex curta. The moss layer is dominated by a carpet of Sphagnum squarrosum with some S. recurvum. Other mosses include Acrocladium stramineum, Aulacomnium palustre and Drepanocladus aduncus. In some of these places birch and willow scrub is developing. If these community-types represent the ontogenesis of the mire, they are clearly commensurate with the developmental scheme established by BELLAMY (1967; 1968).

Some of the Carex diandra-lasiocarpa stands are diminishing in extent as a result of bush colonisation, which presumably represents the natural succession of the community. Willows are mainly involved - S. cinerea and S. pentandra. Around isolated bushes the composition of the sedge community remains similar to that of the open mire. However, the sedges tend to be confined to the wetter areas away from the tree bases and in any case are overshadowed by Equisetum fluviatile and Filipendula ulmaria, both of which become more prominent. With the establishment of more closed conditions Geum rivale

comes in, often with much Climacium dendroides. These willow carrs, however, tend to remain rather open and many of the open mire species are able to persist, if only in the wetter hollows.

6.5.2. Constant species

The following are constant for all of the community-types:

Carex diandra
C. lasiocarpa
C. rostrata
Cardamine pratensis
Caltha palustris
Eriophorum angustifolium
Galium palustre
Menyanthes trifoliata
Potentilla palustris
Acrocladium cuspidatum
A. giganteum

The following are frequent in most community-types:

Agrostis stolonifera
Carex nigra
C. panicea

Agrostis stolonifera
Angelica sylvestris
Carex nigra
C. panicea
Cirsium palustre
Equisetum palustre
E. fluviatile
Epilobium palustre
Filipendula ulmaria
Galium uliginosus
Mentha aquatica
Molinia caerulea
Succisa pratensis
Valeriana dioica

Aulacomnium palustre

6.5.3. Typical nodum

Characterising species: None. Distinguished by absence of differentials.

Description: This is not a very uniform syntaxon but it contains samples characterised either by a general species poverty or by the absence of other samples with which they

could satisfactorily form a group. It seems likely that further data might permit a re-assessment of the contents.

The dominants are the three sedges, C. diandra, C. lasiocarpa and C. rostrata, though in some C. diandra is absent and in others only C. rostrata occurs. Acrocladium giganteum is constant with A. cuspidatum, Eriophorum angustifolium, Galium palustre and the other normal constants (see 6.5.2.).

The following range of communities are encompassed here:

6.5.3.1. Carex rostrata wet fen. A rather species-poor community-type dominated by Carex rostrata with Menyanthes and Potentilla palustris prominent and much Acrocladium giganteum. S.919 and S.983 are from Tarn Fen, Malham and Tarn Moor, Orton, respectively. The first contains Mnium pseudopunctatum and Mn. rugicum; the second is a more species-poor community developed over old peat cuts. Marchantia polymorpha is in both samples.

6.5.3.2. Carex lasiocarpa wet fen. (S.958) A species-poor stand of wet fen dominated by Carex lasiocarpa at Murder Moss, Selkirk.

6.5.3.3. "Typical" variant. This contains 4 samples, all made at Newton Reigny Moss, Cumberland. This site, which was once a deep swampy morass (HODGSON, 1898), has now substantially dried out, but there are still some good examples of Carex diandra-lasiocarpa mire containing the basic

complement of constant species (see 6.5.2.) and showing the typical community structure. One stand (S.941) is strongly dominated by Carex lasiocarpa but in the others more equal proportions of the main sedges prevail. Scattered plants of Carex limosa can still be found in some of the stands. In one place Schoenus nigricans is prominent but the sample cannot be assigned to the Schoenus-nodum because of the absence of the other species diagnostic for this. However, records from this site by HODGSON (1898) for Carex dioica, C. lepidocarpa, Epipactis palustris, Parnassia palustris, Pedicularis palustris and Primula farinosa, suggest that parts of the mire might once have been referable to this community-type.

6.5.3.4. Carex lepidocarpa variant. Not a well-defined variant composed of some rather well developed, but not species-rich, stands of wet Carex diandra-lasiocarpa fen. These have many similarities with the "typical" variant (above), from which they are distinguished by rather trivial floristic differences, such as the occurrence of Carex lepidocarpa. At Sunbiggin Tarn (S.990) Carex elata is frequent in this community (see HOLDGATE, 1955b).

6.5.4. Cicuta virosa nodum.

Diagnostic species-group: Cicuta virosa, Ranunculus lingua, Scutellaria galericulata.

Description: This nodum is characteristic of certain very wet

types of fen in the Whitlaw Mosses and it is particularly well developed on Murder Moss, where it is transitional to reedswamp. The community is often found as part of a "schwingmoore" developed locally over old peat cuts or, more extensively, over infilling lake basins. It forms moss-rich stands dominated by the sedges Carex diandra, C. lasiocarpa or C. rostrata. The moss cover can, in fact, be very extensive (70% estimated in one sample). Acrocladium cuspidatum is particularly important but also A. giganteum and Campylium stellatum are prominent. Mnioid mosses are well represented and Mn. affine, Mn. longirostrum and Mn. undulatum, all occur. This mossy carpet supports a variety of herbaceous species: Caltha palustris, Epilobium palustre, Eriophorum angustifolium and Filipendula ulmaria, together with the ubiquitous Menyanthes and Potentilla palustris. On firmer areas of more consolidated peat (as round the edge of old peat cuts), the same sort of community-type can occur but with a richer assemblage of associates, including Carex lepidocarpa, Pedicularis palustris and Myosotis caespitosa. In such places Molinia caerulea can be frequent.

6.5.5. Mnium pseudopunctatum nodum.

Characteristic species group: Carex appropinquata (local), Mnium pseudopunctatum; distinguished from typical nodum by Carex lepidocarpa, Fissidens adianthoides, Parnassia palustris, Pedicularis palustris, Riccardia pinguis; from other groups, separated by the absence of differentials.

Description: This community-type has been created from only two samples, both made at Tarn Fen, Malham. Floristically it is clearly distinct from most other community-types, but mainly by the absence of differential species. Positive characterisation, however, is provided by the moss Mnium pseudopunctatum, which is of fairly regular occurrence and, to a lesser extent, by Carex appropinquata, though this is of more local occurrence and is more abundant in other types of plant community (see 6.7.6.; 6.9.2.). The occurrence of this sedge at Malham at 1,230 ft. is notable as it is predominantly a species of south and east England, although on the continent it can attain 1,350 m in the Alps. Interestingly, its growth here within Carex diandra fen is in keeping with its prominence within some of the C. diandra-lasiocarpa fen communities of the Norfolk Broads (see 6.2.12.2.; 6.2.15.).

The Carex rostrata - Carex diandra fens at Malham have been described by PROCTOR (1974), who places them within a Potentilla palustris-Acrocladium nodum. Note, however, that not all of the lists he describes would go into this Mnium pseudopunctatum unit: some of the more species-poor types, e.g. the Carex rostrata-fens, would be placed into the typical nodum (cf. S.919). The dominant species are Carex rostrata and C. diandra with occasional scattered tussocks of C. appropinquata. Associated with them is quite a rich

assemblage of associates with cyperaceous species such as Carex lepidocarpa, C. nigra, C. panicea, Eriophorum angustifolium and dicots such as Caltha palustris, Epilobium palustre, Mentha aquatica, Ranunculus flammula, Parnassia palustris, Pedicularis palustris and large amounts of Menyanthes and Potentilla palustris. The moss layer is well developed with much Acrocladium cuspidatum and A. giganteum and, in some places, A. cordifolium. Other species include Bryum pseudotriquetrum, Fissidens adianthoides, Cratoneuron filicinum, Marchantia polymorpha, Mnium pseudopunctatum and Pellia endiviifolia.

Note that the two samples represent rather different developments of the community. S.920 is the most typical type and corresponds best to the lists given by PROCTOR in his Potentilla palustris-Acrocladium nodum. S.918 represents a rather drier version containing plants such as Molinia caerulea, Crepis paludosa, Sanguisorba officinalis and Climacium dendroides. It has evident affinities with the Crepis paludosa nodum.

6.5.6. Pyrola rotundifolia nodum.

Characterising species: Carex limosa, Pyrola rotundifolia, Salix repens, Viola palustris, Sphagnum contortum, S. warnstorfianum.

Description: A most interesting vegetation type recorded only from Northern Britain where it is well developed at Beanrigg Moss and the adjacent Blackpool Moss in the Whitlaw Mosses

N.N.R. The community is a form of very wet fen with pools and wet areas separated by more elevated parts created by tufts and tussocks of sedges, swelling mounds of mosses and the basal portions of small shrubs.

The physiognomic dominant is Phragmites communis, which forms a prominent upper stratum to the community. However, the cover is actually rather low (20-40%) and the main components of the community are the sedges of the rush layer: Carex diandra, C. lasiocarpa and C. rostrata - the exact proportions varying in different parts. Carex paniculata is occasional forming scattered, robust tussocks. Carex limosa is a constant species, often in rather small quantity. In one very wet part of Beanrigg Moss, however, it becomes locally dominant.

The community is rich in plants with parts of Beanrigg having up to 60 species in a $10m^2$ quadrat. This is comprised in part of taller herbaceous species such as Angelica sylvestris, Filipendula ulmaria and Succisa, but also there is a wide diversity of smaller herbs: Cardamine pratensis, Caltha palustris, Galium palustre, Lychnis flos-cuculi, Pedicularis palustris, Rhinanthus minor, Sagina nodosa and Valeriana dioica. On elevated mossy hummocks Pyrola rotundifolia and Viola palustris are frequent. The rare grass Hierachloë odorata is abundant, though by no means confined to this phytocoenose. The taller, drier hummocks

serve as oxyphilous nuclei. They support species such as Calluna, Drosera rotundifolia, Erica tetralix, Luzula multiflora, Molinia caerulea and Potentilla erecta. In a few places Carex curta, C. echinata and Dactylorhiza ericetorum can be found.

Between the hummocks are wet depressions. These contain much Equisetum fluviatile, Menyanthes trifoliata, Potentilla palustris and Potamogeton poligonifolius. Ranunculus lingua sometimes also occurs.

The moss layer is very well developed. Hummocks, which can be locally extensive, are formed by a Sphagnum, which appears to be largely S. warnstorfianum but the closely related S. rubellum may also occur. These provide acidophilic habitats for some of the species mentioned above and, often creeping over them, are the long, trailing shoots of Vaccinium oxycoccus. The rare rich fen species, Sphagnum contortum, also forms frequent hummocks.

Other mosses are frequent as well including Acrocladium cuspidatum, A. giganteum, Campylium stellatum, Bryum pseudotriquetrum and Riccardia pinguis with Scorpidium scorpioides in some of the wetter parts.

Bushes occur in the community but are not prominent. They are mainly small specimens of Salix cinerea, S. pentandra, S. repens and Betula pubescens.

In terms of physiognomy, structure and floristic

composition these stands have many affinities with those forming the Schoenus-nodum in North Wales, and may form a geographical variant. Schoenus nigricans is curiously absent from the Whitlaw mosses. It occurs not far away at Adderstonelee Moss near Hawick, but apparently not as a member of this community-type (BELLAMY, pers. comm.).

6.5.7. Schoenus nigricans nodum.

Characterising species Group: Schoenus nigricans, Dactylorhiza purpurella, D. traunsteineri, Drosera rotundifolia, Epipactis palustris, Eriophorum latifolium, Fissidens adianthoides, Mnium pseudopunctatum, Utricularia spp.

Description: This is a community of swampy areas of rich fen in parts of North Wales. It has been recorded from three main sites: On Anglesey it occupies quite extensive areas of Cors Goch - an elongate, wet, peat-filled hollow in the Carboniferous limestone. The other two areas are both on the Lleyn peninsula. They are not on Carboniferous limestone but are associated with calcareous drift deposits. One is the extensive wetland complex of Cors Geirch, developed over a post-glacial lake in a long (2½ miles), narrow valley wet of Pwllheli. This has received some description by LACEY (1955). The other is from the same area - a rich, but little known mire occupying a small, spring-fed basin near Hirdre Uchaf, between Tudweiliog and Edern.

The wettest development of the community is at Cors Goch where the alkaline water (pH 6.5-8.0), derived from springs

at the base of the limestone scarp which forms the southern edge of mire, is above the surface in the lowest parts even during mid-summer. Here there is an upper layer of c. 1m high formed by a sparse covering of Phragmites communis and Cladium mariscus. The dominants, however, are plants of the rush layer - Carex diandra, C. lasiocarpa, Juncus subnodulosus and Schoenus nigricans. The latter occurs throughout the stands but shows a tendency to form patches of local dominance. In the numerous, shallow pools there is much Menyanthes trifoliata and also Potamogeton poligonifolius and Utricularia species. Both U. intermedia and U. neglecta have been recorded.

The moss layer is generally well developed, usually constituting some 30% of the total vegetation cover. Acrocladium cuspidatum, A. giganteum and Campylium stellatum are abundant with Scorpidium scorpioides in the wetter parts. Sphagnum plumulosum is frequent forming locally extensive polsters. Other mosses include Aulacomnium palustre, Bryum pseudotriquetrum, Drepanocladus revolvens, Fissidens adianthoides, Mnium seligeri, Riccardia pinguis and R. sinuata. Other mosses of interest include Cinclidium stygium, Mnium pseudopunctatum and the rare Sphagnum contortum. Bryum weiglii has also been recorded.

In the relatively open conditions of this community and especially in association with some of the moss carpets,

there is a varied assemblage of associates: Carex dioica, C. lepidocarpa, C. nigra, C. panicea, Eriophorum angustifolium, E. latifolium, and herbaceous species such as Anagallis tenella, Parnassia palustris, Pedicularis palustris and, rarely, Pinguicula vulgaris. Orchidaceous plants are abundant - Epipactis palustris, but in particular Dactylorchids: D. incarnata, D. purpurella and D. traunsteineri. Taller species frequent in the vegetation include Angelica sylvestris, Eupatorium cannabinum and Succisa pratensis.

At Cors Geirch and Hirdre Uchaf the community is in many ways similar but in general the areas are not so wet and, in drier places, species such as Briza media, Carex flacca and Molinia caerulea become important with the moss Ctenidium molluscum.

Phytogeographically the floristics of this community-type shows a mixture of southern and northern elements. Species such as Cladium mariscus, Epipactis palustris, Eupatorium cannabinum and Juncus subnodulosus, are predominantly southern, whilst Carex dioica, C. limosa and Dactylorhiza purpurella are mainly northern.

This vegetation unit has strong affinities with some of the communities belonging to the Carex nodum of the Cladium-Phragmites fens of the Norfolk Broads (6.2.15.3.) both in terms of habitat - wet, swampy morasses and floristics - not least the prominence of Carex diandra, C. lasiocarpa and

Cladium mariscus. The main points of distinction are the absence of broadland species such as Cicuta virosa, Lysimachia vulgaris, Peucedanum palustre, Ranunculus lingua and Sium latifolium and the presence of species more typical of hyper-atlantic rich fen - Drosera rotundifolia and Potamogeton polygonifolius and the northern species mentioned above.

6.5.8. Crepis paludosus nodum.

Characterising species-group: Crepis paludosus, Geum rivale, Sanguisorba officinalis, Climacium dendroides, Hylocomium splendens, Juncus acutiflorus, Lophocolea bidentata, Rhytidiadelphus squarrosus.

Description: This community, although represented by only three releves, is nonetheless distinct and well characterised. It occurs in the same mire systems as some of the other Carex diandra-lasiocarpa community-types, of which it represents a drier version, transitional to certain types of fen meadow.

Sedges still remain important components within this community but there are numerous associated herbaceous plants. Dicots become particularly prominent. In addition to species such as Angelica sylvestris, Cirsium palustre, Filipendula ulmaria, Galium palustre, Mentha aquatica and Succisa pratensis, the differential species Crepis paludosus, Geum rivale and Sanguisorba officinalis, produce a rather tall (up to 1 m) and colourful community. These are species more characteristic of wet grassland and fen meadow than swampy mesotrophic mire, and other associates confirm this trend to drier

conditions: Molinia caerulea, Agrostis stolonifera, Holcus lanatus, Ranunculus acris etc. However, plants such as Equisetum fluviatile, Menyanthes trifoliata and Potentilla palustris still remain.

The complement of bryophytes reveal the same trend. In general, the bryophytes cover is not extensive (5-10%) and the main species are those more typical of fen meadow: Climacium dendroides, Ctenidium molluscum, Lophocolea bidentata and Rhytidiadelphus squarrosus. These replace Acrocladium giganteum, though A. cuspidatum still occurs.

This community-type has been recognised from two main sites: Newlaw Moss in Kirkubright and Tarn Fen, Malham. Each of the three releves represents a different facies. At Newlaw Moss, Carex paniculata is important with much Carex lasiocarpa and a little C. diandra. At Malham one sample is dominated by C. lasiocarpa (very localised here) and C. nigra with the grass Calamagrostis stricta being frequent and Sphagnum contortum growing in the moss layer. In the other the tussocks of Carex appropinquata predominate with some C. diandra. Both of these last two samples have similar associates (including mire species such as Eriophorum latifolium and Parnassia palustris and the shrub Salix repens).

The communities at Malham have been described by PROCTOR (1974). He placed the Carex lasiocarpa stand within the category of "miscellaneous Carex stands"; his stands

dominated by Carex appropinquata all appear to be located within the Carex nigra-Sanguisorba officinalis nodum. However, the Carex appropinquata stand recorded here would seem to represent a wetter community.

6.5.9. Juncus subnodulosus nodum

Characterising species-group: Juncus subnodulosus; plus the absence of differentials for other groups.

Description: In south and east England Carex diandra-lasiocarpa vegetation types are only occasionally found. They may be readily separated from their northern counterparts by the presence of the fen rush, Juncus subnodulosus. This species occurs in the Schoenus nigricans nodum recorded from Anglesey (see 6.5.7.), but this may be readily distinguished by its own differential species.

This type of community is often developed only in very fragmentary form and at rather disjunct localities and this may in part account for the variability within the nodum. However, two variants may be readily discerned:

6.5.9.1. Carex elata variant. Recorded only from East Walton Common and Thompson Common in W. Norfolk where it forms local areas of "schwingmoore" in some of the small depressions which are a feature of these commons (see 6.1.2.2.). The vegetation mat tends to be rather poor in species. Phragmites and Cladium form a sparse upper

stratum. In the rush layer Carex diandra and C. elata predominate with C. lasiocarpa in one place. Small bushes of Salix cinerea can be found growing on some of the C. elata tussocks. The moss layer is quite extensive (contributing some 20% of the vegetation cover) but rather poor in species. Acrocladium cuspidatum, A. giganteum and Campylium stellatum predominate but in one pool Scorpidium has been recorded and Acrocladium cordifolium has also been found.

6.5.9.2. Typical variant. Recorded from three disjunct sites and in each one the community is only fragmentarily developed. It can be easily distinguished from the Carex elata variant by the absence of C. elata, Cladium, Acrocladium giganteum and Pedicularis palustris, though this latter most probably once occurred in the Buckinghamshire site (S.436) (DRUCE, 1926). This is a small area of swamp developed over a spring. In the other two sites the community forms a slightly swinging raft over small depressions.

6.5.10. Related community-types in Britain

There has been only a very limited description of this type of wetland vegetation from Britain and very little is strictly comparable with the species-rich lowland community-types that are described here. However, HOLDGATE (1955b) has given some account of this type of vegetation from Sunbiggin Tarn, Westmorland (cf. S.983; S.990), and

describes the Carex rostrata dominated fens that surround much of the Tarn. These are, in fact, rather variable in their floristic content but would appear to be members of the typical nodum established here. PROCTOR (1974) has documented the upland Carex fens at Malham Tarn. He describes Potentilla palustris-Acrocladium nodum to accommodate the wet fen areas dominated by Carex diandra and/or Carex rostrata.

From Scotland various types of Carex rostrata and C. lasiocarpa fens have been described. Thus, SPENCE (1964, p.344) has distinguished a Carex rostrata-Acrocladium cordifolium/cuspidatum sociation. This is composed of rather species-poor stands with Carex rostrata, Galium palustre, Potentilla palustris and Acrocladium cuspidatum/cordifolium as constants. Menyanthes trifoliata is also well represented. Rather similar to this is the Potentilla-Acrocladium cordifolium sociation (p.352), where Potentilla palustris is the dominant with Carex rostrata and Acrocladium cordifolium as constants. There is also a Carex nigra-Acrocladium sociation (p.349) with Carex nigra as the dominant and with C. rostrata, Potentilla palustris and Acrocladium cuspidatum as constants. None of these community-types are closely related to any described here as such species-poor areas of wet fen of neutral pH are outside the range of this survey.

From Skye BIRKS (1973) has recognised a Carex lasiocarpa-Menyanthes trifoliata Association dominated by Carex lasiocarpa

and with much Menyanthes. Carex rostrata, C. nigra and C. limosa are also important and constant species with Equisetum fluviatile. As BIRKS seems to recognise this is clearly a heterogeneous Association containing, on the one hand, oligo-mesotrophic stands (pH c.5.0) with Sphagnum palustre and S. recurvum and, on the other, more base-rich stands containing the rich fen moss Scorpidium scorpioides.

IVIMEY-COOK & PROCTOR (1966) have described a related Carex nigra-Acrocladium giganteum nodum from the Burren.

McVEAN & RATCLIFFE (1962) (RATCLIFFE, 1964) give details of a Carex rostrata-Sphagnum warnstorfianum mire. This is a rare montane (1400-2700 ft) nodum of calcareous areas confined to the Central Highlands and associated with areas of relatively stagnant but base-rich water. Carex rostrata dominates the community but Sphagna have a large amount of cover - these are mainly relatively eutraphentous types such as S. squarrosum, S. subsecundum. In particular, S. teres and S. warnstorfianum are given as constants and S. contortum also occurs. Other mosses include Camptothecium nitens, Drepanocladus revolvens and Mnium pseudopunctatum.

6.5.11. Syntaxonomy

In considering the syntaxonomy of the Carex diandra-lasiocarpa communities, two considerations are relevant:

(a) that the noda have not been formed on the basis of the dominance of a particular sedge;

(b) that, although some of the community-types have strong affinities with certain calcareous mire communities, nonetheless, floristically and physiognomically they display a certain unity.

Plant communities similar to the ones discussed here have frequently been described from the European continent. However, they have become surrounded by a certain degree of syntaxonomic confusion, asscciated (i) with the existence of a whole series of communities characteristic of more acid conditions, and (ii) with the attempt to differentiate syntaxa on the dominant species.

In its original concept the Caricetum lasiocarpae Koch 26 contained basiphilous vegetation of wet fens dominated by Carex lasiocarpa. Carex diandra and Eriophorum gracile occurred in some stands and, with the C. lasiocarpa, constituted the character species. A similar community-type was described by LIBBERT (1932). However, as he pointed out, 'Mann kann Carex lasiocarpa-Bestände beobachten, in denen Sphagnum-Arten, Carex limosa, Vaccinium oxycoccus und Andromeda polifolia auftreten, die auch noch zahlreiche echte Flachmoorarten

besitzen'. This indicates a major syntaxonomic problem presented by Carex lasiocarpa stands, for the sedge is a species of wide ecological amplitude and will tolerate water of varying pH and base status. At the extremes of the pH range (DUVIGNEAUD, 1948, gives pH 4-7), although it remains the dominant species, there are very different associates. Thus, the acidophilic Caricetum lasiocarpae of JONAS (1935) is a very different community-type to that of KOCH (1926) with a prominence of species of Sphagnum.

This problem has been resolved in two ways. The first is shown by SCHWICKERATH (1942) who, illustrating the use of differential species, treated the community as a single Association with a series of sub-communities. This effectively united stands with few species in common except for the dominant sedge. The other approach has been to subdivide the community. Thus, DUVIGNEAUD & VANDEN BERGHEN (1945) recognised an oligomesotrophicum sub-ass. and a eutrophicum sub-ass. with only the latter relating to KOCH's Association. This distinction has been maintained by DUVIGNEAUD (1948; 1949) and LEBRUN et al. (1949). VANDEN BERGHEN (1952) renamed the sub-associations sphagnetosum and scorpidietosum.

DUVIGNEAUD (1949) created from the parts two Associations: Caricetum lasiocarpae acidoclinum and the Caricetum diandro-lasiocarpae basiclinum and this independent status is reflected in the two Associations used by PASSARGE (1964) - the acidophilous Sphagno-Caricetum lasiocarpae Steffen 31 and the basiphilous

Eriophoro-Caricetum lasiocarpae (Vollmar 47) Passarge 64. These however, are not synonymous with DUVIGNEAUD's Associations because PASSARGE, following JONAS (1933) has regarded communities with much Carex diandra as belonging to an independent Association. For JONAS described a Caricetum diandrae composed of vegetation dominated by Carex diandra. A similar community has also been recognised by OBERDORFER (1957), JESCHKE (1959), SCHEEL (1962), KRAUSCH (1968) and BALATOVA-TULACKOVA (1972) amongst others. Although many of these descriptions refer to basiphilous communities, as with Carex lasiocarpa, acidophilous ones also occur (e.g. see SCHEEL, 1962; KRAUSCH, 1968). PASSARGE (1964) has therefore created two independent Associations to contain these - by emending the Caricetum diandrae Jonas 33 to refer to the acidophilous development and by using the Eriophoro-Caricetum diandrae Jeschke 59 for the other.

However, it would be inappropriate to separate the material of this survey into two Associations based upon the prominence of either Carex diandra or C. lasiocarpa, because the floristic affinities of the stands are not dependent upon the dominant species and, in any case, mixed populations often occur. This is in accordance with the observations of SEGAL (1966; 1968) who suggested that the separation of Carex diandra and C. lasiocarpa Associations seemed to be more on the basis of dominance than floristic distinctions. (It may be noted that this is not necessarily true for the area of the optimal development of the "Caricetum diandrae" - N.E. Europe. Here

BALATOVA-TULACKOVA (1972) points to its close affinities with the Caricetum appropinquatae Aszod 36). Thus, WESTHOFF & DEN HELD (1969) return to a composite association encompassing both dominance types. They still, however, retain the distinction between the acidophilous and basiphilous forms of the community: for the acidophilous version they have revived the Sphagno-Caricetum lasiocarpae Steffen 33 - an Association of stands dominated by Carex lasiocarpa combined with various Sphagna. The basiphilous version has been named the Scorpidio-Caricetum diandrae - a renaming of KOCH's original Caricetum lasiocarpae.

This latter Association would appear to be suitable for the material presented here. However, Scorpidium scorpioides, although occurring in some of my samples, is not at all frequent. In contrast, Acrocladium giganteum is a constant species and appears to be optimally developed in this community. (It also occurs in certain Schoeneto-Juncetum communities, but so also does Scorpidium). A more appropriate name for the Association would thus seem to be Acrocladio (giganteii)-Caricetum diandrae. As well as the communities dominated by Carex diandra and/or C. lasiocarpa, related species-poor wet fen communities with only Carex rostrata as the dominant may also be placed here (cf. VAN DONSELAAR, 1961). Similarly, communities developed in very wet "mud-bottom" areas of rich fen which have Carex limosa as dominant may also be included. Such stands have been placed into the Caricetum limosae Br.-

Bl. 21 (e.g. KOCH, 1926) or, in order to distinguish them from Carex limosa types of ombrotrophic mires, into a Caricetum limosae eutrophicum (DUVIGNEAUD, 1949). Here, however, the communities are often so small and intermingled with Carex diandra-lasiocarpa types, that they are perhaps best regarded just as a development of these (cf. Caricetum lasiocarpae caricosum limosae Koch 26).

There are no good single character species that appear satisfactory for the Association, although Carex diandra and Acrocladium giganteum are possible weak characters. However, C. diandra with C. lasiocarpa and A. giganteum probably constitute a good character combination.

6.5.12. Syntaxonomic placement

The variability of the Carex diandra-lasiocarpa communities has led to their assignment to various higher syntaxa. KOCH (1926), whilst noting some affinities to his Rhyncosporion albae, placed the Caricetum lasiocarpae unambiguously within the Caricion fuscae. (= the later Caricion davallianae). However, the subsequent recognition of the very different acidophilic and basiphilic subunits of the Association caused it to become partitioned between the Caricion curto-nigrae and the Caricion davallianae. But, subsequently, the Association was able to come together again by the creation of an appropriate syntaxon - the Caricion lasiocarpae (see

VANDEN BERGHEN, 1952). This Alliance was used by LEBRUN et al. (1949), OBERDORFER (1957) (using the synonymous Eriophorion gracilis Prsg. apud Oberd. 57) and HOLUB et al. (1967) etc., but, with their rejection of this Alliance as a valid syntaxon, WESTHOFF & DEN HELD (1969) return the communities to the Caricion curto-nigrae and the Caricion davallianae.

The Acrocladio-Caricetum communities are in many ways very different from other Caricion davallianae types - representing a vegetation of wetter conditions with Phragmition species such as Ranunculus lingua - and they form a rather distinct unit. There would seem many advantages in placing them within an independent Alliance such as the Caricion lasiocarpae. However, as data from other (acid) Carex lasiocarpa-diandra types are currently not available to indicate how satisfactory such an Alliance would be and as Caricion davallianae character species are fairly well represented in most, but not all, community-types of the Association (extremely well represented in some), it is considered, with reservations, appropriate to class the Association in the Caricion davallianae.

It may be noted that one community-type - the Acrocladio-Caricetum caricetosum Schoenus var. - is apparently transitional between this Association and the Schoeneto-Juncetum. It could equally well have been placed in the latter.

6.5.13. Synopsis of Carex diandra-lasiocarpa-rostrata communities.

PARVOCARICETEA Den Held et Westhoff 69

TOFIELDIETALIA prsg. apud Oberd. 49

CARICION DAVALLIANAE Klika 34

Acrocladio (giganteii)-Caricetum diandrae (Koch 26) nom. nov.

typicum (6.5.3.)

Carex rostrata var. (6.5.3.1.)
Carex lasiocarpa var. (6.5.3.2.)
typical var. (6.5.3.3.)
Carex lepidocarpa var. (6.5.3.4.)

cicutetosum (6.5.4.)

caricetosum

Mnium pseudopunctatum var. (6.5.5.)
Pyrola rotundifolia var. (6.5.6.)
Schoenus nigricans var. (6.5.7.)

crepetosum (6.5.8)

juncetosum (subnodulosi)

Carex elata var. (6.5.9.1.)
typical var. (6.5.9.2.)

6.6. Group 6. Rich fen meadow communities - Table 6.

This category is not susceptible to precise definition. Essentially it contains wetland vegetation of medium height (50-80 cms), dominated by sedges and/or rushes developed upon a substratum that is wet throughout the year with a water-table only just below the surface. A number of turf-forming grasses occur but these are almost always subordinate to the sedges and rushes and do not usually form a closed turf. Associated herbs include species of rich-fen and of wet grassland. The irrigating water is usually base rich and of high pH (6.5-8.0) and the communities fall into the categories of "rich fen" or "extreme rich fen", although they must also be recognised as being transitional to grassland. These are thus referred to as "rich fen meadows" to distinguish them from related community-types of lower base status. This type of vegetation is not easy to distinguish from some forms of wet meadow and intermediates most certainly occur. Wet meadows, however, have a greater prominence of grasses and a reduced complement of rich fen species. The substratum is often a gleyed mineral soil rather than a peat, and they are subject to a different hydrological regime with the possibility of very high water levels during the winter, or of superficial drying out during the summer. In contrast, fen meadows are developed where there is a water-table that is constantly high, more or less, throughout the year and

where there is water-flow by some form of seepage. They often occupy sloping ground.

There is in fact a variety of types of vegetation which may develop on such wet slopes, including communities dominated by rushes such as Juncus acutiflorus, J. effusus and J. inflexus. Many of these marshes - even some of the more acidic types - have very firm floristic affinities to what is here regarded as rich fen meadow. They have not, however, been found in most of the areas examined in this survey and have largely been excluded from its scope, although it is clear that for a fuller understanding of this type of vegetation such areas need to be examined in some depth.

Within these constraints rich fen meadow vegetation has been examined in detail, and over 200 samples have been made from various parts of England and Wales.

6.6.1. Rich fen meadow communities.

6.6.1.1. Introduction

Physiognomically the plant communities described here form a very distinct category. In the ungrazed state they consist of closed stands of vegetation with a height of between 50-80 cms, dominated by various species. In many examples, rushes are particularly prominent. Juncus articulatus, J. acutiflorus and J. inflexus can all be principal components but, in the

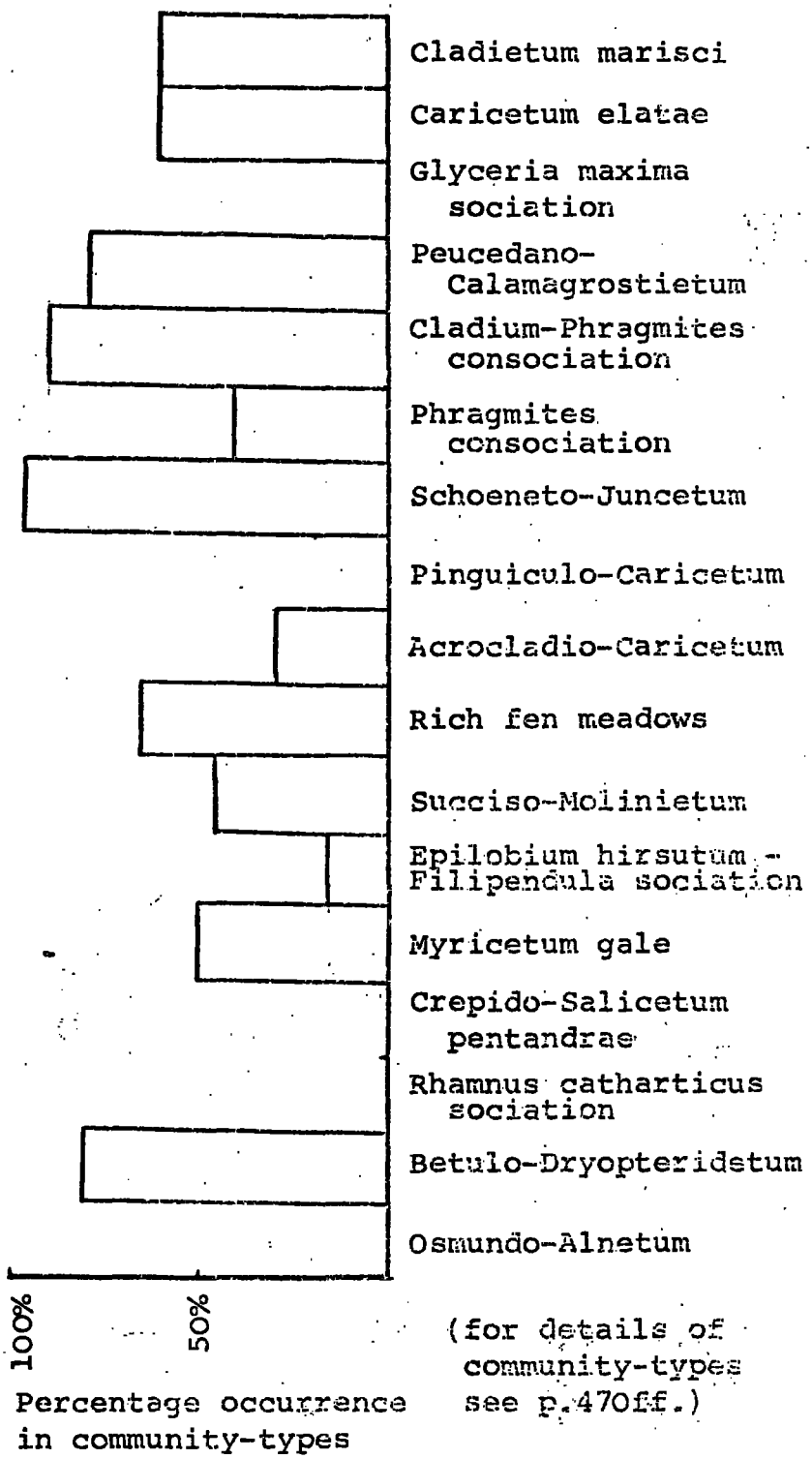
greater proportion of stands considered in this survey, it is the fen rush, Juncus subnodulosus, that is the characteristic species.

Juncus subnodulosus, a plant distributed mainly in southern and eastern England, is found in a wide range of rich fen communities (see Fig. 6.6.II), but it is most abundant in certain fen meadow community-types. It is a creeping hemicryptophyte with a well developed sympodial rhizome system which can often form a dense intertwined mat just below the surface. Shoots arise from this at frequent intervals (0.5-3 cms apart) and, where the plant is abundant, often provide very dense stands. The bright green sterile shoots are produced in the autumn and persist throughout the winter, though often not extending greatly until the spring when they can grow up to 100 cms, but more often to about 60-80 cms. During the spring the flowering shoots are produced and these give rise to the tawny lax inflorescences. J. subnodulosus is one of the earliest flowering members of the Septati section of rushes. It normally flowers in July and early August, before J. articulatus and much before J. acutiflorus. In summer the shoots gradually become light brown and they show a marked tendency towards prostration. This is mainly induced by exposure to wind and heavy rain but cattle have been noted to have a similar influence. The result is a springy mattress of shoots which gives a characteristic

Fig. 6.6.II.

Sociological amplitude of

Juncus subnodulosus



(for details of community-types see p.470ff.)

appearance to Juncus subnodulosus stands in the summer. Small herbaceous species - especially late-flowering ones such as Mentha aquatica - can often be found growing up through it. The mat of shoots, however, can blanket the associated plants and when large banks of dead shoots accumulate there are often very few other species present. But often the rush mattresses do not develop and, with the incidence of grazing pressure - in which the effects of trampling and poaching seem to be particularly influential - much more open conditions are maintained. Grazing pressure does not seem detrimental to the rush (although under constant trampling it may be replaced by J. articulatus), and its tolerance to mowing is important in maintaining it against the advance of taller fen species (LAMBERT, 1946).

In other examples of rich fen meadow sedges play an important part, sometimes as do-dominants with the rushes but also as dominant species by themselves. Two species are especially important: Carex acutiformis and Carex disticha.

The lesser pond sedge, Carex acutiformis, has long, creeping rhizomes from which tufts of shoots arise at intervals. The plants are robust (up to 1.5 m, but usually 70-90 cms) and, when abundant, the coarse, glaucous leaves can strongly dominate the vegetation cover sometimes to produce extensive sedge meadows. When the incidence of trampling is low and especially on a comparatively dry substratum, there can also

be the accumulation of a substantial litter of dead leaves between the tufts of the plant.

In contrast to the fen rush and the pond sedge the brown sedge (Carex disticha) is only occasionally dominant in the samples considered here but when it is the monopodial, bright green shoots which are often only about 40-60 cms tall produce a very distinct facies.

Phragmites communis occurs occasionally - usually in stands with little or no grazing pressure - but it is rather sparse and at the most forms a rather open upper stratum of 100-150 cms height.

Thus, the main contributors to the vegetation cover are graminoid monocotyledons of 50-80 cms height. And, although in the summer this mantle is usually overtopped by the flowering heads of taller herbaceous dicots - especially Angelica sylvestris, Cirsium palustre, Filipendula ulmaria, Lythrum salicaria - it usually looks like stands of coarse grassland. These affinities with grassland are, in fact, confirmed upon closer examination as a large number of graminaceous species can be found. In addition to the more robust species - Deschampsia cespitosa, Festuca arundinacea and Molinia caerulea - which tend to be restricted to certain community-types where the rough tussocks can form distinct facies, there are also smaller turf-forming grasses - Agrostis stolonifera, Anthoxanthum odoratum, Festuca rubra, Holcus lanatus and Poa trivialis -in abundance. With these,

though less frequently, Briza media and Arrhenatherum elatius often occur and in some places - particularly the drier areas - Cynosurus cristatus, Lolium perenne and Phleum pratense.

These associations with grassland are confirmed by the occurrence of other species which can be regarded as more characteristic of wet grassland than of rich-fen. They include Cardamine pratensis, Cerastium holosteioides, Lathyrus pratensis, Lotus uliginosus, Ranunculus acris, Rumex acetosa and Vicia cracca as constant species. Others often found, but with lower constancies, are Centaurea nigra, Plantago lanceolata, Potentilla anserina, P. reptans, Prunella vulgaris, Ranunculus repens and the clovers, Trifolium pratense and T. repens.

As well as these grassland types there is still a good complement of general wetland species. Juncus subnodulosus comes into this category and others are Angelica sylvestris, Carex panicea, Cirsium palustre, Caltha palustris, Filipendula ulmaria, Hypericum tetrapterum, Scrophularia aquatica and Valeriana dioica. However, many of these occur in wet meadows as well as in peat fens. More typically "fen" plants are restricted to certain community-types. On the one hand, species of soligenous calcareous mires such as Anagallis tenella, Carex dioica, C. hostiana, Eriophorum angustifolium, Epipactis palustris, Parnassia palustris, Pedicularis palustris, Pinguicula vulgaris and mosses like

Bryum pseudotriquetrum and Drepanocladus revolvens can be found. On the other hand, species of taller fen such as Calamagrostis canescens, Iris pseudacorus, Lysimachia vulgaris, Lythrum salicaria, Thalictrum flavum, Symphytum officinale and Valeriana officinalis also may occur, though in rather different situations.

Thus, a range of species may be present and some stands support a high species diversity: where the dominant is not too repressive more than 60 species per sample have been recorded, though some taxa may be represented only by one or two individuals. But in contrast some community-types are typically poor in species with only about 15-20 species per sample.

A characteristic feature of rich fen meadow is the very reduced part played by bryophytes. In some stands none have been found at all and in many places only Acrocladium cuspidatum and Brachythecium rutabulum occur and then often only in small quantity. But even when the moss cover is more extensive there are few additional species.

In a similar way shrubs tend to be rare. Only Alnus glutinosa and Salix cinerea can usually be found.

6.6.1.2. Constant species. The following species may be regarded as constant for the range of community-types considered here:

Agrostis stolonifera	Hypericum tetrapterum
Angelica sylvestris	Lathyrus pratensis
Anthoxanthum odoratum	Lychnis flos-cuculi
Caltha palustris	Mentha aquatica
Cardamine pratensis	Rumex acetosa
Cirsium palustris	Valeriana dioica
Equisetum fluviatile	Vicia cracca
Filipendula ulmaria	
Galium uliginosus	Acrocladium cuspidatum
Holcus lanatus	Brachythecium rutabulum

The following are also constant in a wide variety of community-types:

Cerastium holosteoides	Poa trivialis
Dactylorhiza fuchsii	Scrophularia aquatica
Festuca rubra	Succisa pratensis

Together these two groups constitute the typical "constant species" of rich fen meadow, which is referred to in the subsequent descriptions.

6.6.1.3. Life form spectrum. The majority of species in the above lists are hemicryptophytes. This reflects the life-form both of the main dominants and the associates. Considering the most frequent species (and excluding species differential for specific sub-groups), the full life-form spectrum from 56 species is:

Helophytes	1.0%
Hemicryptophytes	67.5%
Protohemicryptophytes	25.0%
Semi-rosette hemicryptophytes	41.0%
Rosette hemicryptophytes	.5%
Geophytes	.5%
Herbaceous chamaephytes	.5%
Therophytes	.2%
Moss	.5%

6.6.1.4. Habitat:

Communities of this type occupy two distinct habitats:

(i) Spring fen meadows: These are marshy areas developed on slopes beneath springs and (more generally) areas of water seepage. Such areas occur on hill slopes, over-steeped valley sides, around the margins of mire complexes or in shallow mire basins. They can vary in the degree of slope from a negligible amount to 30° or more. They vary also in the degree of flushing and often a hydrological gradient may be observed extending from the very wet central spring area - which may have water at the surface throughout much of the year - into slightly flushed grassland around the periphery. To this may be related changes in the vegetation cover. Most of the sites included here are wet throughout the year with a high sub-surface water-table even in the summer (although this may be reduced substantially in the most peripheral areas). The pH of the water ranges from 6.5 to 8.0. The mean from all of the sites measured is 7.3. The substratum is usually a black peaty gley often only 30-40 cms deep. It normally conforms to the topography of the area where it has developed. Examples are known, however, especially from shallow slopes, where the spring mire has an eccentric convex profile - presumably created by hydrostatic pressure and the accumulation of organic material. In general, the water seeps down the mire slopes to issue at

the bottom into a stream or a topogenous mire complex, or even to be lost in a more permeable substratum. Less frequently, there may be discrete water channels and soakways within the mire, usually associated with the most active springs.

Undulations in the topography of the spring slopes coupled with variations in the intensity and duration of irrigation can create a complex network of inter-grading plant communities which often seems irresolvable into discrete components. This may create substantial problems of sampling. These are often exacerbated by another characteristic feature of the spring mires namely their small size: some of the smaller have an extent of only some 100 square metres. Two matters arise from this. First the amount of "edge" to "middle" is rather high and the composition of the wetland community can often be much influenced by the intussusception of species from the surrounding vegetation. Secondly, within this small area a whole series of plant communities may be developed in response to a range of hydrological regimes. From the point of view of a regional phytosociological survey, it might thus be expedient to ignore such areas. However, these often represent the only examples of rich fen over large sectors of the English countryside.

(ii) Topogenous fen meadows: The second main habitat is that provided by flat, low-lying situations, which are not

normally irrigated directly by springs but which may receive water derived from springs (and spring fens) on the neighbouring slopes. Such areas can be found in a variety of contexts: badly drained marshy meadows in valley bottom areas; water meadows alongside rivers; in mire basins - especially in marginal areas surrounding lakes and wetter types of fen; and on drained mire surfaces.

Such areas cannot always be clearly separated from spring fen meadows and in some rich-fen systems the slopes of a mire basin or wet valley may be occupied by seepage fens, whilst the floor supports a topogenous fen meadow-type. In other situations irrigation may be by the influence of dykes or sluggish rivers or streams; or the topography may maintain generally wet conditions without any clear seepage areas. Such sites are exposed to a less constant hydrological regime than the spring fens with a greater possibility of flooding during the winter and of at least superficial drying out during the summer. The plant communities tend to be more variable too as, in addition to variations in height of the meadow surface, other factors such as proximity to streams and sub-surface drainage patterns most probably help to determine the distribution of species.

The substratum can also vary and the community has been found developed upon deep fen peat, on peaty gleys and also on alluvial deposits.

Fen meadows of this type can sometimes be quite extensive.

Large areas are known on some flat grazed commons in Norfolk; examples still occur on some of the drained grazing levels of the valley of the R. Yare (cf. LAMBERT, 1948). Previously mowing marshes of the wet fens associated with the Norfolk Broads supported large areas of this vegetation type (LAMBERT, 1946) and, although it is now infrequent in such places, examples still occur and in some droves through the marshes related communities may be found.

6.6.1.5. Utilisation.

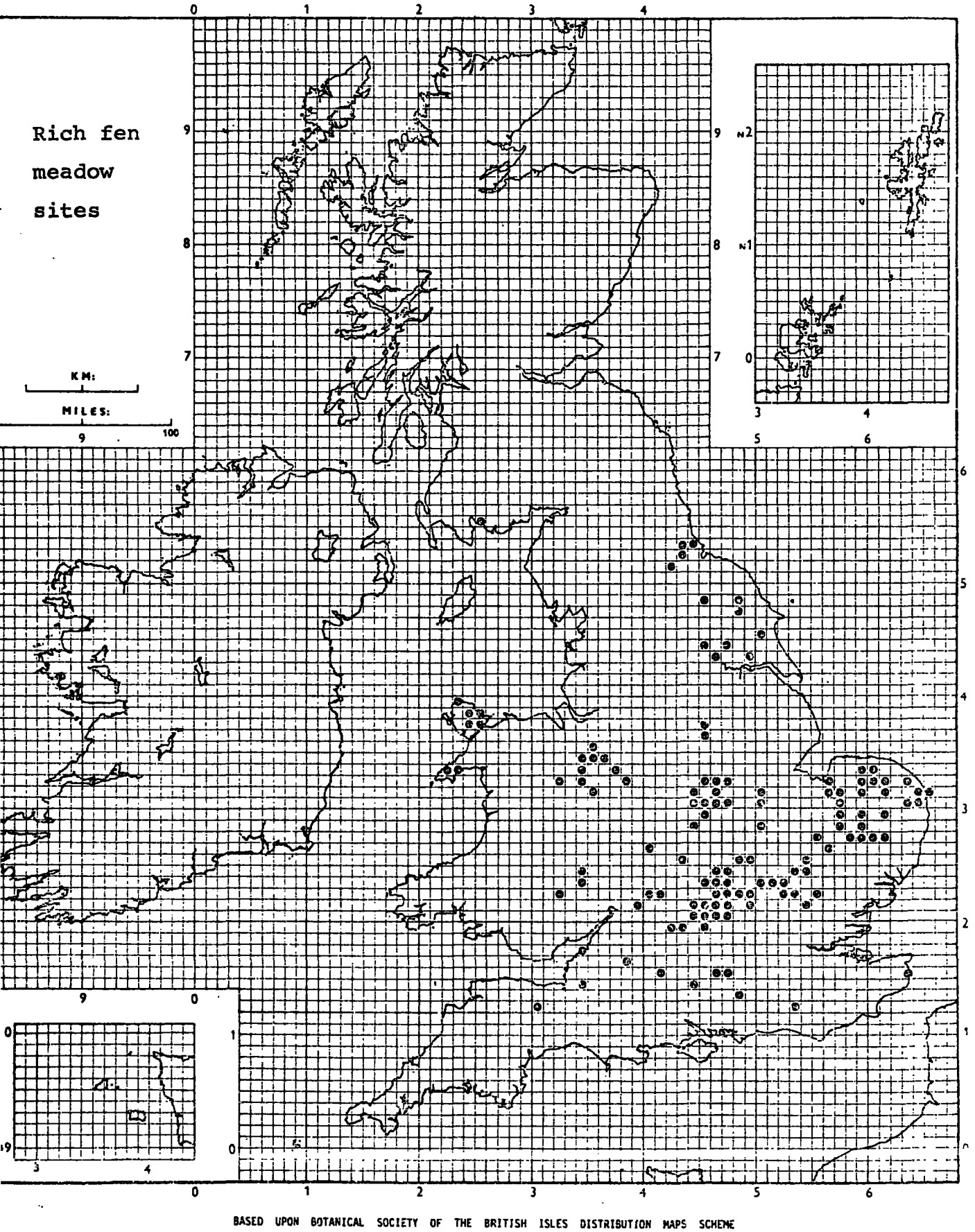
One of the most characteristic features of fen meadow communities is their occurrence in association pastoral agriculture. The sites often occur as small pockets within grassland used for pasturing stock throughout the year. Or, alternatively, they may occupy small low-lying boggy fields where the areas of rough grassland and fen meadow are used to provide poor summer grazing. Both Carex acutiformis and Juncus subnodulosus are eaten - even if rather unenthusiastically - by cattle. This does not seem to seriously reduce their vigour and indeed light grazing may well enhance it (though LAMBERT (1948) suggests that heavy grazing is deleterious to Juncus subnodulosus). Grazing can modify the physiognomy of the stands by reducing the height of the rushes and sedges and thus exposing some of the lower-growing herbs. The trampling pressure undoubtedly also helps to maintain partly

open conditions and in particular may be important in breaking up accumulations of rush and sedge litter. In the wettest areas the ground may become heavily poached.

Some data as to the influence of grazing on fen meadow vegetation have been obtained by management experiments in Thriplow meadows, Cambridgeshire. This work has been summarised by CROMPTON & HEPBURN (1972). Considering the numbers of flowering spikes produced by the marsh orchids Dactylorhiza incarnata and D. praetermissa, they have shown that grazing by both horses and cattle supports large numbers of orchid spikes. An ungrazed control strip provided the least satisfactory conditions with a much lower count but also a strip mown during the summer months had low totals as well. Casual observations made during this survey also suggest that grazing is instrumental in maintaining a high species-diversity in fen meadow communities.

6.6.1.6. Distribution. Fen meadows represent the most widely distributed type of rich-fen community in England and Wales, as is reflected in the large number of samples that have been collected. This is largely because they are able to co-exist with the anthropogenic organisation of the landscape and indeed sometimes represent the residual communities of format mire surfaces which have largely been destroyed by drainage. Hence, together with the closely related

Fig. 6.6.III



BASED UPON BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

marshes and boggy meadows that have not been encompassed by this survey, they can be found throughout much of the country. The types considered here are, however, rather more restricted distributionally and their association with irrigating water of fairly high pH and base status means that they are developed particularly in association with calcareous strata in S.E. England.

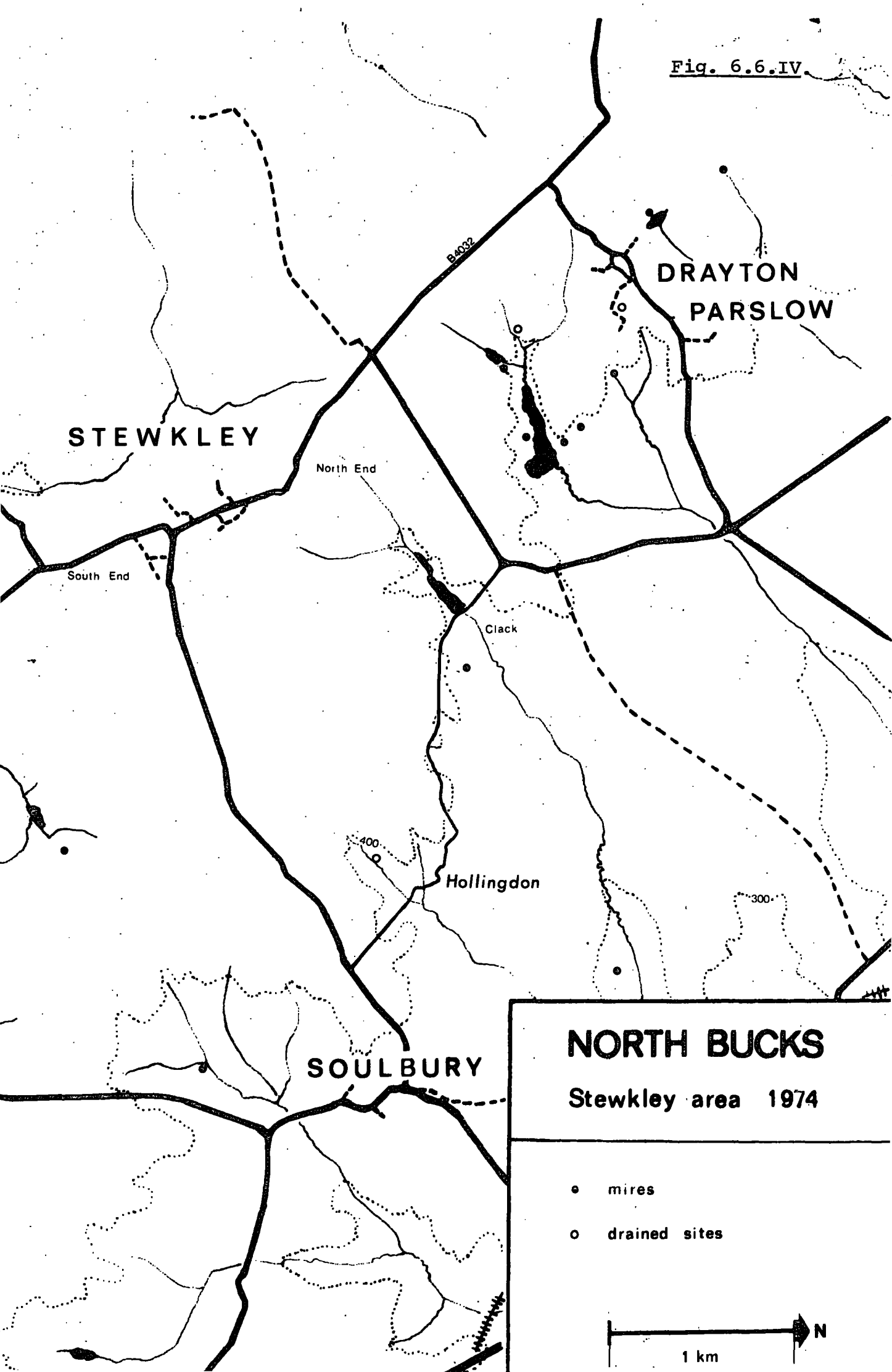
The distribution of rich fen meadow, as shown in this survey, is indicated in Fig. 6.6.III. This reveals a high concentration of sites in East Anglia where, in fact, within each 10 km grid square there are often a large number of places where the community occurs. It is found in almost all of the calcareous mire systems in Norfolk - associated with the chalk in the west and with the glacial deposits overlying the Norwich Crag in the East. It often occurs peripherally to other rich-fen types forming a distinct and characteristic zone around the margins of the mire basins. But it can also occur in isolated areas by itself, though here it is sometimes the product of the modification of some other community. The community is not very frequent in broadland where the absence of regular mowing or grazing permits the establishment of other vegetations. It can occur, however, in places and a number of examples have been noted in marginal locations - particularly on the mineral slopes at the edge of the fen basins (where seepage is most probably important for irrigation).

Extending S.W. from East Anglia there is a whole range of sites. These are developed along the N.W. edge of the Cretaceous scarp from the Gog Magog hills in Cambridgeshire down to Salisbury Plain. In fact, there are only a few fen-meadows directly associated with the Chalk itself, although where the Lower Chalk has washed down onto the Gault to form the Chalk Marl, several marshy areas occur. Sites are also found associated with the Coralline Limestones, particularly in parts of Berkshire. However, in South Central England many of the fen meadows are developed - often as very small pockets - in association with the glacial deposits northwest of the chalk. North Buckinghamshire has proved to be particularly rich in such sites. Here, in areas of outwash sands and gravels mixed with chalky boulder clay, numerous small marshes have developed especially in association with the headwaters of some of the small streams draining the area (see Fig. 6.6.IV).

North of this area - in N. Bucks, N. Bedfordshire and Northamptonshire, some small spring fens have developed on the Jurassic Oolites and Cornbrash. On the same formation other examples also occur much further S.W. on the Gloucestershire Oolites.

In southern England only a few examples of rich fen-meadow have been found - mainly in association with the chalk. In Central England also the community-type is only occasional but some records have been made from the Keuper Marl in

Fig. 6.6.IV


B4032
DRAYTON PARSLOW
STEWKLEY
North End
South End
Clack
400
Hollingdon
300
SOULBURY
NORTH BUCKS
Stewkley area 1974
mires
drained sites
N
1 km

Leicestershire. An isolated locality at Redditch is on the same formation and here suitably calcareous conditions seem to have resulted from layers of gypsum within the rock. Similar examples are also known from parts of Staffordshire and Cheshire. In these parts, however, it is the numerous peat-filled glacial hollows of the Cheshire-Shropshire plain that provide the main centres for fen meadow, especially those associated with more calcareous conditions (cf. GORHAM, 1957).

The Carboniferous Limestones of North Wales provide suitable irrigating water for fen meadow. Sites occur beneath exposures on the north-eastern Marches, but the main area is much further west in the limestone basins of the Anglesey mires and in parts of the Lleyn peninsula.

There are only a few samples from Yorkshire; mainly from the calcareous areas of the Wolds and from the area around Driffield, but examples have also been noted in the North York Moors. In Durham some sites are known on the Magnesian Limestone with a few examples also from parts of Teesdale.

It must, however, be appreciated that this account of the distribution of fen meadow reflects more the sites which it has been possible to examine than the actual distribution pattern. Other examples of vegetation clearly belonging to this category have been given by DONY (1952, 1967) for Bedfordshire and Hertfordshire (respectively), by MESSENGER (1971) from Rutland and by NEWTON (1971) from Cheshire. Indeed many of the records of Juncus subnodulosus in local

floras probably indicate the occurrence of this type of vegetation and the distribution pattern of this species (PERRING & WALTERS, 1962) may more accurately reflect the distribution of the community.

6.6.1.7. Types of rich fen meadow communities.

The analysis of the fen meadow samples has been the least satisfactory of any undertaken in this project. The initial examination of the data by Information Analysis produced some lower-order groupings that were rather nebulous, which could not easily be defined with reference to their floristic content, and which did not seem to correspond to any distinct ecological situation. This is perhaps partly a reflection of the species-poverty of many of the stands together with a large amount of variation in floristic content - which may be related to factors such as management history and the nature of surrounding vegetation types etc. Nonetheless, some better defined groups were obtained and in many cases it was possible to recognise trends of floristic variation even if discrete groups could not be delimited.

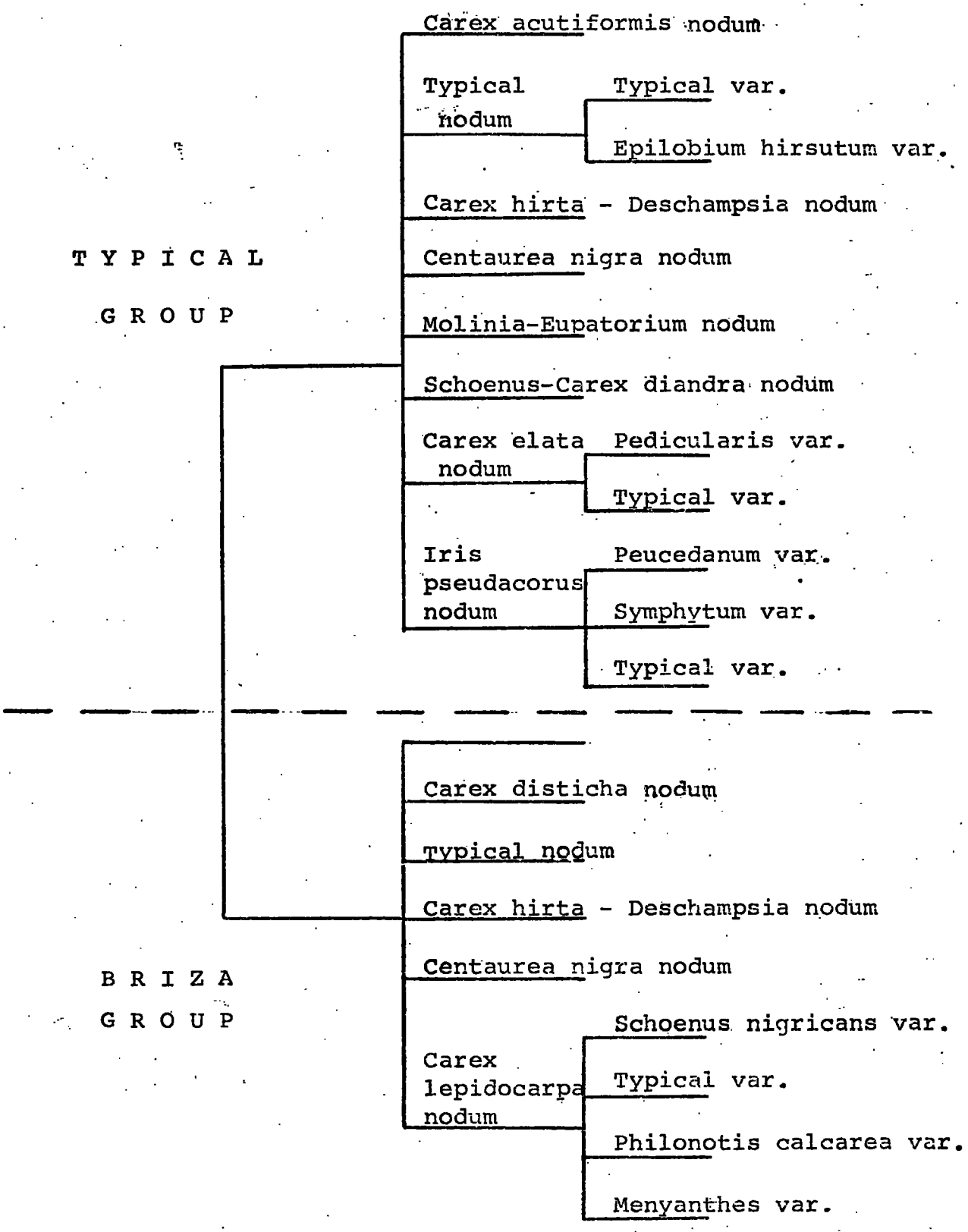
The data were further analysed by a quantitative version of Ward's Method using the estimated cover-abundance values of the species transformed as suggested by MOORE et al. (1971). The classification produced by this was in many ways similar to that of Information Analysis. However, because of the weighting given to the more abundant species some of the

lower-order groupings became defined as dominance-types. This seemed a more acceptable approach as it incorporated a floristic definition of the higher-order groupings but also a clear segregation of these into facies defined by the dominant plant. The groupings produced were still not entirely satisfactory and there was always the possibility that the dominance-groups were in fact spurious groupings with the dominance of a particular species obscuring very real floristic differences between the stands. An attempt was thus made to re-arrange the species-releve matrix by hand but this proved to be equally unsatisfactory. It was thus decided to use the results of the Ward's method analysis as the basis for categorising different community-types though in the realisation that some of the groupings defined by dominance might not be optimal on the basis of total floristics. Indeed in a few cases some stands were subjectively re-allocated to new groupings where it was felt they more appropriately belonged.

Despite these problems it is felt that the main vegetational types recognised here represent "real" vegetational units which can be at least loosely defined on the basis of their floristic content. What is more in question is (a) whether certain stands could be better placed in other units, or (b) whether additional floristic units could be created from the data.

Fig. 6.6.I.

HIERARCHICAL RELATIONSHIPS
OF RICH FEN MEADOW COMMUNITIES



Because of the various re-allocations of stands that have been made, the dendrogram produced by Ward's method is no longer valid and will not be reproduced. It is worth noting, however, that the two penultimate groups that existed before the final fusion were well characterised floristically. One which may be called the Briza-group was characterised by a species-group containing Briza media, Carex nigra, Prunella vulgaris, Trifolium pratense, T. repens and Triglochin palustris. The other, the "typical"-group, had none of these. In a similar way the application of Association Analysis to the same data set selected Briza media as the first division species. (Interestingly, Briza was also selected as the first division species of the Group 4 (calcareous mire) data). It is not, however, clear that this corresponds to a fundamental floristic or ecological division of the data set and indeed in some places it cuts across what would seem to be more "meaningful" floristic groupings. Thus, whilst it is convenient to retain this hierarchical structure for economy of description of the various groupings, it would seem more useful to discard it when constructing the final syntaxonomic arrangement.

Fig. 6.6.I. shows the hierarchical relationships of the communities that is used for the subsequent description.

6.6.A. Briza series.

Community-types 6.6.1. to 6.6.6. are characterised by

the occurrence of a species-group containing Briza media, Carex nigra, Prunella vulgaris, Trifolium pratense, T. repens, and Triglochin palustre. These are largely absent from the non-Briza series of community-types (viz. 6.6.7.-6.6.14.).

6.6.2. Carex lepidocarpa nodum.

Characterising species-group: Anagallis tenella, Carex flacca, C. lepidocarpa, Eriophorum angustifolium, Pedicularis palustris, Parnassia palustris; plus differentials of the sub-groups.

Description: A rather loosely defined group composed of fairly species-rich stands of vegetation (up to c. 40 spp./ 10 m^2). These are often developed on flushed slopes and are characteristically small in extent (e.g. 2 m x 2 m), frequently occurring just as fragments intermixed with wet grassland. The phanerogam cover is usually more open that is often the case in these grassy fens with open runnels and/or a better developed bryophyte layer with frequent Campylium stellatum in addition to Acrocladium cuspidatum. The characterising species are listed above. It should be observed, however, that these are only tenable as a group and individual species may be absent from a number of the stands. Carex lepidocarpa is, however, relatively constant. As well as these species others, such as Carex pulicaris, Epipactis palustris, Gymnadenia densiflora and Bryum pseudotriquetrum are sometimes found and together these indicate the close relations of these stands to some of

the Schoenus-Juncus subnodulosus communities.

Four variants may be distinguished:

6.6.2.1. Menyanthes variant: Generally a rather short herbaceous community of 30-40 cms dominated by small sedges - Carex lepidocarpa, C. nigra and C. panicea, and often with large amounts of Menyanthes trifoliata. Juncus subnodulosus does not occur, the main rushes being J. articulatus and J. inflexus - both usually in rather small quantity. Often a rather open community (70-80% cover) with Triglochin palustris prominent and sometimes with Carex dioica and Pinguicula vulgaris. Species like Agrostis stolonifera, Anthoxanthum odoratum, Angelica sylvestris, Filipendula ulmaria and Rumex acetosa, which are generally constant in fen meadows, are largely absent here. Cratoneuron commutatum can be abundant in places.

Recorded from the Oolites in Gloucestershire, the Chalk in Yorks. and the Magnesian Limestone in Co. Durham.

The remaining variants may all be distinguished from the first by the occurrence of Molinia caerulea, Hydrocotyle vulgaris and Potentilla erecta with fairly high constancy:

6.6.2.2. Philonotis calcarea variant: A very species-rich community (c. 60 spp./sample) developed on spring fens in parts of Norfolk (especially at Buxton Heath). The bryophyte layer is well developed with about 50% cover

containing, in addition to the predominant Acrocladium cuspidatum, species such as Drepanocladus revolvens (intermedius), Philonotis calcarea, Riccardia pinguis and Sphagnum palustre. Juncus subnodulosus is the dominant angiosperm.

6.6.2.3. Typical variant. Designated by the absence of the species of the other variants. Encompasses species-rich stands (64 species in one 10 m^2 sample) dominated by Juncus subnodulosus. Small sedges - Carex panicea, C. nigra and C. hostiana are frequent but Carex lepidocarpa is either absent or poorly represented. The moss layer is often poorly developed. Normally developed in fen areas slightly aside from the main influence of water seepage.

6.6.2.4. Schoenus nigricans variant. Characterised by the occurrence of Schoenus nigricans in small quantity. This has been recorded mainly from the slopes of some of the fen basins in Anglesey and is particularly well developed around Cors y Farl. In such sites Dactylorhiza purpurella, Luzula multiflora, Oenanthe lachenalii and Serratula tinctoria are often found as well. A less rich example has been recorded from Flordon Common, Norfolk (S.289), which may represent a piece of former Schoenus fen that has largely dried out.

6.6.3. Centaurea nigra nodum.

Characterising species-group: Centaurea nigra, Plantago lanceolata, Potentilla anserina, Ranunculus repens.

Description: This is a rather nebulous nodum representative of a fairly species-rich fen meadow vegetation which is widely distributed in England and Wales. The stands are dominated usually by Juncus subnodulosus with J. articulatus as a constant subordinate species which can be abundant in some places. The cover is closed (95-100%) but nonethless the stands are quite rich in associates (average species number = 41/10 m^2). Molinia is constant and abundant in some sites with most of the constant species being well represented, except for Scrophularia aquatica which is completely absent and Hypericum tetrapterum which are rare. Molinia caerulea is constant and abundant in some stands. In general the larger sedges are not prominent as, although both Carex acutiformis and C. disticha occur occasionally, it is usually only with low cover.

The characterising species-group is not well developed with only Centaurea nigra being constant.

Other species frequently occurring include Carex panicea, Epilobium palustre, Galium palustre, Lythrum salicaria and Succisa pratensis.

Mosses are poorly developed - often only Acrocladium cuspidatum and Brachythecium rutabulum occur.

The community has been recorded from damp fen meadows in

flat low-lying valley bottom areas, where they can sometimes be extensive. Such areas are not directly irrigated by seepage water. It also occurs as a zone just above, or alongside, seepage areas on slopes. In both circumstances it is usually subject to grazing. One development of this community is from the Gordano valley in Somerset (cf. WILLIS & JEFFERIES, 1959, who list a similar fen meadow community). This contains much Carex nigra with acidophilic species such as Carex demissa, C. echinata and Sieglingia decumbens, and is rather different from the other stands grouped together here.

6.6.4. Carex hirta-Deschampsia caespitosa nodum.

Characterising species-group: Carex hirta, Deschampsia cespitosa, Potentilla reptans, Cynosurus cristatus.

Description: A comparatively distinct community-type representing one of the driest forms of fen-meadow such as is developed at the transition between wet fen and drier grassland, at the edge of fen systems, or on the site of marshes that have largely dried out. The diagnostic species for this community are, (i) the species of the Centaurea nigra group (6.6.3., particularly Centaurea nigra, Plantago lanceolata and Potentilla anserina), together with the characterising species listed above. In addition, other species such as Achillea millefolium, Betonica officinalis, Galium verum, Listera ovata, Senecio erucifolius, Silaum silaus and Pulicaria dysenterica can be found here.

The main ruch is Juncus subnodulosus, usually with J. articulatus and often with J. inflexus. However, by and large the rush cover is not great and graminaceous species may play an equally important part. Especially where there has been little grazing, the community often appears as a form of rough grassland with the prominence of coarse tussocks of Deschampsia cespitosa and Festuca arundinacea. Tufts of Molinia caerulea may be frequent as well. In addition to these the usual grasses of fen meadow (see 6.6.1.2.) are often abundant and Holcus lanatus can be very conspicuous. Arrhenatherum elatius and Calamagrostis epigejos can also occur. Filipendula ulmaria can sometimes be plentiful, again especially under reduced grazing pressure.

In general, sedges are not very important, though Carex panicea is a constant of the group. As a rule both Carex disticha and C. acutiformis are just occasional.

The constant species of fen meadow are generally well developed, though mosses, as usual, are poor, often restricted to a few scattered strands of Acrocladium cuspitatum. Overall, these stands tend to be species rich ranging between 40-60 spp./sample.

Where the community has developed in association with drying out areas of calcareous fen the tor-grass, Brachypodium pinnatum, may sometimes be found. In situations where a relatively short turf has been maintained species

such as Euphrasia nemorosa may appear. At the edge of one such area at Dernford Fen in Cambridgeshire, some Blackstonia perfoliata and Gentianella amarella also occur.

6.6.5. Typical nodum.

Characterising species: None. Separated from the other groups by the absence of differential species.

Description: This is not a well defined nodum and basically serves just to accommodate stands dominated by Juncus subnodulosus and with a full complement of the constant-species of fen meadow. With the fen rush there are varying proportions of the two other common Junci of fen meadow, J. articulatus and J. inflexus. Sedges, however, are relatively unimportant though Carex panicea is a constant species. In some of the stands Centaurea nigra and Pulicaria dysenterica occur.

The stands all came from seepage areas on gentle slopes.

6.6.6. Carex disticha nodum.

Characterising species: Carex disticha.

Description: This nodum - which is only rather weakly characterised by the constancy of Carex disticha - encompasses some of the most typical developments of spring fens in lowland England and Wales. The characteristic location is on the marshy slopes of small stream valleys, often near

the headwaters, where there are springs and areas of water seepage. Such areas have a constant throughflow of water maintained at, or just below, the surface throughout the year. Often they are rather small, developed only in the areas immediately influenced by the irrigating water. Outside of this they show a transition to wet meadow.

The stands included here have a full representation of the constant species of fen meadow and, in addition, others such as Ajuga reptans, Arrhenatherum elatius, Dactylorhiza fuchsii, D. incarnata, Ranunculus flammula, Rhinanthus minor and, occasionally, Menyanthes trifoliata. It is often inappropriate to speak of a dominant species: frequently, there is a mixture of several important species and the proportions may vary within the stand. These include Carex disticha, sometimes C. acutiformis, Juncus articulatus, J. inflexus, J. subnodulosus and, in one place, Equisetum palustre. Holcus lanatus and Festuca rubra can also be plentiful.

It is clear from Table 6 that this community-type can be subdivided into two variants. In the first Juncus inflexus is an important species and growing with it there is often Carex hirta, Deschampsia cespitosa, Epilobium parviflorum and Pulicaria dysenterica. In the other, Juncus subnodulosus is more prominent, often with J. inflexus and Carex acutiformis.

6.6.B. Non-Briza series. The subsequent community-types are all characterised by the absence of the species-group characteristic for the Briza media series, although stands may contain one or two of the species.

6.6.7. Iris pseudacorus nodum.

Characterising species-group: Iris pseudacorus, Lythrum salicaria, Valeriana officinalis; plus the species differential for each sub-group.

Description: A rather variable, though fairly clearly defined unit, composed in the main of stands of topogenous fen meadow. It is particularly associated with some of the fen basins of East Anglia, where often the community would seem to be derivative from the species-rich tall fen vegetation of 6.2.

The characterising species are not very well developed. Iris is fairly constant, but Lythrum salicaria and Valeriana officinalis only occur in some of the stands. However, in association with the species of the sub-groups (below) and the general prominence of Phragmites communis and Hydrocotyle vulgaris the group is reasonably well delimited. Another feature of the group is that some of the "constant" species of fen meadow have only poor representation here. In particular, Anthoxanthum odoratum, Lathyrus pratensis, Hypericum tetrapterum and Scrophularia aquatica occur only sparingly, whilst others, such as Agrostis stolonifera, Equisetum palustre and Cardamine pratensis have their frequency reduced.

This most probably reflects the relatively recent origin of many stands from a Magnocaricion type of vegetation.

The appearance of the community tends to be rather different to that of more typical fen meadow. This is partly due to the prominence of some of the taller herbaceous species such as Iris and Lythrum, but it is also due to Phragmites communis which often forms a rather sparse upper stratum to the stands. However, dominance remains firmly within the rush layer and is normally held by Juncus subnodulosus. Indeed, other rushes are often little in evidence: Juncus articulatus occurs just occasionally and J. inflexus is even more restricted. Sedges, however, are more plentiful. Both Carex acutiformis and C. disticha can come in considerable quantity and in some stands the tussocks of Carex paniculata are prominent. Carex elata is also sometimes found.

As in many other fen-meadow types mosses are only poorly developed. Acrocladium cuspidatum is constant and Brachythecium rutabulum remains frequent. In addition, Campylium stellatum and Mnium longirostrum often occur but otherwise there are few other species.

Within this Iris pseudacorus-nodum certain sub-groups may be distinguished:

6.6.7.1. Typical variant. This is composed of rather

variable species-poor stands (average = 15 spp./sample) and lacks positive characterisation. Even the constant species of fen meadow are poorly developed here and, in addition to those mentioned in 6.6.7. (above), others like Cerastium holosteoides, Festuca rubra, Galium uliginosum, Poa trivialis, Ranunculus acris and Valeriana dioica are largely absent from the stands. Examples of this can be found in places around Hickling Broad in East Norfolk and in various fen systems elsewhere.

6.6.7.2. Symphytum variant. Characterised by the occurrence of Symphytum officinale and Thalictrum flavum, this includes areas of wet Juncus subnodulosus fen with Carex paniculata alongside the R. Test at Bransbury Common, Hants. This vegetation has many similarities to the Carex paniculata-Phragmites fen (6.3.2.3.) of the same area and most probably represents a grazed version. Also included here are two areas of fen meadow near Wicken fen, Cambs. and also samples of the vegetation from the droves at Wicken. These areas, kept open by regular mowing, support some of the richest vegetation of the fen. In addition to Symphytum and Thalictrum they also have Lysimachia vulgaris and Calamagrostis canescens, together with Molinia caerulea and many lower-growing species notably Carex distans, C. flacca, C. hostiana, C. lepidocarpa, C. panicea, Eleocharis quinqueflora, Dactylorhiza incarnata, Ranunculus flammula and Rhinanthus

minor. Lathyrus palustris can also be found. The vegetation of such droves is clearly derived from that of the surrounding fen and typical fen meadow species such as Equisetum palustre, Lathyrus pratensis, Lotus uliginosus and Vicia cracca tend to be absent. In the absence of regular mowing the droves would revert to high fen.

6.6.7.3. Peucedanum palustre variant. This has been recorded from areas of fen meadow associated with the peat basins of the East Norfolk river valleys. Characteristic of these stands is the occurrence of species of the Cladium-Phragmites fens (6.2.), in particular Peucedanum palustre, Calamagrostis canescens, Lysimachia vulgaris and Stellaria palustris. With these there is also Equisetum fluviatile, Dactylorhiza praetermissa, Menyanthes trifoliata, Potentilla palustris, Ranunculus flammula and also, in some places, Carex appropinquata, Epilobium palustre and Oenanthe fistulosa.

Such areas of fen-meadow, dominated by Juncus subnodulosus, have only been found occasionally. The community is richly developed over parts of the grazed Burgh Common alongside the Muckfleet. Here there are additional species such as Carex diandra, C. lepidocarpa, Eriophorum angustifolium and Pedicularis palustris. An example is also known from the Sutton Broad area and from the Wheatfen complex. Here, however, it is of very restricted occurrence, mainly along the western fen margin. It was once a more widely distributed

community, with the dominance of the fen rush maintained by regular mowing (LAMBERT, 1946). With the cessation of mowing there has been a reversion to Phragmites-dominated communities and the establishment of fen carr.

As at Wicken fen related communities are maintained by the regular mowing of droves and these permit low-growing species to persist. The following list was made from a pathway in the Upton Broad fen basin:

Upton, South Walsham, Norfolk. TG 385138.

Sample area: 1 m x 20 m

Cover: Moss: 30% Herbs: 80%

Anagallis tenella	-	Juncus subnodulosus	2,3
Agrostis stolonifera	+	Luzula multiflora	+
Calamagrostis canescens	+	Molinia caerulea	+
Cardamine pratensis	+	Parnassia palustris	+
Carex diandra	+	Pedicularis palustris	+
C. elata	2,3	Peucedanum palustris	+
C. flacca	+	Platanthera bifolia	+
C. lepidocarpa	1,1	Pyrola rotundifolia	+
C. panicea	1,1	Potentilla erecta	+
Cirsium palustre	+	Schoenus nigricans	1,1
C. dissectum	+	Succisa pratensis	+
Cladium mariscus	+	Thelypteris palustris	+
Dactylorhiza incarnata	+	Valeriana dioica	+
D. praetermissa	+		
Epipactis palustris	+	Acrocladium cuspidatum	+
Filipendula ulmaria	+	Hypnum cupressiforme	+
Galium palustre	+	Mnium punctatum	+
G. uliginosum	+	Sphagnum fimbriatum	+,2
Hydrocotyle vulgaris	+	S. plumulosum	+

Many of these species were completely absent from the adjoining Cladium fen. In a similar way Parnassia palustris occurs on a path in the Reedham marshes, but seems to be completely absent from the other areas.

6.6.8. Carex elata nodum.

Characterising species: Carex elata.

Description: This is a community of spring-fed hollows characterised by the occurrence of the tussock sedge, Carex elata, often in quite large amounts. Juncus subnodulosus is usually the dominant plant, though it may just be do-dominant with the sedge. J. articulatus normally occurs but only in small quantity. Other species characteristically occurring are Carex panicea, Epilobium palustre, Galium palustre and Hydrocotyle vulgaris. Potentilla palustris is also constant and can be present in quite large amounts. Phragmites communis is usually present as well and forms a rather sparse upper stratum to the community.

Two distinct variants can be recognised:

6.6.8.1. Typical variant. In this community-type the constant species of fen meadow are largely well developed. It is not widespread and appears to be confined to East Anglia. Characteristically it occurs in small, shallow depressions where water is able to accumulate so that even during the summer the bottom is normally wet (though not necessarily with standing water). Examples have been found at Shepreth Moor in Cambridgeshire, Pashford Poor's Fen near Lakenheath in Suffolk, Blo' Norton Fen near Thelnetham (also in Suffolk) and Sculthorpe Moor in Norfolk.

6.6.8.2. Pedicularis palustris variant: This is a very distinctive variant separated from the typical community not only by Pedicularis palustris, but also by a range of other species including Menyanthes trifoliata, Ranunculus flammula and R. lingua. Also, many of the constant species of fen meadow are completely absent or poorly represented. These include Anthoxanthum odoratum, Cerastium holostoides, Cirsium palustre, Festuca rubra, Holcus lanatus, Galium uliginosus, Lotus uliginosus, Lychnis flos-cuculi, Hypericum tetrapterum, Poa trivialis, Scrophularia aquatica, Rumex acetosa and Brachythecium rutabulum.

The community is well developed at Thompson Common in Norfolk, where it forms a clear zone of wet fen around the periphery of Carex elata swamp in the depressions of the common (see 6.1.2.). The slopes of these depressions are often occupied by a rather dry version of Juncus subnodulosus fen meadow belonging to the Carex hirta-Deschampsia cespitosa group (6.6.4.). At the base of the slope conditions are much wetter and here this Carex elata community forms a transitional zone to the swampy parts. Frequently this zone is narrow and fragmentarily developed. However, where at the base of the slope there is a larger area of virtually flat ground the community is often well developed. The stands - which are well grazed and trampled by stock - are characteristically low-growing. Both Mentha aquatica and Pedicularis

palustris are often abundant and there may be quite large amounts of Potentilla palustris too. Menyanthes can be frequent and, in some places at least, forms small floating rafts. In come places Calamagrostis stricta is abundant. The moss layer is extensive though mainly composed only of Acrocladium cuspidatum.

A similar community has also been recorded from a wet depression at Cors Bodelio in Anglesey.

6.6.9. Schoenus nigricans - Carex diandra nodum.

Characterising species-group: Carex diandra, C. flacca, Schoenus nigricans.

Description: A rather distinct community-type created from 3 samples all made in Anglesey - two from Cors Bodelio and one from a wet bog near Simdda-wen, Llanbadrig. In each case the community was developed in fairly small, shallow wet depressions.

Juncus subnodulosus predominates with much Carex panicea and Molinia caerulea. Constants include Carex diandra, C. flacca, Equisetum fluviatile, Epilobium palustre, Galium palustre, Pedicularis palustris and Ranunculus flammula. Schoenus nigricans occurred in two stands, though only sparingly; Carex lepidocarpa in one. Acrocladium cuspidatum forms a fairly extensive bryophyte layer with some Brachythecium rutabulum and Mnium longirostrum.

6.6.10. Molinia caerulea - Eupatorium cannabinum nodum.

Characterising species-group: Molinia caerulea, Eupatorium cannabinum, Hydrocotyle vulgaris, Potentilla erecta; plus absence of differentials for other groups.

Description: Juncus subnodulosus dominant. Other rushes are infrequent and unimportant. Species that are fairly constant include the characterising species (above), Carex panicea and the normal constant species of fen meadow, though Anthoxanthum odoratum, Agrostis stolonifera, Ranunculus acris, Rumex acetosa and Scrophularia aquatica are all infrequent. Carex acutiformis and C. disticha are only occasional.

This community can be found both in flat, low-lying wet areas and also in association with springs. In this latter case species such as Anagallis tenella, Epipactis palustris, Gymnadenia densiflora and Pinguicula vulgaris sometimes come in, the moss layer becomes more extensive and Cratoneuron commutatum and Pellia endiviifolia grow with Acrocladium cuspidatum.

6.6.11. Species-poor Centaurea nigra nodum.

Characterising species-group: Centaurea nigra, Plantago lanceolata, Ranunculus repens. Differs from 6.6.3. by the absence of Briza media, Carex nigra, Hydrocotyle vulgaris, Molinia caerulea, Potentilla erecta, Prunella vulgaris, Trifolium pratense, T. repens.

Description: This community-type is very similar to that of 6.6.3., of which it represents a species-poor version. The dominant species are either Juncus subnodulosus, J. articulatus

or Carex acutiformis. The habitat is normally relatively dry during the summer, even when the community is on spring slopes.

Some stands are transitional into the next community-type.

6.6.12. Species-poor Carex hirta-Deschampsia cespitosa nodum.

Characterising species-group: Carex hirta, Deschampsia cespitosa, Festuca arundinacea, Potentilla reptans. Differs from 6.6.4. by the absence of Briza media, Hydrocotyle vulgaris, Molinia caerulea, Potentilla erecta, Prunella vulgaris, Trifolium pratense, T. repens.

Description: A community-type paralleling that of 6.6.4., of which it represents an impoverished version. The dominant is Juncus subnodulosus, but Juncus inflexus can be very prominent and some stands can also support quite large quantities of Carex acutiformis or C. disticha.

This community is also characteristic of dry conditions, but unlike the species-rich Carex hirta-Deschampsia group (6.6.4.) it tends to be developed only in a fragmentary form. It thus may occupy small shallow depressions on drying out moors; it has been recorded from spring fens where drainage has been attempted; and it can also occur around the periphery of wetter spring fens where it is only subject to a limited degree of seepage.

6.6.13. Typical nodum.

Characterising species-group: None. Separated from other groups by the absence of differentials and by the occurrence of Juncus subnodulosus, usually as a dominant.

Description: Included here are a large number of generally species-poor stands (values range from 15-30/sample), which are categorised mainly by the absence of any differentiating species. Juncus subnodulosus is a constant species and is normally abundant in the stands, often being the predominant plant. With this come the constant species of fen-meadow mainly developed quite well with the exceptions of Anthoxanthum odoratum, Cerastium holostecides, Festuca rubra, Poa trivialis, Rumex acetosa and Succisa pratensis - all of which are only sporadic. There are often only a few additional plants in many stands.

The group may be subdivided into two:

6.6.13.1. Epilobium hirsutum variant. Here Epilobium hirsutum and Arrhenatherum elatius are defining species. Two facies may be recognised:

(a) Carex paniculata facies: Carex paniculata is abundant often forming large and closely-set tussocks, which determine the physiognomy of the stand. The tussock-tops often support strands of Acrocladium cuspidatum and, especially, Brachythecium rutabulum. Sallow (Salix cinerea) may also grow here. Such stands are often located in some of the wettest parts of rich fen systems: e.g. on flattish spring mire surfaces where throughflow of water is impeded or, in the bottom of shallow valleys in areas maintained constantly wet

by springs. Carex paniculata can occur on the slopes of spring fens but often only as isolated tussocks.

(b) Carex acutiformis facies: Here Carex acutiformis is co-dominant with the fen rush and can form quite extensive sedge meadows in low-lying flat valley bottoms, etc. The facies can also develop in a more localised form around springs and seepage areas.

6.6.13.2. Typical variant: This is rather similar to the foregoing community-type but lacks the Epilobium hirsutum and Arrhenathenum elatius. Juncus inflexus and J. articulatus occur along with J. subnodulosus but they are of low constancy and also usually of low cover. Three facies can be discerned:

(a) Typical facies: Juncus subnodulosus is the dominant plant. With it Juncus articulatus, J. inflexus and Carex disticha may occasionally be important. These stands may often be species-poor (e.g. c. 19-20 spp./sample). They can occur as fen meadow in damp depressions, but are particularly characteristic of sloping spring mire surfaces. In very wet conditions, such as where seepage from the springs coalesces to form distinct runnels or where it is ponded back in some way, Berula erecta can be frequent.

(b) Carex acutiformis facies: Carex acutiformis is either the most important plant of the stands or is co-dominant with Juncus subnodulosus. With it are often Iris

pseudacorus, Lythrum salicaria, Epilobium palustre and Galium palustre. It is particularly important on sloping mire surfaces, especially in the wettest parts associated with the main outfall of seepage water. Here these rather impoverished stands can occupy some of the most central seepage areas on very soft, open muds and peats. They grade outwards into a richer community where the seepage is less vigorous and where a more closed vegetation cover has developed.

(c) Phragmites communis facies. A version of the fen-meadow community which tends to develop if grazing pressure is not too severe.

6.6.14. Carex acutiformis nodum.

Characterising species-group: Carex acutiformis; plus absence of differentials.

Description: Encompassed here are stands of vegetation thoroughly dominated by the lesser pond sedge, Carex acutiformis. This plant can form extensive sedge meadows of some 75 cms high often with very few associated species. Rushes occur in small quantity. Sometimes Juncus subnodulosus, but more often J. articulatus or J. inflexus, and J. effusus can be found. Epilobium hirsutum is often present, sometimes in quite large amounts, and with it Urtica dioica and Galium aparine. Mosses can be completely absent, or represented by just a few stands of Brachythecium rutabulum.

These sedge meadows are often found in relatively dry situations, away from the major influence of seepage water. In some cases they form "sea" surrounding "islands" of Carex acutiformis versions of Juncus subnodulosus-dominated spring fens (represented often by the Carex acutiformis facies of the typical group (6.6.13.2b.)). Carex acutiformis seems to be quite an aggressive species. Examples are known where it has formed fairly pure stands upon invading former damp grassland after the cessation of mowing for hay. Cattle grazing seems to have little affect upon its vigour.

6.6.15. Other rich fen meadow communities in Britain.

There have been very few descriptions of rich fen meadows of the type considered here. LAMBERT (1946, 1948) has described Juncus subnodulosus dominated fen communities from parts of the Norfolk Broads region. CROMPTON (1962) has given some description of the Triplow fen meadows near Cambridge, but otherwise there is remarkably little documentation.

Related communities have been described from Scotland. SPENCE (1964) has a Juncus articulatus-Angelica community from grazed fens which is similar to some of the fen meadows. McVEAN & RATCLIFFE (1962) and RATCLIFFE (1964) describe Juncus acutiflorus-Acrocladium cuspidatum mires, but these refer to vegetation-types not compassed by this survey, though there are obviously very close similarities.

6.6.16. Syntaxonomy

Stands of vegetation dominated by Juncus subnodulosus have often been united into a single Association, the Juncetum subnodulosi Koch 26, later split by OBERDORFER (1957) into a lowland Crepido-Juncetum subnodulosi (Libbert 32) Tx. 37 and a montane Trollio-Juncetum subnodulosi Oberd. 57. The status of the syntaxon has, however, been contentious - mainly because the fen rush is a species of wide sociological amplitude and can be prominent in a variety of community-types. Some types have floristics related to Caricion davallianae vegetations, especially to Schoenus nigricans-dominated types (e.g. KOCH, 1926; LIBBERT, 1932; ZOBRIST, 1935; TÜXEN, 1937; VOLLMAR, 1947; JESCHKE, 1959), though even here it is evident that there are also very strong affinities with the vegetation of enriched wet meadows. Indeed, Juncus subnodulosus seems to be particularly well developed in the "Feuchtwiesen" of the Calthion Tx. 37 em. Tx. 51 (OBERDORFER et al., 1967) and many descriptions refer to this type of community (e.g. OBERDORFER, 1957; KORNECK, 1963; KRAUSCH, 1964; PASSARGE, 1964; KLOSS, 1965). In addition, the rush may also be the dominant species in certain pioneer communities of shallow swamps (6.1.5.). These have sometimes been encompassed within the Juncetum subnodulosi (e.g. JESCHKE, 1959), although others (e.g. KRAUSCH, 1964; PASSARGE, 1964; KLOSS, 1965; OBERDORFER et al., 1967) have preferred to regard them as independent

communities.

As might be anticipated, the Juncetum subnodulosi is only weakly characterised floristically. Crepis paludosus and Camptothecium nitens have been suggested as character species (e.g. KOCH, 1926; VOLLMAR, 1947) but these seem to have had only local applicability and, effectively, the community-type has come to be defined by the dominance of the fen rush (SEGAL, 1968). Thus, doubt has been cast upon the validity of the Association. WESTHOFF & DEN HELD (1969) do not accept it and OBERDORFER et al. (1967) have raised the possibility of allocating the material to Juncus subnodulosus-sub-communities of other, better defined, Associations.

In this survey it has already been decided that Juncus subnodulosus-stands of shallow swamps should be placed within the Phragmition (see 6.1.5.2.) and that those closely related to Schoenus nigricans-vegetations are best united with these into a Schoeneto-Juncetum subnodulosi Association (see 6.4.6.; 6.4.7.). The residue - which, in fact, represents the main development of Juncus subnodulosus stands in Britain - comprises the rich fen meadow communities. If the Juncetum subnodulosi is to be retained at all then it would be best restricted to refer only to these. However, such a unit would seem to be of limited value for, as the present work has shown, closely related to the Juncus subnodulosus-stands of rich fen meadow are other types in which the rush is absent. The partitioning

of the data in the classification has not consistently been based upon the presence or absence of the Juncus (although it may be noted that some of the community-types are characterised by the invariate occurrence of the rush whilst in others it tends to be absent). It thus seems likely that a more appropriate syntaxon would be one of wider compass than the Juncetum subnodulosi which would also accommodate certain fen meadow vegetation-types with dominants other than the fen rush. Whether such a syntaxon, of suitable homogeneity and floristic characterisation, is feasible remains to be established for it is considered that additional data are required from other fen meadow-types before the matter can be resolved. For the present the community-types recognised from rich fen meadow will not be given a formal classification but simply regarded as noda of undecided status. It is not evident even whether they conform to a single syntaxon or whether they would be best allocated to several.

6.6.17. Syntaxonomic placement.

Of the constant species of rich fen meadows (6.6.1.2.) a large proportion have been used in some way to characterise the higher syntaxa of the Molinio-Arrhenatheretea Tx 37. (see 2.4.). Cardamine pratensis, Cerastium holosteoides, Festuca rubra, Holcus lanatus, Lathyrus pratensis, Poa trivialis,

Ranunculus acris and Rumex acetosa have been given as Class character species and a number of other species of lower constancy (e.g. Plantago lanceolata) have been given similar status. Angelica sylvestris, Cirsium palustre, Equisetum palustre, Filipendula ulmaria, Galium uliginosum, Lotus uliginosus and Lychnis flos-cuculi have been to characterise the Molinietalia Koch 26. As these species are well developed throughout the noda it seems appropriate to refer all of these to the Molinietalia, though it is worth noting that a number of the plants are also prominent in the Schoenus nigricans-Juncus subnodulosus communities that have been assigned to the Caricion davallianae.

Within the Molinietalia it would seem as if the noda should be placed within the Calthion. Calthion character species (from WESTHOFF & DEN HELD, 1969) which occur fairly constantly are Caltha palustris, Carex disticha, Lotus uliginosus, Lychnis flos-cuculi and Myosotis scorpioides (local and of low constancy). Succisa pratensis (given as a Junco-Molinion character) is also constant, but the precise diagnostic value of this is uncertain as, in this survey, it has been shown to be widespread and well developed in a number of rich fen vegetation types as well as in Junco-Molinion communities. It can, however, be noted that some of the noda in which Molinia is particularly prominent (e.g. the Molinia-Eupatorium nodum, 6.6.10.) may have affinities with the Junco-Molinion.

6.6.18. Synopsis of rich fen meadow communities.

MOLINIO-ARRHENATHERETEA Tx. 37

MOLINIETALIA Koch 26

CALTHION PALUSTRIS Tx. 37 em. 51.

- Juncus-Carex lepidocarpa nodum (6.6.2.)
  - Menyanthes var. (6.6.2.1.)
  - Philonotis calcarea var. (6.6.2.2.)
  - Typical var. (6.6.2.3.)
  - Schoenus nigricans var. (6.6.2.4.)
- Juncus-Centaurea nigra nodum
  - Briza media var. (6.6.3.)
  - Typical var. (6.6.11.)
- Juncus-Carex hirta-Deschampsia cespitosa nodum
  - Briza media var. (6.6.4.)
  - Typical var. (6.6.12.)
- Juncus subnodulosus typical nodum
  - Briza media var. (6.6.5.)
  - Molinia caerulea-Eupatorium cannabinum var. (6.6.10.)
  - Typical var. (6.6.13.)
    - Epilobium hirsutum sub-var. (6.6.13.1.)
    - Typical sub-var. (6.6.13.2.)
- Juncus-Carex disticha nodum (6.6.6.)
- Juncus-Iris pseudacorus nodum (6.6.7.)
  - Typical var. (6.6.7.1.)
  - Symphytum var. (6.6.7.2.)
  - Peucedanum var. (6.6.7.3.)
- Juncus subnodulosus-Carex elata nodum (6.6.8.)
  - Typical var. (6.6.8.1.)
  - Pedicularis palustris var. (6.6.8.2.)
- Juncus subnodulosus-Schoenus-Carex diandra nodum (6.6.9.)
- Carex acutiformis sociation (6.6.14.)

6.7. Group 7. Molinia caerulea communities - Table 7.

This group is composed of 53 samples all made from vegetation dominated by Molinia caerulea. This type of fen grassland forms a distinct physiognomic category within rich fen systems. It is found particularly in relatively dry parts, often in marginal locations, frequently just occurring as small fragments. Such areas are only of peripheral interest to this survey and have mainly been included because of the clear floristic affinities shown with wetter fen communities from which, in some cases at least, they have developed.

As these are marginal to the main survey and only relatively few data have been collected, together with the fact that there are other forms of Molinia-dominated grassland and mires outside of the rich fen context, the communities will only be described in limited detail. It is felt that a fuller description, together with an assessment of their syntaxonomic status, must await further data pertinent to Molinia-vegetation, so that a more comprehensive and better-balanced account can be given.

The group constitutes a clear category and there was little doubt as to which samples should be assigned to it. The only problem arising was with regard to certain stands that seemed to be transition to certain calcareous mire (Group 4) communities. In all cases these were assigned to Group 4 and only the unambiguous examples of Molinia-fen-grassland were incorporated into Group 7. The samples were

analysed by Information Analysis. Relocation procedures using the Information statistic were applied at the 10-cluster stage, but only a few individuals were re-allocated and the resultant clusters represented essentially the same vegetational categories. Mention will also be made here of a Carex nigra-Molinia community-type that was not included within the original analyses.

6.7.1. Molinia caerulea communities.

The purple moor grass, Molinia caerulea, has a rather wide sociological amplitude and is an important component of a variety of rich fen plant communities. In such communities it is usually a sub-ordinate species and may be present only in small quantities. However, in many rich fen systems, areas can often be found where the grass is strongly dominant. These are usually comparatively dry places with a fluctuating water-table and may occur in various situations: at the edge of fen systems away from the major influence of the ground water; in elevated areas associated with peat workings or mineral "islands" within the fen; and, occasionally, in areas of water seepage along fen margins which tend to be fairly dry during the summer months. Similar communities can also be formed by the insurrection of Molinia caerulea within rich-fen vegetation either as part of the autogenic successional sequence associated with the accumulation peat or in response to a similar drying out of the fen surface as

a result of drainage or a general reduction in the level of the water-table, etc.

Molinia usually occurs as rather robust tussocks of some 25-50 cms tall, but in some situations this tussocked-habit is lost and the plant can form a fairly even turf (cf. JEFFRIES, 1915). The stands are often poor in species, especially where Molinia is strongly dominant. There are usually some associates, however, even though many of them may be present only in small quantity and confined largely to the spaces between the tussocks. They are grasses such as Anthoxanthum odoratum, Briza media, Deschampsia caespitosa and Holcus lanatus, small sedges such as Carex hostiana and C. panicea, rushes such as Juncus articulatus, J. conglomeratus and J. subnodulosus and a variety of herbaceous dicots. These may include relatively tall species such as Angelica sylvestris, Cirsium palustre and Filipendula ulmaria (which form a rather sparse layer over-topping the Molinia), together with various species of smaller stature - Galium verum, Linum catharticum, Potentilla erecta and Valeriana dioica. There is an overwhelming pre-eminence of semi-rosette hemicryptophytes.

Characteristically, the moss layer is poorly developed. Molinia tussocks do not usually support a rich epiphytic moss flora and the accumulation of litter between them presents unfavourable conditions for the growth of bryophytes. However, in some of the damper, more open sites, bryophytes may become more important. The usual species is mainly Acrocladium

cuspidatum, though Psuedoschleropodium purum is also frequent and Brachythecium rutabulum may occur as well.

This vegetation type thus represents a form of fen grassland. Grasses predominate accompanied by various grassland species. But, the close affinities to rich fen vegetation are indicated by the occurrence, to a greater or lesser degree, of mire species, although these may only be poorly developed in some versions of the vegetation.

6.7.1.1. Types of Molinia caerulea communities.

Table 7 shows the community-types that have been recognised. It is evident that brought together here are vegetation-units with rather different species compositions, united through the dominance of Molinia caerulea (and also the constant occurrence of Potentilla erecta and Succisa pratensis). It is also apparent that many of the groupings cannot easily be defined by the presence or absence of a few differential species. Rather they have been formed by various overlapping combinations of 22 fairly well defined groups of species. Thus, for the purposes of description and characterisation, it is most convenient just to refer to the species-groups that constitute each community-type.

The contents of these groups are as follows:

Species groups.

1: Molinia caerulea
Potentilla erecta

2: Briza media
Valeriana dioica

3: Acrocladium cuspidatum
Carex hostiana
C. panicea

4: Angelica sylvestris
Cirsium palustre
Lotus uliginosus

5: Galium uliginosum
Vicia cracca

6: Centaurea nigra
Deschampsia cespitosa
Filipendula ulmaria

7: Cardamine pratensis
Carex nigra
Eriophorum angustifolium
Juncus articulatus
J. conglomeratus
Ranunculus acris

8: Achillea ptarmica
Dactylorhiza fuchsii
Caltha palustris
Lychnis flos-cuculi
Poa trivialis

9: Achillea millefolium
Hypericum tetrapterum
Potentilla anserina
P. reptans
Pulicaria dysenterica
Trifolium pratense

10: Calluna vulgaris
Erica tetralix
Hypnum cupressiforme
Sieglingia decumbens

11: Carex flacca
Agrostis stolonifera
Linum catharticum
Prunella vulgaris

12: Ctenidium molluscum
Euphrasia nemorosa
Fissidens adianthoides
Pinguicula vulgaris

13: Hylocomium splendens
Rhytidiadelphus squarrosus
Selaginella selaginoides

14: Dactylorhiza incarnata
Juncus inflexus
Ranunculus flammula
Triglochin palustris

15: Aulacomnium palustre
Drosera rotundifolia
Platanthera bifolia
Polygala serpylifolia
Sphagnum plumulosum

16: Myrica gale

17: Calystegia sepium
Cirsium arvense
Cladium mariscus
Lysimachia vulgaris
Salix repens
Calamagrostis canescens
C. epigejos

18: Cirsium dissectum
Juncus subnodulosus
Schoenus nigricans

19: Eupatorium cannabinum
Lythrum salicaria
Phragmites communis

20: Brachythecium rutabulum
Equisetum palustre
Mentha aquatica

21: Cerastium holostoides
Festuca rubra
Lathyrus pratensis
Leontodon autumnalis
Plantago lanceolata

22: Anthoxanthum odoratum
Carex pulicaris
Luzula multiflora

In the following descriptions the species-groups present in each community-type will be given. An asterisk (*) after a group means that the group is only poorly represented in that community-type. A line beneath a group-number means that that species-group is particularly diagnostic for the community-type concerned.

Clearly with a whole range of overlapping species-groups of varying amplitude, such as occur here, various hierarchical sub-divisions of the set of releves are tenable: there are several potential higher-order groupings each of which could be well characterised floristically and, although the final vegetation units are themselves well defined, it is not altogether clear what represents the best arrangement of them into higher order groups. Indeed it might be most appropriate not to invoke any hierarchical organisation at all. However, Information Analysis of the data has produced a satisfactory hierarchical classification and it would seem acceptable to utilise this.

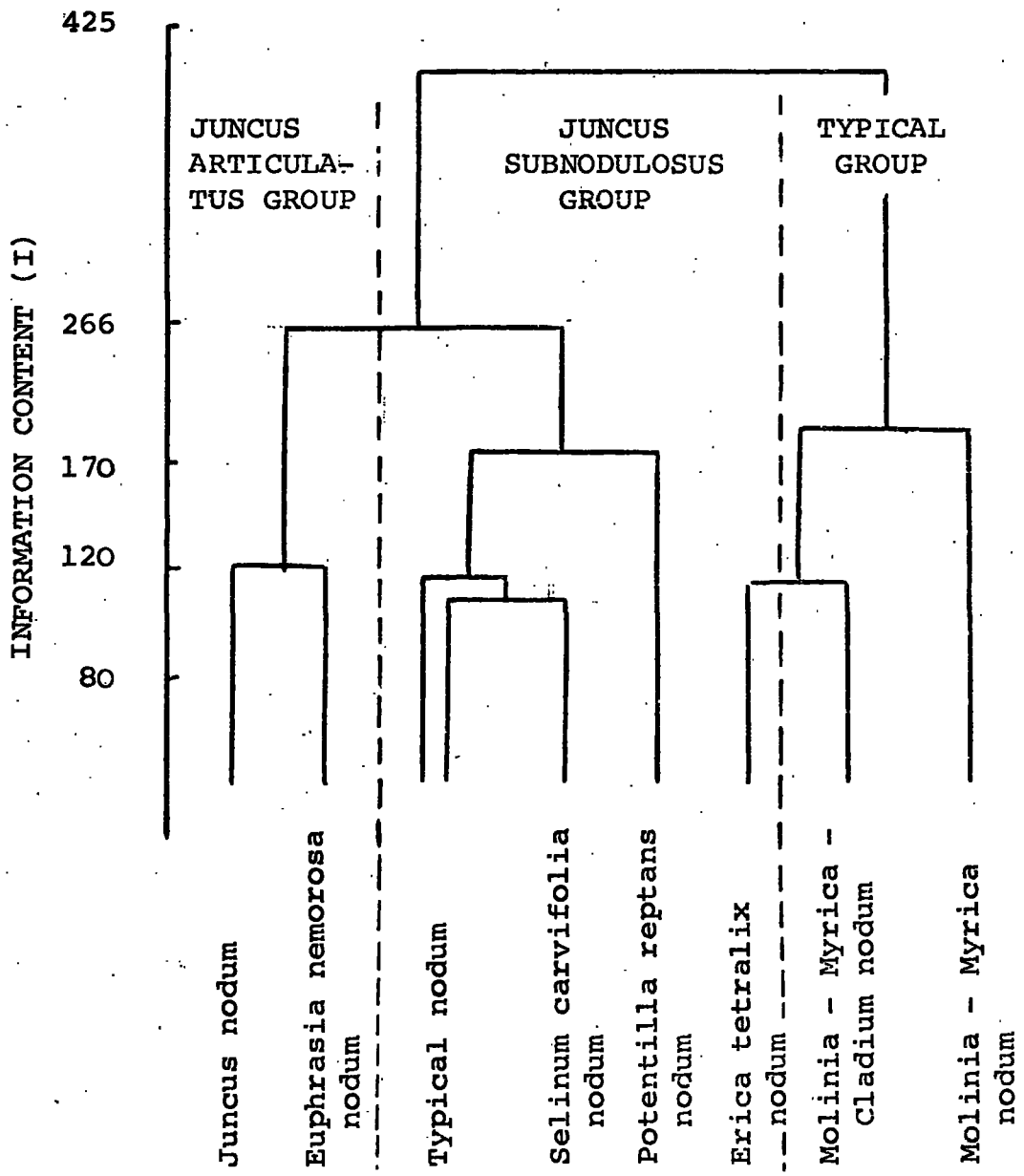
The Information Analysis dendrogram is given in Fig. 6.7.I. Essentially three major groupings have been produced:

(i) Juncus subnodulosus group - defined mainly by the occurrence of the species of Group 18, viz.: Juncus subnodulosus, Cirsium dissectum and Schoenus nigricans.

(ii) Juncus articulatus group - defined mainly by the

Fig. 6.7.I.

INFORMATION ANALYSIS OF
MOLINIA CAERULEA FEN GRASSLAND



occurrence of Group 7 and, to a lesser extent, Group 8 species.

These two groups may be jointly distinguished from the third by the common possession of species-groups 2, 3 and 21.

(iii) Typical group - a heterogenous group which serves to contain a variety of rather dissimilar community-types.

6.7.2. Juncus subnodulosus group.

This group includes releves containing Juncus subnodulosus, Cirsium dissectum and, occasionally, Schoenus nigricans. A number of variants may be distinguished.

6.7.2.1. Typical nodum.

Species groups: 1,2,3,4,5,6,18,21*,22.

Most of the releves included here represent Molinia grassland developed peripherally to wetter depressions containing Schoenus nigricans-Juncus subnodulosus communities. Juncus subnodulosus is an abundant constant and Schoenus occurs at some sites. Tussocks of Molinia caerulea dominate the community with some Holcus lanatus and Deschampsia cespitosa. Mosses are generally rare with just a few scattered plants of Acrocladium cuspidatum and Pseudoschleropodium purum.

This community is typical of calcareous Molinia-grassland developed in drying out fens and supports a variety of species. Amongst others Brachypodium pinnatum and Polygala vulgaris can occasionally be found as well as certain orchidaceous species:

Epipactis palustris, Gymnadenia densiflora and Listera ovata.

6.7.2.2. Potentilla reptans nodum.

Species groups: 1,2,3,4,5,6,9,11*,18,21*.

Similar to the typical variant but distinguished by the occurrence of some of the species of groups 9 and 11, in particular Achillea millefolium, Agrostis stolonifera, Linum catharticum, Potentilla reptans and Trifolium pratense. Galium verum is also frequent here. This also is characteristic of drying-out fen margins and often forms an edge community to rich fen systems, particularly to some of the Breckland fens (cf. "Molinia-edge" community, HASLAM, 1965). Frequently, it occupies a zone between a Schoenus nigricans-Juncus subnodulosus community and calcareous grassland and a mixture of plants both of rich fen and calcareous grassland occurs. Thus, Schoenus nigricans can be found and, although usually in rather sparse quantity, is often flowering and fruiting well despite the dry conditions. Species of calcareous grassland are rather well developed and include Campanula rotundifolia, Cirsium acaulon, Festuca ovina, Ononis spinosa, Plantago media, Polygala vulgaris, Poterium sanguisorba, Thymus drucei and Viola hirta. Mosses are generally rare and sometimes none can be found.

Occasional plants of Cladium mariscus and Phragmites communis can sometimes be found (cf. S.619) but they are usually only in a stunted vegetative state.

6.7.2.3. Selinum carvifolia nodum.

Species groups: 1,2,3,4,5,6*,11,18,19,20.

This variant of fen grassland has only been recorded from Chippenham Fen in Cambridgeshire, where it occupies an extensive area along the northern margin. Phragmites communis forms a sparse upper layer to the community with occasional Cladium mariscus and also taller dicots such as Angelica sylvestris, Cirsium palustre, Eupatorium cannabinum and Lythrum salicaria. Of particular note is the occurrence of the umbellifer Selinum carvifolia. This species formerly occurred in Nottinghamshire and Lincolnshire, but is now restricted to a few sites in Cambridgeshire. It is still abundant at Chippenham where the closely related Peucedanum palustris is curiously absent. It occurs in a range of communities from the Molinia meadows to areas of Cladium fen.

Beneath these taller herbs are dense tussocks of Molinia with much Juncus subnodulosus and, in a few places, Schoenus nigricans. Associates include Carex flacca, C. hostiana, C. panicea, Centaurea nigra, Equisetum palustre, Gymnadenia densiflora, Linum catharticum, Mentha aquatica, Serratula tinctoria and, occasionally, Dactylorhiza incarnata and Epipactis palustris. The moss layer, though sparse, is better developed than in some Molinia-communities with Acrocladium cuspidatum, Brachythecium rutabulum and Campylium stellatum occurring as constants.

Molinia-dominated vegetation containing Selinum carvifolia occurs also in other parts of Chippenham fen, especially along the ridges of the old peat workings, but it is not so well developed and a number of species are absent (S.473, S.476).

6.7.2.4. Erica tetralix nodum.

Species groups: 1,2,3,10,12,15,18,19*,22.

This nodum has been recorded from three sites in East Anglia. At Redgrave Fen and at Lopham Little fen, on either side of the R. Waveney along the Norfolk-Sufolk border, small gravelly islands in amongst the wet calcareous peat support areas of Molinia-dominated acidophilic vegetation (cf. BELLAMY & ROSE, 1961) which is referable to this community-type. The other site is at Buxton Heath in Norfolk, where there is damp calcareous grassland developed at the transition between the oligotrophic wet heath of the upper valley slopes and the rich fen along the central mire axis (v. ROSE, 1953).

In this community Molinia is dominant with much Juncus subnodulosus. Schoenus nigricans also occurs sparingly. With them various oxyphilous plants can be found: Calluna vulgaris, Drosera rotundifolia, Erica tetralix, Genista anglica, Luzula multiflora, Polygala serpylifolia, Sieglingia decumbens and, at Buxton Heath, Platanthera bifolia. Bryophytes include Aulacomnium palustre, Hypnum cupressiforme and Sphagnum plumulosum, together with Calypogeia fissa,

Cephalozia bicuspidata, Dicranella heteromalla, Lepidozia setacea and Pohlia nutans. There are, however, rich fen species as well: Anagallis tenella, Epipactis palustris, Parnassia palustris and Pedicularis palustris with mosses such as Campylium stellatum, Drepanocladus revolvens and Fissidens adianthoides.

Related oxyphilous communities may sometimes also be found on ridges in old peat workings, where Calluna vulgaris and Erica tetralix are prominent.

6.7.3. Juncus articulatus group.

Characterising species-group: Group 7 species, viz.: Cardamine pratensis, Carex nigra, Eriophorum angustifolium, Juncus articulatus, J. conglomeratus and Ranunculus acris; plus differentials for the variants.

The communities in this group are characteristically shorter (c. 40-50 cms) than those of the Juncus subnodulosus group, in some cases at least simply as a response to heavy grazing pressure. In general, they are more species rich as well. In some case the pre-eminence of Molinia as the dominant is reduced and polydominant situations arise with species such as Carex hostiana, C. nigra, C. panicea and Juncus articulatus becoming much more important.

A number of variants have been distinguished:

6.7.3.1. Juncus nodum.

Species groups: 1,2,3,4,5,6*,7,8,9*,11,14,20,21,22.

Characterised mainly by the species of Group 14: Juncus effusus, J. inflexus, Ranunculus flammula and Triglochin palustris. Rushes are important in the community and, in addition to the two listed above, Juncus conglomeratus can often be found in quite large quantities. Grasses are plentiful: Agrostis stolonifera, Anthoxanthum odoratum, Briza media and Holcus lanatus can all be found. Carex nigra is often abundant, C. panicea is constant and Carex flacca, C. hostiana and C. pulicaris can occasionally occur.

There is also a fairly rich assemblage of herbaceous species such as Caltha palustris, Dactylorhiza fuchsii, D. incarnata and Lychnis flos-cuculi. Mosses are but poorly developed though Acrocladium cuspidatum is constant.

Two variants may be distinguished. The Deschampsia cespitosa var. has a number of differential species, all characteristic of grassland: Centaurea nigra, Cerastium holosteoides, Festuca rubra, Filipendula ulmaria, Leontodon autumnalis and Rumex acetosa with others like Hypericum tetrapterum, Potentilla anserina and Pulicaria dysenterica. Betonica officinalis and Silaum silaus also occasionally occur. This community is usually found in rather damp rough pasture.

The other variant - the Epipactis var. - has only been recorded from Allimore Green in Staffordshire and Hatch, near Basingstoke in Hampshire. It occupies small wet depressions

slightly flushed with base-rich water (pH 7.0) and is characterised (i) by the absence of the species of the Deschampsia var.; (ii) by the semi-dominance of Carex nigra; and (iii) by the occurrence of species such as Anagallis tenella, Epipactis palustris, Parnassia palustris, Pinguicula vulgaris and Carex dioica. This variant has clear affinities with the next community-type.

6.7.3.2. Euphrasia nemorosa nodum.

This nodum encompasses Molinia-vegetation developed on slight slopes where seepage maintains a high sub-surface water-table even during the summer months. Such conditions can occur around the margins of some mire basins or on flushed slopes in heathland etc. Here there is only limited accumulation of organic material and the substratum is often a primitive gleyed mineral soil.

Diagnostic species include character species of both the Tofieldietalia and the Nardetalia: Carex demissa, C. lepidocarpa, Euphrasia nemorosa, Festuca ovina, Nardus stricta, Parnassia palustris, Pedicularis palustris, P. sylvatica. Of these Euphrasia nemorosa is the most constant but it is absent from some of the sites and its use as a label for the variant is largely because of the absence of anything more appropriate.

The Molinia, with the Festuca ovina and Nardus forms a

rather open low-growing turf. There are other grasses such as Anthoxanthum odoratum and Briza media and Festuca rubra may occur as well. Carex nigra is often abundant and with it may be other small sedges: Carex dioica, C. hostiana, C. echinata and C. pulicaris. In contrast, however, rushes are usually not well developed. The rush complement is mainly composed of Juncus articulatus - which may often be very low growing (20-30 cms). Less constant are Juncus acutiflorus and J. conglomeratus. With all of these various small herbs can be found: Linum catharticum, Hypericum pulchrum, Prunella vulgaris, Rhinanthus minor and Selaginella selaginoides.

On slightly elevated areas Calluna vulgaris, Erica tetralix and Sieglingia decumbens can be found. There may also be more acidophilic species - Drosera rotundifolia, Narthecium ossifragum, Aulacomnium palustre, Polytrichum commune, Sphagnum palustre and S. plumulosum.

This type of vegetation can be found in various parts of England and Wales. Many of the examples recorded in this survey, however, were derived from the slopes of the mire basins of the Whitlaw Mosses on the Selkirk/Roxburgh border.

6.7.4. Typical group.

This is a rather heterogenous group containing four dissimilar community-types, united mainly by the common absence of species of Groups 2, 3 and 21.

6.7.4.1. Molinia societies.

Stands of vegetation completely dominated by the purple moor grass can occasionally be found in rich fen complexes. Such stands normally occupy small, dry areas of fen often on the elevated baulks in a peat-cutting complex.

Few, if any, associated species can be found, with Anthoxanthum odoratum, Potentilla erecta and Succisa pratensis being the most frequent, sometimes with Galium saxatile. Invasion by Pteridium aquilinum has been observed and also colonisation by trees, particularly Betula pendula.

6.7.4.2. Species-poor Molinieta

This is a heterogenous grouping into which has been placed various stands dominated by Molinia caerulea, which are of variable floristic composition and are characterised mainly by a paucity of species. It is perhaps best left as a general "dustbin"-group to accommodate such samples until further data are available to clarify their sociological status.

6.7.4.3. Molinia-Myrica nodum.

Species groups: 1,16.

A floristically poor but very distinct community-type which can cover quite large areas in certain rich fen systems. Molinia caerulea forms large, dense tussocks and with these are

associated numerous bushes of Myrica gale. Associates are few and variable and the five samples available can only give a preliminary picture of the vegetation. They demonstrate two broad trends, however:

(i) stands containing rich fen species - Juncus subnodulosus, Eupatorium cannabinum, Filipendula ulmaria, Galium palustre, Mentha aquatica, Phragmites communis.

(ii) stands with calcifuge species - Calluna vulgaris, Drosera rotundifolia, Erica tetralix, Narthecium ossifragum, Platanthera bifolia, Sphagnum plumulosum.

These two elements can be found together in some stands in which case the rich fen species occur between the Molinia tussocks, whilst the calcifuge species occupy oxyphilous nuclei such as the tussock tops.

This community is not common in rich fen systems. It is extensively developed in the Cors Erddreiniog-Cors Nantisaf wetland complex in Anglesey. It occurs also in some West Norfolk fens, e.g. Dersingham Fen, Roydon Common.

Similar communities have been described from rather acid soligenous sites elsewhere in Britain. RATCLIFFE (1964) has described Molinia-Myrica mires from Scotland, especially the western parts and BIRKS (1973) has recognised a similar community on Skye. The community at Roydon Common has received some documentation by DANIELS & PERASON (1974). Related communities occur also in the New Forest, Hants.

(NEWBOULD, 1960).

Some of the Myrica gale stands of the Norfolk Broads have clear affinities to this community. These, however, have been referred to a Myrica gale consociation (6.9.5.).

6.7.4.4. Molinia-Myrica-Cladium nodum.

Species Groups: 1*,4,5*,6*,16,17,19.

This nodum has been created from three stands made from parts of Woodwalton Fen. In these Molinia caerulea is abundant and with it are patches of Myrica gale, Cladium mariscus and, in places, Calluna vulgaris. Associated with these are various fen species: Angelica sylvestris, Calamagrostis canescens, C. epigejos, Cirsium palustre, Lysimachia vulgaris, Lythrum salicaria and Phragmites communis. Achillea ptarmica and Hydrocotyle vulgaris also occur and there are bushes of Salix repens. Scrambling through the vegetation is Calystegia sepium, Lotus uliginosus and Vicia cracca. Mosses are largely absent.

This community has also been described from Woodwalton by POORE (1956), who relates its occurrence on the Fen to the distribution of oligotrophic fen peat. No other comparable communities have been located in this survey.

6.7.5. Other British Molinieta.

A variety of Molinia caerulea grassland types have been

documented from Britain. Acidic Molinieta have been described from upland areas in the Pennines and also from parts of Scotland (e.g. MOSS, 1911; SMITH, 1911; JEFFRIES, 1915, 1917; FRASER, 1933; TANSLEY, 1939; McVEAN & RATCLIFFE, 1962; KING & NICHOLSON, 1964). Molinia-dominated communities occur in association with some of the New Forest valley bogs (RANKIN, 1911; ROSE, 1953) and wet heath Molinieta have also been recognised (TANSLEY, 1939; BRIDGEWATER, 1970). There have, however, only been a few accounts of the communities associated with fens. PEARSALL (1918) described a very species-poor Molinietum from the Esthwaite Fens; GODWIN & TANSLEY (1929) give an account of the "litter" of Wicken Fen - a Molinia-dominated community which was maintained by annual mowing. And from Ireland, DUFF (1930) and WHITE (1932) mention Molinieta within the Lough Neagh fens.

6.7.6. Syntaxonomy.

Molinia caerulea has a broad ecological amplitude and grows in a variety of plant communities ranging, in Atlantic regions, from ombrotrophic bog to calcareous grassland. Indeed, GUINOCHET & LEMEE (1950) have suggested that there are four different varieties of the species each occupying a specific habitat and community-type.

In consequence a number of different Molinia caerulea community-types have been described from Europe (see, for

example, BALATOVA-TULACKOVA, 1972, pp. 56-59). Some of these have been recognised as independent communities (e.g. by PHILIPPI, 1960; KORNECK, 1962). PASSARGE (1964) however, recognises two basic Association-Groups: Eu-Molinietum coeruleae Koch 26 containing species-rich Molinia-meadows and a Succisietum pratensis with species-poor communities.

Some of the earliest descriptions of Molinieta referred to s tands associated with calcareous mires (e.g. ALLORGE, 1922; KOCH, 1926; LEMEE, 1937). From Atlantic regions LEMEE described a Molinietum caeruleae atlanticum recognising within it both acidophilic and basiphilic community-types (see also DUVIGNEAUD & VANDEN BERGHEN, 1945; DUVIGNEAUD, 1949; LEBRUN et al., 1949; VANDEN BERGHEN, 1951). A similar community has been described by Dutch workers - the Cirsio-Molinietum Sissingh et De Vries 42 (see VANDEN BERGHEN, 1951; WESTHOFF & DEN HELD, 1969). Communities of this kind in calcareous mires can have a strong floristic affiliation to Schoenus nigricans communities (see ALLORGE, 1922; TÜXEN, 1937) and indeed BEGER (1922) regarded Schoenus communities as a sub-association of the Molinietum.

Of the communities considered here the Juncus subnodulosus-group could be accommodated within the Cirsio-Molinietum and the same may apply to some of the other community-types. However, it is felt that more data pertinent to other types of Molinieta in Britain are required before a firm systematic

scheme can be constructed and in particular clarification of the relationships to certain Carex nigra-dominated stands is necessary. Until this is achieved it seems best to place all of the noda identified into an ad hoc Succiso-Molinietum community.

Syntaxonomic placement

Molinia-dominated vegetation associated with base-rich mires has been placed into the Molinion Alliance by many phytosociologists (e.g. KOCH, 1926). Thus it would seem likely that the Molinieta described could be similarly placed here, or, at least, in the Atlantic counterpart, the Junco-Molinion Westhoff 69. However, certain problems arise. First, of the character species suggested by WESTHOFF & DEN HELD (1969) for this Alliance, Viola stagnina and Potentilla anglica have not been recorded; Juncus conglomeratus is only of local occurrence and also occurs (admittedly with low constancy) in rich fen meadow communities (and also in other mire communities not covered by this survey); and Succisa pratensis, though well developed (perhaps optimally) in these Molinia communities is also constant and well developed in rich fen meadow types and, particularly, in the Schoeneto-Juncetum.

The second problem is that Calthion species are quite well represented, at least in certain community types, especially Lotus ulignosus but also Caltha palustris and Lychnis flos-cuculi.

However, these are not very constant and also, of the species given by WESTHOFF & DEN HELD to differentiate the Junco-Molinion from the Calthion, Sieglingia decumbens, Parnassia palustris and (very rarely) Platanthera bifolia do occur in at least some stands.

The third problem is of long standing and concerns the oft-noted affinities between Molinion and Caricion davallianae communities - created, at least in part, by the seral relationships between the two types. In the present data it is evident that species such as Carex hostiana, C. panicea, C. pulicaris and Cirsium dissectum, whilst perhaps optimally developed in the Molinieta, are also very well represented in some Caricion davallianae communities, especially the Schoeneto-Juncetum. Conversely, calcareous mire species like Epipactis palustris or Schoenus nigricans occur, at least sporadically, in a number of Molinieta community-types. In particular, the Euphrasia nemorosa nodum of the Juncus articulatus group (6.7.3.2.) has a large number of calcareous mire species including Carex lepidocarpa, Pinguicula vulgaris, Drepanocladus revolvens etc. It would be tempting to classify the nodum with the Caricion davallianae communities were it not for the occurrence of certain Nardetalia species as well. The problem is exacerbated by the Schoeneto-Juncetum containing a good representation of certain Molinia-Arrhenatheretea and Molinietalia character species.

These issues are only likely to be resolved by study of other Molinion communities in Britain as, clearly, the present examples are biased towards the vegetation of base-rich mire. It would seem best for the time being, to follow the precedent of Continental phytosociologists and place the communities within the Molinion, though from the present data I have been unable to isolate any species which satisfactorily characterise this Alliance.

6.7.7. Carex nigra-Molinia fen.

Included within this group are stands representing a relatively dry form of fen vegetation dominated by the common sedge, Carex nigra and the purple moor grass, Molinia caerulea. This has mainly been recorded from the drier parts of some rich fen systems of Northern Britain, as in the Tarn Fens at Malham, W. Yorks., at Sunbiggin Tarn, Orton, in Westmorland, and in association with some of the Whitlaw Mosses of the Roxburgh-Selkirk border.

Only a few samples of this type of vegetation are available and as these show substantial variation only a preliminary account will be given here.

The dominant monocots are Carex nigra and Molinia caerulea which combine with other species to produce a tussocky closed sward of up to 75 cms high. Other constant graminoid species include the sedge Carex panicea and the grasses Agrostis stolonifera, Anthoxanthum odoratum and Holcus lanatus. Juncus articulatus is the most constant rush but J. acutiflorus can occur and also J. conglomeratus. Luzula multiflora is quite frequent and in some places Carex disticha can be abundant.

Dicotyledonous species are prominent in the vegetation. In particular, Filipendula ulmaria can reach high cover values. Other constant dicots include:

Angelica sylvestris
Caltha palustris
Cardamine pratensis
Centaurea nigra
Cirsium palustre
Galium palustre
Galium uliginosum
Lychnis flos-cuculi
Potentilla erecta
Succisa pratensis
Valeriana dioica

In places Achillea ptarmica, Crepis paludosa, Geum rivale and Sanguisorba officinalis can also be found, with Serratula tinctoria and Trollius europaeus in the community at Malham.

At Beanrigg moss the holy-grass, Hierachloë odorata is abundant in this community. In the Malham Tarn fens Carex appropinquata is a frequent component. Mosses are fairly well developed. Acrocladium cuspidatum is constant and often abundant. Others include Brachythecium rutabulum, Mnium longirostrum, Mn. undulatum and Rhytidiadelphus squarrosus. Climacium dendroides is often abundant.

This type of vegetation has received very little documentation. However, the communities at Sunbiggin have been described by HOLDGATE (1955b) and those at Malham by PROCTOR (1974). PROCTOR has united the stands at Malham into a Carex nigra-Sanguisorba officinalis nodum, recognising within it two facies, one dominated by Carex nigra and the other by Carex appropinquata.

The relationship of this community to other rich fen types is not entirely clear but there are obviously close affinities to the Juncus articulatus group of Molinia-dominated communities (6.9.2.).

6.7.8. Synopsis of Molinia-dominated communities.

MOLINIO-ARRHENATHERTEA Tx. 37

MOLINIETALIA Koch 26

JUNCO (SUBULIFLORI) - MOLINION Westhoff 69

Succiso-Molinietum community

Juncus subnodulosus group (6.7.2.)

Typical nodum (6.7.2.1.)
Potentilla reptans nodum (6.7.2.2.)
Selinum carvifolia nodum (6.7.2.3.)
Erica tetralix nodum (6.7.2.4.)

Juncus articulatus group (6.7.3.)

Juncus nodum (6.7.3.1.)
Euphrasia nemorosa nodum (6.7.3.2.)

Myrica nodum (6.7.4.3.)

Myrica - Cladium nodum (6.7.4.4.)

Species-poor Molinieta (6.7.4.2.)

Molinia societies (6.7.4.1.)

Carex nigra - Molinia community (6.7.7.)

(= Carex nigra-Sanguisorba officinalis nodum Proctor 74)

6.8. Group 8. Epilobium hirsutum-Filipendula ulmaria tall herb fen communities - Table 8.

This small group contains stands of vegetation dominated by the great willowherb, Epilobium hirsutum and/or the meadowsweet, Filipendula ulmaria.

Only a few data are available for this community-type. They represent a very characteristic type of vegetation in which Epilobium hirsutum and Filipendula ulmaria are strongly dominant forming dense, leafy stands of about 1 m tall in which there are usually only a small number of associated species. Carex acutiformis is sometimes an important additional species, but the most usual associates seem to be Angelica sylvestris, Galium aparine and Urtica dioica. This last species is abundant in certain stands and can contribute up to 20% of the vegetation cover. Another species which can be prominent in some sites is Cirsium arvense. The bryophyte layer is typically poorly developed and may be completely missing. Brachythecium rutabulum is the only moss frequently found. In some of the wetter sites it may be quite abundant and is especially conspicuous during the winter months when the taller vegetation has died back.

Because of the small number of samples available, these data have not been processed by Information analysis. However, a manual re-ordering of the species-sample matrix suggests the occurrence of three broadly defined floristic groupings.

6.8.1. Typical nodum.

A very species-poor community-type containing in the main just the species mentioned above.

6.8.2. Lotus uliginosus-Cirsium palustre nodum.

A poorly defined variant containing the following additional species:

Arrhenatherum elatius	Lotus uliginosus
Cirsium palustre	Mentha aquatica
Equisetum palustre	Rumex acetosa
Galium ulignosum	Scrophularia aquatica
Holcus lanatus	Solanum dulcamara
Lathyrus pratense	Vicia cracca

This has clear affinities with rich fen meadow vegetation and Juncus subnodulosus can occasionally be found.

6.8.3. Glyceria maxima-Phragmites communis nodum.

Characterising species-group: Phragmites communis, Glyceria maxima, Eupatorium cannabinum.

Description: This community-type, which again is not very well defined, is characterised by the occurrence of tall-growing graminoids such as Glyceria maxima, Phragmites communis or Phalaris arundinacea with the Epilobium and Filipendula. It represents a rather variable nodum and more data would almost certainly lead to its division. It has been recorded from both wet and dry places in rich fen systems. However, Filipendula is reduced, or even completely absent, in the

wettest places. The nodum has clear affinities with some Epilobium and Filipendula rich stands of the Phragmites communis sociation (6.3.2.1.).

6.8.4. Occurrence.

This type of vegetation often occurs as small fragments at the drying out margins of certain rich fen systems. It can, however, occupy extensive surfaces. It is particularly characteristic of dry sites, especially those which have been drained or disturbed in some way. It can also occur, often extensively, on ungrazed, flat, alluvial flood plains alongside rivers, where the substratum is subject to periodic inundation but otherwise remains relatively dry for much of the year. It may also occur, however, in similar situations where there is a high water-table throughout the year. In such contexts it has most often been noted on low-lying areas of mineral soil, but it has also been recorded from peat fens alongside rivers. In this case it is usually best developed alongside the river or bordering dykes and inlets extending into the fen, especially where there are deposits of silt. Here Urtica is often especially prominent. Inwards, this fringe vegetation gives way to other communities, frequently to rather species-poor areas dominated by Phragmites.

Occasionally this type of vegetation occurs in spring fens, sometimes just confined to some wet, central portions,

but often developed over all, or most, of the mire. Some good examples have been located in the spring fens of North Buckinghamshire. Here it occupies sites where drainage has been attempted, but also it is well developed in places which have a high water-table that is constant for most of the year, and which have apparently not been subject to disturbance. All of them occur, however, in the vicinity of arable fields used for cereal cultivation and receive surface or sub-surface run-off from these.

HASLAM (1965) has described an Epilobium-Galium-Urtica community, which is very similar to those considered here, from dry valley fens in the Breckland and also from disturbed places of wetter headwater mires. She has related the occurrence of this type of vegetation to the presence of relatively high levels of available phosphate and potassium in the substratum. Some analyses made of the ground water and peat of the undrained spring mires of North Bucks. which support this community has indicated they too have markedly higher levels of phosphorus in the peat than in nearby spring mires (situated amongst pasture land), which support fen meadow vegetation dominated by Juncus subnodulosus. It seems possible that here the development of Epilobium hirsutum dominated communities may be related to a process of eutrophication of the irrigating waters as a result of the application of agricultural fertilisers to the adjoining arable fields. However, evidence relating to this is at present inconclusive.

Filipendula dominated vegetation has been described from Malham by PROCTOR (1974) and from Semerwater by INGRAM et al. (1959). SPENCE (1964) has recognised a Filipendula-Acrocladium sociation from Scotland.

6.8.5. Syntaxonomy.

Because of the floristic poverty and variability of these communities, together with the small amount of available data, it seems most appropriate, at least for the time being, to regard them as components of a sociation defined by the dominance of Filipendula ulmaria and Epilobium hirsutum. However, the clear relationship between this unit and the Valeriano-Filipenduletum Siss. apud Westhoff et al. 46 of Continental phytosociologists may be noted.

On the basis of the physiognomy of the stands together with the prominence of Epilobium hirsutum (a characterising species of the Filipendulion) and Filipendula ulmaria (often given as a character species of the Valeriano-Filipenduletum which is assigned to this Alliance), the present Epilobium-Filipendula communities would seem to be best placed within the Filipendulion.

6.8.6. Synopsis of Epilobium hirsutum-Filipendula ulmaria communities.

MOLINIO-ARRHENATHERETEA Tx. 37

MOLINIETALIA Koch 26

FILIPENDULION (Duvig. 46 p.p.) Segal 66

Epilobium hirsutum-Filipendula ulmaria sociation

(= Valeriano-Filipenduletum Siss. apud Westhoff et al. 46 ?)

typical var. (6.8.1.)
Lathyrus pratense - Cirsium palustre var. (6.8.2.)
Glyceria maxima - Phragmites communis var. (6.8.3.)

6.9. Group 9. Mire forest communities - Table 9.

This group contains stands of forest vegetation developed within rich fen systems. Following TANSLEY (1911) such areas will be referred to as "fen carr".

Mire forest is extensively developed in some rich fen systems. It was not, however, regarded as a major vegetation type to be considered in this survey and, accordingly, has not been examined exhaustively. Nonetheless, some 100 samples were available for analysis. These mainly included stands dominated by Alnus glutinosa, Rhamnus catharticus and Salix pentandra, together with a Betula pubescens-Myrica gale scrub. There were also a few stands with Salix cinerea as the dominant, but in general Salix cinerea scrub has not been considered.

The results of Information Analysis are shown in Fig. 9.I. The samples were examined for re-allocation at the 10 cluster stage, but the contents of the groups were stable. A clear distinction was made between alder carr, Salix pentandra carr, Rhamnus carr, and the Betula pubescens-Myrica gale scrub. The few stands of Salix cinerea scrub all segregated with the Alnus stands. It is thus convenient to recognise four major groupings:

(a) alder carr (+ Salix cinerea carr).

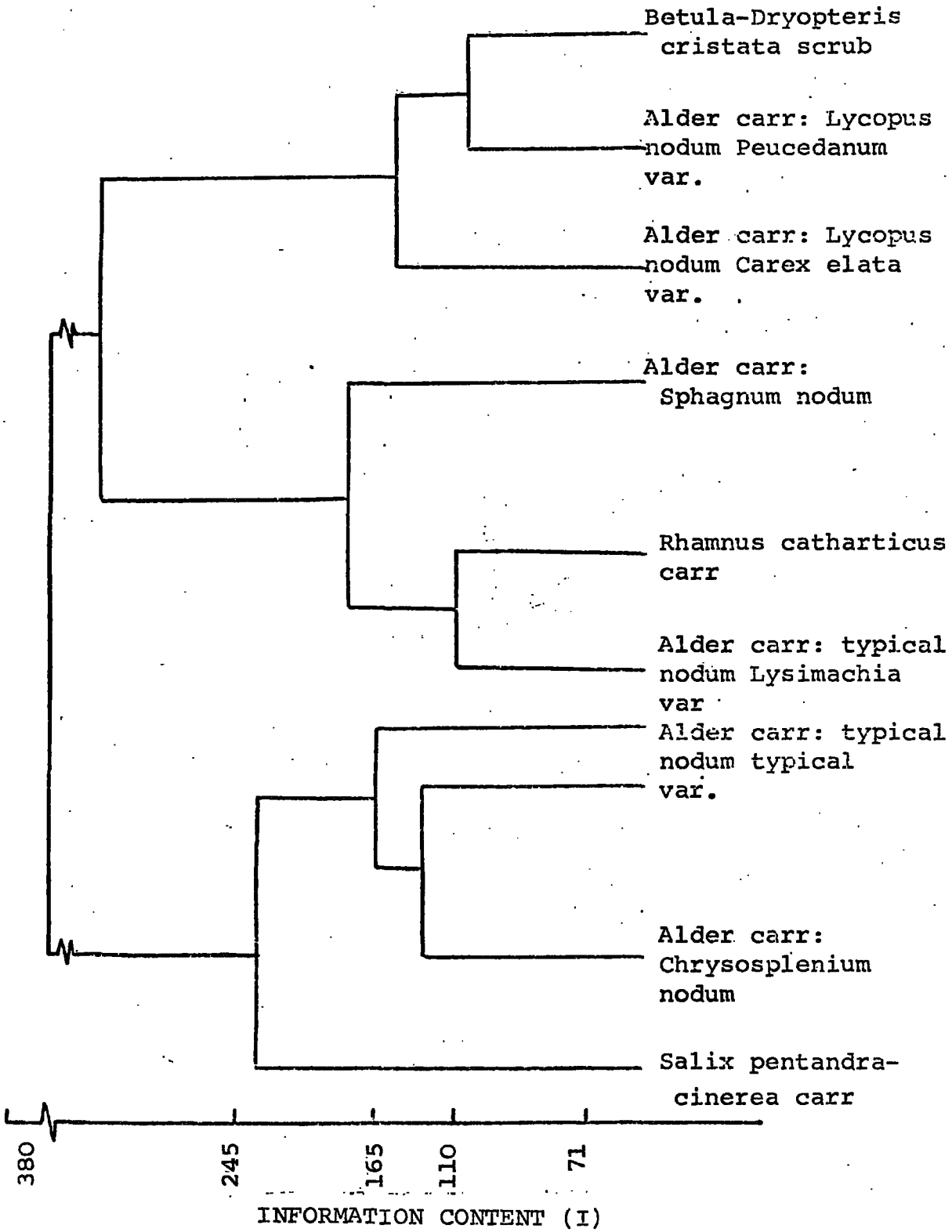
(b) Salix pentandra carr.

(c) Betula pubescens-Myrica gale scrub.

(d) Rhamnus catharticus carr (with Frangula alnus carr).

Fig. 6.9.I.

INFORMATION ANALYSIS ON
MIRE FOREST VEGETATION



In addition two other community-types are recognisable from some samples that were not subject to numerical analysis. These will also be considered here as:

(e) Myrica gale scrub.

(f) fen oakwood.

6.9.1. Alder carr vegetation - Table 5.

Encompassed here are stands of mire forest dominated by Alnus glutinosa. This tree, which can grow up to about 20 m, can form fairly pure stands, but usually there are at least some other arboreal associates. Betula pubescens is frequent and in some stands Fraxinus excelsior and Quercus robor can also occur. The willow Salix cinerea is a constant component of the vegetation. In mature alder forest it may only occur in small quantity forming a second storey below the alder canopy. But often it is co-dominant with the alder and may even predominate.

The stands frequently have a dense shrub layer which may make them difficult to penetrate. Salix cinerea is again a major component in this, but various other shrubs may occur: Crataegus monogyna, Frangula alnus, Ligustrum vulgare, Rhamnus catharticus etc. - together with bushes of Ribes nigrum and R. sylvestre. Rubi are usually prominent and, especially in drier situations, Rubus fruticosus can form a dense undergrowth.

Lianas of various species may contribute to the structural complexity of the forest and trees and shrubs can be found entwined with Solanum dulcamara and, in drier parts, Lonicera periclymenum. Bryonia dioica, Humulus lupulus and Calystegia sepium sometimes occur and also the long arching shoots of Rosa canina.

The herb layer is normally tall and luxuriant. Particularly characteristic and constant are the two sedges Carex acutiformis and C. paninculata. The tussocks of the latter are usually a prominent feature of the stands. Growing up with these are various tall herbs. They include Cirsium palustre, Eupatorium cannabinum, Filipendula ulmaria, Iris pseudacorus, Lysimachia vulgaris, Urtica dioica and Valeriana officinalis. Together they form a rather tall herb layer of about 1 m high. Ferns may also contribute to this - especially Dryopteris dilatata, but also Athyrium filix-femina.

As well as these tall-growing plants smaller species can also occur, such as Caltha palustris and Cardamine pratensis. Often a distinct patterning may be observed in the herb layer. Thus, in the drier places around the bases of trees there can be species such as Circaea lutetiana, Oxalis acetosella and Stachys sylvatica - plants that are normally absent from the wetter parts.

The extent of the bryophyte layer is variable. Sometimes only isolated patches of mosses may occur - mainly Acrocladium cuspidatum - but elsewhere there may be a richer development with Brachythecium rutabulum, Eurhynchium praelongum and Mnioid species such as Mnium affine, Mn. punctatum and Mn. undulatum. In more acidic conditions Sphagna may be abundant.

In the gloomy, dripping interior of the forest the moist environment provides favourable conditions for the growth of cryptogameous epiphytes and some stands may be very rich

in these. Rotting trunks and fallen branches may also support a number of species. On this type of substratum various bryophytes may be found. Amongst the mosses, Aulacomnium androgynum, Dicranoweissia cirrata, Hypnum cupressiforme, Leskea polycarpa, Orthotrichum affine, O. lyellii, Plagiothecium denticulatum and Thamnium alopecurum. And amongst the liverworts, Frullania dilatata, Lophocolea heterophylla, Metzgeria furcata and Radula complanata. In some carrs lichens can form growths over the branches. They include species of Caloplaca (e.g. C. citrina), Lecanora (e.g. L. carpinea) and Parmelia (e.g. P. caperata, P. physodes) with Evernia prunastri, Ramalina farinacea and Usnea sp. A fuller list is given by ELLIS (1965).

Various examples of alder wood have been described from Britain - MOSS et al. (1910), PALLIS (1911), RANKIN (1911), TANSLEY (1939), ROSE (1950), LAMBERT (1951), McVEAN (1956) and KLÖTZLI (1970).

Types of alder carr

Four distinct types of alder carr have been recognised together with several minor variants. These are described below:

6.9.1.1. Typical nodum.

Characterisation: Absence of species differential for other groups.

Description: This community-type is composed of a number of rather different releves representing patches of alder carr from fen systems in various parts of England and Wales. It is designated as typical both because it lacks characterising differential species and also because it represents the most widespread type of alder carr associated with rich fen systems.

The dominant tree is Alnus glutinosa with Betula pubescens and Fraxinus excelsior growing up with it at some sites. Salix cinerea also normally occurs, either as small bushes or forming a secondary canopy beneath the alder. There is normally some development of a shrub layer, often with much Salix cinerea but other shrubs may be numerous as well. Crataegus monogyna, Frangula alnus, Ligustrum vulgare, Rhamnus catharticus and Viburnum opulus can all frequently be found, sometimes all at the same site. Rather less frequent are Ribes nigrum and R. sylvestre. Ribes uva-ursi occasionally occurs. Very occasionally the midland hawthorn, Crataegus oxyacanthoides has been recorded. In addition, Rubi are normally prominent. Both Rubus caesium and R. idaeus have sometimes been found but the main representatives of the genus are various species of the Rubus fruticosus aggregate. Such brambles can often be abundant, especially in drier areas.

In the herb layer Carex acutiformis is nearly always found, often as the dominant species. With it there are normally tussocks of the greater tussock-sedge, Carex paniculata.

These may be very robust (up to 1.5 m high) and numerous, covering a large proportion of the woodland floor and sometimes supporting a rather poor epiphytic flora which includes species such as Dryopteris filix-mas, Oxalis acetosella and Geranium robertianum. Various tall herbaceous species are also constant: Angelica sylvestris, Cirsium palustre, Iris pseudacorus and Filipendula ulmaria. Other frequent species include Eupatorium cannabinum and Valeriana officinalis. In some places Urtica dioica can be abundant sometimes managing to grow to a height of well over 1 metre. Sometimes standing above this herbaceous vegetation are shoots of Phragmites communis. This, however, is normally only sparsely developed and in a vegetative state, although where there are breaks in the tree canopy vigorous colonies can usually be found. Cladium mariscus is not a characteristic component of carr vegetation but occasionally sterile clumps are encountered as relicts of a former open vegetation type.

Ferns are often important. Dryopteris dilata is frequently abundant and D. filix-mas often grows with it, though mainly in the slightly drier, more elevated parts. Athyrium filix-femina is occasional, Dryopteris cartusiana rare. The marsh fern, Thelypteris palustris, is largely absent, though it has been recorded from Ham Fen in Kent. It was once recorded from the alder thickets at Pont-y-spig (Monmouthshire) (WADE, 1970), but now appears to be extinct.

It is also present in some of the alder carrs associated with the meres of the Cheshire-Shropshire plain (see below).

A variety of smaller herbaceous species can also occur: Ajuga reptans, Caltha palustris, Cardamine pratensis, Mentha aquatica and Valeriana dioica. Around the base of the trees some species more characteristic of drier situations can often be found: Circaea lutetiana and Geranium robertianum in the damper parts and Oxalis acetosella in the upper drier areas. Pteridium aquilinum may sometimes grow here to.

Cutting across these horizontal strata are climbing and scrambling species. The most constant of these is Solanum dulcamara, but Lonicera periclymenum also is frequent and Humulus lupulus is occasional. Mosses are not normally abundant on the forest floor, often only constituting 5-15% of the total cover. Acrocladium cuspidatum, Brachythecium rutabulum and Eurhynchium praelongum are the most constant. Amblystegium serpens is only occasional and Hypnum cupressiforme is found mainly in association with the tree bases. Mnioid species are not uncommon - mainly Mnium affine, Mn. hornum, Mn. punctatum and Mn. undulatum.

It is clear from Table 9 that this community-type is rather variable in composition and that different associates tend to occur at different sites. With the few data presently available it seems premature to attempt to distinguish variants and a more thorough examination of the community is required.

No clear distinction has yet emerged between the wetter and drier examples of the community, though in the field this often appears evident due to greater quantities of brambles and Dryopteris filix-mas in the latter. This indistinction may be due to the fact that, even in the wetter woods, elevated areas provide a suitable autenvironment for some of the less wet-tolerant species.

There are, however, two distinct variants:

6.9.1.1.1. Lysimachia vulgaris variant.

This is developed in the fen woodland surrounding some of the meres of the Cheshire-Shropshire plain. These woodlands are rather fragmented and variable in floristic composition but some samples that were taken from them form a rather definite group. In the tree layer Salix fragilis frequently occurs with Alnus and Salix cinerea but Betula pubescens is absent. In the herbaceous strata there is usually Phalaris arundinacea - often in substantial quantity. Other herbs include Lysimachia vulgaris and Lythrum salicaria. Both Calamagrostis canescens and Thelypteris palustris have been recorded from some samples. These stands appear to lack many of the constant species of other alder carrs, particularly shrubs like Crataegus monogyna, Ligustrum vulgare and Viburnum opulus (see Table 9).

This variant has been recorded from Fenemere in Shropshire and Quoisley Mere in Cheshire. It seems likely that a

similar community occurs surrounding the nearby Norbury Meres (NEWTON, 1971, p.54).

6.9.1.1.2. Scirpus sylvaticus variant.

This constitutes a rather species-poor variant with Scirpus sylvaticus as an important component of the herb layer. In many cases the characteristic sedges of the herb layer - Carex acutiformis and C. paniculata - are completely absent.

6.9.1.2. Chrysosplenium nodum.

Characterising species-group: Chrysosplenium oppositifolium, C. alternifolium (rare), Oenanthe crocata, Pellia epiphylla.

Description: A very characteristic type of fen woodland typically found below springs and seepage lines along the sides of small, shallow, peat-lined valleys cut back into areas of acidic, nutrient-poor bedrock. Here, in rheotrophic conditions, there is mire forest usually dominated by the alder, Alnus glutinosa, and with a characteristic associated flora.

In Southern Britain such sites have been found in Surrey and Sussex and along the border of Buckinghamshire and Bedfordshire. They are developed in association with various beds of the Lower Greensand, often in association with Ironsand deposits. Elsewhere in Britain they are with Permo-Triassic sandstones.

The substratum is usually a black, fibrous, semi-brushwood peat. Between springs and around the base of trees it is often relatively dry and firm but where water comes to the surface it may be a treacherous slurry. Such areas may show iron mottling and small iron-stained runnels are often developed below them. Thus, there is usually a mosaic of habitats ranging from very wet to relatively dry and this permits the growth of fen carr species together with others more typical of drier woodland.

In its mature state the trees of the community are often well developed. Alder can grow up to about 25 m and the high canopy with limited scrub development permits easy penetration. Alnus is usually dominant with a sub-storey of Salix cinerea. Betula pubescens, Ilex aquifolia and Sorbus aucuparia sometimes occur and bushes of Salix caprea and S. aurita may also be found. Corylus avellana, Fraxinus excelsior and Quercus robur are occasional in drier areas. Rubus fruticosus, though usually not abundant, is constant and Ribes nigra, Rosa spp. and Viburnum opulus may be present in some places.

In the herb layer Carex paniculata is often the dominant sedge, though it frequently forms local colonies rather than covering the whole area - often being restricted to the lower portions of the mire slope. Carex acutiformis is frequent and Carex remota may also occur. Occasionally, Scirpus sylvaticus is present in quantity. Ferns may be abundant, particularly Dryopteris dilata and Athyrium filix-femina, but

also Dryopteris filix-mas. Thelypteris palustris can be found occasionally and it may once have been more frequent (the records for it from Bedfordshire and Buckinghamshire (DONY, 1953; DRUCE, 1926, respectively) almost certainly refer to this community-type). At Waldridge Fell in Co. Durham Osmunda regalis persists in this type of woodland. With these there are other tall herb species - Cirsium palustre, Eupatorium cannabinum, Filipendula ulmaria and Valeriana officinalis. Rushes tend to be infrequent, mainly Juncus acutiflorus and J. effusus.

There are a variety of smaller dicots: Caltha palustris, Galium palustre, Mentha aquatica, Ranunculus acris, R. repens and Valeriana dioica. Cardamine pratensis is frequent and C. amara and C. flexuosa may also occur. Equisetum palustre is occasional and E. sylvaticum can sometimes be found. The same applies to Myosotis caespitosa and M. secunda.

The species which serve to identify the community are often present in substantial quantity. These are Chrysosplenium oppositifolium, Oenenanthe crocata and Pellia epiphylla. The Chrysosplenium is often present in very large amounts, particularly in the wettest areas where it can form an almost continuous carpet and is especially associated with Caltha palustris and Mentha aquatica.

The bryophyte layer can be well developed composing up to 50% of the vegetation cover on the ground. The liverwort

Pellia epiphylla is particularly characteristic. Acrocladium cuspidatum, Eurhynchium praelongum, Mnium undulatum and Brachythecium rutabulum are all constant. Brachythecium rivulare can also sometimes be found. Mnium hornum and Mn. punctatum are frequent. Sphagna may be found, especially in areas least affected by the springs. Sphagnum palustre and S. squarrosum are the most frequent but S. fimbriatum, S. plumulosum and S. recurvum may also be present.

In drier areas more typically woodland species can occur:

Anenome nemorosa	Mercurialis perennis
Circaea lutetiana	Oxalis acetosella
Festuca gigantea	Primula veris
Geranium robertianum	Pteridium aquilinum
Hedera helix	Ranunculus ficaria
Lonicera periclymenum	Silene dioica
Lysimachia nemorum	Veronica chamaedrys

Some of these (e.g. Anenome nemorosa) may also encroach upon much wetter parts of the mires.

Distribution. As this type of vegetation has only been of peripheral interest in the present survey, and as it has received very little documentation no account of its distribution can be given. It is, however, most probably a fairly widespread type and in this survey has been recorded in Southern England, South Wales, the Midlands and the North-East of England. It is perhaps particularly characteristic of peaty gullies in acid sands in the South. Thus, most of the samples included here came from mires in Sussex and Surrey. GROSE (1954) has given an account of this community from the Lower Greensand in Spye

Park, Wilts. and it is evident from GROSE (1957) that similar stands have occurred elsewhere in Wiltshire. Similarly, BOWEN (1968, p.36) has given a list from the alder gullies of the Plateau Gravels of S. Berks, which seems to be referable to this community-type. From Northern Britain the community at Waldridge Fell, Co. Durham (S.992, S.993) has received some description from JEFFREYS (1916) and BELLAMY (1970).

It is important to note that flushed areas containing many of the species of this community (especially Chrysosplenium oppositifolium) can occur on slopes in various types of deciduous woodland.

6.9.1.3. Sphagnum nodum.

Characterising species-group: Molinia caerulea with Sphagna; plus the absence of differentials for other groups.

Description: In parts of some rich fen systems isolated from the main influence of moving ground water (e.g. at the periphery of a fen basin adjoining nutrient-poor mineral ground or in association with derelict peat-workings containing stagnant water) a species-poor acidophilic type of alder wood can sometimes develop. Alder is the dominant tree but with it Betula pubescens is abundant. The associated flora is very much reduced and many typical alder wood species (e.g. Carex acutiformis, C. elata, C. paniculata, Cirsium palustre, Solanum dulcamara) are either absent or rare. In their place is Molinia caerulea - sometimes in large quantity - and

sphagnaceous species. These mosses can often form a complete carpet. The main species are Sphagnum palustre and S. recurvum but S. fimbriatum and S. squarrosum can sometimes occur in abundance, occasionally with S. cuspidatum and S. subsecundum. With them Polytrichum commune is frequent. Phanerogamic associates are few and variable and may only account for 20-30% of the ground cover. They include Carex curta, C. echinata, C. rostrata, Juncus effusus, Menyanthes trifoliata and Viola palustris. Affinities to more typical alder carr are retained by the occasional persistence of species like Carex elata, C. paniculata, Lysimachia vulgaris and Phragmites communis.

In general, shrubs are poorly represented but Frangula alnus, Myrica gale, Salix aurita and S. cinerea can be found at some sites.

6.9.1.4. Lycopus nodum.

Characterising species-group: Lycopus europaeus, Peucedanum palustre, Lysimachia vulgaris, Lythrum salicaria, Thelypteris palustris.

6.9.1.4.1. Peucedanum variety.

Description: Included within this group are mature stands of alder carr sampled from the fens of East Norfolk, mainly those alongside the Ant and Bure rivers.

The dominant tree is Alnus glutinosa which can sometimes have a canopy reaching over 25 metres. Growing up with it

there may be Betula pubescens or Fraxinus excelsior and, very occasionally, in the drier sites occasional trees of Quercus robur. Beneath this upper tree layer Salix cinerea is usually frequent. Other smaller trees such as Frangula alnus, Ilex aquifolia, Rhamnus catharticus, Sorbus aucuparia and Viburnum opulus also occur at some sites. Of the lower-growing shrubs Rubus fruticosus is the most frequent and constant but others also sometimes occur as well, such as Rubus caesius, Rosa sp., Ribes nigrum and R. sylvestre.

In the herb layer scattered plants of Phragmites communis can sometimes be found but the species is completely absent from many stands. The dominants are usually Carex acutiformis and C. paniculata, although C. elata may be important as well. Carex remota is also a typical component of these carrs, though it is rarely prominent. The other plants of the herb layer include tall herbs such as Angelica sylvestris, Cirsium palustre, Eupatorium cannabinum, Filipendula ulmaria, Iris pseudacorus and Valeriana officinalis. Additionally, there are also the species which serve to characterise the group - Lycopus europaeus, Lysimachia vulgaris, Lythrum salicaria and Peucedanum palustre.

Ferns are well represented in these woods. In particular the fronds of Thelypteris palustris are prominent in the field layer. Dryopteris dilata is often abundant, sometimes with D. filix-mas and Athyrium filix-femina. But perhaps the most

notable species is the royal fern, Osmunda regalis. This is widespread through the area and, although absent from many stands, can be abundant. In one place near Sutton High Fen it forms the dominant species of the herb layer with a total cover of about 50%.

Mosses are frequent on the woodland floor with a cover of between 5-20%. The most usual are Acrocladium cuspidatum, Eurhynchium praelongum and Mnium hornum but other species - like Amblystegium serpens and Mnium undulatum - are also frequent. In some places Sphagna are prominent. Various species have been recorded from different locations but Sphagnum squarrosum and S. fimbriatum appear to be the most frequent. Viola palustris is also often found in these more acidic situations.

A structural variant of this community is swamp carr (see LAMBERT, 1951), which originates through the colonisation of the Carex paniculata tussocks of the semi-floating Caricetum paniculatae communities (q.v.) by Alnus and Salix cinerea. This type of fen carr is characterised by the huge tussocks of Carex paniculata. Some of these support the trees of the forest, which often are not growing vertically in consequence of the instability of the basal tussocks. Between the tussocks are treacherous pools and areas of liquid mud-supporting but little vegetation cover. Frequently, dead and rotting trees occur - presumably as a result of subsidence below the water-table.

Alder carr of this community-type occurs in various parts of broadland. It is particularly well represented over vast areas of the Bure valley, where it has developed both as part of the hydroseral encroachment of vegetation into the open water of the broads and also by the development of scrub over former mowing marsh. Most of this carrland, however, has not been examined in this survey. LAMBERT (1951) has given some account of it. Carr is more localised in the R. Ant fens, but in places it is very well developed and the Herons Carr area of Barton Broad contains some of the finest stands of alder carr that have been recorded in this survey. In the Wheatfen complex of the Yare valley similar communities also occur (see also ELLIS, 1934; TANSLEY, 1939, p.461). Here alder is often not the dominant species, but Salix cinerea and Fraxinus excelsior are prominent. The buckthorn, Rhamnus catharticus, is also particularly frequent and other trees, for example, Euonymus europaeus, may also be found.

There are other stands of alder carr elsewhere in lowland England and Wales that would also seem to be referable to this community-type. These constitute a varietal form distinguished by a paucity of the characterising species so that, out of the four species listed above, only one or two may be present. In particular, Peucedanum palustre is absent: this has only been recorded from carr in Broadland. Carex elata, however, is constant and is often present in large amounts. This variety may thus be referred to as a Carex

elata variety to distinguish it from the Peucedanum variety.

6.9.1.4.2. Carex elata variety. This has been recorded from a number of sites. Much of the fen carr at Askham Bogs in East Yorkshire is referable to this variety. Here Peucedanum palustre is absent but other species such as Lythrum salicaria and Calamagrostis canescens occur. Thelypteris palustris grows in places and there are scattered plants of Osmunda regalis. Similarly, most of these species are also found in two other examples of this variety. There are from two small mires occupying hollows in glacial sands and gravels in Staffordshire. One, near Balterley Heath (S.821), is particularly rich with Dryopteris carthusiana, Osmunda and Thelypteris palustris. Both of these sites - along with part of the Askham Bog complex - are notable for the occurrence of Carex elongata - a sedge rare in Britain (being completely absent from the carrs of broadland), but which is widespread in certain alderwood communities on the continent.

The carr at Sweat Mere, Salop. (S.357; see also TANSLEY, 1939, p.464; SINKER, 1962) and at Hatchmere, Ches. (S.320; see also LIND, 1950) may also be referred to this community. Also, some of the fen carr of Broadland - particularly some stands from the Yare valley - seem appropriately placed here.

Clearly this variant is in some respects transitional to the "typical" alder carr community (6.9.1.1.).

6.9.1.5. Syntaxonomy.

KLÖTZLI (1970) in a survey of alderwoods in Britain placed them into two Associations: the Osmundo-Alnetum of nutrient-rich habitats and the Pellio-Alnetum of nutrient-poor conditions. Both of these are related to an Association described frequently from the continent, the Carici elongatae-Alnetum Koch 26 em. Tx. et Bodeux 55.

As both TUXEN (1937) and BODEUX (1955) have pointed out some workers (e.g. MALCUIT, 1929) have placed stands containing much Alnus glutinosa into an "Alnetum glutinosae" without reference to their true floristic affiliations. BODEUX has thus attempted to define the Association more rigorously to accommodate only stands of mire forest that are dominated by the tree. Such communities are widespread throughout Northern Europe and accordingly he found it necessary to delimit two geographical Association-groups to contain the floristic variation. One of these contains just one Association, the atlantic Cariceto laevigatae-Alnetum (Allorge 22) Schwickerath 37, characterised by Carex laevigata, Osmunda regalis, Salix atrocinerea and Scutellaria minor. The other Association group contains three Associations of which one, the Carici elongatae-Alnetum, is the most widespread. This has Carex elongata, Calamagrostis canescens, Peucedanum palustre and Thelypteris palustris as diagnostic species.

WESTHOFF & DEN HELD (1969) have adopted these two Associations for the alder forests of Holland. They correspond, more or less, to two Associations defined by DOING (see

DOING, 1962), viz. Sphagno-Alnetum and Irido-Alnetum. The correspondence is not exact, however, as the separation of these last two Associations is not primarily geographical but edaphic.

Within the Carici elongatae-Alnetum BODEUX (1955) recognised three sub-associations: a betuletosum sub-ass. of acid sites with Betula pubescens and Sphagna; a symphytetosum sub-ass. of richer sites with Symphytum officinale and Eupatorium cannabinum; and a ranunculetosum repentis sub-ass. of intermediate conditions.

From Belgium NOIRFALAISE & SOUGNEZ (1961) have essentially followed the system of BODEUX (1955), but instead of the Carici elongatae-Alnetum they have two Associations: the Peucedano-Alnetum of flood-plain mires and a Glycerio-Alnetum of small valley mires. However, WESTHOFF & DEN HELD (1969) have allocated these two Associations of NOIRFALAISE & SOUGNEZ as sub-associationswithin the Carici elongatae-Alnetum.

6.9.1.6. Syntaxonomy of the British material.

The alder carrs described here are clearly similar to the Caricetum elongatae-Alnetum. However, there are pronounced differences such as the occurrence of Osmunda and the rarity of Carex elongata. It is thus felt that KLOTZLI's (1970) recognition of an Osmundo-Alnetum as atlantic vicariant of the Caricetum elongatae-Alnetum provides a suitable phytocoenon

for the British material. Therefore, it is proposed to unite all of the alder carr stands described here into this Association. The Chrysosplenium community (6.9.1.2.) raises some problems as it has clear relationships to the Pellio-Alnetum, but because of the affinities with other rich fen alder forest types, it would seem appropriate with reservations, to retain this in the Osmundo-Alnetum. The Lycopus community (6.9.1.4.) corresponds well with the Lycopus sub-association recognised by KLÖTZLI. However, the results of this survey do not support the existence of a Hydrocotyle sub-association as he suggested.

Thus, the following syntaxonomic scheme is proposed:

Association: OSMUNDO-ALNETUM Klotzli 70 (Alnetum glutinosae Tansley 39)

Osmundo-Alnetum Klötzli 70

typicum subass. nov.

typical var. (= Hydrocotyle sub-ass Klötzli 70 p.p.) (6.9.9.1.)
Lysimachia vulgaris var. (6.9.1.1.1.)
Scirpus sylvaticus var. (6.9.1.1.2.)

chrysosplenietosum subass. nov. (= Pellio-Alnetum Klötzli 70 p.p.) (6.9.1.2.)

sphagnetosum subass. nov. (6.9.1.3.)

lycopetosum Klötzli 70 (6.9.1.4.)

Peucedanum palustre var. (6.9.1.4.1.)
Carex elata var. (6.9.1.4.2.)

The systematic placement of this Association is clearly within the Alnetea glutinosae though some of the stands of the chryosplenietosum sub-ass. have some floristic affinities with the Querco-Fagetea.

6.9.2. Salix cinerea-Salix pentandra carr - Table 9.

Fen carr occurs in some of the rich fen systems of Northern Britain. In some stations it is only primitively developed as small areas of willow thicket but in other larger areas ofmore mature fen woodland exist. Owing to the relative rarity of rich fen systems in N. Britain and also to absence of woodland from many of them, only a few samples are available as a basis for the description of the vegetation. Nonetheless, they indicate a community very different from the alder carrs of Southern Britain.

For one thing Alnus glutinosa is not an important tree, confined mainly to the more lowland fens and even here often only sporadic. Instead Salix pentandra and S. cinerea are the major trees, often with Betula pubescens (and with Salix phylicifolia at Malham Tarn). These are often only about 5-8 m tal and form a fairly low and open canopy. Beneath this shrubs such as Rubus fruticosus are normally absent and in the well-lit conditions there is the development of a rich herbaceous flora. Equisetum fluviatile and Geum rivale are abundant and can form local societies - and indeed the occurrence of large quantities of the Equisetum shoots (up to 1 m tall, usually well-branched) is one of the most characteristic features of the ground layer of these woods. Angelica sylvestris, Cirsium palustre, Dryopteris dilata, Filipendula ulmaria and Valeriana officinalis are all characteristic associates. In wetter

places Carex rostrata, Menyanthes trifoliata and Potentilla palustris are frequent. In general, sedges are not the most important components of the herb layer, though Carex diandra and C. lasiocarpa are occasionally found in shallow pools amongst the roots of trees etc. and at Malham, Carex appropinquata can dominate the herb layer in some of the carr. However, of the sedges so typical of the lowland alder woods, Carex paniculata is only of occasional occurrence and Carex acutiformis has not been recorded in this survey. Similarly, other familiar species are absent: Eupatorium cannabinum, Iris pseudacorus, Lysimachia vulgaris, Lythrum salicaria, Solanum dulcamara and Urtica dioica.

Herbs of lower stature are plentiful: Caltha palustris, Cardamine pratensis, Dactylorhiza fuchsii, Equisetum palustre, Galium palustre, Lychnis flos-cuculi and Poa trivialis. Also, the northern species Crepis paludosa is frequent. The saprophytic orchid Corallorhiza trifida has been found in three sites. The round-leaved wintergreen, Pyrola rotundifolia, has been recorded from the woodland at Blackpool Moss, Selkirks. and Newham Bog, Northumberland. It is most abundant in the rather immature shrub transitional between open fen and the woodland. At Newton Reigny, Cumberland, the lesser wintergreen, Pyrola minor, occurs (as in other fen woodlands in N.W. England, e.g. Moorthwaite Moss, Cumberland).

The moss layer is well developed, covering up to 60% of the ground. Climacium dendroides is characteristic and

abundant. With this are Acrocladium cuspidatum and Eurhynchium praelongum. Mniums are well represented with Mnium affine, Mn. longirostrum, Mn. punctatum, and Mn. undulatum. Mnium pseudopunctatum and Mn. rugicum have also been recorded from the woods at Malham Tarn. In some stands Sphagna occur, mainly on elevated parts covering roots etc. The most usual species is Sphagnum recurvum but others can occur and at Temple Sowerby Moss (Westmorland) Sphagnum subsecundum and S. squarrosum were also recorded.

In the stands represented by lists S.923, S.928 and S.961 quite large areas of fairly level wet carr were available from which the lists could be made. At the other sites, however, undulations in fen surface, created by former turbary, produced a distinct environmental and vegetational pattern. In these situations the more elevated areas provide suitable conditions for the abundant growth of Molinia caerulea. Sphagna, especially S. palustre and S. squarrosum can also be found here and Betula pubescens is particularly associated with these higher areas.

Most of these Salix pentandra — S. cinerea communities have probably developed from Carex diandra — lasiocarpa fen (see 6.5.1.). It is not clear what communities might follow them in seral development, although it seems likely that with drying out Betula pubescens will become more prominent and acidification is likely to be accompanied by an expansion of Sphagna.

This type of fen woodland has very little documentation in the literature. The community has been described from the fens at Malham Tarn (PROCTOR, 1974; see also PROCTOR, 1960; SINKER, 1960) and from Semerwater in Yorkshire (INGRAM et al., 1959). Its distribution is at present uncertain due to insufficient information. It is most probably largely a rather localised community of rich fen systems in Northern Britain. However, similar stands have been observed in the rheotrophic parts of some poor fen systems in N.W. England.

Syntaxonomy: An Association - the Salicetum pentandro-cinereae Passarge 61 - has been described (see PASSARGE, 1961; WESTHOFF & DEN HELD, 1969), in which Salix pentandra is an important component. However, this has very different floristics to the community discussed above. It would, therefore, seem appropriate to recognise an independent Association for which the name Crepido-Salicetum pentandrae is suggested. It may be placed, along with other Salix scrub within the Salicion cinereae Müll. et Görs 58 Alliance of the Franguletea Doing 62 em. Westhoff 68.

6.9.3. Betula pubescens-Dryopteris cristata community - Table 9.

Characterising species-group: Dryopteris cristata, Calamagrostis canescens, Caldium mariscus, Dryopteris cartusiana, Juncus subnodulosus, Myrica gale, Pyrola rotundifolia.

Description: The crested buckler-fern, Dryopteris cristata, has for long been regarded as a rarity of the broadland area of East Norfolk. Although a widespread species of the European continent (JALAS & SUOMINEN, 1972), it is of very restricted occurrence in the British Isles. It was once more widely distributed (see BENNETT, 1904) but has suffered from drainage and collecting and is now mainly restricted to Norfolk where it occupies a handful of sites (PETCH & SWANN, 1968; SWANN, 1975). This survey has indicated, however, that the plant remains quite frequent in some of the fens associated with the Thurne and Ant rivers.

The fern occupies a rather specific community where patches of immature Betula pubescens scrub form small acidic nuclei within the rich fen vegetation. These often occur amongst very wet tall fen communities with Phragmites communis and Typha angustifolia.

The origin of these areas is not clear but characteristically theyconsist of Betula pubescens bushes 2-3 m high mixed with Alnus glutinosa, Myrica gale, Salix cinerea, Rubus fruticosus and, occasionally, R. caesius. With these are open fen species - much Phragmites communis and, usually in small amounts, Calamagrostis canescens, Eupatorium cannabinum, Juncus

subnodulosus, Lysimachia vulgaris, Lythrum salicaria, Peucedanum palustre and, sporadically, Cladium mariscus. Interestingly, Molinia caerulea has not been recorded. The floor of the scrub is covered by large inflated polsters of Sphagna. Sphagnum fimbriatum, S. palustre, S. plumulosum and S. recurvum have all been found in large amounts with other bryophytes such as Calypogeia muellerana, Campylopus pyriformis, Dicranella heteromalla and Plagiothecium denticulatum. Associated with the mosses is Hydrocotyle vulgaris and, in one place in the Ant fens, Drosera rotundifolia - perhaps its only current broadland record, though ELLIS (1965, p.99) indicates that it was formerly more abundant (see also PALLIS, 1911, p.233).

Ferns are particularly well-developed in these small areas: Thelypteris palustris is frequently abundant with Dryopteris dilatata, D. carthusiana and, less frequently, D. filix-mas (in one place with D. borreri), Athyrium filix-femina and Osmunda regalis. With these, in many of the birch stands, a few fronds of Dryopteris cristata and/or hybrids with D. carthusiana can be found. D. cristata seems to be most characteristic of the marginal carr and it rarely occurs in better developed scrub away from the edges. The same seems to apply to another species often present in this community, Pyrola rotundifolia. In the Ant marshes this often seems to be most abundant at the boundary between Betula-Myrica scrub and Phragmites fen and at Upton Broad it is often found where immature carr borders the droves.

Distribution. This community is most probably restricted to a few sites in the East Norfolk fens.

Syntaxonomy. Due to the distinct structure and floristic composition of this community, which is clearly very different from other types of fen scrub that have been recognised, it would seem appropriate to recognise it as an independent Association. The name Betulo-Dryopteridetum cristatae is proposed for this. The characterising species-group given above may be regarded as diagnostic and Dryopteris cristata can be considered as a fairly good faithful species (at least in East Anglia). The community may be assigned to the Salicion cinereae Alliance of the Franguletea. Related communities that have been described are the Dryopterido-Sphagnetum Segal 66 and the Frangulo-Salicetum auritae Doing 62.

6.9.4. Frangula alnus-Rhamnus catharticus communities.

Characterising species-group: Frangula alnus or Rhamnus catharticus as dominants.

Stands of fen carr dominated either by Frangula alnus or Rhamnus catharticus have only been recorded from Wicken Fen, Cambs. in this survey. These communities have already received documentation by GODWIN & TANSLEY (1929), GODWIN (1936) and GODWIN et al. (1974) and will only be considered briefly.

6.9.4.1. Frangula alnus carr. YAPP (1908) pointed to Frangula alnus (= Rhamnus frangula L.) as a species forming extensive thickets on Wicken. As indicated by GODWIN & TANSLEY (1929) and GODWIN (1936), the species colonises sedge fen to form a dense scrub beneath which only a few associates occur.

The following sample was taken:

Wicken Sedge Fen, Wicken, Cambs.

Frangula alnus	3,3,3	Calystegia sepium	+
Salix cinerea	1,1	Eupatorium cannabinum	+
S. repens	+	Poa trivialis	+
Ligustrum vulgare	+	Phragmites communis	+
Rubus fruticosus	+		
		Acrocladium cuspidatum	+
Cladium mariscus (includes both living and dead material)	3,3	Brachythecium rutabulum	+

This represents fairly immature Frangula carr. The bushes were about 3 m tall forming an almost continuous canopy. Beneath them Cladium mariscus was the major component but most

of the leaves seemed to be dead.

The following is an example of more mature carr containing more associates:

S.152 Wicken Poor's Fen, Wicken, Cambs.

Frangula alnus	3,3	Phragmites communis	1,1
Salix cinerea	+	Poa trivialis	+
Rhamnus fruticosus	+	Symphytum officinale	+
Rubus fruticosus	+	Urtica dioica	+
Crataegus monogyna	+		
		Acrocladium cuspidatum	+
Carex elata	+	Brachythecium rutabulum	1,1
Cladium mariscus (dead)		Campylium stellatum	1,1
Eupatorium cannabinum	+	Eurhynchium praelongum	+
Iris pseudacorus	+	Fissidens adianthoides	+
Mentha aquatica	+	Pseudoschleropodium purum	+
Molinia caerulea	+		

6.9.4.2. Rhamnus catharticus carr - Table 9.

Here Rhamnus catharticus is the dominant species forming a carr community some 5 m tall. Frangula alnus often occurs with it but usually in small quantity. Dead bushes have been found. The composition of the community is shown in Table 9. Where Rhamnus forms a dense canopy there are often few associated species but in the mature stands, where the canopy is fairly high and there are spaces between some of the crowns, a more diverse ground flora is able to develop. This includes bushes of Rubus caesius and R. fruticosus, along with scattered shoots of Phragmites communis and in places even Cladium mariscus has been able to persist. Herbaceous species include Filipendula ulmaria, Eupatorium cannabinum, Iris pseudacorus, Lythrum salicaria, Lysimachia vulgaris and Urtica dioica. In some places Thelypteris palustris can be abundant. Grasses include Agrostis stolonifera and Poa trivialis and in one stand Calamagrostis canescens was recorded.

Mosses can be well developed forming extensive carpets over the floor of the carr. Acrocladium cuspidatum and Brachythecium rutabulum are both abundant and with them can be Campylium stellatum, Eurhynchium praelongum, Mnium affine and Mnium longirostrum.

6.9.4.3. Syntaxonomy. It seems most appropriate to regard the above communities as sociations characterised by the dominance of Frangula alnus and Rhamnus catharticus respectively.

They may be referred to the Salicion cinereae Alliance of the Franguletea.

6.9.5. Myrica gale community - Table 9B.

Characteristic species: Myrica gale (dominant).

Description: Only two samples are available to describe this community, both from corners of mowing marshes in the Ant valley where the vegetation has been allowed to pass into Myrica scrub. However, related stands have been observed elsewhere in the East Norfolk fens.

The predominant feature of the vegetation is Myrica gale, which occurs as numerous straggly bushes of up to 2 m tall. There are only a few associated species, but Phragmites communis still occurs in quantity growing up between the bushes and Cladium mariscus can also be found. Associated herbs vary but specimens of Peucedanum palustre, Lysimachia vulgaris, Eupatorium cannabinum, Calamagrostis canescens and Thelypteris palustris can often be found. Mosses tend to be absent.

The community is related to Myrica-rich stands of open Phragmites-Cladium fen (6.2.10.), from which it may have developed in some places.

Syntaxonomy. Myrica gale scrub has frequently been described but usually as a community of nutrient-poor conditions with acidophilic species (e.g. Myricetum sphagnosum Jonas 35; Sphagneto-Myricetum Gale Duvigneaud 49; Sphagneto papilloso-imbricati Jonas 35 var Myricetosum Vanden Berghen 51; Frangulo-Myricetum Tüxen & Passarge 60). However, versions of the community from more nutrient-rich situations with species such

as Calamagrostis canescens, Cirsium palustre, Lysimachia vulgaris, Peucedanum palustre, and Phragmites communis, have also been described (JONAS, 1933; DUVIGNEAUD & VANDEN BERGHEN, 1945). FISCHER (1967) has created two subassociations of the Myricetum gale (Gadeceau 09) Jonas 35, to accommodate these different developments: an Erica tetralix sub-ass. characterised by Erica tetralix, Calluna vulgaris, Drosera rotundifolia and Eriophorum angustifolium and also a Peucedanum palustre sub-ass. characterised by Peucedanum palustre, Calamagrostis canescens, Galium palustre and Lysimachia vulgaris.

The stands described here are clearly related to the second sub-association, which would, in fact, appear to represent a suitable placement for this community-type.

The Myricetum gale has been placed within the Order Salicetalia auritae Doing 62 both by WESTHOFF & DEN HELD (1969) and OBERDORFER et al. (1967).

TABLE 9B.

Myrica gale scrub.

	707	728
Alnus glutinosa	+	+
Myrica gale	4,4	4,4
Phragmites communis	2,3	1,1
Cladium mariscus	1,1	+
Peucedanum palustre	+	+
Calamagrostis canescens		+
Filipendula ulmaria	-	
Juncus subnodulosus		+
Eupatorium cannabinum	+	
Lysimachia vulgaris	+	
Lythrum salicaria		+
Thelypteris palustris	+	

Releve sites:

707: Barton Turf, Norfolk. TG 368204
728: Catfield, Norfolk. TG 369213

6.9.6. Fen Oakwood.

It is not clear to what extent fen carr represents a climax community. TANSLEY (1939) suggested that, in East Anglia at least, oak forest might be expected to succeed carr vegetation. GODWIN & TURNER (1933) considered that at Calthorpe Broad, in the East Norfolk fens, a zone of oakwood developed over Phragmites peat might represent a natural successional development. And, CLAPHAM (in TANSLEY, 1939) has described an oak forest as the culmination of the hydrosere at Sweat Mere in Shropshire, though there is some doubt as to whether it truly does represent this (see SINKER,

1962). LAMBERT (1951) also questions if all carr communities may be expected to become sufficiently dry to accommodate oakwood. However, examples of oakwood most certainly can be found on the drier parts of some rich fen systems. Two lists, one (S.1084) made from Wicken Fen, Cambridgeshire, and the other (S.1098) made from Calthorpe Broad in Norfolk, give some indication of the floristics of fen oakwood:

	1084	1098
Quercus robur	2,3	3,3
Fraxinus excelsior	1,1	
Crataegus monogyna	+	1,1
Salix cinerea	+	+
Rhamnus catharticus	+	
Rosa canina	+	
Rubus fruticosus	+	+
Carex acutiformis	+	+
Cirsium palustre	+	
Dryopteris filix-mas	+	+
Eupatorium cannabinum	+	
Galium palustre		+
Geranium robertianum		+
Iris pseudacorus	+	+
Phragmites communis		+
Poa trivialis	+	+
Solanum dulcamara	+	+
Urtica dioica	+	+
Amblystegium serpens	+	+
Atrichum undulatum	+	
Brachythecium rubabulum	+	+
Mnium hornum	+	+
Mn. undulatum	+	+

Under certain (relatively acid) circumstances a rather different community has been recorded. Here an open shrub layer of Myrica gale occurs and Molinia caerulea strongly

dominates the ground layer. This is seen in two lists: S.1036 from Askham Bog, Yorks.; and S.1057 from the mire complex to the north of Upton Broad, Norfolk.

	1036	1057
Quercus robur	3,3	3,3
Myrica gale	1,2	1,3
Betula pubescens	1,3	1,3
Frangula alnus	+	
Sorbus aucuparia	+	
Molinia caerulea	4,4	4,4
Dryopteris filix-mas	+	+
Lonicera periclymenum	1,1	+
Phragmites communis	+	+
Potentilla erecta		+
Quercus seedlings	+	+
Rubus fruticosus agg.	+	2,2
Solanum dulcamara	+	
Plagiothecium denticulatum		+

6.9.7. Synopsis of rich fen forest communities.

FRANGULETEA Doing 62 em. Westhoff 68

SALICETALIA AURITAE Doing 62 em. Westhoff 68

SALICION CINEREAE Th. Müll. et Görs 58

Myricetum gale (Gadeceau 09) Jonas 35

Peucedanetosum Fischer 67 (6.9.5.)

Betulo-Dryopteridetum cristate ass. nov. (6.9.3.)

Frangula alnus sociation (6.9.4.1.)

Rhamnus catharticus sociation (6.9.4.2.)

Crepido-Salicetum pentandrae (6.9.2.)

ALNETEA GLUTINOSAE Br.-Bl. et Tx. 43 em. Th. Müll. et Görs 58

ALNETALIA GLUTINOSAE Vlieger 37 em. Th. Müll. et Görs 58

ALNION GLUTINOSAE (Malcuit 29) Meijer Drees 36

Osmundo-Alnetum Klötzli 70

typicum subass. nov.

typical var. (= Hydrocotyle sub-ass Klötzli 70 p.p.) (6.9.9.1.)
Lysimachia vulgaris var. (6.9.1.1.1.)
Scirpus sylvaticus var. (6.9.1.1.2.)

chrysosplenietosum subass. nov. (= Pellio-Alnetum Klötzli 70 p.p.) (6.9.1.2.)

sphagnetosum subass. nov. (6.9.1.3.)

lycopetosum Klötzli 70 (6.9.1.4.)

Peucedanum palustre var. (6.9.1.4.1.)
Carex elata var. (6.9.1.4.2.)

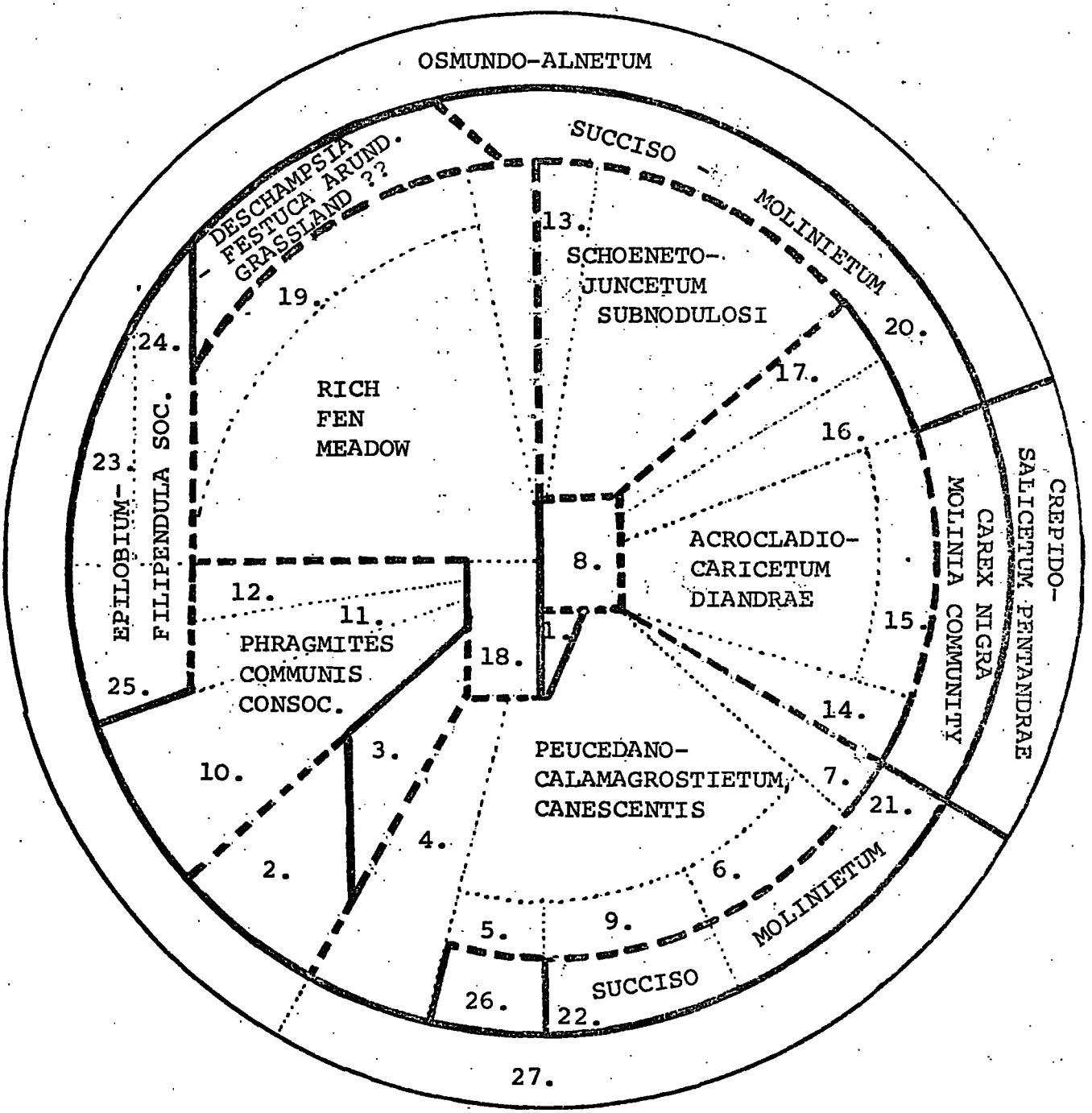
Chapter 7.

The rich fen circle of vegetation.

Discussion and summary.

Fig. 7.I.

THE RICH FEN CIRCLE OF VEGETATION



7. The rich fen circle of vegetation

In some respects the title of this Chapter is misleading. It is debatable as to how legitimate it is to refer to a rich fen "circle of vegetation" for, as has become evident, rich fen plant communities have strong floristic ties to other vegetation types outside of the concept of rich fen. Nonetheless, the vegetation types described do not just represent a purely arbitrary 'chunk' of wetland vegetation, but rather constitute a series of inter-related community-types with at least some measure of natural circumscription. They are thus considered to compose a "circle of vegetation", albeit a broken one. Fig. 7.I. attempts to display some of the inter-relations of some of the syntaxa within this.

The cohesion given to this circle of vegetation is a product of the manifold floristic inter-relations of the various component communities, together with intergradations between different types. However, there are no species that occur in all of the communities. Only the moss Acrocladium cuspidatum comes close to doing this. Several species, however, occur in most of them except for the Pinguiculo-Caricetum dioicae and, to a lesser degree, the sedge swamp communities. These are Angelica sylvestris, Cirsium palustre, Filipendula ulmaria and Mentha aquatica.

The application of Information analysis to synoptic data representing all of the noda recognised led to the construction

of two main classes. One contained the communities of sedge swamp vegetation, fen vegetation of Groups 2 and 3 and alder carr communities, together with the communities of the Pinguiculo-Caricetum. The other contained the Acrocladio-Caricetum diandrae, the Schoeneto-Juncetum subnodulosi, the Succiso-Molinietum, the Group 6 communities of rich fen meadow and the Filipendula ulmaria - Epilobium hirsutum communities of Group 8. The most notable feature here is the classification of the Pinguiculo-Caricetum away from the other calcareous mire communities of the Caricion davallianae.

Sedge swamp communities

Little need be said about the sedge swamp communities. These sublittoral communities represent some of the earliest phases of the hydrosere that may be referred to as fen. Indeed, the deep-water stands of Cladium mariscus are best regarded as reedswamp: they were only included here for the purpose of comparison with more terrestrial Cladium-dominated types.

The sedge swamp communities have essentially been defined on the basis of the dominant sedge. Thus, the Cladietum marisci Zobrist 35 em. Pfeiffer 61 contains Cladium-dominated swamp (not the more terrestrial Cladium communities). A single stand of Carex appropinquata swamp has been referred to a 'Carex appropinquata community' - whose relationship with

the Caricetum appropinquatae Aszod 36 remains uncertain. Both of these are rather species-poor communities with only tenuous affiliations with the bulk of the rich fen circle. A similar observation can be made about the Carex elata swamp types that have been included within the Caricetum elatae Koch 26. However, in the Carex paniculata swamp ("Tussock fen"; Caricetum paniculatae Wangerin 15) a fair number of fen plants are represented, such as Epilobium hirsutum, Lythrum salicaria and, in broadland, Peucedanum palustre, Thelypteris palustris. These are able to come in here through the elevated substratum provided by the robust, upstanding tussocks of the sedge, and in broadland the community has clear floristic links with the more terrestrial Peucedano-Calamagrostietum communities; it also has seral links with the Osmundo-Alnetum as the tussock-tops are colonised by saplings of Alnus glutinosa and Salix cinerea as the preliminary phase of the development of swamp carr (LAMBERT, 1951).

Magnocaricion fen

The tall growing communities of open fen (groups 2 and 3) form a distinct vegetation unit, but nonetheless, it is difficult to find species that characterise this. Occurring with fairly high constancies are Calystegia sepium, Iris pseudacorus, Lycopus europaeus, Scutellaria galericulata and Solanum dulcamara. These show a distinct affinity to this

unit but this is by no means absolute. They occur also, with rather high constancies in certain communities of the Osmundo-Alnetum and also in certain rich fen meadow vegetation types, especially in the Juncus subnodulosus-Iris pseudacorus nodum.

The Peucedano-Calamagrostietum communities (encompassing much of the herbaceous fen vegetation of east Norfolk) are clearly linked floristically to those of the sociations of Group 3 (i.e. species-poor Phragmites fen vegetation) by species that they have in common, such as the above-mentioned together with others such as Valeriana officinalis and Thalictrum flavum. In particular, the Phragmites-Carex paniculata sociation has clear floristic affiliations through species such as Lysimachia vulgaris. In general, however, the Group 3 sociations seem to be rather distinct from the Peucedano-Calamagrostietum types. This partly reflects their general poverty of species, but also the occurrence of species such as Urtica dioica, Galium aparine and Scrophularia aquatica - species that are largely absent from the Peucedano-Calamagrostietum

The Peucedano-Calamagrostietum itself has Peucedanum palustre and Calamagrostis canescens, as constant species with a high level of fidelity. Considering only the data of this survey, a fidelity degree of 4 has been estimated (following the criteria of SZAFER and PAWLOWSKI in BRAUN-BLANQUET (1964)). The reason why a value of 5 cannot be given is mainly due to the occurrence of these species in certain mire forest types, notably the Osmundo-Alnetum lycopetosum Peucedanum var.

Other species which also show the same trend of occurring both in Peucedano-Calamagrostietum and alder carr are Carex elata, Lysimachia vulgaris and Thelypteris palustris. As these species are able to flourish in the carr environment they are not to be regarded just as relicts of a former phase of herbaceous fen (as, for example, is Cladium mariscus which usually occurs in carr only in a moribund, vegetative state). Clearly, there must be certain parallels between the fen and carr environment that are conducive to the growth of these species. It would be of interest to identify them.

From this point of view, Thelypteris palustris is of considerable interest. Although this plant is of fairly wide occurrence throughout the Peucedano-Calamagrostietum, it is particularly well developed in certain community-types, as for example in the Myrica gale variant of the typicum subassociation. In the mowing marshes of the Norfolk broads area it has been noted to be particularly characteristic of areas with some shrub development. Furthermore, its present abundance in certain parts of the marshes may, in at least some instances, reflect the previous occurrence of scrub or carr in the not-too-distant past, though there is no evidence to suggest that this is universally so. It seems best developed in communities that produce considerable accumulation of litter.

Other species that have their main occurrence within the Peucedano-Calamagrostietum are Carex appropinquata, Lathyrus palustris, Rumex hydrolapathum and Stellaria palustris.

A number of the more characteristic species of the Peucedano-Calamagrostietum also occur in certain rich fen meadow community types. As well as those already mentioned, Peucedanum itself, Calamagrostis canescens, Lysimachia vulgaris, Lathyrus palustris, Carex appropinquata, Thelypteris palustris and others have all occasionally been found in this context. They mainly occur, however, only in one community-type, the Juncus subnodulosus-Iris pseudacorus nodum, and, within this, in the Symphytum and Peucedanum varieties. As already mentioned in 6.6.7., these constitute rather atypical fen meadow communities which, in many cases at least, have been derived from Peucedano-Calamagrostietum fen by mowing and grazing, and which would almost certainly revert to high fen in the absence of these factors.

Lathyrus palustris and Lysimachia vulgaris have both been regarded by some Continental phytosociologists as character species for the Molinietalia Koch 26 (e.g. OBERDORFER, 1962; WESTHOFF & DEN HELD, 1969). This status, however, is not confirmed by the present survey which suggests that both species are mainly confined to Magnocaricion communities (amongst herbaceous types). Interestingly, KORNECK (1963) also regards Lathyrus palustris as a Magnocaricion species. It may, however, be noted that at Wicken Fen, where the plant is abundant, Molinia is an important component of the community (the Peucedanum-Calamagrostietum typicum Molinia-Symphytum var.),

whereas it is not normally in this Association. Indeed, the vegetation at Wicken may well be developing into a Molinietum by gradual acidification and drying out (GODWIN & TANSLEY, 1929). Similarly, at Catcott Heath, where the plant is again abundant, Molinia is also a prominent component of the vegetation and the same applies in many places where it occurs at Upton Broad in Norfolk. The plant also grows in a rather dry fen meadow in Yorkshire. However, in the fens of the R. Yare in Norfolk, where Lathyrus is again plentiful it is not associated with Molinia. The plant, in fact, shows a curious distribution in English fens, and it would be of interest to identify some of the factors determining this.

The discussion above makes it clear that some stands of the Peucedano-Calamagrostietum show floristic relationships to Molinia-dominated vegetation. This is through species such as Molinia caerulea, Carex panicea, Dactylorhiza incarnata, Potentilla erecta and Succisa pratensis. This trend is shown by the Molinia-Symphytum var. of the typical subassociation and by the typical var. and Stellaria palustris var. of the caricetosum subassociation. A similar trend is displayed by the species-poor Cladium-Molinia fen communities that have also been recognised.

Caricion davallianae communities

The communities of calcareous mire, rich fen meadow and areas dominated by Molinia caerulea are all bound together by a group of species which occur fairly constantly. These are Potentilla erecta, Succisa pratensis, Carex panicea and, with generally lower constancies, Molinia caerulea and Carex nigra. These are most constant in the Schoeneto-Juncetum and the Succiso-Molinietum, but are also fairly constant in the Acrocladio-Caricetum diandrae, the Pinguiculo-Caricetum dioicae and in the communities of rich fen meadow, though here, in some of the most species-poor noda (e.g. Carex acutiformis sociation), they may hardly be represented. Nonetheless, they serve to impart a measure of coherence to these community-types: something which is enhanced by further inter-relationships.

The Pinguiculo-Caricetum dioicae is clearly very different from the other vegetation units in terms of its floristic composition as is demonstrated by it being grouped with the alder carr, Peucedano-Calamagrostietum fen etc. in the Information Analysis classification of the synoptic data, rather than with the other calcareous mire types. Indeed, it cannot really be considered a genuine component of the lowland circle of rich fen vegetation. As it is composed predominantly of samples made in upland parts of northern England, this is, perhaps, not surprising! It is distinguished by the low

constancies or complete absence of a number of species that are otherwise generally rather frequent throughout the range of communities. These include Angelica sylvestris, Cirsium palustre, Filipendula ulmaria, Galium palustre, Lotus uliginosus, Lychnis flos-cuculi, Mentha aquatica and Vicia cracca. These species include a number normally given some diagnostic value within the Molinio-Arrhenatheretea, though they also occur in Acrocladium-Caricetum diandrae/Schoeneto-Juncetum communities, and not always with low constancies. Here, however, they are largely absent. One important exception, however, is in the Pinguiculo-Caricetum filipenduletosum, which includes some of the most lowland representatives of the Association. The significance of this feature however, cannot be evaluated until further data are available concerning other types of mire and wet grassland from upland Britain. It may, however, be noted that these species also are not particularly well developed in the serratuletosum sub-association of the Schoeneto-Juncetum which includes the calcareous mires of Anglesey. The Pinguiculo-Caricetum has a number of species in common with the Schoeneto-Juncetum. These include:

Carex flacca*	Bryum pseudotriquetrum
C. lepidocarpa*	Cratoneuron commutatum
C. hostiana*	Ctenidium molluscum
C. pulicaris*	Drepanocladus revolvens
Eriophorum latifolium	Fissidens adianthoides
Parnassia palustris*	Pellia endiviifolia
Pedicularis palustris	Riccardia pinguis

Many of these species have been given as character species for the Caricion davallianae, or for the Parvocaricetea. They are particularly well developed in these two above-mentioned Associations, but also may be found in others as well. Those marked with a * are all prominent in the Juncus articulatus and Juncus subnodulosus groups of the Succiso-Molinietum, pointing towards the close affinities that have long been recognised between certain Caricion davallianae and Molinion communities. This is particularly noticeable in certain community-types. Thus, nearly all of the above-listed species also occur in the Euphrasia nodum of the Juncus articulatus group of the Succiso-Molinietum. Some of them also occur in rich fen meadow communities as well, but here they are usually only sporadic, though important exceptions are found within the Juncus-Carex lepidocarpa nodum.

The Schoeneto-Juncetum subnodulosi (which basically includes calcareous mire of lowland S.E. England dominated either by Schoenus nigricans or Juncus subnodulosus) itself is fairly distinct from the Pinguiculo-Caricetum. In addition to the Molinio-Arrhenatheretea species mentioned above, the Schoeneto-Juncetum has a number of differentiating species. Those which are of fairly high constancy include Anagallis tenella, Cirsium dissectum, Dactylorhiza incarnata, Epipactis palustris, Gymnadenia densiflora, Oenanthe lachenalii and Sphagnum plumulosum. Schoenus nigricans, although particularly characteristic of the Association, also occurs to some extent

in the Pinguiculo-Caricetum. Again, all of these species are fairly well represented in the Succiso-Molinietum, particularly in the Juncus subnodulosus group, emphasising the affinities between these two community-types. In particular, the Succiso-Molinietum Juncus subnodulosus Group Selinum var. has strong floristic affinities with the Schoeneto-Juncetum, and may perhaps be best regarded as occupying a transitional position. This similarity is not surprising in view of the ontogenetic relationships between the two community-types.

In a converse way, typical "grassland" species of the Succiso-Molinietum can also be found in certain community-types of the Schoeneto-Juncetum. Thus, species such as Trifolium repens, Plantago lanceolata, Linum catharticum, Leontodon taraxacoides and Polygala vulgaris are found in certain Schoeneto-Juncetum communities, particularly in the leontodetosum and serratuletosum subassociations. In the latter, species such as Hypericum pulchrum and Genista anglica also occur. Even the fly orchid, Ophrys insectifera, recognised by OBERDORFER (1962) as occurring within the Molinion, is found in association with the Schoenus tussocks; for even in the wettest sites the tussock-tops can provide a favourably dry autenvironment. Such niches also permit acidophilous plants to enter what is otherwise a highly basiphilous community.

The occurrence of Sphagna in the Schoeneto-Juncetum is of some interest. The main species is S. plumulosum, though others may also occur. CLAPHAM (1940) has pointed out that the

Sphagnum normally occurs on elevations above the calcareous mire surface, on hypnaceous mosses and around the base of woody plants etc. These observations have been largely confirmed in the present survey. It may, however, be noted that occasional inundation by calcareous fen water may not be particularly detrimental to the plant. SKENE (1915) has indicated that fairly high levels of calcium carbonate are not injurious per se to the rich fen species Sphagnum contortum. Other salts, however, such as phosphates may perhaps be more harmful, though SKENE points out that the toxicity of these is mitigated by the presence of calcium sulphate. Thus, in a calcareous fen, where the level of available phosphate seems anyway to be rather low (HASLAM, 1965) inundation by the ground water may have little affect upon the growth of the moss. However, any eutrophication of the irrigating water, might be expected to lead to more deleterious consequences.

The recognition of the apparent low nutrient-status of mires supporting the Schoeneto-Juncetum subnodulosi (which requires to be confirmed in more detail) also may help to explain the occurrence of other acidophilic species (such as Drosera rotundifolia). It also makes the occurrence of Schoenus nigricans on blanket peat in Ireland (TANSLEY, 1939) a little less surprising.

The Acrocladio-Caricetum diandrae exhibits some interesting inter-relationships with other community-types. Itself, it

is a coherent unit containing as defining constant species (which are also often dominant) Carex diandra, C. lasiocarpa and Acrocladium giganteum. Menyanthes trifoliata and Potentilla palustris are also very well developed, and this Association seems to be optimal for them amongst rich fen types. Other species, also rather characteristic, are Carex limosa, Cinclidium stygium, Mnium pseudopunctatum and Sphagnum contortum.

However, the above-mentioned species are not exclusive to this unit. They occur also, to some extent, in certain community-types of the Schoeneto-Juncetum subnodulosi and the Peucedano-Calamagrostietum canescentis and it is with these two Associations that the syntaxon shows its closest relationships.

The relationship with the Schoeneto-Juncetum is mediated through the occurrence of various Caricion davallianae species, such as Carex lepidocarpa and Bryum pseudotriquetrum, together with other species of calcareous mire such as Pedicularis palustris, Drepanocladus revolvens, Fissidens adianthoides, Riccardia pinquis and, less often, Eriophorum latifolium and Epipactis palustris. These occur in some, but not all, of the communities with varying degrees of constancy. On the other hand, the affinities with the Peucedano-Calamagrostietum are maintained by certain wet fen species. Thus, Potentilla palustris is a species well developed in both Associations though of rather restricted occurrence in other rich fen types. More specifically, however, the main inter-relationship of

the Acrocladio-Caricetum is with the cicutetosum and caricetosum subassociations of the Peucedano-Calamagrostietum, as these communities also contain large amounts of Carex diandra and Carex lasiocarpa and Acrocladium giganteum - sometimes developed as a semi-floating raft of vegetation in just the same way as is so characteristic of the Acrocladio-Caricetum. Similarly, some of the species characteristic of the Peucedano-Calamagrostietum cicutetosum, namely Cicuta virosa, Ranunculus lingua and Scutellaria galericulata also occur in certain Acrocladio-Caricetum communities, especially the cicutetosum subassociation. In some respects at least, the Peucedano-Calamagrostietum cicutetosum represents a community-type intermediate between this Association and the Acrocladio-Caricetum. It could, in fact, readily have been classified as a Peucedanum subassociation of this last syntaxon.

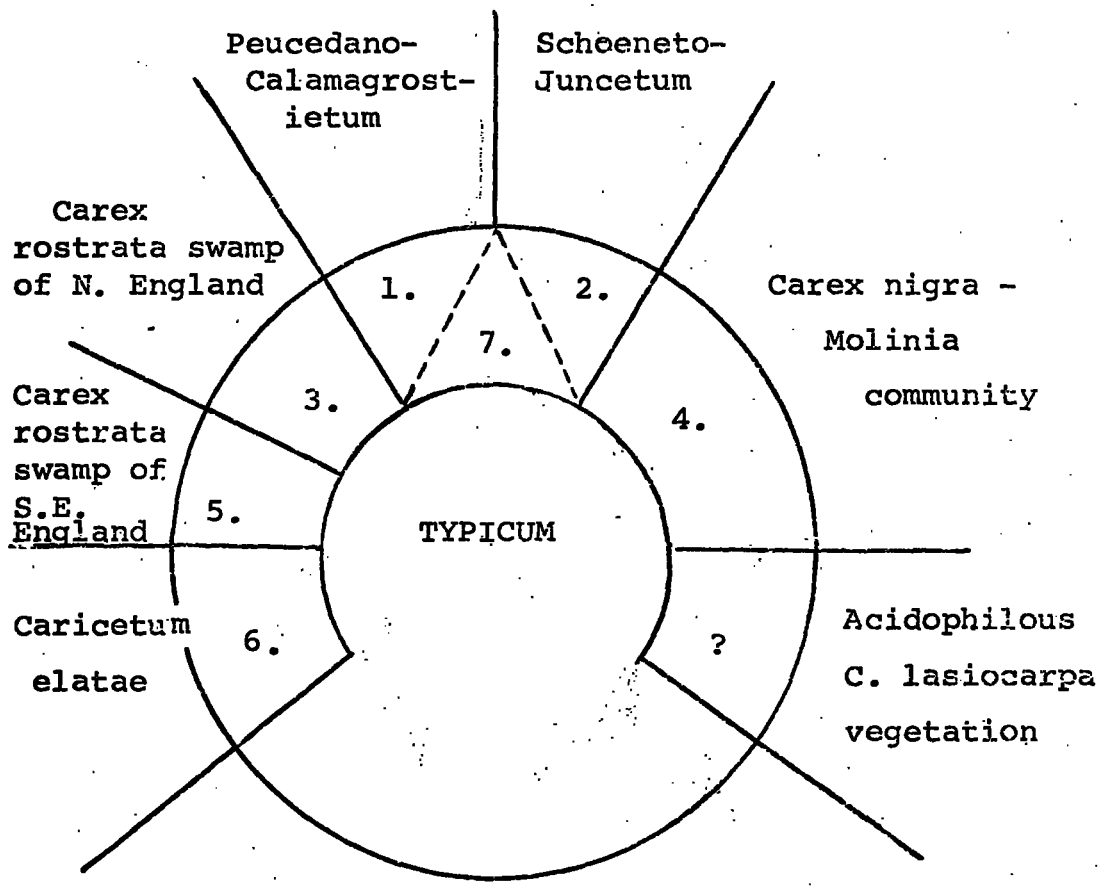
One community-type, assigned to the Acrocladio-Caricetum has particular affinities with the Schoeneto-Juncetum. As well as containing the calcareous mire species mentioned above, this community, the Acrocladio-Caricetum caricetosum Schoenus var., has, in addition, Anqallis tenella, Cladium mariscus and both Juncus subnodulosus and Schoenus. It is perhaps best regarded as a community transitional between the two Associations and the decision to keep it within the Acrocladio-Caricetum was only based upon the prominence of Carex diandra and C. lasiocarpa. Particularly interesting is that this community-type - recorded only from the mires of North Wales -

has a parallel in broadland, the Peucedano-Calamagrostietum caricetosum. Floristically, this stands on the boundary not only of the Acrocladio-Caricetum and the Schoeneto-Juncetum, but also is transitional to the Peucedano-Calamagrostietum. It incorporates elements from all three Associations. This community is of particular interest in that it serves to introduce into the often rather species-poor flood-plain mires of broadland a very wide species diversity, including a number of Tofieldietalia-Caricion davallianae species which otherwise are largely absent from these sites - such as Epipactis palustris, Carex lepidocarpa and even Anagallis tenella. Similarly, Acrocladio-Caricetum species such as Carex limosa and Cinclidium stygium. But of especial interest is that certain (rather wet) developments support a number of species not particularly characteristic of any of the "parent" Associations, notably Liparis loeselii, Hypericum elodes and Platanthera bifolia. Drepanocladus vernicosus and Pyrola rotundifolia also occur together with hydrophytes such as Baldellia ranunculoides, Hottonia palustris and Utricularia spp.

A further direction of variation is shown by the Acrocladio-Caricetum crepetosum, which incorporate stands transitional between the typical development of the Association and wet grassland communities (such as the Carex nigra-Molinia community 6.7.7.). However, as few data are available concerning such fen meadow types, little comment may be made. The same has to be said about another major direction of

Fig. 7.II.

Acrocladio-Caricetum diandrae:



Acrocladio-Caricetum communities:

1: cicutetosum (6.5.4.)
2: caricetosum Schoenus var. (6.5.7.)
3: typicum Carex rostrata var. (6.5.3.1.)
4: crepetosum (6.5.8.)
5: juncetosum typical var. (6.5.9.2.)
6: juncetosum Carex elata var. (6.5.9.1.)

Peucedano-Calamagrostietum community:

7: caricetosum (6.2.15.)

variation in which the Association is involved, namely that along pH gradient and the transition to more acidophilic community-types. Other developments of the community are also known which (Acrocladio-Caricetum typicum Carex rostrata var.) are transitional to Carex rostrata swamp, and (Acrocladio-Caricetum juncetosum Carex elata var.) to the Caricetum elatae.

This Association, then, has numerous clear affiliations with other community-types to which many of its sub-communities represent transitional forms. Nonetheless, it retains a nucleus of characteristic species as is demonstrated by its distinctive physiognomy and structure.

An attempt to illustrate the inter-relationships is given in Fig. 7.II.

It is thus evident that the precise floristic limits of calcareous mire vegetation are not sharp, and although Caricion davallianae species are very well represented in the communities that have been assigned to this Alliance, they also occur, to some extent, elsewhere - in the Magnocaricion and, particularly, the Molinion (or the Junco-Molinion).

These considerations, together with inadequate information relating to other vegetation types, make it premature to establish character species for the higher order syntaxa of calcareous mires. Nonetheless, it may be observed that from the communities examined here most of the character species proposed by WESTHOFF & DEN HELD (1969) (see 2.2.) for the

Caricion davallianae, and higher syntaxa, have not been excluded from this possible role. Exceptions are Stellaria palustris, which seems to be better developed in the Peucedano-Calamagrostietum than in Parvocaricetea communities (though it is known from some of these). Another is Potentilla palustris, which is also well developed in various Magnocaricion communities, especially the Peucedano-Calamagrostietum. It may be noted, however, that many of the character species are very local.

Rich fen meadow communities

These community-types (the noda of Group 6) together constitute a fairly discrete class. Characteristically developed as sedgy or rushy fen meadows in association with base-rich irrigating water, they have loose affinities both with the Succiso-Molinietum and the Schoeneto-Juncetum subnodulosi. These are maintained by a group of species that are fairly constant in each ofthe three syntaxa (though generally most constant in the fen meadows) and which have only restricted occurrence outside of them, namely:

Anthoxanthum odoratum	Festuca rubra
Centaurea nigra	Holcus lanatus
Dactylorhiza fuchsii	Ranunculus acris

and, to a lesser degree, Dactylorhiza incarnata and Trifolium repens.

The following species are also shared with the Succiso-Molinietum:

Deschampsia cespitosa	Pulicaria dysenterica
Lathyrus pratense	Rumex acetosa

There are, however, a number of species largely confined to the fen meadows, though with occasional representation in other groups (again, especially in the Succiso-Molinion). Some of the more constant are:

Arrhenatherum elatius	Juncus inflexus
Carex acutiformis*	Poa trivialis
C. disticha	Scrophularia aquatica
Epilobium parviflorum	
Hypericum tetrapterum	Brachythecium rutabulum*

(* = also constant in alder carr)

Other species of lower constancy largely confined to the group (often restricted to certain community-types) are:

Carex hirta	Ranunculus repens
Cynosurus cristatus	Rumex conglomeratus
Festuca arundinacea	Rumex sanguineus
Phleum pratense	Stellaria graminea
Potentilla anserina	Veronica beccabunga

The group, however, is not exceptionally well characterised as many of the above species are of rather low constancies. Furthermore, there are a number of different community-types. Some of these show floristic affinities to communities outside the scope of this survey, such as Deschampsia cespitosa-Festuca arundinacea grassland and little can be said about them, except that they are often developed on the drier margins around wetter fen meadow areas or in sites that have partially dried out. The Juncus-Carex lepidocarpa nodum shows firm

affinities to certain calcareous mire types with species such as Carex lepidocarpa, Pinguicula vulgaris etc., and indeed various other communities may also contain a smattering of Caricion davallianae species. The close relationships with the Succiso-Molinietum are seen particularly in the Juncus-Carex hirta-Deschampsia nodum which has many similarities with the Succiso-Molinietum Juncus articulatus Group Juncus nodum Deschampsia variant. As has already been noted, affinities with the Peucedano-Calamagrostietum are displayed by the Juncus subnodulosus-Iris pseudacorus nodum. There are also relationships between the Juncus subnodulosus typical nodum and the Group 3 Phragmites-Juncus subnodulosus sociation, as seen by the occurrence of Arrhenatherum elatius, Carex acutiformis, Lathyrus pratense, Scrophularia aquatica and Brachythecium rutabulum, amongst others, in the latter. In some cases at least it is known that the Phragmites-Juncus sociation has developed from Juncus subnodulosus fen meadow following the cessation of grazing.

Some comment must be briefly made concerning taxa that have been proposed as character-species for the higher order syntaxa of fen meadow (Calthion, Molinietalia, Molinio-Arrhenatheretea) (see Chapter 2), as a number of them do not seem to be well confined to these units. Thus, of the species listed for these syntaxa in Chapter 2, it may be noted that the following occur widely in other rich fen communities, especially those of the Caricion davallianae:

Angelica sylvestris	Filipendula ulmaria
Cardamine pratensis	Lotus uliginosus
Caltha palustris	Lychnis flos-cuculi
Cirsium palustre	Valeriana dioica
Equisetum palustre	Vicia cracca

Although these may be developed optimally in the Molinio-Arrhenatheretea, nonetheless, some of them, such as Vicia cracca, Valeriana dioica, are constant and often abundant in other community-types, especially in the Schoeneto-Juncetum. Other species, however, such as the Class characters Cerastium holosteoides, Festuca rubra, Holcus lanatus, Lathyrus pratensis, Plantago lanceolata, Ranunculus acris, Rumex acetosa and Trifolium pratense, do seem to be much more restricted to Molinio-Arrhenatheretea community-types.

Fen carr communities

The very different structures of herbaceous and woody rich fen community-types is reflected in their floristic distinctions: the ecesis of carr in herbaceous fen is marked by a very pronounced change of floristics. The process of carr development should not necessarily be thought of in terms of a gradual replacement of taxa so that the most mature carr contains the least number of species of open fen. Indeed, the converse is true, at least in some cases: that species of herbaceous fen are often least well developed in the initial stages of carr development, when the immature bushes are

tightly crowded together casting a dense shade. This has been observed to be the case with certain examples of Salix cinerea scrub. It is also true of Frangula alnus scrub (the Frangula alnus sociation) where the immature carr can often have a highly impoverished ground flora (GODWIN, 1936). By contrast, in the later, more open phases of more mature carr, species of open fen are once again able to become more prominent.

The sharp distinction between herbaceous and woody fen types is shown well by the Betulo-Dryopteridetum cristatae. This is an Association of certain places in the Norfolk broads area. It is characteristically developed as small islands of Betula pubescens scrub amongst sedge or reed communities. Most certainly various open fen species occur - Phragmites, Eupatorium, Juncus subnodulosus etc. - but the notable feature is the content of species that are absent or very rare in the surrounding acres of open fen. This is particularly true of the ground layer which consists of extensive polsters of Sphagna developed around the bases of the trees, but also there are specific herbaceous species too, not least Dryopteris cristata, Pyrola rotundifolia and, in one place, Drosera rotundifolia. The boundary between the scrub and the surrounding fen is always very sharp, no doubt partly in response to the different community-structures.

The same, however, is not so true for the willow thickets of the Crepido-Salicetum pentandrae. Of all the mire forest

communities observed this retains the greatest floristic connections with the surrounding open fen vegetation - which, in the sites examined in this survey, have usually be communities of the Acrocladio-Caricetum - and species such as Carex diandra and C. lasiocarpa may often persist in wet hollows in the woodland floor. It may be noted that the Association has considerable differences from the Osmundo-Alnetum: not least, the rarity or absence of species such as Eupatorium cannabinum, Iris pseudacorus and Urtica dioica which are so characteristic of the latter.

The Osmundo-Alnetum, containing the alder forest communities of rich fen systems, forms a very discrete syntaxon. These climax (or subclimax) communities have undoubted ontogenetic relationships with open fen communities, yet one of the interesting points emerging from this survey is the infrequency with which extensive intermediate phases between fen and alder carr have been observed.

The Association retains a number of the constant species of rich fen. Among the most frequent are:

Angelica sylvestris	Filipendula ulmaria
Caltha palustris	Galium palustre
Cardamine pratensis	Mentha aquatica
Equisetum palustre	Acrocladium cuspidatum

It may, however, be noted that some of the typical dominants of open fen are not well represented in the woods. In particular, Cladium mariscus is hardly ever found, even though the carr may be developed upon Cladium peat (LAMBERT &

JENNINGS, 1951). In fact, the plant is not shade tolerant (CONWAY, 1937) and is usually ousted from the vegetation with the ecesis of carr. If it persists at all then it is usually in an unhealthy and infertile state. Similarly, Juncus subnodulosus is virtually completely absent from fen carr. The same is not true, however, for Phragmites which is fairly frequent, though usually absent from the most shaded parts, or only persisting as weak, sterile haulms. It is best developed beneath openings in the canopy. A species of similar structure which seems able to withstand a greater degree of shading is Phalaris arundinacea. This plant most probably has quite high nutritional demands - and indeed, in the alder wood context, is normally best developed alongside rivers etc. in woods on mineral soils which are periodically flooded. Nonetheless, it does occur in alder carrs of peat fens, even though it may be completely absent from the surrounding open fen communities. Two other species that can similarly be found in fen woodland but often not in the adjoining fens are Galium aparine and Urtica dioica. These, like Phalaris, usually occur in the most nutrient-rich parts of mires and Urtica is known to have high requirements both of phosphate and nitrate.

The Osmundo-Alnetum also shares a number of species with other community-types. With fen meadow it has Carex acutiformis and Brachythecium rutabulum in common and sometimes the grass

Poa trivialis is abundant as well. As has already been mentioned, a number of species have optima both in the Osmundo-Alnetum and in the Peucedano-Calamagrostietum. Another plant that may be mentioned in this context is Osmunda itself. This species, which is largely restricted to acidic alder woods in Continental Europe seems to be of wider amplitude in Britain. In rich fen systems it has been recorded mainly from the Osmundo-Alnetum lycopetosum, particularly from stands in the Norfolk broads area. Its precise status here is of interest for, whilst undoubtedly a native component of the alder carr flora, it has also been widely planted in the past, as it was once harvested in large quantities. It occurs locally also in certain stands of the Peucedano-Calamagrostietum, the open habitat reflecting its similar occurrence in wet heaths and acid mires in parts of western Britain. The extent to which the occurrence of Osmunda in mowing marsh is as a relict from former carr is not entirely clear. It has been observed that its survival is enhanced by the fact that it is often not mown with the rest of the vegetation. In keeping with its acidophilic tendencies, the species has been recorded only from the more mesotrophic parts of rich fen systems. In the Norfolk broads area it has been found mainly in parts which are probably little influenced by circulating water. And it has not been found in alder carr associated with calcareous springs.

The Osmundo-Alnetum is fairly rich in bryophytes, even though some are of rather low constancy overall. Species such as Amblystegium serpens and Eurhynchium praelongum tend to be particularly well developed here. Others, however, also occur widely in fen meadow types and in the Schoeneto-Juncetum. These include Lophocolea bidentata, Mnium affine, Mn. longirostrum, Mn. punctatum and Mn. undulatum. They are not, however, usually found in Peucedano-Calamagrostietum communities. Further parallels with the Schoeneto-Juncetum are seen in the growth of Sphagna. The elevation of the woodland floor and acidification of the peat can provide suitable conditions for Sphagna to establish and grow and sometimes a thick carpet can develop (cf. GODWIN & TURNER, 1933).

Although various subassociations and variants within the Osmundo-Alnetum have been recognised, nonetheless, the essential uniformity of alder forest must be emphasised. The Association can develop on highly calcareous spring mires, in acid fens, in mesotrophic glacial hollows with stagnant topogenous water, on the flood-plain mires of East Norfolk (either as a community encroaching upon the open water of the broads or developed upon the more consolidated peat between them), but nonetheless, it has remarkable floristic uniformity. The uniformity is by no means absolute, as the existence of subassociations and variants indicates - for example, the chrysosplenietosum subassociation is associated with rather

acidic valley mires; the Peucedanum var. of the lycopetosum subassociation is associated with the mires of East Norfolk where its characterising species are well developed. Different seral sequences may produce different versions of the community - at least initially (LAMBERT, 1951). But, nonetheless, when compared with the wide viersity of rich fen communities that might be anticipated to occupy the various habitats in the absence of alder forest, the floristic uniformity is notable.

This unformity is most probably largely created by the vegetation itself. The environmental constraints presented by the development of a structured forest will help to select for certain species, perhaps largely over-riding the influence of other habitat differences. But also, the development of mire forest may actually serve to moderate habitat distinctions - the growth of a nitrogen-fixing tree may help to enhance the nitrogen balance of nitroge-deficient habitats. The accumulation of brushwood peat elevating the woodland floor above the main influence of the ground water, may help to produce a fairly uniform substratum irrespective of the precise ionic composition of the irrigating water - especially if superficial acidification is able to develop.

The convergence of a wide diversity of vegetation types into a single, relatively uniform community, appears to be the normal process of seral development and is implicit in the concept of climax vegetation. The extent to which the

Osmundo-Alnetum may be regarded as a climax type is debatable. GODWIN & TURNER (1933) described an oakwood at Calthorpe Broad, which may represent a successional phase but, as TANSLEY (1939) observed "many of the alder carrs show little or no signs of invasion by drier types of vegetation" (p.463). It is questionable as to whether all sites may be expected to dry out sufficiently to support oakwood. In any case, it is possible that in some sites the establishment of Sphagna could lead to a climax of ombrotrophic mire.

The above discussion indicates some of the floristic inter-relations between different rich fen community-types. It is evident that the varying sociological amplitudes of rich fen species on the one hand serve to define certain types of vegetation with a 'kernel' of characterising species, but on the other, serve to unite them into a complex circle of vegetation. No attempt has been made to specify character species, but nonetheless it would appear that at least some vegetation units (especially those corresponding to Alliances)

have species that are more or less restricted to them. In others this does not appear to be the case. Here, the particular combination of species is more useful for defining the unit.

It would seem likely that the complex inter-relationships of the rich fen circle of vegetation are paralleled by complex interactions between determinative habitat factors. The rich fen habitat may be regarded as being formed of a network of co-acting environmental gradients. Some of the more obvious of these, which are by no means necessarily independent of one another, form the axes pioneer:climax, unstable:stable, wet:dry, base-rich:base-poor, eutrophic:oligotrophic etc. But, in particular, the importance of geographical location in determining the composition of rich-fen vegetation has become evident. Thus, on a large scale, the Schoeneto-Juncetum subnodulosi is largely confined to calcareous mires in S.E. England, whereas the Pinguiculo-Caricetum dioicae is found mainly in Northern Britain. The Acrocladio-Caricetum dioicae is mainly an Association of N.W. England and S. Scotland - though this may represent nothing more than the absence of suitable sites in the south-east. The same is probably true of the Peucedano-Calamagrostietum canescentis - confined largely to the few remaining areas of flood plain mire in East Anglia.

But even on a more local scale, location is important.

Considering the Peucedano-Calamagrostietum, not only are there the two chorological variants of "Yare valley fen" and "Bure valley fen" identified by PALLIS (1911), but also many of the other variants recognised are confined to specific areas of the mire complexes. Each different area often seems to produce its own distinctive version of the community. And this is true elsewhere. Indeed, one of the most obvious aspects of rich fen systems is that no two are the same - each has its particular characteristics, each its particular pattern of species-distributions combining to differentiate the vegetation cover into a pattern of plant communities. Nonetheless, the results of this survey suggest that regularly-recurring combinations of plant species can be found and that these permit the identification of the various types of rich fen vegetation which, although showing intergradations to other types, can nevertheless, be recognised and characterised.

-o-o-O-o-o-

Summary of Associations and Other Main Units

PHRAGMITETEA Tx. et Preising 42
PHRAGMITETALIA Koch 26
PHRAGMITION (COMMUNIS) Koch 26 em. B.-T. 63

Cladietum marisci Zobrist em. Pfeiffer 61 (6.1.1.).

Cladium-dominated swamp of pools and wet places in fens.

typicum (6.1.1.1.) - no differential species

caricetosum lasiocarpae (6.1.1.2.) - Carex lasiocarpa an important species.

Glyceria maxima sociation (6.3.1.)

Glyceria-dominated swamp and fen; few associates.

Juncus subnodulosus swamp (6.1.5.)

MAGNOCARICION Koch 26

Carex appropinquata swamp (6.1.4.)

Caricetum elatae Koch 26 (6.1.2.)

Carex elata-dominated swamp in pools and wet fens.

Caricetum paniculatae Wangerin 16 (6.1.3.)

Carex paniculata-dominated swamp.

Peucedano-Calamagrostietum canescentis ass. nov. (6.2.7.-6.2.15.)

Tall fen dominated by Phragmites, Cladium or Calamagrostis canescens, mainly in Nrofolk broads. Characteristic species: the above, plus Peucedanum palustre, Lysimachia vulgaris, Juncus subnodulosus, Carex elata, Thelypteris palustris etc.

typicum (6.2.7.-6.2.11.) - no differentials.

glycerietosum (6.2.9.) - mainly from the R. Yare valley Glyceria maxima, Epilobium hirsutum, Thalictrum flavum, Lathyrus palustris, Solanum dulcamara.

schoenetosum (6.2.13., 6.2.14.) - mainly R. Ant and R. Thurne fens; Schoenus nigricans, Oenanthe lachenalii.

cicutetosum (virosae) 6.2.12.) - wet fen areas; Cicuta virosa, Carex pseudocyperus, Berula erecta, Ranunculus lingua, Sium latifolium, Typha angustifolia.

caricetosum (diandro-lasiocarpae) 6.2.15. - wet or relatively dry fen; rare; Carex diandra, C. lasiocarpa, C. appropinquata, Epipactis palustris, Pedicularis palustris, Valeriana dioica, Schoenus nigricans, Carex lepidocarpa, Acrocladium giganteum.

Cladium-Phragmites consociation (6.2.4.; 6.2.5.) - dominated by Cladium or Phragmites; in broadland and elsewhere; often species-poor; Peucedano-Calamagrostietum species largely absent.

Phragmites communis consociation (6.3.2.)

Generally species-poor vegetation dominated by Phragmites; Carex paniculata sometimes important.

PARVOCARICETEA Den Held et Westhoff 69
TOFIELDIETALIA Prsg. apud Oberd. 49
CARICION DAVALLIANAE Klika 34

Schoeneto-Juncetum subnodulosi ass nov. (6.4.1.-6.4.9.)

Sedge communities of calcareous, soligenous (mainly) fens, normally on oozing peat; chiefly in S.E. Britain; Schoenus nigricans and/or Juncus subnodulosus dominate with the following species: Anagallis tenella, Epipactis palustris, Cirsium dissectum, Dactylorhiza praetermissa, Eupatorium cannabinum, Phragmites communis, Galium uliginosum, Oenanthe lachenelii; plus the species of the Pinguiculo-Caricetum, below. Bryophytes abundant; Sphagnum plumulosum.

callunetosum (6.4.2.) - 'mixed mire'; Aulacomnium palustre, Calluna vulgaris, Drosera rotundifolia, Erica tetralix, Myrica gale, Juncus bulbosus, Sphagnum plumulosum, S. palustre, S. subsecundum.

cladietosum (6.4.3.2.) - characterised by Cladium mariscus in conjunction with absence of other differentials.

caricetosum rostratae (6.4.3.4.) - wet Schoenus fen; Carex rostrata, Menyanthes trifoliata, Potamogeton coloratus, Utricularia sp.

leontodetosum (6.4.3.5.) - often fairly dry; Leontodon taraxacoides, Polygala vulgaris, Anthoxanthum odoratum, Centaurea nigra, Gymnadenia densiflora, Luzula multiflora.

typicum (6.4.3.1.,6.4.4.1.,6.4.4.2.) - no differentials; often small, isolated mires.

serratuletosum (6.4.5.) - Anglesey mires; Serratula tinctoria, Dactylorhiza purpurella, Gymnadenia densiflora, Linum catharticum, Sieglingia decumbens, (Hypericum pulchrum, Plantago maritima); absence of Cirsium dissectum, Galium uliginosum, Valeriana dioica.

Dactylorhiza purpurella nodum (6.4.3.3.) - from N. England; characterised by Dactylorhiza purpurella plus absence of other differentials.

Pinguiculo-Caricetum dioicae Jones 73 em. (6.4.10.-6.4.19.)

Communities of calcareous soligenous mires on peat or mineral gleys in N. Britain; typical species: Carex lepidocarpa, C. flacca, C. hostiana, C. dioica, Eriophorum latifolium, Parnassia palustris, Pedicularis palustris, Pinguicula vulgaris, Bryum pseudotriquetrum, Cratoneuron commutatum, Drepanocladus revolvens, Fissidens adianthoides, Riccardia pinguis, Molinia caerulea, Potentilla erecta, Succisa pratensis, Ctenidium molluscum. These species also occur in Schoeneto-Juncetum and Acrocladio-Caricetum; distinguish from these by the absence of their characterising species and by the presence of local characterising spp., e.g. Primula farinosa.

molinietosum (6.4.11.-6.4.13.,6.4.15.2.) - upland and lowland calcareous mires with Molinia important and characteristic with Eriophorum latifolium and Succisa pratensis; includes certain Schoenus mires; also 'turfy marshes' of Upper Teesdale with species like Bartsia alpina, Kobresia simpliciuscula, Sesleria caerulea, Tofieldia pusilla.

filipenduletosum (6.4.14.) - lowland community with wet meadow species: Filipendula ulmaria, Anthoxanthum odoratum, Lotus uliginosus, Luzula multiflora.

Scorpidium nodum (6.4.11.) - open flush with rich development of Scorpidium scorpioides, Cratoneuron commutatum, Drepanocladus revolvens, Riccardia pinguis.

Saxifraga aizoides-Chara nodum (6.4.15.1.) - open flushes; similar to Scorpidium nodum, but Scorpidium rare, Saxifraga aizoides frequent. Recorded from Upper Teesdale.

Acrocladio-Caricetum diandrae (Koch 26) nom. nov. (6.5.3.-6.5.9.)

Communities of base-rich, wet, topogenous fen usually over peat; may be developed as a floating raft. Carex diandra, C. lasiocarpa and Acrocladium giganteum abundant and characteristic; Carex rostrata, Eriophorum angustifolium, Menyanthes trifoliata, Potentilla palustris abundant; Pedicularis palustris, Carex lepidocarpa in some communities.

typicum (6.5.3.) - no differentials; most widespread type in N. England.

cicutetosum (6.5.4.) - infrequent type of very wet fen - old peat sites etc.; Cicuta virosa, Ranunculus lingua, Scutellaria galericulata.

caricetosum (6.5.5.-6.5.7.) - species-rich communities with many calcareous mire species: Carex lepidocarpa, Eriophorum latifolium, Fissidens adianthoides, Parnassia palustris, Pedicularis palustris; also Carex limosa, Sphagnum contortum, Mnium pseudo-punctatum.

crepetosum (6.5.8.) - drier communities with fen meadow species in N. Britain with fen meadow spp.: Crepis paludosus, Geum rivale, Sanguisorba officinalis, Climacium dendroides, Hylocomnium spendens, Juncus acutiflorus.

juncetosum (subnodulosii) - communities in S.E. England, often fragmentary and comparatively species-poor. Juncus subnodulosus is characteristic together with absence of other differentials.

MOLINIO-ARRHENATHERETEA Tx 37
MOLINIETALIA Koch 26
CALTHION PALUSTRIS Tx. 37 em. 51

Fen meadow noda (6.6.2.-6.6.14.)

Rush or sedge dominated stands on wet ground; mosses poorly developed; widely distributed; wet grassland species are prominent: Caltha palustris, Cardamine pratensis, Carex acutiformis, C. disticha, Cerastium holosteoides, Dactylorhiza fuchsii, Epilobium parviflorum, Hypericum tetrapterum, Juncus articulatus, J. inflexus, J. subnodulosus, Holcus lanatus, Lathyrus pratense, Plantago lanceolata, Poa trivialis, Ranunculus acris, Rumex acetosa, Trifolium repens.

Juncus-Carex lepidocarpa nodum (6.6.2.) - infrequent around base-rich springs etc.; transitional to Schoeneto-Juncetum; Anagallis tenella, Carex lepidocarpa, Eriophorum angustifolium, Pedicularis palustris, Parnassia palustris. (Schoenus, Carex hostiana, Pinguicula).

Juncus-Centaurea nigra nodum (6.6.3.-6.6.11.) - freq. in rather dry places; Centaurea nigra, Plantago lanceolata, Potentilla anserina, Ranunculus repens.

Juncus-Carex hirta-Deschampsia nodum (6.6.4.,6.6.12.) - freq. in rather dry places; Carex hirta, Deschampsia cespitosa, Potentilla reptans, Cynosurus cristatus, Centaurea nigra, Plantago lanceolata, Potentilla anserina.

Juncus subnodulosus typical nodum (6.6.5.,6.6.10.,6.6.13.) - Frequent, usually in wet places; no good differentials but Juncus subnodulosus constant and usually dominant.

Juncus-Carex disticha nodum (6.6.6.) - frequent in wet places; poorly characterised, but Carex disticha constant and often abundant, but not always.

Juncus-Iris pseudacorus nodum (6.6.7.) - occasional; topogenous fen meadow (usually); Iris pseudacorus, Phragmites communis, (Lythrum salicaria, Valeriana officinalis, Calamagrostis canescens, Lysimachia vulgaris, Peucedanum palustre, Symphytum officinale, Thalictrum flavum).

Juncus subnodulosus-Carex elata nodum (6.6.8.) - infrequent; topogenous fen in hollows; Carex elata (often plentiful), Epilobium palustre, Potentilla palustris (Pedicularis palustris).

Juncus subnodulosus-Schoenus-Carex diandra nodum (6.6.9.) - recorded only from Anglesey in topogenous fen; often only fragmentarily developed; Juncus subnodulosus, Carex diandra, Pedicularis palustris, Schoenus nigricans.

Carex acutiformis sociation (6.6.14.) - species-poor sedge meadows dominated by Carex acutiformis.

JUNCO (SUBULIFLORI)-MOLINION Westhoff 69

Succiso-Molinietum community (6.7.2.-6.7.4.)

Poorly characterised; basically fen grassland in which Molinia caerulea is dominant; may include many species of fen meadow or of the Schoeneto-Juncetum or Pinguiculo-Caricetum; species often well developed are: Carex panicea, C. hostiana, Potentilla erecta, Succisa pratensis, Gymnadenia densiflora, Linum catharticum, Leontodon taraxacoides, Rumex acetosa, Hypnum cupressiforme. Mosses poorly represented.

Juncus subnodulosus nodum-group (6.7.2.) - mainly S.E. England as communities at the dry margins at the edge of calcareous fens; often bordering Schoeneto-Juncetum communities; Juncus subnodulosus, Cirsium dissectum, Schoenus nigricans.

Juncus articulatus nodum-group (6.7.3.) - occasional in both S. and N. England often on slopes (slightly) flushed with base-rich water; Molinia dominance often reduced; Cardamine pratensis, Carex nigra, Eriophorum angustifolium, Juncus articulatus, J. conglomeratus. Caricion davallianae often well represented.

Myrica nodum (6.7.4.3.) - Molinia co-dominant with Myrica gale; often in more acid parts of rich fen systems.

Myrica-Cladium nodum (6.7.4.4.) - only from Woodwalton Fen; Molinia abundant with Myrica, Cladium, Calluna, Achillea ptarmica, Calamagrostis canescens, Lysimachia vulgaris.

Species-poor Molinieta (6.7.4.2.).

Molinia societies (6.7.4.1.).

FILIPENDULION (Duvig. 46 p.p.) Segal 66

Epilobium hirsutum-Filipendula ulmaria sociation (6.8.1.-6.8.3.)

Species-poor vegetation dominated by Epilobium hirsutum and/or Filipendula with Galium aparine and Urtica dioica. In nutrient rich places alongside rivers, in dry fens etc. Bryophytes often completely absent.

FRANGULETEA Doing 62 em. Westhoff 68
SALICETALIA AURITAE Doing 62 em. Westhoff 68
SALICION CINEREAE Th. Müll. et Görs 58

Myricetum gale (Gadeceau 09) Jonas 35

peucedanetosum Fischer 67 (6.9.5.) - Myrica gale scrub; from Norfolk broads area; Phragmites, Cladium, Peucedanum palustre, Lysimachia vulgaris, Calamagrostis canescens, Thelypteris palustris.

Betulo-Dryopteridetum cristatae ass. nov. (6.9.3.)

Immature Betula pubescens scrub with Myrica and Sphagnum carpeted floor. Characterising species: Dryopteris cristata, D. carthusiana, D. uliginosa, Pyrola rotundifolia, Cladium mariscus, Calamagrostis canescens, Juncus subnodulosus, Peucedanum palustre. Fens in R. Ant valley, broadland.

Crepido-Salicetum pentandrae ass. nov. (6.9.2.)

Salix pentandra and/or Salix cinerea carr of topogenous fens of N. Britain. Betula pubescens frequent; Equisetum fluviatile, Geum rivale, Crepis paludosa; well developed bryophytes with Climacium dendroides, Mnia, Sphagna.

Frangula alnus sociation (6.9.4.1.)

Low, dense scrub dominated by Frangula; esp. at Wicken. Few associates, cryptogam or phanerogam.

Rhamnus catharticus sociation (6.9.4.2.)

Carr dominated by Rhamnus; esp. at Wicken.

ALNETEA GLUTINOSAE Br.-Bl. et Tx. em. Th. Müll. et Görs 58
ALNETALIA GLUTINOSAE Vlieger 37 em. Th. Müll. et Görs 58
ALNION GLUTINOSAE (Malcuit 29) Meijer Drees 36

Osmundo-Alnetum Klötzli 70 (6.9.1.1.-6.9.1.4.).

Alder carr; widespread in lowland fens; Alnus glutinosa, Betula pubescens, Salix cinerea (Fraxinus excelsior), Carex acutiformis, C. paniculata, Eupatorium cannabinum, Iris pseudacorus, Lythrum salicaria, Solanum dulcamara, Urtica dioica.

typicum (6.9.1.1.) - no differentials; widespread.

chrysosplenietosum (6.9.1.2.) - valley fen woods below spring lines often on acidic substrata; Chrysosplenium oppositifolium, Oenanthe crocata, Pellia epiphylla.

sphagnetosum (6.9.1.3.) - Betula pubescens prominent; poor herb layer with Molinia (Carex curta, C. echinata, Viola palustris); extensive Sphagnum carpets. Infrequent.

lycopetosum - mainly East Anglia, in broadland; Lycopus europaeus, Peucedanum palustre, Carex elata, Lysimachia vulgaris, Thelypteris palustris, Peucedanum palustre, (Osmunda regalis).

REFERENCES

ADAM,P., BIRKS, H.J.B., HUNTLEY, B. & PRENTICE, I.C. 1975. Phytosociological studies at Malham Tarn Moss and Fen. Vegetatio, 30, 117-132.

ALLORGE, M.P. 1922. Les associations végétales du vexin française. Rev. Gén. Bot., 33.

--- 1937. Le problème du Schoenus nigricans L. Ann. Des. Sci. Nat. Bot., 10, 1-5.

ANDERSON, D.J. 1965. Classification and ordination in vegetation: controversy over a non-existent problem ? J. Ecol. 53, 521-526.

ASZOD, L. 1936. Adatok a nyírségi homoki vegetació ökologiájához és szociólogiájához. Acta geobot. hung. 1, 75-107.

BALÁTOVÁ-TULÁČKOVÁ, E. 1963. Zur Systematik der europaischen Phragmitetea. Presila 35, 118-122.

--- 1965. Cnidion venosi, ein neuer Molinietalia-Verband. Biológica, 20, 294-296.

--- 1968. Beitrag zur Systematik zur Molinietalia-Gesellschaften. In, Pflanzensoziologische Systematik, ed. R. Tuxen. Den Haag.

--- 1972. Flachmoorwiesen im mitteleren und unteren Opava-Tal (Schleisen). Vegetace CSSR A4. Prague.

BARKMAN, J.J. 1968. Das synsystematische Problem der Mikrogesellschaften innerhalb der Biozönosen. In Pflanzensoziologische Systematik ed. R. Tuxen, Den Haag. 21-53.

BAUMANN, E. 1911. Die Vegetation des Untersees (Bodensee). Archiv. fur Hydrobiol. Suppl. 1.

BECKING, R.W. 1957. The Zürich-Montpellier School of phytosociology Bot. Rev., 23, 411-488.

BEGER, H. 1922. Assoziationsstudien in der Waldstufe des Schanfiggs. Jahresber. Naturforsch. Ges. Graubundens. 1.

BELLAMY, D.J. 1967. Ecological studies on some European mires. Ph.D. thesis. London.

--- 1968. An ecological approach to the classification of the lowland mires of Europe. Proc. 3rd. Int. Peat Cong., Quebec. 74-79.

--- 1970. The vegetation. In 'Durham County and City with Teeside', ed. J.C. Dewdney, 133-141.

--- 1972. Templates of peat formation. Proc. 4th. Int. Peat Cong., Helsinki. 7-18.

--- & RIELEY, J. 1967. Some ecological statistics of a minature bog. Oikos, 18, 33-40.

--- & ROSE, F. 1961. The Waveney-Ouse valley fens of the Suffolk-Norfolk border. Trans. Suff. N. Soc. 11, 367-385.

BENNETT, A. 1899. Senecio paludosus and S. palustris in East Anglia Trans. Norf. Norwich N. Soc., 6, 457-462.

--- 1902. Liparis loeselii and Teucrium scordium in England. Ibid, 7, 333-338.

--- 1903. Distribution of Peucedanum palustre and Layhtrus palustris in Britain. Ibid, 7, 467-476.

--- 1904. On Carex paradoxa and Lastrea cristata in Britain. Ibid, 7, 695-700.

BIRKS, H.J.B. 1969. The late-Weichselian and present vegetation of the Isle of Skye. Ph.D. thesis. Cambridge.

--- 1973. Past and present vegetation of the Isle of Skye. A palaeo-ecological study. Cambridge.

BOER, A.C., 1942. Plantensociologische beschrijving van de orde der Phargmitetalia. Ned. Kruidk. Arch. 52, 237-302.

BODEUX, A. 1955. Alnetum glutinosae. Mitt. Flor-soz. Arbeitsg. N.F. 5,114-135

BOWEN, H.J.M. 1968. The Flora of Berkshire. Oxford.

BRADSHAW, M.E.B. 1970. The Teesdale flora. In 'Durham County and City with Teeside' ed. J.C. Dewdney, 141-152.

BRADSHAW, M.E.B. & CLARK, W.A. 1965. Flora and vegetation. In 'The natural history of Upper Teesdale', ed. D.H. Valentine. Newcastle.

BRAUN-BLANQUET, J. 1921. Prinzipien einer Systematik der Pflanzen-gesellschaften auf floristicher Grundlage. Jahrb. St. Gallen Naturw. Ges. 57, 305-351.

--- 1928. Pflanzensoziologie. 1st ed. Berlin.

--- 1949. Übersicht der Pflanzengesellschaften Ratiens. III. Vegetatio, 1, 129-156.

--- 1964. Pflanzensoziologie. 2nd ed. Wien-New York.

--- & TUXEN, R. 1952. Irische Pflanzengesellschaften. In 'Die pflanzenwelt Irlands' ed. W. Lüdi 224-415. Bern.

BRIDGEWATER, P. 1970. Phytosociology and community boundaries of the British heath formation. Ph.D. thesis. Durham.

BRISSE, H. & GRANDJOUAN, G. 1971. Adaptation d'une méthod de classification multivariable par similitudes à l'écologie végétale en milieu naturel. I. Oecol. Pl. 6, 163-187.

BULOW, K.V. 1929. Allgemeine Moorgeologie - Handbuch der Moorkunde 1. Berlin.

BURR, E.J. 1970. Cluster sorting with mixed character types. II. Fusion strategies. Aust. Comp. J. 2, 98-103.

BURRELL, W.H. & CLARKE, W.G.1910. The fauna and flora of Flordon Common. Trans. Norf. Norwich N. Soc. 2, 170-186.

BUTTERY, B.R. & LAMBERT, J.M. 1965. Competition between Glyceria maxima and Phragmites communis in the region of Surlingham Broad. I. The competition mechanism. J. Ecol. 53, 168-181.

ČEŠKA, A. 1973. Češka-Roemer program: specifications. Mscr.

--- & ROEMER, H. 1971. A computer program for identifying species-releve groups in vegetation studies. Vegetatio 23, 255-277.

CHRISTIANSEN, W. 1955. Pflanzenkunde von Schleswig-Holstein. 2nd ed. Neumunster.

CLAPHAM, A.R. 1936. Overdispersion in grassland communities and the use of statistical methods in plant ecology. J. Ecol. 24, 232-251.

CLAPHAM, A.R. 1940. The role of bryophytes in the calcareous fens of the Oxford district. J. Ecol. 28, 71-80.

CLAPHAM, A.R. & CLAPHAM, B.N. 1939. The valley fen at Cothill, Berkshire. Data for the study of post-glacial history. II. New Phytol. 38, 167-174.

--- & GODWIN, H., 1948. Studies in the post-glacial history of British vegetation. VIII and IX. Phil. Trans. B. 233. 233-273.

---, TUTIN, T.G. & WARBURG, E.F. 1962. Flora of the British Isles. 2nd ed. Cambridge.

CONWAY, V.M. 1936. Studies in the autecology of Cladium mariscus R.Br. I.Structure and development. New Phytol. 35, 177-204.

--- 1937. IV. Growth rates of the leaves. Ibid. 37, 254-278.

--- 1938. V. Fistribution of the species. Ibid. 37, 312-328.

CRAWFORD, R.M.M. & WISHART, D. 1967. A rapid method for the detection and classification of groups of ecologically related species. J. Ecol. 55,505-524.

CROMPTON, G. 1972. History and flora of Thriplow meadows. Nature Cambs. 15, 25.

--- & HEPBURN, I. 1972. Management experiment on Thriplow meadows, Cambridgeshire. Nature Cambs. 15, 21-25.

CURTIS, J.T. 1959. The vegetation of Wisconsin: an ordination of plant communities. Madison.

DAGNELIE, P. 1960. Contribution à l'étude des communautés végéta les par l'analyse factorielle. Bull. Serv. Carte. Phytog. B5, 7-71; 93-195.

DAHL, E. 1957. Rondane. Skr. norske Vidensk.-Akad; mat-naturv. Kl. 1-374.

?-- & HADAC, E. 1949. Homogeneity of plant communities. Studia bot. Cechosl. 10, 159-176.

DALE, M.B. & ANDERSON, D.J. 1972. Qualitative and quantitative Information analysis. J. Ecol. 60, 639-653.

---, LANCE, G.N. & ALBRECHT, L. 1971. Extensions of Information analysis. Aust. Comp. J. 3, 29-34.

--- & QUADRACCIA, L. 1973. Computer assisted sorting of phytosociological data. Vegetatio 28, 57-73.

DANIELS, R.E. 1973. A preliminary survey of Beanrig Moss, a fen in south Scotland. Trans. Bot. Soc. Edin. 42, 507-516.

--- & PEARSON, M.C. 1974. Ecological studies at Roydon Common, Norfolk. J. Ecol. 62, 127-150.

DARBY, H.C. 1956. The draining of the Fens. 2nd ed. Cambridge.

DAUBENMIRE, R. 1966. Vegetation: identification of typal communities. Science, N.Y. 151, 291-298.

DAWKINS, C.J. 1939. Tussock formation by Schoenus nigricans: the action of fire and water erosion. J. Ecol. 27, 78-88.

DIJK, J. VAN & WESTHOFF, V. 1955. De plantengroei der naturgebieden in N.W. Overijsel. Natuur en Landschap 9, 33-57.

DOING, H. 1962. Systematische Ordnung und floristiche zusammensetzung Niederlandische Wald- und Gebüschgesellschaften. Wentia 8

--- 1963. Ubersicht der floristischen zussammensetzung, der struktur und der dynamischen beziehungen Niederlandischer Wald- und Gebüsch-gesellschaften. Meded. Landbouwhogeschool Wagen. 63.

DONSELAAR, J. VAN. 1961. On the vegetation of former river beds in the Netherlands. Wentia 5, 1-85.

DONY, J.G. 1953. Flora of Bedfordshire. Luton.

--- 1967. Flora of Hertfordshire. Hitchin.

DRUCE, G.C. 1926. The Flora of Buckinghamshire. Arbroath.

DUFF, M. 1930. The ecology of the Moss Lane region, Lough Neagh. Proc. Roy. Irish Acad. 39B, 477-496.

DUFFEY, E. 1971. The management of Woodwalton Fen: the multidisciplinary approach. In 'Scientific management of animal and plant communities for Conservation' ed. E. Duffey & A.S. Watt. Oxford.

DU RIETZ, G.E. 1921. Zur methodologischen Grundlage der modernen Pflanzensoziologie. Uppsala.

--- 1936. Classification and nomenclature of vegetation units 1930-1935. Svenske Bot. Tidskr. 30, 580-589.

--- 1949. Huvudenheter och -granser i Svensk Myrvegetation. Ibid 43, 299-309.

--- 1950. Phytogeographical mire excursion to northeastern Smaland and Ostergotland. 8th Int. Bot. Congr. Excurs. guide AIIb2,

--- 1954. Die Mineralbodenwasserzeigergrenze als Grundlage einer naturlichen Zweigliederung der nord- und mitteleuropaischen Moore. Vegetatio 5/6, 571-585.

DUVIGNEAUD, P. 1946. La variabilité des associations végétales. Bull. Soc. Roy. Bot. belg. 78, 107-134,

--- 1948. La tourbière eutrophe à Carex lasiocarpa (Caricetum diandro-lasiocarpae) dans les marais de la Haute Semois. Lejeunia 12, 5-26.

--- 1949. Classification phytosociologique des tourbières de l'Europe. Bull. Soc. Roy Boy. Belg. 81, 59-129.

--- & VANDEN BERGHEN, C. 1945. Associations tourbeuses en Campine Occidnetale. Biol. Jaarb. Dodonae, 12, 53-90.

EGLER, F.E. 1942. Vegetation as an object of study. Phil. Sci. 9, 245-260.

ELLENBERG, H. 1954. Zur Entwicklung der Vegetationssystematik in Mitteleuropa. Fest. Aichinger, Angew. Pflanzensoz. 1, 134-143.

--- 1956. Aufgaben und Method der Vegetationskunde. In 'Einfuhrung in die Phytologie IV(1) ed. H. Walter. Stutgart.

--- & CRISTOFOLINI, G. 1964. Sichtlochkarten als Hilfsmittel zur Ordnung und Auswertung von Vegetationsaufnahmen. Ber. geobot. Inst. ETH. Rubel 35, 124-134.

ELLIS, E.A. 1934. Wheatfen Broad, Surlingham. Trans Norf. Norwich N. Soc.13.

--- 1965. The Broads. London.

GEHU, J.-M. 1961. Les groupements végétaux du Bassin de la Sambre francaise. Vegetatio 10, 69-148.

GIBBONS, E.J. 1975. The Flora of Lincolnshire. Lincoln.

GILMOUR, J.S.L. & WALTERS, S.M. 1964. Philosophy and classification. Vistas in Botany 4, 1-22.

GLEASON, H.A. 1939. The individualistic concept of the plant association. Am. Midl. Nat. 21, 92-110.

GODWIN, H. 1931. Studies in the ecology of Wicken Fen. I. The ground water level in the fen. J. Ecol. 19, 449-473.

--- 1936. Ibid. III. The establishment of fen scrub (carr). 24, 82-116.

--- 1941a. Studies on the post-glacial history of British vegetation III and IV. Phil. Trans. B. 230, 239-303.

--- 1941b. Ibid. VI. New Phytol. 40, 108.

--- 1948. Ibid. X. Phil. Trans. B. 233, 275.

--- & CLIFFORD, M.H. 1938. Ibid. I and II. Phil. Trans. B.229, 323-406.

---, CLOWES, D.R. & HUNTLEY, B. 1974. Studies in the ecology of Wicken Fen. V. Development of fen carr. J. Ecol. 62, 197-214.

---- & GODWIN, M.E. 1934. Pollen analysis of peats at Scolt Head Island, Norfolk. In 'Scolt Head Island' ed. J.A. steers. Cambridge.

--- & TANSLEY, A.G. 1929. The vegetation of Wicken Fen. In 'The natural history of Wicken Fen' ed. J.S. Gardiner, 387-446. Cambridge.

--- & TURNER, J.S. 1933. Soil acidity in relation to vegetational succession in Calthorpe Broad, Norfolk. J. Ecol. 21, 235-262

GOODALL, D.W. 1953a. Objective methods for the classification of vegetation. I. The use of positive interspecific assoication. Aust. J. Bot. 1, 39-63.

--- 1953b. Ibid. II. Fidelity and indicator value. Aust. J. Bot. 1, 434-456.

--- 1954a. Ibid. III. An essay in the use of factor analysis. Aust J. Bot. 2, 304-324.

---- 1954b. Vegetational classification and vegetational continua. Festschr. Aichinger, Angew. Pflanzensoziol. 1, 168-182.

--- 1963. The continuum and the individualistic association. Vegetatio 11, 297.

--- 1973a. Sample similarity and species correlation. In Whittaker (1973).

--- 1973b. Numerical methods of classification. In Whittaker (1973).

GORHAM, E. 1957. The chemical composition of some waters from lowland lakes in Shropshire, England. Tellus 9, 174-179.

GÖRS, S. 1958. Ein Beitrag zur Kenntnis des Crepido-Juncetum acutiflori (Br.-Bl.15) Oberd.56. auf basenreichen Standorten in Südwest-Deutschland. Beitr. naturkdl. Forschung SW-deutsch. 17, 8-10.

---- 1963. Beitrage zur Kenntnis basiphiler Flachmoorgesellschaften (Tofieldietalia Prsg. apud Oberd. 49). I. Das Davallseggen-Quellmoor (Caricetum davallianae Koch 28). Veröff. Landesst. Natursch. u. Landschaftpfledge Baden-Württemberg 32, 7-42.

--- 1964. Ibid. II. Das Mehl-primel-Kopfbinsen-Moor (Primulo-Schoenetum ferruginei Oberd. (57) 62. Ibid. 32, 7-42.

GOUNOT, M. 1961. Les methodes d'inventaire de la végétation. Bull. Serv. Carte phytogeogr. B6, 7-73.

GRIFFITH, J.E. 1895. Flora of Anglesey and Carnarvonshire. Bangor.

GREIG-SMITH, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. Ann. Bot. 16, 293-316.

--- 1971. Application of numerical methods to tropical forests. In 'Statistcial ecology' Ed. G.P. Patil et al., 195-204.

GROSE, D. 1954. A botanical survey of Spye Park. Wilts. Arch. N. Hist. Mag. 55, 263-276.

--- 1957. The flora of Wiltshire. Devizes.

GUINOCHET, M. & LEMÉE, G. 1950. Contribution à la connaisance des races biologiques de Molinia caerulea (L.) Moench. Rev. gen. Bot. 57.

HADAC, E. 1939. Zur nomenklatur und Systematik der Moorgesellschaften. Studia bot. Cech. 2, 97-106.

--- & VÁNA, J. 1967. Plant communities of the mires in the western parts of the Krkonose mountains, Czechoslovakia. Fol. Geobot. Phytotax. 3, 213-254.

HASLAM, S.M. 1965. Ecological studies in the Breck Fens. I. Vegetation in relation to habitat. J. Ecol. 53, 599-619.

--- 1966. The Breck fens. Trans. Suffolk N. Soc. 13, 137-146.

HESLOP-HARRISON, J. 1953. A synopsis of the Dactylorchids of the British Isles. Ber. Geobot. Forsch. Rübel Zürich, 1953, 55-82.

HODGSON, W. 1898. Flora of Cumberland. Carlisle.

HOLDGATE, M.W. 1955a. The vegetation of some springs and wet flushes on Tarn Moor near Orton, Westmorland. J. Ecol. 43, 80-89.

--- 1955b. The vegetation of some British upland fens. J. Ecol. 43, 389-403.

HOLUB, J., HEJNY, S., MORAVEC, J. & NEUHÄUSL, R. 1967. Ubersicht der höheren Vegetationseinheiten der Tschechoslowakei. Prague.

HOLZNER, W. & STOCKINGER, F. 1973. Der Einsatz von Elektronrechernern bei der pflanzensoziologischen Tabellenarbeit. Osterr. Bot. Z. 121, 303-309

HOPKINS, B. 1955. The species-area relations of plant communities. J. Ecol. 43, 410-426.

HORST, K., KRAUSCH, H.-D., & MÜLLER-STOLL, W.R. 1966. Die Wasser- und Sumpfpflanzengesellschaften im Elb-Havel-Winkel. Limnologica 4, 101-163.

HUECK, K. 1931. Erläuterung zur vegetationskundelichen Karte der Lebauehrung (Ostpommern). Beitr. Naturdenk. 14, 107-214.

IVIMEY-COOK, R.B. 1972. Association analysis - some comments on its use. In.'Grundfragen und Methoden in der Pflanzensoziologie' ed. R. Tuxen, 89-97. Den Haag.

--- & PROCTOR, M.C.F. 1966. The plant communities of the Burren, Co. Clare. Proc. Roy. Irish Acad. 64B. 211-302.

JACCARD, P. 1912. The distribution of the flora in the alpine zone. New Phytol. 11, 37-50.

JALAS, J. & OKKO, V. 1951. Botanical and geological analysis of the Cladium mariscus station in Joroinen. Arch. Soc. Zoo. Bot. Fenn. 'Vanamo' 5, 82-101.

--- & SUOMINEN 1972. Atlas Florae Europaeae. Pteridophyta. Helsinki.

JEFFRIES, R.L., WILLIS, A.J. & YEMM, E.W. 1968. The late- and post-glacial history of the Gordano valley, North Somerset. New phytol. 335-348.

JEFFERIES, T.A. 1915. Ecology of the purple heath grass (Molinia caerulea). J. Ecol. 3, 93-109.

JEFFREYS, H. 1916. On the vegetation of four Durham coal-measure fells. I. General description of the areas and its vegetation. J. Ecol. 4, 174-195.

JENNINGS, J.N. & LAMBERT, J.M. 1951. Alluvial stratigraphy and vegetational succession in the region of the Bure valley broads. I Surface features and general stratigraphy. J. Ecol 39, 106-119.

JESCHKE, L. 1959. Pflanzengesellschaften einiger Seen bei Fledberg in Mecklenburg. Feddes Repert. Beih. 138, 161-214.

JONAS, F. 1933. Der Hammrich. Feddes Repert. Beih. 71.

--- 1935. Die Vegetation der Hochmoore im Nordhümmling. Feddes Repert. Beih. 78, 1-143,

JONES, A.V. 1973. A phytosociological study of Widdybank Fell in Upper Teesdale. Ph.D. thesis. Durham.

KENNETH, A.G. 1971. An orchid new to Scotland. Glasgow Nat. 18, 589.

KENT, D.H. & LOUSLEY, J.E. 1956. A hand list of the plants of the London area. London.

KERSHAW, K.A. 1957. The use of cover and frequency in the detection of pattern in plant communities. Ecology, 38, 291-299.

KING, J. & NICHOLSON, I.A. 1964. Grasslands of the forest and sub-alpine zones. In 'The vegetation of Scotland' ed. J.H. Burnett, Edinburgh.

KLIKA, J. 1929. Příspěvek ke geobotanikému prozkumu středního Polabí. Věstník Král. čes. Spol. Nauk, Prague 2, 1-25.

--- 1934. Die pflanzengesellschaften auf Travertinen bei Stankovany in der Slowakei. Bull. intern. Ac. Tcheque Sc. 35, 41-44.

KLOSS, K. 1965. Schoenetum, Juncetum subnodulosi und Betula pubescens-Gesellschaften der kalkreichen Moorniederung Nordost-Mecklensburgs. Feddes Repert. Beih. 142, 65-117.

KLÖTZLI, G. 1970. Eichen, Edellaub-, und Bruchwälden der Britischen Inseln. Schweiz. Zeitschr. Forstwesen 121, 329-366.

KOCH, W. 1926. Die Vegetationseinheiten von Linthebene unter Berücksichtigung der Verhältnisse in ther Nordostschweiz. Jahr. St.-Gallischen Naturwiss. Ges. 61.

--- 1928. Die höhere Vegetation der subalpinen Seen und Moorgebiete des Val Piora. Zeitschrift Hydro. 4.

KORNECK, D. 1963. Die Pfeifengraswiesen und ihre wichtigstens Kontaktgesellschaften in der nördlichen Oberrheinebene und im Schweinfurther Trockengebiete. III. Kontaktgesellschaften. Beitr. naturk. Forschung SW-Deutschl. 22, 19-44.

KOPECKY, K. 1967. Mitteleuropäischen Flussröhrichtgesellschaften des Phalaridion arundinacea-Verbandes. Limnologica 5, 39-79.

--- & HEJNY, S. 1965. Allgemeine Charakteristik der Pflanzengesellschaften des Phalaridion arundinaceae-Verbandes. Preslia 37, 53-78.

KOVACS, M. Die Moorwiesen Ungarns. Budapest.

KRAUSCH, H.-D. 1964. Die Pflanzengesellschaften des Stechlinsee Gebietes. II. Röhricht und Grossseggengesellschaften. Limnologica 2, 423-482.

--- 1965. Zür Gliederung des Scirpo-Phragmitetum medioeuropaeum W.Koch 26. Limnologica 3, 17-22.

--- 1968. Die Pflanzengesellschaften des Stechlinsee-Gebietes. IV. Die Moore. Limnologica 6, 321-380.

KUCHLER, A.W. 1967. Vegetation mapping. New York.

KUHN, L. 1961. Die Verlandungsgesellschaften des Federseerieds. In 'Die Federsee' Ed. W. Zimmerman, 1-69. Stuttgart.

LACEY, W.S. 1955. Orchis traunsteineri Saut. in Wales. Proc.B.S.B.I. 1,297-300.

----& ROBERTS, R.H. 1958. Further notes on Dactylorchis traunsteineri (Saut.) Vermeul. in Wales. Proc. B.S.B.I. 3, 22-27.

LAMBERT, J.M. 1946. The distribution and status of Glyceria maxima (Hartm.) Holmb. in the region of Surlingham and Rockland Broads, Norfolk. J. Ecol 33, 230-267.

--- 1947a Glyceria maxima (Hartm.)Holmb. J.Ecol. 34, 310-344.

--- 1947b A note on the physiognomy of Glyceria maxima reedswamps in Norfolk. Trans. Norf. Norwich N. Soc. 16, 246-249.

--- 1948 A survey of the Rockland-Claxton level, Norfolk. J. Ecol. 36, 120-135.

--- 1951. Alluvial stratigraphy and vegetational succession in the region of the Bure valley broads. III. Classification, status and distribution of communities. J. Ecol. 39, 149-170.

--- 1965. The vegetation of Broadland. In 'The Broads' (Ellis, 1965).

--- 1972. Theoretical models for large scale vegetation surveys. In 'Mathematical models in ecology, ed. J.N.R. Jeffers. Oxford.

--- & DALE, M.B. 1964. The use of statistics in phytosociology. Adv. Ecol. Res. 2, 59-99.

--- & JENNINGS, J.N. 1951. Alluvial stratigraphy and vegetational succession in the region of the Bure valley broads. II. Detailed vegetational-successional relationships. J. Ecol. 39, 120-148.

----,----, SMITH, C.T., GREEN, C. & HUTCHISNON, J.N. 1960. The making of the broads. R.G.S. Res. Mem. 3.

--- & WILLIAMS, W.T. 1966. Multivariate methods in plant ecology. VI. Comparison of information analysis and association analysis J. Ecol 54, 635.

LANCE, G.N. & WILLIAMS, W.T. 1966. Computer programs for hierarchical polythetic classification. Comput. J. 9, 60-66.

--- & --- 1967. A general theory of classificatory sorting stratevies. I. Hierarhical systems. Comput. J. 9, 373-380.

--- & --- 1968. Ibid. II. Clustering systems. Comput. J. 10, 271-277.

LEBRUN, J. NORIFALAISE, A., HEINEMANN, P. & VANDEN BERGHEN, C. 1949. Les associations végétales de Belgique. Bull. Soc. Roy. Bot. Belg. 82, 105-199.

LEMÉE, G. 1937. Recherches écologiques sur la végétation du Perche. Paris.

LIBBERT, W. 1932. Die Vegetationseinheiten der neumärksichen Staubecken-landschaft unter Berucksichtigung der angrenzenden Landschaften. Verh. Bot. Ver. Prov. Brandenb. 74, 10-93; 229-348.

LIND, E.M. 1950. Vegetation and history of some Cheshire Meres. Mem. Proc. Manch. Lit. Phil. Soc. 90, 17-36.

LOHMEYER, W. et alii 1962. Contribution a l'unification du systeme phyto sociologique pur l'Europe moyenne et nord-occidental. Melhoramento 15, 137-151.

MALCUIT, G. 1929. Les associations végétales de la vallée de la Lauterne. Arch Bot. 2.

MALMER, N. 1965. The southern mires. Acta phytog. Suec. 50, 149-158.

--- 1968. Uber die Gliederung der Oxycocco-Sphagnetea und Scheuchzerio-Caricetea fuscae. Ber. Int. Symp. Pflanzensoz. Syst. Stolenzau/Weser 1964.

McINTOSH, R.P. 1967. The continuum concept of vegetation. Bot. Rev. 33.

McVEAN, D. & RATCLIFFE, J. 1962. Plant communities of the Scottish Highlands. London.

MEIJER DREES, E. 1951. Capita selecta from modern plant sociology and a design for rules of phytosociological nomenclature. Rapp. Bosb. Proefst. Bogor 52, 1-68.

MESSENGER, G. 1971. Flora of Rutland. Leicester,

MESSIKOMMER, E. 1928. Verlandungserscheinung und Sukessionen im Gebiete des Pfuffikersees. Festschrift H. Schinz, Viertaljahrsschr. Naturf. Ges. Zurich 73.

MOORE, J.J. 1962. The Braun-Blanquet system: a reassesment. J. Ecol. 50, 761-769.

--- 1968. A classifcation of the bogs and wet heaths of Northern Europe (Oxycocco-Sphagnetea Br.-Bl. et Tx 43.) Ber. Int. Symp. Pflanzensoc. System., Stolenzau/Weser 1964. 306-320.

--- 1971. Phyto - a suite of programs in Fortran IV for the manipulation of phytosociological tables according to the principles of Braun-Blanquet.

---, FITZSIMMONS, S.J., LAMBE, E. & WHITE, J. 1970. A comparison and evaluation of some phytosociological techniques. Vegetatio 20, 1-20.

MOORE, P.D. & BELLAMY, D.J. 1974. Peatlands. London.

MORAVEC, J. 1966. Zur syntaxonomy der Carex davalliana-Ges. Folia Geobot. Phytotax. 1, 3-25.

MÖRNSJÖ, T. 1969. Studies on vegetation and development of a peatland in Scania, S. Sweden. Opera bot. 24

--- 1971. Peatland types and their regional distribution in S. Sweden. Geol. Fören. i Stock. Fordhandlingar 93, 587-600.

MOSS, C.E. 1911. In 'Types of British vegetation' ed. A.G. Tansley, Cambridge.

---, RANKIN, W.M. & TANSLEY, A.G. 1910. The woodlands of England. New Phytol. 9, 113-149.

MUELLER-DUMBOIS, D. & ELLENBERG, H. 1973. Aims and methods of vegetation ecology. New York.

NEUHÄUSL, R. 1959. Die Pflanzengesellschaften des südöstlichen Teiles des Wittingauer Beckens. Preslia 31, 115-147.

--- 1965. Vegetation der Röhrichts und der sublitoralen Magnocariceten im Wittingauer Beckens. Vegetation C.S.S.R. A1. Prague.

NEWBOULD, P.J. 1960. The ecology of Cranesmoor, a New Forest valley bog, I. The present vegetation. J. Ecol. 48. 361-383.

NEWTON. A. (1971). Flora of Cheshire. Chester.

NICHOLSON, W.A. 1906. A preliminary sketch of the bionomical botany of Sutton and the Ant district. Trans. Norf. Norwich N. Soc. 8, 265-289.

NOIRFAILAISE, A. & SOUGNEZ, N. 1961. Les forets riveraines de Belgique. Bull. Jard. Bot. de l'etat. 30, 199-288.

NORDHAGEN, R. 1936. Versuch einer nuen Einteilung der subalpinen-alpinien Vegetation Norweges. Bergens Mus. Arbok 7.

--- 1940. Ett nytt funn av Cladium mariscus i Norge. Act.phtyog. Suec.13, 201.

--- 1943. Sikilsdalen og Norges Fjellbeiter. Bergens Mus. Skr. 22.

NOY-MEIR, TADMOR, N.H. & ORSHAN, G. 1970. Multivariate analysis of desert vegetation. I. Isreel J. Bot. 19, 561-591.

OBERDORFER, E. 1957. Suddeutsche Pflanzengesellschaften. Jena.

--- 1962. Pflanzensoziologische Exkursionflora fur Suddeutschland. Stuttgart.

--- et alii 1967. Systematische Ubersicht der westdeutschen Phanaerogamen und Gefässkryptogamen-Gesellschaften. Schr. Reih. Vegetationsk. 2, 7-62.

ORLOCI, L. 1968. Information analysis in phytosociology: partition, classification and prediciton. J. theor. Biol. 20, 271-284.

--- 1973. Ordination by resemblance matrices. In Whittaker (1973) 251-286.

O'SULLIVAN, A.M. 1965. A phytosociological survey of Irish lowland meadows and pastures. Ph.D. thesis. Dublin.

--- 1968a. The lowland grasslands of County Limerick. Dublin.

--- 1968b. Irish Molinietalia communities in relation to those of the Atlantic region of Europe. Ber. Int. Symp. Pflanzensoz.Syst., Stolenzau/Weser 1964, 273-280.

PALLIS, M. 1911. The river valleys of east Norfolk: their aquatic and fen formation. In 'Types of British vegetation'. ed. A.G. Tansley.

PASSARGE, H. 1961. Zur soziologischen Gliederung der Salix cinerea-gebüsche norddeutschlands. Vegetatio 10, 209-228.

--- 1964. Pflanzengesellschaften des nordostdeutschen Flachlands I. Jena.

PATON, J.A. 1962. The genus Calypogeia Raddi in Britain. Trans. Br. Bryol. Soc. 4, 221-229.

PEARSALL, W.H. 1918. The aquatic and marsh vegetation of Esthwaite Water. J. Ecol. 6, 53-74.

PERRING, F. 1962. Hints on the determination of some critical species, microspecies, subspecies, varieties and hybrids in the British flora. Proc. B.S.B.I. 4, 359-383.

--- & WALTERS, 1962. Atlas of the British Flora. London.

PERSSON, A. 1962. Mire and spring vegetation in an area north of Lake Torneträsk, Torne Lappmark, Sweden. Opera bot, 6, 1-187.

PETCH, C.P. 1947. Fenlands of west Norfolk. Trans. Norf. Norwich N. Soc. 16.

--- & SWANN, E.L. 1968. Flora of Norfolk. Norwich.

PFEIFFER, H.H. 1961. Soziologische Stellung, Gesellschaftshaushalt und Entwicklung des gefahrdeten Cladietum marisci. Feddes Rep. Beih 139, 250-262.

PHILIPPI, G. 1960. Zur Gliederung der Pfeifengrasweisen im südlich und mittleren Oberrheingebiet. Beitr. naturk. Forsch, SW-Deutschl. 19, 138-187.

PIGNATTI, S. 1953. Introduzione allo studio fitosociologica della pianura Veneta orientale. Atti Inst. Bot. Univ. Lab. Crittogamico serie 5 9, 92-258.

--- 1957. La vegetazione delle risaie pavesi. Ach.Bot. Biogeog. Ital. 32.

PIGOTT, C.D. The vegetation of Upper Teesdale in the North Pennines. J. Ecol 44, 545-586.

POORE, M.E.D. (1955a,b,c; 1956a) The use of phytosociological methods in ecological investigations. I-IV. J. Ecol, 43, 226-244; 245-269; 606-651; 44, 28-50.

--- 1956b. The ecology of Woodwalton Fen. J. Ecol 44, 455-492.

--- 1962. The method of successive approximation in descriptive ecology. Adv. ecol res. 1, 35-69.

POTONIE, R. Aufbau und Vegetation der Norddeutschlands. Engl. Bot. Jahrb.90.

PRAEGER, R.L.J. 1934. The botanist in Ireland. Dublin.

PROCTOR, M.C.F. 1960. Mosses and liverworts of the Malham district. Fld. std. 1.

--- 1974. The vegetation of the Malham Tarn fens. Fld. std. 4, 1-38.

--- & IVIMEY-COOK, R.B. 1966. The application of association analysis to phytosociology. J. Ecol 54, 179-192.

RANKIN, W.M. 1911. In 'Types of British vegetation' Ed. A.G. Tansley, Cambridge.

RANWELL, D. 1960. Newborough Warren, Anglesey. II. Plant associes and succesional cycles of the sand dune and dune slack vegetation. J. Eccl. 48, 117-141.

ROBERTS, R.H. 1959. Notes on the fen habitat of Ophrys insectifera in Anglesey. Proc. B.S.B.I. 3, 274-278.

RATCLIFFE, D.A. 1964. Mires and bogs. In 'The vegetation of Scotland' ed. J.H. Burnett, 426-478. Edinburgh.

ROSE, F. 1950. The east Kent fens. J. Ecol., 38, 292-302.

--- 1953. A survey of the ecology of the British lowland bogs. Proc. Linn. Soc. 164, 186-211.

ROUSSINE, N. & GOUNOT, M. 1957. A propos d'un manuel recent de phytosociologie. Bull. Serv. Carte. Phytogeogr. B 2, 51-61.

RUUHIJARVI, R. 1960. Über die regionale Einteilung der nordfinnischen Moore. Ann. Bot. Soc. 'Vanamo' 31, 1-360.

SALWAY, P., HALLAM, J.S. & BROMWICH, J. 1970. The Fenland in Roman times. R.G.S. Research series 5.

SCAMONI, A. & PASSARGE, H. 1959. Gedanken zu einer naturlichen Ordnung der Waldgesellschaften. Arch Forstwes. 8, 386-426.

SCHEEL, H. 1962. Moor- und Grünlandgesellschaften im oberen Briesetal nordlich von Berlin. Wiss. Z. pad. Hochsch.Potsdam, Math-Nat.R.7, 201-230.

SCHWICKERATH, M. 1942. Bedeutung und Gliederung des Differentialartenbegriffs in der Pflanzengesellschaftslehre. Beih. Bot. Zentralbl. 61B, 351-383.

SEDDON, B. & DAVIES, T.A.W. 1966. Carex appropinquata in Pembrokeshire. Nature Wales, 10, 43-44.

SEGAL, S. 1966. Ecological studies of peat-bog vegetation in the North-western part of the province of Overjisel (the Netherlands). Wentia 15, 109-141.

--- 1968. Schwierigkeiten der Systematik von Moorgesellschaften. Ber. Int. Symp. Pflanzensoziol. Syst., Stolenzau/Weser 1964. 220-229.

SHIMWELL, D.W. 1968. The phytosociology of calcareous grasslands in the British Isles. Ph.D. thesis. Durham.

--- 1971. Description and classification of vegetation. London.

SINKER, C.A. 1960. The vegetation of the Malham Tarn area. Proc. Leeds Phil. Lit. Soc. 8.

--- 1962. The north Shropshire meres and mosses: a background for ecologists. Fld. Std. 1, 101-138.

SJORS, H. 1948. Myrvegetations i Bergslagen. Acta Phytogeogr. Suec. 21.

--- 1950. On the relation between vegetation and electrolytes in North Swedish mire waters. Oikos 2, 241-258.

SKELLAM, J.G. 1952. Studies in statistical ecology. I. Spatial pattern. Biometr. 39, 346-362.

SKENE, M. 1915. The acidity of Sphagnum and its relation to chalk and mineral salts. Ann. Bot. 29, 65-87.

SMITH, W.G. 1911. In 'Types of British vegetation' ed. A.G. Tansley, 282-287. Cambridge.

SNEATH, P.H.A. & SOKAL, R.R. 1973. Numerical taxonomy. San Francisco.

SPARLING, J.H. 1968. Biological flora of the British Isles: Schoenus nigricans. J. Ecol. 56, 883-899.

SPENCE, D.H.N. 1964. The macrophytic vegetation of freshwater lochs, swamps and associated fens. In 'The vegetation of Scotland', ed. J.H. Burnett, 306-425. Edinburgh.

--- 1970. Scottish serpentine vegetation. Oikos 21, 22-31.

SUMMERHAYES, V.S. 1968. Wild Orchids of Britain. 2nd ed. London.

SWANN, E.L. 1975. Supplement to the Flora of Norfolk. Norwich.

TALLIS, J.H. 1973. The terrestialization of lake basins in north Cheshire with special reference to the development of a 'schwingmoor' structure. J. Ecol. 61, 537-567.

TANSLEY, A.G. (ed.) 1911. Types of British vegetation. Cambridge.

--- 1939. The British islands and their vegetation. Cambridge.

--- & ADAMSON, R.S. 1926. Studies of the vegetation of the English chalk. IV. A preliminary survey of the chalk grassland of the Sussex downs. J. Ecol. 14, 1-32.

THUNMARK, S. 1942. Über rezente Eisenocker und ihre Mikroorganismengeme inschaften. Akad. Avh. Bull. Geol Inst. Upsalla, 29.

TÜXEN, 1937. Die Pflanzengesellschaften Nordwestdeutschlands. Mitt. Flor.-soz. Arb. Gem. Niedersach. N.F. 3.

--- 1954. Pflanzengesellschaften und Grundwasser Ganglinien. Angew. Pflanzensoz. Stolenzau/Weser. 8, 64-99.

--- 1955. Das System der nordwestdeutschen Pflanzengesellschaften. Mitt. Flor.-soz. Arb. Gem. Niedersach. 5, 155-176.

--- & PREISING, E. 1942. Grundbegriffe und Methoden zur Studium der Wasser- und Sumpfpflanzengesellschaften. Deutsche. Wasserwirts. 37.

VANDEN BERGHEN, C. 1951. Les praries à Molinia de Belgique. Bull. Soc. Roy. Bot. Belg. 83, 373-403.

--- 1952. Contribution à l'étude des bas-marais de Belgique. Bull. Jard. Bot. de l'Etat. 22, 1-64.

VLIEGER, J. 1937. Aperçu sur les unités phytosociologiques supérieures des Pays-Bas. Ned. Kruidk. Arch. 47, 335-353.

VOLLMAR, F. 1947. Die Pflanzengesellschaften des Murnauer Moores. Ber. Bayer. Bot. Ges. 27, 13-97.

WADE, A.E. 1970. The flora of Monmouthshire. Cardiff.

WALLIS, A. 1904. In 'Handbook to the natural history of Cambridgeshire', Marr, J.E. & Shipley, A.E. 209-237. Cambridge.

WALTERS, S.M. 1965. Natural history. In 'The Cambridge Region', ed. J.A. Steers. Cambridge.

--- 1974. The rediscovery of Senecio paludosus L. in Britain. Watsonia 10, 49-54.

WARD, J.H. 1963. Hierarchical grouping to optimize on objective function. J. Amer. Stat. Assoc. 58, 236-244.

WATT, A.S. 1947. Pattern and process in the plant community. J. Ecol. 35, 1-22.

WEBB, D.A. 1954. Is the classification of plant communities either possible or desirable ? Bot. Tidsskr. 51, 362-370.

WEBB, L.J., TRACEY, J.G., WILLIAMS, W.T. & LANCE, G.N. 1967. Studies in the numerical analysis of complex rainforest communities. II. The problem of species-sampling. J. Ecol. 55, 525-538.

WEBER, C.A. 1908. Aufbau und Vegetation der Moore Norddeutschlands. Englers Bot. Jahrb. 90.

WESTHOFF, V. 1951. An analysis of some concepts and terms in vegetation study or phytocoenology. Synthese 8, 194-206.

--- & DEN HELD, A.J. 1969. Plantengemeenschappen in Nederland. Zutphen.

--- & MAAREL, E. VAN DER, 1973. The Braun-Blanquet approach. In WHITTAKER, 1973,617-726.

WHEELER, B.D. & WHITTON, B.A. 1971. Ecology of Hell Kettles I. Terrestial and sub-aquatic vegetation. Vasc. 56, 25-37.

WHITE, J.M. 1930. Recolonisation after peat cutting. Proc. Roy. Irish Acad. 39(B), 453-476.

WHITTAKER, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monog. 26, 1-80.

--- 1962. Classification of natural communities. Bot. Rev. 28, 1-239.

--- 1970. The population structure of vegetation. In 'Gesellschaft-morpholgie (Strukturforschung)' ed. R. Tuxen. Ber. Symp. int. Vegetationskunde, Rinteln 1966. 39-62.

--- 1973 (ed.) Handbook of vegetation science. Part V. Ordination and classification of communities. Den Haag.

WILCOX, H.A. 1933. The woodlands and marshlands of England. London.

WILLIAMS, W.T. 1971. Principles of clustering. Ann. Rev. Ecol. System. 2,303.

---, CLIFFORD, H.T. & LANCE, G.N. 1971. Group size dependence: a rationale for choice between numerical classifications. Comp. J. 14, 157-162.

WILLIAMS, W.T. & DALE, M.B. 1962. Partitioned correlation matrices for heterogenous data. Nature 196, 602-603.

--- & --- 1965. Fundamental problems in numerical taxonomy. Adv. bot. res. 2, 35-68.

--- & LAMBERT, J.M. 1959. Multivariate methods in plant ecology. I. Association analysis in plant communities. J. Ecol. 47, 83-101.

--- & --- 1960. Multivariate methods in plant ecology. II. The use of an electronic digital computer for Association analysis.

---, --- & LANCE, G.N. 1966. Multivariate methods in plant ecology. V. Similarity analysis and Information analysis.

WILLIS, A.J. 1967a. The vegetation of Catcott Heath, Somerset. Proc. Bristol Nat. Soc. 31, 297-304.

--- 1967b. A new locality for Liparis loeselii. Proc. B.S.B.I. 6, 352.

--- & JEFFERIES, R.L. 1959. The plant ecology of the Gordano valley. Proc. Bristol. Nat. Soc. 29, 469-490.

WILLIS, E.H. 1961. Marine transgression sequences in the English fenlands. Ann. N.Y. Acad. Sci. 95, 368-376.

WILLMANS, O. 1959. Ein Gerät zur Mechanisierung von Tabellenarbeit. Ber. dt. bot. Ges. 72, 419-420.

WILSON, A. 1938. Flora of Westmorland. Kendal.

--- 1956. The altitudinal range of British plants. Arbroath.

WISHART, D. 1969. Clustan 1A. User manual. St. Andrews.

WITTING, M. 1948. Preliminärk meddelande om fortsatta katjonbestämmigar i myrvatten sommaren 1947. Sv. Bot. Tidskr. 42.

YAPP, R.H. 1908. Sketches of vegetation at home and abroad. IV. Wicken Fen. New Phytol. 7, 61-81.

--- 1909. On stratification in the vegetation of a marsh and its relation to evaporation and temperature. Ann. Bot. 23, 275-319.

ZOBRIST, L. 1935. Pflanzensoziologische und bodenkundliche Untersuchung des Schoenetum nigricantis im nordostschweizerischen Mittellande. Beitr. Geobot. Landesaufn. d. Schweiz 18, 1-144.

ZWILLENBERG, L.O. & DE WIT, R.J. 1951. Observations sur le Rosmarineto-Lithospermetum schoenetosum du Bas-Languedoc. Acta Bot. Neer. 1, 310-323.

Addenda

DA SILVA, A.R. PINTO. 1954. Sera-t-il possible de mecaniser la preparation des tableaux phytosociologiques ? Vegetatio 5/6 16-17.

FIELD, J.G. 1969. The use of the information statistic in the numerical classification of heterogenous systems. J. Ecol. 57, 565-570.

FISCHER, W. 1967. Beitrage zur Verbreitung, Soziologie und Ökologie von Myrica gale mit besonderer Berücksichtingung der Vorkommen in der Niederlausitz. Arch. Naturschutz u. Landschaftsforsch. 7, 129-151.

FRASER, G.K. 1933. Studies of Scottish moorlands in relation to tree growth. Bull. For. Comm., Lond. 15.

FRENKEL, R.E. & HARRISON, C.M. 1973. Comparison of traditional phytosociological and numerical classificatory methods and their uses in ecology. Occasional paper 20, Dept Geography, University College, London.

FRÜH, J. & SCHRÖTER, C. 1904. Die Moore der Schweiz mit Berücksichtingung der gesamten Moorfrage. Beitr. z. Geol. Schweiz, Geotech. Ser. III. Bern.

GREIG-SMITH, P.1964. Quantitative plant ecology. 2nd ed. London.

Appendix 1. The syntaxonomy of the higher vegetation-units of rich fen and related wetland types.

This Appendix contains a short account of the evolution and usage of some of the higher syntaxonomic units that have been proposed to contain the vegetation types of rich fen and related wetlands.

PHRAGMITETEA Tx. et Prsg. 42

KOCH (1926) recognised the Order Phragmitetalia and included within it two Alliances, the Phragmition communis containing helophyte communities characterised by a low level of organisation and the Magnocaricion elatae, with the 'Großseggengesellschaften' of marshes and lake margins etc. This basic division was retained by TÜXEN (1937), VLIEGER (1937) and also by TÜXEN & PREISING (1942). These last workers, however, brought the communities together into a Class, the Phragmitetea. In 1942 BRAUN-BLANQUET & SISSINGH (in BOER, 1942) created an additional Alliance within the Phragmitetalia. This w as the Glycerio-Sparganion, containing some communities that had previously been referred to the Phragmition, notably low-growing Glyceria-Sparganium types.

One of the chief emendations to this framework was made by PIGNATTI (1953), who established with the Phragmitetea three Orders - essentially an upgrading of the earlier Alliances - Phragmitetalia, Magnocaricetalia and Nasturtio-Glycerietalia. This

scheme has been widely accepted (e.g. by BALATOVA-TULACKOVA, 1963; PASSARGE, 1964; WESTHOFF & DEN HELD, 1969), although OBERDORFER et al. (1967) have retained the Phragmitetalia as the only Order of the Class. NEUHAUSL (1959) also uses only one Order but has named it the Phragmiteto-Magnocaricetalia as the single Order of the Class Phragmiteto-Magnocaricetea Klika 44 (synonymous with the Phragmitetea). Additional Alliances have also been added to the Class, notably the Oenanthion aquaticae Hejny 48, but this Alliance has not received wide acceptance and OBERDORFER et al. (1967) do not incorporate it into their systematic scheme but keep the relevant Associations in the Phragmition. It has, however, been maintained by KOPECKY & HEJNY (1965) and HOLUB et al. (1967), who regard it as part of the Oenanthetalia aquaticae Hejny 65. It has also been adopted by WESTHOFF & DEN HELD (1969) who, however, place it as a second Alliance of the Phragmitetalia.

PHRAGMITETALIA Koch 26 em. Pignatti 53 denuo em. Segal et Westhoff 69

Initially, this was the only Order of the Phragmitetea, but with the creation of other Orders by PIGNATTI (1953) it became defined more narrowly with only the Phragmition remaining within it. More recently, however, PASSARGE (1964) has added a Carici-Rumicion hydrolapathi Passarge 64 and WESTHOFF & DEN HELD (1969) placed the Oenanthion aquaticae Hejny 48 here.

PHRAGMITION (COMMUNIS) Koch 26.

With the removal of the Glyceria-Sparganium types of vegetation to the Glycerio-Sparganion this Alliance has effectively become defined by its life-form, encompassing tall reedswamp vegetation of lakes, rivers and estuaries. The syntaxon has retained its identity since KOCH's initial description but there has been wide divergence of opinion concerning its subdivision into Associations, largely because the vegetation shows a tendency to develop as facies dominated by a particular species. These have often been treated as subunits of a single syntaxon, the Scirpo-Phragmitetum Koch 26 (e.g. BOER, 1942; LEBRUN et al., 1949; VAN DONSELAAR, 1961; KRAUSCH, 1965), but more recently there has been a tendency (e.g. by PASSARGE, 1964; OBERDORFER et al., 1967; WESTHOFF & DEN HELD, 1969) to treat the facies of some of the species as independent Associations.

MAGNOCARICETALIA Pignatti 53

Originally the Magnocaricetalia was an Order containing but one Alliance, the Magnocaricion, a well defined syntaxon initially established by KOCH (1926). However, NEUHÄUSL (1959) pointed out that, whereas KOCH was only concerned with sub-littoral 'Großseggengesellschaften' others have also included eu-littoral types within the Alliance. He thus suggested that the Alliance should be redefined to give a Magnocaricion elatae Koch 26 s.s. containing the communities

of deeper water and proposed the creation of a new Alliance, the Caricion gracilis, to contain eu-littoral communities characterised by a sub-surface summer-water table, a more closed vegetation cover, the absence of aquatics and a reduction in the moss layer. As well as including the exclusively eu-littoral community-types this would also include the eu-littoral forms of communities with sub-littoral representatives (e.g. Caricetum elatae Koch 26). This division was also recognised, though in a somewhat modified form, by PASSARGE (1964) and HOLUB et al. (1967). Related to it is a subdivision put forward by GEHU (1961) who, following J. DUVIGNEAUD (1958), classified the communities on the basis of the richness of the irrigating water into the Magnocaricion gracilis of mesotrophic waters and the Magnocaricion elatae of alkaline bogs.

BALATOVA-TULACKOVA (1963) proposed a rather different division of the Order which reflects distinctions in floristic composition, hydrological regime and trophic status. She created a Caricion rostratae containing mesotrophic communities of mires and lake margins and a Caricion gracilis (non sensu Neuhausl 57) with eutrophic communities of lake edges and river flood-plains. This classification has been accepted by KRAUSCH (1964) and HORST et al. (1966) and, at the sub-alliance level, by OBERDORFER et al. (1967). On the other hand, WESTHOFF & DEN HELD (1969) prefer to retain the Magnocaricion (elatae) as a single unit.

MAGNOCARICION (ELATAE) Koch 26

This has been regarded as a well defined Alliance encompassing those swamp and marsh communities dominated by large sedges, either helophytes or hemicryptophytes. Although sometimes the communities are represented by almost pure stands of a particular sedge with poor floristic characterisation, nonetheless, in terms of structure, synecological requirements and position within the hydrarchal sequence, the Alliance has had sufficient integrity for its recognition by many workers (LIBBERT, 1932; TÜXEN, 1937; 1955; BOER, 1942; LEBRUN et al., 1949 etc.). More recently, however, proposals for the subdivision of the Alliance have been put forward (see above.)

The Alliance represents a unit cutting across the hydroseral gradient with Phragmition swamps on one side and drier wetland types on the other. Within it, Associations are often defined on the basis of the dominant species of sedge. However, the dominance of a particular sedge often extends along the hydroseral gradient, starting within the swamp and continuing into drier fen vegetation. Not only does this mean that the Associations themselves are often not very coherent units but also that they show a marked non-conformity within the limits of the Magnocaricion. Thus, an overtly Magnocaricion stand may, on the one hand, contain more of the character species of the Phragmition or, on the other, of, say, the Caricion davallianae than of the Magnocaricion itself. The same

comments may also be made about other Alliances and syntaxa that are implicated in the hydrosere or, at least, in the zonation around open water. Instead of recognising Associations based upon a dominant taxon, there is much to commend the idea of basing them upon comparable phases or zones cutting across the hydrosere and involving more than one dominant (cf. SEGAL, 1966).

NASTURTIO-GLYCERIETALIA Pignatti 53

PIGNATTI (1953) included within the Order one Alliance, the Glycerio-Sparganion Br.-Bl. et Sissingh 42 and in this has been followed by BALATOVA-TULACKOVA (1963) and KRAUSCH (1964). PASSARGE (1964), however, expanded the concept of the Order to include two new Alliances, the Eleocharido-Sagittarion and the Phalaridio-Glycerion, although WESTHOFF & DEN HELD (1969) do not accept these for the Netherlands: the Phalaridio-Glycerion, like the Phalaridion arundinaceae Kopecky 61 (described from the montane regions of Central Europe) does not seem to be valid Alliance for the lowlands of N.W. Europe (KOPECKY, 1967; WESTHOFF & DEN HELD, 1969). Instead WESTHOFF & DEN HELD expanded the Order otherwise to contain the Cicution virosae Hejny 60 together with a new Alliance, the Apion nodiflorae Segal 69.

CICUTION VIROSAE Hejny 60 em. Segal 69

BOER (1942) described a Cicuto-Caricetum pseudocyperi Boer et Siss. 42. It included vegetation previously assigned to the Scirpo-Phragmitetum and was itself placed within the Phragmition. Subsequently it has also been placed within an independent Alliance, created to contain it, the Cicution virosae Hejny 60 (= Carici-Rumicion hydrolapathi Passarge 64). However, KOPECKY & HEJNY (1965) and HOLUB et al. (1967) have not maintained the Alliance and OBERDORFER et al. (1967) have refused to accept it. But, by contrast, WESTHOFF & DEN HELD (1969) decided to retain the Alliance because of its clear floristic, structural and ecological identity. However, whereas PASSARGE (1964) had placed his Alliance within the Phragmitetalia WESTHOFF & DEN HELD recognised that it had affinities also with both the Magnocaricetalia and the Nasturtio-Glycerietalia and they chose to place it within the latter Order.

SCHEUCHZERIO-CARICETEA FUSCAE Tx. 37

(Note that in the following discussion Carex nigra = C. fusca = C. Goodenoughii; Carex curta = C. canescens)

Commonly two major categories of mire vegetation have been recognised (e.g. by LEBRUN et al., 1949; TÜXEN, 1955; LOHMEYER et al., 1962; OBERDORFER et al., 1967; HOLUB et al., 1967).

The first is the Scheuchzerio-Caricetea fuscae Tx. 37 which includes the communities of transition and rheotrophic mires (sensu BELLAMY, 1967, 1968) of mesotrophic to eutrophic status together with certain wet hollow communities of ombrotrophic bogs. The second is the Oxycocco-Sphagnetea Br.-Bl. et Tx. 43 which contains the other community-types of ombrotrophic mires together with those of wet heaths.

The Scheuzerio-Caricetea fuscae is a heterogenous unit of wide compass containing the rather different vegetations of both highly calcareous mires and oligotrophic hollows in ombrotrophic mires. In general, these have been partitioned between three Orders - the Caricetalia nigrae Koch 26 em. Nordh. 36 denuo em. Tx. 37, the Tofieldietalia Prsg. apud Oberd. 49 and the Scheuchzerietalia palustris Nordh. 36. The nature and contents of these syntaxa will be discussed below. It may, however, be noted that, in order to reflect the rather weak floristic affinities of the Scheuchzerietalia communities with the other communities of the Class, a recent proposal has been to allocate these to an independent Class, the Scheuchzerietea Den Held, Barkman et Westhoff 69 (see WESTHOFF & DEN HELD, 1969). These authors have re-named what remains of the Scheuchzerio-Caricetea as the Parvocaricetea Den Held et Westhoff 69. Thus, in this scheme there are three main classes: the Parvocaricetea and the Oxycocco-Sphagnetea, together with the acidophilic, species-poor communities of the Scheuchzerietea, which occupy a floristically intermediate

position.

CARICETALIA NIGRAE Koch 26 em. Nordh. 36 denuo em. Tx. 37

In the scheme of KOCH (1926) all mire vegetation was grouped into a single Order - the Caricetalia fuscae - which thus effectively represented the same unit as the Scheuchzerio-Caricetea fuscae. As such it contained two Alliances, the Caricion fuscae and the Rhynchosporion albae. The first main change to this was made by NORDHAGEN (1936), who subdivided the order to produce a Caricetalia nigrae of more restricted compass and a new Order, the Scheuchzerietalia palustris. Into this second Order was placed the Rhynchosporion. The Caricetalia fuscae thus contained KOCH's Caricion fuscae which, by this time, had itself been split by KLIKA (1934) into a more-narrowly defined Caricion fuscae of rather acid mires and a Caricion davallianae containing basiphilous communities. The Caricetalia thus contained both of these Alliances and also an additional one that had been newly created by NORDHAGEN to contain certain base-rich mire communities of sub-artic and alpine areas - the Caricion bicoloris-atrofuscae. A year later, however, the contents of the Order were again modified, this time by TÜXEN (1937), who placed only one Alliance - the Caricion fuscae - within it. The Caricion davallianae he placed elsewhere. (The Caricion bicoloris-atrofuscae was not considered). This thus produced what

has come to be the current conception of the Order. It may, however, be noted that this was not adopted immediately by all phytosociologists. Thus, some (e.g. VLIEGER, 1937; DAHL, 1957) maintained the Caricetalia fuscae sensu Nordhagen and indeed others (LEBRUN et al., 1949; VANDEN BERGHEN, 1952) have preferred to use it in the original sense of KOCH (1926).

Since the work of TÜXEN (loc. cit.) some expansions of the Order have been suggested. DOING (1963) put forward the idea of combining the Caricion curto-nigrae (see below) with certain Molinion communities to produce a Junco-Caricetalia nigrae. And OBERDORFER et al. (1967) combine the Caricion with the Rhyncosporion, Caricion lasiocarpae and Eriophorion scheuzchzerii to produce a Scheuchzerio-Caricetalia fuscae (Koch 26) Görs et Th. Müll. 67. It may be noted that the Eriophorion scheuchzerii Hadac 39 - containing certain high alpine mire communities - has also been placed in the Carietalia nigrae by several authors. Both OBERDORFER et al. (1967) and WESTHOFF & DEN HELD (1969) regard its status as dubious, however.

CARICION CURTO-NIGRAE Koch 26 em. Nord. 36.

The Caricion fuscae was introduced by KOCH (1926) to contain the plant communities of slightly acid to alkaline mires. Later (KOCH, 1928), he also included within it Associations of more acidic situations, thereby producing a rather heterogenous

unit. With the splitting of the Alliance by KLIKA (1934) the basiphilous communities were referred to the Caricion davallianae and the more acidophilous types to the Caricion fuscae. Two years later these latter were grouped by NORDHAGEN (1936) into his new Caricion canescentis-Goodenoughii (which, with current nomenclature, is now referred to as the Caricion curto-nigrae). This is thus an Alliance of rather acidic, base-poor soligenous mires, developed in areas saturated in water with a pH range of about pH 4-6. The communities are usually fairly species-rich with sedges and rushes normally predominating in the herb layer, and with both Carex nigra and C. curta often being prominent. The moss layer is normally fairly well developed and may contain both hypnoid mosses and Sphagna.

With the use of the name Caricion canescentis-Goodenoughii by NORDHAGEN the Caricion fuscae was made superfluous. Nonetheless, it has persisted to some extent in the phyto-sociological literature. Thus, HOLUB et al. (1967) continue to use this name instead of Caricion curto-nigrae. A more confusing use has been adopted by VANDEN BERGHEN (1952) (see also LEBRUN et al., 1949), who, considering that KOCH's original Alliance referred mainly to basiphilous communities, has adopted the name as a synonym for the Caricion davallianae.

TOFIELDIETALIA Preising apud Oberdorfer 49

TÜXEN (1937), recognising the affinities between Caricion davallianae communities and some of those of the Molinion, placed the two Alliances together in the Molinietalia. The same procedure was also adopted by HADAC (1939). However, BRAUN-BLANQUET (1949) created a new Order in which the Alliance could be accommodated. This was the Caricetalia davallianae Br.-Bl. 49. At the same time a similar unit also emerged under the name of the Tofieldietalia Prsg. apud Oberd. 49. This name may be regarded as synonymous with the Caricetalia and has come to be the accepted name for the Order.

Four Alliances have been placed within the Order. Of these, two have been widely recognised: the Caricion davallianae and the Caricion bicoloris-atrofuscae. A third was described from Rondane by DAHL (1957) as the Sphagneto-Tomenthypnion - an Alliance of base-rich locations, often occurring as a zone between base-rich mires on the one side and dry land, or acidic peatland, on the other. PASSARGE (1964) has also included here an Eleocharition pauciflorae containing open pioneer communities of muddy-ground at the edge of mesotrophic lakes etc. Of these only the Caricion davallianae will be discussed further.

CARICION DAVALLIANAE Klika 34

This Alliance includes species-rich stands of mire vegetation developed under the influence of base-rich ground water. Carex species are prominent in the herb layer and a hypnaceous moss layer is usually well developed.

The syntaxon was created by KLIKA (1934). It is synonymous with the Schoenion ferruginei Nordh. 36, the Epipacto-Schoenion ferruginei Duvign. 49 and also with certain usages of the name Eriophorion latifolii. WESTHOFF & DEN HELD (1969) comment that the original usage of the Eriophorion latifolii was by BRAUN-BLANQUET & TÜXEN (1943) to distinguish from the Caricion davallianae other communities of base-rich mires characterised both by the absence of alpine and sub-alpine species and also by a general poverty of Scheuchzerio-Caricetea fuscae species. As such the Alliance was placed within the Molinietalia. (Subsequently, SOO (1957) and KOVACS (1962) have made the same distinction but in precisely the opposite way). However, the current usage of the name is normally as a synonym for the Caricion (e.g. LOHMEYER et al., 1962; PASSARGE, 1964; OBERDORFER et al., 1967).

PASSARGE (1964) makes an interesting distinction between the Caricion davallianae and the Eriophorion latifolii, in that he has used the Caricion to refer specifically to one of the two vicariant sub-alliances he created by subdividing the Eriophorion. It encompasses calcareous mires of southern and

Central Europe. The second sub-alliance - with a northern distribution - is the Eriophorion gracilis. This contains communities which have often otherwise been placed within the Eriophorion gracilis Prsg. apud Oberd. 57 - an independent Alliance synonymous with the Caricion lasiocarpae Vanden Berghen 49. WESTHOFF & DEN HELD (1969) also place these communities within the Eriophorion latifolii but they do not recognise the sub-Alliance as they feel that a geographical division of the Alliance is not the most satisfactory.

Most authors have placed the Caricion davallianae within the Tofieldietalia. However, the affinities with Molinietalia vegetations noted by TÜXEN (1937) and HADAC (1939) have already been mentioned and this relationship has also been emphasised by other authors. Some have expressed this by placing the two types of vegetation together in the same Class. Thus, SOO (1957) has used the Molinio-Juncetea Br.-Bl. 57 - a class created by the partitioning of the Molinio-Arrhenathertea into two independent units - as a convenient syntaxon. On the other hand, MALMER (1968) has raised the possibility of including both the Molinion and Calthion within the Tofieldietalia - which might then perhaps be elevated to the status of an independent Class, the Tofieldietea. However, in general the Alliance has been placed within the Scheuchzerio-Caricetea fuscae (TÜXEN, 1955; OBERDORFER, 1962; LOHMEYER et al., 1962; DOING, 1963; PASSARGE, 1964 etc.).

SCHEUCHZERIETALIA PALUSTRIS Nordh. 36

This Order was created by NORDHAGEN (1936) to accommodate the Rhyncosporion albae Koch 26. It has normally been regarded as a member of the Scheuchzerio-Caricetea nigrae but in WESTHOFF & DEN HELD (1969) it has been assigned to an independent Class, the Scheuchzerietea Den Held, Barkman et Westhoff 69. This was because of the substantial differences between communities of the Scheuchzerietalia and other Scheuchzerio-Caricetea types and also because of a general impoverishment in Class character species.

As well as the Rhyncosporion other Alliances have also been placed within this order. They include the Stygio-Caricion limosae Nord. 43 and the Leuco-Scheuchzerion Nordh. 43, both of which have mainly been recognised by Scandinavian workers. The Caricion lasiocarpae Vanden Berghen 49 has also been located here.

The Stygio-Caricion limosae is described by DAHL (1957) as "consisting of calcicolous-eutrophic vegetation in localities of stagnant water in hollows of mires". It may, perhaps, be regarded as a vicariant of the Caricion lasiocarpae. It has been placed within the Scheuchzerietalia by NORDHAGEN (1943), DAHL (1957) and MALMER (1968) but WESTHOFF & DEN HELD (1969) suggest a placement in the Tofieldietalia.

The Leuco-Scheuchzerion is also described by DAHL as "strictly oligotrophic and strongly acidophilous communities

in mires where the water-table is permanently high and the water is stagnant or with little movement". It has been regarded as a vicariant of the Scheuchzerion by HADAC & VANA (1967), although WESTHOFF & DEN HELD point to the substantial floristic overlap between the two syntaxa. The Scheuchzerion itself is a widely distributed Alliance which contains communities of wet depressions in ombrotrophic mires and poor fens. The herb layer is species-poor and often poorly developed but there is normally a well developed moss layer in which species of Sphagnum are prominent.

CARICION LASIOCARPAE Vanden Berghen 49

This Alliance was created by VANDEN BERGHEN (in LEBRUN et al., 1949; see also VANDEN BERGHEN, 1952) to accommodate communities containing Carex rostrata, C. lasiocarpa, Eriophorum gracile, Calla palustris, Menyanthes trifoliata and Potentilla palustris as characteristic species. Such communities occupy wet hollows in mesotrophic mires where they may often develop as floating mats of vegetation, frequently encroaching upon open water. The syntaxon has been adopted by a number of phytosociologists either as the Caricion lasiocarpae (e.g. LEBRUN et al., 1949; LOHMEYER et al., 1962; HOLUB et al., 1967) or as the Eriophorion gracilis Prsg. apud Oberd. 57 (e.g. OBERDORFER et al., 1967; KRAUSCH, 1968). The two names may be regarded as synonymous.

Before the creation of the Alliance the communities composing it were placed in either the Caricion curto-nigrae or the Caricion davallianae. This is demonstrated by DUVIGNEAUD (1948) who placed the oligomesotrophicum sub-association of his Caricetum diandro-lasiocarpae into the first of these and the eutrophicum into the second. It is also reflected in the observation of VANDEN BERGHEN (1952) that the communities of the Caricion lasiocarpae have floristic and ecological affinities with the Rhyncosporion albae, the Caricion curto-nigrae and the Caricion davallianae. Indeed "L'Alliance constitue ainsi un pont entre des unites phytosociologiques à première vue assez distinctes" (p.20). This intermediate status has caused doubt to be cast both upon the systematic placement of the Alliance and also upon its validity as a vegetational unit. In general, the syntaxon has been placed with the Rhyncosporion into the Scheuchzerietalia but WESTHOFF & DEN HELD (1969) consider that, for the greatest part, its relationships are with the Tofieldietalia rather than with this. Not only do they feel that the Alliance should not be grouped with the Scheuchzerion but also, following MALMER (1968), they suggest that its contents could be satisfactorily apportioned between this Alliance and the Caricion curto-nigrae and Caricion davallianae. The matter remains to be clarified. Most certainly some phytosociologists have found the Caricion lasiocarpae to serve as a useful syntaxon.

Other classificatory schemes

One of the most important deviations from the classification of mire vegetation described above was that proposed by DUVIGNEAUD (1949). Being impressed by the complex inter-relationships and intergradations between different mire community-types he looked to the possibility of creating a single syntaxon in which they might all be placed. Thus, following VLIEGER (1937), he created a new Class, the Sphagno-Caricetea fuscae, which included, not only all of the characteristic mire communities, but also some Molinion and Filipendulo-Petasition communities as well. The scheme adopted was:

SPHAGNO-CARICETEA FUSCAE

MOLINIO-CARICETALIA FUSCAE

Parvocaricion canescentis-fuscae
Epipacto-Schoenion ferruginei
Caricion bicoloris-atrofuscae
Molinio-Juncion acutiflori
Filipendulo-Petasition

ERICO-SPHAGNETALIA

Vaginato-Sphagnion europaeum
Trichophoro-Ericion tetralicis
Scheuchzerio-Rhyncosporion albae

The Epipacto-Schoenion ferruginei is synonymous with the Caricion davallianae. Interestingly, DUVIGNEAUD included within this the Cladietum marisci - an Association normally placed in the Magnocaricion or Phragmition.

DUVIGNEAUD put forward a number of species to serve as character taxa for the Class, but the value of these has been

brought into doubt by WESTHOFF & DEN HELD (1969), and in general the classification seems to have received little acceptance.

It may be noted that the two main divisions of this scheme relate broadly to the separate Classes used by other authors. The Molinio-Caricetalia corresponds to the Scheuchzerio-Caricetea fuscae modified by the addition of the Molinietalia and the omission of the Scheuchzerietalia, whereas the Erica-Sphagnetalia largely corresponds to the Oxycocco-Sphagnetea plus the Scheuchzerietalia.

A further classificatory scheme which may be considered is that of DU RIETZ (1949; 1954). This consists of two main units - the Ombro-Sphagnetea, or bog formation, and the Sphagno-Drepanocladetea, or fen formation. The boundary between these corresponds to the 'Mineralbodenwasserzeigergrenze' or the 'fen plant limit'. The ombrotrophic Ombro-Sphagnetea has broad parallels with the Oxycocco-Sphagnetea, but does not include minerotrophic wet heath communities. The minerotrophic Sphagno-Drepanocladetea is subdivided:

Apiculatetalia	Euapiculation	extreme poor fen
	Subsecundo-apiculation	transitional poor fen
Scorpidietalia	Warnstorfio-scorpidion	transitional rich fen
	Euscorpidion	extreme rich fen

This Class has broad affinities with the Scheuchzerio-Caricetea fuscae containing the minerotrophic vegetations of the Caricetalia nigrae, the Tofieldietalia and (in part only)

the Scheuchzerietalia. However, an interesting feature of this Class is that Magnocaricion communities were also included within it (DU RIETZ, 1949) - a recognition of the close ties that these have with mire vegetation types (but see WESTHOFF & DEN HELD, 1969).

Various other schemes have also been suggested. MALMER (1968) put forward some tentative proposals in which, amongst other things, acidic mire communities belonging to the Caricion canescentis nigrae are placed with the communities of ombrophilous bogs rather than with the base-rich mires of the Tofieldietalia. Scheuchzerietalia communities are also placed here or else regarded as belonging to an independent Class, the Caricetea limosae. He also suggests the placement of the contents of the Molinietalia within the Tofieldietalia with the possible upgrading of this Order into a new Class, the Tofieldietea. An interesting approach has also been suggested by SEGAL (1966; 1968) in which communities occupying similar successional zones are grouped together. Such a classification would cut across the rich-poor nutritional gradient which has provided the basis for more classificatory schemes.

In sum it may be said with WESTHOFF & DEN HELD (1969) that "the classification of the vegetations of fens and bogs has always caused many difficulties which even now are only partly solved" (p.194). Not only are there complex inter-relations

within these vegetations but also there are close links, forged by floristic and successional relationships, with other vegetation-types. There are affinities, not only with the reedswamps and fen of the Phragmitetea and the wet grasslands and riverside communities of the Molinio-Arrhenatheretea, but also with certain spring community-types of the Montio-Cardaminetea Br.-Bl. et Tx. 43, the 'disturbed'wetland types of the Plantaginetea majoris Tx. et Preisg. 50 and also some of the various communities of the margins of pools and lakes. Nonetheless, in any classification, it is necessary for boundaries to be drawn somewhere.

MOLINIO-ARRHENATHERETEA Tüxen 37

The Molinio-Arrhenatheretea is composed of the man-made vegetation of moist grasslands, together with the semi-natural vegetation of riversides and of certain types of mire. The Class was created by TÜXEN (1937) to contain two Orders, the Molinietalia and the Arrhenatheretalia. There have, however, been differences in opinion as to the precise rank of these units and a major syntaxonomic modification was made in 1947 by the creation of two independent Classes, the Molinio-Juncetea Br.-Bl. 47 and the Arrhenatheretea Br.-Bl. 47. This scheme was adopted by BRAUN-BLANQUET (1949) and LEBRUN et al. (1949) among others (see also OBERDORFER et al., 1967). It was maintained also by SOO (1957) and KOVACS (1962) but these

additionally incorporated Tofieldietalia communities within the Molinio-Juncetea. However, the present tendency (e.g. by LOHMEYER et al., 1962; PASSARGE, 1964; HOLUB et al., 1967; WESTHOFF & DEN HELD, 1969) has been just to recognise the Molinio-Arrhenatheretea as a single Class. WESTHOFF & DEN HELD (1969) point to the need for a thorough syntaxonomic study of the Class together with an examination of its relationships with the Tofieldietea and the Nardo-Callunetea Prsg. 49.

As well as the two Orders mentioned above two others have also been placed in the Class. One is the Holoschoenetalia Br.-Bl. 31 of the Northern Mediterranean region. The other is the Deschampsietalia caespitosae Horvatic 56 which includes the vegetation of periodically flooded grassland. This has been adopted by PASSARGE (1964). Others, however (e.g. HOLUB et al., 1967) have accommodated its Alliances within the Molinietalia, whilst WESTHOFF & DEN HELD (1969) suggest that most of the communities would be better contained within the Agropyro-Rumicion crispae Nordh. 40 em. Tüxen 50 of the Plantaginetea majoris Tx. et Prsg. 50.

MOLINIETALIA Koch 26

KOCH (1926) created the Order Molinietalia and included within it one Alliance, the Molinion coeruleae. Since then a number of additional Alliances have also been placed here and the Order now constitutes a rather wide-ranging floristic unit.

As well as the Molinion, TÜXEN (1937) included within the Order the Caricion davallianae and a new Alliance, the Calthion palustris. Of these, the Caricion was subsequently transferred to the Tofieldietalia but the Calthion has come to be an accepted part of the Molinietalia, even though in its original conception it seems to have been an unsatisfactory unit (SCHWICKERATH, 1949; WESTHOFF & DEN HELD, 1969). A further Alliance was introduced by DUVIGNEAUD (1946) as the Filipendulo-Cirsion oleracei (see Filipendulion below) and this was followed in 1947 by the Juncion acutiflori Br.-Bl. 47. This Alliance has been generally used to contain vegetations of wet areas rich in Juncus acutiflorus (the (Crepido)-Juncetum acutiflori (Br.-Bl. 15) Oberd. 57) (e.g. by LEBRUN et al., 1949; OBERDORFER, 1962; OBERDORFER et al., 1967). However, O'SULLIVAN (1968b) has pointed out that the main distribution of the Alliance is in S.W. Europe and, concordantly, WESTHOFF & DEN HELD (1969) consider that it is, in fact, absent from N.W. and W.-Central Europe and that the (Crepido)-Juncetum acutiflori would be better placed within the Calthion (cf. GÖRS, 1958; PASSARGE, 1964). They have also introduced a further change in the sub-division of the Order by recognising a Junco-(subuliflori)-Molinion Westhoff 69 as an Atlantic version of the Molinion coeruleae Koch 26.

Other Alliances that have been placed in this Order by other authors are those containing communities of periodically

flooded grassland. They include the related Alliances, the Deschampsion caespitosae Horvatic 30 and the Alopecurion pratensis Passarge 64. PASSARGE (1964) observed, however, that these syntaxa contain a well developed complement of species of the Agropyro-Rumicion crispae Nordh. 40 em. Tx. 50 and WESTHOFF & DEN HELD (1969) suggest that the communities could, in fact, largely be satisfactorily accommodated within this Alliance. BALATOVA-TULACKOVA (1965; 1968) has also introduced a new Alliance, the Cnidion venosi, to contain continental Molinieta subject to regular flooding. She considers it a vicariant of the Deschampsion.

JUNCO (SUBULIFLORI) MOLINION Westhoff 69

Only one Alliance was originally recognised within the Molinietalia by KOCH (1926), namely the Molinion coeruleae. This has persisted as a well defined syntaxon comprising communities of relatively nutrient-poor situations in unmanured moist meadows in which Molinia caerulea is usually an important component. The Alliance was created on the basis of the species-rich, basiphilous communities of Central Europe but the poorer, atlantic and sub-atlantic Molinieta have usually been grouped here as well (e.g. the Junco-(effusi)-Molinietum Tx. et Prsg. 51). However, WESTHOFF (in WESTHOFF & DEN HELD (1969), considering the Dutch material, concluded that as most of the Molinion character-species were absent or

poorly developed and that as the Molinion has come to contain a number of independent Associations (e.g. see OBERDORFER et al., 1967) - albeit by the splitting of the "Molinietum coeruleae" Koch 26 - which all contained the Alliance character-species it was appropriate to create a new Alliance, the Junco-(subuliflori)-Molinion, to accommodate the impoverished atlantic material.

CALTHION PALUSTRIS Tx. 37 em. Tx. 51

This incorporates communities of manured, wet meadows developed on relatively nutrient-rich clayey or peaty soils. In its original conception the syntaxon was unsatisfactory (See WESTHOFF & DEN HELD, 1969) basically because '... le Calthion est un vaste "depottoir" ou s'entassent des groupements appartenant aux unités phytosociologiques les plus diverses;' (DUVIGNEAUD, 1946). The syntaxon was subsequently emended (as the Bromion racemosi Tx. 51) to contain a floristically and structurally more uniform set of community-types.

PASSARGE (1964) has distinguished two sub-alliances - the Holco-Juncion of calcium-poor soils and the Cirsion oleracei of calcium-rich conditions. WESTHOFF & DEN HELD (1969) feel that this subdivision is not justified.

WESTHOFF & DEN HELD (1969) point out that floristically, structurally and ecologically the communities show transitions to the Artemisietea vulgaris Lohm., Prsg. et Tx. 50. DOING (1963), in fact, suggested that the Filipendulo-Petasition should be grouped with the Convolvuletalia sepium Tx. 50 to form the Filipendulo-Calystegietalia sepium - an Order ofhis newly created Class, the Urtico-Cirsietea, thereby bringing the Filipendulo-Petasition together with the Artemisietea communities. However, SEGAL (1966), OBERDORFER et al. (1967) and WESTHOFF & DEN HELD (1969) have considered it adequate just to place part of the Alliance (including the Petasites communities) into the Artemisietea. The remainder has been renamed the Filipendulion and has been kept within the Molinietalia.