Studies of the performance of Eriophorum Angustifolium L. and Sphagnum Recurval L. along an ecological gradient

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Studies of the performance of ERIOPHORUM ANGUSTIFOLIUM L. and SPHAGNUM RECURVUM L. along an ecological gradient.

INTRODUCTION.

The 'science' of production ecology is at present time the only in the stage of the collection and collation of information.

Production data relating to various species in their specific habitiats of various definable ecosystems has been gathered together, but it is very difficult to drae any concrete conclusions from the data collected from such varying sources.

The information forming the basic staructure of this new science has nit yet been collected for the following reasons:-

1) It is virtually impossible to distinguish between the endogenous and exogenous information, ei that information formed by an organism as a direct consequence of its specific nature, habitat and performabce, and that information formed as a result of the random variation in these results.

2) There has been no distinguishing of the variation between sites, and also too much variation within sites (both due to random distribution) to make this time consuming operation as methodology of data collection and sorting worth while.

Information linking the production and mineral cycling of specific ecosystems and their component species exists at the present time. BAZ'LEVICH (1968) -here is already enough information collected to show specific differences in these attributes between phytogeographically distinct areas, eg between ecosystem components of the major world vegetation belts. There is as yet little information regarding variation between ecosystem types within such phytogeographically distinct regions.

The related study of phytosociology allows for the discernment and regognition of species characteristic to the specific roles carried out in the production ecology studies. These species are selected objectively from a 'matrix of information' built up from objective study and data collection in the habitats of the suspected species. In these specific habitats however, the species grow and find their 'full expression', in the specific niche into which they have evolved, to be adapted as closely and as fully as possible to exploit to the maximum the factors existing in that habitat where they will assuredly find their greatest perfofmance. It is to be noted that there are no references to any investigation into the *degree* of adaptation of plants to their natural habitat.

Phytosociology has, for Europe, produced a system of vegetational classification which allows the regognition of floristic units; associations, alliances, orders, and classes which have their specific phytogeographical meaning. BRAUN-BLANQUET (1932). Although these units cannot be regarded as ecosystems in the true sense of the word, they are populations of primary producers evolved under specific abiotic (habitat) conditions.

In any succession complex eg the mire hydrosere there is an interrelated chain of biotic and abiotic factors in the habitat. This interwoven chain in brought about and furthers itself in the process of energy fixation. As this 'energy flux of succession' drives along and causes vast changes in the microenvironmental factors one might expect certain species able to tolerate these changes in the environment to show a marked variation in performances through the succession of floristically determinable components of a sere. One could therefore use the varying environmental factors to investigate an delimit the factors to which these particular species are sensitive.

In order to investigate the above statements to a greater extent, and to try to understand the process of environmental plasticisation in performance and growth the following potentially fruitful line of investigation is suggested. It links phytosociology with production ecology and is intended to measure the primary production and mineral cycling of the sociological unit and their component species over their phytogeographical range.

To test the feasability of this approach it was decided to study the performance measured as net aerial production of two species which are characteristic of a specific phytosociological unit over an environmental gradient.

The two species selected were ERIOPHORUM ANGUSTIFOLIUM and SPHAGNUM RECURVUM both typical component species of the OXYCOCCO - SPHAGNETEA. The environmental gradient was that created by hydroseral succession from open mire communities, referable to the Order ERICO SPHAGNETALIA of the class OXYCOCCO SPHAGNETEA, to closed mire forest referable to the order VACINIO PICETALIA of the class VACINIO PICETEA.

The method selected and developed was one of 'growth analysis' in the field and will be called

SINGLE SPECIES INCREMENT CROPPING.

THE SUCCESSION (Summary)

This is;-

OPEN MIRE → CLOSED FOREST.

This seems to be the only variable, the seral stages being edaphically and hydrologically similar. The peat consistency, constituents and nutrient contents being of the samw order of magnitude, if not being quite identical, through the seral succession.

The variable chosen for investigation was therefore STABILISATION OF THE PEAT SURFACE.

Through this facter the system was built up through the process of energy accumulation in the substrate, and finally the vertical extension of the plant habitat. Through this method of soil consolidation and vertical plant growth the ecosystem was extended vertically upward to a considerable degree. There was however no downward vertical extension of the ecosystem, this being shown by the fact that all the forest tree roots are to be found <u>only</u> in the upper 40 cms. of the substrate

SELECTION OF SPECIES.

ERIOPHORUM ANGUSTIFOLIUM - this species is found throughout the mire system, and is characteristic of thos areas termed 'transition mires' (see phytosociology section). Also it usually finds its optimal expression in open areas particularly the ERICO SPHAGNETALIA of the class OXYCOCCO SPHAGNETEA.

SPHAGNUM RECURVUM - this species also is characteristic of transition mires, and is found throughout the mire system. In a supplementary rôle to that of ERIOPHORUM ANGUSTIFOLIUM it usually finds its optimal expression in the shade, often in the VACCINIO PICETALIA OF THE CLASS VACCINIO PICETEA.

COMPARISONS BETWEEN PLOTS.

Calculations:-

The graphs and histograms were erected from information derived from theinitial cropping and weighing results, which contained the mean weight, standard deviation of the mean, standard error of the mean and finally the standard limit of the mean. Figures were calculated for all the various organs of the plants.

Discussion:-

The results of the increment croppings are shown in table of appendix ,as in fig. . More detailed breakdowns of the figures are shown in fig. .

For the above data it may be seen that:-

Area 1

Open Sphagnum lawn community referable to the SCHEUCHZERIO CARICETEA FUSCAE. Here Eriophorum Angustifolium, acting as a pioneer plant, shows its poorest performance, peak standing crop being in late June.

Peak standing crop grammes per individual.

Area 2

Peak standing crop is similar to the above, but at this site there is a more stabilised sphagnum lawn. The stand of Eriophorum is dense and one would suppose it to be under the effects of intraspecific competition.

Peak standing crop is not significantly higher than at site 1, but the peak standing crop is at least 14 days earlier.

Peak standing crop grammes per individual.

Area 4

The Eriophrum is growing as a shade plant of the herb layer of a dense pine forest. PINUS SILVESTRIS.

Its peak standing crop is significantly greater than at the other three sites. Also, after peak standing crop is attained there is rapid and massive loss to litter, not shown at any other site.

Peak standing crop grammes per individual.

Area 5

Eriophorum is here growing as part of a diverse, mixed community typical of the OXYCOCCO SPHAGNETEA.

Peak standing crop is here very indeterminate. There are indications of an early and a late peak which is discussed in the Addendum on bienniol perennielism.

Peak standing crop grammes per individual.

CHEMICAL ANALYSIS.

The results of the chemical analysis are shown in table of appendix , as in fig. . More detailed breakdown and a recombination of the chemical analysis with production figures gives the 'POTASSIUM FLUX' which are shwon in fig. .

Potassium Results:-

In all cases it may be seen that Potassium is removed from the leaves at or before death. It may be seen as an intergral part of efficient recycling of this mineral, unless a rapid 'wash out' is assumed.

Similar results have been shown by J. Rieley for CAREX FLACCA and CAREX PANICEA, also members of the Family CYPERACEAE with ERIOPHORUM ANGUSTIFOLIUM.
Ref. (J.Riely Ph D thesis (1967) Durmah Univ. Bot. Dept.)
It would appear that this is analogous to the process of recycling as shown also by Goodman and Perkins for Eiophorum vaginatum.
ref. (Goodman G. T. and PERKINS D. F. (1959) Nature vol 184 pp467 - 468.)

It is interesting to note that only at site 4 is there any significantly larger Potassium content per gramme. This indicates a better supply of this mineral at the site, probably due to nutrients falling as pine needles from the tree canopy. However, as the withdrawal of potassium from the dead leaves would appear to be just as efficient at this site, one would suppose that saturation of the requirement of the species have not yet been reached.

DISCUSSION :-

The technique.

The technique of single species increment cropping has been developed in order to compare the 'performance' of species, measured as nett annual production.

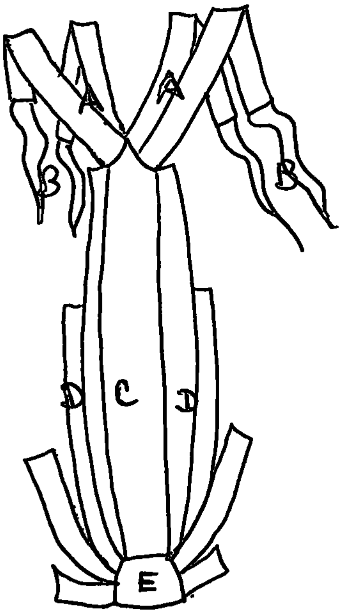
The progress curves of the cotton grass with their remarkably small standard errors and standard limits, indicated on the graphs show that this is a useful and valid technique.

Fig shows the theoretical situation.

Using this techniqueeverything is measured except the loss to litter. The assumption is that the actual loss can be directly obtained by adding any decreases either in the deadleaves or dead sheaves. There is no other possible source of litter for it cannot come from the live sheaves or leaves in the shoot interval of two weeks between cropping. Any litter must come from the dead plant organs. One fact must be born in mind. Using this technique the worker must make detailed observations of the plants each time the site is visited. A good visual assessment of the growth processes must be obtained. Therefore it would seem reasonable to assume that any positive increment between sample dates does actually represent a gain in tissue mass and therefore a measure of nett production may be obtained by adding these.

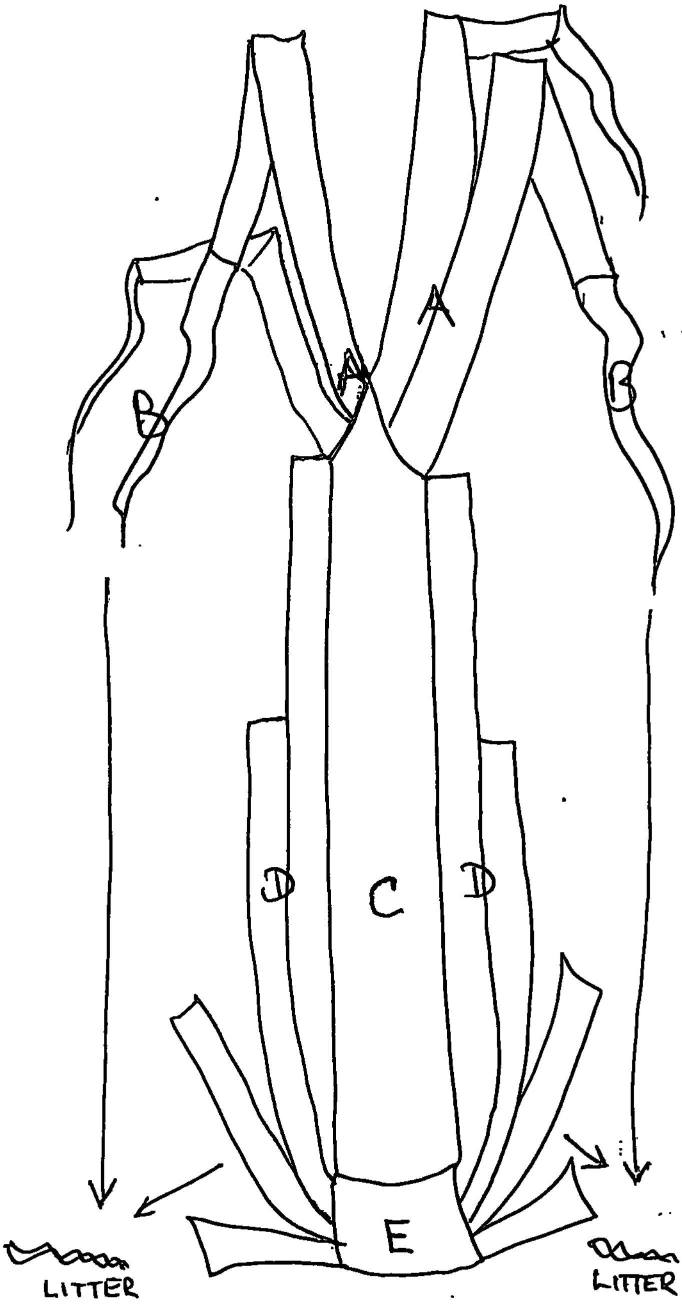
However it must be assumed that there is no loss from a particular fraction of the plant if there is a gain observed. For example, while a fraction A of the plant is increasing rapidly it must be assumed that there is no loss to B. In fact both processes could well be taking place; that is both growing and dying processes will occur but the former at a greater rate than the latter so obviating it in its entirety.

Ther is little or no evidence available however from



Time 1

0 days



Time 2.

1 e x days,

NB only B & D → litter –

the observations and the experimental data that there is a constant and massive loss of material from the plant which is actually masking the amount of production which is taking place. The observations show a regularised sequence of GROWTH, DEATH and LOSS, not a continuous flux continuing ant a basic level for all three factors.

As shown above the sequence of growth, death and loss are distinct processes which are accelerated and slowed down at various parts of the annual growth cycle of the plant. It must be emphasised that growth is not a continuous process whose overall rate is changed. It is in fact the sum effect of a number of sub-operations whose rates differ at varying but overlapping periods of the year.

It seems reasonable to assume therefore that the measurements and the calculations have some absolute meaning. They are used as such within the context of the following discussion.

There is a further unknown factor. All estimates of production from measurement of the biomass are open to the criticism that there is an unknown quantity of dieback occuring between cropping dates. To minimise this source of error the cropping dates were as close together as possible and this was fixed at once every fourteen days to enable the vast task of dissection, sorting, weighing and the further treatment of the plant to be completed before the next cropping.

ADVANTAGES OF THE TECHNIQUE.

The technique described above has a number of advantages over other methods, eg the biomasstechniques usually employed.

1) It is a rapid technique in that only a few individuals are cropped and weighed on each occasion; rather then the interminable sorting necessary when dealing with total cropping of known fixed areas.
eg. WEIGART and EVANS methos using paired plots
Nevertheless sorting of the material still took up a significant portion of the whole available experimental time.

2) The setting up of complicated and costly enclosures was not necessary, for if any plant was founf to be damaged in any way at all after cropping, it could be and was discarded.

3) There were enough (30) samples obtainable and obtained at most of the croppings to allow at least some statistical treatment. The most valuable calculations were those of standard error and standard limit. The problems of producing comparable statistical estimates using the paired plot technique would ahve been enommous unless a vastly larger number of workers had been employed.

It is important to realise that one of the few advantages of the more time consuming method using paired plots is that accurate plot production figures are directly available. These figures are however easily obtained using the method simply by multiplying the mean individual plant production figures by the mean number of individuals per unit area within the community.

4) The growth pattern of the species in each plot can be ~~assessed~~ obtained using this method hence PHRENOLOGICAL PERFORMANCE (performance throughout a fixed and named period

of time) of each species within each plot can be assessed.

5) Any chemical analysis performed will give a direct insight into the role of the species within its specific community and the mineral cycling of the plant within this specific habitat community or ecosystem in quantity and quality (ie different ions) and in time

SUMMARY.

This method even though relatively simple to carry out when compared with the 'plot' biomass techniques appears to give meaningful results for the comparative studies of performance of species between sites.

Also it gives the worker the possibility of dissecting the primary producers of an ecosystem, studying each separately at first, then following this stage with detailed study reassembling the ecosystem to obtain results per unit area.

It is argued that such a study as this takes no longer than and usually represents a considerable saving of time when compared with any of the currently used techniques in the study of primary production.

In contrast to these other, more generally used techniques, it appears to yeild much more detailed information about the makeup of the ecosystem and is therefore of much greater value to the ecologist.

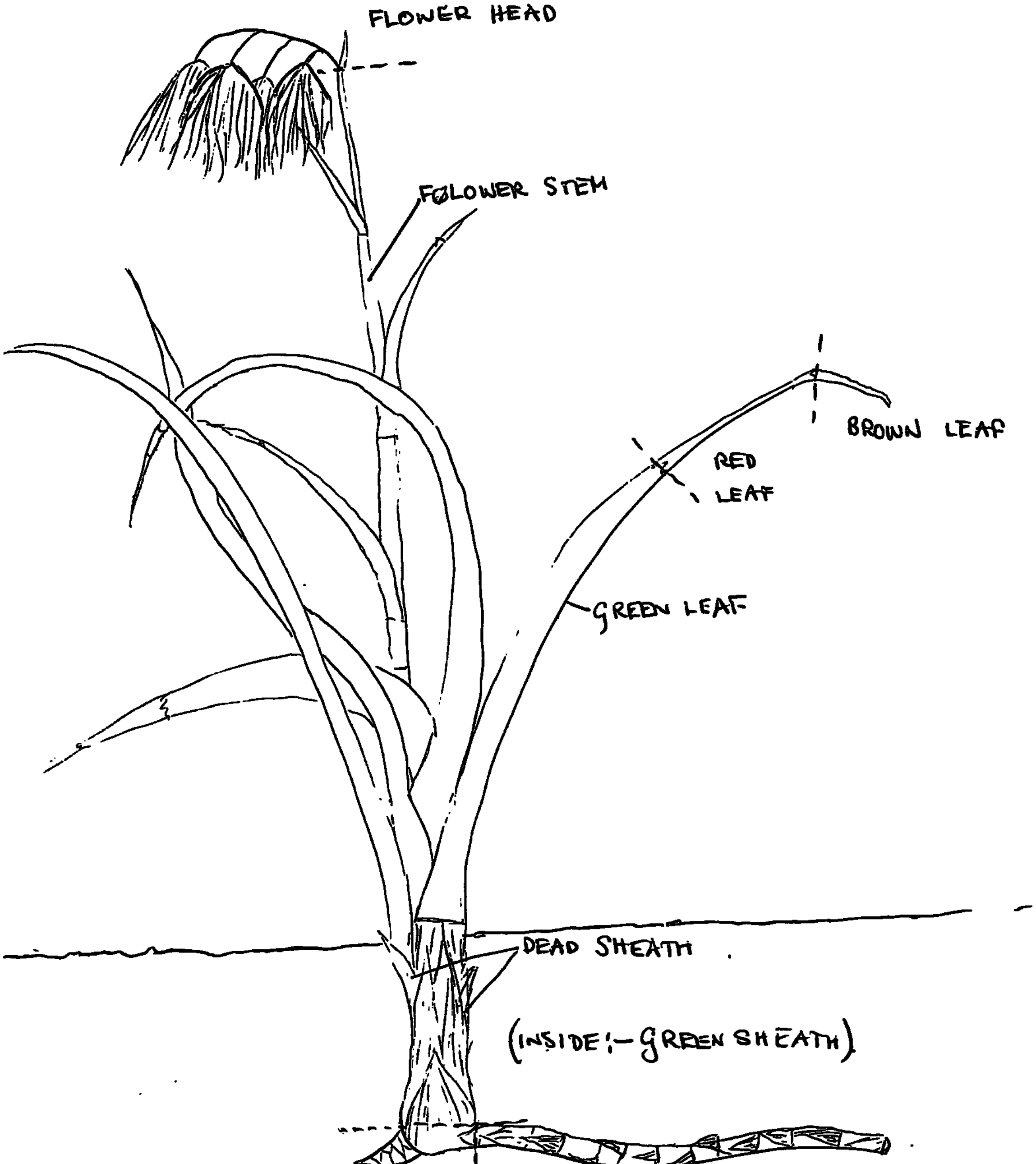
The method however seems applicable only to the aerial portion of the plants.

ADDENDUM.

There is one further interesting problem in the interpretation of the data collected on the ERIOPHORUM ANGUSTIFOLIUM. The species seems to exhibit the phenomenon of 'BIENNIEL PERENNIELISM' which has been investigated and substantiated by other workers.

Each shoot is purely vegetative for one year, therhizomes producing leaves and extending the root system in that year. It is not until the following year that the plant flowers, fruits, and produces more rhizomes. Detailed phrenological knowledge of each species is therefore essential before the method can be used.

ERIOPHORUM ANGUSTIFOLIUM · x 1 → x ½



APPENDIX I

Preliminary surveys.

These were completed in the Michaelmass Term of 1966, and consisted of two visits to Moorthwaite Moss to study the situation found there.

The system consisted of a domed ambrophilous mire with a ring lagg in places. The whole was surrounded by arable land which doubtless contributed minerals by surface water drainage and also by dust blowing. The dominant tree in the wooded areas was Pinus sylvestris. These were large and seemed to be a native species, probably not having been introduced. Towards the centre of the mire the pine trees were smaller and more stinted and in the middle there were only seedling surrounding a swampy pool, the centre of the centripetal bog development in the mire hydroseral succession.

At various points on the bog surface there were dry areas which may have been caused by peat cutting in surrounding areas, so taking away the surface waters. On these dry areas the pines were particularly well developed, often surrounded by luxuriant heather growth.

Also throughout the system there were runnels, these were probably richer in nutrients than the rest of the surface for here especially Eriophorum angustifolium grew very vigorously in the rich damp conditions.

It was notable that E. angustifolium and Sphagnum recurvum grew in all the habitats. These species were selected for further study in the comparison of the environmental conditions.

In the Epiphany Term further visits were made, water samples taken and a provisional association table drawn up. From this it can be seen that the two indicator species selected were the two most easily studied of the wide-ranging species.

Later on a different, expanded association table was drawn up.

Also, specimens were gathered from various habitats to compare the sizes to which individuals of the same species grew under different shade, water flow (and nutrient?) regimes. It was notable that Eriophorum angustifolium grew about 1 metre high in the woods where it occurred and perhaps only 20 cms. in the centre of the mire near the pool. The growth forms of individuals of Sphagnum recurvum were also noticeably different in the several types of habitat, being longstemmed, long leaved and weakstemmed in the wetter areas and grading into a more compact and sturdy type where drier, also being darker green in shaded areas.

Similar changes could be seen in Pinus silvestris, Erica tetralix and Calluna vulgaris, all being members of the wide-ranging group of species.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4109

Plan of the Investigation.

From the preliminary investigation a number of interesting facts were discovered, some very obvious but nonetheless still pertinent to an investigation.

1) The area was a mire, therefore minerals available to the plants were found in the ground water solution. Presumably the nutrients in the peat were not available to the plants. Because of this continuous ground water system the concentrations of the minerals would be quite uniform, free flow of ions being possible. Therefore any deficiency of ions in an area would be immediately buffered by a similar inflow from elsewhere.

2) The flora of the mire varied across it. There were presumably ecological gradations causing this:-

(a) Variations in the mineral content of the ground water over large areas (the deductions from 1) being presumably limited to a relatively small area.

(b) Variations in the advancement of the ecological succession.

i. Centripetal bog development is occurring and so forming the raised ombrophilous mire - the main resultant of this being shade variation, but also in the degree of wetness of the substrate e.g. the pinewoods were dry underfoot.

ii. Hummock Hollow bog development is also taking place.

There is therefore in the wideranging species a considerable tolerance of varied conditions. Gradations in the system can be easily seen and are

1 - Wet -> Dry
2 - Shaded -> Open.
(3 - Nutrient rich -> Nutrient poor)
4 - Flowing groundwater -> still groundwater

This is not very apparent

The purpose of the investigation was therefore to find how the performance (nutrient & trophic dynamics) of these two species varied with their environment. The steps in the investigation could therefore be enumerated thus.

1) Description of the vegetation and demarcation of associations.

2) Recording the environmental factors.

3) Investigating the numeral uptake and energy fixation of individuals of the two species in named associations and described conditions.

Step 1 had already been accomplished in the preliminary investigation.

2 consisted of

a) Recording weekly rainfall and its analysis to find incoming nutrients.

b) Analysis of ground water at various points throughout the system.

c) Using controlled and cultivated plants as control.

The plants used should preferably be very phenotypically variable and of a genetically identical stock. Plants chosen were Balsam - Impatiens balsamfera var. "Camellia flowered double finest mixed" the only variable was the amount of anthocyamis in the petals causing variation in flower colour from indigo to white.

It was decided that at each cropping station, situated in a defined community the following control station should be set up. see Fig.

Each cropping station consisted of the following:-

1) Two seed trays, with drainage holes, of vermiculite down with Impatiens on 28th. April, 1969 grown in a greenhouse for two days to induce germination. These were placed in position on 30th. April for cropping at monthly intervals. Thinned .

2) 9 x 10 cm plant pots of vermiculite sown with approximately four Impatiens seeds each on the 29th. April and placed on the bog in a dry area to allow germination, then placed in position on the 7th. May. While placed on the bog to germinate they were covered with perforated polythene to conserve moisture and to retain heat,

3) 9 Individuals of Impatiens growing in the native peat. Originally these were planted in a seed tray of vermiculite, as were those in 2) and treated similarly to them until 7th. May when planted out into the native peat after removing most of the vermiculite from the roots.

4) Sumps. These were dug on 30th. April to collect ground water for analysis.

Plants in 2 and 3 were to be cropped one a week for nine weeks removing them in the order 5, 1, 3, 7, 9, 2, 8, 4, 6.

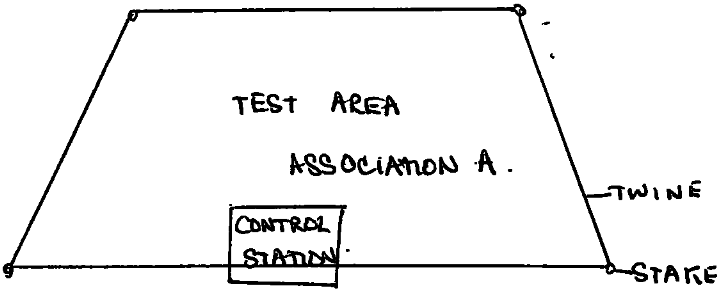
```
x x x   x x x   o x x   o x o   o x o

x x x   x o x   x o x   x o x   x o x

x x x   x x x   x x x   x x x   o x x
```

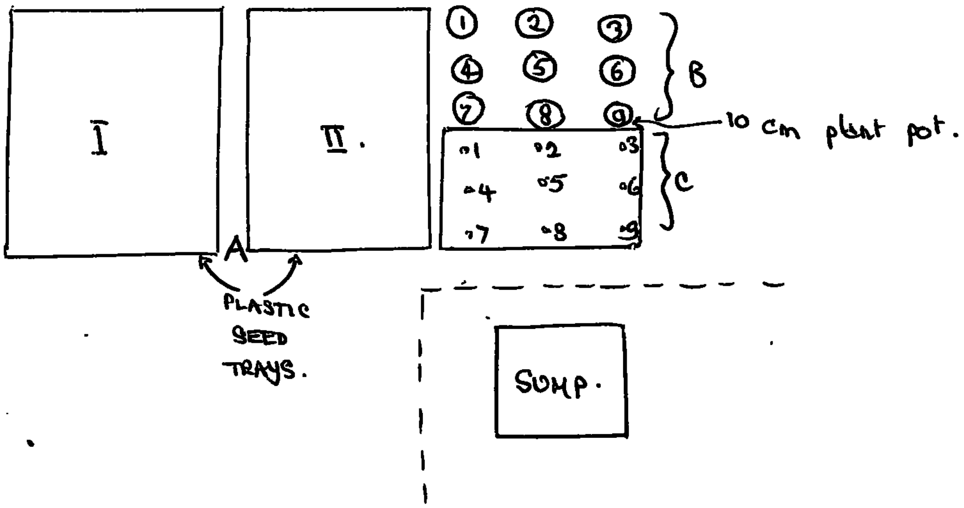
```
o x o   o o o   o o o   o o o   o o o

x o x   x o x   x o x   o o x   o o o

o x o   o x o   o o o   o o o   o o o
```

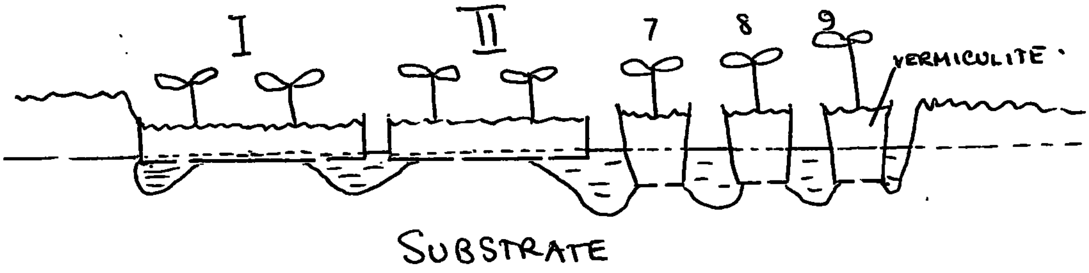
When cropped they were to be treated as the other test plants.

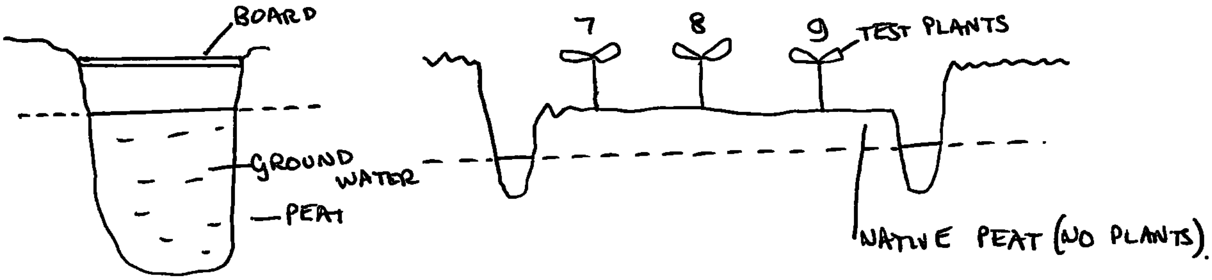
3) Consisted of analysis and bomb calorimetry

We can therefore draw a flow diagram of the methodology.

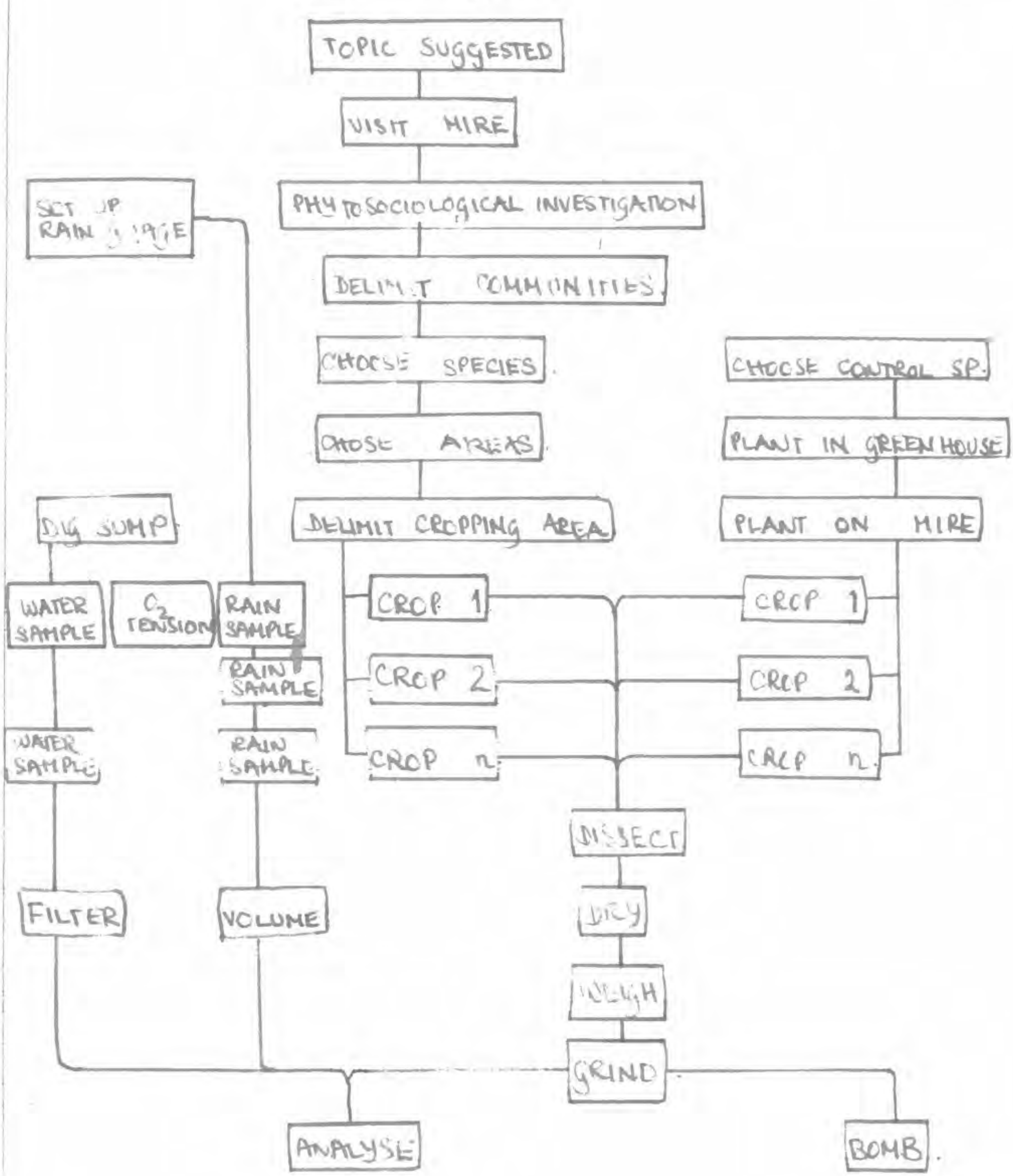

TEST AREA
ASSOCIATION A.
TWINE
CONTROL STATION
STAKE


I
II.
① ② ③
④ ⑤ ⑥
⑦ ⑧ ⑨
B
10 cm plant pot.
1 2 3
4 5 6
7 8 9
C
A
PLASTIC SEED TRAYS.
SUMP.


I
II
7
8
9
VERMICULITE
SUBSTRATE


BOARD
GROUND WATER
PEAT
7
8
9
TEST PLANTS
NATIVE PEAT (NO PLANTS).

FLOW DIAGRAM.



CROPPING.

In situations where herbivore animals are not important and where a steady static condition is never reached, the harvest method can be used. Weighing the growth produced is straightforward; the productivity is easily calculated. It is better to take harvest samples at intervals during the season than to rely on a single terminal harvest (see Penfound 1956; E.P.Odum, 1959). Such a method cannot be used where the food produced is being removed as it is produced, as it is in many natural communities, other methods should then be used.

Since food used by the plants themselves is not included, the harvest method always measures net production.

Ref: Odum Fundamentals of Ecology 1967.

As far as was ascertainable from brief looks at the wire system it did not seem that there were many herbivorous animals and certainly none that could be excluded; e.g. rabbits, voles, mice, deer. The method used to study the system was therefore the harvest method.

Eriophor$\overset{u}{a}$m

A minimum sample was found from previous experience of cropping this species by other workers to be about 30 individuals. Accordingly for every cropping 30 plants were dug up randomly. This was done by starting at one edge of the plot and marking out a 50 cm. band across it. The plants were then dug up with roots and all dead leaves attached, proceeding across the strip and digging the <u>next</u> plant encountered.

The plants were put into polythene bags, labelled and taken back to the laboratory.

Sphagnum recurvum.

Several methods for cropping this plant were tried.

1) Random sampling of, e.g. 100 plants - discarded because it did not provide for any increase in height of the plants with growth in weight. There was no fixed point of reference.

2) Hair net - to prevent loss of light energy by any coarser material - increment - broke down - moss pushed up net.

3) Fishing net - coarser and stronger - but still the moss pushed it up - light loss due to coarseness of material.

4) Wire netting - zinc - killed moss.

5) Fixed area live growth cropping - this proved to be much more satisfactory and allowed larger and therefore more valuable samples to be taken,

In fact no method was satisfactory. Results were taken but in fact not used in this investigation

TREATMENT OF CROPS.

The plants when obtained were put into labelled polythene bags which were returned to the laboratory and treated in the following manner as soon as possible.

1. Taken out of the polythene bags and separated from each other.

2. Dissected into the component parts, 1) green leaves, red leaves.
11) non green living leaves and sheaths.
see diagram 111) dead leaves.
1V) dead sheaths.
V) roots.
V1) flower stems.
V11) flower heads.

3. For each plant these were put into separate cellophane bags. These were put into a small brown paper bag and these in turn into a large labelled brown paper bag.

4. The crops were then dried in an oven at 80°C for 48 hours, it had been found that drying at 105°C dries off lipids as well as water.

5. Constituent plant parts were weighed and the results tabulated.

6. All the similar constituent parts from a cropping, e.g. all flowers from an area, were put into the cellophane bags for storage.

7. Samples were milled and restored and before "bombing" were pressed into pellets of about 1 gram weight.

8. The energy content per gram of the constituent parts were found by bomb calorimetry. From these results the total calories per plant and then per cropping could be found.

9. Nutrient content was found by acid digestion and mineral analysis. From these results the total nutrients per plant and per cropping were found.

Bomb Calorimetry.

Introduction.

The classical methods for determining the calorie value of foodstuffs are both long and tedious, and a number of alternative methods have been suggested for assessing the energy value of foods based on an analysis of the foodstuff and the use of factors with each of the chemical components to give energy content. None of these methods is really satisfactory, and when a high level of accuracy is required direct calorimetry must be used.

The adiabatic method used by Raymond, Canaway & Harris (1957) reduced the time taken for a determination to approximately 30 min, but the equipment is complicated and expensive. A fundamental feature of this and the classical procedure is that the quantity of heat produced is measured by a small rise in temperature of a large mass of material, resulting in long equilibration times and the need for great accuracy of temperature measurement.

Description of Apparatus.

The vessel consists of two main parts, the lower portion being the receptacle for the complicated upper portion which is in reality the main part of the bomb.

Externally the upper portion has two protrusions, one for the insertion of the thermocouple terminals and the plugs for the electric firing when the bomb has been placed in position, and the other for the admittance of oxygen and release of waste gases. This latter part has a valve to prevent loss of gas while the experiment is in progress.

Internally the upper portion has two "arms", each of which has a hole in which to place the ignition wire of standard type and length, (5cm) and a fastening for each end of the wire. Black cotton of standard type and length (5 cm) is used to join the sample and the ignition wire.

One arm of the apparatus has an extension on to which is fastened a housing to contain the removable crucible and its sample.

The two main parts of the bomb are held together by means of a brass-threaded collar and the rubber '0' ring provides a gas-tight seal.

The bomb is places in the inner water bath in its niche. The insulating lid with the thermometer on its housing is swung over and lowered into position.

Method of use.

Samples for combustion are placed in a crucible of 5 ml capacity located horizontally by a ring. Ignition is effected by means of a short length of cotton one end of which is tied to the platinum filament and the other placed in contact with the sample.

The thermocouple is of copper-constantan, the junction being soldered to the tip of a spring-type wander-plug; the connecting wires pass down through a hole drilled through the spring. The thermocouple is connected to a galvanometer through a series resistance which turns on a heater in the outer bath so preventing the loss of any heat by maintaining the outer bath at an identical temperature to the inner bath. The inner bath and the outer are of distilled water to prevent the thermocouples from registering any current.

passing, and so turning on the heating when the baths are at the same temperatures.

The apparatus has been calibrated to work when the inner bath with its container weigh 1500 grs. The apparatus must be carefully shielded from draughts. The bomb is inserted and the apparatus switched on and allowed to equilibrate at a temperature about 21°C and the initial temperature is read. The current used to ignite the samples is controlled by means of a clockwork time switch, which operates for 15 sec, so that the heating effect of the ignition current is always the same. The temperature rise due to it and to the burning of the cotton fuse is determined separately, and subtracted as a 'blank' from the peak galvanometer reading.

On combustion of a sample, the temperature of the bomb in the region of the thermocouple rises rapidly to a peak value and then falls off, rapidly at first as heat is conducted away through the walls, and then more slowly. This causes a rapid initial rise in temperature shown by the Beckmann's thermometer, which is read by an eye piece, and also by the "heating" light switching on and off rapidly. Later the temperature rise rate slows until it equilibrates and the final temperature is read off to three places of decimals as is the first temperature reading.

Oxygen filling system.

This includes a needle valve and a pressure gauge which has a safety front and a blowout back. Union fittings are provided for a nylon oxygen supply tube and a nylon bomb filling tube. A hand tightening union nut with a toroidal ring is used to seal the filling tube to the bomb.

Accuracy. (Proc. Nutr. Soc. 1964, 23 xxxvii).

Current experimental work on the dietary energy component has afforded the opportunity to make a comparison between the rapid determination of gross energy values of food and faeces using a ballistic bomb calorimeter and those determined on the more conventional static bomb calorimeter. The summarized data from over 600 determinations are given in the table to illustrate the repeatability and relative accuracy of the two methods.

		%of determinations with each accuracy range.			
% accuracy between determinations		1%	2%	2½%	3%
conventional calorimeter	- duplicates	16.7	50.0	100.0	-
ballistic calorimeter	- duplicates	34.0	63.0	73.0	78.1
	- triplicates	82.0	92.0	96.1	98.0

When duplicates of each sample are taken for analysis 50% of the duplicate determinations are accurate to within 2% of each other and all are within 2½% when the conventional bomb calorimeter is used; 63% of duplicate determinations on the ballistic bomb calorimeter are accurate to within 2% and 73% to within 2½%. With a further single determination (i.e. triplicate determinations) a 2% accuracy can be obtained with 92% of all samples examined. The range of variability obtained with the ballistic bomb calorimeter is only slightly greater than that obtained with the conventional calorimeter, and against this must be offset the time factor since it has proved possible to complete twelve determinations/h with the ballistic bomb calorimeter compared with one/h on the conventional bomb calorimeter. Using the ballistic bomb calorimeter the above patterns of repeatability were virtually the same in data from three separate trials with difference operators and with samples from pig and poultry trials. Our findings with regard to the preparation of materials are in agreement with those of Miller and Payne (1959) and Sibbald (1963) that determinations on finely powdered preparations are far more accurate than when pelleted.

Possible sources of error.

Variations in oxygen pressure. Over the range 300-500lb/in^2 the peak deflection/kcal liberated was found to be the same. Below 300 lb/in^2 the time taken to reach the peak temperature was extended and below 200 lb/in^2 combustion was obviously incomplete. For these reasons, and in accordance with other methods 400 lb/in^2 (25 atm.) was selected for routine operation.

Variations in initial temperature. Since the peak galvanometer deflection is a measurement of temperature difference, it seemed unlikely that small variations in initial temperature would be a source of error. For normal use the initial temperature of the bomb casing was about 20°. When samples were being combusted at short intervals it was achieved by cooling with tap water.

Summary.

1. An adiabatic bomb calorimeter is described, which enables three determinations to be carried out in an hour with an accuracy as good as with most methods. The characteristics of the bomb were investigated and the chosen operating conditions were at an oxygen pressure of 400 lb/in^2, an initial temperature of 20°C, with a sample weight of approximately 1 g.

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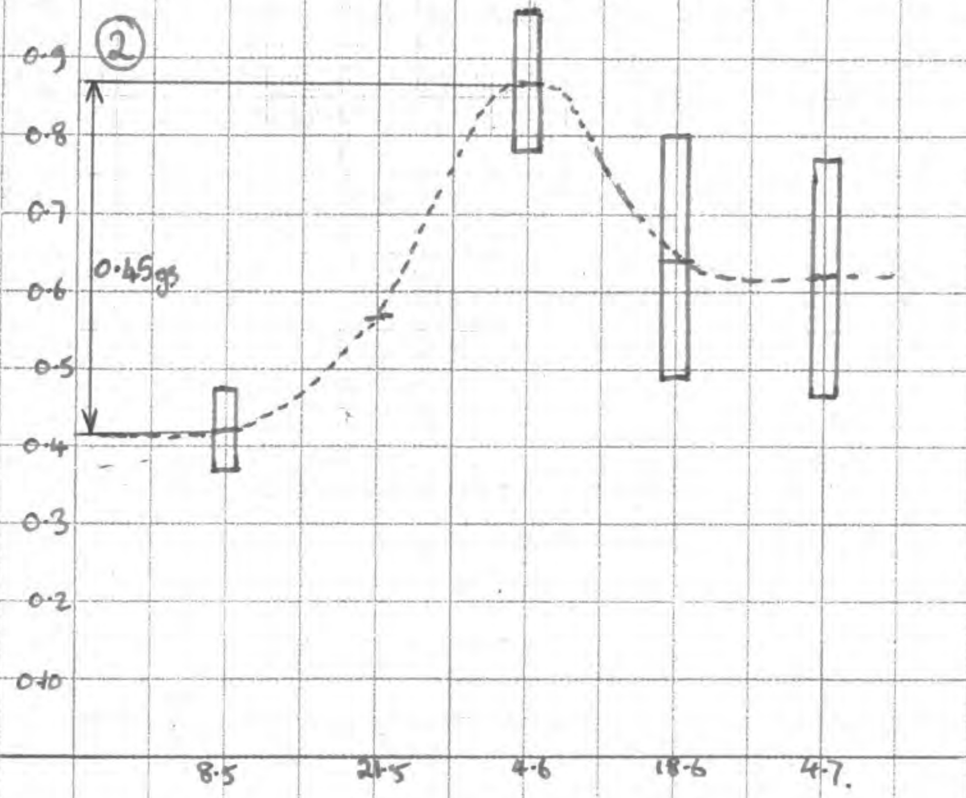
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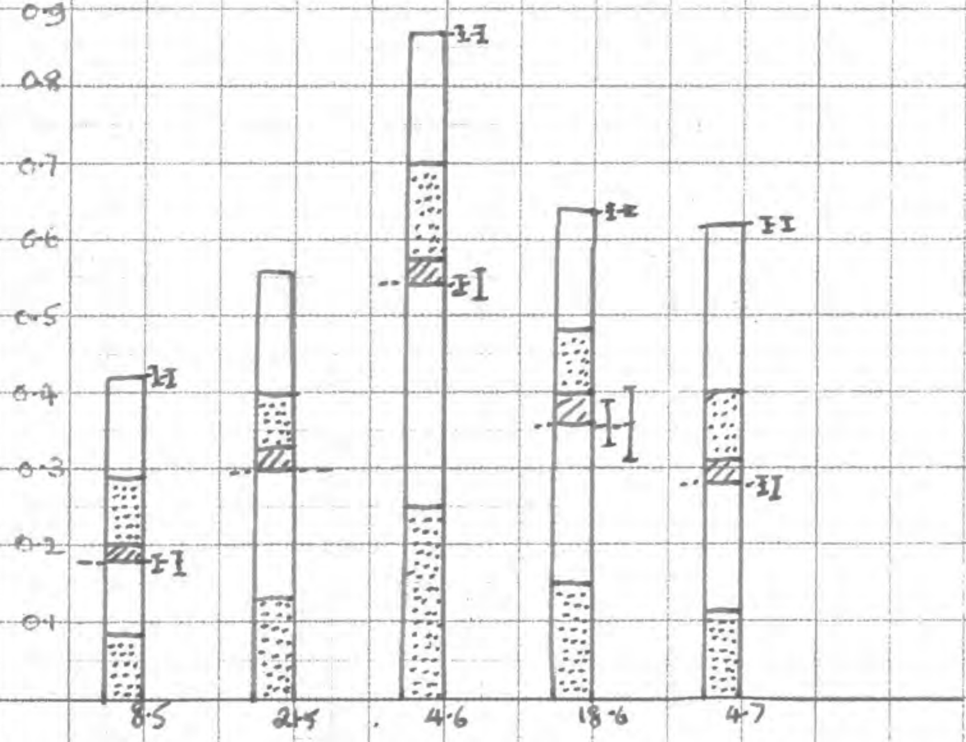
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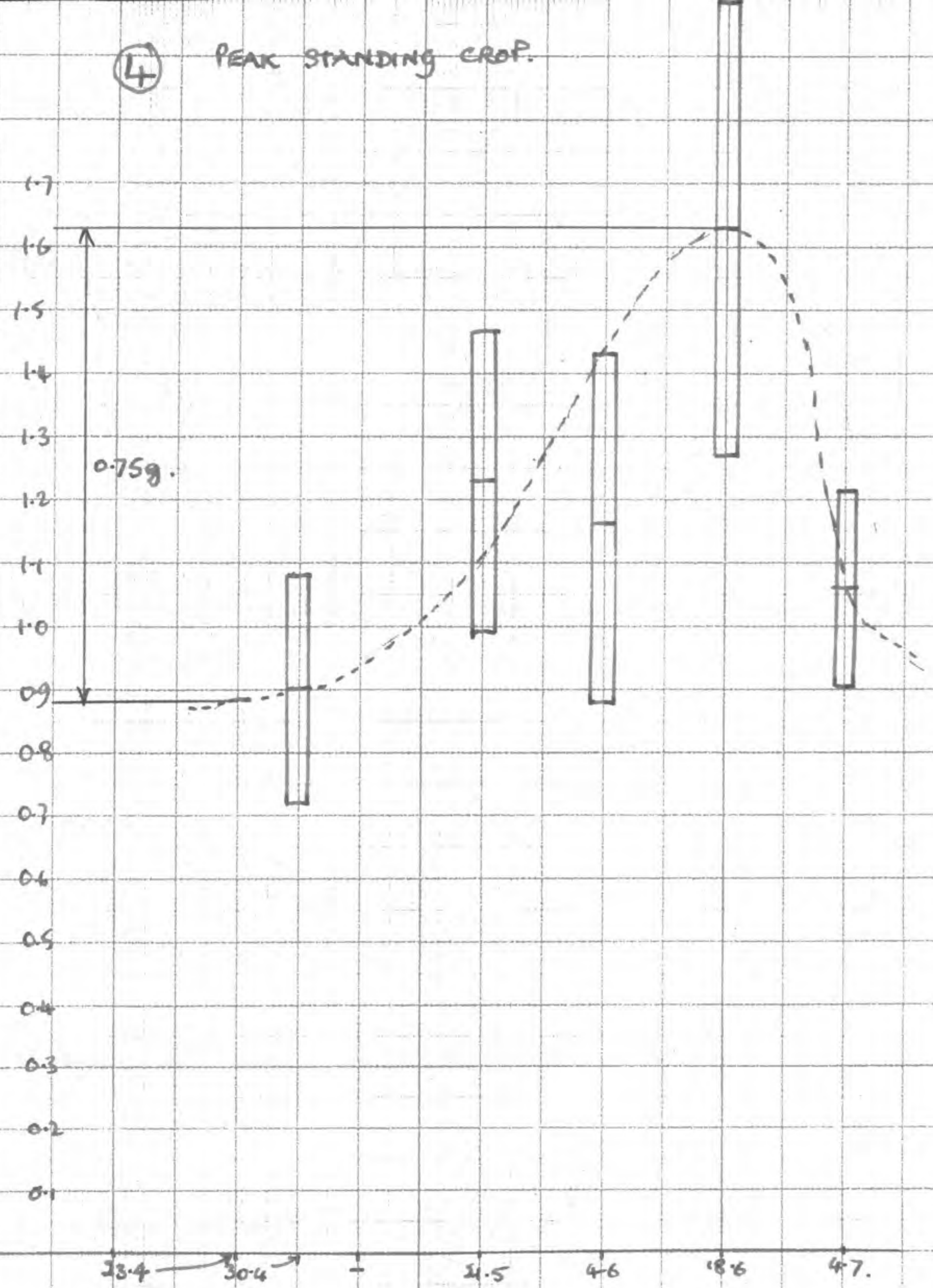

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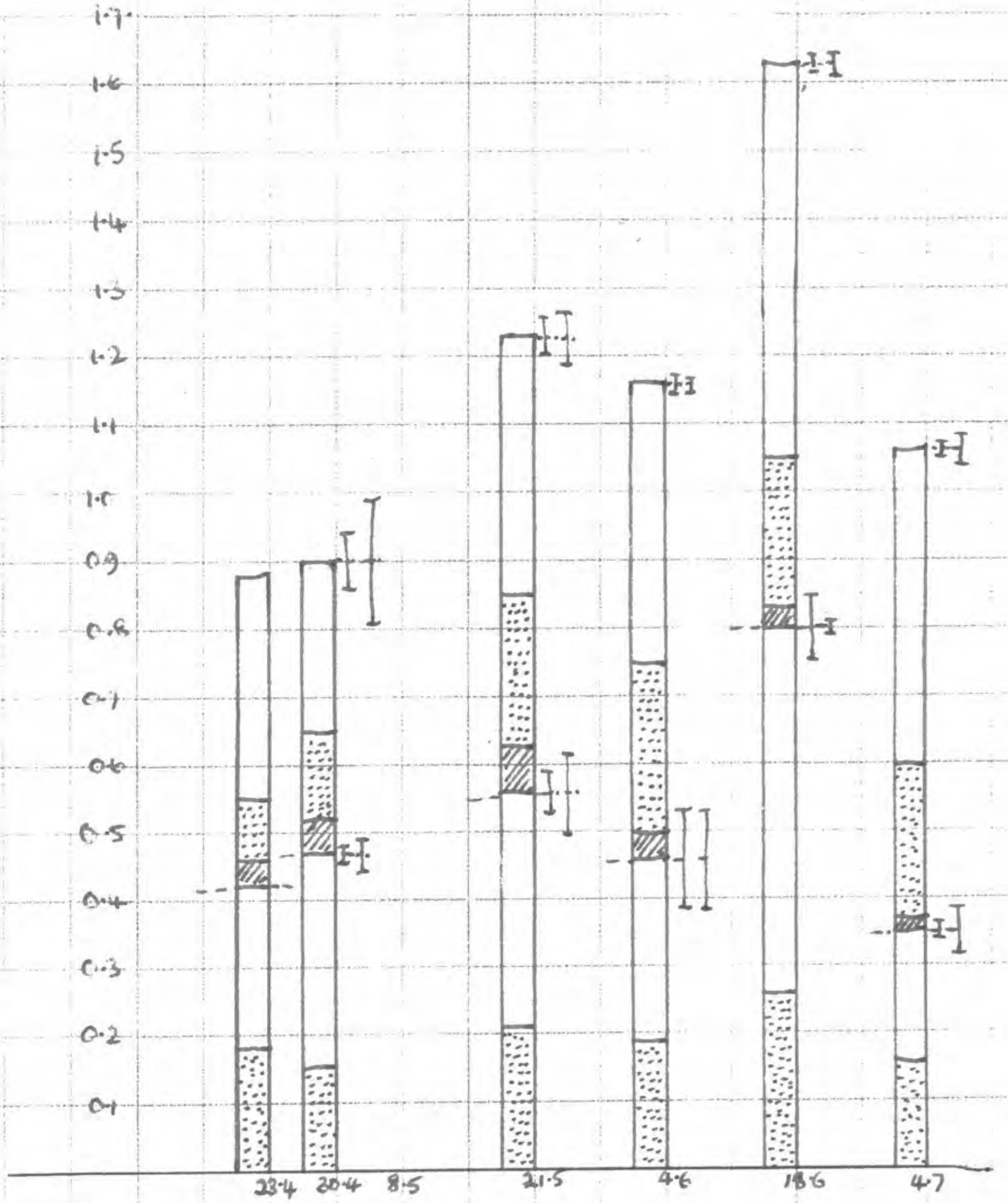
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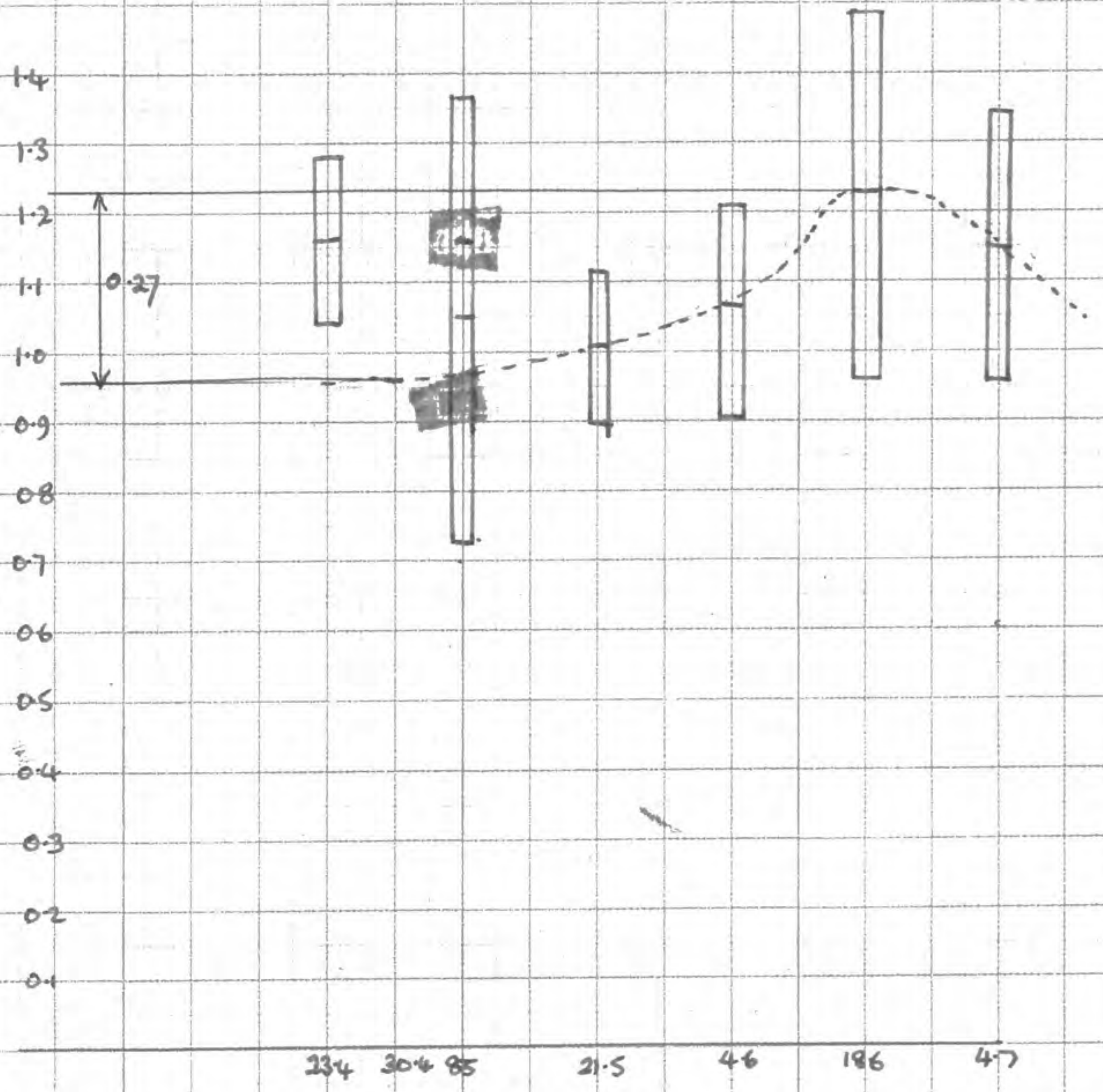


Hollow-Hummock Cycle.

Raised bog vegetation is mixed, like that of blanket bog, and contains most of the same species, but there is a genetic sequence, or rather series of sequences, in the layers of peat which have built up the bog. When the bog has been raised on a substratum of fen the lower layers of the peat record the structure of the fen, and above this come successive cycles of different kinds of bog peat. The existence of these cycles depends upon the fact that the surface of a bog at any given time is not uniform, but consists of alternating hummocks and hollows inhabited by different species. The peat at the bottom of each hollow is built up by the vegetation in the natural process of autogenic succession until it forms a new hummock, the surfaces of the adjacent pre-existing hummocks which have stopped growing thus coming to occupy a lower level than the new hummocks. The old hummocks thus become the sites of new hollows, the old hummock vegetation dies, and is replaced by species characteristic of hollows, these in their turn giving way to new hummock formers. Thus the structure of the peat of a raised bog is lenticular, each lenticle representing a complete cycle of "hollow-hummock" development, and all the phases of the cycle are represented at any given time on the surface of an actively growing bog ("regeneration complex"). The lenticular structure can be clearly seen in vertical section of the peat. The story of raised bog development was first worked out in detail by Osvald in his classical paper on the Swedish bog "Komosse", and the Irish raised bogs are essentially similar, though some of the species are different.

Below are lists of the species occurring in different stages of the "hollow-hummock" development on a typical raised bog surface south of Athlone, in the middle of the central plain.

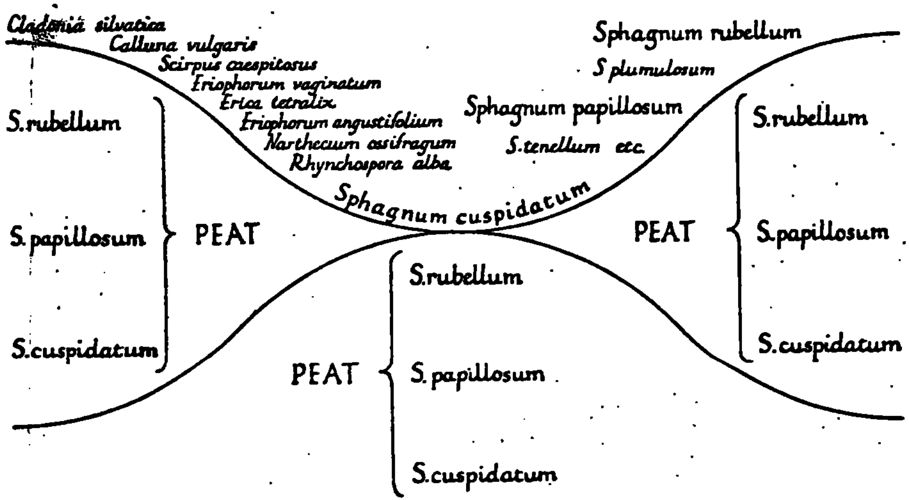


Fig. 189. Diagram of the succession of Species forming the Peat in a typical "Hollow-Hummock" cycle (Regeneration Complex)

Vegetation of seral stages.

Stage 1. Semi-aquatic Sphagnum phase - wet hollow:

Sphagnum dusenii+	d	Rhynchospora alba	o
Eriophorum angustifolium	o		

+ The dominant species of the hollows is generally S. cuspidatum.

Sphagnum cymbifolium and one plant of Narthecium occurred along the margin.

This community is increasingly colonised by vascular plants, species of semi-aquatic bog moss remaining dominant in the lower layer; and thus develops into

Stage 2. Rhynchospora phase - hollow.

Rhynchospora alba	d	Eriophorum vaginatum	o

Narthecium ossifragum	f	Oxycoccus palustris	o
Erica tetralix	f	Sphagnum cuspidatum	d
Andromeda polyfolia	o	S. tenellum	f
Calluna vulgaris	o	Lepidozia sp.	
Drosera anglica	o	Cladonia uncinalis	o
D. rotundifolia	o		

Stage 3. Narthecium phase - hollow.

Narthecium tends to assume dominance at the expense of Rhynchospora, while the semi-aquatic Sphagna and other species retrogress.

In this stage the following list was made.

Narthecium ossifragum	d	Rhynchospora alba	o
Erica tetralix	f	Scirpus caespitosus	o
Andromeda polyfolia	o	Sphagnum papillosum	f
Drosera anglica	o	S. rubellum	o
D. rotundifolia	o	S. tenellum	o
Eriophorum vaginatum	o	Lepidozia sp.	o
Calluna vulgaris	o	Kantia sp.	o

Stage 4. Calluna - Sphagnum rubellum stage.- active phase of hummock formation. In this S. rubellum rapidly assumes dominance in the lower, and Calluna in the upper layer:

Calluna vulgaris	d	Oxycoccus palustris	o
Erica tetralix	f	Rhynchospora alba	o
Eriophorum vaginatum	f	Sphagnum rubellum	d
Andromeda polyfolia	o	Hypnum schreberi	o
Drosera rotundifolia	o	Kantia sp.	o

Eriophorum angustifolium	o	Mylia sp.	o
Narthecium ossifragum	o		

Stage 5. - Calluna - Cladonia stage - last stage of hummock, in which the Sphagna have lost dominance and are dying.

Calluna vulgaris	d	Cladonia sylvatica	a
Erica tetralix	f	C. uncialis	o
Eriophorum vaginatum	f	Sphagnum rubellum	) f
E. angustifolium	o	S. plumulosum	) but
Andromeda polyfolia	o	S. tenellum	) dying
Narthecium ossifragum	o	Kantia sp.	
Oxycoccus palustris	o	Riccardia sp.	a
Scirpus caespitosus	o	Lepidozia sp.	

+ Sir A.G. Tansley. The British Islands and their Vegetation.

APPENDIX III

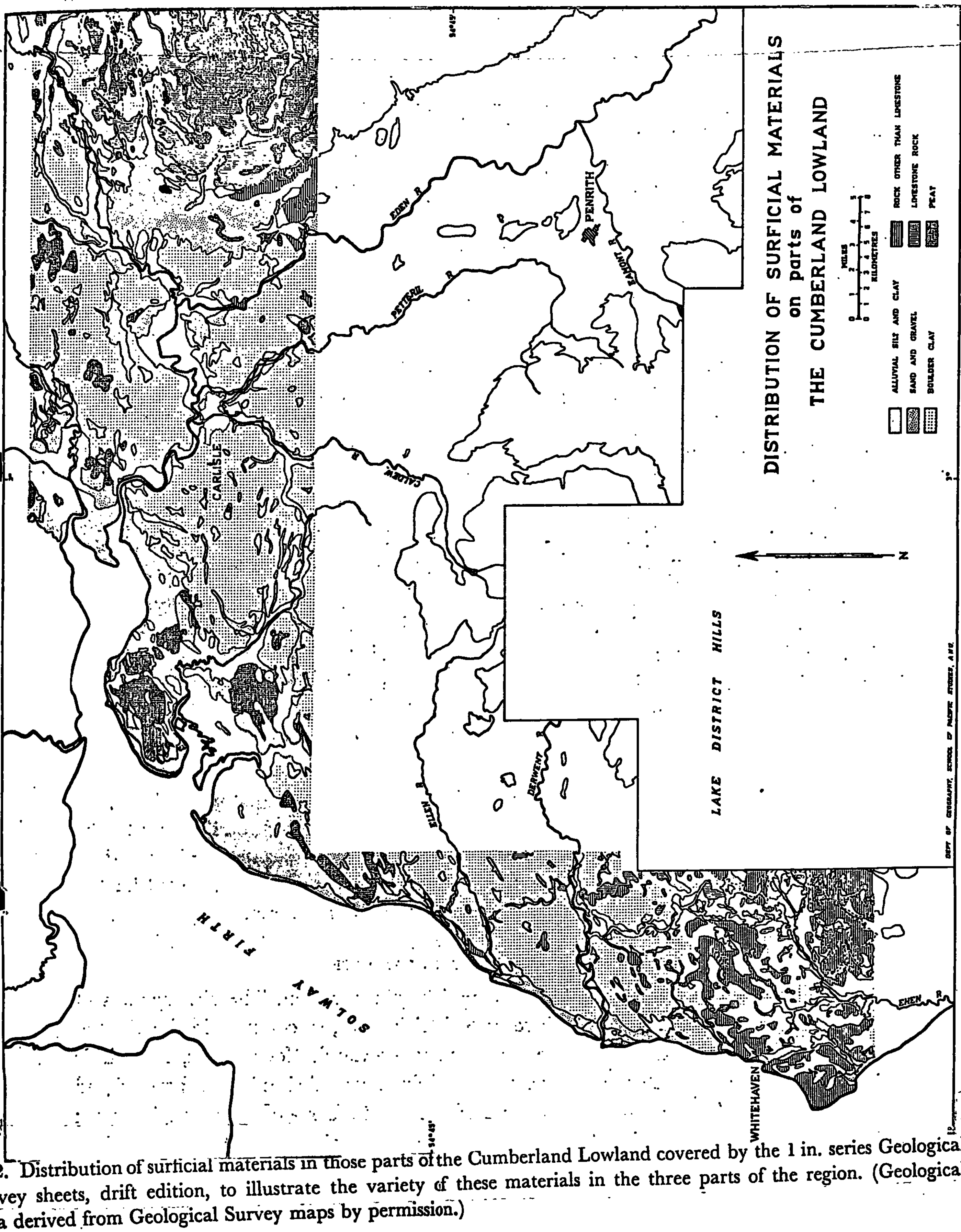
INTRODUCTION

Foreword

The choice of the Cumberland Lowland offered the possibility of allowing the investigation of the significance of the Scottish Readvance Glaciation and the chronology and extent of the post-Glacial marine transgression and regression. Moreover, the history of human settlement of the area is comparatively simple.

Of the parts which follow this introduction, three are devoted entirely to the presentation of factual information together with the minimal interpretation which is necessarily implied in the very zonation of the pollen diagrams. The next part presents data from sites associated with changes in land and sea level and goes on to discuss the chronology of these changes. The final three parts, which are of a more speculative nature, strive to interpret these data in terms of the ecological history of the region and to derive such conclusions as seem valid about the geographical processes, climatic changes and history of human settlement.

All the work on which this paper is based was carried out between 1949 and 1961 whilst the author was a member of the University Sub-department of Quaternary Research,



IGURE 2. Distribution of surficial materials in those parts of the Cumberland Lowland covered by the 1 in. series Geological Survey sheets, drift edition, to illustrate the variety of these materials in the three parts of the region. (Geological data derived from Geological Survey maps by permission.)

Cambridge. Any valuable contribution which it may contain is due to the constant help and guidance of Professor Harry Godwin, F.R.S. and to the author's colleagues during that time, particularly Dr. A.G. Smith, Dr. R.G. West, Dr. E.H. Willis, Dr. F. Oldfield and Miss R. Andrew. The help given by Miss C.A. Lambert is acknowledged with especial gratitude. In the early stages of the work the advice of Professor S.E. Hollingworth and of the late Professor W.B.R. King was of inestimable value. In the field the work was greatly facilitated by the ready co-operation of the landowners on whose property it was carried out and by those who helped either physically or with good advice, amongst them Dr. D.A. Ratcliffe, Dr. B. Seddon, Mr. B. Blake, Mr. W.H. Alp, Miss K.S. Hodgson and Miss C. Fell. Mr. H. Gunther and Mrs. C. Daniel drew the maps for this Introduction and Mr. L. Pancino prepared many of the other diagrams. To all of these the author is most grateful, but his greatest debt is undoubtedly to Mr. E. Blezard, Curator of Tullie House Museum, Carlisle, whose depth of understanding of Cumberland natural history has been an inspiration to many and whose personal interest in this work has so often revitalized the author when his enthusiasm has flagged.

GEOGRAPHY AND GEOLOGY OF THE REGION

The county of Cumberland lies in the north-west corner of England, between the Pennine Hills and the sea, from about 54° 10' N on the west coast and 54° 40' N inland near Penrith to 55° 0' N at the head of the Solway Firth and 55° 15' N in the north-east where it meets the boundaries of Scotland and Northumberland. In the north-east of the county the high Pennines join the Southern Uplands of Scotland and the greater part of the south-west is occupied by a part of the mountainous English Lake District (or Lakeland Hills). Between these two blocks of high ground the Rivers Caldew, Petteril, Eden, Irthing, Lyne and their tributaries drain wide lowland valleys into the head of the Solway Firth near Carlisle. The lowland extends south-westwards from the Carlisle district around the edge of the Lake District Hills narrowing to about 11.5 km (7) near St. Bees Head and to less than 1.5 km (1) farther south.

The Cumberland Lowland, as the term is used in this paper, is arbitrarily defined as that part of the area described above which lies below the 230 m (750 ft.) contour of altitude and excluding valleys below that level but less than 5 km (3) wide. Between the Lake District Hills and the Pennines, the county boundary with Westmorland, which there runs along the Rivers Eamont and Eden and Crowdundale Beck (about 54° 40' N), is used. The northern boundary lies along the River Lyne from the Solway Firth to Bewcastle; then south-south-eastwards across the River Irthing to Denton Fell, thereby excluding the upland moorland areas of the Irthing catchment and the Tyne Gap. Thus defind, the Cumberland Lowland forms a crescent the arms of which are the coastal strip and the Eden-Petteril valleys, with a slight north-eastern extension. It is the south-eastern part of a more extensive, more natural, unit which includes all the lowland bordering the Solway Firth. The central area of the crescent is frequently referred to as the 'Carlisle Plain', the eastern arm as 'Eden-side' and the western arm as the 'coastal fringe'. The hills which border so much of the region rise steeply from the 230 m contour, or from just below it, except in the district immediately north-west of Penrith where the tract of Carboniferous Limestone rises gently westwards to the foot of the steeply climbing Ordovician hills.

The Cumberland Lowland contains few striking topographic features which are not ascribable to drift deposits, either Glacial or post-Glacial in origin. The River Eden, however, has carved deeply through the drift and into the underlying sandstone creating a gorge along several miles of its course. On each side of the river the sandstone occasionally rises above the 230 m contour, as at King Harry's Common (240m) and Lazonby Fell (245m) but these 'islands' of higher land are never more than 2 km^2 in extent. In the south-west, the normally gentle meeting of the coastal fringe with the sea is broken at St. Bees Head by a block of sand stone about 13.5 km^2 in area rising to 147 m O.D. forming a cliffed coastline 91 m high and about 5 km long.

Apart from these features, where the solid rock is exposed or covered with a thin layer of sedentary soil or peat, the whole region is shrouded in glacial drift which in turn is partially covered by post-Glacial deposits. Trotter and Hollingworth (1932a) have compared the sequence of glacial drifts in the region with that in Southern Scotland (Charlesworth 1926) and in Northumberland (Smythe 1912 and have suggested correlations with drift sheets elsewhere in England. Smith (1931) correlated the glacial episodes of Cumberland with those of the Isle of Man. The general sequence of glaciations and interglacials developed by these authors seems to have been generally accepted (Charlesworth 1957) in spite of the contrary views of Carruthers (1939, 1947, and in Hollingworth et al. 1950).

An early glaciation of Scottish origin (the Early Scottish) has been proposed to account for the occasional outcrops of boulder clay below the Main Glaciation drift and separated from it by laminated clays; as at Langwathby (Goodchild 1875), or sand and gravel, as near Whitehaven (Eastwood, Dixon, Hollingworth & Smith 1931). This early boulder clay is usually deeply weathered and rich in Scottish erratics. It is to this glaciation that the transport of

Lake District rocks to the east coast of England via the Tyne Gap (150 m O.D.) is attributed together with the piling of ice around the Isle of Man. These distributions can only be explained by assuming a great reservoir of ice in the northern part of the Irish Sea which flowed outwards, overtopping the Lake District and forcing ice up the Eden Valley. The melting of this ice is documented only by gravel, sand and laminated clay in isolated occurrences indicating that the ice certainly retreated from the lower ground. But the only evidence for a temperate climate before the onset of the next glacial phase is a tooth of ox found in sand beneath Main Glaciation boulder clay near Appleby (Dakyns, Tiddeman & Goodchild 1897). Since it is not known whether Early Scottish drift occurs beneath this sand, this evidence indicates, at the most, a climate tolerable by this animal at any time before the onset of the Main Glaciation. There is therefore no critical evidence for an interglacial period in the modern sense of the terms (West & Godwin 1958; Jessen & Milthers 1928) between the deposition of the Early Scottish drift and that of the Main Glaciation.

At the onset of the Main Glaciation, ice moved outwards from the Lake District Hills on to the coastal fringe, the Carlisle Plain and the Eden Valley. Ice from Scotland deflected the north-bound Lake District ice westwards around the northern fringe of the hills and southward down the west coast. The ice ponded up in Edenside escaped over Stainmoor (440 m O.D.) and Grayrigg (260 m O.D.) and across a col into the South Tyne valley at 570 m (1900 ft.) O.D. The distribution of erratics suggests that the ice in the Eden Valley during the maximum of the Main Glaciation stood about 760 m above present sea level and only the highest of the northern Lake District peaks can have escaped glaciation. The absence of well-marked frontal moraines in the region and the wide distribution of kettle-holed sand and gravel drift suggest that there was little intermittent forward movement during the general retreat from the Main Glaciation, except in the case of the Gosforth Oscillation (Trotter, Hollingworth, Eastwood & Rose 1937), but that the ice melted more or less in situ from its shallower edges northward towards Scotland.

After the ice had vacated the gegion, there was a separate readvance from Scotland onto the Carlisle Plain and the coastal lowland known as the Scottish Readvance Glaciation (Trotter 1929; Trotter & Hollingworth 1932a). The distinct and separate nature of this glaciation depends on the evidence of large areas of sand, gravel and water-deposited clay of the retreat from the Main Glaciation which are overlaid by and partly incorporated into an overlying boulder clay containing Scottish erratics. The time interval between the two glaciations is unknown but must have been long enough for the withdrawal of ice north of the Solway Firth and the accumulation of considerable depths of varved clay later overridden by the readvancing ice (e.g. at Linstock Castle, Lanercost). A peat bed exposed beneath supposed Scottish Readvance boulder clay south of St. Bees Head and from which plants of temperate modern distribution were recovered (Eastwood et al. 1931), is not now available for study. Similar deposits in the same cliff are not covered by boulder clay and date from the late-Glacial and post-Glacial periods after the Scottish Readvance (Walker 1956). It is possible that the boulder clay above the originally described peat was not in its primary position and that the plants contained in the peat were therefore no indication of conditions during the Main Glaciation - Scottish Readvance interval. The Readvance was probably rapid and of short duration. Only a few drumlins were formed and pre-existing drumlins of the Main Glaciation were only slightly modified. It left no terminal moraine but, at its maximum, the outflow of the Eden and adjacent rivers was blocked by ice and the lake so formed drained eastwards for a short period through the Gilsland overflow at 133 m O.D. In the earliest stage of retreat the level fell to 121 m O.D. and drainage was westwards to the Irish Sea. Although the stages of its retreat northwards are well documented by overflow channels (e.g. Hollingworth 1931), the outwash fans are small and the strand-lines and notches of pro-glacial lakes were impersistent. These features suggest that the ice was relatively clean and that it melted fairly rapidly.

There is evidence, therefore, for three invasions of the region by ice: the Early Scottish Glaciation, the Main

Glaciation and the Scottish Readvance. The Main glaciation is undoubtedly a part of the Newer Drift Glaciation of Great Britain and there is little evidence within the region of the length or climatic character of the intervals before it and between it and the Scottish Readvance Glaciation.

The main event which has considerably modified the topography left by the melted ice, apart from local solifluction, soil creep, etc., has been the inundation of the coastal areas by the sea and the consequent modification of the river valleys, particularly in their lower reaches.

The river systems draining the region must have been affected by these changes in base level, at least in their lower courses. During the early period of low relative sea level it is probable that the rivers excavated quite deep valleys in the soft drift lowlands but, with the rising sea, these valleys would be flooded and the transporting power of the streams diminished. A multiplicity of terraces exists along most of the river valleys but, although those at similar levels have been grouped for ease of mapping and description, it is not possible certainly to equate any riverine stage with events on the coast. Ignoring the uppermost group of terraces, which are restricted in distribution and probably of late-Glacial date, alluvial terraces are well developed up to about 110 m O.D. in the Irthing valley, about 60 m O.D. on the Gelt and about 45 m O.D. on the Eden, but hardly exist on the Rivers Ehen and Irt. The development of terraces clearly depends on a complex of geographical factors, amongst which the base level, represented by the sea, is only one although a most important one in the estuaries. Nevertheless, it is useful to note that at no time during the post-Glacial period was the area of riverine flood plain more than twice its area at the present day.

The hollows in the glacial drift are invariably partly filled with sand and gravel, but many also contain peat bogs (e.g. Hayton Moss, Moresby Moss, Hallsenna Moor) or fens (Bigland's Moss). Large bogs have developed on some of the marine deposits near the coast (e.g. Bowness Common, Wedholme Flowe, Salta Moss) and smaller ones on associated river alluvium (e.g. Pow Beck valley, St. Bees). Some of the lower drift hills carry bogs which are totally ombrogenous (e.g. Broomhill Moss) but the main spread of Pennine blanket bog does not extend far below the 500 m contour, although on the western margins of the Lake District fells it is not uncommon down to 300 m O.D.

The nature and distribution of these various superficial deposits allows the Cumberland Lowland to be divided into subregions.

The first of these lies between the River Petteril and the foothills of the Pennines, including the Eden Valley. Here the topography is broken; there are very few areas which are even moderately flat. The dominant topographic unit is the steep-sided hill or ridge, separated from its neighbours by deep, narrow, channels in which the drainage is often impeded. There are also many completely enclosed hollows of a variety of depths and sizes but all with steep banks. A little solid rock, mostly coarse-grained sandstone, outcrops at the surface. The hilltop soils are light, leached and covered by a mor humus where they have escaped disturbance. In the hollows has accumulated much of the finer grain material from above, although, even so, the soils are but rarely clayey. Many such localities are perennially waterlogged. Between these two contrasting situations are the steep, unstable, slopes.

Between the River Petteril and the sea, bounded in the south-west by the River Calder, lies an area of quite different topography. Extensive, rolling, boulder clay flats are cut by steep-sided, wide, meandering channels, uusually flat bottomed and containing misfit streams. Little, if any, solid rock reaches the surface. Soils are heavy and overall drainage is poor, with a strong tendency to fen development in the valley bottoms. Some of the channels contain swifter-flowing rivers or streams which havedeposited alluvium along their banks. Although undistrubed soils are now very rare, in the few profiles observed there is strong evidence of leaching in the uppermost metre but no sign of podzol development.

South of the River Derwent, the third area has characteristics intermediate between those of the other two, than either of which it is much smaller. Small patches of solid rock, mostly limestone and sandstone, frequently occur at the surface. For the rest, broad sweeps of boulder clay are punctuated here and there by small, sharp-featured, patches of sand and gravel. Drainage is good, except on the larger boulder-clay tracts.

These last two areas are much more susceptible to wind blast from the south-west than is the first. There is no significant rainfall gradient across the region and, except for the very edge of the coast, snow lies almost as long in the west as the east.

The Pollen Diagrams

Where the site condition allowed, series of samples for pollen analysis were only made after a thorough stratigraphic investigation of the deposits. This investigation was intended primarily to allow the reconstruction of the processes of accumulation at the site. The stratigraphic data itself was frequently of direct value in assessing ecological changes in and around the site. One series of samples was collected at the site from the point where the longest and least interrupted history of accumulation was expected and where vegetation changes of the most severely local kind were likely to be poorly represented.

The vertical interval of sampling, much of which was carried out with a Hiller-type borer, was determined partly by considerations discussed below and partly by the suspected rates of accumulation of the various materials. Particularly close sampling was usually carried out around major stratigraphic breaks or horizons of special archaeological or geological significance. Only very rarely did the vertical interval between samples exceed 10 cm. Except in special cases the vertical thickness of each sample was restricted to 1 cm. All samples were stored wet and prepared by treatment with dilute potassium hydroxide followed by acetolysis and chlorination. The pollen grains were then stained and mounted in glycerine jelly or glycerine. The debris sieved off after the potash masceration was examined and rough assessments made of the abundance of the various identifiable and unidentifiable consituents. These results are presented with the pollen diagram and provide another valuable control on interpretation comparable with that of the stratigraphic record.

A pollen spectrum is a good estimate of the actual pollen content of a sample only if a sufficient number of pollen grains contribute to it. The size of this 'sufficient number' depends on the number of different pollen types present in the sample and the accuracy with which their separate frequencies need to be determined. In general practice the total number of pollen grains counted from a sample is usually much greater than the number of types identified and no serious error is introduced here. Throughout a diagram, however, the number of types may change suddently as, for instance, between the end of the late-Glacial and the beginning of the post-Glacial. In such cases the frequencies of any particular pollen type from sample to sample have significance which is not constant because the bases on which they are calculated (i.e. the 'pollen sum') should be related to the number of types in the sample. In most parts of pollen diagrams this consideration is not likely to be a serious source of error because the number of types counted varies only slightly from one sample to the next.

Attempts to improve the accuracy with which the frequencies of individual types can be determined have led to the use of very large 'pollen sums' in much recent critical work. The minimum total count which gives a dependable and reproducible estimate of the real frequency of types in a sample is clearly smaller for the few types which contribute the bulk of the sample than it is for those which occur only rarely in it. On the other hand, where the same 'pollen sum' is used for calculating the frequencies of both common and rare types, the random error in the assessment of the latter remains much greater than in the assessment of the former. Comparable percentage changes at very different absolute levels e.g. 40 to 20% and 0.4 to 0.2%, are not equally significant. Only the use of exceedingly large 'pollen sums' can give the assessment of very small frequencies useful statistical significance. These limitations apply particularly to comparisons between two samples only. Where a change in frequency progresses in one direction through a series of samples the validity of this change is enormously enhanced. It is evident, therefore, that for a given effort, i.e. a given total of pollen grains to be counted in a whole diagram, more reliable information can be obtained by counting a large number of closely spaced samples than by counting very large 'pollen sums' in a few widely spaced samples, provided always that the 'pollen sum' of each sample is large compared with the number of types in it.

In the analyses presented in this paper, therefore, detail was investigated by close sampling rather than by recourse to large counts of a few samples. Moderately small 'pollen sums' were used (150 to 500 grains) in numerous samples, closely placed (2 to 5 cm). Little significance is attached to the appearance of a pollen type in an isolated sample, whatever its frequency there, except as a record of its presence. Similarly, changes of frequency which in reality represent only differences of a very few grains between a pair of counts are not generally used for interpretation. Progressive changes of frequency in one direction through a series of samples, however small, are given considerable weight, as are phenomena which occur in comparable positions in several diagrams from different sites or from different points at one site. In order to detect significant changes to which pollen types individually present in insignificant amounts contribute, such types have often been grouped together. Indiscriminate grouping produces biologically meaningless results and every effort has been made to include only ecologically similar plants within any one group.

In the majority of the analyses reported in this paper the primary counts and zonation were based on pollen sums comprising the tree types only. Improved technique, and sheer abundance of data, now result in pollen diagrams which include a wealth of information about the vegetation they represent far in excess of that required for this kind of zonation. Details of the floristic composition of communities, ecological differentiation from place to place as well as information on the processes of change from time to time can be discerned. Without detriment to the standard zonation scheme, therefore, additional 'zonations' may often be applied to pollen diagrams in order that these details and processes may be more easily compared from site to site within a region. In order to retain its chronological validity, the standard zonation must depend only on the widely distributed, anemophilous, physiognomic dominants of the vegetation and on major changes in their components. These are the criteria which have been used in the standard zonation of the diagrams presented in this paper. A subsidiary zonation might not seek chronological validity as its primary aim, however; rather should it attempt to define both periods of change and periods of stability in the vegetation represented at a site and in this way to focus attention on process and change and ecological differentiation! But the data from each site are themselves complex and derive from a variety of ecological situations. In order to achieve anything, therefore, each subsidiary zonation must apply only to closely related ecological groups. In the primary diagrams from the Cumberland Lowland one subsidiary zonation has been applied throughout whilst a second, related only to forest clearance phenomena, has also been used where it seemed appropirate to the data. The first subsidiary zonation is based on the curves for trees, shrubs and land herbs. Where the significance of changes is in doubt, the plants of wetter habitats, including trees such as Betula and Alnus, have been excluded from consideration in favour of those more certainly restricted to dry land. In practice, as might have been expected, this subsidiary zonation has resulted mainly in the subdivision of the standard British zonation. Partly because of this parallelism and the basis on which the subsidiary zonation is founded and partly because the same sequences of events were detected in almost all the diagrams under consideration, this subsidiary zonation is thought to have some limited and approximate chronological value within the Cumberland Lowland and has been styled the 'Cumbrian Zonation'. It is certainly not anticipated that it will prove of any value outside the region. The extensive, but variable, impact of human activities on the vegetation during the last 5000 years has been such that it is unlikely that a chronologically valid zonation of wide application will ever be achieved which does not depend on a physical dating technique. In the present work every effort has been made to dissociate the initial zonation from the more obvious manifestations of human activity, but it would be misleading to pretend that many of the features used in this zonation might not be amongst the more subtle effects of human interference with the ecosystem. Until human economic prehistory is much better documented than at present, any zonation of post-Mesolithic vegetation history must remain chronologically suspect.

In zoning the pollen diagram an attempt has been made to distinguish regional from local phenomena. Thus, in the post-Glacial period the general trend of the curves for the commoner trees which were certainly not contributing to any hydrosere, viz. Quercus, Pinus and Ulmus, were used to give a very broad general indication of changes in the forest at large. The technique employed was to recalculate the frequencies of these pollen types as percentages of their combined sum and then to smooth the resulting curves arithmetically. Although a general picture of progressive changes amongst the physiognomic dominants of the dry-land forest was obtained in this way, it was hardly representative of the vegetation as a whole so that the position of zone boundaries, generally indicated as described above, were finally fixed by taking a wider range of pollen types into consideration.

STRATIGRAPHY AND POLLEN ANALYSIS AT MOORTHWAITE MOSS

Moorthwaite Moss lies in a kettle hole in the Main

Glaciation drift outside the limit of the Scottish Readvance Glaciation, south-east of Carlisle in Cumberland. The bog has developed over a lake initiated early in the deglaciation of the region and pollen diagrams, zoned according to the standard British and local Cumbrian schemes, indicate accumulation of deposits from a very early stage of the late-Glacial period. The present bog surface is secondary and anthropogenic but, in spite of removal or oxidation of the upper peat, undisturbed deposits as young as about 1500 B.C. are thought to be present at the site. The ecological history of the mire has been reconstructed so far as the stratigraphic and pollen analytical data allows. Among the most interesting subfossil remains recorded are those of Betula nana, Cardaminopsis cf. petraea, Koenigia islandica, Linum usitatissimum, Potamogeton filiformis and Lycopodium annotinum.

Introduction

Moorthwaite Moss occupies a kettle hole in the drift of the Main Glaciation at about 120 m O.D. Moorthwaite Moss is 11 km (7) east-south-east of Carlisle on the east bank of the River Eden. Along this part of its course the River Eden flows northward between steeply sloping banks which rise on each side between 30 m and 75 m. The bedrock, Penrith Sandstone, is exposed in this gorge but the greater part of the surface is overlaid by thick deposits of glacial drift. 5 km east of Moorthwaite the main slopes of the Cross Fell range begin to rise and peaks almost 600 m high lie within 13 km of the site. The narrow strip of land between the river and the foot of the mountains is thickly spread with deposits, mostly sand and gravel, of the Main Glaciation, except where hills of solid rock, sandstones and shales, protrude to heights of about 230 m O.D. The drift features themselves are very fresh, pocked by kettle holes and cut by overflow channels. Westwards, the valley of the River Eden is divided from that of the River Petteril by a strip of land about 5 km wide in which the sandstone hills again rise to over 210 O.D. In this region the overlying drift is predominantly boulder clay, of the Main Glaciation in the south and the Scottish Readvance in the north, and in consequence the features are less steep than those east of the River Eden. The south-eastern limit of the Scottish Readvance Glaciation lies 1 km from Moorthwaite Moss.

GEOGRAPHY AND STRATIGRAPHY

Moorthwaite Moss (Nat. Grid.Ref. 510510)

Moorthwaite Moss lies in a hollow on top of a hill at 120 m O.D., 2 km south-south-east of Cumwhitton village. Westwards, the hill falls fairly evenly to the River Eden, 2 km away (1) at 40 m O.D. To the south and east it falls within 0.5 km to the Chapplewell Beck running just below the 120 m contour. Northward, 0.5 km from the Moss edge, the hill forms the south-western edge of a partially enclosed hollow containing a larger bog, Cumwhitton Moss. The crest of the hill surrounding Moorthwaite Moss does not rise more than 9 m above its surface. The slopes of the hollow are not very steep above the peat surface. There are no natural inflowing streams, but the narrowest and lowest part of the surrounding rim at the north-west corner, across which an artificial drainage ditch has now been dug, probably served intermittently as a natural outflow in the past. The hill is mainly composed of a rather sandy boulder clay, but its eastern flanks are covered by outwash sand of Stages K and M in the retreat of the Main Glaciation ice, an extension of which drift forms an ose train around the northern edge (Trotter 1929). Deltaic sands of a later stage are banked against the slope of the valley of the River Eden 1 km west of Moorthwaite and rise to 114 m O.D. The limit of the Scottish Readvance Glaciation lies immediately west of this accumulation.

The hollow now occupied by Moorthwaite Moss became free of the general ice cover after Stage M of the retreat of the Main Glaciation ice. When the delta was formed at 114 m O.D. the rim of the hill surrounding the hollow must have stood above the waters of the pro-glacial lake and presumably, as the ice retreated farther northward and westward, more and more land emerged as the lake level fell. Subsequently, when the Scottish Readvance ice at its maximum stood across the valley of the River Eden here, its pro-glacial lake stood at 133 m O.D. completely immersing the Moorthwaite hill. It had emerged again, however, by the first documented retreat stage of

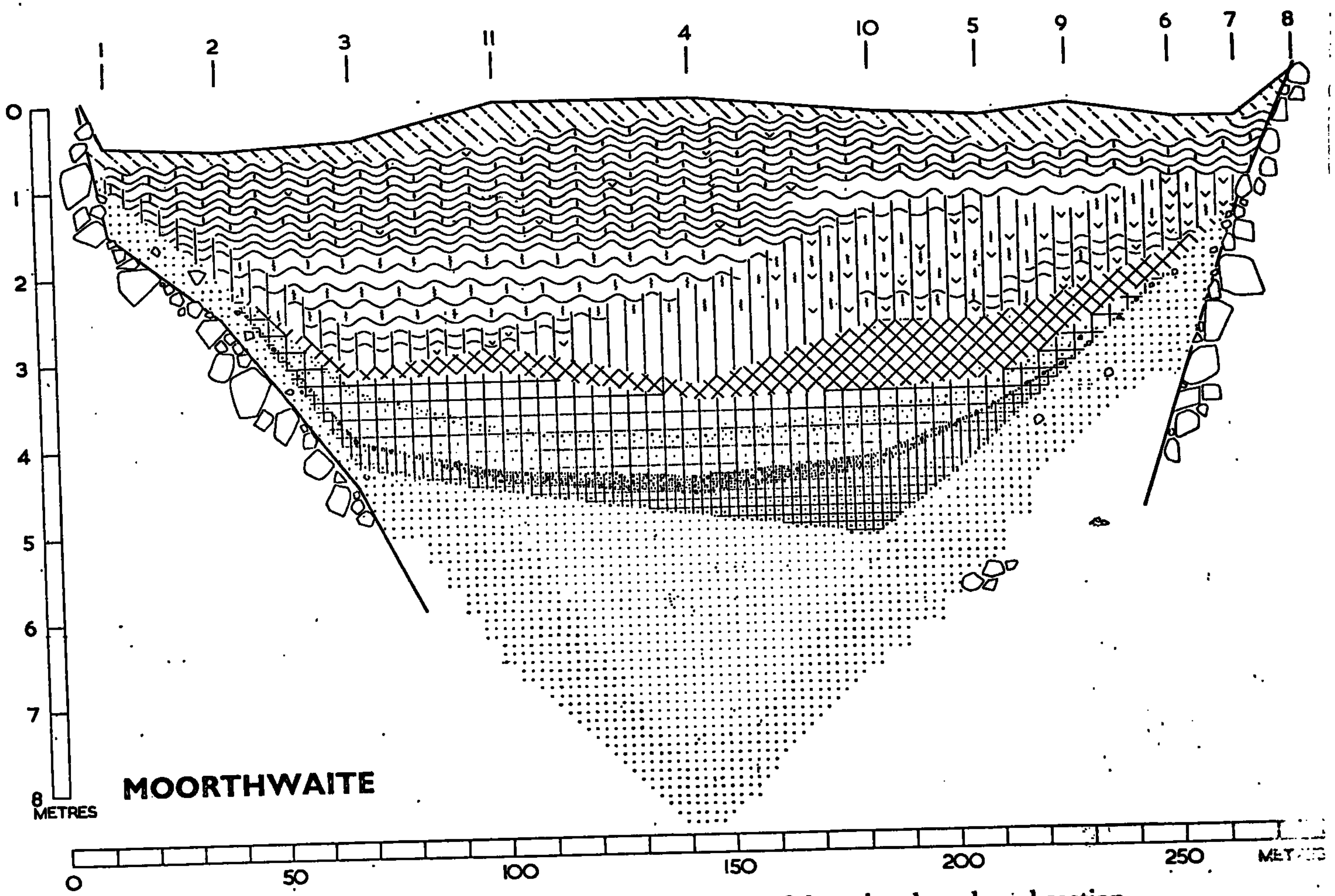


FIGURE 12. Moorthwaite Moss. Stratigraphy of deposits along bored section (cf. figure 11*b*).

the Scottish Readvance (stage R.A., Trotter 1929) when the glacial lake stood at 115 m O.D. and the hollow on the hill contained an isolated pond.

Moorthwaite Moss is now roughly oval in shape, enclosed by gently rising slopes. The surface peat has been cut away for fuel in the past as the old cutting banks and the boundary stones show. It is now covered with a more or less open woodland of Pinus sylvestris with some Betula pubescens, both of which are regenerating and which might all be subspontaneous from an old plantation, now destroyed, on the southern margin of the bog. The drier areas, particularly the baulks of peat left between the old cuttings, bear a vegetation dominated by Calluna vulgaris, but here and there this is replaced by Vaccinium myrtillus and Molinia caerulea. The cuttings themselves are filled with undulating swards of Sphagnum dominated communities amongst which S. magellanicum and S. papillosum and particularly abundant. Oxycoccus palustris, Rhyncospora alba, Narthecium ossifragum and Erica tetralix are also common in these communities.

The stratigraphy of the deposits was investigated by a single series of borings running across the bog, the findings of which were confirmed by six additional borings made near the eatern end of the basin. The boulder-clay slopes fallaway very steeply within the limits of the basin and were not proved in the centre where borings did not penetrate more than 9 m from the surface. Lining all but the rim of the basin, and increasing in thickness towards the centre, is a deposit of red sand and gravel, occasionally containing lenses of clay. In the centre, this deposit surrounds a deep pocket of compact, stiff, pink silt with occasional laminae of sand and clay. The maximum depth of this pocket is about 3 m and at the top the silt passes upwards into a grey, silty, clay-mud with rare coarse sand grains. The uppermost layers of this material extend laterally beyond the edges of the silt-filled pocket where they directly overlie the basal sand and gravel fill. A layer, 10 to 15 cm deep, in which the clay-mud is coarsely sandy, marks the top of the silt-filled pocket. The uppermost 15 cm of the clay-mud contains abundant coarse sand and gravel and is difficult to penetrate in some places. Over the greater part of the section this gravelly clay-mud and the sandy gravel into which it passes marginally are overlaid by a layer of brown nekron mud up to 1 m in thickness and containing frequent remains of Potamogeton spp. and Myriophyllum alterniflorum. Sand and silk are, on the whole, rare in this material except in a rather well marked zone up to 20 cm in thickness where coarse sand occurs commonly in closely spaced horizontal laminae. Except at the extreme edge of the section the nekron mud passes almost insensibly upwards into a mud darker incolour, richer in organic detritus and entirely free of sand or silt. Fragments of sedge leaves are frequent as are seeds of Nymphaea alba ar fruit-stones of Potamogeton spp. Over the greater part of the section this mud becomes more coarsely detrital at the top, remains of Carex spp. and Phragmites communis becomming very common. Sphagnum leaves (mostly S. cuspidatum) are frequently found in this layer and, over the soutern half of the section, become progressively more abundant as the mud grades into the Sphagnum peat which directly overlies it. At its deepest continuous part this peat is 2.5 m thick, of a slightly varying, deep brown, colour and varying humification (H- 5-7). Nohorizontally consistant changes were traced between borings. Over the northern half of the section the detritus mud is coarser and rich in wood fragments (particularly Betula and Alnus) and reaches a maximum thickness of 2 m. It is overlain by the northern extension of the Sphagnum peat. The interface between the detritus mud and the Sphagnum peat rises northward between borings 10 and 11, suggesting that the two deposits were accumulating over the same period whilst the peat-producing communities slowly encroached on those producing the detritus mud. The uppermost layer is composed of the peat, which there contains occasional woody fragments and frequent remains of Eriophorum vaginatum. The surface has been cut and the deposits are commonly distrubed to a depth of 30 to 50 cm.

POLLEN DIAGRAMS AND CHRONOLOGY

At Moorthwaite Moss samples for pollen analysis were collected from Boring 10 where the deposits were described in the field as follows:-

cm	
0 - 50	disturbed and oxidized peat
50 - 75	dark brown, coarsely fibrous peatl H8
75 - 95	medium brown Sphagnum peat with some Eriophorum vaginatum. H5
95 - 105	unconsolidated, woody, Sphagnum peat. H7
105 - 120	very woody, medium brown, coarse detritus mud
120 - 185	medium brown coarse detritus mud with frequent fragments of Alnus and Betula wood
185 - 191	yellow wood in peaty matrix
191 - 218	dark brown, amorphous, mud with traces of Sphagnum
218 - 240	Carex-Sphagnum peat, medium brown, with abundant Menyanthes seeds at 225 - 230 cm
240 - 250	transitional mud
250 - 294	moderately fine detritus mud with frequent seeds of Nymphaea alba and potamogeton natans
294 - 320	dark brown nekron mud with occasional laminae of lighter brown mud
320 - 348	medium brown, slightly sandy, nekron mud with laminae of lighter coloured, more sandy, mud
348 - 350	abundant sand laminae in buff mud matrix
350 - 371	abundant sand in mud
371 - 377	slightly sandy, dark brown, mud with indistinct laminae
377 - 395	coarse sand and pebbles in mud matrix
395 - 411	fine grey sand with occasional pebbles
411 - 475	grey, silty clay-mud with rare sand

cm	
475 - 482	transition
482 - 490	pink sandy clay-mud
490 - 700	coarse red sand

ECOLOGICAL DEVELOPMENT OF THE MIRE

Moorthwaite Moss

The deep, steep-sided, basin now occupied by Moorthwaite Moss is almost certainly a kettle hole created by the melting of a residual ice block left behind after the general retreat from the locality of the ice cover of the Main Glaciation. There is no way of knowing at what stage in the general deglaciation this block finally melted, except that is must have post-dated Stage M of the retreat and is unlikely to have persisted very long under climatic conditions which resulted in the general deglaciation of the Carlisle Plain. It is very likely that the red sand and gravel lining the hollow is morainic material which melted out of the isolated ice block itself. By that time, the hollow containing a lake was probably isolated from the pro-glacial lake between the ice front to the north-west and the Pennine foothills and Penrith Sandstone ridge to the east. Much of the surrounding countryside would still have been flooded and only hills rising above 150 m O.D. are likely to have been entirely free of the effects of a high water-table. The Moorthwaite hollow itself can never have received very much drainage water, the area of land from which it could possible do so being rather less than 1 km^2. The only outlet, however, was across the watershed

Table 2

		Moorthwaite Moss						Abbot Moss					
		I	II	III		IV–V	VI	I		II	I–II	IV–V	VIIa
		C	C	C	C	C	C	C	C	C	C	C	C
species	remains	4	5	7	8	9	10	3	4	5	3+4 +5	9	14
Betula nana	fr	.	.	.	.	.	.	+	.	.	.	.	.
*B. pubescens**	fr+sc	.	.	.	.	+	+++	+	.	.	++	++	.
B. verrucosa	sc	.	.	.	.	.	+	.	.	.	.	.	+++
Cardaminopsis cf. *petraea*	s	.	.	.	.	.	.	.	.	.	+	.	.
Carex sp.	n	.	.	+	+	.	.	+	.	.	.	.	.
Cirsium cf. *heterophyllum*	fr	.	.	.	.	.	.	.	.	.	+	.	.
Corylus avellana	n	.	.	.	.	.	+	.	.	.	.	.	.
Cyperus sp.	n	.	.	.	.	.	.	.	.	.	+	.	.
Eleocharis palustris	fr	.	.	.	.	.	.	.	.	.	+	.	.
Eleogiton fluitans	fr	.	.	.	.	.	.	.	.	.	+	.	.
Myriophyllum alterniflorum	s	.	.	.	.	.	.	+	.	.	.	.	.
Nymphaea alba	s	.	.	.	.	+	++	.	.	.	.	.	.
Polygonum minus	s	.	.	.	.	.	.	.	.	.	+	.	.
Potamogeton filiformis	f.st	.	.	.	.	.	.	.	.	.	+	.	.
P. natans	f.st	.	.	.	.	+++	++	.	.	.	.	.	.
Ranunculus cf. *flammula*	s	.	.	.	.	.	.	.	.	.	+	.	.
R. sect. *Batrachium*	s	.	++	+++	+++	.	.	.	.	.	.	.	.
Ceratodon purpureus	l	.	.	.	.	.	.	+	.	.	.	.	.
Fissidens osmundoides	l	.	.	.	.	.	.	.	+	.	.	.	.
Hypnum cf. *cuspidatum*	l	++	.	.	.	.	.	.	.	.	.	.	.
H. riparium	l	.	.	.	.	.	.	.	.	.	+	.	.
Polytrichum cf. *juniperinum*	l	.	.	.	.	.	.	.	.	+	.	.	.
P. piliferum	l	.	.	.	.	.	.	+	+	.	+	.	.
Polytrichum sp.	l	.	.	.	.	.	.	+	.	.	.	.	.

Fr = fruits; f.st = fruit stones; l = leaves; n = nutlets or nuts; s = seeds; sc = catkin scales. + = rare; ++ = occasional; +++ = frequent.

* Full records for *B. pubescens* accompany the pollen diagrams.

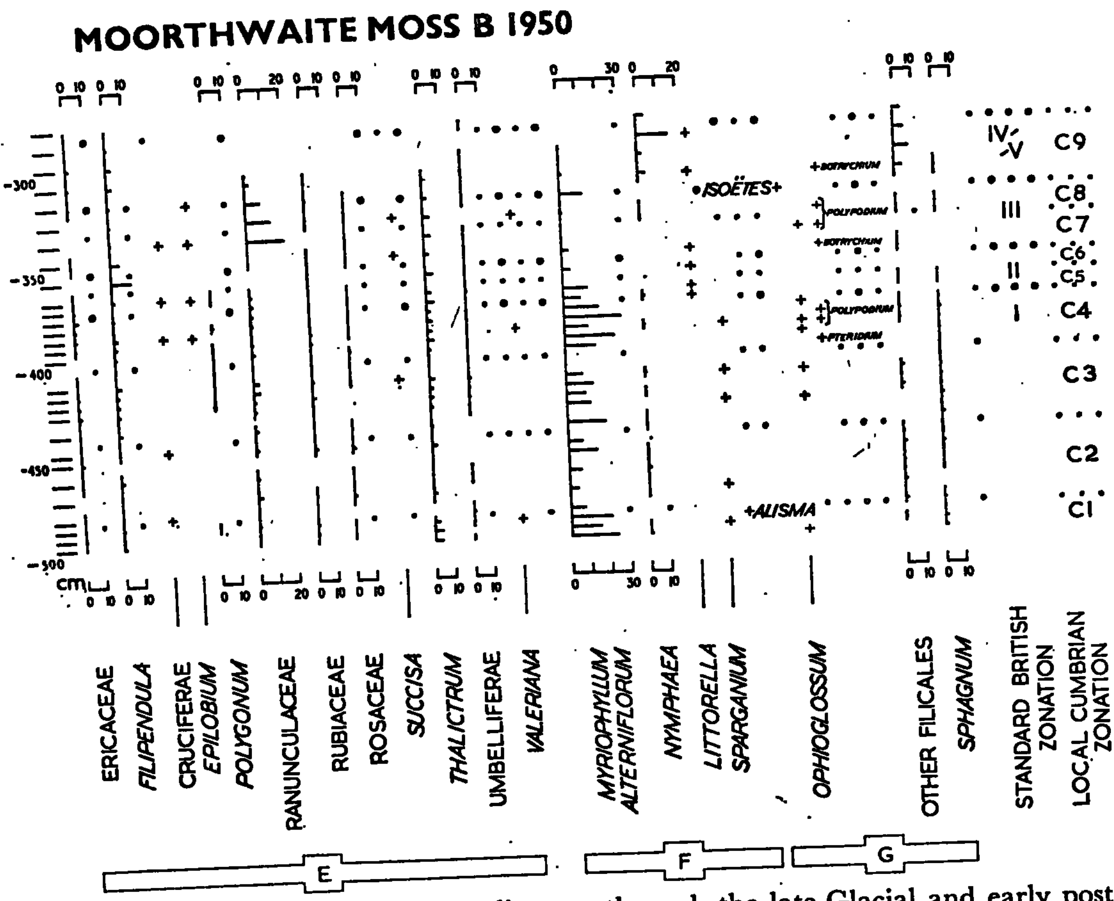


Figure 14. Moorthwaite Moss B. Pollen diagram through the late-Glacial and early post-Glacial deposits at boring 10 (cf. figure 12.) Section A: individual trees. Section B: individual shrubs. Section C: individual land herbs. Section D: summary curves for land flora (A+B+C+Ericales). Section E: individual taxa of uncertain ecology. Section F: individual aquatic herbs. Section G: individual Pteridophyta and Bryophyta. The pollen frequencies in Section A are shown as percentages of the sum of Section A pollen (= arboreal pollen total) of the appropriate sample. The pollen and spore frequencies in the other sections are shown as percentages of the basic pollen sum (A+B+C+Ericales) of the appropriate sample.

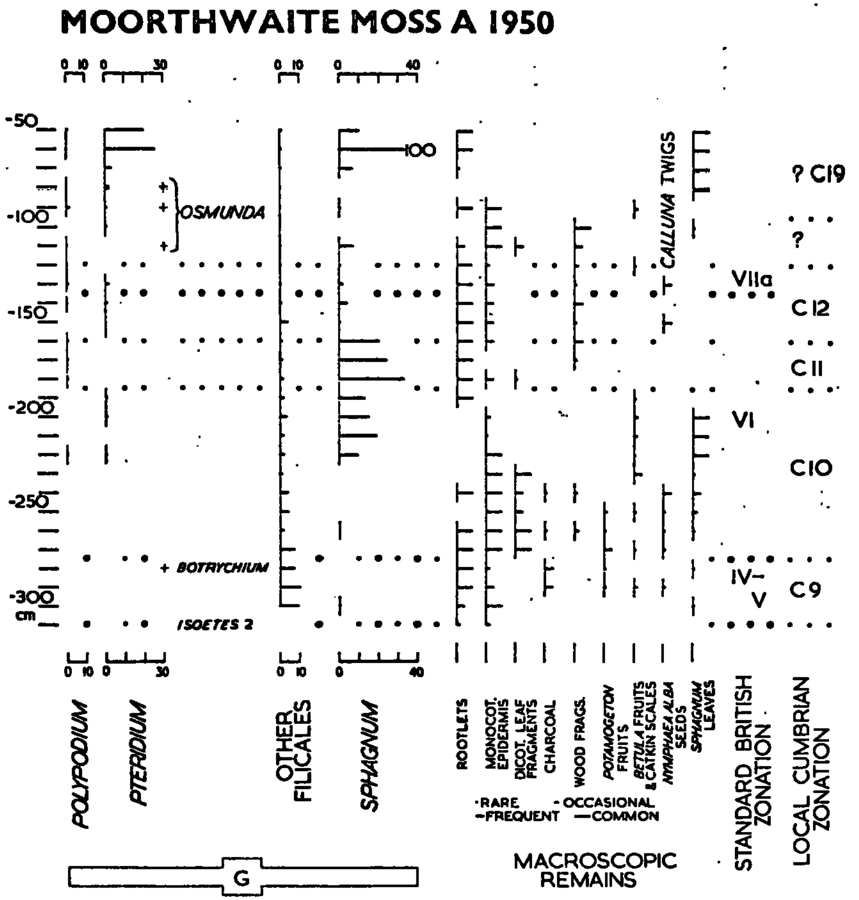
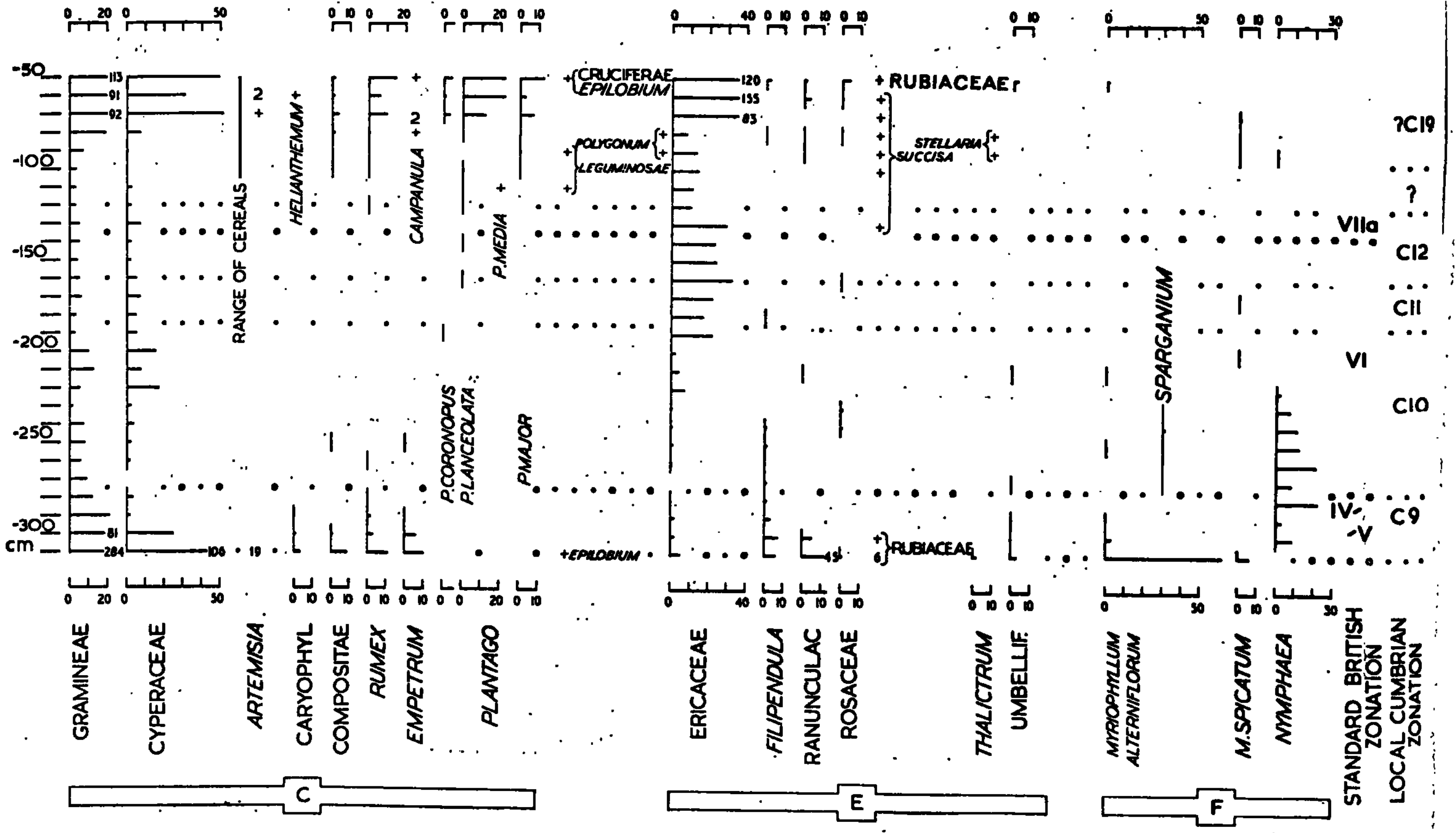


Figure 16. Moorthwaite Moss A. Pollen diagram through the post-Glacial deposits at boring 10 (cf. figure 12). Section A: individual trees. Section B: individual shrubs. Section C: individual land herbs. Section E: individual taxa of uncertain ecology. Section F: individual aquatic herbs. Section G: individual Pteridophyta and Bryophyta. The frequencies of pollen or spores of all taxa are shown as percentages of the arboreal pollen total (Section A) of the appropriate sample.

MOORTHWAITE MOSS A 1950



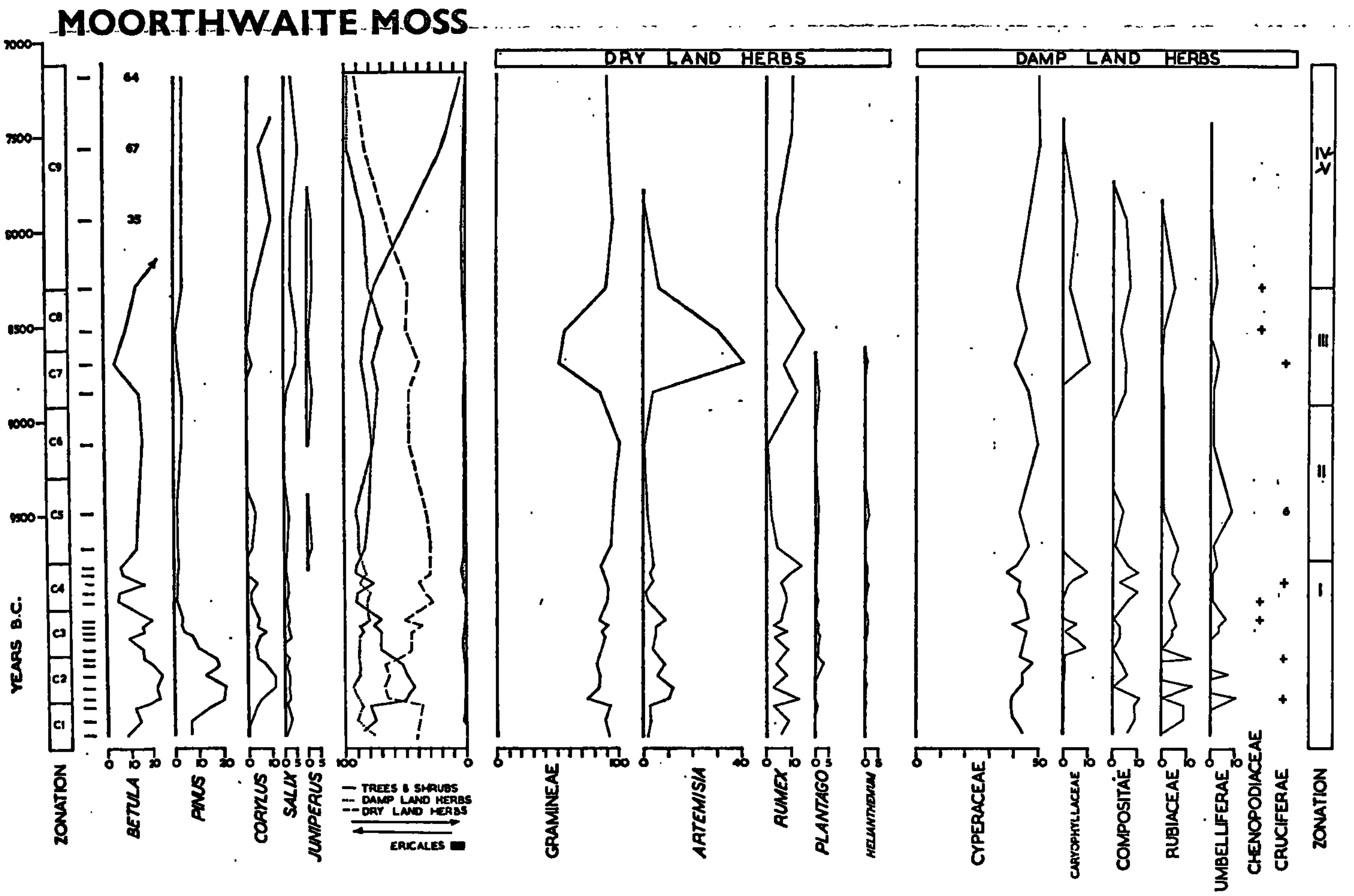
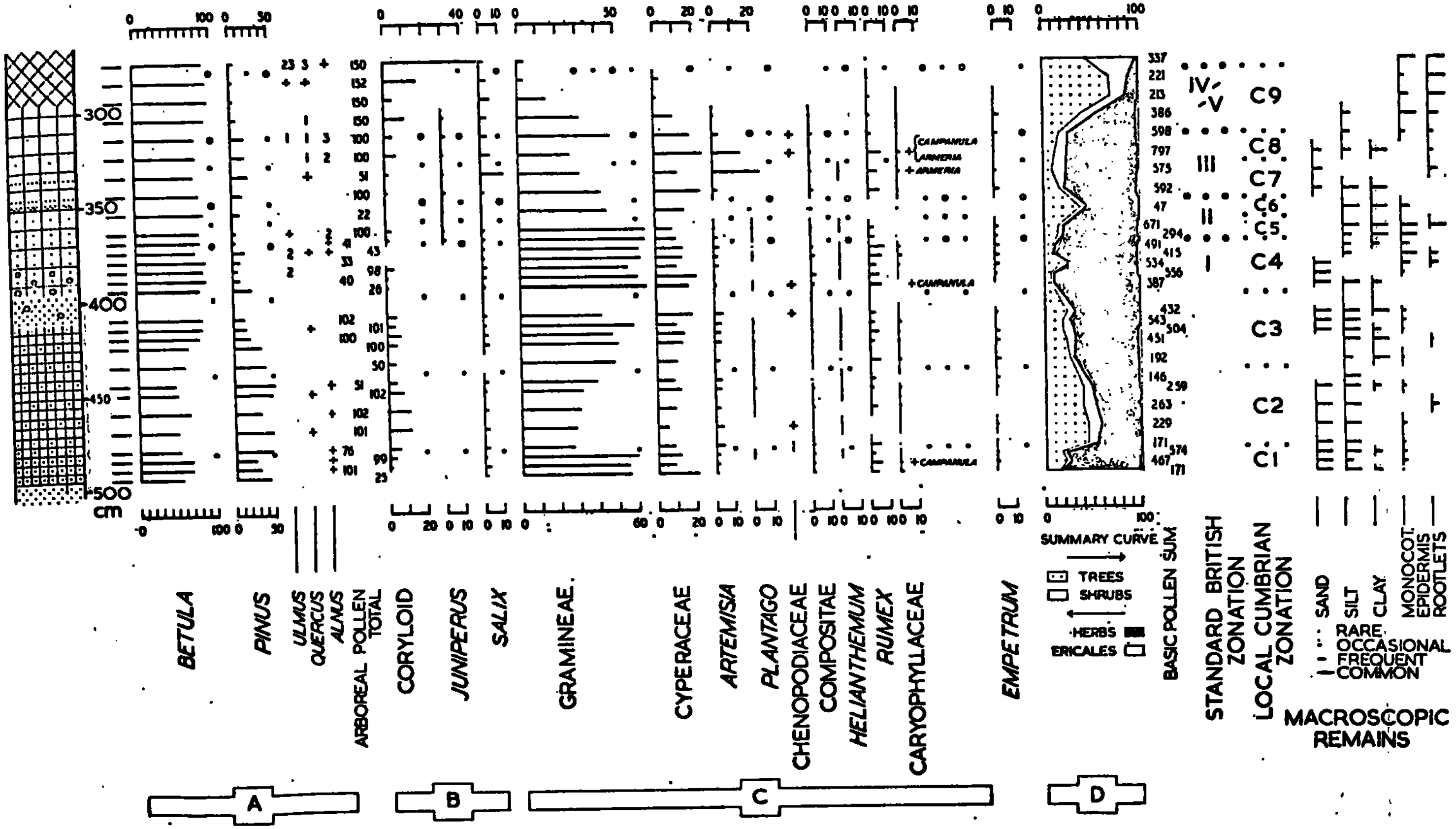
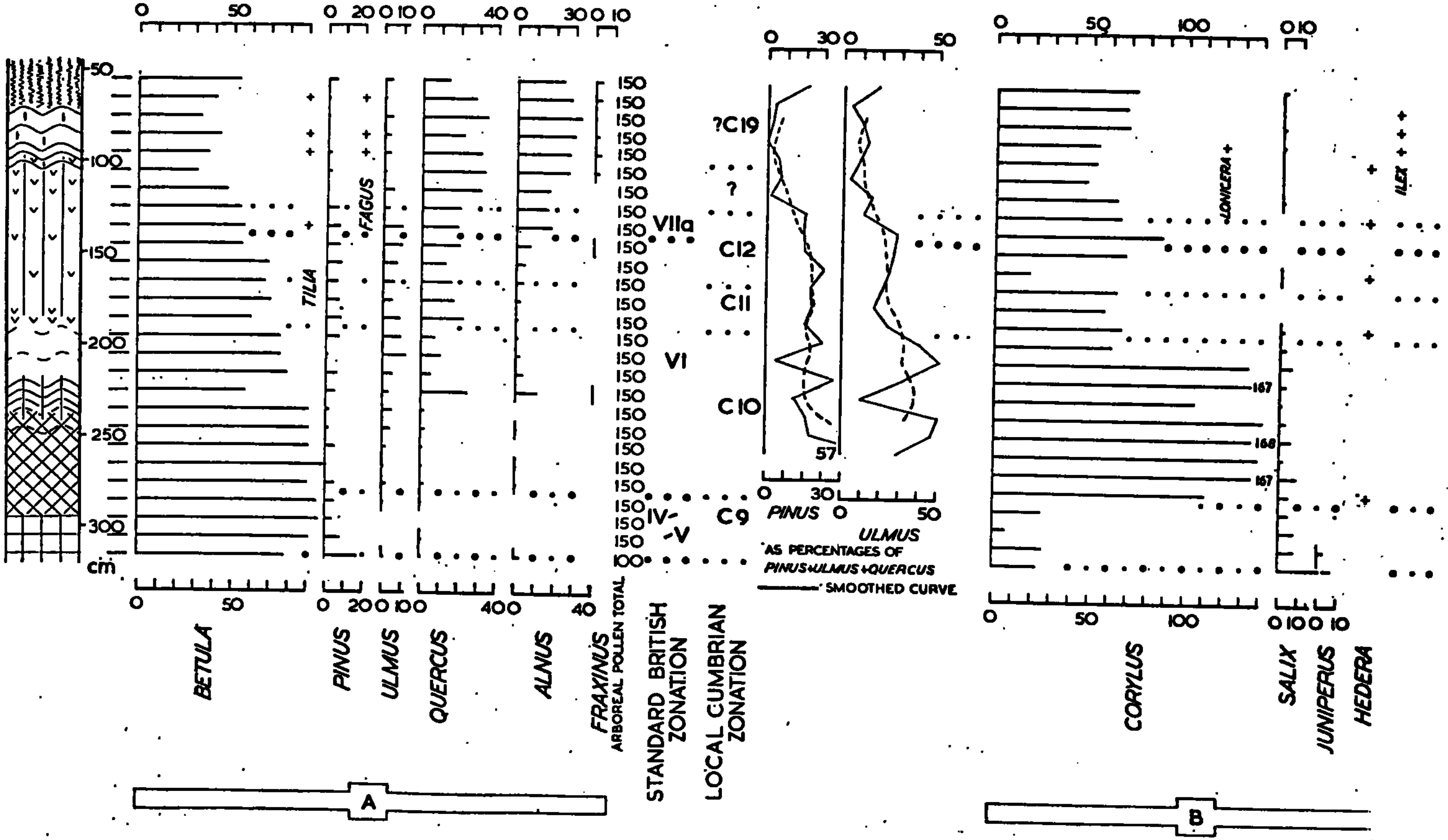


FIGURE 33. Selected pollen curves from the lower deposits at Moorthwaite Moss, recalculated from the data presented in diagram Moorthwaite Moss B. The vertical scale has been adjusted to give an approximately linear timescale above 9000 B.C. as indicated by the radiocarbon dates from Scaleby Moss. Frequencies of trees and shrubs and of the groups trees + shrubs, dry-land herbs, damp-land herbs and Ericales are expressed as percentages of the total of these four groups. Frequencies of individual pollen types within the groups dry-land herbs and damp-land herbs are expressed as percentages of the total for the appropriate group alone. The zonation is derived from the diagram Moorthwaite Moss B.

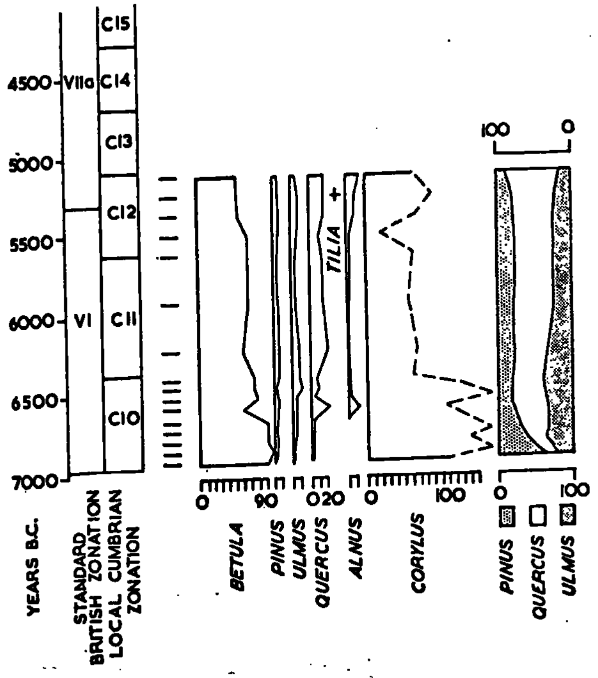
MOORTHWAITE MOSS B 1950



MOORTHWAITE MOSS A 1950



MOORTHWAITE MOSS



Laboratory methods for analyses ~~and Growth Chamber methods~~.

The dried peat samples were taken and 2.5 grams of each was weighed out. For each sample an ion extraction column was set up. These were prepared by putting a little glass wool at the bottom of a separating funnel and then packing in the dried peat which had previously been sieved through a 2mm. sieve. More glass wool was put on top of the peat to prevent it from being disturbed as the exchange solution was added. The top of each separating funnel was closed and 250-mils. of N1 Ammonium acetate solution was passed through slowly by adjusting the tap to deliver about 2-mils. a minute. The liquid was collected in a 250-mil. volumetric flask and was then filtered through a Whatman No.42 filter paper, transferring the filtrate to a 400-mil. wide-necked flask. The liquid was evaporated to about 100-mils. in the fume-chamber and allowed to cool before being made up to the mark in a 250-mil. volumetric flask with distilled water. The solution was stored in a polythene bottle which had been rinsed out with ammonium acetate to displace all ions absorbed on to the bottle surface, and then rinsed with distilled water and dried. The bottle was labelled with the peat's place of origin and method of extraction.

The samples were also analysed in the following manner, as were the plant samples, to find the total ions present. 1-gram of each sample was therefore weighed out and put into a 400-mil. wide-necked conical flask. The acid-digestion mixture, consisting of 20-mils of concentrated nitric acid, 5-mils of conc. hydrochloric acid and 5-mils of conc. perchloric acid. Goggles were worn during the manipulations. The flask was warmed over a low flame in the fume-chamber and then boiled until only a small amount of the perchlorate remained. Care was taken not to boil the solution dry or the mixture would have exploded. The solution was then diluted with about 170-mils. of distilled water and then filtered through a Whatman No.1 filter paper. The solution was transferred to a 250-mil. volumetric flask and made up to the mark with distilled water, then stored in a labelled, polythene bottle.

The extracted solutions were analysed for calcium and magnesium by Atomic Absorption Spectrophotometry (A.A.S.) and for sodium and potassium by Flame Photometry. The methodology for these is as follows:-

FLAME PHOTOMETRY.

The gas supply and air compressor were connected to the instrument and it was switched on at the mains. The gas was turned on and the flame lit and adjusted to give a steady flame. The compressed air was turned on and adjusted to 10 lbs/sq.in. The gas supply was adjusted, first to give one, large, central cone in the blue flame and then gradually turned down to give just ten small cones within the central flame. The glass testing vessels were all washed, rinsed in distilled water, and then dried. This was to eliminate any inaccuracies caused by dried solutions in the vessel and water clinging to its sides, and so diluting the solutions to be analysed.

A sample vessel was filled with distilled water and put on the stage below the capillary suction tube. Then the stage was raised to put the end of the tube well under the liquid surface and a steady but minute stream of liquid was drawn up and squirted into the flame. At this point the appropriate filter was inserted into its position next to the flame and the reading was adjusted to zero.

After this, a standard solution of 100-ppm was used and the reading at the top of the scale was reduced to 100 by the sensitivity control. The distilled water was used again and adjusted to 0 by the zero control and the solutions were used alternately until distilled water always gave 0 and the standard solution always gave 100. When this had been done the instrument was considered as calibrated.

All the solutions were tested now and if any were off-scale they were diluted either twice, four-fold or ten-fold, to bring the reading on to scale. When all the sodium determinations had been done the method was repeated for potassium. After all were determined the readings were converted to parts per million by using the calibration curve graph for the appropriate mineral.

Theory:

A standard flame is started with and obtained by the methodology found at the beginning. The appropriate filter is inserted to allow through only light of the specific wavelength of the mineral to be estimated. The distilled water was injected into the flame and the reading reduced to 0 by the zero control. A standard solution was then injected and the increase in intensity of the light of the mineral's specific wavelength was registered on the scale. This is brought to 100 by the sensitivity control. A calibration curve is constructed by drawing a graph of p.p.m. against the reading a solution of such a p.p.m. causes.

The graph is not linear. Any solution of unknown concentration when injected into the controlled flame will cause emission of light of the mineral's specific wavelength of such an intensity which varies directly with the solution's concentration.

The reading so obtained can be reconverted to p.p.m. by using the calibration curve and so the concentration of the ion, being investigated, in any solution, can be found.

This method is more easy to use than any other method, for example, titration; is faster to use and more accurate and reliable than any other method.

ATOMIC ABSORPTION SPECTROPHOTOMETRY. to be used for Ca^{2+} Mg^{2+}.

Reference: T.S. West. Endeavour. January 1967.

Theory:

Small amounts of some materials can cause a vast difference in many systems. The normal method of absorption spectrophotometry cannot be extended for these purposes where great accuracy is required, as the probability of interaction of a molecule being rather low and the selectivity being poor. Atomic absorption spectrophotometry was first discovered in 1955 by A. Walsh and he also discovered atomic fluorescence spectrophotometry (AFS).

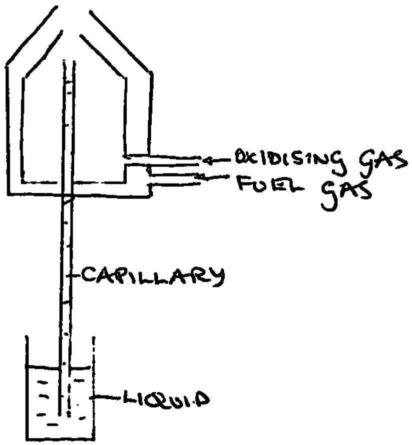
AAS: Atoms as well as molecules can absorb light by the promotion of electrons out of their ground state levels into higher, excited levels. Only light of the energy which is equal to the difference in energy levels between the ground and excited states will be absorbed by the atoms or molecules. Atoms are simple in comparison with molecules so that the number of energy levels they possess is relatively small and the interactions between them are relatively infrequent. Dissolved molecules show rather broad absorption bands over the range 100-1000Å because of the complexity of their electronic structures, whereas free atoms show very narrow absorption bands. All these bands are in the ultra-violet and visible range of the spectrum and many bands can be identified within this wide range.

A dilute solution of the atoms must be produced, much as in absorption spectrophotometry. The free atomic particles cannot be produced in a solution, but are introduced into a flame as a finely divided solution of the compound.

e.g.

$$\mathrm{NaCl\ (solution)} \rightarrow \mathrm{NaCl\ } \underbrace{\mathrm{(solid)} \rightarrow \mathrm{NaCl\ } \underbrace{\mathrm{(liquid)} \rightarrow \mathrm{NaCl\ (vapour} \rightarrow \mathrm{Na^{\circ}} + \mathrm{Cl^{\circ}\ (gas)}}_{\text{dissociation}}}_{\text{sublimation}}$$

SPRAY MECHANISM.



The flame therefore acts on an atom reservoir within which measurements of atomic absorbancy may be made. The flame must be a steady state or monochromatic one and there must be a detection device to measure the decrease in the signal from the source when the atoms are ontroduced.

<u>Source</u>: In the A.S. in the ultra-violet and visible part of the spectrum, a deuterium or hydrogen discharge lamp is used as a source for 2000 to 3500Å and a tungsten filament lamp for 8,000 - 10,000Å. The light from these continuous sources is made monochromatic by dispersion through a prism system, or by a diffraction grating, or by both. This method, however, is not sensitive enough for A.A.S. so a narrow-line source, a hollow cathode lamp, which emits radiation much marrower in band width than the A.A.band is used.

Various flames can be used according to which temperature is required.

Fuel	Oxygen	Air.
Town gas	3000°K	2000°K
Propane	3100	2200
Butane	3200	2200
Hydrogen	2950	2400
Acetylene	3400	2500
	3230(NO_2)	3230(N_2O)
Cyanogen	4800	

The temperatures for the various flames are shown above. The cool air flames are perfectly satisfactory for many metals but others require hotter flames. These however raise difficulties of high emissive and absorptive backgrounds.

During the ten years in which the method has been available it has been vastly improved, and recognised as one of the most rapid techniques available. Its advantages are that it is:-

1. Specific for all elements to which it can be applied and it can be easily adapted to operate over the range 0.1-100p.p.m.
2. It can be applied to 60 elements with an error of only ± 1%
3. The technique involves only the dissolution of the sample in an organic or inorganic solvent and needs no further chemical or physical manipulation.
4. It is rapid and easy to operate by even unskilled staff and can be easily automated to give direct, digital readings.
5. Instruments are cheap, £600 - £2500, in comparison with other techniques. The maintenance costs are low and no special housing is needed except for good ventilation for the flue gases.

These are the reasons why the A.A.S. was used instead of any method using titration of any sort. Many of the advantages are also shared by the flame photometer.

The apparatus is complicated to set up however, but once this is done and it is calibrated it is relatively a simple operation to use it. As with the flame photometer, readings are gained by the solution being sucked up through a capillary and into the flame where the atomic absorbance is measured, instead of emission of a light of a specific wavelength as in the flame photometer. The method is as above for magnesium estimation but for calcium estimation the method is complicated as phosphate has a similar absorbance to calcium. This effect is eliminated by diluting the solution to half the original concentration with a solution of

so that the calcium flame absorbs only light of its required energy and not also that of phosphate.

SODIUM AND POTASSIUM (E.E.L. Flame Photometer).

Apparatus. Same for Na. & K.

i. Pipettes. 1 x 1ml, 1 x 2 ml, 1 x 5 ml, 1 x 10 ml.

1 x 10 ml. graduated.

Range for sample dilutions.

ii. Volumetric Flasks.

12 x 100 ml.

Several 25 ml, 50 ml for sample dilutions.

iii. Conical Flasks, one 250 ml for filtering each sample.

iv. Filter funnel, one for each sample.

v. Filter paper.

Method.

Set up flame photometer and use according to manufacturers instructions.

Solutions.

1) a) Stock sodium solution 2.542 g. NaCl made up to 1000 mls with distilled water 1.00 ml - 1.00 mg. Na.

b) Stock potassium solution 1.907 g. KCl made up to 1000 mls with distilled water 1.00 ml - 100 mg.K.

2) Standard solutions.

Dilute 10.0. ml. stock sodium solution to 100.0. mls.

1 ml. = 0.10 mg. Na.

Dilute 10.0. ml. stock potassium solution to 100.0 mls.

1 ml = 0.1 Mg. K.

Calibration Curve.

Use the following mls. of standard Na or K solutions made up to 100.0 mls.	Concn. of Na or K Mgs./l.
1	1
2	2
3	3
4	4
5	5
6	6
7	7
8	8
9	9
10	10

CALCIUM AND MAGNESIUM (E.E.L Atomic Absorption Spectrophotometer)

Apparatus.

1. Pipettes for sample dilutions

1 x 1 ml.	12 x 1 ml.
1 x 1 ml.grad. Mg.	1 x 1 ml.grad. Ca.
1 x 2 ml.	1 x 2 ml.

2. Volumetric Flasks.

   12 x 50 mls.

   1 x 25 ml. for each element.

   1 x 100 ml.

3. Conical Flasks.

   1 x 250 mls for filtering samples.

4. Funnels for filtering samples.

5. Filter paper.

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APPENDIX II

ERIOPHORUM ANGUSTIFOLIUM - Species Habitat

Eriophorum Angustifolium is a circumpolar plant which occurs throughout the arctic and sub-arctic regions, and is described by Polunin as common throughout the Canadian Eastern arctic. It is found as far North as 83°N in Greenland. It is placed by Matthews in his arctic-alpine category, but it is a plant of very wide geographical and climatic range, as is indicated for instance by Hulten's map which shows it as frequent throughout the whole of Scandinavia. Although also recorded throughout the British Isles, it is now very rare or perhaps extinct in some parts of the South and East, possibly as a result of the cutting of peat and drainage of suitable habitats.

\+ Goodwin. History of the British Flora p.249.

ERIOPHORUM ANGUSTIFOLII - Community Habitat

This community is very local in the southern Pennines, but more extensive on the northern part of the chain. According to Watson (1932) it is much more frequent on the Somerset moorlands than E. vaginati and limited are described by Pethybridge and Praeger (1905) at high altitudes (about 500 - 700m) on the Wicklow mountains in eastern Ireland. The Wicklow Eriophoreta are small in extent and "below the uniform waving foliage of the cotton-grass is a continious dense stinted growth of Calluna with several of the plants of the Calluna and Scirpus associations. The peat is "sopping wet" and spongy unlike that of the Scirpetum caespitosi (see below), which is the characteristic community of most of the Wicklow mountain plateau. The species recorded from three sample areas were as follows:-

Eriophorum angustifolium d
Calluna vulgaris sd

All three areas:

Eriophorum vaginatum
Empetrum
Scirpus caespitosus
Vaccinium Myrtillus

Cladonia sp (2 areas)
Erica tetralix (1 area)
Vaccinuim vitis-idaea (1 area)
Sphagnum spp. (1 area)

The Eriophoretum angustifolii described by Lewis (1904) from the northern Pennines has Eriophorum vaginatum mixed in smaller quantity, together with a few individuals of R chamaemonis, Erica tetralix and Empetrum nigrum.

Eriophorum angustifolium often occupies wet channels and depressions in the blanket bogs of E. vaginatum, and colonises cracks in the bare peat of such hollows by means of its creeping rhizomes.

BRYOPHYTES Watson (1932) remarks that many Bryophytes present in the Eriophoretum vaginati are absent or rarer in the wetter E. angustifolii. He records the following species from the last-named community (of the Somerset moors) not listed from the E. vaginati.

Aulacornnium palustre
Campylopus brevipilus
Cephalozia fluitans
Drepanocladus aduncus
D. fluitans
D. revolvens

Lepidozia setacea
Leptoscyphus anomalus
Odontoschizma sphagni
Sphagnum ocutifolium
S. phumulosum

The Hydroseral Succession and Peat Formation.

As a generic term, peat refers to the partially decomposed plant remains which form stratified layers in old lake basins or over wet grounds.

The classification of kinds of peat is a complicated subject (Dachnowski 1912; Huels 1915) Oversimplifying the situation it can be said that four main types are common - sedge peat, sphagnum peat, hyprum peat and woody peat, their origins being indicated by their names.

The peat substrates are briefly characterised as being highly acid, very wet and very low in oxygen. The anaerobic conditions are largely responsible for the lack of decay in the peat, as the most active micro-organisms are unable to function in such an environment. The water retaining capacities frequently average 600 - 700 per cent.

(As the areas are so wet, considerable evapo-transpirational losses are incurred by the system during the day, this causes night mists and fogs to develop) which bathes the swamp plants in a saturated atmosphere for periods of eight to ten hours. Considerable condensation on to twigs and leaves takes place. The abundance of lichens and bryophytes is largely due to this nocturnal condition of high moisture.

(There is), however another important feature of the microclimate of the conifer swamps. This is the great shortening of the growing season caused by the insulating qualities of the sphagnum moss. The tops of plants may be subject to high temperature while the roots, at the same time, are bathed in ice-water. In N. America the bog ericads such as Ledum (Labrador tea) Andromeda (bog rosemary) and Kolmia (bog laurel) are adapted to such conditions, and may even burst into flower while the ground is still solidly frozen. In Europe, Erica tetralix, Andromeda polyfolia, Vaccinium spp. take their place.

The same insulating qualities of the Sphagnum which hold the ice in spring also prevent its rapid formation in the Autumn.

The general influence of the forest community on its microclimate is thus a moderating one. Summers tend to be shorter, cooler and more humid than the surrounding lands, whilst winters are warmer and of more even temperature.

+ Curtis - The Vegetation of Wisconsin.

Moorthwaite Moss was Probably a eutrophic lake at its formation. Its development could have been along the following lines, its vegetation being controlled by limiting factors.

In a hydrosere the limiting factors for plant growth are the depth of the water and lack of aeration : the trend of the succession is towards the accumulation of silt, raising the soil above the water level, and eventually lowering the water table. The first colonists grow in open water in a pond, lake or sluggish stream. These are the submerged aquatics, usually with dissected leaves, like Ranonculus aquatilis sub. pp., Ceratophyllum demersum or Myriophyllum spicatum. They are anchored in the mud (though Ceratophyllum has no roots) and the maximum depth at which they can survive must have a light intensity above their compensation point. In water with a good deal of plankton or other suspended matter to absorb the light this maximum depth may not be much more than two metres. If there is any silting up of the pond at this point, it will raise the level of the bottom and allow the growth of species like Nuphar luteum, N. pumila, Nymph ea alba for which the limiting depth is not so great. The floating leaves shade out the submerged species and prepare the way for the next stage in the succession. Their remains help to raise the substrate level and further this. Some free-floating aquatics : Lemna gibba, L.minor, L.major, L.trisulca, Hydrocharis morsus-ranae, Stratoides alrides (Azolla filiculoides, Riccia fluitans, Salvinia having been introduced in the South and East of the British Isles and occurring spontaneously for a few years then dying out). occur in the floating leaf zone amongst emergent vegetation. Their only restriction to shallow water is that they must overwinter at the bottom of the pond, but though theoretically free-lance they seem to be kept to the margin of the pond by surface wind currents. In shallower water the horizontal spread of floating leaves is replaced by a thick upward growth of species with aerial leaves, like Phragmites, Juncus, Irish psendacornus, Typha, Alisma plantago - aquatica, Sagittaria sagit folia, Butomus umbellatus and Typha Their dense growth hastens the accumulation of silt, and the effect of their transpiration must make some contribution towards lowering the water table of the pond. This sequence may be seen as concentric zones of vegetation round the margin of any suitable pond, and is illustrated in the profile chart Fig. If the succession progresses these zones migrate bodily out into deeper water and the banks of the pond close in behind them.

In the stages following the reed-swamp community the vegetation is terrestrial at first with a high water-table and poorly aerated soil. Such conditions tend to favour the development of soil acidity, and the pH. of the standing water may well determine the future course of the sere if it is sufficiently base-rich to counteract this acid tendency, then fen vegetation arises, with grasses, sedges and later alders and willows. These effect a gradual lowering of the water table, and prepare the way for ashwoods and eventually a climax of oak.

In areas where the pond or lake water is poor in bases the succession may be deflected by increasing acidity after the reed swamp stage. Sphagnum may enter and the succession proceed no further than bog vegetation, under drier conditions this will raise the surface of the mire forming a domed ombrophilous mire, as Moorthwaite Moss is, which usually drains in time and gives rise to heath vegetation with Calluna vulgaris, Vaccinium myrtillus as dominants. Although heath vegetation can give place to birches, pines and eventually climax oakwood, the soils of these areas is generally too nutrient poor to allow much tree colonization. However, the ecoseral development may stop at any place according to the nutrient requirements of the next sere. Moorthwaite Moss obviously does not have enough minerals for mixed mesaphytic oakwood. This is therefore an "edaphic climax".

Domed embrophilous mires or raised bogs take their name from their convex, cushion like shape, which is due to the sloping margins where lateral extension of the Sphagnum moss, the chief peat-forming agent, is prevented by the collection of relatively base-rich drainage water from the surrounding mineral soil. These sloping margins (German Rand) are better drained than the bog centre and carry different communities, often pronouncedly zoned and dominated by such species as Calluna, Molinia caeralea, Trichophorum caespitosus and Betula pubescens. The drainage water from the Rand and from the adjacent mineral soil falls into a wet marginal area known as the "lagg" where the higher base-status of the water is reflected in the occurrence of the more eutrophic species characteristic of fens. The central portion of the raised bog has a very gentle curvature indeed and carries highly characteristic communities dependent in their nature upon the conditions of the bog and it s climatic and drainage relationships.

In the more oceanic climates such as those of central Ireland the undrained bog will still be actively growing and will present a mosaic of open pools and of hummocks of growing sphagna. This system is spoken of as the "regeneration complex" and it produces a characteristic branded peat in which the vegetation of the pools and of the hummocks can be traced in constant alternation with one another. Highly constant species of the regeneration complex fall within such oligstrophic genera as Calluna, Erica, Eriophorum, Andromeda, Oxycoccus, Drosera, Narthecuim and Rhynehospora, as well as equally typical mosses and liverworts in profusion.

Raised bogs in continental climates tend to have their surfaces bush or tree-covered, and in this country bogs which are artificially or naturally drained pass over a "standstill complex" in which dominance is taken over by Calluna or Eriophorum vaginatum, Sphagna are less important and peat growth is reduced in rate or ceases, and the peat type produced is more humified than under regeneration complex. Such Callina-Eriophorum bogs are drier altogether than the active Sphagnum-dominated raised bogs.

Raised bogs very commonly occur in former periglacial regions, often upon the sites of lakes created by the laying down of terminal moraines across glaciated valleys.

The stratigraphy of such bogs shows all the early stages of colonization of more or less eutrophic lakes, the open-water lake muds being progressively replaced, marginally at first, by reed swamp, fen and perhaps fenwood. Only at these later stages of vegetational development, when peat formation had carried the ground surface above the reach of the lake waters, was ombrogenous peat formation able to begin. From this stage onwards Sphagnum growth can be seen to have dominated the bog's development. In the excellent vegetational studies made by Steffen on the shores of the Baltic near Koningsberg we may find displayed together the zonation of living lake, fen and raised bog communities and the stratification in the raised bog deposits entirely corresponding with the zonation; such correspondence has indeed long been recognised (see Oswald's boring Edenberry Bog).

PEAT PROFILES

Edenberry bog shows retrogression.

Table XXII. *Section of bog south of Edenderry through moss (bog) peat and underlying fen and carr peat to basal glacial clay. H = degree of humification (scale of humification* 1 *to* 10).

Metres		H.		
0	Sphagnum cuspidatum—Narthecium	9	Current cycle	7
	Sphagnum rubellum, Eriophorum vaginatum Sphagnum papillosum	3	Complete cycle	6
0·5	Sphagnum cuspidatum with Eriophorum vaginatum and Sphagnum papillosum	2		
	Sphagnum and Calluna	7	Incomplete cycle	5
	Sphagnum rubellum	2		
1·0	Sphagnum papillosum—Sphagnum rubellum	1		
	Sphagnum	5	Incomplete cycle	4
1·5	Sphagnum imbricatum	2 to 3		
	Sphagnum	5	Incomplete cycle	3
2·0	Sphagnum, Calluna and Oxycoccus	7		
2·5	Sphagnum imbricatum	3		
	Sphagnum	8	Incomplete cycle	2
	Sphagnum imbricatum	4		
3·0	Sphagnum	8	Incomplete cycle	1
	Sphagnum imbricatum and much Eriophorum vaginatum	4		
3·5	Sphagnum with Calluna	8	Typical first stage of moss	
	Sphagnum ? rubellum	4		
4·0	Sphagnum, Calluna, Oxycoccus	4		
	Sphagnum with Calluna, Oxycoccus and much Eriophorum vaginatum	8		
4·5	Carex—Sphagnum	6	Last stage of fen	

Table XXII *continued*

Metres		H.	
5·0	Much Equisetum and Cladium	6	Second development of fen consequent on reflooding
	Carex	6	
5·5	Carex Amblystegium with Equisetum and Cladium	5	
6·0	Carex—Amblystegium	5	
	Amblystegium	5	
6·5	Calluna—Sphagnum		First development of moss
	Carex with Phragmites and Menyanthes	6	Fen and reedswamp consequent on flooding of carr
7·0	Carex with Myrica and Menyanthes	4	
7·5	Muddy sedge peat with Cladium and Phragmites	8	
8·0	Wood peat with Carex	9	Fen carr probably in hollow of glacial clay
	Wood peat with Birch and Alder	8	
8·5	Wood peat with some Carex	9	
	Bluish grey clay		
9·0	Bluish grey clayey gravel		
9·5			

SUB-CLIMAX.
CARR WOOD
INITIATION of
ECOSERAL
DEVELOPMENT

Inter-relationships between bog types and vegetational types in the hydroseral succession.

Moss (Moorthwaite Moss) and bog (Irish blanket bog) are used in this article synonymously for the wet, acid peat vegetation, and moor and moorland are used only in the wide, popular sense. The plant communities which form and inhabit wet acid peat have often been divided into "lowland" and "upland", but are more naturally classified as valley bog, raised bog and blanket bog - names which refer to real differences in habitat, structure and mode of development.

Valley bog and Raised bog. Valley bog is developed where water, draining from relatively acidic rocks, stagnates in a flat bottomed valley or depression, so as to keep the soil constantly wet. In such situations species of Sphagnum and associated plants appear and produce a bog limited to the area of wet soil. Such bogs are common in the mountainous regions of Palaeogenic rocks in the north and west of the British Isles, but they have not been investigated ecologically, and very little is known of their structure and development. The "wet heath" communities (see pp.734-41) occurring in depressions of the English lowland heaths, where the ground water is nearly level with the surface, are essentially of this type.

In a sufficiently moist climate the characteristic raised bog (German Hochmoor) may develop on the top of a valley bog. The valley bog itself, however, being fed by drainage water, is never so poor in soluble mineral constituents as a raised bog, and it contains plants, such as species of Juncus and Carex, which have no part in a typical raised bog. The stream running through a valley, however stagnant it may become in parts of its course and however acidic the rocks which it drains, brings a certain quantity of soluble salts from the upper reaches where erosion is taking place, and the water of a valley bog is typically less acid than that of a bog depending on precipitation alone. When a raised bog develops on the top of valley bog the stream is blocked or diverted by the growth of the bog vegetation and the peat which it forms. The original water course may thus be forced to one side, or split into two streams which find their way round the sides of the bog: part may run below the surface of the bog. The marginal watercourses form the lagg (a Swedish term) of raised bog, and the vegetation of the lagg is characteristically less extremely oxyphilous than that of the general surface of the raised bog.

Usually, however, raised bog is developed not on valley bog but on fen. As we saw in the last chapter, Sphagnum and associated plants, which require acid water in their habitat, locally colonise the surface of fen, especially where the large tussocks of certain fen plants have raised the level above the neutral or alkaline ground water, so that the natural acidity of the humus formed by the debris of the tussock is not neutralised. The small communities of oxyphilous plants arising in this way may remain very limited in extent, but there is abundant evidence in the British Isles, as well as on the continents of Europe and North America, that they have, in times past, spread over and superseded fen vegetation, replacing it by wide extents of the highly characteristic moss or bog formation. Where this formation has thus arisen on a fen localised in a basin it has itself remained restricted to the basin, though this may be of considerable extent, up to several miles in diameter. The surface of the moss is characteristically convex, sloping gently from the centre towards the periphery, where it ends in a relatively steep bank bounded by a ditch or watercourse (lagg) representing the original drainage channels of the fen basin and receiving the water draining from the bog. Beyond the lagg fen vegetation, not yet covered by the moss, may often be seen. Thus the moss as a whole is raised above the immediately surrounding fenland, and this is the origin of the German term Hochmoor. This is the type of bog so common in the great central limestone plain of Ireland, where they are based on the local fen basins, and are known as "red Bogs" from the red-brown colour of the dominant vegetation. Similar raised bogs occur in Scotland, northern England and Wales, and were formerly much commoner, many having been destroyed by draining and peat cuttings.

Blanket bog. It seems probable that raised bogs are formed in climates intermediate between that of the East Anglian fens, where the air seems too dry for the bog-moss vegetation to extend vigorously in dependence upon atmospheric moisture, and that of the west of Scotland and the west of Ireland, where the rainfall is high and the air so constantly moist that bog is the climatic formation, not necessarily arising in fen basins but covering the land continously except on steep slopes and outcrops of rock. This is the third type of bog met with in the British Isles and may be called blanket bog, because it covers the whole land surface like a blanket. The contrast can be well seen in the bogs developed east and west of Galway city in the west of Ireland. To the east is the great plain of Carboniferous Limestone with raised bogs developed in the numerous small fen basins. To the west is a region of acidic rocks under an extreme oceanic climate, and bearing almost continuous blanket bog. Blanket bog is independent of localised water supplies, depending on high rainfall and very high average atmospheric humidity. Raised bog, on the other hand, seems always to have an aquatic or semi-aquatic origin, being built upon fen, marsh or valley bog, so that the bog peat is often underlain by fen peat and lacustrine or estuarine silt. The climate in which raised bog is developed must, however, provide sufficient atmospheric humidity to make the upward growth of the bog possible.

Bog or moss communities. The dominants and associated species of blanket bog and raised bog are mostly, though not entirely, the same; but, as we have seen, the habitats (in the wide sense) are different, and the structure and development also differ in several respects. Blanket bog has never been studied by modern methods, but we know more about the development of raised bog, thanks to the labours of continental workers and to some quite recent work in the British Isles. The main plant communities of bog or moss are six - Sphagnetum, Rhynchosporetum, Schoenetum, Eriophoretum, Scirpetum and Molinietum - and of these Sphagnetum is the first and most fundamental.

(1) Sphagnetum. The species of the genus Sphagnum, as is well known, have a highly specialised vegetative structure. The surface of the stem is covered with a layer of large empty cells, whose walls are strengthened by ribs and pierced by relatively wide holes;

the leaves consist of a single layer of cells, the framework composed of cells similar to those covering the surface of the stem, and running between them are lines of narrow living cells containing chlorophyll. The network of fine capillary channels formed by the empty cells with their pierced walls results in the plants absorbing liquid water in contact with their shoots through the holes in the cell walls and holding it like a sponge, so that a considerable quantity can be easily squeezed out with the fingers from a living tuft of Sphagnum. Water is also held between the surfaces of the leaves and the stems. When this surface water has been lost by evaporation that contained in the cells is slowly evaporated into the air, the actual rate of evaporation depending of course primarily on the saturation deficit of water vapour in the air as well as on the structure of the plant.

Variation of habitat and structure. Some species of Sphagnum are aquatic mosses, growing immersed in water: others live on constantly wet soil or more commonly on the wet bases of the aerial shoots of other plants. The habitat of these must be pretty constantly wet, either from soil water or abundant precipitation, and the "terrestrial" Sphagna are most abundant and flourish most luxuriantly under conditions of very high average atmospheric humidity. The species which live in the less constantly wet habitats, as Watson (1918) points out, possess xeromorphic characters in greater or less degree - compactness of habit, close imbrication of leaves on the branches, infolding of the leaf edges - characters which check loss of water by evaporation to the air. The more aquatic species are least xeromorphic and least able to resist desiccation.

Acidity and mineral requirements. The sphagna are well known to flourish only where they are in contact with more or less acid water and to be killed by exposure to alkaline solutions. The acid substances held in their cell walls absorb the bases of nutrient salts, setting free the acid ions and thus maintaining an acid medium in contact with the moss. While this is true of all the species they vary a good deal in sensitiveness to an alkaline medium, and this is correlated with the degree of their own acidity. (Skene, 1915.) Broadly speaking the least acid species grow in the less acidic habitats, where they can usually obtain a greater supply of mineral salts, while the extremely acid species, most readily killed by alkaline solution s, have a very low mineral requirement and grow in the most acidic habitats. Thus Skene found that Sphagnum contortum, a species which, judged from its habitats, is of relatively high mineral requirements, had an average "primary acidity" (measured in terms of grams of acid hydrogen per hundred grams of Sphagnum material after thorough washing out of the absorbed bases) of 0.0715, while S.rubellum, a hummock-forming spec es of highly acidic raised bog, had an average primary acidity of 0.1092. This correlation is not however exact. Skene found that the acidity of different samples of the same species varied a good deal and that their ranges of acidity overla ped considerably; and there is evidence that what appears to be the same species may differ markedly in acidity and habitat in different regions. Further research is required on the relation of acidity and mineral requirements to habitat, and on the possible existence of different ecotypes of the same species.

Oxidation-reduction potential.

Pearsall (1938) found that the p^H values in the Sphagnetum of raised bog, where the conditions were optimal for the growth of the bog moss (species not stated), varied between 4.17 and 4.62 at 10cm depth, most determinations giving a reading of 4.2 or 4.3 These soils are "reducing".

Water requirements. The following species of Sphagna are arranged in order of water requirement and mineral requirement.

S. Cuspidatum	low	mineral	requirement
S. squarrosum	high	"	"
S. Papillosum	high	"	"
S. tenellum	intermediate		"
S. Magellanicum	low	"	"
S. Fuscum	low	"	"
S. Imbricatum	low	"	"
S. Rubellum	low	"	"

Role of Sphagna in vegetation. Certain species of the genus are the characteristic dominants and primary peat formers of the many mosses or bogs which cover wide areas of flat or gently sloping or undulating land in the cooler regions of the northern hemisphere, more especially the uneven morainic ground left by the Pleistocene ice-sheets. Starting with aquatic species in the innumerable pools or lakelets occupying the hollows, or with less hydrophytic species on valley bog, fen or forest vegetation in a sufficiently moist climate, the bog mosses may spread far and wide over surrounding vegetation, the more hydrophytic being succeeded by less hydrophytic species. In this way the moss bogs have destroyed and buried great areas of fen or forest more than once in post-glacial times, probably always as the result of change from a drier to a wetter climate. Owing to the peculiar structure of its tissues already described Sphagnum carries its own water with it as it grows upwards and outwards. Thus a pad or cushion of one of the less hydrophytic bog mosses forms an extending shoot saturated with water and with a convex upper surface, and the raised bog as a whole is an aggregate of such shoots, also with a slightly convex surface, since the centre of the bog represents its oldest and therefore its highest part.

The older, lower layers of the moss are cut off from light and air by the living surface layer, and progressively die. Compressed by the increasing superincumbent weight as the moss rises higher, and unable to decay completely owing to absence of free oxygen and of the normal action of soil bacteria, the lower layers of moss are converted into typical acid bog or moss peat, whose antiseptic properties are well known from the wonderfully complete preservation after many centuries of various objects, including the bodies of animals and men, that have been buried in the bog.

Such a raised bog is not however a simple mass of Sphagnum, but has a complex structure. In the first place it is composed of very numerous aggregated Sphagnum cushions or hummocks, in each of which progression from aquatic or subaquatic species at the base can be traced upwards to the more xeromorphic species at the summit of the cushion. And secondly it is inhabited by a number of species of oxyphilous vascular plants whose remains form part, sometimes the greater part, of the peat. The shape an d growth of the individual cushions reflect in petto those of the bog as a whole. The structure of a raised bog will be described in more detail in connexion with the Irish raised bogs.

Sphagnetum in Great Britain. A great deal of Sphagnum peat has been formed in the British Isles during the wetter climatic epochs of the post-glacial period. But in the lowlands of England Sphagneta are now mainly met with in sandy heath areas where the drainage is impeded so that acid soil water accumulates. These "wet heath" Sphagneta with their associated species of flowering plants are really "valley bogs" of limited extent, and show a floristic composition quite similar to, though not identical with, those of raised and blanket bogs. Other species of Sphagna occur in certain wet woods and on certain fens under appropriate conditions. On the uplands Sphagnetum does not now cover any large areas of Great Britain. In many upland regions peat is now being actively eroded, though in the wettest climates, and locally where the necessary edaphic conditions are realised, peat is still being formed. Tansley 1939 says that "it is doubtful if an unspoiled example now exists, though there may be some in the Lake District and neighboring regions ......

..... The only available description of a Scottish raised bog "with which to compare Moorthwaite Moss" is that of a small but very perfect example completely enclosed by mature pinewood on the South-Western side of Loch Maree in Ross-shire.

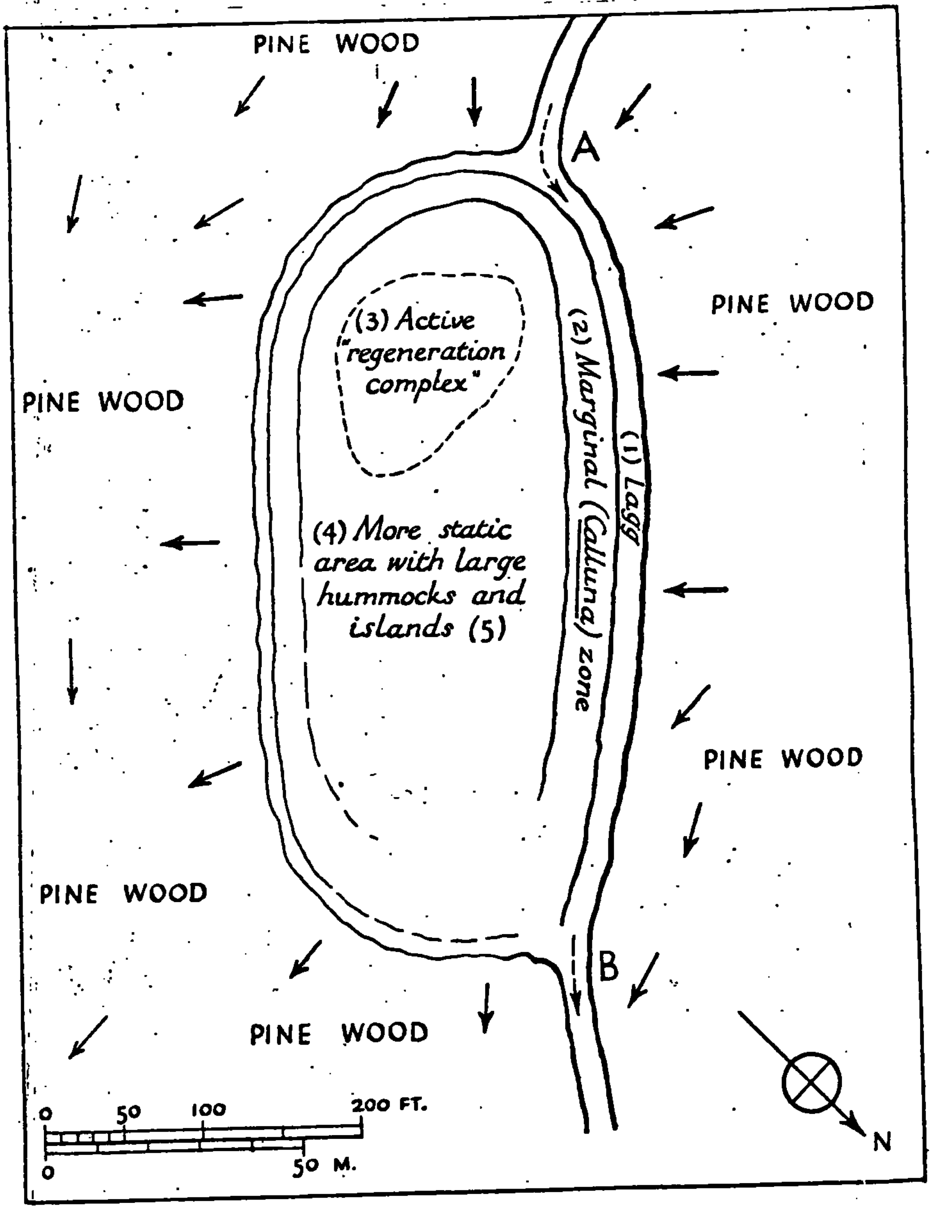


FIG. 138. DIAGRAM OF SMALL RAISED BOG AT LOCH MAREE (ROSS-SHIRE)

The bog is developed on a terrace of the steeply sloping hillside and is entirely surrounded by native pinewood. The thicker arrows show the steeper slopes. (This diagram is drawn from memory and the boundaries and scale are only approximate.) Cf. Pl. 115, phot. 282, which is taken from the hillside at the south-west end of the bog (top of the diagram), approximately from the position of the vertical arrow.

The following species were recorded in a small raised bog at Loch Maree.

(1) Lagg (in and near the stream):

		Molinia caerulea	d
Sphagnum papillosum	cd	Calluna vulgaris+	f
S. recurvum	cd	Carex panicea	f
S. plumulosum	f	Potentilla erecta	f
Juncus effusus	o-la	Erica tetralix	o

+ Not flowering freely

(2) Marginal Calluna zone:

Calluna vulgaris+	d	Potentilla erecta	f
Molinia caerulea	a	Drosera rotundifolia	o
		Sphagnum papillosum	f

+ Flowering freely.

(3) Regeneration complex:

In pools and hollows		Forming hummocks	
Sphagnum cuspidatum var. submersum	a	Sphagnum papillosum	a
S. inundatum	r	S. plumulosum	f-a
Rhynchospora alba	a	S. magellanicum (medium)	o
Drosera anglica	a	S. rubellum (summits)	f
Eriophorum angustifolium	f-a		
Carex pulicaris	o		

Sphagnum tenellum (molluscum), Rhacomitrium lanuginosum and Hypnum cupressiforme were scattered on the hummocks.

(4) More static area. This contained the following additional species:

Eriophorum vaginatum	a-ld	Erica tetralix	f
Narthecium ossifragum	a	pedicularis sylvatica	o-lf
Molinia caerulea	f-la	Juncus squarrosus	o
Potentilla erecta	f-la	Scirpus caespitosus	r-o
Drosera rotundifolia	f	Carex panicea	o
Calluna vulgaris	f	C.stellulata	r

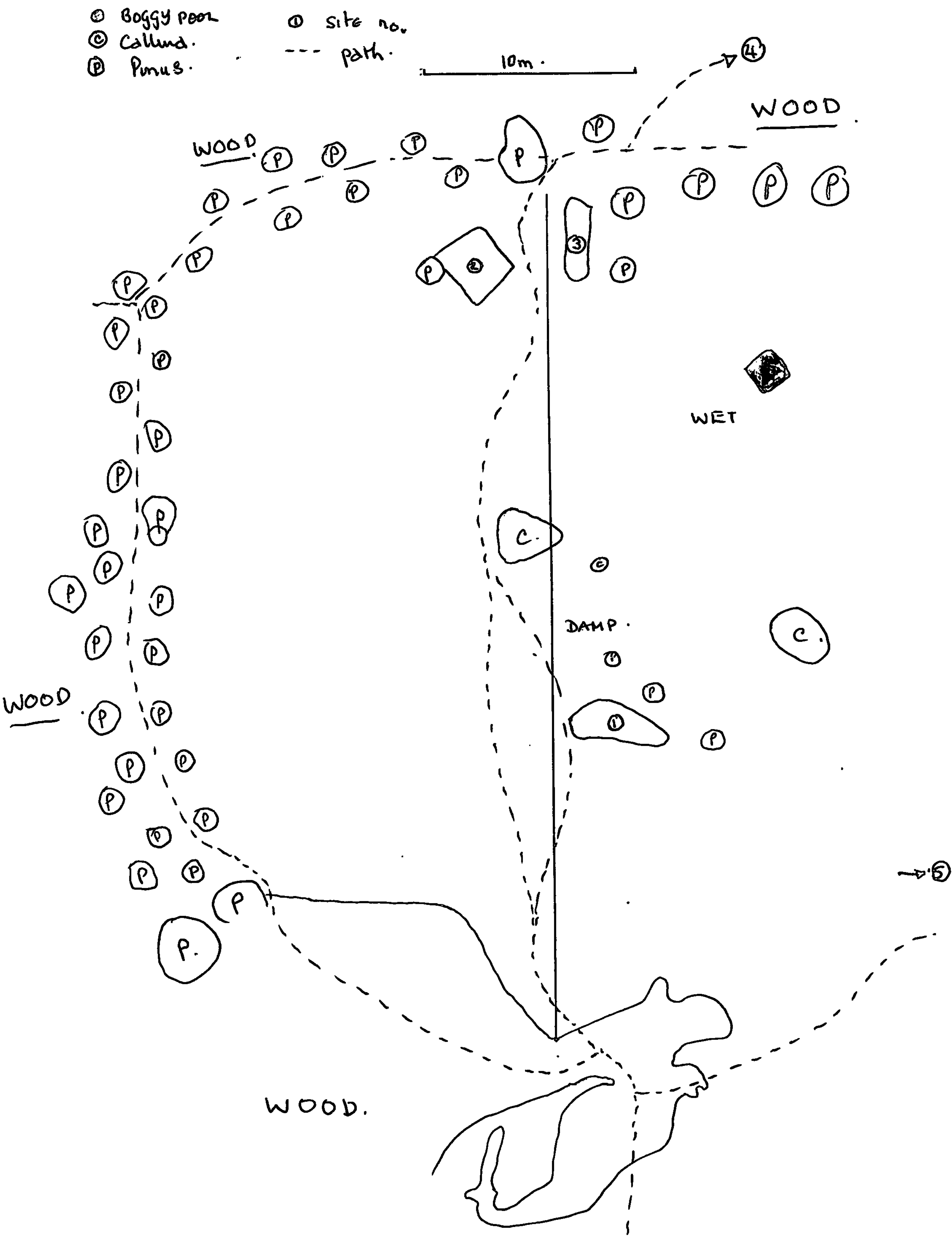
Seedlings of Pinus sylvestris were abundant.

(5) "Islands" (rock outcrops):

Calluna vulgaris	a-d	Hypnum schreberi	f
Molinia caerulea	f	Dicranum scoparium	o
Pteridium aquilinum	f	Hylocomium loreum	o
Agrostis canina	o	H.splendens	o
Juncus effusus	o	Thuidium tamariscinum	o
Vaccinium myrtillus	o		
Pinus silvestris (dwarfed)	F	Cladonia sylvatica	o
Ilex aquifolium	o	C.uncialis	o

Compare this with -

Moorthwaite Moss Cumberland. P.T.O.


Boggy pool
Calluna.
Pinus.
① site no.
--- path.
10m.
④
WOOD
WOOD
P
C.
①
②
③
WET
DAMP.
C.
WOOD
⑤
WOOD.

tion of its success.

It is reasonably clear, however, that during the past 5000 years or more the dominant determinant of vegetation has been human activity with deaphic and climatic factors playing but a secondary role.

THE CLIMATIC OPTIMUM

The concept of a period of post-Glacial climatic optimum is difficult in apply in the face of increasing knowledge of the autecologies of different species. In the Cumberland Lowland itself there were no vegetation changes certainly indicative of 'improved' thermal conditions after about 6000 B.C. In the region immediately south of the Lake District hills, however, the occurrence of Tilia cordata on base-rich soils (Smith 1958, 1959; Oldfield 1960b; Walker 1955a) cannot be similarly dismissed. The pattern of the spread of T. cordata through Great Britain (Godwin 1956) certainly suggests that its extension was slowed by competition from the existing closed forests of oak and elm and that it did not reach the north-west until very late, possibly long after the region became climatically suited to it. Its very establishment at the limit of its range in Zone VIIa under these conditions argues a change in the factors determining forest composition which is difficult to attribute to anything other than climate. The virtual absence of Tilia in Cumberland at the time may have been due to the absence of suitable soils but it might equally have been true that any climatic change failed to transgress the threshold of tolerance for Tilia in that region.

The humidity of the region was evident already in late-Clacial time (part VI). There is no pollen analytical evidence for a dry period at any time in the post-Glacial. The extension of Alnus glutinosa in Zones C12 (Boreal-Atlantic Transition) is attributed to an effective increase in rainfall which may have been going on for some time already (part VII). It is certain, however, that evidence of increased precipitation is more likely to be preserved in organic deposits than is evidence of desiccation, so that a lack of evidence for dryer periods does not preclude their having occurred.

As far as it goes, therefore, the evidence suggests that a thermal 'optimum' might have been achieved early in the post-Glacial and that increases in precipitation, evaporation ratio occurred from time to time throughout the period.

APPENDIX IV

I.

Date: 4·7·69 Plot: 1 Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0·09	0·02	0·01	0·19	0·22			0·02
2.		0·12	0·10	0·05	0·03	0·08			0·01
3.		0·19	0·40	0·10	0·06	0·08			0·02
4.		0·20	0·10	0·02	-	0·10			0·01
5.		0·39	0·26	0·10	-	0·11			0·04
6.		0·15	0·29	0·03	0·01	0·15			0·07
7.		0·26	0·16	0·03		0·02			0·02
8.		0·12	0·07	0·01		0·01			0·01
9.		0·40	0·17	0·01		0·07			0·02
10.		0·09	0·03	0·01		0·01			0·02
11.		0·15	0·10	-	0·02	0·08			0·02
12.		0·08	0·08	0·01	0·05	0·16			0·01
13.		0·28	0·12	0·03		0·08			0·02
14.		0·30	0·17	0·03		0·06			0·01
15.		0·18	0·10	0·07		0·15			0·05
16.		0·51	0·28	0·11		0·10			0·02
17.		0·49	0·22	0·10		0·10			0·02
18.		0·15	0·10	0·01	0·14	0·10			0·02
19.		0·38	0·32	0·05	0·01	0·04			0·02
20.		0·30	0·12	0·02	-	0·02			0·01
21.		0·30	0·10	0·06	0·01	0·06			0·01
22.		0·28	0·19	0·09	0·24	0·14			0·01
23.		0·30	0·14	-	-	0·01			0·01
24.		0·20	0·10	0·03	0·10	0·05			0·04
25.		0·57	0·30	0·01	0·08	0·06			0·03
26.		0·15	0·03	0·08	0·01	0·03	0·06	0·02	0·01
27.		0·01	0·02	0·02	0·36	0·28			0·03
28.									
29.									
30.									
31.	17·82	8·87	4·18		1·49	2·41	0	08	0·79
32.									
33.									
34.									
35.									

.~~995~~Σ	6·64	4·09	1·09	1·31	2·37			0·58
m·995	0·246	0·151	0·040	0·049	0·088			0·021
σ	0·017	0·011	0·001	0·008	0·004			0·0002
SE	0·003	0·002	0·0003	0·002	0·0008			0·00004
df	2·056							
SL.	0·006	0·004	0·0006	0·004	0·0016			0·00008

I

Date: 18·6·69 Plot: 1 Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0·20	0·10	-	-	0·03			0·01
2.		0·56	0·31	0·05	-	0·10			0·02
3.		0·21	0·09	0·03	-	0·03			0·01
4.		0·11	0·04	-	0·01	0·07			0·01
5.		0·24	0·10	0·03	0·09	0·14			0·02
6.		0·12	0·10	0·16	0·18	0·14			0·02
7.		0·39	0·12	0·07	0·39	0·35	0·18	0·05	0·03
8.		0·25	0·13	0·03	-	0·10			0·02
9.		0·18	0·09	-	0·01	0·03			0·01
10.		0·01	0·03	0·03	0·42	0·28	0·01	0·01	0·02
11.		0·20	0·10	0·02	0·01	0·04			0·02
12.		0·35	0·13	0·02	-	0·07			0·02
13.		0·43	0·22	0·08	-	0·09			0·02
14.		0·22	0·14	0·01	0·01	0·03			0·01
15.		0·41	0·23	0·12	0·05	0·12			0·02
16.		0·08	0·02	0·10	0·40	0·43	0·10	0·02	0·03
17.		0·28	0·18	0·10	0·05	0·10			0·02
18.		0·21	0·01	0·09	0·10	0·22	0·09	0·02	0·03
19.		0·22	0·17	0·10	-	0·09			0·02
20.		0·31	0·19	0·01	-	0·06			0·02
21.	13·84	5·95	2·65	(1·05)	1·51	2·60	0·51		0·62.
22.									
23.									
24.									
25.									
26.									
27.									
28.									
29.									
30.									
31.									
32.									
33.									
34.									
35.									

Σ	4·78	2·51	1·05	1·72				0·40
m	·239	0·126	0·053	0·086				0·02
σ	0·023	0·006	0·025	0·021				0·00004
SE	0·005	0·001	0·005	0·005				0·00001
df	2·093							
SL	0·01	0·002	0·01	0·01				0·00002
ΣSL	0·20	0·04	0·20	0·20				0·00040

3III

Date: 4-6 ~~15·5~~·69 7 Plot: I Species: Eriophorum angustifolium

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.	0·29	0·11		0·01	0·04	0·05	0·01	0·01
2.	0·06	0·08		0·36	0·35			0·09
3.	0·01	0·06		0·10	0·03			0·01
4.	0·24	0·13		-	0·06			0·03
5.	0·16	0·10		0·26	0·23			0·01
6.	0·02	0·03		-	0·06			0·03
7.	0·18	0·12		0·12	0·08			0·03
8.	0·16	0·10		0·46	0·37	0·13	0·03	0·06
9.	0·03	0·10		0·18	0·07			0·02
10.	0·08	0·08		0·50	0·38	0·06	0·02	0·09
11.	0·12	0·08		0·17	0·13			0·03
12.	0·20	0·12		0·12	0·12			0·03
13.	0·18	0·10		-	0·06			0·03
14.	0·10	0·05		0·03	0·06			0·03
15.	0·08	0·08		0·17	0·17	0·08	0·02	0·04
16.	0·25	0·13		0·05	0·08			0·03
17.	0·18	0·08		0·03	0·06			0·04
18.	0·08	0·08		-	0·06			0·02
19.	0·03	0·03		-	0·03			0·01
20.	0·08	0·02		0·02	0·02			0·01
21.	0·25	0·13		0·01	0·08			0·05
22.	0·80	0·07		0·02	0·57	0·14	0·01	0·09
23.	0·22	0·10		-	0·08			0·06
24.	0·18	0·09		0·13	0·11			0·03
25.	0·28	0·13		0·07	0·09			0·05
26.	0·30	0·18		0·06	0·08			0·04
27.	0·20	0·12		0·05	0·08			0·03
28.	0·21	0·11		0·01	0·05			0·03
29.	0·11	0·08		-	0·07			0·02
30.	0·08	0·07		-	0·06			0·01
31.	0·09	0·08		-	0·05			0·03
32.	0·07	0·06		-	0·06			0·02
33. 509						0·46	0·09	
34.								
35. 15·26	5·58	2·76		2·93	2·56	0·55		0·88

Σ.	5·32	2·90	3·11	3·84	1·11
m.	0·166	0·0191	[illegible]	0·17	0·035
σ	0·021	0·001	0·023	0·162	0·0005
SE	0·004	0·0003	0·004	0·003	0·0001
df	2·041				
SL	0·008	0·0006	0·008	0·006	0·0002
ΣSL	0·256	0·0192	0·256	0·192	0·0064

IV

Date: 21.5.69 Plot: 1 Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0.10	0.03	0.01	0.04	0.08			0.01
2.		0.17	0.07		0.01	0.01			0.01
3.		0.16	0.08		0.01	0.02			0.01
4.		0.18	0.07		0.01	0.08			0.01
5.		0.10	0.08	0.01	0.04	0.01			0.02
6.		0.07	0.02		0.01	0.02			0.01
7.		0.30	0.11	0.01	-	0.04			0.02
8.		0.01	0.02		0.01	0.01			0.01
9.		0.06	0.07		0.01	0.01			0.01
10.		0.51	0.02		0.17	0.56	0.13	0.01	0.02
11.		0.31	0.10	0.09	0.09	0.22			0.03
12.		0.24	0.10		0.03	0.05			0.01
13.		0.16	0.01	0.01	-	0.05			0.01
14.		0.22	0.09		-	0.02			0.01
15.		0.30	0.11	0.02	-	0.05			0.02
16.		0.06	0.11	0.01	0.22	0.08			0.01
17.		0.17	0.08		-	0.04			0.01
18.		0.18	0.08		0.62	0.05			0.02
19.		0.05	0.02	0.01	0.01	0.01			0.01
20.		-							- -
21.									
22.									
23.									
24.									
25.									
26.	7.84	3.80	1.37	(0.17)	0.60	1.52	0.13		0.42
27.									
28.									
29.									
30.									
31.									
32.									
33.									
34.									
35.									

Σ	3·35	1·27	0·17	0·68	1·41			0·26
m	0·176	0·067	0·009	0·033	0·074			0·014
σ	0·16	0006	0·0004	0·006	0·016			0·00005
SE	0·04	0·001	0·0001	0·001	0·004			0·00001
SL	0·08	0·002	0·0002	0·002	0·008			0·00002
ΣSL	0·152	0·038	0·0038	0·038	0·152			0·00038
df	2·101							

5

Date: 4.7.69 Plot: 2. Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0·20	0·08	0·01	0·10	0·13			0·01
2.		0·26	0·09	0·03	0·10	0·08			0·01
3.		0·14	0·09	0·05	0·39	0·24			0·02
.		0·03	0·02	0·06	0·29	0·19			0·01
.		0·01	0·05	0·03	0·03	0·09			0·01
.		0·17	0·02	0·05	0·04	0·05			0·03
7.		0·20	0·09	0·03	0·30	0·15			0·02
8.		0·21	0·11	0·10	–	0·21			0·04
.		0·12	0·07	0·01	0·08	0·02			0·01
10.		0·03	0·06	0·01	0·40	0·38	0·11	0·04	0·02
1.		0·14	0·24	0·08	0·32	0·21			0·06
2.		0·01	0·02	0·01	0·01	0·03			0·02
3.		0·30	0·17	0·03	0·11	0·04			0·01
4.		0·52	0·19	0·01	0·15	0·12			0·03
5.		0·10	0·10	0·06	0·18	0·11			0·01
6.		0·12	0·07	0·01	0·08	0·02			0·01
7.		0·17	0·02	0·02	0·04	0·14			0·02
8.		0·03	0·04	–	–	0·01			0·01
.		0·05	0·01	0·01	0·36	0·16			0·03
.		0·18	0·10	0·04	0·08	0·17			0·02
1.		0·28	0·18	0·10	0·07	0·08			0·02
2.		0·07	0·05	0·01	0·80	0·48	0·12	0·01	0·01
.		0·08	0·01	0·02	0·22	0·21			0·01
4.		0·14	0·07	0·01	0·04	0·07			2
5.		0·20	0·09	0·02	0·07	0·07			2
6.		0·20	0·08	0·02	0·01	0·04			2
7.		0·08	0·02	0·02	0·12	0·08			2
8.		0·19	0·06	0·01	0·03	0·08			1
.		0·10	0·08	0·10	0·05	0·02			2
0.		0·30	0·16	0·02	0·10	0·11			2
1.		0·16	0·09	0·04	–	0·01			2
2.	·563						0·33		0·59
3.	19·18	6·67	2·65		4·81	3·83			
4.									
5.									

Σ	4.79	2.36	1.01	4.77	3.97			
m	0.155	0.076	0.0033	0.154	0.126			0.61 0.019
σ	0.012	0.014	0.009	0.031	0.034			0.00012
SE	0.002	0.003	0.00002	0.006	0.017			0.00002
df	2.042	~~0.006~~	0.00004					
SL	0.004	0.006	↓	0.012	0.034			0.00004
ΣSL	0.12.	0.18	0.0012	0.362	1.054			0.0012

6

Date: 18·6·69 Plot: 2 Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0·10	0·07	0·30	0·10	0·13			0·02
2.		0·12	0·04	0·02	0·04	0·07			0·02
3.		0·17	0·20	-	1·72	1·03	0·08	0·07	0·10
4.		0·09	0·04	0·01	0·01	0·07			0·01
5.		0·04	0·04	0·04	0·13	0·10			0·01
6.		0·01	0·03	0·10	0·13	0·21			0·01
7.		0·01	0·02	0·01	0·01	0·03			0·01
8.		0·05	0·02	0·05	0·08	0·10			0·02
9.		0·05	0·06	0·08	0·13	0·32	0·20	0·06	0·01
10.		0·08	0·08	0·10	0·40	0·21	0·10	0·03	0·02
11.		0·02	0·01	0·02	0·44	0·27	0·05	0·01	0·01
12.		0·12	0·04	0·02	-	0·05			0·01
13.		0·16	0·10	0·18	0·06	0·18			0·06
14.		0·10	0·06	0·09	0·10	0·03			0·01
15.		0·11	0·02	0·04	0·01	0·04			0·02
16.		0·10	0·03	0·01	0·01	0·02			0·01
17.		0·31	0·10	0·02	—	0·08			0·01
18.		0·02	0·06	0·10	0·30	0·41	0·10	0·01	0·02
19.		0·20	0·10	0·01	-	0·03			0·01
20.		0·06	0·03	0·01	0·30	0·23			0·01
21.		0·17	0·10	0·04	0·23	0·013			0·02
22.		0·20	0·08	0·01	-	0·01			0·02
23.		—	0·15	—	0·28	—			0·05
24.		0·20	0·10	0·12	0·02	0·02			0·02
25.		0·19	0·13	0·09	—	0·08			0·02
26.		19	0·10	0·09	0·07	0·04			0·01
27.		0· —		—	0·13	0·36	0·10	0·02	0·05
28.		0· 08	0·07	0·02	0·31	0·14			0·04
29.		0· 20	08	0·02	0·07	0·11			0·02
30.		0· 02	-01	0·01	—	0·01			0·01
31.		0· 10	0· —	—	0·48	0·25			0·02
32.		- 10	0· 10	0· 12	0·08	0·04			0·02
33.	0562	03	0· 01	0·01	0·04	0·12			0·01
34.	21·20	5·40	2·55		6·35	5·15	0·75		1·00
35.									

Σ	3·4	2·08	1·74	5·68	4·92	4·32		0·71
m	0·0193	0·063	0·053	0·172	0·0149	0·0149		0·0224
σ	0·006	0·002	0·004	0·097	0·037	0·037		0·0004
Σ	[illegible]				0·006	0·006		0·00007
SE	0·001	0·0003	0·007	0·016				
df	2·041							
SL	0·002	0·006	0·014	0·033	0·012			0·00014
ΣSL	0·066	0·0198	0·0462	1·089	0·396			0·0046

VII

Date: 4·6·69 Plot: 2. Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0·09	0·08		0·09	0·04			1
2.		0·08	0·02		0·01	0·03			1
3.		0·12	0·07		0·03	0·07			1
4.		0·13	0·04		0·18	0·07			2
5.		0·10	0·13		0·88	0·29	0·20	0·02	5
6.		0·31	0·16		0·63	0·42			5
7.		0·03	0·04		0·49	0·26	0·02	0·01	3
8.		0·21	0·08		0·10	0·12			4
9.		0·30	0·21		0·04	0·05			1
10.		0·07	0·10		0·42	0·41	0·08	0·01	7
11.		0·10	0·12		1·00	0·76	0·17	0·02	5
12.		0·10	0·18		0·98	0·65	0·08	0·02	2
13.		0·13	0·05		0·02	0·11			1
14.		0·15	0·08		0·01	0·02			1
15.		0·19	0·21		0·70	0·34	0·20	0·09	1
16.		0·16	0·09		0·02	0·01			1
17.		0·12	0·10		0·01	0·01			1
18.		0·21	0·11		0·13	0·07			1
19.		0·10	0·17		0·58	0·33	0·13	0·02	2
20.		0·02	0·07		[illegible]	0·01			1
21.		0·12	0·05		0·03	0·01			1
22.		0·12	0·08		–	0·01			1
23.		0·15	0·10		0·05	0·06			1
24.		0·15	0·09		0·02	0·03			1
25.		0·10	0·13		0·62	0·41	0·13	0·05	0·03
26.		0·18	0·11		0·73	0·50	0·17	0·03	6
27.		0·13	0·09		0·27	0·17			5
28.		0·09	0·10		0·30	0·20			2
29.		0·12	0·08		0·25	0·25			7
30.		0·12	0·08		0·18	0·20	0·02	0·01	2
31.									
32.	26·22	4·65	3·52		9·00	6·52	01·21	0·39	0·93
33.									
34.									
35.									

Σ	4.00	3.02		8.84	6.41			0.78
m	0.13	0.101		0.295	0.214			0.026
σ	0.005	0.003		0.107	0.054			0.0005
SE	0.0009	0.0005		0.024	0.01			0.001
df	2.045							0 --
								0.0002
SL	0.0018	0.001		0.04	0.02			0
ΣSL	0.054	0.03		0.12	0.06			0.0006

8

Date: 21·5·64 Plot: 2 Species: Eriophorum angustifolium

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.	0·12	0·11	0·06	0·15	0·17			0·03
2.	0·09	0·14	0·08	0·92	0·51	0·26	0·11	0·10
3.	0·13	0·07	0·06	0·23	0·15			0·05
4.	0·08	0·10	0·10	0·08	0·12			0·03
5.	0·11	0·10	0·04	–	0·03			0·04
6.	0·06	0·10	0·06	0·32	0·30	0·11	0·04	0·03
7.	0·10	0·08	0·03	0·20	0·13	0·03	0·03	0·06
8.	0·06	0·10	0·06	0·27	0·18			0·04
9.	0·14	0·19	0·12	0·27	0·10			0·07
10.	0·18	0·13	0·05	0·10	0·08			0·04
11.	0·05	0·07	0·02	0·08	0·08			0·03
12.	–	0·05	0·08	0·28	0·16			0·10
13.	0·24	0·20	0·07	0·05	0·08			0·06
14.	0·10	0·10	0·08	0·06	0·10			0·05
15.	0·10	0·07	0·07	0·05	0·04			0·06
16.	0·15	0·10	0·08	0·03	0·03			0·08
17.	0·08	0·04	0·07	0·19	0·12			0·03
18.	0·02	0·01	0·04	0·12	0·12			0·03
19.	0·04	0·09	0·08	0·24	0·31			0·03
20.	0·07	0·04	–	0·01	0·02			0·01
21.	0·01	0·04	–	–	0·01			0·01
22.	0·07	0·10	0·03	0·10	0·10			0·02
23.	0·02	0·20	0·12	0·46	0·98	0·21	0·07	0·01
24.	0·25	0·17	–	0·02	0·03			0·04
25.	0·29	0·10	0·02	0·07	0·09			0·01
26.	0·17	0·11	–	0·02	0·01			0·01
27.	0·08	0·08	0·06	0·01	0·02			0·02
28.	0·08	0·01	0·01	–	0·01			0·01
29.	0·07	0·09	0·06	0·07	0·03			0·02
30.	0·13	0·08	0·01	0·02	0·02			0·01
31.	0·10	0·06	0·01	0·02	0·02			0·01
32. total	0·11	0·14	0·05	0·74	0·46	0·12	0·06	0·05
33. mean ·658	0·18	0·03	0·03	0·08	0·08			0·02
34.	0·10	0·05	0·02	0·01	0·02			0·02
35.	0·10	0·03	0·03	–	0·01			0·01
1954	4·78	2·67	(1·68)	5·98	4·33	0·72	0·25	0·81

Σ	2·78	3·25	1·70	5·21	14·72	1·019
m	0·126	0·105	0·057	0·116	0·157	[illegible]
σ	0·002	0·002	0·001	0·046	0·039	0·040
SE	0·0004	0·0003	0·0002	0·008	0·007	0·0036
df	2,031					0·0001
SL	0·0008	0·0006	0·0004	0·016	0·014	0·0002
ΣSL	0·028	0·021	0·014	0·560	0·490	0·0070

9

Date: 18.5.(3 ? Plot: 2 Species: Eriophorum angustifolium

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0.11	0.13		0.30	0.22	0.07	0.02	0.03
2.		0.22	0.12		0.04	0.07			0.02
3.		0.07	0.06		–	0.04			0.01
4.		0.11	0.06		0.04	–			0.01
5.		0.12	6.10		0.18	0.12			0.01
6.		0.10	0.07		0.05	0.02			0.02
7.		0.14	0.09		0.01	0.02			0.01
8.		0.11	0.05		0.01	0.01			0.01
9.		0.09	0.03		0.01	0.05			0.01
10.		0.03	0.04		0.18	0.13			0.01
11.		0.07	0.08		0.11	0.03			0.01
12.		0.03	0.01		–	0.01			0.01
13.		0.12	0.12		0.18	0.11			0.02
14.		0.07	0.03		0.03	0.04			0.02
15.		0.10	0.13		0.16	0.11			0.02
16.		0.09	0.06		+	0.03			0.01
17.		0.13	0.10		0.02	0.06			0.01
18.		0.18	0.08		0.08	0.03			–
19.		0.10	0.12		0.38	0.20			0.02
20.		0.10	0.05		0.16	0.15			0.01
21.		–	0.01		–	0.01			0.01
22.		0.07	0.18		0.37	0.20	0.07	0.01	0.01
23.		0.19	0.07		0.01	0.08			0.02
24.		0.05	0.02		–	0.01			0.01
25.		0.11	0.19		0.43	0.20	0.09	0.02	0.09
26.		0.08	0.09		–	0.02			0.01
27.		0.28	0.26		0.14	0.10			0.02
28.		0.14	0.10		0.01	0.04			0.02
29.		–	0.01		0.41	0.21			0.02
30.		0.11	0.05		–	0.01			0.01
31.	·416 12.60	3.38	2.71		3.10	2.61	0.22	0.05	0.53
32.							0.27		
33.									
34.									
35.									

Σ	3·12	2·51		4·01	2·33			0·49
m	0·104	0·084		0·134	0·078			0·016
σ	0·004	0·003		0·045	0·005			0·0003
SE	0·0007	0·0006		0·008	0·001			0·00005
df	2·042							0·0001
SE	0·0014	0·0012		0·016	0·002			0·003
ΣSL	0·042	0·036		0·480	0·060			

10

Date: 4·7·69 Plot: 4 Species:

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.	0·70	0·30	0·08	0·05	0·04			0·02
2.	0·43	0·21	0·03	0·01	0·01			0·01
3.	0·55	0·20	0·01	0·06	0·06			0·01
4.	0·25	0·05	0·01	0·01	0·08			0·01
5.	0·77	0·40	0·18	0·71	0·40			0·06
6.	1·22	0·54	0·11	0·70	0·59			0·02
7.	0·48	0·21	0·13	–	0·10			0·01
8.	0·57	0·23	0·10	0·22	0·17			0·02
9.	0·52	0·20	0·13	0·21	0·13			0·02
10.	0·53	0·23	0·10	0·47	0·43			0·05
11.	0·77	0·27	0·10	1·04	0·70			0·02
12.	0·32	0·11	0·02	0·09	0·01			0·01
13.	0·40	0·19	0·08	0·01	0·01			0·02
14.	0·38	0·14	–	0·17	0·21			0·01
15.	0·41	0·18	0·09	0·01	0·12			
16.	0·31	0·10	–	0·01	0·01			0·01
17.	0·35	0·31	0·01	–	0·03			0·02
18.	0·38	0·19	0·19	0·30	0·021			0·01
19.	0·35	0·21	0·08	0·03	0·03			0·02
20.	0·29	0·18	0·10	0·07	0·10			0·01
21.	0·29	0·20	0·05	0·19	0·11			0·01
22.	0·28	0·10	0·07	0·37	0·15			0·02
23.	0·29	0·13	0·03	0·02	0·01			0·01
24.	0·43	0·14	0·02	0·42	0·18			0·01
25.	0·12	0·10	0·02	0·02	0·01			0·01
26.	0·50	0·19	0·01	–	0·14			0·01
27.	0·50	0·26	0·08	–	0·01			0·01
28.	0·41	0·13	0·05	0·22	0·11			0·02
29.	0·30	0·19	0·10	0·20	0·15			0·02
30.	0·47	0·19	0·12	0·25	0·19			0·02
31.	0·59	0·25	0·09	0·05	0·10			0·02
32. 10114	14·36			5·99	4·93			0·92
33. 32·81		6·61						
34.								
35.								

Σ	14.07	6.09	2.19	5.91	4.59			0.54
m	0.47	0.203	0.073	0.197	0.153			0.018
σ	0.049	0.009	0.003	0.066	0.029			0.0001
SE	0.009	0.002	0.0005	0.012	0.005			0.00002
df	2.042							
SL	0.018	0.004	0.001	0.024	0.01			0.00004
ΣSL	0.~~609~~ 558	0.121	0.037	0.744	0.31			0.0012

11 black wax pencil

Date: 18.6.69? Plot: 4 Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0.66	0.28	0.05	0.02	0.07			–
2.		0.70	0.32	0.08	0.30	0.21			0.02
3.		0.19	0.22	0.16	0.38	0.13			0.01
4.		0.25	0.19	0.06	0.10	0.08			0.02
5.		0.51	0.20	0.19	1.51	0.65			0.06
6.		0.60	0.29	0.04	1.11	0.46			0.04
7.		0.52	0.33	0.06	1.23	0.41			0.03
8.		0.38	0.23	0.08	0.02	0.09			0.02
9.		0.62	0.30	0.11	0.72	0.52			0.09
10.		0.24	0.12	0.03	0.26	0.10			0.01
11.		0.53	0.29	0.12	1.17	0.51			0.08
12.		0.68	0.43	0.14	0.77	0.40			0.04
13.		0.63	0.40	0.08	0.31	0.18			0.02
14.		0.47	0.29	0.05	0.49	0.34			0.03
15.		0.30	0.18	0.02	0.77	0.47			0.09
16.		0.43	0.21	0.06	0.10	0.10			0.01
17.		0.57	0.26	0.06	0.17	0.10			–
18.		0.60	0.27	0.01					0.05
19.		0.69	0.29	0.12	0.19	0.06			0.08
20.		0.39	0.20	0.21	0.51	0.18			0.03
21.		0.39	0.20	0.13	0.79	0.431			0.03
22.		0.51	0.30	0.09	0.44	0.18			0.03
23.		0.40	0.17	0.08	0.15	0.10			0.02
24.		0.67	0.32	0.02	0.02	0.05			0.02
25.		0.48	0.08	0.06	0.23	0.31			0.01
26.	1.511					6.40			1.01
27.	40.82	14.58	6.35		11.98				
28.									
29.									
30.									
31.									
32.									
33.									
34.									
35.									

Σ	12·35	4·57	2·11	11·76	6·16			0·85
m	·494	·183	·084	·470	·246			·034
σ	·032	·022	·063	·194	·038			·0007 ~~·00~~
SE	·006	·004	·0006	·039	·008			·0001
df	2·064							
SL	·012	·008	·0012	·080	·016			·0002
ΣSL	·03	·02	·003	·20	·044			·005

12

Date: 4·6·69 ? Plot: 4 ? J paper Species:

	Whole plant.	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0·26	0·03	0·01	0·10	0·801			-
2.		-0·22	0·09	-	0·01	0·06			0·01
3.		0·42	0·20	-	0·68	0·02			0·07
4.		0·32	0·20	0·16	0·02	0·28			0·06
5.		0·23	0·20	0·21	0·51	0·17			0·01
6.		0·12	0·06	0·01	0·10	0·01			0·01
7.		0·38	0·20	0·16	0·76	0·31			0·03
8.		0·10	0·01	0·01	0·21	0·09			0·01
9.		0·53	0·28	0·13	0·28	0·18			0·03
10.		0·38	0·14	0·17	0·88	0·35			-
11.		0·20	0·21	0·09	1·00	0·51			0·11
12.		0·36	0·21	0·09	0·10	0·02			0·01
13.		0·50	0·29	0·10	0·30	0·12			0·01
14.		0·41	0·23	0·02	-	0·01			0·03
15.		0·38	0·25	0·11	0·59	0·25			0·01
16.		0·07	0·08	0·01	0·41	0·09			0·02
17.		0·38	0·29	0·01	0·07	0·06			-
18.		0·40	0·20	0·12	0·39	0·22			0·03
19.		0·08	0·03	-	0·01	0·01			0·01
20.		0·62	0·43	0·18	1·34	0·74			0·05
1.		0·37	0·20	0·01	0·04	0·08			0·01
2.		0·43	0·25	0·09	0·18	0·10			0·02
3.		0·22	0·27	0·17	1·01	0·30			0·08
4.		0·38	0·22	0·18	0·11	0·09			0·01
25.		0·12	0·01	0·03	0·01	0·08			0·01
26.		0·20	0·15	-	0·10	0·03			0·01
27.									
28.	1·129								
29.									
30.									
31.	30·22	10·43	4·73	(9·07) incl in green	9·18	4·99			0·89
32.									
33.									
34.									
35.									

Σ	8·00	4·73	2·04	9·2	4·19			0·59
m	·308	·182	·078	·354	·184			·023
σ	·027	·012	·028	·149	·052			·0005
SE	·005	·0042	·00042	·063	·028			·00021
df	2·060							
SEL	·001	·004	·0004	·06	·02			·0002
ΣSL	·25	·100	·010	1·5	·050			·005

13

Date: 21-5-·69 Roman Loxton

Plot: 4

Species:

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.	084	0·28	0·09	0·82	0·39			0·08
2.	0·21	0·22	0·19	0·89	0·35			0·10
3.	0·19	0·17	0·01	0·02	0·02			0·01
4.	0·13	0·12	0·02	0·39	0·18			0·02
5.	0·27	0·20	0·05	0·32	0·12			0·05
6.	0·19	0·12	0·05	0·18	0·17			0·01
7.	0·13	0·06	0·01	0·02	0·01			0·01
8.	0·50	0·55	0·26	0·77	0·30			0·10
9.	0·29	0·20	0·09	0·12	0·10			0·01
10.	0·21	0·11	0·03	0·31	0·11			0·03
11.	0·31	0·21	0·12	0·18	0·21			0·02
12.	0·40	0·31	0·07	0·72	0·30			0·07
13.	0·38	0·29	0·11	0·22	0·10			0·02
14.	0·19	0·15	0·04	0·20	0·12			0·03
15.	0·38	0·32	0·15	0·32	0·41			0·08
16.	0·23	0·26	0·04	0·01	0·06			0·01
17.	0·35	0·18	0·02	0·05	0·04			0·02
18.	0·19	0·16	0·06	0·68	0·45			0·08
19.								
20. 1·14								
21. 22·26	6·72	4·05	(1·41) incl in green	6·93	3·78			0·98
22.								
23. Σ	4·79	3·91	1·41	6·22	3·44			0·75
24.								
25. m	·266	·217	·078	·346	·191			·043
26.								
27.								
28. σ	·085	·015	·005	·096	·022			·001
29.								
30. SE	·020	·004	·0051	·023	·005			·0003
31. df	2·052							
32.								
33. SL	·04	·008	·002	·047	·010			·0006
34.								
35. ΣSL	·72	·144	·036	·846	·180			·0108

14 Date: 30·4·69 Plot: 4 Species:

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
	0·34	0·21		0·19	0·08			–
	0·34	0·15		0·17	0·11			0·08
	0·03	0·05		0·05	0·04			0·01
	0·03	0·03		0·05	0·06			0·01
	0·29	0·22		0·53	0·25			0·04
	0·28	0·28		0·33	0·42			0·08
	0·26	0·13		0·15	0·10			0·02
	0·21	0·22		0·29	0·33			0·01
	0·20	0·09		0·17	0·09			0·03
	0·64	0·07		0·01	0·01			–
	0·66	0·01		0·04	0·04			0·02
	0·13	0·28		0·26	0·13			0·09
	0·34	0·33		0·41	0·13			0·01
	0·36	0·30		0·35	0·316			0·10
	3·10	1·76		3·05	2·00			0·59
Σ	4·11	2·27		3·00	1·95			·50
m	·294	·162		·214	·139			·0357
σ	·041	·103		·028	·015			·001
SE	0·011	·03		·007	·004			·0003
df	2·169							
SL	·024	·065		·015	·009			·0006
Σ	·336	·91		·210	·126			·008

15 TEST CROPPING

Date: 23·4·69 Plot: 4 damp pine 70% shade Species: Eriophorum angustifolium

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.								
2. TOTALS	11·10	2·84		8·34	6·81			1·27
3. no 33								
4.								
5.								
6.								
7.								
8.								
9.								
10.								
11.								
12.								
13.								
14.								
15.								
16.								
17.								
18.								
19.								
20.								
21.								
22.								
23.								
24.								
25.								
26.								
27.								
28.								
29.								
30.								
31.								
32.								
33.								
34.								
35.								

16

Date: 4.7.69 Plot: 5 Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0.50	0.21	–	0.05	0.02			0.02
2.		0.36	0.18	0.06	0.06	0.11			0.03
3.		0.40	0.22	0.02	–	0.02			0.02
4.		0.58	0.20	0.12	0.08	0.19			0.06
5.		0.48	0.17	0.13	0.08	0.18			0.02
6.		0.20	0.12	0.04	–	0.04			0.02
7.		0.11	0.01	0.05	0.01	0.02			0.02
8.		0.50	0.30	0.12	0.01	0.16			0.02
9.		0.20	0.09	0.05	0.13	0.09			0.01
10.		0.47	0.20	0.06	0.01	0.03			0.06
11.		0.18	0.12	0.03	1.11	0.60	0.33	0.02	0.02
12.		0.42	0.21	0.10	–	0.12	–		0.02
13.		0.20	0.40	0.03	0.02	0.11			0.02
14.		0.68	0.28	0.13	0.5	0.31			0.09
15.		0.10	0.13	0.10	0.01	0.11			0.01
16.		0.29	0.10	0.04	0.11	0.05		–	0.01
17.		0.32	0.29	0.09	– 0.07	0.11			0.03
18.		0.20	0.19	0.05	–	0.09			0.01
19.		0.26	0.15	0.10	0.25	0.20			0.01
20.		0.70	0.41	0.12	0.42	0.65			0.05
21.		0.27	0.18	0.10	0.01	0.08			0.02
22.		0.20	0.09	0.01	–	0.02			0.02
23.		0.28	0.30	0.12	0–	0.10			0.05
24.		0.25	0.14	0.09	0.08	0.10			0.02
25.		0.69	0.43	0.13	0.01	0.20			0.10
26.		0.43	0.33	0.15	0.25	0.29			0.05
27.		1.05	0.47	0.18	0.31	0.37			0.04
28.		0.73	0.43	0.37	0.21	1.11			0.15
29.		0.11	0.05	0.02	0.01	0.03			–
30.		0.20	0.18	0.29	0.51	0.42			0.07
31.	1.040	15.22	6.88		5.18	6.08			1.28
32.	34.64								
33.									
34.									
35.									

Σ	11.36	6.58	2.90	4.31	5.93			1.07
m	.378	.219	0.0966	.144	.197			.035
σ	.056	.016	.0065	.057	.057			.001
SE	.01	.063	.0011	.01	.01			.0002
df	2.045							
SL	.02	.006	.002	.02	.02			.0004
ΣSL	.60	.18	.06	.60	.60			.012

17

Date: 18·6·69 Plot: 5 Species:

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.	0·35	0·21	–	–	0·08			0·02
2.	0·39	0·28	0·11	–	0·12			0·05
3.	0·30	0·18	–	–	0·06			0·02
4.	0·30	0·18	0·10	0·03	0·14			0·04
5.	0·20	0·12	0·02	–	0·02			0·02
6.	0·42	0·33	0· 09	0·05	0·17			0·05
7.	0·18	0·45	0· 17	1·33	0·02	0·18	0·04	0·01
8.	0·38	0·22	0· 02	0·11	0·08			0·02
9.	0·20	0·18	0· 05	0·11	0·10			0·01
10.	0·20	0·14	0· 01	–	0·01			0·02
11.	0·08	0·19	0· 11	0·60	0·80	0·18		0·03
12.	0·46	0·24	0· –	0·01	0·04			0·03
13.	0·04	0·06	– 21	0·42	0·20			0·03
14.	0·57	0·24	0· 11	0·10	0·21			0·05
15.	1·57	0·11	0· 09	0·10	1·01	0·22	0·11	0·02
16.	0·19	0·28	0· 11	0·50	0·60			0·05
17.	0·17	0·09	0 01	0·51	0·40			0·06
18.	0·07	0·40	0·10	0·78	0·10			0·02
19.	0·23	0·25	0·10	0·31	0·20			0·04
20.	0·07	0·07	0·01	0·08	0·03			0·01
21.	–	0·20	0·	0·39	0·30			0·08
22.	0· 21	0·16	0·03	0·09	0·31			0·02
23.	0·19	0·13	0·09	0·10	0·07			0·01
24.	0·04	0·09	0·08	0·34	0·44	0·12	0·01	0·01
25.	0·18	0· 11	0·02	0·31	0·22			0·02
26.	0·32	0·33	0·22	0·70	0·30			0·02
27.	0·15	0·10	0·07	0·40	0·21			0·02
28.	0·18	0·10	0·02	0·40	0·40			0·04
29.	0·70	0·46	0·23	0·15	0·35			0·07
30.								
31. 1·114							1·64	1·20
32. 35·67	10·48	6·21		8·91	7·23			
33.								
34.								
35.								

								8
Σ	8·28	5·85	2·18	8·12	6·93			0·87
m	·286	·202	·075	·28	·241			·03
σ	·084	·014	·005	·039	·058			·0004
SE	·016	·003	·0009	·018	·011			·00008
df	2·048							·00016
SL	·033	·066	·0018	·037	·022			·00016
ΣSL	·957	·174	·052	1·073	·638			·0044

18

Date: 4·6·69 Plot: 5 Species:

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
	0·34	0·18	0·08	0·44	0·28			0·05
	0·32	0·28	0·12	0·33	0·23			0·02
	0·24	0·08	0·02	0·02	0·04			0·01
	0·03	0·16	0·02	0·24	0·06			0·01
	0·19	0·31	0·10	0·63	0·48			0·03
	0·10	0·07	0·02	-	0·01			0·01
	0·24	0·64	0·22	0·41	0·70			0·03
	0·24	0·14	0·12	0·31	0·48			0·02
	0·02	0·07	0·03	0·13	0·08			0·01
	0·13	0·11	0·03	0·15	0·20			0·01
	0·09	0·06	0·02	0·03	0·02			0·01
	0·34	0·26	0·12	0·67	0·49			0·02
	-	0·20	0·08	0·50	0·60	0·04	0·01	0·08
	0·60	0·64	0·27	0·30	0·20			0·08
	0·22	0·33	0·09	0·01	0·15			0·03
	0·18	0·21	0·02	0·18	0·18			0·03
	0·34	0·20	0·04	0·01	0·08			0·02
	0·14	0·16	0·07	0·43	0·41			0·01
	0·28	0·12	0·03	0·01	0·03			0·01
	0·30	0·20	0·16	0·08	0·10			0·03
	0·18	0·10	0·02	0·	0·01			0·01
	0·34	0·21	0·01	0·40	0·67			0·05
	0·68	0·71	0·23	0·42	0·29			0·05
	0·04	0·02	0·02	0·18	0·19			0·01
	0·31	0·27	0·04	0·37	0·45			0·02
	0·31	0·10	0·02	-	0·02			0·01
	0·07	0·08	0·02	0·22	0·21			0·02
	0·24	0·14 0·39	0·05	0·25	0·17			0·01
	0·55	0·16	0·12	0·05	0·12			0·01
	0·21		0·15	-	0·01			0·01
1·019 34·55	11·56	7·38	(2·44)	7·59	7·04	0·05		0·93

Σ	7·27	6·48	2·44	6·77	6·90			·72
m	·242	·216	·081	·226	·230			·024
σ	·031	·033	·006	·042	·044			·0004
SE	·006	·006	·001	·008	·008			·00007
df	2·045							
SL	·012	·012	·002	·016	·016			·00014
ΣSL	·360	·360	·060	·480	·480			·0042

19

roman letters

9-6 21-5
Date: ~~15~~·5·69? Plot: 5 Species:

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0.11	0.05		0.09	0.07			0.01
2.		0.40	0.23		0.28	0.10			0.01
3.		0.22	0.18		0.72	0.09			0.01
4.		0.60	0.67		0.15	0.10			0.07
5.		0.05	0.30		0.14	0.15			0.09
6.		0.21	0.11		0.58	0.54			0.10
7.		0.67	0.05		0.05	0.37			0.05
8.		0.17	0.21		0.32	0.18			0.02
9.		0.24	0.10		0.12	0.15			0.02
10.		0.18	0.08		0.86	0.50			0.0[illegible]
1.		0.02	0.03			0.01			-
2.		0.16	0.17		-	0.03			0.01
3.		0.10	0.07		0.01	0.01			0.01
4.		0.13	0.13		0.41	0.21			0.0 1
5.		0.52	0.34		0.59	0.21			0.0 2
6.		0.38	0.21		0.19	0.11			0.0 1 0.01 2
7.		0.39	0.23		0	0.01			0.02 2
8.		0.20	0.10		0.22	0.20			0.02 1
9.		0.24	0.13		-	-			
10.		0.50	0.47		0.43	0.11			0.02
1.		0.51	0.36		0.25	0.10			0.021 0.01 --
2.		0.18	0.13		-	0.04			0.01
3.		0.19	0.20		0.20	0.09			0.1 2
4.		0.08	0.14		0.26	0.65			0.1 2
5.		0.08	0.03		0.02	0.32			
6.		0.49	0.40		0.36	0.10			0 01
7.		0.29	0.22		0.02	0.10			0.01
8.		0.29	0.49		0.75	0.31			0.02
9.		0.21	0.28		0.35	0.15			0.02
10.	.916								
1.	28.33	8.83	6.00		7.27	5.21			1.02
2.									
3.									
4.									
5.									

Σ	8·21	5·91		6·77	4·71			1·37
m	·283	0·204		·233	·162			·034
SEσ	·00633	·021		·057	·011			·004
SE	·086	·004		·011	·002			·0008
[illegible]	2·0048							
SL	·012	·008		·022	·004			·0016
ΣSL	·348	·232		·638	·116			·0464

20

Date: 8·5·69 Plot: 5 Species: 13 [illegible]

	Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.		0·21	0·12		0·50	0·20			0·01
2.		0·20	0·12		0·43	0·22			0·01
3.		0·19	0·11		0·20	0·13			0·02
4.		0·52	0·35		0·42	0·20			–
5.		0·10	0·05		–	0·03			0·01
6.		0·28	0·17		0·27	0·18			0·02
7.		0·23	0·11		0·40	0·24			0·05
8.		0·29	0·10		–	0·12			0·02
9.		0·32	0·12		0·05	0·06			0·01
10.		0·33	0·10		0·32	0·29			0·01
11.		0·15	0·04		0·12	0·30			0·01
12.		0·02	0·01		0·01	0·01			0·01
13.		0·61	0·28		1·08	0·48			0·04
14.		0·20	0·17		0·51	0·15			0·02
15.		0·49	0·29		1·29	0·52			0·02
16.									0·33
17.		4·30	2·31		5·74	3·12			~~2·24~~
18.									
19.									
20.									
21.									
22.									
23.									
24.									
25.									
26.	Σ	4·14	2·21		5·60	3·13			·260
27.					·373	·209			·017
28.	m	·276	·147						
29.									
30.	σ	·031	·01		·254	·024			·0002
31.	SE	·008	·003		·066	·006			·00005
32.	df	2·064							
33.									
34.	SL	·017	·006		0·136	·013			·001
35.	ΣSL	·255	·09		2·04	·195			·015

21

Date: 30·4·69 Plot: 5 Species:

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
	0·31	0·38		0·84	0·49	0·14		0·25
	0·29	0·28		0·43	0·22	0·10		0·14
	0·12	0·10		0·19	0·12			0·10
	0·09	0·06		0·16	0·06			0·02
	0·29	0·35		0·48	0·18	0·20		0·21
	0·07	0·20		0·12	0·05			0·04
	0·10	0·15		0·36	0·21			0·10
	0·15	0·02		0·11	0·39			0·05
	0·22	0·15		0·25	0·17			0·10
	0·07	0·14		0·74	0·38			0·15
	0·03	0·05		0·28	0·15			0·08
	0·15	0·11		0·29	0·19			0·08
	0·13	0·19		0·23	0·16	0·10		0·03
	0·11	0·18		0·12	0·05			0·07
								0
13·89	2·13	2·36		4·30	2·81	0·54		1·42
Σ	2·13	2·36		4·60	2·82			1·42
m	·152	·169		·328	·201			·0101
σ	·010	·014		·060	·020			·005
SE	·001	·002		·008	·003			·0002
df	2·160							
SL	0·002	0·004		·017	·006			·015
ΣSL	0·028	·056		·238	·084			·210

22 TEST CROPPING

Date: 23.4.69 Plot: 5 Species: Eriophorum angustifolium

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1.								
2. TOTAL								0·58
3. 12·78	2·19	1·51		5·34	3·14			
4. no 11								
5.								
6.								
7.								
8.								
9.								
10.								
11.								
12.								
13.								
14.								
15.								
16.								
17.								
18.								
19.								
20.								
21.								
22.								
23.								
24.								
25.								
26.								
27.								
28.								
29.								
30.								
31.								
32.								
33.								
34.								
35.								

23

Date: 21·5·69 Plot: 2 . Species:

Whole plant	green leaves	living sheath	red leaves	brown leaves	dead sheath	flower stem	flower head	plant root
1. 2. 3. 4. 5.	0·10 0·05 0·21 0 10 0·11	0·16 0·03 0·18 0·10 0·10		0·54 0·08 0·72 0·04 0·91	~~0·30~~ ~~0·08~~ 0·66 0·15, 0·82.			0·02 0·01 0·03 0·01 0·02
6. 7. 8. 9. 10.	0·22 0·73 0·19. 0·18. 0·09	0·29 0·15 0·21 0·14 0·10		0·47 1·19 0·74 0·76 0·74	0·21, 0·74. 0·57. 0·45. 0·37.	0·05 0·19		0·02 0·03 0·03 0·03 0·01
1. 2. 3. 4. 5.	0·08, 0·10. 0·11 . 0·01 0·11.	0·02 0·15 0·08 0·04 0·18		0·03 0·08 0·07 – 0·40	0·04. 0·24. 0·09, 0·01 , 0·28.			0·01 0·01 0·01 0·01 0 02
6. 7. 8. 9.	0·21 0·22. 0·15 0·29. 0·02,	0·17 0·23 0·11 0·28 0·02		0·79 0·90 0·02 0·14 –	0·65 . 0·49 : 0·09, 0·08. 0·01 .			0·03 0·02 0·01. 0·02 0·01
1. 2. 3. 4.	0·13 . 0 25. 0·13 .. 0·05. 0·10	0·04 0 26 0·13 0·09 0·70		0·02 0·19 0·38 0·14 0·70	0·04. 0·07. 0·20. 0·04 0·12	0·10		0·02 0·01 0·02 0·01 0·20
6. 7. 8. 9.	3·79	3·26		5·50	6·86.			0·57
1. 2. 3. 4. 5.	15 ×2	13·0		31·6	27.	13		23.

	·394	·396	10·05	6·70	·062
	·158	·158	·402	·268	·025
	·020	·020	·376	·629	·001
	·004	·004	·075	·121	·008
df	2·064				
SL	·008	·008	·154	·250	·0006
Σsu	·20	·20	3·85	6·25	·015

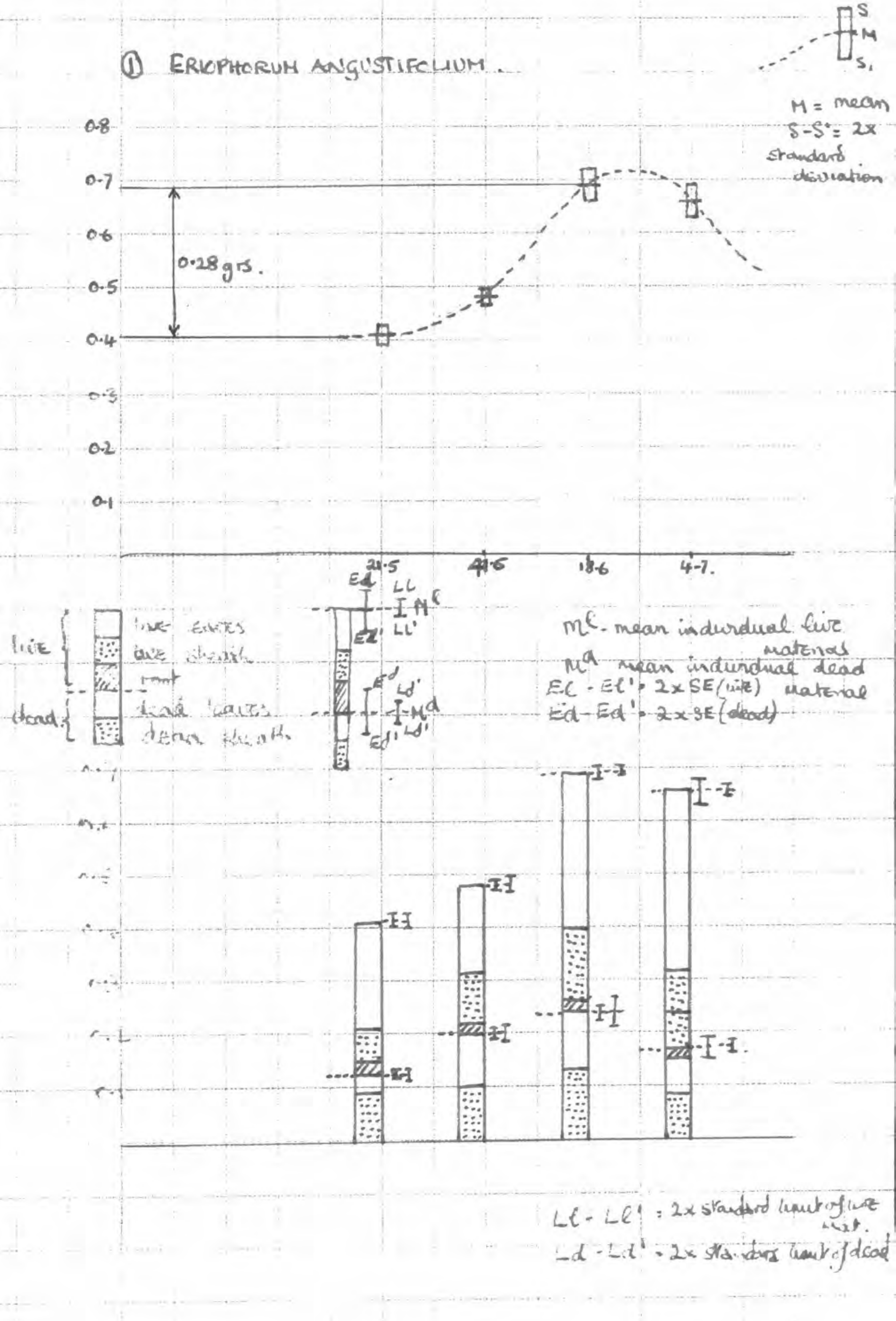
dry weight yield per 100 plants
(with flower data
per 100 flowering plants.)

		23·4	30·4	8-5	21-5	4-6	18-6	4-7
Totals 1		-	-	-	41	48	69	66
2		-	-	42	56	87	64	62
4		88.	~~123~~ 90.	-	123	116	163	106
5		116.	96	105	101	107	123	115
green 1		-	.	-	20	17	30	33
2		-	-	11	14	16	16	21
4		33	24	-	37	40	58	46
5		20	15	28	32	39	36	51
livesheath 1		-	-	-	7	9	13	15
2		-	-	9	7	12	8	9
4		9	14	-	22	18	27	21
5		14	17	15	21	25	21	23
total alive 1		-	-	-	27	26	43	48
2		-	-	20	21	27	24	30
4		42	37	-	50	58	86	68
5		38	32	44	53	62	57	74
dead lb 1		-	-	-	3	9	8	6
2		-	-	10	17	30	19	16
4		25	23	-	38	35	48	19
5		49	33	38	26	25	31	17
dead sheath 1		-	-	-	8	8	13	9
2		-	-	9	12	22	16	12
4		18	15	-	21	19	26	16
5		29	20	21	19	23	25	20
total dead 1		-	-	-	11	17	21	14
2		-	-	19	29	52	35	28
4		42	39	-	59	54	73	35
5		77	53	59	44	49	55	38
roots 1		-	-	-	2·2	1·6	3·1	2·9
2		-	-	1·8	2·3	3·1	3·0	2·8
4		3·8	4·5	-	5·4	3·4	4·0	2·9
5		5·3	10·1	2·2	3·6	3·1	4·1	4·3
fls 1		-	-	-	13·0	11·0	12·7	8·0
2		-	-	9·0	19·4	16·3	12·5	16·5
4		-	-	-	-	-	—	—
5		-	13·5	-	-	5·0	4·1	--

Dry wt yield per plot - bracketed figure = no of plants sampled.

	23·4	30·4	8·5	21·5	4·6	18·6	4·7
Totals 1				1·84 (19)	15·26 (32)	13·84 (20)	17·82 (27)
2			12·60(30)	19·54(35)	26·22 (30)	21·20 (33)	19·18 (31)
4				22·26 (18)	30·22 (23)	40·82(25)	32·81 (3
5	12·78(11)	13·85(14)	-	28·33(29)	34·55(30)	35·61(29)	34·64(30
green 1				3·80 (21)	5·58	5·95	8·87
2			2·38(30)	4·78(35)	4·65	5·40	6·67
4	11·10	3·10(14)		6·73(18	10·43	14·58	14·36
5·	2·19	2·13(14)	4·30 (15)	8·83(29)	11·56	10·48	15·22
lvs sh 1				1·37	2·76	2·65	4·18
2			2·71	2·67	3·52	2·55	2·65
4	2·84	1·76		4·05	4·73	6·85	6·61
5	1·51	2·36	3·31	6·00	7·38	6·41	6·88
d. ws sh 1				0·60	2·93	1·51	1·49
2			3·10	5·98	9·00	6·35	4·81
4	8·34	3·05		6·93	9·18	11·95	5·39
5	5·34	4·80	5·74	7·27	7·59	5·91	5·18
dead sh lvs 1				1·52	2·56	2·60	2·41
2			2·61	4·33	6·52	5·15	3·83
4	5·81	2·00		3·78	4·92	6·40	4·93
5	3·14	2·81	3·12	5·21	7·04	7·23	6·08
d.sh 1							
2							
4							
5							
roots 1				0·42	0·88	0·62	0·19
2			0·53(30)	0·98	0·93	1·00	0·89
4	1·27(33)	0·59(14)		0·81	0·89	1·01	0·92
5	0·58(11)	1·42(14)	0·33(15)	1·02	0·93	1·20	1·28
fls 1				0·13	0·55	0·51	0·08
2		-	0·27	0·97	1·60	0·75	0·33.
4		-		0·98	-	-	
5.		0·54(4)	-	-	0·05	1·64	

① ERIOPHORUM ANGUSTIFOLIUM.



M = mean
S-S' = 2x standard deviation

M^l - mean individual live material
M^d mean individual dead material
$El - El' = 2 \times SE$ (live)
$Ed - Ed' = 2 \times SE$ (dead)

$Ll - Ll'$ = 2x standard limit of live wt.
$Ld - Ld'$ = 2x standard limit of dead

northward into the Cumwhitton Moss basin, but this could only have functioned if the water level had stood above 120 m O.D., an order of level for which there is no evidence in the stratgraphy.

The melting of the ice block was followed by the accumulation of a sandy silt which became progressively more muddy as time went on but never became very organic. This deposit might represent only a remnant of a formerly greater extension, removed from the edges of the basin by subsequent erosion. Above it, silty clay-mud was laid down during Zones C1, C2 and early C3 (I). The pollen diagram indicates how barren was the vegetation of this period. Only Myriophyllum alterniflorum could really flourish in such oligotrophic conditions, although Alisma plantago-aquatica, Sparganium sp. and Nymphaea cf. alba were sparsely represented whilst grasses, sedges, Thalictrum sp. and Filipendula ulmaria formed poor fringing fens, probably incompletely covering the ground and hardly distinguishable from the communities occupying the drier and higher land. The later half of Zone C3 (I) witnessed the deposition first of fine sand and then (in Zone C4) of coarse sand and gravel which can oly have resulted from the re-distribution of earlier-deposited material from the upper slopes of the basin. A pronounced change in water-table may have been sufficient to account for this, but the upper parts of the deposit are very mixed, suggesting the downslope solifluction movement of unsorted material under freeze-thaw conditions. The pollen analytical data do not indicate any major ecological change in the basin during this period. The consistent presence of Sphagnum spores (ca. 20% A.P.) is perhaps of interest, but might be due to their secondary incorporation with soliflucted material.

After this episode the formation of truly organic deposits in the basin began. The first stage, covering Zones C5, C6 and early C7 (II and early III) resulted in up to 49 cm of nekron mud being deposited beneath the lake up to a maximum height of 3.5 m below site datum, i.e. about 117 m O.D. The pollen diagram is rather uninformative about the lake vegetation during this period. Tt is evident that Myriophyllum alterniflorum was much less important than formerly but there is no indication of what replaced it. It may be that the more stable conditions around the margins, resulting in a diminution in the quantity of inorganic material supplied to the lake, thereby rendered the lake water intolerably poor in nutrients to anything other than micro-organisms. Apart from an isolated maximum of Filipendula ulmaria pollen and the persisting Thalictrum sp. the fringing fens must have been largely dominated by grasses.

During the latter part of Zone C7 and Zone C8 (III) sand was once again washed into the lake, although not on the scale of Zones C3 and C4. Indeed, no more rigorous conditions than a change in water table, or the slight exposure of surrounding slopes to water erosion, seem necessary to explain this change, particularly as the deposition of nekron mud contin continued throughout. The only recorded floristic change of any substance was the continued diminution of M. alterniflorum, punctuated at the top of Zone C8 (III) by a temporary maximum, perhaps only at the site of the pollen diagram, and the sudden abundance of Ranunculus sect. Batrachium. In the fringing fens, as in the dry-land vegetation, sedges perhaps replaced grasses in part, but there is no other indication of change there.

With the opening of Zone C9 (IV-V), allochthonous material became very rare in the lake mud, whilst in the latter part of the zone the muds became finely detrital, suggesting overgrowth and the initiation of a hydrosere, at least at the edges. During Zone C9 at least half a metre of organic mud accumulated and the water level cannot have been more than 2.5 below site datum, i.e. below 118 m O.D. As the curves for M. alterniflorum and R. sect. Batrachium fall in the pollen diagrams, that of Nymphaea rises to take their place whilst abundant macroscopic remains near the top of the zone indicate the presence of N. alba and Potamogeton natans in quantity. Marginally grass and sedge fens undoubtedly began to encroach on the lake; Thalictrum first and then Filipendula ulmaria dimished in importance, presumably as organic accumulations reduced the accessibility of mineral soil. During this zone, therefore, the organic productivity of the lake and the surrounding mires was evidently much increased. There is no stratigraphic evidence of enrichment by the inflow of new materials from the surroundings, nor was the nature of the sediment on the lake bottom markedly different from that which had been available since the end of Zone C4 (I). It seems probable, therefore, that this marked, and fairly rapid, change was largely the result of the climatic amelioration at the beginning of the post-Glacial period (sensu stricto).

During Zone C10 (VI) the overgrowth of the lake by mire communities continued. The stratigraphy is confusing but there seems little doubt that fens encroached from the northern margin, through the deposits of which the pollen diagram passes. By the middle of Zone C10 these fens had replaced the aquatic communities of N. alba and P. natans, which had been joined at the beginning of the zone by aquatic species of Sphagnum, suggesting the beginning of acidification of the lake. The fen deposits of this period still contain a large sedimentary fraction indicating that they were still being laid down below water level, which cannot have stood more than 2 m below the site datum, i.e. 118 m O.D., at the end of Zone C10. The abundant remains of trees in the mud, particularly those of Betula pubescens, suggest that the initial colonizing communities were of the swamp-carr type (Lambert 1951). At the south side of the basin, however, Sphagnum peat, at first with a few sedges, directly overlays the lake muds attributable to Zone C9. Moreover, unless their origin be ascribed to the neighbouring Cumwhitton Moss, the high values of Sphagnum spores and Calluna pollen in the diagram from late in Zone C10 onwards must indicate the active growth of bogs in the basin. It therefore seems necessary to suppose that, whilst swamp-carr occupied the northern part of the basin, a Sphagnum bog was developing on the southern banks and aquatic Sphagna were invading the water surface of the lake itself. (It may be significant in this connexion that the field immediately to the south of the basin until very recently contained a woodland growing over a Calluna heath on shallow peat over a very well-developed podzol profile). This pattern persisted throughout Zones C10, C11 and C12 (VI), the bog steadily encroaching on the swamp-carr and finally replacing it. This replacement was probably not a very regular process and its uncertainties account for the chronological hiatus in the pollen diagram between the top of Zone C12 and the base of Zone C19, an interval represented by only 25 cm of deposits.

Early in Zone C19, Sphagnum bog extended as far northward as the site of the pollen diagram and probably rapidly covered the rest of the mire thereafter. It is difficult to determine when, if ever, this bog became independent of topogenous water. The high Calluna values at the top of the pollen diagram might indicate this change, with which an increased frequency of drier habitats would probably have been associated, but they might equally derive from vegetation on heaths outside the basin itself. It is evident from historical records and microtopographic evidence, however, that Moorthwaite Moss had grown up to considerably above its present surface level by the Middle Ages, presumably as an ombrogenous raised bog.

The most notable ecological changes at Moorthwaite Moss which which stratigraphic breaks are associated are: (i) the accumulation of sandy clay mud in an oligotrphic lake during Zones C1 and C2 leading, in Zone C3, to the deposition of what is probably a solifluction deposit; (ii) the beginning of organic accumulation immediately after this event; (iii) the overgrowth of the lake by swamp-carr from the north and Sphagnum from the south, beginning in Zone C10; and (iv) the final overgrowth of the whole basin by Sphagnum-dominated bog communities. There is no strong evidence for major changes in water level at any time, although the lowest water level compatible with accumulation of the deposits naturally rises as the basin fills. The instability of the marginal slopes resulted in the inwash of inorganic material into the lake. At Moorthwaite Moss it extended from the latter part of Zone C7 (III) through Zone C8 (III).

The inwash of inorganic materials and accumulation of inorganic sediments ceased at the beginning of Zone C9 (IV - V). From that time onwards there is no indication in the sediments of the physical conditions of the soils of the surrounding slopes.

VEGETATION

Aquatic vegetation

The general development of the hydrosere hasbeen described. At Moorthwaite Moss the basin harboured an open pool with varying frequencies of Myriophyllum alterniflorum and rare Nymphaea alba, Alisma plantago aquatica and poor and narrow marginal fens throughout Zones C1 to C8 (I-III). Zone C9 (IV-V) witnessed the beginning of rapid extension of swamp carr and Sphagnum rafts into the open water. Some deterioration in conditions was being reflected in the increasing barrenness of the lakes at Moorthwaite Moss. Once the inhibitions of Zones C7 and C8 (III) were passed, however, hydrosere development was very quick.

Land Vegetation

Some aspects of the pollen diagram from the site are summarized in figures. In the figure a common vertical scale has been adopted, A purely arbitrary span has been allotted to Zones C1 to C4 inclusive. Finally, sample levels from the separate sites have been distributed through each separate zone at distances proportional to their original intervals at the points of sampling. The pollen frequencies shown on the diagram have been recalculated on a new basis. The new 'pollen sum' comprises all commonly occurring trees and shrubs (Betula spp., Pinus, Corylus, Salix, Juniperus), and herbs judged to be at least mainly occupying mineral soils at most sites, and the Ericales (Calluna, Empetrum). The herb section is divided into two components, viz. those types thought to derive from drier soils (Gramineae, Artemisia, Rumex, Plantago, Helianthemum, Armeria) and the others more likely to represent communities on damper soils (Cyperaceae, Caryophyllaceae (Stellaria type), Compositae, Cruciferae, Rubiaceae, Umbelliferae, Chenopodiaceae). In the first section of the diagram the curves for each tree and shrub type are shown, individual frequencies being calculated as percentages of the 'pollen sum', as well as composite curves for each of the four main sections of the pollen rain referred to above calculated on the same basis. The second part of the diagram illustrates frequency variations within the group of herbs characteristic of dry ground, values being percentages of the total for this group of pollen types alone. In the third section the herbs of damp group are similarly treated. The original zonation of this part of each of the original pollen diagrams (parts II to IV) was based on the changing balance between the curves for the pollen of trees and shrubs and that for the sum of herbaceous heliophytes of dry land. Variations of individual curves amongst the herbs did not contribute to that primary zonation so that any correlation now established between such individual curves or between them and the primary chronology is not simply the result of the original zonation technique.

The most striking feature of these diagrams is the dominance of herb pollen over that of trees and shrubs from Zone C4 to Zone C8 inclusive. In view of the criteria on which the herbaceous components have been selected this must imply a predominantly open, almost treeless, vegetation throughout the late-Glacial period. During Zone C2 (Moorthwaite), however, there is evidence for more abundant tree growth.

The rate at which the herbaceous communities were replaced by trees and shrubs is interesting. At Moorthwaite change was hardly completely accomplished in 1000 years.

All the trees and shrubs which were available at the site increased their frequencies more or less simultaneously during Zone C5. This must imply a lack of competition between these plants all of which must have been within the limits of their climatic tolerance and readily available from outside the area or from isolated stands within it. Indeed, competition between the woody plants seems not to have been important until the end of Zone C9 when Corylus began its great expansion. The shade-intolerant Juniperus persisted at least from the middle of Zone C8 throughout Zone C9 until the expansion of Corylus began. This, as well as the parallel but less continuous occurrence of many herbs (e.g. Rumex cf. acetosella), must indicate that the high birch frequencies of Zone C9 are not necessarily to be interpreted as the product of closed uniform birch forest but of birch woodland with abundant clearings and open places fringed, or totally occupied, by juniper and willow thickets and into which the hazel could quickly penetrate, e.g. the end of Zone C9. At Moorthwaite a particular change takes longer to achieve and, as a corollary, is usually not well defined for a number of otherwise separate phenomena necessarily overlap. At Moorthwaite herbs of the dry soil group preponderate throughout.

Within the framework of these general observations, and using evidence from all the pollen diagrams and from macroscopic identifications from the site, the sequence and pattern of vegetation development during thispioneer period will be described.

During the Cumbrian Oscillation (Zones C1 to C4 inclusive) the vegetation appears to have been predominantly herbaceous. A wide variety of genera are represented in the pollen diagrams (e.g. Artemisia, Rumex, Filipendula, Thalictrum, Campanula, Armeria, Koenigia), but it is difficult to associate these in distinct ecological groups except by picking out those most characteristic of drier soils. This is the group which suffered most at the expansion of Betula and Pinus which characterizes Zone C2 and which almost certainly represents a greater expansion of woodland areas than occurred at any subsequent time during the late-Glacial period. It is notable that Juniperus is not recorded before the end of Zone C4. It seems very likely that Zone C1 was a period of more or less complete vegetation cover most of which was herbaceous and susceptible to rapid and ephemeral change induced by physical changes which must have been relatively frequent during the early topographical and soil development following the retreat of the Main Glaciation ice. Betual (probably including B. nana) and Pinus were already present and expanded onto the drier, and probably more stable, soils toward the end of the zone to establish the vegetation pattern diagnostic of Zone C2. In that zone there is little doubt that thevegetation was still diagnostic of Zone C2. In that zone there is little doubt that thevegetation was still predominantly herbaceous but with a liberal scatter of birch and pine although how far these were of severely local significance is difficult to judge from a single diagram from this period. In Zone C3 these trees, particuarly the pine, became less frequent and the vegetation seems virtually to have returned to its Zone C1 condition. Those changes continued into Zone C4 in which the plants of drier soils, notably Gramineae and Rumex cf. acetosella, seem to have assumed even greater importance amongst the herbaceous flora, at least in the upper part of the zone at Moorthwaite. It is difficult to avoid interpreting these records as indicative of an open tundra-or steppe-like vegetation with rare tree birches, and possibly pines, in particularly favoured localities (by reason of their aspect or soil) but more extensive shrubberies of dwarf birch and willows. It may well have been a vegetation in which communities were not well differentiated for, as in the earlier zones, there is little of the interplay between the curves for for various species which becomes such a characteristic of the following late-Glacial period.

During Zone C5, which is correlated with the beginning of the Allerød period, birches became generally more abundant over the whole region. The increase of birch pollen in the pollen rain seems due largely to the expansion of tree birches and was maintained during Zone C6. The pine expanded later (i.e. in Zone C6) and less markedly than the birch and this might indicate only a slight extension of its range beyond its Zone C4 refugia or alternatively a greater vigour within those same areas. Nevertheless, a positive increase in the success of Pinus is indicated and there can be no doubt that the tree was in Cumberland in late-Glacial time, although apparently less abundant then than at the height of the Cumbrian Oscillation. Juniperus first assumed importance in Zone C5 and seems to have been more abundant then than in Zone C6. This might be explained by supposing the shrub to have occupied sites during C5 which were subsequently colonized by birch or pine. But if the relative frequencies of pollen types are any guide, these sites must have been few for herbaceous pollen is still clearly dominant. Empetrum must have been an infrequent, but widely distributed, plant during this time.

The gentler hills beyond the immediate margins of Moorthwaite Moss, must have been covered by a predominantly grassy vegetation in which ruderals played a relatively insignificant part.

Zones C5 and C6, therefore, witnessed the extension of wooded areas and the stabilization of the remaining herbaceous swards. It is possible that small patches of more or less closed woodland did develop but the weight of evidence suggests that these were uncommon. Differentiation between the drier slopes with closed grassland and the damp hollows with poor fens became pronounced.

Already towards the end of Zone C6 the frequency of the trees had begun to decrease and the equilibrium which had taken place between 300 and 400 years to achieve and had been maintained for a rather shorter period, took only about 150 years to disrupt. At all the sites the transition from Zone C6 to C7 which marks this disruption is characterised by a diminution in importance of the pollen of trees and a disproportionate increase in the importance of pollen of damp soil herbs when compared with than of herbs from drier habitats. This phase of apparent success of damp soil plants was probably about 750 years at Moorthwaite. The genera contributing to this expansion varied but undoubtedly the Cyperaceae played the major part. At the time of the initiation of these changes, the dry-soil component of the herbaceous vegetation began a sequence of highly characteristic changes. The frequencies of grass pollen in the diagrams from the drier sites fall whilst those of Rumex cf. acetosella sustain temporary, but well marked maxima. This is followed by a considerable increase in the frequency of Artemisia pollen together with a more or less pronounced fall in the relative level of Rumex. The phase of abundant Artemisia is not clearly marked but there can be no doubt that this was a period of promouned vegetational instability in which a reassortment of communities took place. The final diminution of Artemisia coincided with a small maximum of Rumex cf. acetosella which then remained as a fairly small but consistent component of the herbaceous vegetation until the great expansion of the forest trees in Zone C10. This sequence of vegetation changes lasted for about 800 years. The points on the pollen diagram from which this time period is assessed are, of course, more or less arbitrarily determined because the changes from one phase to another are rarely sharply defined.

The period of vegetational instability broadly covers Zones C7 and C8 (III). The instability is further emphasised by the records of Armeria vulgaris from the two zones.

The performance of both pine and birch clearly deteriorated throughout the region at the beginning of Zone C7 (III) as did that of juniper at sites where it had been of some significance before. Salix seems to have become more abundant. This might be significant in view of the increased importance of herbs tolerant of damp soil at the same time.

The recovery of the trees which began during the latter part of this predominantly herbaceous period was restricted almost entirely to Betula by the end of Zone C8, Pinus having by then assumed the subordinate role which it was to keep throughout the rest of the pioneer period. Moreover, although Juniperus might have begun to increase slightly with Betula it nowhere reached its highest or most consistent values until the expansion of the birch was well advanced. The birch cover was never complete, that continuous tree birch forests were not established. Further indications of the same face lie in the low but consistently maintained pollen frequencies of Gramineae and Rumex acetosella throughout the zone and the occasional records of Campanula, Polemonium, Artemisia, Plantago maritima and Ophioglossum. In addition Corylus avellana, which can hardly have been fertile under a closed birch canopy, attained considerable importance. At Moorthwaite the trees gained supremacy considerably slowly, indeed a steady state was not achieved until after the expansion of Colylus and the establishment of more thermophilous trees at about 6900 B.C.

Empetrum had clearly been present throughout the late-Glacial period in the region as a whole, although usually rate and probably restricted to small areas of base-poor sand or rocky outcrops.

During Zone C9 the vegetation of the region remained patchy. The mosaic was composed of open-canopy birch woodlands with Juniperus, Corylus or Salix along the margins and in the clearings, together with grasslands and with herb-rich communities on the less stable soils and Empetrum in places where soil acidity had quickly developed. These treeless patches were encroached upon by woodlands within which, however Corylus continued to play an ever more important role largely at the expense of herbs and Salix and, in some case, of juniperus. It was Corylus, too, which was able quickly to take advantage of the reduction in success of the birches in some localities, which coincided with the first establishment of Ulmus and Quercus and which brought to an end this period of pioneer vegetation at about 6800 B.C.

The following major tendencies were exhibited by the vegetation as a whole:

(a) During Zone C2 of the Cumbrian Oscillation Betula and Pinus trees became an important component of the vegetation, only to lose this importance in the subsequent Zones C3 and C4.

(b) On the whole, the relatively undifferentiated or widely diverse herbaceous communities of the later part of the Cumbrian Oscillation and the beginning of the Allerød Oscillation (Zones C3 and C4) were replaced by more stable communities in Zones C5 and C6 in which trees were of moderate importance.

(c) This stability was broken down in a particularly characteristic way during the latter part of Zone C6 and Zone C7.

(d) With the opening of Zone C9, trees began to play a more important part in the vegetation cover than ever before, in spite of their incomplete cover and differences in the degrees of their importance from site to site.

The Causes of Vegetational Change

None of the plants recorded from the full- and late-Glacial periods demand high artic or alpine conditions in their modern habitats although some, e.g. Betula nana, Salix herbacea, Montia fontana, Koenigia islandica, from other sites nearby are certainly tolerant of such conditions. Only two species of this group seem likely to be limited in their southerly extension by high maximum summer temperatures, viz. Koenigia islandica (24 °C) and Salix herbacea (26 °C) (Dahl 1951), the limits for which are modified to 21 to 22 °C and 23 to 25 °C respectively for the British Isles (Conolly 1961). Many more seem to be intolerant of extreme cold at the present day, e.g. Armeria maritima, Helianthemum chamaecistus, Hippophae rhamnoides, Schoenoplectus lacustris, Potamogeton trichoides. The time available was certainly adequate for a much greater development of birch woodlands than the pollen diagrams indicate. A major ecological factor must have inhibited them. In view of the suitability of all other ecological conditions for their spread it is difficult to avoid ascribing their failure to a climatic check. At the present day B. pubescens seems to be tolerant of both oceanic and continental climates but reaches its northern limit at the 10 °C July isotherm. It therefore seems necessary to assume low summer temperatures during some parts of the full-and late-Glacial periods.

In Zone C1 at Moorthwaite Moss there are no records other than those of Helianthemum and Empetrum, Betula and Pinus which impose restrictions on a climatic interpretation. In the general vegetational and sedimentary context the Pinus frequencies are difficult of interpretation but neither these nor the tree birch pollen records are sufficiently substantial to indicate summer temperatures often exceeding 10°C. The Helianthemum record, however, though represented by only a few pollen grains, suggests that winter temperatures were not extreme, i.e. consistently below - 2°C (Proctor 1956). Such conditions would not prevent the local growth of the oceanic Empetrum nigrum. Moreover, they do not necessarily imply serious physical disturbance of the soil as a result of freeze-thaw action, a fact which corresponds well with the apparent continuity of the herbaceous vegetation cover and the lack of accumulation of soliflucted material into the basin. The plants of Zone C2 are neither more nor less restrictive on climatic interpretation except that the increase in real abundance of Betula and Pinus pollen must indicate a climatic amelioration, probably a small rise in the maximum summer temperature, whilst the relative abundance of the latter might suggest less oceanic conditions than applied at other times. The records from Zone C3 are hardly more diagnostic. The falls in Betula and Pinus pollen curves at Moorthwaite Moss imply a return to more exacting temperature conditions. The continued presence of Helianthemum indicates the infrequency of extreme winter temperatures. This zone has been correlated with the Scottish Readvance glaciation and culminated in severe solifluction movements at Moorthwaite Moss. The vegetation data, whilst allowing a cooling of the climate during this period and possibly a slight decrease in continentality, do not require high arctic conditions to have pertained around the edge of the Scottish Readvance ice. The vegetation seems to indicate a mean January minimum somewhat above Manley's estimate of 16°F (-9°C) for inland Lake District at this stage (Manley 1951, 1953).

Similar conditions seem to have continued into Zone C4. In the latter part of this zone, which is thought to have been contemporary with the final melting of the Scottish Readvance ice, changes began which continued through Zone C5 and culminated in Zone C6. Juniperus, first recorded in Zone C4, became significant in Zone C5. The absolute frequency of this pollen type is never high however, and if the diminutions in Zone C6 are correctly interpreted as the result of competition with trees for favourable sites, Juniperus cannot have formed very extensive thickets of tall bushes except in particularly favoured spots. According to Iversen's (1954) interpretation of juniper ecology this might imply that many otherwise suitable habitats were still snow-covered in winter. Helianthemum cf. chamaecistus was present indicating the general infrequency of very cold winters. It is possible that summer temperatures were only a little lower than at present in the Cumberland Lowland. The general climatic indications for this period, therefore, are of an amelioration in which the summer temperatures increased markedly whilst the winters remained cold enough for much of the considerable precipitation to fall as snow. Such a regime, which need have involved little regular freezing of the ground, would accord well with the absence of solifluction material in the basins and the beginnings of organic accumulation there. The expansion of the trees, however, was clearly inhibited more than the supposed summer temperature levels demand, and this might have been the effect of long, if comparatively warm, winters. It might also have been an effect of severe wind blast which would be likely to have modified the success of trees and shrubs more than that of herbaceous plants. The overall implication that summer temperatures improved more than did winter temperatures is in agreement with Manley's (1951, 1953) estimates of a rise of 7°F (4°C) in July mean but of only 1°F (0.5°C) in January mean.

Frost-thaw movement of the ground and the establishment of permafrost are inimical to the development of a continuous and stable vegetation (Benninghoff 1952). The conditions suggested for the Allerød period in this region, on the contrary, seem likely to have been conducive to the formation of a more or less complete herbaceous cover, with the consequent stabilization of the ground surface.

A new vegetational instability had already begun during the latter part of Zone C6 and continued through Zone C7 into Zone C8. There was a small but regional diminution in the success of trees, suggestive of a slight climatic deterioration of some kind. Juniperus was also less frequent than before, indicating that areas newly vacated by trees were not reoccupied by Juniperus presumably, although not necessarily, because of some climatic limitation such as low temperature or exposure to cold winds. The herbaceous plants do not indicate any marked temperature changes from the immediately preceding period. Helianthemum cf. chamaecistus was much diminished, however, even at St Bees, suggesting the possibility of a decrease in mean maximum winter temperature below - 2°C. Armeria maritima, remains witness to the oceanicity of the climate, as does Littorella uniflora. The minimal temperature changes required between the height of the Allerød period and the most regorous conditions of Zones C7 and C8 (III) seem to be a lowering of the maximum summer and minimum winter temperatures by a very small amount. Yet pronounced changes in the pattern of herbaceous vegetation took place which suggest (a) an increased area of effectively wet soil, and (b) a complete disruption of the dry-soil communities which remained leading to the unprecedented abundance of the runderal Artemisia there. An associated indication of soil conditions at the time is the accumulation of limited solifluction materials in all the basins investigated. If winter temperatures fell sufficiently to induce moderately frequent winter freezing of the ground water and the formation of patterned ground, this would almost certainly inhibit the free drainage of soil water during the summer thaws, even in areas formerly well drained. The areas most favoured for drainage would still be distrubed and the growth of runderals would be encouraged there at the expense of continuous turf. There is positive evidence of the depauperation of the phanerogamic flora at some time during Zones C7 and C8 perhaps implying a small temperature change which was insufficient to affect the rest of the aquatic fauna and flora. It seems that all the recorded vegetational and stratigraphic changes during Zones C7 and C8 (III) can be accounted for by a small fall in winter temperatures enough to produce periodic freeze and thaw of the ground and resultant solifluction movements. The climatic indications of individual species, such as they are, suggest winter temperatures commonly falling below - 2°C but rarely exceeding - 8°C and summer temperatures regularly falling below 10°C, perhaps for only a relatively short period, and frequently rising to about 14°C in favoured localities.

Manley (1951, 1953) does not require such a fall in winter temperatures but reaches a somewhat similar conclusion about the fall in mean maximum summer temporatures between the Allerød and the post-Allerød climatic deterioration. His modification of those conclusions for the north-west of England particularly (Manley 1959), seems to be in much closer agreement with the present vegetational interpretation.

In Zone C9 richly organic mud accumulated and the hydrosere at the points of pollen analysis progressed without any apparent environmental check.

The herbaceous vegetation had hardly gained stability before it was substantially replaced by trees and shrubs. None of the plants recorded from the zone require climatic conditions more rigorous than those found in the Cumberland Lowland today. It is only necessary, therefore, to try to assess the degree and rate of the climatic amelioration implied. Continuous forests were not immediately established although the components were available in profusion. The temporary abundance of Juniperus, as well as its continued frquency later, must imply the growth of juniper thickets independent of snow cover. The expansion of Betula pubescens indicates the early achievement of mean summer maxima considerably above 10°C.

During Zone C9, Corylus avellana certainly became established early but not until the end of the zone did it expand very markedly. Tree cover was not complete so that competition for sites ~~is~~ unlikely to have inhibited its spread: it seems likely that temperature conditions restricted it to more favoured localities. This would imply that mean July temperatures did not generally exceed about 15°C over the region as a whole. This condition does not conflict with the known tolerance of any of the other plants recorded from the zone, although possibly somewhat marginal for Pilularia globulifera. Winter temperatures are difficult to assess, even approximately, during this period. It is clear from the behaviour of Juniperus, as well as from that of Corylus, that snow did not lie long in winter. This may have been a result of pronounced oceanicity of the climate with relatively mild winters. As Corylus was established during this period, if only in favoured localities, it is difficult to imagine that the development of closed Betula pubescens forest was inhibited by a climatic factor alone. The climate cannot have been sufficiently favourable for tree growth for its effects to overcome the selective effects of local edaphic conditions, particularly where communities were already established which were particularly well adapted to both climatic and edaphic conditions.

The opening of Zone C10 (VI) at about 7000B.C. was marked by a great expansion in the abundance of Corylus avellana which must indicate a complete lack of climatic inhibition and mean maximum summer temperatures of at least 15°C and an absence of late spring frosts. The climatic amelioration from the middle of Zone C8 until the end of Zone C9, a period of about 1500 years, need not have been great in order to account for the vegetation changes and, if it was not great, it evidently progressed slowly. The rapid and marked change took place at about 7000 B.C., a change of which those trees and shrubs already established within the region in a pioneer role were able most quickly to take advantage.

The determinants of vegetation change during the full- and late-Glacial and early post-Glacial periods were primarily climatic changes of small magnitude which nevertheless crossed and recrossed the tolerance thresholds of communities and individual species, causing an almost continuous reassortment of these communities both directly and by affecting soil conditions.

The General Vegetation Pattern of the British Isles

The place of the Cumberland Lowland in the developing vegetation pattern of the British Isles is best appreciated by comparing the record there with those from critically zoned sites elsewhere omitting those within the larger upland masses. The sites considered are Drymen (Donner 1957), Garscadden Mains (Mitchell 1952; Donner 1957), Cannons Lough (Smith 1961b), Neasham (Blackburn 1952), Witherslack Hall and Helton Tarn (Smith 1958), Skelsmergh Tarn (Walker 1955a), Hawes Water (Oldfield 1960b), Star Carr (Walker & Goodwin 1954), Moss Lake (Godwin 1959), Aby (Suggate & West 1959) and Hockham Mere (Godwin & Tallentire 1951). These authors' own interpretations of their diagrams have been accepted and comparisons attempted using the general British zonation scheme without subdivision.

Even the latter part of Zone I has not been widely documented in the British Isles. Nowhere, however, was closed woodland established then and the vegetation was at the best dominated by herbs with occasional shrubberies and rare pioneer trees. At this stage the vegetation of the Cumberland Lowland seems to have been quite undifferentiated from that of the rest of the Lowland Britain.

In Zone II, however, some regional differentiation of vegetation can be discerned. From East Anglia to Cumberland birch woodlands were established, their continuity roughly decreasing from East Anglia and Lincolnshire, where pine was also undoubtedly established, towards the north-west where, in all but the most favoured niches, herbaceous and shrub-dominated communities still remained of paramount importance. Beyond, in Northern Ireland and Southern Scotland, treeless communities still predominated. At this time, therefore, the Cumberland Lowland was in the van of tree migration.

During Zone III, whilst trees seem to have been less successful than before all over the region considered with the exception of the Hawes Water basin, extension of herbaceous communities seems to have been most marked in the north of England. At most sites all elements of the Zone II vegetation seem to have persisted, many in a drastically reduced condition. At Cannons Lough in Northern Ireland shrubs and possibly rare birch trees became established, suggesting that their former absence might have been due solely to lack of time for migration from farther south and east.

At Hockham Mere it is evident that the expansion of the birch to form closed forests was rapidly accomplished at the beginning of the post-Glacial period, and the same is true of the Star Carr region. Farther west there seems to have been considerable variation from site to site. At Moss Lake, Witherslack Hall and Helton Tarn the rate of closure of the forest seems to have been intermediate between that already referred to and the fairly slow spread documented in the Cumberland Lowland and at Cannons Lough. At Hawes Water, Skelsmergh Tarn and Drymen forests seem to have been quickly established. It may be conjectured that climatic conditions on the whole were less conducive to forest development in the north-west but that their effects were offset to some extent by other peculiarly favourable ecological conditions (e.g. soil, aspect) in many localities. The generally greater abundance of the hazel in early post-Glacial time in the north and west might well have been a direct reflexion of a climatic gradient but it might also have been due to the more open nature of the vegetation already established there which allowed the hazel ample opportunity to establish and flower profusely before the arrival of the true forest trees.

b THE PERIOD OF THERMOPHILOUS VEGETATION

Hydrosere Development

Sphagnum-dominated bog grew at Moorthwaite by Zone C12, the surface was still below the water-table of the surrounding land and therefore not readily susceptible to any small changes in precipitation. At Moorthwaite Moss, the acidification change took place in a large reservoir of open water surrounded by fringing vegetation into which a considerable volume of drainage water must regularly have discharged. The development of oligotrophy under these circumstances argues base-poor drainage water which in turn suggests the development of leached and acid soils on the surrounding slopes.

At Moorthwaite Moss the site is unaffected by marine changes during this period, and there is some slight evidence for lower water levels in Zones C12 and C13 than at earlier times.

At Moorthwaite Moss woodlands of thw swamp carr type were important, at least during Zones C10 to C12 (VI) and from C14 (VIIa) onwards respectively. It may have been the establishment of a drier type of fen woodland in Zone C12 which reduced accumulation at Moorthwaite Moss until true bog conditions developed in Zone C19 (VIIb).

There was the tendency for open water, euthophic, lakes to progress towards oligotrophy and the final establishment of a Sphagnum-dominated bog, with or without an intercalated fen woodland stage. There is no indication of any development from fen woodland towards the vegetation of the dry land of the time. Seedlings and young trees, whilst intensley light-demanding, are well able to survive on all but the most waterlogged soils and these characteristics, together with its short generation time and in the vegetation took place during Zone C12. Betula pubescens was evidently further reduced at that time. It therefore seems very likely that birch woodlands were largely replaced by alder woodlands on waterlogged soils. It is also possible that some of the wetter elm and oak woodlands were, at least temporarily, affected by competition from alder around their edges and possibly by the intrusion of alder into their regeneration cycles. The success of the alder over the birch seems to have been less marked at Moorthwaite Moss; places evidently existed where birch remained an important dominant throughout the forest period.

Pollen of Tilia cordata is recorded most commonly from different zones: The number of grains recorded is so small, however, as to make it virtually certain that this species was not part of the vegetation of the Cumberland Lowland. Hedera helix was clearly a frequent and flowering plant from Zone C11 onwards. Only one pollen grain of Hedera is recorded from Zone C10 at Moorthwaite but subsequently there is no significant difference in the distribution of this pollen type from zone to zone or site to site, if its occurrences are assessed against the number of samples examined.

The Causes of Vegetational Change

Three processes, active during this period, must be explained, viz. (a) the great expansion of Corylus followed by the arrival of Ulmus and Quercus and their establishment as the most significant dominants in the vegetation; (b) the encroachment of Quercus throughout the period on areas occupied by Pinus and Ulmus; and (c) the establishment and expansion of Alnus in competition with Betula.

Corylus was already a constituent of the vegetation in Zone C9 (IV-V), although probably restricted to the most favourable, frost-free, localities. Its failure to extend substantially outside these for over a thousand years seems to imply a climatic limitation which was evidently overcome at the beginning of Zone C10 (VI); i.e. at about 7000 B.C. Followed, as it was, by the immigration of Ulmus and Quercus from great distances away, the most likely cause of the Corylus expansion into the Betula woodlands seems to have been a rise in summer temperatures together with an almost total eradication of spring frosts. Mean maximum summer temperatures above 15°C seem probable. Corylus expanded before Ulmus and Quercus because its slightly greater tolerance of cold, together with its short generation time and its aggressive invasion of light habitats, allowed it to cross Europe ahead of the others. The first arrivals in the British Isles may, indeed, have followed a western route, with its more oceanic climate, in order to spread rapidly north-ward. Ulmus and Quercus arrived in the area at about the same time. It may be that the oceanicity of the west favoured the germination of the frost-susceptible acorns and so, at least in part, offset the superficially more efficient dispersal mechanism of the elm. The arrival and first establishment of these trees does not indicate any substantial amelioration in climate beyond that already required by the behaviour of Corylus. The apparent failure of the oaks to spread so quickly as the elm once both had arrived may well have been the result of the oaks' need for long warm summer periods for repeated production of heavy crops of fruit. Judging from the records of Hedera helix such conditions had developed by Zone C11 (about 6300BC) when also the mean temperatures for the coldest winter month must have exceeded about 1.5°C.

The forests which were so established were not stable, although the explanation of their establishment implies that they were in balance at least with the temperature conditions of the prevailing climate. The progressive modification of the forest composition, resulting from the success of Quercus at the expense of Pinus and more particularly Ulmus, could have been due to the depauperation of the soil and the formation of mor by leaching under the oceanic conditions which prevailed.

The immigration behaviour of Alnus glutinosa has been interpreted principally as its replacement of Betula pubescens on poor, waterlogged soil and its slight intrusion into the forest of dryer and better soils. It has frequently been observed that the temperature requirements of A. glutinosa are no less great than those of the forest trees which were growing in western Europe long before its arrival there. The relative delay in its establishment is variously attributed to insufficiently damp conditions along its migration route (Godwin 1956) or to a want of adequate summer warmth in the west (Firbas 1949; Kubitzki 1961) or to inefficient seed dispersal without the aid of suitable running water (McVean 1956b). There can be no doubt that a few alder trees grew in the Cumberland Lowland during Zone C11 and that these were in inland, as well as coastal, sites. The expansion during Zone C12 (Boreal-Atlantic Transition) occurred both within and beyond the tract immediately affected by the rising sea of the time, so this factor alone cannot have been directly and totally responsible for the change in the vegetation. In competition with B. pubescens, stable spring weather (i.e. the absence of late cold spells and strong winds) and more consistently high ground water tables with but rare periods of drought for the seedlings seem likely to have been the factors most conducive to the spread of A. glutinosa. Although not all aspects of and extremely oceanic climate are favourable to the alder (McVean 1956b), it is difficult to see how the changes documented above could have been attained other than by an increase in the precipitation: evaporation ratio through a critical range during Zone C12. It does not seem necessary, however, to suppose this to have been sudden. On the contrary, the evidence suggests that in this region it was the culmination of climatic tendencies which had been reducing the competitive power of the birch for some time.

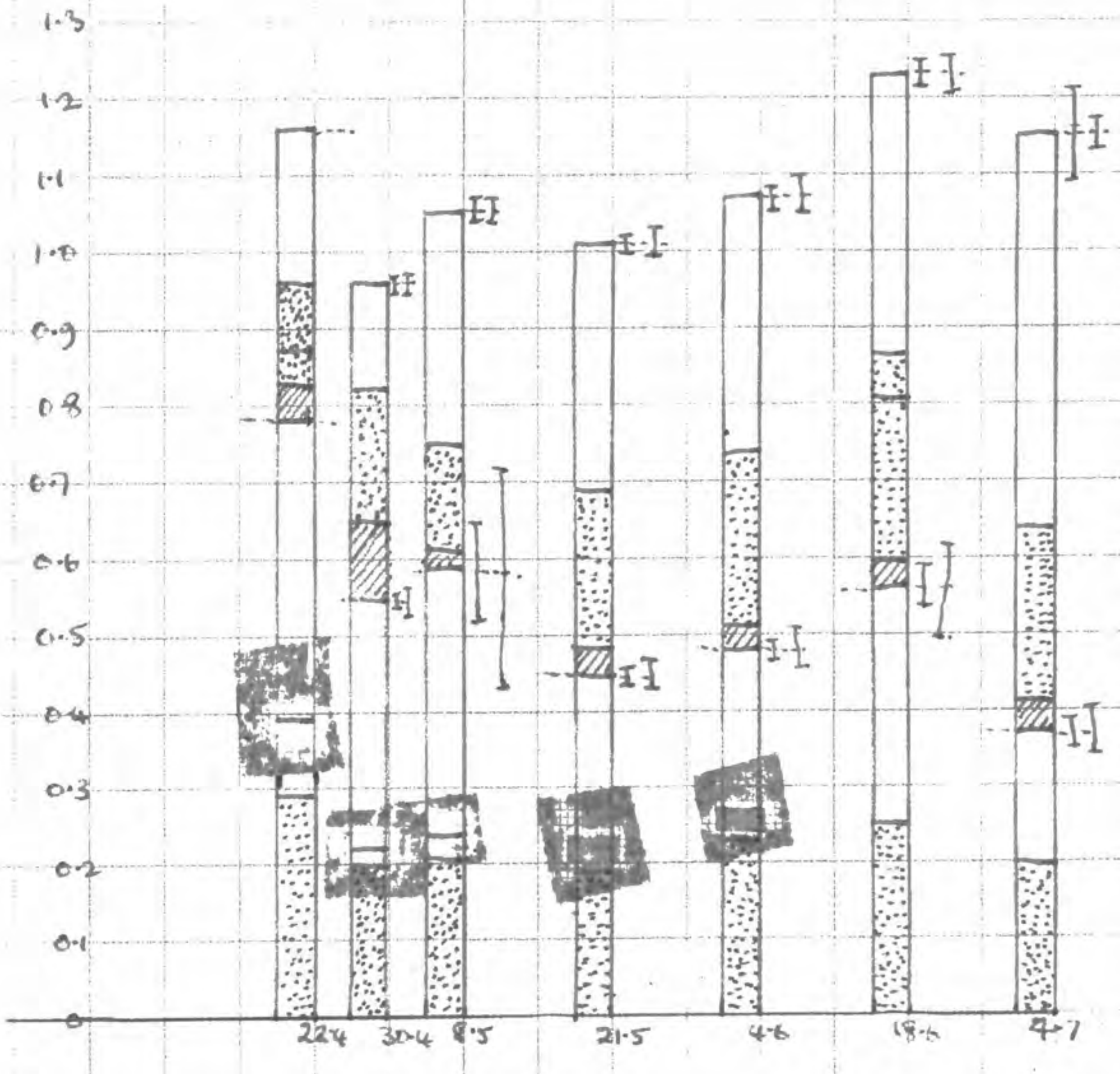
The major vegetational changes during this period seem to be accountable by assuming a substantial rise in summer temperature maxima and winter temperature minima at about 7000 B.C. and a subsequent increase in precipitation: evaporation ratio. These are two components of a markedly oceanic limate but they did not apparently progress at directly related rates. Thus the temperature change is best envisaged as the culmination of the rather slower amelioration which had been in progress since about 8500 B.C., under humidity conditions which had already long before become distinctly oceanic. The rainfall was learly adequate then to allow the development of 'mor' soils but it was not until about 5500 B.C. that a further rise in the precipitation: evaporation ratio first began to affect the vegetation of the partially waterlogged soils. It is conveivable, that even though precipitation might have increased regularly from the earliest post-Glacial (C9, IV) onwards, the establishment of forests itself temporarily retarded the overall effects of this increase, by raising the rate and amount of water loss by transpiration. There is no positive evidence for a 'Boreal' period of pronounced dryness in this region. It seems likely that the temperature changes were part of a general amelioration accompanying deglaciation while the humidity chage was the result of the eustatic extension of the oceans exacerbated in this region by the extensive flooding of the shallower areas of the Irish Sea to which it gave rise.

HYDROSERE DEVELOPMENT

The tendency for bog to replace more eutrophic formations developed in Zone C16 (VIIa). Thereafter, proably into the Christian era, the mire grew upwards as Sphagnum-dominated units. So far as can be ascertained, the greater part of the central area of each of these bogs rose above the main effects of ground water during the following zone, C19.

The time of achievement of independence of ground water was a function of factors local to the site. The general

⑤



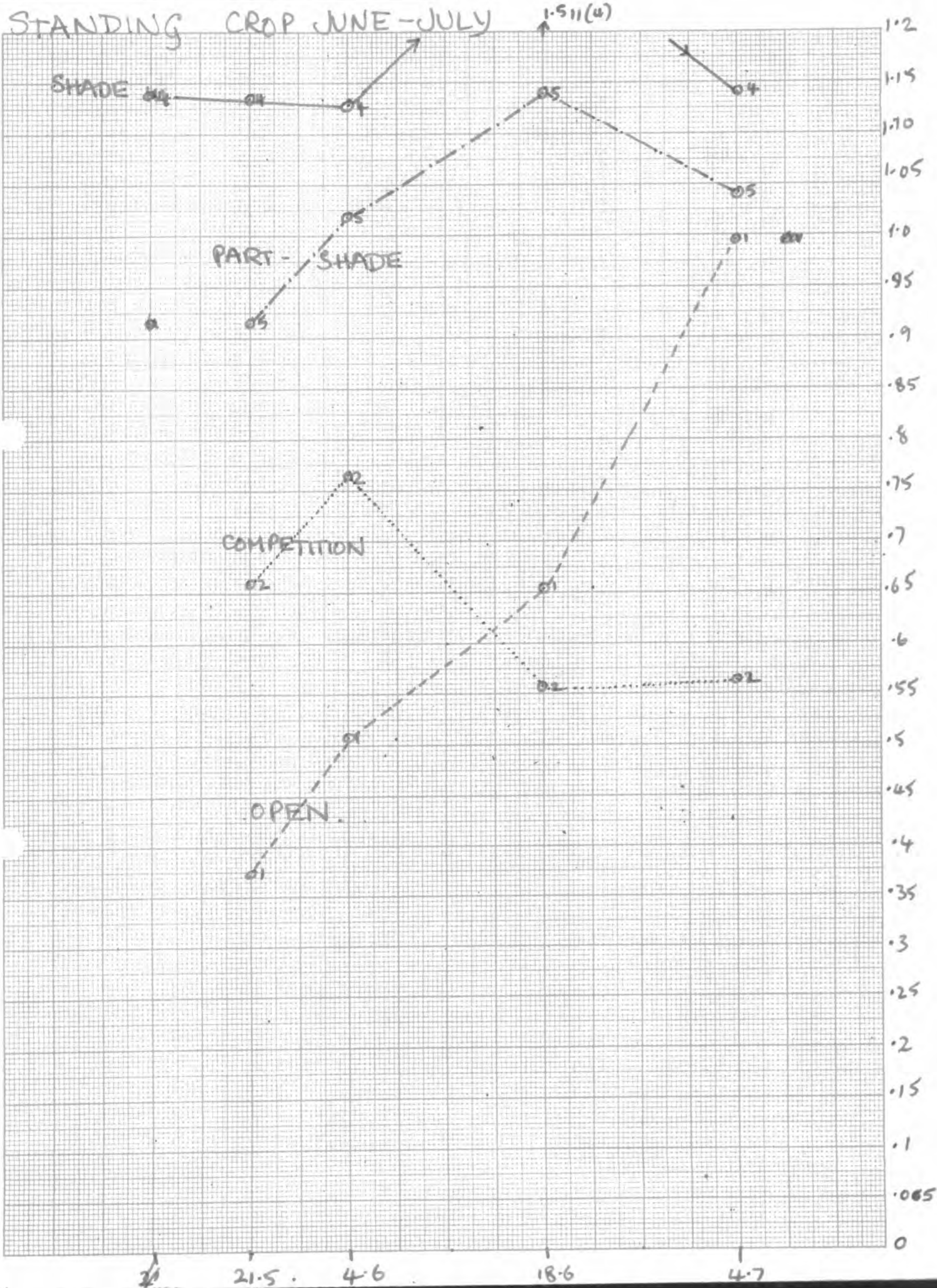
Dry weight increments per cropping.

		→30.4	8.5.	21.5.	4.6.	18.6.	4.7.	Total.
1.	gr lvs	-	-	-	-0.03	+0.13	+0.03	+0.013
	gr sh.	-	-	-	+0.02	+0.04	+0.02	+0.08
	d. lvs	-	-	-	+0.06	-0.01	-0.02	+0.03
	d. sh.	-	-	-	·	+0.05	-0.04	+0.01
	root.	-	-	-	-0.006	+0.015	-0.002	+0.007
2.	gr lvs	-	-	+0.03	+0.02	·	+0.05	+0.10
	gr sh.	-	-	-0.02	+0.05	-0.04	+0.01	·
	d. lvs	-	-	+0.07	+0.13	-0.11	-0.03	+0.06
	d. sh.	-	-	+0.03	+0.10	-0.06	-0.04	+0.03
	root.	-	-	-0.005	+0.008	-0.001	-0.002	·
4	gr lvs.	-0.09	+0.06	+0.07	+0.03	+0.18	-0.08	+0.17
	gr sh.	+0.05	+0.04	+0.04	-0.04	+0.09	-0.06	+0.12
	d. lvs.	-0.02	+0.07	+0.08	-0.03	+0.13	-0.29	-0.06
	d sh.	-0.03	+0.03	+0.03	-0.02	+0.07	-0.10	-0.02
	root.	-0.07	+0.004	+0.005	-0.02	+0.006	-0.011	-0.017
5	gr lvs.	-0.05	+0.13	+0.04	+0.07	-0.03	+0.15	+0.31
	gr sh.	+0.03	-0.02	+0.06	+0.04	-0.04	+0.02	+0.09
	d. lvs.	-0.16	+0.05	-0.12	-0.01	+0.06	-0.14	-0.32
	d. sh.	-0.09	+0.01	-0.02	+0.04	+0.02	-0.05	-0.09
	root.	+0.048	-0.079	+0.014	-0.005	+0.01	-0.002	-0.017
Total.	1	·	·	·	+0.046	+0.225	-0.012	+0.259
	2	·	·	+0.106	+0.308	-0.241	-0.012	+0.191
	4	-0.097	+0.204	+0.225	+0.08	+0.476	-0.541	+0.187
	5	-0.222.	+0.091	-0.026.	+0.135	+0.02.	-0.022	-0.024.

Dry wt. increment cropping – increase per plant per Y days in grams

	30·4	8·5	21·5.	4·6	18·6	4·7.
1. gr ws	·	-	-	-0·03	+0·13	+0·03
gr sh.	-	-	-	+0·02	+0·04	+0·02
d ws	-	-	-	+0·06	-0·01	-0·02
d sh.	·	-	-	·	+0·05	-0·04
root.	·	-	-	-0·006	+0·015	-0·002
2. gr ws	-	-	+0·03	+0·02	0	+0·05
gr sh.	·	-	-0·02	+0·05	-0·04	+0·01
d ws.	·	-	+0·08	+0·13	-0·11	-0·03
d sh.	·	-	+0·03	+0·10	-0·06	-0·04
root.	·	·	-0·005	+0·008	-0·001	-0·02
4 gr ws.	-0·18	+0·10	+0·08	+0·03	+0·18	-0·08
gr sh.	+0·10	+0·07	+0·04	-0·04	+0·09	-0·06
d ws	-0·04	+0·12	+0·09	-0·03	+0·13	-0·29
d sh	-0·06	+0·05	+0·03	-0·02	+0·07	-0·10
roots	-0·14	+0·07	+0·005	-0·02	+0·006	-0·01
5. gr ws.	-0·10	+0·23	+0·04	+0·07	-0·03	+0·15
gr sh.	+0·06	-0·03	+0·06	+0·04	-0·04	+0·02
d ws	-0·32	+0·09	-0·13	-0·01	+0·06	-0·14
d sh	-0·18	+0·02	-0·02	+0·04	+0·02	-0·05
roots.	+0·096.	-0·013.	+0·015.	-0·005	+0·01	-0·002
pl. increase.						
1	—	—	—	+0·044	+0·235	+0·048
2	—	—	+0·114	+0·308	-0·041	+0·058
4	-0·094	+0·357	+0·242	-0·03	+0·476	-0·151
5	+0·056	+0·134	+0·130	+0·145	+0·02.	+0·168
loss to litter.						
1	—	—	-	0	-0·01	-0·06
2	—	—	0	0	-0·17	-0·07
4	-0·1	0.	0	-0·05	0	-0·39
5.	-0·50	0.	-0·15.	-0·01	0	-0·19

STANDING CROP JUNE-JULY

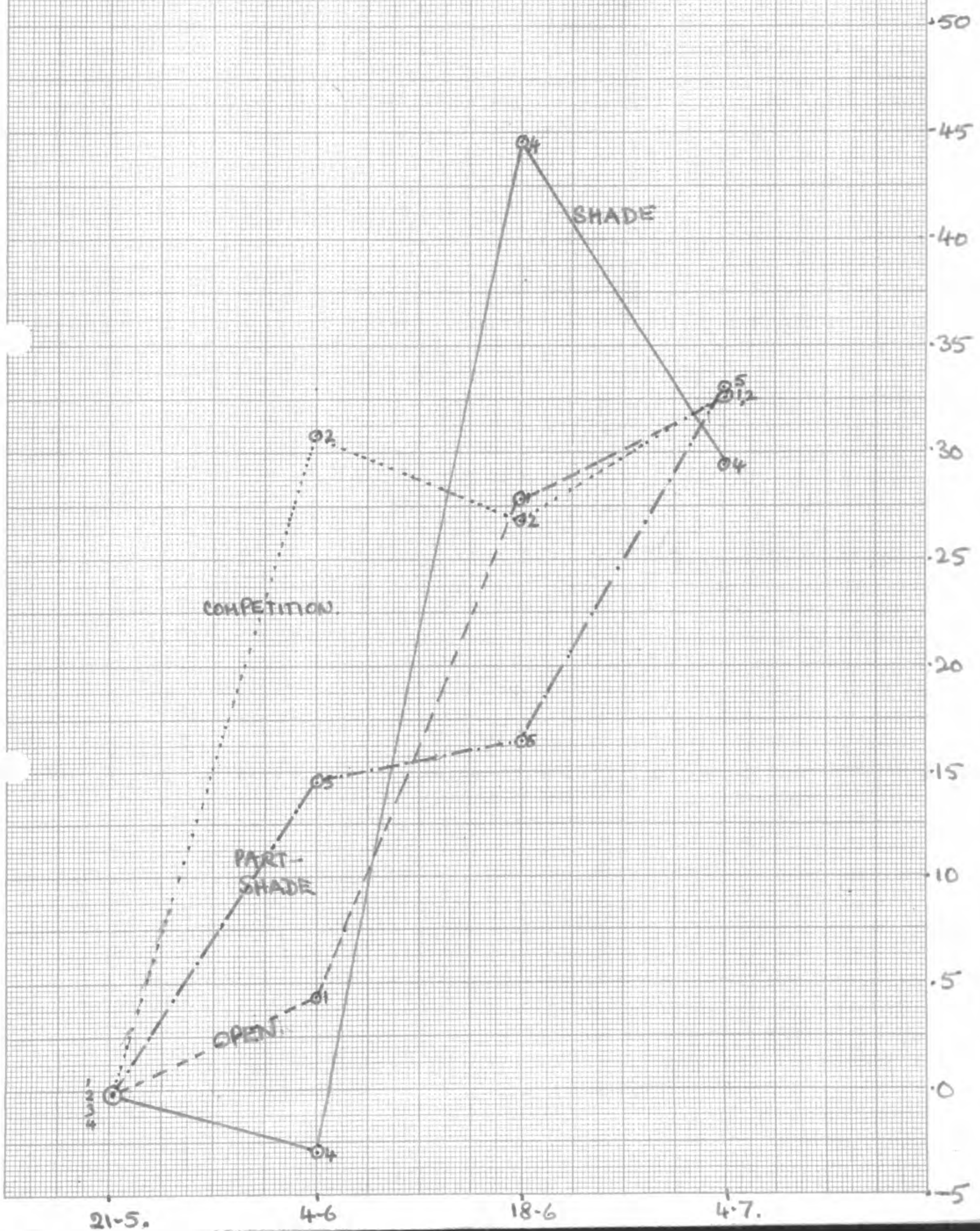


26. dry wt increment cropping.

	23·4	30·4	8·5	21·5	4·6	18·6	4·7	* Total
1 gr lvs	-	-	-	-	-0·03	+0·13	+0·03	+0·013
gr sh	-	-	-	-	+0·02	+0·04	+0·02	+0·08
dead lvs	-	-	-	-	+0·06	-0·01	-0·02	+0·03
d. sh.	-	-	-	-	0	+0·05	-0·04	+0·01
root.	-	-	-	-	-0·006	+0·015	-0·002	+0·007
2 gr lvs	-	-	-	+0·03	+0·02	0	+0·05	+0·10
gr sh	-	-	-	-0·02	+0·05	-0·04	+0·01	0
d lvs	-	-	-	+0·07	+0·13	-0·11	-0·03	+0·06
d sh	-	-	-	+0·03	+0·10	-0·06	-0·04	+0·03
root	-	-	-	-0·005	+0·008	-0·001	-0·02	0
4 gr lvs	-	-0·09	av. +0·06	av +0·07	+0·03	+0·18	-0·08	+0·17
gr sh	-	+0·05	av. +0·04	av +0·04	-0·04	+0·09	-0·06	+0·12
d lvs	-	-0·02	av +0·07	av +0·08	-0·03	+0·13	-0·29	-0·06
d sh	-	-0·03	av +0·03	av +0·03	-0·02	+0·07	-0·10	-0·02
root.	-	-0·07	av +0·04	av +0·005	-0·02	+0·006	-0·011	-0·017
5 gr lvs	-	-0·05	+0·13	+0·04	+0·07	-0·03	+0·15	+0·31
gr sh	-	+0·03	-0·02	+0·06	+0·04	-0·04	+0·02	+0·09
d lvs	-	-0·16	+0·05	-0·12	-0·01	+0·06	-0·14	-0·32
d sh.	-	-0·09	+0·01	-0·02	+0·04	+0·02	-0·05	-0·09
root.	-	+0·048	-0·079	+0·014	-0·005	+0·01	-0·002	-0·017
total 1	-	-	-	-	+0·046	+0·225	-0·012	+0·259
i.e. all. 2	-	-	-	+0·106	+0·308	-0·211	-0·012	+0·191
4	-	-0·097	+0·204	+0·225	-0·08	+0·476	-0·541	+0·187
5	-	-0·222	+0·091	-0·026	+0·135	+0·02	-0·022	-0·024
total plant 1	-	-	-	-	+0·046	+0·235	+0·048	0·761
2	-	-	-	+0·106	+0·308	-0·041	+0·58	0·953
4	·	-0·047	+0·204	+0·225	-0·03	+0·476	-0·151	0·677
5	-	+0·028	+0·091	+0·114	+0·145	+0·02	+0·168	0·856
loss to soil 1	·	-	-	-	0	-0·01	-0·06	0·07
2	·	-	0	0	0	-0·17	-0·07	0·14
4	·	-0·105	0	0	-0·05	0	-0·39	0·49
5	·	-0·25	0	-0·14	-0·01	0	-0·19	0·59

STANDING CROPS JUNE - JULY

RELATIVE CHANGES. JUNE 4 = 0.



ANALYSIS RESULTS.

object		ppm	ug/gr.
rain	1.5.69.	6	1.5
	8.5-69	2.5	0.625
	14.5-69	2.0	0.5
	4-6-69	0.5	0.12
	11-6-69	3.0	0.75
	18-6-69	29	7.25 !
	25-6-69	3.5	0.875
	4-7-69	10.	2.5 !

		4-7	4-6	1st	4-7.	4-6	1st.
①	l lvs.	55	55	55.	16	16	16.
	l sh	80	116	104	20	29	26.
	d lvs	17	18	20	4.25	4.5	5
	d sh	14	17	14	3.5	4.25	3.5
	roots	95	100	100	24.	25	25
	fls.	-	114	155	..	28.5	38
②	l. lvs	65	70	96	16	17.5	24
	l sh	114	102.	148	28.5	25.5	37
	d l.	7	11	12	1.75	2.75	3
	d sh.	14	12	18	3.5	3	4.5
	roots	100	102.	94	25	25.5	23.5
	fls.	-	114	155	..	28.5	38
④	l lvs	89	88	88.	22.25	22	22.
	l sh	87	89	144	21.75	22.25	36.
	d l.	6	7	7	1.5	1.75	1.75
	d sh	15	18	20	3.75	4.5	5
	roots	106	130	123	26.5	32.5	30.75
	fls.	-	-	-	-	-	-
⑤	l lvs	70	60	70	17.5	15	17.5
	l sh	65	66	61	16.25	16.5	15.25
	d l.	7	10	8	1.75	2.5	2.
	d sh	7.5	10	13	1.82	2.5	3.25
	fls ~~roots~~	-	117	155	-	28.25	38.75
	rts	57	67	65	14.25	16.75	16.25

Analysis results contd.

Object	[illegible]	ppm				mg/g.			
ground water	⑤	22	24	22	26.	5·5	6	5·5	6·5
	②, ③	12	-	10	10	3	-	2·5	2·5
	①	12	14	15	12	3	3·5	3·75	3
	⑪	26	27	25	28	6·5	6·75	6·25	7
	⑥	10	12	14	17.	2·5	3	3·5	4·25
Bog centre			48.				2.		

Calculations of K^+ flux				K ppm			K flux.		
increments	·4·6	·18·6	·47·	·4·6	·18·6	·47	·4·6	·18·6	·4·7
1 live lvs	-3	+13	+3	55	55	55	-165	+715	+165.
l sh	+2	+4	+2	116	96	80	+232	+384	+160
d lvs	+6	-1	-2	18	17·5	17	+108	-17·5	-34
d sh	0	+5	-4	17	15·5	14	-	+77·5	-64
roots	-·5	+1·5	-·2	100	97·5	95	-47·5	+146·2	-19
gain							+127·5	+1322·7	+306
loss to litter.								-17·5	-98
2 live lvs	+2	0	+5	70	67·5	65	+140	0	+325
l lvs	+5	-4	+1	102	108	114	+540	-432	+114
d lvs	+13	-11	-3	11	9	7	+117	-99	-21
d sh	+10	-6	-4	12	13	14	+140	-78	-64
roots	+·8	-·1	-2	102	101	100	+808	-10	-200
gain							+1745	-442	+239
loss to litter.								-177	-85
3. live lvs	+3	+18	-8	93	90	87	+279	+1620	-696
l sh	-4	+9	-6.	89	84·5	80	-320	+760·5	-480
d lvs	-3	+13	-29	7	6·5	6.	-18	+84·5	-174
d sh	-2	+7	-10	18	16.5	·15	-30	+45·5	-15
roots	-2	+·6	-1·1	130	118	106.	-212	+708	-11·6
gain							-253	+1760	-1187·6
loss to l.							-48	-	-189
4 live lvs	+7	-3	+15	60	65·0	70.	+420	-202·5	+1050
l sh	+4	-4	+2	66	65·5	65	+264	-262	+130
d lvs	-1	+6	-14	10	8·5	7	-10	+51	-98
d sh.	+4	+2	-5	10	8·5	7·5	+40	+17	-37·5
roots	-·5.	+1.	-·2.	67	62	57	-33·5	+62	-11·4
gain							+690·5	-334·5	+1168·6
loss to l.							-43·5	-	-135·5

Absolute plottable K^+ flux. – ppm

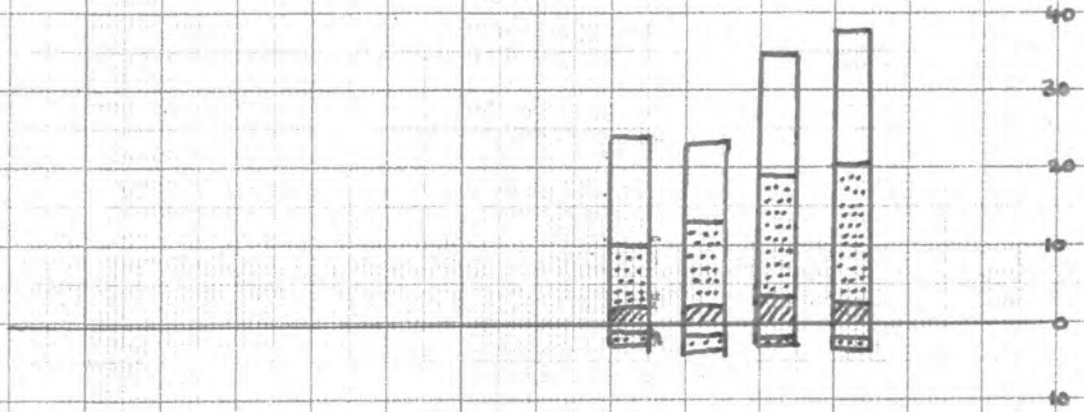
ppm x wt.

1.	0	-127.5	1450.2	1756.2
	0	0	-17.5	-115.5.
2.	0	1745	1303	1542
	0	0.	-177	-262.
4.	0	-253	1501	319.4
	0	-48	-48	-231
5.	0	690.5	356	1524.6.
	0.	-43.5	-43.5	-179.

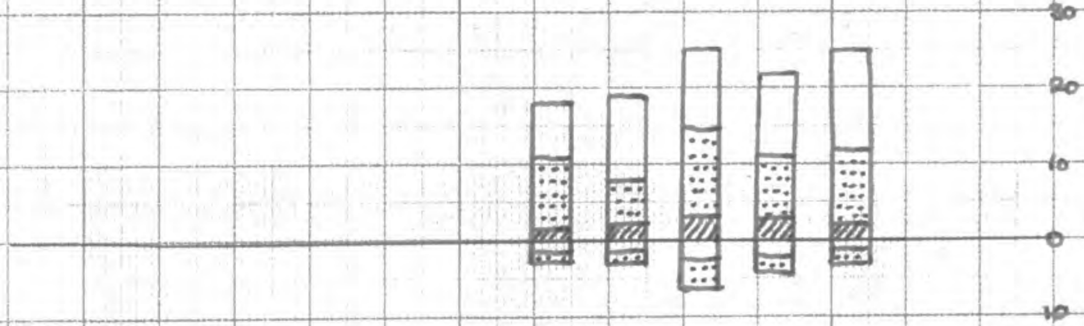
mgs per plant.

1.	0	-32	362.	439.
	0	0.	-4.75	-28.8.
2.	0	436	3423.	385.5.
	0	0	-44	65.
4	0	-63	377	79.8
	0	-12	-12	-57
5.	0	172.	89	381.1
	0	-11	-11	-45.

K flux ①



② K^+ flux



FINAL ASSOCIATION TABLE

MOORTHWAITE MOSS 27·1-69

CLASS: OXYCOCCO-SPHAGNETEA
ORDER: SPHAGNETALIA MAGELLANICI
ALLIANCE: ERICO-SPHAGNION

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 28 29
1 2 3 4 17 19 21 10 11 8 9 6 7 26 13 18 27 12 5 15 25 22 23 24 14 16 26

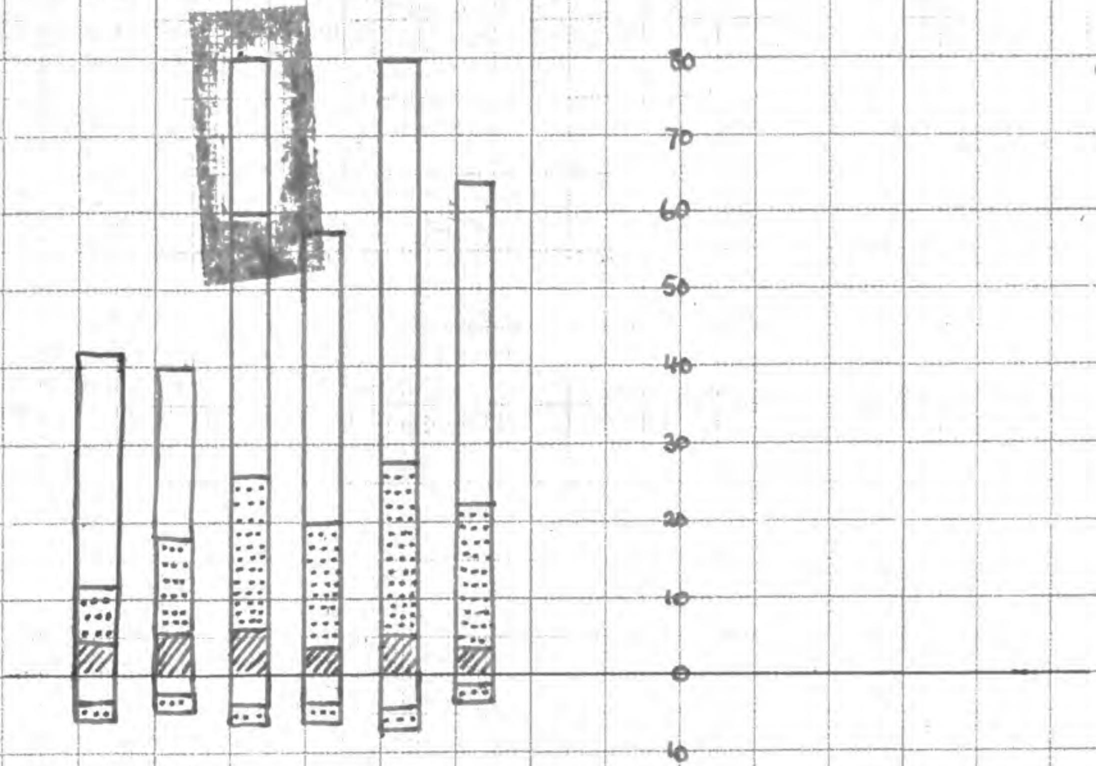
ERIOPHORUM ANGUSTIFOLIUM	2·2 2·2 2·2 + 2·2 2·2 3·3 4·2 3·2 3·3 2·2 2·2 + 1·1 + ✓ + + + ✓ ✓ 1·1 1·1 ✓ – 3·3 4·4
ERICA TETRALIX	1·1 + 3·3 + 2·2 1·1 2·2 1·1 + 1·1 1·2 1·2 1·2 2·2 2·2 + 1·2 2·2 4·4 1·1 – 4·4 4·4 3·3 – 2·2 1·1
AULACOMNIUM PALUSTRE	3·3 1·2 3·3 + 1·2 1·1 1·1 + 4·4 4·4 4·4 2·2 – – 2·2 4·4 + 1·1 – 2·2 1·1 – – – 1·1 – 1·1
OXYCOCCUS PALUSTRIS	3·3 – 3·3 2·2 2·2 2·2 2·2 2·2 1·1 3·3 3·2 2·2 – 2·2 – – + 2·2 2·2 – – 2·2 2·2 1·1 – 2·2 1·1
MYLIA ANOMOLA	4·4 + – – 1·2 + + – 2·2 2·2 2·2 1·2 – – – – – + – + – – – – – – 1·1
PINUS SYLVESTRIS	1st 1·1 + – + 1st 1st 1st + 1st 1·1 1·1 1st 1·1 1·1 – + 1·1 4·1 – + 1·1 1·1 1·1 1st + 1·1
PARMELIA PHYSODES	+ – – – + + – – + + + + 2·2 2·2 1·1 1·1 1·1 – – – + – – 1·1 1·1 + –
SPHAGNUM RECURVUM	+ 5·5 2·2 – 2·2 3·3 3·3 2·2 – 2·2 – – 2·2 2·3 – – 1·1 2·2 4·4 3·3 + 1·1 2·2 3·3 – – –
CALLUNA VULGARIS	+ + – – 1·1 – + – 3·2 1·2 2·2 2·2 4·4 3·3 3·3 2·3 3·3 2·2 2·2 1·2 1·1 · – + – –
NARTHECIUM OSSIFRAGUM.	3·3 + 3·3 + 1·1 1·1 2·2
ANDROMEDA POLYFOLIA	1·1 + – + + + + +
DROSERA ROTUNDIFOLIA	+ + – 1·1 + + 1·1
SPHAGNUM MAGELLANICUM	4·4 2·2 3·2 · 4·4 2·2 3·3 4·4 1·1 1·2 1·1
ERIOPHORUM VAGINATUM	+ 2·2 + 4·2 3·2 2·2 3·3 1·2 3·2 3·3 3·2 2·2 + 3·3 2·3 3·3 2·2 +
PLEUROZIUM SCHREBERI	2·2 2·2 1·1 3·3 3·3 2·2 1·3 3·3 2·2 4·4 1·1 3·3 2·3 1
CLADONIA IMPLEXA	1·1 1·2 4·4 4·4 4·4 1·3 1·1 4·4
VACCINIUM MYRTILLUS	+ · 1·3 4·4 4·4 2·3 2·3 2·2
EMPETRUM NIGRUM	+ 1·2 1·1 + 1·1 +
SPHAGNUM RUBELLUM	5·5 3·3 3·3 2·2 1·2 1·2
CALYPOGIA SPHAGNICOLA	1·2 2·2 1·2 + 1·1
SPHAGNUM MAGELLANICUM PAPPILOSUM	1·2 2·2 3·3 1·1 + 2·2
DICRANUM SCOPARIUM	1·2 + +
DICRANUM BONJEANI	+ 1·2
HYPNUM CUPRESSIFORME	+ 1·2 2·2
TRICHOPHORUM CAESPITOSUM	+
RHYNCHOSPORA ALBA	+
CLADONIA SYLVATICA	+ 1·1
BETULA PUBESCENS	1st. +
POLYTRICHUM STRICTUM	+
SPHAGNUM CUSPIDATUM	+
SPHAGNUM TENELLUM	+ +
ODONTOSCHISMA SPHAGNNI	2·2 + + 1·1
CEPHALOZIA CONNIVENS	2·3 2·2 + 12
JUNCUS EFFUSUS	×
MOLINIA CAERULEA	×
LEPIDOZIA SETACEA	
LEUCOBRYUM GLAUCUM	×
DRYOPTERIS SPINOSA	×
DIGITALIS PURPUREA	×
EPILOBIUM ANGUSTIFOLIUM	×
RUBUS SP	×
HEDERA HELIX	×
SALIX SP	
LISTERA OVATA	1·2

× - BORDER SP

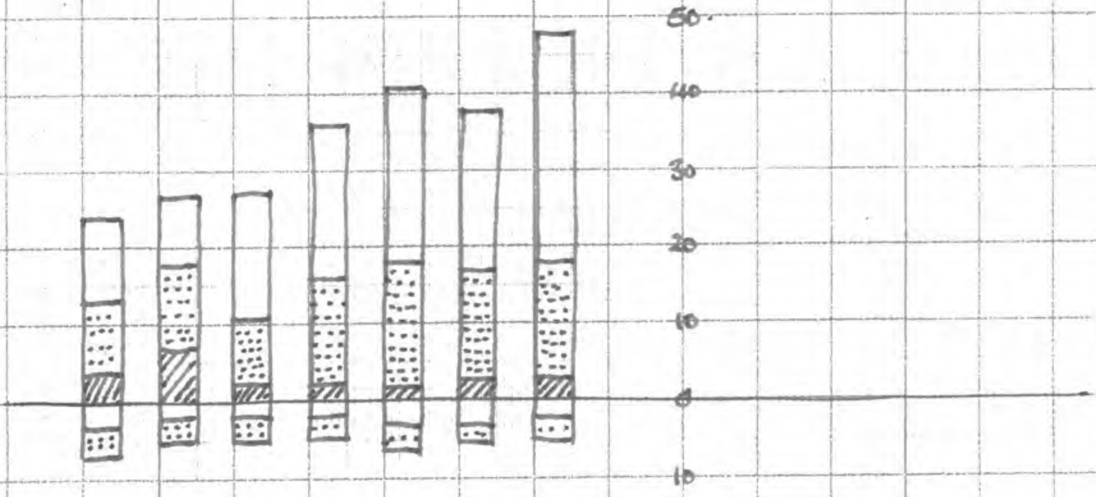
QUERCUS SP	1st
ILEX AQUIFOLIUM	1st
ACER PSEUDO PLATANUS	1st


4
2
3
1
5

④ K. flux.



⑤ K flux.



KD32

4·6·69

①	green leaves	1·12	22·142	24·169	2·027	1·810
②	green leaves	0·92	21·947	23·513	1·566	1·702
④	green leaves	0·74	23·540	24·603	1469	1·571
⑤	green leaves	0·83	23·741	24·987	1·246	1·501
①	live sheath	0·69	23·423	24·728	1·305	1·891
②	live sheath	0·74	22·698	24·085	1·387	1·874
④	live sheath	0·69	22·417	23·734	1·317	1·909
⑤	live sheath	0·75	22·321	23·715	1·394	1·859
①	brown leaves	0·95	22·113	23·962	1·849	1·948
②	brown leaves	0·84	22·355	23·995	1·640	1·952
④	brown leaves	0·97	22·547	24·478	1·931	1·991
⑤	brown leaves	0·76	22·749	24·236	1·487	1·957
①	dead sheath	0·93	22·541	24·271	1·730	1·860
②	dead sheath	0·95	22·340	24·078	1·738	1·830
④	dead sheath	1·13	21·953	22·224	2·271	2·010
⑤	dead sheath	1·01	22·643	24·636	1·993	1·973
①	flowers	0·72	22·468	23·657	1·189	1·652
②	flowers					
~~④~~	~~flowers~~					
⑤	flowers					
①	root	0·83	22·435	23·900	1·465	1·765
②	root	0·92	22·394	24·052	1·658	1·802
④	root	0·71	22·715	23·988	1·273	1·793
⑤	root	0·75	22·691	24·052	1·361	1·814
①	moss	0·51	22·710	24·444	0·734	1·440
②	MOSS	0·67	22·362	23·515	01·154	1·721
④	moss	0·59	21·825	22·828	1·003	1·701
④	MOSS	0·72	22·648	23·666	1·018	1·414
⑤	MOSS	0·63	22·325	23·334	1·009	1·601

31

BOMB CALORIMETRY RESULTS.

4-7-69

	weight	initial temp	final temp	temp. change	°C change/gr
⑤ 4·7·69 dead sheath	1·28	21·297	23·998	2·701	2·110
④ dead sheath	1·15	22·062	24·056	1·994	1·734
④ dead lvs	1·09	22·602	24·779	2·177	1·997
④ live sheath	1·35	22·536	25·0 98	2·562	1·898
⑤ live sheath	1·01	22·722	24·647	1·925	1·905
④ green leaves	1·01	22·092	24·015	1·923	1·904
⑤ ?	1·01	22·893	24·665	1·770	1·754
⑤ roots	0·71	22·110	23·588	1·478	2·081
① live leaves	1·09	21·912	23·869	1·792	1·953
① roots	0·64	21·601	22·539	0·938	1·460
① dead sheath	0·69	22·728	23·972	1·244	1·800
④ dead leaves	1·21	21·631	23·678	2·047	1·692
①,②,⑤ flowers	0·69	22·475	23·604	1·129	1·636
③ live sheath	1·04	23·045	24·952	1·907	1·834
④ MOSS (long)	0·75	22·530	23·765	1·235	1·645
⑤ green leaves	0·81	21·298	22·566	1·268	1·565
② green leaves	1·21	23·001	25·062	2·061	1·703
① live sheath	1·09	22·735	24·779	2·044	1·875
① brown leaves	0·81	22·012	23·593	1·581	1·952
③ brown leaves	1·03	23·041	25·112	2·071	2·011
⑤ brown leaves	0·97	22·119	24·287	2·068	2·132
② dead sheath	1·24	22·950	25·105	2·155	1·738
② root	0·85	22·571	24·866	1·295	1·523
④ root	0·90	22·612	24·414	1·802	2·002
③ MOSS	0·91	22·730	24·022	1·292	1·420
④ MOSS (short)	0·78	22·578	23·884	1·306	1·675
⑥ MOSS	0·90	21·901	24·354	1·453	1·614
⑥ MOSS	0·87	22·375	23·760	1·385	1·592
1 gram benzoate	1·00	21·915	24·514	2·599	2·599
0·5 " "	0·50	22·042	23·342	1·300	2·600

terms of the actual floristic composition existing at the time of study; only after this composition is described are communities delimited and successional relations considered. In essence the approach is based upon two beliefs :

1) That there are distinct species combinations which repeat themselves in nature and

2) That because of the complex inter-action of plants and habitat, the floristic composition of the vegetation as a unit is more meaningful than a list of component species. Study procedures follow two steps, sub-divided as follows:-

1) Field Analysis.

(a) selection of a site and its position and size. The species-area curve (Oosting 1956; Vestal 1949; and especially Goodall 1952) is widely used to determine proper size and number of sample plots - The sites "aufnahme", "relevéo" or description i.e. its geographical position, altitude etc. are given.

(b) description of the stand. The average height and percentage cover of each layer of vegetation are given, also the full floristic list , absolutely no species being left unidentified to ensure the validity of the results. Then every species is given a value for cover abundance and degree of sociability. Density which is the % of plots occupied may also be given. Then finally soil profiles may be given and also a figure for the area of the stand.

2) Data synthesis.

This is used to determine the degree of association of plant populations. This was done by using an association table to sort out the characteristic plants into groups to typify the plant communities or associations. The ecologist uses other concepts to help him define the associations of these the most important is fidelity, the firm adherence of a species to an association, which is a good taxonomic character. Numbers denoting various degrees of fidelity are therefore assigned to each species.

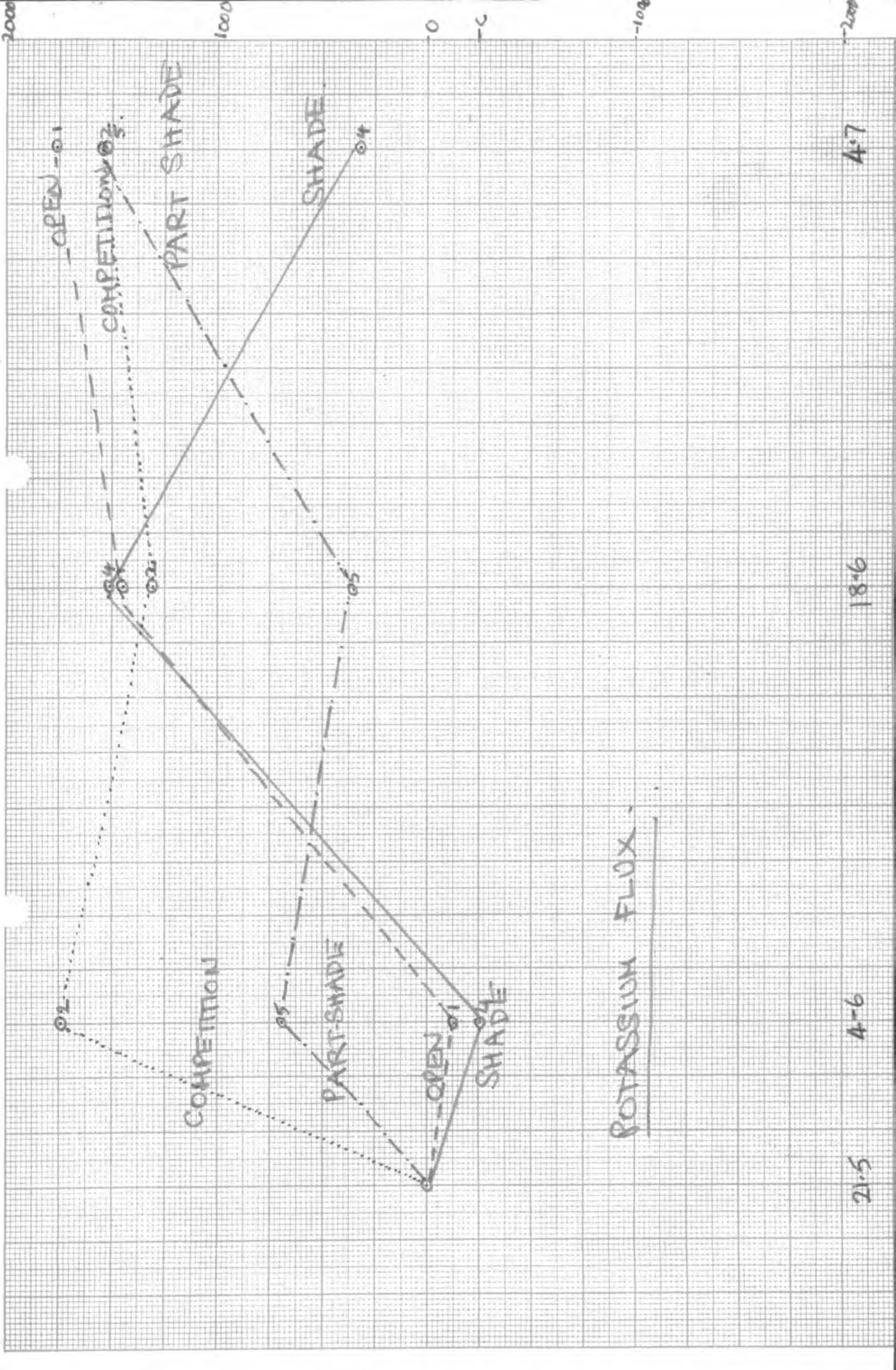
5 - exclusive - entirely confined to one community.

4 - selective - found most frequently in one community.

3 - preferential - dominant in one but found in many communities.

2 - indifferent - no pronounced affinity to any community.

1 - strange - intruders into another country, or relic species with fidelities of 5, 4 or 3 are called characteristic species "characterarten".



POTASSIUM FLUX

Rainwater

14·5·69	212 ccs.
21·5·69	482 ccs.
28·5·69	
4·6·69	263 ccs.
11·6·69	201 ccs
18·6·69	262 ccs.
25·6·69	239 ccs.
4·7·69	145 ccs

for a cylinder 10cm diam.

Statistical Formulae.

$$\sigma = \sqrt{\frac{\sum x^2}{n-1} - \bar{x}^2}.$$

$$SE = \frac{\sigma}{\sqrt{n}}.$$

df. = calculated from table using n-1.

$$SL = df . SE$$

$$\sum SL = SL . n.$$

PRELIMINARY ASSOCIATION TABLE

RELEVÉ	0	40	70	10	20	30	50	60
ERIOPHORUM ANGUSTIFOLIUM		32	+	21	[illegible]	[illegible]	+	+
ERICA TETRALIX	11	23	+	21	+1	+	+	+
AULACOMNIUM PALUSTRE		[illegible]	+	[illegible]	[illegible]	12	+	+
[illegible]		[illegible]	+	[illegible]	[illegible]	[illegible]	+	+
[illegible]				1	11	11	+	+
SPHAGNUM [illegible]	33	11	23	11	32	23	33	33
CALLUNA [illegible]	22	11	+	+	11	+	•	+
ANDROMEDA POLIFOLIA		+		+1	+	+	+	+
DROSERA ROTUNDIFOLIA					1	+		
SPHAGNUM MAGELLANICUM				2+	[illegible]	[illegible]	+	1
SPHAGNUM PAPILLOSUM		•		+	1		+	+
ERIOPHORUM VAGINATUM	22	[illegible]	+				+	
[illegible]	[illegible]	[illegible]	+			+		
CLADONIA IMPLEXA	1	•	+	[illegible]			[illegible]	+
EMPETRUM NIGRUM		1						
SPHAGNUM [illegible]			+					
DICRANUM SCOPARIUM				13	+	33	+	
ODONTOSCHISMA SPHAGNI				12	+	11	+	+
DICRANUM [illegible]					+	[illegible]		+
SPHAGNUM CUSPIDATUM							+	+

[illegible]

33

21·5·69					
① non-green leaves	1·16	21·526	23·440	1·914	1·650
① root	0·98	21·538	23·137	1·599	1·632
① flowers	0·17	22·328	22·613	0·285	1·676
① green leaves	1·16	21·232	23·189	1·957	1·687
① green sheath	0·93	22·280	23·815	1·535	1·651
① nongreen sheath	1·05	22·623	24·313	1·690	1·610
8-5-69					
② non green sheath	0·89	21·232	22·665	1·433	1·610
② root	1·10	21·288	23·078	1·790	1·627
② green leaves	1·19	21·003	23·042	2·039	1·713
② green sheath	1·17	21·600	23·515	1·915	1·637
② non green leaves	0·81	22·532	23870	1·338	1·652
② + ⑤ flowers	0·74	22·325	23·548	1·223	1·653
23-4-69					
④ green leaves	0·88	22·515	24·006	1·491	1·694
④ non green leaves	0·76	22·782	24·036	1·254	1·698
④ green sheath	0·92	22·266	23·793	1·527	1·660
④ nongreen sheath	0·81	21·878	24·180	1·302	1·607
④ root	0·88	22·424	23·884	1·460	1·659
⑤ green leaves	0·96	22·573	24·214	1·641	1·709
⑤ non green leaves	0·71	22·251	23·415	1·164	1·639
⑤ green sheath	1·02	22·742	24·429	1·687	1·654
⑤ non green sheath	1·16	22·845	24·703	1·868	1·602
⑤ root	0·93	22·367	23·887	1·520	1·684
③ green sheath	1·10	21·575	23·400	1·825	1·659
MOSS					
③	0·88	22·416	23·464	1·048	1·491
④ sh.	0·74	22·352	23·640	1·288	1·740
④ long.	0·83	22·921	23·334	1·413	1·702
⑤	0·86	22·962	23·194	1·232	1·432
⑥	0·63	21·676	22·685	1·009	1·602

CALORIES PER GRAM OF TISSUE.

4.7.69	1	2	4	5	6.
gr lvs	4568	4441	4630	3973	
gr sh	4560	4413	4616	4633	
d l	4747	4891	4857	5185	
d sh	4378	4227	4217	5132	
fl.		← 3979 →			
roots	3551	3704	4869	5061	
mono		3. 3453	4073 4001	3925	3871
4.6.69					
g l	4402	4139	3821	3650	
g sh	4599	4558	4643	4521	
d l	4738	4747	4842	4753	
d sh	4523	4450	4888	4798	
fl		← 4018 →			
roots	4292	4382	4360	4411	
mono		3. 3502	4185 4137	3439	3893
21.5.69	21.5.69	6.5.69	23.4.69		
gl	4103	4185	4120	4156	
g sh	4015	3981	4037	4022	
d l	4013	4018	4008	3986	
d sh	4523	3915	3908	3896	
fl	4076	4020	—	—	
roots		3957	4035	3974	
mono		3, 3626	4231 4139	3482	3896.

CALORIES PER CROPPING

	1	2	4	5	6.
4-7-69					
g l.	143836	8698	213015.	194134	
l sh.	68408	40147	95946	106571	
br lvs	28486	7826.	92288	88756	
br sh	39403	50728	67481	102643	
fl	31833	65657	-	-	
roots	10298	10372.	14121	21765.	
moss					

	1	2	4	5	6.
4-6-69					
g l.	74841	66233	152846	142384	
live sh.	41395.	54697	83578	113041	
br lvs	42643	142435	159495.	119000	
d sh	36192.	97924	92889	1100375	
fl.	44199	65496		20129	
roots	6868	13587	14827	13677	
moss					

	1	2	4	5	6.
green lvs.					
live sh.	82065	45831	135970	83136.	
br lvs.	28110	35835	36338	56322	
d sh	12039	40181	100210	99663	
fl	36192.	35243	70356	113000	
roots	5299	36185	-	-	
moss		7123	15333	21064	

CALORIFIC VALUES OF PLANTS & PARTS. cals / plant or per part.

		1	2	4	5
4-7-69	whole	3,222	3321	4838	5128
	live	2543	2031	3240	3224
	dead	678	1289	1597	1907
4-6-69	whole	2461 1673	4411 ~~[illegible]~~	13,354	5186
	live	788	2007 ~~[illegible]~~	2512	2892
	dead	~~[illegible]~~	2403 788	2623	2793
1st cropping					
	whole	1637	2004	3942	3131
	live	1154	1249	2579	1605
	dead	482	754	1362	2126

APPENDIX V

8·5·69 Sphagnum recurvum.

	3	4	5	6
1	0·56	0·54	0·55	
2	0·60	0·36	0·17	
3	0·32	0·43	0·14	
4	0·29	0·32	0·17	
5	0·24	0·36	0·15	
6	0·19	0·26	0·14	
7	0·21	0·25	0·07	
8	0·13	0·23	0·05	
9	0·14	0·18	0·05	
10	0·15	0·18	0·03	
11	0·15	0·16	0·02	
12	0·17	0·14	0·01	
13	0·23	0·13	0·01	
14	0·20	0·13	0·01	
15	0·15	0·07		
16	0·13	0·05		
17	0·07	0·		
18	0·05			
19	0·05			
20	0·01			
x	0·	0·12		
21	0·02			
22	0·03			

+ individual weights

+ individual weights

1003 roman letters

Sphagnum recurvum.

	3	4	5	6
1	0·56	1·23	1·45	0·78
2	0·74	1·22	1·26	0·87
3	0·55	1·42	0·75	0·83
4	0·69	1·60	0·84	0·85
5	0·76	1·82	0·90	0·57
6	0·80	1·11	0·91	0·51
7	0·90	1·07	0·81	0·64
8	0·46	0·96	0·75	0·41
9	0·67	0·66	0·71	0·40
10	0·50	0·65	0·67	0·28
11	0·46	0·47	0·71	0·23
12	0·45	0·33	0·65	0·20
13	0·44	0·26	0·75	0·19
14	0·41	0·22	0·57	0·17
15	0·42	0·16	0·38	0·14
16	0·26	0·11	0·25	0·06
17	0·26	0·20	0·13	0·03
18	0·23		0·08	0·03
19	0·13		0·05	0·05
20	0·25			0·03
21				
22				
23				
tips	0·43	0·80	0·12	0·15

1024

8·5·69 Sphagnum recurvum Erica tetralix 5

1	0·75	individual plant weights taken.
2	0·31	
3	0·28	
4	0·25	
5	0·20	
6	0·16	
7	0·15	
8	0·13	
9	0·15	
10	0·14	
11	0·09	
12	0·06	
13	0·07	
14	0·05	
15		

1085

18.6.69 Sphagnum recurvum

	3	4	5	6.
1	0·92	1·89		
2	1·27	1·70		
3	1·60	1·96		
4	1·50	2·51		
5	1·36	2·68		
6	1·40	2·85		
7	1·30	2·38		
8	1·43	1·85		
9	1·44	1·61		
10	1·51	1·22		
11	1·48	0·95		
12	1·51			
13	1·48			
14	1·39			
15	1·24			
16	1·18			
17	1·27			
18	1·00			
19	0·90			
20	0·87			

1096

4·7·69 Sphagnum recurvum.
Wood at entrance

0·62
0·67
-
0·70
0·90
0·85
0·95
0·69
0·37
0·41
0·28
0·25
0·24
0·07
0·22
0·12
0·05

1807

4·7·69 Sphagnum recurvum

	3	4 short	4 long	5	6
1	1·52	0·55	0·35		
2	1·51	0·53	0·43		
3	1·35	0·59	0·53		
4	1·39	0·59	0·55		
5	1·21	0·47	0·55		
6	1·20	0·35	0·43		
7	1·23	0·40	0·35		
8	1·09	0·27	0·35		
9	1·01	0·27	0·35		
10	1·02	0·22	0·35		
11	1·08	0·17	0·26		
12	1·00	0·13	0·18		
13	1·02	0·10	0·27		
14	0·98	0·03	0·12		
15	0·89		0·11		
16	0·91				
17	0·88				
18					
19					
20					

BOMB CALORIMETRY — DEGREES DEFLECTION PER GRAM MATERIAL

4·7·69

	1	2	4	5	6
green leaves	1·792	1·703	1·904	1·565	
live sheath	1·875	1·834	1·898	1·905	
brown leaves	1·952	2·011	1·997	2·132	
dead sheath	1·800	1·738	, 1·734	2·110	
flowers	← 1·636 →				
roots	1·460	1·523	2·002	2·081	
moss	- ·	3, 1·420	1·675 sh 1·645 long	1·614	1·592

4-6-69

green leaves	1·810	1·702	1·571	1·501	
live sheath	1·891	1874	1·909	1·859	
brown leaves	1·948	1·952	1·991	1·957	
dead sheath	1·860	1·830	2·010	1·973	
flowers	← 1·652 →				
roots	1·765	1·802	1·793	1·814	
moss	—	3, 1·440	1·721 sh 1·701 long	1·414	1·601

21·5-69 → 1		8·5·69 2	23·4·69, 4	23·4·69, 5	23·4·69, 6	23·4·69, 3
green leaves	1·687	1·713	1·694	1·709		
live sheath	1·651	1·637	1·660	1·654		
brown leaves	1·650	1·652	1·648	1·639		
dead sheath	1·610	1·610	1·607	1·602		
flowers	1·676	1·653 →				
roots	1·632		1·659	1·634		
moss	—	—	1·740 sh. 1·702 long.	1·432	1·602	1·491

BOMB CALORIMETRY - DEGREES DEFLECTION PER GRAM MATERIAL

4.7.69

	1	2	4	5	6.
green leaves	1.792	1.703	1.804	1.565	
live sheath	1.875	1.834	1.898	1.905	
brown leaves	1.952	2.011	1.997	2.132	
dead sheath	1.800	1.738	1.734	2.110	
flowers	←	1.636	→		
roots	1.460	1.523	2.002	2.081	
moss	–	3. 1.420	1.675 sh 1.645 long	1.614	1.592

4-6-69

	1	2	4	5	6.
green leaves	1.810	1.702	1.571	1.501	
live sheath.	1.891	1.874	1.909	1.859	
brown leaves	1.948	1.952.	1.991	1.957	
dead sheath	1.860	1.830	2.010	1.973	
flowers	←	1.652.	→		
roots	1.765	1.802.	1.793	1.814	
moss	–	3. 1.440.	1.721 sh. 1.701 long	1.414	1.601

21-5-69	1	8.5.69 2.	23.4.69 4		
green leaves	1.687	1.713	1.694	1.709	
live sheath	1.651	1.637	1.660	1.654	
brown leaves	1.650	1.652	1.648	1.639	
dead sheath	1.610	1.610	1.607	1.602.	
flowers	1.676	1.653. →			
roots	1.632	–	1.659	1.634	
moss	–	– 23.4.69 3. 1.491	1.740 sh. 1.702 long.	1.432	1.602

Impatiens.

The results of the Impatiens balsaminifera experiments were rather dissapointing. Despite all the precuations which could be designed, the plants suffered serious losses through grazing and rotting of the root system. They were also attacked by fungal mycelia at the base of the stem. By the time precautions had been taken, many of the plants and seeds had bee lost, leaving only a statistically invalid number remaining to crop.

Grazing losses were reduced be covering the crops with fine guage nylon netting. This eliminated the major pests, which were found to be large black slugs living in the matted roots of the Eriophorum plants. However, even so the smaller 'keel' slugs found their way in and destroyed large numbers of remaining plants.

The problem of rotting of the root systems was tackled by raising seed boxes, in which the plants were growing, above the (varying) water level prevalent in the bog at the time. Water availability was ensured by placing peat and Sphagnum moss under the seed boxes. Only capillary water was attracted to the vermiculite rooting medium, so it was hoped that it would contain sufficient air and oxygen to allow the roots to survive. However, the situation was not relieved to any large extent and the cropping results of the impatiens controls were si low as to be insignificant.

Similarly when thesen low level crops were harvested and put into the cool room, at 4°C, the plants died and rotted, thus destroying the first harvest completely.

Control plants grown in garden soil in Durham at St. Chad's College had only reached 20cm. in height by August 26th. They only weighed 3grs. dry weight, so this part of the experiment also gave insignificant results.

Conclusions

It is suggested that a more hydrophytic indicator - control plant be used, one which can withstand greater amounts of waterlogging, but one which can also withstand dry land conditions. Suggested plants may include Cardamine pratensis
Veronica beccabunga
Mimulus guttatus

The latter would probably be the most preferable, as it can withstand a large variation in water regime, and is a useful indicator of prevailing nutrient conditions.

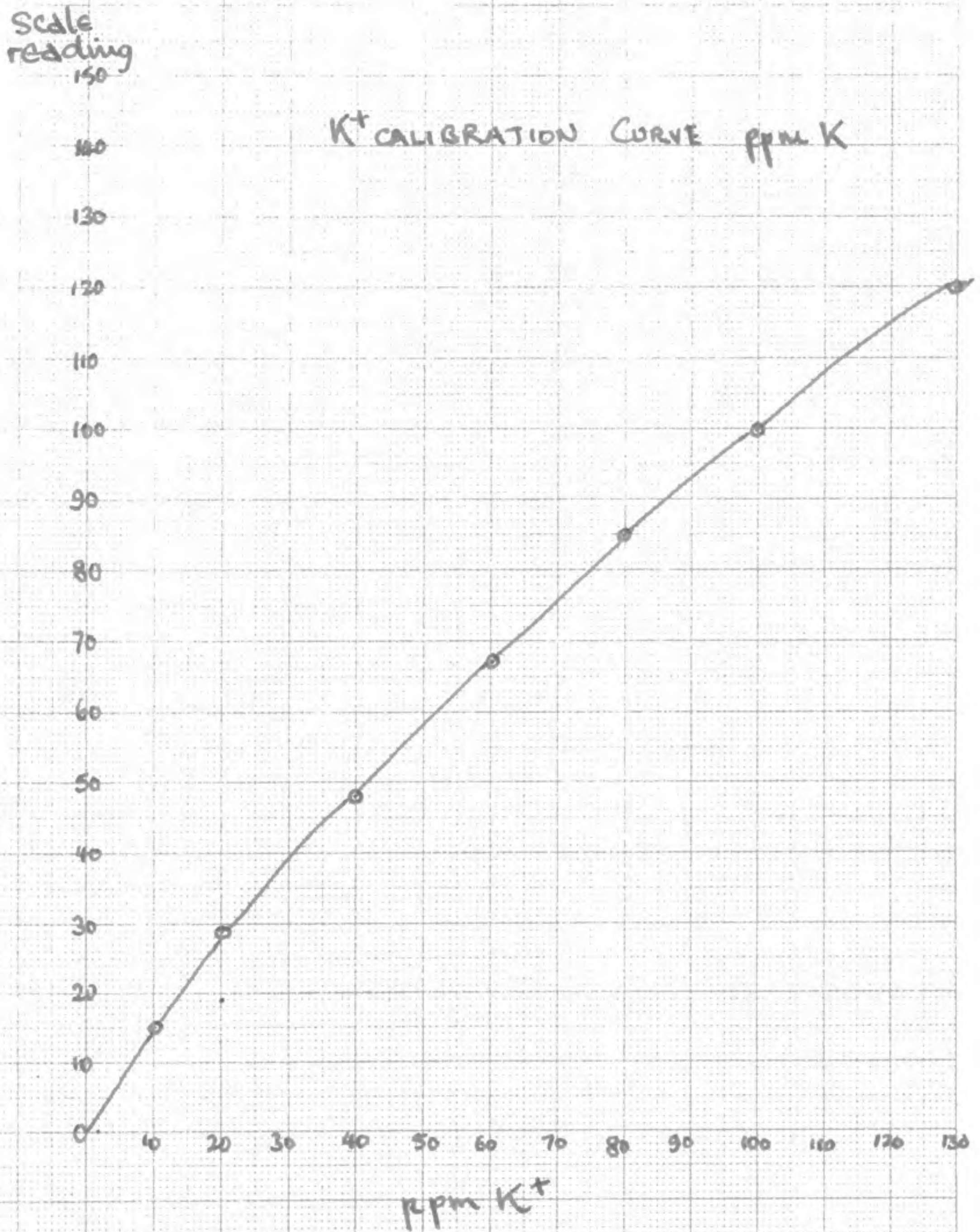
Addenda

% dry weight Sphagnum recurvum - 2341% water retention ref. Green B. H. (1965) Some studies of water / peat / plant relationships with special reference to Wybunbury Moss, Cheshire.

rain analysis	ppm Na	K	Ca
	1.8	0.1	1.9
	0.9	0.3	1.6
pine wood	8.1	6.2	9.8
	8.1	4.0	15.0
	12.1	4.5	5.2
	5.1	0.5	3.4
Sphagnum lawn	3.4	1.6	4.0
	4.3	3.8	3.6
	5.4	0.5	3.5
	4.5	1.1	1.5
Soak (standing water in Sphagnum recurvum)	6.0	1.0	1.8
	6.3	0.3	1.9

Sphagnum lawn communities	625 (25by25) cm^2 quadrats
Oxycoccus palustris	100
Sphagnum recurvum	98
Eriphorm vaginatum	82
Eriophorm angustifolium	70
Drosera rotundifolia	54
Erica tetralix	38
Empetrum nigrum	32
Calluna vulgaris	30
Polytrichum silvaticum	24
Aulacomnoum palustre	20
Sphagnum papillosum	18
S. cuspidatum	14
S. rubellum	12
Mylia anomola	12
Carex rostrata	10

J. Ecol. (1964)
vol. 52 p. 299.


K+ CALIBRATION CURVE ppm K
Scale reading
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
110
120
130
ppm K+