A field and laboratory study of the bryophyte associations of an area of mixed mire (sensu du rietz)

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Photographs of site unavailable due to long delays in processing.

A FIELD AND LABORATORY STUDY OF THE BRYOPHYTE ASSOCIATIONS OF AN AREA OF MIXED MIRE (SENSU DU RIETZ)

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TO MY PARENTS

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CONTENTS

1. INTRODUCTION

The site chosen for this study was Tarn Moor, near Orton in Cumbria. The vegetation of this area has been described by Holdgate (1955). Tarn Moor is an area of undulating moorland on the western slopes of the Pennines and, like most of the surrounding land, supports an almost total cover of blanket bog. However, in the stream valleys cutting through the blanket bog certain interesting formations occur, especially in the valley of Tarn sike (see map 1). Here the blanket bog covered hillock to the north meets a level plain which, at point B, stretches for some 25 metres between the foot of the hillock and Tarn sike. The underlying rock of this area is problematical being a limestone bedrock overlain by a glacial drift of unknown composition. However, the surface soil is a limestone-rich marl and the dominant abiotic factor here is the calcium carbonate-rich water from the springs which occur in many places on this plain (especially along the foot of the hillock). Many of these springs arise from the centre of a mound built up above the level of the plain (see photograph). The structural material of these mounds is a friable deposit of calcium carbonate known as Tufa and hence these spring mounds are termed Tufa mounds, and they support a characteristic bryophyte flora.

In effect the whole of this plain may be regarded as one large tufa plateau with springs coming to the surface at many points. This spring water is very rich in calcium carbonate and gives rise to a *'rich fen' vegetation which dominates much of the plain. However within

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* The terms 'rich fen', 'poor fen' and 'acid bog' are used throughout the text and are based on the classification of Sjors (1948), though the term 'acid bog' is substituted for Sjors' 'moss' inorder to avoid confusion with the bryophytes studied.

this area of rich fen, hummocks composed mainly of sphagnum, with associated species of acid bog, arise.

This close juxtaposition of rich fen and acid bog constitutes a mixed mire in the sense of Du Rietz (1949), and a consideration of how much an area may have developed poses several questions.

We have here a situation where the propagules of many of the species of bryophyte typical of acid bog are landing or (on being washed down from the blanket bog onto) an area of rich fen. Somehow these 'acid bogs' species are gaining a foothold, as it were, in the rich fen areas and are growing up above the level of the fen to form these miniature raised bog (Bellamy and Riely 1967).

Thus the development of this mixed mire would appear to be entirely biotically determined. This is an ideal situation in which association between bryophyte species may be studied in some detail.

Work by K. Giles (unpublished) has shown that the presence of the common woodland moss Mnium hornum causes inhibition of the production of protonema by the leaves of Mnium punctatum in an experimental situation. This line of approach was followed in the present study on the bryophytes of Tarn Moor in order to discover any allelopathy that might occur between pairs of species.

Allelopathy is usually understood as a biochemical inhibition among higher plants under natural conditions that is caused by the release of metabolic substances. The question of whether or not allelopathy plays a significant role in controlling plant distribution under natural conditions has not yet been fully clarified (Mueller-Dombois and Ellenberg 1974).

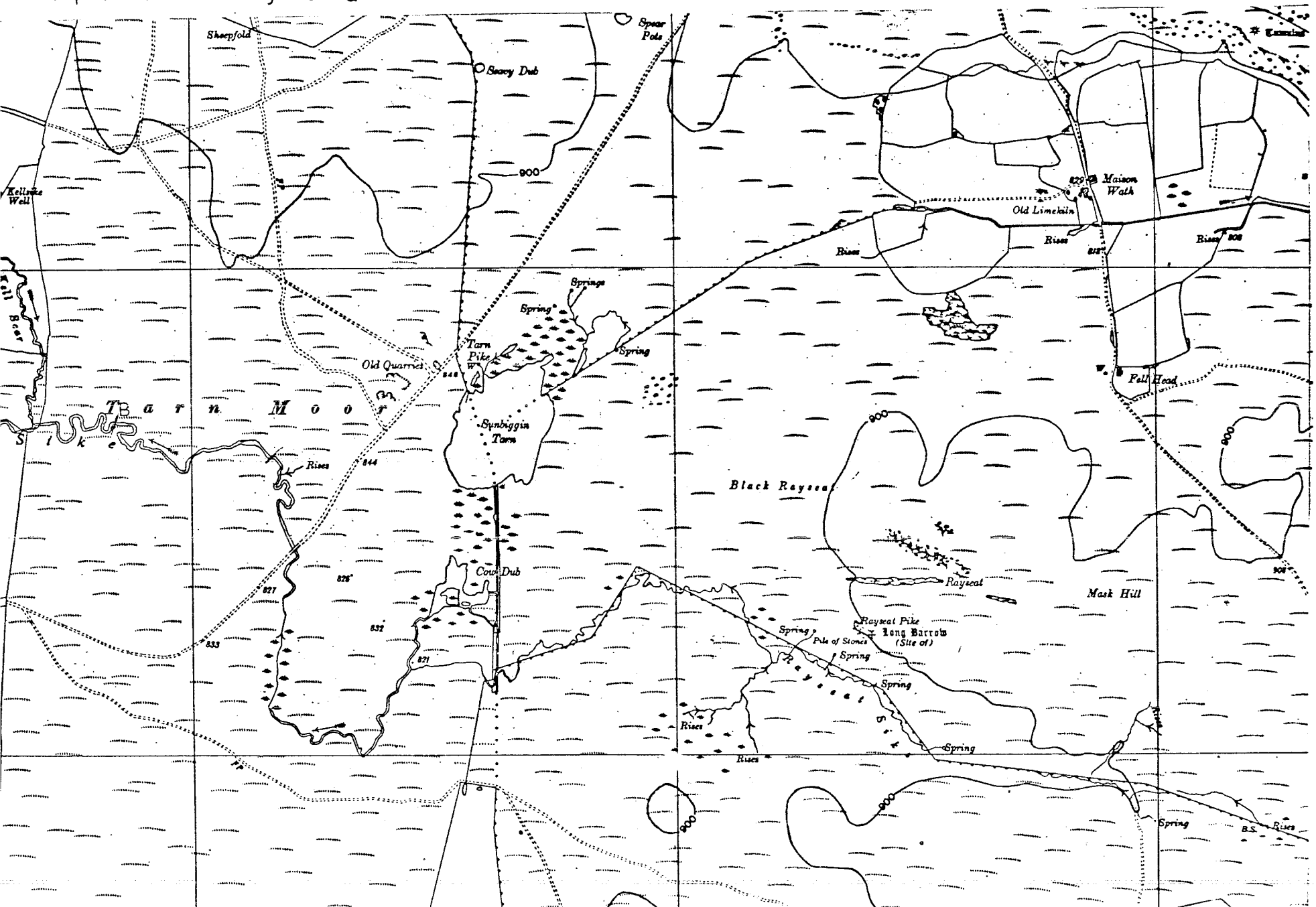
The laboratory experiments on allelopathy, were supported by investigations into the bryophyte distributions in the field using the technique of association analysis.

It was hoped that some links might be discovered between the laboratory studies on allelopathy and the field studies on distribution in order to account for some of the bryophyte distribution, and to gain an insight into the biotic factors controlling the development of this mixed mire complex.

For a detailed account of the vegetation, geology and climate of the Tarn Moor area see Holdgate (1955).

The nomenclature used throughout is that of Watson (1955), except that Cratoneuron falcatum is regarded as a species and not as a variety of Cratoneuron commutatum.

Map 1: The study area



2. METHODS

2.1 LABORATORY EXPERIMENTS

A. Preliminary experiments were carried out using the common woodland moss, Mnium hornum (collected from the Cathedral banks in Durham City) in order to ascertain the best method for setting up the later experiments using mosses from Tarn moor, Mnium hornum was chosen as the previously mentioned study of K. Giles (unpublished) had shown that the leaves of this moss readily produced protonema in an experimental situation. Four experimental regimes were set up which were designated A, B, C and D. Four replicas were also set up under each regime.

The basic preparation method used, was based on that of Gemmel (1953). A pad of 2 filter papers (Whatmans No. 1) were placed in a 5 cm petri dish and saturated with the relevant culture solution (see below). Excess liquid was drained off and twenty-five leaves of Mnium hornum were placed on the pad in five rows of five leaves each to facilitate examination and counting. The leaves had been previously stripped from a number of stems, avoiding the very old and very young leaves and stored in water in a small dish. They were then transferred on a brush to the filter paper pads. The plates were arranged in a Latin square on a bench in the corner of the laboratory furthest from all windows so that the light received by all of the dishes was reasonably equal. The temperature in the laboratory rarely varied much from 65^{o}F throughout the course of all the experiments.

The four culture regimes were as follows:-

(a) Leaves in 6% Knop solution and given a whiff of natural gas.

(b) Leaves in 6% Knop without a whiff of natural gas.

(c) Leaves in tap water and given a whiff of natural gas.

(d) Leaves in tap water without a whiff of natural gas.

The tap water was allowed to stand for about an hour in order to lose some of the chlorine. The whiff of gas was given directly from the gas tap in the laboratory immediately before the lids were placed on the petri dishes. This was done in the hope that the ethylene contained in the gas might promote the production of protonema by the moss leaves.

The plates were kept moist by periodic additions of the appropriate culture solutions by means of a small pipette.

B. The second set of experiments were set up using 19 species of moss and one leafy liverwort collected on an early trip to Tarn moor. This set of experiments was again a preliminary; this time designed to test a new range of mosses for the production of protonema and to look for any indication of allelopathy.

316 petri dishes were prepared as before and all set up under regime A. The species used were:

Aulacomnium palustre
Dicranum scoparium
Bryum pseudotriquetrum
Polytrichum strictum
Acrocladium cuspidatum
Philonotis fontana
Pleurozium schreberi
Climacium dendroides
Scorpidium scorpioides
Mnium rostratum
Leocobryum glaucum
Cratoneuron filicinum
Scapania undulata
Drepanocladus intermedius
Cratoneuron falcatum
Ctenidium molluscum
Sphagnum palustre
Sphagnum plumulosum
Campylium stellatum
Rhacomitrium lanuginosum

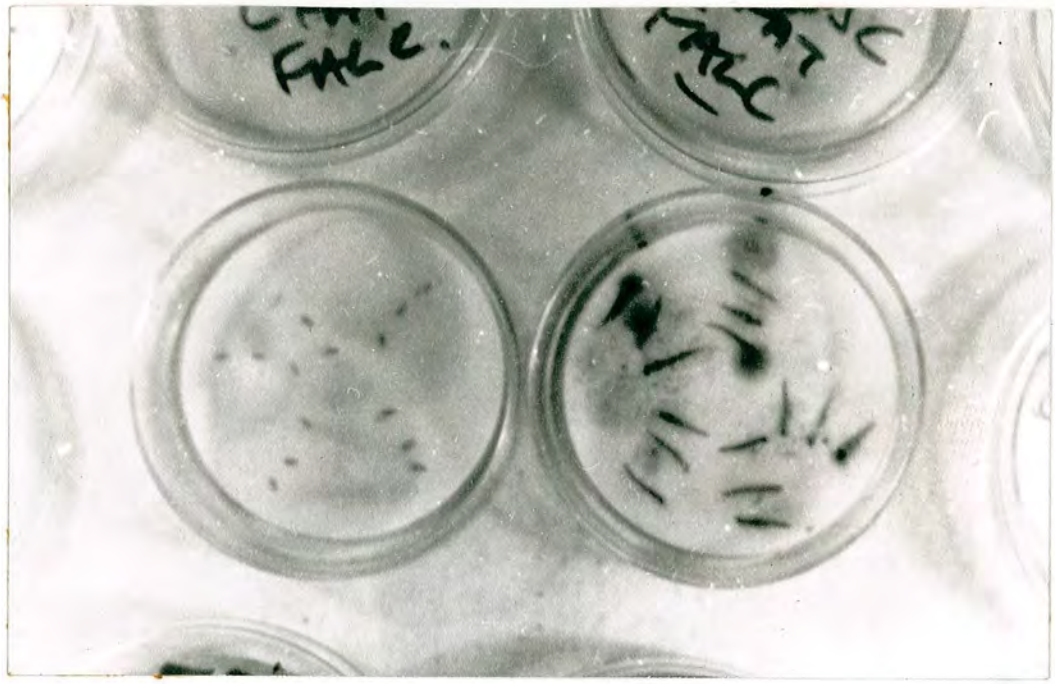


Plate I Leaves of Acrocladium cuspidatum (left) and Dicranum scoparium (right) in control situation. Note fungal infection of D. scoparium leaves.

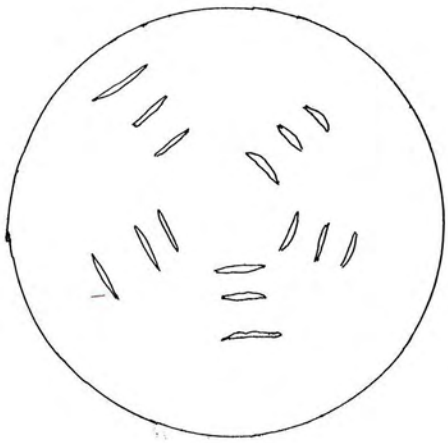


Fig 1 Leaves of Dicranum scoparium in control situation

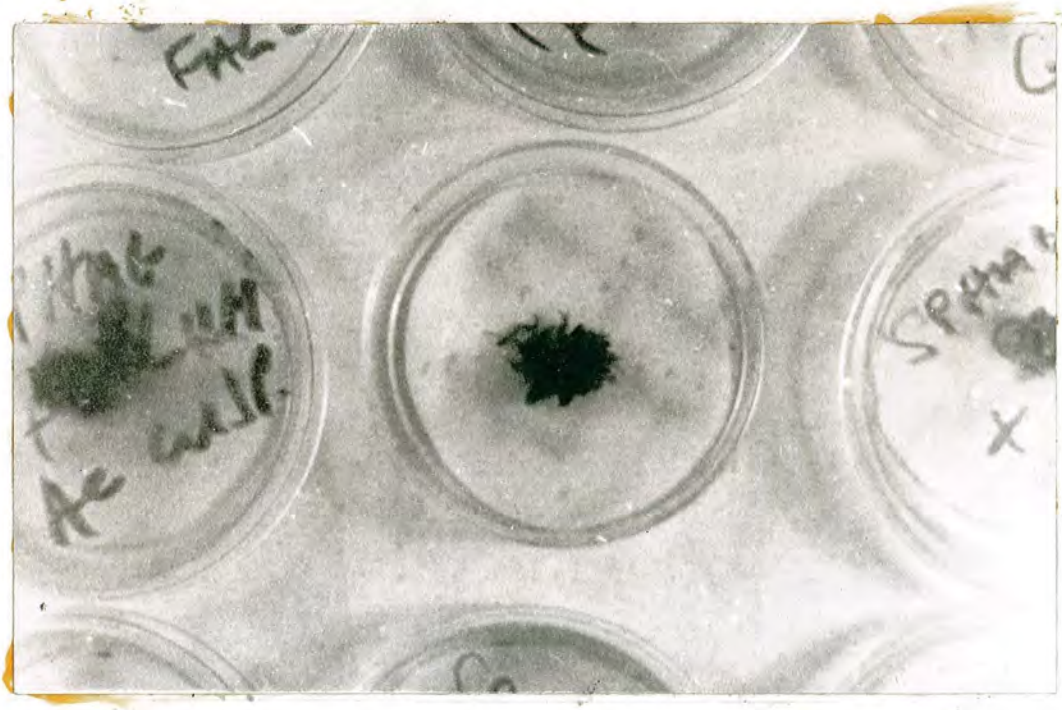


Plate II Sphagnum plumulosum (sprig) and Acrocladium cuspidatum (leaves) in experimental situation.

Plate III Petri dishes arranged on the bench

Each of the twenty species was set up alone as a control and also set up with every other species to test for possible allelopathic effects between species. In each case five rows of three leaves each were used and the dishes were set up as shown in the diagram (Fig. 1) and the photographs opposite. With such a large number of dishes and tests it was impossible to arrange the dishes in a Latin square. However, the dishes were set up in reasonably consistent environmental conditions as before and were all placed on large sheets of paper which were rotated at regular intervals (see photograph).

C. A third set of experiments was prepared on the basis of the results of the second set and on some of the early results of the phytosociology and field observations.

Two hundred and forty dishes were set up under regime C. The fourteen species being employed were set up in appropriate pairs to test for allelopathy and also set up alone as controls. A further twelve dishes were set up under a new regime, E, which involved the exposure to a whiff of natural gas as before, and the use of water collected from a Tufa spring at Tarn Moor as the culture medium. Also a further 20 dishes were set up under a regime, F, identical to E except that water collected from an area of rich fen at Tarn Moor was employed as the culture medium in this case. In both regimes (E and F) the natural waters were filtered, and each dish contained one species only as in the earlier controls.

D. Finally a fourth set of dishes was plated out under regime C. Nine species were used to test for allelopathy with the relevant controls being set up also. This set of experiments was designed to test some of the more "interesting" results of the third set of experiments. (See Table 3 and Discussion I).

In all cases the dishes were examined intermittently and the results recorded after thirty days, and again after forty days in the case of the third and fourth sets of experiments only.

2.2 FIELDWORK

A preliminary reconnaisance of the area was carried out, and on the basis of this a sample plot of 25 m^2 was marked out. This plot was subjectively assessed to be representative of the mixed mire area of Tarn Moor and to exhibit most of the variation therein. This area was mapped in some detail and also photographed in order to provide a permanent field background to the data collected. (See Map 2 in rear pocket, and photographs

Within the sample plot, detailed sampling of the bryophyte vegetation was carried out to fulfil the requirements of field data for the allelopathy experiments. These requirements were:-

A. An analysis of positive and negative interspecific association at the site, to suggest the pairs of species to test for allelopathy.

B. An analysis of the distributional pattern of the species by abstract statements of interrelationships whose properties might be explicable in environmental terms. (To ascertain whether any of the distribution might be due to allelopathic effects, if any were found in the experiments and to allow comparisons to be drawn between possible effects of allelopathy and possible effects of changes in environmental factors (pH, minerals, etc.) on species distributions).

To fulfil the above requirements and to give a good description of vegetation with small scale variation it was decided to adopt a point quadrat sampling method based on that of Yarranton (1967), for use within the 25 metres square sample plot. This method uses a net (a one inch

mesh herring net in Yarrantons case) as a sampling grid in which the net intersections are taken as individual sample points. The density of sampling can be varied (e.g. every fourth, eighth or twelfth intersection etc.) to suit both the physical scale of the vegetation being examined, and the purposes of the investigation. By definition a point sample can only touch one species, but if the point is removed to the line of contact between two individuals it is possible to imagine the point containing two species with an interspecific distance of zero. This method was adapted to suit the present case and two distribution sampling schemes were carried on within the 25 metres square sample plot.

First a net method virtually identical to that of Yarranton was used. A piece of one inch mesh garden netting, 40 inches square (approximately one metre square) was employed as the sample grid and samples were taken at every tenth intersection of the net. Thus the samples were each 10 inches apart and 25 were taken in each grid.

At each sample point the species actually touched by the grid intersections was recorded along with the species touching the first nearest to that point. In effect the sample point is moved to the line of contact between the two species. Recording of the same contact in neighbouring samples was avoided without difficulty. Where the species hit by the sample point did not touch another species, or where it occurred as a pure stand over an area greater than the circle with a 5 inch radius drawn around the sample point, then the sample was recorded as "No contact". "No contact" was then treated as a species and analysed along with all of the other species.

The grids were distributed at random within the 25 metres square plot by throwing a metre rule over the shoulder and then laying the net along the line of the rule. The rule was first thrown from a corner of

the plot and then from each subsequent grid site, direction only being subjective so far as keeping the rule within the sample plot was concerned. Thus the pseudo-randomly distributed set of grids with systematic sampling within each one, gave a partial random sampling method by which 625 species pairs were obtained. This number was reckoned to be sufficient to include almost all of the species of bryophyte present within the plot. A species pair with quadrat number curve was drawn as a check from the results. (See Fig. 2).

A second sampling method was developed in order to compare partial random sampling with strictly systematic sampling of the site. For this method a 25 metre tape measure was employed as the sampling device. This was laid across the site from A-D to B-C at 25 one-metre intervals, starting from line AB and moving towards line CD (see map 2 and photgraph). At each line 25 point samples were taken, one at each metre mark on the tape from 0 to 24 metres inclusive. At each point the sample was taken in the same manner as with the nets. This method again gave 625 species pairs, this time by a rigorous systematic technique. The species pair with quadrat number graph for these data is shown in figure 2 .

Fig. 2A Species pair/quadrat number curve for "nets" data

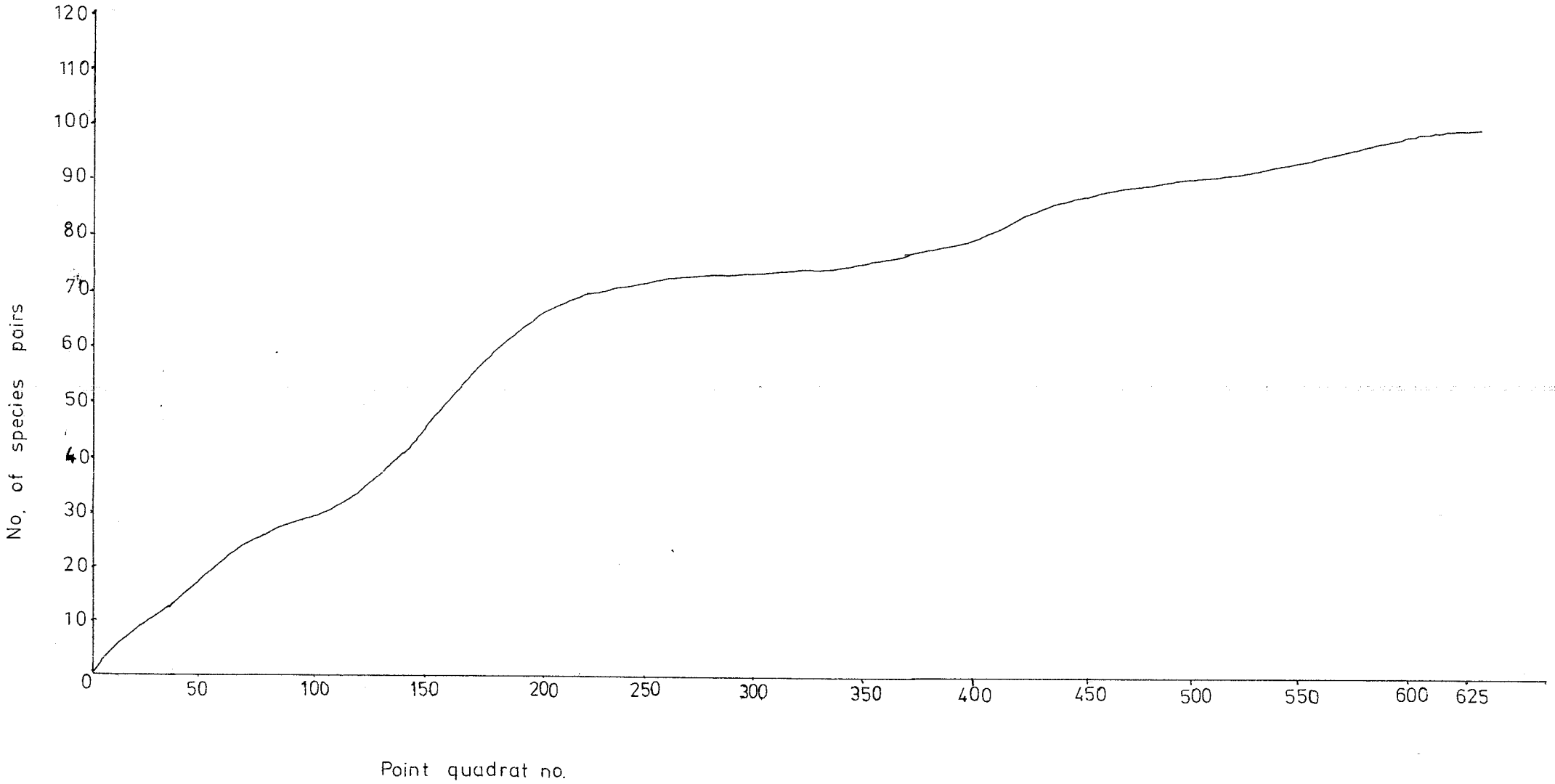
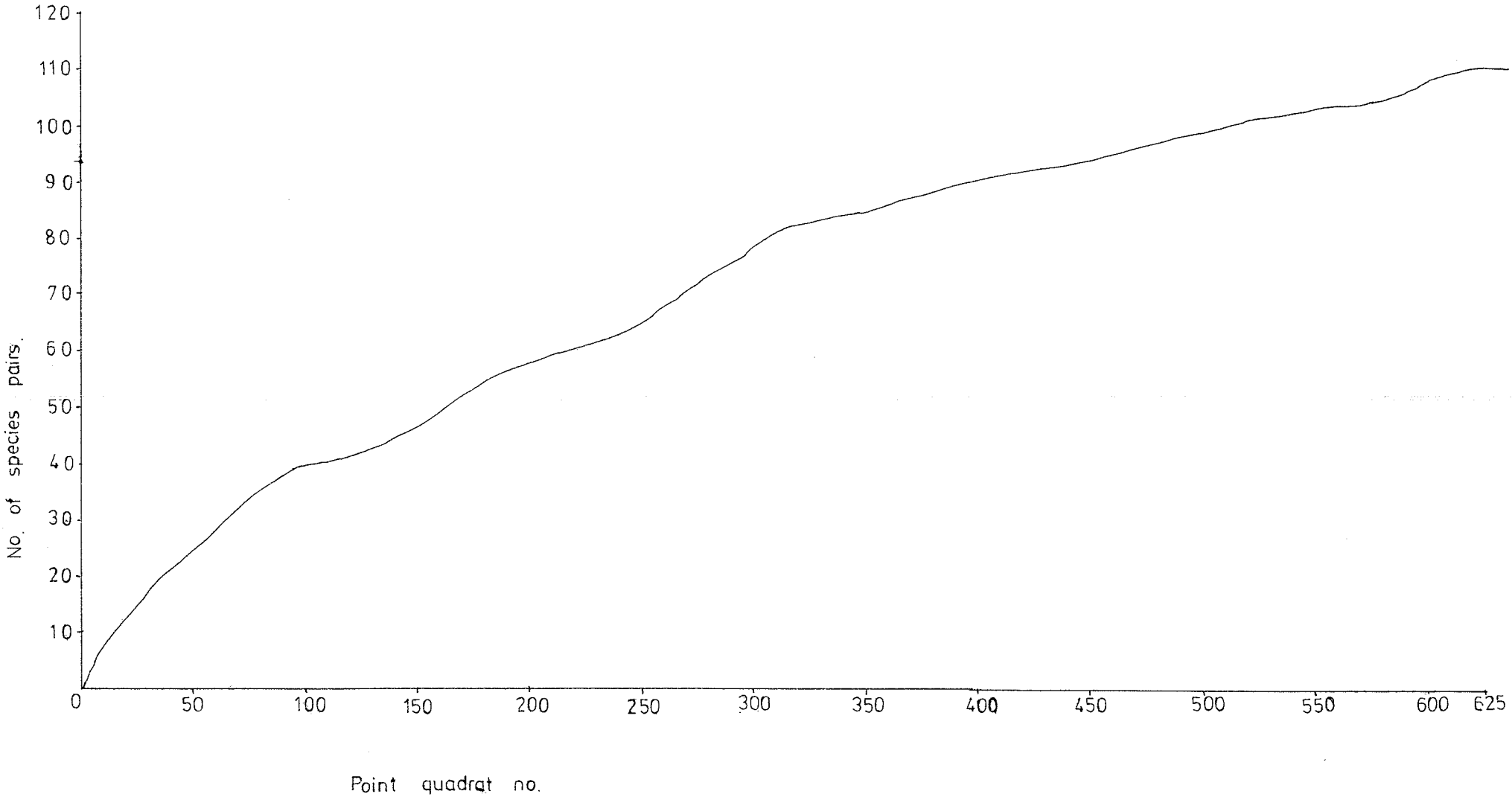


Fig. 2B. Species pair/quadrat number curve for "tapes" data.



3. ANALYSIS OF DATA

3.1 LABORATORY EXPERIMENTS

The results of the first set of experiments were not recorded as such but were used only as a basis for settling up the second set. They are examined fully in 4.1 below.

The results of the second set of experiments are shown in Appendix I. Due to the close similarity in numbers of leaves producing protonema in each concentric ring, the numbers have been grouped into total numbers of leaves producing protonema in each dish. These results could not be submitted to any statistical tests as no replicate dishes were set up and the results were taken only as indications of which of the species would readily produce protonema in the experimental situation, and which of the species pairs showed signs of allelopathic effects. In this way experiments with nil results could be avoided in the third set of experiments and thus more time concentrated on setting up replicates of experiments likely to give significant results.

In the third set of experiments only situations where the experimental result differed from that of the control are shown in Table 1 and 2. Other results were discarded (see section 4.1). The results displayed are the total numbers of leaves producing protonema in a four dish set of replicates, each replicate containing 15 leaves. The results were grouped due to the small variation between the numbers of leaves producing protonema in concentric rings in any four dish set, (see section 2.1 and Fig. 1). The totals for each experimental, and its respective control situation were arranged into a 2 x 2 contingency table and tested for significance of difference by the chi-square test.

For example,

Null hypothesis:- There is no significant difference between the numbers of leaves producing protonema in the experimental and the control situations below:

Acrocladium cuspidatum (sprig) with Dicranum scoparium (leaves)

	No. of leaves producing protonema	not producing protonema	
Experimental	60 (a)	0 (b)	60 (a+b)
Control	5 (c)	55 (d)	60 (c+d)
	65 (a+c)	55 (b+d)	120 (n=a+b+c+d)

Using the formula $$X^2 = \frac{n(ad-bc-\frac{n}{2})^2}{(a+b)(b+d)(a+c)(b+d)}$$

(This formula includes Yates' correction).

We get in this case $X^2 = 97.879$.

Entering the X^2 tables of significance with one degree of freedom we find that this figure is significant at the 0.1% level of probability ($p < 0.001$).

Therefore the null hypothesis is disproved and we may state that significantly more leaves produce protonema in the experimental than in the control situation, indicating that Acrocladium cuspidatum promotes the production of protonema in the leaves of Dicranum scoparium in this experimental situation.

The results of the chi-square tests and their respective levels of significance are shown also in Tables 1 and 2.

The more unexpected results of this set, along with those showing high significance, were tested again in the fourth set of experiments.

TABLE 1

Results of the third set of experiments (those under regime C, see section 2.1).

Sprig species	Leaf species	No. of leaves producting protonema (out of 60) tap water pH 9.3, in: Experiment	Control	X^2 value	Significance Level
1. Acrocladium cuspidatum	Dicranum scoparium	60	5	97.879	0.1%
2. A. cuspidatum	Drepanocladus intermedius	6	0	4.385	5%
3. D. intermedius	A. cuspidatum	21	0	23.088	0.1%
4. Sphagnum fuscum	Campylium stellatum	9	0	7.687	1%
5. S. fuscum	Cratoneuron falcatum	22	5	12.234	0.1%
6. Leocobryum glaucum	Pleurozium schreberi	9	5	0.727	not significant
7. P. schreberi	L. glaucum	53	17	42.000	0.1%
8. Sphagnum plumulosum	L. glaucum	51	17	36.975	0.1%
9. L. glaucum	Aulacomnium palustre	11	3	3.962	5%
10. A. palustre	L. glaucum	9	19	2.405	not significant
11. D. scoparium	A. palustre	20	3	12.569	0.1%
12. A. palustre	D. scoparium	49	5	62.255	0.1%
13. S. fuscum	A. cuspidatum	7	0	5.461	5%
14. S. plumulosum	A. cuspidatum	8	0	6.562	5%
15. S. plumulosum	C. falcatum	12	5	2.467	not significant
16. D. intermedius	A. palustre	13	3	5.841	5%
17. D. intermedius	L. glaucum	2	17	12.526	0.1%

TABLE 2

Results of the third set of experiments (regimes E and F, see section 2.1)

Culture medium	Leaf species	No. of leaves producing protonema (out of 60) in:- Experiment	Control Tap water pH 9.3	X^2 value	Significance Level
1. Tufa spring water pH 8.2	A. palustre	6	3	0.480	not significant
2. Tufa spring water	C. falcatum	8	5	0.345	not significant
3. Tufa spring water	Cratoneuron commutatum	30	8	16.983	0.1%
4. Fen water pH 7.6	A. palustre	8	3	1.601	not significant
5. "	C. commutatum	45	8	43.796	0.1%
6. "	C. falcatum	21	5	9.904	1%
7. "	L. glaucum	0	17	17.544	0.1%
8. "	Polytrichum strictum	0	7	5.461	5%

Culture medium	Leaf species	No. of leaves producing protonema (out of 60) in:- Experiment	Control Fen water pH 7.6	X^2 value	Significance Level
1. Tufa spring water pH 8.2	A. palustre	6	8	0.0808	not significant
"	C. falcatum	8	21	6.5479	
"	C. commutatum	30	45	6.968	

TABLE 3

Results of the fourth set of experiments

Sprig species	Leaf species	No. of leaves producing protonema (out of 60) in:- Experiment	Control	X^2 value	Significance Level
1. Cratoneuron falcatum	Cratoneuron filicinum	25	36	3.334	not significant
2. Campylium stellatum	C. filicinum	26	36	2.703	not significant
3. Acrocladium cuspidatum	C. filicinum	15	36	13.640	0.1%
4. Drepanocladus intermedius	A. cuspidatum	6	11	1.096	not significant
5. Sphagnum fuscum	C. stellatum	17	0	17.544	0.1%
6. S. fuscum	C. falcatum	9	0	7.687	1%
7. S. fuscum	C. filicinum	30	36	0.841	not significant
8. Aulacomnium palustre	Leocobryum glaucum	1	17	14.705	0.1%
9. S. fuscum	A. cuspidatum	18	11	2.228	not significant
10. Sphagnum plumulosum	C. falcatum	5	0	3.339	not significant
11. A. palustre	C. filicinum	47	36	3.907	5%
12. L. glaucum	C. filicinum	33	36	0.136	not significant

The data obtained were similarly treated and the results are shown in Table 3.

The chi-square tests were, in both cases, carried out on the results of the examination and count after 30 days. This was because in the majority of cases there was very little difference in the results after 30 days and those after 40 days. However, in some cases there were less leaves producing protonema after the second count. Careful examination of these few cases often revealed protonema lying around the leaves though not attached. This could be due to disturbance during the watering of the dishes or during the examination and counting after 30 days. It is also possible that it could be due to counting errors or a 'natural' occurrence such as lack of nutrients in the culture medium.

The results of these experiments are discussed fully in sections 4.1 and 4.3 below.

3.2 FIELDWORK

First the species totals from the two sampling schemes (i.e. nets and tapes) in the 25 metres square plot were compared as lists by a correlation coefficient. The resultant 'r' value was 0.93 and this represents a positive correlation between the two sets of data significant at the 0.1% ($p < 0.001$) level of probability. Thus the two sampling schemes had yielded almost identical results as far as species totals were concerned.

The species with species data were collected individually (Fig. 3A) and then grouped into a contingency matrix (Fig. 3B). These data were first investigated for interspecific association using 2 x 2 contingency tables and the chi-square test, the elements of the contingency matrix (Type B Fig. 3) being the top left hand cells of the

Sample

Species	1	2	3	4	5	6	7	8
a	x	x		x			x	x
b	x		x				x	
c			x	x	x	x		x
d		x			x	x		

Species

Species	a	b	c	d
a	5	2	2	1
b	2	3	1	0
c	2	1	5	2
d	1	0	2	3

N=8

Fig. 3. Types of data provided by contact sampling.

A. Original data: B. Contingency matrix.

2 x 2 tables. Chi-square values were calculated in the usual way, employing Yates' correction and using the formula:-

$$X^2 = \frac{n(ab-cd-\frac{n}{2})^2}{(a+b)(c+d)(a+c)(b+d)}$$

based on the contingency table:-

Species A

Species B	+	-	
+	a	b	a+b
-	c	d	c+d
	a+c	b+d	n=a+b+c+d

(See Kershaw 1964, Mueller-Dombois and Ellenberg 1975, Shimwell 1971).

The data were actually processed on an IBM 370/168 computer and the results were obtained as a contingency matrix showing positive and negative associations at the 5% ($p = 0.05$) significance level of probability. The results of this test are presented in figures 4A and 4B. The major differences are discussed in Discussion 2. At this point it was decided that, due to the highly significant positive correlation of species totals, and the advantages of combining data collected at two periods in the growing season, these data sets could be combined into one large set of data for further analysis. This large set of data (Nets plus Tapes) was first processed for chi-square. The results of this test are shown as a tracing overlay to the correlation matrix in figure 6.

Next, the data were tested for interspecific correlation by comparing all possible pairs of columns in the symmatical contingency matrix (Fig. 5). The analysis was carried out as shown below.

Example from figure 5.

	Column 4	Column 8
1	0 (x)	0
2	16	11
3	19	4
4	378	151
5	15	12
6	64	119
7	18	6
8	151	481
9	42	139
10	33	1
11	5	18
12	0	10
13	3	0
14	1	0
15	0	1
16	0	0
17	0	0
18	9	4
19	0	1
20	0	2
21	1	1
22	1	0
23	1	0
24	2	1
25	0	0
26	0	0
27	0	0
28	0	0
29	0	0
30	0	0

Discounting 0-0 occurrences we have,

$$n = 21$$
$$\Sigma x = 756$$
$$\Sigma y = 962$$
$$\Sigma x^2 = 173824$$
$$\Sigma y^2 = 274249$$
$$\Sigma xy = 143837$$

applying these data to the formula,

$$r = \frac{\sum (x-\bar{x})\ (y-\bar{y})}{\sqrt{\sum(x-\bar{x})^2 \sum (y-\bar{y})^2}}$$

where, $\sum (x-\bar{x})^2 = \sum x^2 - \frac{1}{n} (\sum x)^2$

$$\sum (y-\bar{y})^2 = \sum y^2 - \frac{1}{n} (\sum y)^2$$

$$\sum (x-\bar{x})(y-\bar{y}) = \sum xy - \frac{1}{n} (\sum x)(\sum y)$$

we get, $$r = \frac{10925}{\sqrt{146608 \times 230180.24}}$$

$$= 0.5770$$

significant at the 1% level of probability, ($p < 0.01$), with 20 degrees of freedom

Column 4 is Cratoneuron falcatum and column 8 is Campylium stellatum, the two dominant species of the sample plot as a whole. The above figure for r shows that Cratoneuron falcatum and Campylium stellatum have closely, positively correlated distributions. That is, where we find one of these species we are very likely to find the other very close by.

The correlation coefficients calculated from the symmetrical contingency matrix are based on the occurrence of each species pair with all the other pairs. The data were processed for this test also on the IBM 370/168 computer and the results obtained as a list of correlation coefficients from which a correlation matrix was drawn up.

Fig 4A Association matrix for nets' data

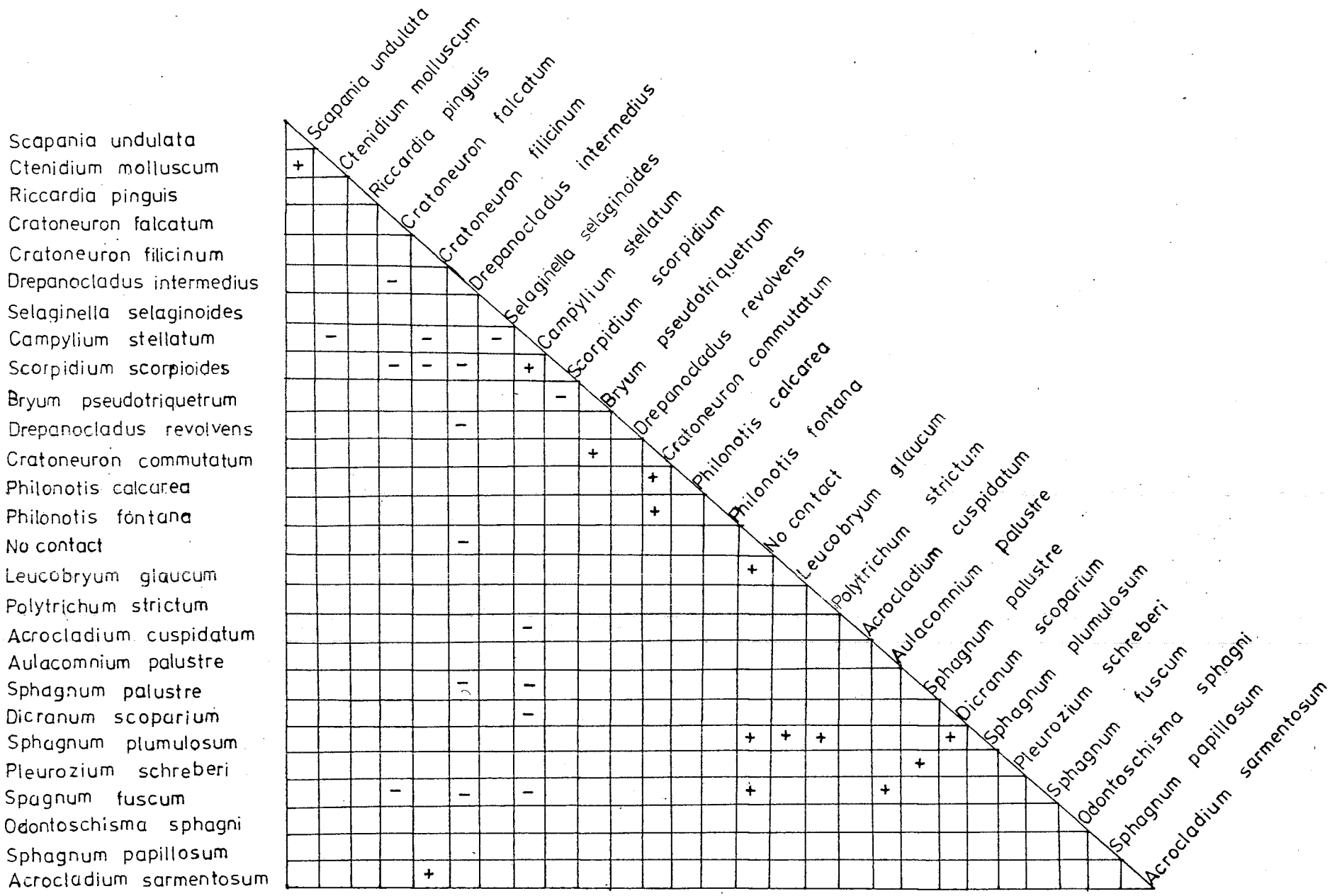


Fig 4B Association matrix for "tapes" data.

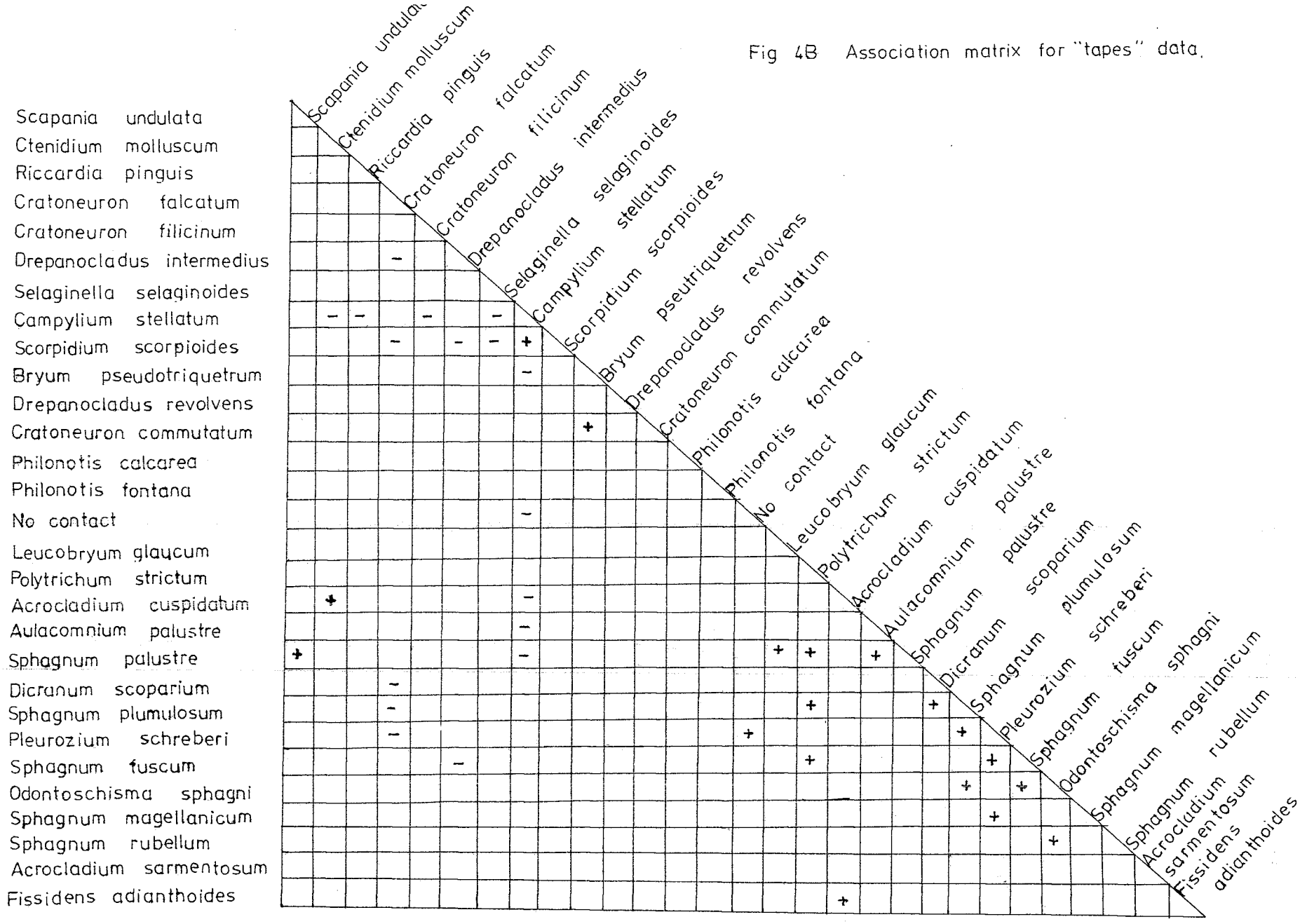


Fig. 5. Symmetrical contingency matrix for "nets plus tapes" data.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1 Scapania undulata	2	1																		1										
2 Ctenidium molluscum	1	56		16	2	12	4	11		1								5			1		1	2						
3 Riccardia pinguis			46	19	2	9		4	8	1		2						1												
4 Cratoneuron falcatum		16	19	378	15	64	15	151	42	33	5		3	1				9			1	1	1	2						
5 Cratoneuron filicinum		2	2	15	79	21	3	12	5	7			1	1				3				1		3			3			
6 Drepanocladus intermedius		12	9	64	21	302	13	119	20	26	1	3	1	1	1			4		1	1			3						2
7 Selaginella selaginoides		4		15	3	13	48	6	2									3		2										
8 Campylium stellatum		11	4	151	12	119	6	481	139	1	18	10			1			4	1	2	1			1						
9 Scorpidium scorpioides			8	42	5	20	2	139	24	4	3	2	2		17															
10 Bryum pseudotriquetrum			1	33	7	26		1	4	94	4	12	2					1		1				1						
11 Drepanocladus revolvens				5		1		18	3	4	35	1	2					1												
12 Cratoneuron commutatum			2			3		10	2	12	1	38	4	2				2												
13 Philonotis calcarea				3	1	1			2	2	2	4	15																	
14 Philonotis fontana				1	1	1						2		5																
15 No contact						1		1	17						71	9				1		16	9	16					1	
16 Leucobryum glaucum															9	15				1		5								
17 Polytrichum strictum																	41			7		20	1	12				1		
18 Acrocladium cuspidatum		5	1	9	3	4	3	4		1	1	2						48	4	3	1	2	1	2						2
19 Aulacomnium palustre								1										4	32	7	5	7	2	4		1			1	
20 Sphagnum palustre	1					1	2	2		1					1	1	7	3	7	55	4	8	13	3	1					
21 Dicranum scoparium		1		1		1		1										1	5	4	63	31	6	9	1	1	1			
22 Sphagnum plumulosum				1	1										16	5	20	2	7	8	31	124	17	1	12		1	1	1	
23 Pleurozium schreberi		1		1											9		1	1	2	13	6	17	65	10		1		3		
24 Sphagnum fuscum		2		2	3	3		1		1					16		12	2	4	3	9	1	10	83	12			2		
25 Odontoschisma sphagni																				1	1	12		12	29				3	
26 Sphagnum papillosum																			1		1		1			3				
27 Acrocladium sarmentosum																					1	1					5			
28 Sphagnum magellanicum																	1					1	3	2				8	1	
29 Sphagnum rubellum															1				1			1			3			1	7	
30 Fissidens adianthoides						2												2												4

4. DISCUSSION

4.1 RESULTS OF LABORATORY EXPERIMENTS

The Mnium hornum leaves set up in Knop solution in the first set of experiments produced protonema after approximately 10 days, and after 20 days had all produced large numbers of protonema. However, counting had become very difficult by this time as the places were almost covered by dense growths of fungi and algae. The M. hornum leaves set up in tap water took up to 30 days to produce protonema but did not become infested by fungi or algae to any great extent. The second set of experiments were set up after the first set had run for only 20 days, and knop solution was again used as it seemed to produce good results at this time. In hindsight it would have been more profitable to have set up the second set of experiments in tap water, but time and previous results militated against this.

As expected, many of the dishes in the second set of experiments were infested by growth of fungi and algae (see plate), some very dense, and counting had to be carried out very carefully. From the results of this set of experiments (Appendix I) it can be seen that only 13 species out of the 20 used produced any protonema in the control situation, and of these only Aulacomnium palustre, Climacium dendroides, Leucobryum glaucum and Cratoneuron filicinum produced protonema from seven or more of the fifteen leaves set up. It is noted also that the leafy liverwort, Scapania undulata did not produce any protonema and this result was expected. Scapania had only been included as a possible inhibitor of protonema production in the mosses. The species of sphagnum used S. palustre and S. plumulosum also showed no production of protonema in the control situation, and though they appear to have produced a very small number of protonema in some of

the experimental situations this may be due to examination error, as none were observed in any of the later experiments. In certain cases it was very easy to mistake fungal hyphae for protonema in the badly infected dishes.

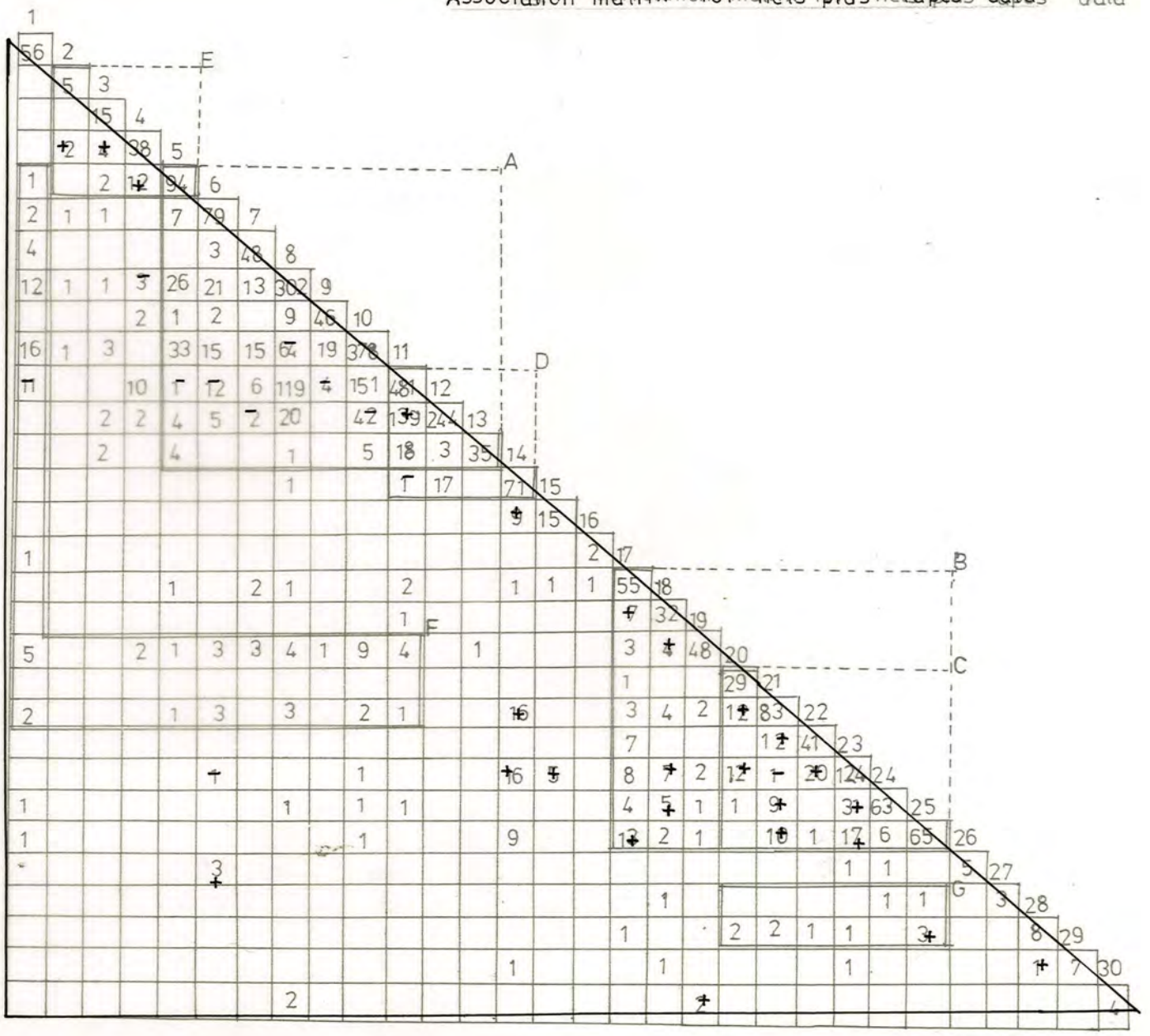
As a whole the second set of experiments gave useful results with several leads to be followed, not only on possible allelopathic effects but also on possible occurrences of promotion which had, hitherto not been anticipated.

The results of the third set of experiments (Tables I and 2) were of much more value than either of the previous sets. There was very little infection by fungi or algae and this is thought to be due to the chlorine present in the tap water used as a culture medium. Out of the 46 experiments set up, 21 produced results identical to the results of the respective controls. This was in every case a situation of no production of protonema in either the experiment or the control. These results were discarded and the remaining 25 experiments were examined in detail. The discarded experiments contained every situation where a species of Sphagnum was present as the leaf species thus suggesting that the Sphagma tested (S. palustre and S. plumulosum) are incapable of producing protonema from abscised leaves in such an experimental situation. It is possible that the pH of tap water (9.3) used is too high for the Sphagnum leaves to survive. This question is reexamined in Discussion 4.3.

As mentioned above, examples of promotion of protonema production by one species on another were not at all anticipated. However, in Table I it is seen that this occurred 15 times out of 17, though it was only significant at the 5% level or above in 13 of these cases. This is a most interesting phenomena and opens a new angle of discussion on the basis and formation of mixed mires (see Discussion 4.3).

In order to discover how important the culture medium might be in terms of pH and mineral composition, regimes E and F were set up. The results (Table 2) for Aulacomnium palustre and Cratoneuron filicinum in tufa water show an insignificant departure from the controls in both cases. However, Cratoneuron commutatum shows a remarkable increase in the number of leaves producing protonema in this case. C. commutatum is rarely found anywhere but in the immediate vicinity of the tufa springs at Tarn Moor (which have the highest pH levels in the area). This suggests that C. commutatum has a requirement for the high pH (8.2) or some other factor present in the tufa spring waters. The important factor is unlikely to be pH alone though, as the average pH of the tap water used was higher at 9.3 (max. 9.5; min. 8.7). This situation is further complicated when it is observed that significantly more leaves of C. commutatum produce protonema when plated in fen water which has an even lower pH of 7.6. Significantly more leaves of C. falcatum produce protonema in this situation also. On the basis of these observations it is suggested that the fen water is nearer than the tufa water, to the optimum pH for the growth of both C. falcatum and C. commutatum, but that C. commutatum may be eliminated from the areas of fen by competition with the closely related species C. falcatum. C. commutatum seems better able to survive than C. falcatum in the areas of slightly higher pH around the tufa springs which are probably near to its upper level of tolerance to pH. (It is interesting to note here that Watson (1955) includes both of these species in a single species. (Viz. C. commutatum and C. commutatum var. falcatum) and also suggests that the variety falcatum appears to be less exacting in requirements). It is unfortunate that these two species were not chosen to be plated out together, as, if the above suggestions of competition are correct,

Fig 6 Association matrix for nets plus "tapes" data



1 Ctenidium molluscum
2 Philonotis fontana
3 Philonotis calcarea
4 Cratoneuron commutatum
5 Bryum pseudotriquetrum
6 Cratoneuron filicinum
7 Selaginella selaginoides
8 Drepanocladus intermedius
9 Riccardia pinguis
10 Cratoneuron falcatum
11 Campylium stellatum
12 Scorpidium scorpioides
13 Drepanocladus revolvens
14 No contact
15 Leucobryum glaucum
16 Scapania undulata
17 Sphagnum palustre
18 Aulacomnium palustre
19 Acrocladium cuspidatum
20 Odontoschisma sphagni
21 Sphagnum fuscum
22 Polytrichum strictum
23 Sphagnum plumulosum
24 Dicranum scoparium
25 Pleurozium schreberi
26 Acrocladium sarmentosum
27 Sphagnum papillosum
28 Sphagnum magellanicum
29 Sphagnum rubellum
30 Fissidens adianthoides

some allelopathic effect would be expected between them.

The other species tested on fen water were Leucobryum glaucum and Polytrichum strictum. Neither of these species produced any protonema in this situation. This again poses interesting questions. Both species are found to grow solely on the summits of the Sphagnum plumulosum and S. fuscum hummocks, at Tarn Moor, where the pH values are between 4.0 and 4.5 (Bellamy and Riely 1967, Edwards 1975 pers. comm.). Thus if the pH alone were important these species would be expected to produce more protonema on the fen water (pH 7.6) than on the tap water (pH 9.3). It is evident that more work is required on the culture media and their mineral composition. L. glaucum leaves produced many more protonema when plated with a sprig of S. plumulosum on tap water and this suggests that the 'promotional' effects observed may be due to the addition of minerals to, and a lowering of the pH in, the dishes by the spriggspecies in many cases. In any future work it would be advisable to sample for pH within the dishes to ascertain whether any pH gradient occurs between the sprig and the edge of dishes (see figure 1).

These suggestions can be, at best, only tentative and will be reexamined, in the light of the fieldwork results in Discussion 4.3.

Table 3 shows the results of the fourth set of experiments, which were run mainly as a check on the third set. Cratoneuron filicinum was tested against several other species in this set as it had been shown to be a prolific producer of protonema in the second set of experiments but had been mis-identified when the third set were prepared.

In general the occurrences of 'promotion' seen in the third set results were again observed in this set. Especially interesting is the effect that S. fuscum appears to have on promotion of protonema production in Cratoneuron falcatum and Campylium stellatum. Also in

several cases where S. fuscum and S. plumulosum were employed as the sprig species the leaves of Cratoneuron falcatum and Campylium stellatum were observed to produce shoots directly as well as protonema. These findings are discussed in relation to the development of mixed mire in Discussion 3 .

Two examples of possible allelopathy occurred in the fourth set of experiments. Acrocladium cuspidatum appears to inhibit the production of protonema by leaves of Cratoneuron filicinum and Aulacomnium palustre is seen to have a similar effect on leaves of Leucobryum glaucum. The results are, in both cases, statistically significant at the 5% level or above.

As already mentioned, many of these results become more meaningful when studied in the light of field observations of association between the species. The next section discusses the field results and the combined results are discussed in Discussion 4.3.

4.2 RESULTS OF FIELDWORK

The association matrices for the net samples and the tape samples are shown together in figure 4. Selaginella Selaginoides is included in both cases as, although it is a pteridophyte, it is of the same growth habit and habitat as many of the bryophytes studied.

The main differences in the association matrices shown, occur in the bottom right hand corner, which contains the sphagna and other species found on the hummocks. These differences can be explained by the fact that the two sets of samples were collected about 6 weeks apart. At the collection of the later (tapes) samples the whole area of Tarn Moor was relatively dry and, on many of the hummocks, a large amount of Odontoschisma sphagni had appeared, thus altering, to some extent, the associations recorded for this community type in the second

sample. The O. sphagni probably appears at this time due to the slowed rate of growth of the dominant sphagna during the dry weather.

Also in the bottom right hand corner of the matrix are most of the species with small total occurrences, and these often tend, by their small numbers, to have high degrees of association in the few species pairs in which they do occur. These should perhaps be excluded from the matrix altogether.

It was decided that the combination of the tapes and net samples was justified by the close correlation exhibited between species totals, and also by the fact that an overall sample from the site at two periods in the growing season would be obtained.

The symmetrical contingency matrix for the combined data is shown in figure 5. The correlation matrix was obtained from this as outlined in Analysis and Data 2. The matrix was actually constructed by hand from the correlation coefficients produced by the computer. Species pairs having the highest positive correlation coefficients were placed together and then the species having the next highest coefficient was added and so on until the matrix was completed. Where this procedure became at all dubious (e.g. in cases of a species having a low but equal correlation coefficient to one or more other species) a knowledge of the site and of the ecology of the species was employed. In this way the final correlation matrix produced is fairly objective but also biologically meaningful.

Certain groups of species can be selected from (and these are delimited on) the correlation matrix figure 6. These groups are labelled A, B, C, D, E, F and G. It is suggested that the groups labelled A, B and E represent distinct communities and that these may be regarded as 'taxa', of an unknown rank, in the sense of Braun Blanquet (1932). It is difficult to suggest hierarchical rank into which any

"bryophytes only" community would fit as the taxonomic system is based on all orders of plants from bryophytes to angiosperms.

The species of group A tend to occur in general in the rich fen area of the mixed mire complex, i.e. between the individual sphagnum hummocks. This group contains most of the dominant bryophytes at the site e.g. Drepanocladus intermedius, Cratoneuron falcatum, Campylium stellatum and Scorpidium scorpioides. This is not surprising as the rich fen community covers by far the largest area of any within the 25 m^2 plot. Several negative associations occur within this group which may be due to the inclusions of some species with much lower total occurrences than those mentioned above. Alternatively it may be that species associations in this seemingly quite homogeneous community are more discrete than can be easily shown by the sampling regime employed.

This community is linked to group E, containing the species associated with the tufa springs, by Bryum pseudotriquetrum which occurs widely in both areas.

The species of group D do not really constitute a separate taxonomic unit in the Braun Blanquet sense but are more representative of the open water areas of the rich fen where Scorpidium scorpioides is often the only bryophyte present; hence the inclusion of "no contact" with this group.

"No contact" might be justifiably linked also with group B which contains the species found on the Sphagnum hummocks in general. On these hummocks S. plumulosum and S. fuscum often occur as pure stands over areas as large as 25 cm^2 and thus would often be recorded as associated with "no contact".

Sphagnum palustre and Aulacomnium palustre occur mainly on the larger (older) hummocks capped with Calluna vulgaris, and also where

two or more hummocks have

Acrocladium cuspidatum is present around the edge of virtually all of the hummocks and is, strictly speaking, a plant of the narrow transition zone between the rich fen and the acid sphagnum hummocks (i.e. of the poor fen).

If we remove these species from group B we are left with group C, which is really a mean community of all of the smaller (younger) hummocks of Sphagnum. If we were to split group C into two groups, one excluding S. fuscum and the other excluding S. plumulosum. (Note that these two species are the only negatively associated pair in group C). We should have a pair of bryophyte species lists fairly presentative of any one of the smaller hummocks at the site. However group C as a whole gives a generalised Sphagnum hummock community representing all of the smaller hummocks in the area, each of which might be regarded as a fragmentary stand (sensu Braun Blanquet 1932).

Group F represents some of the associations occurring in the very narrow boundary zone between the rich fen and the Sphagnum hummocks and to be complete, it should include the associations between A. cuspidatum and the other species of group B. If the correlation matrix were rearranged this 'transition zone' group might conceivably represent a taxa (sensu Braun Blanquet) with A. cuspidatum as its line character species in the same sense. A. cuspidatum is in fact a recognised character species of poor fen on 'transition' mires on a larger scale.

The species to the right of group B are excluded from all of the groups due to their low numbers of occurrences. Group C is designed solely to demonstrate that the Sphagna all occur on the hummocks.

Ctenidium molluscum is rather a 'problem species' which is included in group F though it represents mainly the rich fen side of

the "transition" or poor fen community.

4.3 COMBINED RESULTS

The occurrence of promotion of the production of protonema by leaves of one species of moss due to the presence of a second species had not been anticipated. From a comparison of the results for Leucobryum glaucum alone in tap water, alone in fen water, and with Sphagnum plumulosum in tap water, it appears that the promotional effects may well be due to the diffusion of ions out from the central sprig to the leaves in the dishes. In hindsight it would have been rewarding to have sampled selected dishes for pH values at several points from the central sprig outwards to the edge of the dishes. The use of larger dishes, if available, would also have been an advantage in this case.

As further support for the suggestion in 4.1 that competition between Cratoneuron falcatum and C. commutatum controls, to some extent, their distribution; it is seen from figure 6 that they were not found to occur together at all in the field samples.

It is interesting to note that the Sphagnum species used never produced protonema (except perhaps in the second set of experiments - see 4.1). This may be due to the high pH of the tap water (9.3) compared to that of the normal habitat of these Sphagna. (4.0-4.5). However on a quite deep (but by no means exhaustive) investigation into the literature, no account could be found of any species of Sphagnum producing protonema from abscised leaves and Parihar (1959) lists one of the fundamental features of Sphagnum as "No special means of vegetative reporduction". Further work is required on this matter before any conclusions can be drawn.

One case where allelopathy seemed to occur in the experiments was

in the effect that Aulacomnium palustre has on leaves of Leucobryum glaucum. In the field both of these species grow mainly in pure clumps on the sphagnum hummocks though they were not recorded as a species pair in the field data. It is thus difficult to conclude much from these results except that the effects observed might be of some importance in cases of direct competition between these two species, if this occurs.

A comparison of Tables 1 and 3 with figure 6 shows that most of the statistically significant results occur among species from group B and also where species from group B are the 'sprig species'. In all cases this could be due to the lowering of the pH of the culture medium in the dishes by the presence of a sprig of moss with a low pH value, from which ions may be constantly diffusing. (It could possibly be due also to the production of 'growth promoters' of some kind by these 'sprig species' but this is thought to be unlikely). These suggestions may have some bearing on the development of this mixed mire complex.

In the introduction we saw that the most important abiotic factor on the site is the calcium carbonate-rich spring water, and this has been found to be reasonably uniform in ion content and pH over the site as a whole except for the water actually issuing from a tufa spring at any one time. (K. Edwards pers. comm.). (The water leaving a tufa spring deposits some of its load of calcium carbonate as tufa thus continuing the construction of the tufa mound).

We can assume then, that the development of the mixed mire is predominantly determined by biotic factors. The major problem is in discovering how the Sphagna establish themselves in the rich fen areas well enough to develop the hummocks. From the results obtained from the laboratory experiments and fieldwork carried out, the following hypothesis

is offered as a possible explanation.

The area is imagined as having been originally a plain, supporting a relatively homogeneous rich fen vegetation, with blanket bog-covered slopes to the north and west. Within this blanket bog there are areas of acid bog and poor fen, and thus the rich fen area would receive a constant supply of the propagules of many acid bog and poor fen species of moss, both from the air and in the run-off from the slope to the north, ('propagule' is in this case, taken to mean anything from a Sphagnum spore to a clump of several stems of moss that might be dislodged by a cow or sheep). If these propagules were to land on a slightly less base-rich area of the rich fen (e.g. where peat or sandy drift had been washed down from the blanket bog), then the hummock forming process might be set in motion. A small clump of Acrocladium cuspidatum (a species characteristic of poor fen) might be able to develop and survive in such an area, especially if a clump of Sphagnum were present also. Together these species might reduce the pH of the area slightly and also change the mineral compositions, thus favouring their continuing development.

If the results of the experiments in sets three and four (Tables 1, 2 and 3) have been interpreted correctly (see section 4.1) then the change in environmental factors (or possibly the mere presence of the alien species alone) would be expected to stimulate growth in Cratoneuron falcatum, Campylium stellatum and Drepanocladus intermedius growing on the rich fen in the vicinity. It is also possible that the propagules of the poor fen and acid bog species might land on a pre-existing dense clump of Cratoneuron falcatum, Campylium stellatum and Drepanocladus intermedius (which are seen to exist in the present areas of rich fen). The surface of these clumps, being slightly further from the groundwater level, might be expected to provide a slightly less

base-rich environment than most of the rich fen area.

Thus by developing at the surface of such a clump, be it pre-existing or stimulated, the acid bog and poor fen species escape, to some extent the continuous replacement of bases in the groundwater. This would allow first Acrocladium cuspidatum and then the Sphagna to develop. As the Sphagna grow upwards, the groundwater will be diverted and they will increase the acidity of their immediate environment.

Evidence supporting this hypothesis comes from work by K. Edwards (pers comm.) who has found large amounts of the rich fen species Campylium stellatum, Cratoneuron falcatum and Drepanocladus intermedius at the base of hummocks examined at Tarn Moor. These species have been associated, in this position, with the poor fen and acid bog species, Acrocladium cuspidatum, Sphagnum palustre (more tolerant of less acid conditions than many Sphagna, Watson 1955), and S. plumulosum. The first and third of these species are seen from Tables 1 and 3 to promote the production of protonema by the abscised leaves of the associated rich fen species.

The results in Tables 1 and 3 also indicate that Sphagnum fuscum significantly promotes the production of protonema by leaves of Cratoneuron falcatum and Campylium stellatum, whereas similar promotion by S. plumulosum is not statistically significant. Of these two species of Sphagnum, however, S. plumulosum is the one most often found at the bottom of the hummocks and on the lower hummocks, and is generally reckoned to be one of the main hummock 'generators'.

This might be considered as a failure by the experimental evidence to support the hypothesis. However, these results must be examined in the correct way. As S. fuscum occurs mainly on the tops of the hummocks and on the larger hummocks, it would be expected to be growing

at a slightly lower pH than most of the S. plumulosum. Thus in the experimental situation a sprig of S. fuscum is likely to be more effective than one of S. plumulosum in altering the mineral composition of the culture media in the dishes, and thus promoting production of protonema in the experimental situation.

It is true that a large step has been taken in assuming from promotion of protonema production that promotion of general growth might also occur. However, as mentioned earlier (section 4.1), it was found that in several cases where the Sphagna were the sprig species employed shoots as well as protonema were produced directly from the abscised leaves of the above mentioned rich fen species.

As the hummocks increase in size they present favourable conditions for development to the propagules of other poor fen and acid bog species which may be carried from the neighbouring areas of blanket bog. Thus each hummock builds up its species content until it can be regarded as a fragmentary stand (sensu Braun Blanquet) of acid bog or a "miniature raised bog" (Bellamy and Riely 1967).

On the larger (older) hummocks at the site, and also where two or more hummocks have coalesced Calluna vulgaris and Sphagnum palustre, indicators of dry and wet heath communities (Holdgate 1955) occur.

Figure 7 depicts a model which represents concisely the ideas and arguments, put forward in the hypothesis, as to the development of this mixed mire complex.

The poor fen stage of the succession described is probably quite short occurring only while the Sphagnum species develop to well above the groundwater level. After this stage the poor fen species are eliminated from the hummocks due to the build up of acid conditions and become confined to the narrow belt around the hummocks, which might be considered as the "sphere of influence" of the hummock on the pH

of the surrounding area. This agrees with the results of the fieldwork in which Acrocladium cuspidatum, a true indicator of poor fen, was found to occur mainly in a narrow belt around individual hummocks.

The succession outlined above follows that of Weber (1908), e.g.

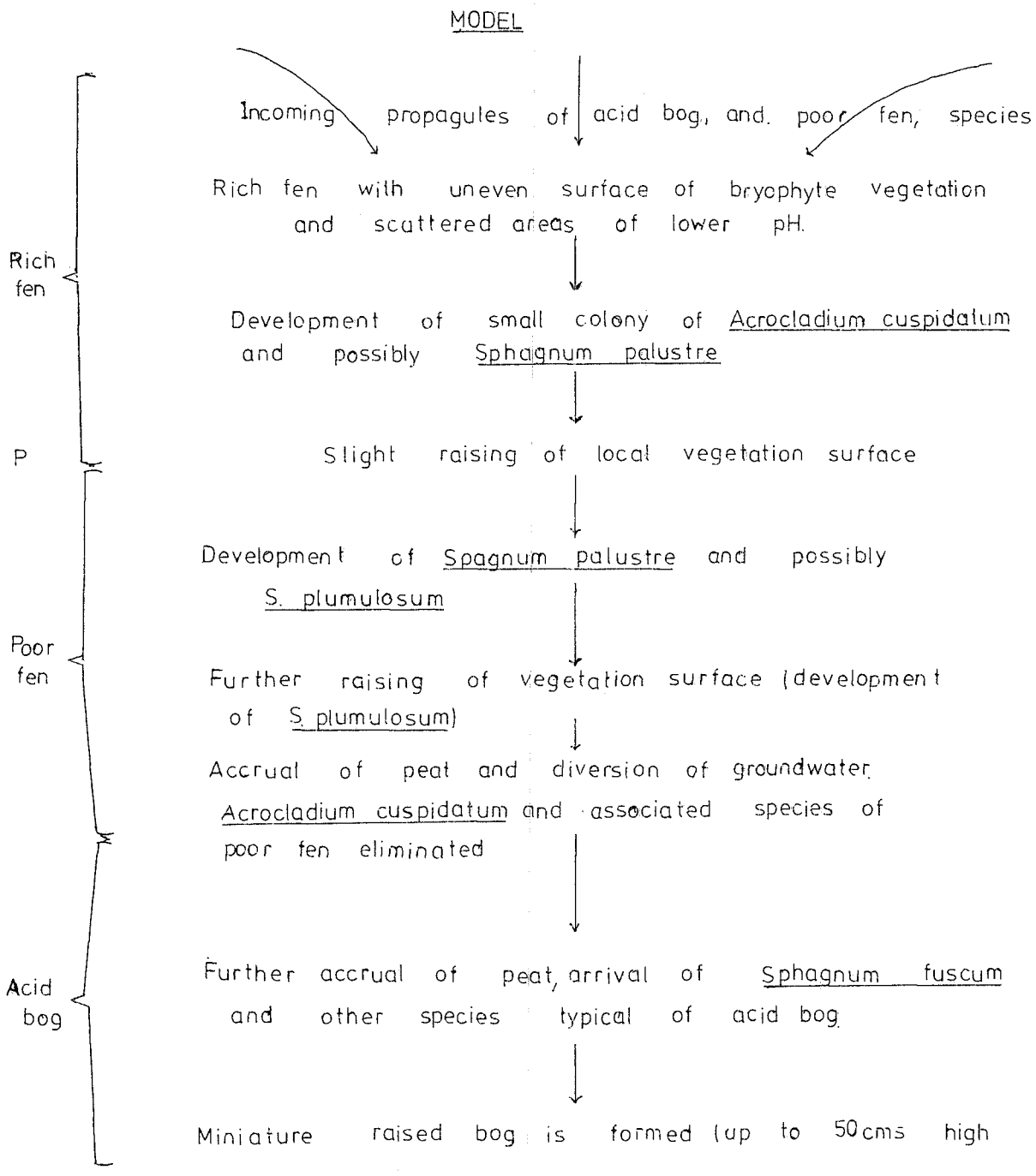
Niedermoore ——→ Ubergangsmoore ——→ Hochmoore (Weber)

Rich fen ——→ Poor fen ——→ Acid bog

and all three types of mire can be seen within an area as small as one metre square at Tarn Moor (see Map 2 and figure 7).

This hypothesis is drawn, in parts, from quite scanty information and several assumptions are made. However, it is considered to be worthwhile as it neatly consolidates the results of the present work and arrives at a picture of the mire type succession at Tarn Moor which backed by evidence from the laboratory and the field, agrees with the classical concept of mire type succession put forward by Weber in 1908.

It is appreciated that more work is required both on and around this hypothesis. To this end the next section consists of a list of suggested lines along which further work on the subject, and the site, might proceed.


MODEL
Incoming propagules of acid bog, and poor fen, species
Rich fen with uneven surface of bryophyte vegetation and scattered areas of lower pH.
Development of small colony of Acrocladium cuspidatum and possibly Sphagnum palustre
Slight raising of local vegetation surface
Development of Spagnum palustre and possibly S. plumulosum
Further raising of vegetation surface (development of S. plumulosum)
Accrual of peat and diversion of groundwater
Acrocladium cuspidatum and associated species of poor fen eliminated
Further accrual of peat, arrival of Sphagnum fuscum and other species typical of acid bog
Miniature raised bog is formed (up to 50cms high
Rich fen
P
Poor fen
Acid bog

5. SUGGESTIONS FOR FURTHER WORK

1. More detailed work is required on the setting up of the experiments and the measurement of all variables (pH, major ions etc.) within the dishes. Also larger dishes should be used.

2. Some other types of growth experiments would be desirable in order to verify some of the assumptions made in constructing the hypothesis.

3. Other species pairs, especially those suggested in the discussions (i.e. Campylium stellatum, Cratoneuron falcatum, and Drepanocladus intermedius with Sphagnum palustre; and Cratoneuron falcatum with C. commutatum) should be tested for allelopathy/promotion.

4. More detailed point sampling using a random technique to investigate the more discrete species associations especially in the area of rich fen.

5. In conjunction with 4 above, point sampling also for abiotic factors such as pH and major ions.

6. Physiological work on the key species mentioned in the discussions (especially those mentioned in section 4.3), in order to discover more about their tolerance limits to pH and the major ions such as $H^+, Na^+, K^+, Mg^{++}, Ca^{++}$, SO_4^-, Cl^-

7. Floristic and chemical analysis comparisons of Tarn Moor with other areas of mixed mire in Europe.

8. Detailed sampling of the peat within the hummocks to discover more about its species content.

9. Combination of all the above work with work on the higher plants of mixed mires.

6. SUMMARY

Bryophyte species from an area of mixed mire are tested individually for the production of protonema from abscised leaves and also for possible effects of inhibition/promotion of this production by the presence of a second species.

The bryophyte distribution in the field is investigated using point quadrats distributed in both a partial random, and a systematic manner.

Tables of results show species which readily produce protonema in this experimental situation and also pairs of species which show inhibition/promotion of this production on one another.

The floristic data are ordinated to give a picture of communities into which the bryophytes of this area are grouped.

The results of the laboratory experiments and the fieldwork are combined and a hypothesis is put forward to explain the development of the mixed mire studied.

It is hoped that this hypothesis will lead to further work on the subject and to this end a list of suggestions is given.

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APPENDIX I

A. CONTROLS

Species No.	Species	No. of leaves producing protonema (X)
1.	Aulacomnium palustre	8
2.	Dicranum scoparium	2
3.	Bryum pseudotriquetrum	6
4.	Polytrichum strictum	0
5.	Ucrocladium cuspidatum	0
6.	Philonotis fontana	2
7.	Pleurozium schreberi	2
8.	Climacium dendroides	7
9.	Scorpidium scorpioides	0
10.	Mnium rostratum	0
11.	Leucobryum glaucum	15
12.	Cratoneuron filicinum	15
13.	Scapania undulata	0
14.	Drepanocladus intermedius	4
15.	Cratoneuron falcatum	2
16.	Ctenidium molluscum	4
17.	Sphagnum palustre	0
18.	Sphagnum plumulosum	0
19.	Campylium stellatum	1
20.	Rhacomitrium lanuginosum	1

Tables of results of the second set of experiments. All dishes employed Knop solution as the culture medium. All counted after 20 days. All numbers are from a possible total of 15.

B. EXPERIMENTS

L.sp = Leaf species no. X = No. of leaves producing protonema.

Sprig species	L.sp	X
Aulacomnium palustre	2	3
	3	2
	4	4
	5	0
	6	6
	7	0
	8	7
	9	0
	10	0
	11	0
	12	14
	13	0
	14	5
	15	0
	16	0
	17	0
	18	2
	19	0
	20	0

Sprig species	L.sp	X
Dicranum scoparium	1	9
	3	4
	4	14
	5	4
	6	0
	7	1
	8	4
	9	0
	10	4
	4	15
	12	9
	13	0
	14	5
	15	0
	16	5
	17	0
	18	4
	19	0
	20	0

Sprig species	L.sp	X
Bryum pseudotriquetrum	1	7
	2	2
	4	15
	5	4
	6	7
	7	5
	8	2
	9	0
	10	3
	11	13
	12	11
	13	0
	14	1
	15	1
	16	1
	17	0
	18	0
	19	0
	20	0

Sprig species	L.sp	X
Polytrichum strictum	1	10
	2	2
	3	3
	5	3
	6	6
	7	6
	8	0
	9	0
	10	5
	11	15
	12	8
	13	0
	14	1
	15	0
	16	4
	17	0
	18	1
	19	0
	20	1

Sprig species	L.sp	X
Ucrocladium cuspidatum	1	3
	2	2
	3	1
	4	14
	6	0
	7	0
	8	0
	9	0
	10	3
	11	15
	12	1
	13	0
	14	1
	15	3
	16	1
	17	0
	18	1
	19	0
	20	0

Sprig species	L.sp	X
Philonotis fontana	1	1
	2	0
	3	7
	4	12
	5	3
	7	0
	8	1
	9	0
	10	8
	11	14
	12	0
	13	0
	14	0
	15	0
	16	0
	17	0
	18	0
	19	0
	20	0

Sprig species	L.sp	X
Pleurozium schreberi	1	3
	2	2
	3	2
	4	6
	5	0
	6	0
	8	1
	9	0
	10	0
	11	15
	12	0
	13	0
	14	2
	15	0
	16	1
	17	0
	18	0
	19	2
	20	0

Sprig species	L.sp	X
Climacium dendroides	1	1
	2	1
	3	10
	4	12
	5	6
	6	7
	7	2
	9	0
	10	6
	11	13
	12	0
	13	0
	14	3
	15	0
	16	2
	17	0
	18	0
	19	0
	20	5

Sprig species	L.sp	X
Scorpidium scorpioides	1	9
	2	0
	3	5
	4	8
	5	13
	6	1
	7	0
	8	0
	10	7
	11	15
	12	0
	13	0
	14	0
	15	3
	16	5
	17	0
	18	0
	19	1
	20	0

Sprig species	L.sp	X
Mnium rostratum	1	3
	2	4
	3	2
	4	0
	5	0
	6	0
	7	0
	8	1
	9	0
	4	14
	12	15
	13	0
	14	5
	15	3
	16	4
	17	0
	18	0
	19	0
	20	1

Sprig species	L.sp	X
Leucobryum glaucum	1	3
	2	0
	3	7
	4	0
	5	0
	6	1
	7	5
	8	0
	9	0
	10	10
	12	0
	13	0
	14	0
	15	0
	16	1
	17	0
	18	0
	19	0
	20	1

Sprig species	L.sp	X
Cratoneuron filicinum	1	3
	2	0
	3	9
	4	0
	5	0
	6	0
	7	0
	8	0
	9	0
	10	10
	11	12
	13	0
	14	4
	15	3
	16	6
	17	0
	18	0
	19	1
	20	2

Sprig species	L.sp	X
Scapania undulata	1	2
	2	2
	3	6
	4	0
	5	1
	6	2
	7	4
	8	0
	9	0
	10	12
	11	12
	12	11
	14	5
	15	0
	16	2
	17	0
	18	0
	19	1
	20	0

Sprig species	L.sp	X
Drepanocladus intermedius	1	1
	2	4
	3	9
	4	2
	5	4
	6	2
	7	1
	8	0
	9	1
	10	13
	4	10
	12	10
	13	0
	15	1
	16	1
	17	0
	18	0
	19	0
	20	0

Sprig species	L.sp	X
Cratoneuron falcatum	1	0
	2	2
	3	8
	4	0
	5	14
	6	6
	7	0
	8	1
	9	2
	10	13
	11	7
	12	14
	13	0
	14	2
	16	6
	17	0
	18	0
	19	1
	20	0

Sprig species	L.sp	X
Ctenidium molluscum	1	0
	2	4
	3	13
	4	0
	5	3
	6	0
	7	6
	8	2
	9	0
	10	13
	11	12
	12	13
	13	0
	14	3
	15	0
	17	0
	18	0
	19	0
	20	3

Sprig species	L.sp	X
Sphagnum palustre	1	5
	2	2
	3	1
	4	0
	5	2
	6	5
	7	2
	8	0
	9	0
	10	13
	11	15
	12	4
	13	0
	14	3
	15	0
	16	1
	18	0
	19	0
	20	0

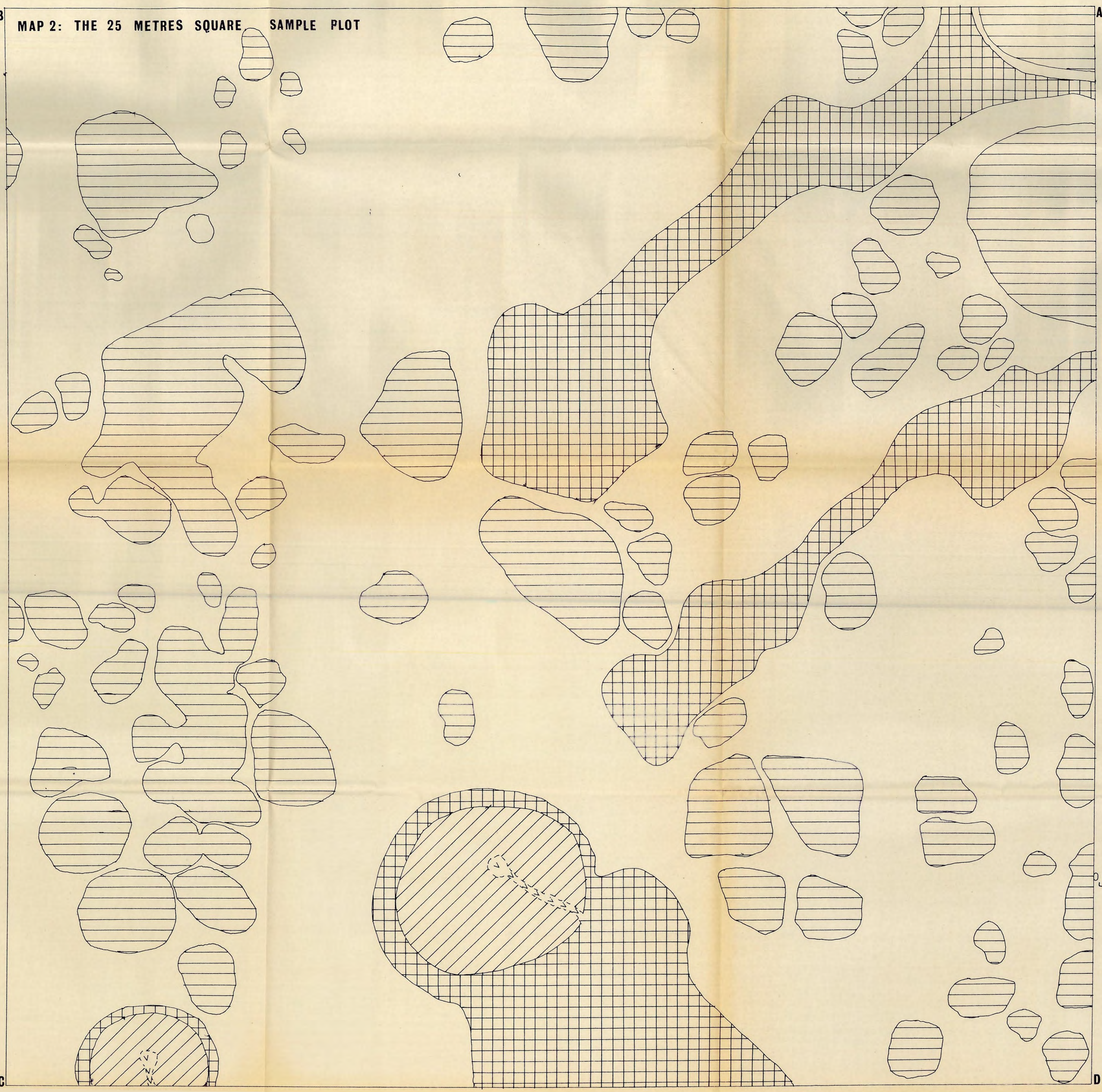
Sprig species	L.sp	X
Sphagnum plumulosum	1	11
	2	1
	3	9
	4	0
	5	6
	6	2
	7	4
	8	0
	9	0
	10	9
	11	15
	12	4
	13	0
	14	3
	15	0
	16	0
	17	0
	19	0
	20	1

Sprig species	L.sp	X	Sprig species	L.sp	X
Campylium stellatum	1	8	Rhacomitrium lanuginosum	1	1
	2	0		2	0
	3	9		3	4
	4	0		4	0
	5	0		5	1
	6	4		6	1
	7	4		7	1
	8	0		8	0
	9	0		9	0
	10	13		10	5
	11	7		11	11
	12	3		12	10
	13	0		13	0
	14	0		14	0
	15	1		15	3
	16	6		16	5
	17	0		17	0
	18	0		18	0
	20	0		19	0

B

A

MAP 2: THE 25 METRES SQUARE SAMPLE PLOT



C

D

KEY:

Sphagnum hummocks, typical habitat for species of group B.

Areas of standing water, typical habitat for species of group D.

Tufa mound, typical habitat for species of group E.

Tufa mound with active spring

Areas of rich fen, typical habitat for species of group A.

All species groups named are shown in figure 6.

To be used in conjunction with sections 4.2 and 4.3, and also with figure 6.

Scale:

0 1 2 3 4 5 6 metres