# An objective analysis of the plant communities on Claish Moss, Argyll: the relationship of these to environmental parameters, and the floristics of the development of the hummook-hollow complex

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**How to cite:**

Snobel, N.S. (1978) An objective analysis of the plant communities on Claish Moss, Argyll: the relationship of these to environmental parameters, and the floristics of the development of the hummook-hollow complex. Masters thesis, Durham University.

# An objective analysis of the plant communities on Claish Moss, Argyll; the relationship of these to environmental parameters, and the floristics of the development of the hummock-hollow complex.

by N.S.Snobel

Graduate Society

Dissertation submitted in part fulfillment of the requirements for the degree of Master of Science in Ecology by advanced course, at the University of Durham.

# ACKNOWLEDGEMENTS

My thanks are due to my supervisor, Dr.D.J.Bellamy for originally suggesting Claish Moss as a suitable site for fieldwork, and for stimulating discussion of the subject thereafter. Also to Dr.D.K.Daniels of the I.T.E. for providing some information on Claish Moss, and kindly giving his permission for it to be used in this dissertation.

Mr.Tom Brett carried out the analysis for cations by atomic absorption spectrophotometry.

I should also like to express my appreciation to the Botany department technicians, the Workshop and Mr.John Richardson for providing equipment, from paper bags, to our daily travel, in the form of a boat with outboard motor.

Finally, I should like to thank in advance my typist, Miss Doreen Danter, for being able to take on the work at such short notice.

This work was undertaken while I was in receipt of an advanced course studentship from the Natural Environmental Research Council, without which the work would not have been possible.

## SUMMARY

Claish Moss, Argyll, is an eccentrically domed mire, well outside the normal climatic zone for this mire type, and is characterized by the hummock-hollow complexes (fig.2), of which it provides the best example in Britain.

The floristics were analyzed by association analysis (method of Agnew), and by the Curtis and McIntosh ordination. The results given by the association analysis depended on the effective quadrat size used in sampling, and this was attributed to the very different habitat conditions present in a small area of the hummock-hollow complex.

The ordination gave correlations between communities of both vascular and non-vascular species, and water table stability and peat depth. Water table stability could be acting directly to affect species composition. Alternatively or additionally, it might have an affect though ground water flow. The correlation with peat depth is postulated to be due to an effect of ground water flow.

No correlation between floristics and hydraulic conductivity was found, nor between the latter and other environmental factors, but the measurements for conductivity were incomplete, and the method is rather crude.

No chemical differences between any of the sites were found, except that site immediately adjacent to the drog stream; the $Ca^{2+}$ and $Mg^{2+}$ levels corresponded to HMT 7 (Bellamy scale) or moss type (Sjors scale). On the basis of total ionic concentration, $NA^{+} : H^{+}$ and $Cl^{-} : SO_4^{2-}$, the mire has some oceanic character, intermediate between ombrophilous proper, and intermediate ombrophilous, as defined by Bellamy.

No explanation was found for the occurrence of the fen window, though an explanation for the slightly anomalous floristic and structual character of a highly eroded part of a hummock-hollow complex is suggested, in terms of possibly (artificially) increased drainage of the area.

A study of the hummocks of the hummock-hollow complex as islands revealed a sequence in the plant cover of hummocks of increasing height, which might correspond to a cyclic successional change if one accepts the biotic theory of

the hummock-hollow complexes (van Post and Sernander). The discovery that species richness of the hummocks depends on their size lends support to the idea that competition is a continually occuring process on the mire; the species cover of a hummock is not predetermined from the point of hummock formation.

It was observed that there was a big difference in the floristic composition of the mire between early May and mid-June. This would probably mainly be due to phenological differences between the species. The annual establishment of seedling and immature plants probably depends mainly on intraspecific competition, though there may also be an interspecific component which might explain the size-dependence of the species richness of hummocks.

## Introduction

Claish Moss in Argyllshire, Scotland (Grid Ref. : NM 710677) is formed between the western end of Loch Shiel, and higher ground to the south (fig.1). It is an eccentrically domed ombrotrophic mire complex, as defined by Bellamy (1), with surface patterning due to an arrangement of pools and hummocks at right angles to the slope, and eccentrically round the domes (fig.2).

The particular type of mire complex that develops in an area depends partly on topography, particularly slope and area of the catchment which supplies water to the mire (2). However, because of the importance of precipitation and evapotranspiration in determining mire type, there is generally a good correlation between geographical region, and the principal mire type that is found (fig.3,(3)).

Claish Moss is far out outside the normal climatic limits for eccentrically domed mires, which are defined by climatic zone 5 (see fig.3), and no explanation has been advanced for the presence of such a mire complex type in climatic zone 8, which is typified by Blanket bog as described by Tansley (26). Furthermore, the Nature Conservancy says of Claish Moss, referring to the surface patterning, that: 'The large amplitude and total scale of the pattern (linear ridges following the contours of the mire surface which form successive terraces each of which has its own water table) in unparalled in Britain and these mires are more closely allied to Scandinavian patterned mires than anything else in Britain'.

The aim of this study was to gain more information regarding the mire complex and especially the patterned area, with a view to discovering what factors may be involved in producing this anomalous mire type for this region.

It may be that topography is the chief factor involved. However, because of the area involved - 1,198 acres, and the difficulty in making the relevant measurements, the problem was not approached from this angle. Instead, the floristics of the mire were studied for comparison with environmental factors, to see what special conditions, if any, are required to produce the surface patterning.

The other possible explanation of this anomalous mire type is that the local climate of Claish Moss is not typical of Western Scotland. If this were the case, it would have to be an extremely local effect, as the climate of the Ardnamurchan and Ardgour districts is warm and moist, in common with other areas of Western Scotland.

In order to investigate such an effect it would be necessary to make rainfall and temperature records over a long period of years, rather than the period of weeks for which the rainfall was actually measured on Claish Moss. In any case, it hardly seems likely that the climate could be very far removed from the typical one for the region, compared to that of the North Karelian region of Finland, where the climate is continental, with mean winter temperatures well below freezing point. The ratio of $Cl^-$ to $SO_4^{2-}$ concentrations should give a measure of the oceanicity of the mire (see on); other than that, the question of the effect of climate is dealt with in more detail in Mr.C.F.Palmer's dissertation.

In this analysis, the detection of natural groupings of species was attempted by the use of the so-called objective methods. There are two main reasons for this, which arise from the fact that in Western Scotland, the hummock-hollow complexes seem to be exceptional and little studied mire types, which give the overwhelming subjective impression of being floristically dissimilar from the plant communities of blanket mire (mainly because of the Rhacomitrium hummocks). Firstly, will the objective methods separate the plant communities of the hummocks and hollows from those of the lawn communities (the more familiar ones of blanket bog), and will they separate different areas of hummocks and hollows floristically? Secondly, on a much smaller scale, will the objective methods separate different communities within the individual hummocks and terraces? With the difficulty of the somewhat arbitrary choice of minimum sampling area encountered in the Braun-Blanquet system of study this question of the identification of communities within individual hummocks may be difficult by any means except by the objective methods. Hence the objection that no phytosociological method can ever be entirely objective is irrelevant; if a method produces a result that could not be produced by the

Braun-Blanquet system, it is valid to use it.

Association analysis and ordination methods are used to detect the natural groupings of species; the results of these analyses can then be compared with the various environmental parameters that were investigated.

Environmental factors interact in a complex way, and if a correlation is discovered between a parameter and, say, a certain plant community, this does not imply a causal relationship. For example, a correlation with relative $Na^+$ ground water concentration may be discovered. This may reflect the dependence of the vegetation on the degree of flushing with rain water (containing high relative $Na^+$ due to salt spray) *compared* to spring water (which may contain low relative $Na^+$ concentration). But the causal effect might be the *total* flushing of the vegetation, which, in other circumstances, may not be correlated with relative flow due to different inputs, or $Na^+$ concentration.

Considerations such as these mean that predictions about other sites, or even other areas within this site, cannot be made on the basis of any correlations that may be discovered. Nevertheless, these correlations will give some understanding of the variation in the floristics of this site, which is a valid object in itself, for the reasons that have been explained.

Experiments involving manipulation of the communities - transferring plants between different areas - might have given some information about causal relationships, by following the performance of different species within a community under different conditions. Such manipulative experiments were, however, considered beyond the scope of this investigation, because of the need to study the long term effects of transferring the plants. The results of short term experiments would have been greatly complicated by, for example, the differential seasonal growth and dying out of a particular species in different areas of the mire.

The various environmental parameters that were measured in connection with the floristics are described in the 'Methods' section.

The other study that was made was on the floristics of the hummock-hollow complex. The method used was to estimate the cover (see 'Methods' for explanation of this term) of the plant species on individual hummocks, completely surrounded by open water or bare mud bottom. The advantage of this 'island' study is that each hummock can be regarded as a discrete community, thus circumventing problems of sampling.

The subjective impression gained from inspection of the hummock-hollow complexes is that stages of development can be recognised, from the height of the hummocks above free water or mud bottom; also from the degree of erosion of the hummocks, and area of bare peat on the latter; also from the vegetation (or lack of it) present in the hollows or pools. Thus the purpose of the study of the floristics of the hummocks in relation to their height is to see if the latter confirms this subjective impression. The causes of such a development, and the implication, if any, for the theories of the origin of the hummock-hollow complex are discussed.

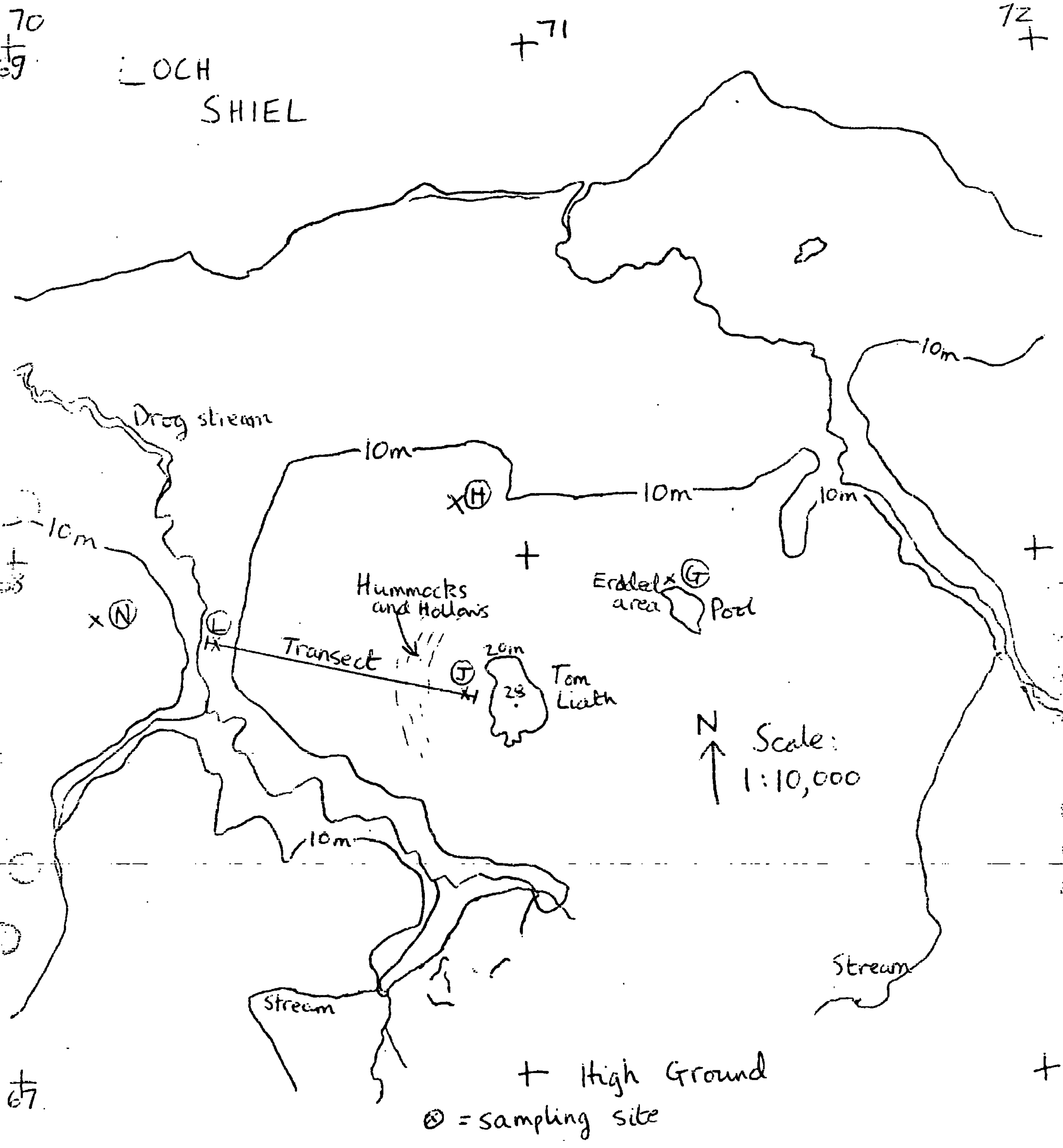


Fig. 5 Map of transect and off-transect sampling sites

## METHODS

The first step in deciding how to sample the plant communities on Claish Moss was to examine an aerial photograph. Different areas of the Moss appear differently on the photograph, corresponding to different plant communities and surface features. Thus the hummock-hollow complexes stand out particularly well. A line was sought on the photograph which would cross all the communities which would be identified, as different by their appearance. Since most of the sampling was to be along this line, it was desirable that all the communities should be encountered in a conveniently short distance. The line which was chosen was identified on the Ordnance Survey Map, scale 1: 10,000 (fig.5).

The plant communities were sampled at 14 sites on the Moss; these were designated A through to P (excluding I and O). Sites A,B,C,D,E,F.J.K.L.M and P were approximately equidistant on the line shown in fig.5 (but not in that order on the line). Sites G,H,N were elsewhere on the bog. These sites were chosen to represent plant communities or surface features not encountered on the line.

Site G was in an area of seemingly highly eroded hummocks and hollows, characterized by large pools with bare mud bottoms, which readily dried out after a short drought period. The hummocks were large, and had steep sides of bare peat, and were sometimes mushroom-shaped, due to erosion or oxidation of peat (fig.4).

Site H was characterized by shallow pools, dense with Sphagna, and low hummocks. Both pools and hummocks were very elongated, giving the appearance of ridges and furrows.

Site N was in the 'fen window' - an area in the middle the familiar lawn vegetation of blanket bog, where there is a 'pocket' of Phragmites.

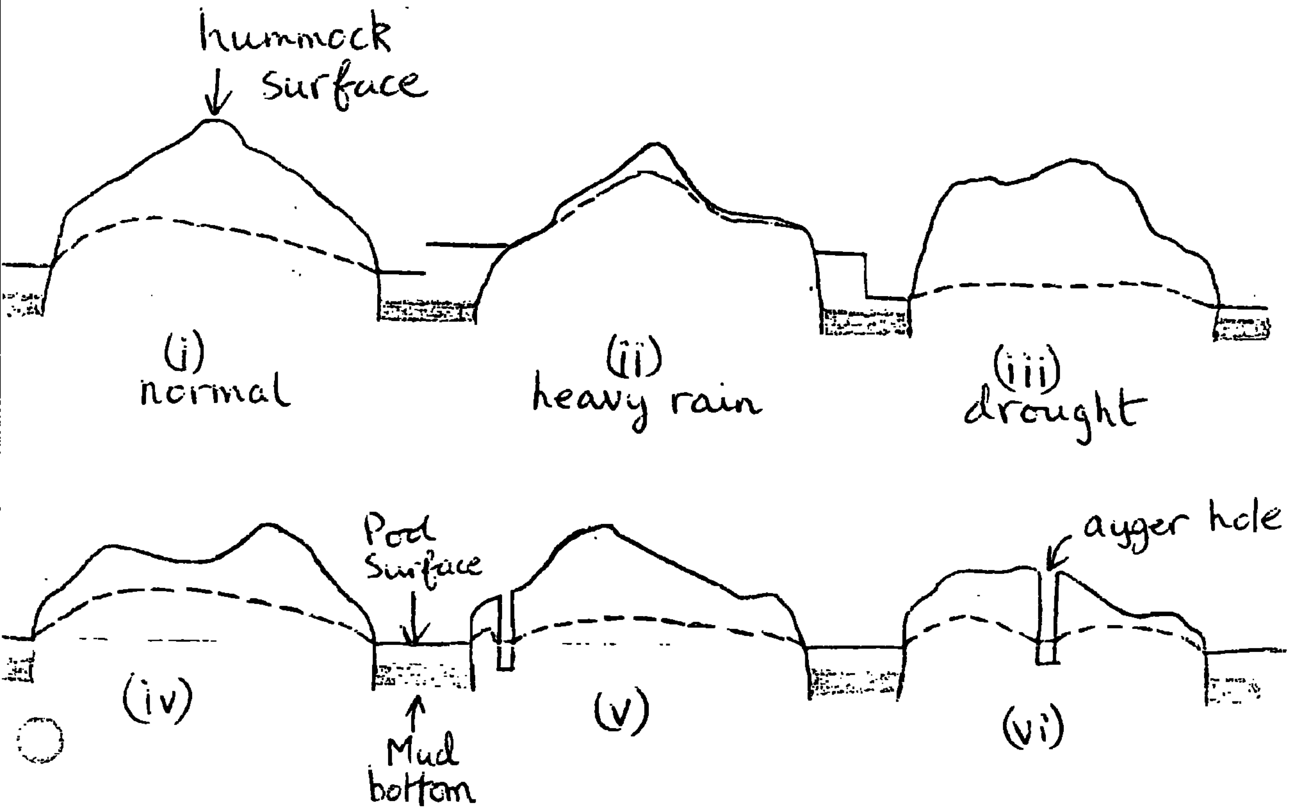
To sample the plant communities at each of the sites, a stake was used to which was tied a string, one metre in length, with ten knots tied at random intervals along the metre length. The other end of the string was tied to another stake, the stakes being positioned so that the string lay approximately along the transect, across the moss; in the case of sites G,H,N, the string was simply positioned to lie across the vegetation it was desired to study, in a consistent direction for each site. For each site the string was set six times, so that data was collected for six one metre lengths.

For each knot in succession, all the plants that were in contact with it, or were vertically below it or above it as seen by looking directly over the knot were recorded. Additionally, a pinch of the vegetation was taken from the very surface of the soil or peat directly below each knot, and the plants thus obtained were recorded. This is a variation on the point quadrat method used by Goodall (4). It was necessary here both to record the plants above and below the knot, and to take a sample at the peat surface, because here we are dealing with two strata of vegetation. There are the mainly vascular plants that project away from the physical influence of the mire surface (especially from the free water surface, where there is waterlogging); then there are then mainly non-vascular plants which mostly constitute the surface of the peat, except where the latter is bare (eroded hummocks - see on), or covered in dry litter - as on the Calluna - dominated areas.

The data was accumulated in two ways; firstly, for each metre length of string, the presence or absence of plant species was recorded; so for each site, there are six columns of presence and absence data (six metres were sampled at each site). This data is shown in table 1. Secondly, for each site the total number of strikes of each species was added up, to give an estimate of the cover of each species at that site (table 2)(12). The methods used in deterimining the environmentel parameters at each site are now described under headings.

## Peat Depth

A sounding rod was used at three points, all within about a foot of each other, at each sampling site, to give an average peat depth for each site. On the peat itself, bedrock was struck at clearly defined depths. However, on the peaty soils adjoining the drog streams, these depths were not so clearly defined, making it difficult to obtain consistent results.



Probable effect of humidity ( i,ii,iii) and sinking auger hole (iv,v,vi) on water table profile in hummock. Notice in i,ii,iii there is greater variation of level in hummock compared to pool.

------ = water table profile

Fig. 6 Water table profile in hummock

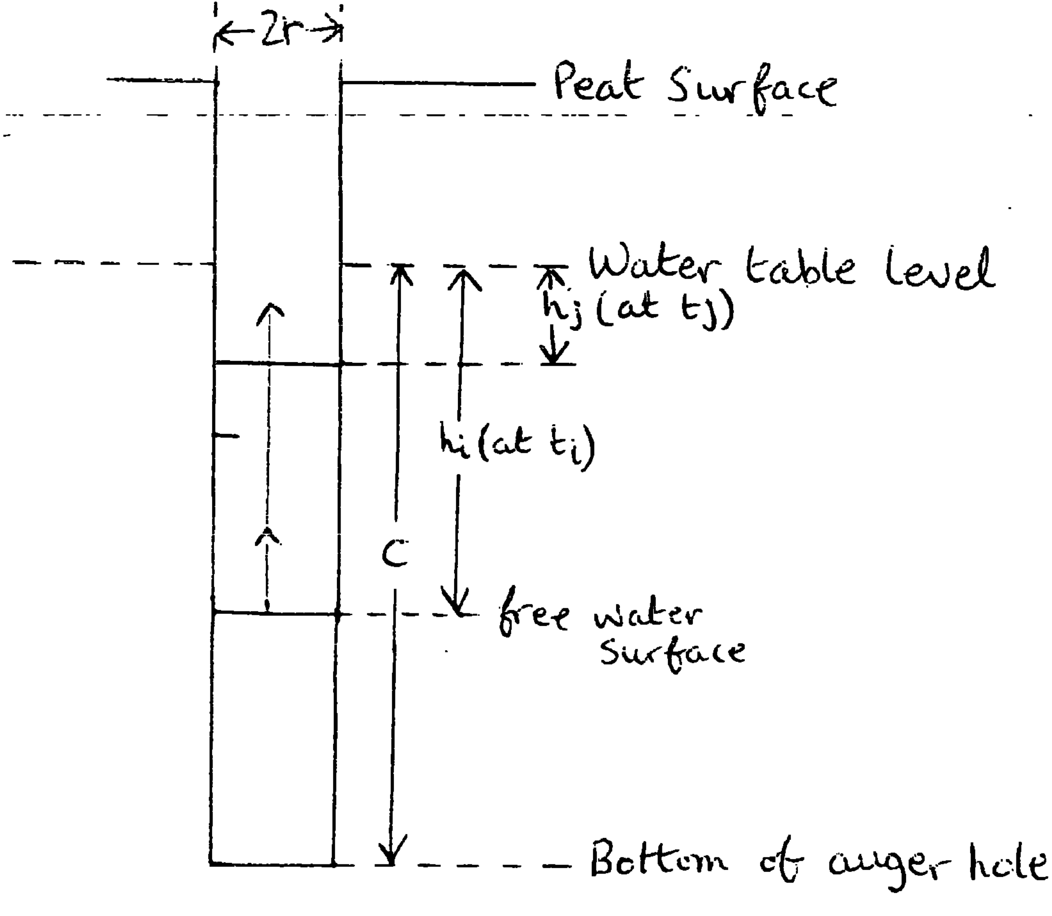


Fig. 7 Measurement of hydraulic conductivity

## Water Table and Hydraulic Conductivity

At each site, a soil corer was used to bore a hole in the peat surface; the water table was then simply taken as the distance from the surface to the free water in the hole. At nearly all the sites there was some uneveness in the surface, so the water table that would be obtained would depend on at what point the core was taken (for example, whether through a hummock or hollow). No attempt was made to standarize the water table to the average level of the mire surface at each site, so the absolute water tables at each site do not have much significance. However, it is the changes in the water tables at each site with time that will be considered, and these can be compared.

In the case of the hummock-hollow complexes, where the hollows are permanently under free water, the question of the level of the water tables in the hummocks is more complicated (5); in each hummock, the water table is likely to be very far from flat (fig. 6), and the profile at the point where the core is taken is likely to be greatly altered by the process of taking a core. The only measurement that can be reliably made is the vertical distance from a fixed point on the hummock to the free water surface on the pool. Variations in this distance will then represent movement of the pool surface up and down with respect to the hummock. This was the measurement that was in fact made; the method used was to take a core at the side of the hummock, and measure it down to the free water in the hole; it was found that this free water had the same level as the pool. Thus in the case of the hummock-hollow complexes, the results given for changes in the water table refer only to the margins of the hummocks.

Hydraulic conductivity of peat is a measure of the rate at which water will flow through a fixed volume under a fixed pressure (6). It is related to the degree of humification of the peat, the density of it, and some other factors, which are discussed in more detail below. One of the ways in which it can be measured is to remove or add water to the holes which were bored for measurement of the water table (see above), and follow the return of the water level back to the equilibrium. The particular method used was that of the auger hole (7), which is illustrated in fig. 7. The hydraulic conductivity is given by the empirical solution of Hooghoudt (8):

$$K = \frac{2.3rA_h}{(2c+r)\ (t_j - t_i)} \times \text{Log}_{10}\ \frac{hi}{hj} \qquad * \ (\text{eqn.}1),$$

Where $h_i$ and $h_j$ are the level displacements recorded at times ti and tj respectively. The peat is assumed to be homogeneous and istropic; the former assumption is called into question by the results (see on). Leaving that aside, provided measurments are made when

$$hj < c/4,$$

Lathin (9) believes that results are yielded correct to within 10-20%. $A_h$ is the shape factor, which has dimensions of length:

$$A_h = ro/o.19$$ , for lengths measured in metres.

The constancy of the shape function arises from Hooghoudt's assumption of a uniform potential gradient in the vicinity of the well; in fact, errors are introduced due to the gradient varying with depth-being greatest near the base of the well-and hence the shape factor changes as the hole fills up (10,11). From eqn.1, a graph of log h (where h is the distance of water from water table level) against t will be a straight line, of gradient $\frac{K\ (2c + r)}{2.\ 3rA_h}$ . Hence K may be found.

However, heterogeneity of the peat, and lack of constancy of the shape function, both due to theoretical considerations discussed above, and due to the non-uniformity of the water table level over a short distance in the hummocks, militate against a straight line being produced to find K. Thus it may be difficult to give more than a rough estimate for hydraulic conductivities, and the results must be treated with caution.

Experiments were performed involving both depletion and recharge of the water in the auger holes, and following the return to equilibrium levels in some cases over a period of minutes, in some over a period of hours. At some sites, auger holes were sunk both in the hummocks and hollows (where the latter were dry) in order to obtain a comparison.

## Water Chemistry

At each site, and from the drog stream itself, samples of water were taken for chemical analysis. At those sites where a free water surface was present, collection of a sample of superficial water presented no problem; at sites where no free water surface was present, free water was collected from the auger holes used in the hydrological studies (see above). At all sites, water was collected from squeezed peat samples. Any living mosses and liverworts were stripped off the surface of the peat; peat was then extracted to a depth not greater than about 3 cms. Water was squeezed from this peat to produce further water samples.

Water samples were collected from sites on the 7th May (7/5) after heavy rain when the water tables were at a peak. Also on 27th May, after a dry period, when the water tables were much lower.

Water samples were stored in polypropylene bottles which had been washed in acid and equilibrated with distilled water.

pH of the water samples was measured using a Pye Unicam field pH meter, model 293. Electrical conductivity was measured using an electrical conductivity set, model MC-1, Mark V, supplied by Electronic Instruments Ltd., Chertsey, Surrey. Generally, the conductivities were measured using the temperature compensation control, which allows for a 2% conductivity increase per degree C, to standardise them to 25°C.

Analyses for $Na^+$, $K^+$, $Mg^{2+}$ and $Ca^{2+}$ by atomic absorbtion specrophotometry, were kindly undertaken by Mr. Tom Brett.

Analysis for $HCO_3^-$ in those samples with pH 4.5 was by titration against 0.001N HCL using a microburette, the end point being detected using a pH meter, B.D.H. 4.5 indicator did not give a satisfactory endpoint.

Analysis for $Cl^-$ was by titration against 0.0141N $AgNO_3$, using a microburette, and potassium chromate as an indicator.

$SO_4^{2-}$ concentration was found by balancing equivalent concentrations of anions and cations. The results of such calculations must be treated with caution, as there is the possibility that there are charged colloidal particles derived from the peat in the samples, so that the concentration of free ions would not balance.

### Density and Water Content of Peat

Cores of peat of standard length were taken from each site, and loaded into tins. Each core consisted of the top 7.9 cms. of peat, with living plants stripped off the surface. The tins were weighed to give the density of the peat, and then stored in an oven for 18 days at 100°C, and reweighed to give the water content.

### Island Study

In the case of the island study, the area of the islands was estimated by measuring the sides of a rectangle that would be of approximately an equivalent area. The height of the island was taken as the vertical distance of the surface mosses at the top of the hummock down to the mud bottom of the pool, since the latter would fluctuate less in height on subsequent days than the height of the free water surface. Any special features, such as shape, of the hummocks were noted.

For each hummock, a complete list of species present was drawn up. Then for each species, an estimate was made of the cover of that species *relative to the maximum cover seen for that species anywhere on the bog.* That is not the normal definition of cover, which is the proportion of ground occupied by perpendicular projection on to it of the aerial parts of individuals of the species under consideration (12). For most plants, the maximum cover seen on the bog was 100%; so the cover defined by either definition would be the same. In the case of a few plants maximum density did not appear to give 100% cover; in the case of *Narthecium ossifraga*, this was because the plants were only in the process of emerging at the time at which the study was undertaken. It was felt that a better picture of the differences in vegetation between the hummocks would emerge by taking cover as relative to the maximum seen for a particular species, as a result of excluding factors such as seasonal effects on cover.

For each species, relative cover was designated as follows:

| | |
|---|---|
| | present |
| 2 | 20% |
| 4 | 40% |
| 6 | 60% |
| 8 | 80% |
| 10 | 100% |

Because cover was taken relative to the maximum for the species, and because individuals of different species can overlap, the total cover for a particular hummock, even for one of the two strata of vegetation, could be well over 100%.

12 hummocks, chosen to cover a range of heights and areas, were studied at each of four sites: F, M, P and G.

Note that the cover here was estimated by inspection i.e.subjectively. This was necessary simply to examine a sufficient number of islands to obtain meaningful results.

# RESULTS

| Site ↓ | Transect no. ↓ | Molinia caerulea | Eriophorum vaginatum | Calluna vulgaris | Erica tetralix | Eriophorum angustifolium | Trichophorum caespitosum | Hypnum cupressiforme | Sphagnum recurvum[1] | Sphagnum rubellum | Sphagnum cuspidatum | Sphagnum palustre | Sphagnum papillosum | Sphagnum magellanicum | Rhacomitrium lanuginosum | Pleurozia purpurea | Drosera rotundifolia | Cladonia impexa | Cladonia arbuscula | Calypogeia fissa | Odontoschisma sphagni | Mylia anomala |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| L | 1 | X | | | | | | X | X | | | | | | | | | | | | | |
| | 2 | X | | | | | | | | | | | | | | | | | | | | |
| | 3 | X | | | | | X | | X | | | | | | | | | | | | | |
| K₂ | 4 | X | | | | | | X | X | X | | X | | | | | | | | X | X | X |
| | 5 | X | | | | | | X | X | X | X | X | | | | | | | | X | X | X |
| | 6 | X | | | | | | X | X | X | | X | | | | | | | | X | | |
| K₁ | 7 | X | | | X | | | X | | | | | | | | | | X | | | X | |
| | 8 | X | | X | X | | X | X | | | | | | | | | | X | | | X | |
| | 9 | X | X | X | X | | | X | X | | | | | | | | | | | | X | |
| A | 10 | X | X | X | X | | | | X | | | | | | | | | | | | | |
| | 11 | X | X | X | X | | | X | | | | | | | | | | X | | X | X | |
| | 12 | X | X | X | | | | X | | | | | | | | | | | | | X | |
| | 13 | X | X | X | X | | | X | X | | | | | | | | | | | X | X | X |
| | 14 | X | X | X | X | | | X | X | X | | | | | | | | | | X | X | X |
| | 15 | X | X | X | X | | | X | X | | | | | | | | | | | | X | X |
| B | 16 | X | X | X | X | X | | X | X | X | | | | | | | | | | | X | X |
| | 17 | X | X | X | X | X | X | | X | X | X | X | | | | | | | | | X | X |
| | 18 | X | X | | X | | X | | X | | X | | | | | | | | | | X | X |
| | 19 | X | X | X | X | X | X | | | | | | | | | | | | | | X | X |
| | 20 | X | X | | X | | X | | | X | X | | | | | X | X | | | | X | X |
| | 21 | X | X | | X | | X | X | X | X | | | | | | | | | | X | X | X |
| C | 22 | X | X | X | X | X | X | | | X | | | | | X | | | X | X | | X | X |
| | 23 | X | X | X | X | X | X | | X | | | X | | | | | | | X | | X | X |
| | 24 | X | X | X | X | X | X | | | | X | X | | | | | | | | | X | X |
| | 25 | X | | X | X | X | X | | X | | X | | X | | | | | X | | | X | |
| | 26 | X | | X | X | | X | X | X | | | | | | | | | X | | | X | X |
| | 27 | X | | X | | | X | X | X | X | | | | | X | | | X | | | X | X |
| D | 28 | X | X | X | X | | X | | X | X | | | | | X | | X | X | | | X | X |
| | 29 | X | | X | | X | X | X | X | X | X | | | X | | | X | X | | | X | X |
| | 30 | X | X | | X | X | | | | | X | | | | | | | | | | X | X |
| | 31 | X | | X | X | X | X | | X | X | | | | X | | | | | | | X | X |
| | 32 | X | X | X | X | X | | | | | X | | X | | | X | | | | | X | |
| | 33 | X | X | X | X | X | X | | X | X | X | | | | X | | | X | | | X | X |
| E | 34 | X | X | X | | X | | | X | X | | | | | X | | | X | | | X | |
| | 35 | X | | X | | X | X | | X | X | | | | | X | X | | X | X | | X | |
| | 36 | X | X | X | X | | X | | X | X | X | X | | | X | X | | X | X | | X | |
| | 37 | | | X | | X | X | | | | | X | X | | X | | | | | | | |
| | 38 | X | | X | | X | X | X | X | X | | | | X | X | X | X | X | X | X | X | |
| | 39 | X | | X | X | X | X | | X | X | X | | | X | X | | | X | X | X | X | |
| F | 40 | X | X | X | | X | | | | | | | X | | X | | | X | X | | | |
| | 41 | | | | | X | X | X | | | | | | | X | | | X | X | | | |
| | 42 | | X | X | | X | X | | | | | | | | X | | | X | | | | |
| | 43 | X | | X | | X | | | | | | | | | X | | | | X | | | |
| | 44 | X | X | X | | X | X | X | | X | | | X | | X | | | X | X | | X | X |
| | 45 | | | X | | | | | | X | X | | | X | | | | | | | X | X |
| M | 46 | X | X | | X | | | | | | X | | X | | | | X | | | | | |
| | 47 | | | X | X | | X | | X | X | X | | X | X | X | | | X | | | X | |
| | 48 | X | X | X | X | X | X | | | X | | | X | | X | X | | X | X | | X | |
| | 49 | X | X | X | X | | | X | | | | | | | X | X | | X | X | | | |
| | 50 | X | | X | X | X | | | | | | | X | | X | | | | | | | |
| | 51 | X | | X | | X | | X | | | | | | | X | | | X | | | | |
| P | 52 | X | X | X | X | X | X | | | X | X | | X | X | | | X | | | | | |
| | 53 | X | X | X | X | X | X | X | | X | | X | X | X | | | X | X | | | X | |
| | 54 | X | X | X | X | X | | | X | X | | | X | X | X | X | X | X | X | | X | X |
| | 55 | X | X | X | X | | X | | X | | | X | X | X | X | X | X | X | | X | X | X |
| | 56 | X | X | X | X | X | X | | X | X | | | X | X | X | X | X | X | | X | X | X |
| | 57 | X | | X | X | | X | | X | | | X | X | X | | X | X | X | | | X | |
| J | 58 | X | X | | X | | | X | | X | | | | | | | | X | | | X | |
| | 59 | X | X | | X | | | | X | X | | X | | | | | | X | | | | X |

Note: Only species present at least 10 times included here

[1] Sphagnum rubellum may frequently have been misidentified for Sphagnum recurvum. Sphagnum recurvum may only have been present at sites L, $K_2$, and J.

Table 1 Presence and absence data for on-transect sites, based on sampling in 1 metre lengths

| Site | | L | K2 | K1 | A | B | C | D | E | F | M | P | J | G | H | N1 | N2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | on-transect | | | | | | | | | | | | off-transect | | | |
| Vascular plants: | | | | | | | | | | | | | | | | | |
| Molinia caerulea | 1 | 14 | 26 | 23 | 31 | 50 | 40 | 12 | 10 | 7 | 12 | 21 | 20 | 12 | 22 | 12 | 7 |
| Myrica gale | 1 | 13 | 4 | | | | | | | | | | | | | | |
| Carex nigra | 1 | | 3 | | 1 | | | | | | | | | 2 | | | |
| Ranunculus ripens | 1 | | | 1 | | | | | | | | | | | | | |
| Ranuculus ficaria | 1 | | 1 | 2 | | | | | | | | | | | | | |
| Ranunculus acris | 1 | 1 | | | | | | | | | | | | | | | |
| Poa pratensis | 1 | 2 | | | | | | | | | | | | | | | |
| Festuca ovina | 1 | | 1 | | | | | | | | | | | | | | |
| Filipendula ulmaria | 1 | | | 1 | | | | | | | | | | | | | |
| Veronica officianalis | 1 | 2 | | | | | | | | | | | | | | | |
| Potentilla erecta | 1 | 1 | | | | | | | | | | | | | | | |
| Anemone nemorosa | 1 | 1 | | | | | | | | | | | | | | | |
| Agrostis tenuis | 1 | 1 | | | | | | | | | | | | | | | |
| Eurhynchium praelongum | 1 | 1 | | | | | | | | | | | | | | | |
| Phragmites communis | 1 | | | | | | | | | | | | | | | 10 | |
| Eriophorum vaginatum | 2 | | | | 54 | 19 | 5 | 8 | 6 | 5 | 3 | 10 | 16 | 1 | 8 | 18 | 14 |
| Trichophorum caespitosum | 3 | | | 3 | | 26 | 25 | 16 | 10 | 5 | 4 | 23 | | | 4 | 1 | |
| Narthecium ossifragum | 3 | | | | | | | | | 3 | 8 | 16 | | 1 | 2 | 1 | 4 |
| Calluna vulgaris | 4 | | | 8 | 45 | 7 | 18 | 13 | 23 | 22 | 24 | 19 | | 16 | 15 | 32 | 10 |
| Menyanthes trifoliata | 4 | | | | | | | | | 1 | 1 | | | | | | |
| Eriophorum angustifolium | 5 | | | | | 10 | 5 | 22 | 16 | 21 | 10 | 6 | | 9 | 12 | | |
| Erica tetralix | 5 | | | 8 | 12 | 23 | 16 | 19 | 2 | | 11 | 18 | 5 | 4 | 13 | 7 | 6 |
| Rhynchospora alba | 5 | | | | | | | 7 | 6 | | 4 | | | | | | |
| Non-vascular plants | | | | | | | | | | | | | | | | | |
| Sphagnum recurvum | 1 | 5 | 20 | 1 | 18 | 8 | 12 | 7 | 11 | | 1 | 7 | 1 | | | 18 | 6 |
| Sphagnum palustre | 1 | | 15 | | | 1 | 2 | | 2 | | | 3 | 1 | | | | |
| Ctenidium molluscum | 1 | 5 | | | | | | | | | | | | | | | |
| Plagiothecium undulatum | 1 | 3 | 8 | 2 | | | | | | | | | | | | | |
| Rhytidiadelphus squarrosus | 1 | | 4 | | | | | | | | | | | | | | |
| Hypnum cupressiforme | 2 | | 6 | 15 | 20 | 7 | 6 | 3 | 2 | 2 | 8 | 1 | 9 | 2 | 5 | 37 | 15 |
| Dicranum scoparium | 2 | | 2 | 5 | 4 | 4 | | | | | | | | | 2 | | |
| Thuidium tamariscinum | 2 | | 2 | 2 | | | | | | | | | | | | | |
| Campylopus flexuosus | 2 | | | 1 | | | | | | | | | | 1 | | | |
| Leucobryon glaucum | 2 | | | | | | | | | | | | | | | 3 | 2 |
| Sphagnum rubellum | 3 | | 14 | | 3 | 20 | 4 | 22 | 15 | 4 | 3 | 13 | 3 | | 16 | 1 | 11 |
| Sphagnum cuspidatum | 3 | | | | | 6 | 3 | 14 | 3 | 1 | 3 | 2 | | 1 | 16 | | |
| Sphagnum compactum | 3 | | | | | | | 5 | | | | | | 4 | | | |
| Pleurozia purpurea | 4 | | | | | 1 | | 3 | 8 | | 3 | 16 | | | 2 | | |
| Sphagnum plumullosum | 4 | | | | | | | | | | | 16 | | | 1 | | |
| Shagnum magellanicum | 4 | | | | | | | 3 | 4 | 2 | 2 | 13 | | | 4 | 1 | 6 |
| Sphagnum papillosur | 4 | | | | | | 1 | 3 | 1 | 3 | | 9 | | | 10 | | |
| Drosera rotundifolia | 4 | | | | | 1 | | 2 | 1 | | 1 | 12 | | | 1 | 2 | 1 |
| Hylocomium splendens | 4 | | | | | | | | | | | | | | 1 | | |
| Cladonia impexa | 5 | | | 5 | 1 | | 7 | 6 | 34 | 10 | 18 | 14 | 7 | 1 | 1 | 5 | 1 |
| Sphagnum inundatum | 5 | | | | | | | 1 | | | 6 | | | 1 | | | |
| Campylopus atroviriens | 5 | | | | | | | | | | 5 | | | | | | |
| Rhacomitrium lanuginosum | 6 | | | | | | 12 | 1 | 21 | 35 | 17 | 3 | | 31 | 1 | | |
| Cladonia arbuscula | 6 | | | | | | 2 | | 6 | 8 | 4 | 1 | | | 4 | | |

Notes:
a) Figures in left-hand column are climax adaptation numbers
b) Underlined species are leading dominants
c) At most sites, six metres were sampled, and the number of strikes for each species recorded. However, because this lenght was not invariable, total number of strikes for each site are not comparable as community performances.

Table 2 Data for cover of vascular and non-vascular species at all sites

| Quadrat no. n. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Gleocystis | | X | | | X | X | | X | | | | | | | | | | | | | | | | | | | |
| Sphagnum tenellum | | | X | X | | X | X | X | X | | | | | | | | | | | | | | | | | | X |
| Sphagnum rubellum | | X | X | X | X | X | X | X | X | X | X | X | X | | | | | | | | | | | | | X | X |
| Rhacomitrium lanuginosum | | | | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| Hypnum cupressiforme | | | | | X | | | | X | X | X | X | X | | | | | | | | | | | X | X | X | X |
| Cladonia uncialis | | | | X | X | X | X | X | X | X | X | X | X | | | | | | | | | | | | X | X | X |
| Cladonia impexa | | | X | X | X | X | X | X | X | X | X | X | X | X | X | | | | | | | | | X | X | X | X |
| Trichophorum caespitosum | | | X | | | | | | X | X | X | | | | | | | | | | | | | X | | | |
| Rhynchospora alba | | X | | X | | X | X | X | | | | | | | | | | | | | | | | | | | |
| Narthecium ossifragum | | | X | X | X | | X | X | X | X | X | X | X | | | | | | | | | | | | | | X |
| Drosera rotundifolia | | | X | X | X | X | X | X | X | X | X | | | | | | | | | | | | | | | | X |
| Molinia caerulea | | | X | X | X | X | X | X | | | | | | | | X | | | | | | X | X | X | X | X | X |
| Eriophorum angustifolium | X | X | X | X | X | X | X | X | X | | X | X | X | X | X | | | | | | | | | | | | X |
| Erica tetralix | | X | X | X | X | X | X | X | | | | | | | | | | | | | | | | | | X | X |
| Calluna vulgaris | | | X | X | X | X | X | X | X | X | X | X | X | | | | | | | | | | X | X | X | X | X |

| Quadrat no. n. | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Gleocystis | | | | | | | | | | | X | | | X | | | X | X | X | X | | | | | | | |
| Sphagnum tenellum | | | X | X | | | | | | | | | | X | X | X | X | X | X | | | | | | | | |
| Sphagnum rubellum | X | | X | X | | | X | | | | | | X | X | X | X | X | X | X | X | | | | | | | |
| Rhacomitrium lanuginosum | | | X | X | X | | X | X | X | X | X | X | | | X | X | X | | | X | | X | X | X | X | X | X |
| Hypnum cupressiforme | X | | | X | X | X | X | | | | | | | X | X | X | X | | | | | | | | | | |
| Cladonia uncialis | | X | X | X | | | | | | | | | | X | X | X | X | X | X | | X | | X | X | | | |
| Cladonia impexa | X | | X | X | X | X | X | X | | | | X | | | X | X | X | X | X | | | | X | X | | | |
| Trichophorum caespitosum | X | X | | X | | | | | | | | X | | | | | | | | | | | | X | | | |
| Rhynchospora alba | | X | X | | | | | | | | | | X | X | X | X | X | X | X | X | X | | | | | | |
| Narthecium ossifragum | X | X | X | X | X | | | | | | X | X | X | X | X | X | X | X | X | X | X | | | | | | |
| Drosera rotundifolia | X | X | X | X | | | | | | | | | X | X | | | | X | X | | | | | | | | |
| Molinia caerulea | X | X | X | X | X | X | X | X | | | | X | X | X | X | X | X | X | X | X | X | | X | X | | | X |
| Eriophorum angustifolium | X | X | X | X | X | | | X | | | X | X | | | | | X | X | X | X | X | X | X | X | X | X | X |
| Erica tetralix | X | X | X | X | X | X | X | | | | | | X | X | X | X | X | X | X | X | | | | | | | |
| Calluna vulgaris | X | X | X | X | X | X | X | | | | | X | X | X | X | X | X | X | | | | | X | X | | | X |

Notes: a) Only quadrats falling entirely over hummocks are included here; data for quadrats falling entirely or partially over pools not shown.

b) Only species with at least ten occurences shown.

c) Species association table based on this data shown in table 5.

Table 4 Presence and absence data for hummocks based on 20cm. quadrats

Table 3 Chi-square matrix for on-transect stands, showing positive and negative species relationships present

| | Eriophorum vaginatum | Calluna vulgaris | Erica tetralix | Eriophorum angustifolium | Trichophorum caespitosum | Hypmum cupressiforme | Sphagnum recurvum | Sphagnum rubellum | Sphagnum cuspidatum | Sphagnum palustre | Sphagnum papillosum | Sphagnum magellanicum | Rhacomitrium lanuginosum | Pleurozia purpurea | Calipogeia fissa | Odontoschisma sphagni | Mylia anomala | Cladonia impexa | Cladonia arbuscula |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eriophorum vaginatum | | | | | | | | | | | | | | | | | | | |
| Calluna vulgaris | | | | | | | | | | | | | | | | | | | |
| Erica tetralix | ++ | | | | | | | | | | | | | | | | | | |
| Eriophorum angustifolium | | ++ | | | | | | | | | | | | | | | | | |
| Trichophorum caespitosum | | | | + | | | | | | | | | | | | | | | |
| Hypmum cupressiforme | | | | -- | | | | | | | | | | | | | | | |
| Sphagnum recurvum | | | | | | | | | | | | | | | | | | | |
| Sphagnum rubellum | | | | | | | ++ | | | | | | | | | | | | |
| Sphagnum cuspidatum | | | ++ | | | -- | | | | | | | | | | | | | |
| Sphagnum palustre | | | | | | | | | | | | | | | | | | | |
| Sphagnum papillosum | | | | | | - | -- | | | | | | | | | | | | |
| Sphagnum magellanicum | | ++ | | ++ | | | | + | | | ++ | | | | | | | | |
| Rhacomitrium lanuginosum | | ++ | | ++ | | | | | | | | | | | | | | | |
| Pleurozia purpurea | | | | | | | | | | | + | | | | | | | | |
| Calipogeia fissa | | | | | | ++ | | | | | | | | | | | | | |
| Odontoschisma sphagni | | | + | | | | | ++ | | | | | | | | | | | |
| Mylia anomala | | | | | | | | ++ | | | | | | | | ++ | | | |
| Cladonia impexa | | +++ | | ++++ | | | | | | | | | +++ | | | | | | |
| Cladonia arbuscula | | | | | | | | | | | | | +++ | | | | | ++ | |
| Drosera rotundifolia | | | | | | | | | | | ++ | +++ | | +++ | | | | | |

$\left.\begin{matrix}+\\-\end{matrix}\right\}$ P<0,02

$\left.\begin{matrix}++\\--\end{matrix}\right\}$ P<0,01

+++ P<0,001

Species constellatoin diagram based on this table shown in fig.9

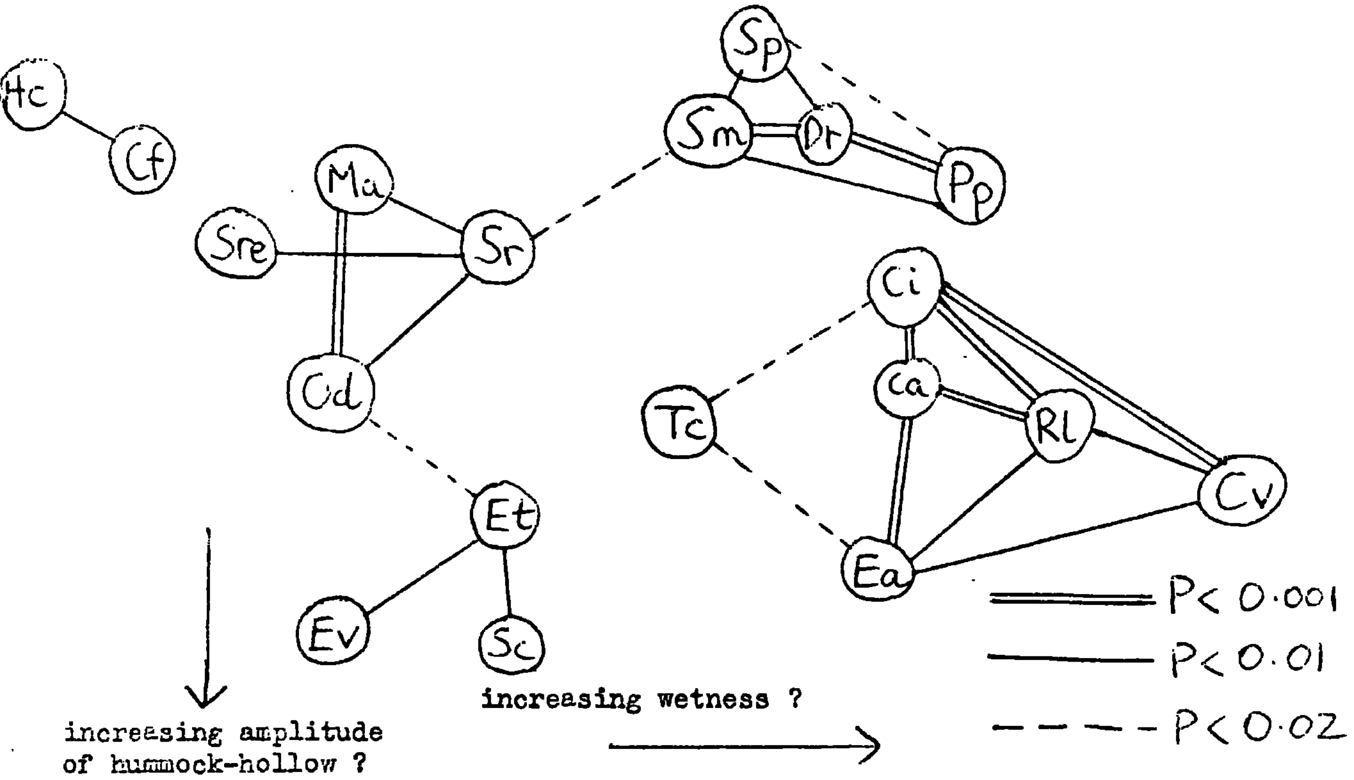
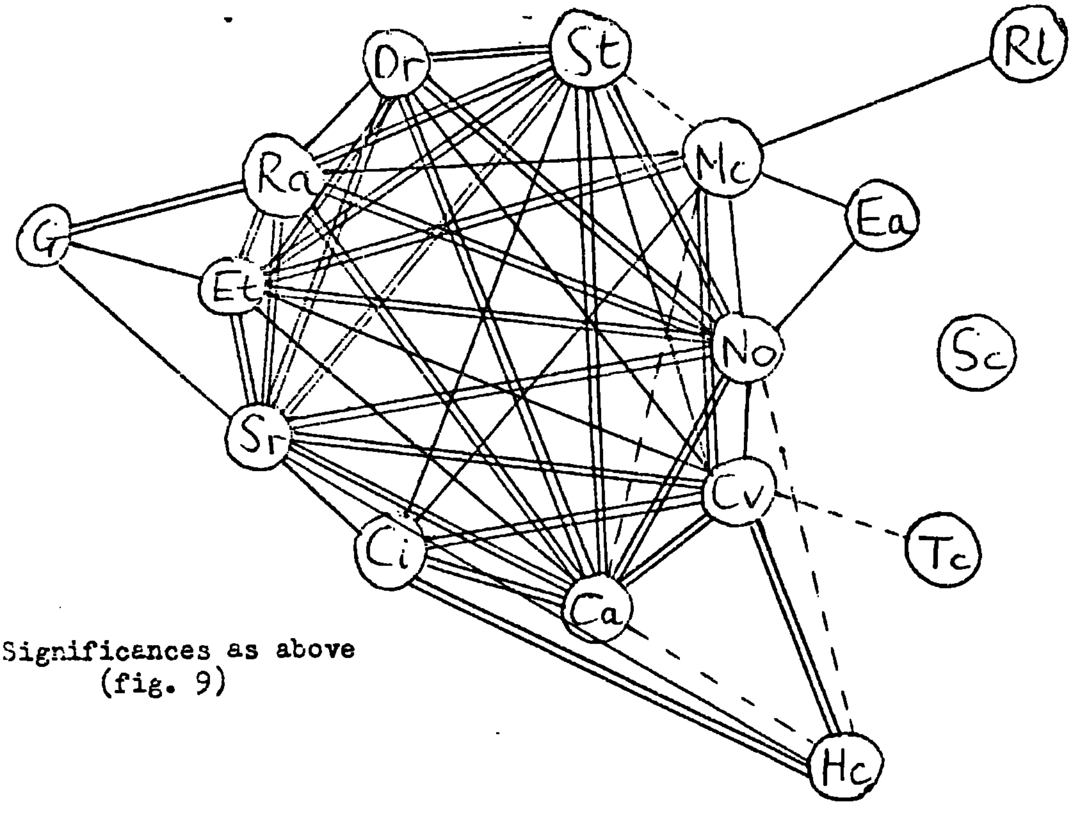


Fig. 9 Species constellation diagram - all sites

| | | | | | |
|---|---|---|---|---|---|
| Ca | Cladonia arbuscula | G | Gleacystis | Rl | Rhacomitrium lanuginosum |
| Ci | Cladonia impexa | Hc | Hypnum cupressiforme | Sc | Sphagnum cuspidatum |
| Cf | Calypogeia fissa | Ma | Mylia anomala | Sm | Sphagnum magellanicum |
| Cv | Calluna vulgaris | Mc | Molinia caerulea | Sp | Sphagnum papillosum |
| Dr | Drosera rotundifolia | No | Narthecium ossifragum | Sr | Sphagnum rubellum |
| Ea | Eriophorum angustifolium | Od | Odontoschisma sphagni | Sre | Sphagnum recurvum |
| Et | Erica tetralix | Pp | Pleurozia purpurea | St | Sphagnum tenellum |
| Ev | Eriophorum vaginatum | Ra | Rhynchospora alba | Tc | Trichophorum caespitosum |



Significances as above (fig. 9)

Fig. 10 Species constellation diagram - hummocks and hollows

## RESULTS

The first method that was used to analyze the floristic data was a simple ordination obtained by using $X^2$ as a measure of association between the species pairs. The method of Agnew (13) was used, except that any species that occurred in presence or absence table (table 1) less than ten times was eliminated to simplify the construction of the species constellation diagram. *Molinia caerulea* was also eliminated, as it occurred in 54 out of 59 metre lengths; no significant correlations could be found for such an ubiquitous species, except possibly by reducing the effective quadrat size (or length of string) used in sampling. Only data from the transect (fig. 5) were included in the association analysis; it would not be valid to include data from sites C, H and N, as they do not lie within the area defined for sampling. The floristics of these sites can be compared with the constellation diagram produced from the transect data.

The correlations obtained are tabulated in table 3. These are used to construct the species constellation diagram (fig. 9) by the method of Agnew, using reciprocal $X^2$ values. From fig. 9, the following species groupings emerge:

### Group 1

*Eriophorum vaginatum*, *Erica tetralix*, *Sphagnum cuspidatum*

### Group 2

*Calipogeia fissa*, *Hypnum cupressiforme*

### Group 3

*Odontoschisma sphagni*, *Mylia anomala*, *Sphagnum recurvum*, *Sphagnum rubellum*

### Group 4

*Sphagnum magellanicum*, *Sphagnum papillosum*, *Drosera rotundifolia*, *Pleurozia purpurea*

### Group 5

*Tricophorum caespitosum*, *Eriophorum angustifolium*, *Rhacomitrium lanuginosum*, *Calluna vulgaris*, *Cladonia impexa*, *Cladonia arbuscula*

In determining these groups, correlations obtained significant only at the 5% level were ignored, since with twenty species, giving 100 $X^2$ values, five correlations at the 5% level would be expected purely by chance, and 2½ of these positive.

One can attempt to identify where these species groupings occur along the transect line.

Group 1 occurs once at sites E, M, P, and 2 or 3 times at sites, B, C, D. It is not characteristic of the hummocks and hollows (site F), nor the mire margin or lagg communities (sites J, K, L) nor the 'dry lawn' community (site A). It is, therefore, most characteristic of the 'wet lawn' community of the mire expanse.

Group 2 occurs at sites A (3 times), K (2 times), B and E (once). It is difficult to generalize here, because C. fissa would be easily overlooked, being a small leafy liverwort. H. cupressiforme is most abundant in the mire margin (site K) and dry lawn (site A), and is often associated with roots of Calluna, though this has not emerged from the association table.

Group 3 occurs at site B (3 times), K, P, D (2 times), A and C (once). Thus, like group 1, it is not characteristic of the hummocks and hollows, but extends further towards the dry lawn and mire margin sites (A, K).

Group 4, which is a very 'tight' group on the species constellation diagram, occurs only at one site - P - four times, although three of the four species occur more widely, particularly on the hummocks and hollows. Site P is between the lagg and the hummocks and hollows, and consists of low ridges and shallow hollows, the latter consisting of mainly vascular plants, particularly Molinia caerulea. Group 4 could, therefore, be said to be characteristic of a partially developed hummock-hollow complex.

Group 5 occurs at sites C, F, M (once), and E (3 times). Of all the groups it is therefore the one most characteristic of the hummock-hollow complex.

Having decided where the communities occur in the mire, it is now theoretically possible to relate the species constellation diagram to environmental factors by superimposing axes of co-ordinates on it, and deciding what 2

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Calluna vulgaris | | | | | | | | | | | | | | |
| ++ | Ericatetralix | | | | | | | | | | | | | |
| | | Eriophorum angustifolium | | | | | | | | | | | | |
| +++ | +++ | ++ | Molinia caerulia | | | | | | | | | | | |
| ++ | +++ | | | Drosera rotundifolia | | | | | | | | | | |
| ++ | +++ | ++ | ++ | +++ | Narthecium ossifragaum | | | | | | | | | |
| | +++ | | ++ | ++ | +++ | Rhynchospora alba | | | | | | | | |
| + | | | | | | | Trichophorum caespitosum | | | | | | | |
| +++ | | | + | +++ | +++ | +++ | | Cladonia unciales | | | | | | |
| +++ | | | ++ | | | | | +++ | Cladonia impexa | | | | | |
| +++ | | | | | + | | | +++ | + | Hypnum cupressiforme | | | | |
| | -- | | ++ | - | | - | | | | | Rhacomitrium lanuginosum | | | |
| +++ | +++ | | | +++ | +++ | +++ | | ++ | +++ | ++ | | Sphagnum rubellum | | |
| ++ | +++ | | + | +++ | +++ | +++ | | ++ | +++ | | | +++ | Sphagnum tenellum | |
| | ++ | | | | | +++ | | | | | | ++ | | Gleacystis |

Significances as for table 3

Species constellation diagram derived from this data shown in fig. 10

Table 5 Chi-square matrix from 20cm quadrat data

| | on-transect | | | | | | | | | | | off-transect | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | L | $K_2$ | $K_1$ | A | B | C | D | E | F | M | P | J | G | H | $N_1$ | $N_2$ |
| Continuum index, $c_v$ | 100 | 100 | 238 | 270 | 272 | 284 | 381 | 361 | 373 | 364 | 312 | 187 | 330 | 321 | 283 | 286 |

These data shown graphically in fig.11

Table 6 Curtis and McIntosh continuum indices based on vascular plants

| Site | L | $K_2$ | $K_1$ | A | B | C | D | E | F | M | P | J | G | H | $N_1$ | $N_2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Continuum index, $c_n$ | 100 | 156 | 273 | 174 | 246 | 344 | 308 | 426 | 533 | 457 | 386 | 313 | 526 | 378 | 207 | 248 |

These data shown graphically in fig. 12

Table 7 Continuum indices based on non-vascular plants

N.B. The order of the transect sites given in tables 6,7 (L J) is the order in which they occur along the transect. Much of the data is presented graphically against this direct ordination. Thus figs. 11,12 show the indirect ordinations (based on continuum indices) plotted against the direct one.

environmental gradients would be most appropriate to correspond with the axes. Thus one might be average water table level, and the other increasing differentiation between hummock and hollow (fig. 9). In this way, the species groupings and therefore by extension, the sampling sites, will have been ordinated.

However, the terms that were used to describe the habitat preferences of the species groups were vague, and relied on subjective observations of the habitats, rather than the precise measurements that were actually made. The latter can be more effectively used by the Continuum approach of Curtis and McIntosh (14, 15), which will give a more objective ordination of species and plots, which can be used to test which environmental variables are the important ones.

The correlations obtained that are used to construct the species constellation diagrams depend on the area of vegetation for which the presence or absence of species is checked. To see if further plant communities or relationships between species could be discovered, just within the hummock-hollow complexes, some data kindly provided by Dr. D.K. Daniels of the I.T.E. were analyzed, in the same way as the data above. This data (table 4) was for presence or absence of species in 20 cm. quadrats instead of 1 metre lengths. Because the communities of the hummocks and hollows are so different, the data was subdivided between the two. The correlations obtained are tabulated in Table 5, and are used to construct the species constellation diagram (fig. 10).

The main findings are that Rhacomitrium lanuginosum is strongly negatively correlated with many species (which is not surprising, from the observations that it forms large cushions on top of the hummocks), which is perhaps the basis of the large number of highly positive correlations between many of the remaining species. Hypnum cupressiforme is found to be highly correlated with Calluna and Cladonia, which accords well with subjective observations, but which does not emerge in the species groupings in fig. 9.

In those quadrats which fell over the boundary between hummocks and hollows, an association of Molinia caerulia, Eriophorum angustifolium and Narthecium

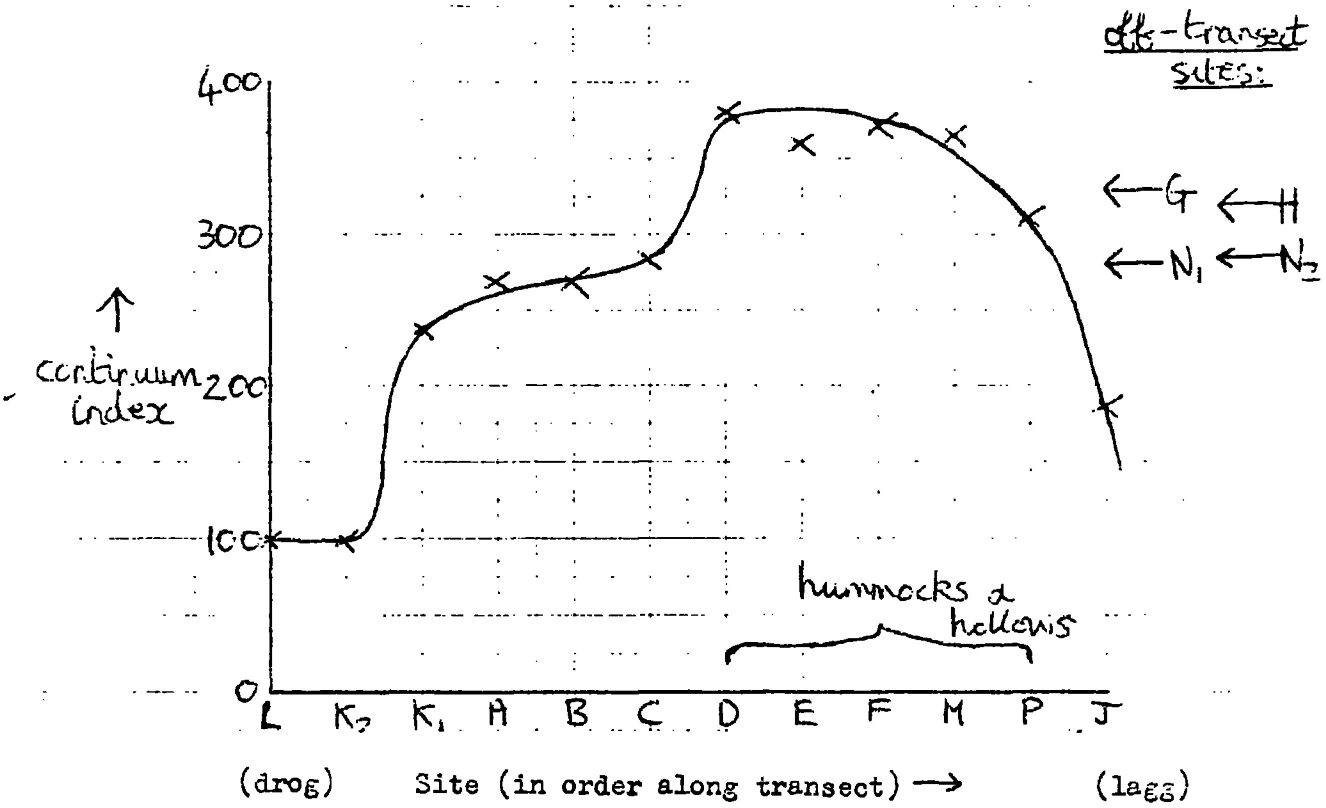


Fig. 11 Plot of continuum indices based on vascular plants

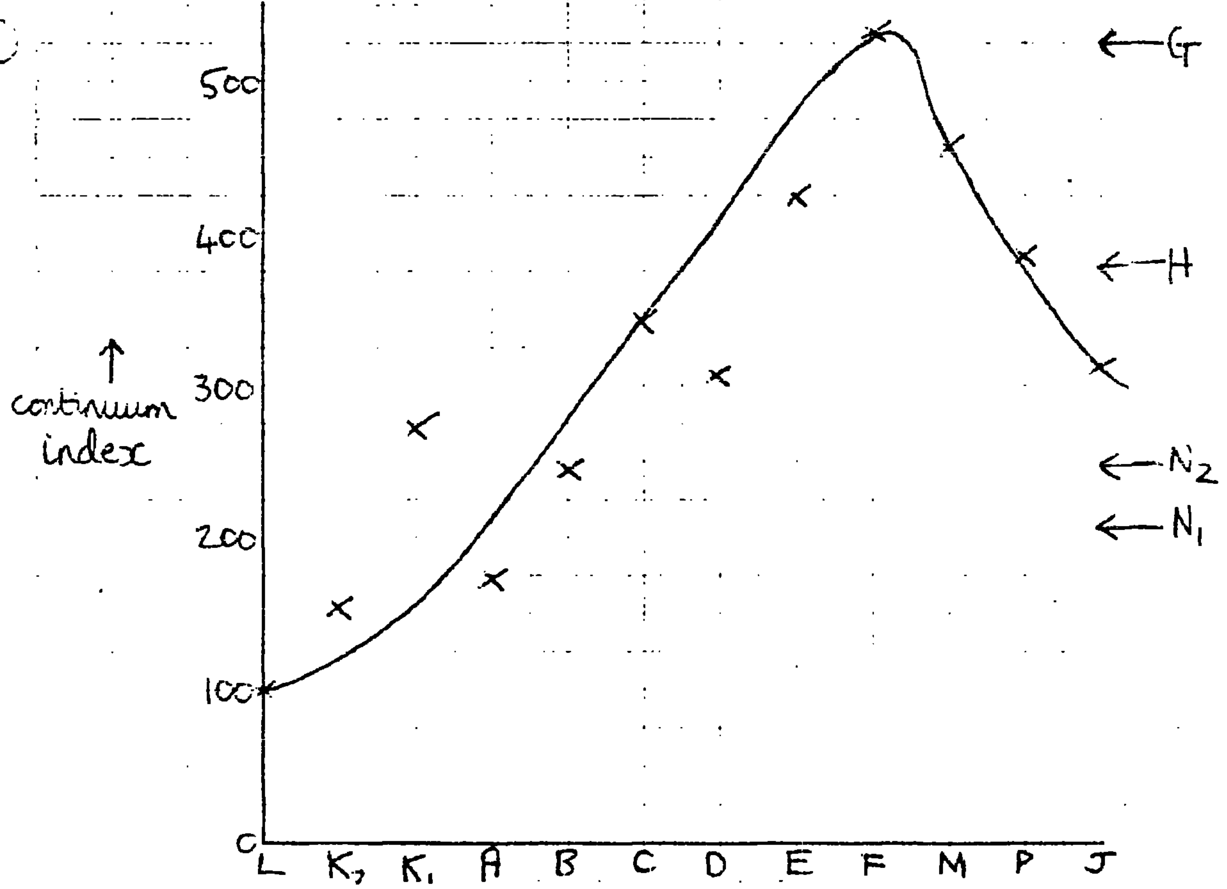


Fig. 12 Plot of continuum indices based on non-vascular plants

ossifraga was elucidated, indicating that this latter association may be typical of the edges of the hummocks (of the three, only E. angustifolium would be likely to grow in open water).

Sphagnum rubellum, Sphagnum cuspidatum and Erica tetralix all emerge from this latter analysis as being associated with the other species of the hummock-hollow complexes, though they did not in the first analysis based on the table 1 data. However, in neither analysis did Eriophorum vaginatum appear to be part of hummock-hollow complex associations.

## The Curtis and McIntosh Ordinations

These ordinations are based on the data shown in table 2. Data for the vascular plants minus Drosera spp. have been separated from non-vascular plants plus Drosera spp., since these two represent two different strata of the vegetation (see 'Methods'), and the two strata are likely to be responding to different environmental gradients. Thus non-vascular plants are likely to be more sensitive to humidity than vascular ones, as they lack the adaptations to water stress of the latter; Drosera spp. are included with these latter because they seem to belong more to this stratum of the vegetation.

These two groups of plants are treated separately.

For each site, total community performance is total number of strikes for all species; the importance value of each species is then taken as:

$$\frac{\text{Number of strikes of that species} \times 100}{\text{Community performance}}$$

The leading dominants and climax adaptation numbers are then assigned according to the method of Brown and Curtis, but only using the transect sites, L to J (table 6). Using the climax adaptation numbers so obtained, the continuum indices for all the sites are now calculated, including sites G, H and N (table 6), for vascular plants, by the method of Brown and Curtis (16).

Continuum indices are plotted against distances along the transect line in fig.11.; the results accord well with the subjective impression gained of the sites; L and $K_2$ were similar - dense Molinia tussocks by the side of the drog. A, B and C were similar lawn communities on the mire plane.

D,E,F and M were characterized by hummock-hollow complexes; P was intermediate between these, and the Molinia lagg,J.

It is notable that sites $N_1$ and $N_2$, the former on the fen window, and the latter just off it, have similar continuum indices to the lawn sites at A,B and C.

These observations are discussed in more detail when the relationship to environmental parameters is explored.

Table 7 shows the ordination for the non-vascular plants; the liverworts are not included, because it was felt that the figures for the number of strikes for the liverworts probably vastly overestimate the importance of these species, as defined by Brown and Curtis (16); the cover given by the point quadrat method (4) for liverworts, which should be the method used to give relative dominance (which is a factor in the importance value of Brown and Curtis), would be much lower than that estimated by the method used here (see above). In fact the relative dominance of the liverworts is probably very low, so they can be excluded from the ordination.

Continuum indices are plotted against distances along the transect line in fig.12. The result is different from that for fig.11, indicating that the non-vascular plants are responding to different environmental gradients than the vascular ones (which was to be expected). Further, the relative positions of the sites off the transect (G,H and N) are different, indicating that the environmental factors that operate here have different effects on the vascular and non-vascular plant communities (see 'Discussion').

The value of this method is that it enables comparisons to be made directly with environmental parameters. Before these comparisons are made, the results of the measurements on environmental parameters are reported.

## Peat density and water content

Peat density varied around a mean of 0.834 g cm-3. There was no obvious trend in the values along the transect line of sites, though the value for the sample from site L (Next to the drog) was easily the highest at 1.249 - presumably due to the high mineral content of this sample - it was noticeably sandy. Samples from pools or furrows were more dense (mean 0.908) than those from hummocks or ridges (mean 0.799), $P<0.05$. This could be due to the higher water content of the former.

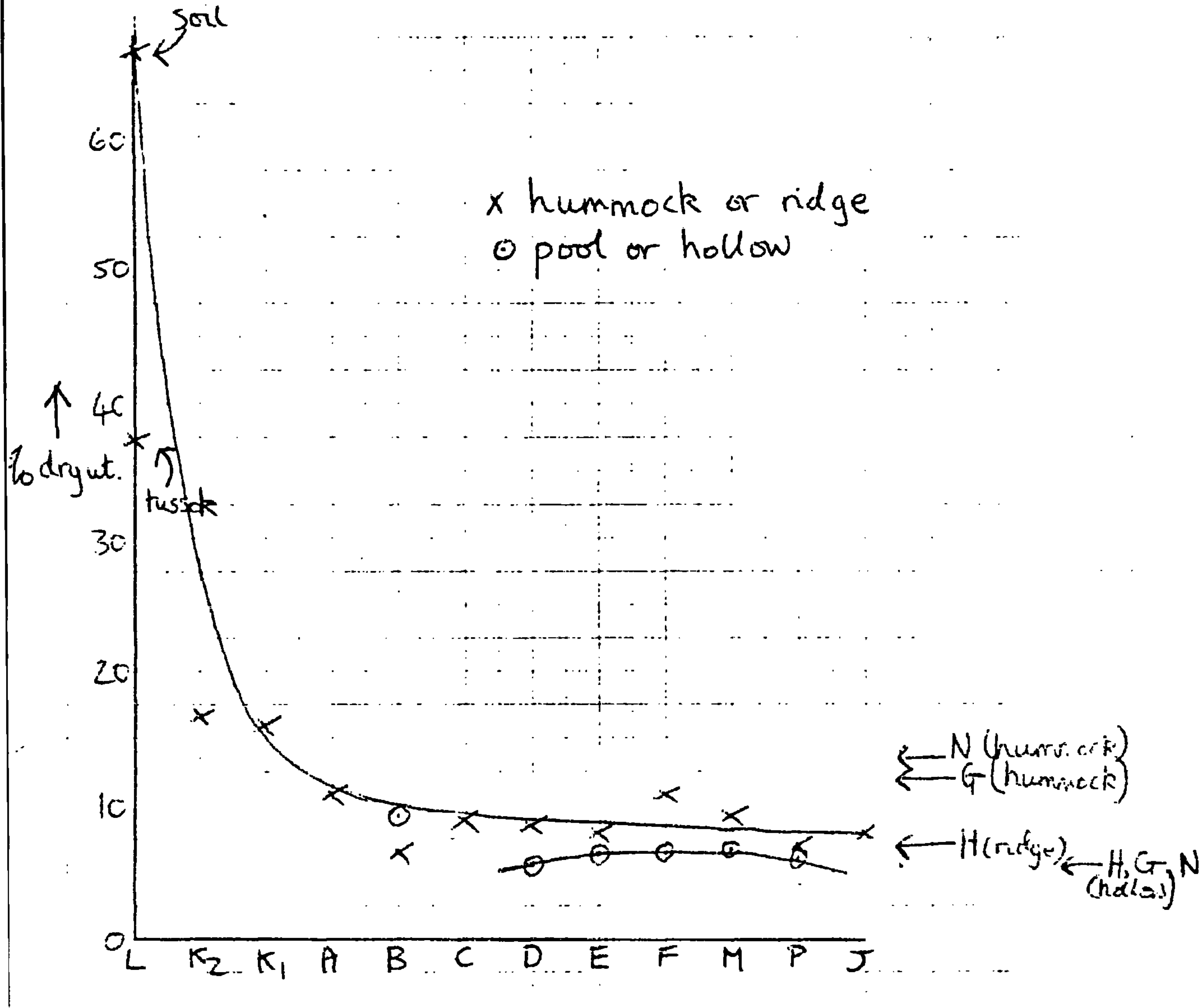


Fig. 13 Graph of % dry wt. content of peat against site

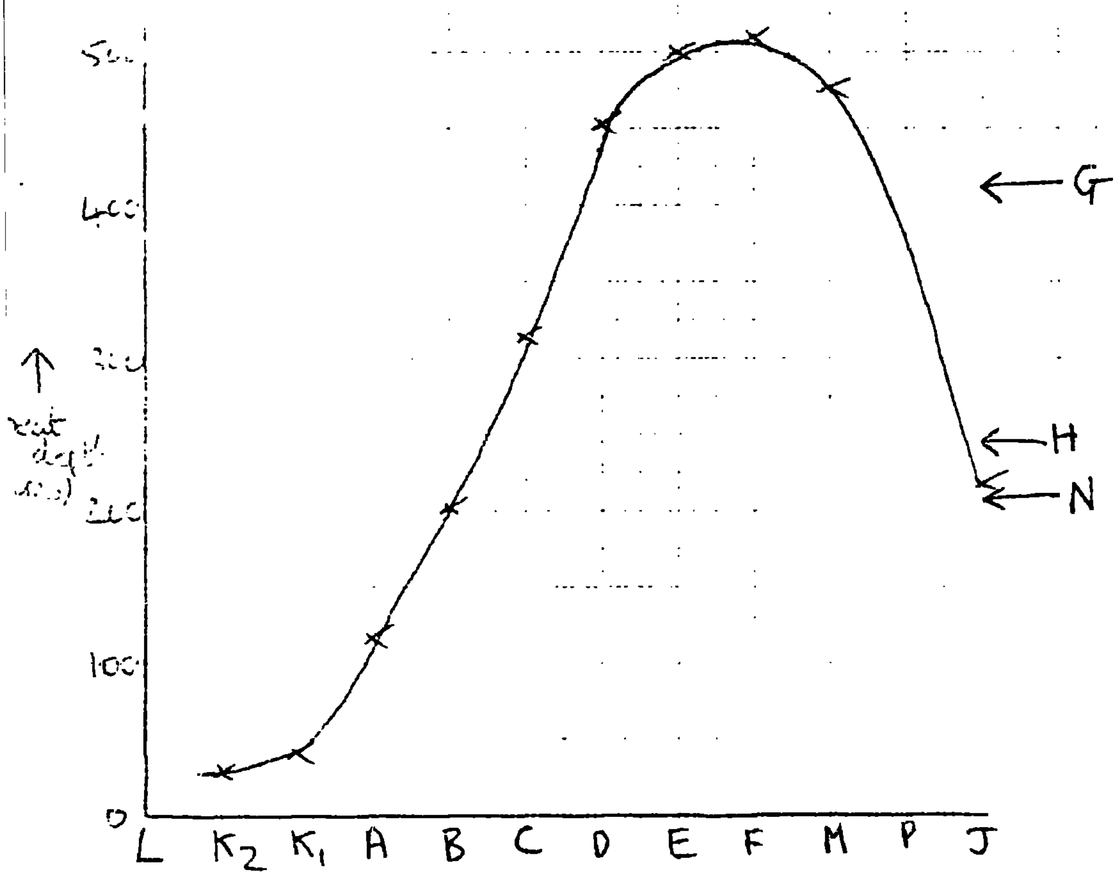


Fig. 14 Graph of peat depth against site

Samples taken 7/5/77 -after heavy rain

| Mean levels for sites A B C D E | pH | Conduct. µmhos | $Na^+$ meq $l^{-1}$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $Cl^-$ | $SO_4^{2-}$ | $HCO_3^-$ |
|---|---|---|---|---|---|---|---|---|---|
| Superficial water | 4·15 | 69 | ·207 | ·010 | ·028 | ·078 | ·217 | ·106 | - |
| Water sqeezed from peat | 4·30 | 74 | ·322 | ·082 | ·048 | ·094 | ·307 | ·244 | - |

| Ratio of equivalent concentrations | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $H^+$ | $Cl^-$ | $SO_4^{2-}$ | $HCO_3^-$ |
|---|---|---|---|---|---|---|---|---|
| Superficial water | 1 | ·048 | ·135 | ·377 | ·324 | 1·049 | ·512 | - |
| Sqeezed water | 1 | ·255 | ·149 | ·292 | ·149 | ·938 | ·758 | - |

Samples taken 27/5/77 -after dry period

| | pH | Cond. | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $Cl^-$ | $SO_4^{2-}$ | $HCO_3^-$ |
|---|---|---|---|---|---|---|---|---|---|
| Drog stream | 6·4 | 90·5 | ·405 | ·036 | ·206 | ·148 | not taken | | ·375 |
| Superficial water) | 4·15 | 82·5 | ·321 | ·022 | ·030 | ·096 | ·366 | ·103 | - |
| Squeezed water ) | 4·25 | 125 | ·236 | ·050 | ·038 | ·082 | ·206 | ·200 | |
| mean for sites D,E,F,M J;G,H,N | | | | | | | | | |
| Site M (squeezed) | 4·0 | 148 | ·386 | ·020 | ·030 | ·146 | ·507 | ·075 | - |
| Site G (squeezed) | 4·0 | 205 | ·813 | ·051 | ·130 | ·400 | ·747 | ·647 | |

| Ratios of equivalent concentrations | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $H^+$ | $Cl^-$ | $SO_4^{2-}$ | $HCO_3^-$ |
|---|---|---|---|---|---|---|---|---|
| Drog | 1 | ·089 | ·509 | ·366 | - | not taken | | ·926 |
| Superficial water | 1 | ·069 | ·093 | ·298 | ·227 | 1·140 | ·321 | - |
| Squeezed water | 1 | ·212 | ·161 | ·347 | ·247 | ·873 | ·847 | - |
| site M | 1 | ·052 | ·078 | ·378 | ·259 | 1·313 | ·194 | - |
| site G | 1 | ·063 | ·160 | ·492 | ·123 | ·919 | ·796 | - |

**Table 8** pH, electrical conductivity and mineral content of water samples

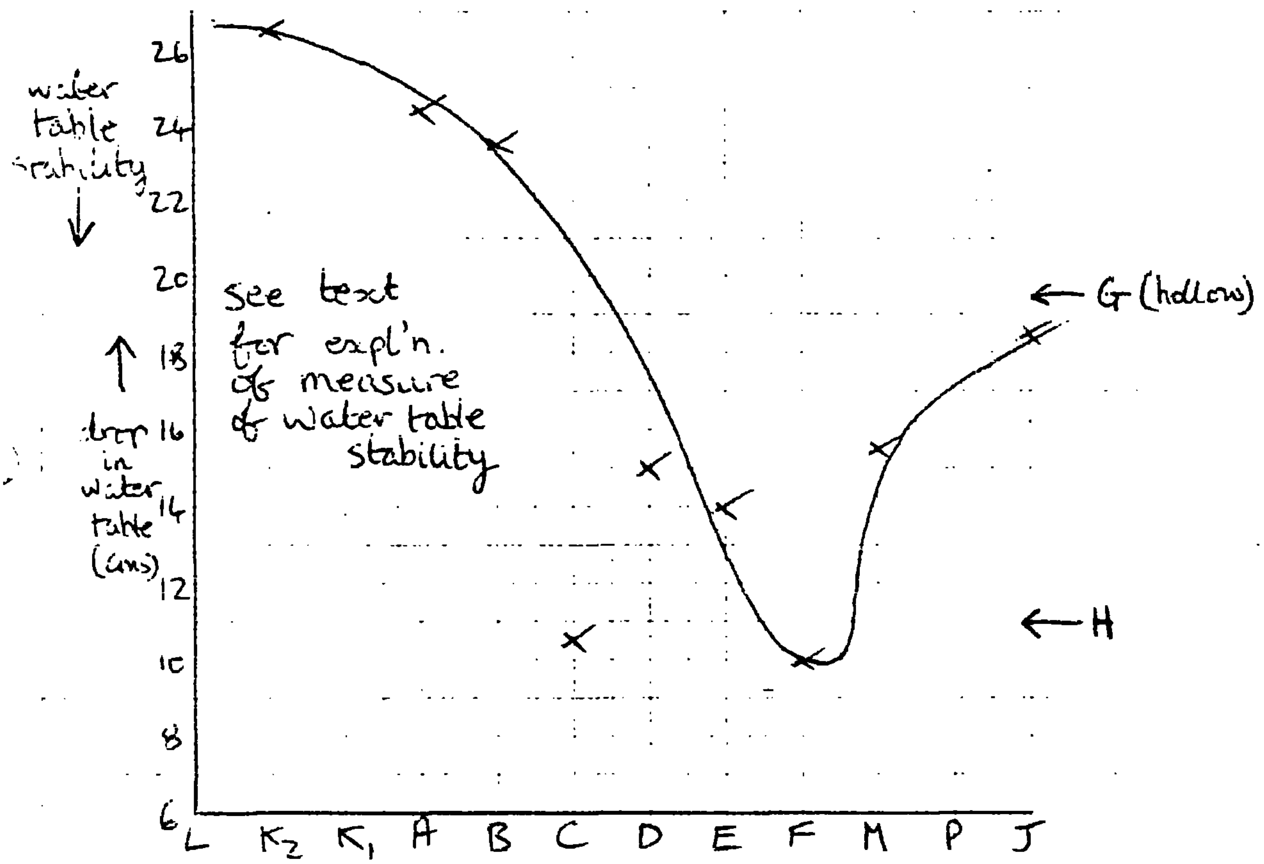


Fig. 15    Graph of ground stability against site

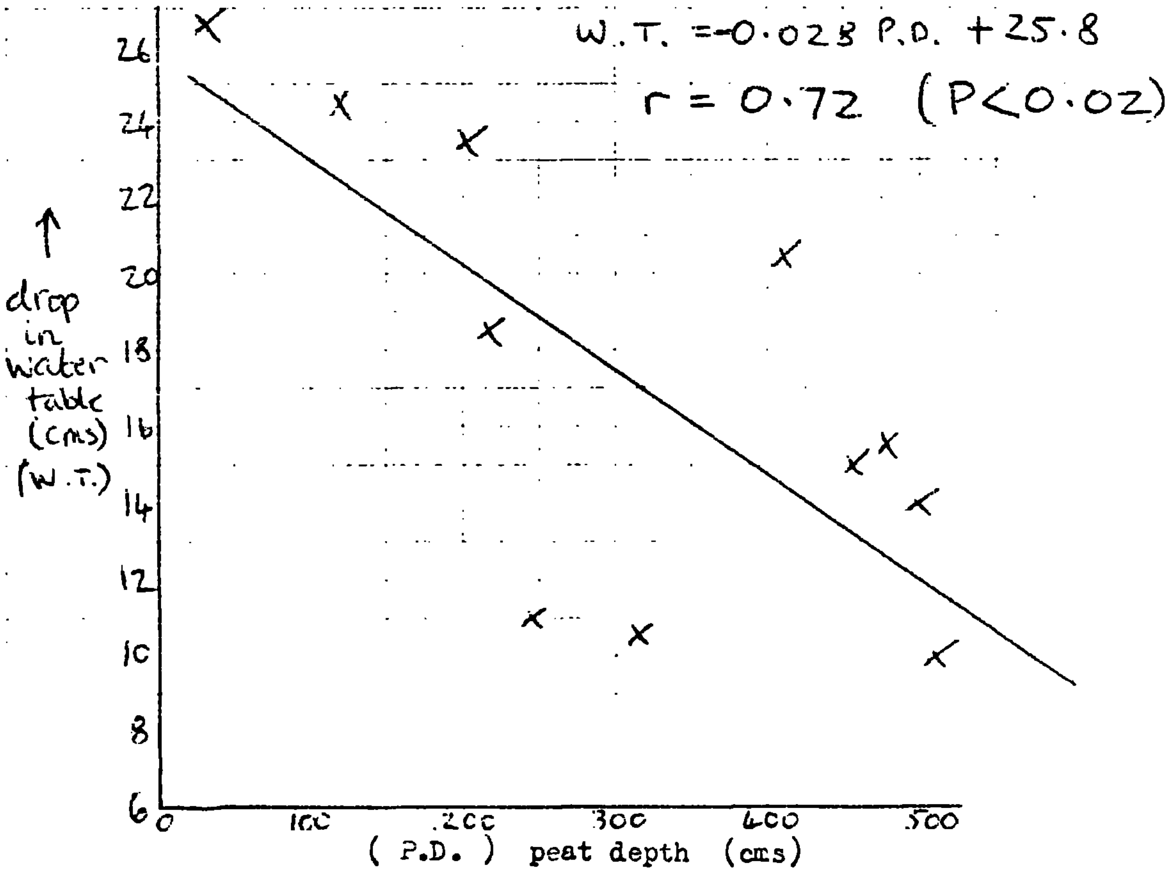


Fig. 16    Correlation between water table stability and peat depth

| Site | L | $K_2$ | $K_1$ | A | B | C | D | E | F | M | P | J | G | H | $N_1$ | $N_2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Peat depth (cms) | soil | 31 | 43 | 118 | 203 | 314 | 456 | 500 | 510 | 478 |  | 217 | 412 | 245 | 207 | 207 |

values are the mean of three readings

results shown graphically in fig.14

Table 9 Peat Depths

| Site | L | $K_2$ | $K_1$ | A | B | C | D | E | F | M | P | J | G | H | $N_1$ | $N_2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Drop in water table (cms) |  | $26\frac{1}{2}$ |  | $24\frac{1}{2}$ | $23\frac{1}{2}$ | $10\frac{1}{2}$ | 15 | 14 | 10 | $15\frac{1}{2}$ |  | $18\frac{1}{2}$ | $20\frac{1}{2}$ | 11 |  |  |

Results for sites B,C,D,E,F obtained directly; other results by extrapolation (see text)

Figures given are for drop in water table between 18/5 and 21/6. They are used as an inverse measure of water table stability (see fig. 15)

Table 10 Fall in water table levels

| Site | B | C | D | E | F | M | J | G | H | N |
|---|---|---|---|---|---|---|---|---|---|---|
| $K(m^2 min^{-1}) X10^4$: | ·095 | ·271–<br>·644 | 2·96 | 1·31 | >100 | ·125–<br>·630 | ·268 | ·261–<br>2·8 | 2·66 | 15·6 |
| Ridges or Hummocks (i)by depletion |  |  |  |  |  |  |  |  |  |  |
| (ii)by repletion |  |  |  |  |  | ·043 | ·027 |  |  |  |
| Hollows- by depletion | ·289 |  | 7·45 |  |  | 54·5 |  | ·300 | 30·8 |  |

Note the wide limits given on three of the values (see figs. 17,18)

In three cases out of four, the results for the hollows (which may be dried out pools) are much bigger than for hummocks at the same site, suggesting the peat to be less humified in the pools(see text). However little reliance is placed on these results for the hollows, and they are not commented on further.

Table 11 Hydraulic conductivities (K) as measured by the auger hole method

There was less variation in the % dry weight of the samples; values for samples from $K_1$,$K_2$ and L were higher than the rest; in the last case considerably so; the results are represented graphically in fig.13. Where samples were taken from both hummocks and hollows, the mean dry weight content of the former (8.60%) was higher than for the latter (6.90%) - $P<0.05$ - this is not a trivial point; when the measurements were taken pools had dried up at the surface at least, at all the sites except F.

## Water Chemistry

Here again, although some interesting results were obtained, there was no significant trend that would be revealed by plotting continuum indices for the sites against any of the chemical parameters. Apart from the water of the drog stream itself, there was little variation in the values; mean figures are given in table 8. However, ionic concentrations for samples from sites M and G were elevated, particularly in the squeezed water samples. The significance of this will be referred to below.

## Peat Depth

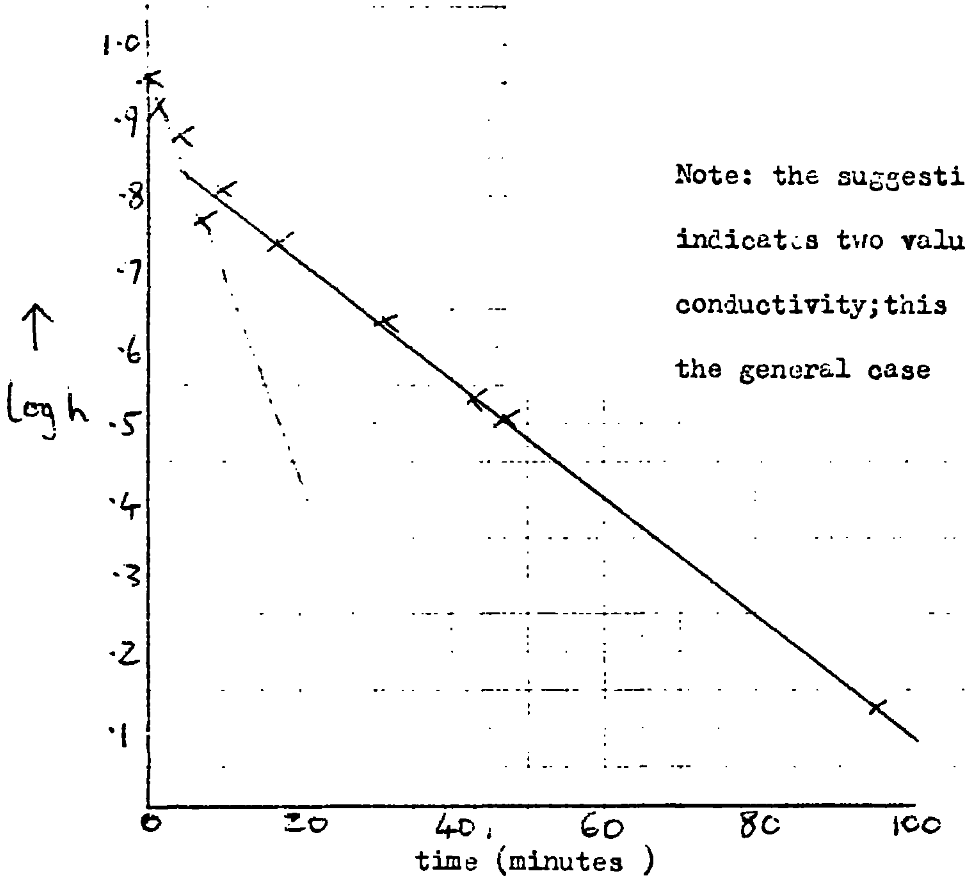
A significant trend of these values was evident (table 9 and fig.14). In the case of station L, a depth of 199 cms was recorded, but since this was of soil rather than peat (the profile could be seen as a bank of the drog stream), this value was disregarded.

## Water Table Movement

The period 18th May - 21st June, when water table measurements were made, was one of little rain, and the water tables fell consistently during this period. For some of the sites, where measurements were not taken from the beginning, it was necessary to extrapolate to estimate the fall in the water table between these dates.

This fall in the water table, from the 18th May - 21st June, at each site, is taken as a measure of the stability of the water table at that site. The values, either measured or estimated by extrapolation, are shown in table 10 and fig.15.

There is significant correlation between peat depth and water table stability (fig.16); $r = 0.72$ ($P<0.02$).



Note: the suggestion of two gradients indicates two values for hydraulic conductivity; this is an example of the general case

Fig. 17 Graph of log h against time for site C to determine hydraulic conductivity (see text for expl'n.)

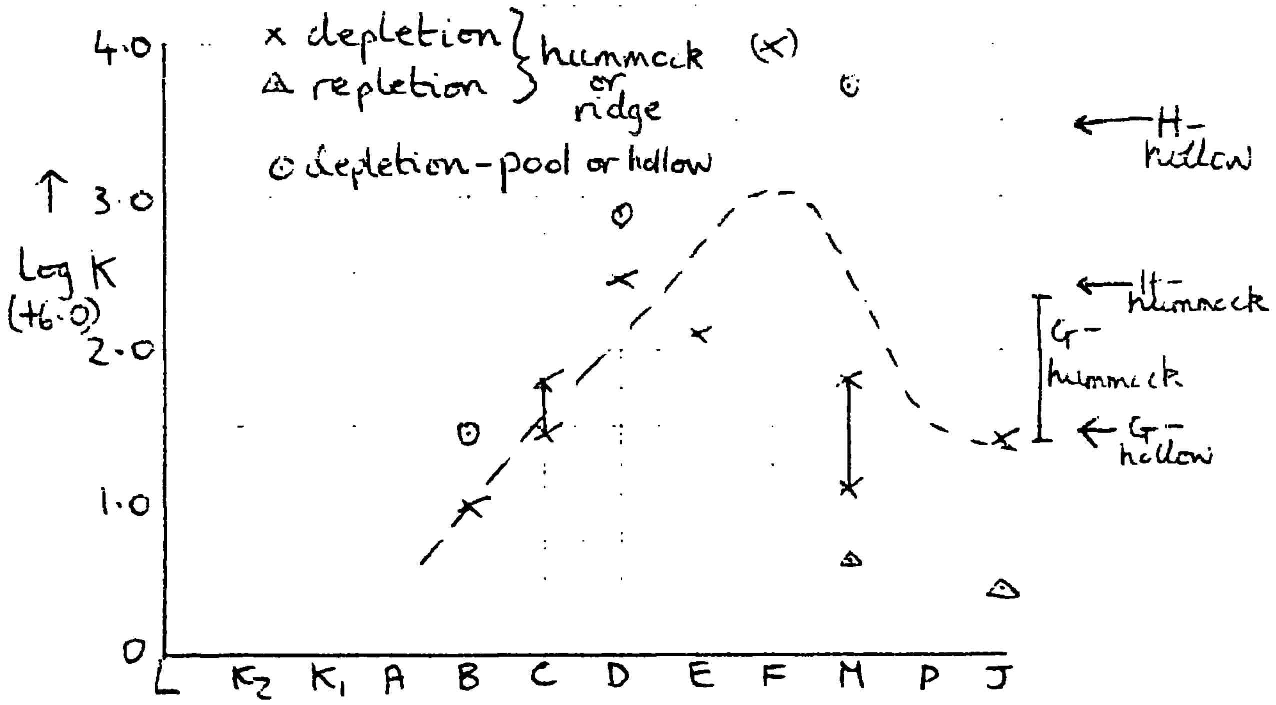


Fig. 18 Graph of hydraulic conductivity against site

## Hydraulic Conductivity

As was explained in the introduction, various theoretical and practical factors militate against a straight line being produced in the graph of log (distance of water level from equilibrium) against time. However, in some of the plots that were made, it seemed that two district gradients were produced (see fig.17 for an example). This might indicate a change in the quality of the peat with depth. Normally, one would expect the surface layers of peat to be less humified than the deeper ones. As mentioned in the introduction, this might mean the surface layers would have a higher conductivity than the deeper ones. The converse of this situation seems to be indicated by some of the results - partly by discontinuities in the graphs; partly by the lower conductivities given by the water addition experiments as opposed to the water depletion ones - indicating the surface layers to be more humified (see table 11). The explanation for this might be that in rising through a hummock, humification increases. The implications of this idea are discussed below.

No significant correlation between either peat depth, or water table stability with hydraulic conductivity was found; however, not all the sites were covered for the latter measurement, which in any case gave rather inconsistent results. More complete data may have shown such correlations; there is an indication that hydraulic conductivity may increase with peat depth and water table stability.

A graph of hydraulic conductivity along the transect line is shown in fig.18.

## Comparison of environmental parameters with continuum indices

Of the two remaining environmental parameters that can be compared with the two sets of continuum indices, peat depth and water table stability, it would be unlikely that there could be a direct effect of peat depth on the species composition. It would probably be through some other effect such as water table stability (with which peat depth is correlated ) , or through some factor that has not been studied, such as ground water flow. Unfortunately, there is insufficient data to use multi-variate analysis to determine if there is a significant effect of peat depth, not explicable in terms of water table stability.

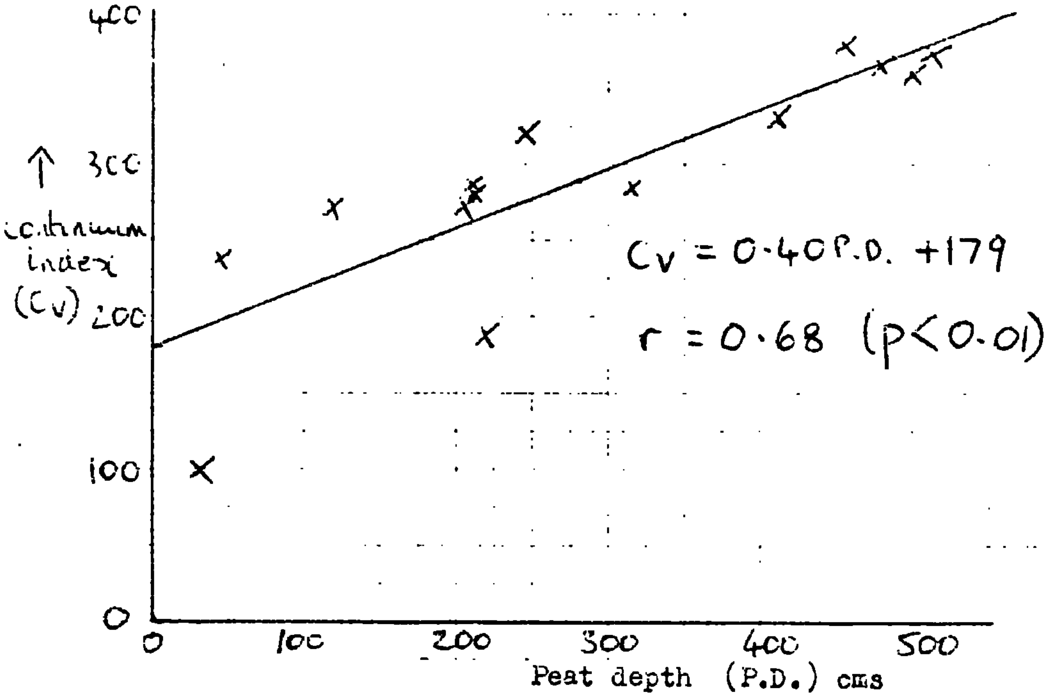


Fig. 19 Correlation between continuum index (vascular plants) and peat depth

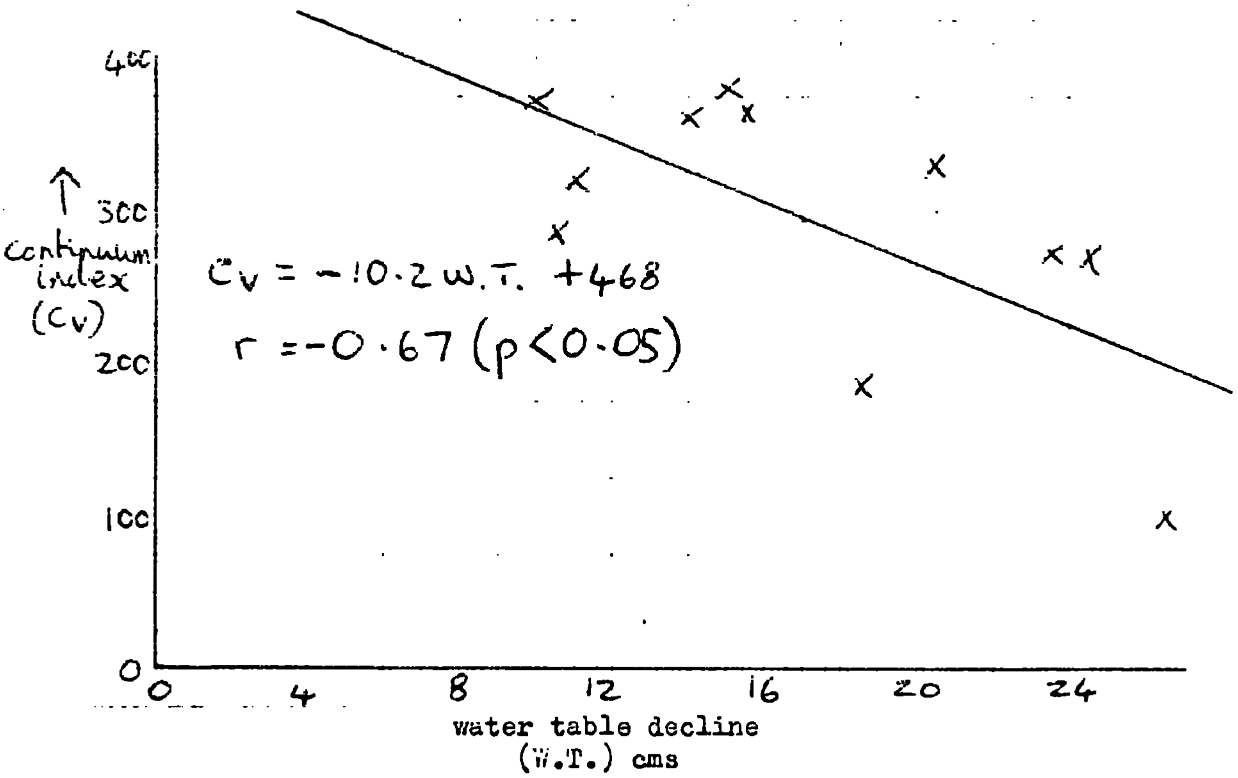


Fig. 20 Correlation between continuum index and water table stability

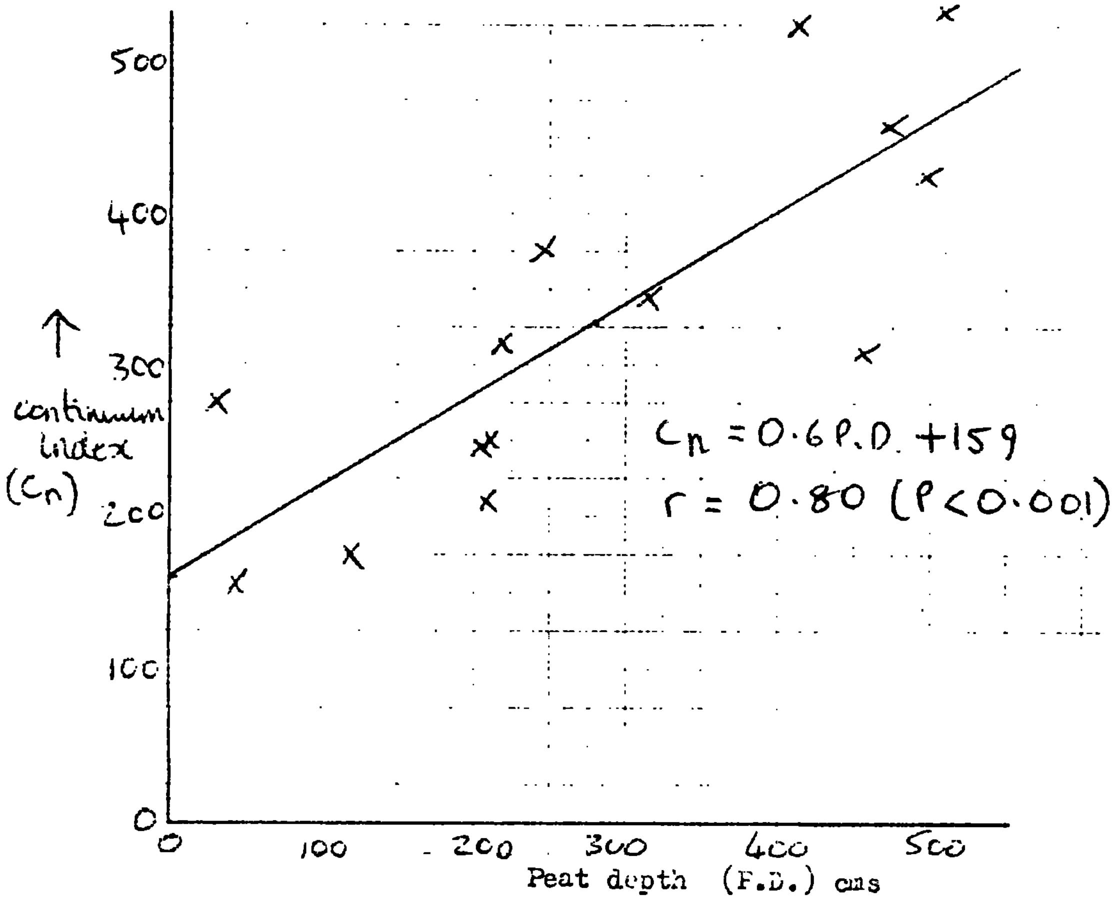


Fig. 21 Correlation between continuum index (non-vascular) and peat depth

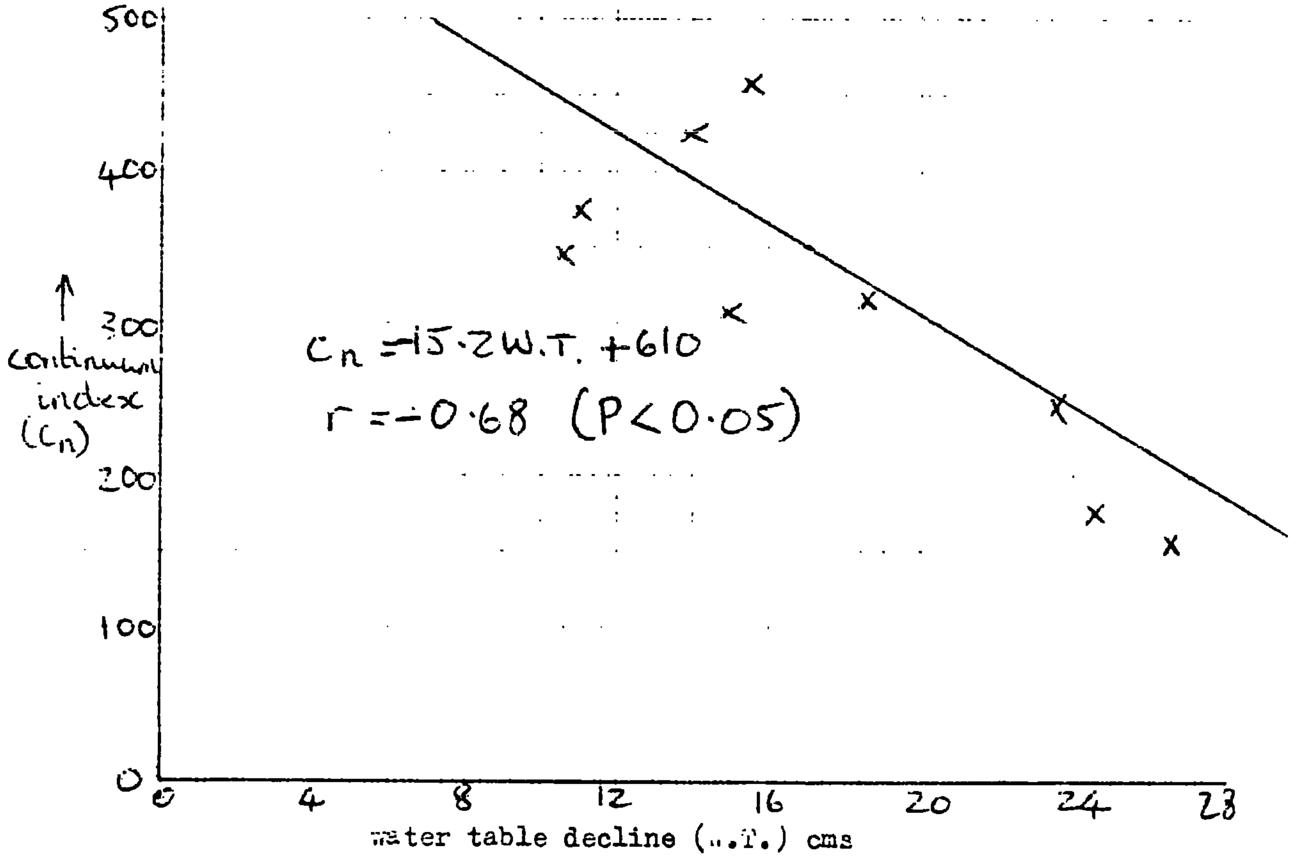


Fig. 22 Correlation between continuum index (non-vascular) and water table

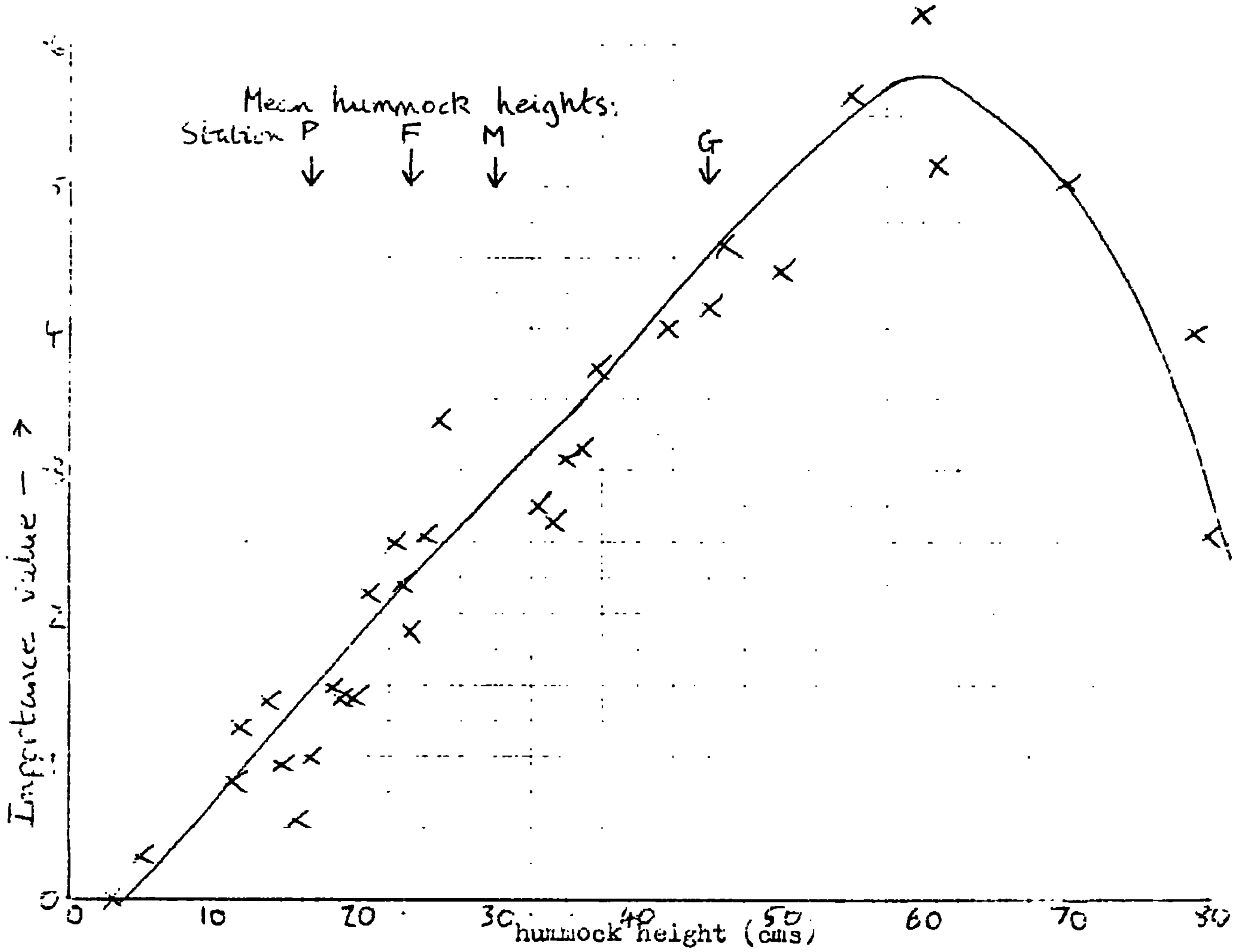


Fig. 23 Importance value of Calluna vulgaris in relation to hummock height

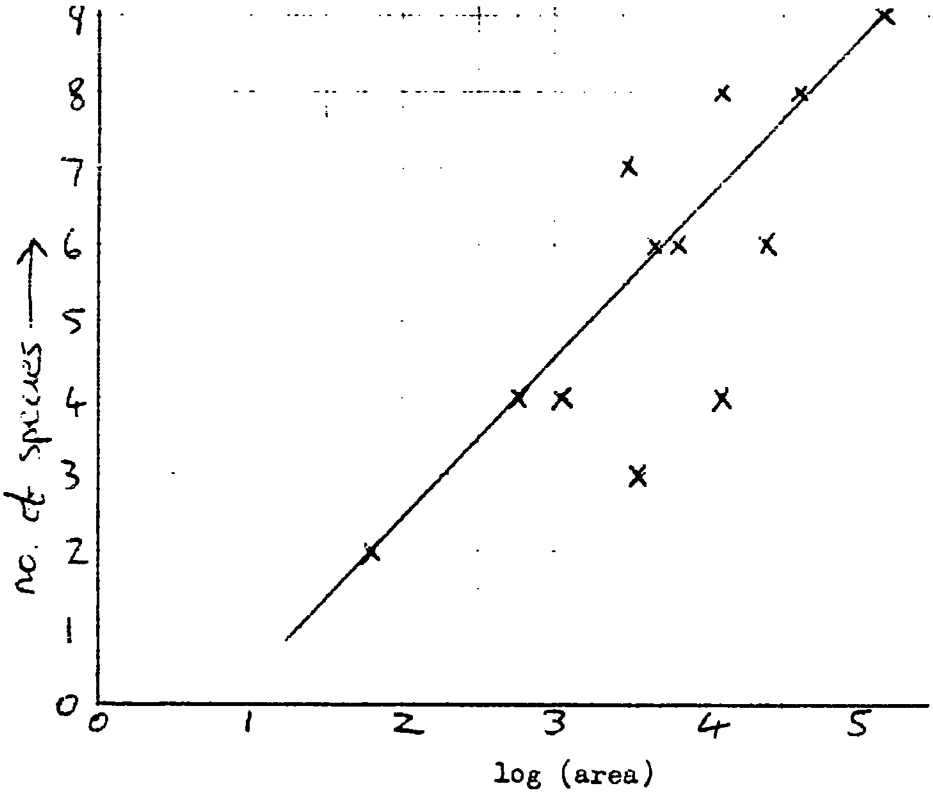


Fig. 25 Graph showing species richness against log (area) of hummock at site F

|  | Peat depth (cms), d | Water fluctuation (cms), w |
|---|---|---|
| Continuum index, vascular plants, $c_v$ | $c_v = 0\cdot40d+179$<br>$r = 0\cdot68$ $(P<0\cdot01)$ | $c_v = -10\cdot2w + 468$<br>$r = -0\cdot67$ $(P<0\cdot05)$ |
| Continuum index, non-vascular plants, $c_n$ | $c_n = 0\cdot60d+159$<br>$r = 0\cdot80$ $(P<0\cdot001)$ | $c_n = -15\cdot2w + 610$<br>$r = -0\cdot68$ $(P<0\cdot05)$ |

There is a correlation between water table fluctuation and peat depth:

$$w = -0\cdot028d + 25\cdot8$$
$$r = 0\cdot72 \quad (P<0\cdot02)$$

These correlations are shown in figs.16 and 19–22

Table 12 Summary of correlations between environmental factors and continuum indices

| Site<br>Species | P<br>peak import. | <br>height | F<br>peak import | <br>height | M<br>peak import | <br>height | G<br>peak import | <br>height |
|---|---|---|---|---|---|---|---|---|
| Rhynchospora alba | ·40 | 14 |  |  |  |  |  |  |
| Narthecium ossifragum | ·825 | 16 |  |  |  |  |  |  |
| Trichophorum caespitosum |  |  | ·37 | 19½ |  |  |  |  |
| Eriophorum angustifolium |  |  | ·60 | 21 |  |  |  |  |
| Molinia caerulea |  |  |  |  | ·50 | 45 |  |  |
| Calluna vulgaris |  |  |  |  |  |  | ·58 | 60 |
| Sphagnum magellanicum | ·73 | 14 |  |  |  |  |  |  |
| Pleurozia purpurea | ·67 | 18½ |  |  |  |  |  |  |
| Sphagnum papillosum |  |  | ·64 | 18 |  |  |  |  |
| Sphagnum rubellum |  |  | ·625 | 21 |  |  |  |  |
| Sphagnum plumullosum |  |  | ·475 | 21½ |  |  |  |  |
| Rhacomitrium lanuginosum |  |  | ·95 | 42 |  |  |  |  |
| Cladonia impexa |  |  |  |  | ·445 | 34 |  |  |
| Hypnum cupressiforme |  |  |  |  |  |  | ·22 | 60 |
| Campylopus flexuosus |  |  |  |  |  |  | ·22 | 43 |

The table shows at which site each species has maximum importance, and at what height. See text for explanation and fig. 24 for graph of results.

Table 13 Sequence of dominant species of hummocks

The correlations that were obtained are shown table 12 and fig. 19-22. Thus there is no evidence for hydraulic conductivity as a determinant of the plant communities.

Island Study

For each group of 12 hummocks, the procedure was as follows: firstly, data for the vascular and non-vascular (+ Drosera spp.) species were separated, so the two strata were dealt with separately. Next, for each stratum, the total cover for all the species on each hummock was added up to give a measure of community performance. Next, the dominant species of each hummock was identified. For each dominant species, the importance value on each hummock was calculated, as: $\frac{\text{cover}}{\text{community performance}}$. It was found that there was a relationship between the importance value of a species, and height of the hummock (fig.23). There is a considerable scatter of points, and the data are smoothed by a standard procedure given by the formula:

$$B = \frac{a + 2b + c}{4}$$

where B is the smoothed value of b, where a and c are the adjacent points (17). From these curves, the height at which a species has its maximum importance value can be read off (table 13). In this table, the four sites are arranged in order of the mean height of the hummocks; P,F,M and G. Site P was an area of shallow pools and low ridges, like H. Site F was an area of the classic hummock and hollow complex; site G was an area of eroded hummocks and hollows (see 'Methods'), and site M was intermediate between F and G.

Let us first consider the vascular plants of table 13. Certain trends in the plant cover can be identified across the series P→G. The word performance here is used in the sense of cover.

Rhynchospora alba is only dominant at site P, though it is present at the other sites.

Narthecium increases in importance between P and M, and is then absent in G. Its peak performance occurs at heights well below the mean hummock heights; this accords with its position in the species constellation diagram (fig.10) between

Note: The floristic data used in the construction of this figure were based on the estimation of species cover of hummocks as described in the introduction; and the hummock shapes from general observations made while this data was collected.

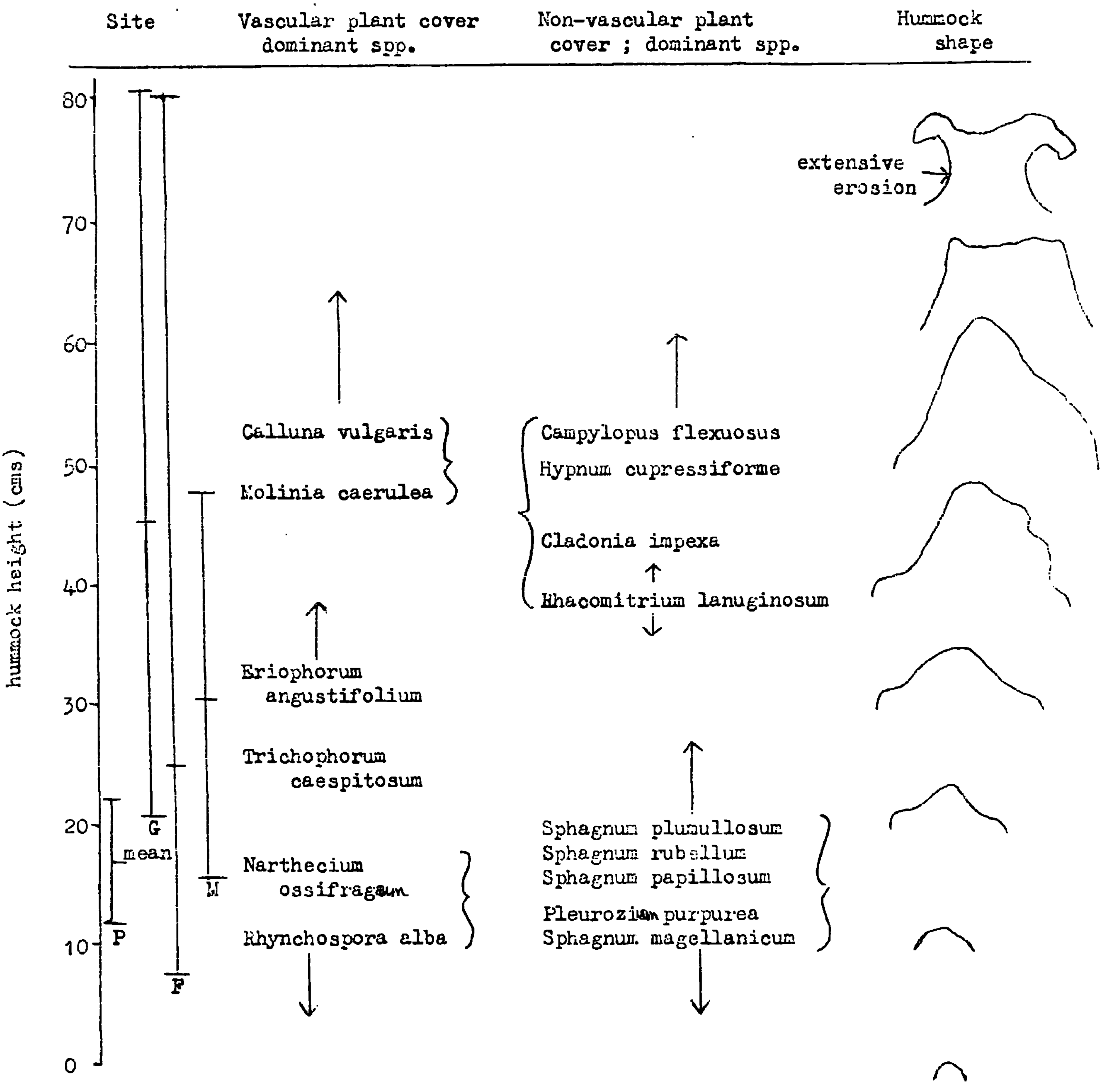


Fig. 24 Species cover of hummocks of increasing height

the hummock and pool species.

*Tricophorum* also has its peak performance at site M; at sites M and G, it is more dominant on the lower hummocks.

*E.angustifolium* peaks at site F; its preferred height increases with the mean height of hummocks from P→G.

*Calluna* and *Molinia* both have their peak performances at site G. Particularly at sites F and M, *Calluna* tends to dominate the higher hummocks. At site G, the lower hummocks may have a high cover of bare peat; this may often be associated with a high *Molinia* cover.

We now come to the non-vascular plants.

Firstly, there is a group of species which overlap with Group 4 of the species, constellation diagram (fig.10). These are: *Sphagnum papillosum*, *S.magellanicum*, *S.plumullosum*, *S. rubellum* and *Pleurozia purpurea*; these all peak at sites P or F; at site P, they all have peak performance at about the average height of the hummocks; at sites F and M, they peak at heights well below the average heights - they are associated more with the lower hummocks.

*Rhacomitrium lanuginosum* peaks at sites F and M, and tends to dominate the higher hummocks. Likewise at site G, where the cover falls somewhat. At site G, a lot of the *Rhacomitrium* was very dried out, and some of it partly decomposed; in the latter case, the hummocks were sometimes very eroded (and much lower), and had a high cover of *Molinia* and *Campylopus flexuosus*. The *Hypnum cupressiforme* of site G was mainly associated with the high *Calluna* cover.

These results all suggest a pattern for the species cover of hummocks of increasing size (fig.24). This sequence may or may not be an actual successional development. That depends on the theory of the origin of the surface patterning that one accepts.

Finally, it was found that there was a relationship between the species richness of a hummock, and its area. A graph of no. of species against log (area) gave an approximately straight line relationship (fig.25). Such a relationship is explained in terms of island biology by postulating an equilibrium between immigration and extinction of species depending on island size, and proximity of sources of colonizing species (18) . This implies that at some stage after hummock formation, immigration or extinction of species is an active process.

Alternatively, the size-dependence on species richness of the hummock could be a manifestation of the minimal area required for the hummock communities. There is little information on what factors might determine such minimal areas. Indeed, one of them might be the area-dependent survival of various species i.e. an 'island' effect on species extinction rate.

## Discussion and Conclusions

### Species constellation diagrams (figs.9,10)

Fig. 9 was based on association analysis of different communities on the mire : the hummock and hollow complexes, the lagg, the lawn communities, and those round the drog stream; fig.10 was based only on the hummock and hollow complex. Nevertheless, it is striking how different the two diagrams are. In fig. 9, the hummock species, Rhacomitrium and Calluna, Eriophorum etc. emerge as associated species, whereas in fig.10 Rhacomitrium emerges as negatively associated with some of the other hummock species. This suggests a hierarchical structure of the plant communities, with species relationships occurring at different levels, detectable at different block sizes (i.e. quadrant size used in sampling).

The problem is that species that appear to be associated at one block size (and are therefore assumed to have similar habitat requirements), may not be at another block size, and may in fact have different habitat requirements. This is likewise a problem with the McIntosh and Curtis ordination. Thus a hummock may represent a different environment for a plant at its crown (covered with Rhacomitrium) compared to its margin (with a Sphagnum cover). This may cast doubt on the validity of attempting to measure environmental parameters for the hummock and hollow complex as a whole, and comparing with a species ordination based on sampling sites that span several hummocks and hollows. Any correlations that are discovered only apply to the sum total of the species at a site; it must not be assumed that all the species have the same habitat requirements.

### The Ordinations

The Curtis and McIntosh ordination was used, because although not the simplest (which is the polar ordination), it gives more information on species relationships and habitat preferences.

Comparison of environmental factors with continuum index is only likely to give a good correlation where the environmental factors changing along the transect line which affect species composition do so in similar ways. Where opposing factors are involved, good correlations will not be obtained.

Thus the leading dominants (table 2) which have climax adaptation numbers furthest apart are assumed to be adapted to two opposite environmental extremes along the transect. Those with intermediate climax adaptation numbers are adapted to conditions intermediate between the two extremes. This likewise applies to the sub-dominant species that have their highest importance values at the same sites as one or other of the leading dominants.

Thus the continuum index of a site along a transect line, is the sum of all the products of importance value X climax adaptation for each species present there. It is therefore a measure of the position of the environment there between the two extremes as 'seen' by the plant community at that site. Sites with continuum indices furthest apart have the opposite environmental extremes of the transect. Where conditions are intermediate between the two extremes, the continuum index will have an intermediate value.

Because the derivation of continuum index is rather arbitrary - in that climax adaptation numbers are based only on the relationship between the leading dominants, the relative values in themselves are not of much significance, though they can be used to compare the similarity of sites (see figs. 11,12, where continuum indices are plotted against simple ordinations, based on positions of sites along the transect line) , It is the relationship of continuum index to environmental factors that is of more significance.

For both vascular and non-vascular plants, peat depth and water table stability emerged as the factors most highly correlated with continuum indices. The latter of these two factors will be considered first.

The idea of water table stability affecting plant communities is not new. Sjörs (5) says that species of carpets and mud-bottoms require an even and high water level. In Bergslagen, where concentrically domed mire predominates, these species include Rhynchospora alba and Sphagnum cuspidatum, which also occur in the hollows and pools on Claish Moss, at sites of high water stability. Species of hummocks, on the other hand, are said to be susceptible to inundation. This illustrates the very different habitat requirements of species present at one site.

In fact the water table levels in hummocks probably vary greatly depending on short-term rainfall (fig.6). These fluctuations were not measured, and there would be great difficulty in measuring them, because taking out a core from a hummock to create a well would greatly distort the water table profile, because of the limited supply of capillary water in the hummock.

It was the change in water table level at the hummock margin that was measured, which would reflect the level of the pool, and therefore the conditions to which the species at the hummock margins were subject.

Sjors (5) suggests that the reason forthe stable water level of the pools is that, of the precipitation received by the hummock and hollow complex, most is kept and stored by the framework of hummocks, which therefore act as a sort of buffer. This might therefore explain the high stability of the water level in the pools. Likewise, the existence of pools would prevent the hummocks from becoming inundated (by acting as drainage ditches), so permitting the spatially close coexistence of species with very different habitat requirements.

Stability of the water table is not just important in determining the constancy of the humidity at the peat surface; it also determines the extent to which roots of vascular plants are subjected to horizontal ground water flow; also, instability can convey nutrient ions from one horizon to another, as well as increasing soil aeration, by inspiring and expiring air from the soil voids (19).

Further, Sjörs suggests that water table stability is also connected with ground water flow. Ingram (19) is more specific about this, and suggests that fluctuations in the water table may be of lower amplitude in peats of high conductivity, with larger soil voids. It is implied that a higher hydraulic conductivity is associated with a higher ground water flow. However, the latter also depends on the slope of the ground water table. In a domed mire, the peat near the surface of the dome is usually thought of as being poorly humified, ombrogeneous peat, compared to the mire margins (2). It would therefore be likely, according to Ingram (6), to have a high hydraulic conductivity. But the ground water flow is generally considered to be least at the dome, since this is likely to be furthest from the water tracts. Thus one cannot equate hydraulic conductivity with ground water flow.

In fact the values for hydraulic conductivity did not correlate with water table stability or the floristics, though the data was incomplete, and the values obtained were inconsistent; also, values given by extraction and repletion of water in the auger holes did not agree. In fact Ingram (21) measured hydraulic conductivities at Dun Moss (in the Grampian foothills, Grid ref.: NO 167558) using the seepage tube method, rather than the auger hole, since with the latter method, there was a problem with water draining rapidly from superficial layers of scarcely humified peat. This could be the explanation for the discontinuity in the plots (fig.17), rather than a change in the humification of the peat at greater depths in the hummock. Such a change might be postulated to be due a hummock developing from a hollow or pool bed of well humified peat. Such a hypothesis would be at odds with the stratigraphical evidence however (22). Even the values for K giving by Ingram (21) by the seepage tube are quoted over a wide range (1-2 orders of magnitude); there is also an order of magnitude of difference in values given by depletion and recharge (less than that in the results quoted here). Nevertheless the range of the conductivities given here and by Ingram agree.

It is clear that the theory and method of measurement of hydraulic conductivities will need further development before these can be routinely used to compare with other environmental factors and floristics.

There was a strong correlation between peat depth and continuum indices (table 12, figs. 21,22). It is hard to see how peat depth could affect the plants directly at any of the sites except L and $K_2$, since at all the other sites, it would be too deep for vascular plant roots to reach down to the underlying substratum. One possibility is that peat depth is correlated with ground water flow, as suggested in the model for the development of a domed mire (20). Ingram (19) lists the ways in which water flow can affect plants:

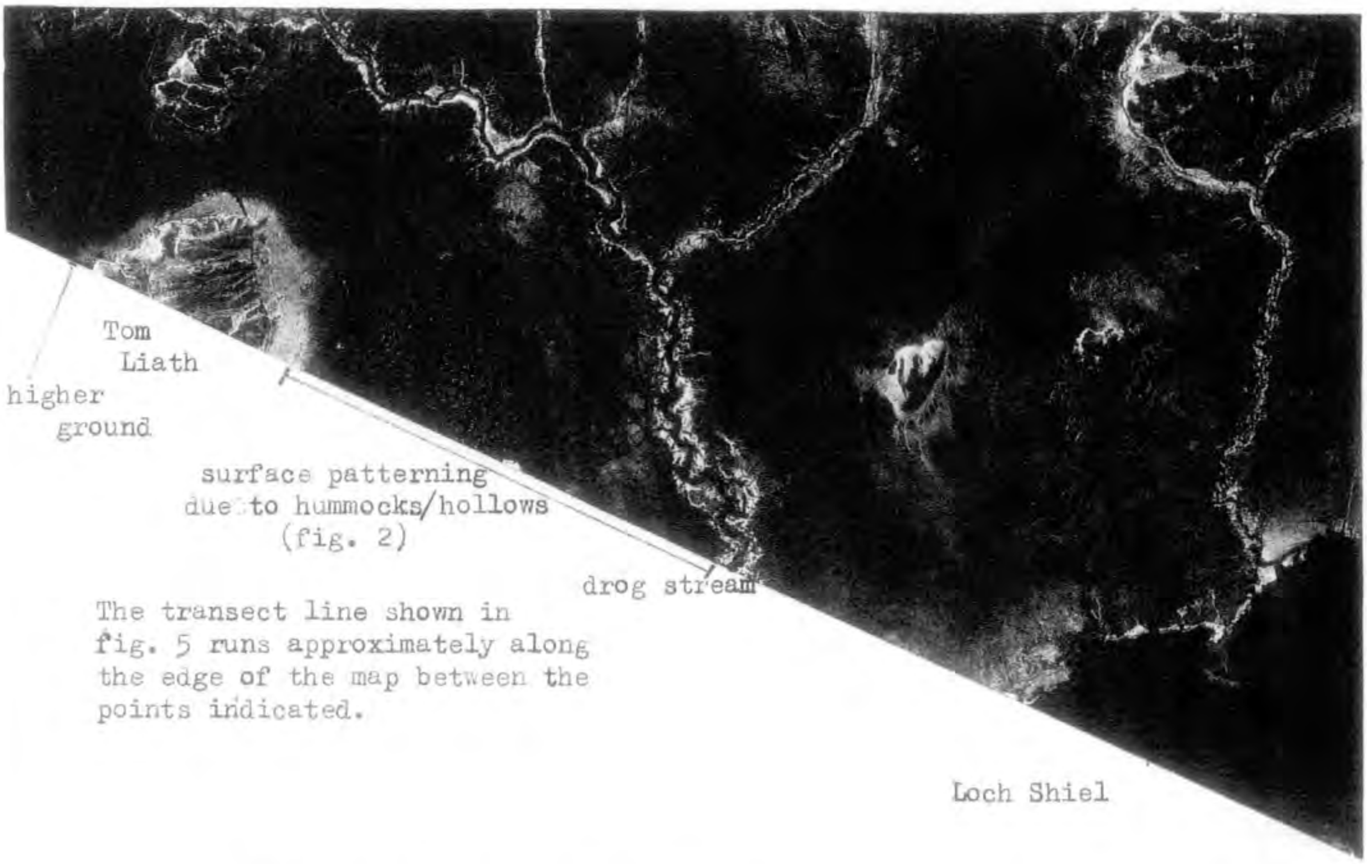
1) effect on soil atmosphere
2) solubility of toxic metal ions
3) high concentration of $CO_2$ and $S^{2-}$ that would accumulate round roots in static water
4) water movements may convey soligenous ions from beyond mire boundary and gather ombrogenous ions from mire expanse (24).
5) water flow might determine the rate of ion uptake by plants.

Obviously it would be desirable to measure ground water flow on Claish Moss, but to do this directly would require a rather sophisticated instrument - the hot wire anenometer (23).

## Chemistry

Water flow can affect uptake of mineral ions by plants, and also local concentrations of these ions by the roots. These effects would be difficult to detect under field conditions. However, water movements also affect overall ion concentrations (see point 4 above), which might have an effect on floristics, since mineral availability is said to be a limiting factor on primary productivity on ombrogenous mire (19). Although in a mature plant community, sufficient mineral salt may have accumulated, and be recycled to sustain that community, low mineral availability in litter would affect seedling establishment and performance of immature vegetation, so governing the species competition of the community.

In fact, in this study, no significant variation in pH or mineral content over the mire was found (table 8). Ionic concentrations at sites M and G were elevated in the squeezed water samples. At both these sites, there were signs of erosion of the hummocks; the increased mineral content could be due to oxidation of the peat following lowering of the water table, and release of complexed mineral ions.



The transect line shown in fig. 5 runs approximately along the edge of the map between the points indicated.

Fig. 1 Aerial view of Claish Moss

Fig 2 Arrangement of hummocks and pools

The ionic composition of the water from the drog stream is similar to that draining granite or mica schist (Gorham, 1961) - it is very poor in $Ca^{2+}$, $Mg^{2+}$ and $K^{+}$. In fact the underlying rock of Claish Moss consists of feldspathic schists, which are likewise poorly mineralized.

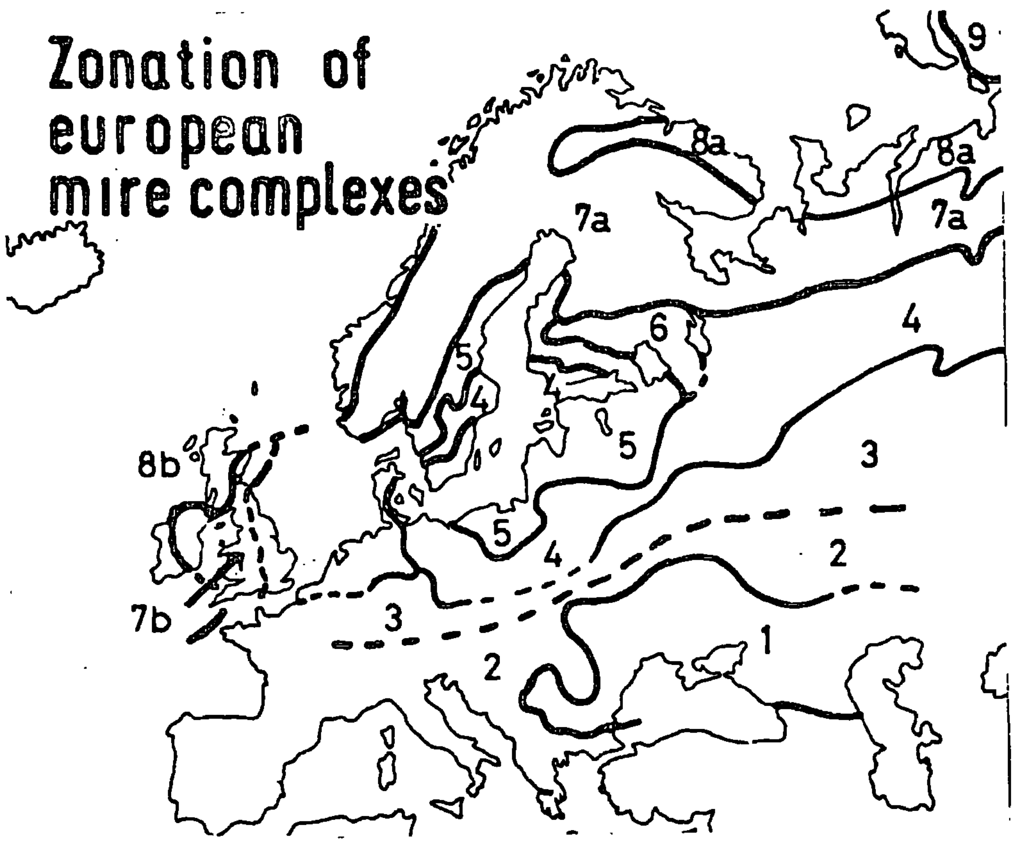
On the basis on the mean $Ca^{2+}$ and $Mg^{2+}$ levels (averaged over the entire mire expanse), the mire complex fits into hydrological mire type 7 (Bellamy), or 'moss' type, as described for Scandinavian mires by Sjörs. However, on the basis of pH, the mire complex would fit into HMT6, or extreme poor fen. The explanation for this discrepancy would be the 'rainfall effect'. The effect that this has on ground water pH and ionic composition for the blanket mires of Western Ireland has been described by Bellamy (25). The highest mean total ionic concentration found for Claish Moss, was for the squeezed water for the dry period; this was 1.19 meq $L^{-1}$. This is intermediate between the ombrophilous intermediate type (1.25 meq $L^{-1}$), and the ombrophilous mires proper (0.96-1.05 meq $L^{-1}$), as defined by Bellamy (25). This accords with a ratio of equivalent concentrations of $Cl^{-}$ to $SO_4^{2-}$ in the superficial waters of between 2:1 and 4:1 (table 8), and of $Na^{+}$ to $H^{+}$, of between 3:1 and 4.5:1. Thus this is not a strongly oceanic mire; one would predict $<$1000 mm of rain; 225-250 rain days per year.

### The off-transect sites - G,H,$N_1$,$N_2$.

What conclusions can be drawn about any special factors that are operating at the above sites? Each site will now be considered in turn.

### Site G

The hummock and hollow pattern was most accentuated at this site, in terms of the height of the hummocks above the mud bottoms of the hollows. This was in accordance with the continuum indices for the site based on non-vasular plants, which was close to that for site F (which had the most pronounced hummock and hollow effect of the on-transect sites) - see fig.12. This high continuum index at site G is due to the high *Rhacomitrium* and *Cladonia* cover, both of which are hummock species.



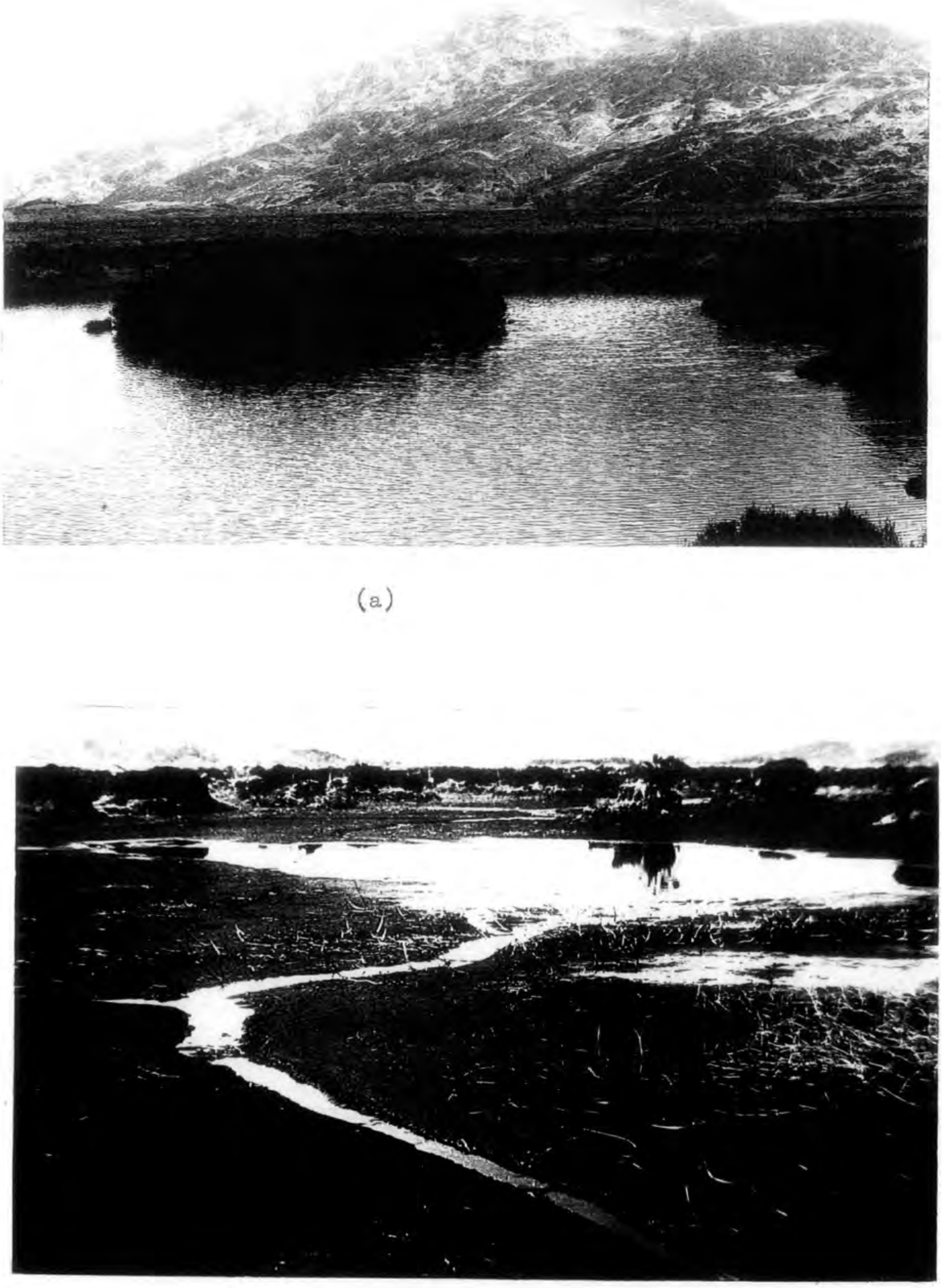
In this map, zone 5 is typified by concentrically domed mires
zone 6 '' '' eccentrically domed mires
zone 7 '' '' Aapamire (with surface patterning)

Topography plays some part in determining which of these three mire complexes are formed at one site.

zone 8b (in which Claish Moss) is typified by blanket bog

Fig. 3 Normal geographical limits of mire complex types

Map reproduced from 'The peatlands'; see ref. 20



(a)

(b)

Fig. 26 The drop in water table at site G between early May (a) and mid-June (b)

These photographs were taken of the same pool from different aspects. Note the course of the drainage channel in (b).

However, the continuum index based on the vascular plants was rather lower than for the other hummock and hollow sites (fig.11), and this could be attributed to the rather high Molinia cover at this site. Molinia is a plant more usually associated with the mire margins and lagg, where there is low water table stability, and possibly higher ground water flow. Both of these factors may operate at this site; water table stability is low (see fig.15 and 26). Low water table stability and high ground water flow may be due to increased drainage at this site; in the lower picture of fig.26, a drainage channel can be seen, down which there was a noticeable flow. In the aerial photograph, this channel appears to lead into a very straight ditch, which may have been dug at some point.

The flow of water might be the direct cause of erosion of the hummocks (fig.8), or the lowering of the water table, and consequent drying out of the hummocks, may result in oxidation of the peat, giving the appearance of erosion. Certainly, some of the Rhacomitrium appeared to be in a decomposing state, so the cover and performance of even the non-vascular plants may be declining at this site. Some of the hummocks had areas of bare peat, which appeared to be partly colonized by Campylopus flexuosus.

Site H

On the basis of both vascular and non-vascular plant communities, this site had a continuum index intermediate between the lawn community sites (A,B,C) and the hummock and hollow sites (D,E,F). In both cases it had a continuum index close to site P, which it also resembled in appearance - low ridges and shallow furrows, the latter dense with Sphagna. The only puzzle with this site was the high water table stability, in comparison with peat depth and floristics (figs.15,19,20). Possibly, a hummock-hollow complex is in the process of active development here. The position of this site (fig.5) was just below a hummock-hollow complex, and adjacent to the eroded area of site G. The high water table stability might be due water draining out of the hummock-hollow complex above, which acts as a reservoir; alternatively, it may be an old, eroded hummock-hollow complex (like site G), where the bare peat has been recolonized by new species. The measurements that have been made here, though, do not give any evidence as to these possible successional changes.

### Sites $N_1$ and $N_2$

On the basis of the vascular communities these two sites are indistinguishable from each other, and the mire lawn communities, in the ordination (fig. 11).

On the basis of the non-vascular communities, they are not so close together, but still well within the range for the mire lawn communities of sites A.B.C (fig. 12).

There is no chemical factor or other environmental factor which appears to give possible reasons for the occurrence of the fen-indicator species, Phragmites communis, at site $N_1$. One can only speculate that this plant is deeply rooted (it has deep roots) in more rheotrophic peat, which is perhaps the remnant of an water tract.

### The island study

In fig.24, a sequence of the species cover of hummocks of increasing height is shown. This sequence immediately recalls the cycle theory of the origin of hummock-hollow complexes of Van Post and Sernander. That is that hummocks and hollows alternate thus: where environments conditions are favourable, any slightly raised area of the mire tends to become invaded by hummock forming species, so that a hummock, above the general level of the mire surface becomes established. The hollows in between become filled with water, which becomes rich in algae; the oxygen produced by the latter causes oxidation of the peat of the mud bottoms, causing these to sink further relative to the hummocks. At a later stage, the pools become colonized with Sphagnum cuspidatum, and them Menyanthes trifoliata as the flow diminishes. Next, the hummock attains a maximum height, as it dries at the surface, and there is a more rapid peat accumulation in the pools, until eventually, the pools are colonized by hummock forming species, and the old hummocks, now bare of vegetation, form the mudbottoms of the new pools.

It is tempting to suppose that the sequence of fig.24 represents part of this cyclic successional development. However, it is not incompatible with the other theory of the origin of the hummock-hollow complex: that the hollows are due to 'cracking' of the surface of the peat mass, due to tension at the surface, generated by the weight of peat on a slope. The evidence for this theory against the other one is from stratigraphy: Walker and Walker found that the positions of the main hummocks and pools remain constant with depth, though the pools showing a periodic expansion and contraction. On this theory, certain species would tend to colonize hummocks and hollows of certain amplitudes, which might give a sequence as in fig.24.

To distinguish between these possibilites it would be necessary to look at the stratigraphy of the hummock-hollow complexes in more detail. If the sequence in space of fig.24 also turned out to be a sequence in time, this might lend weight to the biotic theory of development of hummock-hollow complex.

The other conclusion to emerge from the island study concerns competition between the species of hummock-hollow complex community. In fig.25, it was shown that the species richness of a hummock depended on the area of the latter and it was pointed out that this meant that either establishment or extinction of new species must be a process that occurs after hummock formation, after it has become isolated from other hummocks, and that these processes are not predetermined by the species that are already present (or one would not expect an effect of size). Thus competition is a process that occurs continually, that might operate through the chances of seedling establishment, or survival of immature plants.

In fact, the overwheliming impression was that there were big seasonal differences in the species composition of the bog (as well as in physical factors - see fig.26), and that for a lot of species that might be thought of as perennial, there was a lot of dying out and re-establishment each year. For example, pools rich in Sphagnum cuspidatum at the beginning of May had completely dried out by mid-June, with the moss in an advanced state of decay. Recolonisation of the pool when it fills up again presumably depends on competative effects between Sphagna, algae and vascular plants.

Thus the bog should not be thought of as a stable community with some slight seasonal effects on the floristic content, but a dynamic system, where the floristic composition each year depends on the interaction between environmental factors (which may vary between years) and interspecific competition.

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