A COMPARISON OF SUBJECTIVE AND OBJECTIVE METHODS OF ANALYSIS OF THE VEGETATION OF HARTLAND MOOR.

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I. Introduction to the problem.

The investigation was undertaken for three main reasons :-

1). An investigation was needed in ecology into the comparison of subjective and objective methods of the classification of vegetation. It has long been debated (Goodall 1954, Ashby 1948) whether subjective assessments of the vegetation of an area bear any relation to those obtained by objective methods, i.e. whether the subjective, human element outweighs and obscures important vegetational features when an attempt is made to classify the vegetation into communities "by eye".

2). The work would serve as an extension of that being carried out in the Botany Department of Southampton University on the analysis of vegetation by fully objective methods such as association-analysis (Williams and Lambert, 1959 and in preparation). Several relatively simple areas containing either few species or few quadrats have already been investigated with promising results. It was now appropriate that a more complex area with both a larger number of species and quadrats should be analysed.

3). The results should incidentally give a clearer understanding of the specific ecology of Hartland Moor. In the last thirty years our knowledge of British lowland bogs has greatly increased and many areas have been intensively studied. Hartland Moor however was previously relatively understudied and the new ecological tool of association analysis might elucidate further the nature of the vegetation of another British lowland bog.

The classification of vegetation has the function of systematising natural communities into discrete units that can be comprehended, compared and studied (Becking, 1957). It has emerged from being an aspect of plant geography into a fundamental and independent part of the modern science of the study of the eco-system. Between the fully subjective assessment of the area and the fully objective association-analysis there exist many methods of recording, describing and analysing vegetation. These intermediate methods generally belong to the current schools of phytosociologists and one such method was used in modified form in this investigation for comparison with the subjective and objective results; there is however inherent in all phytosociological methods a great element of subjectivity and a further attempt was made to reduce this by applying more rigid, statistical methods of community discrimination.

To avoid any influencing of the subjective assessment by the results of the wholly or partially objective methods, the investigation was carried out in four successive stages :- (a) subjective assessment (b) phytosociological classification (c) statistical phytosociological study and (d) association-analysis. Each stage was completed and the written account produced before the next stage was started, and the resulting maps and accounts were then compared.

A subsidiary part of this investigation was to find the effect of omitting certain groups of species estimated as relatively unimportant from the data used for classification. Such species might form either numerically or physiognomically a subsidiary part of the total vegetation. If the results are not radically altered when compared with those gained from a full species analysis, such species might be legitimately excluded and the surveying and calculation time of such analyses would thereby be greatly reduced.

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II. Description of the experimental area.

A. Introduction

Hartland Moor appeared to be a suitable area for study because

1). It has two main types of community :- (i) those that are more or less distinct and generally recognised by most British ecologists (bog, wet heath and dry heath) and (ii) those that are less clearly delimited and accepted (the various subdivisions of the bog). The interest lay in whether or not the distinct communities are retained by all classification methods and the extent to which the secondary communities have any objective reality.

2). The vegetation has no well defined seasonal aspects and was therefore suitable for prolonged surveying.

3). The area was relatively free from interference such as grazing and burning when compared with similar local vegetation types.

4). Some information already exists in the files of the Nature Conservancy as to the general ecological background of the area, and additional information was obtained from the notes of the several ecologists and systematists of the Nature Conservancy and the Universities, who have visited Hartland Moor in the course of their specialist researches. Such pre-existing information would be used in the general ecological interpretation of the results.

B. General description of Hartland Moor.

(1) The present features.

Hartland Moor (National Nature Reserve) in the north Purbeck region of the Dorset heaths conservation area, occupies an almost complete drainage basin of about 600 acres, and extends from near the Corfe/Wareham road to the sea at Middlebere Creek on the west side of Poole Harbour, a total distance of about 1½ miles.

The Reserve consists of two valleys separated by a knoll (100 ft. O. D.) and joining below it to give a single seaward valley. There are a number of smaller tributary "basins" (e.g. Tramway bog) lateral to the main valley.(see map 1).

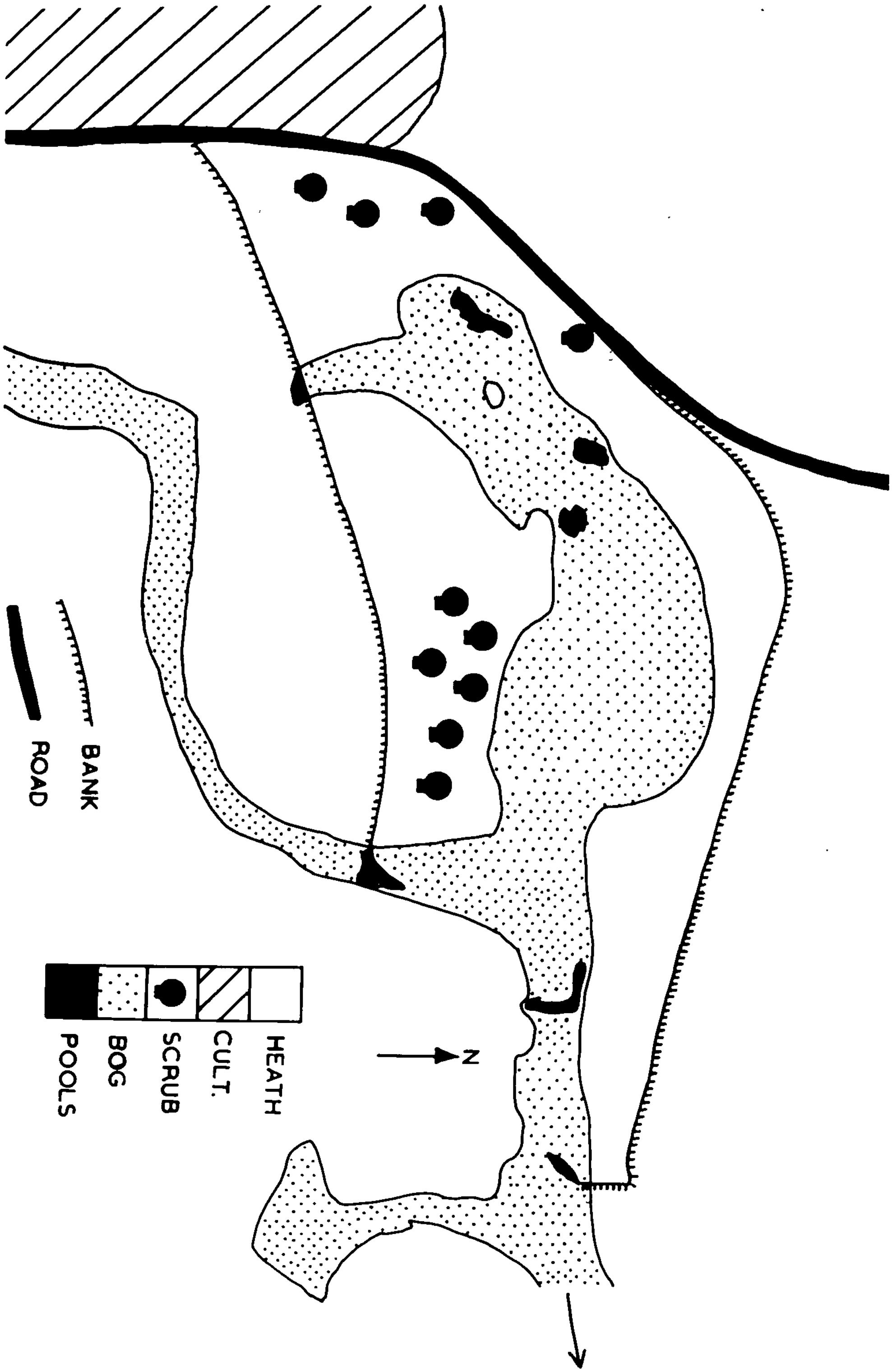
Underlying most of the Reserve are Bagshot beds which in this area are mainly granitic sands with some pipe-clay lenses, the higher areas being capped with Plateau Gravels and Ironstone concretions. The drier parts of the Reserve lying roughly above the 25 feet O.D. contour line have a podsolised soil. The wetter parts have peat over a mineral soil that is composed of sand with many clay lenses. There is no evidence of a podzol underlying the peat. The peat is about 130 cm. deep in the deepest part, just below the confluence of the two valleys.

The wider of the two valleys bears a central zone of bog vegetation bordered by wet heath and grading upwards into dry heath bearing occasional patches of scrub. The narrower valley is similar except that its peat vegetation is of the fen type, the latter also occurring below the junction of the two valleys. This fen grades into reedswamp as the sea is approached and ultimately into salt marsh. Pools of various sizes occur in the bog and fen valleys. (see map 2)

Surrounding the Reserve are undulating heaths, some of which have been ploughed and sown, and are now used as pasture and

Map 1. Contour map of Hartland Moor.

Scale : approx. 6 ins. = 1 mile.



Map 2. General features of Hartland Moor.

Scale : approx. 6 ins. = 1 mile.

arable land.

Burning of some of these surrounding heaths is periodically carried out to provide fresh grazing for cattle and sheep and these fires sometimes spread to the reserve. Accidental fires are occasional and are caused generally by trippers, who are becoming more numerous annually owing to the disappearance of other heathlands in the area through increasing exploitation.

Cattle and sheep from neighbouring heaths and pastures occasionally stray on the Reserve and graze a little but the bog itself is rarely touched, the wet heath being the only zone on which damaged plants have been noted. Deer - three species are to be found in the neighbouring parklands - occasionally escape and visit Hartland but little damage is done.

(2) History of the area.

The early history of the area is uncertain although a barrow on the top of the knoll is almost certainly of Bronze age origin, suggesting a fairly open vegetation at the time.

The origin of the bog itself is still debatable. Rose (1953) believes that " .... the vast quagmire of Hartland Moor is a floating mat developed over a lake, now reduced to a few small lakelets with a small form of *Nymphaea alba*" but he cites no evidence. Peat borings carried out by Mr. M. J. Hudson (of the Botany Department of Southampton University, who has been studying the origin and development of the bogs of the Hampshire basin) suggest that Hartland Moor is not a floating mat at least in its upper reaches although there is liquid peat below the surface skin in its lower fen reaches. There is as yet no stratigraphical evidence to support the assumption of an original lake, and local evidence suggests that the pool with Nymphaea alba had an artificial origin as a decoy pool.

It is possible that the water-level has been raised at some time in the past since artificial balks of clay and sand with straight vertical sides and about one metre wide are found across the main valley. These balks are too regular to be natural and have no connection with the bluffs of sandy heathland which run into the bog in places. Moreover they are very similar to banks used as boundaries on many of the Dorset heaths and similar examples in the New Forest (e.g. Bishop's Dyke near Beaulieu Road station) date from the Middle Ages. In addition there has been a certain amount of peat cutting in the past. Such peat cutting is known to have been regularly carried out by local people and by a London firm until the outbreak of the first world war. During the course of peat cutting operations straight-sided balks of compacted peat were left across the bog and probably served to hold up the drainage water further, since the upstream water level is several cm. higher than that below them. It is plausible that much of the bog vegetation has colonised these former peat cuttings, with only the balks representing the original peat. Local evidence has suggested that the areas of open water on Hartland Moor have decreased within living memory. This is in accordance with the gradual colonisation of flooded peat cuttings and also may account for Rose's (loc. cit.) contention that the bog had developed from an original lake.

About 1880, the northern side of the reserve, except the wet-heath and the bog, were planted with pine to form the Slepe Plantation of the Ordnance Survey maps. This plantation was destroyed by fire in about 1915 and the remaining trees were felled shortly afterwards. Pines occur on the reserve today but do not reach any considerable size and there is no large scale regeneration similar to that at Morden Decoy reserve three miles to the north of Hartland Moor.

The heaths surrounding the bog were used as a military training ground during the second world war and resulted in the appearance of mortar holes in the wet heath. Flame throwers were used just after the war to clear the heath of unexploded bombs and this process so drastically burnt the dry heath that regeneration of the flora had to start from bare soil. A short description of the area by J. Heslop-Harrison in 1952 (Nature Conservancy reserve record) suggests that the ground was then covered by a mat of *Metzgeria furcata* and *Ceratodon purpureus* together with a few caespitose angiosperms.

C. The area studied.

The whole reserve was too large for a complete detailed survey and therefore only a part, about 300 by 800 metres, comprising a large portion of the bog valley and its surrounding heaths, was chosen for further study. Since the area appeared to be divided into fairly homogeneous communities, it offered a good test as to whether such communities had any objective reality and whether further communities could be distinguished by statistical analysis.

Small hardwood poles were driven into the substrate at taped intervals of 20 metres to produce a grid. (see map 3). This grid served as a co-ordinate reference system for any point on the area and for placing the quadrats.

Peat depths were measured at every quadrat point and from these values a peat depth contour map was constructed. (see map 4). This map also served to show the general configuration of the sub-surface of the submerged area.

A little crude information on peat acidity was also obtained, the pH. observations of Newbould (1953) and Newbould et al. (1957) being supplemented by similar readings along transects across the area and at scattered points. Newbould et al. (l.c.) also give details of specific conductivity (K corr.) measurements and potassium, sodium and calcium determinations (mg./l.) per water from points on a transect across the gridded area. (see table 1.)

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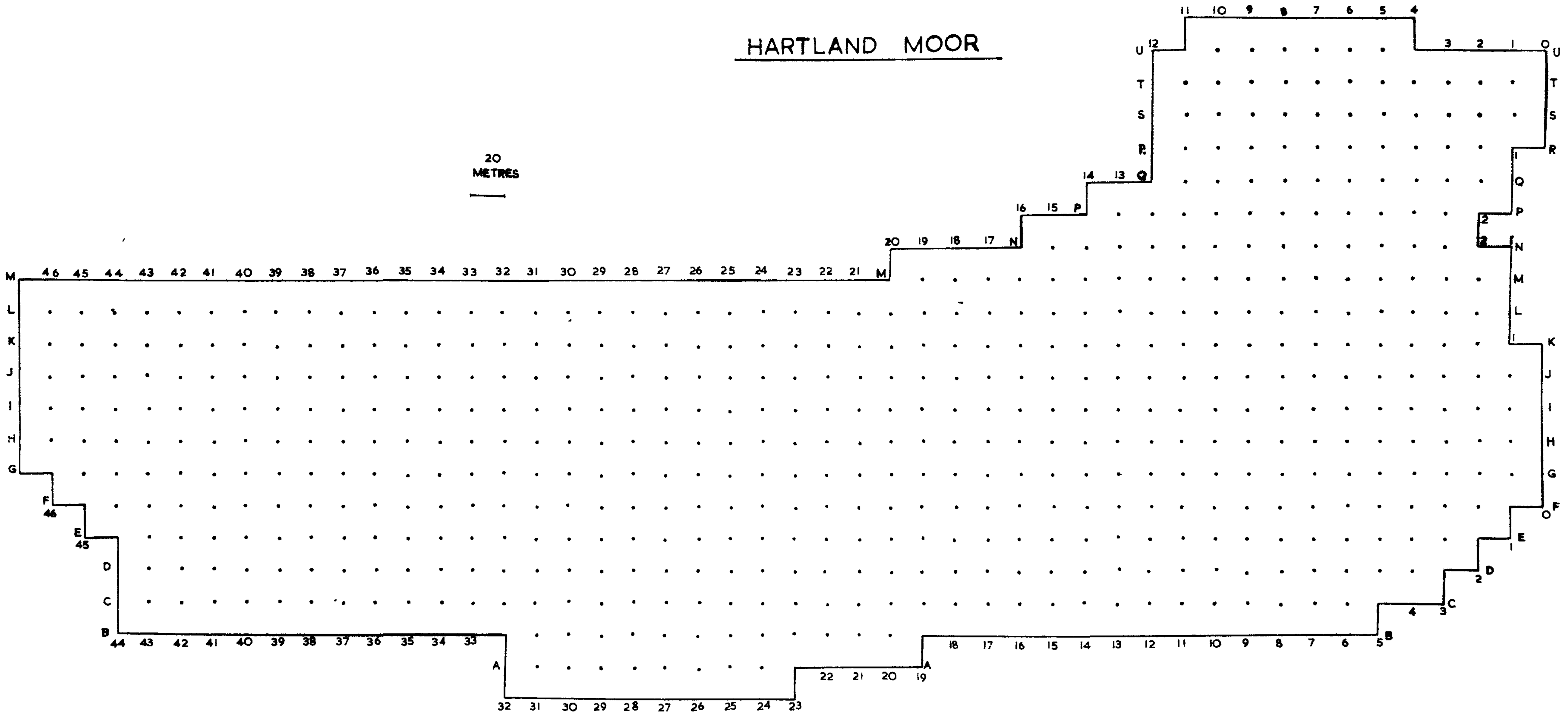
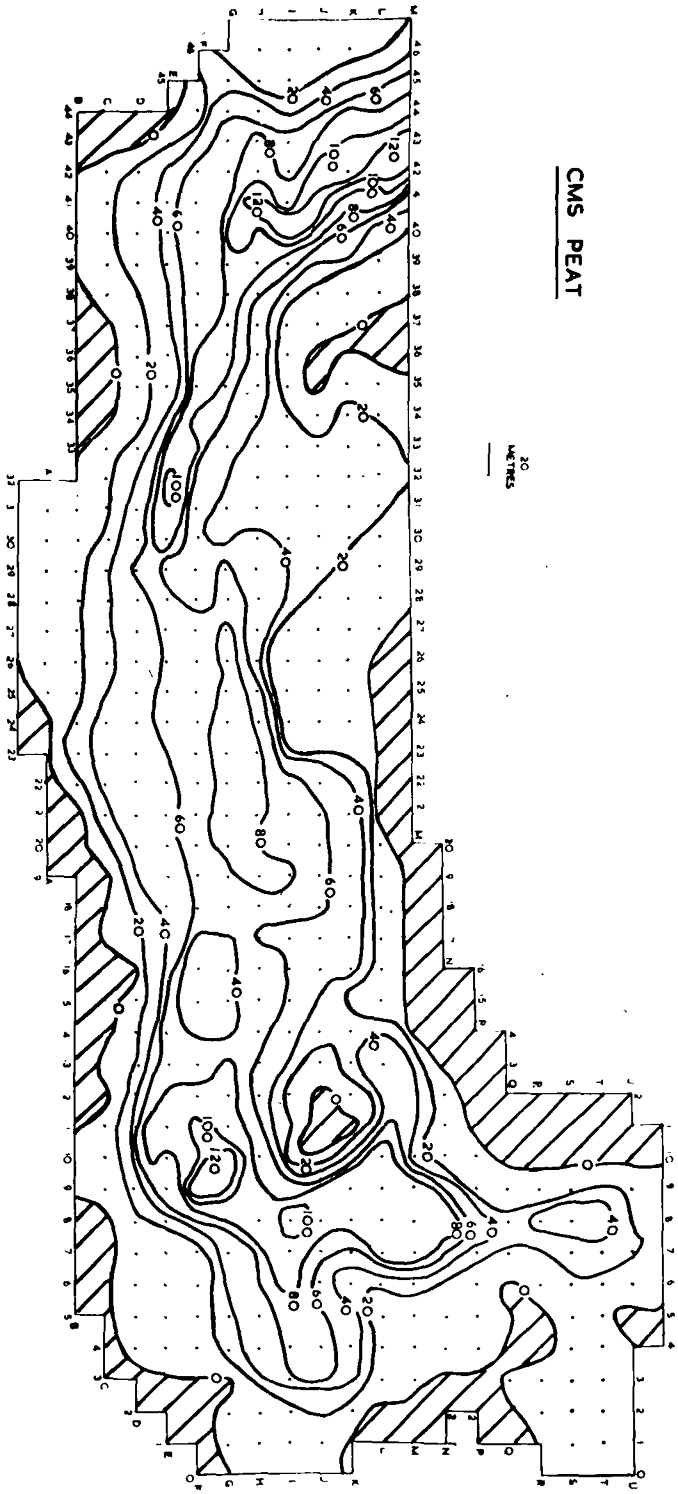
111. Subjective analysis of the vegetation.

A. Methods.

Subjective methods of classifying and mapping vegetation give varying results depending on the worker's previous experience of similar vegetation elsewhere and his knowledge of the written and verbal descriptions of similar areas by other workers. Not one but many criteria are used for the delimitation of the units observed, and the size, distribution and definition of the units will vary as it is unlikely that two or more workers will use the same criteria in the same proportion. In addition to the actual floristic composition of a community, aspects commonly taken into consideration are :-



Map 3. Grid map (= quadrat placings) of experimental area.



Map 4. Peat depths in cm. Shaded areas indicate no peat present.

TABLE 1.

Quadrat No.	Water pH	Water K corr. (mhos x 10^{-6})	Water K (Mg/l.)	Water Na (Mg/l.)	Water Ca (Mg/l.)	Peat pH
A 24	3.6	-	-	-	-	-
A 31	3.7	-	-	-	-	-
B 24	3.8	-	-	-	-	-
B 31	3.7	-	-	-	-	-
* C 15	3.9	239	2.0	31.5	5.0	3.8
C 24	4.1	-	-	-	-	-
C 31	3.5	-	-	-	-	-
* D 15	4.4	112	1.4	21.5	3.8	4.5
D 24	4.5	-	-	-	-	-
D 31	3.6	-	-	-	-	-
* E 15	4.5	87	0.9	18.0	2.0	4.7
E 24	3.8	-	-	-	-	-
E 31	3.7	-	-	-	-	-
* F 8	4.4	97	1.3	17.0	2.0	-
* F 15	4.7	87	0.4	17.0	1.0	4.8
F 24	3.6	-	-	-	-	-
F 31	3.7	-	-	-	-	-
* G 6	4.4	98	-	-	-	-
* G 15	4.7	85	0.3	16.0	2.0	4.4
G 24	3.5	-	-	-	-	-
G 31	3.7	-	-	-	-	-
* H 15	4.4	82	0.4	16.5	2.0	4.8
H 24	3.8	-	-	-	-	-
H 31	4.5	-	-	-	-	-
* I 15	4.3	100	0.8	19.0	3.5	4.8
I 24	3.8	-	-	-	-	-
I 31	4.7	-	-	-	-	-
I 40	3.8	-	-	-	-	-
* J 15	4.5	112	1.1	18.0	2.75	4.7
J 24	3.5	-	-	-	-	-
J 31	4.6	-	-	-	-	-
J 41	4.0	-	-	-	-	-
* K 7	4.5	112	0.5	14.6	3.5	-
* K 15	4.4	107	3.6	20.0	5.0	4.4
K 24	3.5	-	-	-	-	-
K 31	4.6	-	-	-	-	-
K 42	4.9	-	-	-	-	-
* L 15	4.0	-	-	-	-	3.7
L 24	3.6	-	-	-	-	-
L 31	4.1	-	-	-	-	-
L 43	5.1	-	-	-	-	-
* M 15	3.8	-	-	-	-	-
* N 15	3.8	-	-	-	-	-
T 1	3.5	-	-	-	-	-
T 2	3.5	-	-	-	-	-
T 3	3.3	-	-	-	-	-
T 4	3.3	-	-	-	-	-
T 5	3.5	-	-	-	-	-
T 6	3.7	-	-	-	-	-
T 7	3.7	-	-	-	-	-
T 8	3.8	-	-	-	-	-
T 9	3.6	-	-	-	-	-
T 10	3.9	-	-	-	-	-
T 11	3.9	-	-	-	-	-

Values as at March 1959, except those marked *

which are July 1957.

1. The relative abundance of the species.

2. The relative amounts of the various life-forms present.

3. The physiological state of the species affecting the seasonal aspect of the vegetation.

4. The nature of the substrate and the amount of it visible in relation to the cover of the species.

These are all subconsciously integrated to give rather indeterminate units (such as dry heath, wet heath and bog) reflecting the general physiognomy of the vegetation.

Subjective maps (No. 5 & 6) of the gridded area of Hartland Moor were produced in July 1957 on these lines by drawing the boundaries of the communities recognised on squared paper, the corners of the squares representing the grid posts. In addition to the main communities that were mapped, small mosaics could be distinguished in most places, but were of insufficient extent to be represented on the map. Sometimes one of the constituents of the mosaics formed a small but distinct community in which case it was specifically indicated on the map.

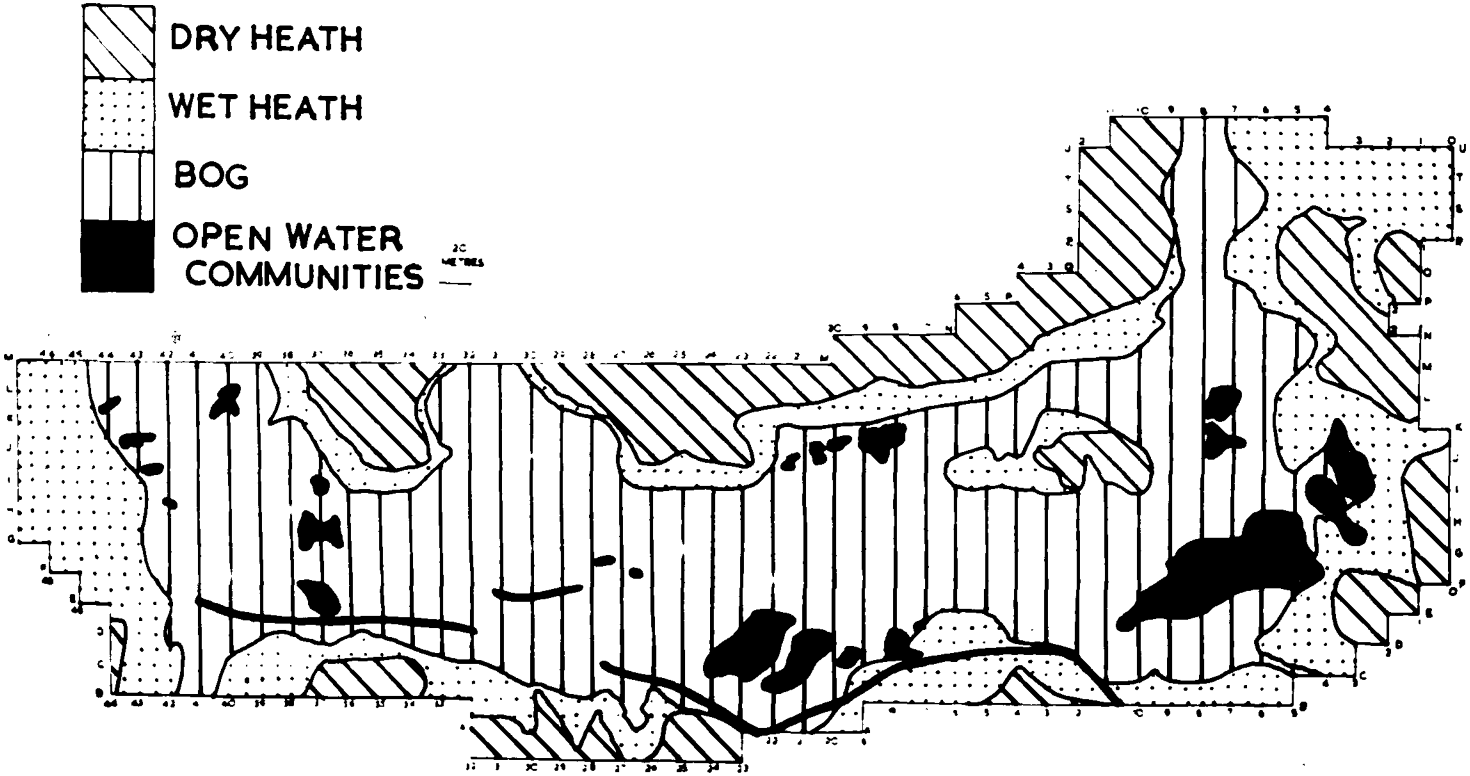
B. Results.

The Main Communities.

Four main communities could be distinguished at first sight. (see map 5).

(1) Dry heath.

"Dry heath" as defined by Tansley (1953) is an ericaceous community developed on a podsolised soil. On Hartland Moor, Calluna is dominant on a sandy podsol occupying a large peripheral area of



Map 5. General subjective vegetational groupings.

the grid; other species, although widespread, only attain local dominance.

(2) Wet heath.

"Wet heath" is an area of heath where the ground water reaches the surface in local hollows and remains fairly constant in relation to the soil surface; it is further characterised by certain typical species listed by Tansley (*loc. cit.*). The flora of areas of Hartland Moor where the ground water is just below the surface agrees with this list except for the occurrence on Hartland of *Erica ciliaris* which here reaches its most easterly station in Great Britain. No single species appears to be dominant over most of the area.

(3) Bog.

This is generally defined as an area of vegetation developed on acid peat where the water table is at or above the soil surface. On Hartland this consists of a more or less continuous carpet of *Sphagnum* spp. dominated in parts by non-tussocky *Schoenus nigricans*, *Carex rostrata*, *Rhynchospora alba* and *Eriophorum angustifolium*. *Molinia caerulea* appears to be the most widespread angiosperm on the bog but there is also much *Calluna*, *Erica tetralix*, *E. ciliaris*, *Narthecium* and *Drosera rotundifolia*.

(4) Open water vegetation.

This is a rather heterogeneous collection of small communities occurring in the pools on the bog or on the wet heath.

Further Subjective Subdivisions of the vegetation.

Whereas the four main divisions are more or less based on physiognomy, further subdivision takes into account specific idiosyncrasies of the area such as the dominance of a single species or a single habitat peculiarity. The following variations were recognised. (see map 6)

(1) Within Dry Heath

a). Calluna areas.

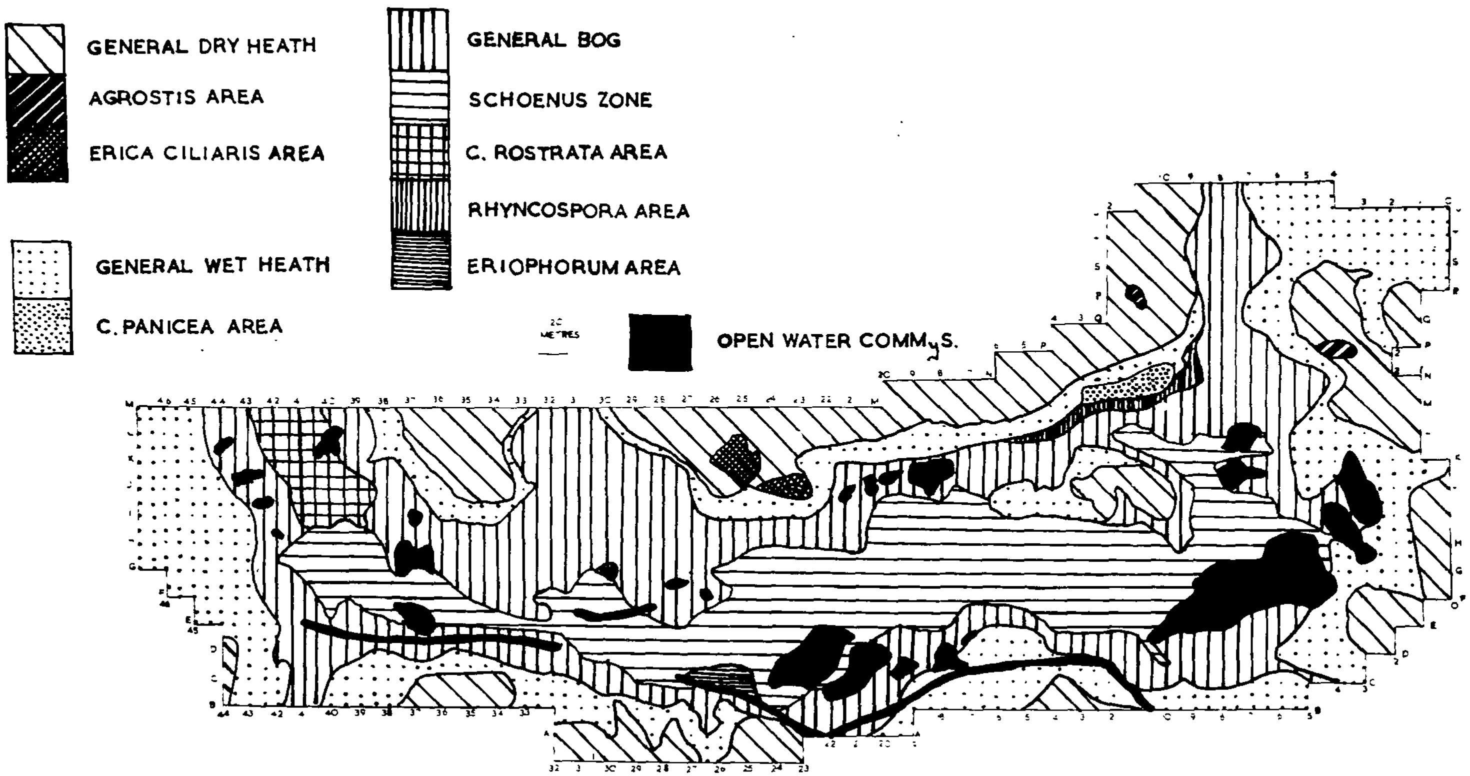
The Calluna is found as the dominant over large areas of the dry heath. It varies in height from about 70 cm. on the western part of the knoll to plants of 15 cm. only in the more sheltered damper regions. The former area has a fairly pure flora of Calluna only but the latter is being invaded by small birches and sallows together with a few stunted pines. Between these two extremes are varying amounts of Molinia, Erica tetralix, E. ciliaris and E. cinerea. Ulex europaeus occurs in isolated chumps and Ulex minor forms a close mat on the more frequented paths and trackways. These variations are apparently continuous and therefore not separately mapped.

b). Erica ciliaris areas.

Although Erica ciliaris, pure or as its hybrid with E. tetralix (E. x watsonii), is found over practically the whole bog and heath, it is only dominant on some damper areas of the dry heath especially on the north side of the knoll. It is not found as a completely monospecific community but has an admixture of Molinia and Erica cinerea and often some Calluna.

c). Agrostis setacea areas.

Several small patches of relatively pure sandy soil (i.e. very little humus present) are dominated by Agrostis setacea to the



Map 6. Detailed subjective vegetational groupings.

exclusion, or at least diminution, of other species.

(2) Within Wet Heath.

a). General wet heath.

Typically this consists of a discontinuous cover of *Sphagnum compactum*, *S. tenellum* and *S. molle* with *Lepidozia setacea* and often *Gymnocolea inflata*, *Campylopus brevipilus*, a small form of *Polytrichum commune*, and blankets of *Zygogonium* "*ericetorum*", all bearing an angiospermous flora of *Scirpus cespitosus*, *Gentiana pneumonanthe*, *Molinia*, *Erica ciliaris*, *E. tetralix*, *Calluna*, *Eriophorum angustifolium* and *Narthecium* with no obvious local concentrations. In the wetter parts, *Lycopodium inundatum*, *Juncus acutiflorus* and *J. squarrosus* are found and also *Sphagnum subsecundum* var. *auriculatum* and *Rhynchospora alba* towards the bog.

b). Carex panicea area.

Carex panicea is found in large, slight depressions in the wet heath, especially those that are subjected to prolonged flooding after heavy storms. *Molinia* and a few lichens are generally the only other colonisers of these hollows.

(3) Within Bog.

a). General bog.

The areas of the bog where no single species is apparently dominant in the *Sphagnum* carpet have been termed "general bog". This consists of dead and living *Sphagnum papillosum*, *S. pulchrum*, *S. magellanicum*, *S. subsecundum* var. *auriculatum* and associated bryophytes (*Lepidozia setacea*, *Cephalozia* spp., *Odontochisma sphagni* and *Cephaloziella starkei* being the commonest) bearing an angiospermous flora. *Molinia* is again the most widespread species although *Drosera rotundifolia* and *Erica* spp. (except *E. cinerea*) are found in most places. *Rhynchospora alba* is patchy in its distribution as also is *Narthecium ossifragum*, both of which apparently form mosaics too small to be mapped on the scale used. In the drier places *Polygala serpyllifolia* and *Potentilla erecta* are found and on the *Sphagnum pulchrum* mats there are occasionally found specimens of *Polygala oxyptera* (= *P. vulgaris*).

b). *Schoenus nigricans areas.*

A non-tussocky form of *Schoenus* is the dominant plant forming a distinct community down the centre of the bog. *Molinia* is subdominant and there are many widespread species such as *Eriophorum*, *Sphagnum papillosum*, *S. pulchrum* and *S. subsecundum* var. *auriculatum* in all but the densest *Schoenus* concentrations. Slight hollows among the *Schoenus* have the water table just above the surface and are colonised by *Potamogeton polygonifolius*, *Hammarbya paludosa* and *Sphagnum subsecundum*. Several leafy liverworts occur on the lower parts of the stems of the *Schoenus* and include such species as *Cephalozia* spp. (4), *Cladopodiella fluitans*, *Calypogeia fissa*, *Mylia anomala* and *Odontochisma sphagni*.

c). *Carex rostrata area.*

Carex rostrata swamp with much open water and some *Schoenus* occurs in the lower reaches of the gridded portion of the bog. It probably represents the sites of artificial pools of which the infilling process has not yet quite reached completion.

d). Rhynchospora alba area.

The *Rhynchospora* forming the zone between wet heath and bog was mentioned above. It was especially noted at the base of the knoll and was there about fifteen metres wide, well demarcated on the wet heath side but merging into the bog the other.

e). Eriophorum angustifolium area.

Bordering the Slepe plantation is an area of *Eriophorum angustifolium* rooted in very wet and black peat and excluding nearly all other species except *Drosera intermedia*.

(4) Open water communities.

Several types could be recognised but all intergraded and often one pool had several separate floristic assemblages. Some pools in the general bog especially those to the west of the small "island" have an almost pure community of *Carex limosa*. This species mixed with others such as *Eriophorum*, *Juncus bulbosus*, *Carex rostrata*, *Potamogeton* and *Molinia* are the colonisers of several pools of various sizes. These pools often have many tussocks each of which bears vegetation typical of the *Schoenus* or general bog communities. The shallows of these pools are dominated by *Sphagnum subsecundum* var. *auriculatum* and *Eleocharis quinqueflora*. Most of these pools have a more or less continuous subsurface mat of a bacterial iron scum.

Other pools are seasonal in nature and are generally colonised by *Sphagnum cuspidatum*. These occur on the wet heath zone and consist of mortar holes, old peat cuttings, cart ruts and the disused ditches of the Slepe plantation. Other species occurring in such places are Sphagnum subsecundum, S. plumulosum, Juncus acutiflorus, J. bulbosus, Molinia, Drosera intermedia, Eriophorum and often a lush growth of Polytrichum commune.

The remaining pools, generally the deepest, have no colonisers.

No attempt was made to subdivide the open-water vegetation further for the map.

It should incidentally be noted that although Hartland Moor has relatively little seasonal variation, much Cirsium dissectum was noted in the general bog in the region of grid post D 35 when the area was revisited in May 1958. At the time of the original map the species had flowered and therefore was not so conspicuous as in May, otherwise it would most certainly have been mapped as a separate community.

C. Discussion.

It can be seen that from the subjective divisions that the criteria used are by no means consistent for all the communities. Whereas the major subdivisions depend on a combination of floristic composition with an arbitary estimation of the wetness of the soil, the minor divisions are based more specifically on presence or lack of a single dominant species. Some examination is now needed as to whether these vegetation units bear any relation to other available habitat factors not specifically used in the original delimitations.

Calluna areas.

This occurs where there is a 10 cm. maximum of peat and often no peat at all. The pH. ranges from 3.5 to 4.1

Erica ciliaris areas.

These occur where there are less than 20 cm. of peat but never where peat is absent.

Agrostis setacea areas.

These occur where peat is absent.

General wet heath.

This community was found on up to 20 cm. of peat but some facies can occur where there is very little humus on or in the soil. The pH. of the peat and the soil water in the wet heath areas varies from 3.3 to 4.7

Carex panicea area.

This community is found where there is a maximum of 40 cm. of peat.

General bog.

This community was developed where there is peat between 20 and 80 cm. in depth and the pH. is below 4.8 and where Schoenus nigricans or Carex rostrata is not dominant.

Schoenus nigricans area.

This community occupies a similar habitat to the general bog except that it can occur on peat up to 120 cm. in depth and therefore tends to occupy the deepest parts of the basin where there is assumed to be more water flow.

Carex rostrata area.

This is developed in all places where there is over 80 cm. of peat and the pH. is fairly high - the highest value for Hartland

Moor 5.1 was recorded from the *Carex rostrata* area. Its position on Hartland at the outlet of the basin suggests that it has a fairly high mineral requirement as at this position the mineral supply is presumed to be the highest in the area.

Rhynchospora alba area.

This is found where there are 40 cm. or under of peat.

Eriophorum angustifolium area.

This is found where there are 40 cm. of peat.

Open-water vegetation.

The pools bear no apparent relation to the subsurface contours.

It can be seen that the larger divisions do bear some relationship with the detailed habitat factors but the smaller divisions are based either solely on the habitat factors noted in their subjective recognition or on factors which were not noted in this investigation.

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IV. Phytosociological Classification of the Vegetation.

A. Introduction.

Whereas subjective methods use an integration of floristic and habitat data, phytosociological methods use only floristic data which is necessarily of a much more detailed nature than that required for a subjective survey.

Of the various schools of phytosociological thought, there are only two that are apparently well documented, the *Zurich-Montpellier* school (Braun-Blanquet, 1928, 1951; Poore 1955 etc.) and the *Uppsala* school (Du. Rietz, 1921 etc., Dahl, 1956). Controversy has existed for many years over the relative merits of these two schools. The basic concept of the Zurich-Montpellier school is that plant communities can be classified according to the presence or absence in them of small groups of characteristic species much more common in one particular community than in any other. The Uppsala school in contrast, uses the dual criteria of constancy and dominance of individual species as a basis for vegetation units.

Both schools take into account abundance as well as other criteria but in order to bring the present investigation into line with later methods only presence and absence data were collected, i.e. giving frequency only, using quadrats placed systematically at the grid points. The Uppsala method could not be used as no suitable data was available but the Zurich-Montpellier method requiring frequency and abundance, of which the former was available, could be used after suitable modification.

B. The principles of the Zurich-Montpellier school.

The degree to which a species is characteristic was recognised by Braun-Blanquet as a variable property which he termed "fidelity". Originally, no quantitative expression of the fidelity of a species to a particular community was attempted and verbal definitions only were used. The five grades were as follows, (Goodall, 1953 b.) :-

1. Strange (fremde) : species that are rare and accidental intruders from another plant community or relics of a preceding community.

2. Indifferent (vage) : species without pronounced affinities for any community.

3. Preferential (holde) : species present in several communities more or less abundantly but predominantly or with better vitality in one certain community.

4. Selective (feste) : species found most frequently in a certain community but also, though rarely, in other communities.

5. Exclusive (treue) : species completely or almost completely confined to one community.

This method inevitably gave cause for disagreement in allotting a grade of fidelity to a particular species in a particular community. Later, a more precise meaning was given to these five grades of fidelity by Szafer et al. (1926), quoted by Braun-Blanquet (1928) with slight modification. Table 2 shows this scheme.

Many objections have been put forward against the use of fidelity as a criterion for the classification and distinction of plant communities. Perhaps the commonest criticism is that, as fidelity depends on presence and abundance and this latter depends on cover and density (and also this is based on verbal descriptions rather than quantitative definitions), it is a highly composite factor. An index such as this does not lend itself to exact treatment and is therefore bound to be largely arbitary (Goodall 1953b). It therefore seems preferable to base it upon one type of measurement only and it should then reflect the continuous variation in the feature it measures and be capable of fairly exact treatment. It is preferred

TABLE 2.

Scheme for the determination of the fidelity of the species to a given association.

Each species in each community is given a degree of presence number (P) and an index of abundance (A) according to the following grades.

The degree of presence.

1. Species in 1-20% of the stands (Rare)
2. Species in 21-40% of the stands (Seldom present)
3. Species in 41-60% of the stands (Often present)
4. Species in 61-80% of the stands (Mostly present)
5. Species in 81-100% of the stands (Constantly present)

The index of abundance.

x. Sparsely or very sparsely present, cover very small.
1. Plentiful but of small cover value.
2. Very numerous or covering at least 5% of the area.
3. Any number of individuals covering 25-50% of the area.
4. Any number of individuals covering 50-75% of the area.
5. Covering more than 75% of the area.

Relationship of species with approximately same vitality and abundance.

In given association	In other associations.
Fidelity 5 :	
-	P 1 : A to 1.
P 4-5 : A 3-5	P 1-2 : A to 1.
P 4-5 : A x-2	P 1 : A x-2
P 1-3 : A any degree	lacking or very rare.

Table 2. contd.

Fidelity 4 :	P 2-3 : A x-2
-	P 3-4 : A x-1 (as association relicts or pioneers)
P 4-5 : A x-2	P 2-3 : A x-1 (2)
P 3-4 : A x-2	P 1-2 (3) : A x-1 (2)
P 1-3 : A x-2	P trifling : A v. trifling.
Fidelity 3 :	
P anything : A 3-5	P x-3 : A x-2
P anything : A anything	P and A trifling or rather trifling : or A trifling and vitality reduced.
Fidelity 2 :	
P, A and vitality in two or more associations approximately equal.	P, A and vitality in two or more associations approximately equal.
Fidelity 1 :	
P 1 : A x-1 vitality reduced.	P 1 : A x-1 vitality reduced.
Species occurring only on the outskirts or on disturbed parts of the stand.	P 1 : A x-1 vitality reduced.

to use only frequency in this investigation.

Apart from the shifting emphasis on the relative importance of presence and abundance in the assessment of the fidelity grades and the asymmetry of the grading scheme, the use of fidelity is suspect in that its determination too easily involves a hidden circular argument: the original choice and grouping of sample plots is itself based on the concept of fidelity, the community being selected on species that have a narrow ecological amplitude and the association itself based on the species showing fidelity towards it.

C. <u>Modification of the method for use in this investigation.</u>

Modification of the Zurich-Montpellier method was necessary because :-

1. Since abundance data were not available, a scheme for determination of fidelity from frequency data only was necessary. By restriction to a single criterion, moreover, the shifting emphasis between presence and abundance was obviated.

2. The circular argument that was alleged to be used in the selection of sample plots was obviated by using a regular grid for collecting the data and by using the originally subjectively assessed communities, based on criteria other than fidelity, as the starting point for the primary extraction of faithful species.

3. The gradings of fidelity were adjusted to form a symmetrical scheme with equal numbers of grades above and below the neutral point.

The following method was finally evolved :-

1. Each vegetational unit recognised subjectively was originally taken as representing an "association" of the phytosociologists.

2. Each quadrat was taken as representing a "stand", and the species list from a quadrat represented the species list from a stand.

Small communities were excluded in line with Braun-Blanquet (1936) who ignores small facies. Since the association-analysis method to be used later does not deal with communities of less than eight quadrats, communities with this number or fewer were disregarded here as well. Moreover to enable comparison to be made with the results from the association-analysis the actual number of species to be considered was reduced. The maximum number of species that can be used by the electronic computer is 76. Ninety-two species of lichens, bryophytes, pteridophytes and spermaphytes were found in the quadrats but by omission of the sixteen which were found in one quadrat only the required number of seventy-six species was left.

3. The scheme for the determination of fidelities was formulated and is given as table 3. Each species was given the appropriate index of fidelity.

The species with fidelities of 3, 4 and 5 were taken as being the characteristic species of their associations.

4. An association, having been characterised, was then examined to see if any of its constituent quadrats were alien or more like those of another association in terms of characteristic species, resulting in some reshuffling of the quadrats of the original communities.

Braun-Blanquet used visual comparison of written species lists from the stands. In this investigation the species lists from the quadrats were transferred to edge-punched cards (see Appendix 2);

TABLE 3.

Presence in given assn.	Presence in other assns.	Index of Fidelity in given assn.	Index of Fidelity in other assns.
4-5	1-2	5	0
1-3	Rare	5	0
4-5	2-4	4	0
3-4	1-3	4	0
1-3	Rare	4	0
1-5	1-3	3	0
2-5	2-5	2	2 if equal <u>or</u> 0 if less.
1	1	1	1 <u>or</u> 0
Less than others	More than in given	0	1-5

these enabled comparison and subsequent sorting to be carried out more quickly, more accurately and more objectively.

As the original subjective groupings were not based on fidelity an association may have no characteristic species. In such cases their constituent quadrats were reallocated to those communities of which they had the greatest proportion of characteristic species.

5. Any stands which appeared equally representative of two or more associations were provisionally labelled as transitional. Braun-Blanquet (1936) states that transitionals should be ignored but in this investigation they were noted and mapped.

6. All the stands remaining unassigned after the above processes, i.e. those quadrats with very few or no characteristic species of any association were examined individually and placed in that association which they most resemble floristically (taking into account all species and not only the characteristic ones).

7. A characterisation of these revised associations was then made using the fidelity scheme as previously. The transitionals were included in this final characterisation to see whether any of them were associations in their own right. A final map was then produced showing all associations and the true transitionals.

8. A new system of nomenclature of the associations was devised. The name of an association should indicate the most frequent species that has been selected as important in the delimitation of that community. The associations were named on that species which had the

highest fidelity in that association. In the case of more than one species with the same fidelity value, presence was used as a secondary criteria.

D. Results of the application of the revised method.

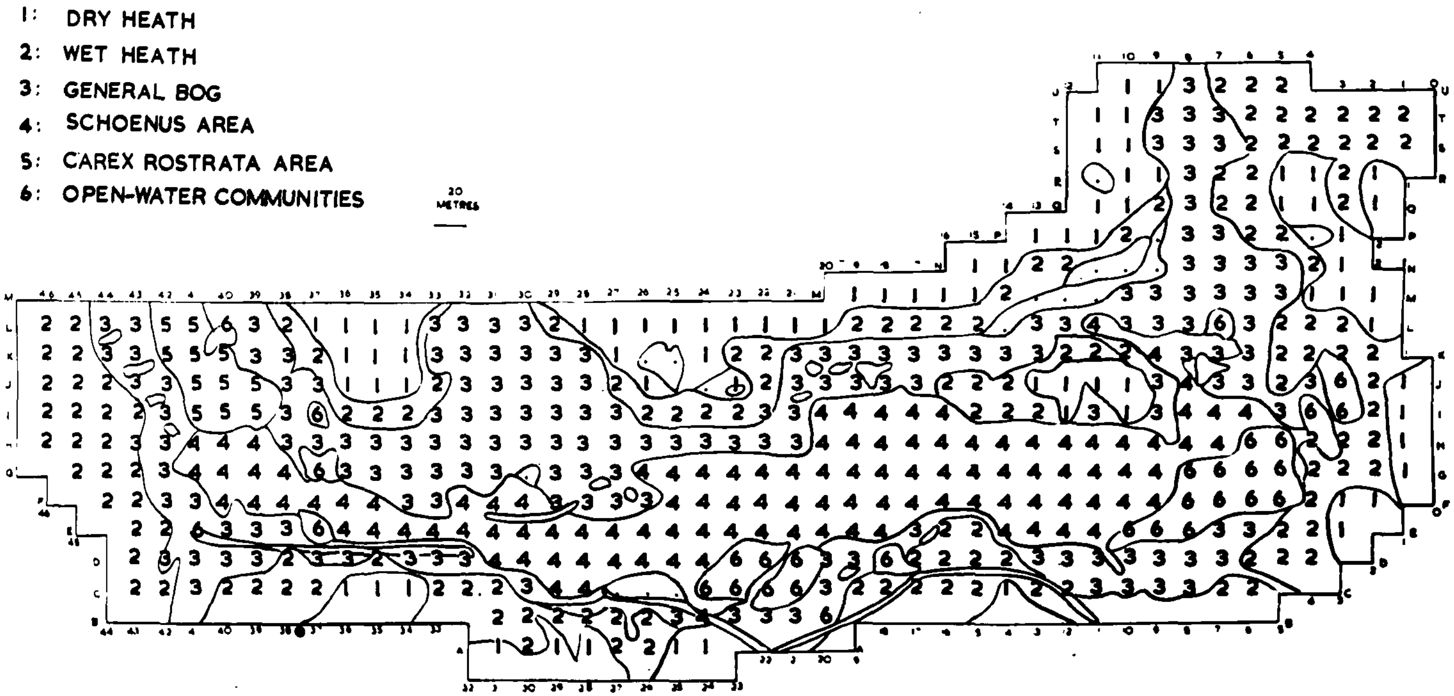
(1) Map 7 shows the quadrats of the six subjective communities that were considered in the allocation of fidelity numbers. These communities comprised the following numbers of quadrats.

1.	Dry heath	81 quadrats
2.	Wet heath	125 "
3.	General bog	159 "
4.	*Schoenus nigricans* area	118 "
5.	*Carex rostrata* area	11 "
6.	Open water vegetation	32 "

The following were omitted because they contained less than eight quadrats :-

Rhynchospora alba area	7 quadrats
Erica ciliaris area	4 "
Eriophorum angustifolium area	3 "
Carex panicea area	2 "
Agrostis setacea area	2 "

(2) The number of quadrat occurrences of each species in each of the six associations was counted and this number expressed as a percentage of the total number of quadrats in that association. A presence number could then be given to each species in each association. Using the modified fidelity scheme the characteristic



Map 7. Quadrats used for phytosociological characterisation. Boundaries as in map 6.

species of each association were found. (see table 4).

Dry heath

	Fidelity
Pteridium aquilinum	5
Ulex minor	5
Cladonia strepsilis	4
Campylopus brevipilus	4
Polytrichum commune	4
Erica cinerea	4
Cladonia coccifera	3
Calluna vulgaris	3

Wet heath

	Fidelity
Sphagnum compactum	4
Sphagnum tenellum	4
Polygala serypyllifolia	4
Drosera intermedia	4
Scirpus caespitosus	4
Erica ciliaris	4

General bog

No characteristic species were found.

Schoenus nigricans area

	Fidelity
Utricularia intermedia	5
Cirsium dissectum	5
Hypericum elodes	5
Dactylorchis incarnata subsp. incarnata	5
Sphagnum papillosum	4

TABLE 4.

Phytosociological characterisation of species.

Species arranged in order of decreasing frequency over the whole area.

For each species in each community is written.

- $^{N}/_{x}$: Number of quadrat occurrences (where x is number of quadrats in the community)
- % : Percentage frequency
- P : Presence number
- F : Index of Fidelity

TABLE 4.

Spp. Nos.	Species	Total Area		I Dry heath				II Wet heath				III General Bog				IV Schoenus area				V Carex rostrata				VI Open Water				Rhyn. alba		Erica ciliaris		Erioph. ang.		Carex panicea		Agrostis setacea	
		N 544	%	N 81	%	P	F	N 125	%	P	F	N 159	%	P	F	N 118	%	P	F	N 11	%	P	F	N 32	%	P	F	N 7	%	N 4	%	N 3	%	N 2	%	N 2	%
59	Molinia caerulea	506	93	57	70	4	2	122	98	5	2	156	98	5	2	115	97	5	2	11	100	5	2	28	88	5	2	7	100	4	100	3	100	2	100	1	50
49	Erica tetralix	414	76	50	61	4	2	111	89	5	2	131	82	5	2	81	69	4	2	11	100	5	2	18	56	3	2	6	85	2	50	1	33	2	100	1	50
51	Eriophorum angustifolium	392	72	17	21	2	0	85	68	4	2	136	86	5	2	101	86	5	2	9	82	5	2	13	94	5	2	7	100	4	100	3	100	2	100	1	50
50	Erica x watsonii	340	63	19	23	2	0	81	65	4	0	118	74	4	0	86	73	4	0	10	91	5	4	16	50	3	0	3	43	3	75	2	67	1	50	1	50
61	Narthecium ossifragum	334	61	7	9	1	0	66	52	3	0	126	79	4	0	97	82	5	2	11	100	5	2	17	53	3	0	5	71	1	25	3	100	1	50	-	-
38	Calluna vulgaris	309	57	77	95	5	3	100	80	4	0	80	50	3	0	27	23	2	0	1	9	1	0	14	44	3	0	4	57	3	75	-	-	1	50	2	100
45	Drosera rotundifolia	307	56	19	23	2	0	73	58	3	2	105	66	4	2	73	62	4	2	7	64	4	2	20	63	4	2	5	71	2	50	3	100	-	-	-	-
47	Erica ciliaris	291	53	35	43	3	0	78	62	4	3	92	57	3	0	61	52	3	0	4	34	2	0	9	28	2	0	6	85	2	50	2	67	1	50	1	50
68	Rhynchospora alba	262	48	9	11	1	0	44	39	2	0	91	57	3	0	81	69	4	3	5	45	3	0	18	56	3	0	5	71	1	25	3	100	-	-	-	-
29	Sphagnum papillosum	242	44	3	4	1	0	19	15	1	0	88	55	3	0	95	81	5	4	8	73	4	0	21	66	4	0	4	57	1	25	3	100	-	-	-	-
16	Lepidozia setacea	223	41	11	14	1	0	37	30	2	0	83	52	3	2	66	56	3	2	6	55	3	2	10	31	2	0	7	100	1	25	2	67	-	-	-	-
31	Sphagnum pulchrum	214	39	1	1	1	0	22	18	1	0	77	48	3	0	82	69	4	2	5	45	3	0	20	63	4	2	4	57	-	-	3	100	-	-	-	-
22	Campylopus brevipilus	147	27	58	72	4	4	57	46	3	0	22	14	1	0	1	1	1	0	-	-	-	-	1	3	1	0	3	43	3	75	-	-	2	100	-	-
18	Odontochisma sphagni	141	26	5	6	1	0	21	17	1	0	60	38	2	2	41	35	2	2	1	9	1	0	6	19	1	0	5	71	1	25	1	33	-	-	-	-
71	Schoenus nigricans	134	25	-	-	-	-	3	2	1	0	25	16	1	0	84	71	4	2	7	64	4	2	13	41	3	0	1	14	-	-	1	33	-	-	-	-
65	Potentilla erecta	118	22	8	10	1	0	46	47	2	2	48	30	2	2	9	8	1	0	-	-	-	-	2	4	1	0	2	29	-	-	2	67	-	-	1	50
66	Polygàla serpyllifolia	117	22	22	27	2	0	53	42	3	4	35	22	2	0	4	3	1	0	-	-	-	-	1	3	1	0	1	14	1	25	-	-	-	-	-	-
2	Cladonia strepsilis	112	19	49	60	3	4	55	44	3	0	2	1	1	0	-	-	-	-	1	9	1	0	1	3	1	0	-	-	1	25	-	-	2	100	1	50
32	Sphagnum subsecundum var. auriculatum	110	20	1	1	1	0	8	6	1	0	35	22	2	0	47	39	2	0	1	9	1	0	14	44	3	4	1	14	-	-	3	100	-	-	-	-
26	Sphagnum compactum	107	20	14	17	1	0	54	43	3	4	29	18	1	0	2	2	1	0	1	9	1	0	2	4	1	0	3	43	1	25	-	-	-	-	1	50
74	Ulex minor	100	18	58	70	4	5	28	23	2	0	13	8	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	25	-	-	-	-	-	-
41	Carex panicea	97	18	6	7	1	0	35	28	2	0	32	19	1	0	9	8	1	0	5	45	3	4	2	6	1	0	5	71	-	-	1	33	2	100	-	-
33	Sphagnum tenellum	96	18	10	12	1	0	49	39	2	4	31	19	1	0	3	3	1	0	-	-	-	-	2	6	1	0	-	-	1	25	-	-	-	-	-	-
12	Cephalozia macrostachya	82	15	5	6	1	0	9	7	1	0	32	19	1	0	27	23	2	2	3	27	2	2	3	9	1	0	2	29	-	-	1	33	-	-	-	-
9	Cephalozia bicuspidata	81	15	4	5	1	0	12	10	1	0	35	22	2	0	17	14	1	0	6	55	3	4	5	16	1	0	-	-	-	-	2	67	-	-	-	-
25	Polytrichum commune	73	13	33	41	3	4	20	16	1	0	14	9	1	0	-	-	-	-	1	9	1	0	1	3	1	0	-	-	2	50	-	-	-	-	2	100
72	Scirpus cespitosus	72	13	11	14	1	0	35	28	2	3	19	12	1	0	-	-	-	-	-	-	-	0	2	6	1	0	2	30	1	25	-	-	2	100	-	-
14	Cephaloziella starkei	69	13	2	2	1	0	7	6	1	0	30	18	1	0	17	14	1	0	5	45	3	4	4	13	1	0	2	30	1	25	1	33	-	-	-	-
44	Drosera intermedia	63	12	6	7	1	0	25	20	2	3	21	14	1	0	6	5	1	0	-	-	-	-	2	6	1	0	1	14	1	25	1	33	-	-	-	-
8	Calypogeia fissa	59	11	1	1	1	0	4	3	1	0	25	16	1	0	19	16	1	0	4	36	2	3	3	9	1	0	1	14	-	-	2	67	-	-	-	-
11	Cephalozia fluitans	56	10	2	2	1	0	3	2	1	0	21	14	1	0	19	16	1	0	5	45	3	4	5	16	1	0	-	-	-	-	1	33	-	-	-	-
64	Potamogeton polygonifolius	55	10	-	-	-	-	-	-	-	-	6	4	1	0	39	33	2	3	2	18	1	0	7	22	2	0	-	-	-	-	1	33	-	-	-	-
27	Sphagnum cuspidatum	51	9	1	1	1	0	9	7	1	1	28	18	1	1	7	6	1	0	-	-	-	-	3	9	1	1	3	43	-	-	-	-	-	-	-	-
5	Cladonia sylvatica	49	9	11	14	1	1	19	15	1	1	12	8	1	1	4	3	1	0	-	-	-	-	2	6	1	0	-	-	1	25	-	-	-	-	-	-
54	Juncus acutiflorus	47	9	4	5	1	0	18	14	1	1	16	10	1	1	8	7	1	0	1	9	1	1	1	3	1	0	-	-	-	-	-	-	-	-	-	-
46	Eleocharis quinqueflora	46	8	-	-	-	-	2	2	1	0	8	5	1	0	23	19	1	0	3	27	2	2	10	37	2	2	-	-	-	-	-	-	-	-	-	-
3	Cladonia impexa	44	8	10	12	1	1	18	14	1	1	11	8	1	0	2	2	1	0	-	-	-	-	2	4	1	0	1	14	-	-	-	-	-	-	-	-
15	Gymnocolea inflata	42	8	4	5	1	0	14	11	1	1	16	10	1	1	3	3	1	0	-	-	-	-	3	9	1	0	1	14	-	-	-	-	-	-	1	50
36	Agrostis setacea	42	8	19	23	2	2	13	10	1	0	6	4	1	0	-	-	-	-	-	-	-	-	1	3	1	0	-	-	2	50	-	-	-	-	1	50
48	Erica cinerea	42	8	30	37	2	4	7	6	1	0	2	1	1	0	2	2	1	0	-	-	-	-	-	-	-	-	-	-	1	25	-	-	-	-	-	-
10	Cephalozia connivens	30	5	2	2	1	0	5	4	1	0	5	3	1	0	12	11	1	1	1	9	1	1	3	9	1	1	1	14	-	-	1	33	-	-	-	-
23	Hypnum cupressiforme (E)	29	5	-	-	-	-	5	3	1	0	16	10	1	1	4	3	1	0	-	-	-	-	3	9	1	1	1	14	-	-	1	33	-	-	-	-
52	Gentiana pneumonanthe	28	5	5	6	1	0	18	14	1	0	5	3	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	Cladonia coccifera	27	5	19	23	2	3	5	4	1	0	2	1	1	0	-	-	-	-	-	-	-	-	1	3	1	0	-	-	-	-	-	-	-	-	-	-
6	Cladonia uncialis	23	4	9	11	1	1	11	9	1	1	3	2	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42	Carex rostrata	20	4	-	-	-	-	1	1	1	0	5	3	1	0	5	4	1	0	8	73	4	5	1	3	1	0	-	-	-	-	-	-	-	-	-	-
54	Juncus bulbosus	19	3	-	-	-	-	1	1	1	0	6	4	1	0	7	6	1	0	2	18	1	3	3	9	1	0	-	-	-	-	-	-	-	-	-	-
4	Cladonia pyxidata	18	3	10	12	1	1	6	5	1	0	1	1	1	0	-	-	-	-	-	-	-	-	1	3	1	0	-	-	-	-	-	-	-	-	-	-
30	Sphagnum plumulosum	18	3	4	5	1	1	2	2	1	1	6	4	1	1	5	4	1	1	-	-	-	-	1	3	1	1	-	-	-	-	-	-	-	-	-	-
58	Menyanthes trifoliata	17	3	-	-	-	-	1	1	1	1	7	4	1	1	6	5	1	1	-	-	-	-	3	9	1	1	-	-	-	-	-	-	-	-	-	-
21	Aulocamnium palustre	16	3	-	-	-	-	2	2	1	0	5	3	1	0	4	3	1	0	1	9	1	0	4	13	1	1	-	-	-	-	-	-	-	-	-	-
20	Riccardia sinuata	15	3	2	2	1	1	1	1	1	1	8	5	1	1	2	2	1	1	-	-	-	-	2	6	1	1	-	-	-	-	-	-	-	-	-	-
19	Riccardia pingius	15	3	-	-	-	-	-	-	-	-	6	4	1	1	9	8	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	Carex limosa	14	3	-	-	-	-	-	-	-	-	4	3	1	0	6	5	1	0	-	-	-	-	4	13	1	1	-	-	-	-	-	-	-	-	-	-
7	Hypogymnia physodes	14	3	6	7	1	1	4	3	1	1	3	2	1	1	-	-	-	-	-	-	-	-	1	3	1	1	-	-	-	-	-	-	-	-	-	-
24	Leucobryum glaucum	13	2	1	1	1	1	4	3	1	1	6	4	1	1	-	-	-	-	-	-	-	-	2	6	1	1	-	-	-	-	-	-	-	-	-	-
17	Mylia anomala	13	2	1	1	1	1	3	2	1	1	6	4	1	1	-	-	-	-	-	-	-	-	3	9	1	1	-	-	-	-	-	-	-	-	-	-
39	Carex echinata	12	2	1	1	1	1	-	-	-	-	7	4	1	1	4	3	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Cephalozia media	11	2	-	-	-	-	1	1	1	1	5	3	1	1	4	3	1	1	-	-	-	-	1	3	1	1	-	-	-	-	-	-	-	-	-	-
75	Utricularia minor	11	2	2	2	1	1	-	-	-	-	2	1	1	1	6	5	1	1	-	-	-	-	1	3	1	1	-	-	-	-	-	-	-	-	-	-
67	Pedicularis sylvatica	8	1	-	-	-	-	6	5	1	1	-	-	-	-	2	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
73	Ulex europaeus	8	1	3	4	1	1	2	2	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	50
76	Utricularia intermedia	6	1	-	-	-	-	-	-	-	-	-	-	-	-	6	5	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
69	Salix cinerea ssp. atrocinerea	4	1	-	-	-	-	-	-	-	-	1	1	1	1	3	3	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
57	Juncus squarrosus	4	1	1	1	1	1	2	2	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
53	Hypericum elodes	4	1	-	-	-	-	-	-	-	-	-	-	-	-	4	3	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
43	Cirsium dissectum	4	1	-	-	-	-	-	-	-	-	-	-	-	-	4	3	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
37	Betula pendula	4	1	1	1	1	1	2	2	1	1	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34	Pteridium aquilinum	4	1	4	5	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70	Salix repens	3	1	1	1	1	1	2	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
56	Juncus effusus	3	1	-	-	-	-	2	2	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28	Sphagnum molle	3	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
62	Dactylorchis incarnata	2	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	5	-	-	-	-	-	-	-	-	-	-	-	-	1	33	-	-	-	-
60	Myrica gale	2	1	-	-	-	-	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	Pinus sylvestris	2	1	1	1	1	1	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
63	Pinguicula lusitanica	2	1	-	-	-	-	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

<u>Schoenus nigricans area</u> contd.

Rhynchospora alba Potamogeton polygonifolius	Fidelity 3

<u>Carex rostrata area</u>

Carex rostrata	" 5
Cephaloziella starkei Cladopodiella fluitans Cephalozia bicuspidata Erica x watsonii Carex panicea	" 4
Calypogeia fissa Juncus bulbosus	" 3

<u>Open-water vegetation</u>

Sphagnum subsecundum var. auriculatum	" 4

It will be noted that in the original general bog there are no characteristic species. This suggests that general bog is not a true community but an ill-defined assemblage of bog species marked only by subjectively recognised <u>Sphagnum</u> dominance.

The open-water vegetation had only one characteristic species (<u>Sphagnum subsecundum</u> var. <u>auriculatum</u>); this was only to be expected as this grouping of convenience was admittedly a heterogeneous collection of smaller communities.

(3) The quadrats of the general bog together with alien quadrats from the more clearly defined communities were then

reallocated. Similarly since it was thought unwise to base an association on one characteristic species only the quadrats of the open-water vegetation were examined and transferred to the community to which they had most floristic resemblance leaving only those which had no obvious affinities with any other community.

This process resulted in each quadrat being placed in either that association it most closely resembled or it was noted as being transitional. The positions of the quadrats of the associations and provisional transitionals after the re-allocation process are shown in map 8.

(4) Table 5 shows the final characterisations of the revised associations and the provisional transitionals. The lists of characteristic species for each association and the transitional groups are given below.

Community 1. (124 quadrats) Campylopus brevipilus association, basically derived from the original dry heath.

	Fidelity	Presence
Campylopus brevipilus	5	5
Ulex minor	5	4
Polytrichum commune	5	3
Agrostis setacea	5	2
Erica cinerea	5	2
Pteridium aquilinum	5	1
Cladonia strepsilis	4	3
Cladonia coccifera	4	1
Cladonia pyxidata var. chlorophaea	4	1

TABLE 5.

Final phytosociological characterisation of species.

(For key to arrangement of table see table 4)

TABLE 5.

Spp. Nos.	Species	I Dry heath N 124	%	P	F	II Wet heath N 105	%	P	F	III Schoenus N 144	%	P	F	IV Carex rostrata N 86	%	P	F	V Open water N 25	%	P	F	Carex rostrata/ Schoenus N 30	%	P	F	Wet heath/ Schoenus N 11	%	P	F	Wet heath/ Dry heath	Wet heath/ Carex rost.	Dry hth./ Carex rost.	Carex ros./Schns./ Wet heath	Wet hth./Dry hth./Schoenus
59	Molinia caerulea	98	79	4	2	103	98	5	2	143	99	5	2	86	100	5	2	20	80	5	2	29	97	5	2	10	91	5	2	8	4	2	1	2
49	Erica tetralix	76	62	4	2	100	95	5	2	104	73	4	2	83	85	5	2	10	40	3	0	26	87	5	2	8	73	4	2	8	3	1	1	2
51	Eriophorum angustifolium	29	24	2	0	81	77	4	2	128	90	5	2	79	92	5	2	24	96	5	2	28	94	5	2	10	91	5	2	4	5	1	1	2
50	Erica x watsonii	30	25	2	0	76	74	4	2	98	68	4	2	78	91	5	2	13	52	3	0	27	91	5	2	9	82	5	2	3	3	1	1	1
61	Narthecium ossifragum	6	5	1	0	72	69	4	0	126	88	5	2	74	86	5	2	9	36	2	0	30	100	5	2	9	81	5	2	2	3	0	1	1
38	Calluna vulgaris	118	95	5	3	81	77	4	0	41	30	2	0	33	38	2	0	4	16	1	0	11	35	2	0	5	45	3	0	8	4	2	1	1
45	Drosera rotundifolia	19	16	1	0	78	75	4	2	106	74	4	2	56	65	4	0	8	32	2	0	23	80	4	2	6	54	3	0	4	4	1	1	1
47	Erica ciliaris	66	53	3	0	69	66	4	3	70	48	3	0	48	56	3	0	6	24	2	0	13	43	3	0	4	36	2	0	8	3	1	1	2
68	Rhynchospora alba	4	3	1	0	54	51	3	0	115	80	4	0	38	44	3	0	9	36	2	0	30	100	5	4	6	54	3	0	1	3	0	1	1
29	Sphagnum papillosum	2	2	1	0	15	14	1	0	129	90	5	2	59	69	4	0	4	16	1	0	29	97	5	2	3	27	2	0	0	0	0	1	0
16	Lepidozia setacea	9	7	1	0	44	42	3	0	89	62	4	2	48	56	3	2	7	28	2	0	16	51	3	2	3	27	2	0	1	4	1	0	0
31	Sphagnum pulchrum	2	2	1	0	20	19	1	0	115	80	4	4	42	49	3	0	8	32	2	0	21	70	4	0	4	36	2	0	1	0	0	1	0
22	Campylopus brevipilus	103	83	5	5	25	24	2	0	1	1	1	0	4	5	1	0	0	0	0	0	1	3	1	0	1	9	1	0	5	3	2	0	2
18	Odontochisma sphagni	3	2	1	0	23	22	2	0	61	42	3	2	28	33	2	0	3	12	1	0	16	51	3	2	3	27	2	0	1	2	0	1	0
71	Schoenus nigricans	0	0	0	0	0	0	0	0	101	70	4	5	25	29	2	0	0	0	0	0	8	27	2	0	0	0	0	0	0	0	0	0	0
65	Potentilla erecta	16	13	1	0	50	48	3	3	12	8	1	0	24	28	2	0	1	4	1	0	7	23	2	0	3	27	2	0	5	0	1	0	0
66	Polygala serpyllifolia	33	27	2	0	59	56	3	3	5	3	1	0	9	10	1	0	3	12	1	0	2	7	1	0	1	19	1	0	3	1	0	1	0
2	Cladonia strepsilis	76	58	3	4	25	21	2	0	0	0	0	0	6	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	2
32	Sphagnum subsecundum var. auriculatum	1	1	1	0	8	8	1	0	61	42	3	0	18	21	1	0	16	64	4	3	4	13	1	0	1	9	1	0	0	0	1	0	0
26	Sphagnum compactum	14	11	1	0	67	64	4	4	3	2	1	0	3	3	1	0	2	8	1	0	1	3	1	0	5	45	3	0	5	5	1	0	1
74	Ulex minor	88	71	4	5	8	5	1	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
41	Carex panicea	6	5	1	0	38	36	2	2	4	3	1	0	33	38	2	2	0	0	0	0	4	13	1	0	1	10	1	0	2	5	1	1	2
33	Sphagnum tenellum	9	7	1	0	64	61	4	5	5	3	1	0	8	9	1	0	0	0	0	0	2	4	1	0	2	18	1	0	4	2	0	0	1
12	Cephalozia macrostachya	3	2	1	0	10	9	1	0	31	22	2	2	25	28	2	2	0	0	0	0	8	27	2	2	2	18	1	0	1	1	0	0	1
9	Cephalozia bicuspidata	5	4	1	0	9	8	1	0	11	8	1	0	45	52	3	4	3	12	1	0	4	13	1	0	0	0	0	0	0	1	2	0	1
25	Polytrichum commune	56	45	3	5	10	9	1	0	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0
72	Scirpus cespitosus	12	10	1	0	50	48	3	5	1	1	1	0	5	6	1	0	0	0	0	0	2	7	1	0	0	0	0	0	0	1	0	0	1
14	Cephaloziella starkei	9	7	1	0	4	4	1	0	10	8	1	0	33	38	2	3	1	4	1	0	7	23	2	0	0	0	0	0	0	4	1	0	0
44	Drosera intermedia	6	5	1	0	34	32	2	3	10	8	1	0	6	7	1	0	1	4	1	0	1	3	1	0	0	0	0	0	2	2	1	0	0
8	Calypogeia fissa	3	2	1	0	5	5	1	0	17	12	1	0	28	33	2	3	0	0	0	0	6	20	1	0	0	0	0	0	0	0	0	0	0
11	Cephalozia fluitans	2	2	1	0	1	1	1	0	22	16	1	0	24	28	2	3	1	4	1	0	5	17	1	0	0	0	0	0	0	1	0	0	0
64	Potamogeton polygonifolius	0	0	0	0	0	0	0	0	44	31	2	2	4	5	1	0	7	28	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
27	Sphagnum cuspidatum	3	2	1	0	14	13	1	1	14	11	1	0	9	10	1	0	2	8	1	0	5	17	1	1	1	9	1	0	0	2	0	0	1
5	Cladonia sylvatica	14	11	1	1	19	18	1	1	8	6	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	9	1	0	5	1	0	0	0
54	Juncus acutiflorus	7	5	1	0	13	12	1	1	6	4	1	0	14	16	1	1	0	0	0	0	1	3	1	0	1	9	1	0	2	1	1	0	1
46	Eleocharis quinqueflora	0	0	0	0	1	1	1	0	27	19	1	0	5	6	1	0	11	44	3	4	2	6	1	0	0	0	0	0	0	0	0	0	0
3	Cladonia impexa	18	15	1	1	16	15	1	1	6	4	1	0	2	2	1	0	0	0	0	0	1	3	1	0	0	0	0	0	1	0	0	0	0
15	Gymnocolea inflata	4	3	1	0	12	11	1	0	6	4	1	0	5	6	1	0	4	16	1	0	3	10	1	0	3	27	2	3	3	2	0	0	0
36	Agrostis setacea	39	31	2	5	1	1	1	0	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	Erica cinerea	41	33	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
10	Cephalozia connivens	3	2	1	0	2	2	1	0	11	8	1	1	8	9	1	1	2	8	1	1	1	3	1	0	1	9	1	1	1	1	0	0	0
23	Hypnum cupressiforme (€)	2	2	1	0	5	5	1	0	11	8	1	1	8	9	1	1	1	4	1	0	2	6	1	0	0	0	0	0	0	0	0	0	0
52	Gentiana pneumonanthe	4	3	1	0	20	19	1	3	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	Cladonia coccifera	23	19	1	4	2	2	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
6	Cladonia uncialis	11	9	1	1	8	8	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9	1	1	2	0	0	0	0
42	Carex rostrata	0	0	0	0	1	1	1	0	3	2	1	0	15	17	1	3	1	4	1	0	1	4	1	0	0	0	0	0	0	0	0	0	0
55	Juncus bulbosus	0	0	0	0	1	1	1	0	9	6	1	0	5	6	1	0	4	16	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Cladonia pyxidata	16	13	1	4	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	Sphagnum plumulosum	0	0	0	0	3	3	1	0	3	2	1	0	8	9	1	1	0	0	0	0	2	6	1	0	1	9	1	1	0	0	1	0	0
58	Menyanthes trifoliata	0	0	0	0	0	0	0	0	11	8	1	0	2	2	1	0	3	12	1	3	1	3	1	0	0	0	0	0	0	0	0	0	0
21	Aulacomnium palustre	2	2	1	0	1	1	1	0	9	4	1	1	4	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	Riccardia sinuata	1	1	1	0	5	5	1	1	2	1	1	0	6	7	1	1	0	0	0	0	1	3	1	0	0	0	0	0	0	0	0	0	0
19	Riccardia pinguis	0	0	0	0	0	0	0	0	9	6	1	1	4	5	1	1	0	0	0	0	2	6	1	1	0	0	0	0	0	0	0	0	0
40	Carex limosa	0	0	0	0	0	0	0	0	8	6	1	0	1	1	1	0	5	20	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Hypogymnia physodes	8	6	1	3	3	3	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	3	1	0	0	0	0	0	1	0	0	0	0
24	Leucobryum glaucum	3	2	1	0	5	5	1	1	1	1	1	0	4	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	Mylia anomala	2	2	1	0	2	2	1	0	3	2	1	0	4	5	1	1	0	0	0	0	2	6	1	1	0	0	0	0	0	0	0	0	0
39	Carex echinata	0	0	0	0	0	0	0	0	5	3	1	1	7	8	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	Cephalozia media	0	0	0	0	2	2	1	0	6	4	1	1	2	2	1	0	0	0	0	0	0	0	0	0	1	9	1	1	0	0	0	0	0
75	Utricularia minor	2	2	1	0	0	0	0	0	7	4	1	3	1	1	1	0	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	Pedicularis sylvatica	4	3	1	1	2	2	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	Ulex europaeus	6	5	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9	1	0	0	0	0	0	0
76	Utricularia intermedia	0	0	0	0	0	0	0	0	6	4	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	Salix cinerea ssp. atrocinerea	0	0	0	0	3	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9	1	1	0	0	0	0	0
57	Juncus squarrosus	2	2	1	1	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	Hypericum elodes	0	0	0	0	0	0	0	0	4	3	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	Cirsium dissectum	0	0	0	0	0	0	0	0	4	3	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	Betula pendula	2	2	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	Pteridium aquilinum	4	3	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	Salix repens	0	0	0	0	3	3	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	Juncus effusus	0	0	0	0	2	2	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	Sphagnum molle	0	0	0	0	3	3	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62	Dactylorchis incarnata	0	0	0	0	0	0	0	0	2	1	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	Myrica gale	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	Pinus sylvestris	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	Pinguicula lusitanica	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Calluna vulgaris	3	5
Hypogymnia physodes	3	1
Ulex europeaus	3	1

Community 2. (105 quadrats) Sphagnum tenellum association, basically derived from the original wet heath.

	Fidelity	Presence
Sphagnum tenellum	5	4
Scirpus cespitosus	5	3
Salix repens	5	1
Sphagnum molle	5	1
Sphagnum compactum	4	4
Erica ciliaris	3	4
Potentilla erecta	3	3
Polygala serpyyllifolia	3	3
Drosera intermedia	3	2
Gentiana pneumonanthe	3	1

Community 3. (144 quadrats) Schoenus nigricans association, basically derived from the original Schoenus nigricans area.

	Fidelity	Presence
Schoenus nigricans	5	4
Utricularia intermedia	5	1
Hypericum elodes	5	1
Cirsium dissectum	5	1
Dactylorchis incarnata	5	1
Sphagnum pulchrum	4	4
Utricularia minor	3	1

Community 4. (86 quadrats) *Cephalozia bicuspidata* association, basically derived from the original *Carex rostrata* area.

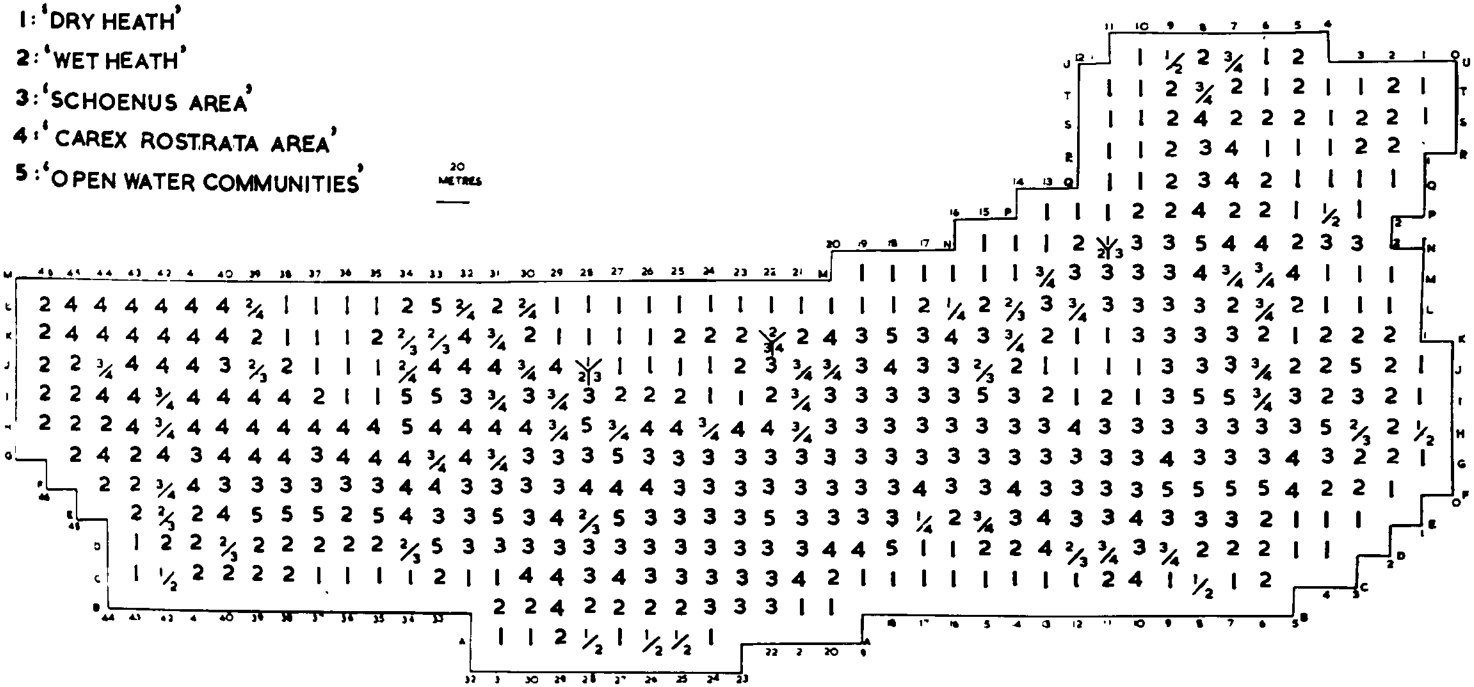
	Fidelity	Presence
Cephalozia bicuspidata	4	3
Cladopiella fluitans	3	2
Cephaloziella starkei	3	2
Calypogeia fissa	3	2
Carex rostrata	3	1

Community 5. (25 quadrats) *Eleocharis quinqueflora* association basically derived from the original open-water vegetation.

	Fidelity	Presence
Eleocharis quinqueflora	4	3
Sphagnum subsecundum var. auriculatum	3	4
Juncus bulbosus	3	1
Menyanthes trifoliata	3	1
Carex limosa	3	1

Community 6. (30 quadrats) *Rhynchospora alba* association, basically derived from the *Schoenus/Carex rostrata* transitionals.

	Fidelity	Presence
Rhynchospora alba	4	5



Map 8. Positions of quadrats after the re-allocation process.
Small figures indicate transitional quadrats.

Community 7. (11 quadrats) Gymnocolea inflata association, basically derived from the original wet heath/ Schoenus transitionals.

	Fidelity	Presence
Gymnocolea inflata	4	5

Map 9 shows the true transitionals and the new associations

Map 10 shows the positions of the stands of the revised associations, the new associations and the true transitionals. Map 11 shows the boundaries of these associations.

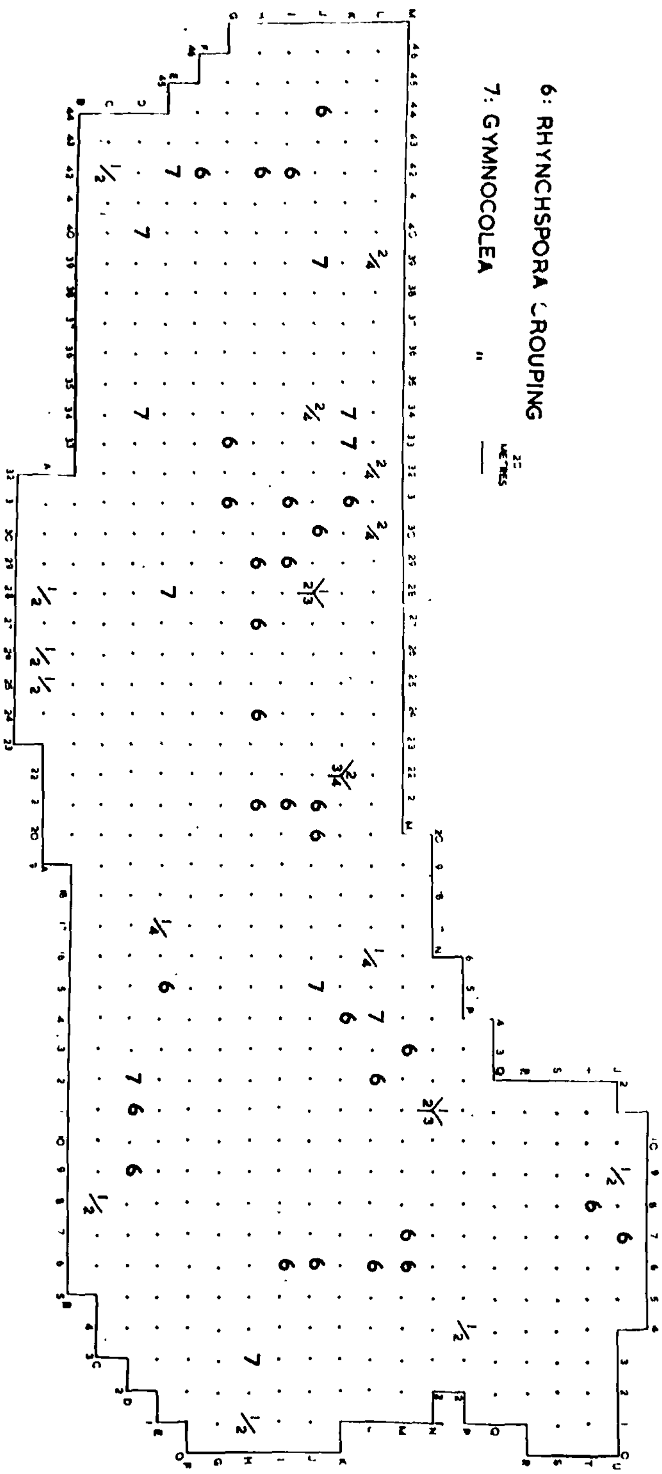
Table 6 compares the number of quadrats and characteristic species in the phytosociological process.

E. Discussion.

A comparison of the final maps (10 and 11) with the subjective maps (5 and 6) together with Table 6, shows that in general the boundaries of most communities do not alter greatly, suggesting that the original subjective assessment is borne out by the more detailed floristic analyses.

In the case of the dry heath the increase in characteristic species is accompanied by an increase in the number of quadrats and suggests an assimilation of closely similar facies from other communities. In the case of the wet heath and open water communities however, where the number of quadrats decreases the better floristic definition is more likely to be due to redistribution of quadrats.

The major point of difference however is that the general bog is no longer a discrete unit but its quadrats have been divided



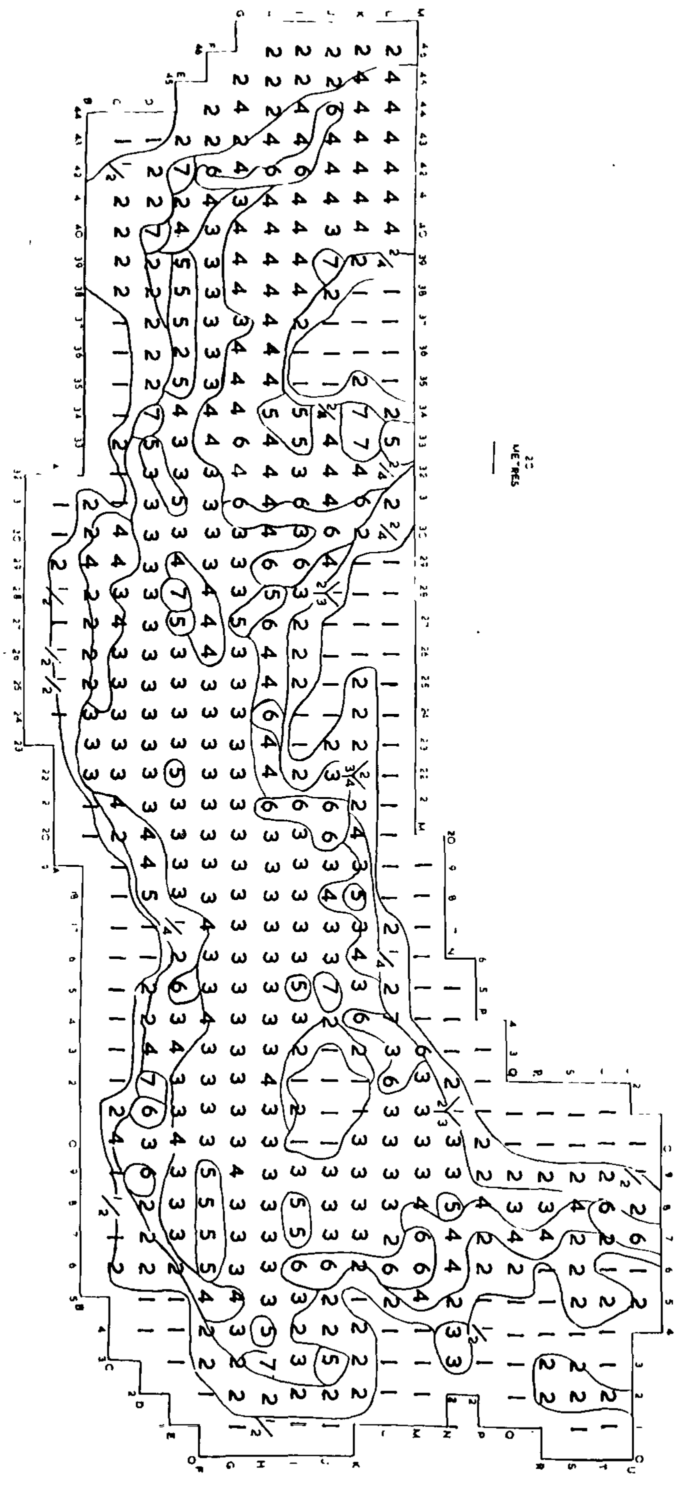
Map 9. Characterisation and re-allocation of transitional quadrats. Small figures indicate "true" transitional quadrats.

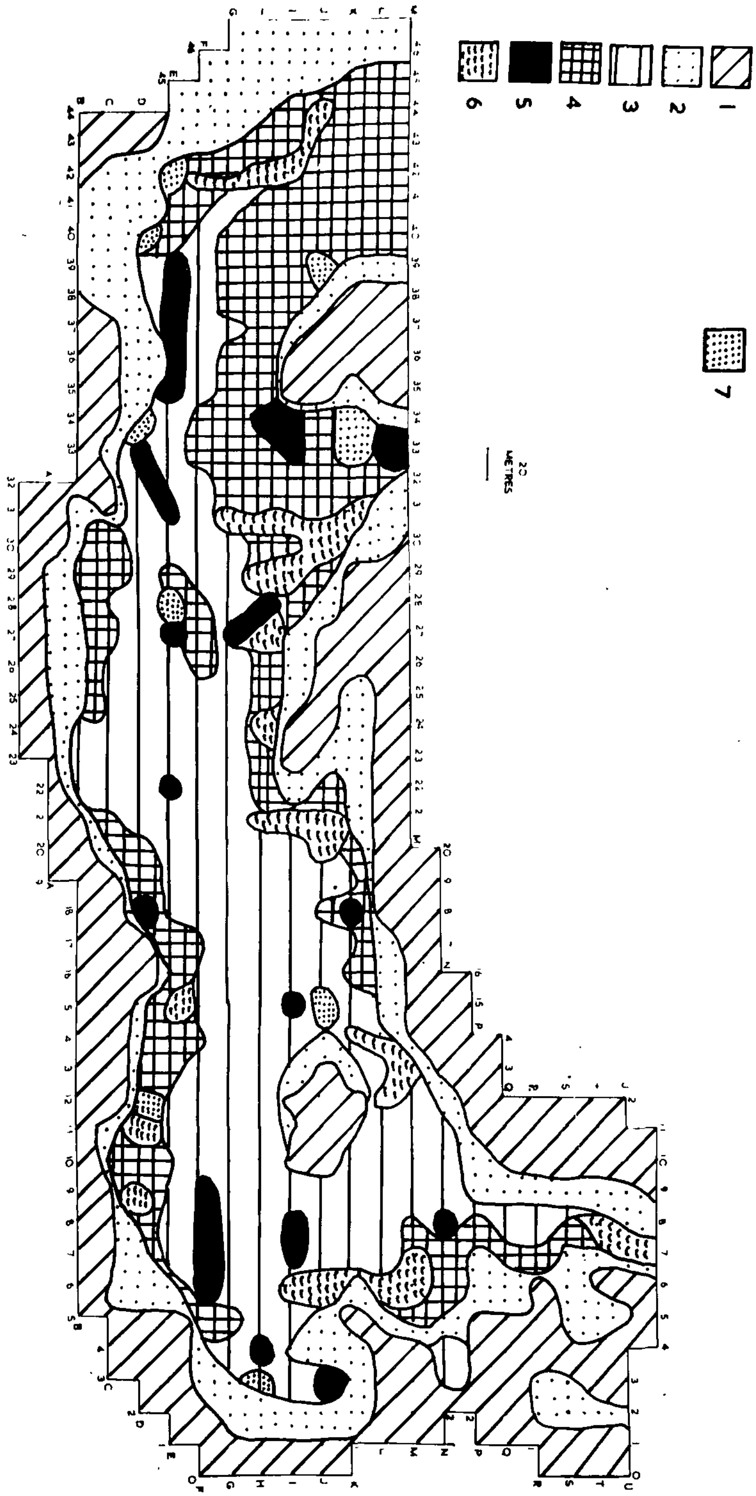
MAP 10.

Final positions of quadrats after the phytosociological processes. Large figures indicate communities as under :

1. Campylopus brevipilus association
2. Sphagnum tenellum association
3. Schoenus nigricans association
4. Cephalozia bicuspidata association
5. Eleocharis quinqueflora association
6. Rhynchospora alba association
7. Gymnocolea inflata association

Small figures indicate "true" transitional quadrats.





Map 11. Final phytosociological communities (generalised form of map 10). Key to communities as for map 10.

TABLE 6.

Original subjective groupings.

Community	No. of quadrats	No. of characteristic spp.
Dry heath	81	8
Wet heath	125	6
Schoenus nigricans area	118	7
General bog	159	0
Carex rostrata area	11	8
Open-water vegetation	32	1
Communities not considered		
Rhynchospora alba area	7	0
Erica ciliaris areas	4	0
Eriophorum angustifolium area	3	0
Carex panicea area	2	0
Agrostis setacea areas	2	0

Phytosociological associations.

Community	No. of quadrats	No. of characteristic spp.
Campylopus brevipilus	124	12
Sphagnum tenellum	105	10
Schoenus nigricans	144	7
Cephalozia bicuspidata	86	5
Eleocharis quinqueflora	25	5
Additional communities		
Gymnocolea inflata	11	1
Rhynchospora alba	30	1
True transitional communities		
Wet heath/Dry heath	8	0
Wet heath/*Carex rostrata*	4	0
Dry heath/*Carex rostata*	2	0
Carex rostrata/*Schoenus*/Wet heath	1	0
Dry heath/Wet heath/*Schoenus*	1	0

between the original Schoenus and the original Carex rostrata communities.

Arising from this is the extension of the original Schoenus community into the present Schoenus association with a change in identity but not in the number of characteristic species, and the much greater increase in the original Carex rostrata community to the present Cephalozia bicuspidata association with a decrease of species. The problem now exists as to whether this latter association in particular is ecologically real or whether the small size of the original sample was responsible for spurious fidelities to give a false basis for the subsequent analysis.

When the area was revisited in March 1959, the boundaries of the Cephalozia bicuspidata association could in fact be recognised: it formed a more closed community than the rest of the original general bog and occupied two definite zones, one continuous with the original Carex rostrata community and running from east to west at the base of the higher ground of the knoll, and the other in the west of the area where the quadrats are grouped.

Although some decrease of the number of characteristic species has taken place with the "dilution" by these extra quadrats, the greater quadrat numbers involved give more confidence in the remaining characteristic species. The enlarged community is no longer confined to the areas of deepest peat but nevertheless has a definite ecological zoning at the lower end of the bog and around the margins of the basin, with the latter occupied by the enlarged Schoenus community.

At first sight the ecological picture is less striking, since the original correlation of the *Carex rostrata* community with areas of deep peat has now been obscured. However the original subjective classification may have merely picked out the preference of a single conspicuous species rather than that of a community as a whole, and the available ecological information is insufficient to show whether the new zoning reflects a better habitat relationship.

The dry heath, wet heath and pools have remained more or less constant and the main fluctuations have occurred in the bog where less zoned habitat conditions occur, as reflected in constant pH. over the area.

The zoning of the whole experimental area is reminiscent of that found in a raised bog: there is a large central bog area with communities usually associated with slightly more mesotrophic conditions downstream and towards the marginal "lagg".

--------oOo--------

V. The application of statistics to the phytosociological classification of the vegetation of Hartland Moor.

A. Introduction.

The previous method of classification involved the estimation of fidelity by means of an arbitrary scoring system. This section shows the result of an attempt to replace this system by a statistical method. The theoretical background has been set out by Williams (unpublished) and is given as Appendix 3. He emphasises that since fidelity is a relative criterion, i.e. the fidelity of a given species to a given group can only be determined in comparison with its occurrence in other groups, it is necessary first to decide which groups are to be compared. The occurrence of a species in a given group can be compared with its occurrence in (a) the complete population, (b) the complete population less the selected group, (c) the next most similar group, or (d) all the other groups taken individually. Statistically the last method is the most satisfactory and is in fact the method used in the Braun-Blanquet system.

Moreover, for any comparison an <u>index</u> of fidelity is required. Williams (<u>l.c.</u>) examines earlier attempts by Cole (1949) and Goodall (1953 a) to produce new indices but shows that these have serious disadvantages and that the conventional indices Q (the coefficient of association) or <u>r</u> (the correlation coefficient) are more acceptable.

However, if a species is present or absent in all quadrats or stands of one but not both of the communities under comparison, the fidelity as measured by Q or similar indices is by definition perfect whatever the proportion in the other community; and this irrespective of the possibility that, if the number of quadrats or stands concerned is small, a zero record may be obtained by mere sampling error. This disadvantage is not possessed by <u>r</u>, which has the additional advantage that its degree of significance can easily by ascertained.

A multiple contingency table can be used to place the species in order of their value for discrimination between groups: those species with the highest index can then be further analysed by calculation of the <u>r</u> values to ascertain their actual affinities for each individual group. On the basis of this the original groups can be redefined in the most economical form possible, i.e. by reference to the smallest number of species.

B. Method.

1. The same quadrat data as used in the previous method, similarly restricted to seventy-six species and six communities, were used in this section.

2. The species were arranged in order of descending frequency and the χ^2 calculated for each species in turn from 2 x 6 contingency tables until a level was reached at which the χ^2 consistently fell below the 0.001 significance level, i.e. in practice only species with an occurrence in over 9% of the quadrats were calculated. (see table 7)

3. χ^2 values were then calculated (by means of 2 x 2 contingency tables - for each pair of communities) for those species with a total of χ^2 (from the 2 x 6 tables) of over the arbitary value of 100. Such species were deemed sufficient to include those necessary for the redefining of the original communities.

Table 8 shows the results for the eleven species.

4. On the basis of the above calculations table 9 was constructed showing for each species the communities with which it was positively, negatively or non-significantly associated.

5. The original groupings were then redefined on the presence or absence of single species using the information in table 9 to arrange the new set of groupings in an hierarchy.

6. Species lists from each of six communities were made, the species being arranged in descending frequency over the whole area.

TABLE 7.

The χ^2 values given by the 2 x 6 contingency tables are as follows arranged in order of discrimination value.

	χ^2	Percentage of total area
Schoenus nigricans	214.98	25%
Ulex minor	189.39	18%
Sphagnum papillosum	176.83	44%
Campylopus brevipilus	174.20	27%
Cladonia strepsilis	170.13	19%
Calluna vulgaris	160.80	57%
Narthecium ossifragum	150.06	61%
Eriophorum angustifolium	138.40	72%
Carex panicea	134.30	18%
Sphagnum pulchrum	131.82	39%
Potamogeton polygonifolius	102.77	10%
Molinia caerulea	79.71	93%
Polytrichum commune	79.58	13%
Rhynchospora alba	78.80	48%
Erica x watsonii	73.93	63%
Sphagnum compactum	73.63	20%
Sphagnum subse/cundum var. auriculatum	73.28	20%
Polygala serpyllifolia	65.44	22%
Sphagnum tenellum	64.39	18%
Lepidozia setacea	61.71	41%

Table 7. contd.

	χ^2	Percentage of total area
Potentilla erecta	51.86	22%
Scirpus cespitosus	46.37	13%
Drosera rotundifolia	44.11	56%
Odontochisma sphagni	41.09	26%
Erica tetralix	38.06	76%
Cladopodiella fluitans	32.72	10%
Calypogeia fissa	30.53	11%
Cephaloziella starkei	30.39	13%
Cephalozia bicuspidata	28.83	15%
Cephalozia macrostachya	24.40	15%
Sphagnum cuspidatum	22.37	9%
Drosera intermedia	17.85	12%
Erica ciliaris	16.83	53%
(Hypogymnia physodes	7.63	3%)

TABLE 8.

χ^2 values for each of the eleven species for each pair of communities, i.e. from 2 x 2 contingency tables. The χ^2 values are omitted if less than 15 : i.e. if P. is below the 0.001 level. (N.B. there is 1 degree of freedom) as preliminary work by Williams and Lambert (unpublished) showed that major vegetational divisions are made at about this level.

Schoenus nigricans

	I.	II	III	IV	V
II					
III					
IV	99.78	124.96	87.3		
V	55.7	55.65	15.45	2.76	
VI	37.18	40.67			

Ulex minor

	I.	II	III	IV	V
II	47.92				
III	97.34				
IV	113.53	27.48			
V	19.43				
VI	43.86				

Sphagnum papillosum

	I	II	III	IV	V
II					
III	60.79	48.03			
IV	113.35	103.95	19.13		
V	43.83	21.03			
VI	52.58	34.12			

Campylopus brevipilus

	I	II	III	IV	V
II					
III	80.59	35.16			
IV		66.90			
V	21.31				
VI	43.11	19.73			

Cladonia strepsilis

	I	II	III	IV	V
II					
III	97.52	70.23			
IV	82.23	59.43			
V					
VI	25.09	15.79			

Calluna vulgaris

	I	II	III	IV	V
II					
III	47.49	26.57			
IV	100.30	79.38	21.50		
V	55.48	26.59			
VI	38.52	16.83			

Narthecium ossifragum

	I	II	III	IV	V
II	41.89				
III	108.27	22.35			
IV	104.17	23.76			
V	51.36	91.70			
VI	27.13				

Eriophorum angustifolium

	I	II	III	IV	V
II	43.46				
III	96.76				
IV	83.06				
V	17.68				
VI	49.99				

Carex panicea

	I	II	III	IV	V
II					
III					
IV		16.90			
V					
VI					

Sphagnum pulchrum

	I	II	III	IV	V
II					
III	54.48	29.29			
IV	92.04	70.05			
V	31.06				
VI	56.90	26.21			

<u>Potamogeton polygonifolius</u>

	I	II	III	IV	V
II					
III					
IV	33.29	49.21	42.05		
V	15.05	23.07			
VI	18.89	28.62			

TABLE 9.

Species	I	II	III	IV	V	VI
Schoenus nigricans (215)	-	-		+	+	
Ulex minor (189)	+		-	-	-	-
Sphagnum papillosum (177)	-	-		+	+	+
Campylopus brevipilus (174)	+		-			-
Cladonia strepsilis (170)	+	+	-	-		-
Calluna vulgaris (161)	+	+		-	-	-
Narthecium ossifragum (150)	-			+	+	+
Eriophorum angustifolium (138)	-	+	+	+	+	+
Carex panicea (134)	-			-	+	-
Sphagnum pulchrum (131)	-	-		+		+
Potamogeton polygonifolius (103)	-	-	-	+		

Number (e.g. IV) refers to community nos. (1-6) of map 7.

Number e.g. (134) under species name : χ^2 value from 2 x 6 table

- : species negatively associated with community

+ : species positively associated with community

No sign : species "neutral" towards community

C. Results.

The hierarchy is shown as Fig. 1. and the new groupings produced and their quadrats are illustrated by means of maps 14 and 15, and the floristic lists on table 10.

The quadrats are mapped also at the three community level (χ^2 of 180) see maps 12 and 13, as this gives an easier comparison with the broad categories of the subjective assessments.

D. Discussion.

1. χ^2 minimum of 180.

The first division of the hierarchy on *Schoenus* appears reasonable as it separates off the vegetation of the wettest facies of the bog which corresponds more or less with the original *Schoenus* area.

The - *Schoenus* area divides on *Ulex minor* which separates the driest facies of the dry heath as discontinuous patches around the periphery of the area.

At this level of the hierarchy the original general bog and the original wet heath are still undifferentiated being together represented by the - *Schoenus* and - *Ulex minor* community, whereas the *Schoenus* boundary assumes prime importance.

2. χ^2 minimum of 120.

The next division of the hierarchy is on *Sphagnum papillosum* which gives a discontinuous zone of quadrats around the periphery of the *Schoenus* area and corresponds with the wetter facies of the general bog. This can be explained by the fact that this association is derived from the original open water vegetation by

FIGURE 1.

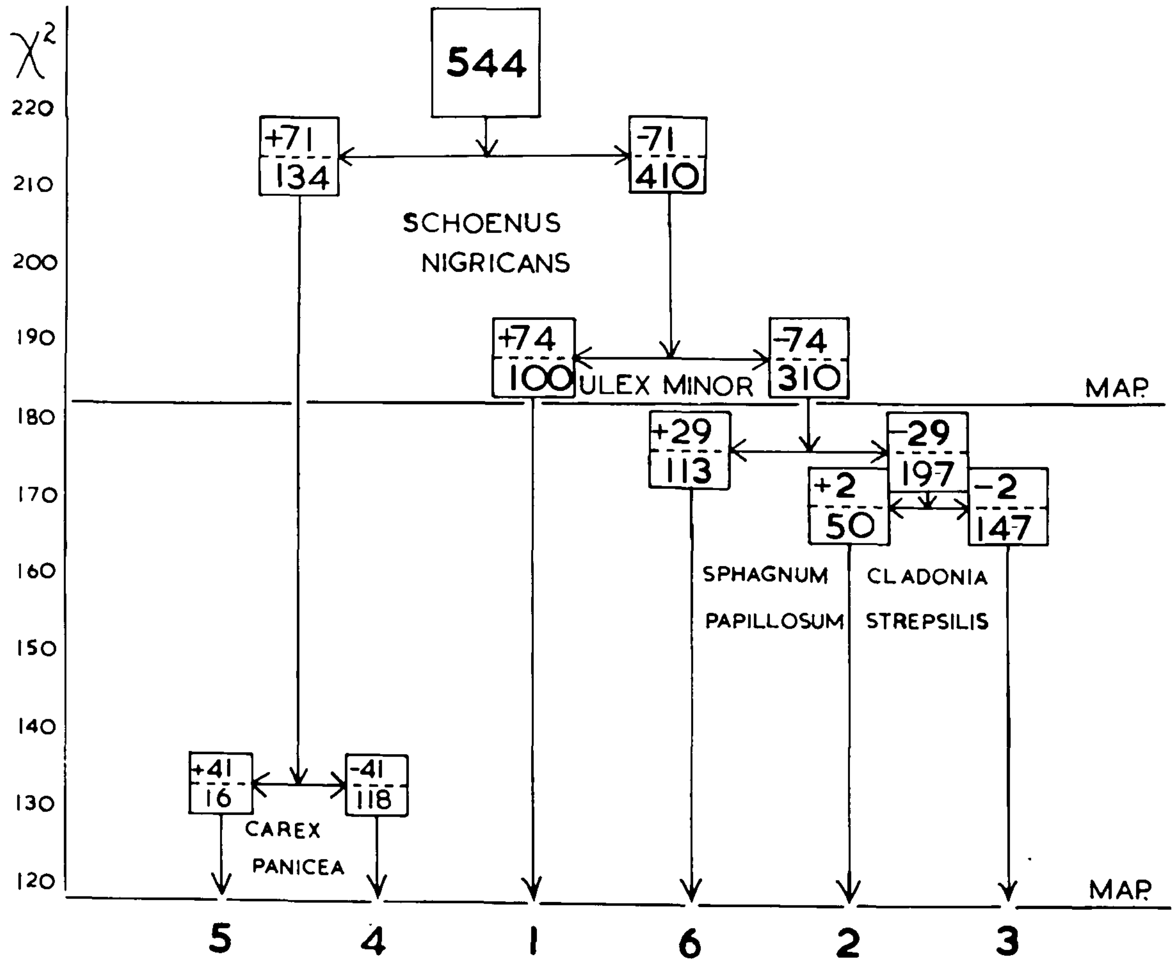
Hierarchial arrangement of communities after the statistical phytosociological procedures.

THE HIERARCHY

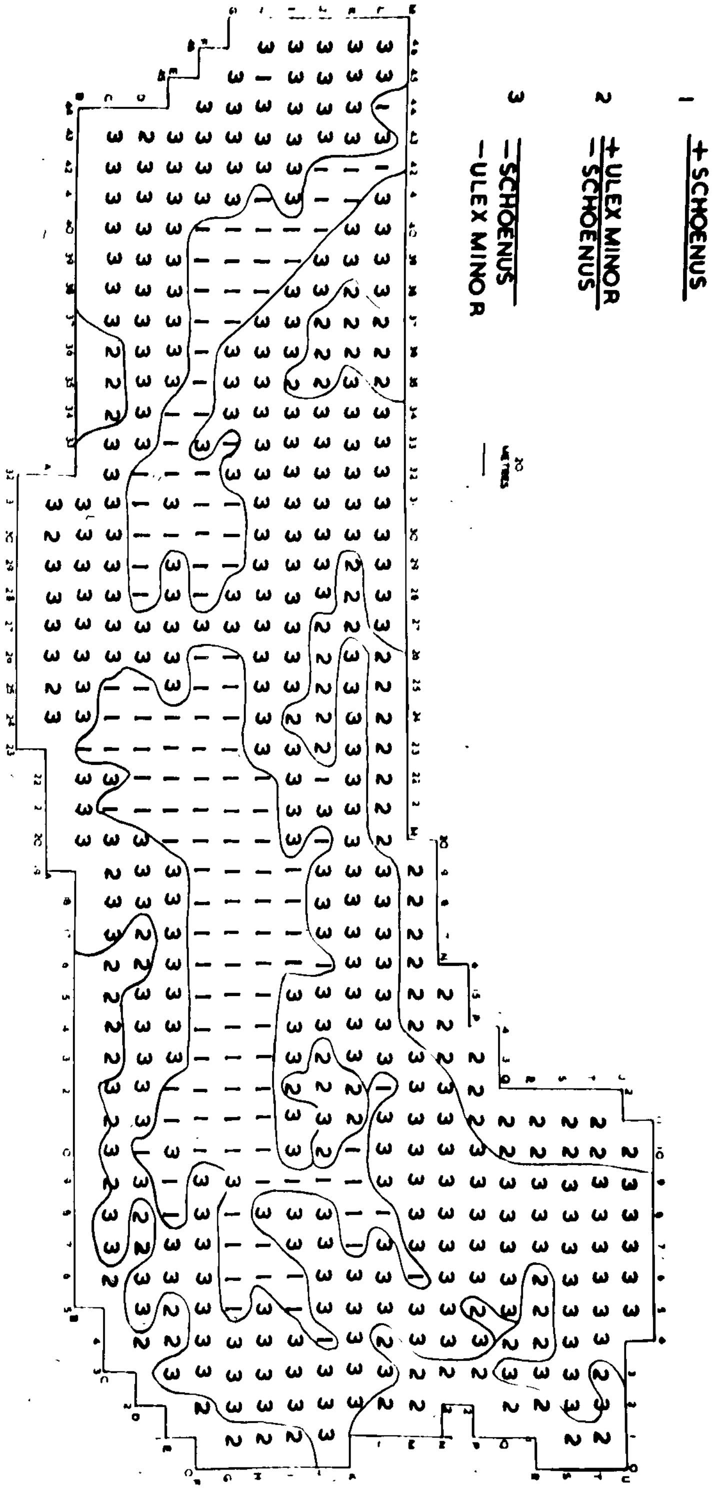
The upper number in each square indicates the serial number of the species on which the preceding division has been made

The lower number in each square indicates the number of quadrats in each subdivision

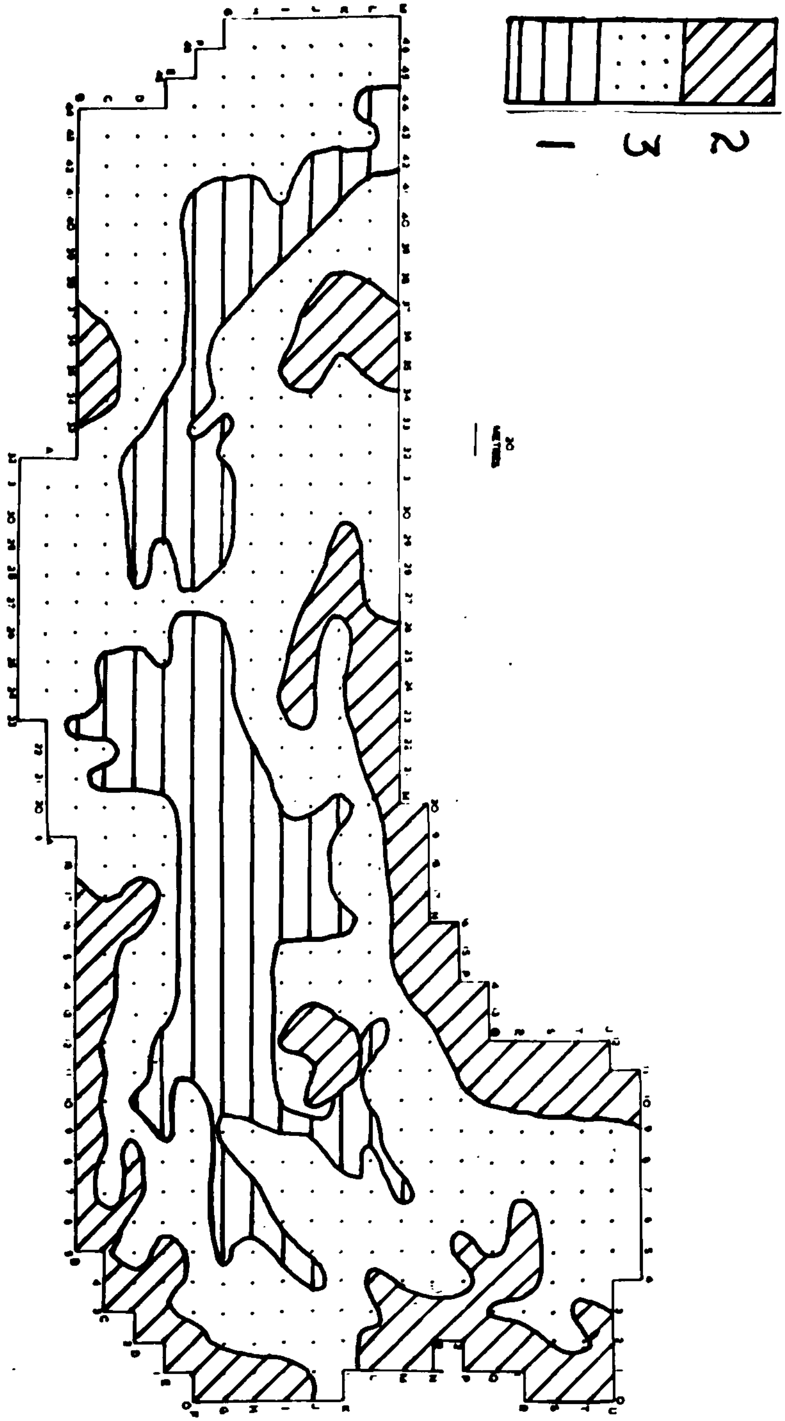
The horizontal lines indicate the value of the highest single χ^2 (with Yates's correction) encountered in the class which has been divided.



χ^2
220
210
200
190
180
170
160
150
140
130
120
544
+71
134
-71
410
SCHOENUS
NIGRICANS
+74
100
-74
310
ULEX MINOR
MAP
+29
113
-29
197
+2
50
-2
147
SPHAGNUM
PAPILLOSUM
CLADONIA
STREPSILIS
+41
16
-41
118
CAREX
PANICEA
MAP
5
4
1
6
2
3



Map 12. Quadrats of the communities present at a minimum χ^2 of 180.



Map 13. Communities present at a minimum χ^2 of 180 (generalised form of map 12). Key as for map 12.

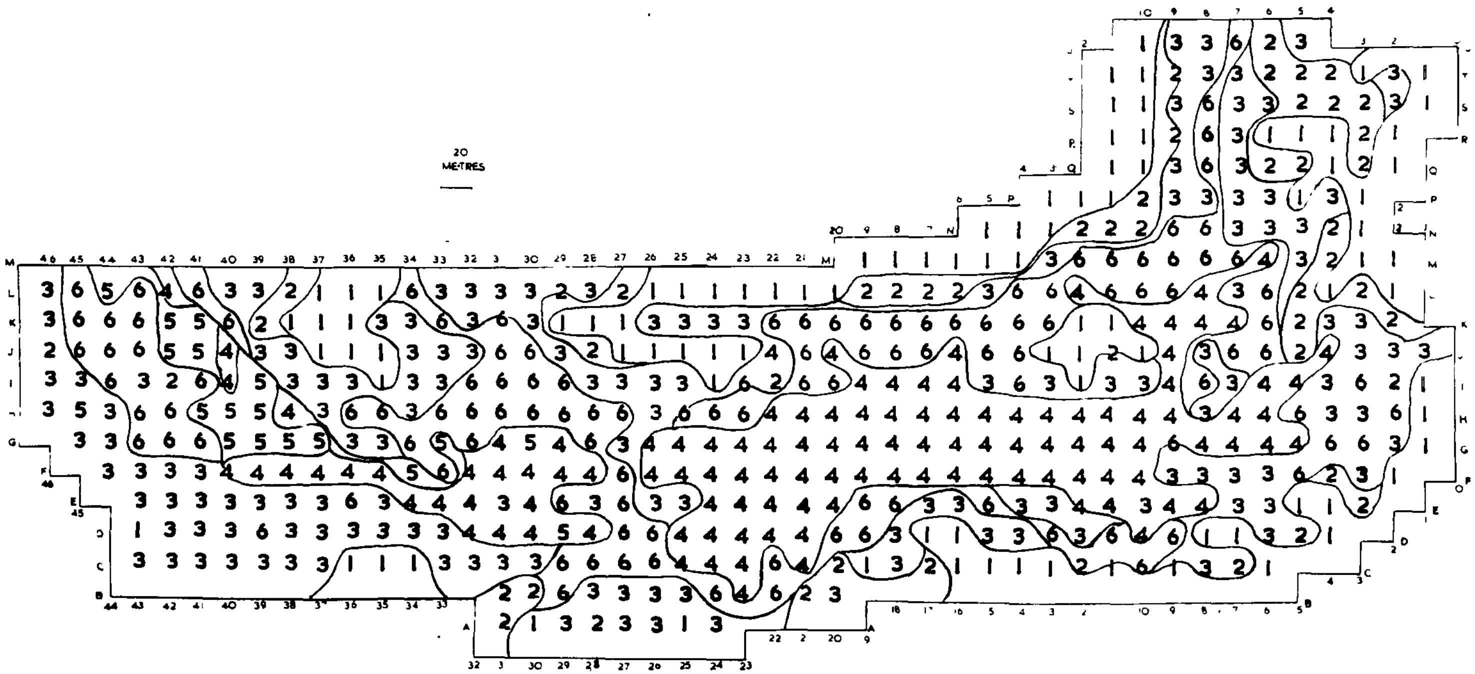
MAP 14.

Quadrats of the communities present at a minimum χ^2 of 120.

The key to communities is as under (see table 10)

1. *Ulex minor* community
2. *Cladonia strepsilis* community
3. *Myrica gale* / *Pinus sylvestris* community
4. *Sphagnum pulchrum* community
5. *Oarex panicea* community
6. *Odontochisma sphagni* community

N.B. These are the re-defined original subjective communities - see map 7. for subjective names.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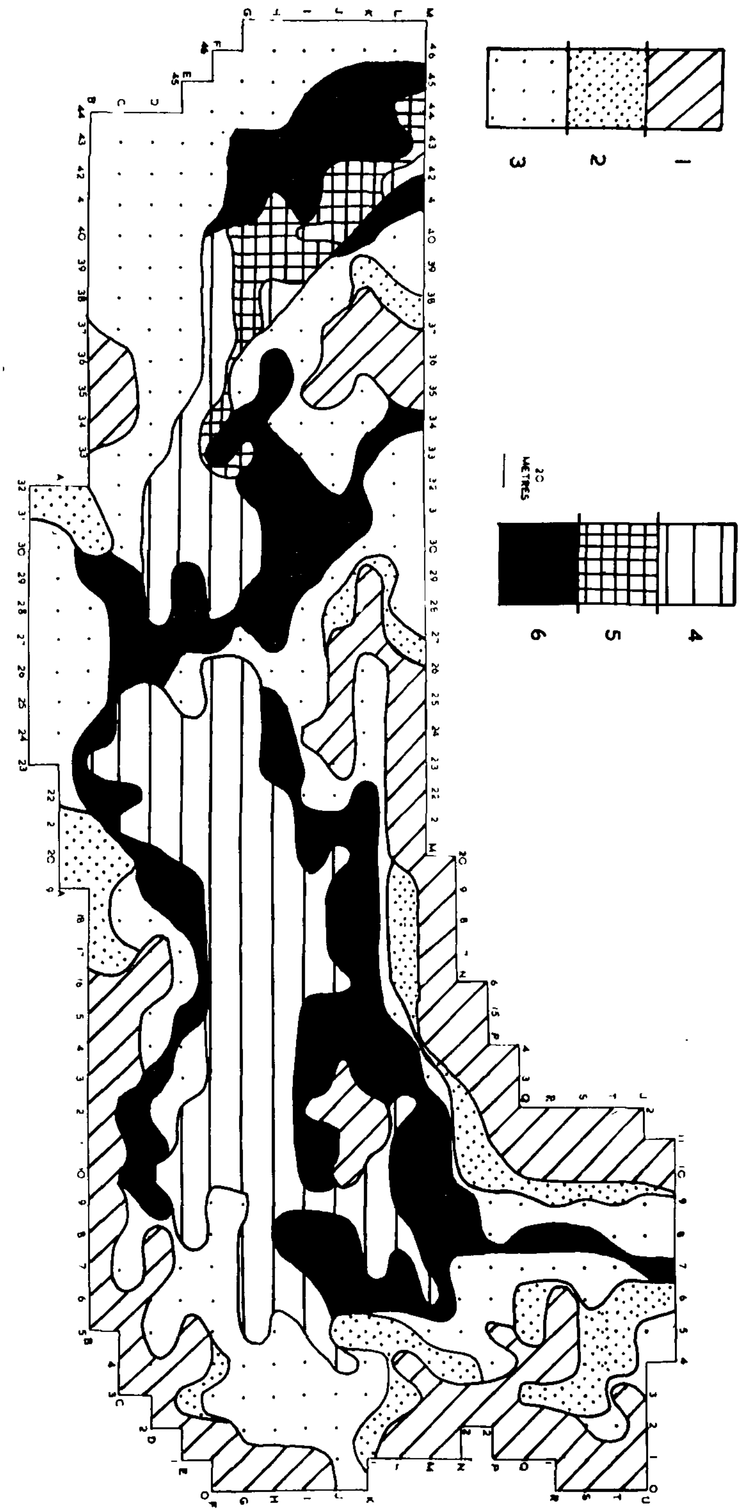


Map 15. Communities present at a minimum χ^2 of 120 (generalised form of map 14). Key to communities as for map 14.

annexation of additional quadrats, so that the open-water vegetation loses its identity.

The outline of the wet heath and the general bog is only established as a relatively low level in the hierarchy when the - *Sphagnum papillosum* quadrats divide on *Cladonia strepsilis* whose presence is indicative of wet heath areas. The remaining quadrats, that is those without *Schoenus*, *Ulex minor*, *Sphagnum papillosum* or *Cladonia strepsilis* occupy the remainder of the wet heath and general bog.

The final hierarchial division on *Carex panicea* divides the + *Schoenus* area into communities corresponding very closely with the original *Schoenus* area and the original *Carex rostrata* area, this latter species generally co-existing with the *Carex panicea* of the bog quadrats.

The chief advantage of the method over the former is that the defining species, whether positive or negative, are now absolute in conjunction with one another, and the boundaries between the communities are statistically more rigid. Moreover, the hierarchial structure of the analysis gives some indication of the relative importance of their respective boundaries. Ecologically the picture is only slightly changed from that of the original subjective classification except for the assimilation of the open-water vegetation with a wet facies of the bog, and this was only to be expected in view of the fact that the method has merely defined the original communities more economically with only slight re-assortment of the quadrats.

It remains to compare the complete species of these newly

TABLE 10.

Characteristic species of the six communities re-defined by the statistical phytosociological method

COMMUNITY I. (100 quadrats) + Ulex minor / - Schoenus nigricans

Species	Fidelity	Presence
Ulex minor	5	5
Polytrichum commune	3	3
Agrostis setacea	3	2
Erica cinerea	3	2
Cladonia coccifera	3	1

Hence the name is the Ulex minor community.

COMMUNITY II. (50 quadrats) + Cladonia strepsilis /- Schoenus nigricans - Ulex minor, - Sphagnum papillosum.

Species	Fidelity	Presence
Cladonia strepsilis	4	5
Erica ciliaris	3	4
Cladonia uncialis	3	1

Hence the name is the Cladonia strepsilis community.

COMMUNITY III. (147 quadrats) - Schoenus nigricans, - Ulex minor, - Sphagnum papillosum, - Cladonia strepsilis

Species	Fidelity	Presence
Myrica gale	5	1
Pinus sylvestris	5	1

Hence the name is the Myrica gale / Pinus sylvestris community.

COMMUNITY IV. (118 quadrats) + Schoenus nigricans /- Carex panicea

Species	Fidelity	Presence
Sphagnum pulchrum	4	3
Cladopodiella fluitans	3	2
Potamogeton polygonifolius	3	2

Hence the name is the Sphagnum pulchrum community.

COMMUNITY V. (16 quadrats) + Schoenus nigricans, + Carex panicea

Species	Fidelity	Presence
Carex panicea	5	5
Carex rostrata	5	3
Juncus bulbosus	5	1
Juncus effusus	5	1
Cephaloziella starkei	3	3
Eleocharis quinqueflora	3	2

Hence the name is the Carex panicea community.

COMMUNITY VI. (113 quadrats) + Sphagnum papillosum /- Schoenus nigricans, - Ulex minor.

Species	Fidelity	Presence
Odontochisma sphagni	3	3
Sphagnum cuspidatum	3	2

Hence the name is the Odontochisma sphagni community.

TABLE 11.

Original subjective groupings				Re-defined associations		
Community	No. of quadrats	No. of characteristic species		Community	No. of quadrats	No. of characteristic species
General bog	159	0	→	*Myrica gale*/ *Pinus sylvestris*	147	2
Schoenus nigricans area	118	7	→	*Sphagnum pulchrum*	118	3
Carex rostrata area	11	8	→	*Carex panicea*	16	6
Open-water vegetation	32	1	→ *Odontochisma sphagni*	*Odontochisma sphagni*	113	2
Wet heath	125	6	→ *Odontochisma sphagni*; → *Cladonia strepsilis*; → *Ulex minor*	*Cladonia strepsilis*	50	3
Dry heath	81	8	→	*Ulex minor*	100	5

defined communities to give some estimate of whether the more rigid definition is accompanied by any marked phytosociological change. Since it is impossible to compare the complete species lists by eye, the criterion of the presence of "positive characteristic species" formerly used (see page 20) has been adopted here (together with the crude nomenclature scheme) in the full realization that the method is not related to the present statistical system. Furthermore, it should be noted that all comparisons should be independent and should have equal value. This is true of all comparative methods (see appendix 3) but it is the fault of the phytosociological system that if any one comparison has a null result all others are taken as null whatever their value. This means that characteristic species can always be removed by the addition of a related community. If any one community has been split up among others, the characteristic species are lost. Nevertheless a comparison on this admittedly crude basis may give a certain amount of information.

The results are given in tables 10 and 11 and show that the number of positive characteristic species actually decrease by more than half in four of the six communities and increases only slightly in the other two cases, i.e. in community IV. (derived from the original general bog) and community V. (derived from the original *Carex rostrata* area); moreover it should be noted that the two characteristic species - *Pinus* and *Myrica* - for the redefined general bog only occur in two quadrats each. This situation contrasts markedly with the considerable increase in the number of characteristic species in most communities resulting from the more typical phytosociological method of the previous section.

The statistical method here employed obviously requires a re-orientation of traditional phytosociological thinking. Since a phytosociological unit is normally recognised more easily in the field by the presence of species rather than by their absence, a system which involves definition by negatively as well as positively defining species is not very easy to apply subjectively without practice. There is a danger that the present method which involves a mixture of subjective and objective stages may lose the specific advantages of both.

--------oOo--------

VI. A Completely Objective Analysis of the Vegetation.

A. Introduction.

In addition to the questions associated with the sampling method and criteria to be adopted, it is clear that the two phytosociological methods are entirely dependent in the first instance on community boundaries laid down in the first subjective assessment. In this section it is proposed to analyse the same sample data by a completely objective statistical method which is completely independent of any preconceived community boundaries.

Such a method has been devised (Williams and Lambert 1959, and in preparation) using both Goodall's criterion of homogeneity of vegetation (Goodall 1953 a) and the new concept of efficient subdivision of the data. This method has been termed association-analysis.

B. Principles of association-analysis.

Goodall suggests that statistically significant associations between presence and absence of different species recorded in quadrats implies heterogeneity in the population of quadrats and hence in the vegetation itself. A homogeneous unit of vegetation is defined as one in which all species associations are indeterminate (either or both species in a species-pair being present or absent in all quadrats) or non-significant, the latter being regarded as the more important criterion (Williams and Lambert l.c.). If the quadrat data can be divided so that within each subdivision no interspecific associations occur, these subdivisions represent an objective elementary classification of the vegetation in terms of underlying factors.

By sorting the quadrat on that species with the highest associative power represented by the sum of its correlation coefficients ($\Sigma\sqrt{\frac{\chi^2}{N}}$) at the level of the highest value for individual pairs of species. The use of this parameter is discussed fully in Williams and Lance (1958) and Williams and Lambert (l.c.). By this means a hierarchy of the subdivisions is produced; such a hierarchy is preferred to successive pooling of the residuum at each stage (c.f. Goodall l.c.) since this latter takes longer to achieve essentially the same result, obscures important discontinuities and makes it impossible to note the route by which the final classes were obtained.

C. The use of the computer for association analysis.

Preliminary work in this department showed that by hand calculation with the aid of a mechanical calculating machine a 396 quadrats area with 10 species took approximately 21 man days for an association-analysis to be computed. The time required for an analysis is related linearly to the number of quadrats and also increases as the square of the number of species: and Hartland Moor with 544 quadrats and 76 species to be analysed would thus take many months of hand computation for an association-analysis so this type of work could only be carried out for Hartland by using electronic computer facilities.

A programme has been prepared for the digital electronic computer at Southampton University, a Ferranti "Pegasus" which will process areas of up to 1680 quadrats and 76 species in about 60 - 70 hours. Although the results used in this section were obtained from the Mark III programme, certain preliminary information was obtained by the earlier but slower Mark II programme.

Appendix 4 gives details of the programme, the preparation of the data for acceptance by the computer and the form of the results.

D. <u>The application of the method to the vegetation of Hartland Moor.</u>

The basic data used was the same as that for the previous methods, the species number already having been reduced to 76 in anticipation of this method (see page 21). The quadrat occurrences of the species were transferred from the punched cards to punched paper tape and the type-out from this basic data tape is shown in appendix 4.

E. <u>Results.</u>

(1) <u>The hierarchy.</u>

The preliminary run under the Mark II programme gave seventy-two final groups at the $P = 0{,}05$ significance level but as this programme did not indicate the relative significance levels of the various divisions of the hierarchy the data was later rerun on Mark III programme to provide this information. Since the number of final groups produced in the first run was far too large to be assessed, the later run took the analysis as far as the limits set by the "short division" modification of the programme (see page 92) Table 12 shows the output (results) sheet of the association-analysis and figure 2 the hierarchy thereby constructed.

(2) The maps.

The hierarchy was more or less stratified to give three groupings that were mapped at the χ^2 of 60 level, six at the χ^2 of 45 level and eleven at the χ^2 of 30 level. The minimum χ^2 of 17 gave twenty communities but these were not mapped as the situation here becomes very complex and no longer gives a useful picture for comparison.

F. Discussion.

(I) Major divisions to a minimum χ^2 of 60 : (maps 16 & 17)

The principal division on *Sphagnum papillosum* appears reasonable as it divides that area into two parts corresponding to the subjective groupings of bog and heath.

The quadrats of the + *Sphagnum papillosum* community are mostly found where there are more than 20 cm. of peat. The further division of the - *Sphagnum* on *Narthecium ossifragum* gives communities roughly corresponding with the original wet heath and dry heath. The former (+ *Narthecium*/-*Sphagnum*) is generally developed on peat of

TABLE 12.

Association - analysis results from computer -

All (76) spp.

ANALYSIS TYPE-OUT

N	=	number of quadrats in class under examination
X/MAX	=	highest single χ^2 (with Yates's correction) encounted in the class under examination
S	=	serial number of species on which class is to be divided
FINAL		implies that no χ^2 value in the class attains 17.
END		is the signal that all quadrats have been accounted for and that the subdivision is complete.

•••
6/11/58---9

ASSOCIATION ANALYSIS (D.L.,MK.III)

J 23.0
HARTLAND MOOR

ALL (76) SPP.

SHORT (X/MIN = 17)

N 544
X/MAX = 237.41
S 29

N 240
X/MAX = 51.00
S 2

N 6
FINAL

N 234
X/MAX = 49.66
S 64

N 37
FINAL

N 197
X/MAX = 31.98
S 38

N 85
X/MAX = 20.25
S 71

N 28
FINAL

N 57
FINAL

N 112
X/MAX = 18.09
S 68

N 78
X/MAX = 18.99
S 11

N 18
FINAL

N 60
FINAL

N 34
FINAL

N 304
X/MAX = 141.32
S 61

N 122
X/MAX = 32.98
S 26

N 61
X/MAX = 33.15
S 16

N 28
FINAL

N 33
FINAL

N 61
X/MAX = 23.49
S 45

N 36
X/MAX = 17.28
S 65

N 9
FINAL

N 27
FINAL

N 25
FINAL

N 182
X/MAX = 55.62
S 49

N 114
X/MAX = 41.60
S 1

N 12
FINAL

N 102
X/MAX = 37.10
S 2

N 49
X/MAX = 26.40
S 45

N 12
FINAL

N 37
FINAL

N 53
X/MAX = 18.45
S 16

N 11
FINAL

N 42
FINAL

N 68
X/MAX = 27.28
S 74

N 42
FINAL

N 26
X/MAX = 19.96
AMB 22/25
S 22

N 5
FINAL

N 21
FINAL
END
I

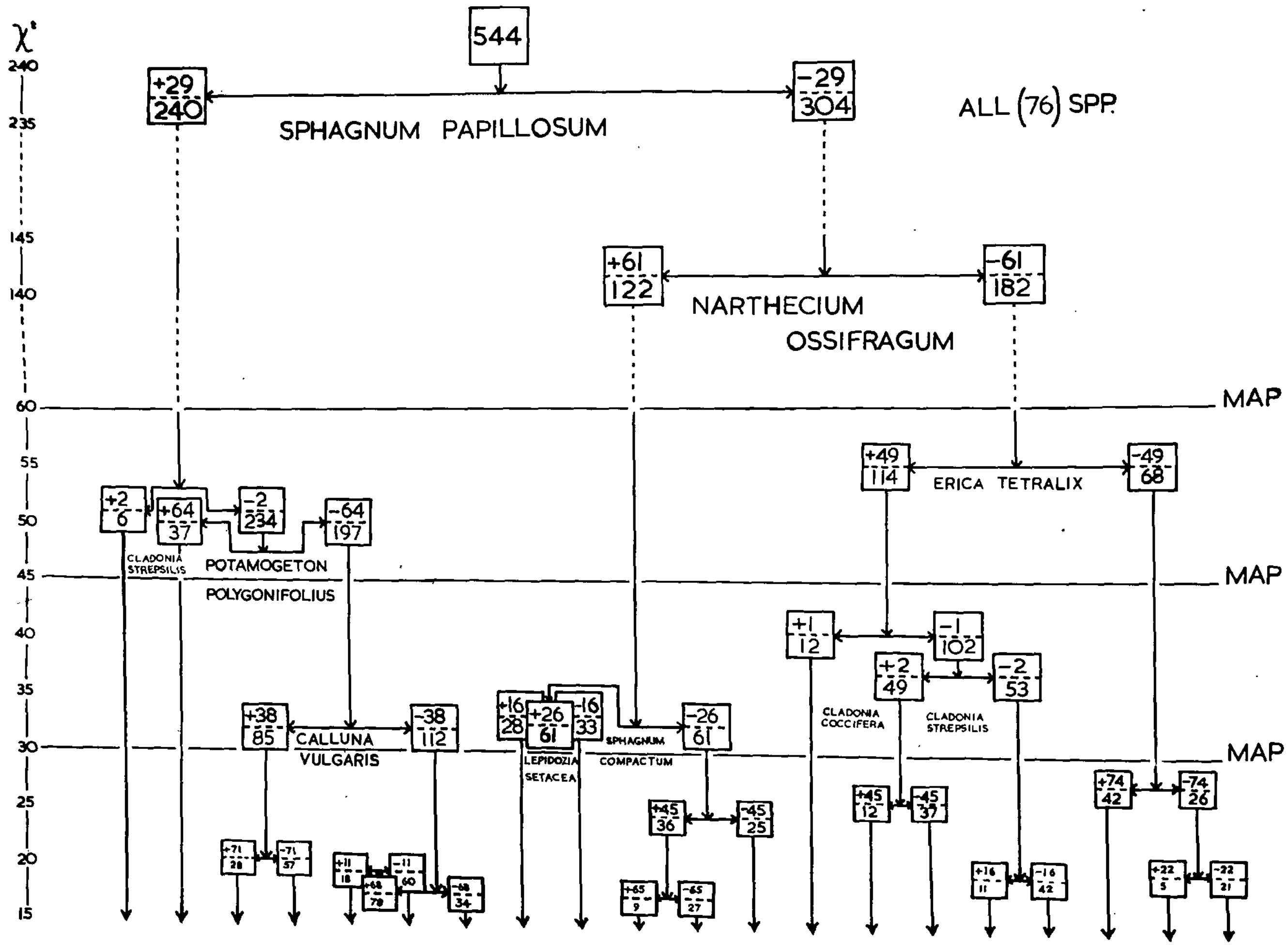


Figure 2. All (76) spp. hierarchy.

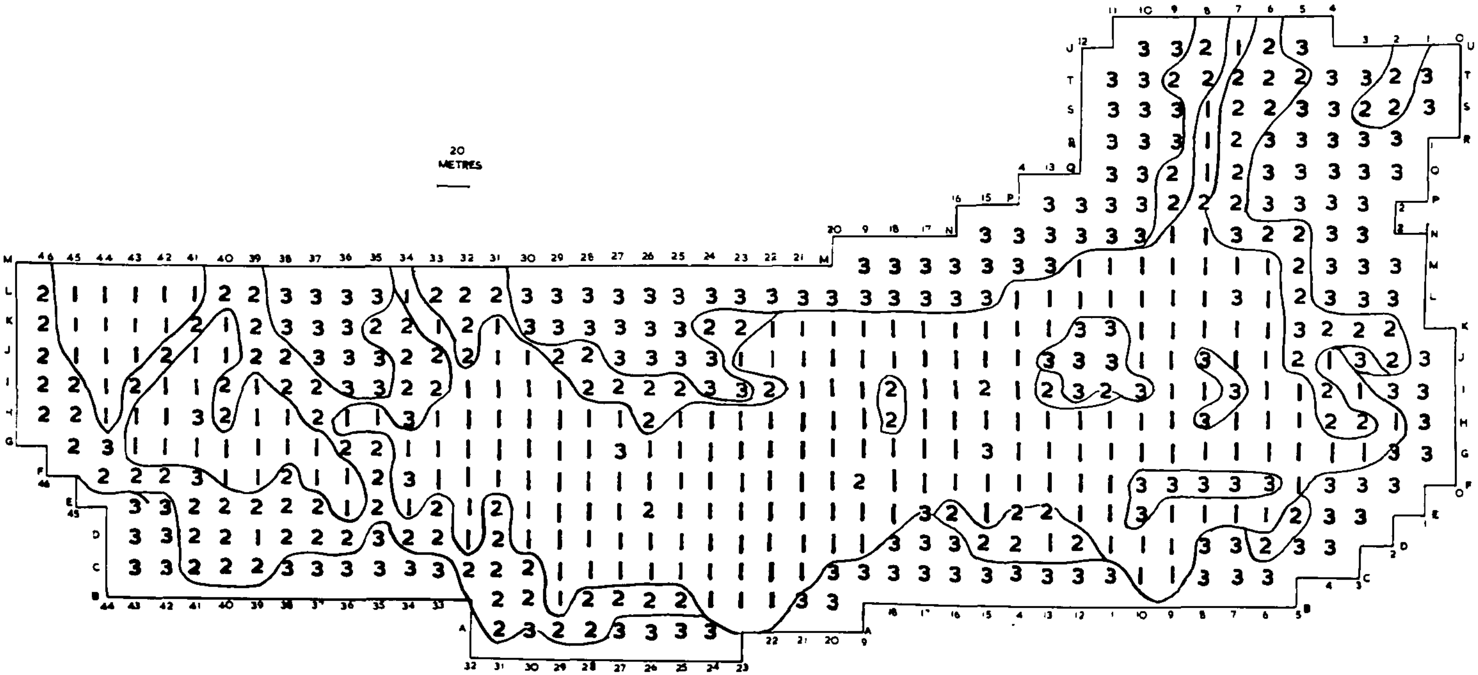
MAP 16.

All (76) spp. analysis.

Quadrat positions of the communities present at a minimum χ^2 of 60.

Key

1. +*Sphagnum papillosum*
2. -*Sphagnum papillosum*/+*Narthecium ossifragum*
3. -*Sphagnum papillosum* -*Narthecium ossifragum*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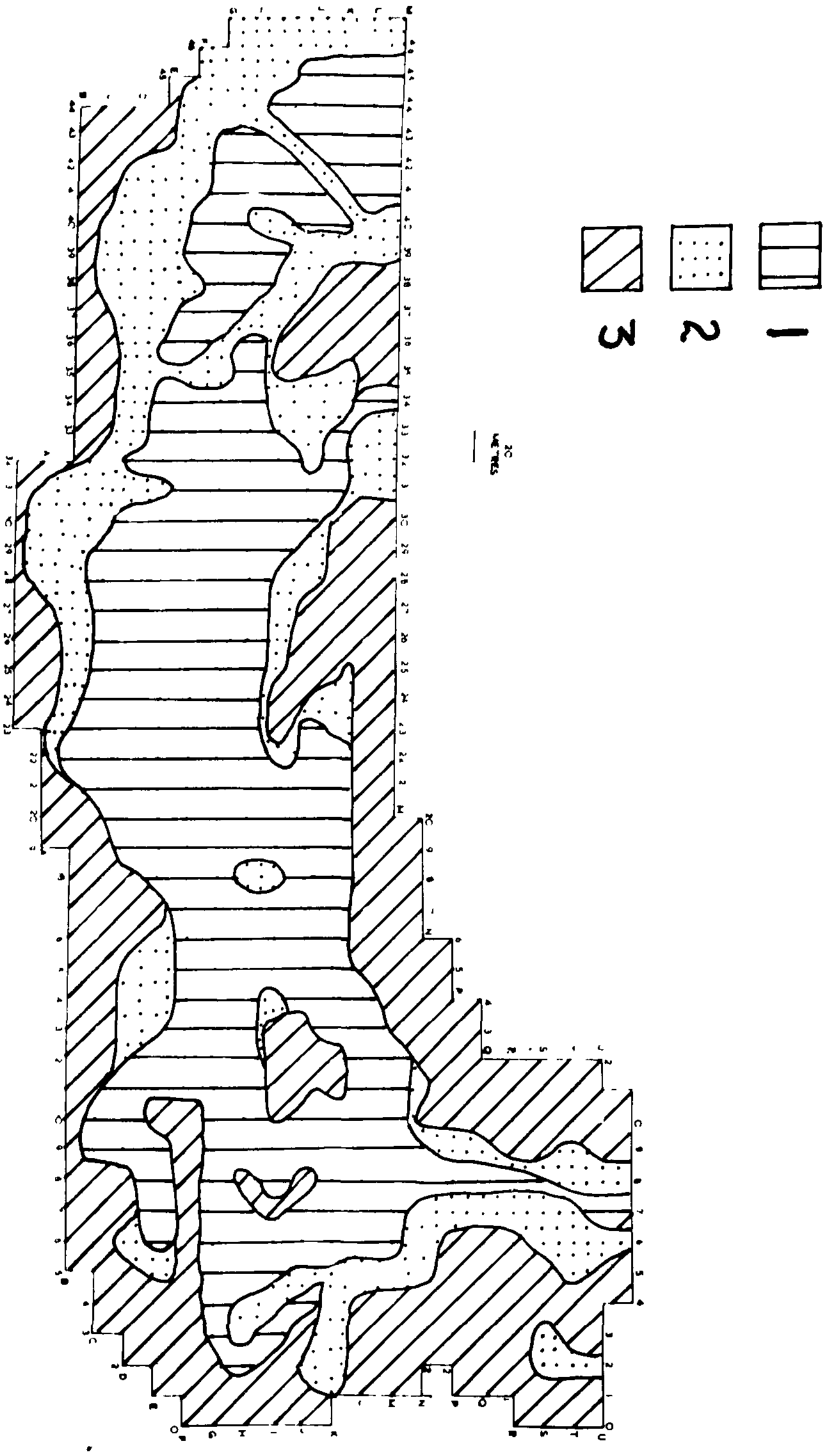


Map 17. Communities present at a minimum χ^2 of 60, (generalised form of map 16).

Key as for map 16.

up to 20 cm. in depth. Quadrats of this community occur in the region of I 43, J 42, K 41, E - G 35, G 36 and H 37. When enclosed by a boundary line, the similar areas of wet heath either side of the bog become bridged by these wet heath quadrats. These "bridges" were found on return to the area to correspond with compacted peat balks noted on page 6 and were much more noticeable then (March 1959) than at the time of the original subjective survey owing to the dead Narthecium along their surface.

In the subjective map there is a well-demarcated zone of wet heath in the J, K, L, 13 - 22 quadrat region but the association analysis gives no + Narthecium zone there. The probable reason for this subjectively unrecognised floristic difference is that in this part of the original "wet heath" where the bog opens into a wide basin (v. map 4) there is probably only a little seasonal fluctuation in water level compared with other parts of the area where the valley is narrower, and where the drainage water would tend to be "piled up". It is suggested that the possibly greater seasonal fluctuation resulting in the narrower parts is necessary for the survival of Narthecium and its associates.

In the central mass of + Sphagnum papillosum there are several more or less isolated quadrats of + Narthecium.

A possible explanation for their occurrence is that the actual sample was taken from a small hummock arising above the general bog surface. These hummocks were too small to be mapped but being slightly higher than the bog surface and therefore slightly drier they bore a flora of wet heath species.

The last of the three communities (- Sphagnum, -Narthecium) is developed generally on those areas where there is no peat, but is occasionally found on up to 10 cm. of peat if the valley is only very slightly shelving.

There are some quadrats of this community in the + Sphagnum area. Inspection showed that some of these could be accounted for by the presence of very high and dry hummocks on the bog surface. Others appear by virtue of the fact that these two extreme habitats, pools and dry heath, are both poor in species and represent the residuum after the bog and wet heath have been extracted. Quadrats F6 - 10 represent a pool that was subjectively recognised and later objectively characterised by the absence of Sphagnum papillosum and Narthecium.

2. Divisions to χ^2 of 45 : (maps 18 & 19).

(1) + Sphagnum papillosum, + Cladonia strepsilis. (6 quadrats)

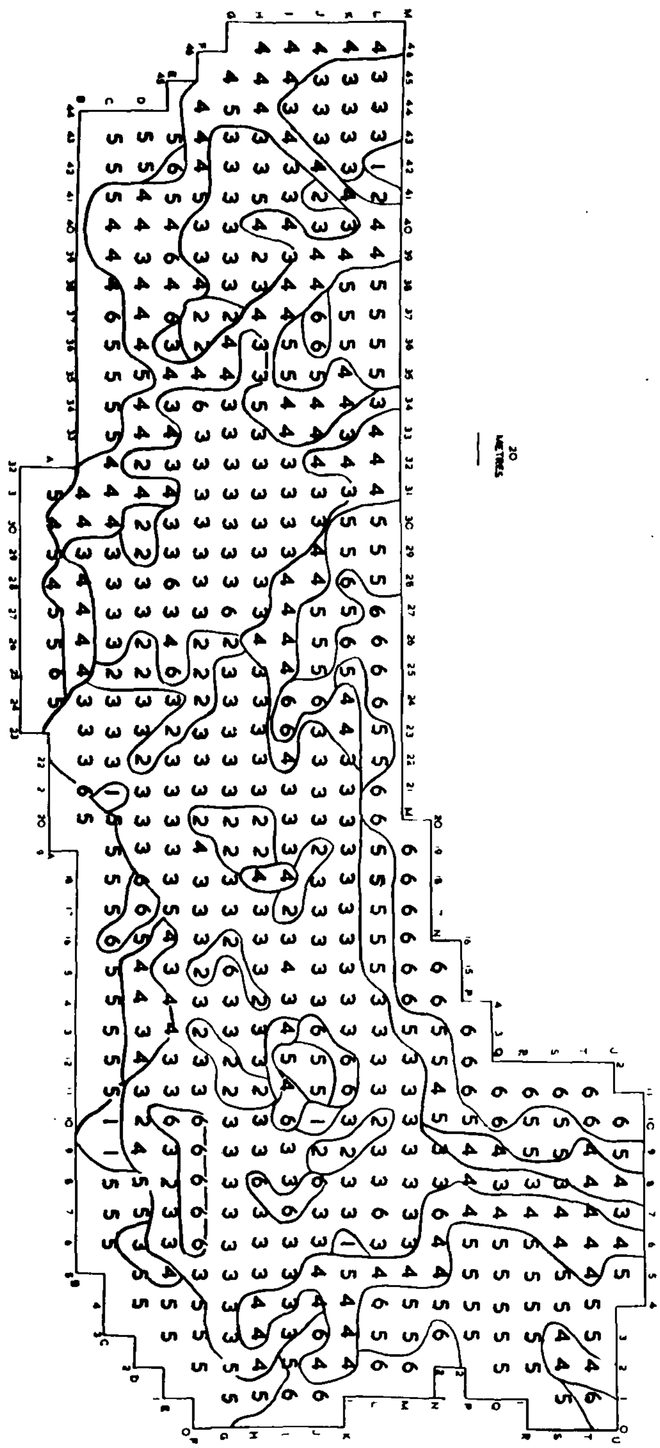
This community is found as scattered quadrats at the juxtaposition of bog and wet-heath on relatively uncolonised areas, and possibly burnt by flame-throwers during the war (see page 7).

(2) + Sphagnum papillosum, + Potamogeton polygonifolius/ - Cladonia strepsilis. (37 quadrats)

These quadrats form one of the wettest zones, and occur as a discontinuous community down the centre of the bog.

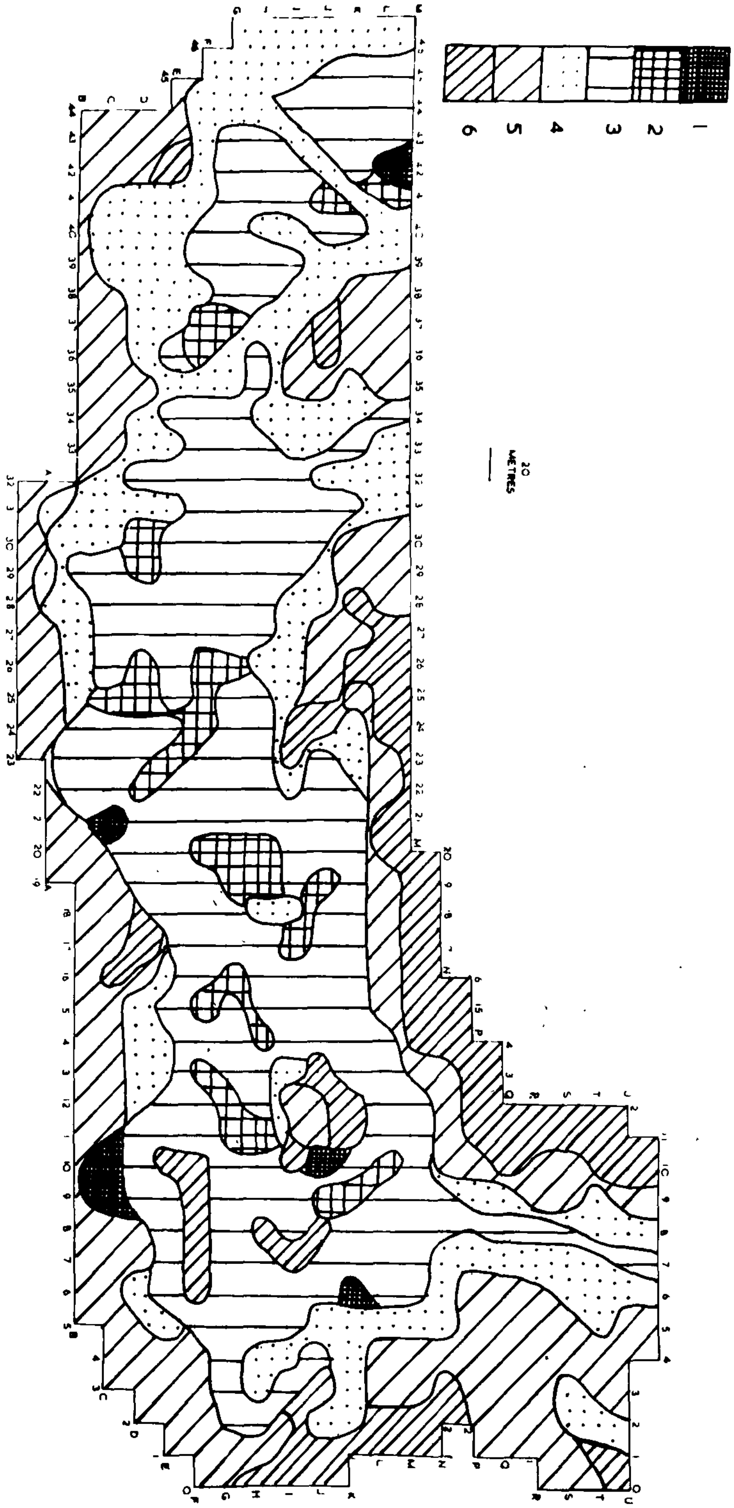
(3) + Sphagnum papillosum/ -Cladonia strepsilis, -Potamogeton polygonifolius. (197 quadrats)

These quadrats comprise the original general bog and all



Map 18. Quadrats of the communities present at a minimum χ^2 of 45.

For key see pages 42 and 43.



Map 19. Communities present at a minimum χ^2 of 45.

For key see pages 42 and 43.

except the wettest facies of the Schoenus area.

(4) - Sphagnum papillosum/+ Narthecium ossifragum (122 quadrats)

The wet heath has not divided further and its distribution has already been discussed.

(5) -Sphagnum papillosum, -Narthecium ossifragum/+Erica tetralix (114 quadrats)

This represents the wetter parts of the original dry heath with Erica tetralix added to the typical dry heath species. This community is confined to those parts of the area with a peat depth between 0 and 20 cm.

(6) -Sphagnum papillosum, -Narthecium ossifragum, -Erica tetralix. (68 quadrats)

This grouping still comprises the quadrats of the most extreme habitats - deep pools and driest facies of the dry heath, with insufficient species to distinguish statistically at this level.

Ignoring the +Cladonia strepsilis community (no. 1) as it occupies a small, specialised area, and dividing the negative community (no. 6) into dry heath and pool groups we can arrive at a linear zoning of the six communities arranged in relation to increasing wetness of substrate.

Part of 6. "Dry heath"

5. "Dry heath" plus Erica tetralix.

4. "Wet heath"

3. "General bog"

2. Wettest bog with Potamogeton.

Part of 6. Pools.

That this arrangement has been brought out by the association-analysis suggests that these six communities have an ecological reality.

3. χ^2 minimum of 50 : (map no. 20)

The area begins to resolve itself into a mosaic of eleven communities, many of which have no counterpart in the subjective survey. The positions of the quadrats of these eleven communities are shown on map 20. A separate community map was not drawn as it was impracticable to show the parts of the mosaics clearly and the major communities were the same as on the previous maps. These communities are referred to by the numbers shown on the key to map 20.

Communities 1, 2, and E are the same as 1, 2, and 6 respectively of the previous map (map no. 19).

The + Sphagnum papillosum / -Cladonia strepsilis -Potamogeton polygonifolius community (no. 3 of map 18) has now divided into a mosaic of two parts on the presence or absence of Calluna vulgaris (represented on this map as communities 3 and 4). It is probably that the + Calluna quadrats are on slightly drier peat than the -Calluna ones. Small tussocks of Calluna were noted on the bog surface but were not related to the contours and topography, but apparently inherent in the structure of the bog and were reminiscent of a regeneration complex. A suggestion that an incipient regeneration complex does occur in British lowland bogs has been put forward by Rose (1953).

The "wet heath" + Narthecium ossifragum / -Sphagnum papillosum that

MAP 20.

All (76) spp. analysis

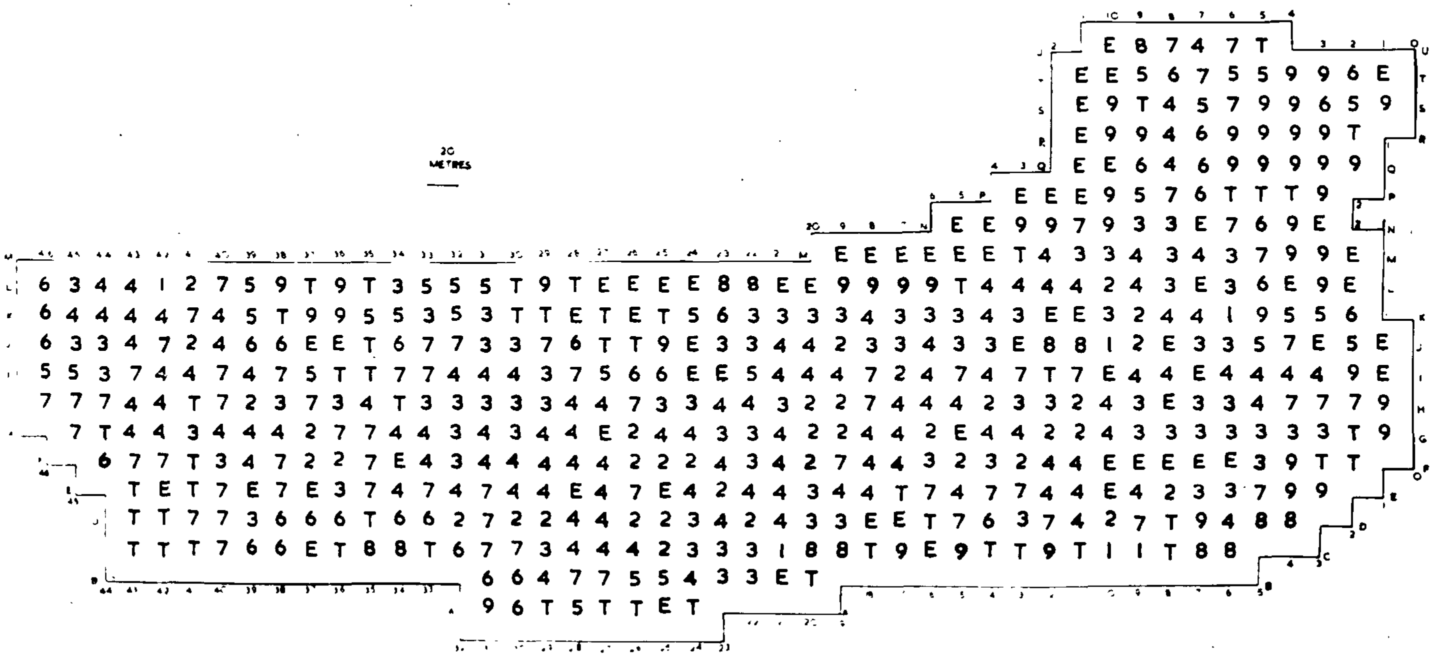
Quadrats of the communities present at a minimum χ^2 of 30.

Key

1. + *Sphagnum papillosum*, + *Cladonia strepsilis*
2. + *Sphagnum papillosum*, -*Cladonia strepsilis*, + *Potamogeton polygonifolius*
3. + *Sphagnum papillosum*, -*Cladonia strepsilis* -*Potamogeton polygonifolius*, + *Calluna vulgaris*
4. + *Sphagnum papillosum*, -*Cladonia strepsilis* -*Potamogeton polygonifolius*, -*Calluna vulgaris*
5. -*Sphagnum papillosum*, + *Narthecium ossifragum*, + *Sphagnum compactum*, + *Lepidozia setacea*
6. -*Sphagnum papillosum*, + *Narthecium ossifragum*, + *Sphagnum compactum*, + ~~Sphagnum compactum~~, -*Lepidozia setacea*
7. -*Sphagnum papillosum*, + *Narthecium ossifragum*, -*Sphagnum compactum*
8. -*Sphagnum papillosum*, -*Narthecium ossifragum*, + *Erica tetralix*, + *Cladonia coccifera*
9. -*Sphagnum papillosum*, -*Narthecium ossifragum*, + *Erica tetralix*, - *Cladonia coccifera*, + *Cladonia strepsilis*

T. -*Sphagnum papillosum*, -*Narthecium ossifragum*, + *Erica tetralix* -*Cladonia coccifera*, -*Cladonia strepsilis*

E. -*Sphagnum papillosum*, -*Narthecium ossifragum*, -*Erica tetralix*.


20 METRES
E 8 7 4 7 T
E E 5 6 7 5 5 9 9 6 E
E 9 T 4 5 7 9 9 6 5 9
E 9 9 4 6 9 9 9 T
E E 6 4 6 9 9 9 9
E E E 9 5 7 6 T T T 9
E E 9 9 7 9 3 3 E 7 6 9 E
E E E E E E T 4 3 3 4 3 4 3 7 9 9 E
6 3 4 4 1 2 7 5 9 T 9 T 3 5 5 5 T 9 T E E E E 8 8 E E 9 9 9 9 T 4 4 4 4 2 4 3 E 3 6 E 9 E
6 4 4 4 4 7 4 5 T 9 9 5 5 3 5 3 T T E T E T 5 6 3 3 3 3 4 3 3 3 4 3 E E 3 2 4 4 1 9 5 5 6
6 3 3 4 7 2 4 6 6 E E T 6 7 7 3 3 7 6 T T 9 E 3 3 4 4 2 3 3 4 3 3 E 8 8 1 2 E 3 3 5 7 E 5 E
5 5 3 7 4 4 7 4 7 5 T T 7 7 4 4 4 3 7 5 6 6 E E 5 4 4 4 7 2 4 7 4 7 T 7 E 4 4 E 4 4 4 4 9 E
7 7 7 4 4 T 7 2 3 7 3 4 T 3 3 3 3 3 4 4 7 3 3 4 4 3 2 2 7 4 4 4 2 3 3 2 4 3 E 3 3 4 7 7 7 9
7 T 4 4 3 4 4 4 2 7 7 4 4 3 4 3 4 4 E 2 4 4 3 3 4 2 2 4 4 2 E 4 4 2 2 4 3 3 3 3 3 3 3 T 9
6 7 7 T 3 4 7 2 2 7 E 4 3 4 4 4 4 4 2 2 2 4 3 4 2 7 4 4 3 2 3 2 4 4 E E E E E 3 9 T T
T E T 7 E 7 E 3 7 4 7 4 7 4 4 E 4 7 E 4 2 4 4 3 4 4 T 7 4 7 7 4 4 E 4 2 3 3 7 9 9
T T 7 7 3 6 6 6 T 6 6 2 7 2 2 4 4 2 2 3 4 2 4 3 3 E E T 7 6 3 7 4 2 7 T 9 4 8 8
T T T 7 6 6 E T 8 8 T 6 7 7 3 4 4 4 2 3 3 3 1 8 8 T 9 E 9 T T 9 T 1 1 T 8 8
6 6 4 7 7 5 5 4 3 3 E T
9 6 T 5 T T E T

first occurred at a minimum χ^2 of 60 has now divided into three communities, 5, 6, and 7, forming a complex mosaic at the edge of the bog and dry heath. Community 5 and community 6 are facies of the wet heath whose ecological interpretation is not yet clear. Community 7 is composed of two elements -

1. Wet heath with few bryophytes owing to a dense mat of phanerogams and a carpet of Zygogonium "ericetorum".

2. Parts of the general bog with neither Sphagnum papillosum nor wet heath cryptogams. These quadrats represent the compacted peat bridges referred to on page 6 and shown on map 17 .

Communities 8, 9 and T are subdivisions of the + Erica tetralix zone of the dry heath i.e. the wetter facies of the dry heath.

Community 8 is further characterised by the presence of Cladonia coccifera. This species was noted to occur where the angiosperm cover was fairly dense and where presumably the underlying lichen species are not subject to big ranges of microclimatic conditions.

Community 9 is further characterised by the presence of Cladonia strepsilis. It is found in similar specialised habitats as Community 1 (+ Sphagnum papillosum) except that 9 has no

(+ Cladonia strepsilis)

Sphagnum papillosum and therefore presumably the water table is below the surface.

Community T comprises the remainder of the wetter facies of the dry heath where Erica tetralix does not form a dense cover but is composed of fairly evenly spaced small tussocks of young plants of this species.

G. General Discussion.

Again some consideration of the actual floristic composition of the groupings at the six-community level may be useful. Using the same criterion of "positive characteristic species" as before (see page 20 and 36) the results are given as tables 13 and 14. Since however, the new community boundaries have altered considerably from those of the previous analyses, a less direct comparison with the results of the other methods can be made and the lists must be examined in their own right. It is clear from the table that all communities except that derived from the general bog have at least one characteristic species, while the very small grouping of the six rather specialised quadrats of community 1 has as many as eleven (it is noteworthy that in the standard phytosociological method of section IV, where communities of less than eight quadrats were not assessed this community would have been disregarded).

It is interesting that a general bog, with no positive characteristic species, appears again here and suggests that this community has a truly objective basis. It confirms the original subjective estimate of its position and suggests that the original phytosociological attempt (section IV) to redistribute its quadrats among other communities may have falsified both the ecological and phytosociological picture. This is a clear case of a community defined both subjectively and statistically more by absence than by

TABLE 13.

COMMUNITY I. (6 quadrats) + Sphagnum papillosum, + Cladonia strepsilis

Species	Fidelity	Presence
Cladonia impexa	5	4
Cladonia strepsilis	4	5
Calypogeia fissa	4	3
Juncus acutiflorus	4	3
Hypogymnia physodes	4	2
Mylia anomala	4	2
Erica ciliaris	3	5
Cladopodiella fluitans	3	3
Cephalozia connivens	3	2
Cladonia coccifera	3	2
Cladonia uncialis	3	2

Hence the name is the Cladonia impexa community.

COMMUNITY II. (37 quadrats) + Sphagnum papillosum, + Potamogeton polygonifolius, /- Cladonia strepsilis

Species	Fidelity	Presence
Potamogeton polygonifolius	5	5
Sphagnum subsecundum	5	5
Schoenus nigricans	4	5
Eleocharis quinqueflora	4	2
Rhynchospora alba	3	5

Hence the name is the Potamogeton polygonifolius, Sphagnum subsecundum community.

COMMUNITY III. (197 quadrats) + Sphagnum papillosum /- Potamogeton polygonifolius, - Cladonia strepsilis

No characteristic species

COMMUNITY IV. (122 quadrats) + Narthecium ossifragum /- Sphagnum papillosum

Species	Fidelity	Presence
Sphagnum compactum	4	3
Sphagnum tenellum	4	3
Carex panicea	3	2

Hence the name is the Sphagnum compactum, Sphagnum tenellum community.

COMMUNITY V. (114 quadrats) + Erica tetralix /- Sphagnum papillosum, - Narthecium ossifragum

Species	Fidelity	Presence
Campylopus brevipilus	3	4

Hence the name is the Campylopus brevipilus community.

COMMUNITY VI. (68 quadrats) - Sphagnum papillosum, - Narthecium ossifragum, - Erica tetralix

Species	Fidelity	Presence
Erica cinerea	5	3
Pteridium aquilinum	5	1
Ulex minor	4	4
Polytrichum commune	3	3
Agrostis setacea	3	2

Hence the name is the Erica cinerea community.

TABLE 14.

Original subjective groupings

Community	No. of quadrats	No. of characteristic species
Open-water vegetation	32	1
Carex rostrata area	11	8
Schoenus nigricans	118	7
General bog	159	0
Wet heath	125	6
Dry heath	81	8

New associations

Community	No. of quadrats	No. of characteristic species
Potamogeton polygonifolius/*Sphagnum subsecundum*	37	5
"+*Sphagnum papillosum*/ -*Potamogeton polygonifolius* -*Cladonia strepsilis*"	197	0
Cladonia impexa	6	11
Sphagnum compactum, *Sphagnum tenellum*	122	3
Campylopus brevipilus	114	1
Erica cinerea	68	5

Communities not considered

Community	No. of quadrats	No. of characteristic species
Rhynchospora alba area	7	0
Erica ciliaris areas	4	0
Eriophorum angustifolium areas	3	0
Carex panicea area	2	0
Agrostis setacea areas	2	0

presence of species, and it appears to represent a basic bog vegetation from which other more specialised bog communities are derived by the addition of more ecologically restricted species.

The general reduction in the numbers of the positive characteristic species in the heath communities may be accounted for by the fact that three separate communities now exist within the area occupied by the original two communities. The separation of a wet facies from the dry heath with floristic relationships with the other two has obviously made any one of these phytosociologically less distinct but nevertheless has shown a real discontinuity between all three in terms of positive characteristic species. This is a concrete example of the failure of the traditional concept of characteristic species, where the addition of a related community reduces the total number of such species (see appendix 3 and page 36).

The original Schoenus community with seven characteristic species, no longer exists as such as the amalgamation of its wetter quadrats with those of the more typical pools has now produced a community with five characteristic species compared with the single faithful species of the open-water vegetation.

The phytosociological picture thus produced is necessarily rather different in certain respects from those produced by the previous analyses but it gives a slightly better phytosociological picture than the statistical phytosociological method as far as total number of positive characteristic species are concerned, although it does not approach the numbers of the traditional phytosociological method. In compensation, completely objective discontinuities have now been revealed between the communities which bear some relation to the habitat itself and give more confidence in the actual characteristic species which appear. Moreover it must be remembered that these discontinuities between communities are usually reinforced by "negative species relationships" which do not appear in the crude method here used to compare the species lists.

--------oOo--------

VII.

The effects of removal of certain groups of species from the data considered for analysis.

A. The Problem.

A subsidiary part of this investigation was to ascertain whether the omission of selected categories of species had any effect on the general analysis of the vegetation of Hartland Moor by a selected method. In the areas studied by Williams and Lambert (1959) vascular plant data only were considered. Lower plants, subjectively at least, appeared to play only a minor role in these areas. Hartland Moor, however, contains a large area of bog in which traditionally *Sphagnum* species and other bryophytes were considered to play an important part. By considering non-vascular plants only in an analysis the part played by these species in any assessment of an area could be studied - whether their presence merely strengthened the delimitation of communities by reflecting the divisions based on vascular plants, or whether they formed distinct communities in their own right transgressing the boundaries of other communities; whether in fact the omitting of any systematic group from an analysis radically altered the general picture of the vegetation of the area.

Of the analytical methods described in the previous sections association-analysis gave a sufficiently objective basis for a further investigation of this type.

Associated with the above is therefore the problem of finding methods for the reduction of data collection time and computing time in any such statistical work, to give results that are without major changes when compared with an all species and all quadrats classification. Such methods must necessarily involve reduction either in the number of quadrats or the number of species considered. From the point of view of data collection, omission of a group such as the bryophytes with their consequent difficulties in identification would considerably reduce the time; moreover where computer time is concerned the omission of species is far more economical in time than the omission of quadrats (see p.94). It was therefore decided in this investigation to concentrate on species reduction rather than quadrat reduction.

B. Method.

The standard association-analysis computer programme contains a device for masking individual species so that it was very easy to omit certain categories and thereby produce a series of separate analyses for comparison. If it can be shown that elimination of lower plants does not provide a reasonable safe method of reducing species there is still the possibility of the elimination of certain numerically unimportant species occurring in less than a certain number or percentage of the quadrats. Though this might give a considerable saving in computer time, it is statistically less desirable and it loses the advantage in data collection time. Omission of a systematic group is preferable since the association-analysis would be done on a "complete" given set of data whereas the omission of species in less than a certain percentage or number of the quadrats is ecologically less preferable as the data is incomplete and one is perhaps erroneously assuming that the species in less than a certain number of the quadrats are those that are least highly associated. Work on other areas in this Department has shown that in a 396 quadrat area a species in only 11 quadrats was very highly associated and the omission of it from an association analysis falsified the ecological picture considerably.

C. Results of the omission of groups of systematically related species.

Table 15 shows the times of the various association analyses compared with that of the all (76) species analysis. The results are given as tables 16, 17 and 18, the hierarchies are shown as figures 3, 4 and 5, and the maps are numbered 21 to 30. These maps were drawn where stratification of the hierarchies allowed and where comparison of previous maps could be equated.

D. Discussion of results.

1. Vascular Plants only. (Bryophytes and Lichens omitted)

(a) : χ^2 of 125 : 3 community level. (maps 21 and 22)

TABLE 15.

Association-analysis	Mark II. Time (Hrs.)	Mark III. Time (Hrs.)
"All (76) species"	21.40	16.35 (short division)
"Vascular plants only"	06.18	04.55 " "
"Bryophytes only"	02.23	01.35 " "
"Lichens and Bryophytes"	04.13	03.00 " "
"2% omitted"	09.30	-
"5% omitted"	07.25	-
"10% omitted"	05.24	-
"15% omitted"	01.55	-

TABLE 16.

Association-analysis results from computer

Vascular Plants only

(for interpretation see table 12)

J 23.0
HARTLAND MOOR

VASCULAR PLANTS ONLY

SHORT (X/MIN = 17)

N 544
X/MAX = 237.41
S 74

N 95
X/MAX = 29.39
S 51

N 20
FINAL

N 75
X/MAX = 20.45
S 47

N 31
FINAL

N 44
X/MAX = 17.34
S 49

N 13
FINAL

N 31
FINAL

N 449
X/MAX = 145.60
S 64

N 55
X/MAX = 23.49
S 71

N 39
FINAL

N 16
FINAL

N 394
X/MAX = 123.76
S 61

N 292
X/MAX = 38.18
S 66

N 63
FINAL

N 229
X/MAX = 43.19
S 41

N 52
FINAL

N 177
X/MAX = 23.19
S 49

N 147
X/MAX = 21.94
S 51

N 138
X/MAX = 24.35
S 71

N 53
FINAL

N 85
X/MAX = 17.52
S 46

N 7
FINAL

N 78
FINAL

N 9
FINAL

N 30
FINAL

N 102
X/MAX = 19.84
S 49

N 77
X/MAX = 18.25
S 47

N 59
FINAL

N 18
FINAL

W 25
FINAL
END
*0***X

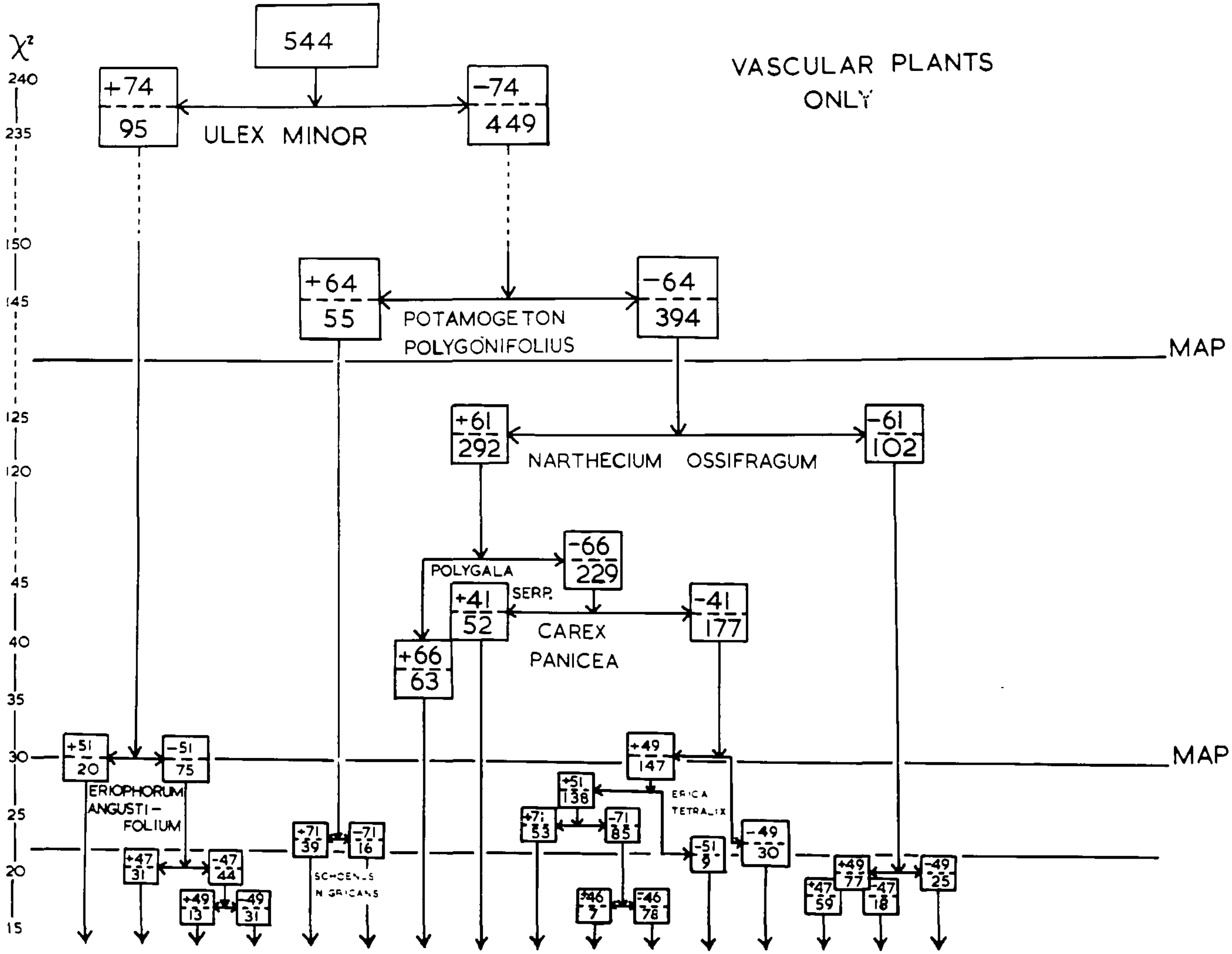
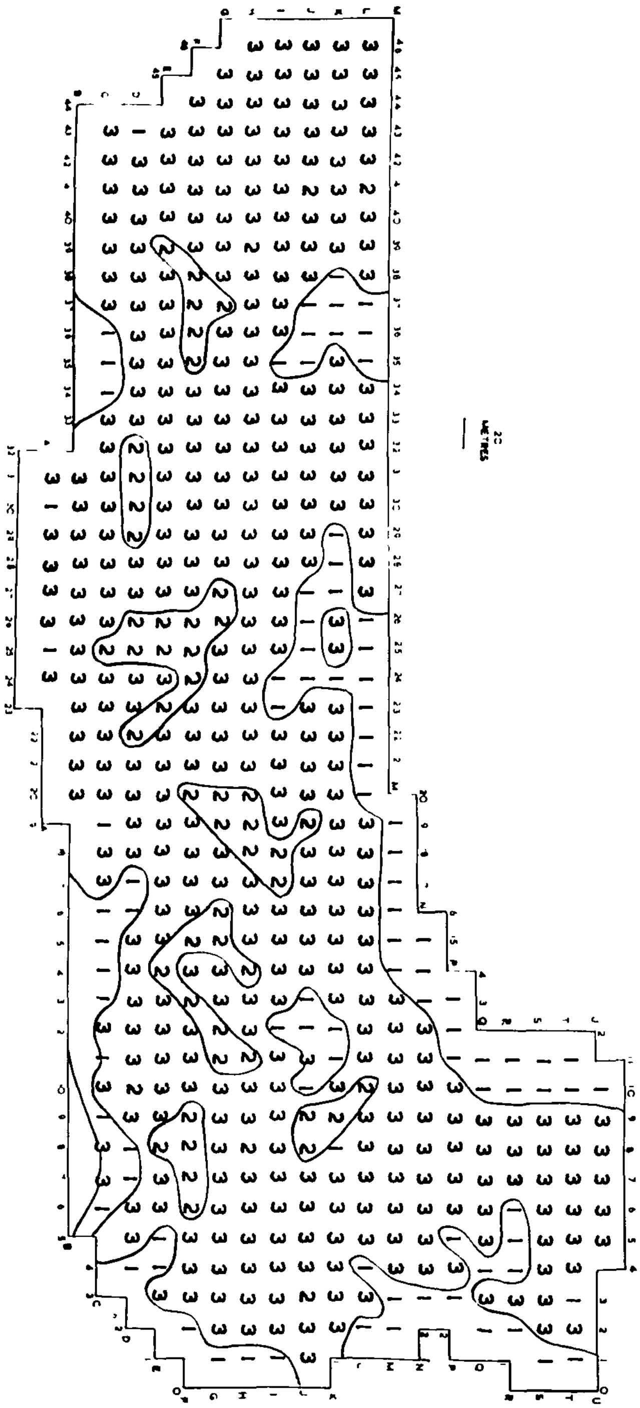
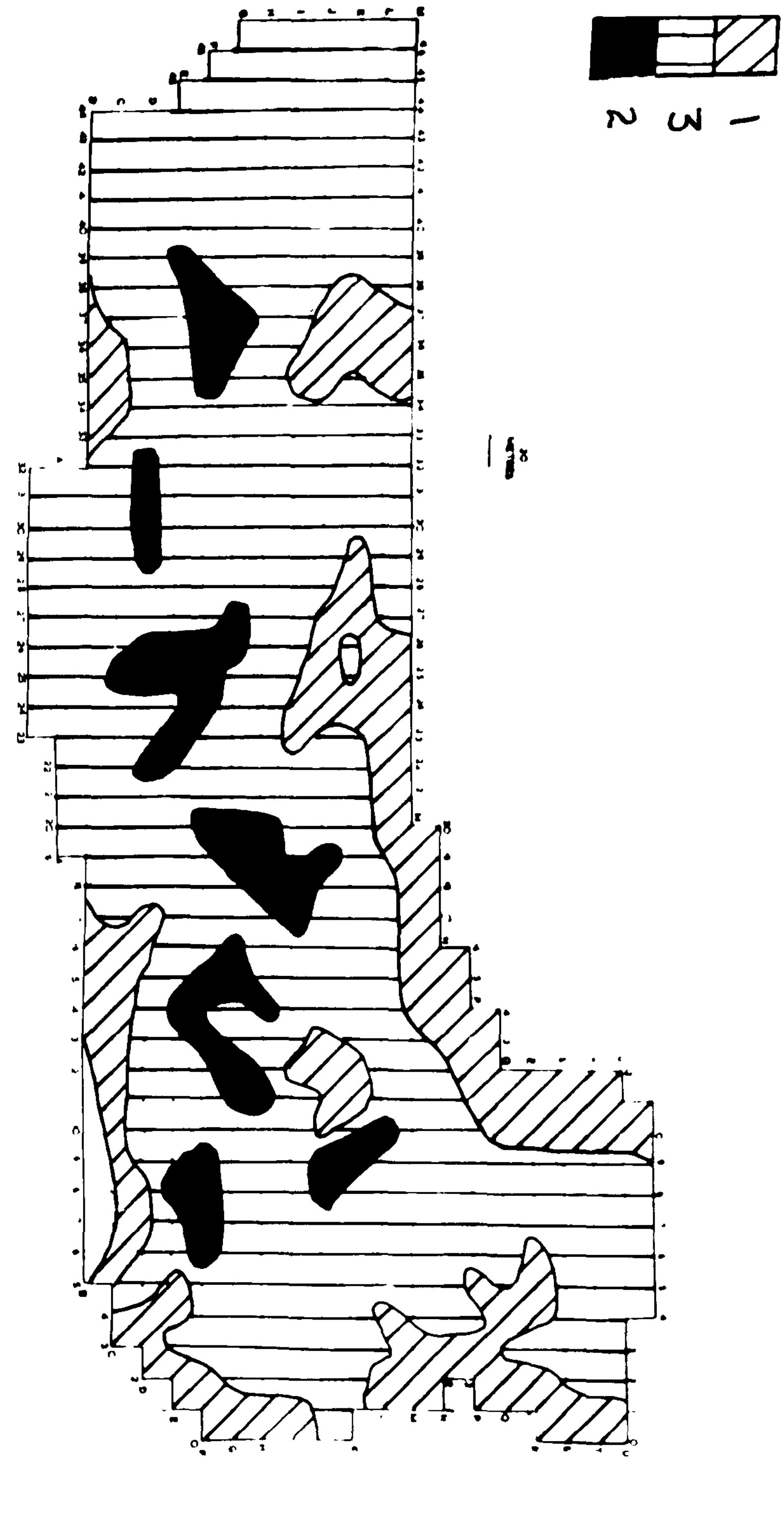


Figure no. 3 : Vascular plants only association-analysis hierarchy.



Map 21. Quadrats of the communities present at a minimum χ^2 of 125. For key to communities see page 51.



Map 22. Communities present at a minimum χ^2 of 125. (Generalised form of map 21). For key to communities see page 51.

The first division of the hierachy on Ulex minor separates the dry facies of the dry heath from the rest of the area. The + Ulex is mapped as community 1.

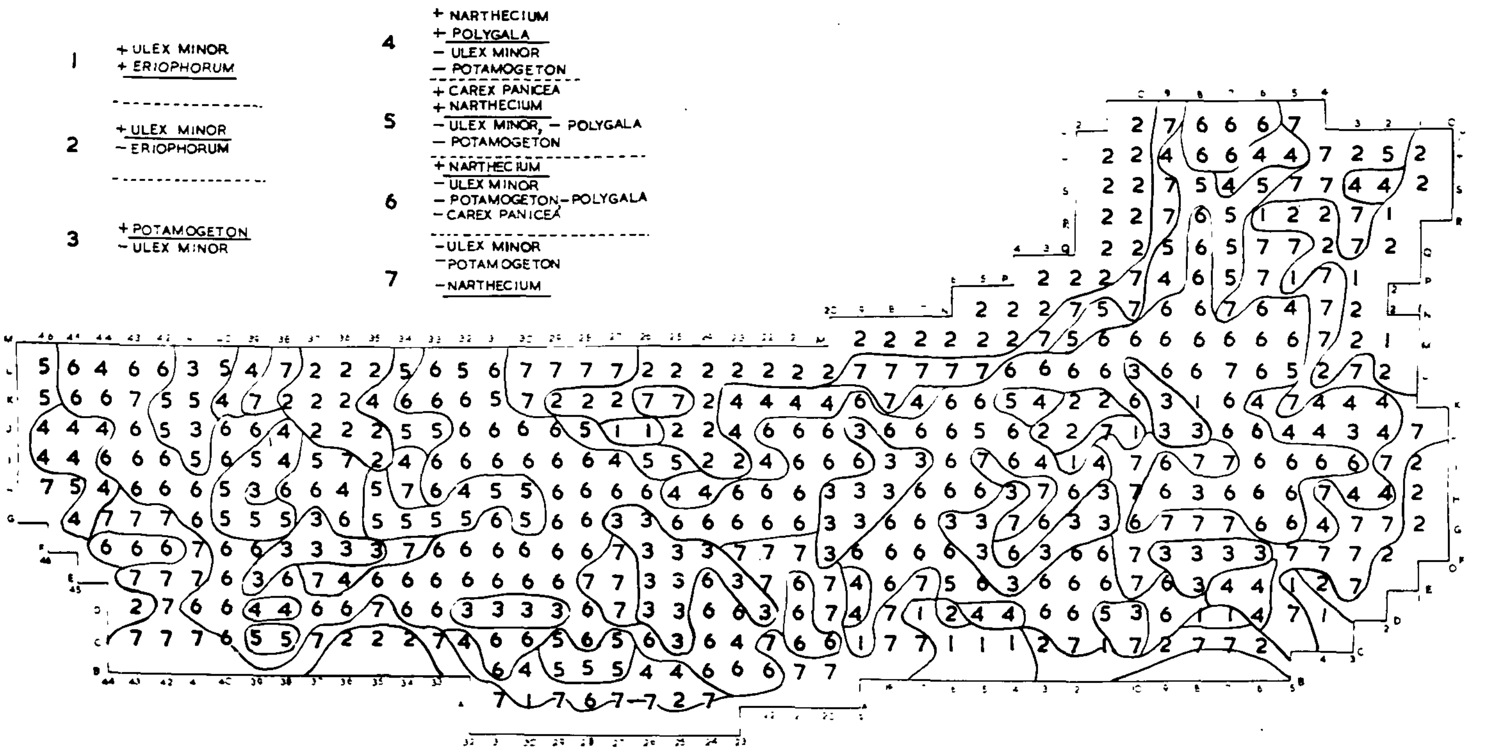
Community 2 is the + Potamogeton polygonifolius division of the -Ulex quadrats. It is concentrated in patches of about 15 quadrats each in the centre of the original Schoenus nigricans area. It comprises the open water communities and the very wettest parts of the Schoenus area.

Community 3 is the residuum left after the communities of the extreme habitats (wettest and driest) have been removed.

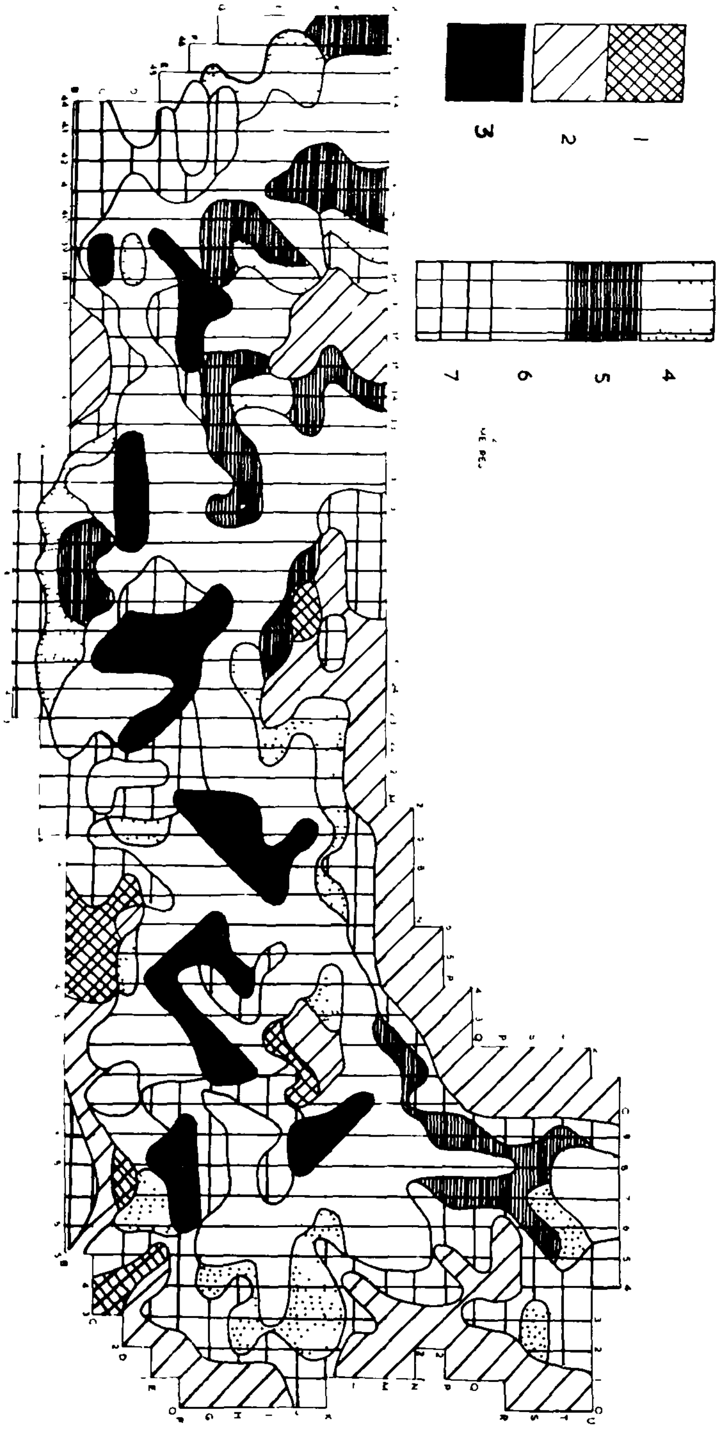
It is obvious that if this map is compared with the "3 community level" of the complete analysis (map 17) there is quite a considerable change in communities shown. The + Ulex minor community corresponds well with the -Sphagnum papillosum, -Narthecium of maps 16 and 17 except that the open-water communities are no longer included with the dry heath. On the other hand the "vascular-plants-only" analysis has not brought out the wet heath at this stage but has separated the wettest parts of the bog, while leaving the wet heath and general bog undifferentiated. This is a similar situation to that found at a similar stage in the hierarchy of the statistical phytosociological classification.

(b) : χ^2 of 30 : 7 community level. (maps 23 and 24)

The + Ulex minor quadrats which divide on the presence of Eriophorum angustifolium gives communities 1 and 2, the first (i.e. the +Eriophorum) being found as isolated patches in the original dry



Map 23. Quadrats of the communities present at a χ^2 of 30.



Map 24. Communities present at a χ^2 of 30.
(Generalised form of map 23).
For key see map 23.

heath probably due to slight damp hollows bearing an incipient bog flora, and the second, (i.e. -Eriophorum) occupying the remainder of the dry heath.

Community 3 is the same as community 2 of the previous map, the + Potamogeton, -Ulex minor community not having further divided. Comparison with the 6 community level map of the complete analysis which has a + Potamogeton community shows that the boundaries of this community agree very closely.

The -Ulex -Potamogeton quadrats divide on Narthecium and then Polygala serpyllifolia to give community 4 which occupies a discontinuous area peripheral to the original bog and which can be approximately compared with the subjective wet heath and the + Narthecium -Sphagnum of the full analysis but is much smaller in extent.

The quadrats without Polygala divide on Carex panicea to give community 5 which occupies the majority of those parts of the original wet heath and the + Narthecium -Sphagnum which were not occupied by the previous community, no. 4.

Community 6, + Narthecium, -Ulex, -Potamogeton, -Polygala and -Carex panicea, occupies the original general bog and those parts of the original Schoenus area not occupied by the present + Potamogeton community and by the very negative community no. 7. This latter occurs as scattered patches of about 4 - 7 quadrats in the original Schoenus area and also in the original dry heath and wet heath.

Comparison of the maps at this stage shows that the apparent divergences shown by the previous comparison are not maintained as the bog and wet heath have become differentiated although this latter is now represented by three communities, 4, 5, and 7.

At a minimum χ^2 of 22 there were eleven communities present (for their quadrats, see map 24) but these were not mapped as they appeared to form a complex mosaic.

2. Bryophytes only. (Vascular Plants and Lichens omitted)

(a) : χ^2 minimum of 60 : 3 community level. (maps 25 and 26)

The first division of the hierarchy on *Sphagnum papillosum* is the same as with the all species analysis and for a discussion of the +*Sphagnum* and -*Sphagnum* communities see page 40.

The -*Sphagnum papillosum* quadrats next divide on *Lepidozia setacea* to give communities 2 (+*Lepidozia*) and 3 (-*Lepidozia*). The former occupies some of the original wet heath and the +*Narthecium* -*Sphagnum* of the all species analysis and a few quadrats are scattered in the general bog. One of the compacted peat balks bridging the bog in the region of quadrats I 43 and K 41 and which was first brought out as a +*Narthecium* -*Sphagnum* community in the all species analysis is shown by the present analysis by the presence of *Lepidozia setacea*.

Community 3 occupies all the original dry heath and the parts of the wet heath not occupied by the +*Lepidozia*.

It is obvious that there is a reasonable correspondence with the communities of the all species analysis, the major point

TABLE 17.

Association-analysis results from computer

Bryophytes only

(for interpretation see table 12)

25/11/58--18

ASSOCIATION ANALYSIS (D.L.,MK.III)

HARTLAND MOOR

BRYOPHYTES ONLY.

SHORT (X/MIN = 17)

N 544
X/MAX = 210.54
S 29

N 240
X/MAX = 34.73
S 31

N 177
X/MAX = 28.25
S 17

N 9
FINAL

N 168
X/MAX = 25.20
S 16

N 110
FINAL

N 58
FINAL

N 63
FINAL

N 304
X/MAX = 64.16
S 16

N 71
FINAL

N 233
X/MAX = 46.12
S 10

N 4
FINAL

N 229
X/MAX = 49.94
S 22

N 116
X/MAX = 33.80
S 9

N 4
FINAL

N 112
X/MAX = 27.26
S 33

N 14
FINAL

N 98
FINAL

N 113
FINAL
END
X

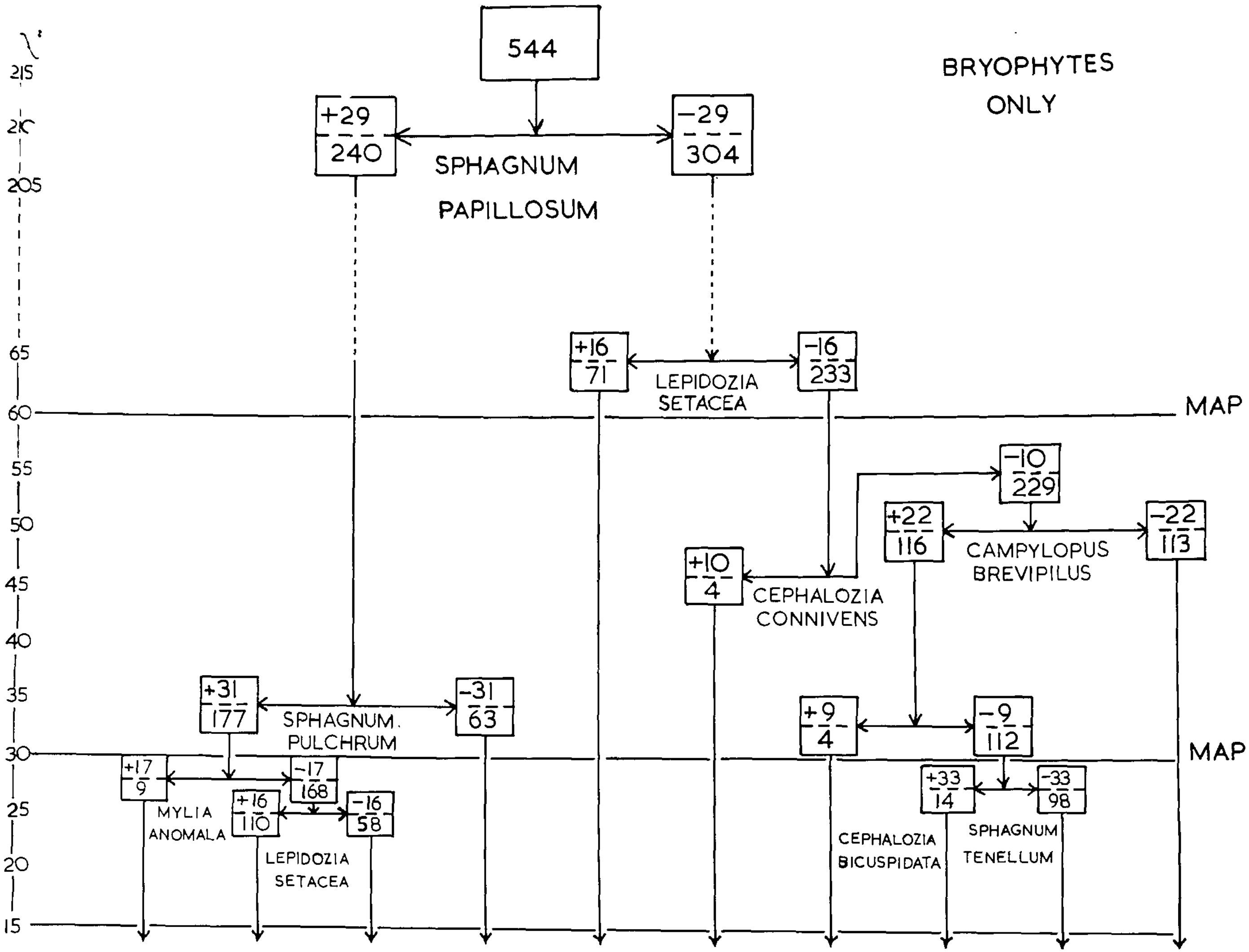
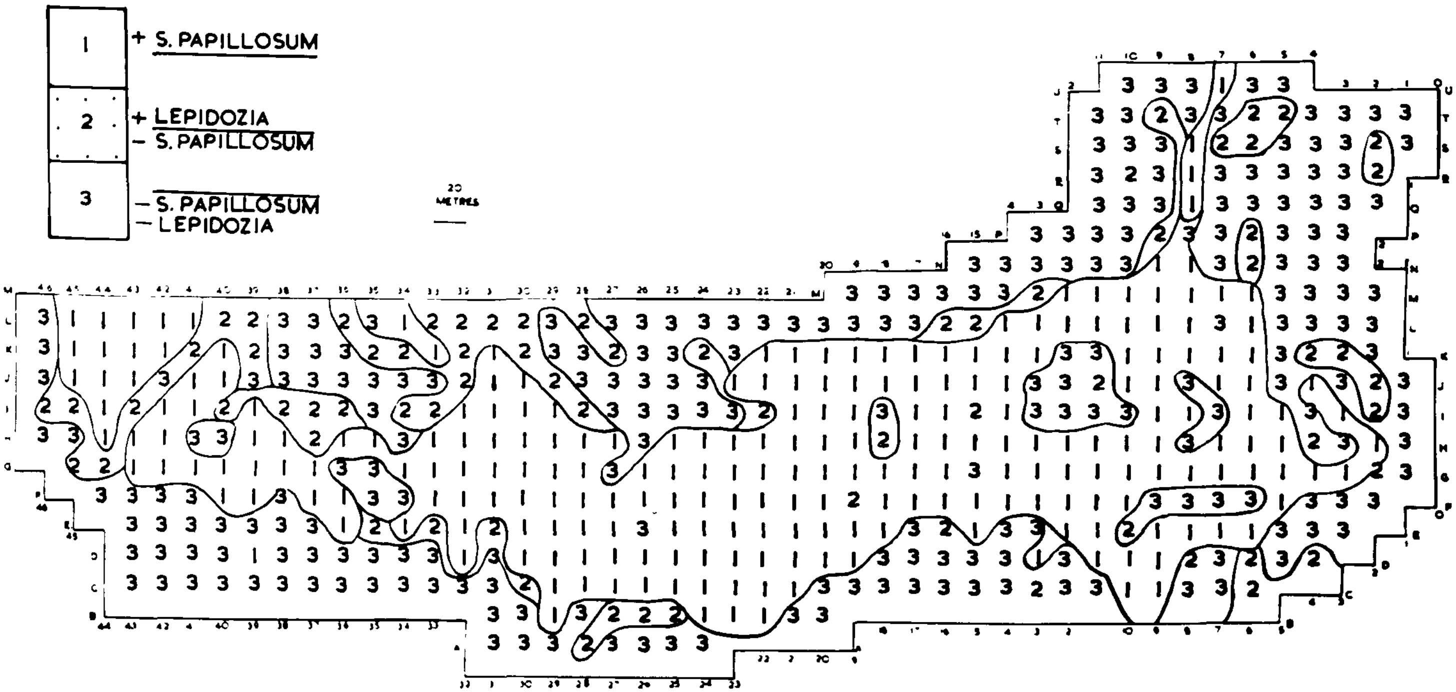
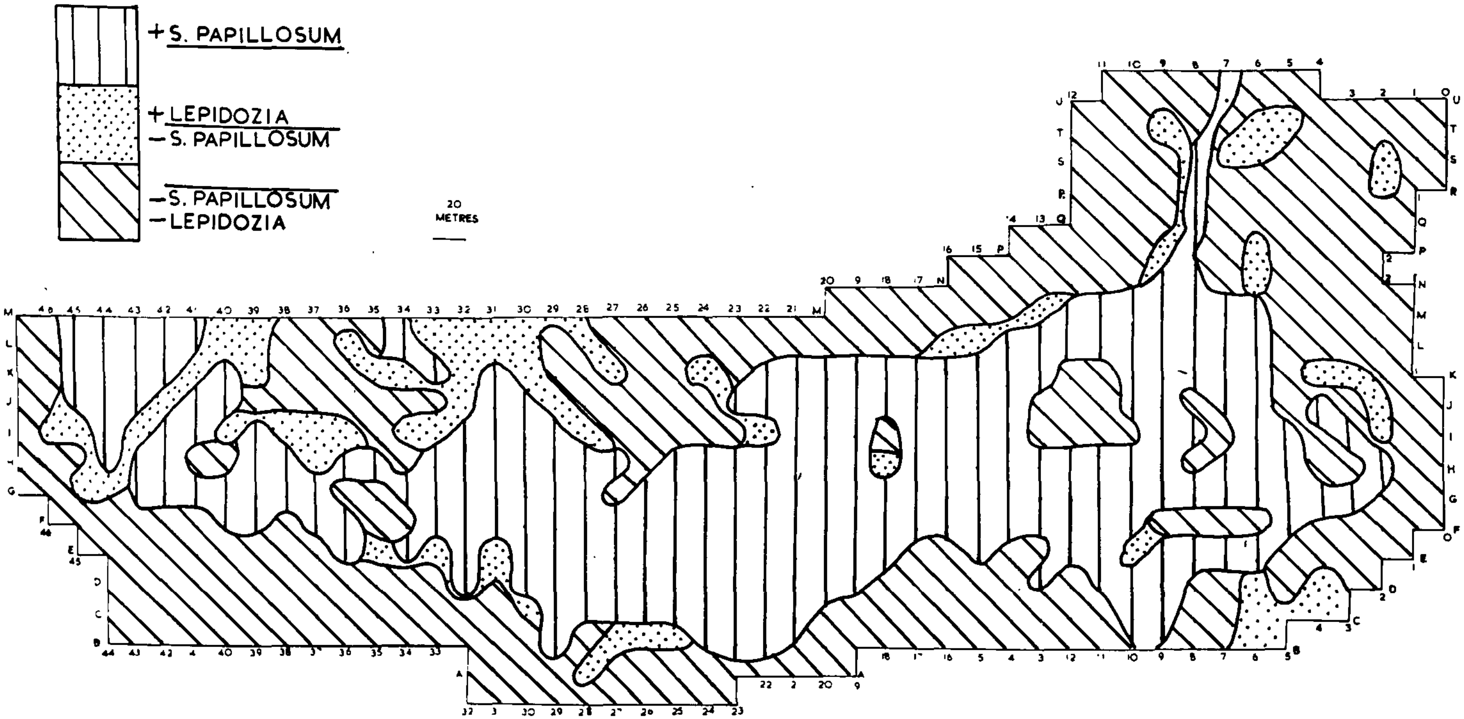


Figure no. 4 : Bryophytes only association-analysis results.



Map 25. Quadrats of the communities present at a minimum of χ^2 of 60.



Map 26. Communities present at a minimum of χ^2 of 60.

(Generalised form of map 25)

of difference is that the "bryophytes only" analysis has reduced the wet heath, by surrender to the "dry heath".

(b) : χ^2 minimum of 30 : 7 community level. (maps 27 & 28)

The area now starts to form a mosaic especially in the regions of the original dry and wet heath.

The + *Sphagnum papillosum* area now divides on *Sphagnum pulchrum* to give communities 1 (+ *Sphagnum pulchrum*) and 2 (-*Sphagnum pulchrum*). The community containing both the *Sphagna* occurs mainly in the upper reaches of the area as a community occupying the wide basin here. It is also found as a more or less continuous string of quadrats in the lower parts of the region. Community 2, i.e. + *Sphagnum papillosum* only, is found as large patches of quadrats in the lower reaches of the area and as a peripheral community in the rest of the area of the original bog community.

Community 3 has remained unchanged from no. 2 of the previous map.

The -*Sphagnum* and -*Lepidozia* community of the previous map divides on *Cephalozia connivens* to give community 4 of which there are only 4 quadrats occurring more or less at the boundary of the bog with the wet heath. The -*Cephalozia connivens* quadrats divide on *Campylopus brevipilus* and then on *Cephalozia bicuspidata* to give communities 5, 6 and 7.

Community 5, +*Campylopus* and +*Cephalozia bicuspidata*/ -*Sphagnum papillosum*, *Lepidozia setacea* and *Cephalozia connivens* is composed of only 5 quadrats which have no apparent definite habitat preferences except that none are found in the original bog communities.

MAP 27.

Bryophytes only association-analysis

Quadrats of the communities present at a minimum χ^2 of 30.

Key

1. +*Sphagnum papillosum*, + *Sphagnum pulchrum*

2. + *Sphagnum papillosum*, -*Sphagnum pulchrum*

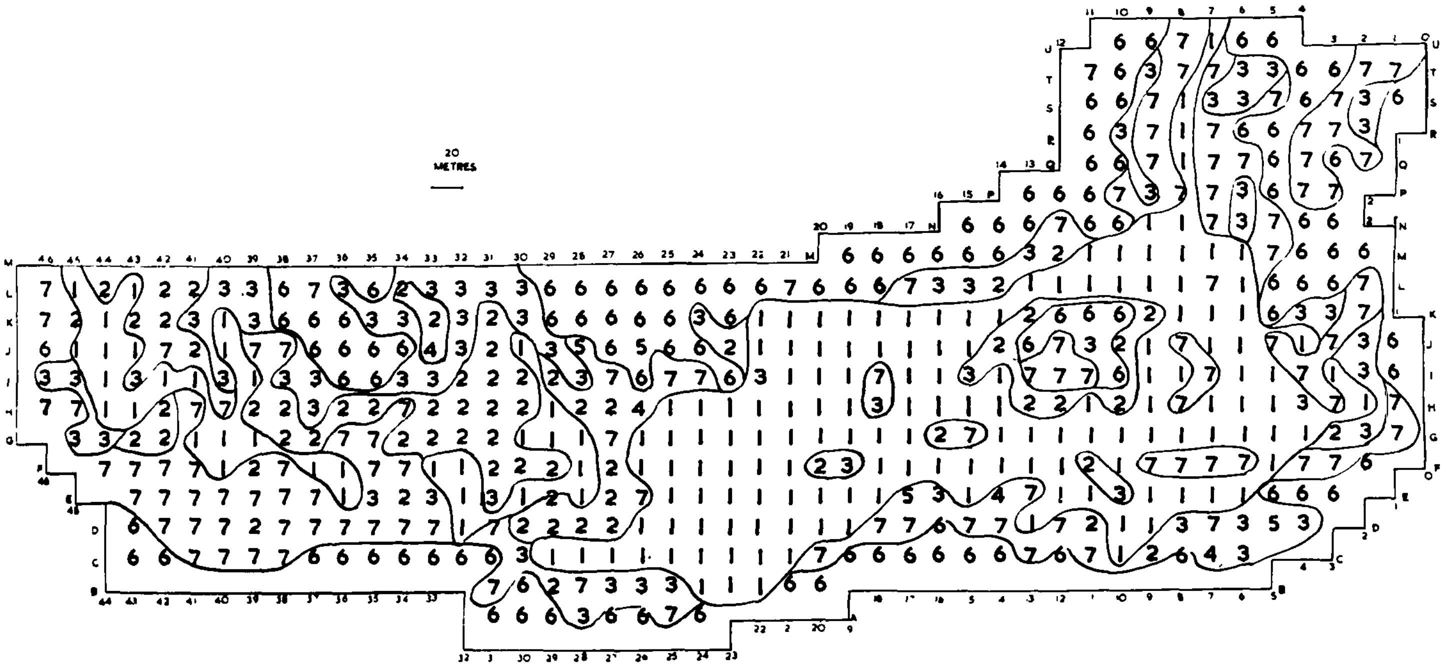
3. -*Sphagnum papillosum*, + *Lepidozia setacea*

4. -*Sphagnum papillosum*, -*Lepidozia setacea*, +*Cephalozia connivens*

5. -*Sphagnum papillosum*, -*Lepidozia setacea*, -*Cephalozia connivens*
   + *Campylopus brevipilus*, + *Cephalozia bicuspidata*

6. -*Sphagnum papillosum*, -*Lepidozia setacea*, -*Cephalozia connivens*
   + *Campylopus brevipilus*, - *Cephalozia bicuspidata*

7. -*Sphagnum papillosum*, -*Lepidozia setacea*, -*Cephalozia connivens*
   -*Campylopus brevipulus*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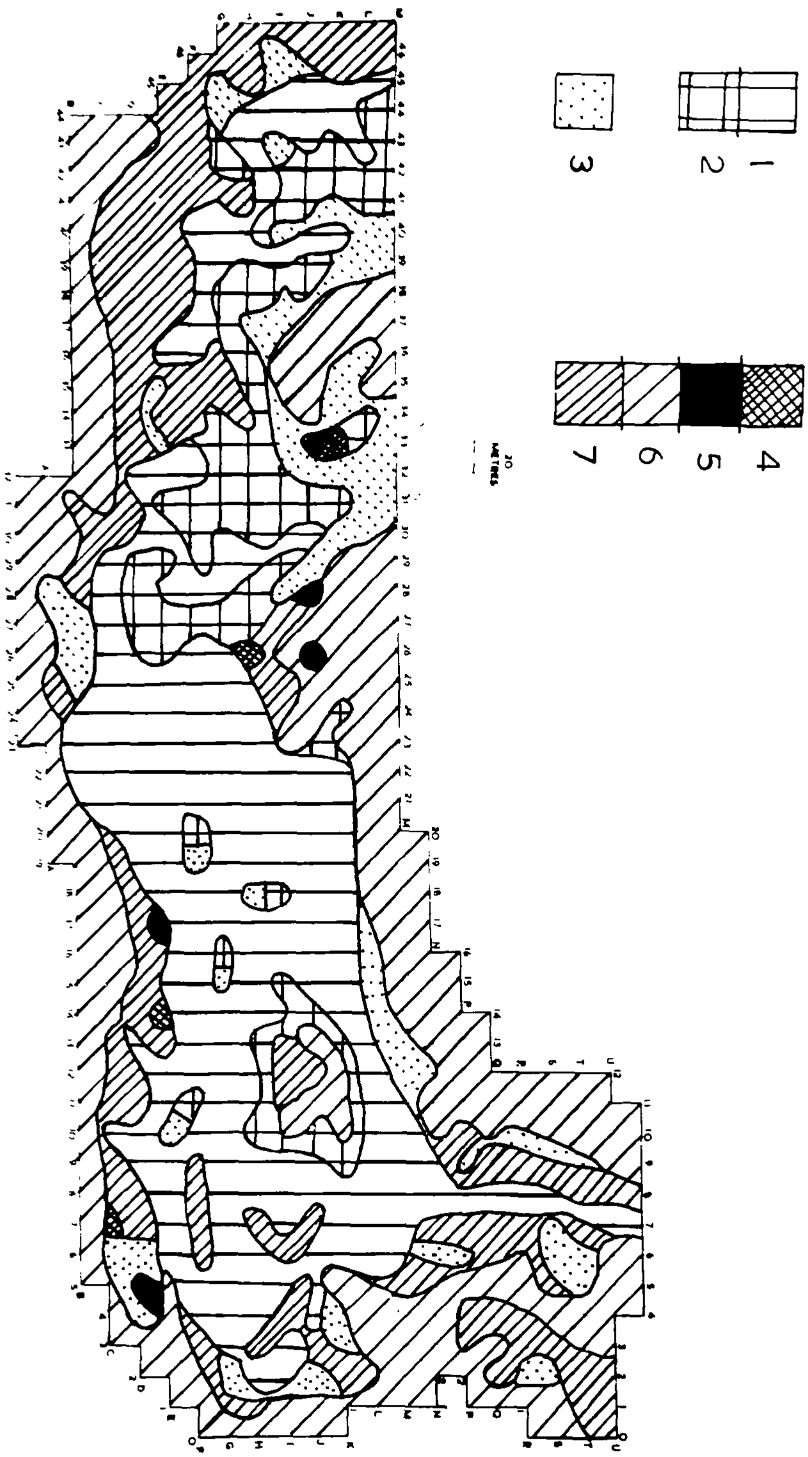


Map 28. Communities present at a minimum χ^2 of 30. (Generalised form of map 27).

For key see map 27.

Community 6, +Campylopus /-Sphagnum papillosum,-Lepidozia, -Cephalozia connivens and-Cephalozia bicuspidata corresponds more or less with the original dry heath.

The community at the very negative side of the hierarchy (no. 7) is composed of at least 5 elements.

a. It is peripheral to the bog and dry heath and therefore is approximately equal to a part of the original wet heath.

b. In the lower reaches it includes the wet heath and parts of the original general bog and Schoenus area.

c. In some places it corresponds with some of the larger pools e.g. the pool in the region of quadrats F 6 - 10.

d. Scattered quadrats of 7 occur in the original dry heath.

e. Scattered quadrats of 7 occur in the main mass of the bog.

Comparison of this map with the 6 community map of the "all species" analysis shows an approximate equivalence as far as the main communities are concerned, the major points of difference being that the very wet parts of the bog, shown as the+Potamogeton community of the full analysis, is not brought out by "bryophytes-only", and the lower reaches of the bog are divided into two communities on the basis of Sphagnum pulchrum in this analysis but remain homogeneous at this level in the "all-species" analysis.

3. Bryophytes and Lichens. (Vascular plants omitted)

(a) : χ^2 minimum of 60. (maps 25 and 26)3 community level.

The first divisions of this hierarchy were on Sphagnum papillosum and Lepidozia setacea respectively to give communities

<u>TABLE 18.</u>

Association-analysis results from computer

Bryophytes and Lichens only.

(for interpretation see table 12)

25/11/58--20

ASSOCIATION ANALYSIS (D.L.,MK.III)

HARTLAND MOOR

VASCULAR PLANTS OMITTED

SHORT (X/MIN = 17)

N 544
X/MAX = 210.54
S 29

N 240
X/MAX = 43.49
S 2

N 6
FINAL

N 234
X/MAX = 35.57
S 26

N 13
FINAL

N 221
X/MAX = 24.80
S 23

N 22
FINAL

N 199
X/MAX = 22.81
S 31

N 152
X/MAX = 19.93
S 6

N 2
FINAL

N 150
X/MAX = 18.91
S 16

N 94
FINAL

N 56
FINAL

N 47
FINAL

N 304
X/MAX = 64.16
S 16

N 71
FINAL

N 233
X/MAX = 46.12
S 32

N 26
FINAL

N 207
X/MAX = 44.98
S 1

N 21
FINAL

N 186
X/MAX = 40.41
S 27

N 9
FINAL

N 177
X/MAX = 38.23
S 33

N 41
FINAL

N 136
X/MAX = 20.28
S 22

N 82
FINAL

N 54
FINAL
END

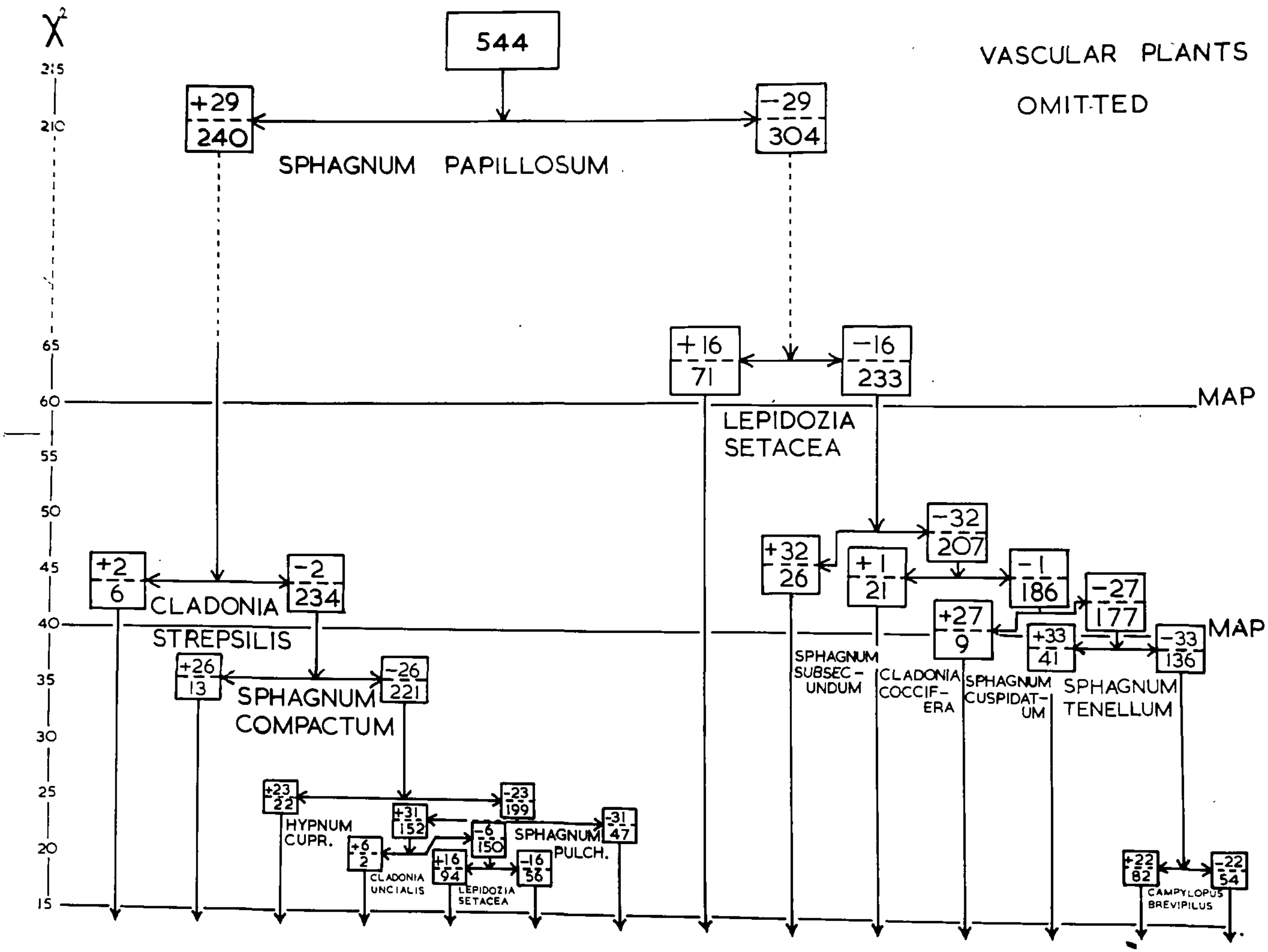


Figure no. 5 : Bryophytes and Lichens association-analysis results hierarchy.

1, 2 and 3 identical with those of the previous analysis. (see pages 40 & 53 and maps 25 and 26).

(b) : χ^2 minimum of 40 : 7 community level (maps 29 & 30)

The Sphagnum papillosum quadrats divide on Cladonia strepsilis to give communities 1 and 2, with and without this species. The 6 quadrats of community 1 are the same as the 6 quadrats of community 1 of map 18 of the "all-species" association-analysis (see page 42).

Community 2 occupies the majority of the general bog, the Schoenus area and the Carex rostrata area.

Community 3 is the same as community 2 of the previous map (see page 51).

The negative side of the hierarchy, i.e. the -Sphagnum papillosum and -Lepidozia setacea divides on Sphagnum subsecundum var. auriculatum to give the 26 quadrats of community 4 which occurs as isolated quadrats and small groups of about 4 quadrats, scattered in the original general bog and Schoenus areas; in both cases they probably represent pools.

The -Sphagnum papillosum, -Lepidozia, -Sphagnum subsecundum community divides on Cladonia coccifera to give community 5 which is to be found at the very periphery of the area in the regions of the dry heath where there is no peat present.

The -Cladonia coccifera quadrats divide on Sphagnum cuspidatum to give 9 quadrats with this species, all occurring as single or double quadrats in the original general bog, Schoenus area

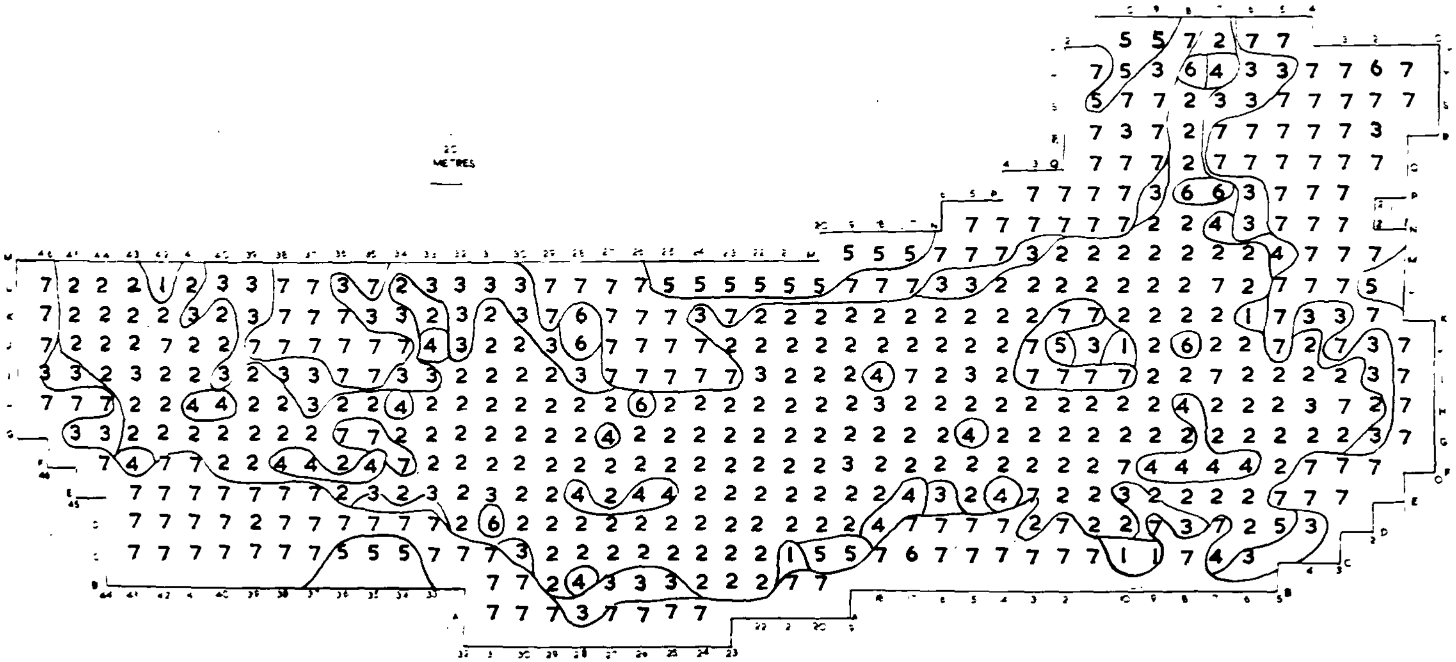
MAP 29.

Bryophytes and Lichens association-analysis

Quadrats of the communities present at a minimum χ^2 of 40.

Key

1. +*Sphagnum papillosum*, +*Cladonia strepsilis*
2. +*Sphagnum papillosum*, -*Cladonia strepsilis*
3. -*Sphagnum papillosum*, +*Lepidozia setacea*
4. -*Sphagnum papillosum*, -*Lepidozia setacea*, +*Sphagnum subsecundum*
5. -*Sphagnum papillosum*, -*Lepidozia setacea*, -*Sphagnum subsecundum*, + *Cladonia coccifera*
6. -*Sphagnum papillosum*, -*Lepidozia setacea*, -*Sphagnum subsecundum*, -*Cladonia coccifera*, +*Sphagnum cuspidatum*
7. -*Sphagnum papillosum*, -*Lepidozia setacea*, -*Sphagnum subsecundum*, -*Cladonia coccifera*, -*Sphagnum cuspidatum*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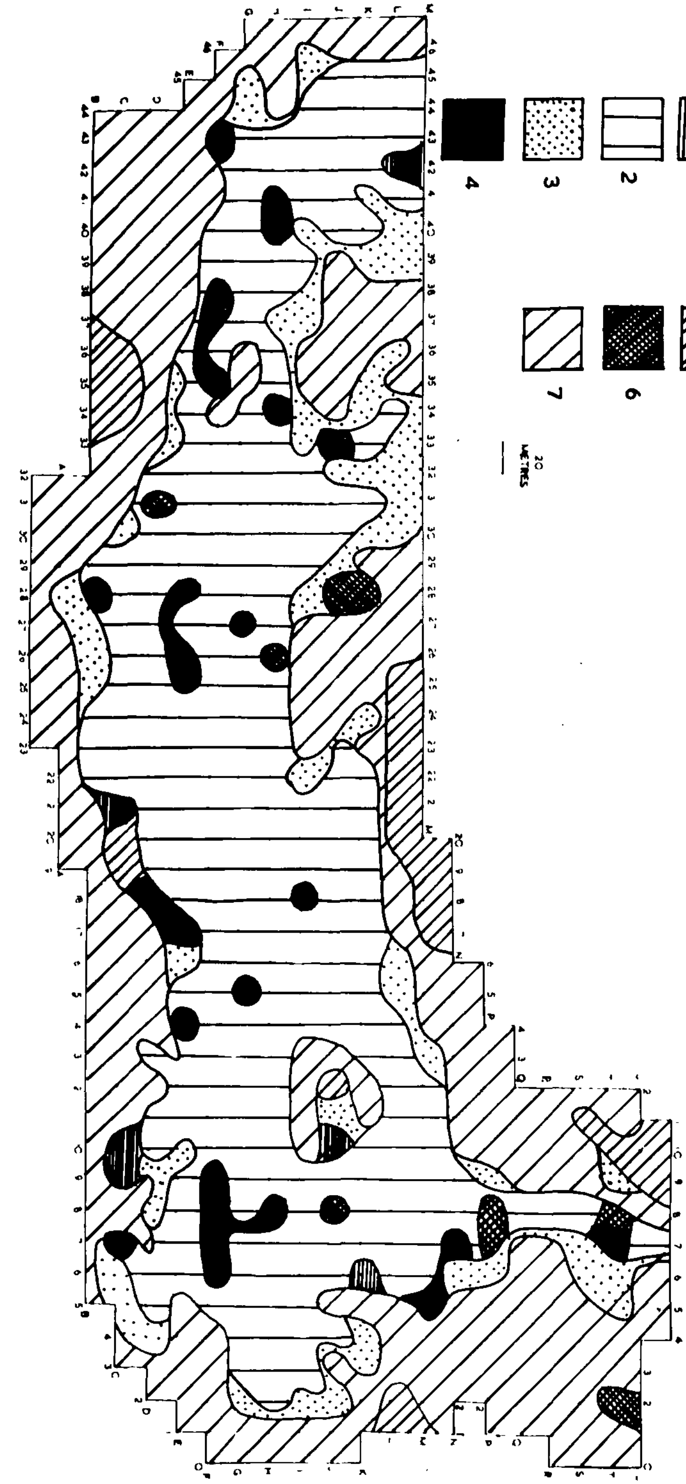


Map 30. Communities present at a minimum χ^2 of 40.
(Generalised form of map 29).
For key see map 29.

and wet heath. They probably are pools of a more intermittent nature than those of the previous community, Sphagnum cuspidatum having been noted to withstand the periods of drought that occur in the open-water communities of the slight hollows of the wet heath.

Community 7, -Sphagnum papillosum, -Lepidozia, -Sphagnum subsecundum, -Cladonia coccifera, -Sphagnum cuspidatum, more or less surrounds the entire experimental area and corresponds with the original dry heath and parts of the wet heath.

E. Conclusions.

These truncated association-analyses have all kept the main divisions of the area, i.e. the dry heath, the wet heath and the bog and brought them out at generally a fairly high level in the hierarchies. There have been boundary changes because the analyses have tended to separate off the extreme elements of the original communities. This is in sharp distinction to the "all species" analysis where the extreme elements, the wettest bog (pools) and the driest heath remained together until a very low point in the hierarchy.

This investigation suggests that the "bryophytes and lichens" analysis probably gives the results most closely resembling that of the full species analysis for this particular area. This is reasonable since bryophytes form such a conspicuous and prominent part of the bog communities, and lichens are a characteristic part of both wet and dry heaths. It is clear that the analysis of vascular plants alone alters the picture considerably even at the highest levels of the hierarchy. This result is in some contrast to a previous analysis of a woodland area (Lambert and Cetik, unpublished) where bryophytes were entirely subordinate to the picture given by the vascular plants.

It is clear therefore that the effect of removal of different groups of systematically related species may vary from one type of vegetation to another and that reduction of species by this method cannot be generally recommended.

F. The omission of numerically unimportant species.

1 : Introduction.

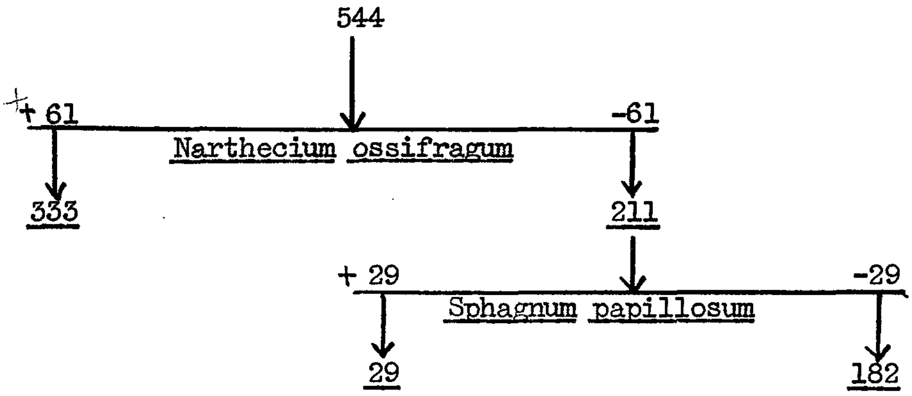
This part of the investigation was not carried very far as only the Mark II programme was available and therefore no significance levels of the hierarchial divisions were known and cross comparison of results must necessarily have been incomplete.

2 : Method.

The species in less than 2%, 5%, 10% and 15% of the quadrats were omitted from the analyses, i.e. 16, 33, 45 and 52 species omitted.

3 : Results.

With the omission of species in less than 2%, 5% and 10% of the quadrats, the first three divisions of the hierarchy remained the same as with the full analysis. When species in less than 15% of the quadrats were omitted the picture was quite changed although the first divisions were on the same species as before, these were used in the opposite order, i.e. the area divided first on *Narthecium* and the negative side divided next on *Sphagnum papillosum*.



4 : Discussion.

As far as this investigation was pursued it appears that this method of omission gave better results than the omission of systematic groups provided the cutting was not too severe. It is in the minor divisions of the hierarchy that the main differences are likely to appear and the general effect is to blur rather than radically alter the general picture. It confirms in fact a preliminary analysis on a simpler community (Williams and Lambert, unpublished).

Since the work in this section was completed a further suggestion had been made that theoretically the best method of reducing species is to omit those calculated to have the lowest associations. These could be ascertained by printing out the first table of $\sum \sqrt{\frac{\chi^2}{N}}$ values for the individual species, i.e. take the analysis as far as the first division and then omit those species that have a value of less than a certain amount. The analysis would then be restarted with these species masked thus giving an analysis of the most highly associated only. Although this would not reduce time for the collection of data and would involve a lengthy preliminary computer calculation it would have the advantage that total computer time would be reduced and the results would be expected to be more reliable. The possibilities of this method are at present under investigation by an undergraduate member of this Department.

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VIII.
DISCUSSION

Three reasons were put forward in the introduction for attempting this problem and this section will discuss these reasons in the light of the results obtained. However, as reason 1 (a comparison of subjective and objective methods of classification of vegetation) and reason 2 (an extension of work on association-analysis) are closely connected it will be convenient to discuss them together.

Association-analysis and the comparison of subjective and objective methods of classification.

The discussions of the previous methods have all related the results to those of the original subjective survey but as it is the association-analysis only that gives results completely independent of the worker, the results of the other methods should now be compared with those of the objective method.

It should be first realised, however, that there are fundamental differences between the subjective and objective methods used. The most important difference is that the association-analysis does not classify vegetation but quadrats, i.e. sample areas of the habitat, and that therefore this method gives primarily an ecological classification and it is only secondarily that the species are examined. A truly phytosociological classification of the vegetation could be obtained by an association-analysis on "inverse data", i.e. where the samples are the species and the attributes are the quadrats, but the scale of the analysis is beyond the reach of any existing computer.

The original assessment used criteria that were a mixture of habitat and vegetation, but the attempts to re-define these subjective communities - the phytosociological methods - are mainly floristic in that they deal with species lists from sample areas and take no account of the other characters of the sample area. The traditional, modified phytosociological method is completely floristic but the statistical method has some element of the habitat (see below).

The attempt to use objective statistical methods for the re-defining of subjective boundaries gives the least satisfactory results of all methods from an ecological and phytosociological standpoint. This is probably an inevitable result of attempting to mix subjective with objective methods. Moreover, the hierarchial arrangement of the re-defined communities of the statistical phytosociological method in a way similar to that of the association-analysis, gives results that are ecological as well as phytosociological, and this combination of subjective and objective methods with ecological and phytosociological results cannot be expected to be very useful.

Objective methods, phytosociological or ecological, appear to be of little use if used on data that were not collected in the first instance in an objective manner.

Taking the broad view, the phytosociological results are further away from the objective results than are the subjective results. This is perhaps because the mode of action of these semi-objective methods is to re-define and thereby strengthen, the subjective boundaries.

The subjective assessment gave approximately the same major divisions as did the association-analysis but it emphasised the _Schoenus_ area which floristically has no counterpart in the association-analysis although part of it was selected out as the wet _Potamogeton polygonifolius_ community. The true pattern of this community was apparently obscured by the relatively large _Schoenus nigricans_.

The method of association-analysis has now been used to process a larger area with more basic data. The results show that this objective method is likely to be a useful ecological tool, not so much for the actual nature of the groups of quadrats produced, but for the manner in which these classificatory units are arranged and related, and for showing up hitherto unnoticed habitat features and for exposing new problems which can later be studied by orthodox methods. It is also very useful for providing an objective background with which later detailed phyto-sociological and other studies may be integrated.

The subjective method, being independent of the samples, should give some idea of the mosaic of the area although the scale used for the drawing of the maps did not allow this to be done in detail. The association-analysis, and to a lesser extent the phyto-sociological methods, give only the pattern of the vegetation that is large in relation to the scale of the sampling. To show the mosaic in detail the size and scale of sampling would have to approximate to the size of the individual parts of the mosaic. Work by Williams and Lambert (unpublished) on similar vegetation types has shown that the closer the sampling the better the mosaic is shown, e.g. the zonation of a bog and the surrounding heaths was exhibited in great detail when the sample was of one-quarter of the area, but Hartland Moor, with only one four-hundredth of its area sampled, could not be expected to show the mosaic in detail.

There is a tendency for some of the smaller, extreme facies of a community to be emphasised at the expense of the main mass of the community by methods with a certain degree of objectivity as they tend to reduce the central matrix of data to order by splitting off the more atypical, extreme elements.

Contributions to the specific ecology of Hartland Moor.

The specific ecology of Hartland Moor has been advanced not so much in the traditional manner of correlating subjectively determined communities with standard observations on the habitat but by pinpointing discontinuities in the habitat as shown by groups of associated species and indicating their relative importance.

It is clear that the major discontinuities produce a zoning which is more distinct and survives throughout all analytical methods in the marginal areas than in the central bog. It is not surprising therefore that it is the bog region which shows most variation from the completely zoned communities of typical valley bog as described by Rose (1953 b). Of the eight zones distinguished by Rose for valley bogs in general only the outer four have clear counterparts at Hartland. These are :-

8. The surrounding dry heath or bracken communities with little or no peat, a typical podsol profile and a deep water table.

7. Dry heath over a thinner peat layer. This is represented on Hartland by the original Calluna areas and also as the -Sphagnum papillosum, -Narthecium ossifragum, -Erica tetralix community of the association-analysis.

6. Damp heath over a damp peat layer. This is brought out in the association-analysis as the +Erica tetralix zone, and is also represented by the Campylopus brevipilus community of the phytosociological method.

5. Wet heath zone. Suggestions of the other zones except

for the central alder carr are scattered within Hartland bog but forming a mosaic whose individual parts are so ill defined that they tend to shift with changes in the criteria used in the various analyses.

In many ways the general pattern of communities is more comparable with that described by Newbould (1953) for the basin bog of Cranesmoor in the New Forest, and the traditional phytosociological analysis in particular gives communities which may be directly compared with Newbould's shielded and flushed areas, but in addition Hartland has certain specific features of its own; the presence of scattered pools, possibly related to the early history of the area, has given communities not usually represented in bogs of this type, and the presence of compacted peat balks has been shown to modify the vegetation locally.

Indeed such impediments to drainage may well have so diffused the general flow of water and this together with shape and size of the valley is possibly responsible for the central ill-defined mosaic. The crude habitat data available is obviously insufficient to explain the vegetational pattern fully, but lines of further work on the area have now to some extent been clarified.

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P. F. HUNT.

1959.

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APPENDIX 1.

Species on punched cards.

(Where no variety or subspecies is noted, the type variety or subspecies is intended)

1. Cladonia coccifera (L.) Willd.
2. Cladonia strepsilis (Ach.) Wain
3. Cladonia impexa Harm.
4. Cladonia pyxidata var. chlorophaea Florke
5. Cladonia sylvatica Hoffm.
6. Cladonia uncialis (L.) Web.
7. Hypogymnia physodes (L.) Wats.
8. Calypogeia fissa (L.) Raddi
9. Cephalozia bicuspidata (L.) Dum.
10. Cephalozia connivens (Dicks.) Spr.
11. Cladopodiella fluitans (Nees) Buch
12. Cephalozia macrostachya Kaal.
13. Cephalozia media Lindb.
14. Cephaloziella starkei (Funk) Schiffn.
15. Gymnocolea inflata (Huds.) Dum.
16. Lepidozia setacea (Web.) Mitt.
17. Mylia anomala (Hook.) S.F. Gray
18. Odontochisma sphagni (Dicks.) Dum.
19. Riccardia pinguis (L.) S.F. Gray
20. Riccardia sinuata (Dicks.) Trev.
21. Aulacomnium palustre (Hedw.) Schwaegr.
22. Campylopus brevipilus B. & S.
23. Hypnum cupressiforme var. ericetorum B. & S.

24. Leucobryum glaucum (Hedw.) Schp.

25. Polytrichum commune Hedw.

26. Sphagnum compactum DC.

27. Sphagnum cuspidatum Ehrh. ex Hoffm. emend.

28. Sphagnum molle Sull.

29. Sphagnum papillosum Lindb.

30. Sphagnum plumulosum Röll.

31. Sphagnum pulchrum (Lindb.) Warnst.

32. Sphagnum subsecundum var. auriculatum (Schp.) Lindb. emend. Åberg

33. Sphagnum tenellum Pers.

34. Pteridium aquilinum (L.) Kuhn.

35. Pinus sylvestris L.

36. Agrostis setacea Curt.

37. Betula pendula Roth.

38. Calluna vulgaris (L.) Hull.

39. Carex echinata Murr.

40. Carex limosa L.

41. Carex panicea L.

42. Carex rostrata Stokes

43. Cirsium dissectum (L.) Hill

44. Drosera intermedia Hayne

45. Drosera rotundifolia L.

46. Eleocharis quinqueflora (F.X. Hartmann) Schwarz.

47. Erica ciliaris L.

48. Erica cinerea L.

49. Erica tetralix L.

50. Erica x watsonii Benth.

51. Eriophorum angustifolium Honck.

52. Gentiana pneumonanthe L.

53. Hypericum elodes L.

54. Juncus acutiflorus Ehrh. ex Hoffm.

55. Juncus bulbosus L.

56. Juncus effusus L.

57. Juncus squarrosus L.

58. Menyanthes trifoliata L.

59. Molinia caerulea (L.) Moench.

60. Myrica gale L.

61. Narthecium ossifragum (L.) Huds.

62. Dactylorchis incarnata (L.) Vermeul. ssp. incarnata

63. Pinguicula lusitanica L.

64. Potamogeton polygonifolius Pourr.

65. Potentilla erecta (L.) Räusch.

66. Polygala serpyllifolia Hose.

67. Pedicularis sylvatica L.

68. Rhynchospora alba (L.) Vahl.

69. Salix cinerea ssp. atrocinerea (Brot.) Silva & Sobrinho

70. Salix repens L.

71. Schoenus nigricans L.

72. Scirpus cespitosus L.

73. Ulex europaeus L.

74. Ulex minor Roth.

75. Utricularia minor L.

76. Utricularia intermedia Hayne

The following species were found in one quadrat each and were those omitted from the phytosociological and objective analyses.

Cladonia furcata (Huds.) Schrad.

Cladonia polydactyla Flörke

Cladonia verticillata (Hoffm.) Flörke

Evernia prunastri (L.) Ach.

Usnea sp.

Pellia epiphylla (L.) Corda.

Dicranum scoparium Hedw.

Dicranella heteromalla (Hedw.) Schp.

Ceratodon purpureus (Hedw.) Brid.

Sphagnum palustre Linn.

Alnus glutinosa (L.) Gaertn.

Chamaenerion angustifolium (L.) Scop.

Carex pulicaris L.

Scirpus fluitans L.

Frangula alnus Mill.

Luzula multiflora (Retz.) Lejeune

The following species were noted from the area during the subjective survey but were not found in any quadrats.

Nymphaea alba L.

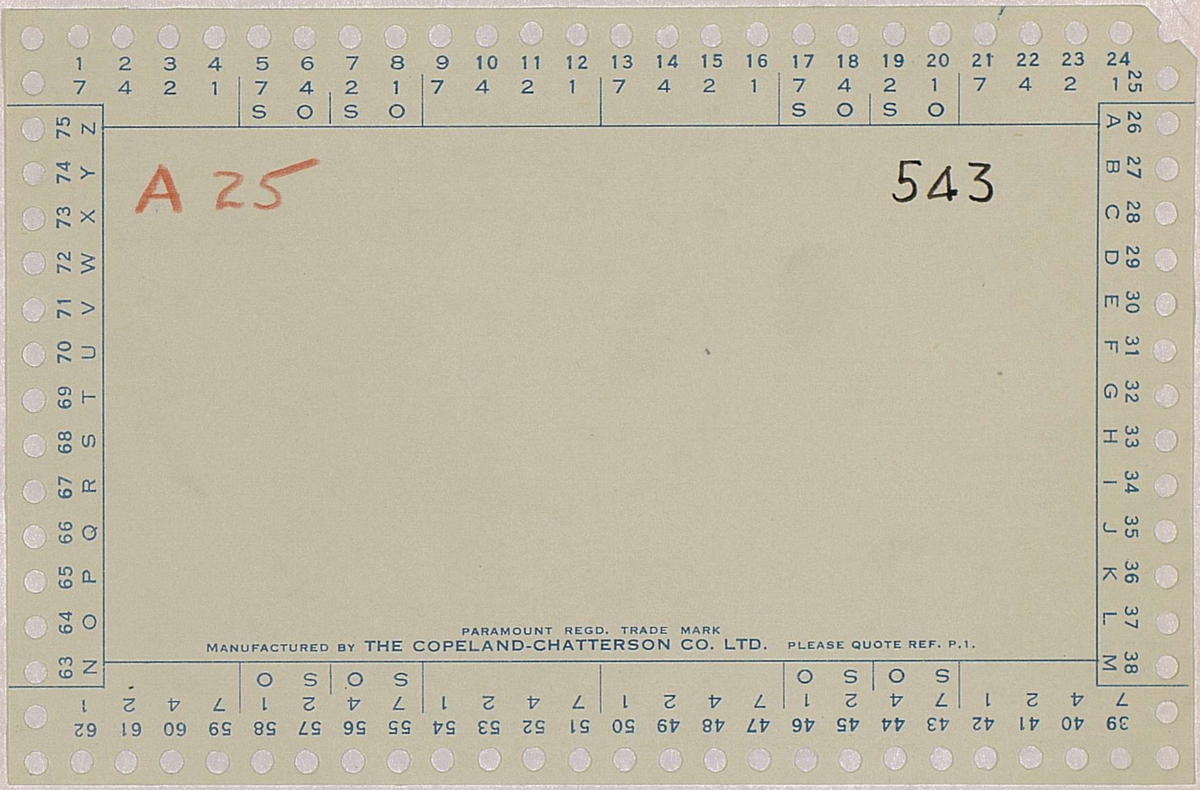
Lycopodium inundatum L.

Zygogonium "ericetorum"

Sphagnum magellanicum Brid.

Polygala oxyptera Reichb. = P. vulgaris L.

APPENDIX 2.



SPECIMEN DATA CARD

A separate card is used for each quadrat. The punched numbers represent the serial numbers of the species present in the quadrat.

The use of punched cards allows the quadrats to be sorted quickly on the species selected by the analysis.

The number in red (e.g. A 25) signifies the position of the quadrat on the grid. The quadrats were also arranged serially (e.g. 543) - quadrat no.1. being U 1 0 and no. 544 being A 24.

APPENDIX 3.

FIDELITY : ITS STATISTICAL MEASUREMENT AND APPLICATION

Introduction

The phytosociological methods of Braun-Blanquet (1928) involve the recording of arbitrarily-selected sample areas of vegetation - "stands" - judged by eye to be homogeneous as to their species-composition. These stands are then classified into groups on the basis of the species they contain. The extent to which a given species is restricted to a given group is called its "fidelity", and is measured by an arbitrary score. Attempts have been made (Cole 1949, Goodall 1953) to place this concept on a sounder quantitative basis, and the primary purpose of this note is to re-examine these attempts.

FIDELITY AS A COMPARATIVE MEASURE

Fidelity necessarily involves a comparison; by virtue of its definition the fidelity of a given species to a given group is not a property of that group alone, but of that group in comparison with one or more reference groups. If the reference groups are changed, the fidelity to the given group will in general change also, and the choice of reference groups is thus fundamental. If the whole population of stands is divided into n groups, any selected one of these may be compared with any of the following reference groups :-

1. The whole population. Such a comparison is valid only when the whole population is presumed homogeneous, and it is desired to test whether the selected group is a representative sample. Since the

reference group here includes the selected group, the concept of fidelity - which is essentially based on restriction - can no longer apply.

2. The whole population, less the selected group. If $n > 2$, the reference group is believed to be heterogeneous, the selected group to be homogeneous. Comparison of such unlike groups is undesirable.

3. The next most similar group. If all species are to be used in defining the reference group, a second subjective step is needed. Designation of the reference group can be made objective by specifying it as that group containing the next smaller proportion of stands containing the given species; but it then incurs the fault of loss of information. No distinction is made between the case in which the proportion is almost identical in groups 1 and 2 but falls to zero in groups 3 to n, and the case in which all groups contain substantially the same proportion.

4. All other groups taken one at a time. This is statistically unexceptionable, but for s species will provide $\frac{1}{2}ns(n - 1)$ measures of fidelity - normally too large a number to handle. Nevertheless, any statistically satisfactory measure should be based on a comparison of this type.

The statistical problem thus resolves itself into the need for simplifying method 4. The number of groups cannot be reduced; but the individual species recorded will be of very different value in discriminating between the groups. If, therefore, the species can be placed in order of discriminatory importance, it may well be found that relatively few species will justify further mathematical treatment. This order can be ascertained by setting up, for each species, a 2 x n contingency table (presence or absence for each group); the χ^2 for the whole table, with (n - 1) degrees of freedom, can be calculated in the usual way and the species listed in order of descending χ^2 value. (Although the contribution for each group is usually calculated separately, these contributions cannot themselves be used as indices of fidelity, since they are not independent). Actual measures of fidelity to each group can then be calculated for each species in turn, the process being terminated when sufficient information has been obtained. The termination can be made objective by setting a lower limit, either of χ^2 itself or of the mean-square contingency χ^2/N, where N is the total number of stands; but such a list can only be set in the light of experience, and this does not at present exist.

INDICES OF FIDELITY

For any given comparison, a measure - an index - of fidelity is required; and, as Goodall has pointed out, such a measure is statistically equivalent to an index of association. We shall here be primarily concerned with qualitative (presence-or-absence) data, so that the association can be expressed in the form of a 2 x 2 contingency table, whose individual entries represent a number of stands :-

	Selected group	Reference group
Given species present	a	b
Given species absent	c	d

We will put $\frac{a}{a+c} = p_1$ and $\frac{b}{b+d} = p_2$; it is these proportions which the index is required to compare.

(A) Requirements and zero-properties of indices of association

Ideally, an index should satisfy three requirements :-

1. It should vary (as is conventional) between -1 for complete dissociation, through zero for independence, to + 1 for complete association. If this requirement is satisfied, different indices can be directly compared.

2. It should remain unchanged if the elements in any one column (or row) are multiplied by a constant. In the table above, this requirement would be fully satisfied if the index remained unchanged when a and c were multiplied by x, and b and d were multiplied by y; i.e., it should remain invariant so long as both p_1 and p_2 remain invarient.

3. It should remain unchanged if all elements are multiplied by the same quantity. If requirement 2 is satisfied, so necessarily is requirement 3; but the reverse is not true.

Indices may be constructed to behave in different ways when one cell, or both cells on a diagonal, become zero; there are two main possibilities:-

1. The association becomes perfect when any one cell becomes zero; I shall call this "zero-property 1".

2. The association becomes perfect only when both cells on a diagonal are zero; I shall call this "zero-property 2".

The practical results of choosing one or other of these properties may be exemplified by the following tables :-

3	0
997	10

(i)

300	0
700	100

(ii)

30	0
0	10

(iii)

For an index with zero-property 2, only (iii) is perfect, and the value of the index for (ii) will normally be higher than that for (i). For an index with zero-property 1, all three tables represent perfect association.

(B) Conventional indices

These fall into two main classes; we need only consider the simplest member of each class.

1. The coefficient of association (Q), where

$$Q = \frac{ad - bc}{ad + bc}$$

This satisfies requirements 1, 2 and 3, and has zero-property 1. Its sampling distribution is known, and its significance can therefore be tested; but its standard error falls to zero if any one cell of the table becomes zero, so that it retains zero-property 1 even if regarded as a sample.

2. The correlation coefficient (r), where

$$r = \frac{ad - bc}{\sqrt{(a+b)(a+c)(b+d)(c+d)}}$$

This satisfies requirements 1 and 3, but not 2; it has zero-property 2. Its distribution is known, but is complex; for qualitative data its significance is best tested by reference to the corresponding χ^2 obtained from the relationship $\chi^2 = r^2 (a+b+c+d)$. It has the incidental advantage that it can be constructed from quantitative data, though its significance then becomes more difficult to test.

(C) Cole's index (Cole, 1949)

Cole took exception on ecological grounds to the use of indices with zero-property 2, and, perhaps unaware of the existence of existing indices with zero-property 1, suggested a new index. It was defined as

$$\frac{a - a_0}{a_{max} - a_0}$$

where a_0 represents the expectation of a (for independence), and a_{max} represents the largest value a can take - i.e., (a + b) or (a + c), whichever is the smaller. We will take $a_{max} = (a + b)$. It is then easily shown that Cole's index is equal to

$$\frac{ad - bc}{(a+b)(b+d)}$$

This satisfies requirements 1, but under rather special conditions. It becomes +1 when b = 0, whatever the values of a, c and 4; but it becomes -1 only when a = d = 0 and b = c. The requirement is associated with more stringent conditions on the negative side than on the positive side. It satisfies requirement 3 but not 2. It has zero-property 1 on the positive side only, in that the association becomes perfect if $b = 0$ but not if $a = 0$.

In extenuation of Cole's index, it must be admitted that traditional considerations of fidelity have been entirely confined to <u>positive</u> associations; but this restriction hardly seems necessary when the simple coefficient Q has all the properties desired and behaves identically for positive and negative associations.

(D) <u>Goodall's index</u> (Goodall, 1953)

Goodall takes exception to the fact that conventional indices are symmetrical; he states that Cole's index "would not be so appropriate as an index of fidelity, however, since it would express association of the community with the species as well as association of the species with the community, only the latter being implied in the concept of fidelity". It is of course perfectly possible to devise asymmetrical indices, so that the value changes when the contingency table is turned on its side, even though the statistical advantages of such indices are not obvious; as a matter of fact, Cole's index is itself asymmetrical. Goodall's own index is fundamentally defined as

$$\frac{p_1 - p_2}{p_2} = \frac{ad - bc}{b(a + c)}$$

This fails to satisfy requirement 1 on the positive side; it ranges from -1 through zero to infinity. It satisfies requirements 2 and 3. It has zero-property 1, but at the expense of becoming infinite on the positive side when b = 0. To overcome this difficulty, Goodall applies Yates's correction to the original table. The concept of continuity is not applicable to an index of association, and its use here serves only to evade the infinite value obtained when b = 0. With Yates's correction the final index (though this is not the form in which Goodall gives it) now becomes equivalent to

$$\frac{2(ad - bc) - (a + b + c + d)}{(2b + 1)(a + c)}$$

It now fails to satisfy any of the three basic requirements, and its zero-properties are complex.

(E) Conclusion

It is clear that, as compared with more conventional indices, the indices of Cole and Goodall have no advantage and several disadvantages. Either Q or r will suffice. Both satisfy requirements 1 and 3; it is for an ecologist to decide whether he prefers Q, which satisfies requirement 2 and has zero-property 1, or r, which fails to satisfy requirement 2 but has zero-property 2. However, if the 2 x n contingency table of the previous section has been used to order the species, an index with zero-property 1 must not be used; for the calculation of χ^2 implies acceptance of a system with zero-property 2, and the system cannot be validly changed in mid-calculation.

THE APPLICATION OF FIDELITY TABLES

The results of the procedures discussed in the foregoing sections will be a series of tables of measures of fidelity for some of the species to all of the groups; it remains to consider the use to which these tables can be put. As fidelity is a comparative measure, it cannot itself be used to define groups *ab initio*; but it can be used to discriminate between them, and one such use suggests itself. Any one species will be positively associated with some groups, negatively associated with others, and not significantly associated with the remainder; the conspectus of such associations may be expected to be simpler if a high significance level is chosen. The presence or absence of species may then be used to re-define the groups, the whole population of stands being hierarchically divided by reference at each stage to the species with the highest available χ^2 in the original contingency-list. A new set of groups will be obtained, very similar to the original groups but defined in the most economical form possible - i.e., by reference to the smallest possible number of species. It must always be remembered, however, that the function of the statistical work here has *only* been to define the original subjective boundaries in this economical form; the primary subjective boundaries are not thereby made objective, and the method remains subjective. The statistical work can only refine the results of the original decision; if that decision was unsound, statistical calculation will not rectify it.

APPENDIX 4.

The computer programme.

I. The association-index

The result of using "corrected" χ^2 as an association-index has been considered in Williams and Lambert (1959). One objection was already clear: the fact that the hierarchy changed with the significance-level. There is, however, a further disadvantage which becomes more serious in a computer programme - the tendency to generate ambiguities. These, it will be recalled, were resolved by reference to the next highest class in which discrimination was possible. However, to hold all the $\Sigma\chi^2$ tables for this purpose would use storage-space that can ill be spared from the quadrats; in the "flexible" programme, therefore, the $\Sigma\chi^2$ tables were punched out. When an ambiguity was reached, the machine was programmed to stop; the hierachy (so far as it had progressed) was constructed, the resolution decided by reference to the appropriate $\Sigma\chi^2$ tables, and the appropriate species-number fed back into the computer. This process wasted a considerable amount of computing-time, partly because of the time taken in punching-out and printing the tables, and partly because of the time taken by the operator to make the decision and communicate it to the computer.

Even so simple a community as Matley produced 4 ambiguities, a situation which was clearly intolerable, and which confirmed us in our preference for one of the two uncorrected indices. There is unlikely to be any great difference between these; $\frac{\chi^2}{N}$ gives rather more weight to individually intense associations than does $\sqrt{\frac{\chi^2}{N}}$, but neither can be claimed to be in any special sense "right". However, we intend ultimately to invoke the full techniques of factor analysis, to which association analysis, as we have previously explained, is a form of approximation. These techniques are normally applied to correlation coefficients - i.e., when presence-or-absence data is in use, to $\sqrt{\frac{\chi^2}{N}}$. We have therefore decided to use the same index for association-analysis. Ambiguities may now be expected to be uncommon; however they are not theoretically impossible, and provision must be made for them. (see below)

II. Ambiguities

Apart from the accidental equality (to the equivalent of 11 decimal digits) of two unrelated $\Sigma\sqrt{\frac{\chi^2}{N}}$ values - a contingency so improbable as to require no provision - ambiguities can arise from two causes :-

(i) Certain species occur together in a group of quadrats, but are all absent from the remainder (likely to occur occasionally at low levels of subdivision in highly heterogeneous areas). Such species are statistically indistinguishable. It is of no importance which is selected for division, since in every case the same group of quadrats would be separated.

(ii) Two species are significantly associated and the remainder indeterminate (extremely unlikely - we have not yet met such a case - but not quite impossible). It is of little importance which species is selected, since only one further division is possible; provided the species concerned are known, the alternative division can be explored at leisure.

Since in neither case is the decision important or irrevocable, an arbitrary decision will serve perfectly well, we have therefore arranged for the machine to note, in its type-out, that an ambiguity has been encountered between certain species-numbers; it will then select the first - i.e., the lowest - species-number for the purpose of the next division.

III. Hierarchy or Pooling

The theoretical objections to Goodall's "pooling" system were considered in the previous paper. Briefly, they are as follows :-

(i) The system is likely to give substantially the same final groups as a hierarchical division, but by a route requiring longer computation;

(ii) In any but a simple community, the final groups will be difficult to characterize, and the route by which they are obtained, unlike the successive divisions of a hierarchy, will be meaningless. The result of a practical test on the Matley data is given in Fig.2.

We note, first, that all the final groups are statistically simple, i.e. they are of the type which would normally be obtained by hierarchical division. Moreover, of the nine groups obtained by both methods, seven are identical. The remaining two in fact differ only in the placing of the 6 quadrats (jdHF); in the hierarchical division these join the 12 quadrats (jdHF) to give thehomogeneous 18-quadrat (jdH), and in the pooling division they join the 37 quadrats (jdhF) to give the homogeneous 43-quadrat (jdF). (Williams and Lambert loc. cit)

Both methods require the scanning of the 9 final groups; but the intermediate groups scanned number 8 in the hierarchical division, 13 in the pooling. Of the 8 in the hierarchy, only 2 contain more than 200 quadrats; of the 13 in the pooling division, no less than 7 exceed 200 quadrats. Moreover, it is these large groups, with few indeterminate species, that require the bulk of the computing time, Our theoretical objections are thus fully upheld by the practical test, and we have discarded the "pooling" system of division.

IV. Significance Levels

Successive orders of division in the hierarchy will not in general be of equivalent importance. According to the nature and disposition of the underlying factors, one subdivision may reduce the residual heterogeneity enormously; a corresponding division on the other side of the hierarchy may bring about very little reduction. We require a measure of the heterogeneity of each class under examination, which can be used as a means both of estimating the fall in level brought about by division, and of terminating the subdivision at some assigned minimum level of heterogeneity. We consider these two aspects in turn.

1. Measures of heterogeneity.

The ideal measure, if we were using the correlation matrix itself, would be the sum of the significant latent roots after the matrix had been reduced to its lowest possible rank by appropriate choice of communities. This would represent the total significant variance of the matrix, and would necessarily fall on subdivision. However, the whole matrix, not merely the column sums, would need to be stored, and the computation required would be so formidable as to make even an approximation to this measure quite impracticable.

Another possibility is to use the first latent root of the contingency matrix. Unfortunately, as the subdivision proceeds, it is likely that a relatively higher proportion of the variance in each sub-group will be concentrated in the first root; if this occurs in practice, the roots may actually rise, A crude estimate of this root can be obtained from the $\Sigma|r|$ values already stored in the computer *, and test-runs on the Beaulieu and Matley data showed that, after an initial fall, the value of the root did in fact rise once more.

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* Let the correlation coefficients be denoted by r_{ij} , and take r_{ij} = 0 when i = j; let s be the number of statistically effective species; then the estimate, λ , actually used was given by

$$\lambda_1 = \frac{s}{s-1} \cdot \frac{\sum_{i=1}^{s} \left(\sum_{j=1}^{s} |r_{ij}| \right)^2}{\sum_{i=1}^{s} \sum_{j=1}^{s} |r_{ij}|}$$

i.e., the sum of the squares of the loadings on the first averoids axis of the matrix ($|r_{ij}|$).

We must therefore have recourse to a cruder test based on the values of the individual elements of the matrix, and may first consider the result of using the highest single $\sqrt{\frac{\chi^2}{N}}$ value.

As the variance due to the main factors is reduced by subdivision, mosaic elements - trivial from the point of view of the analysis as a whole - become predominant; and in small groups of quadrats the association-index may easily rise, for one pair of species or another to its maximum value of unity. Once more, therefore, the highest value may be expected to fall and then rise as subdivision proceeds.

A very different situation obtains with the highest individual χ^2, which has the right properties for the wrong reasons. It will normally fall; but this is primarily due to the fall in the size of the class under examination, and is a measure of the reliability of the association in a sample of that size. It will fall sharply towards the end of the analysis, owing to the increasingly drastic effect of Yates's correction in very small samples. A rise is not impossible, but it will be relatively uncommon. Theoretically, it is barely defensible, since it is a measure of a property quite different from that whose measure is required; but it seems to be the only simple parameter available with approximately the properties required, and its defence must rest on its usefulness in practice. The programme has been designed so that the highest individual χ^2 within the class under examination is punched out.

2. Termination of subdivision.

If the highest single χ^2 is used as a measure of heterogeneity - used, in fact to define the levels of successive divisions - it must also be used for terminating the subdivision. The simplest solution is to fix a constant value; when, in any class, no single χ^2 equals or exceeds this value, the class is designated "final" and is not further subdivided. In Paper I, the value of 3.84 (corresponding to $P = 0.05$) was chosen; with Yates's correction, a class must exceed 7 quadrats before this value can be attained.

Consider a population which has been hierarchically subdivided down to this level, and precisely replicate each quadrat n times. The hierarchy will not change, but all the χ^2 values will be multiplied by n; and additional subdivisions previously below the level of significance, will be added at the lower end. Nevertheless, it is the major divisions which are of the greatest interest, and the addition of this finer subdivision at the lower levels greatly increases the time for the whole process. This difficulty can obviously be overcome by fixing a termination-value which is proportional to the number of quadrats (N) in the whole population before subdivision. From such experience as we have, we have arbitrarily selected this value as $N.\ 2^{-5}$ to the nearest integer. This we designate "short division", and the programme provides a choice between this and the "long division" terminating at 3.84.

Of course, even a group of 7 quadrats can be highly heterogeneous; but the inability of even "long" division to examine groups of this size is unlikely to cause inconvenience in ecological work. However, in certain circumstances subdivision may be called for on occasion, and it is desirable to be able to continue the subdivision until all ultimate groups are completely indeterminate- i.e., their members are identical or differ in respect of only one attribute.

This facility is not built in to the programme; but a "complete subdivision" tape is available which permanently alters the programme in the computer so that it will carry out this operation.

V. Programming restrictions

The method has been programmed for the Ferranti "Pegasus" digital computer, and three restrictions are inevitable:-

(i) Number of species. The working unit of "Pegasus" is the "word" of 38 binary digits. Each of these digits will be taken to represent a particular plant species, with the value 1 if the species is present, 0 if it is absent; each complete "word" will then represent a quadrat. In this form of working, which we shall conventionally refer to as "single-length", the community under study must not contain more than 38 different species, Alternatively, it is possible to use two words to represent each quadrat, the number of permissible species being thereby raised to 76; such a "double-length" programme is necessarily slower to run. Triple- and quadruple-length working are theoretically possible, but, as we shall show, have practical objections so serious as to render them inadmissible.

(ii) Number of quadrats. The amount of information which "Pegasus" can store is limited; it can be greatly increased by the addition of a magnetic-tape unit, but, since this is not likely to be generally available, and has not been available to us, our programme refers to the standard machine. With single-length working the programme can handle up to 3360 quadrats; with double-length, 1680 quadrats. This is the first objection to triple- or higher-order working; it would reduce to an inadmissible extent the number of quadrats which could be handled.

(iii) Time of calculation. Computing-time is both expensive and subject to competing claims; the time of computation should therefore ideally be kept down to a reasonable length - of, say some few hours. Now the time required for an analysis not only depends roughly linearly on the number of quadrats, but increases roughly as the square of the number of species. As a guide, we find that the calculation of the first $\sum\chi^2$ table for 76 species and 100 quadrats - requiring the setting up of 2850 contingency tables and the computation of all the relevant χ^2 values - takes something over an hour. This is the second reason for our rejection of larger number of species.

VI. Masking of species.

The quadrat-data may contain species of very different taxa or life-forms; a wood, for example, will usually contain trees, angiosperm ground-flora, bryophytes, and lichens. It may well be desirable to analyse these groups separately, or to find the effect on the analysis of excluding one or more of them. Provision has therefore been made whereby any species can be "masked", in that while the mask is in operation, the species is excluded from the analysis. The same system is also used to inform the computor that certain of the binary digits are not in use; if, for example, a community contains only 20 species, it is undesirable that computing-time should be wasted in scanning the remaining 18 positions.

VII. Function of Programme.

(1) The programme will accept information defining a set of individuals, each specified by the presence or absence of a number of attributes. This population is subdivided hierarchically in such a way as to reduce the residual variance to the greatest possible extent at each division. The programme is terminated by reference to the highest χ^2 encounted in each class under examination, at one of two possible levels: "short" division, terminating at $\chi^2 = N. 2^{-5}$, where N = number of individuals; and "long" division, terminating at $\chi^2 = 3.84$.

(2) Any attributes may be "masked" and thereby excluded from the analysis.

(3) Facilities are provided for the subdivision of the population on any desired attribute by manual operation of the computer. If a long run has to be removed from the machine, it can later be quickly brought to the same point by hand and the automatic subdivision restarted.

(4) For each class examined, the computer will print :

(a) the number of individuals in the class (as N 258)

(b) the maximum χ^2 encountered (as X/MAX = 78.29) if this is not less than the termination value; or "FINAL" if it is; and "END" if all individuals are accounted for, and subdivision is complete

(c) the serial number of the attribute selected for division (as S 28).

VIII. Mode of Operation.

(1) The computer considers all possible pairs of attributes, and for each sets up a 2 x 2 contingency table. From this is calculated (a) χ^2 with Yates's correction, and (b) the correlation coefficient r. The values of $|r|$ are summed as they are obtained in respect of each attribute. The highest $\Sigma|r|$ is checked against the termination-value; if it is less, the group is designated "final"; if it is not, the highest χ^2 encountered in the class is punched out.

(2) If not final, the attribute with the highest $\Sigma|r|$ is selected and its serial number punched out. The class population is then sorted on this attribute into two groups; the number of individuals which contain the attribute is punched out. This forms the new population for which the process is repeated.

(3) The process works down the positive side of the hierarchy; when a group is designated "final", the computer scans back to ascertain the location and size of the next class awaiting examination. When the whole population is included in "final" groups the computer will print "end", and set itself to receive a new mask for the same set of data.

(Restrictions.

The present programme "D. L. Mk. III" will accept not more than 1680 individuals specified by not more than 76 attributes. A faster single-length programme which will process 3360 individuals specified by not more than 38 attributes is in preparation.)

IX. Working Space.

The programme, and its association storage-locations, occupy blocks B1 - 89 of the main store; the data is in B90 onwards (two addresses are required as a "blank" for sorting; these are initially B90.0 and 90.1). The programme uses the whole of the computing store.

X. Timing.

The bulk of the time is taken in setting up the 2 x 2 tables, each of which requires the scanning of all individuals in the class under examination. The time for any one class is thus approximately proportional to the number of individuals (about 100 can be scanned per second); but is also nearly proportional to the square of the number of attributes not masked in that class.

XI. Procedure for Punching Data - and Mask-Tapes.

(1) General:

Punching the tape is not difficult; it should require only a few minutes' instruction and a little practice. This section is not intended to be intelligible to a reader who has no experience of the tape-punching equipment; it will, however, enable him to prepare his own tapes after instruction. We shall deal with the data- and mask-tapes in turn.

(2) The data-tape:

(a) The name sequence.

The initial leader of blank tape is ignored; everything which immediately follows is treated as a name sequence and (apart from the character "Er") will be copied by the computer into the output tape. The name should begin and end with C R L F, and is followed by blank tape (not more than 2 ɸ 's). Everything which follows this blank tape will be treated as data. The name-sequence must not be omitted.

(b) Species-numbers.

The serial numbers of the species present in each quadrat are punched individually, and separated by " / ". If species 2, 9 and 35 were present they would be punched as 2 / 9 / 35, or as 2 / 35 / 9 - the order is immaterial. If a run of species is present, for example numbers 3, 4, 5, 6, 7, 8, 9 and 10, it should be punched as "3 - 10". The only character which may appear between the digits of a two-figure number, or between a number and the " - " which signifies a run, is "Er". In no circumstances may the same number be punched twice within any one quadrat.

(c) Quadrats.

A quadrat is terminated by " . ". It will usually be convenient to punch C R/L F; but if, in species-poor quadrats, it is desired to hold several quadrats on one line of the type-out, they may be separated by the character "Sp". A typical quadrat would thus be punched as 1 / 4 / 7 - 1 1 / 2 9 / 7 2 - 7 5.C R L F

(d) The check-sum.

After the last quadrat leave a little blank tape (see (V) below) and then punch λ . This must be followed by blank tape (more than 2 ɸs), which is in turn followed by C R/L F + N/C R/L F λ L ɸ, where N is the total number of quadrats on the tape. The tape now ends. If the check-sum does not agree with the number of quadrats - i.e. the number of full-stops, on the tape, the computer will enter a loop stop in U 0. 1+.

(e) <u>Combination of tapes.</u>

It may occasionally be desirable to combine data from two areas and therefore to use the date from two separate tapes; but once the check sum has been reached this is impossible. If, in the blank tape which follows the last quadrat, and before the λ, the character "+" is added, the computer will encounter a 77 stop at that point; the second tape can now be read in.

(f) <u>Unassigned characters.</u>

Any character may appear on the name-sequence; but once the data is reached, the only permissible characters are C R, L F, S p, E r, /, -, +, · , λ, ɸ and the digits 0 - 9. If any other characters appear on the tape there will be a loop stop in U 2 · 1+.

(3) <u>The mask-tape.</u>

Like the data-tape, this <u>must</u> begin with a name-sequence followed by blank tape. The main section takes the form of a single quadrat, ending in " . ", in which the numbers punched are those which it is desired to <u>exclude</u> from the analysis. If, for example, it is desired to exclude species-numbers 1, 2, 5, 6, 7 and 8, and if only 20 species are present, so that 21 - 76 are not represented at all, punch " 1 / 2 / 5 - 8 / 2 1 - 7 6. " Finally punch λ; the tape now ends. Any number of different mask-tapes may, of course, be prepared for the same set of data. Unassigned characters in the mask-tape will cause loop stops as for the data-tape.

THE BASIC DATA TYPE-OUT

The type-out begins with a name sequence.

Each full-stop represents the end of a single quadrat.

The numerals represent the serial numbers of the species present in each quadrat.

The tape ends with the number of quadrats which should have been punched.

The quadrats are arranged in groups of tens to facilitate quick reference.

HARTLAND MOOR

1-4/22/38/74.
1/3/6/22/26/38/44/45/47/49/59.
8/26/31/38/44/45/49/50/51/47/59/61/65/68.
9/12/23/27/29/31/45/47/49/51/59/61/68.
2/22/38/47/48/51/59/61/65/73.
3/22/38/44/45/47/49/50/51/59/72.
2/3/6/38/74.
1-3/6/22/38/48/74.
2/3/8/16/22/26/33/44/45/47/49/57/59/61/65/66/68.
19/24/27/31/44/45/47/49/51/59/61/68.

31-33/44/45/47/49/50/51/59/61/68.
2/3/6/16/26/38/44/45/48/49/59/61/66/68.
2/16/26/38/42/44/45/47/49/50/51/59/61/65/66/72.
2/22/26/38/45/47/49/50/59/65.
2/22/38/47/49/50/59/65/74.
26/27/38/41/44/45/47/49/50/51/59/61/65/67/70.
36/38/47/48/59/73/74.
1-4/6/7/22/38/48/74.
2/22/38/47/48/49/59/74.
26/38/41/44/47/49/50/*59/68/72.

16/27/29/31/32/41/45/47/49/50/51/59/61/65.
16/22/26/27/32/41/44/45/47/49/50/51/59/61/66/68.
16/22/41/44/45/47/49/54/59/61/65/68.
2/38/47/49/59/66/72.
2/22/26/38/47/49/50/59/66.
2/26/33/41/44/45/47/49/50/51/59/61/65/66/68.
3/16/26/33/45/47/49/50/59/61/65/66/70/72.
2/4/6/22/38/47/49/59/66/72/74.
2/22/25/36/38/74.
2/16/22/25/36/38/47/48/49/59/74.

2/6/26/38/44/45/47/49/50/51/59/66/68/72.
16/21/29/31/44/45/47/50/51/59/61/68.
26/41/49-52/54/59/61/65/72.
2/22/36/41/47/49-51/59/66/67/74.
2/22/38/48/49/59/66/72/74.
2/38/49/59/66/74.
2/36/38/41/47/49-51/59/66/67/72.
9/15/16/22/26/28/45/47/49/51/59/65/66/70/72/74.
2/22/38/48/74.
2/22/38/48/74.

26/38/41/44/45/47/49-51/59/61/68/72.
16/18/27/29/31/45/47/49-51/59/61/68.
9/26/36/41/44/45/47/49-51/59/61/65/72.
2/41/47/49-51/59/66/72.
2/22/38/47/49/59/66.
2/36/38/48/49/59/66/74.
2/22/38/47/49/51/59/65/67.
2/36/38/47/49/59/66/74.
2/22/38/48/74.
22/38/48/74.

2/22/38/59/74.
2/26/38/44/45/49/50/59.
16/18/22/24/26/27/31/38/41/45/47/49/51/59/61/66/68/72.
8/27/31/38/41/45/49/50/51/59/61/68.
26/27/31/38/41/44/45/49/50/51/59/61/65/72.
16/22/26/38/41/45/47/49/50/51/65/72.
11/14/15/22/38/47/49/51/59/65/74.
15/25/26/38/47/49-51/59/65/73.
2/36-38/47-49/51/59/65/74.
2/22/25/36/38/74.

2/22/25/36/38/48/74.
2/22/36/38/48/49/59/66/74.
2/38/47/49/59/66.
2/22/41/47/49/50/51/59/61/72.
2/22/38/41/49/51/59/72.
16/18/27/29/31/38/45/47/49/51/59/61/68.
16/18/29/31/38/45/47/49/50/51/59/61/68.
31/32/44/51/55.
8/16/*27/31/32/44/45/49/50/51/59/61/68.
3/26/33/38/44/45/47/49/50/51/59/61/65/66/68.

2/22/26/38/44/47/49-52/59/66/72.
2/22/38/48/74.
1/2/4/5/22/34/38/48/74.
1/4/5/7/22/25/38/48/74.
1/2/4/5/7/22/25/34/38/48/74.
2/22/25/36/38/48/74.
2/4/22/38/48/66/74.
2/22/25/36/38/48/74.
14/15/16/22/26/41/47/49/51/59.
8/12/16/18/27/29/32/41/45/47/51/59/61/65/68.

3/10/12/14/16/18/23/29/31/38/45/47/49/50/51/59/61/65/68.
8/16/18/27/29/31/38/45/47/49/59/61/68/72.
8/16/18/29/31/45/47/49/50/51/59/61/68.
8/16/1*8/29/31/38/45/47/49/50/51/59/61.
10/14/16/18/29/31/32/45/49/50/51/59/*61/68.
8/16/18/29/31/38/45/50/51/58/61/68/71.
3/9/18/31/32/44/45/49/50/51/59/61/68.
2/22/38/45/47/49/50/51/59.
2/22/38/49/50/59/74.
2/22/25/36/38/45/48/59/66/74.

5/26/3*3/38/41/45/49-52/59/61/68.
8/9/15/29/31/38/45/47/49/50/51/56/59/61/65/68.
9/12/14/16/29/32/41/45/47/49/50/51/54/59/61/65/66/71.
8/9/10/12/16/29/31/42/45/47/49/50/59/61.
2/11/12/29/32/42/45/47/49/50/51/59/61/71.
8/12/21/25/29/38/42/46/47/49/50/55/59/61/64.
10/12/16/20/23/41/45/51/50/59/61/68.
5/9/11/41/14/16/18/26/27/33/44/38/45/49/51/59/61/66/68/.
2/22/38/47/49/50/51/59/72.
14/24/25/38/47/49/59/72/74.

2/16/22/25/36/38/48/49/59/74/.
22/25/36/38/47/49/50/59/74.
5/9/11/16/1*8/26/27/29/32/33/38/41/45/47/49/50/51/59/61/68/72.
15/16/18/23/24/26/32/45/47/49/50/51/59/61/68.
12/14/16/18/26/27/33/38/41/45/47/49/50/51/59/61/68.
5/12/14/15/16/18/23/26/27/38/44/47/49/50/51/59/61/68/72.
10/14/16/22/26/38/41/45/47/49/50/51/72/.
2/5/22/38/47/49/50/59.
16/22/25/26/38/47/49/50/59/75.
2/22/25/36/38/47/48/59/75.

22/25/36/38/48/74.
1/22/25/36/38/48/74.
1/22/36/25/38/48/74.
1/22/25/38/49/59/74.
1/22/38/49/59/74.
1/2/5/6/38/48/74.
1/2/22/38/74.
2/5/7/17/22/38/45/49/50/59.
2/22/26/38/44/45/49/50/57/59/72.
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2/9/16/22/26/38/44/45/49/50/54/59.
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