THE UNIVERSITY OF HULL

ECOLOGICAL STUDIES

on the

SILVER FLOWE NATURE RESERVE

being a Thesis submitted for the Degree of

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by

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CONTAINS PULLOUTS

"In the more level parts of the
country, the surface of the peat
is broken up into little pools of
water, which stand at different
heights, and appear as if artificially
excavated"

Charles Darwin, 7th January 1835,

in describing the peat-covered areas of Tierra del Fuego, during the Voyage of the Beagle.

CONTENTS

INTRODUCTION

This thesis is concerned with the development of surface patterns on an area of blanket bog in south-west Scotland. The area concerned forms part of a series of blanket bogs, collectively known as the Silver Flowe, all of which have conspicuous patterns of deep pools or hollows alternating with firmer areas of the bog surface. Such patterns are commonly found on blanket bogs in northern and western districts of Britain, and are particularly well developed on the extensive 'flows' in Sutherland and Caithness. Similar surface patterns have been described from many peatland areas elsewhere in the northern hemisphere, many of which occur on a scale far greater than those of the British peatlands.

The cause of such patterns has long excited speculation. A review of the literature was written by Auer as long ago as 1920 and a recent appraisal is given by Sjors (1961). In Britain bogs exhibiting these features have been curiously neglected by ecologists until quite recently. In 1956 Pearsall briefly described two such bogs in Sutherland and in 1958 Ratcliffe and Walker described the bogs forming the Silver Flowe. Very different interpretations were offered to account for essentially similar features and neither of these contributions provides a completely satisfactory explanation of pattern development. Indeed Pearsall's contribution is largely speculation. More recently Boatman and Armstrong (1968) have described an area of blanket bog in west Sutherland, in which numerous deep elongated pools occur. They suggest a possible mechanism to account for pool alignment parallel to the contours of the bog surface.

My aim, in carrying out the investigations which form the basis of this thesis, has been to investigate in detail one area of patterned blanket bog with a view to understanding some of the processes involved in pattern formation. The Silver Flowe in Galloway was an obvious choice for a study area since, not only was it the nearest area of undamaged patterned bog, but it also had the safeguard of being a National Nature Reserve.

Early in planning the work it was decided that several lines of investigation would be adopted within the one study area. This policy arose from a consideration of the various suggestions which have been made, largely by Scandinavian and North American workers, to account for the development of patterned surfaces. In general terms there are two 'schools of thought'. Many workers have suggested that patterns are produced by physical processes by which peat already formed is subject to displacement, at least in the surface layers. Several distinct and unrelated phenomena have been relied upon to account for the development of essentially similar patterns. These include the lateral movement of peat owing to slope of the underlying mineral ground (Troll 1944, Pearsall 1956, Heinselman 1965); desiccation and subsequent shrinkage of peat, resulting in convolutions of the peat surface (Newbould 1958, Pearsall 1956); also frost-heaving and other phenomena related to periodic freezing and thawing whereby surface irregularities might be produced (Auer 1920, Drury 1956, Drew and Shanks 1965 and Sigafoos, 1952).

Others suggest that patterns are the result of a specialised form of bog growth, the ridges and hollows forming distinct ecological environments which, once initiated, become accentuated by differential rates of peat accumulation (Sjors 1963 1965, Granlund 1932, Lundqvist 1951, Boatman and Armstrong 1968).

In reviewing the subject of pattern development Ratcliffe (in Burnett 1964) suggests that three main problems require explanation. The first is the underlying cause of hummock and hollow development, in whatever situation. The second is the cause of aligned hollows on sloping bogs and the third is the development of extensive pool networks which he considers are due to erosion. These are still the basic problems. It is worth emphasising that many of the ideas advanced from both 'schools of thought' are in fact no more than speculation based on an examination of surface features. It is surprising, in view of the extent of patterned peatland in the Boreal Zone, and the number of areas which have been described in detail, that very few detailed investigations aimed at understanding the process of pattern formation have been carried out (e.g. Granlund 1932, Boatman and Armstrong 1968 and Ratcliffe and Walker 1958).

If patterns result from a physical process involving some lateral movement of peat then it is reasonable to expect that the distribution of patterns will show a relationship with the form of the underlying mineral ground. Accordingly it was decided that this relationship should be investigated in detail in the area selected for study. In addition analysis of peat stratigraphy was chosen as a second line of investigation in view of the fact that it would provide a most direct means of ascertaining the course of 'pool and ridge' formation.

Detailed examination of water level fluctuation in different types of situation within an area of patterned bog was adopted as the third major line of investigation. In considering the possibility that patterns result from a specialised form of bog growth the most obvious relationship is that of plant communities and microtopography to water table. In the case of the Silver Flowe, Ratcliffe and Walker demonstrated clearly the range of tolerance of different plant species in this respect and many other workers notably Sjors (1948) and Drury (1956) have emphasised the different ecological conditions prevailing in hummock and hollow. The behaviour of the water table in these different conditions had not however been investigated in detail at the time when this work was planned and it appeared that this would be a logical first step in understanding the process of pattern formation as it is occurring at present.

During the course of the work two particular features of the present bog surface posed additional problems which were considered to merit attention. One of these was the accumulation of wind-blown litter of Molinia caerulea in pools and wet hollows, a feature which I considered might have an important influence on the present development of the bog surface. The other was the scarcity of aquatic species of Sphagnum in the deeper pools. The small amounts of Sphagnum growing naturally in such situations was observed to disintegrate in the late summer of two successive years and for this reason I decided to investigate the performance of Sphagnum introduced to such conditions.

These various lines of approach to the problem are presented in turn. Each forms the basis of a separate section but throughout the work, wherever it is relevant, the bearing of one line of research on another is discussed. The main points arising from the various sections are drawn together in the final discussion.

ACKNOWLEDGMENTS

I wish to thank Professor N.F. Robertson and Dr. D.J. Boatman for giving me the opportunity to work in the Botany Department of the University of Hull. I am grateful to Dr. Boatman for suggesting the research topic and, as my supervisor, for his continued guidance and helpful discussion.

The study would have been impossible without the willing co-operation of the Forestry Commission and Nature Conservancy. In particular I thank Mr T. Huxley for his assistance in matters relating to the Nature Reserve. Thanks are also due to the staff of the Garraries Forest, in particular Mr W. Semple.

Several people assisted with field work and I am particularly grateful to Dr. A. Lord, Dr. D. Cotton, Mr B. Ringer and Mr J.W. Lamble, who assisted with survey work.

I am indebted to the technical staff of the Botany Department for their ingenuity in constructing special instruments, such as a water level recorder and peat corer. I acknowledge the loan of a Robot Automatic camera from the Department of Zoology.

My thanks are due to Mr P. Wakely and Mr P. Smith for photographic work and to Dr. J.K. St. Joseph for allowing me to include photographs from the Cambridge collection.

During the period of this study I received a University of Hull Research Studentship.

I wish to acknowledge the helpful discussion and criticism on the part of colleagues, especially Mr Ian Smith.

Finally thanks go to my wife Diana who assisted with the drawing of diagrams and has given endless help and encouragement.

The Silver Flowe

The bogs collectively known as the Silver Flowe lie along the floor of a broad gently sloping valley in the Galloway Hills, Kirkcudbright, Scotland (grid reference: NX 475820). Much of the valley floor is covered by blanket bog, the vegetation of which belongs to the lowland western-Scottish type (Trichophoreto-Eriophoretum) described by McVean and Ratcliffe (1962). The flatter expanses of bog are distinguished by pronounced surface patterns of pools or hollows separated by hummocks or ridges. Bogs exhibiting these features form a series, separated by lagg streams, along the valley bottom, and patterns also occur locally on flat-lying areas of blanket bog towards the head of the valley. It is these patterned bogs which give the Silver Flowe its special character and importance.

A general account of the stratigraphy of certain bogs of the series and a description of the vegetation throughout the whole area has been given by Ratcliffe and Walker (1958).

The Silver Flowe was designated a National Nature Reserve by the Nature Conservancy in 1956 in order to maintain the bogs as far as possible in their natural state.

SECTION I

THE STUDY AREA: LONG LOCH BOG B

Introduction

Within a region of fairly uniform blanket bog in the northern part of the Silver Flowe there occur eight areas of patterned blanket bog characterised by either linear pools and ridges or by anastomosing pool networks. The distribution of these is shown in figure 1 in which the naming of sites follows that used by Ratcliffe and Walker (1958). The three larger areas are situated on a low spur which forms the watershed between the Long and Round Lochs of the Dungeon and the valley of the Saugh Burn and its tributary. All three differ from other bogs of the Silver Flowe in that they cannot be clearly distinguished from the adjoining blanket-bog. Other bogs of the series generally show distinct marginal features such as laggs and rands which separate the bogs from each other so that each can be regarded as a separate morphological unit. Indeed Ratcliffe and Walker suggested that in certain external features the lower bogs of the series showed affinities with raised bogs. However the lack of definite marginal features in the three northern bogs and their very position on the watershed led them to regard these sites as true blanket bog.

Differences are apparent between these three areas. Round Loch Bog exhibits a series of linear pools and ridges with a greater amount of *Sphagnum* than in the other two bogs. In this bog many of the pools are interlinked but the pool networks so formed are not extensive. The surface of Long Loch Bog A, the largest of the three, consists of an extensive series of anastomosing pool networks with deep pools separated by ridges.

Most of the pools are steep edged and only the peripheral pools are *Sphagnum* grown.

Long Loch Bog B exhibits a variety of surface features which can be divided broadly into four major types.

1. Extensive steep edged pool networks, with little development of *Sphagnum* dominated communities.
2. Linear pools and ridges with a well defined zonation of plant communities related to the amplitude of the pools and ridges.
3. Areas with hollows and 'flat' dominated by *Sphagnum papillosum*.
4. Areas where pools are absent except for relatively few small non-linear pools.

All these types occur within an area which appears at first sight to be a single morphological unit, the pools and ridges being aligned around one central axis. The other two areas described above are more uniform in their surface morphology and it was for this reason that Long Loch Bog B was selected for detailed investigation.

Shape of the peat body beneath the study area and two smaller areas near to Long Loch

The surface patterns which define the extent of this site occur on a tongue of peat which slopes gently from north to south along the axis of the watershed. Their total extent is included in an area 700 ft. (213 m.) long by 600 ft. (183 m.) wide which is the area investigated in detail. It can be seen from the oblique aerial photograph (figure 2) that the patterns are discontinuous and that they vary in type throughout the site. Parts of the site are lacking in conspicuous surface patterns and in places mineral ground is exposed in the form of granite rocks, some of which may well be erratic boulders.

The general slope of the bog surface is shown in figure 3, in which the contours are drawn on the general level of the bog surface, not taking account of deep pools. For details of survey methods see Appendix 1. The surface of the peat forms a single morphological unit within which three zones can be recognised:-

(a) An extensive central area which appears to be almost flat but which slopes very gently from north to south along the axis of the watershed, at an approximate gradient of 1 in 250, giving a total fall of only 3 ft. along the mid-line of the study area.

(b) A surrounding area continuous with (a) in which the slope increases to a gradient of 1 in 37 (average of 10 profiles) and locally to 1 in 25. In the south west section of the site this zone is less distinct, being wider and flatter (with an average gradient of about 1 in 80).

(c) A relatively steep margin (average gradient 1 in 11) is developed around the southern periphery of the site. Elsewhere zone (b) merges with the surrounding blanket bog in a continuous gentle slope.

In contrast to the peat surface the morphology of the mineral ground is most irregular as can be seen in figures 4-7. A number of basins and ridges underlie the study area, the distribution of which is not reflected in the surface slope therefore the peat depth varies considerably throughout the site. In places the occurrence of mineral ground ridges is reflected in changes of slope of the peat surface but these only occur where the peat is very thin (generally less than 1 m.). Such features give rise to the steep surface slopes around the southern margin and to isolated knolls elsewhere on the peat surface. The sections across the site (figure 6), and those which are extended to include the area to the east (figure 7) (where patterned surfaces are absent), show the contrast between slope of the peat surface and that of the mineral ground on the study area.

Before going on to consider the relationship which exists between the shape of the peat body and the distribution of major surface patterns on the study area details are given of the shape of the peat body underlying two smaller isolated patches of 'pool and hummock' bog which occur within the general blanket bog terrain close to Long Loch. The nature of these sites can be seen in the aerial photograph, figure 8. The general slope of the peat surface in this area is from north to south. Both areas of Sphagnum - dominated vegetation (referred to as pool networks 1 and 2) occur on "terraces" where the peat surface is almost flat (see figures 9a and 10a). Within the pool networks a Sphagnum papillosum - Eriphorum angustifolium[1] association predominates, whereas on the surrounding blanket bog vascular plants prevail, Calluna vulgaris, Molinia caerulea, Trichophorum cespitosum and Eriophorum vaginatum being the main constituents of the vegetation.

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1. Plant nomenclature in this work follows Clapham Tutin and Warburg (1962), Paton (1965), Warburg (1963) and Fritsch (1945, 1948).

Profiles across those sites show that in both cases there is a basin in the mineral ground below the terrace on which the pools occur (figures 9c and 10c). The present extent of the pool networks does not however correspond exactly with the basins. Each basin is filled with soft semi-liquid peat (except at the lowest levels close to the mineral ground) which contrasts with the compact peat, strikingly difficult to penetrate with the peat borer, which covers the peripheral regions of each basin.

It is clear from the profiles that these basins are much simpler structures than the irregular nature of the mineral ground below the study area and for this reason any relationship which might exist between the distribution of surface patterns and the shape of the underlying mineral ground might be inferred from these smaller areas and then applied to the structurally more complex situation of the study area itself. The following features exhibited by these sites are considered to be important in this respect.

(1) Where the pools are present the peat surface is effectively level or only sloping at a very shallow angle.

(2) The presence of pools appears to be related to the presence of a basin in the subjacent mineral ground with a corresponding ridge downslope of the area of pool development.

(3) A considerable thickness of peat may accumulate above such a ridge and in these cases the pools occupy a peat terrace lying well above the height of the rock ridge.

(4) The type of peat which covers the ridges and surrounds the basin is more compact than the semi-liquid peat in the basin itself.

Distribution of the surface patterns on the study area.

In illustrating the distribution of the surface patterns on the study area emphasis has been placed on the pools (rather than the ridges or hummocks) since these, by virtue of their water surfaces, are easily identified for mapping purposes. The distribution of various types of pools is indicated in figure 11 in which the orientation of the long axis is shown for all elongated pools except those in which the maximum dimension is 5 feet or less.

Discrete pools are shown according to certain size categories and this, together with their spatial relationship, provides an indication of the amplitude of pools and ridges on the peat surface. Where long linear pools lie close together there is generally a well defined ridge between any two adjacent pools. In contrast the small pools, less than 10 feet (3 m.) in length, which are widely distributed over the western section of the site, occur within a surface which is less undulating, though occasional tall hummocks occur.

The outlines of three areas referred to as 'pool networks' are shown in figure 11. In the case of the 'eastern' and 'north-west' pool networks detailed maps have been drawn (figures 13 and 15) and the areas concerned are shown in figure 11. The 'south-west' pool network is composed mainly of *Sphagnum* grown pools many of which merge into adjacent linear pools making it difficult to define a boundary. The boundary shown only indicates the area where pools are distinctly interlinked.

Relationship between shape of the peat body and distribution of major types of surface pattern

The distribution of pool networks and various forms of linear hollow shows a relationship with the shape of the peat body in terms of peat depth, shape of the mineral ground and gradient of the peat surface. Comparison of figures 3 and 11 shows that the three areas of pool network are situated on the flattest parts of the bog surface whereas linear hollows occur on gently sloping areas. The pool networks do not however extend throughout the whole of the flattest parts of the bog surface but are restricted to those areas where peat depth exceeds about 7 ft. (2.1 m.), see figure 5. The eastern and north-west pool networks are separated by a zone where there is no pool development (well displayed in figure 2) corresponding with the area of thin peat overlying the mineral ground ridge which follows the long axis of the study area.

Linear pools or hollows occur on the sloping areas of the bog surface and it is clear from a comparison of figures 3 and 11 that the long axes of these features are aligned parallel to the direction of contour lines on the bog surface. Even in the case of very short hollows (5 - 10 ft. in length) this alignment is maintained where the surface gradient is only 1 in 100. The distribution of linear pools and hollows throughout the study area is however very irregular despite the relatively small amounts of variation in surface gradient and again the depth of peat and shape of mineral ground appear to influence the distribution of hollows of various types to some extent. Large linear hollows (such as those between the western and eastern pool network) occur where peat depth exceeds about 7 ft. (2.1 m.) but small hollows are numerous in areas of shallow peat such as that on the west side of the study area. No hollows occur where the peat is very thin (less than about 1 m.).

Although linear hollows are restricted to sloping areas the degree of slope appears to be important in determining their extent. In figure 7 it can be seen that the linear patterns of the study area occur on the gently sloping zone immediately adjacent to the almost flat central area and are not developed on the more steeply sloping areas further to the east. The maximum gradient on which pools are developed is about 1 in 37. The absence of pools from certain sectors of the eastern periphery, might be related to the local increase in slope in these areas (1 in 25-27) but in the case of the area devoid of pools immediately to the east of the eastern pool network the relatively shallow peat is probably also important. Within the small area of pools to the south of this the gradient is only 1 in 43 and this area is of interest in that it is bounded by a mineral ground ridge on the downslope side producing a situation similar to that of the two small areas near Long Loch previously described.

Northern Bogs of the Silver Flowe

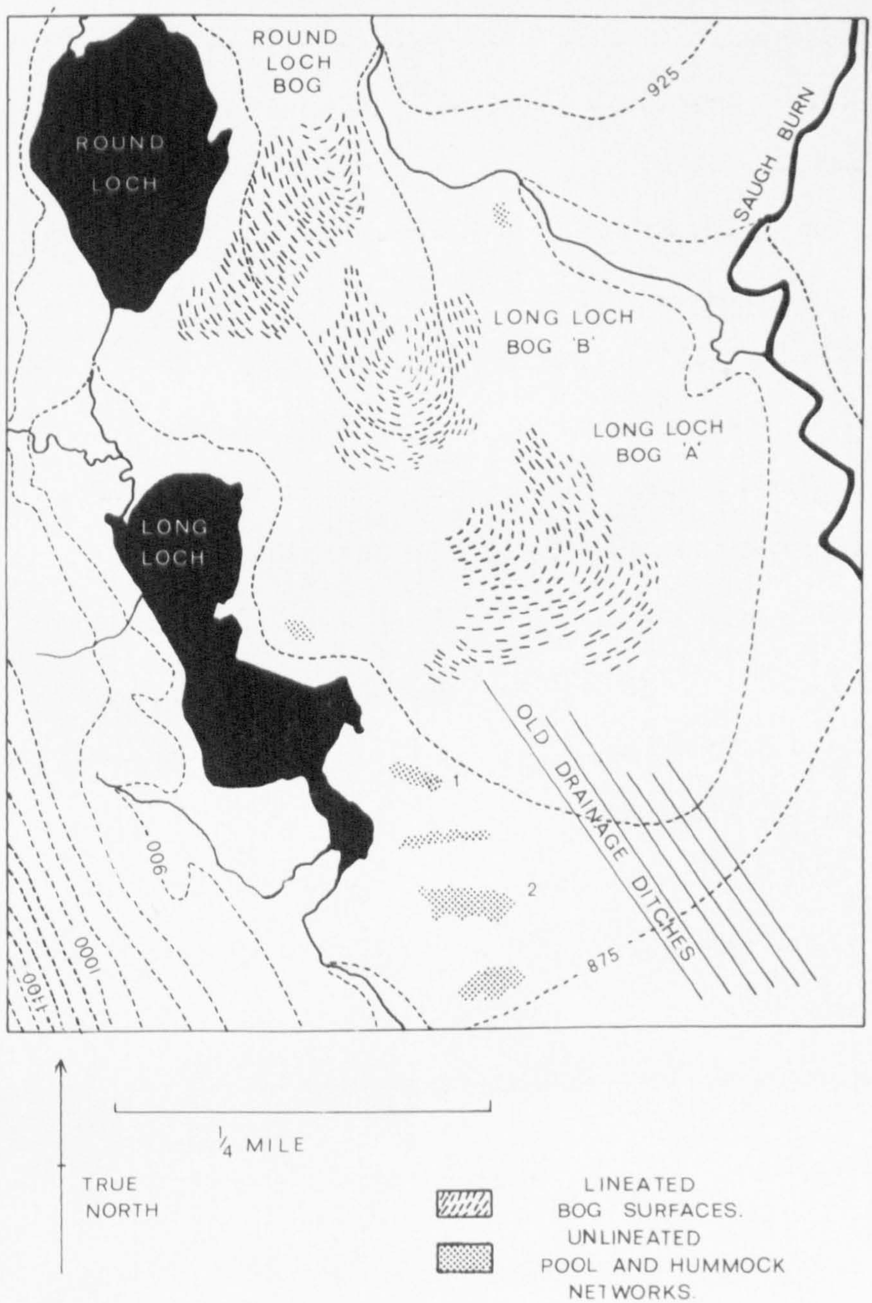


FIG. 1

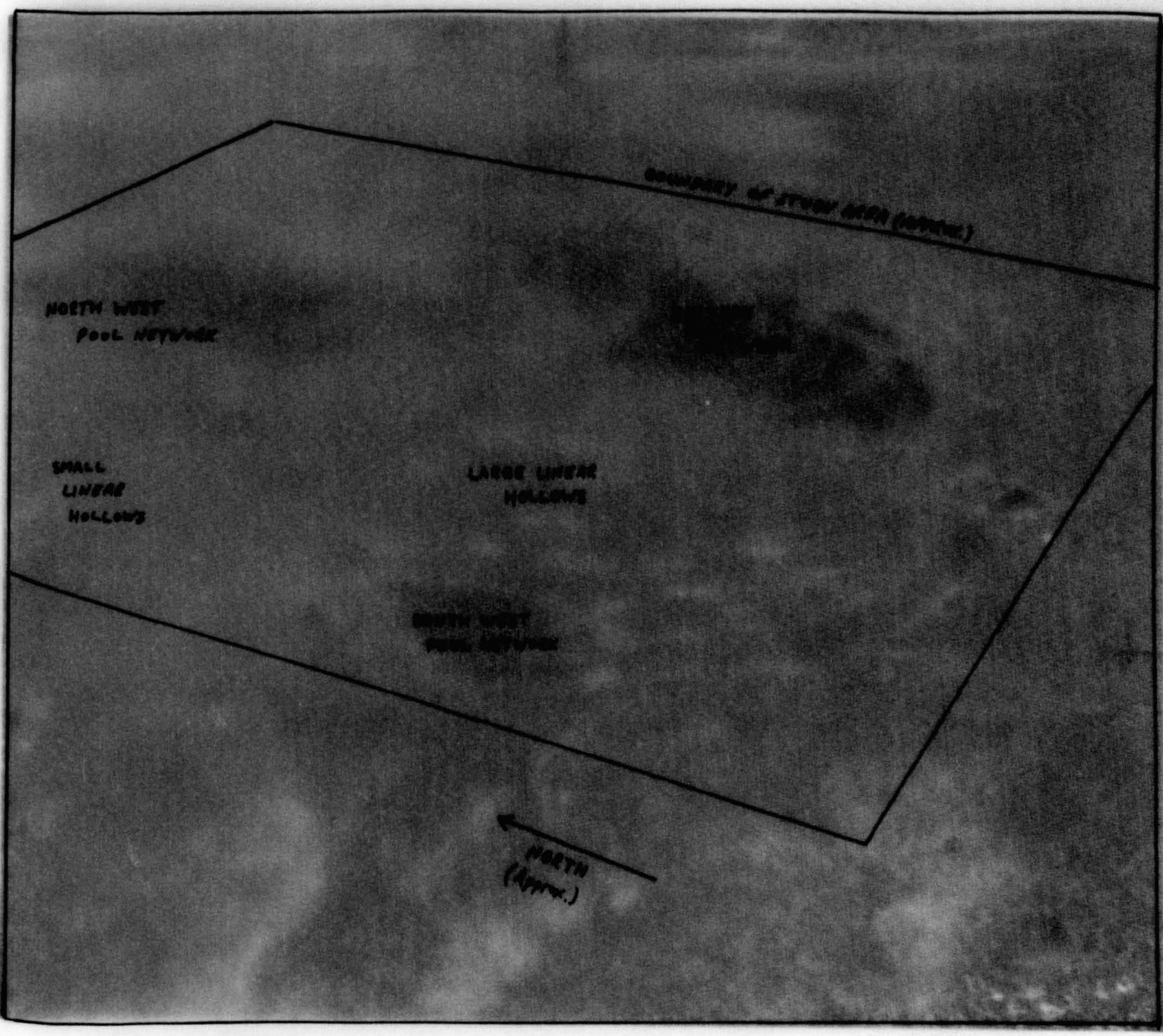
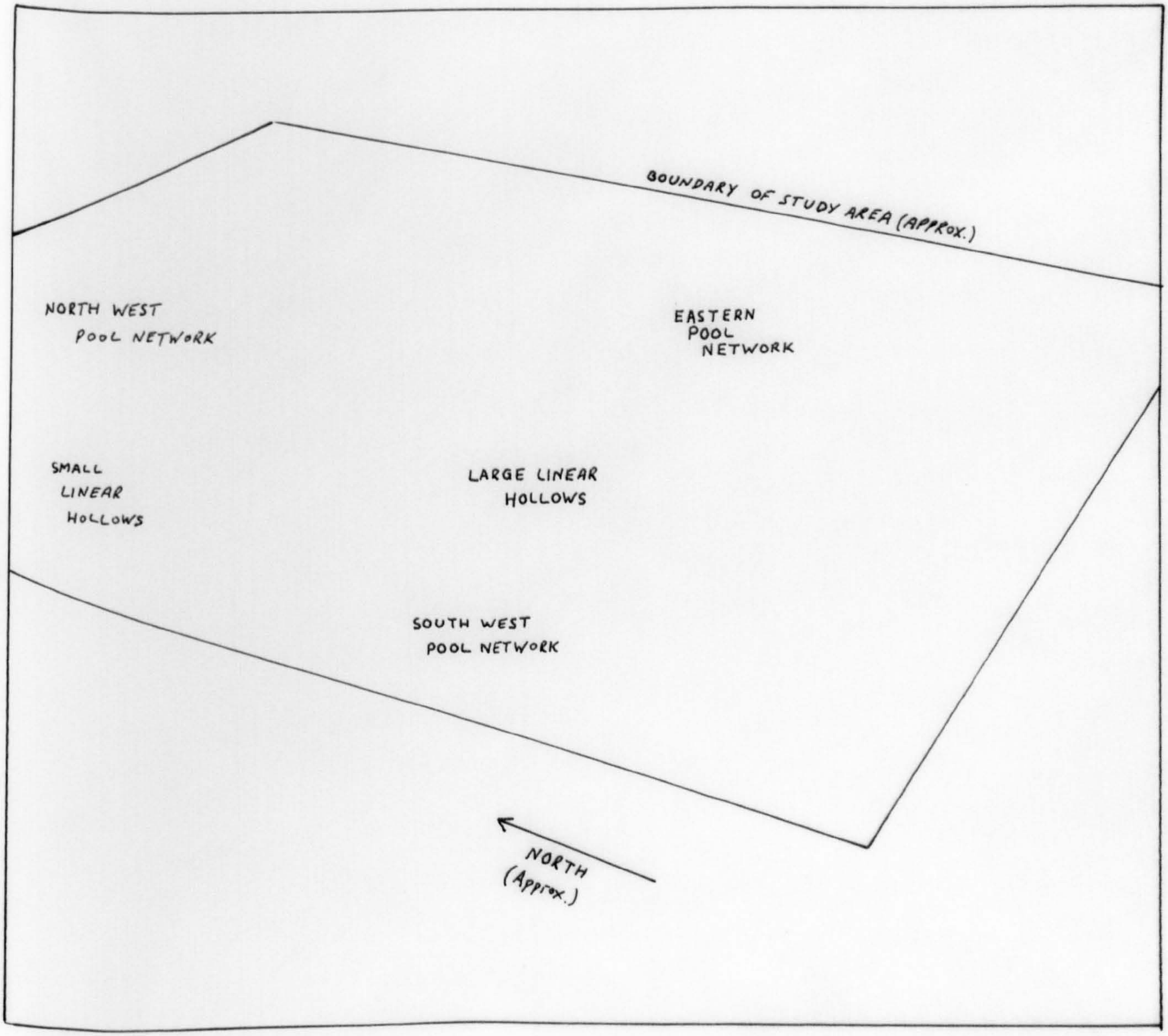


Figure 2. Oblique aerial photograph of Long Loch Bog B from the south west, showing the three separate networks of open pools and discontinuous distribution of linear hollows.

Photo J.K. St. Joseph.


BOUNDARY OF STUDY AREA (APPROX.)
NORTH WEST
POOL NETWORK
EASTERN
POOL
NETWORK
SMALL
LINEAR
HOLLOWS
LARGE LINEAR
HOLLOWS
SOUTH WEST
POOL NETWORK
NORTH
(Approx.)

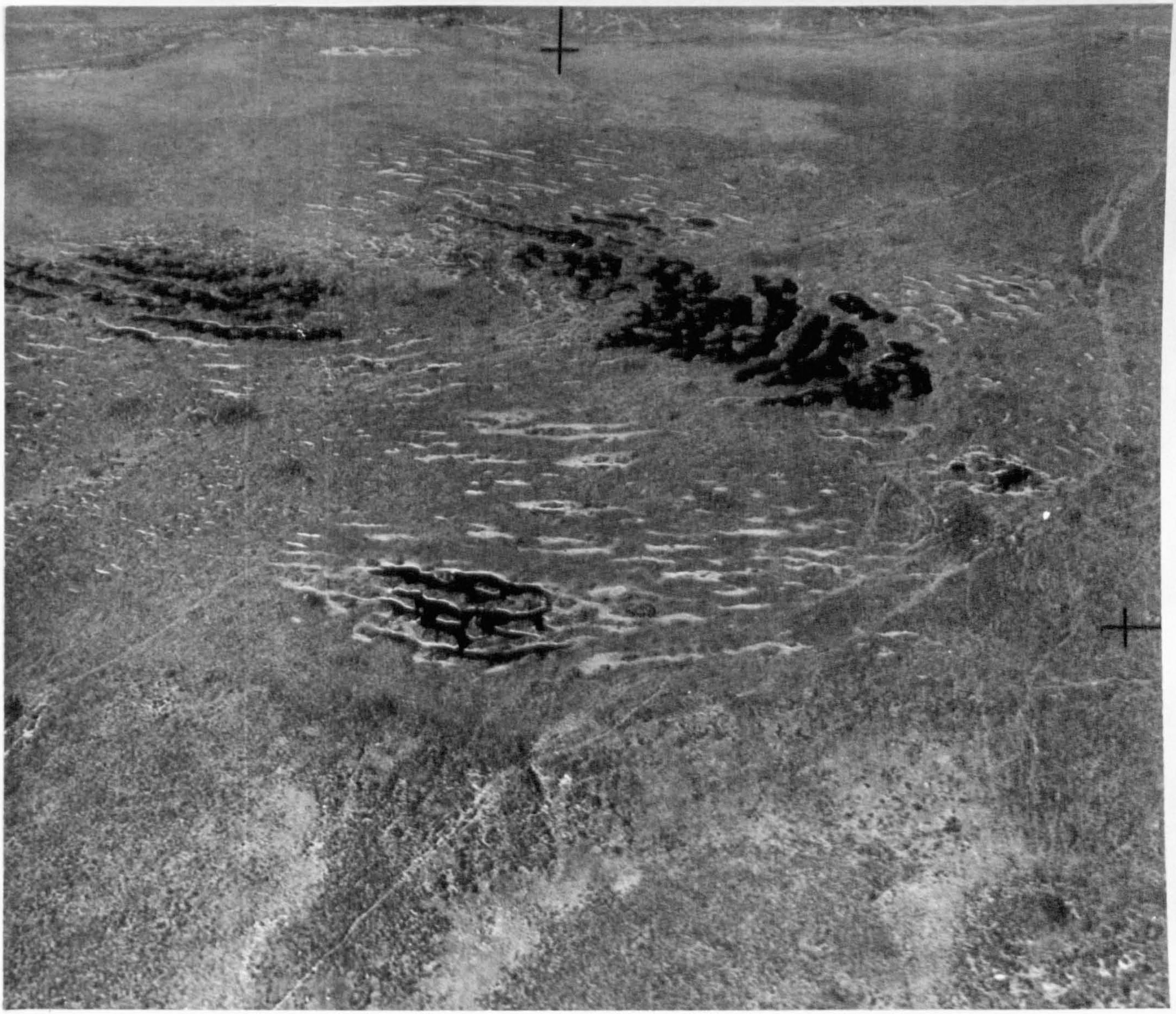
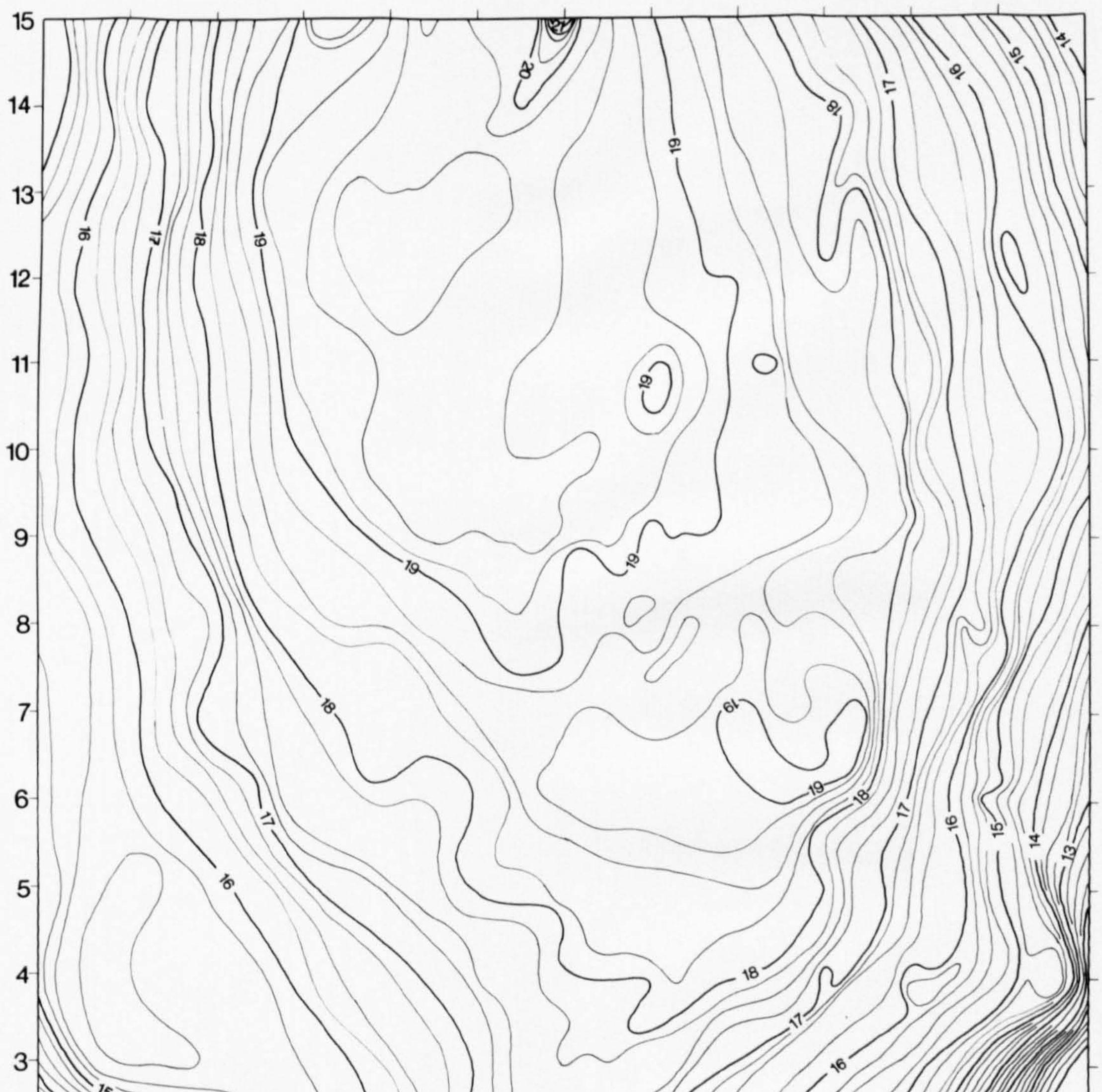


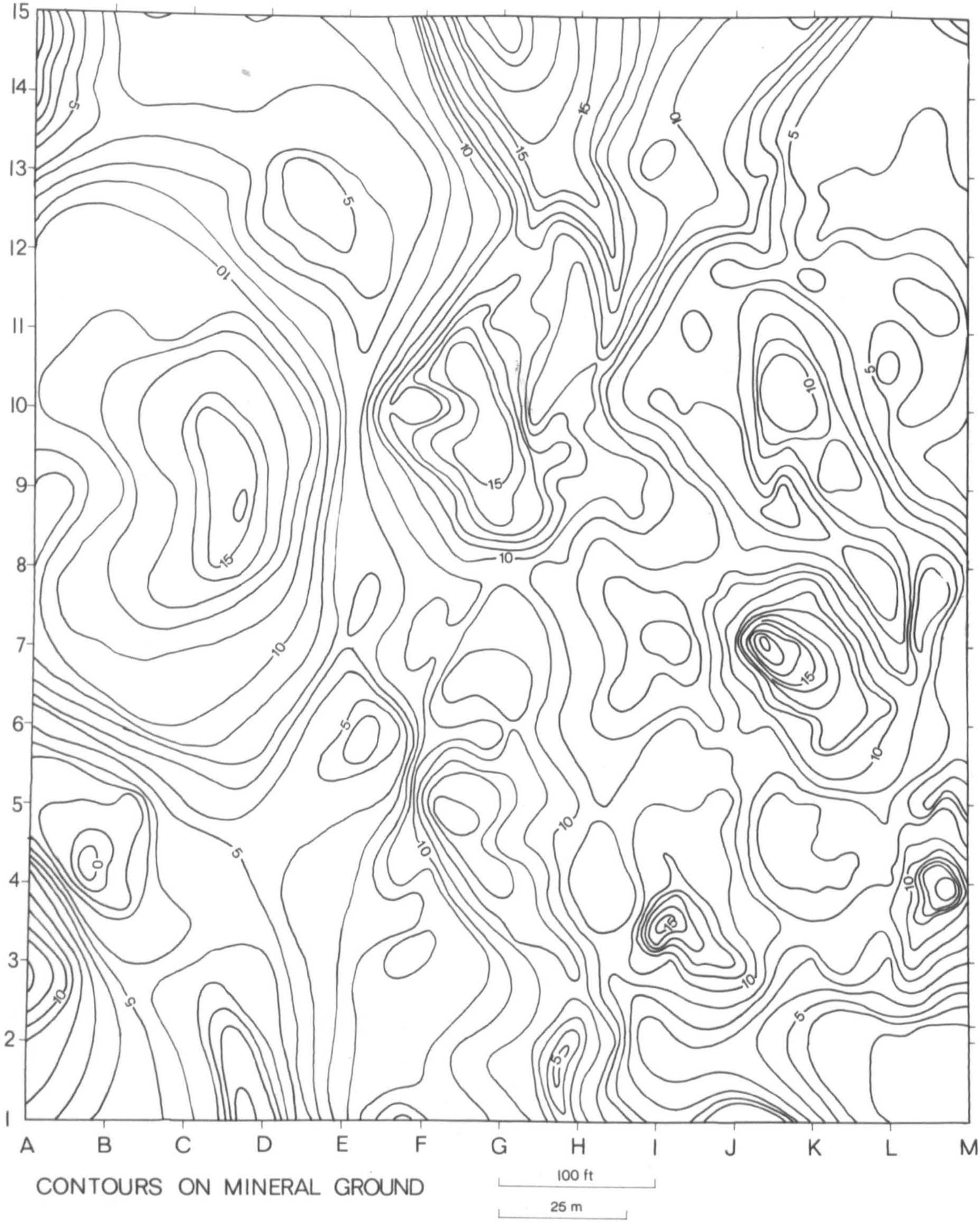
Figure 2. Oblique aerial photograph of Long Loch Bog B from the south west, showing the three separate networks of open pools and discontinuous distribution of linear hollows.

Photo J.K. St. Joseph.



SURFACE CONTOURS ON THE STUDY AREA

FIG. 3



CONTOURS ON MINERAL GROUND

FIG. 4a

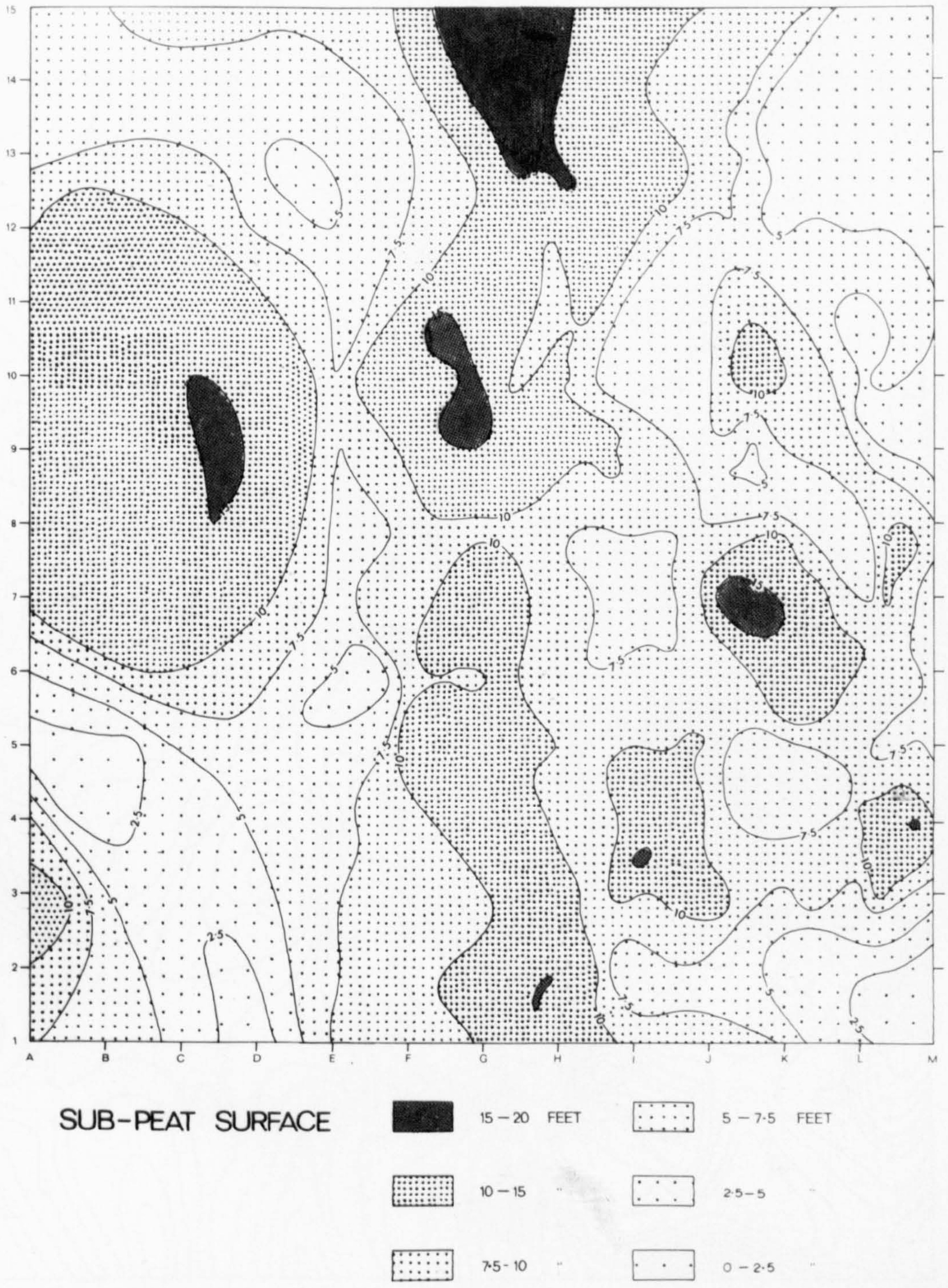
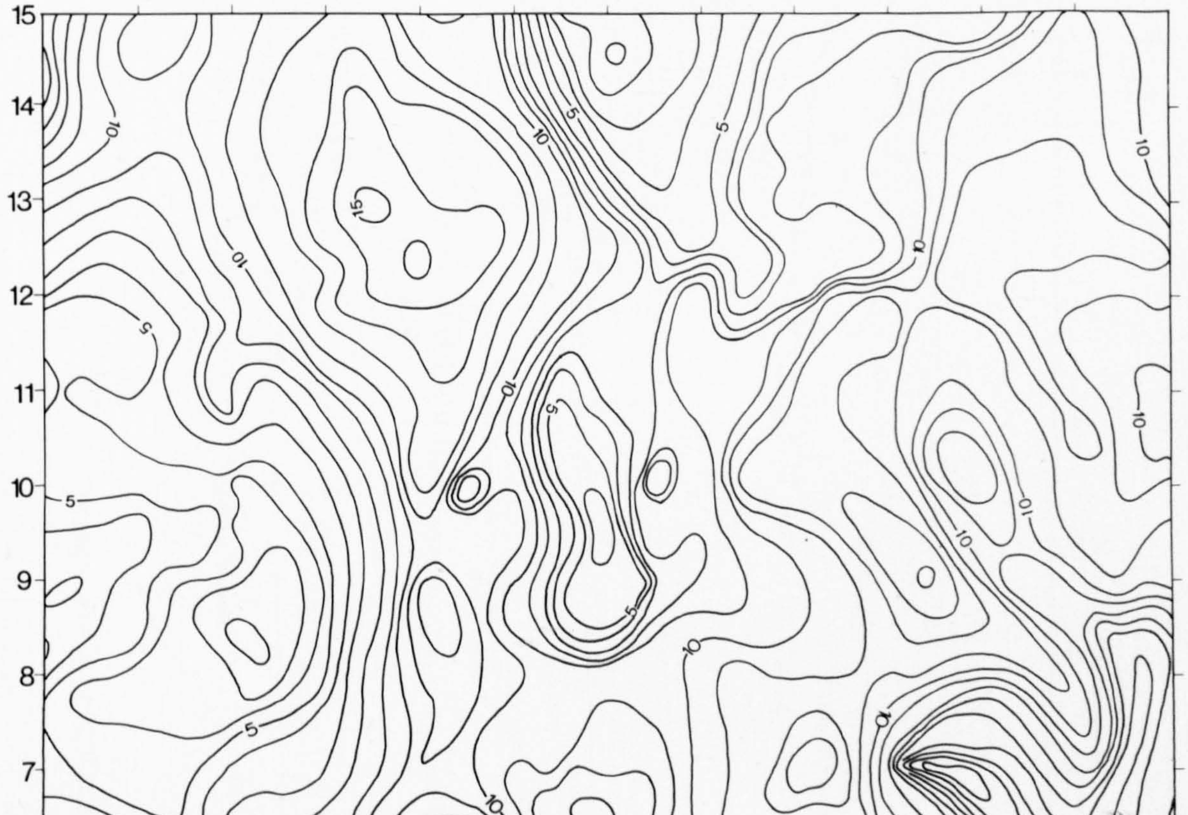

SUB-PEAT SURFACE
15 – 20 FEET
10 – 15 "
7·5 – 10 "
5 – 7·5 FEET
2·5 – 5 "
0 – 2·5 "
A
B
C
D
E
F
G
H
I
J
K
L
M
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

FIG. 4b



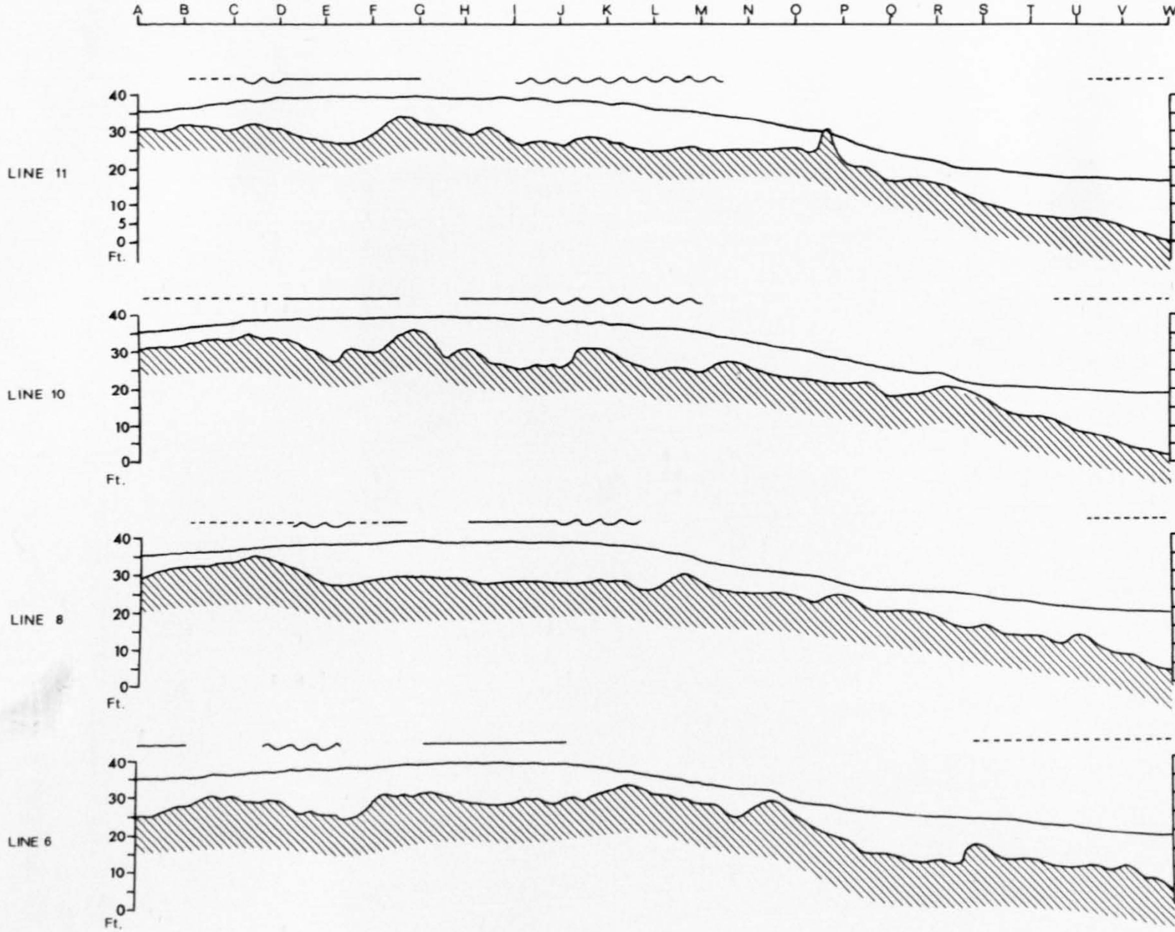
100 ft

25 m

PEAT DEPTH ON THE STUDY AREA

FIG. 5

FIG. 7



PROFILES ACROSS LONG LOCH BOG B
AND ADJACENT AREA TO THE EAST

V. E. × 4

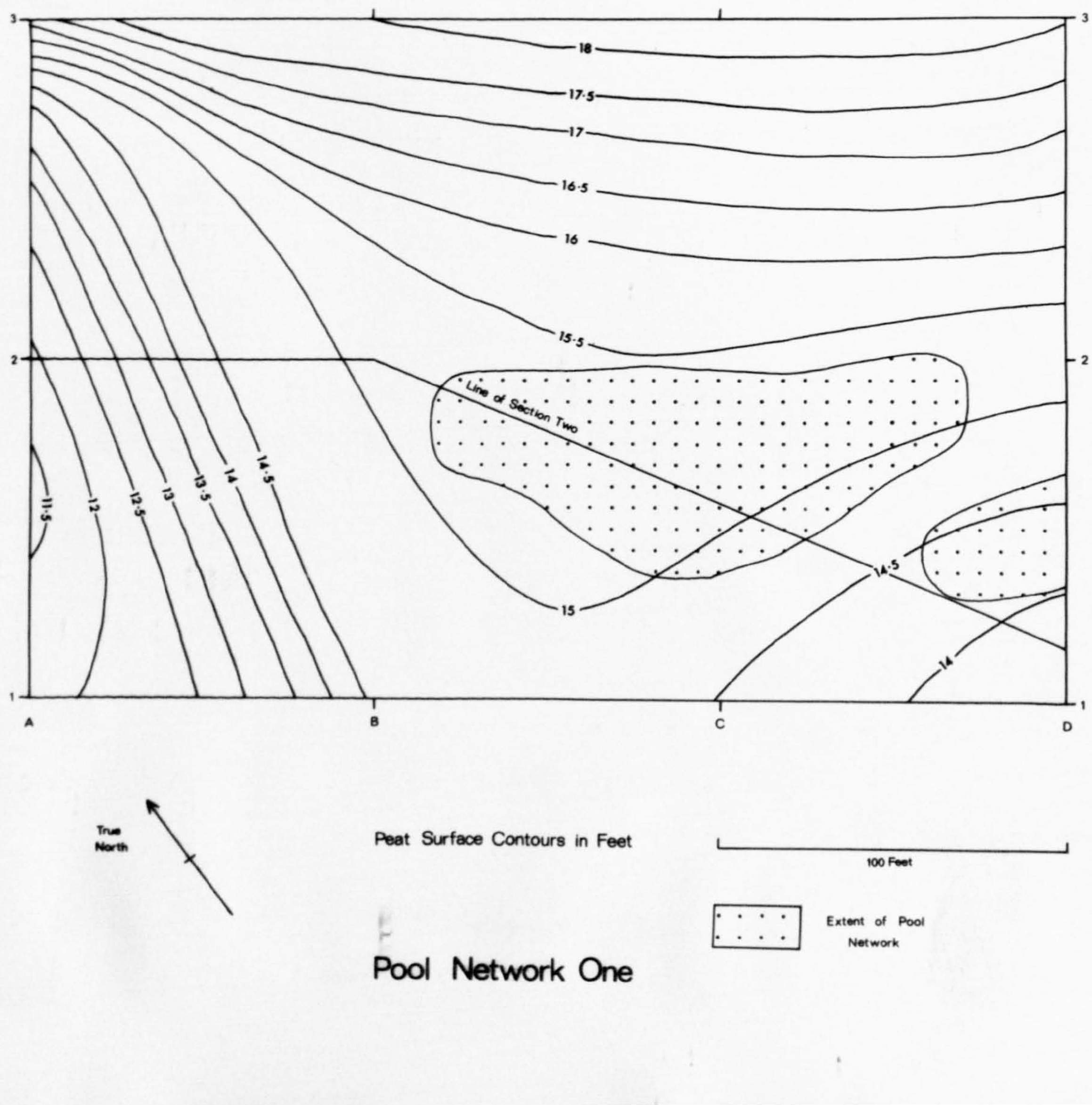
0 200 ft.

0 100 m.

Open pool networks
Linear pools and ridges
Occasional pools present
Vertical height 20 feet corresponds to zero on maps of the study area

Figure 8. Oblique aerial photograph of the small pool and hummock networks close to Long Loch. In the centre is Pool Network 2 and at the top Pool Network 1. A third area of pools lies in the foreground.

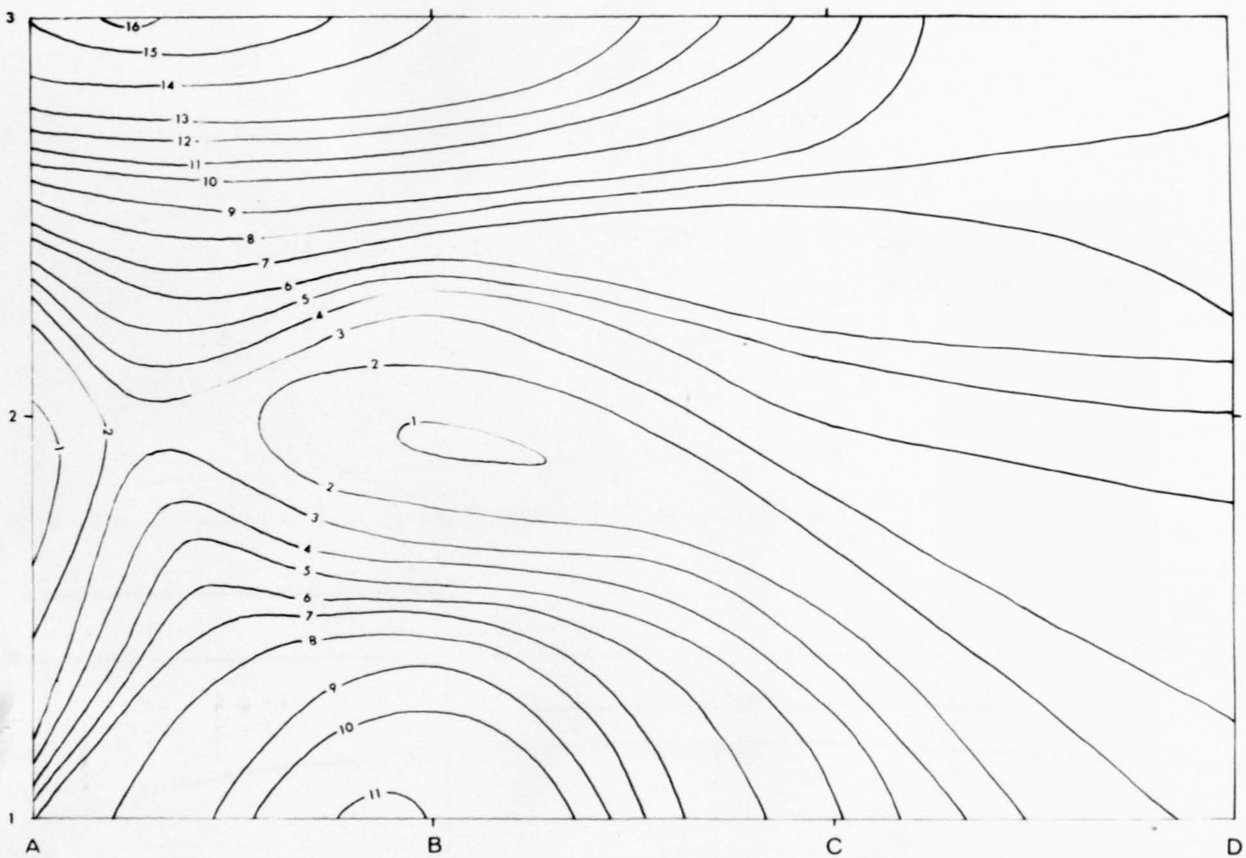
Photo J.K. St. Joseph.



Peat Surface Contours in Feet

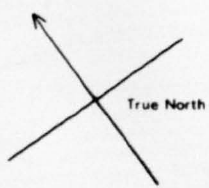
Pool Network One

FIG. 9a



Contours on Mineral Ground in Feet

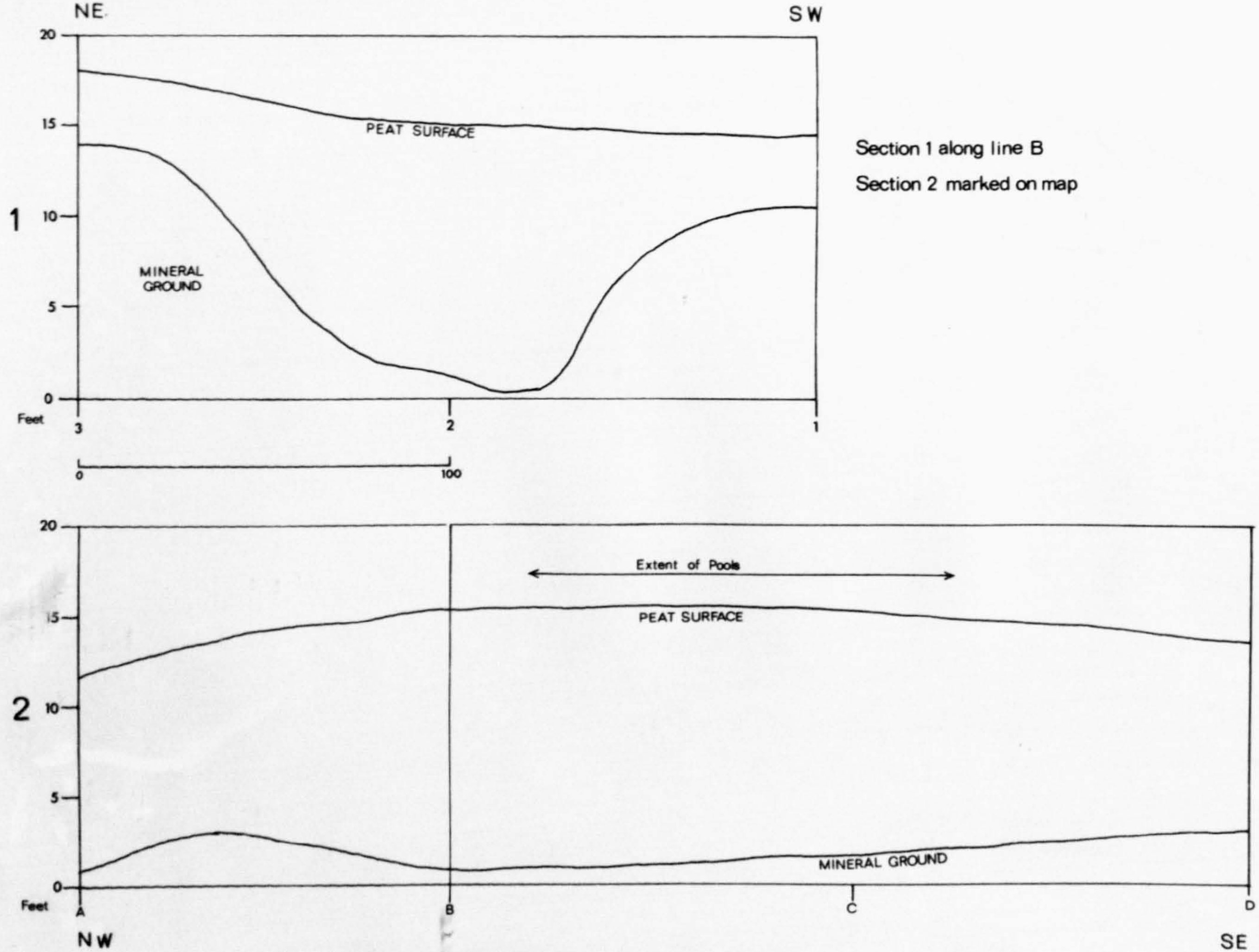
100 Feet



Pool Network One

FIG. 9b

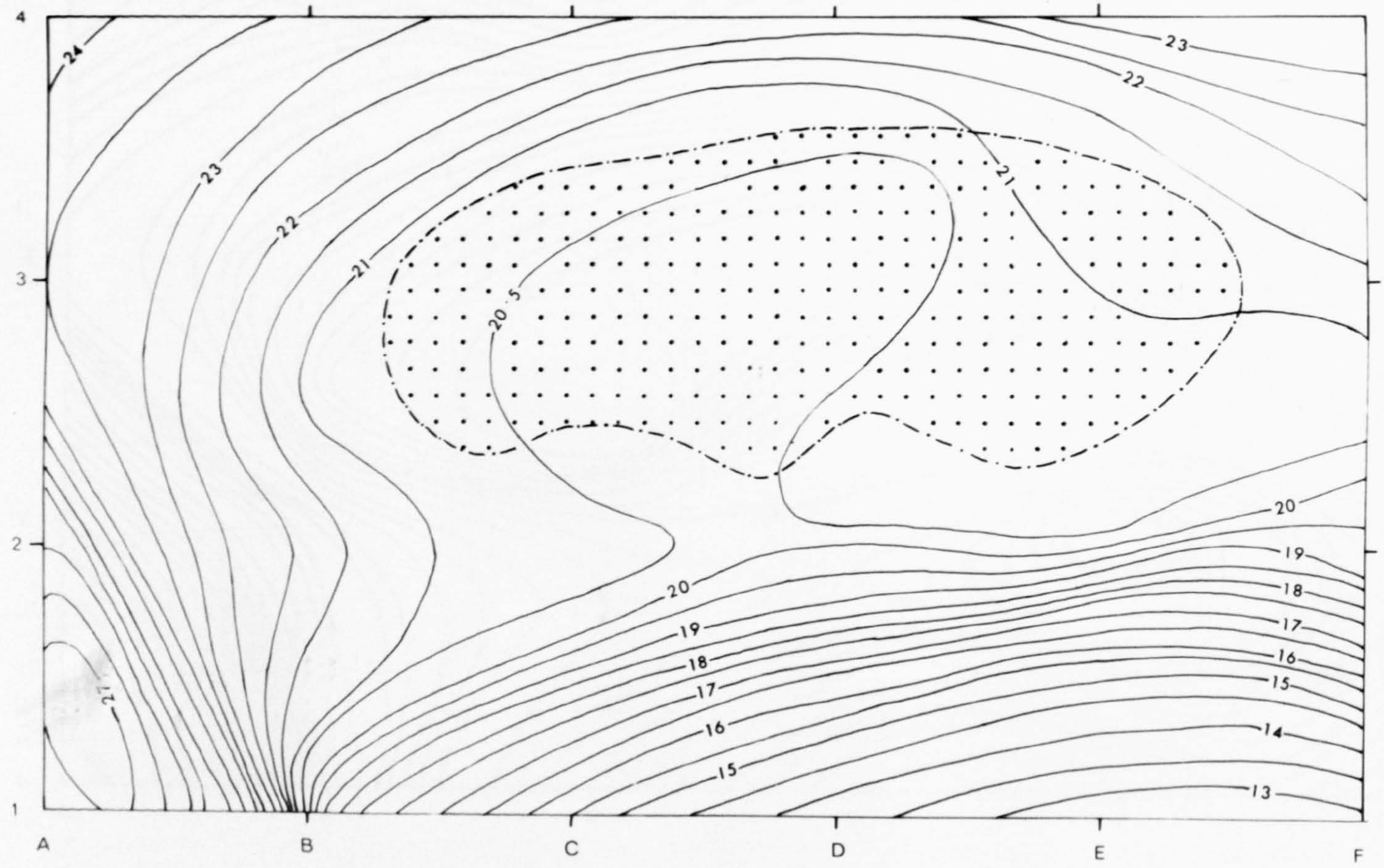
Fig. 9c



Section 1 along line B

Section 2 marked on map

Sections across Pool-Network One



True North

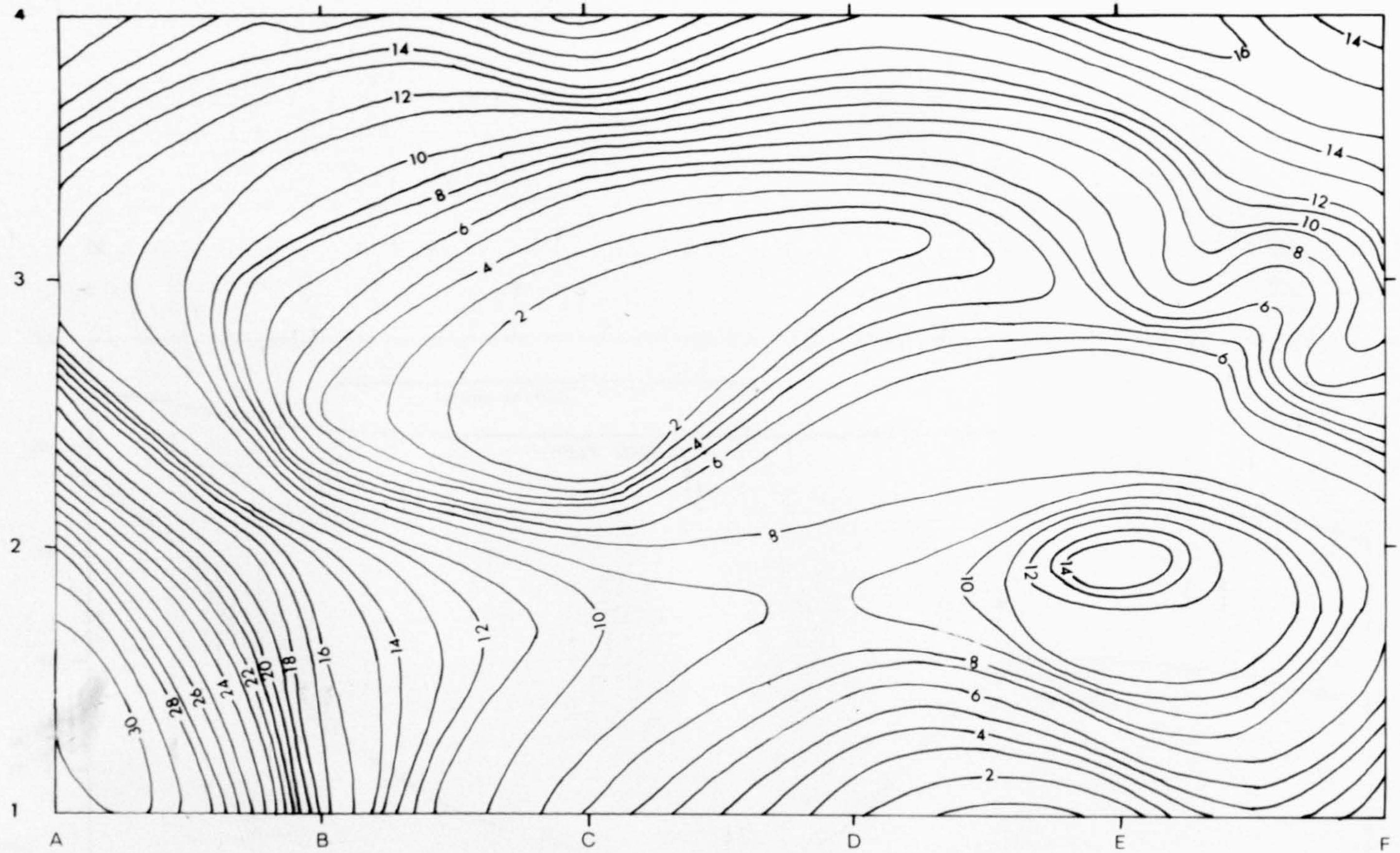
Peat Surface Contours in Feet

Extent of Pool Network

100 Feet

Pool Network Two

FIG. 10a



True North

Contours on Mineral Ground

100 Feet

Pool Network Two

FIG. 10b

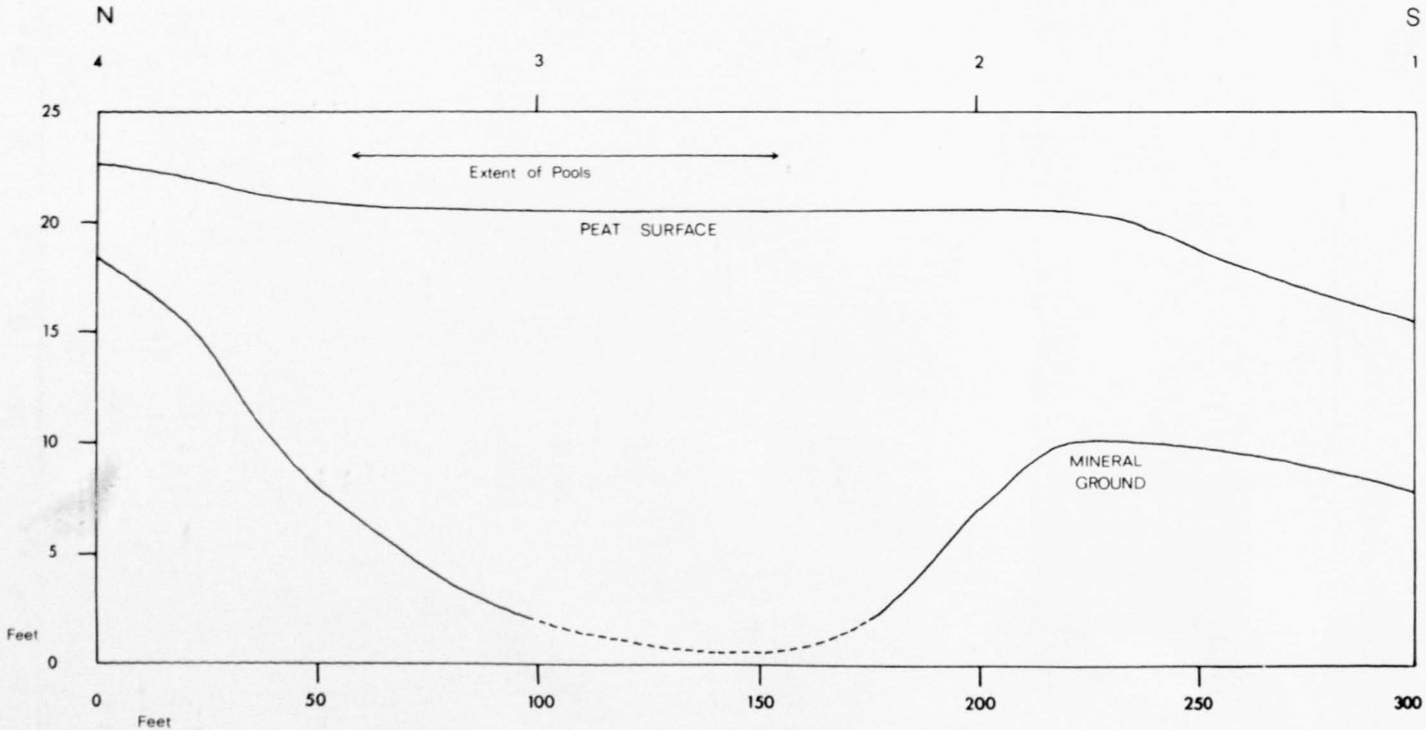
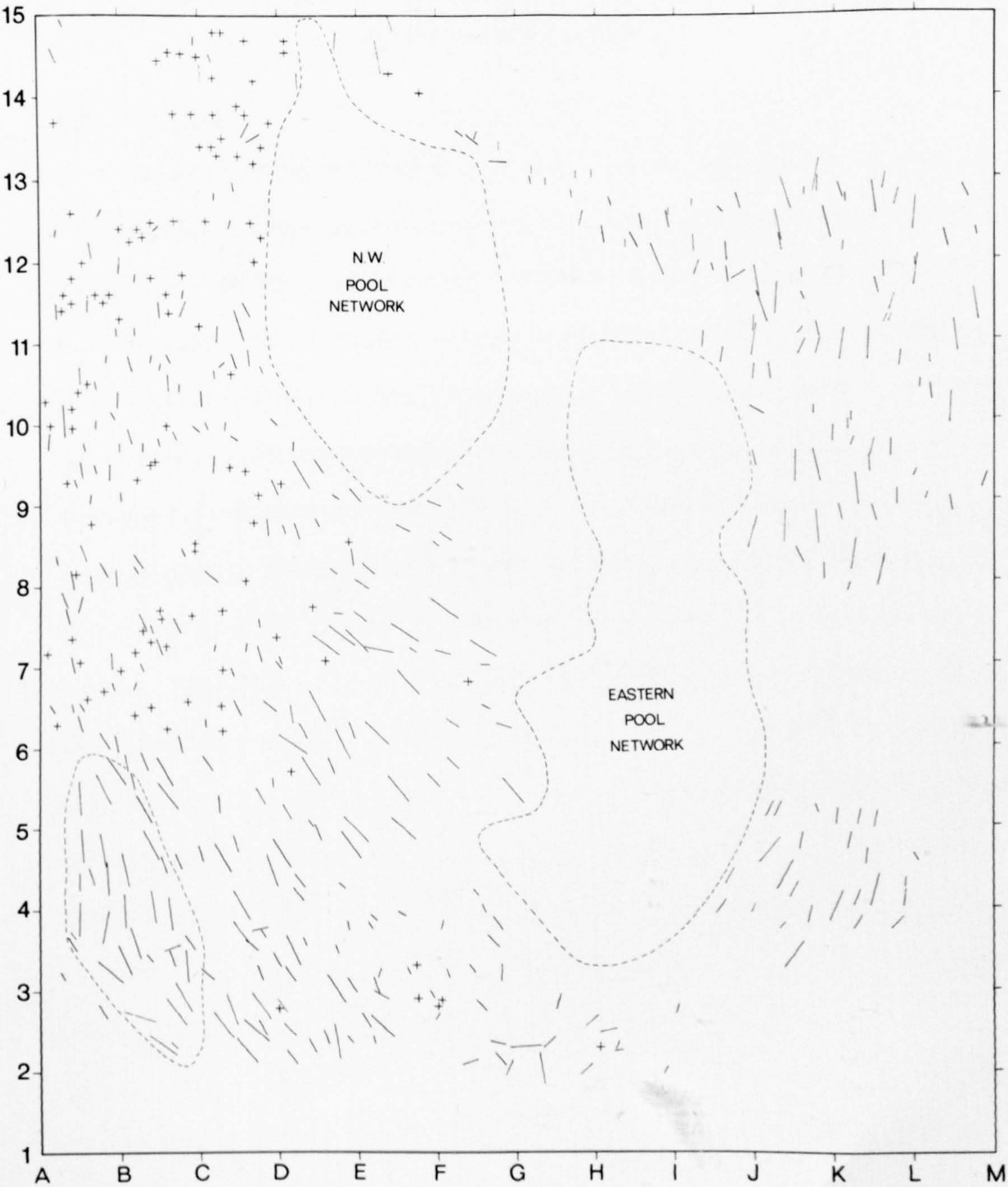


FIG. 10c

Section across Pool-Network Two

ALONG GRID LINE C



DISTRIBUTION AND ORIENTATION OF POOLS ON THE STUDY AREA

FIG. 11

SECTION 2

MORPHOLOGY AND VEGETATION OF SURFACE PATTERNS ON THE STUDY AREA.

Pool Networks

The most striking feature of the surface patterns on the upper bogs of the Silver Flowe is the presence of pool-networks consisting of deep pools (30 - 60 cm.) with steep, often 'undercut', margins and wide expanses of open water in which are situated numerous islands and peninsulas. Three such networks occur on the study area. The pools have a distinctive vegetation, the only macrophytes being Menyanthes trifoliata, which is abundant, producing an open growth throughout the pools, and Eriophorum angustifolium, which is restricted to situations where the pools are shallower than 20 cm., when dense stands of this species may occur. Aquatic Sphagnum species are characteristically absent from these deep pools although there is generally a very sparse fringe of Sphagnum cuspidatum along the edges. Algae are however abundant though this group had not been investigated during the present work. The pools generally contain accumulations of wind-blown litter of Molinia caerulea which forms a compact mat filling the pools completely in the 'bays' and around the ends of elongated pools, but which is semi-floating in the centre of the larger pools. In contrast to the deep open-water areas aquatic Sphagnum species are present in association with deposits of Molinia litter in the bays. Where this litter is relatively thin or absent the pool bottom is seem to be a fairly level bare peat surface covered by a layer of filamentous algae (mostly Batrachospermum sp.).

Areas between the pools are composed of peat ridges, the surfaces of which are approximately level, though isolated hummocks of Sphagnum rubellum and Rhacomitrium lanuginosum occur. Such hummocks are most common where the pool network is developed on a gently sloping surface when they are found on the linear ridges. On the fairly level surfaces of the ridges the vegetation is composed of an association of Sphagnum species and vascular plants, species of both groups having high cover values.

Islands, of variable size, are abundant in the networks. Small islands (less than 25 cm.) are common and usually consist of a single tussock of Trichophorum cespitosum. Larger islands have a vegetation composed of 'high hummock' species i.e. Rhacomitrium lanuginosum, Cladonia impexa, Calluna vulgaris, Sphagnum tenellum, Hypum cupressiforme agg., and Pleurozium schreberi.

To illustrate the vegetation of the pool networks a detailed analysis is shown in figure 12 which shows a transect across the southern part of the eastern pool network. All species except small leafy liverworts were recorded along the exact edge of a tape laid along the transect line, which is 100 ft. long. The numbers refer to the total number of 2 inch units for which the species was recorded in each 1 foot division. The list of species has been arranged in the diagram to facilitate understanding of the distribution of each species and to emphasise the narrow range of vertical distribution. It can be seen that the vegetation of the networks falls into two major categories, these being the communities of the ridge surface and of the pools. Intermediate communities (especially an association of S. papillosum, Trichophorum cespitosum Narthecium ossifragum and Erica tetralix) which are important consitutents of the vegetation outside the pool networks are here confined to narrow zones along the pool edges. This can be seen by comparing the vegetation along this transect with that of the two transect lines in the region of linear hollows and ridges (figures 19 and 20) where the distinction between vegetation 'zones' is much less pronounced.

The patterns of pools and islands on the two major networks in the study area are shown in figures 13 and 15. These maps were compiled from low level aerial photographs (e.g. figure 14) obtained by means of a camera suspended from a balloon at between 100 and 200 feet above the peat surface (details of the method are given in appendix 2). Each pool network is composed of a number of distinct hydrological units in the form of pools with differing water levels separated by peat ridges. Of the five such groups of pools which constitute the eastern pool network (groups A to E in figure 13) groups A to C form a continuous series on a sloping peat surface and illustrate the relation between the downslope width of each pool and the surface gradient. This group C, which is most extensive, occurs on the almost flat surface and the narrow pool system A lies on a steeper slope. This is true in general of the pool networks and moreover the pool systems occupying the flat upper parts of each major pool network (e.g. area E in the eastern pool network) exhibit no orientation, there being simply a mosaic of pools and islands. Such areas contrast with the peripheral areas of the pool networks where there is a distinctly sloping peat surface and the constitutent pools are elongated, the network in such areas consisting of groups of interlinked parallel pools with a common water surface. Narrow peninsulas and strings of islands parallel with the contours of the bog surface occur in such areas. The lower part of the N.W. pool network and group B in the eastern pool network illustrate this very clearly. Although the various groups of interlinked pools form separate hydrological units the difference in water level may be quite small. When measured on a single occasion (23 June, 1967) the difference between various sections of the eastern pool network was A to B 7.8 cm. and B to C 12.4 cm.

Pool complexes constitute a major feature of the surface patterns on the study area and since the processes involved in their development are not at all clear efforts have been made to examine any morphological features which might throw light on this problem. Several such features are now described but first it is necessary to explain why these particular features are considered relevant. Examination of aerial photographs and maps of the individual pool complexes suggests that the development of these extensive areas of pools is dependent on some process of pool expansion and linkage at the expense of the intervening peat surface. In particular the strongly orientated pool networks developed in areas where the overall peat surface is sloping provide features consistent with this theory, especially the linear development of islands and peninsulas and on a smaller scale the presence of many small 'islands' often composed of single tussocks of caespitose vascular plants such as Eriphorum vaginatum or Trichophorum cespitosum, the fibrous remains of which form submerged pillars which may be taller than they are broad. It is difficult to envisage a process by which these features could be produced without such islands once being connected.

Consideration of the implications of pool linkage provides a crude method of investigating whether or not pool systems result from coalescing of several previously discrete pools. On a sloping peat surface where each individual pool has a water level differing from that of adjacent pools up and down slope linkage would result in adjustment of the water levels in those pools furthest upslope to the level of the lowest pool in the network so formed. Consequently, the upslope pools would become shallower and the previously submerged edges would be exposed to some extent. The north west pool network has been examined in order to see if this is in fact the case. Pool depth and shape of vertical pool edge profiles have been measured in the 'highest' and 'lowest' sections of this network. Profiles of pool edges are shown in figure 17. The data were obtained by using a frame through which graduated rods were pushed horizontally at known heights (3" (7.6 cm.) intervals) so that the method was consistent for all profiles. Group A is from the 'highest' part of the network which though it is shown in figure 15 as a discrete pool, has a water level at the same height as the rest of the network. Profiles of Group B are from the 'lowest' pool. The edges of pool A show abundant bare peat surfaces above the water surface which are often colonised by <u>Campylopus atrovirens</u>. The profiles are clearly variable in shape but they are usually concave to some degree especially in the lower half of the profile, i.e. there is a projecting lobe of peat in the upper section and an 'undercut' surface below. The height of the water surface (obtained from a continuous recorder) in relation to the profiles differs in that it is lower in the 'highest' parts of the network (group A) so that the projecting lobe of peat is exposed around the margins of the pool, whereas it is at, or slightly below, the water surface in the lower pools. Pool depth was measured on a single occasion at 10 or more places in each individual section of the network and the average depth (in cm.) is shown in figure 15. The lowest section of this pool network is about 8 - 10 cm. deeper than the upper sections, a difference which corresponds approximately with that already noted in the case of the pool edge profiles. So, although the differences in height are very small, the morphological features of the north west pool network are at least consistent with the conditions to be expected if pool networks result from linkage of previously discrete pools.

It appears that some degree of erosion is involved in the development of pool networks. This has been suggested previously by several authorities but their opinions differ as to exactly how the process operates. It is not relevant to discuss these fully at this stage but an outline of the various ideas is necessary since I have investigated certain features of the pool networks in order to see how far particular theories are applicable to the study area. One school of thought relies on physical erosion involving current or wave action due to wind, including Ratcliffe and Walker (1958), Ratcliffe (in Burnett, 1964), Osvald (1923, 1949) and Pearsall (1956); whilst Sjors (1963, 1965) relies on corrosive oxidation of peat which is essentially a biological process depending on the presence of a film of algae on the bare peat surface below the water level. Boatman and Armstrong (1968) rely on some form of erosion to account for enlargement and linkage of pools but consider that the process depends initially on 'flooding' of the peat surface in the areas which are subsequently eroded.

It might be expected that if wind action is important the direction of greatest pool elongation would be related to that of the prevailing wind and also that the undercut margin might be more pronounced where the greatest fetch is possible. Pool edge profiles have therefore been examined in a variety of situations in the north-west pool network and eastern pool network by the method previously described and these are shown in figures 16 and 17. There does not appear to be any relationship between shape of a profile and its position on the pool system. Furthermore, the extent to which the pool edge is undercut does not depend on the size of the pool or degree of fetch since two profiles which show considerable undercutting (nos. 24 and 25 in figure 16) are from a relatively small pool. Neither is there any clear indication that pool elongation is more pronounced in those cases where pools are aligned parallel to the prevailing wind. The strongly linear pools of the north west pool network lie at 90° to the prevailing wind. The very fact that undercutting occurs at all in the small pool (figure 16) implies that some process other than wind action is involved, though this does not preclude wind action as a factor elsewhere.

It has been shown that linkage of pools on sloping areas (e.g. the north west pool network and the southern part of the eastern pool network) involves narrow straight-edged connections across the intervening ridges. There is no obvious reason why pool linkages due to erosion should have such a constant and characteristic shape. Certain features of the present ridge surfaces have been examined which indicate a possible way in which the process of 'fragmentation' is initiated. These are narrow belts of a distinct vegetation type crossing the continuous ridges which separate the individual hydrological units of each pool network. These are generally 1 - 2m. wide and extend completely across the ridge. Four of these can be seen in figure 14 between groups C and D of the eastern pool-network. The vegetation is characterised by the presence of an algae-covered surface with a sparse distribution of vascular plant species. Floristic data for nine sites on the eastern pool network, and four sites in the north western pool network are given in table 1. Species are shown by presence or absence in five quadrants (15 cm. square) on each site. Certain characteristic species of these sites occur only sporadically in other communities on the study area, e.g. Drosera anglica, Rhynchospora alba, Carex pauciflora and Sphagnum compactum. Other species, especially Eriophorum angustifolium and Narthecium ossifragum are abundant, as also are Sphagnum papillosum and S. cuspidatum which occur as small nuclei rather than a continuous cover. Campylopus atrovirens is characteristic of these sites where it is associated with bare algae-covered surfaces.

EASTERN POOL NETWORK	1	2	3	4	5	6	7	8	9
Drosera anglica	-----	/---/	---//	/////	-----	/-/--	-//-/	-----	-//-/
rotundifolia	/--/-	--///	----/	/---/	-----	////-	/-///	-----	//-/-
Eriophorum angustifolium	///-/	/////	/-///	//-//	/////	/////	/////	/////	/////
Menyanthes trifoliata	---/-	-----	-----	-----	-----	-----	-----	-----	-----
Narthecium ossifragum	-----	/-/-/	-----	/--//	-----	-----	/-///	-----	///--
Rhynchospora alba	-----	-/--/	-----	/-///	-----	-----	-----	-----	-----
Sphagnum compactum	-----	-----	-----	--//-	/----	-/-/-	//---	-----	/--/-
cuspidatum	/////	/--//	-////	/////	/-///	-/-//	-/-//	/////	///--
papillosum	//-//	-////	/////	/////	/////	////-	////-	/////	/--//
rubellum	-----	-----	-----	----/	-----	-----	-----	-----	/----
subsecundum	/////	/----	/--/-	-/---	-//--	-//--	--/--	--/--	-----
Campylopus atrovirens	-----	-----	-----	/-///	-----	//---	-----	-----	-----
Molinia caerulea litter	-----	-----	-----	-----	-----	-----	-----	/////	-----
Algae-covered surface	-----	/////	-/---	/////	////-	///-/	////-	-----	/////

NORTH WESTERN POOL NETWORK	1	2	3	4
Calluna vulgaris	-----	-----	-----	---/-
Carex pauciflora	-----	-----	-----	----/
Drosera anglica	/-/--	-///-	//-//	/--/-
rotundifolia	///-/	-----	---/-	//-//
Erica tetralix	///-/	----/	-----	---/-
Eriophorum angustifolium	///-/	--///	///-/	/////
Molinia caerulea	-----	//---	-----	-----
Narthecium ossifragum	///-/	//---	--/-/	--///
Rhynchospora alba	-----	--//-	-----	-/---
Trichophorum caespitosum	-----	//---	---//	---/-
Sphagnum compactum	-----	-/---	/--//	-/---
cuspidatum	-//-/	/-///	///-/	/////
magellanicum	///--	-----	-----	-----
papillosum	/-/-/	-////	/////	//-/-
subsecundum	-----	-----	/----	-----
tenellum	//---	/----	-----	----/
Campylopus atrovirens	-----	//---	-----	//-/-
Odontoshisma sphagni	-----	-----	-----	/----
Algae-covered surface	/-/--	--///	-----	-/-//

Table 1.

Floristic analysis of nine overflow sites in the eastern pool network and four sites in the north western pool network. The data from five quadrats, each 15 cm. square, are shown for each site by species presence or absence.

The average height (of ten points) of each of these sites is shown in relation to the fluctuation of the water surface in figure 18. The range of height of the ridge surface on which these sites are situated is also shown. All the sites lie within the range of water level fluctuation and are therefore liable to periodic inundation and exposure of the surface. On the north-western pool network the majority of the ridge surface (outside these sites) lies above the highest water levels. The ridge on the eastern pool network is however lower in relation to the adjacent water surface and a greater part of this ridge is subject to inundation (water level fluctuations are described fully in section four). Where a ridge separates two groups of pools in which the level of the water surface differs then the sites described above are not only inundated but there is also flow of water across the ridge when the water level rises sufficiently. For this reason it is proposed that these zones be termed 'over-flow sites'. Similar features have been examined on the large areas of patterned bog known as Claish Moss in Argyll where the lowest points on the ridges between pools at different levels clearly act as overflow sites.

Similar distinct vegetation zones have been described from an area of patterned blanket bog in west Sutherland (Boatman and Armstrong 1968). In this case the zones occur between adjacent pools lying at the same level on a sloping bog surface. Boatman and Armstrong consider these areas, which they term 'bridges', to be frequently flooded. They emphasise that <u>Eriophorum angustifolium</u> is the only vascular plant species present and point out that this species is considered by Armstrong (1964) to be tolerant of low oxidation-reduction potentials. These features are thought by Boatman and Armstrong to represent an early stage in the linkage of pools. They suggest that erosion of the peat forming a bridge occurs once the bridge surface has been permanently flooded which they attribute to the slower upward growth of the peat on the bridge than elsewhere round the pools.

The overflow sites described from the study area are remarkably similar in that there is much bare peat and they are certainly subject to regular inundation. It is tempting therefore to suggest that a similar process to that suggested by Boatman and Armstrong might explain the development of the cross connections between pools on the study area. A further feature of the pool networks on the study area is of interest in this respect. That is the occurance of submerged peat ridges extending between adjacent islands or peninsulas. Three such areas can be seen in figure 14 between the islands to the right of the water level recorder. They are recognisable by the presence of emergent <u>Eriophorum angustifolium</u>. These ridges contrast strongly with other parts of the pool networks since they are relatively shallow (11 - 14 cm. below the lowest recorded summer water level). Their edges are steep, falling 35 - 40 cm. to the floor of the pool and these edges form a line continuous with peninsula and adjacent island in each case. It appears that they represent an intermediate stage in the developmental sequence from overflow channel to steep-edged connection between pools.

These then are some of the morphological features of the pool networks which I consider provide an indication of the way in which these networks have developed. The significance of these features is considered in the light of evidence from other investigations (notably stratigraphy and Sphagnum growth experiments) in the final discussion.

Linear pools and Sphagnum covered hollows on the study area.

It has already been shown that discrete linear pools or hollows are restricted to areas of the peat surface which show a distinct slope and that the long axes of such pools are aligned parallel to the contours on such slopes. In general the pools of this type occur peripherally to the central pool networks (their distribution is shown in figure 11). It is of interest to note that such pools do not occur continuously throughout the peripheral zones of the bog. In fact they are well developed in particular areas the limits of which are clearly defined. One group of pools lies on a projecting tongue of peat to the south-east of the eastern pool network and a more extensive group occurs further to the north, again marginal to the pool network. In this latter case the adjacent section of the pool network consists of a series of inter-linked linear pools and ridges. A further group of large, linear Sphagnum-grown hollows occurs on the gently sloping surface in the south west of the bog. Elsewhere linear pools are developed locally as in the area downslope of the north-west pool network. These various groups of pools are well displayed in figure 2 in which the Sphagnum dominated hollows (S. papillosum and S. cuspidatum) are emphasised by their lighter colouring.

In those areas where linear pools and ridges are developed there is a wide range of variation in surface microtopography and associated vegetation. In order to illustrate the general nature of the vegetation in relation to surface features two areas were selected which represent different morphological types. These are illustrated in figures 19 and 20 by transect lines parallel with the slope and the vegetation is depicted in the same manner as previously described for figure 12. The western transect crosses a number of wide ridges and Sphagnum dominated hollows which lie on a very gentle slope whilst the eastern transect crosses a more steeply sloping surface where the ridge and hollow morphology is on a smaller scale. A section of the eastern transect is shown in figure 21.

In contrast to the pool-networks the linear pools exhibit a continuous vegetation cover (predominantly Sphagnum species). These are probably best described as hollows since the water surface is only visible after a period of rain when it rises above the bryophyte carpet. During the summer period standing water is seen only intermittently. The length of linear hollows varies from only 1 - 2 m. to a maximum of about 20 m. Their width is usually 1 - 2 m. but may be as much as 7 m. in the widest parts. Hollows show considerable morphological variation, as can be seen in figure 2. The amplitude of ridges and hollows lies mainly in the range 10 - 25 cms. (c. 4 - 10 inches). On the steeper slopes there may be an amplitude of up to 30 cms.

The vegetation of the ridge and hollow systems can be divided ideally into three facies.

(1) The ridge vegetation. This is dominated by both vascular plant species and bryophytes in varying proportions. Usually the cover of *Sphagnum* (*S. tenellum*, and *S. rubellum*) as a ground layer below the ericaceous shrubs is discontinuous. *Calluna*, *Molinia* and *Erica tetralix* are widely distributed through the ridge surfaces whereas certain species e.g. *Eriophorum vaginatum*, *Rhacomitrium lanuginosum* and *Hypnum cupressiforme* are more local and restricted to the higher parts.

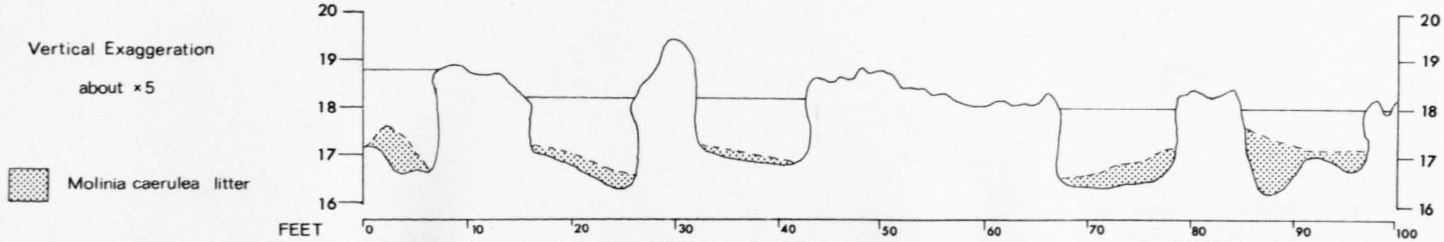
(2) Margins of Hollows. An open *Sphagnum* carpet is characteristic of the periphery of the hollows and is usually dominated by *S. papillosum* though this may be replaced locally by *S. magellanicum* or even *S. rubellum*. Only a sparse association of vascular plants is present including *Drosera rotundifolia*, *Narthecium ossifragum* *Trichophorum cespitosum* and *Eriophorum angustifolium*.

(3) Hollows. These are very constant being dominated by *Sphagnum cuspidatum*, *S. subsecundum* var. *auriculatum* and *Eriophorum angustifolium*. Where both *Sphagnum* species are present the former generally occupies the marginal area and the latter is co-dominant with *E. angustifolium* in the centre. *Utricularia minor* is abundant in some of the shallower hollows and *Menyanthes* is frequent in the larger ones. Further details of the vegetation in some of the linear hollows are given in the section on *Molinia* litter.

In contrast to the open pool networks morphological features of linear hollows provide very little indication of the way in which such features arise and consideration of their development is deferred until the final discussion in which evidence from other lines of investigation (especially stratigraphy and water levels) is significant.

TRANSECT ACROSS THE EASTERN POOL NETWORK SHOWING MORPHOLOGICAL FEATURES AND ASSOCIATED VEGETATION

Frequency values are the number of 2" units per foot in which the species is recorded



Rhacomitrium lanuginosum	---------------------------26651--3666665---------------
Hypnum cupressiforme agg.	------------------------------21------------66-132-21---
Cladonia impexa	--------------------------165-1-------------11-4446--1-----------1--------------61------------------
Cladonia uncialis	------------------------------1---------------1----------------------------------6665---------------
Sphagnum tenellum	----------141-------------------------------11------22-1---------4----------------------------------
Calluna vulgaris	---------4-231-------------142132-----------144633544221----34---11-------------4-3-----------------
Eriophorum vaginatum	-------1----------------------21-----------1-34-411313------11-1-3--------------112-----------------
Sphagnum rubellum*	--------46136663---------------33-----------52-43-265364-----566643------------------------------452
Sphagnum plumulosum	------------1---
Molinia caerulea	-----------211------------3521154----------3-11-132212142--------1------------------------------11-3
Drosera rotundifolia	-------1--112------------------------------12-----422332---12--1-1----------------------------------
Erica tetralix	--------2-2-432-----------53--321-----------2---11121-21-----2-343-------------11---1------------2-1
Narthecium ossifragum	------26243--325----------1-----1----------651-1-------661-----1511------------------------------2-1
Trichophorum caespitosum	------15-----22----------11-----1-----------------------34------214--------------3--6---------------
Eriophorum angustifolium	-------2-15212-2----------1----------------121-------11--221-1111--------22---2-1--1-2------------32
Sphagnum papillosum	------2664641165---------161----2----------162--------5666666666233-----------2-----43----------4664
Sphagnum cuspidatum	---34-132-3-2----1--------6--2---11-----
Sphagnum subsecundum	------1------------------1---2------------------3------------2
Utricularia minor	---3------11--------1-----1------
Menyanthes trifoliata	21----1-1-----2---31-224-------------1-1-------------------------1--2--2--12--------------1---31----
Molinia caerulea litter	6666665---------6666666666------166666662-4-----------------------166666666666-------236666666664---
Open water	6666665--------26666666666------16666666666-----------------------2666666666661------666666666664---

*including Sphagnum capillaceum

FIG. 12

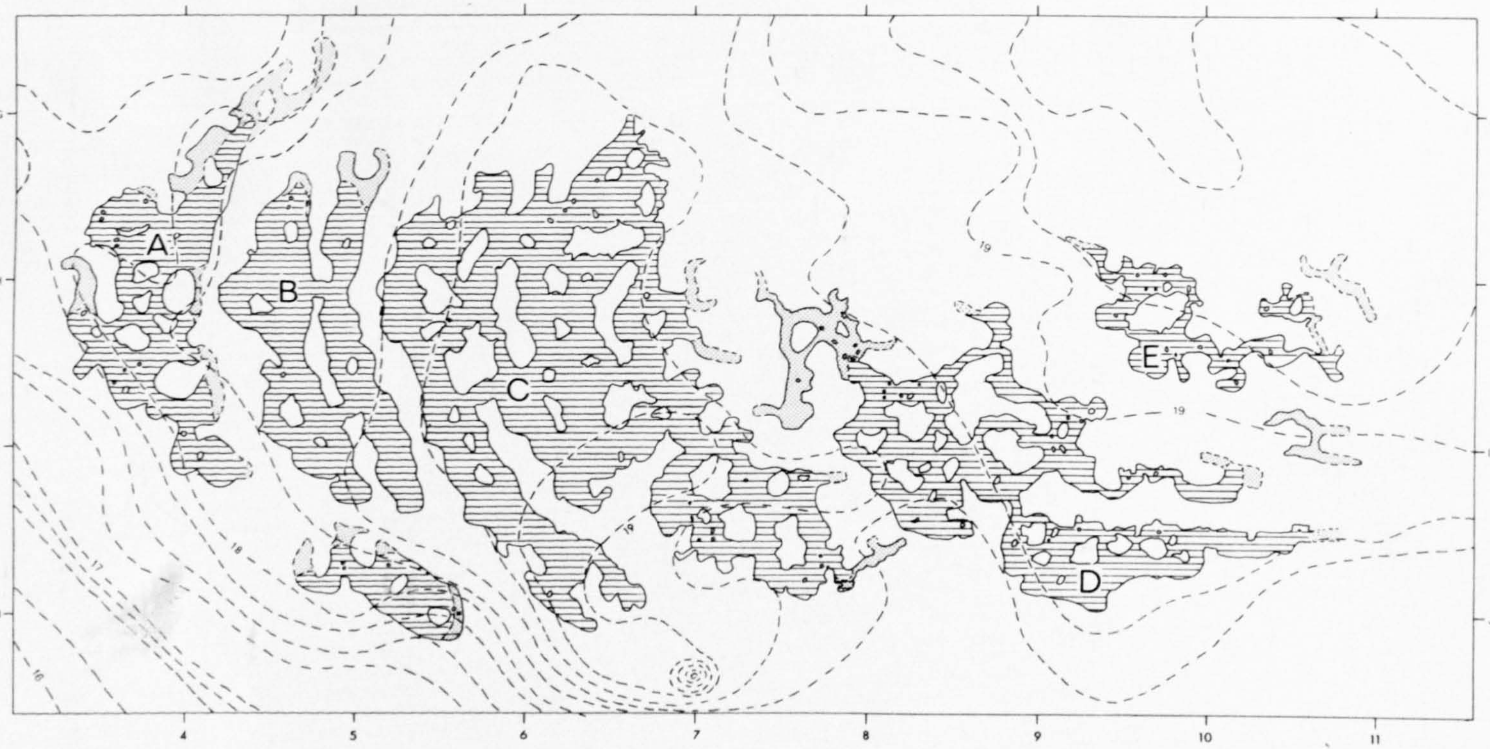


FIG. 13

Eastern Pool - Network on Long Loch Bog 'B'

Compiled from low-level aerial photographs and ground survey

0 50 100 FEET

0 25 m

Contours at 3" V.I.

Open water with *Menyanthes trifoliata*

Areas of pool colonised by aquatic *Sphagnum* spp.

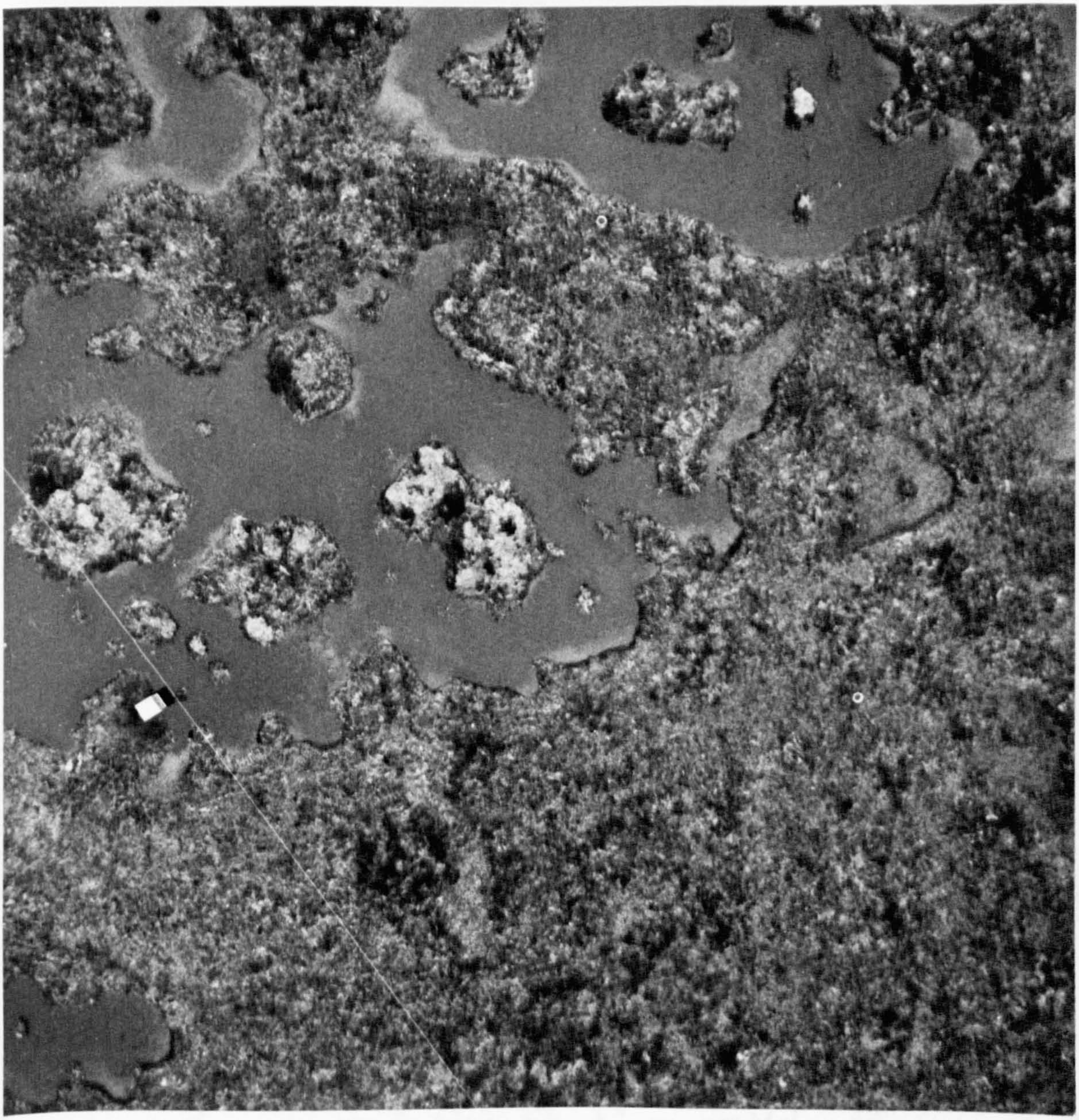
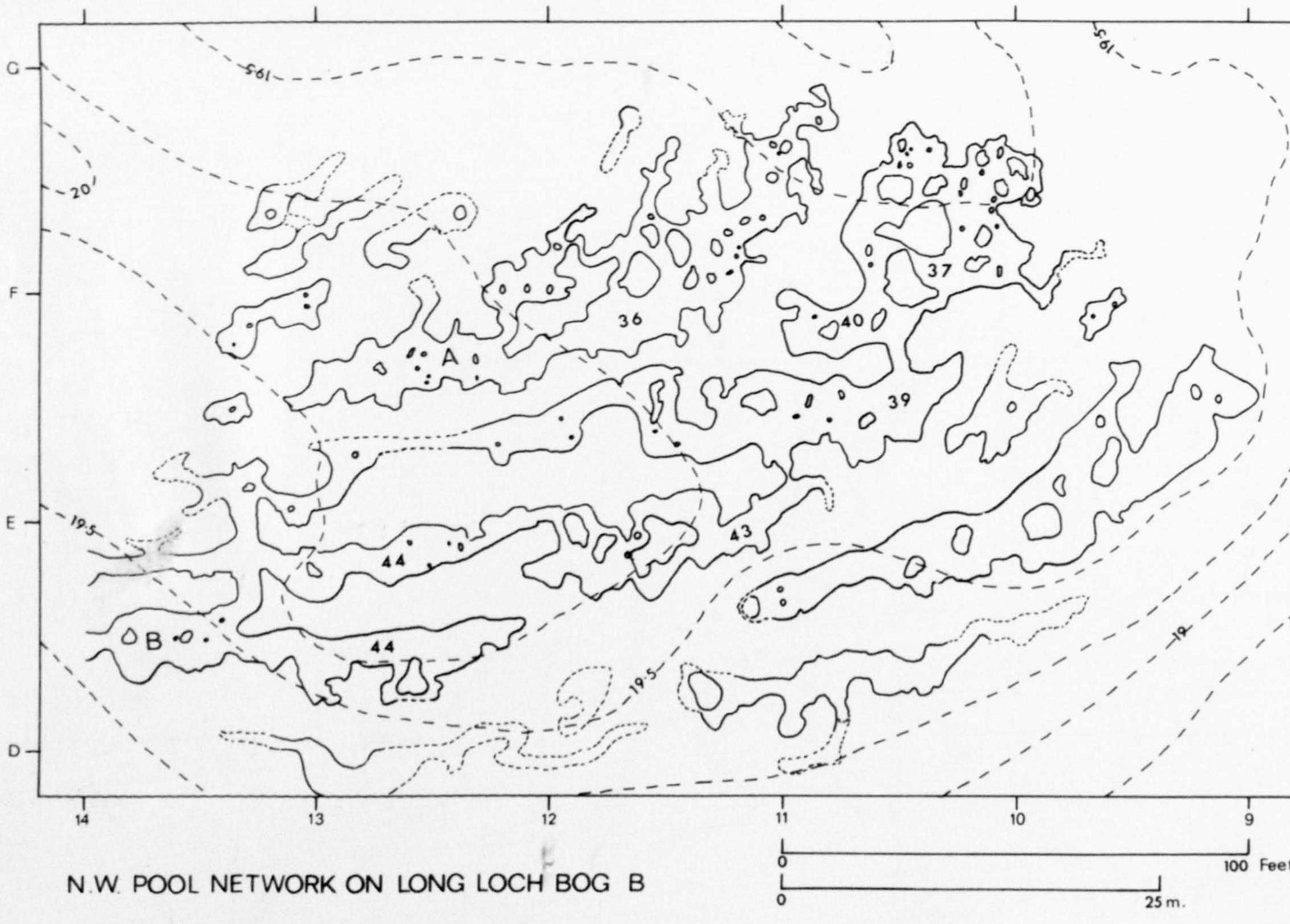
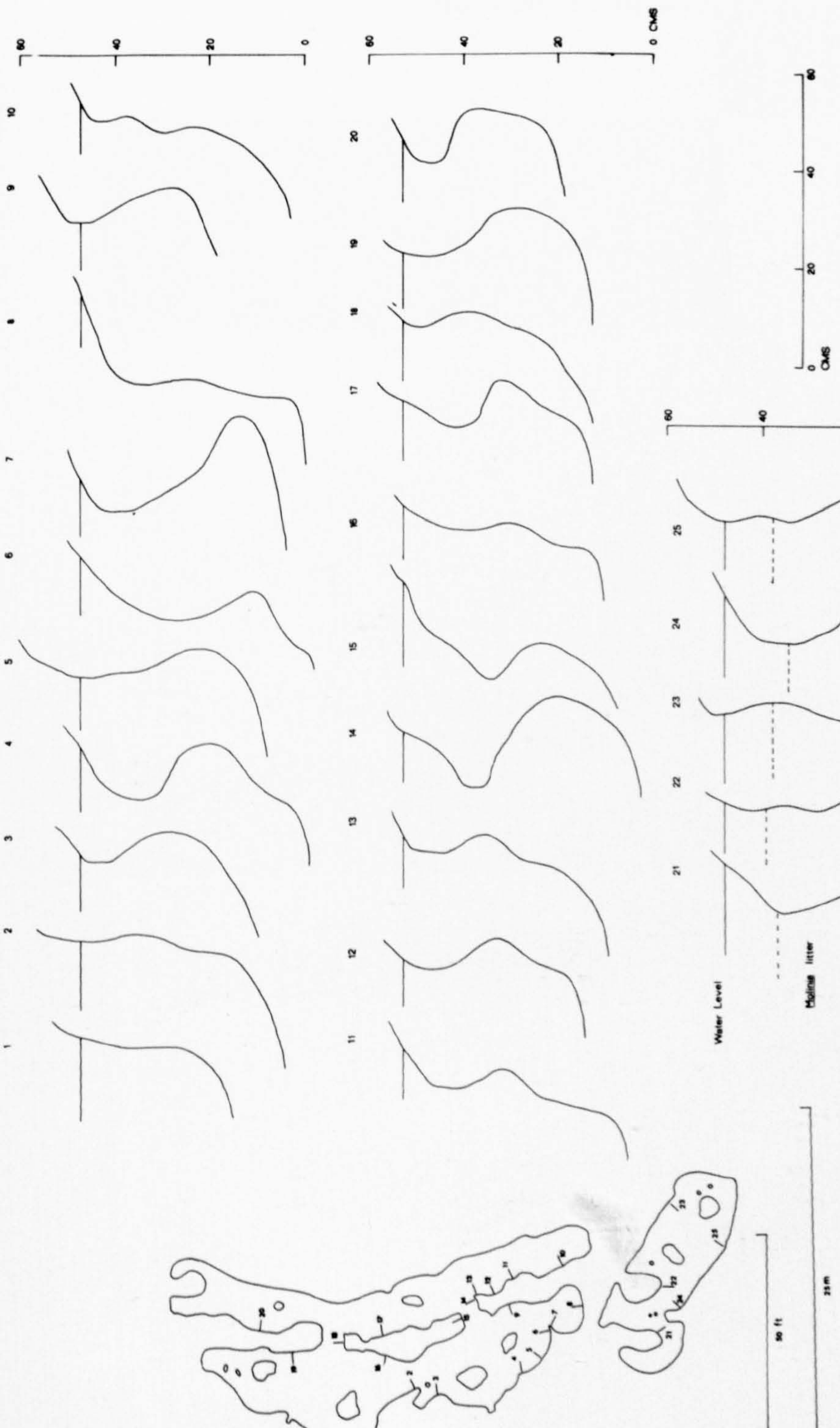


Figure 14. Low level aerial photograph of a part of the Eastern Pool Network (approximately section I - J, 7 - 8 in figure 13).



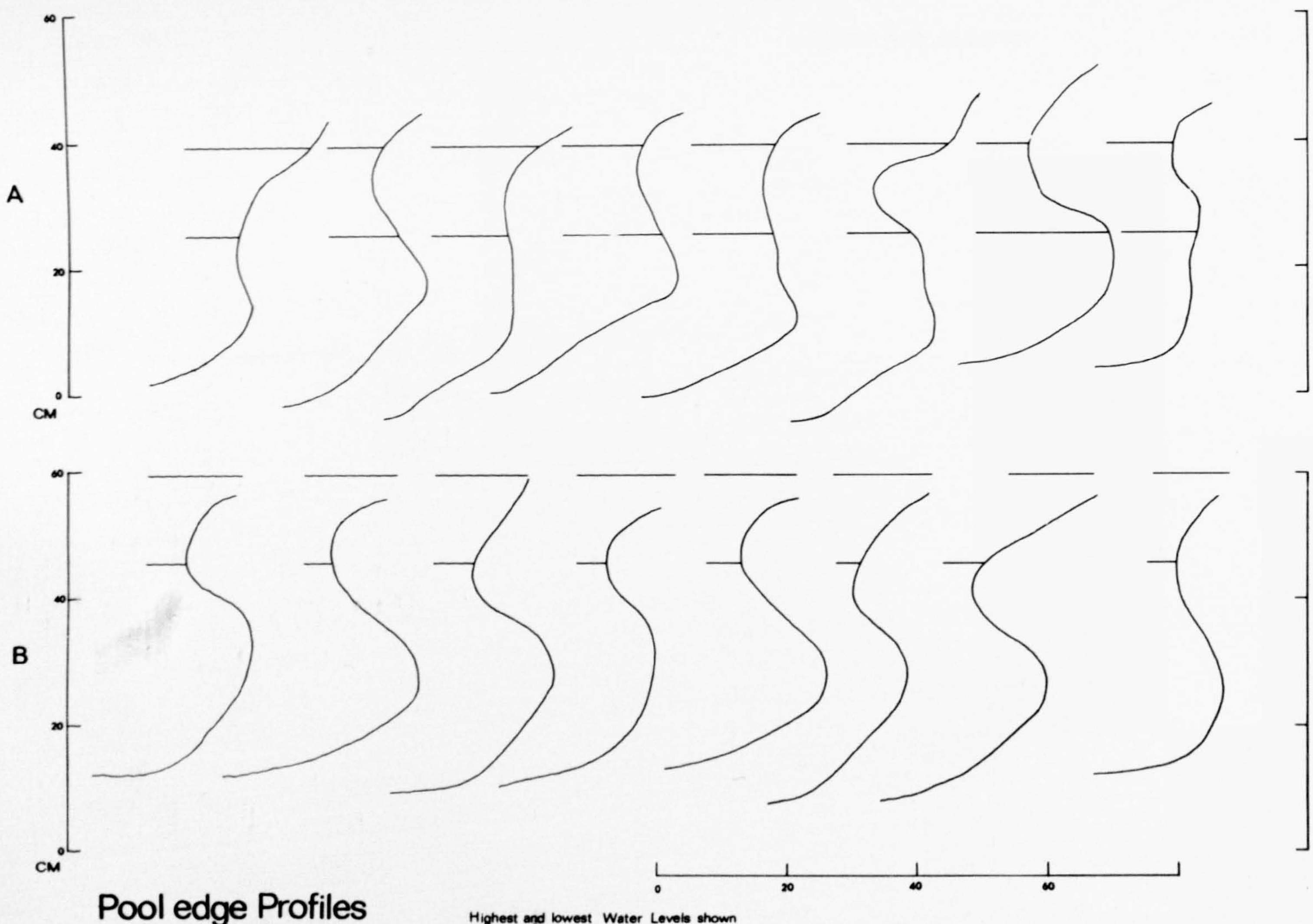
N.W. POOL NETWORK ON LONG LOCH BOG B

FIG. 15



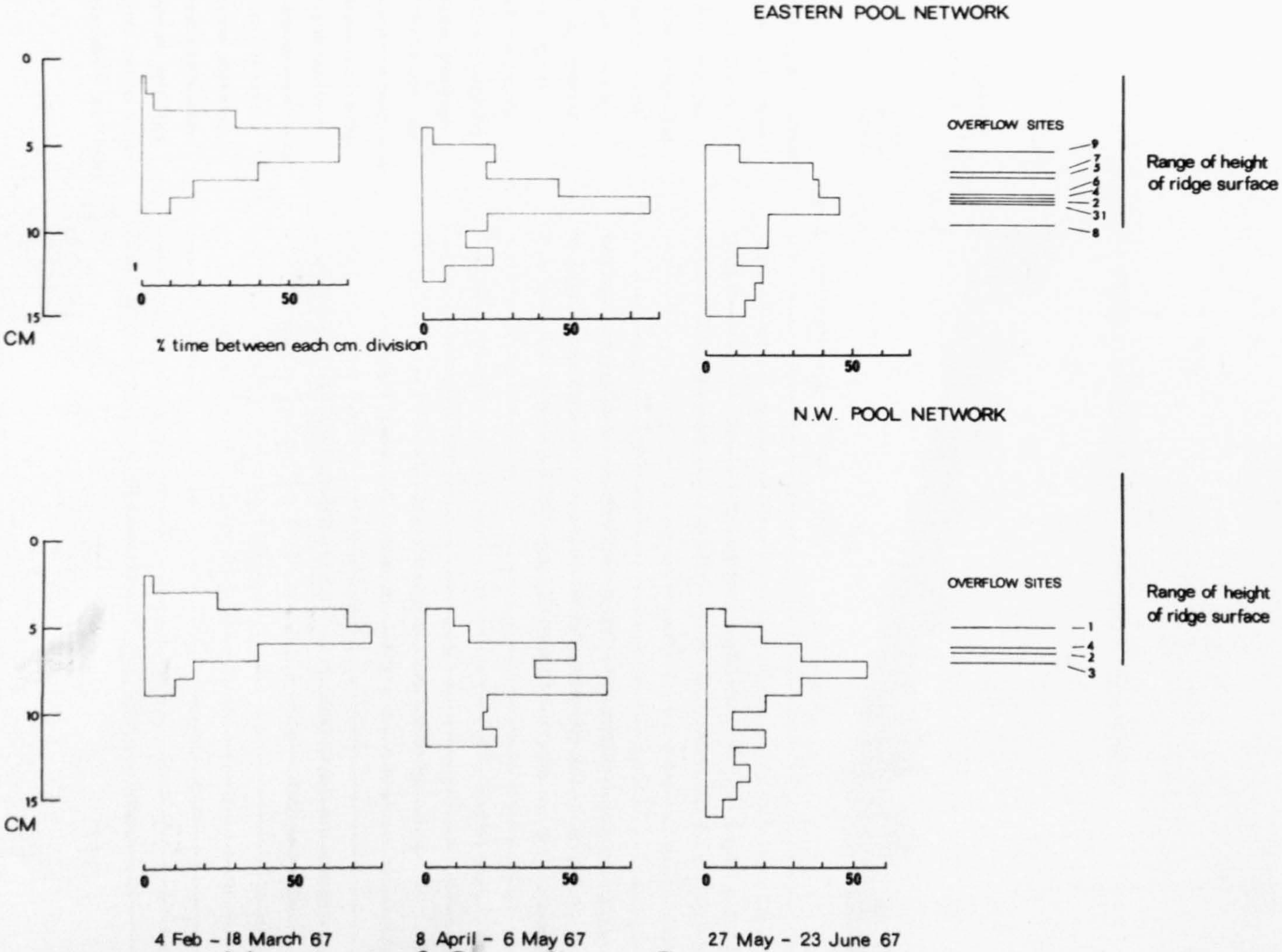
Profiles of Pool Edges

FIG. 16



Pool edge Profiles

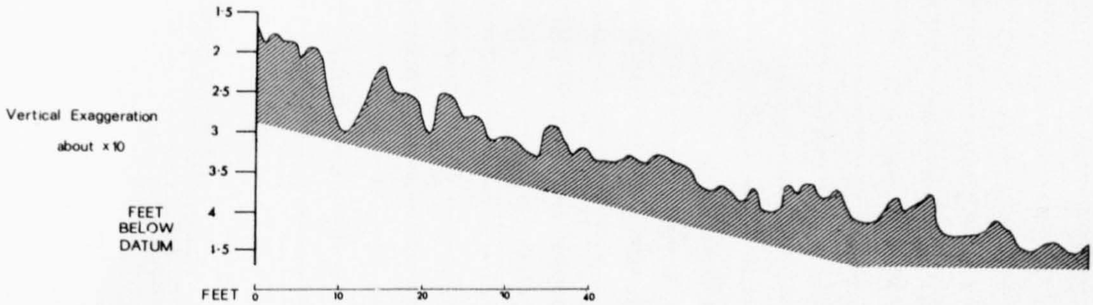
FIG. 17



Relative Heights of Overflow Sites and Water Level

FIG. 18

LINEAR POOLS AND RIDGES : EASTERN TRANSECT

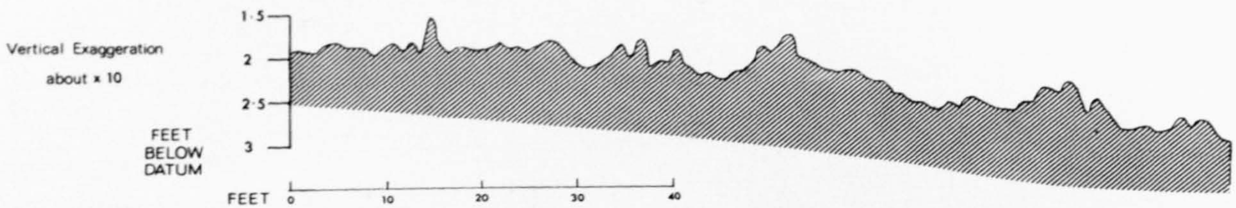


Rhacomitrium lanuginosum	--3---
Hypnum cupressiforme	--22----------1-------12-----------11---------------------------2--2------------23------1----------
Calluna vulgaris	112121-2-------1--------112--------12----22231-31123---333--3----1-4222------4-53432----11--1-141231
Sphagnum tenellum	--2------------2212--24-543---------22131232----1-1-24-112------344311------11--21-----313-12-31---
Eriophorum vaginatum	---2------------------2-1-------------------------------------111-23---------22---------1---------
Cladonia uncialis	----------------22-----------------------------1------2---------------------------------1-----
Molinia caerulea	24462312-----1452432-255333----1--453364433232-24342251443163--22652112-----36423331---326656534341-
Sphagnum rubellum*	43--55-61-----3122--263331111-----1--2-22-54262256625326555662-22223-65-------465-441--1---2-2662111
Erica tetralix	13--5-23------111--1--2122-----1--2221-1-1123--113-224331151----1332434-------122-3-----421452-53-21
Pleurozia purpurea	-------------12---------------1---
Drosera rotundifolia	-----31-2------------1-------1---------------21-----1-----1--------1-------2-2---1----------22-1111
Sphagnum plumulosum	------------------3--------462--------------------3--2--------------------------------------1--5--
Narthecium ossifragum	2----32-------2-----231---1-------2233-1122-12152333-----2-21-355541113----51----------------1-----
Trichophorum caespitosum	1-------1----32-3332-1--3335------3--1-335331-221----26-111----1----5--1----1-----33---13-1335423-11
Sphagnum magellanicum	-----1------------------------------------3---
Sphagnum papillosum	6---12626---1312---151-161-1615666655--------166----2----2--144641---12661--4-3---3563265-----2-6-66
Eriophorum angustifolium	----211-11-223-2111--221--112-3421----2--121--11----1--1--2--1111-------11221-21-1--3353----2---2222
Utricularia minor	------------------------------2-----------------------1------------------------33-------------
Sphagnum cuspidatum	--------366655--11----------121--------332-------------
Sphagnum subsecundum	---------11131------------------2-------------------------43---------16561---------1-------------
Menyanthes trifoliata	-----------1---1-----------1-------------
Molinia caerulea litter	---------6565-------63----------561-1--------------------1---53---------46661-------464-------------

*includes S. capillaceum

FIG. 19

LINEAR POOLS AND RIDGES : WESTERN TRANSECT



Rhacomitrium lanuginosum	------------------------------------5-------------------1-----------------------------------3----1-
Hypnum cupressiforme	-------------26--11----------------1-------------4122--------------------------316511------2-32263-
Cladonia impexa	-----------------------------------15------------2---
Calluna vulgaris	-2-31--1-11--13--221-1-11321------------11------62-15-3-132-2-111------1-------64-341522113122334512
Sphagnum tenellum	-424--2---1-32166222-3---5---------1---51---------22-41---41--2---------2-------22-132-11131-1-21-46
Eriophorum vaginatum	13335----1---11--51-1---1-1---------13-2-1--------1-1211--------------------------1224---42-121443-
Cladonia uncialis	1-1-11-------------2---11------------541--------------1-2----2-2-----------------------224---1-----1
Molinia caerulea	1141-1411---33355442----353-1-----133-3251-----22466554245434222l---------------26356132146366655444
Sphagnum rubellum*	63--2-----131--43-21----62-11---1245111--------11-2413--------1---------1------1-2---1125-11-113-1-2
Erica tetralix	2124224-13112231231524-3-125-----14212133------1-321245512121-222---------------2-123-221521-212323-
Pleurozia purpurea	------1------------------------------2---------4-----------25---------------------------------------
Drosera rotundifolia	---1---11-332-----1-61111-134------1-1-1-31----12------4412-222432-----13-------------22-1111------1
Sphagnum plumulosum	---21--------11-2-1---23----1--
Narthecium ossifragum	-----111-----1-----1-------11----1------155--------3----------331-------1-------5323---------1------
Trichophorum caespitosum	2-1-12-12-2111-----1133112--2--------11--2--------------1-2--1--1----------------------124-1--------
Sphagnum magellanicum	------2----1---1-------------------------------------
Sphagnum papillosum	--113646666642----126466216666666662----4666666651-----663--65466665---6661---461-----253-15--------
Eriophorum angustifolium	331--212511232----121132211-113233111-2---122342------21125611-13-2353251621362--------45212---1---1
Sphagnum cuspidatum	--------2---------------------62-----212--421-5-------------------1566631666663--------------------
Sphagnum subsecundum	------------------------------1------1------422-------------------26661-56661----------------------
Menyanthes trifoliata	---1-1--------------------1------1-1-----------------------
Molinia caerulea litter	---453--------------------6662--56663----------------------

*including S. capillaceum

FIG. 20

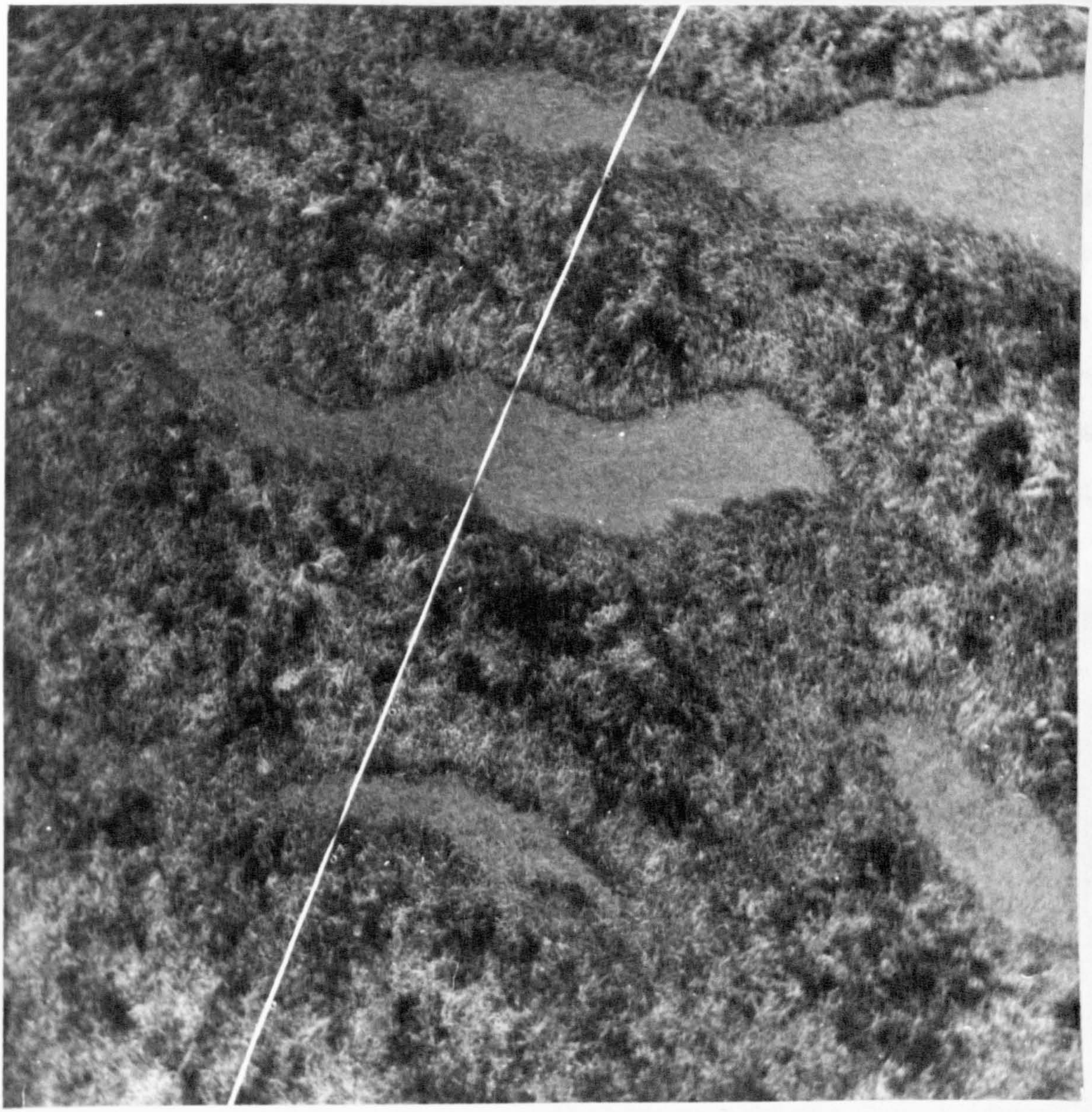


Figure 21. Low level aerial photograph of linear hollows along a section (38 ft. long) of the Eastern Transect. Tube wells can be seen at 5 feet intervals.

SECTION 3

STRATIGRAPHY

In order to obtain information on the past development of pools and hollows on the study area stratigraphical investigations were carried out. It was considered that a study of macroremains in the peat below selected pools and hollows would be the most appropriate course of investigation, rather than to attempt a wider analysis of the stratigraphy in the study area as a whole. Since the pools and hollows of the study area can be divided into two major types (the open pool networks and the linear hollows where S. papillosum forms a carpet or border) these form a basis for separate studies. Together with an initial investigation they constitute the three sections into which this chapter is divided.

(1) Initial investigation.

(2) Examination of peat underlying open pool networks.

(3) Examination of surface peat below linear hollows where S. papillosum is dominant.

(1) Initial investigation

Ratcliffe and Walker (1958) suggest, in their descriptions of Snibe Bog, that initiation of pools and hummocks is a relatively recent phenomenon restricted to the upper layers of the peat and associated with the development of fresh Sphagnum peat above a more humified 'Sphagnum-Molinia bench'. No stratigraphical investigations had been carried out on the upper bogs of the Silver Flowe at the time when the present work was commenced and an initial investigation was made to see whether the situation described by Ratcliffe and Walker also applied in the study area. Two sites were chosen, both of which were situated in pool networks where the peat was deeper than the average for the study area.

Site One

This is an 'island' of firm peat in the south-west pool network, which is completely surrounded by a zone of S. papillosum 'carpet' and pools with Sphagnum cuspidatum. The centre of this island is occupied by a hummock of S. imbricatum. A series of three cores was taken between the centre of the hummock and the pool margin by means of a Hiller sampler. Cores were extracted to a depth of 4 m. below the hummock but only to a depth of 2.8 m. in the case of the profile nearest to the pool owing to difficulty of core extraction. The upper 30 - 40 cms. of each profile were extracted by means of a sharpened aluminium tube (see Appendix 3).

Cores were examined in the laboratory, initially taking units of 2 cm. length at 10 cm. intervals. Procedure was later modified, every alternative 2 cm. unit being examined. Amorphous material was removed by sodium hydroxide digestion and the remaining material examined for its Sphagnum content. Since Rhacomitrium cf. lanuginosum constituted a large proportion of certain cores this was also noted. No attempt was made to identify the remains of vascular plants. Results are shown in figure 1. Relative proportions of different Sphagnum species present are subjective. Three categories have been recognised viz: present, abundant and dominant, indicated respectively by progressively thicker lines in the diagram. The category termed 'dominant' is applied to that species constituting the largest proportion of the Sphagnum content of the sample but this category is not used where the total Sphagnum content is less than about 10% of the whole sample. If two species are equally important they are both shown as dominant. Abundance is also a variable category dependent on amount of Sphagnum in the sample but it generally indicates less than 50% of the total Sphagnum content assessed visually.

The differences between the three profiles can be summarised as follows:

Core 1, at the centre of the hummock, shows abundance of S. imbricatum, relative to other Sphagnum species throughout almost its entire profile. At one horizon where S. imbricatum shows a decline S. papillosum increased in quantity. This latter species is not well represented and 'S. acutifolium'[1] is virtually absent. The frequent abundance of Rhacomitrium is noteworthy.

Core 2 shows association of S. imbricatum with S. acutifolium agg. (mainly S. rubellum) in the lower horizons where S. papillosum is frequently present, but S. imbricatum is absent from the upper horizons where S. papillosum and S. magellanicum constitute the bulk of the Sphagnum. Rhacomitrium is reduced in abundance compared with Core 1, particularly in the lower horizons. S. tenellum is a frequent constituent of the upper horizons.

The lower horizons of Cores 2 and 3 are similar but the upper layers of Core 3 show reduction in both frequency and amount of Rhacomitrium and again S. imbricatum is absent.

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1. Except where otherwise stated S. 'acutifolium' has been used to denote all species of the Acutifolia group. On the present bog surface S. rubellum is the commonest member of the group but both S. plumulosum and S. capillaceum also occur in small amounts.

Abundance of S. imbricatum and S. papillosum can, by analogy with their present habitat requirements, be taken to indicate respectively 'dry' and 'wet' conditions. This being so it can be seen that a wet phase at a certain horizon in Core 1 corresponds, to some extent, with a similar wet phase in the other cores where aquatic Sphagna are recorded in one such instance. The development of wetter phases is more prevalent in the upper horizons in all three cores but it noticeable that they were developed at comparatively low horizons in the case of Core 3.

The implication is that, once established, the centre of pool and hummock have in this case remained constant, though periodic wetter or drier phases have resulted in lateral transgression of vegetation zones. There has been a progressive increase with time in the degree of lateral transgression by wetter communities towards the centre of the hummock.

Differences in vegetation reflecting the present difference between pool and hummock appear to have been initiated at a depth of 2 - 2.5 m. which contrasts with the situation on Snibe Bog where the pools are said to be initiated within 1 m. of the present bog surface (Ratcliffe and Walker 1958). Despite the rather incomplete data of the present work it appears that the horizons below about 2.5 m. are less variable laterally than the upper horizons. Some degree of similarity with the Snibe Bog profiles might therefore be argued, in that both show initiation of pool and hummocks across a relatively uniform surface.

Site Two Following this investigation another site was selected in order to compare the stratigraphy of the surface peat below a ridge and below the adjacent section of a deep pool in the eastern pool network. At the selected site the ridge surface is almost flat, the pool margin undercut and, at the time of sampling, the pool depth was 37 cms. Core 1 was taken at a point on the ridge 10 cms. above the level of the water in the pool by means of a Hiller sampler. Again the upper 30 cms. were extracted by means of the aluminium tube. In the case of Core 2 the soft peat immediately below the pool was extracted to a depth of 50 cms. by means of a special corer (see Appendix 3). Below that depth a Hiller sampler was used.

Cores were examined in the laboratory, the whole core being examined in units of 2 cm. length. Each sample was washed through sieves of 2,000, 210 and 75 micron mesh sizes. The larger macro-remains, e.g. Sphagnum stems and branches, larger parts of vascular plants and certain other material such as the 'capsules' of Donacine beetles were thereby separated from other finer grained material. The 'microfraction', consisting of Sphagnum leaves and other material of similar size, e.g. Menyanthes seeds, was retained in the lower sieve. Amorphous material was retained in a third sieve. The whole macrofraction was examined and the proportions of various identifiable plant remains noted. Only a sample of the microfraction was examined. The amount of amorphous material was noted as an approximate proportion of the total sample. The same subjective categories were used to distinguish the proportions of plant remains present as in the first investigation but in this case and in all subsequent investigations each was compared with the total material of the sample. 'Dominance' indicates over about 40% of the sample. Results are shown in figure 2.

The two profiles show differences which are most pronounced in the upper horizons. Below about 1.2 m. there is a greater degree of similarity between the two cores. Vertical variation is most pronounced in the pool profile which shows an alternation of relatively wet and dry phases which is not so marked in the ridge profile. A point of similarity between the two is that a layer of amorphous peat, darker in colour than the fibrous peat forming the bulk of the profiles, occurs in both profiles at a similar level. Also S. imbricatum, which is absent from the surface vegetation of the eastern pool network, is a major component of the peat beneath both ridge and pool at a depth of 1.2 m. below the level of the ridge surface. Differences between the two profiles include absence of Rhacomitrium cf. lanuginosum, Molinia caerulea and S. acutifolium agg. from the pool profile, all of which are significant components of the upper horizons of the ridge profile. Conversely aquatic sphagna and S. compactum are not represented in the ridge profile, though both occur in the pool profile to a depth of 1 m. below the level of the ridge surface.

Profile 1 shows less distinct vertical trends than Profile 2. S. imbricatum, which is the dominant Sphagnum below the amorphous layer, is absent above that layer. S. acutifolium agg. (mainly S. rubellum) is the dominant Sphagnum species in the upper horizons of the ridge and

Rhacomitrium is relatively more abundant than at the lower levels. Profile 2 exhibits an early 'wet' phase, indicated by an increase in the proportion of S. papillosum and S. subsecundum. The succeeding section of the profile is characterised by presence of E. vaginatum, Calluna, S. imbricatum, and, at one horizon, Leucobryum glaucum and absence of S. papillosum. This corresponds in part with the amorphous layer. It is noteworthy that the species present are all less hydrophilous than those associated with habitats dominated by S. papillosum, which lends weight to the suggestion that this is an oxidised layer. The upper 40 cm. of profile 2 shows progressive decrease in the less hydrophilous species, i.e. S. imbricatum, Calluna and E. vaginatum, so that the layers immediately below the pool are characterised by S. subsecundum, S. papillosum and E. angustifolium with no other vascular plant remains. The presence of S. compactum in profile 2 is of interest. At present this species occurs on bare peat often in association with gelatinous algae or Zygogonium sp., where the surface of the peat is periodically inundated.

So in this case the cores below a ridge and an adjacent pool show differences which are more pronounced immediately below the present pool bottom than at greater depth. The ridge profile shows no pool phases at any stage whereas the pool profile shows two distinct pool phases separated by drier conditions. Certain of the drier elements of the ridge profile are entirely absent from that below the pool. In the upper horizons of the ridge profile above the level of the pool bottom Sphagna of the Acutifolium group form an important constituent which is entirely absent from the pool profile.

A feature of interest is the fact that Sphagnum imbricatum does not occur above the amorphous zone in either profile. This species is present at only three places on the surface of the study area yet it is a major component of the peat below 1 m. at this site and was dominant throughout below 2.5 m. at site 1 where it has survived to the present surface at one point. Abundance of S. imbricatum at lower levels in the peat, contrasting with absence or only sparce occurance in the surface layers is characteristic of many British bogs, (Green 1968). A very similar loss of S. imbricatum associated with a strongly humified horizon is described from Tregaron Bog by Godwin and Conway (1939) who consider that the humified horizon represents a 'retardation layer' indicative of drier climatic conditions.

(2) Examination of peat underlying part of the Eastern Pool Network

It is appreciated that generalizations made on the basis of the features shown in the two sites studied during the initial investigation may not be applicable to the whole study area. Nevertheless one of the features which both sites have in common may be significant. Whereas the profiles below ridge or hummock are relatively uniform, the profiles of the peat below existing pools indicate that there has been a tendancy for wetter conditions to be initiated, which have gradually become dominant. This implies that the pools are not simply surface features but were initiated at depth whilst the ridges have remained fairly constant features. Morphological features of the extensive pool networks suggest that such pools have increased in size by erosion of peat in the intervening areas. If this is so the underlying stratigraphy will differ considerably in various parts of the pools depending on whether the site concerned is an original pool site or whether it is the truncated section of a previous ridge. In order to discover whether this is in fact the case a series of 10 cores was extracted from the peat immediately underlying parts of the Eastern Pool Network.

Distribution of the core sites is shown in figure 24a. Cores were extracted by means of the special sampler at about 6 m. intervals along the two sides of a ridge crossing the eastern pool network. In addition two cores (2c and 2d) were extracted from the peat underlying parts of the pools in line with elongated islands or peninsulas where erosion might be expected to have occurred. In all cases the pool surface was covered with a think layer (1 - 2 cm.) of algae and semi-liquid detrital ooze consisting of Menyanthes seeds, fragments of S. subsecundum and Rhacomitrium lanuginosum, also fragments of many vascular plants including particularly Menyanthes rhizomes and Calluna stems. The whole length of each core was examined in the laboratory (2 cm. units washed through sieves, as described for site two above) and the results are shown in figure 24 a and b.

It is immediately clear that the different cores show a good deal of variation in the sequence of macroremains. Most of the cores consist predominantly of fibrous remains (mainly roots) and amorphous material. Slightly less humified horizons are present, but fresh Sphagnum peat is absent. In the lower sections of most cores the identified macroremains represent only a small fraction of the total material (which is mainly amorphous material and roots). These strongly humified lower horizons are similar, and probably equivalent, to the amorphous horizons of the pool profile in figure 23. Above the predominantly amorphous horizons the profiles generally show an increase in identifiable macro-remains though the proportion of fibrous material, especially roots, is still very high in most cases. It is in these upper horizons that the greatest amount of variation occurs between different cores. Indeed the most significant feature of this series of cores is the fact that there is no common stratigraphical sequence immediately underlying the pools concerned.

All the cores show changes in the macroremains indicative of changing conditions of water table at the time of peat formation. Certain cores show fluctuating wetter and drier phases throughout the whole profile (e.g. 1a and 2 c) but the majority show abrupt breaks in the stratigraphy where humified peat (containing macroremains indicative of dry conditions) is overlain by a peat containing abundant evidence of wetter conditions (e.g. 1d, 1e, 2a, 2d). In some cases these latter profiles show reversion to drier conditions (e.g. 1b, 1e and 2e) whilst others show persistence of the pool phase (e.g. 2a and 2d). It will be clear from the diagram that in some cases humified peat extends very close to the present pool surface (.e.g. 1d and 2 d) whilst in other cores notably 1a and 2c such highly humified peat is restricted to relatively thin horizons.

Of the profiles which show establishment of a distinct pool phase numbers 1e and 2a show the most clearly defined succession. The lower horizons of le show amorphous and fibrous peat with remains of Trichophorum cespitosum, E. vaginatum and abundant Calluna, overlain by corroded S. papillosum. This is immediately followed by a layer of S. subsecundum indicating a pool phase. Numerous branches and leaves of Calluna are associated with this indicating flooding of a Calluna dominated surface. The succession thereafter shows progressive colonization by less hydrophilous elements. The initial phase of pool colonization is very well displayed showing S. papillosum succeeded by S. magellanicum as the dominant bryophyte and there is a well defined succession of vascular plants. The upper horizons contain Calluna and Molinia caerulea with Rhacomitrium indicating a dry community, at which point the profile is terminated by the pool bottom.

Flooding of a humified peat surface is also show in core 2a. In this case S. imbricatum and Calluna are followed by a highly humified peat containing fragments of Calluna and Rhacomitrium. A layer of corroded S. papillosum indicates the onset of wetter conditions this being succeeded by a pool phase dominated by S. subsecundum. The presence of Molinia litter, S. cuspidatum and S. compactum in the upper horizons of this phase provides striking similarity with the profiles below shallow hollows (see figure 52), a similarity which is accentuated by the presence of S. papillosum and E. angustifolium above the pool phase.

The other profiles in which wetter conditions are established over a humified peat show a more attenuated pool or hollow phase. Cores lb, ld, and 1e all show a wet phase characterized by S. papillosum or S. magellanicum, with E. angustifolium and in all three cases this has reverted to a drier phase. Core 2d is unique in that a more distinct pool phase is developed, with Menyanthes and algae present, which persists to the level of the present pool bottom. Indeed this is the only profile in which the succession can be interpreted as being a logical precursor to the present pool condition.

Certain cores particularly 1a and 2c show alternation of dry and wet phases throughout the profile with little development of completely amorphous peat. In neither case is a well defined pool established, the wetter phases being represented mainly by S. papillosum and Trichophorum. In 2c these form narrow inter-collations in a predominantly dry phase peat composed essentially of Rhacomitrium and Calluna remains.

Sphagnum acutifolium agg. (consisting of S. rubellum whenever examined in detail) occurs in only two cores, 2c and 2e. In the latter profile it is a major component of the lower horizons along with Molinia and Calluna, prior to the establishment of an association of S. papillosum, E. angustifolium and Trichophorum.

A number of the features outlined above are thought to be important. Firstly, whilst many of the profiles indicate establishment of wetter conditions in the upper horizons, this has not necessarily led to the development of a pool phase. Where pools have formed, subsequent colonization has occurred in most cases and this has resulted in reversion to drier conditions.

Although the present pool bottom is fairly flat the profiles show no common feature in the succession immediately below the surface. Indeed the present pool bottom bears no relationship to the succession displayed in most of the profiles. In only one core does a succession exhibit the development of a pool immediately below the present pool bottom.

Certain profiles (particularly 1a, 2c and 2e) show predominantly dry conditions with periodic development of S. papillosum. These profiles are similar to the ridge profile in figure 23. In two cases S. 'acutifolium' is present, which is confined to the ridge profile in figure 23 and a further point of similarity is that there is no development of a pool phase in these profiles.

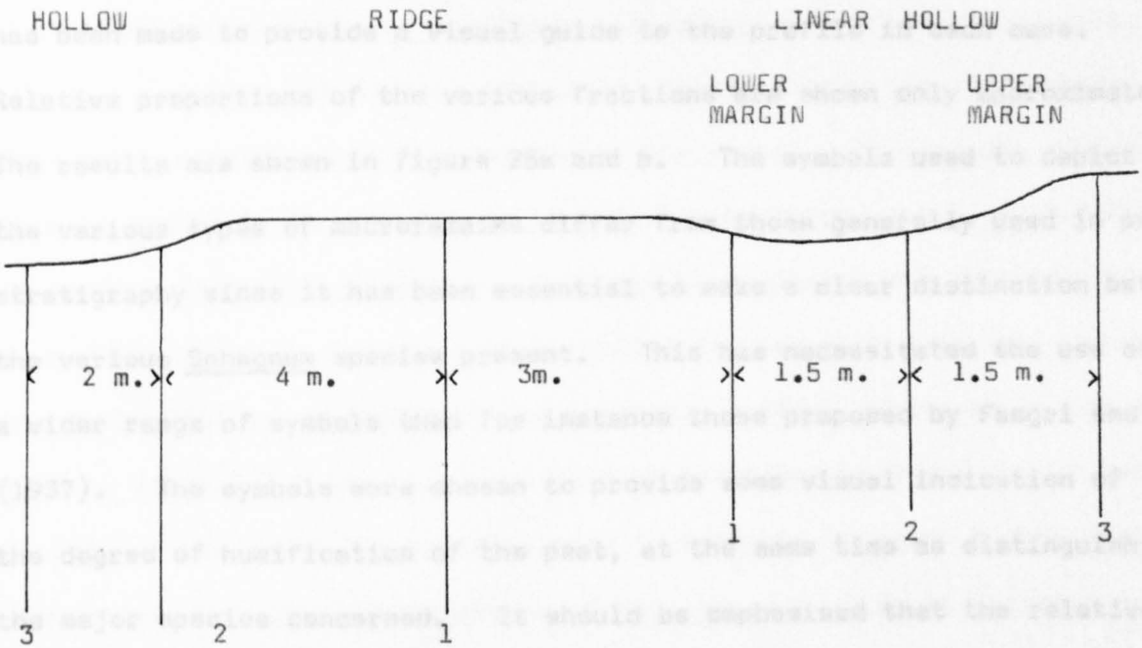
The following interpretation is offered to account for these features. It is clear that wetter conditions have been superimposed on a humified peat surface. In some situations this has resulted in pool formation with subsequent recolonization. In other situations there has been renewed activity of peat growth involving S. papillosum and S. 'acutifolium' with no pool phase. The profiles exhibiting this range of conditions are all truncated by the present pool system, indicating that this is a secondary feature which has been produced by some process involving erosion irrespective of the succession in the profiles concerned. In some cases such 'erosion' may have been pronounced. Evidence suggests that the profiles showing an absence of pool formation (but including wetter phases in a predominantly dry succession) may well represent truncated ridges the upper parts of which have been removed by erosion. The position of these profiles, in line with fragmented ridges (or peninsulas), is consistent with this suggestion. The stratigraphical evidence therefore supports the contention that formation of pool networks involves some degree of 'erosion'.

(3) Examination of surface peat below linear hollows in which S. papillosum is dominant

(a) Large linear hollows

A characteristic feature of the study area is the presence of Sphagnum dominated linear hollows. These may be dominated completely by an association of S. papillosum and E. angustifolium or they may have an auriole of S. papillosum and a central zone of S. cuspidatum or S. subsecundum often with Molinia litter and E. angustifolium. Some of the largest of such hollows are crossed by the western transect line the position of which is shown in figure 27. An analysis of the vegetation is given in figure 20 and the general form of the hollows can be seen in the oblique aerial photograph figure 2 (the hollows concerned lie midway between the pool network in the foreground and the eastern pool network).

In order to investigate the stratigraphy of such hollows six cores were extracted, a series of three across a linear hollow and two from an adjacent S. papillosum-covered hollow. One core was extracted from the intervening 'ridge' widway between these hollows. Relative heights of the bryophyte surface at the core sites was measured. The distribution is shown below.



Cores were extracted by means of the aluminium tube described previously. In the case of the ridge site and the lower margin of the linear hollow it was necessary to obtain additional deeper cores. A Hiller sampler was used for this purpose below about 50 cm. The cores were examined in the laboratory (by sieving 2 cm. units, see previous description of method). In depicting the results the relative abundance of each species has been shown in relation to the total core material at the horizon concerned. In addition since the degree of humification, as well as the contents, shows abrupt changes an attempt has been made to provide a visual guide to the profile in each case. Relative proportions of the various fractions are shown only approximately. The results are shown in figure 25a and b. The symbols used to depict the various types of macroremains differ from those generally used in peat stratigraphy since it has been essential to make a clear distinction between the various Sphagnum species present. This has necessitated the use of a wider range of symbols than for instance those proposed by Faegri and Gams (1937). The symbols were chosen to provide some visual indication of the degree of humification of the peat, at the same time as distinguishing the major species concerned. It should be emphasised that the relative levels of the horizons in different cores as shown on the diagram may well be inaccurate owing to the variation in compaction of the profiles during extraction of the core. (Tests on fresh S. papillosum, which is most subject to compaction, showed that differences of up to 7 cms. could be produced.)

All except one of the profiles show highly humified peat forming the lower horizons. The exception is core 2 below the linear hollow which does not however extend as deep as the other cores.

The profile below the ridge (figure 25a) shows very clearly fluctuating conditions, from dry (Rhacomitrium, E. vaginatum, Calluna) to wet conditions (E. angustifolium, S. papillosum, Trichophorum). A pronounced feature of of the profile is the fresh S. papillosum in the upper layers and the appearance of Molinia caerulea close to the surface, which is absent from the lower horizons. It is notable that S. 'acutifolium' is a major component in the profile.

Profiles below the S. papillosum covered hollow (figure 25a) show a basal amorphous and fibrous peat which does not show the same degree of vertical variation as in the case below the ridge. (Indeed the identified species are restricted to S. papillosum, Trichophorum, and E. angustifolium in profile two and Trichophorum, Calluna, E. vaginatum and Rhacomitrium in profile three.) Certainly the macroremains are much less well preserved and roots form the majority of the material in these cores, as in the case of most cores below the open pool network described in the previous section. In both of the cores the humified peat is overlain directly by the pool mud containing algae and fragments of Menyanthes. This is followed by Molinia litter and S. subsecundum with abundant E. angustifolium which is rooting in the pool mud. Stem bases of E. angustifolium, showing a similar degree of decomposition, were also found in the upper layers of the humified peat, contrasting with the majority of that material and indicating that plants of the pool phase were rooting in the older humified peat. Above the pool phase is fresh S. papillosum with E. angustifolium and S. cuspidatum is present along with these in the upper horizons of both cores.

The pool phase is strikingly similar to that of the present open pool network. It might therefore be inferred that these hollows are similar pools which have become colonized by S. papillosum. However an examination of the margins of the pool showed that there was no distinct pool-edge engulfed by fresh Sphagnum, as would be expected. The depth of fresh Sphagnum papillosum appears to decrease gradually from the hollow towards the firmer peat, the pool phase becoming discontinuous and eventually dying out.

The linear hollow (figure 25b) shows a similar development of fresh Sphagnum over humified peat. In profile 1 strongly humified peat, in which fragments of E. vaginatum are abundant, is succeeded by the peat composed essentially of roots with numerous leaf scales of Trichophorum. Corroded S. papillosum is present and this increases to form the dominant material in the core together with E. angustifolium. This remarkable thickness of fresh S. papillosum shows a drier phase at one horizon, where S. 'acutifolium' forms a significant part of the core and Calluna shoots are present. (It is suggested that this is a lateral extension of a community lying adjacent to the core site since it is unlikely that colonization of the fresh Sphagnum by all the species concerned would occur.) The development of S. papillosum over the humified peat of core three is not such an abrupt change as in core one. Here the macroremains indicate progressively wetter conditions. Following establishment of fresh S. papillosum a short pool phase occurs but the profile shows S. papillosum, with E. angustifolium as the dominant association in core one. Core two, in the centre of the Molinia hollow, shows distinct zones of fresh S. papillosum alternating with S. subsecundum and other material indicative of distinct pool phases. The lowest of these pool phases indicated by S. subsecundum overlies peat dominated by Sphagnum plumulosum and Trichophorum. Unfortunately the lower horizons were not investigated owing to difficulty of extracting deeper cores in the centre of the hollow.

In this region of the bog surface fresh S. papillosum has developed over a humified peat surface the microtopography of which was very irregular. From the few cores examined it appears that the present wet hollows have been produced by flooding of such a surface. A field examination shows that fresh S. papillosum is gradually becoming dominant over the remaining 'ridges' of older humified peat as it has in the ridge profile in figure 25a. Alternation of S. papillosum growth and pool phases is seen in the centres of the hollows possibly indicating a delicate balance between conditions necessary for establishment of a Sphagnum papillosum carpet or a pool, whilst the conditions on the peripheral areas are more consistantly suitable for development of a Sphagnum carpet.

(b) Small linear hollow

In addition to these large hollows numerous small, linear hollows, occur within a zone of vegetation dominated by vascular plants towards the western margin of the study area (north of grid line 6 and west of line D). These generally occur on shallow peat, 1 - 1.5 m. in depth. One such hollow was selected for detailed stratigraphical investigation (lying at 160E and 360N; units in feet from grid zero). Others have been examined in less details and are described in Section 6 in relation to the accumulation of Molinia litter.

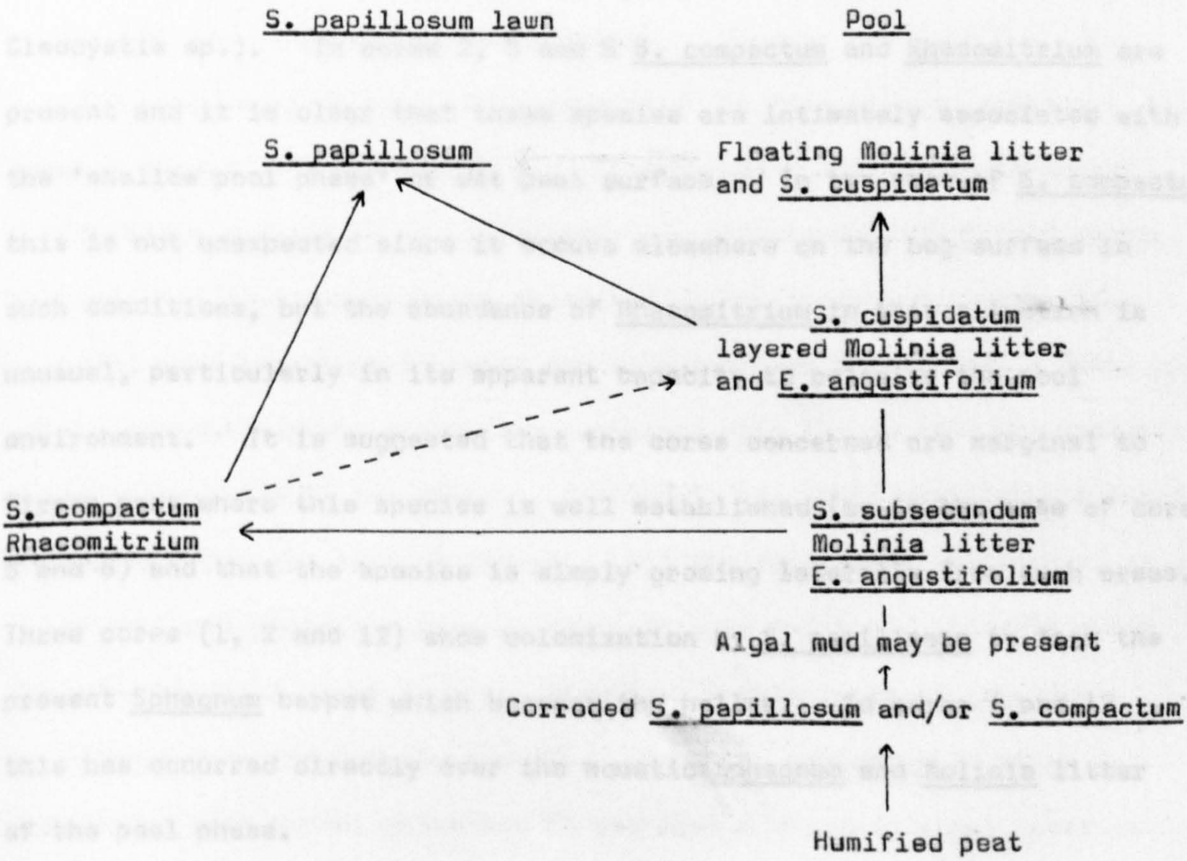
A sketch map of the hollow was drawn in the field (see figure 26) and twelve surface cores 30 - 50 cm. in length were extracted at approximately 1 ft. intervals along a base line following the long axis of the hollow.

Cores were extracted using an aluminium tube as described previously and the whole length of each core was examined in the laboratory. Since the profiles consisted for the most part of fresh peat it was possible to represent the various fractions by symbols for single species. An exception to this is in the lowest horizons where humified peat contains remains of Calluna and E. vaginatum. No attempt has been made to indicate the proportions of various species in such horizons. The results are depicted in figure 26, in which there is a vertical exaggeration of x5. It should be emphasised that possible compaction of the peat during extraction of the cores precludes exact reproduction of the relative heights of horizons in different cores.

A first inspection of the diagram shows that there is a good deal of lateral and vertical variation in the cores. Furthermore it is clear that the range of vegetation represented in these relatively short cores contrasts with the present surface vegetation which is basically divisable into only three types (see sketch map). Three species in particular, which form significant proportions of certain cores, are entirely absent from the present surface in the immediate vicinity of the hollow. These are S. magellanicum, S. compactum and R. lanuginosum.

Perhaps the most striking feature of the profiles is the fact that the hollow has developed on a relatively uniform surface of humified peat. All the cores show lower humified horizons terminated by a layer of corroded S. papillosum which indicates the onset of wetter conditions. Above this the cores show considerable variation, not only in detail but also in the main successional trends. The following account is intended as a guide to the salient stratigraphical features as well as being an interpretation.

Firstly it is apparent that certain cores show a simple succession, following establishment of a pool phase, in which this phase persists to the present surface or else is subject to colonization by S. papillosum. In some cases Rhacomitrium and S. compactum form dominant fractions within a succession which must be regarded as a pool phase. Cores 1 - 5 and 12 exhibit the above features which can be summarised in a diagram.



Core 4 represents the simplest succession, in which a pool phase is established following the layer of corroded S. papillosum overlying humified peat with Calluna and E. vaginatum. The lower levels of this phase are mainly S. subsecundum with Molinia litter and some E. angustifolium. E. subsecundum is replaced abruptly by S. cuspidatum at a higher level, in conjunction with an increase in Molinia litter which forms a more compact, layered deposit. This persists to the present pool where this material is floating. Menyanthes trifoliata is present in the lowest layers of the pool phase in core 1 and a distinct algal layer is present in core 12. This consists of both filamentous and gelatinous algae (including abundant Gleocystis sp.). In cores 2, 3 and 5 S. compactum and Rhacomitrium are present and it is clear that these species are intimately associated with the 'shallow pool phase' or wet peat surface. In the case of S. compactum this is not unexpected since it occurs elsewhere on the bog surface in such conditions, but the abundance of Rhacomitrium in this situation is unusual, particularly in its apparent capacity to colonize the pool environment. It is suggested that the cores concerned are marginal to firmer peat where this species is well established (as in the case of cores 5 and 6) and that the species is simply growing laterally from such areas. Three cores (1, 2 and 12) show colonization by S. papillosum to form the present Sphagnum carpet which borders the hollow. In cores 1 and 12 this has occurred directly over the aquatic Sphagnum and Molinia litter of the pool phase.

The second group of cores (6 - 11) show a more varied stratigraphy. An obvious difference is that humified peat extends closer to the present surface. In the case of core 6 this could be interpreted as a result of a persistent hummock centre. In contrast the stratigraphy exhibited by cores 9 and 10 indicates that an early pool phase has been overtopped by humified peat of a hummock and this in turn is reverting to wetter conditions at present. The rather complex sequence shown by core 9 is a result of its intermediate position between pool and hummock. Whether the secondary hummock development seen in cores 9 and 10 originated in situ or whether it is a lateral extension of humified peat with _Rhacomitrium_ displayed in core 11 cannot be determined directly. However the fact that the initial pool phase in core 10 is terminated by _Rhacomitrium_ implies a lateral spread of drier elements. In contrast a pool phase in cores 7 - 9, which appears to be equivalent, was colonized by _S. magellanicum_ and this has been subsequently inundated by the present pool deposits.

The more important features can be summarised as follows. Simplicity of the present surface vegetation contrasts with the variety of vegetation types represented in the cores. Throughout the whole profile more humified peat lies below the surface layers. All the cores show development of at least one pool phase and in most cases this is initiated slightly above the more humified basal layers, often with a thin layer of _Sphagnum papillosum_ occuring between the two. _Sphagnum_ _compactum_ is often associated with a pool phase and in one case a distinct algal layer is well developed. Subsequent development is variable, some areas remaining as pools and others being colonised by less hydrophilous vegetation which is considered to represent lateral spread from adjacent drier areas. In some cases second pool phases occur. Greatest vertical variation (cores 2, 5, 6 and 9) appears to correspond with present position of pool edges indicating that the zone separating relatively wet and dry areas has remained fairly constant. At both ends of the hollow <u>Sphagnum papillosum</u> has colonised the pool but this has not occurred in the centre of the hollow. There the pool phase persists and in the case of core 4 it has never been interrupted by drier elements.

Summary of stratigraphical investigations

The stratigraphical investigations described in this section provide direct evidence of the way in which particular surface features have developed on the study area. In this respect these investigations differ from other lines of approach to the problem of pattern formation. Other sections of this thesis are concerned more with possible causitive factors rather than the actual course of pattern formation. So the present investigations provide an important basis for discussion of possible causes, which forms the final section of the thesis. In order to emphasise the salient stratigraphical features which have a bearing on pattern development these are now summarised.

In general the peat shows less lateral variation in lower horizons than it does closer to the surface, though the depth at which more uniform conditions occur is variable. At site one where the peat depth is 4.6 m. fairly uniform conditions prevail below 2.5 m. At site 2 there is some indication of more uniform conditions below about 1.2 m. In the case of the linear hollows lateral variation is most pronounced in the surface horizons to a depth of 20 - 60 cm., below which the peat is more strongly humified.

In many cores abrupt changes from strongly humified peat to a pool phase are demonstrated, often with a very thin layer of corroded Sphagnum papillosum at the surface of the humified peat indicating onset of wetter conditions. Such sudden changes to a pool phase indicating flooding of a humified peat are seen in some of the cores below open pools and particularly in the case of the small linear hollow. In some cases the development of a pool phase is associated with an algal layer and often Sphagnum compactum is present. It is significant that on the present bog surface such conditions are found only on the overflow sites described in section two.

Lateral oscillation of wet and dry vegetational elements is demonstrated particularly in the case of site one (figure 22), and can be inferred from the degree of vertical variation exhibited by cores adjacent to pool edges in the case of the small linear hollow. In this case there is a considerable contrast between these marginal cores and that in the centre of the hollow where the pool phase remains dominant throughout. It is suggested that at site one a pool phase was initiated in the region of the present pool centre, that periodic wetter or drier phases have resulted in lateral transgression of vegetation zones and that there has been a progressive increase with time in the degree of lateral transgression by wetter communities towards the centre of the hummock.

Sites one and two show that major centres of pool or hummock remain constant though vertical fluctuations in the small linear hollow (core 10) indicate small-scale alternation of pool and hummock conditions and similar alternations are seen in the peat below open pools in certain cases. Ridges or hummocks on the present bog surface appear to be characterised by the absence of pool development at any horizon in the underlying peat and by abundance of Sphagna of the Acutifolium group in the upper horizons.

On the basis of the present work existing ridges might be regarded as areas where pools have never developed. (It must be remembered, however, that very few ridge sites have been examined during the present work and so these results must be treated with caution.) The peat below present hollows or open pools often shows more pronounced vertical variation than that of the ridges and in some cases this involves alternation of pool and hummock phases as mentioned above.

Regarding the development of the large pool networks it has been shown that there is no common stratigraphical succession below the two pools investigated and indeed only one of the ten cores shows a succession which can be interpreted as a logical precursor to the present pool. This arbitrary truncation of stratigraphical sequences implies that the present pool bottom is an 'erosion phenomenon'. The stratigraphy below the pool bottom in areas in line with linear peninsulas and an intervening island (cores 2c and 2e, figure 24) is more comparable with that of the ridge profiles in that aquatic phases are completely absent and Sphagna of the Acutifolium group are present, which are generally absent from profiles where distinct pool phases are developed. These two sites show the most pronounced anomaly between stratigraphical succession and level of the pool bottom and it is inconceivable that the present level of the pool bottom can be anything other than an erosion feature in this case. The amount of erosion is, however, unknown. Similarity of the profile below a ridge with that of the peat below a gap in the ridge does not necessarily mean that the ridge was once continuous at its present level. The gap may have been initiated by flooding of a section of the ridge at sometime during growth of the ridge and later accentuated by erosion.

Site One

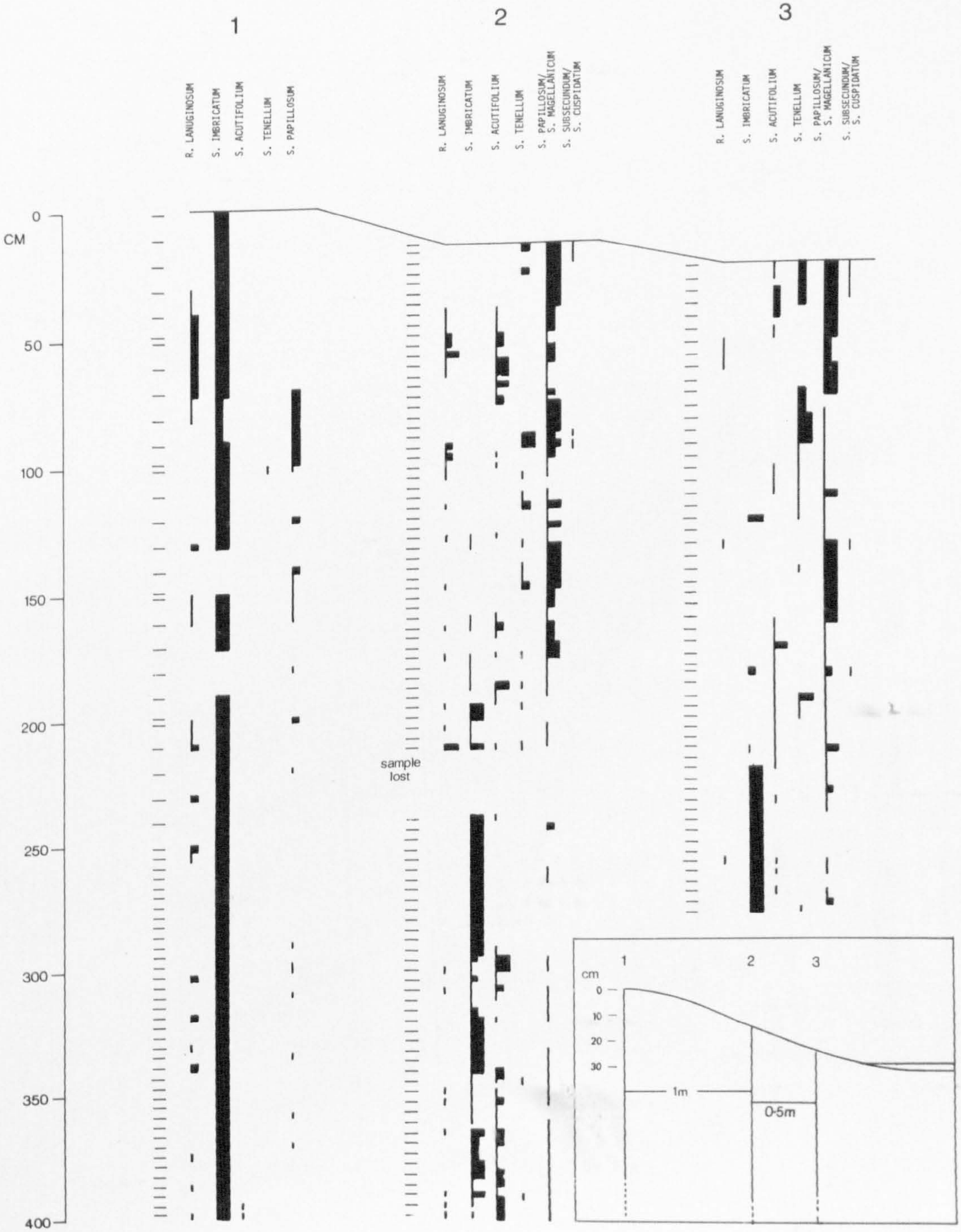


FIG. 22

Site Two

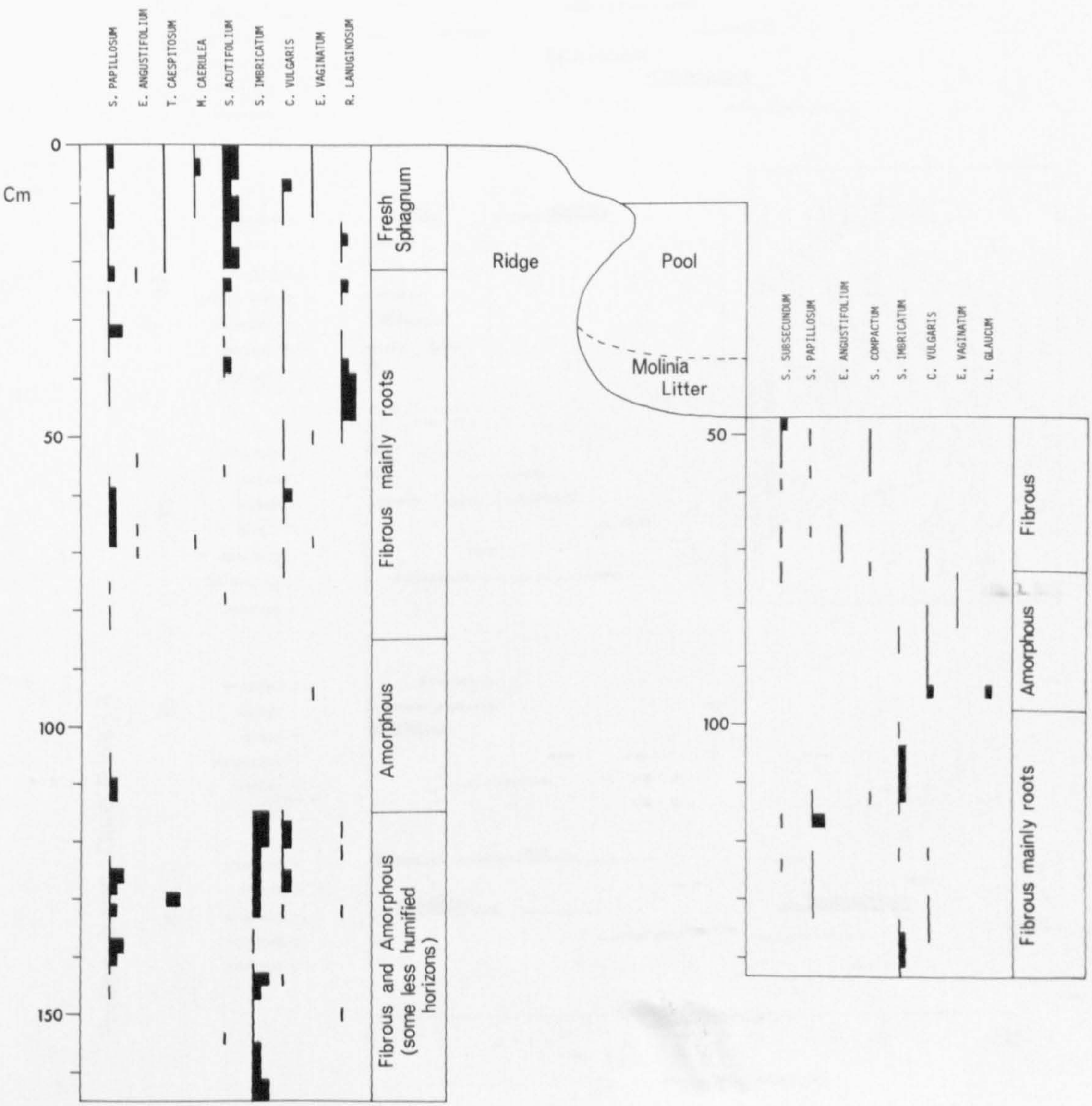


FIG. 23

Profiles below Open Pools : 1

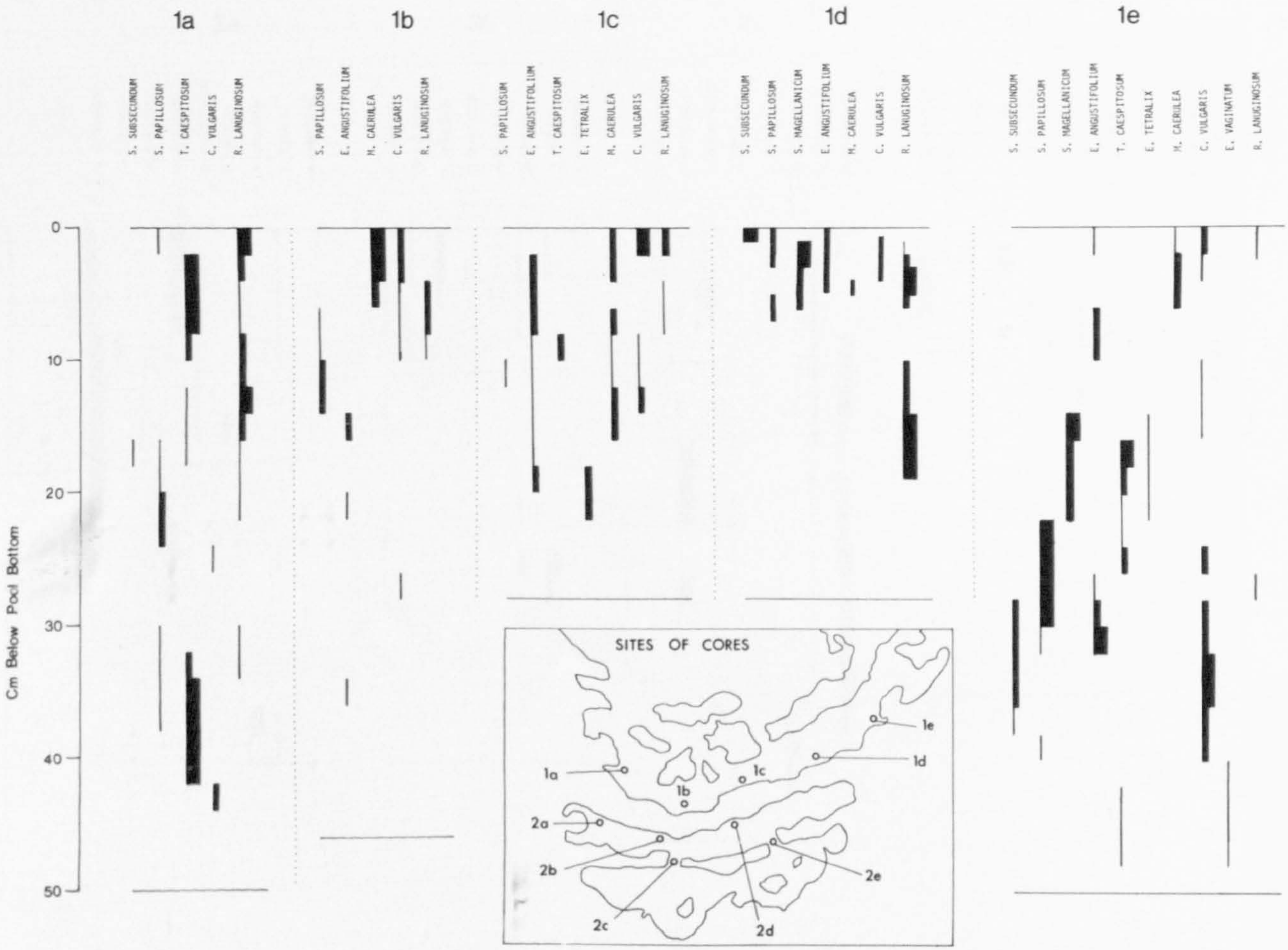


FIG. 24a

Profiles below Open Pools : 2

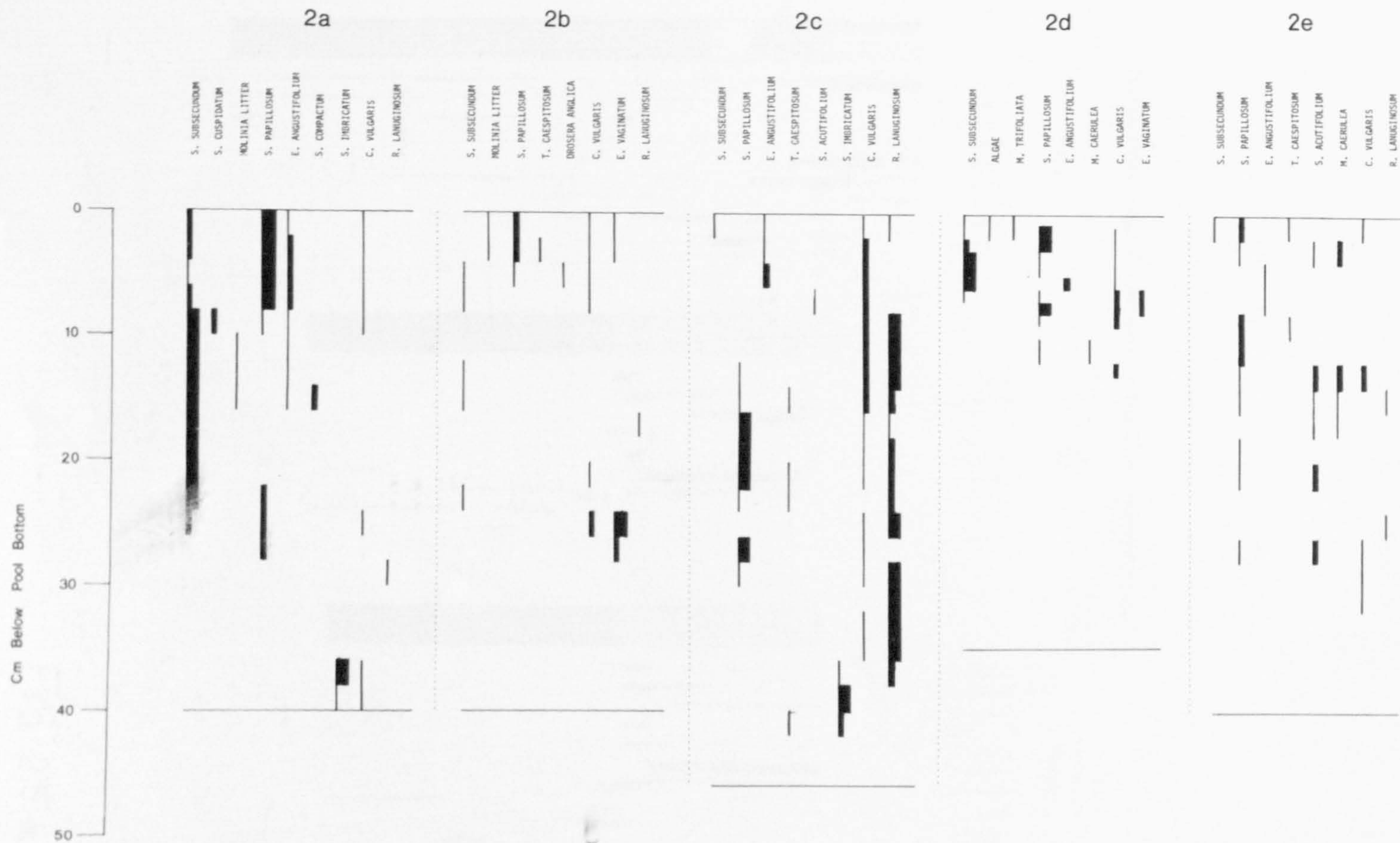


FIG. 24b

Profiles below ridge and adjacent S.papillosum covered hollow

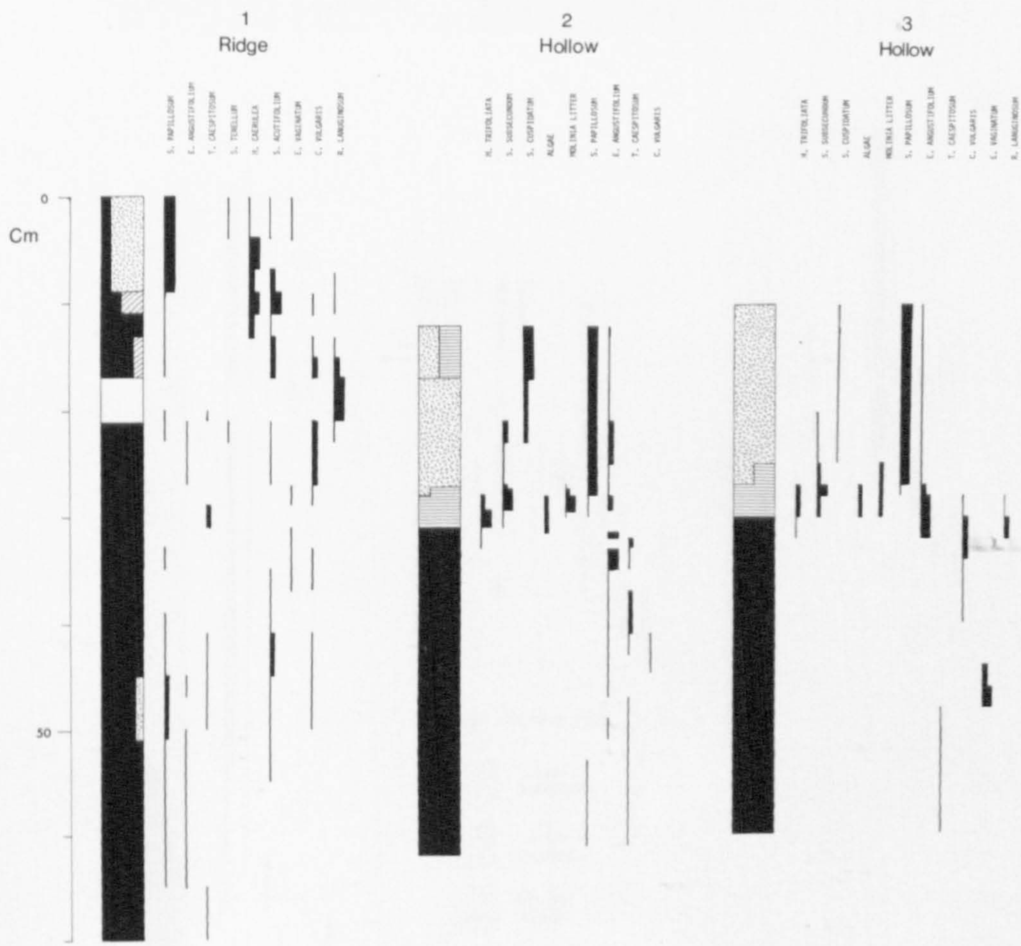


FIG. 25 a

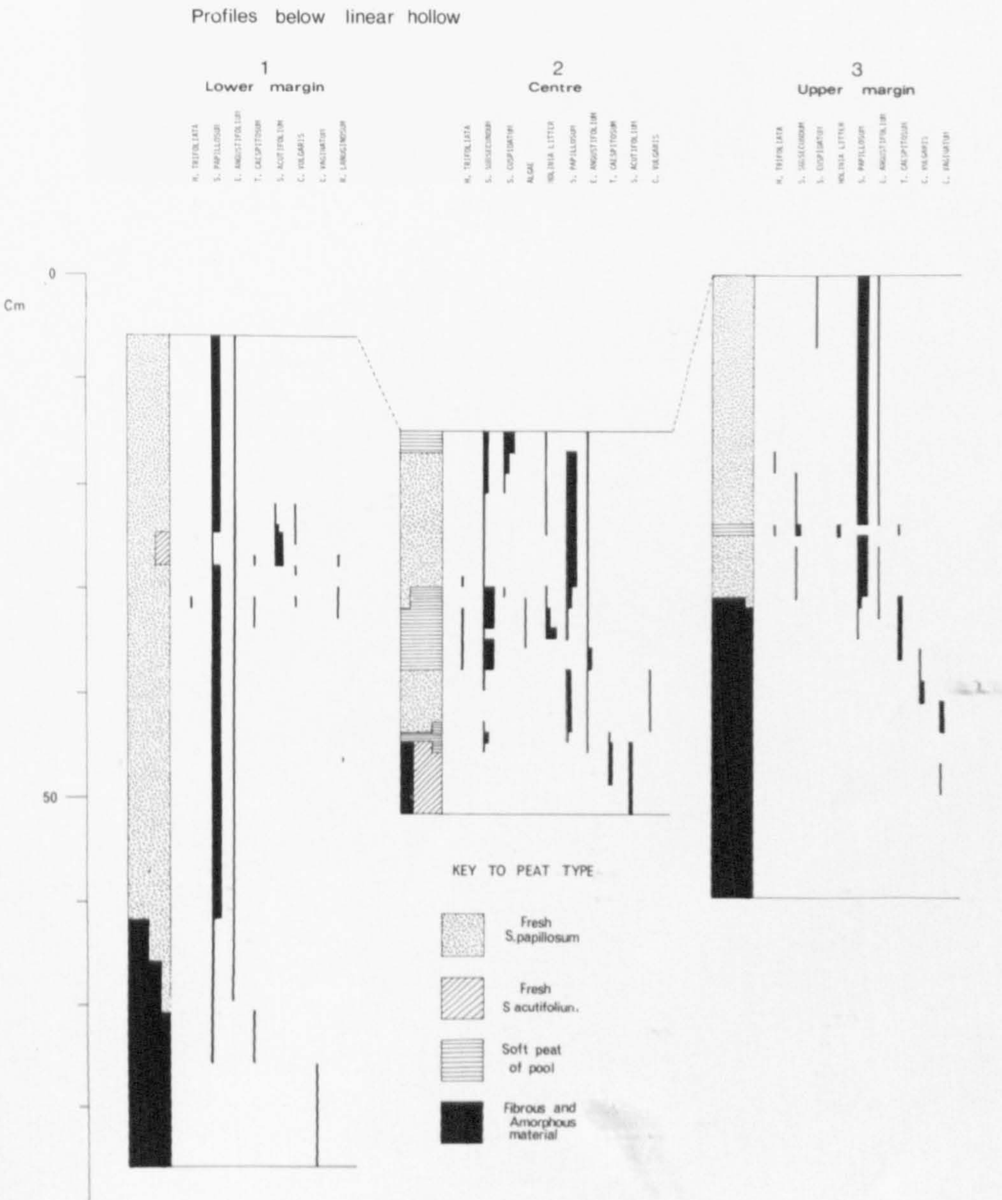

Profiles below linear hollow
1
Lower margin
2
Centre
3
Upper margin
0
Cm
50
KEY TO PEAT TYPE
Fresh S.papillosum
Fresh S acutifoliun.
Soft peat of pool
Fibrous and Amorphous material

FIG. 25b.

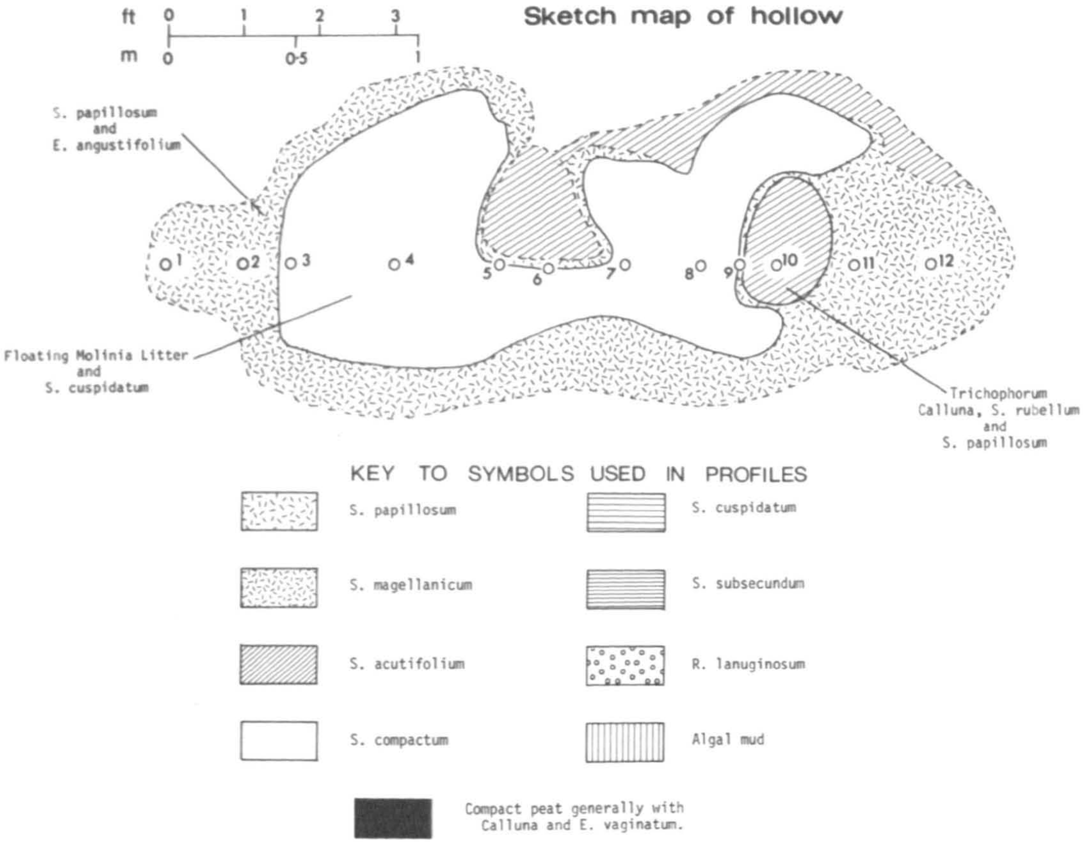

Sketch map of hollow
ft 0 1 2 3
m 0 0·5 1
S. papillosum and E. angustifolium
Floating Molinia Litter and S. cuspidatum
Trichophorum Calluna, S. rubellum and S. papillosum
1 2 3 4 5 6 7 8 9 10 11 12
KEY TO SYMBOLS USED IN PROFILES
S. papillosum
S. cuspidatum
S. magellanicum
S. subsecundum
S. acutifolium
R. lanuginosum
S. compactum
Algal mud
Compact peat generally with Calluna and E. vaginatum.

FIG. 26

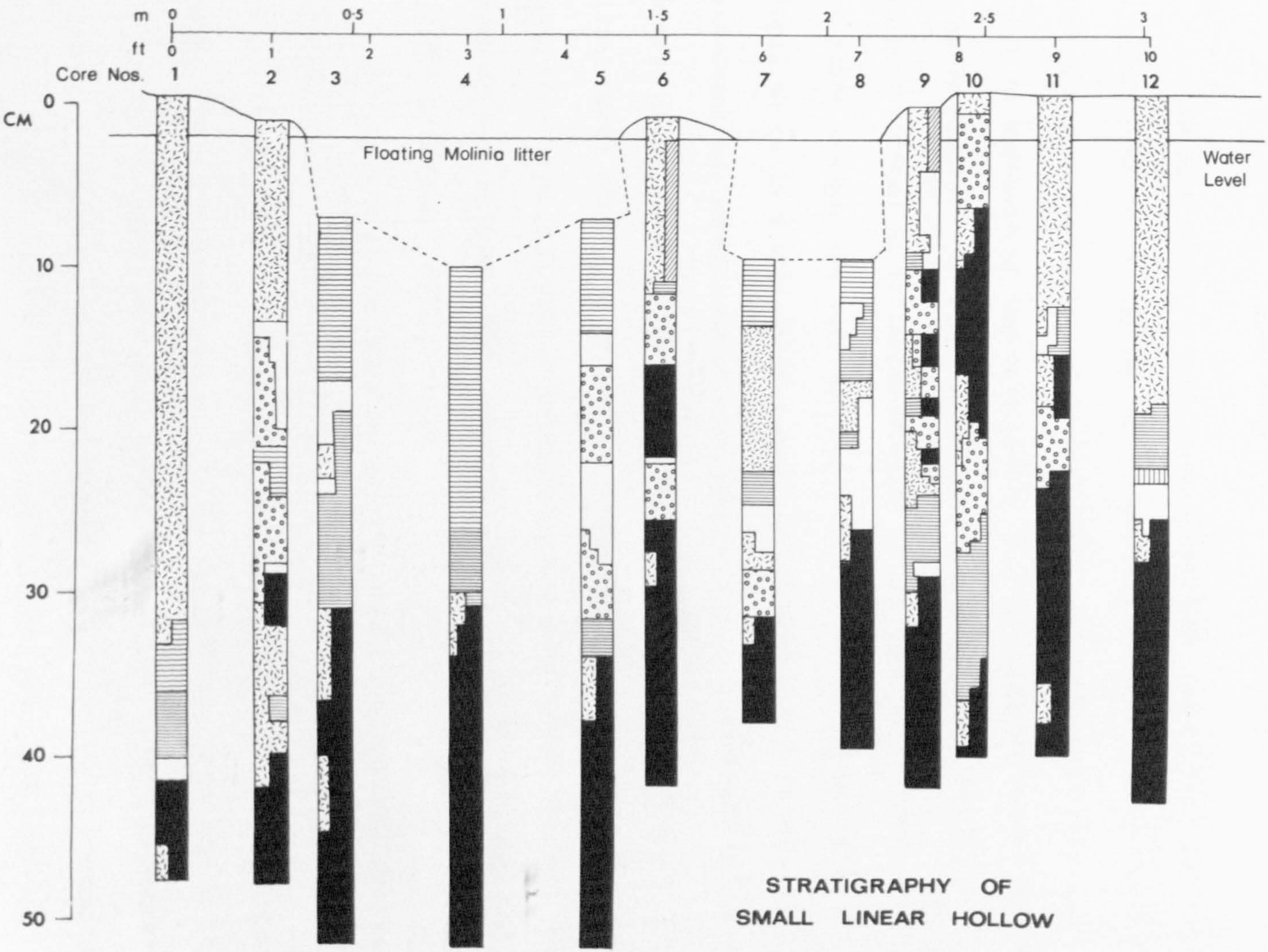

m
0
0·5
1
1·5
2
2·5
3
ft
0
1
2
3
4
5
6
7
8
9
10
Core Nos.
1 2 3 4 5 6 7 8 9 10 11 12
CM
0
10
20
30
40
50
Floating Molinia litter
Water Level
STRATIGRAPHY OF SMALL LINEAR HOLLOW

FIG. 26

SECTION 4

WATER LEVELS

It has been shown in earlier sections that the surface patterns on the study area are an expression of the relationship between the present surface microtopography and water-table. In some cases this consists simply of exposure of the water-table in deep permanent pools separated by drier ridges. In other situations the relationship between water-table and peat surface is reflected largely in the vegetation zones. Most of the plant species are more or less hydrophilous but taking the whole bog flora, there is a considerable range of variation in tolerance to, or dependance on, conditions of high water-table. A vertical zonation of species in relation to the water-table has been demonstrated for the Silver Flows (Ratcliffe and Walker 1958) and the importance of water level as a principal factor determining bog communities has long been accepted e.g. Osvald (1923), Tansley (1939), Sjors (1948), Kulczynski (1949) and Malmer (1962).

The present stratigraphical investigations suggest that pattern initiation is in some way dependent on a rise of water-table with respect to the bog surface. Examination of present water-level fluctuations is relevent to an understanding of pattern development in so far as it indicates the conditions under which patterns are being maintained at present. This in itself is sufficient reason to study the behaviour of water levels. There is the danger however that what is being investigated might be a result of pattern formation rather than a cause and so caution is necessary in relying on present conditions to explain the development of patterns.

Water level fluctuations within the study area were investigated by two separate methods, one producing continuous records and the other intermittant records. The number of sites where continuous records were produced was limited to three partly due to the high cost of the necessary instruments and partly to the need to restrict the amount of ensuing data to manageable proportions. By contrast intermittant records were made at a large number of sites in four distinct groups totalling nearly 100. The distribution of water level recording stations isshown in figure 27. The pattern of groups of stations for intermittant records results from the need to obtain information about the behaviour of the water table both in relation to the whole bog system and also at the local level in individual pools and hummocks.

In the following account the continuous records obtained at the three key stations are described first since they provide a background against which the intermittant records become more meaningful. This is followed by a description of the significant features of the intermittant records and the na ture of water level fluctuation is then summarised in the light of both these types of investigation.

Continuous records of water level fluctuation

Selection of the key sites for continuous records was made on the following basis. Sites 1 and 2 were chosen as representatives of contrasting pool types, site 1 being a large Sphagnum-covered hollow (principally S. papillosum and S. cuspidatum) and site 2 one of the large open pools of the eastern pool network. The third site which lies on the crown of the bog in the north western pool network was established at a later date in order to investigate the degree of water level fluctuation in that part of the system where the only hydrological input is in the form of direct precipitation. Both site 1 and 2 are subject to some degree of run-off from other parts of the study area though this can be expected to be very slight in the case of Site 2.

The instruments chosen to produce continuous records were Munro vertical one-range water level recorders (type 1H89) which are specifically designed to record small changes in water level i.e. less than one foot. Operation is by means of a float operating a pen arm in the vertical plane in conjunction with a rotating chart drum operated by a monthly clock mechanism. The chart drum is 10" (25.5 cm.) in height, sufficient to accommodate the full range of fluctuation on the sites investigated at the natural scale. Each clock was tested for a period in excess of one month before the instruments were set up in the field.

In order to produce absolute stability the instruments were screwed to iron platforms supported at their four corners by conduit piping extending through the peat to mineral ground. It was thought that by this means the record produced would be independent of any vertical movements of the peat mass should such occur. The steel tape bearing float and counter-weight was protected from disturbance in an aluminium casing. In the case of site 1 a small area of Sphagnum papillosum was removed to a depth of about 25 cm. thereby providing a sufficient depth of water for the float, the aluminium casing extending down into the pit so formed. The method of mounting these instruments is shown in figure 28.

Records were commenced at sites 1 and 2 in November 1965 but those at site 3 were not commenced until September 1966. All records continued until August 1967 a period of 20 months in the case of sites 1 and 2. Unfortunately, failure of the instruments for a variety of reasons, in conjunction with the fact that charts were renewed only at monthly intervals, resulted in loss of records over substantial periods as can be seen from the diagram showing mean weekly levels over the entire period (figure 30). For this reason the results have not been subjected to a computer analysis. The records have however been analysed in a number of ways and the results are depicted in figures 30 - 33.

Several selected portions of the continuous charts are shown in figure 29 in order to illustrate the general features of water level fluctuations over periods of several weeks. The main purpose of this diagram is to provide a background against which analysis of the continuous records might be more easily understood. In particular the nature of the vertical scale and its zero datum must be explained. It will be appreciated that especially in the case of the recorder at site 2 in the open pool network undulations of the bog surface in the vicinity of the instrument might well exceed the total range of fluctuation of water level so that it is meaningless to relate water level fluctuations to 'ground surface' since such a value could only be an arbitrary figure with no real significance. This being so the zero value for each instrument is entirely arbitrary but is consistant throughout the results. These arbitrary values are referred to as levels 1, 2 and 3 relating to the site concerned in each case where in practice the zero level consisted of a horizontal line engraved on the aluminium float casing.

This same diagram (figure 29) also serves to illustrate some of the features of water level fluctuations over 'wet' periods during both summer and winter. The charts show a series of rises and falls related to periodicity of rainfall, the rising portions being abrupt and the fall-off curves being exponential curves truncated at each successive period of rain. It will be noted that the pattern of fluctuation is essentially similar at different sites over the same period but that the total range of fluctuation differs, that at site 1 being consistently greater than site 2. Perhaps the most important feature of the charts is the evidence that total range of fluctuation even at site 1 can be very small over periods of several weeks. In the case of these particular charts, which are of winter and summer periods, the maximum range is 6 cm.

The range of fluctuation does of course increase during drier periods and the nature of the continuous charts over such periods can be appreciated from examination of the section of charts from site 1 shown in figure 38. This particular period was the most pronounced dry phase during the whole period of study. It will be noted that the total range of fluctuation is in this case 16 cm. Another feature of interest which is well displayed is the diurnal effect which gives rise to the 'stepped' trace. This effect is found on charts during dry periods throughout much of the year but, as might be expected, is more pronounced during summer since it is a direct reflection of evapotranspiration rates (indeed Heikurainen, 1964, has used this phenomenon to measure evapotranspiration). Another feature of this chart is that the period following the dry phase illustrates very clearly that even in summer the water level can be rapidly raised to a level comparable with that of the wet periods previously described.

These, then, are some of the features of water level fluctuations which can be seen from direct examination of the continuous charts. In order to illustrate the nature of fluctuations throughout the year at different sites the data have been 'condensed' in various ways.

Firstly, the data are shown (figure 30) as mean values for weekly periods, these values being the mean of 14 points in each week((6 a.m. and 6 p.m. each day). This diagram indicates the nature of fluctuations over the year. It can be seen that greater differences between consecutive weekly averages occur during the summer period but a pronounced fall during January 1966 shows that a sufficiently long dry period can have a substantial effect in lowering the water table even during those seasons when evapotranspiration rates are negligible. The diagram shows clearly that the average height of the water table over the year changes gradually, being high in winter and lowest in June-July, but the total difference is remarkably small. The mean weekly values differ by only 10 cm. in the case of site 1 and 8 cm. in site 2 over the whole of the study period.

The diagram referred to above does not include total range of fluctuation in terms of maxima and minima for the weekly periods. Instead the total range and degree of fluctuation of water levels are demonstrated by means of histograms which are drawn to represent sections of the continuous charts by showing the length of time that the water level lay between each 1 cm. division as a percentage of the total period represented. Histograms of water level fluctuations are shown for weekly and longer periods in order to demonstrate both short and long term behaviour of the water table.

Using this method the seasonal fluctuations of the water table are illustrated in figure 31 by means of 9 selected periods of 4 - 6 weeks throughout the year. It is immediately apparent from this diagram that the water levels show a seasonal cycle in terms of both the range of fluctuation and the relative height of the modal values for the periods concerned. The winter periods are characterised by a consistantly narrow range of water level fluctuation (e.g. 8-10 cm. for the three periods between 4 November 1966 and 18 March 1967 at site 1 and 7-8 cm. for the periods at site 3). In contrast periods of similar duration, or less, during summer show considerably greater range of fluctuation. For example the total range of fluctuation at site 1 during a six week winter period (8 December 1966 - 18 January 1967) is less than half that of a four week summer period (27 May - 23 June 1967), the totals for those two periods being 8 cm. and 17 cm. The degree of difference is slightly less pronounced at site 3 where the values for those same periods are 7 cm. and 12 cm. A second point concerning the seasonal variation in range of fluctuation is that the highest water levels in each period are remarkably constant throughout the year. At site 1 there is only a 2 cm. difference between the highest values for all 9 periods and 5 of the 9 periods share the highest value. In contrast the maximum difference between the lowest values for the 9 periods is 11 cm. So although the greater range of fluctuation in the summer is largely caused by lower water levels the effect would be less were it not for the fact that the summer water levels may at times be as high as the highest winter water levels and are frequently within 2 cm. of such values.

This diagram (figure 31) is not shown simply for the purpose of depicting seasonal range of fluctuation. The main purpose is to demonstrate the nature of water level fluctuations more clearly by expressing this in terms of percentage time between particular levels over a given period. The histograms for these periods with their modal values give a clearer indication of the actual behaviour of the water level than do weekly means of total range of fluctuation. Some of the histograms show two separated peaks (e.g. September 22 - 3 November 1966) indicating that the period concerned included the end of a dry phase followed by a phase when the water level remained relatively high. Single peaks are however more usual and it is significant that the seasonal variation of this modal value, although distinct, is quite small. At site 1 the maximum difference of modal levels throughout the year is 8 cm. and in the case of sites 2 and 3 this value is only 3 - 4 cm. Associated with this in the fact that the low summer water levels indicated by the total range of fluctuation constitute only a small proportion of the periods concerned. The four-week period 27 May - 23 June 1967, which includes the most pronounced dry phase during the whole period of study, illustrates this fact very clearly. For example at site 1 the water levels for the whole study period rarely fell lower than 18 cm. below the datum for that site but during this particular period the lowest level reached was 26 cm. below this datum. The time over which these relatively low levels occurred is however only 30% of the four-week period.

The same method has been used to demonstrate the behaviour of the water table over shorter periods and this is shown in figure 32 which comprises 11 consecutive single week periods from 8 April to 24 June 1967. The mean values for these periods are included in figure 30. As in the previous figures the fact that site 1 has a greater range of fluctuation than the other two sites is demonstrated very clearly. The very narrow range of fluctuation which occurs during 'wet' periods (i.e. when the water table is high) is particularly marked. For example the period 22 April - 27 May for which the total fluctuation is 7-8 cm. at site 1 and 4-6 cm. at sites 2 and 3 for the weekly periods. During two consecutive weeks the water level at sites 2 and 3 lay within single 1 cm. units for over 50% of the time. By contrast the total range of fluctuation is seen to increase considerably during a dry period, e.g. 3 - 27 June, when over a period of three weeks the total range was 17 cm. at site 1 and 10-12 cm. at sites 2 and 3. During the last week of this period a rapid rise of water level is demonstrated, a total difference at 14 cm. occurring at site 1. The fact that the water level can in a matter of days regain a level from which it has gradually fallen over a period of 2½ weeks is significant when considering the fact that the highest water levels during the summer periods shown in figure 31 are consistantly very close to the highest winter water levels.

<u>Some aspects of climatic conditions during the period of continuous water level recording as a guide to interpretation of results</u>

Water level fluctuations have been investigated to provide accurate information relating to one variable which is considered to have a significant effect on the distribution of plant communities within the area of patterned blanket bog being studied. It is to be expected that fluctuations in water level will be related to the climatic regime of the area and to the physical properties of the peat body concerned. A full understanding of the causes of water level fluctuation might therefore require a study of the whole hydrological regime including, as well as a total water budget, an investigation of storage capacity and rate of water movement through the peat. For a representative picture to be obtained such a study would have to be made over a considerably longer period than the present study. Indeed unless the particular climatic conditions prevailing during this study can be compared with average conditions over longer periods the value of these observations of water level fluctuations will be very limited. So it is relevant to indicate briefly the extent to which the study period is typical of the prevailing climatic conditions of the area and for this purpose reference is made to Meteorological Office rainfall data for the nearest stations. Examination of these and certain other data relating to the climatic conditions during the study period also allows a more meaningful interpretation to be made of water level movements, particularly in terms of seasonal changes.

The data which have been used are monthly rainfall totals for Loch Dee (which lies at the southern end of the Silver Flowe about three miles from the study area) also monthly rainfall totals and daily values of 'bright sunshine' for the station at Clatteringshaws (seven miles from the study area) which have been used to produce monthly estimates of potential transpiration over the period of study. Data are tabulated in Appendix 4.

In table 1 the monthly rainfall totals for Loch Dee are given alongside the same values expressed as percentages of the average monthly rainfall (based on the period 1916 - 50). This indicates the extent to which any month differed from average both in degree and also whether it was wetter or drier than average. The annual total for 1966 expressed as a percentage of the average annual rainfall is 103.57 which is very close to the average condition. The figures for Clatteringshaws for 1966 show an even closer degree of similarity between actual and average annual rainfall where the total is 100.42% of the average (table 2). For this part of the study period the rainfall conditions can be regarded as average in total but there is clearly a good deal of divergence from average conditions over the monthly periods which is relevant when considering seasonal fluctuations of water levels.

A more significant indication of the extent to which seasonal fluctuations in the climatic regime over the period of study depart from average conditions is obtained by comparing actual and average values of net soil water surplus or deficit for monthly periods. These figures are simply the difference between rainfall and potential transpiration for each month. Average monthly values of potential transpiration are given in the Ministry of Agriculture Technical Bulletin No. 16: Potential Transpiration, in which the method of calculating monthly potential transpiration for particular periods is given. (This requires data on hours of 'bright sunshine' per day and since the station nearest the study area which includes this is Clatteringshaws the figures in tables 3 and 4 are based on data from this station).

In table 3 the monthly rainfall totals are given together with calculated values of potential transpiration and a striking feature is the fact that over the whole period of study only two months show a net soil water deficit and for a considerable proportion of the time rainfall is substantially greater than potential transpiration. The figures are tabulated in order to emphasis this relative small significance of potential transpiration in proportion to rainfall which prevails over eight months of the year. Some indication of the likelihood of a net soil water deficit occurring in any month can be gained from table 5 which shows the minimum amount of rain (expressed as a percentage of the average monthly rainfall) necessary to produce a net soil water surplus under average conditions of potential transpiration. From this it can be expected that a net soil water deficit will be unlikely to occur very often for months other than May, June and July. This then provides a background to the general climatic conditions of the area.

Finally average monthly soil water surplus at Clatteringshaws and the actual monthly totals of surplus or deficit over the study period are given in table 4. Comparison of these two sets of figures provides the most significant indication of the extent to which seasonal fluctuations in climatic regime over the period of study depart from average conditions. A graph of the relationship is given alongside the mean weekly values of water levels in figure 30.

Interpretation of water level fluctuations in the light of climatic data

There is in fact a striking similarity between the seasonal cycle of mean values for water levels on the study area and the values for soil water surplus or deficit at Clatteringshaws (see figure 30). Certain irregularities in the seasonal cycle of water levels already noted are immediately explicable in terms of divergencies during the study period from the average conditions of soil water surplus in each month. For instance, the pronounced fall in January 1966 already commented on occurred during a month when the soil water surplus was only 58% of average. The gradual fall in mean water levels over the succeeding period March - June corresponds with a period when conditions of soil water surplus were close to the average. In contrast the same period in 1967 shows violent oscillations of the water levels with peaks in February - March and May and relatively low levels in April and June. The high water levels of May 1967 can be explained by the fact that net soil water surplus for that month was 383% of average.

Average conditions of soil moisture surplus can thus be used as a crude guide to the expected average seasonal fluctuation of water levels. In addition, comparison of the mean weekly water levels during months in which there was a high net soil water surplus indicates that above a certain water level the high rainfall has no further effect. Admittedly the figures are not strictly comparable since the soil water surplus is for the whole month during which shorter periods with lower values might be expected. Nevertheless it is clear in the case of site 3 that there is very little difference between the mean weekly water levels during the 'high periods' in December 1966 and February - March 1967; also the highest mean value in May 1967 lies at a similar level. Despite the very high soil water surplus in December 1966 the mean water levels are not any higher than those of the later periods and it must be assumed that a considerable amount run-off occurred. A threshold must therefore exist for each site, above which additional rainfall will have no further effect in raising the water levels. The shape of water level fall off curves already described supports this contention since it shows a very steep fall at high levels. This also explains why there is so little difference between the highest water levels of each period shown in figure 31. Since they are not affected by extremes of rainfall it can be expected that the water level maxima recorded over the period of study represent conditions which are frequently repeated.

It is less easy to determine how far the particular low water levels recorded during the period of study are characteristic of the water level regime over long periods. From the graph of average soil water surplus (figure 30) and the proportion of average rainfall necessary to produce a net soil water surplus (table 5) it appears that very low water levels are only likely during April, May, June and July. In order to demonstrate the seasonal variation of rate of water level fall, selected 'fall-off' curves' at different times of year have been superimposed and are shown in figure 33a. This is done simply by using a constant horizontal datum and superimposing as far as possible the steeply falling initial section of the curve in each case. The lower part of each curve is effectively a straight line and so it is possible to produce a value for rate of water level fall. This is shown in figure 33b as potential water level fall per month (30 days) throughout the year.

Obviously the degree of water level fall depends on the length of a single dry period and the evapotranspiration conditions at the time. It can be seen from figure 33b that the rate of water level fall increases considerably over the summer period, the rate for June being twice that for April and August. So the possibility of very low water levels occurring is far greater in the period May to July irrespective of seasonal conditions of rainfall. The longest dry period in summer over the whole period of study was 13 days (June 1967) during which time the fall rate was about 1 cm. per day and this, if continued for one month would cause the water level to fall 15-20 cm. below the lowest level recorded during the present study at site one. So it can be assumed that there is a strong possibility of substantially lower summer water levels occurring than those recorded during the present study. Clearly there is a need to consider the water level fluctuations in relation to rain day frequency but this has not been considered during the present work. It is, however, most unlikely that lower water levels than the extremes recorded during the whole study period will occur during the period August to April.

A comparison has been made between the rate of water level fall throughout the year at site 2 and seasonal variation in average potential transpiration (figure 33c). The figures used for transpiration are based on an altitude of 1,200 ft. (compared with 900 ft. for the site concerned) which represents an error of about 3 mm. in June. More important is the fact that these are figures for average potential transpiration for monthly periods, which may well be exceeded during very dry periods. For this reason it is impossible to comment upon the relationship during periods of high potential transpiration except to note that it is approximately linear. What is interesting is the fact that the sections of fall-off curves used indicate that there is a minimum fall-rate of 10 cm. per month irrespective of seasonal variation in potential transpiration. The rates of fall represent the lower sections of the curves shown in figure 33a. At higher water levels, where the fall rate is more consistent and is primarily a reflection of run-off, the fall rate is about 4 cm. a day. So there is a considerable difference in the effective lowering of the water level due to physical factors alone during periods when the water level is high or low. This indicates the difference in hydraulic conductivity between the surface layers and the slightly deeper horizons of the peat forming the lower margin of the pool concerned.

Chapman (1965) has demonstrated a very close relationship between water-table and run-off on a Sphagnum dominated blanket bog in Northumberland. He shows that when the water level rises to within 8 cm. of the bog surface a very marked increase in the rate of run-off takes place suggesting that that the bulk of the water movement in the system is fairly rapid flow through the very surface layer and that movement in the lower layers is at most very slow. Although no measurements of run-off have been made during the present investigations, nevertheless, the form of the hydrograph and the relationship of this to potential transpiration described above suggests the existence of very similar conditions to those described by Chapman.

Intermittent Records of water levels

In the introduction to this section the point was made that intermittent measurements of water levels have been made in order to understand the behaviour of the water table on the scale of the whole study area and also at the scale of local hummocks and hollows. It was considered impracticable to determine the water level behaviour throughout the whole study area and so the large scale approach is restricted to a transect E - W across the study area along grid line 5 with stations at 50 ft. intervals and a grid system of stations at approximately 30 ft. intervals throughout the eastern pool network. The distribution of these and other water level recording stations is shown in figure 27 and a more detailed map of the grid in the eastern pool network is shown in figure 37. The behaviour of the water table on a local scale was investigated by means of two transect lines (shown as transects A and B in figure 27), along which stations were situated at about 5 ft. intervals. Both these transect lines, each of which is 100 ft. long, follows the local direction of slope and crosses a series of Sphagnum-grown hollows with intervening ridges.

Each of the 92 recording stations consisted of a narrow plastic tube inserted into the peat to provide a free water surface and accurate measurement of the water level was found to require a special instrument to avoid disturbance of the water table during measurement. Tubes were 50 cm. long and 5.1 cm. diameter, with two rows of 5 mm. diameter holes drilled along opposite sides, the holes being spaced at 10 cm. intervals.

Before inserting each tube a core of peat about 40 cm. long was removed by means of an aluminium tube (of 5 cm. diameter). A 60 cm. length of wood (2.5 cm. sq.) was pushed into the peat below the well so formed and a perforated disc of expanded polystyrene was inserted above this to form a support for the plastic tube. It was hoped that by this means the tubes would remain rigidly supported.

Initially water level measurements were made simply by lowering a ruler into the tube and measuring the distance from the water surface to the rim of the tube. However it was soon appreciated that fluctuations in water level were very small and that anomalous results were produced by disturbance of the peat surface adjacent to the tubes. The weight of an observer within 1.5 m. of a tube was found to cause the water surface to rise by as much as 3 cm. in certain tubes. This effect varied according to the vegetation types in which the tube was situated.

An instrument was therefore designed, enabling accurate measurements to be made from outside the critical zone around each tube. This consisted of an aluminium tube 2 m. long bearing a movable graduated rod at one end. The graduated rod was lowered into a plastic tube until the instrument rested on the rim of the tube. It could then be moved up and down by turning a knob at the opposite end of the instrument. At the bottom of the graduated rod were two electriccontacts arranged so that when both touched the water surface an electric circuit was completed. This operated a light on the battery box carried by the operator. The distance between the top of the tube and the water surface could be read from the scale when the instrument was withdrawn. The instrument is illustrated in figures 34 and 35 in which the method of operation can be seen as well as detail of one of the recording tubes.

Owing to the resistance of the water the current passing through the circuit was very small, consequently it was necessary to increase the current through a transistor in order to operate the light. The circuit diagram is shown in figure 36.

The instrument was made as light as possible to avoid any displacement of the plastic tubes. Even so it was necessary to rest the instrument very gently on the tubes. The heights of the tubes on one transect line have been checked three times during the course of the work by means of a quicksett level and the amount of difference in measurements was never more than the error of the level, within about 5 mm. In addition to allowing water levels to be measured without the observer influencing the local water table at the time of measurement, the instrument also allowed the measurements to be made without disturbing the surface vegetation in the immediate vicinity of the tube sites. It was appreciated that regular visits to sites dominated by Sphagnum can lead to rapid deterioration of the surface and that this might in due course influence the water regime under investigation.

Water levels have not been recorded regularly or consistently for all four groups of stations since the objectives varied. Short term fluctuations particularly during the summer have been investigated at the local level along the two short transect lines but it has also been necessary to make intermittent measurements at these same stations throughout the year in order to interpret the short term fluctuations in relation to the expected seasonal fluctuation. The total number of occasions on which water levels were measured for each of the four groups of stations was as follows:

Group in Eastern Pool Network	27
Transect across whole site	15
Western Transect	37
Eastern Transect	14

In presenting the results of this investigation I have decided to select only those features which appear to be most significant rather than reproduce the data in full. This has been necessary because behaviour of water levels and more particularly the relationship between mean water level and ground surface are expressions of both local microtopography and position of a recording station within the whole system. The problem is most acute when considering the water level behaviour over a large part of the study area where presentation of data such as depth of mean water level would be meaningless, unless it could be related to an 'average bog level'. Since it is necessary to distinguish between differences in water level behaviour over the whole area and those on a local scale these factors have been considered separately in the following account except in the final section dealing with the relationship between water levels and vegetation.

Range of water level fluctuation in the region of the Eastern Pool Network and along grid line 5.

Since the data are not produced in full it is necessary to provide evidence as to the reliability of the data prior to interpretation of selected features. Figure 39a shows a series of selected water levels along the western transect throughout the period of study and it can be seen that the water levels behave in a very consistant manner. Although the total amount of fluctuation varies from one station to another the relative positions of the water levels remain remarkably constant. For instance the maximum difference between water levels for the two dates 17.12.65 and 14.3.67 is only 0.5 cm. along the whole transect (100 ft.). It is also true of other recording stations, both in the Eastern Pool Network and along the transect across the whole site, that the differences between any two water levels at separate sites appear to be specific, implying that there is a particular range of fluctuation characteristic of each site.

The most significant feature of the water levels over the area of the eastern pool network is the fact that there is a progressive increase in the range of fluctuation away from the pool system. To demonstrate this lines of equal water level fluctuation have been drawn based on the difference between the maximum and minimum water levels over the whole period of study. Utilisation of the extremes can be justified in view of the apparent consistancy of water level changes described above. Since the isopleths of water level fluctuation relate to data from the water level recording stations they have been drawn in figure 37 solely in relation to the distribution of these stations and irrespective of surface features over the area concerned. The resulting pattern of isopleths has been superimposed on a map of the Eastern Pool Network showing surface contours and pool outlines (figure 37) and the distribution of water level recording stations is also shown.

It can be seen that the difference between water levels on the two dates concerned (4 February 1967, 17 June 1967) increases from 8 cm. to 12 cm. or more around the periphery of the pool system but that the 'gradient' of fluctuation increase varies. One area to the east of the Eastern Pool Network shows a very gradual increase in the range of fluctuation and this corresponds approximately with a distinct zone of linear hollows shown in figure 11. The most pronounced 'gradient' of fluctuation occurs around the south-eastern rim of the pool system, a region where the peripheral slope of the bog surface is steepest and where it also approaches most closely to the margin of the pool system.

Before considering the significance of this progressive increase in water level fluctuation it is necessary to examine the extent to which the different components of fluctuation contribute to it. The map was compiled by comparing extreme conditions but it is not known whether precisely the same effect is produced during periods when the water level is rising or falling. To investigate this two periods have been selected from the continuous water level records at site 1, one a falling period and the other a 'rising' period (see figure 38). In the first period

(9-17 June 1967) the water level fell continuously. The second period (17-23 June 1967) includes sections when the water level fell but is predominantly a period of rising water levels. Selection of these periods was restricted by the dates on which water levels were measured elsewhere in the system. The range of fluctuation during each of these periods at the stations along the transect crossing the whole study area (grid line 5, which crosses the Eastern Pool Network) is shown by lines b and c in section 2 of figure 38. In addition the difference between the maximum and minimum water levels recorded along this transect over the whole period of study is indicated by line a.

All three lines indicate that the lowest range of water level fluctuation occurs in the region H - I of the transect which corresponds with the highest part of the bog surface and the position of the Eastern Pool Network (as in figure 37); they also show that there is a pronounced increase in water level fluctuation to the east of the grid line I and that the range of fluctuation is variable in the western half of the transect. Before considering the water level fluctuations over the two periods it should be emphasised that a meaningful comparison cannot be made between actual amounts of fluctuation indicated by lines b and c since the relative amounts of water gained and lost over the two periods are not known. The object is rather to demonstrate differences in relative amounts of fluctuation during the two periods in different parts of the transect. The greatest difference in this respect is between the highest part of the bog surface and the areas on either side. During both periods the amount of water level change is greater towards the edge of the bog than on the crown but this difference is less pronounced in the falling period. The difference between the two areas is accentuated by the inverse relationship of lines b and c. On the crown of the bog the water level fell more during the first period than it rose during the second whereas the converse applies in the peripheral areas where the rise exceeded the fall.

In order to illustrate in more detail this crossing of the lines b and c, data for the same periods are shown in figure 38 (3) for stations at 5 ft. intervals along the Eastern Transect, 100 ft. in length, which lies close to section J - L of the longer transect (see figure 27). Although local variations in water level fluctuations are more obvious than in the longer transect the relationship between lines b and c is essentially the same.

In considering the reason for progressive increase of water level fluctuation away from the pool network on the crown of the bog it is significant that the feature is less pronounced during a period when water level is falling than when it is rising, but the fact that the feature is characteristic of both periods is probably more important as a guide to the principal causative factor.

* Changes in water level at any particular site must relate to the water balance but the actual amount of change will depend on the pore space of the substrate. Thus for gain or loss of a given amount of water the level will change more in a compact substrate with little pore

space than one with large pore spaces.* Relating this to the study area a difference is to be expected between the amount of fluctuation of water levels in the large pool networks and in the areas of compact peat dominated by vascular plants which occupy the margins of the study area. An intermediate condition will apply in the case of the surface horizons of Sphagnum dominated areas. This might well explain the pronounced 'gradient' of fluctuation around the margins of the Eastern Pool Network but it does not explain why the amount of change should differ during periods when the water level is rising or falling. A possible reason for this is that whereas during dry periods the amount of water level change is dependent on site factors (e.g. porosity and gradient of the surface) and evapotranspiration conditions, during wet periods the amount which the water level rises is eventually limited by a threshold value beyond which run-off occurs as described in the previous section. The effect of this will be to add to the input side of the water budget in the peripheral regions causing water levels to rise higher in relation to those of the pool system during the same period and this will accentuate the already existing difference due to the threshold level. This effect will be most marked in areas of steepest slope and least in the 'flattest' area adjacent to the pool system. It has been shown in the previous section that the threshold value of the pool systems is very pronounced and that the climatic regime is characterised by a high potential soil water surplus during the winter period.

So it may be that there are several factors contributing to the range of fluctuation at any one site including 'porosity' of the surface peat, position of the site in relation to gradient of the bog surface and position in relation to any extensive areas of pools on the bog surface. It should be noted however that those areas where hydraulic gradient is greater due to gradient of the peat surface, will also be the areas subjected to the greatest influx of run-off from higher regions of the bog thus accentuating the differences which might exist due simply to storage capacity. For example the area of Sphagnum-grown hollows on the spur to the south east of the Eastern Pool Network will be subject to less water level drawdown during dry periods and less influx of runoff at high water levels than adjacent areas where the gradient is steeper.

Difference between range of fluctuation of water level in hummock and hollow

It has already been demonstrated in figure 38 (2-3) that in addition to large scale trends in the amount of water level fluctuation across the study area there also occur local variations related to differences in mictrotopography of the bog surface. In this section the nature of such differences is described in the case of the Western Transect (figure 27). This transect crosses several linear Sphagnum-dominated hollows alternating with firmer ridges. The vegetation is shown in figure 20. Unfortunately in order to illustrate the water levels adequately along a line of this length (100 ft.) it has been necessary to exaggerate the vertical scale considerably with the result that the peat surface profile is much distorted.

In figure 39a water levels are shown for 12 selected occasions out of a total of 37 measurements over the period of study. It can be seen that for any particular 'zone' within the total range the behaviour of the water levels is remarkably consistant despite differences of season. For instance the levels for the two dates 28 June 1966 and 31 March 1966 (nos. 4 and 5 down) remain very consistant throughout the transect and the same applies in the case of levels on 4 April 1966 and 20 August 1966. Several anomalous peaks occur (which are more frequent in the lower horizons) and one station (at 26 ft.) shows pronounced peaks below the level 10 cm. On the whole however the resulting water level curves are remarkably smooth considering the small range of fluctuation and the extreme vertical exaggeration. The more pronounced anomalies represent a maximum rise of only 2 cm. over a distance of several feet.

The surface profile shows three major hollows, in which standing water is exposed at times, which lie at successively lower levels along the transect and which are separated by firm ridges. The greatest water level gradient occurs immediately upslope of each hollow. So although change in water level along the transect is restricted to the ridges (as it must be since at high water levels the hollows have effectively a free water surface) it occurs particularly in the downslope section of the ridge, the water level gradient of the upslope section of each ridge being relatively small. This effect is however less pronounced at depth.

A related feature is that total range of fluctuation differs between adjacent ridges and hollows. In order to illustrate this more clearly a section of the transect has been drawn at only half the vertical exaggeration and in this case (figure 39b) the water levels are of successive occasions during two 3-day periods. The upper group of water levels shows morning and evening levels for 3 days (14-16 August 1966) whilst the lower group shows only one reading for each day during a later period (23-25 September 1966). The lowest recorded level is also shown. Within the largest ridge the maximum difference between the highest and lowest levels of the first group is 7.1 cm. whereas in the main hollow it is only 2.6 cm. This lateral variation in difference between particular water levels is less pronounced at depth. For instance the difference between the level for 25.9.66 and the lowest recorded level shows a variation of only 0.5 cm. between hummock and hollow (6.1 and 5.6 cm.).

It is suggested that this difference is again related to differences in 'storage capacity' of the peat. Since the peat of the ridge is more compact the water level will rise and fall more per unit gain or loss of water than it does in the hollow. The situation is not, however, as simple as that. Since at high levels the water-table shows a pronounced gradient, movement of water must occur and this is substantiated by the very rapid fall (4 cm./day) at high levels in the ridge. The fact that the water level falls much more slowly at lower levels suggests that hydraulic conductivity is also involved, as suggested previously. The hydrological regime of each hummock might then be regarded as analogous to that described by Chapman (1965) in which the lower layers of peat are much less permeable than the surface layers.

Sjors (1948 figure 18) demonstrates a very similar effect, though on a larger scale, on an area where broad ridges and pools are aligned parallel to the contour. Although only two unrelated water-levels are shown (July and September) it is clear that the range of fluctuation is greatest in the ridges and least in the pools. Sjors states that during extreme drought the water practically ceases to flow through the peat of the ridge and then the greater fall in the ridge causes the maximum drop of the water surface to be displaced 'upslope'. He implies that a differential rate of fall occurs even at very low water levels, which has not been found to be the case in the present investigations.

Whatever the cause this difference between the behaviour of the water level in ridge and hollow is extremely significant when considering the process of pattern formation since it provides a mechanism by which the two ecologically distinct environments can be maintained. The hollow is by definition an area characterised by hydrophilous plant species which in general require a consistently high water level. From the evidence of continuous water level records it is to be expected that water levels below about the level of the September values in figure 39b will occur only for relatively brief periods during the summer and that for most of the year the water levels will lie within the influence of the effect described above. The consequences of this effect are not however limited to the hollows and indeed the converse argument may be more significant to an understanding of pattern development since greater fall of water level in the ridge might be expected to facilitate growth of less hydrophilous plants. So that despite the persistant soil moisture surplus characteristic of the climatic regime this process will allow development of less hydrophilous species in certain situations.

The main point is that once differences in surface conditions are initiated this process allows them to be perpetuated.

Relation between water levels and vegetation

In order to determine the extent to which differences in range of fluctuation described in the previous section might be important in influencing the distribution of plant species the relationship between water levels and vegetation within the study area has been examined. The vertical distribution of certain plant species with respect to the water table has already been shown for the Silver Flowe (Ratcliffe and Walker 1956) but in that case the water level was measured on only one occasion at each site and there is no indication of the period over which the data were obtained except that it was during the summer months, during which the variation in water level can be expected to be 20 cm. or more in some situations (site 1 of the present study). So it is considered that these data are not suitable as a basis for the present investigation.

In order to examine the relation between vegetation and water levels the vegetation has been examined in a quadrat 25 cm^2 placed at each recording station with the tube in the centre of quadrat. Each species in the quadrat was rated either as present, or as a physiognomic dominant, a subjective rating indicating a major component of the vegetation irrespective of cover value or form of the plant. Thus Eriophorum angustifolium and Sphagnum papillosum might constitute the physiognomic dominants in a community also containing Drosera rotundifolia which is relatively insignificant as a structural component but which might exceed the cover value of Eriophorum angustifolium. The physiognomic dominants were used as a basis for comparison of water level and vegetation which means that the results exclude the occasional occurrence of a species in situations other than where it is dominant.

The procedure was as follows. Twenty dates were selected on which water levels have been measured in the stations throughout the Eastern Pool Network and along the western transect, a total of 54 sites. The dates were chosen to reflect as far as possible the general nature of water level fluctuations indicated by the histograms in figure 31. This was done by varying the spread of selected water levels so that a larger number occur close to the modal level and progressively fewer readings were selected further away from the mode.

The water levels have then been expressed as the number of records occurring in each 1 cm. division above and below the level of the bryophyte surface for all sites where a particular plant species is dominant. Histograms of these values are shown for each species in relation to the level of the bryophyte surface in figure 40. Distribution of total water levels for all sites is shown in the large histogram to facilitate comparison between species. The number against each species refers to the number of sites where the species is dominant. It should be noted that one site usually has several dominants.

The species are arranged approximately in relation to increasing depth of water level, S. cuspidatum at the tope left representing the wettest condition and Calluna at the bottom right, the driest. The mode of water levels at sites in which S. papillosum is a dominant species lies at about 2 cm. below the level of the bryophyte carpet. For sites dominated by Eriophorum angustifolium the water level mode lies at about 2.5 cm. These are higher than the mode for all sites which lies at 5 cm. below the peat or bryophyte surface. The mode of water levels for sites dominated by Calluna, Eriophorum vaginatum and Sphagnum rubellum lies at 7 - 8 cm. below the peat surface. So there is a difference of only about 5 cm. between the water level most often occurring in the two extreme, i.e. those sites dominated by hydrophilous species (hollows) and those dominated by the relatively less hydrophilous species (hummocks). This is a remarkably small difference. In the previous section it was suggested that lateral differences in rate of fall of water levels in the surface peat might be significant in determining the distribution of plant species and thereby in maintaining the conditions of hummock and hollow. In figure 39b the depth over which the rapid rate of fall in water levels occurs in the ridge is about 7 - 8 cm., the corresponding fall in the hollow for the same period being about 3 cm. Below this level the differential effect is not so pronounced. So during relatively high water levels, which it must be remembered represent a large proportion of total water levels, a local differential effect causes the water level of the ridge to be lowered more than that of the hollow by an amount which in this particular case corresponds very nearly with the figure for difference between the water level mode of sites dominated by 'hummock' or 'hollow' species.

Further comparative studies of water level behaviour in adjacent ridges and hollows is necessary in order to ascertain the precise relationship between differences in fall-rate and height of the water level mode, but the facts outlined above strongly support the suggestion that differential rates of fall are important.

Summary

The main features of the water level fluctuations described in this section can be summarised as follows.

Firstly the water levels in the open pool networks which lie on the flatter crown of the bog show a very narrow range of fluctuation. From the regularity of the peaks it is apparent that the upper limit is related to the point at which run-off occurs across the bog surface. Below a certain level the fall-off curve flattens out considerably and it is suggested that this is due to the low permeability of the peat surrounding the networks.

During the whole study period the maximum range of fluctuation in the two pool networks examined was only 15 cm. (about 6 inches) but the longest dry period was only 2 weeks. From climatic data it can be expected that lower levels than those recorded might be expected during the period May, June and July. On the basis of the actual fall-off curve for site 2 in the Eastern Pool Network over 2 weeks in June 1967 it is shown that a fall-rate of 21.5 cm./month (30 days) is possible for the lower part of the fall-off curve. That is below the threshold of rapid run-off. So together with the more constant upper section of the curve the total annual range of fluctuation can be expected to be about 26.5 cm. (or about 10.5 inches) given a single dry period of one month in June.

During winter the frequency of rainfall together with the low evaporation rates combine to maintain a consistently high water level but throughout the year the frequency of rainfall is very important in determining water level. It is particularly significant that a single day of rain can cause very low water levels (resulting from prolonged dry periods in summer) to be raised to the threshold level related to run-off.

A similar pattern of fluctuation occurs in a Sphagnum-grown hollow a little distance from the crown of the bog but there is consistently a greater range of fluctuation at that site. Increase in range of water level fluctuation away from Eastern Pool Network has been demonstrated also by intermittent records throughout the area and this effect is attributed mainly to differences in storage capacity (which is of course greatest in the open pools and least in compact amorphous peat). It has, however, been shown that run-off also contributes to this effect and this is accentuated by the fact that the pool networks have a sharply defined threshold level above which run-off occurs. In the peripheral parts of the bog differences in range of fluctuation are closely related to gradient of the bog surface, those areas with steepest slopes having the greatest range of fluctuation of water level. This can be attributed to both draw-down during dry periods being greater where hydraulic gradient increases and also to the fact that run-off from higher zones of the bog will be channelled through these areas during wet periods.

Local differences in range of fluctuation between adjacent hummocks and hollows have been demonstrated. On a sloping bog surface the rate of fall in a hummock may be three times that of an adjacent hollow when the water-table is high but at lower levels this difference is insignificant. This has again been attributed to differences in storage capacity, but also indicates that the rate of water movement through the peat of a hummock (hydraulic conductivity) must be considerably greater at high water levels than at lower levels. Comparison of rates of water level fall at site 2 (throughout the year) with potential transpiration give a measure of that component of fall which is unaffected by differences in evapotranspiration and therefore a crude measure of permeability of the lower horizons relative to the surface layers. A fall rate of 10 cm./month is given for the lower horizons which contrasts with the fall rate of 4 cm./ day in the upper horizons.

It has been shown that the modal water level depth below the bryophyte surface at sites dominated by plants characteristic of pools and those characteristic of hummocks differs by only 5 cm. and it is suggested that the differences in water level fluctuation due to storage capacity are sufficient to accentuate differences in vegetation between pool and hummock once these are established.

WATER LEVEL MEASUREMENT

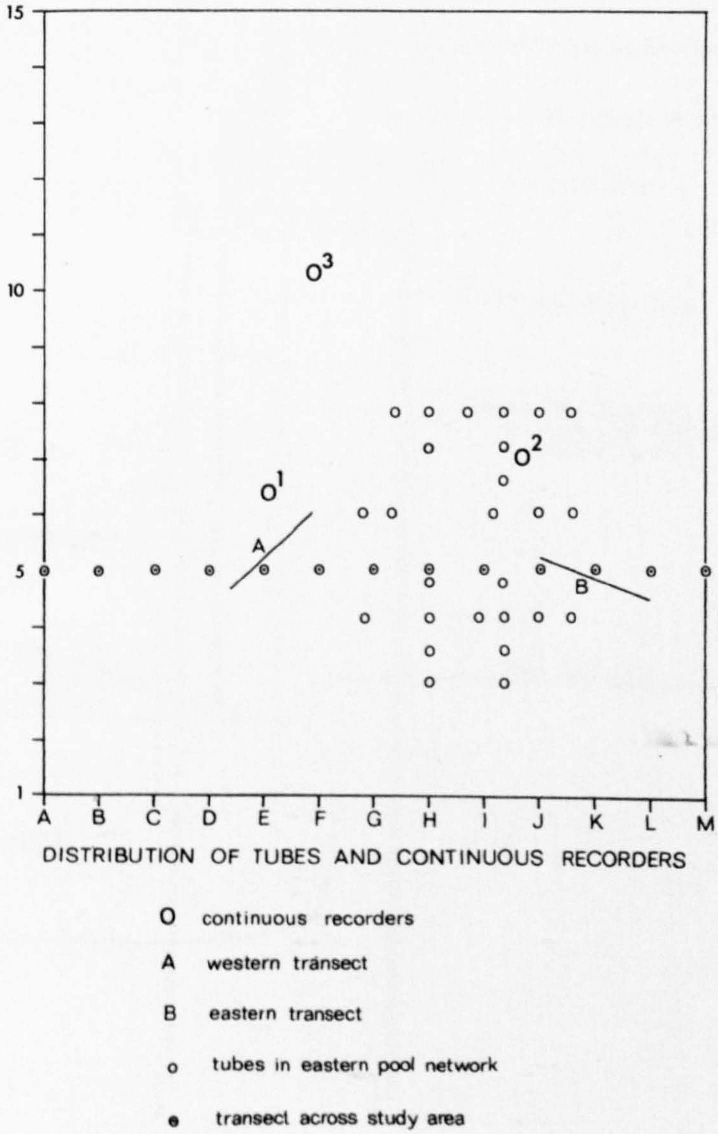


FIG 27

WATER LEVEL RECORDER

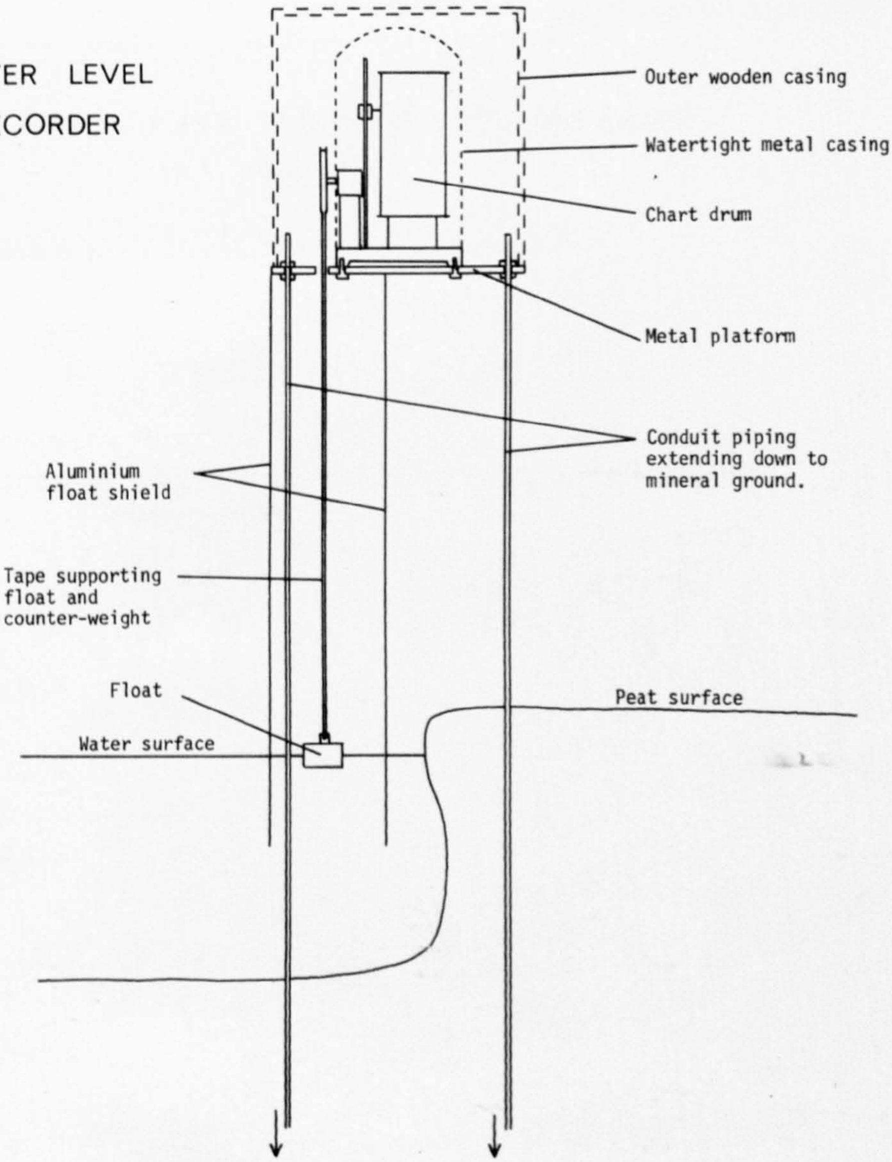


FIG 28

Selected sections of continuous water level records from sites 1 and 2

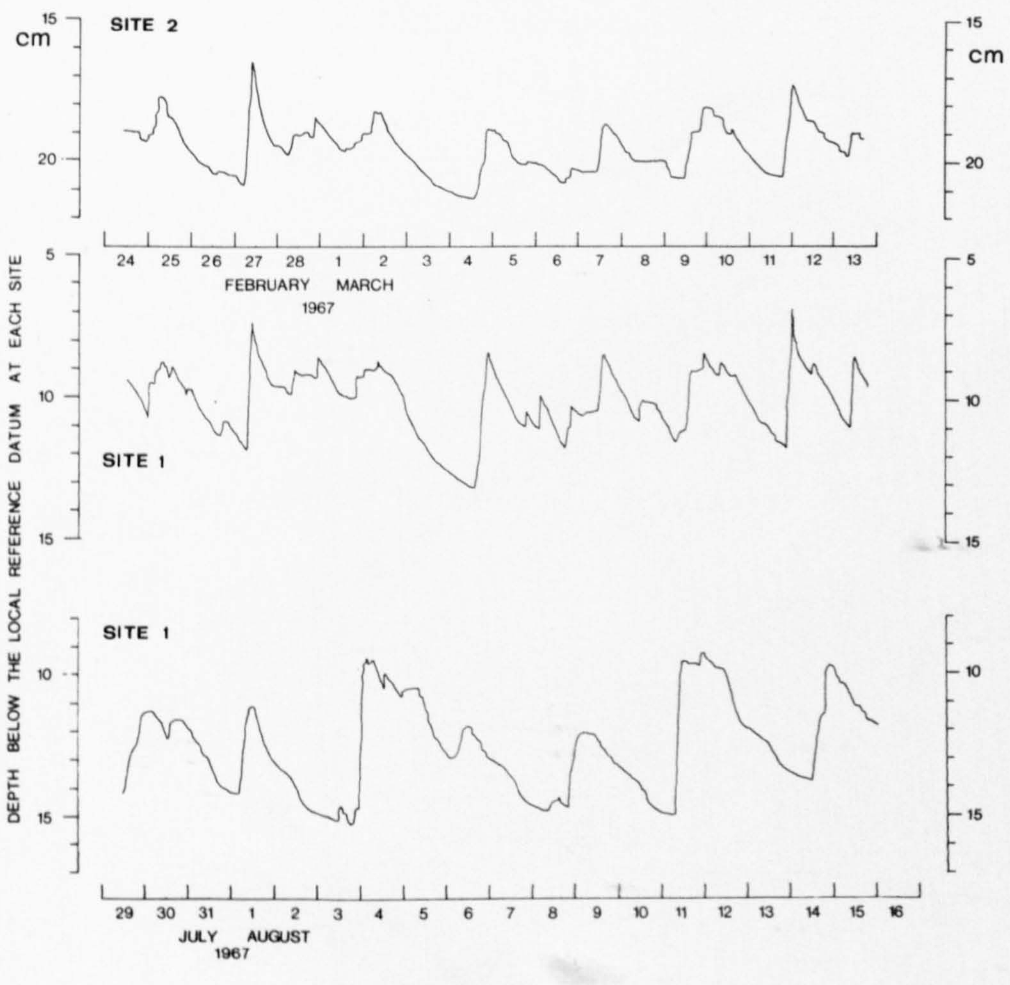
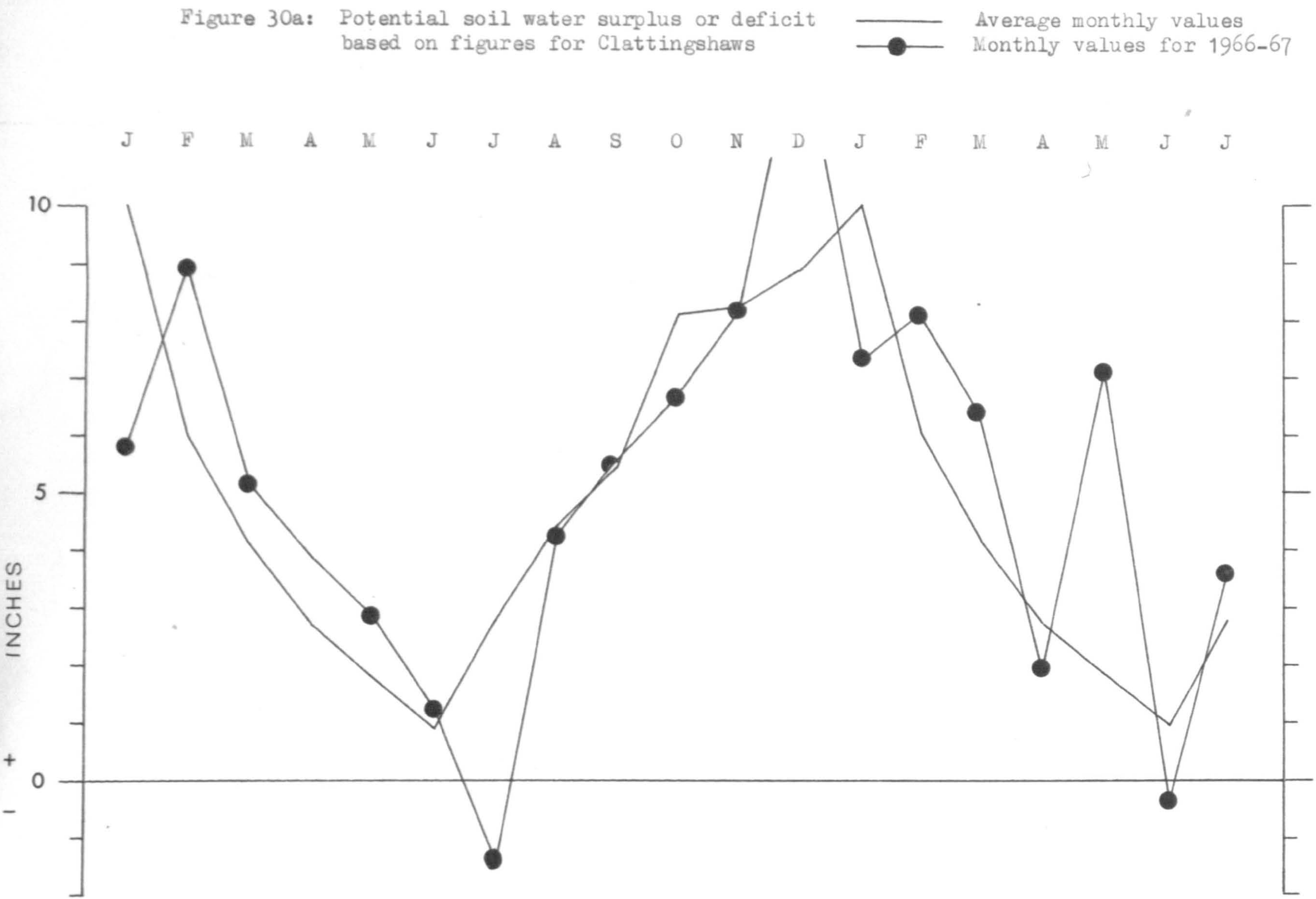
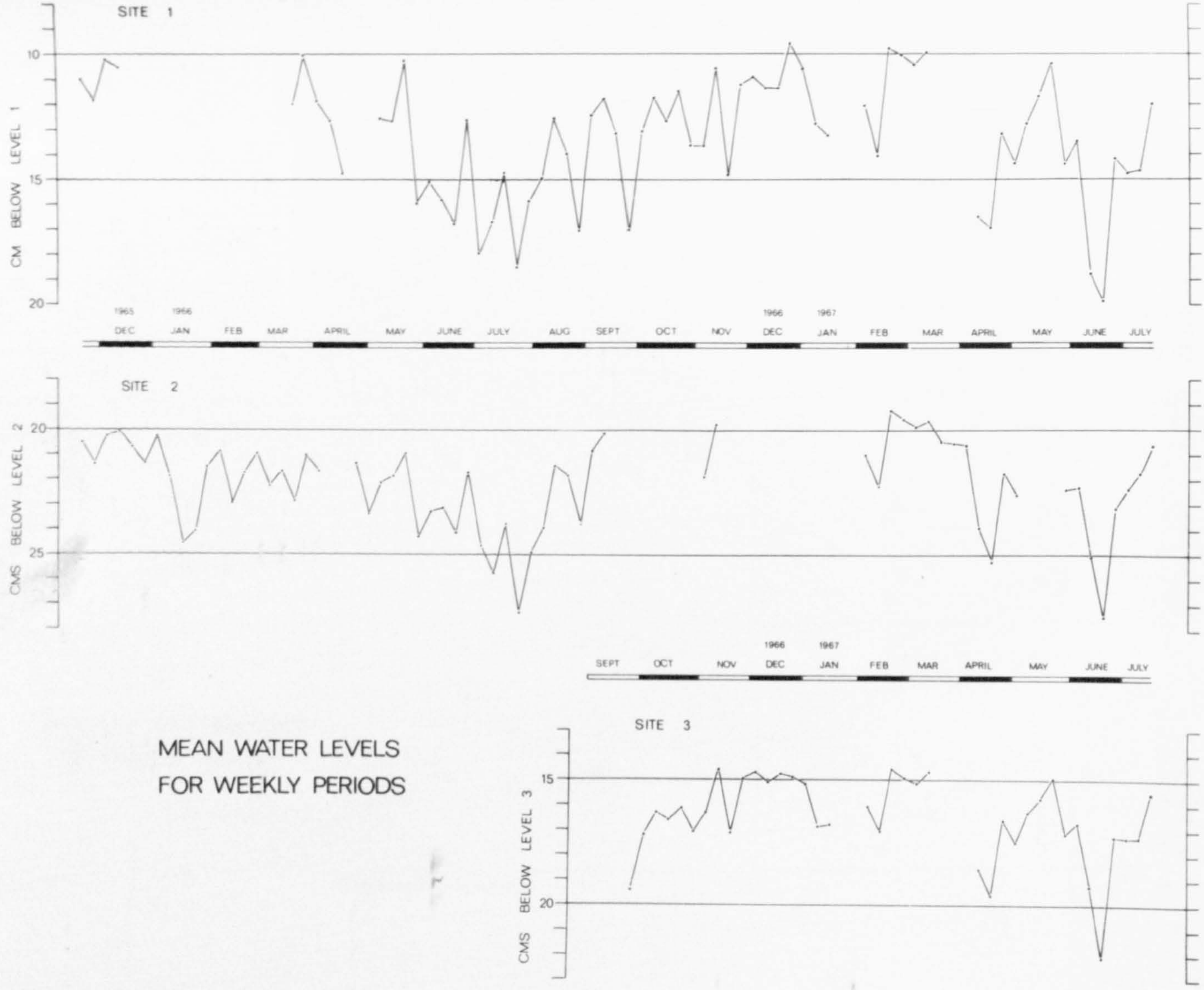


FIG 29

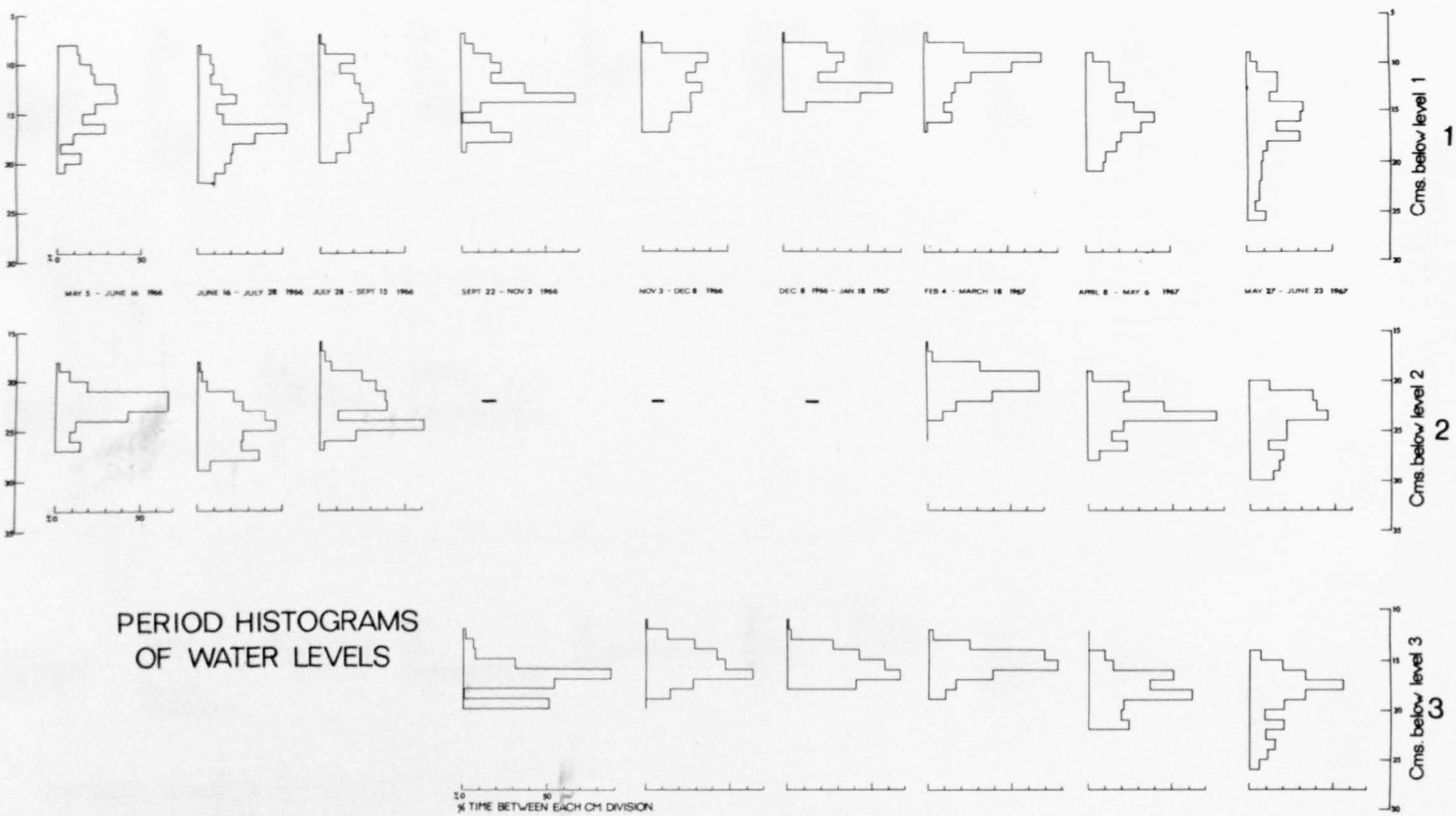
Figure 30a: Potential soil water surplus or deficit based on figures for Clattingshaws





MEAN WATER LEVELS
FOR WEEKLY PERIODS

FIG. 30 b.



PERIOD HISTOGRAMS
OF WATER LEVELS

FIG 31

WEEKLY RANGES OF WATER LEVELS
for the period April 8 to June 24 1967

FIG. 32

Water level fall during dry periods

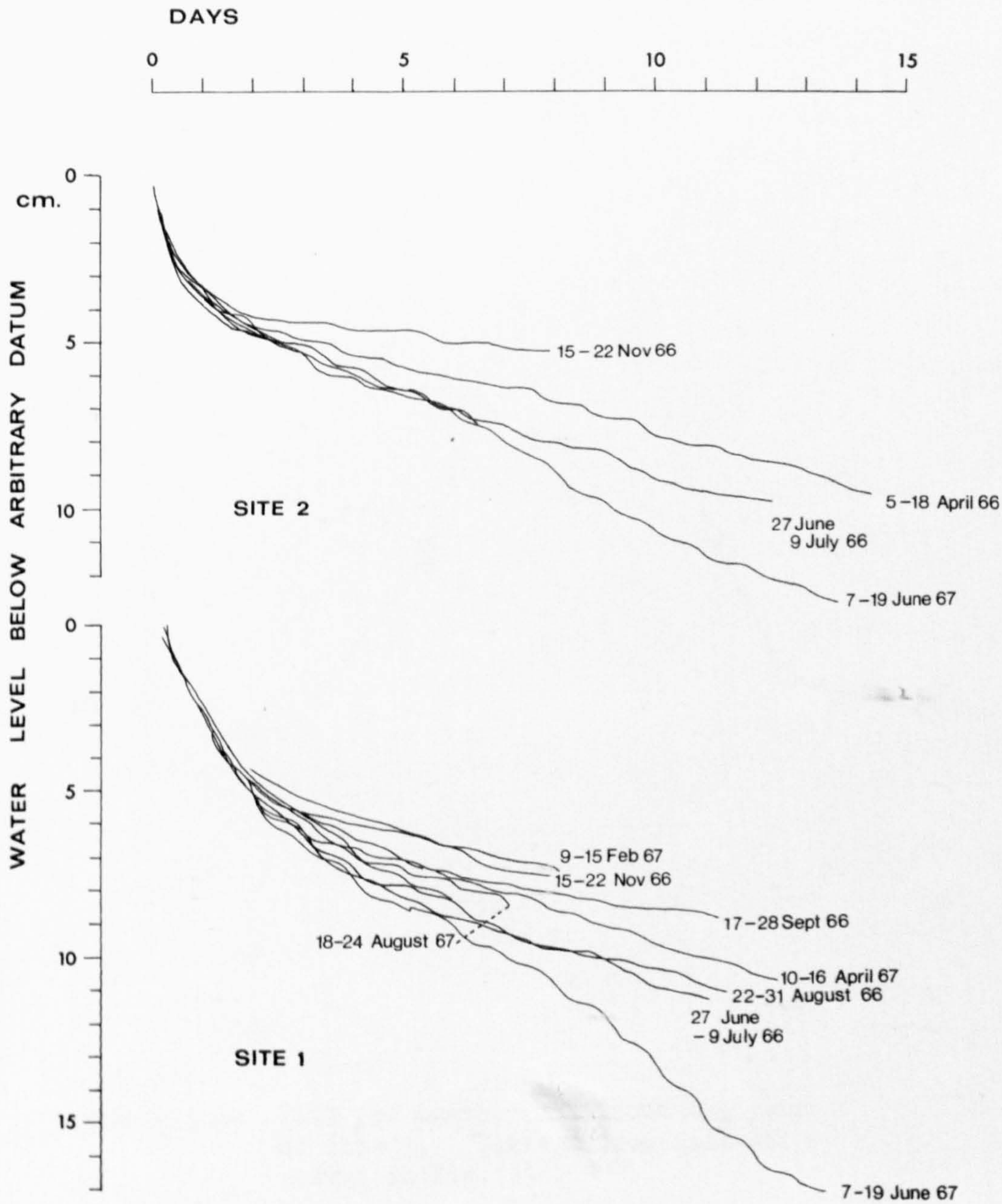


FIG. 33 a

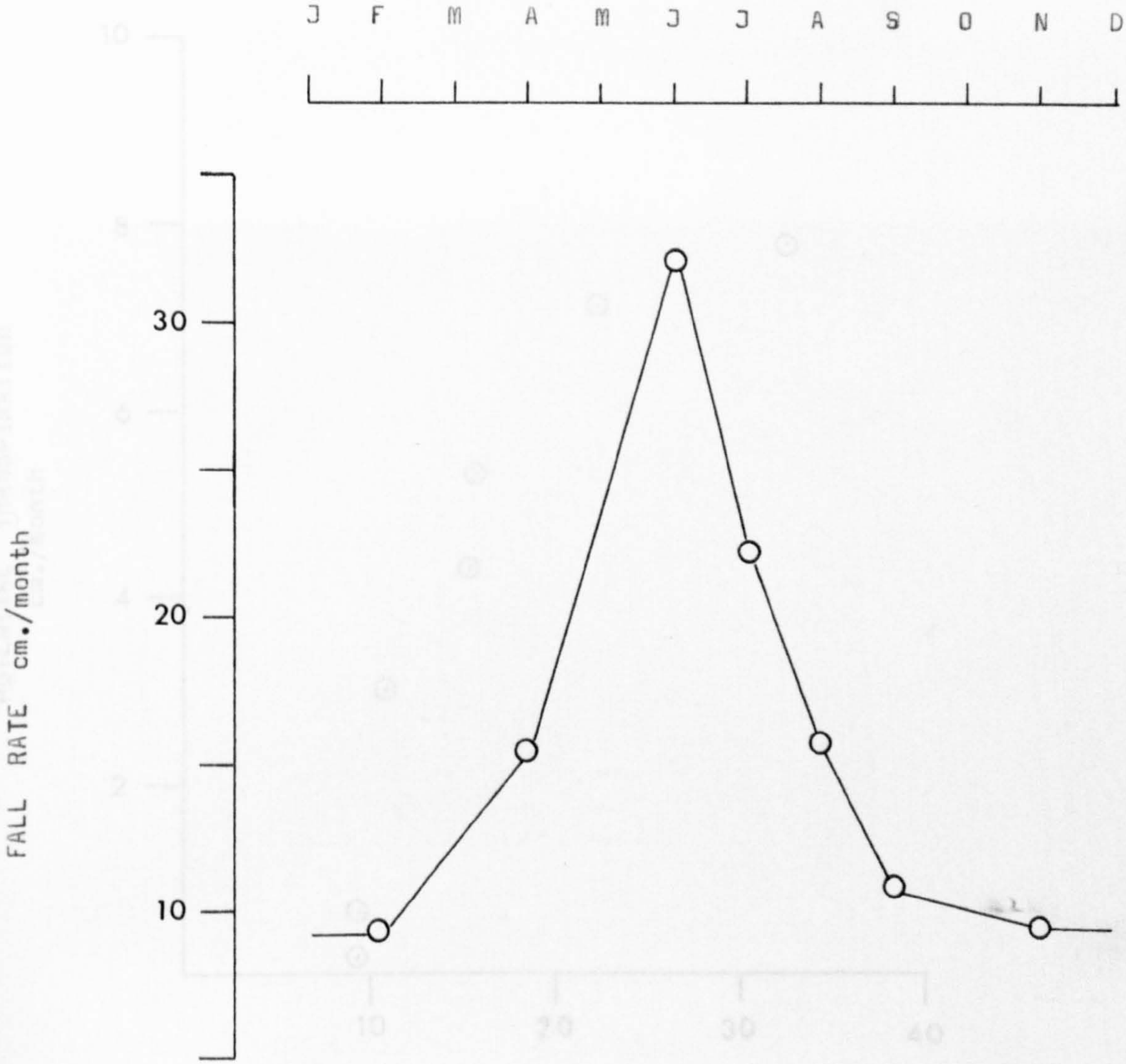


Figure 33b: Fall per month, throughout the year at site 1. Derived from fall-off curves in fig. 33a.

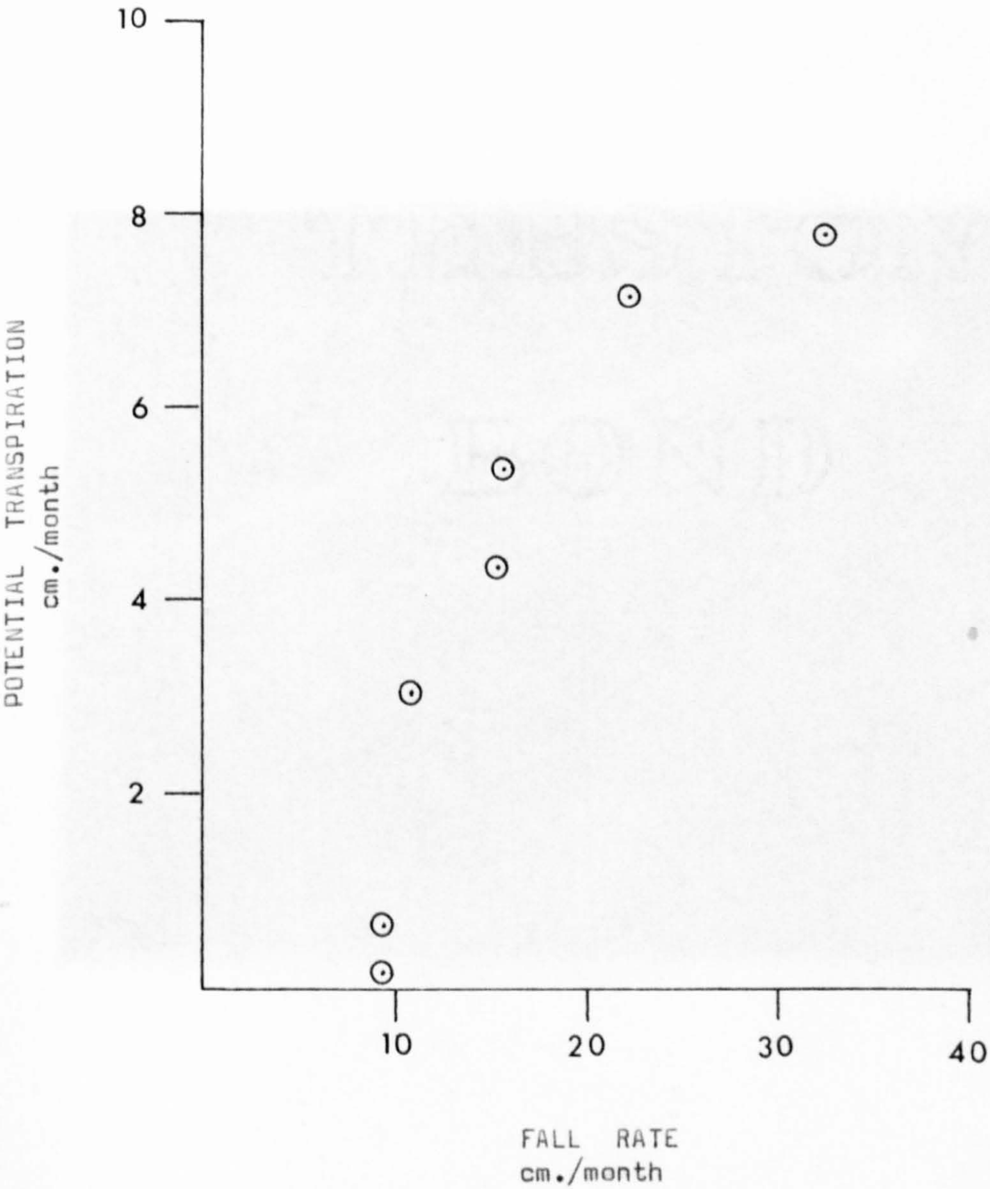


Figure 33c: Relationship between monthly potential transpiration and water level fall rate.

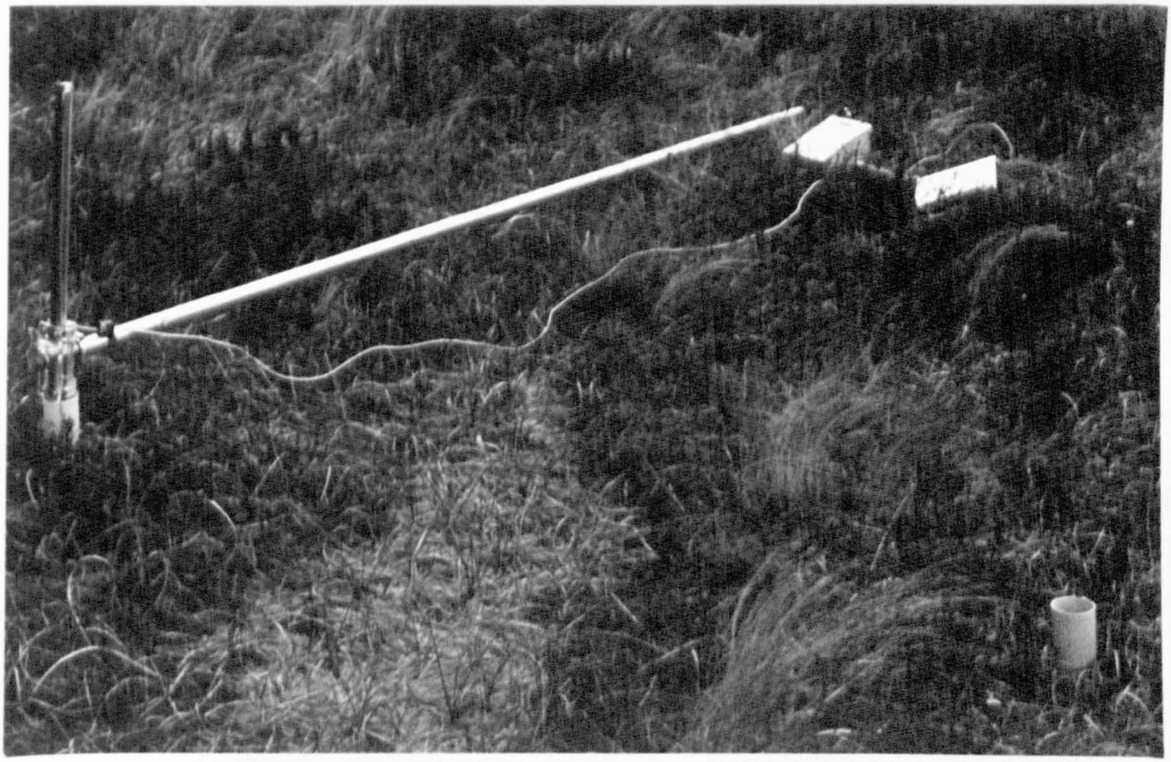


Figure 34. Special instrument for recording water levels in 2" diameter tube-wells from a distance. This enables accurate measurements to be made without proximity of the observer influencing the local water table.

Figure 35. Detail of instrument shown in figure 34 to show the body resting on the rim of a tube-well and the movable arm descending into the tube (operated by a knob at the other end of the horizontal aluminium support).

CIRCUIT DIAGRAM OF WATER LEVEL RECORDER

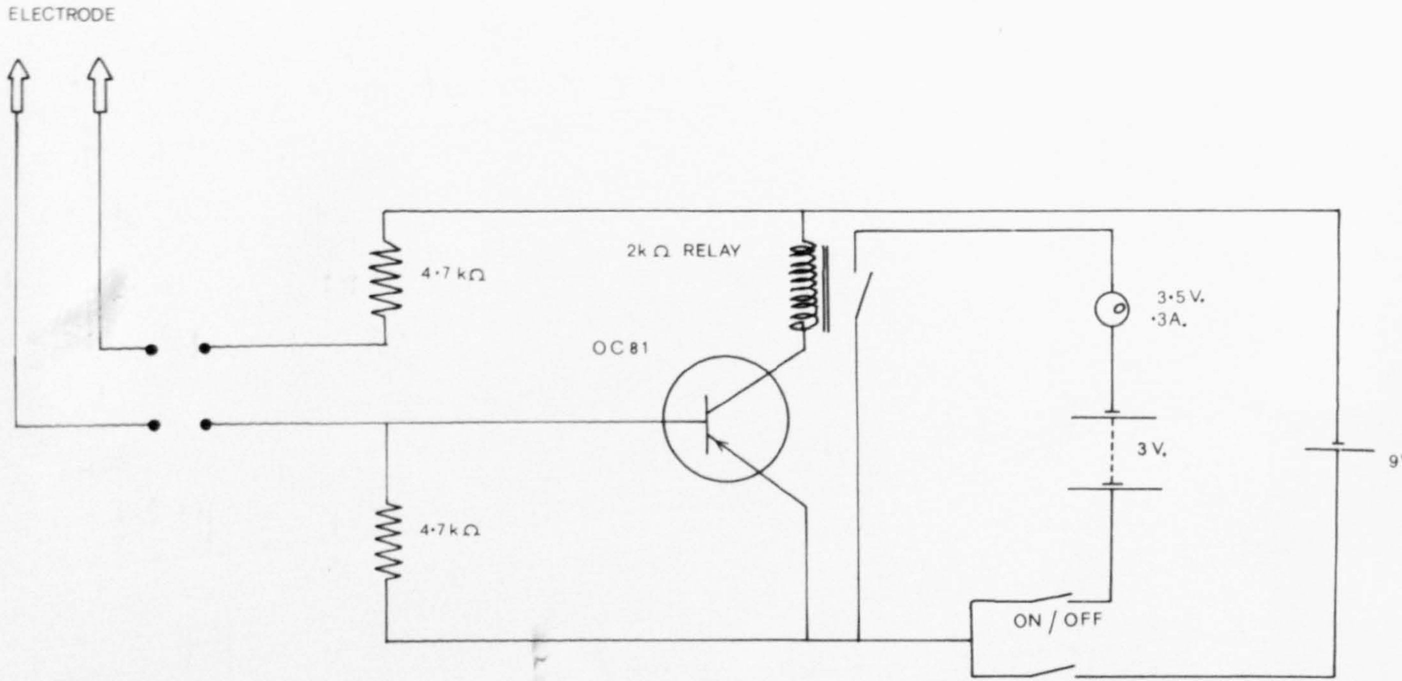


FIG 36

RANGE OF WATER LEVEL FLUCTUATION IN THE REGION OF THE EASTERN POOL NETWORK

———— Lines representing equal ranges of water level fluctuation : at 1 cm. intervals

- - - - - - Surface contours at 10 cm. intervals. (level at 2m. is equivalent to the arbitrary datum used on other maps)

o Sites of water level records

50 feet

25 m.

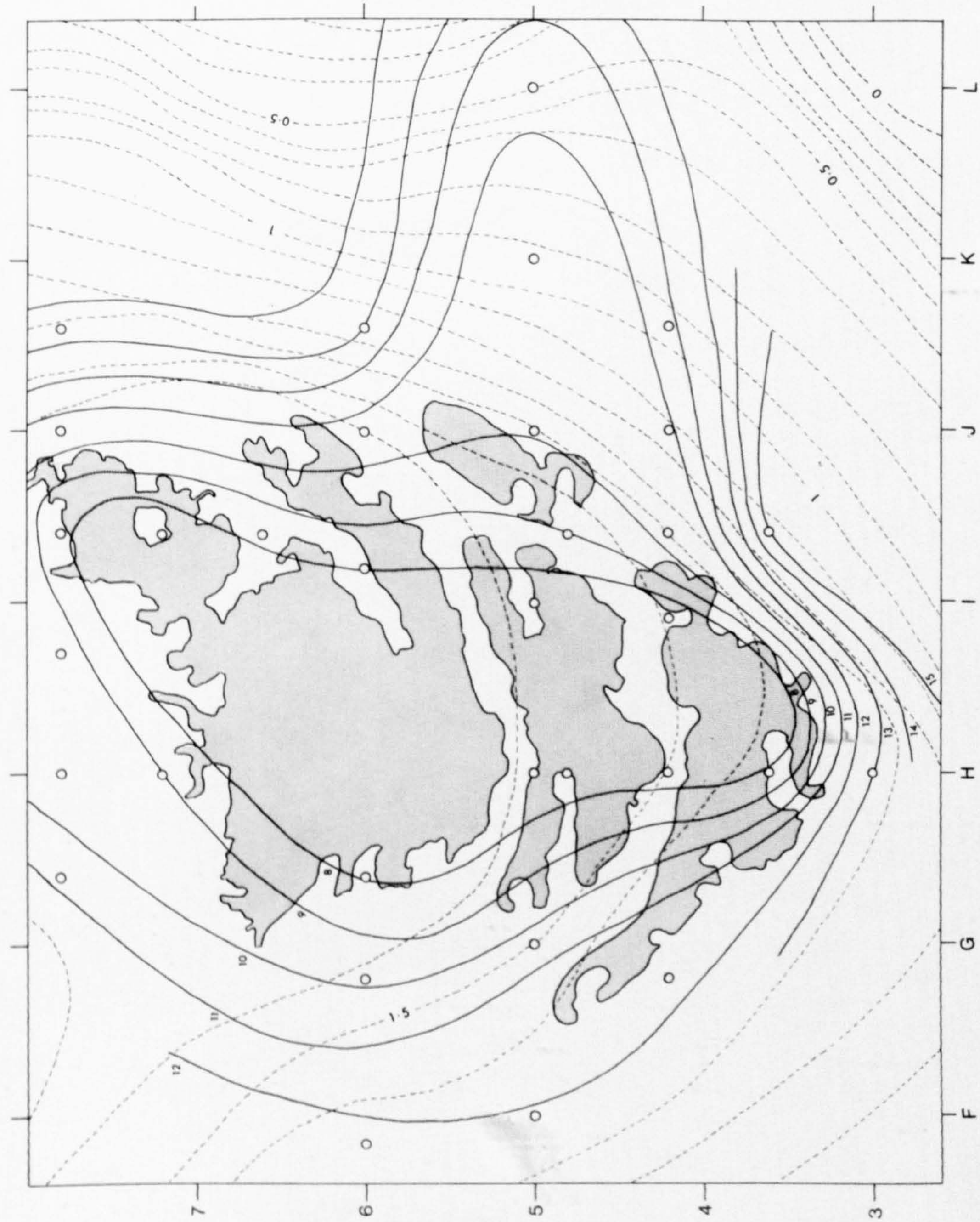
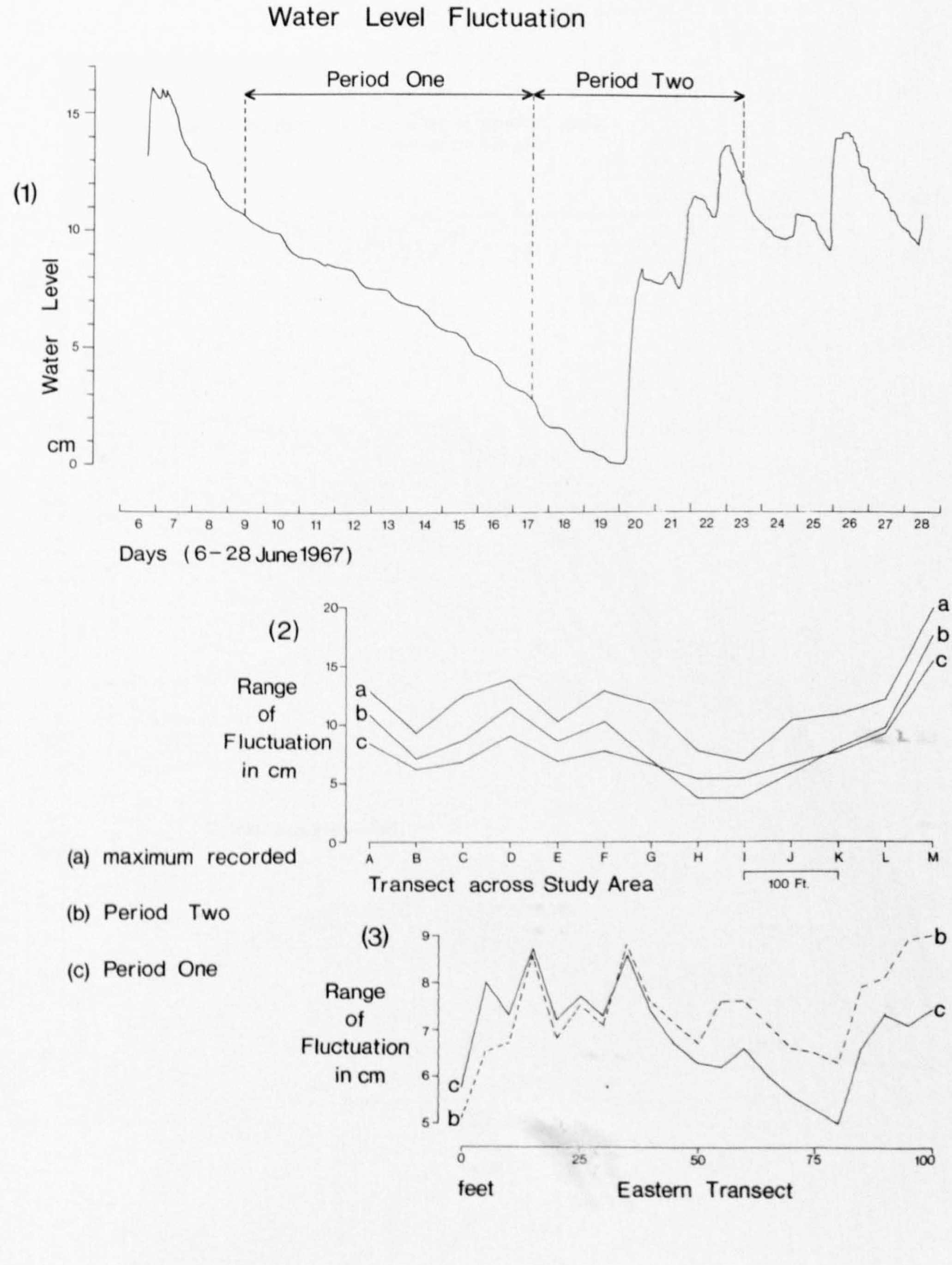


FIG 37

Figure 38: Range of Water Level Fluctuation

1. Trace of water level fluctuations from continuous recorder at site 1 to show the behaviour of the water table over the periods referred to in the lower diagrams.
2. Diagram to show the range of water level fluctuation along a transect across the whole study area (stations 50 ft. apart). The three lines a, b and c refer to the following periods:
   (a) Total range of fluctuation recorded over 18 months of intermittent records.
   (b) Difference between water levels at beginning and end of period 2 above. During this period the water level was progressively raised.
   (c) Difference in water level at beginning and end of period 1 above. During this period the water level showed a gradual fall.
3. Diagram to show the range of fluctuation for periods 1 and 2 along a short transect line (eastern transect) approximately equivalent to the section J - L of the longer transect shown above.



Water Level Fluctuation
(1)
Period One
Period Two
Water Level
cm
15
10
5
0
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Days (6-28 June 1967)
(2)
Range of Fluctuation in cm
20
15
10
5
0
a
b
c
A B C D E F G H I J K L M
Transect across Study Area
100 Ft.
(a) maximum recorded
(b) Period Two
(c) Period One
(3)
Range of Fluctuation in cm
9
8
7
6
5
0 25 50 75 100
feet
Eastern Transect

FIG. 38

Part Of Western Transect
Showing Successive Fall In Water Levels
During Two Periods

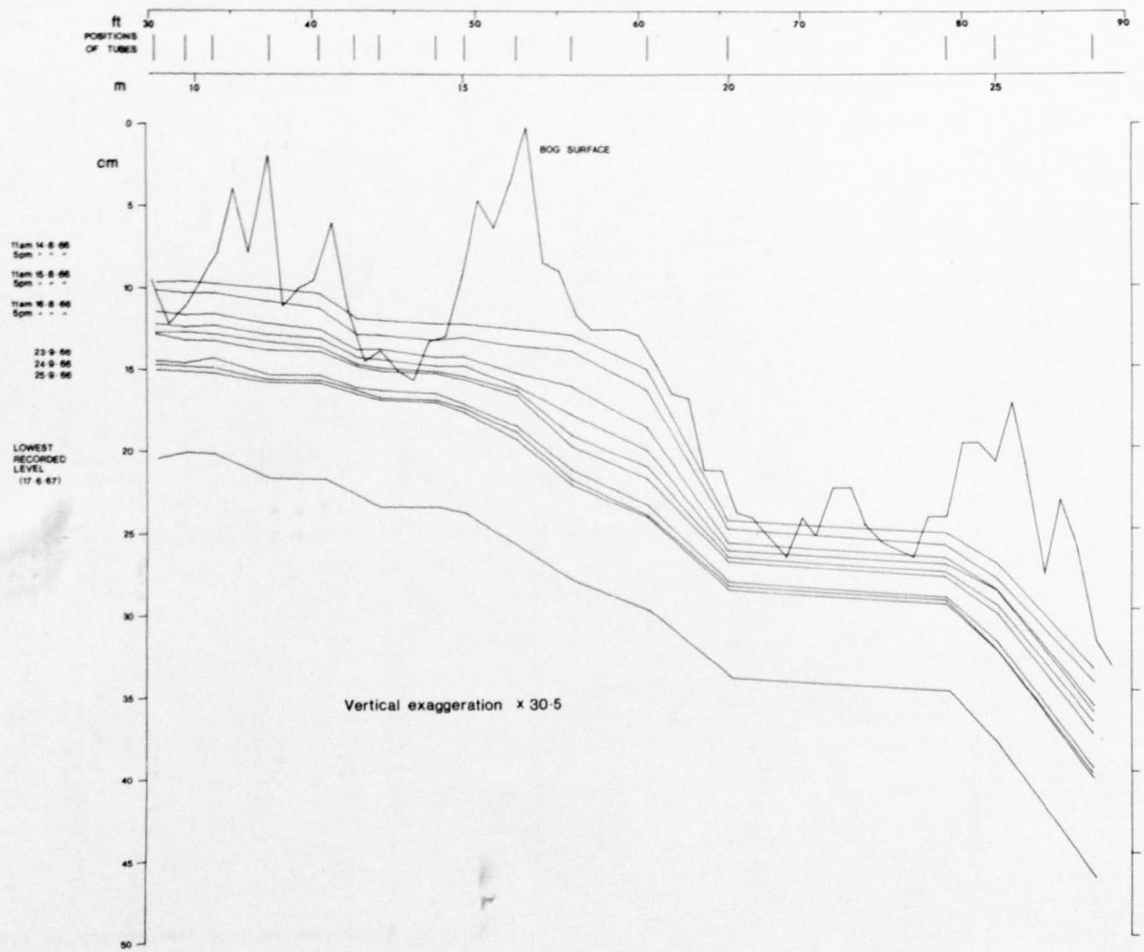
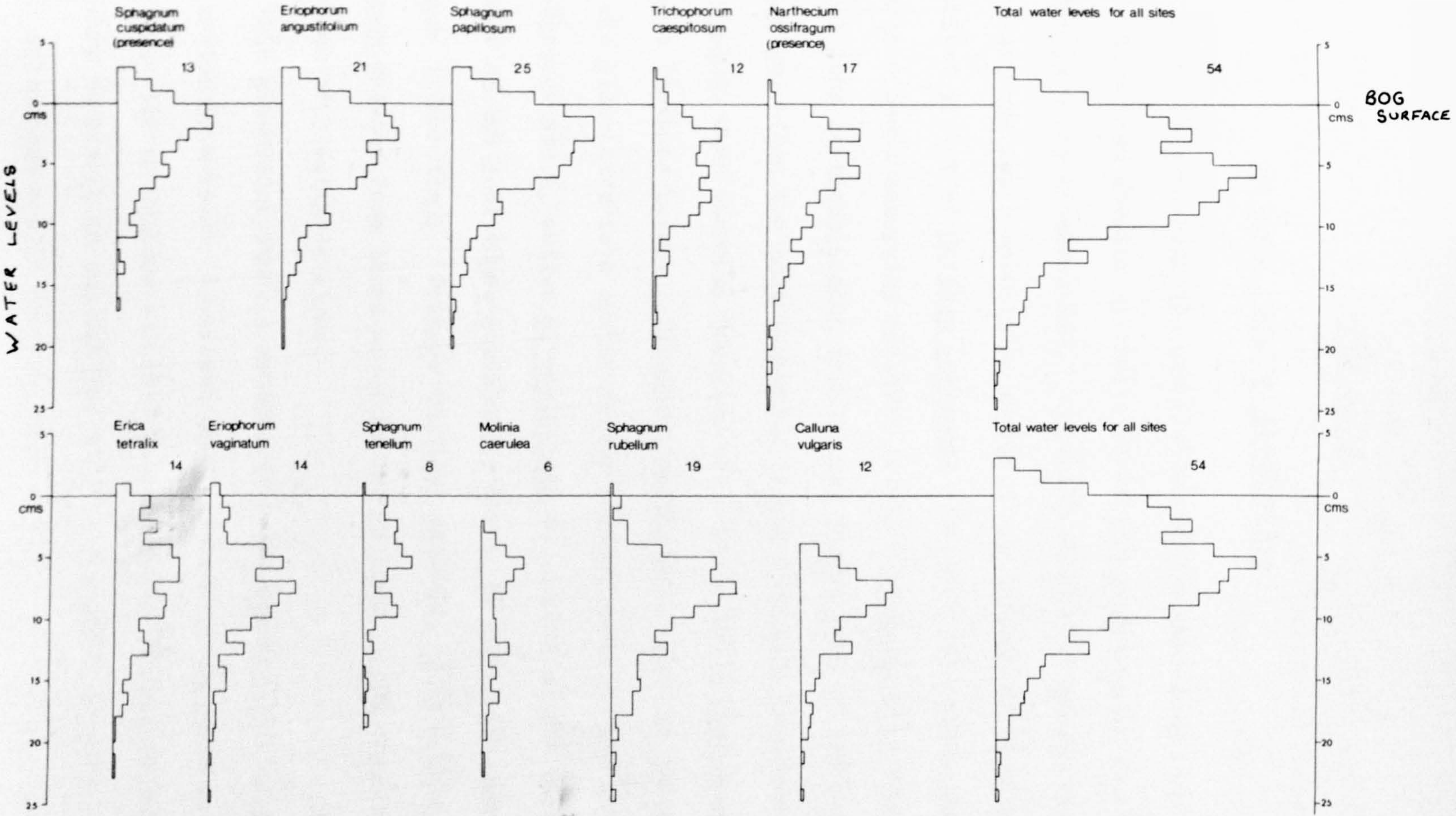


FIG. 39b



RELATIONSHIP BETWEEN PLANT SPECIES AND WATER LEVELS

FIG. 40

SECTION 5

SPHAGNUM GROWTH EXPERIMENTS

It can be seen from the description of the open pool networks on the study area that aquatic or semi-aquatic Sphagnum species are considerably restricted in their distribution. The main centres of growth are at the ends of elongated pools where they appear to be associated with accumulations of wind-blown litter of Molinia caerulea. In such situations three species are usually present occupying adjacent zones. S. papillosum occupies a peripheral zone continuous with that of the firmer peat of the pool edge; S. cuspidatum, often the most extensive, forms a central zone and S. subsecundum var. inundatum, when present, occupies the edge of the Sphagnum-grown area adjacent to the open water. Elsewhere in the pool networks the aquatic species are restricted to a sparse fringe growing close to the water surface on the edges of pools, whilst S. papillosum is present almost throughout the systems on the pool edges immediately above, or partially subject to, water level fluctuation. Perhaps the most striking feature is the absence of Sphagnum species from those areas of the overflow sites which are dominated by a surface of gelatinous algae.

This absence of aquatic sphagna from the deeper parts of the pool systems contrasts with the luxuriant development of those same species in many discrete linear hollows situated in peripheral regions of the bog. It is therefore pertinent to the subject of pool formation to consider why such potential colonisers are in fact absent. Since the stratigraphical investigations described in section 3 support the contention that development of pool networks has involved some degree of lateral extension and coalescing of pools it is clear that such a process must involve some mechanism by which colonisation of open water pools by aquatic Sphagna is prevented. There are indications that certain areas of open pools can be colonised by aquatic Sphagna in particular conditions, notably where Molinia litter has accumulated. Here the Sphagnum 'raft' appears to be lying on the litter and it is feasible that such support is necessary for colonisation of deep pools. In contrast however the shallow overflow sites, where Sphagnum growth would be most likely to occur if support near to the water surface were necessary, show a paucity of Sphagnum growth.

Two field experiments were carried out in order to compare the performance of both S. papillosum and S. cuspidatum in conditions where they are generally absent and in situations where both species normally grow well. Furthermore a number of laboratory experiments were carried out under controlled conditions to investigate the performance of those same species under differing conditions of water depth and exposure.

Field Experiment 1

Specimens of S. papillosum and S. cuspidatum were collected from two pools on the study area. Individual shoots were prepared, each of 10 cm. stem length and with a healthy capitulum. These were then put into groups of 10 shoots secured with plastic covered wire. The bundles of plants were placed in growing conditions on 3 April 1966 as follows:-

(a) 10 groups of each species on an overflow site with apices about 1 cm. above the bare peat surface and the remainder of the plants buried in the peat.

(b) 5 groups of S. cuspidatum placed in a large open (unvegetated) pool, each group being supported close to the surface by a 2" diameter plastic tube (at such a height that the apices were unlikely to be exposed).

(c) 5 groups of S. cuspidatum lying on the bottom of a large unvegetated pool at a depth of about 45 cm., on Molinia caerulea litter. The groups were held in place by cords anchored to stakes on the bottom.

(d) 10 groups of each species in a large hollow dominated by S. papillosum and S. cuspidatum. Apices at about the same height as those of the adjacent S. papillosum when planted.

In order to measure growth one bundle of shoots of each species was removed from each condition on subsequent occasions, at about monthly intervals. Shoot length was measured and the average for each group of 10 recorded. Results are shown in figure 41.

In the case of S. cuspidatum the striking feature is the death and decay of both groups of plants in the open pool condition during August whilst the groups situated in both the overflow site and the S. papillosum hollow continued to grow through the summer period. During the following spring the remaining groups in the overflow site showed very little growth whilst the groups in the S. papillosum hollow continued to grow vigorously. Initially the groups in the pools situations showed greater growth increments than those in the other sites.

S. papillosum showed no significant difference in growth rate between the two sites, indeed the graph shows a remarkable degree of consistency with rapid growth during August in each case.

It is relevant to mention observations made on the various sites at the time of sampling. Death of S. cuspidatum coincided with a luxuriant growth of filamentous algae, both Batrachospermum moniliforme and Zygogonium spp., which coated all solid objects in the water including the plants concerned. This gradually increased in intensity during July and August (see figure 42b). Whilst it is not proven it is suspected that death was in some way related to this phenomenon. The samples collected from the open water in July were relatively free from algae but those collected in August showed a coating of algae and the plants were covered with a layer of gelatinous material. A photograph of a S. cuspidatum leaf coated with algal filaments is shown in figure 42a. Unfortunately insufficient groups had been placed in this habitat so it was not possible to investigate whether the plants so affected would recover. However it appeared unlikely since most of the specimens lost their chlorophyll and were rapidly disintegrating.

During the winter period it was noted that the samples of S. cuspidatum from the overflow site were becoming covered by a layer of gelatinous algae (and also to a lesser extent by filamentous algae). This layer gradually increased and the successive samples were noticeably darker green. It may well be that the decline in the growth rate of S. cuspidatum on this site during the spring is related to the presence of this layer of algae.

Laboratory Experiments

Specimens of S. papillosum and S. cuspidatum were grown in a growth room under controlled conditions of light and temperature but in varying conditions of exposure and immersion of the shoot apices. Fifty plants of each species were selected and cut so that stem length including capitulum was 5 cm. These were washed for a day to remove any algae and then placed in growing conditions. Ten shoots of each species were placed in each of five beakers where they were supported by a peripheral framework of vertical glass rods. Water (from the same pool from which the plants were collected) was filtered and the beakers were filled in varying amounts as follows:-

A: Shoot apices 4 cm. above water surface

B: Shoot apices 2 cm. above water surface

C: Shoot apices about level with water surface

D: Shoot apices 2 cm below water surface

E: Shoot apices 4 cm. below water surface

A cover of polythene was placed over the beaker to maintain maximum humidity since no regulation of humidity was possible in the growth room concerned. Temperature fluctuated between 15° and 20°C but was mainly 17 - 18°C. Water in the beakers was renewed every fortnight from filtered water kept at 0 - 5°C. Growth of the plants is shown in figure 43, the average shoot length of the ten plants in each group being plotted. After about 5 weeks the totally immersed S. cuspidatum showed signs of chlorophyll loss and by the end of the seventh week all the plants had died and were disintegrating. In spite of the fact that measurements of shoot length were made very infrequently, the results show that the plants with their apices above the surface continued to grow whilst those totally immersed did not. Group B produced rather small branches but did not appear to be unhealthy. S. papillosum shows a direct relationship between stem elongation and the degree of immersion, those plants with their apices 4 cm. above the water showing greatest growth. All groups continued to grow to some extent and none appeared unhealthy.

Laboratory Experiment 2

The experiment was repeated, making measurements of shoot length more frequently but with fewer examples of different water level conditions. An additional factor was investigated in the case of Sphagnum cuspidatum. The death of all the S. cuspidatum plants growing totally immersed was unexpected but it was realised that the conditions were very different from those which the plants would experience when immersed in a pool. Perhaps the most important difference is that in the field the water is in motion and this will help to maintain a supply of nutrients and gases to the plants. In order to simulate these conditions more closely replicate beakers in which air was continuously bubbled through the water were included in the second experiment in the case of S. cuspidatum.

In the case of S. papillosum two replicates each containing ten shoots were set up, in each of the conditions:

(1) Apices 2 cms. above the water surface

(2) Apices 2 cms. below the water surface

The results are shown in figure 44.

It is clear that the replicates in each condition behaved in a similar manner initially and that the growth rate was distinctly greater in the exposed shoots. The subsequent greater spread of the replicates does not in fact reflect the true performance of the plants which is better illustrated by figure 45. The totally immersed plants gradually increased in length (particularly during the latter period) but there was an almost total absence of branch development. The experiment was terminated since shoot length was no longer a meaningful measure of performance.

In the case of S. cuspidatum 4 replicates were set up, each containing 10 shoots, in each of the conditions.

(1) Apices 2 cm. above the water surface

(2) Apices 2 cm. below the water surface

In addition 2 further replicates with the apices 2 cm. below the water level were set up and air was continuously bubbled through the water. Results are shown in figure 46.

The difference in performance exhibited by the S. cuspidatum shoots of groups one and two is similar to that shown in the first experiment in that all the totally submerged shoots died whilst the exposed shoots continued to grow. The experiment was terminated owing to the extremely brittle nature of the elongated exposed shoots which could no longer support their own weight. The performance of group 3 in which air was bubbled through is of interest since it shows that totally submerged plants will continue to grow under certain conditions. The reason for this improved performance cannot definitely be attributed to replenishment of an oxygen or carbon dioxide deficiency. It could simply be a physical effect of disturbance. However in view of the fact that the exposed shoots in contact with air generally survive and those totally immersed eventually die it seems probable that the group 3 shoots are maintained by replenishment of either the dissolved oxygen or the carbon dioxide in the water.

Field Experiment Two

In view of the results of the first field experiment it was considered that a similar experiment should be carried out over a second summer period. In addition to placing S. papillosum in an overflow site and in a S. papillosum 'lawn' further groups of plants were placed in the centre of a hollow lying prostrate. These groups were almost continuously covered by water. Eight groups (of ten plants each) were placed in each of the three conditions.

S. cuspidatum was grown in four conditions, viz: overflow site, S. papillosum lawn, in a deep pool but supported close to the surface (and occasionally exposed) and in the same pool at a depth sufficient to ensure that no exposure occurred. (Reference was made to continuous water level records which were produced for the same pool.) Unfortunately one of the tubes together with the last group of shoots growing close to the surface was stolen. However the two groups of plants in the pool had previously behaved in a similar manner. Results are shown in figure 47.

No decline of the submerged S. cuspidatum comparable with that of the previous August occurred, indeed the shoots in the pool showed better growth than in the other conditions, which was the initial tendency during the first experiment. S. cuspidatum shoots on the overflow site again showed progressive development of a layer of gelatinous algae and the final group were disintegrating, the leaves and branches simply dispersing when the plant was immersed in water. It is of interest that no significant development of filamentous algae occurred in the deep pool during the course of this experiment. The quantity of algae was not measured in any objective way but it was noted that the plants growing in the pool did not become 'slimy' as in the first experiment and there was no growth of filamentous algae on them.

The results for S. papillosum again show a remarkable consistency between those of the overflow site and the S. papillosum 'lawn'. The groups growing prostrate in the pool show a strikingly higher growth rate, (three times morein 9 months). Presumably this is a reflection of the greater surface area exposed and consequently higher rate of photosynthesis per shoot. (This may well be important in the progressive colonisation of shallow pools by lateral growth of the Sphagnum papillosum shoots.)

Discussion

A number of points emerge from these experiments which are relevant to the distribution of aquatic and semi-aquatic Sphagna in the deep pools.

1. S. papillosum shows no obvious difference in growth rate between the S. papillosum lawn where it is normally healthy and the overflow site with gelatinous algae where it is normally absent or not well developed.
2. Whereas the growth rate of S. papillosum on overflow sites does not appear to be impeded by the periodic development of gelatinous algae, retardation of the growth rate of S. cuspidatum in similar situations may be due to this phenomenon.
3. The performance of S. cuspidatum supported in deep pools was inconsistent over the two summer periods concerned. Shoots of this species will grow successfully in the pools and it does not appear to make any difference if the apices are periodically exposed or not. Under certain conditions, associated with the development of a 'bloom' of filamentous algae, the S. cuspidatum growing in deep pools dies and disintegrates.
4. S. cuspidatum shoots die when grown totally immersed in the limited artificial environment described. The shoots will however grow successfully if the water is aerated. This may be due simply to disturbance of the water as air is bubbled through, or it could be that aeration is replenishing any oxygen or carbon dioxide deficiency.

The results support the contention that the pools in their present stage of development are not a suitable habitat for successful colonisation by Sphagnum cuspidatum because the periodic luxuriant growth of filamentous algae in some way impedes the growth of S. cuspidatum shoots and indeed appears to result in decay of Sphagnum shoots in contact with the algae. Whether death of the submerged Sphagnum cuspidatum shoots is brought about by direct contact with algae or by depletion of dissolved carbon dioxide is not known. It has been observed that when death and decay of submerged S. cuspidatum occurs naturally (in those limited areas of pools where some degree of colonisation has occurred) it is restricted to the outermost zones of the Sphagnum raft adjacent to the open water where there is a luxuriant growth of filamentous algae. In these circumstances the inner parts of the raft are not subject to such a vigorous growth of algae.

Sjors (1961, 1963, 1965) has suggested that the presence of algae in ombrotrophic bog pools (and in flarks in minerotrophic peatland) limits the development of peat-forming mosses (Sphagna) with the result that peat formation in such situations is retarded. He does not however produce any supporting experimental evidence. The above results and observations are compatible with this suggestion and whilst superficial they do nevertheless indicate that an investigation of competition between aquatic Sphagna and algae might be a rewarding line of research in the ecology of bog pool formation.

The performance of S. cuspidatum and S. papillosum on the overflow sites might be due to the different morphology of these species in that the S. cuspidatum shoots, being unable to support themselves, are more likely to be covered by the layer of gelatinous algae covering the peat surface. This does not explain why S. papillosum is normally only sparsely developed on such sites. The experiment indicates that it grows successfully when shoots are planted. It may be that colonisation by protonema or lateral growth of leafy shoots is less successful. Again the results point to further lines of research which may be more profitable.

FIELD EXPERIMENT ONE

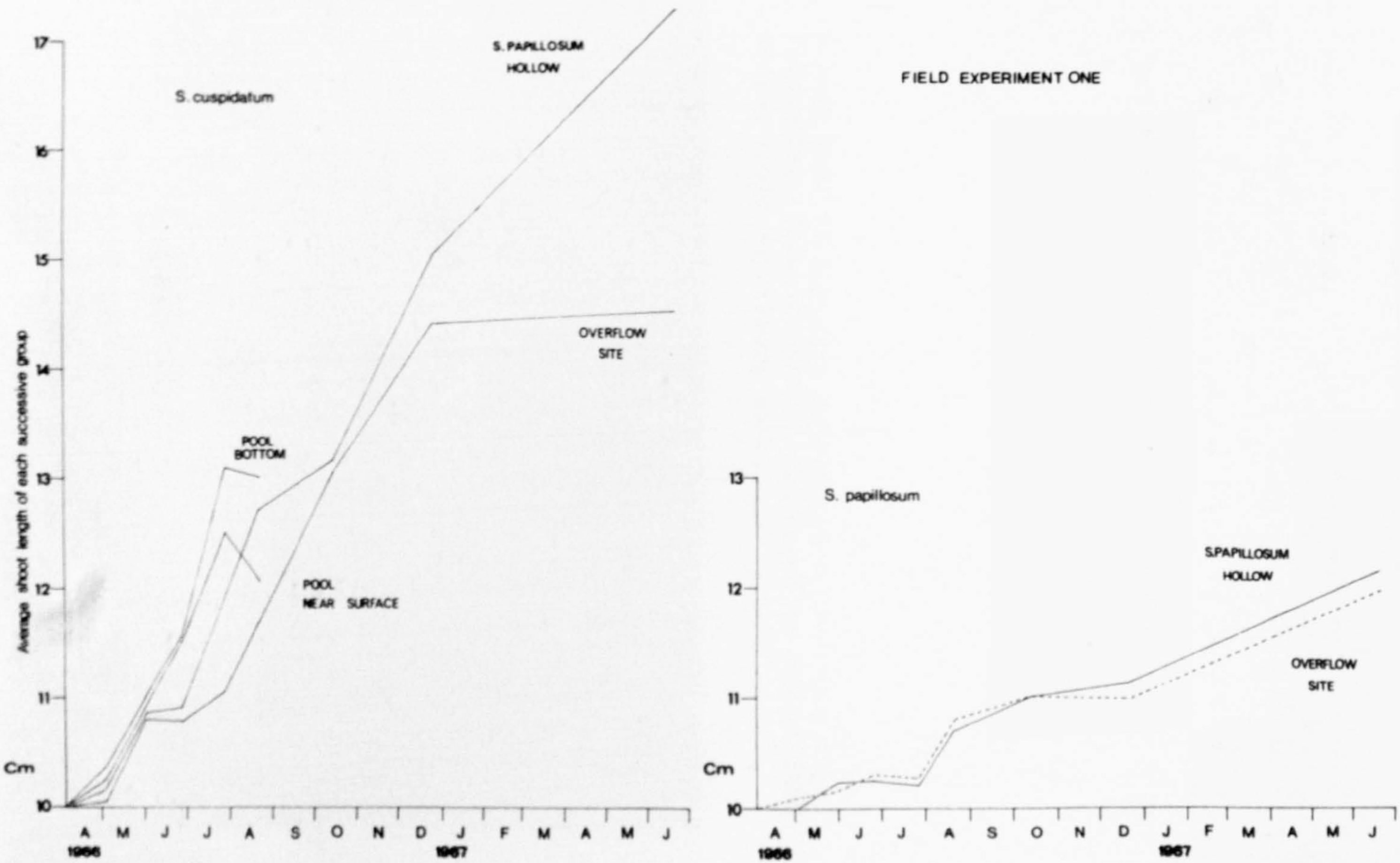


FIG 41

Figure 42a. Branch leaf of Sphagnum cuspidatum coated with algal filaments; from the sample collected in August 1966 during field experiment one.

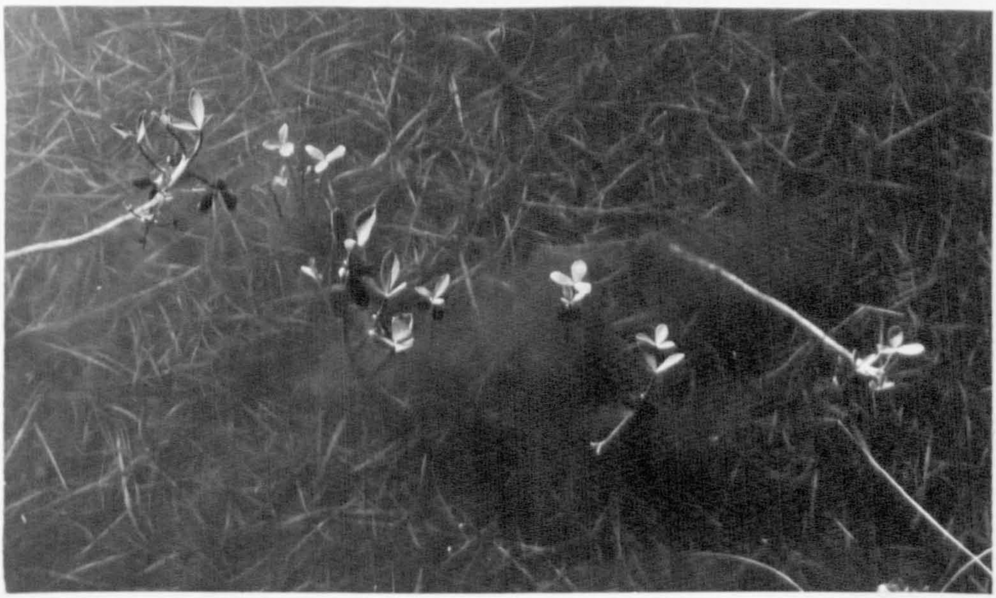


Figure 42b. Part of the open pool in which S. cuspidatum was grown in field experiment one. This photograph shows growth of Batrachospermum supported by stems of Menyanthas trifoliata in August 1966. A deposit of Molinia litter covers the pool bottom.

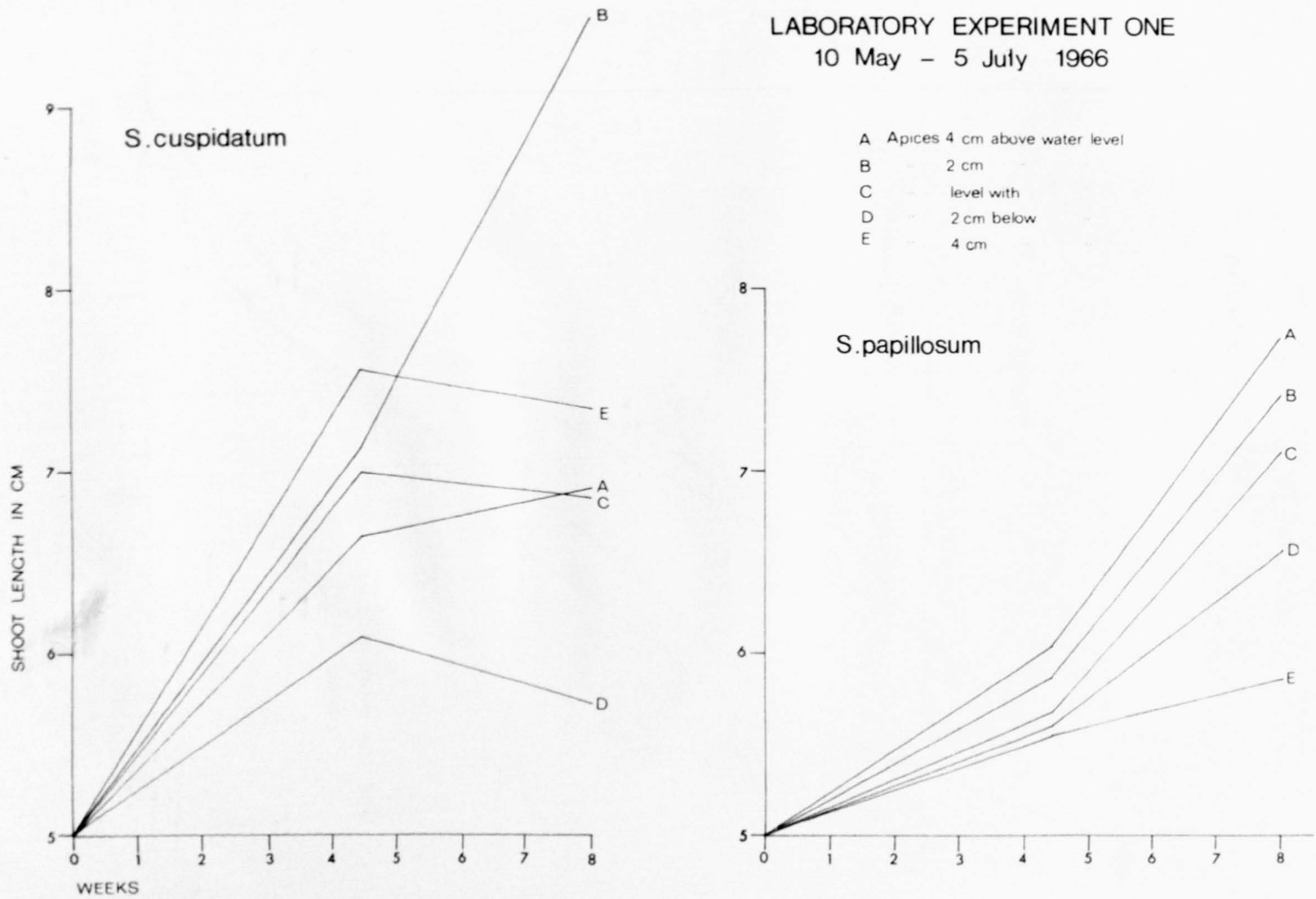

LABORATORY EXPERIMENT ONE
10 May – 5 July 1966
A Apices 4 cm above water level
B 2 cm
C level with
D 2 cm below
E 4 cm
S.cuspidatum
S.papillosum
SHOOT LENGTH IN CM
WEEKS
A
B
C
D
E

FIG. 43

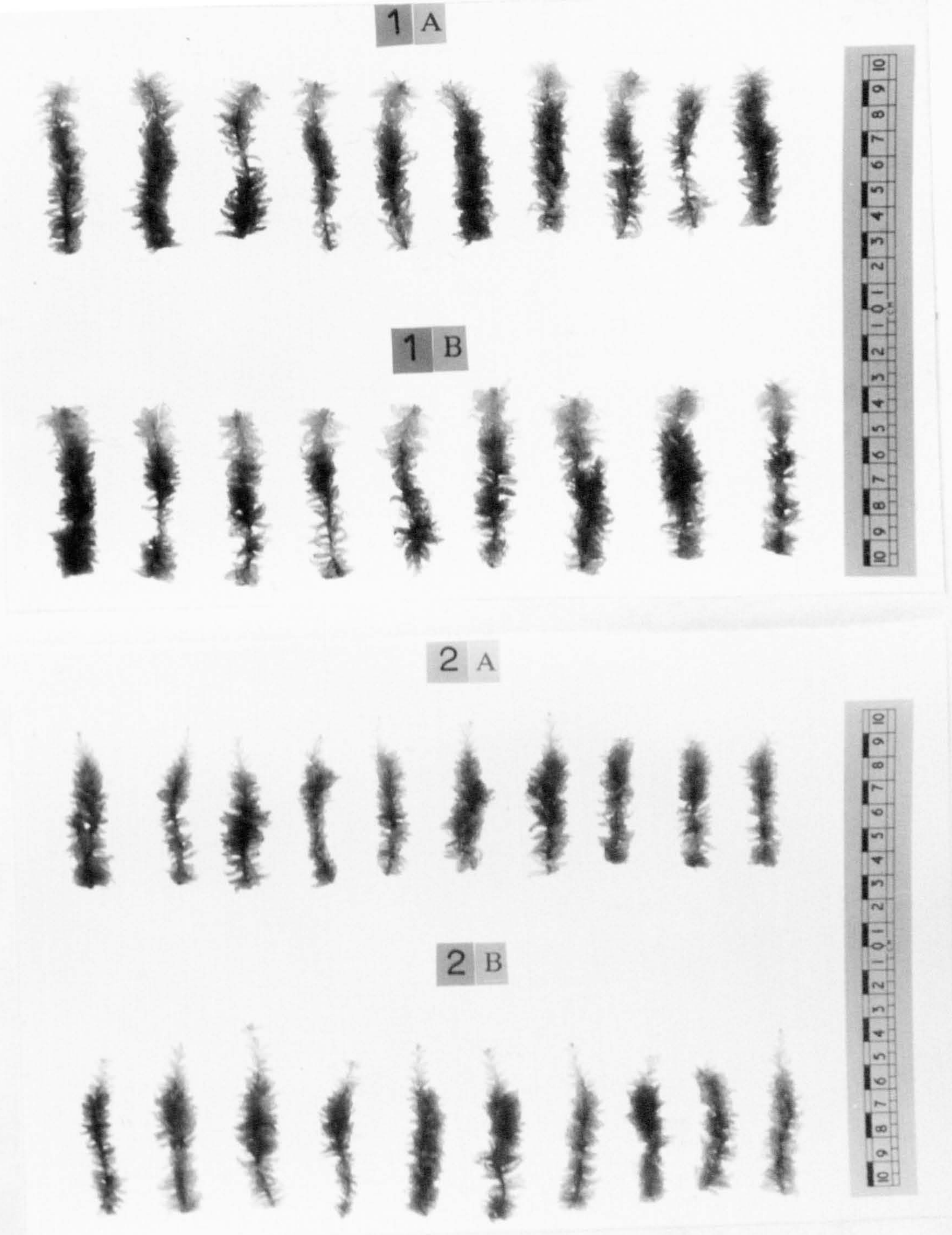
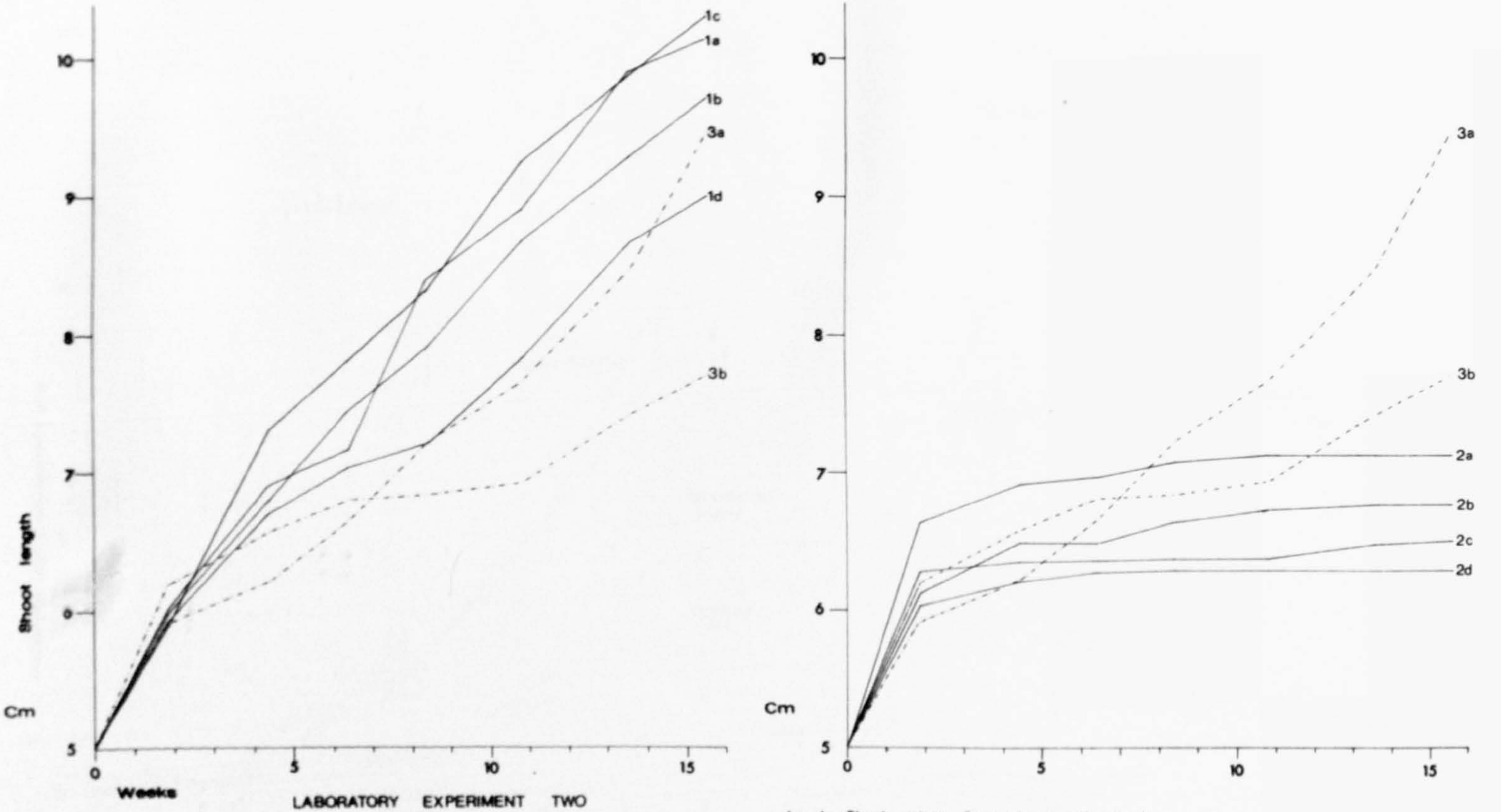


Figure 45. Laboratory experiment 2, showing the difference in form of S. papillosum shoots after 20 weeks. Above 1 A/B with apices of 2 cm. above water surface and below 2 A/B with apices 2 cm. below water surface.



LABORATORY EXPERIMENT TWO

S.cuspidatum 19 Jan - 9 May '67

1a-d Shoot apices 2cm. above water level
2a-d " " " below " "
3a-b " " " " " " and aerated

FIG. 46

SECTION 6

WIND-BLOWN LITTER OF MOLINIA CAERULEA

A characteristic feature of Molinia caerulea is that the dead leaf litter becomes detached during early spring and is easily blown by wind. This has given rise to local names such as 'Blograss' and 'Flying Bent'. In the Galloway uplands, where pure Molinia grassland is very extensive, it is a common sight after a spring gale to see Molinia litter piled up against walls to a depth of several feet. With such quantities of litter available it is not surprising to find that some is blown into rivers and lakes where it is trapped. West (in Murray and Pullar 1910 p. 218) mentions that in Loch Doon (5 miles north of the Silver Flowe) enormous quantities of litter, chiefly of Molinia, are responsible for the extraordinary extinction of the bottom flora at a depth of only 7 feet.

The pools of the Silver Flowe also act as litter traps. In the case of these pools the litter is presumed to have been wind-blown from the surrounding blanket bog where Molinia caerulea has a consistently high cover value. Expanses of pure Molinia grassland are frequent in the blanket bog immediately east of the study area and also cover large areas adjacent to the Cooran Lane and its tributary streams.

Accumulations of wind-blown litter of Molinia which form a characteristic feature of the open pool networks have been described in an earlier section in which it was mentioned that such areas of litter accumulation appear to provide a basis for colonisation of those deep pools by aquatic Sphagnum spp.

It has also been shown, by stratigraphical studies, that a pool phase consisting largely of aquatic Sphagnum spp. in association with Molinia litter may be present below the surface development of S. papillosum in certain hollows now dominated by that species. Furthermore it is relevant to mention that during field investigation of the study area it became apparent that many of the small hollows (1 - 3 m. long) in the western section showed a central mat of Molinia litter, across which shoots of S. papillosum were spreading laterally. During a cursory examination, many hollows totally covered by S. papillosum were found to be underlain by such a mat of litter.

In view of these features it was considered that the accumulation of Molinia litter might be important in assisting, accelerating or even initiating recolonisation of bog pools and for this reason the subject appeared to be worthy of further study. To this end three lines of investigation have been carried out.

1. Litter trapping: to measure the quantity of litter deposited in different areas.
2. Examination of decay rates of litter in a pool and hollow.
3. Examination of the development of hollows where litter is accumulating.

1. Litter Traps

In order to determine how the deposition of Molinia litter varied over the study area and also how it varied between different bogs of the Silver Flowe, a series of litter traps were set up. Ten buckets of equal diameter were placed in the surface peat on each of Long Loch Bog B, Craigeazle Bog and Snibe Bog so that, when water filled, they would trap

Molinia litter. These buckets were placed along transects across a part of each bog. In order that the water in the buckets might be maintained at a high level each was placed in a hollow with its rim level with the peat or Sphagnum surface. Owing to the slight slope of their sides, the buckets did not exhibit a constant area of water surface. Assuming a total range of fluctuation of 10 cm., the water surface varied within the range 470 - 510 sq. cm.

Ten buckets were placed in each of Long Loch Bog B and Snibe Bog on 3rd November 1966. A further ten were placed in Craigeazle Bog on 22nd December 1966. Since the buckets had to be placed in hollows no attempt was made to site them at exact locations on transect lines. On Snibe and Craigeazle Bogs they were at approximately 50 ft. (about 20m.) intervals along lines radial to the convex surface of the bog. In both cases the buckets were numbered inwards from the edge towards the centre, number 1 lying at the outer limit of the sphagnetum. The distribution of buckets on Long Loch Bog B is shown in figure 49.

On both Long Loch Bog B and Snibe Bog the buckets were situated within a system of open pools in contrast to Craigneazle, where they were in an area of wet hollows with Sphagnum cuspidatum and areas of S. papillosum flat.

Unfortunately in some cases litter was washed into buckets from the surrounding hollow during high water level. The buckets concerned were numbers 3 and 4 on Long Loch Bog B, number 10 on Snibe and numbers 9 and 10 on Craigeazle. Bucket 1 on Snibe was missing on 7 May 1967. Figures for these sites have been ignored. A further point in interpreting the results is that litter was collected from Long Loch Bog B on 22nd December 1966 but was not collected from Snibe Bog, which was inaccessible. Collections from all three bogs were made on 7th May 1967 and the sites were visited finally on 10th June 1967. Since trapping did not commence on Craigeazle until 22nd December the figure for Snibe Bog are not directly comparable. They include an additional period of seven weeks which accounted for 6.6% of the total catch (by number of leaves) on Long Loch Bog B.

The results are shown in table 2 and figures 48 and 49. From field observations it is known that most of the litter was deposited during later February and early March 1967. The results show that comparatively little litter was trapped on Long Loch Bog B during the early period (3rd November - 22nd December) the average weekly catch for reliable buckets being about five times greater during the later period. No litter was trapped after 7th May.

Figure 48 shows clearly that over four times more <u>Molinia</u> litter was trapped on Long Loch Bog B than on either of the other two bogs. For the reliable buckets on each site the average content was 286.2 leaves per bucket on Long Loch Bog B, 68.5 on Snibe (including the additional seven weeks) and 50.5 on Craigeazle.

Furthermore there is considerable disparity in the totals for buckets in each site. On both Long Loch Bog B and Snibe Bog the outermost buckets caught considerably more litter than the inner ones. It appears that the position of a bucket within the pool network may influence the amount of litter trapped. Bucket 6 on Long Loch Bog B situated in the centre of the eastern pool network and surrounded by areas of open water caught only

TABLE 2

Amounts of *Molinia caerulea* litter trapped in buckets

1. Long Loch Bog B. 3 November – 22 December 1966.

	1	2	3*	4*	5	6	7	8	9	10	Mean of reliable sites
Dry Wt. (gms.)	0	0.17	0.35	0.38	0.06	0	0.15	0.86	3.05	0.88	0.64
No. of leaves	0	5	8	12	2	0	6	33	90	28	20.5

Long Loch Bog B. 22 December 1966 – 7 May 1967.

	1	2	3*	4*	5	6	7	8	9	10	
Dry Wt. (gms.)	5.16	3.96	5.45	5.25	3.81	1.43	3.71	8.03	10.48	10.55	5.89
No. of leaves	246	185	272	263	190	98	181	400	516	474	286.2

2. Snibe Bog. 3 November 1966 – 7 May 1967.

	1*	2	3	4	5	6	7	8	9	10*	
Dry Wt. (gms.)	-	5.49	2.42	0.66	0.91	0.76	0.46	0.99	0.49	14.77	1.52
No. of leaves	-	240	109	31	44	40	20	36	28	654	68.5

3. Craigeazle Bog. 22 December – 7 May 1967.

	1	2	3	4	5	6	7	8	9*	10*	
Dry Wt. (gms.)	1.23	0.63	0.51	1.04	1.86	0.72	0.53	1.05	2.80	2.61	0.94
No. of leaves	59	31	29	64	94	33	43	51	133	142	50.5

* Unreliable sites, excluded from comparisons

about one-fifth of the amount trapped on the edge of the bog (see figure 49). These results are compatable with the assumption that the majority of the litter is wind blown and originates outside the pool-hummock area.

If it is accepted that a water filled bucket will behave in a similar manner to a pool with a free water surface in its capacity to trap Molinia litter, then the results can be used to explain the pattern of litter accumulation in the pools on the study area. Assuming that the litter is being carried across the bog from outside then the capacity of any pool to accumulate litter will be determined by its position within the pool network. A pool in the centre of the bog is unlikely to trap as much litter as a pool to the windward side of it, i.e. nearer to the periphery. It can be seen from the results that the pools nearer to the periphery will in fact accumulate litter at a faster rate than those in the centre. These peripheral pools will continue to trap litter as long as they exhibit a free water surface but since they are accumulating litter at a faster rate there will be a tendency for them to be filled in before those pools in the centre of the network.

2. Decomposition of Molinia caerulea litter

The effectiveness of Molinia litter in forming a platform over which plants such as S. papillosum can grow will depend on the rate at which the material decays. An experiment was therefore carried out to obtain information on this point, and at the same time to compare the rate of decay in pools of the Eastern Pool Network with that in a hollow nearer to the bog margin.

Dead Molinia leaves were collected from an area of Molinia rich vegetation close to the study area during June 1967. These were air dried and then separated into ten samples, each containing about 8 g. Each sample was weighed and placed in a nylon stocking which was tied to form a bag. Replicate samples were also weighed accurately and then dried to constant weight, to determine the mean dry weight of the sample.

The ten samples in nylon stockings were placed in two pools on the study area on 17th June 1967, five samples in a deep pool (where they were held below the surface on a length of cord) and five samples in a shallow pool within a deposit of Molinia litter and aquatic Sphagnum spp. The deep pool was one of those in the Eastern Pool Network whereas the hollow was situated near the eastern edge of the bog. These samples were removed on 16th February 1968 when they were extracted from the nylon bags and dried to constant weight. The loss in weight (expressed as a percentage) is shown in table 3.

TABLE 3

% loss dry weight

Deep Pool (open water)	1	10.06	Hollow with Sphagnum spp. and Molinia litter	1	10.40
	2	11.01		2	10.36
	3	18.74		3	16.00
	4	11.48		4	10.51
	5	9.02		5	9.10
Mean		12.06	Mean		11.27

It is clear that since only 11 - 12% of the litter is lost by decomposition in 8 months the rate of accumulation from year to year must be considerable. The rise of the floor of a pool receiving large quantities of litter must therefore be rapid. Furthermore the difference in decay rates in the two sites studied is negligible. It can therefore be assumed that any differences in the rate of litter accumulation in pools of the open networks and those situated nearer to the edge of bog is due to differences in litter availability rather than differential decomposition.

3. Litter accumulation in hollows and pools

In order to assess the effect of litter accumulation on the development of bog pools three groups of hollows and pools in different parts of the study area were examined.

(a) A group of large discrete hollows east of the eastern pool network.

(b) A sample of numerous small hollows on the western periphery of the study area.

(c) Examination of litter accumulation in the eastern pool network.

(a) Large Discrete Hollows

A group of large discrete hollows (5 - 15 m. long and 1 - 5 m. wide) east of the eastern pool network demonstrates very clearly that previous open-water pools with little vegetation apart from *Menyanthes trifoliata* have become completely filled with *Molinia caerulea* litter and that a sequence of vegetation changes occurs as the litter accumulates. Seven of these hollows, shown in figure 50, were examined during August 1967 in order to determine the nature of the changes. It was found to be difficult to make corings of the material filling the pools therefore investigation was made in the field by hand to a depth of 0.5 m. Any Sphagnum not clearly recognisable in the field was retained for identification.

Below the litter in each hollow is a layer of dark green algal mud containing numerous seeds and large rhizome fragments of Menyanthes trifoliata, together with smaller fragments of Calluna vulgaris, Rhacomitrium langinosum and other species. This is indistinguishable from the bottom deposit at present found throughout the large unvegetated pool networks and implies that the hollows in question were previously open and unvegetated. It is possible to recognise the 'original' margins of these pools since a firm concave peat surface is present, particularly at the down-slope edges of the hollows.

In all cases (except hollow number 7) the pool mud is directly overlain by litter which covers the whole area of the hollow, though it varies in its degree of compactness. In some parts of the hollows it forms a compact 'layered' deposit and is invariably associated with Sphagnum subsecundum var. auriculatum in the lower layers and S. cuspidatum in the upper layers. (The 'upper' deposits are not however represented in all hollows.) This deposit consists of horizons of compact litter and Sphagnum spp., which sometimes show an alternation, this being particularly marked in the upper layers (S. cuspidatum).

With the exception of number 4, those hollows which were relatively shallow (less than 30 cm. from the present water surface to the algal mud) have filled completely with litter and aquatic Sphagnum. The deeper hollows (numbers 1, 2 and 6) have not completely filled, their centres being occupied by a semi-floating mass of Molinia litter. In the marginal areas of these hollows the litter is concentrated to form dense layered deposits.

The present distribution of all plant species in the hollows was noted. Eriophorum angustifolium occurs abundantly in areas of compact Molinia litter, in which it is rooted. It is absent from areas where the litter is sparse and semi-floating. Menyanthes trifoliata, although present in most of the hollows only produces flowers in areas of open water. In such areas the plants are comparable in stature to those in the unvegetated pool network, whereas the plants occurring in the infilled areas of hollows are dwarfed. Utricularia minor, recorded in all hollows, is most abundant in association with aquatic Sphagnum spp. on a compact mat of litter (nos. 3 and 7).

S. subsecundum var. auriculatum occurs sparsely in a flaccid form in some of the predominantly open-water areas. This species is dominant where the mat of compact Molinia litter does not extend to the pool surface. Here the species has a compact growth form and in some cases occupies the majority of the pool area. S. cuspidatum is the dominant Sphagnum in the margin of the hollow on a dense mat of litter closer to the water surface than the previous species. Elsewhere it occurs as scattered individual plants. In hollow 7 S. cuspidatum is dominant throughout.

S. papillosum is generally restricted to the original margins of pools, where it is dominant. However at the ends and upper (western) edges of certain hollows (where the margin is gently sloping and the hollow has an outer zone of compact litter) S. papillosum is invading the adjacent areas of the hollow by spreading out over such a mat of litter.

It is clear that these hollows have been similar in their morphology to those of the present pool networks, though they were smaller and in general shallower. It is suggested that a sequence can be recognised in the process of infilling of such pools. The process involves colonization of the pools by aquatic Sphagnum spp. and E. angustifolium in association with accumulations of Molinia litter which form a progressively more compact mat. Four stages in the sequence have been recognised though the process must be continuous.

1. Litter is present throughout the open-water pools forming a semi-floating mass. Robust Menyanthes trifoliata is abundant and flowering. S. subsecundum is sparse except around margins where the litter mat may be more compact. (Pool 1 is an example.)
2. Molinia litter is more dense throughout the pool and forms compact mats around the margins. E. angustifolium is present and becomes progressively more abundant, rooting in the litter throughout the pool. S. subsecundum may be dominant in association with the dense litter and E. angustifolium. Menyanthes is less robust, but may be still flowering. Marginal areas may have compact litter with vigorous S. cuspidatum. (Pools 1, 2, 3 and 6.)
3. Molinia litter and S. cuspidatum form a compact mat across the whole pool in which E. angustifolium is rooting. Ultricularia minor is very abundant. Menyanthes is absent or dwarfed and does not flower. (Pools 5 and 7.)

4. Invasion of the hollow by lateral growth of S. papillosum across the compact litter mat. This occurs at the ends and upper edges of the larger hollows (e.g. number 4) but it can be expected that it will occur across the whole area of the hollow as soon as the previous phase is complete.

(b) Small Linear Hollows

Towards the western edge of the study area, on the extensive area of relatively shallow peat (less than 2 m.), are numerous small linear hollows, about 1 - 2 metres long and less than 0.5 m. wide. These hollows occur in an area of blanket bog dominated by vascular plants. All the sites have accumulations of Molinia litter which varies in depth from 10 - 30 cm. In all cases the litter is to some extent covered by a growth of S. papillosum spreading laterally across the hollows. The hollow described in detail in a previous section (figure 26) is a larger example of this type. In the present study eight hollows have been investigated. A brief description of the morphological features and present vegetation was made in the field and the stratigraphy was investigated by extracting cores which were examined in the laboratory. (Cores were extracted by the method described in Appendix 3 using the aluminium tube.)

The stratigraphy and surface features are shown in figures 51 and 52, and the following is a summary of the features displayed. In some cases the cores do not extend to the base of the hollow deposits. In all other cases the hollows are seen to have developed on a surface of compact fibrous and amorphous peat. The depth of hollow deposits varies from 17 cms. in part of pool number 1 to 28 cms. in number 6. An initial phase of S. papillosum is often present at the base of the pool deposits. The pool phase consists initially of S. subsecundum with a rooting zone of E. angustifolium and litter of Molinia usually present. The amount of litter increases towards the higher horizons and S. subsecundum is replaced as the dominant either abruptly or gradually by S. cuspidatum. Where S. cuspidatum and Molinia litter occur together there is in some cases a distinct layering with thin bands of litter (0.5 - 1 cm. thick) separated by thin bands of S. cuspidatum. Where S. papillosum is present at the surface this is seen to overlie the pool-phase deposits. In some cases the interface between pool phase and S. papillosum is abrupt (pools 3 and 4) whilst it is generally between 2 and 6 cms. thick. Core 5a shows the two phases together over a thickness of 18 cms. Further differences exist between the various cores, such as the presence of S. magellanicum, S. plumulosum and S. compactum but these do not cause sufficient divergence from the general trend outlined above to warrant attention in the context of this section. In all the hollows examined E. angustifolium had invaded the infilling pools, rooting in the compact litter and subsequently occurring, though with less frequency, in the S. papillosum carpets.

The carpets of S. papillosum were examined in order to determine the mode of colonization. It was found that in all cases shoot apices adjacent to the central Molinia litter zone could be traced back laterally to the peripheral ridge of compact Sphagnum papillosum.

The initial stages are therefore very similar to those of the hollows described in group 1. Since the hollows under consideration were initially phase of S. papillosum is often present at the base of the pool deposits. The pool phase consists initially of S. subsecundum with a rooting zone of E. angustifolium and litter of Molinia usually present. The amount of litter increases towards the higher horizons and S. subsecundum is replaced as the dominant either abruptly or gradually by S. cuspidatum. Where S. cuspidatum and Molinia litter occur together there is in some cases a distinct layering with thin bands of litter (0.5 - 1 cm. thick) separated by thin bands of S. cuspidatum. Where S. papillosum is present at the surface this is seen to overlie the pool-phase deposits. In some cases the interface between pool phase and S. papillosum is abrupt (pools 3 and 4) whilst it is generally between 2 and 6 cms. thick. Core 5a shows the two phases together over a thickness of 18 cms. Further differences exist between the various cores, such as the presence of S. magellanicum, S. plumulosum and S. compactum but these do not cause sufficient divergence from the general trend outlined above to warrant attention in the context of this section. In all the hollows examined E. angustifolium had invaded the infilling pools, rooting in the compact litter and subsequently occurring, though with less frequency, in the S. papillosum carpets.

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The initial stages are therefore very similar to those of the hollows described in group 1. Since the hollows under consideration were initially shallower the process of infilling has progressed further. Whilst some of the group 1 hollows showed signs of lateral encroachment by S. papillosum this feature is more pronounced in the hollows described in this section. It appears that the lateral spread of S. papillosum was previously prevented by the height of pool edges. Once the Molinia litter - S. cuspidatum mat reaches a certain height, however, the S. papillosum is able to spread across the hollow. As in the case of the group 1 hollows the previous edge of the small hollows can be examined by removing the material which has filled the pool. It is clear that these hollows have resulted from infilling of small steep-edged, shallow pools and it is suggested that the accumulation of Molinia litter has been of importance in this process.

(c) Litter Accumulation in the Eastern Pool Network

Along the transect (figure 12) the depth of litter in the open pools varied from 0 - 25 cm. This is a loose deposit of litter, illustrated in figure 42b. In the 'bays' and ends of the pools the litter is concentrated into more compact masses 30 - 55 cms. thick, with which are associated aquatic Sphagna and often E. angustifolium.

From field observations it is known that immediately after deposition in the pools the litter is blown by wind to the edges where large accumulations later occur in the water. However during the course of observations connected with first experiment described in Section 5 (in which S. cuspidatum was grown on the bottom of one of these pools) it was noticed that Molinia litter became concentrated along the cords indicating that it had been moving and was arrested. Dispersal of litter in the pools, whether by wind or by water movement, leads to an uneven distribution and although the pools are relatively deep (40 - 50 cms., compared with 30 - 40 cms. average for the pools section 1) nevertheless parts of these pools where litter is concentrated will be subjected to infilling owing to the very large surface area of water over which litter is trapped. In those places the process of infilling can be expected to occur in a similar manner to that described in section 1 above.

Discussion

Ratcliffe and Walker (1958) noted that the peripheral pools on the upper bogs of the Silver Flowe were 'Sphagnum grown' but did not offer any explanation for this feature which is well displayed in their illustration of Long Loch Bog A (Plate 12). The above results indicate that the striking development of aquatic Sphagnum spp. and S. papillosum may well be associated with accumulated Molinia litter in these peripheral pools. It is suggested that the pools so modified were previously steep-edged, open-water pools containing little aquatic vegetation, closely comparable with the central pools of the present pool networks where there is an almost complete absence of the Sphagnum species concerned. If this is correct the pool systems of the northern part of the Silver Flowe would have been more comparable with the extensive pool networks developed on blanket peat in the 'flow country' of Northern Scotland where discrete steep-edged pools occur on sloping surfaces around the periphery of the interlinked pool networks. The development of Sphagnum-grown hollows in place of such pools on the upper bogs of the Silver Flowe can be regarded as secondary.

The vigorous growth of aquatic Sphagnum spp. in association with Molinia litter in the discrete hollows described above contrasts with the failure of aquatic Sphagna in the open pool networks as described in Section 5. The fact that pools are being filled in both directly by wind-blown Molinia litter and by aquatic Sphagna in association with the litter implies that there has been an increase in the amount of litter available since such pools were formed. It may be that the mechanism by which aquatic Sphagnum spp. are prevented from colonising deep pool networks is counteracted when a certain degree of Molinia litter accumulation has occurred. Nevertheless the rate of litter accumulation must have been relatively slow for the pools to form in the first place. Unfortunately there is no reliable evidence from other sources to show that the amount of available Molinia litter has been substantially less at any time in the past. Indeed stratigraphical evidence (profile 2a, figure 24b) indicates that deposition of Molinia litter occurred in a pool phase prior to the development of the extensive pool networks. Furthermore Ratcliffe and Walker (1958) term the compact peat underlying pool development on Snibe Bog a 'Sphagnum-Molinia bench' implying that Molinia was an abundant component of the surface vegetation prior to pool formation. On the whole however the stratigraphical investigations on the study area show little development of Molinia on the bog itself except in the uppermost horizons within 0.5 m. of the surface. Some support is found in the suggestion by West (in Murray and Pullar 1910) that the introduction of sheep into the Galloway Uplands led to an increase in grassland communities at the expense of associations of Ericaceae on peatland areas. Unfortunately, although he states that 'the moors have an abundance of ancient peat below the grass, formed there previous to the development of the sheep-rearing industry', he does not in fact provide any definite evidence of such a change taking place and whilst attractive the suggestion cannot be taken any further here.

Results of the litter trapping experiment show that there is at present a considerable disparity in the amounts of litter available in the northern and southern sections of the Silver Flowe. This must be related to differences in the local environment and indeed age differences of the adjacent Forestry Commission plantations provide the most likely explanation of this feature. Young Forestry Commission plantations occupy the whole of the valley to the east and north of the Silver Flowe. The oldest of these are situated at the foot of the valley and the youngest at the valley head. Slopes to the east of Craigeazle Bog were ploughed in 1959 and planted in 1960 whilst an area immediately north-east of the northern bogs was ploughed in 1965 and planted in 1966. In both cases ground mineral phosphate was applied by hand ($1\frac{1}{4}$ cwt./acre). Following ploughing and planting Molinia caerulea showed a considerable increase in its performance on the baulks between the furrows (information from Forest Officer). On the older plantations, e.g. the slopes of Craigeazle, this effect has gradually been reduced and Calluna has now become the dominant species on these baulks. The young trees themselves might be a factor in preventing wind-blow of Molinia litter after several years growth. The trapping of litter was carried out during the winter following planting of the northern area and it is suggested that this may well account for the large differences between the catch on the northern and southern bogs. Whilst a recent increase in available Molinia litter will have produced a more rapid accumulation of litter in the pools it is considered that this will only affect the uppermost horizons of the deposits described in this chapter. However it does serve to illustrate the fact that changes in local environment conditions can have an effect and this might be important if continued over a long period.

QUANTITY OF <u>MOLINIA CAERULEA</u> LITTER TRAPPED

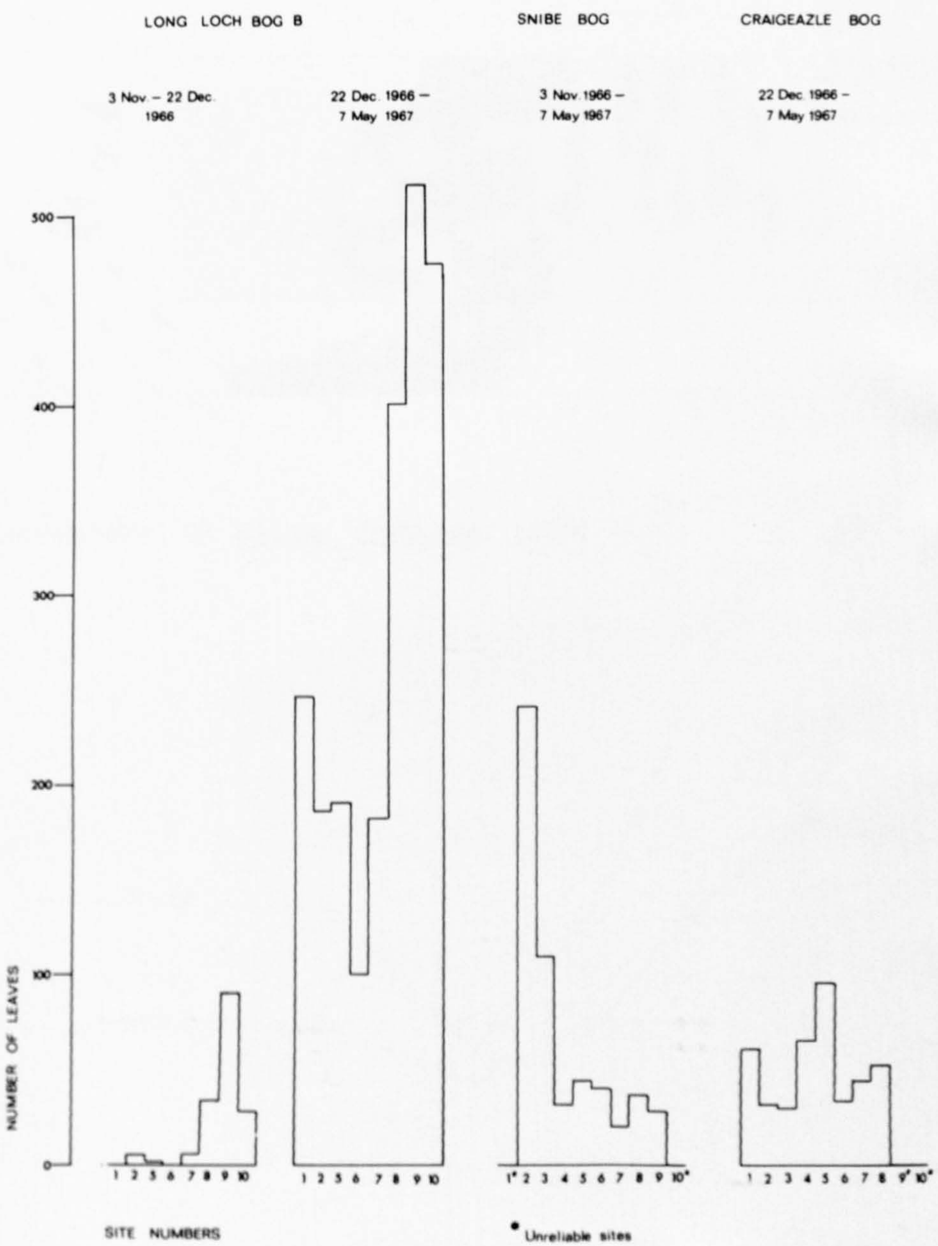
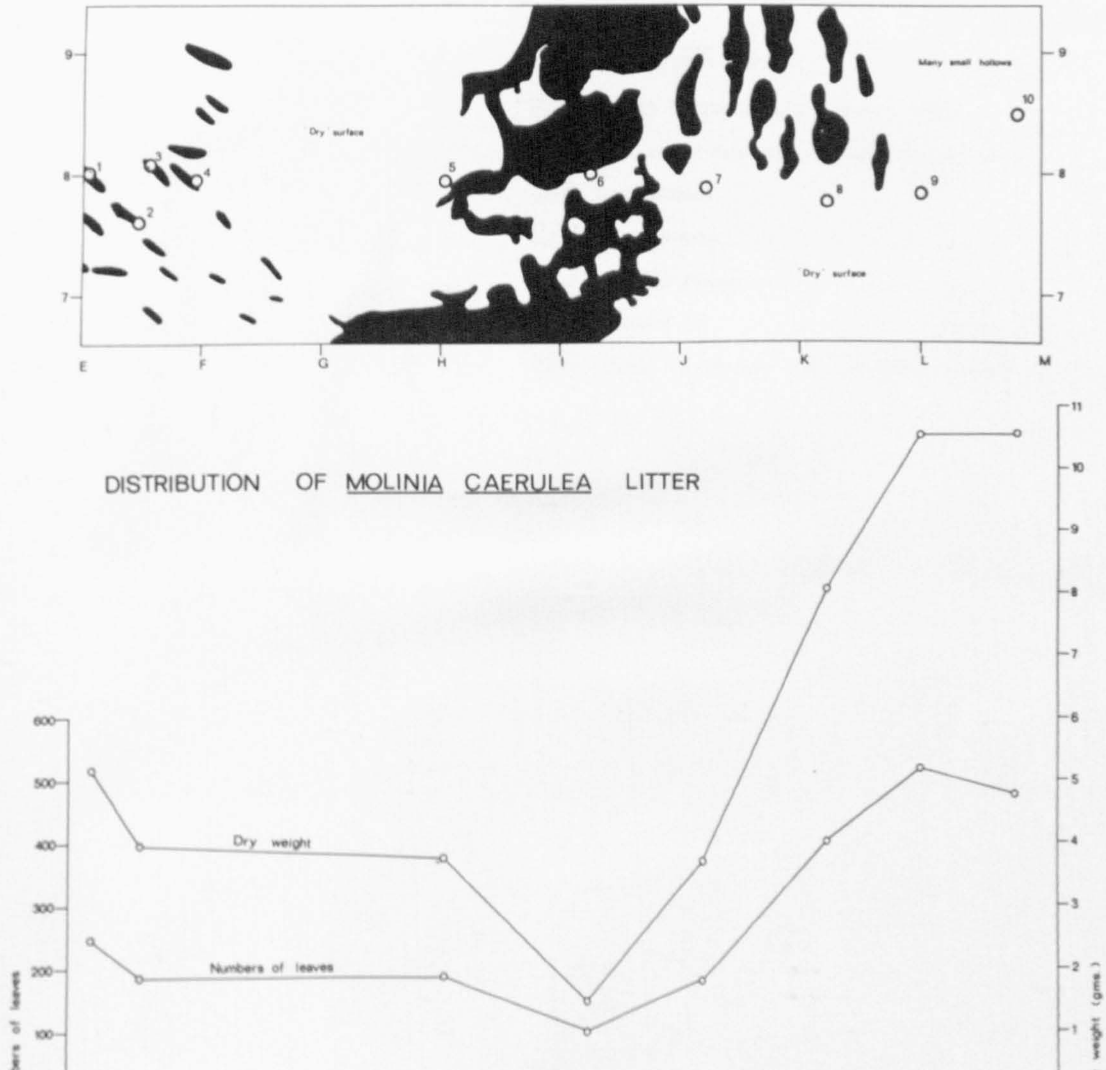


FIG. 48



DISTRIBUTION OF MOLINIA CAERULEA LITTER

FIG. 49

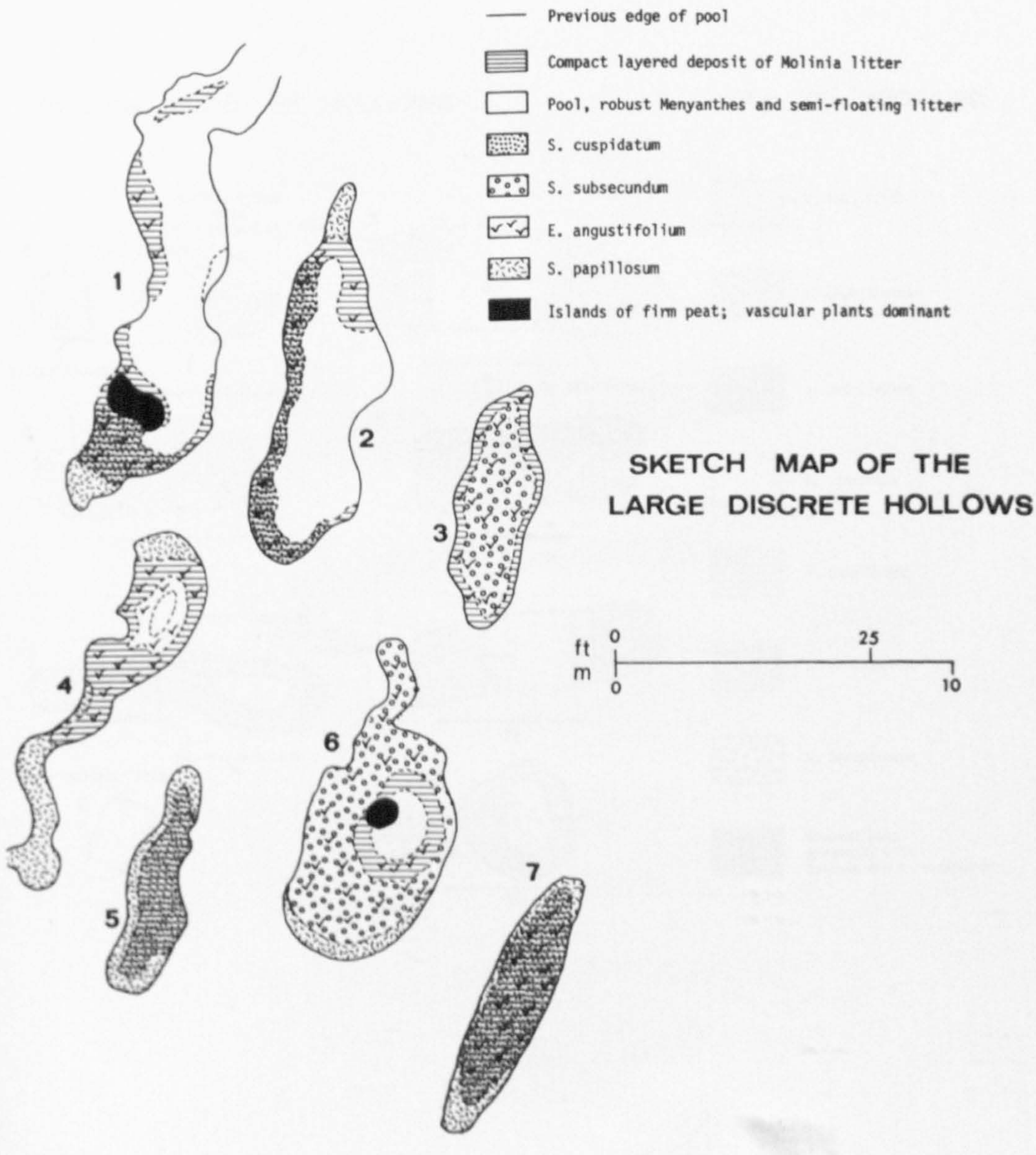
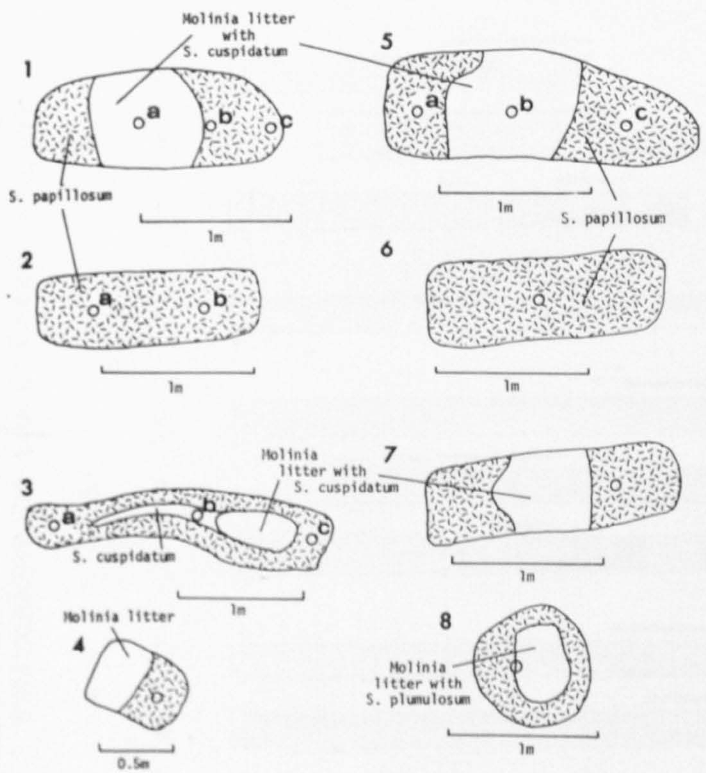

Previous edge of pool
Compact layered deposit of Molinia litter
Pool, robust Menyanthes and semi-floating litter
S. cuspidatum
S. subsecundum
E. angustifolium
S. papillosum
Islands of firm peat; vascular plants dominant
SKETCH MAP OF THE LARGE DISCRETE HOLLOWS
1
2
3
4
5
6
7
ft
m
0
25
0
10

FIG. 50

SKETCH MAPS OF HOLLOWS



KEY TO PROFILES

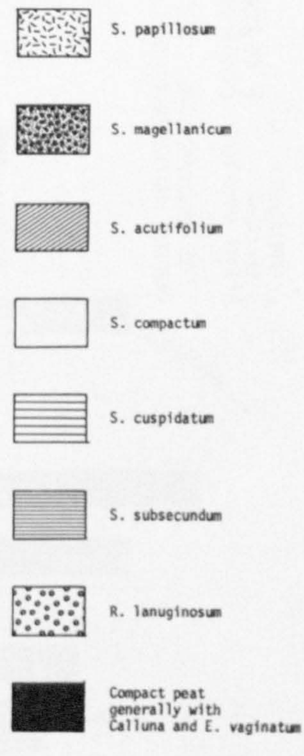


FIG 51

STRATIGRAPHY OF SMALL LINEAR HOLLOWS

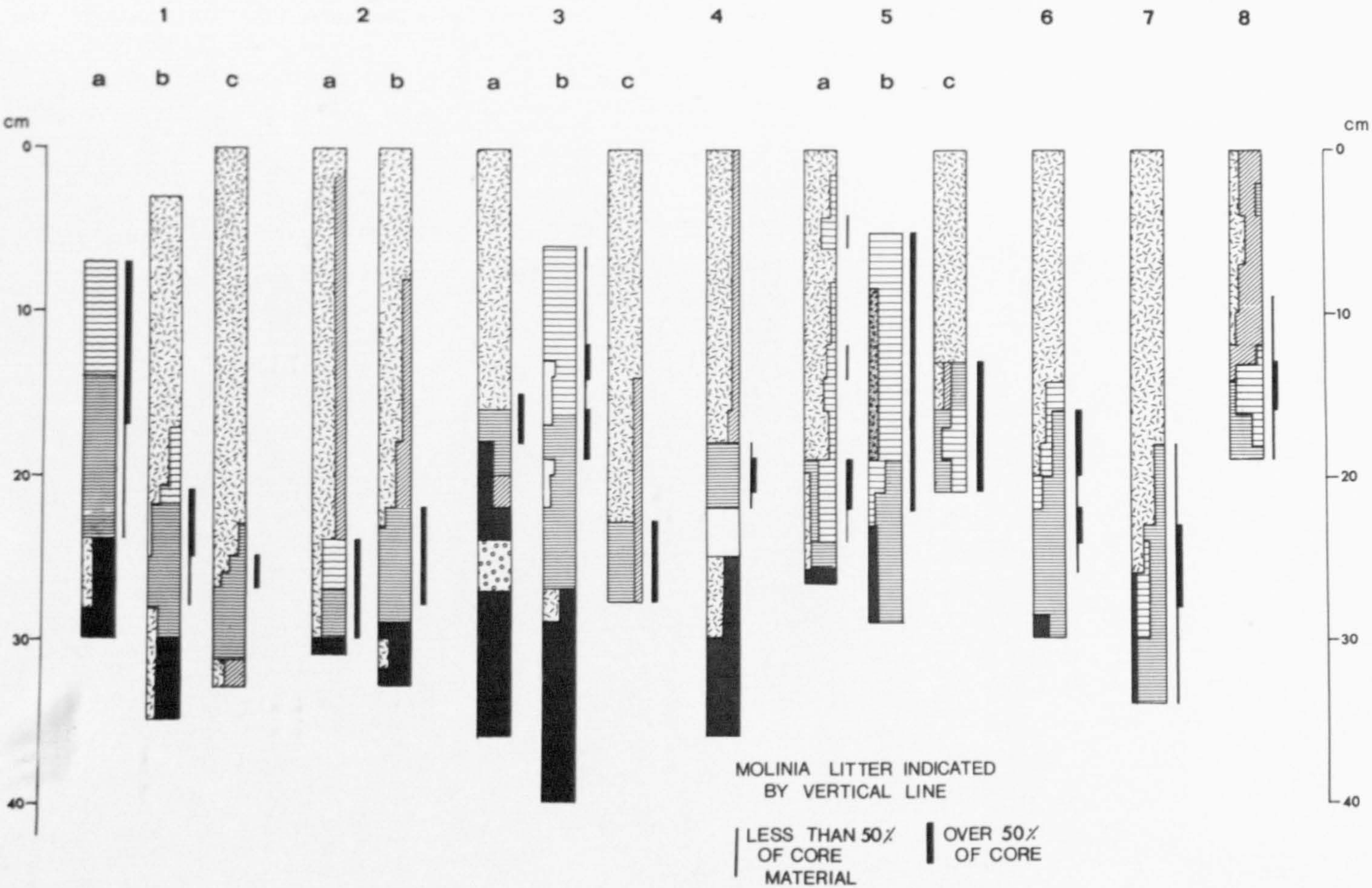


FIG. 52

DISCUSSION

The object of this section is to bring together the main points arising from the various lines of investigation and to consider the extent to which these results contribute to an understanding of pattern development, not only on the study area. The present work indicates that several independent factors and processes are involved in the development of the patterns concerned. Some of these are concerned with the actual establishments of patterns whilst others are important in influencing the form which the patterns take. Consequently it is necessary to consider various aspects of the problem in turn in order to distinguish clearly where any particular factor or process is important.

The main aspects of the problem have already been defined in the introduction and these form the basis of the following discussion. Firstly the extent to which the patterns on the study area are comparable with those described from other areas is considered. The two basic theories which have been advanced to account for pattern development are then outlined and the extent to which the present work supports these ideas is discussed. Following this, processes involved in the development of particular pattern types (e.g. open pool networks or linear hollows) are considered, utilising evidence from the various lines of investigation described.

In the introduction it was pointed out that several theories have been advanced to account for the development of surface patterns of the type described in this work. Some of these have also been referred to in earlier sections in order to explain why a particular line of investigation was adopted. Reference to the literature has, however, been kept to a minimum during the descriptive sections in order to make a clear distinction between the work which forms the basis of this thesis and the various theories which have previously been suggested. Details of these theories are now required but rather than provide a separate review of the literature, which would inevitably result in repetition, the major contributions are described in the relevant section of the discussion which now follows.

Consideration is given first to the extent to which the distribution and form of different kinds of patterned surface on the study area are comparable with other previously described areas. The basic picture, a rather irregular network of pools occupying the flat central areas surrounded by a discontinuous zone of linear pools or hollows, each of which is elongated parallel with the contours, is characteristic of many other domed bogs which show pattern development (e.g. Osvald 1923, Rudolph et. al. 1928, Sjors 1948, 1963 and Tolonen 1967). One of the Finnish raised bogs illustrated by Tolonen (1967 p. 290) Kesonsuo Ilomantsi shows a particularly striking resemblance to the study area, though on a much larger scale, in having a narrow zone of linear pools peripheral to the pool network. Sjors (1948) referring to certain Swedish bogs states that on a completely horizontal surface the hollows are 'isodiametric' but on even the slightest slope hollows are elongated at right angles to the direction of slope. The network of hummocks is pressed together, shortened in the direction of slope and lengthened in the direction of the contour. On the steeper slopes hollows become long and narrow and hummocks string-like.

The present work shows that pools are limited to areas where the surface gradient is less than about 1 in 37 and that the form of the pools is also related to surface gradient in that networks of extensive pools occur on the flattest parts of the surface (a gradient of 1 in 300 in the Eastern Pool Network), whilst narrow linear pools occur where the gradient is steeper (approximately 1 in 100 to 1 in 40). The effect of gradient is, however, partially masked by the fact that peat depth also influences the extent of pool development, pools being best developed where the peat is deepest and totally absent where it is less than about 1 m. deep. The relationship with gradient is best demonstrated by figure 7 which shows that pools are absent from the steeper slopes to the east of the study area. A similar area of bog extending from the Long Loch Bogs towards Brishie Bog, with an average gradient of 1 in 28, is also devoid of pool development. It is of interest that the linear pools on Strathy Bog (Pearsall 1956) terminate where the surface gradient increases abruptly from an average of 1 in 400 to 1 in 35.

Elongated pools seem always to be associated with a sloping peat surface though the slope need not necessarily be very pronounced. According to Sjors (1961) regular linear patterns on minerotrophic peatlands in the Boreal zone often occur across slopes as little as 1 in 1000. The elongated pools on a bog near Rhiconich Sutherland (Boatman and Armstrong, 1968) occur on a surface which slopes at about 1 in 44 whilst very similar features described from Czechoslovakia (Rudolph et. al. 1928) occur where the surface gradient is about 1 in 95.

So the distribution of different forms of pools on the study area is similar to that described for other situations in that it shows a distinct correlation with surface gradient, but the pattern is complicated by variations in peat depth.

In the introduction the variety of explanations advanced to account for pattern formation was outlined and it was emphasised that there are two schools of thought. Some workers consider the patterns to be structural phenomena whilst others regard them as essentially 'ecological', that is the result of a specialised form of bog growth dependent on differential rates of peat accumulation. Suggestions from the structural school fall into two main types some involving frost action and others dependent on slope.

One of the principal exponents of structural processes was Auer (1920) who relied on differential freezing and thawing to explain the development of ridges on Aapamoor (minerotrophic peatland with narrow ridges and wide hollows). Troll (1944) suggested downslope gliding of peat to account for linear ridges which he considered to be accentuated by frost action. Numerous other workers have relied on regelation phenomena to account for the patterned peatlands in areas of permafrost e.g. Sigafoos (1952) and Tantuu (in Cajander 1913). In one case a convolution of the peat within a ridge has been demonstrated in an area subject to permafrost (Drew and Shanks, 1965). Sjors (1961) accepts that patterns have a different form (higher ridges) in permafrost areas and Ruuhijarvi (1960) explains differences between certain types of pattern in Finland on the basis of regelation phenomena, but both these workers emphasise that frost action only modifies the pattern. Sjors

(1946, 1963, 1965) has repeatedly emphasised that pronounced patterns occur in areas where frost action is insignificant. Certainly it seems most unlikely that frost action is a factor in maintaining surface patterns on blanket bog in the temperate maritime climate of Britain, or in the most southerly areas of pattern development in North America (Heinselman, 1965).

Most of the structural explanations of pattern development relate to the very gently sloping minerotrophic mires (Aapamoors or string-bogs). It is probably because the ridges are the sole expression of pattern in such situations that many workers have regarded these as the basis of pattern development, and have therefore turned their attention to physical factors to explain the process. Patterns on ombrotrophic mires have rarely been attributed solely to physical processes, though Newbould (1958) thinks that concentric patterns on a raised bog (Hammarmossen in Sweden) result from the surface skin of vegetation being thrown into folds following desiccation, a suggestion which is not consistant with the stratigraphical evidence (Granlund 1932). More important is the attempt by Pearsall (1956) to account for patterns very similar to those of the present study area by means of structural processes. These patterns occur on two blanket bogs in north Sutherland. In both cases the sloping bog surfaces show a pool and ridge morphology (with pools 20-30 m. long and 2 m. wide) which Pearsall describes as 'furrowed'. In addition, there are, on the crown of each bog, one or more steep-edged pools similar to those forming networks on the present study area. Pearsall suggests that 'in both sites the furrow-ridge systems are distributed in a manner suggestive of pressure ridges'. In the case of Strathy Bog 'the furrow-ridge zone occupies a place where one might expect to find pressure-ridges while the unfurrowed skin of the upper part might possibly represent an area under tension. If this were so the pool on the crown of the bog might represent a 'tear in the skin'. He points out that the general impression is that the patterns are in some way related to the instability of the swollen peat mass. Similarity to crevasses and pressure ridges on glaciers is mentioned. No evidence is given to substantiate such a hypothesis yet Pearsall goes on to outline a hypothetical developmental sequence involving furrowing and splitting in different zones of the surface skin during phases of desiccation of the peat mass.

Ratcliffe and Walker (1958) recognise the essential similarity between the patterns of Strathy Bog and those on parts of the Silver Flowe but they reject Pearsall's suggestions, pointing out that the very small gradients of mineral ground of Snibe Bog (1 in 150) are inconsistent with lateral movement of peat and that the stratigraphy indicates a rising water table rather than desiccation during initiation of pool-hummock morphology. Boatman and Armstrong (1968) showed that the direction of elongation of larger pools over part of a bog in west Sutherland is related strictly to the slope of the peat surface, irrespective of local variations in slope of the underlying mineral ground and they consider that this appears to preclude any possibility of the pools originating as wrinkles or tears. Neither Pearsall's concept of pressure ridges, nor Troll's (1944) suggestion of downslope gliding of peat, can apply in the case of the Aapamoores and other extensive minerotrophic peatlands, where the regularity of the pattern is maintained even when the gradient is only 1 : 1000.

If linear patterns are a response to gravitational effects then greater slope should accentuate the pattern. Reference to the present work (particularly figure 7) shows that this is not in fact the case. Indeed the areas of greatest slope are devoid of pool development. Also, as in the case described by Boatman and Armstrong (1968), the orientation of elongated pools throughout the whole study area is related soley to the present slope of the peat surface and bears no relationship to that of the underlying mineral ground which is extremely irregular. Pearsall's concept of 'pressure ridges' is therefore inconsistent with the form of the peat body in this case and some other process must be involved in the development of linear hollows and ridges. One feature of the patterns on the study area is, however, more compatible with Pearsall's general concept. Whilst orientation of pools is unrelated to shape of the mineral ground, the distribution of pools definitely is related to this. The fact that pools are largest in areas of deepest peat and are absent in areas of thin peat implies that shape of the peat body (if only peat depth) might have some influence on pool development, though not in the precise way which Pearsall conceived. Osvald (1923 p. 283) states that pool complexes on Komosse are nearly always associated with slight depressions of the underlying mineral ground and Lundqvist (1951 figure 122) shows a similar effect on a sloping peat surface. The significance of this feature will be considered later in the discussion.

Ideas based on physical processes to account for pattern development do not appear to be consistant with the patterns described on the study area and it is necessary to consider alternative theories. Sjors (1961, 1963) and Heinselman (1963) have both emphasised the fact that patterns in minerotrophic mires are restricted to zones of water movement through the mire system and Sjors (1948) shows that pool systems on ombrotrophic mires in Sweden are restricted to areas of high rainfall and humidity. It appears that patterns are associated with areas where there is a water 'surplus'. This may seem obvious since pools are an integral component of the pattern. The point is, however, that this lays the emphasis in discussing pattern formation on the pools. In the case of ombrotrophic mires a water 'surplus' will depend upon the climatic regime and also upon the rate of run-off. The slope of the peat surface will be important, shallow slopes providing the lowest run-off rate and greatest possibility of a high water table being maintained. This is at least consistent with the distribution of pools on the study area and provides a basis for discussion.

The idea that pools are the significant components of pattern implies that initial development of patterns must be associated with onset of wetter conditions. A number of previous stratigraphical investigations indicate that pool and hummock development is associated with a resurgence of bog growth, in some cases associated with 'flooding' of the peat surface. Ratcliffe and Walker (1958) show that the pool-hummock topography of Snibe Bog is restricted to the upper horizons of the peat. Fresh Sphagnum peat overlies more humified Sphagnum-Molinia peat and Ratcliffe and Walker suggest that this represents 'flooding' of what was probably a relatively plane surface, subsequent hummock development then determining the extent of interspersed hollows or pools. Walker and Walker (1961) examined the stratigraphy of certain Irish raised bogs and concluded that the great majority of pools seem to have been created by flooding of hollows on a relatively mature bog surface. Lundqvist (1951) showed that pool formation is usually preceded by a period when bog growth was temporarily checked. Tolonen (1967) shows that development of pools and ridges on both Hochmoor and Aapamoor in Finland is associated with superimposition of fresh Sphagnum peat over more humified horizons. Sjors (1961) mentions that in many cases patterns seem to have been lacking during early development of the minerotrophic peatlands where they are now so conspicuous and this is also shown by Heinselman (1963 p. 360). Finally Godwin and Conway (1939 p. 357) show that the pools and hummocks of their 'regeneration complex' have developed over an older drier surface and probably represent some degree of renewed bog growth after a phase of retardation or standstill. They attribute this to climatic change since it occurs in all three of the bogs which they examined.

In addition to the stratigraphical investigations other workers have suggested that 'flooding' of the peat surface is important. Boatman and Armstrong (1968), in accounting for the development of linear pools, suggest that restricted areas of firm peat between adjacent pools at approximately the same level (which they term 'bridges') can be flooded and that the rate of peat accumulation on these flooded bridges is subsequently less than on the surrounding areas. They suggest that the same process might be responsible for pool initiation in general, slight depressions on the bog surface being the centres of pool initiation which once flooded remain as pools under the conditions which they describe. A significant implication of this is that the process of 'flooding' is not in this case restricted to a particular phase in the development of the bog but is a 'continuous' process restricted to particular areas.

The present stratigraphical investigations show that development of distinct hummocks and hollows is associated with the upper horizons of the peat and that the lower horizons show less lateral variation. Establishment of these differences involves the initiation of pools in some areas and resurgence of peat growth in others. Both these conditions imply that the water table was higher in relation to the peat surface at the time when patterns were initiated, than it was previously. In many cores abrupt changes from strongly humified peat to a pool phase are demonstrated, often with a thin layer of *Sphagnum papillosum* at the surface of the humified peat. Presence of *Calluna*, *Eriophorum vaginatum* and often *Rhacomitrium*, together with general absence of *Sphagnum* from the humified peat below the horizons where pools are initiated, indicates that these abrupt changes represent flooding of a relatively dry surface, the thin layer of *Sphagnum papillosum* reflecting onset of wetter conditions. Deep cores indicate that there is a greater degree of vertical variation in cores from sites where pools have developed and it is suggested that ridges on the present surface represent areas where pools have never developed. All the ridge profiles examined show presence of hummock forming species e.g. *Calluna*, *E. vaginatum*, *Sphagnum rubellum* and *S. imbricatum* and there is some evidence (figure 23) that resurgence of peat growth in these situations corresponds in time with pool development in others.

This work supports the contention that patterns depend on establishment of pools on the bog surface. A rise in water table can be taken to infer a change to a wetter climatic regime but sudden changes from humified peat to pool conditions indicate that the conditions of the peat surface itself might be important to the establishment of pools. The fact that pools are absent from areas of very thin peat and are most extensive where the peat is deepest suggests that the form of the peat body might influence the areas of pool initiation. At the time of pool initiation the influence of mineral ground ridges must have been more pronounced than it is now. It has been shown that the first indications of pool initiation at one site in the Eastern Pool Network lies at about 1.2 m. (or about 3'9") below the present bog surface. Reference to figure 6 shows that this is lower than the top of the mineral ground ridge to the west. The surface of the peat covering this ridge must have sloped down to this level and it may be that this slope was sufficient to preclude pool formation. Taking this a step further, it can be argued that the horizon of pool initiation in any one area might correspond with the time when growth of the bog produced a fairly level surface. If this were so then site factors might be more important than climatic change in initiating the patterns in situations, such as the study area, where the mineral ground is very irregular. This can be no more than suggestion, in the absence of more extensive stratigraphical information. Another possibility, though again only conjecture, is that slight contraction of the peat surface associated with desiccation and humification during dry conditions might allow a higher water table to be maintained once wetter conditions are restored. Such an effect could be expected to be more pronounced where the peat fills a wide depression than where it is thin and overlies a convex mineral ground surface. It was noted in section one that the shallow peat on certain parts of the study area and surrounding the smaller basins close to Long Loch is much harder and more compact than the deeper peat filling the basins. These suggestions are offered to account for the present distribution of pools on the study area and in other particular cases referred to earlier (Osvald 1923 and Lundqvist 1951), but it must not be taken to imply that pool development always requires such conditions. Boatman and Armstrong (1968) investigated the possibility that pool development on a sloping bog surface might be related to terracing of the mineral ground but found that this was not so and certainly establishment of a regular alternation of pools and ridges on minerotrophic mires cannot be attributed to differences in the mineral ground topography which is often remarkably uniform (Drury 1956).

Although it appears that pattern formation is initially due to 'flooding' of the bog surface this does not explain how different forms of pattern arise nor the more fundamental problem of how the surface irregularities are maintained once established.

Sjors (1961, 1963, 1965) holds the view that patterns on both ombrotrophic and minerotrophic mires persist because of differences in the rate of peat growth in hummock and hollow. He places the emphasis on retardation of peat growth in the hollows and speaks of 'local cessation of peat formation in waterlogged sites'. Other investigations indicate that the growth rate of hummocks might be increased at the same time as the establishment of pools and that this is important in determining the extent of pools and maintaining the pattern. An extreme case is that described by Granlund (1932) from a Swedish raised bog, Hammarmossen. On this bog the pools are commonly 3-4 m. deep and extend down to a swamp-mud layer which underlies the raised bog peat throughout. Immediately above the swamp-mud at the base of the Sphagnum peat forming the ridges is a layer of highly humified Sphagnum and wood peat. Granlund suggests that this represents birch-clad raised bog hummocks ½ m. high separated by level mud surfaces. He goes on to say that with the change to increased rainfall which corresponds with the surface of the highly humified peat the hollows between the hummocks filled with water and raised-bog growth made powerful headway on the hummocks, thereby maintaining the pattern. Walker and Walker (1961) suggest that on 'mature' bogs where Calluna and Eriophorum vaginatum play dominant roles, hummock development probably depends on successful growth of individual plants of Calluna or caespitose E. vaginatum. They show that such hummocks usually persist during flooding of the bog surface thereby limiting the extent of pools forming over the rest of the surface. They consider that 'these hummocks might themselves be rejuvenated, Sphagna playing an important role in their upward growth which may have been not much slower than that of the surrounding hollows at this stage'. The evidence for a bog surface reacting all over in the same direction to a change in conditions is emphasised. Boatman and Armstrong (1968) in considering the establishment of hummocks favour the view that it is the vascular plants, not the bryophytes, which are the main agents in initiating hummock formation, in providing the necessary support for mosses such as S. rubellum and Rhacomitrium to get above the surrounding saturated peat. Accordingly, areas where such vascular plants are absent during flooding of the peat surface would remain as hollows whilst others would be subject to renewed growth.

There is then general agreement within the 'ecological school' that slight topographic irregularities of the surface being flooded are important in the initiation of more pronounced patterns since they provide situations where different rates of peat accumulation may occur. Even Ruuhijarvi (1960), who relies on frost phenomena and other physical processes to explain the development of pronounced ridges on Aapamoor, considers that differences in 'grades of wetness' must be present before the physical processes can have any effect. 'Only when distinct differences in wetness are developed do regelation and other mechanical forces intervene in the development of the stränge (ridges)'.

In order to determine the precise manner in which the differences between hummock and pool are accentuated it would be necessary to establish values for the rate of peat growth in these two situations. This has not been done in the present study. Nevertheless, some indication of the process can be gained from the stratigraphical investigations. In particular a considerably increased Sphagnum content is apparent in the ridge profile (figure 23) at approximately the same levels as pool phases in the profile below the present pool, which implies that the response to changing water levels is similar to that described by Walker and Walker (1961). No comparison of the actual rate of peat accumulation can be made, despite the basic similarity of the profiles, because different types of corer were used, that for the pool profile producing a possible error due to compaction. This also applies in the case of the linear hollows, in that the corer used involved compaction which might be more pronounced in some types of peat than in others. It could be argued that assuming the establishment of wetter conditions to be synchronous in the small linear hollow (figure 26) then the rate of peat accumulation is least in the pool phase and greatest either where S. papillosum is dominant or where lateral spread of drier elements occurs, but this must remain only a suggestion in view of possible compaction effects.

A completely different aspect of the present work does however have a bearing on the problem of establishment and accentuation of hummock and hollow. This is the behaviour of the water-table, which shows pronounced local differences in fluctuation according to the physical nature of the peat. Fluctuation is least in hollows and greatest in hummocks, a feature which is attributed to differences in storage capacity. It has been shown in the case of ridges and hollows on a sloping surface that when the water level is high the rate of fall in the hummock can be three times that of an adjacent hollow. A similar effect is demonstrated over a wider area by the fact that the range of fluctuation increases by about 3 cm. in the peat immediately surrounding the Eastern Pool Network. It has also been shown that the modal water level depth at sites dominated by plants characteristic of pools and those characteristic of hollows over a large part of the study area differs by only 5 cm. This means that the differences in water level fluctuation due to storage capacity are sufficient to accentuate differences in vegetation between pool and hummock once these are established. So I suggest that this is a possible mechanism by which the two ecologically distinct environments might be maintained, once differences in degree of wetness have been established by flooding of a previously drier bog surface on which hummocks were already established.

Obviously some gradient is necessary for spatial differences in water level to occur. This may be a local gradient between adjacent hummock and hollow, or the gradient of the whole bog surface. If differences in water-level are essential to the establishment of pattern then differences in gradient must also be important. This is because, according to Darcy's Law (see appendix 5), the rate of water movement through a given type of peat is proportional to the hydraulic gradient, the latter being equivalent to the slope of the water table in bog systems (Ingram 1967).

This is of course consistent with the premise made earlier that pattern development depends on establishment of pools where the gradient of the bog surface is not too great. It can be expected that given a constant peat type there will be a certain gradient at which the rate of water movement through the peat will preclude flooding of the bog surface, which is necessary for the establishment of pools. On the study area this appears to be a gradient of about 1 in 37.

But the significance of Darcy's Law to pattern formation is not limited to the <u>distribution</u> of patterns. Together with the evidence of differential water-level fluctuation in hummock and hollow it provides a basis for understanding why patterns are maintained and helps to explain some of the features of the patterns on the study area. This will be referred to in detail in the discussion of particular forms of pattern which now follows.

Development of particular pattern forms

In the previous section it was suggested that initiation of patterns on the study area was due to flooding of a relatively dry peat surface resulting in the development of pools in some cases and causing an increase in the rate of upward growth of hummocks or ridges in others. If pool formation is basic to pattern development then it can be expected that the forms which the pattern takes will be related primarily to the conditions necessary for existence of a pool. In particular the gradient of the bog surface at the time of pool initiation will be important in defining in broad terms, the possible extent of individual pools. Thus flooding of a horizontal, but slightly hummocky, bog surface will result in the production of irregular shallow pools with islands representing former hummock centres. In such situations single pools could be equidimensional. On a similar but sloping bog surface the gradient of slope will limit the extent of a pool in the direction of slope. The maximum width will be a function of the amplitude of the microtopography and average gradient of the bog surface, but the possible extent of a pool along the contour will not be limited in the same way. For a pool to exist another factor is also important, which is most obvious where the bog surface is sloping. That is the permeability of the hummock or ridge downslope of any pool. The relative importance of permeability will vary according to the climatic regime, being most important in a 'dry' climate. For a pool to be maintained the drainage rate through the peat of the hummock must be less than the difference between input (precipitation and inflow from higher areas) and evapotranspiration, per unit time.

If patterns are formed in this way then their persistance depends on the fact that pools are not subject to colonisation and hydroseral succession, otherwise the pattern would be destroyed. This applies particularly to the pool networks but any explanation of pattern development on the study area must also take account of the linear Sphagnum-grown hollows. The basic question is; how far are the present pattern-forms consistant with the concept of pattern being maintained, and perhaps accentuated, simply by relatively rapid upward growth of the ridges, resulting in the pools and hollows being 'left behind'. This leads on to consideration of factors responsible for differential rates of peat accumulation in the two microhabitats. It is also necessary to question how far development of patterns is influenced by 'erosion' since it is clear from the present work that at least in the pool-networks some degree of erosion has occurred.

A brief summary of previous work relevant to these questions is given before considering the implications of the present work. The suggestion that deep pools represent precise areas of pool initiation, which for some reason remain as pools whilst the ridges continue to grow, is supported by the previously described investigations of Granlund (1932). It is also supported by detailed pollen analysis of mires in the Swedish province of Dalarna, where Lundqvist (1951) has shown that almost no peat has been formed in 'flarks' and deep pools during the last 2000-3000 years. In addition Wenner (1947) has demonstrated that positions of ridges and hollows on a mire in Labrador have remained constant since their establishment.

Sjors (1961) strongly supports the idea that patterns are due to cessation of peat growth in waterlogged sites and puts forward a theory

(1963) of corrosive oxidation to account for this. He suggests that a film of algae on the surface of bare peat below the water level gives rise to oxidation conditions which will impede or retard peat formation. Sjors claims that signs of corrosive oxidation are obvious in ombrotrophic bog hollows, where they have usually been believed to represent mechanical erosion. Although he describes (1963 p. 73) how such an oxidation process might operate, he unfortunately fails to indicate the features of this process which distinguishes it from mechanical erosion. He also suggests (Sjors, 1965) that absence of aquatic Sphagna from these sites is due to competition with micro-algae but gives no experimental evidence to support this contention.

Other workers have suggested that the development of pool networks has involved erosion. Thus Ratcliffe and Walker (1958) say that this is a secondary process due to erosion and enlargement of existing hollows by wind and water. A similar view is expressed by Ratcliffe (in Burnett 1964), Osvald (1923 and 1949), and Pearsall (1954). Boatman and Armstrong (1968) consider that erosion of peat occurs, subsequent to the flooding of the peat surface, in certain situations where pool linkage occurs along the contour.

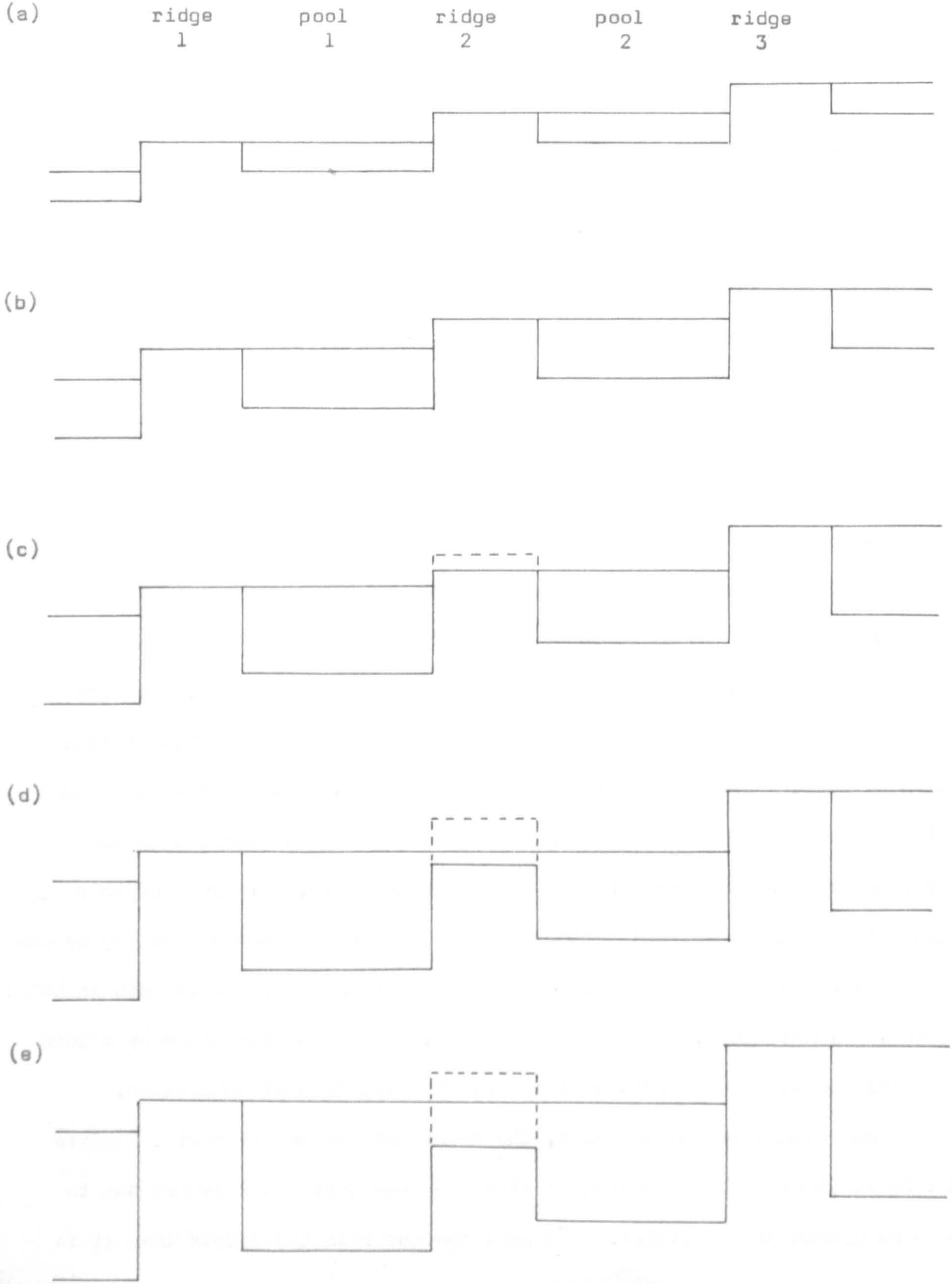
Physical erosion requires that the peat so removed must be transported and deposited somewhere. Since the pools are considered to be enlarged and even deepened by this process (Ratcliffe in Burnett, 1964) it is difficult to see where this material is going. I have examined the pools on the study area during strong winds and found that the water did not show any noticeable 'peat-staining'. Further, it has been shown in section two (p. 15) that undercutting of pool margins is unlikely to be due to wave action, since it occurs on very small pools and indeed many small hollows in the western part of the study area (often less than 1.5 m. in length), have vertical edges of bare peat which are now concealed by accumulations of Molinia litter and lateral spread of S. papillosum. On the other hand there is abundant evidence that peat has been removed by some process. The theory outlined by Sjors (1963) appears to be consistent with features of the study area, not least in the abundance of algae on the bare peat surfaces below the water level.

If this process has in fact operated then it is important to consider the extent to which it has contributed to the present form of the patterns. In this respect it is immediately obvious that if such a process occurred rapidly then the whole pattern would be lost due to lateral expansion and frequent linkage of pools. Although linkage does occur it does not have the form which would be expected if two pools were to expand until they came into contact. Pool linkages only occur by means of straight edged cross-connections through ridges. The very fact that ridges have a very constant width in areas where pool networks are developed on a sloping bog surface implies that there must be a limit to the 'erosion'. (This point is best illustrated by larger networks than those of the study area, e.g. Claish Moss, plate 78 Burnett, 1964). For these reasons I suggest that removal of peat has not caused any appreciable extension of pools subsequent to their initiation but has only been sufficient to accentuate an already established pattern. On this basis the small pillar-like islands would represent the cores of previously slightly larger islands and the discontinuity formed by the present pool bottom can be explained by only a small amount of deepening below the level of pool establishment. This is consistent with the fact that resurgence of peat growth in the ridge profile lies at approximately the same level as the present pool bottom in figure 23.

This implies that the pools have remained open and unvegetated whilst the ridges have grown upwards, as shown by Granlund and Lundqvist. The results of experimental introduction of Sphagnum cuspidatum to these pools during the present work provides some support for the contention by Sjors that absence of aquatic Sphagna from these areas is due to competition with algae, but further work is required on this subject.

The question now is how far other features of the pool networks are consistent with the concept that patterns are due to differential peat growth. I have suggested earlier that extent of a pool on a sloping bog surface will depend on the average gradient and the amplitude of the microtopography. In the case of the pool networks there is a contrast between the amplitude of present ridges and hollows (40-50 cm.) and the small differences between water levels of adjacent pools (generally less than 12 cm.). The point I wish to emphasise is that the large amplitude of the pools and ridges is inconsistent with the relationship between average gradient and frequency of pattern components. To my mind this indicates that the present pattern is simply an upward projection (by growth of the ridges) of a pattern initially dependant on small differences in water level. These would, as suggested earlier, have been determined by a much smaller amplitude of microtopography at the time of pool initiation.

One feature of the patterns, the downslope linkage of pools, appears at first sight to be inconsistent with the idea that patterns are due to upward growth of the ridges. If gaps can occur in the ridges then it is


(a)
ridge 1
pool 1
ridge 2
pool 2
ridge 3
(b)
(c)
(d)
(e)

difficult to see how the pattern can be maintained. I suggest that the process is initiated by 'flooding' of the lowest parts of a ridge, as in the case of the overflow sites described in section two, and that such areas are then subject to a slower rate of peat growth than higher sections of the ridge, which are not flooded. This is comparable with the process envisaged by Boatman and Armstrong (1968) to account for pool expansion along the contour.

Any explanation of this process must take account of the fact that some ridges show no distinct 'overflow sites', whilst in other cases these are well developed. The problem is to explain how the flooding occurs, and why it does not occur in some cases. Assuming that pool networks are the result of upward growth of the peat ridges then it is possible to demonstrate a developmental sequence by which gaps might be formed in certain ridges. This depends on differences in the rate of upward growth of the lowest sections of adjacent ridges.

1. The pattern is accentuated by upward growth of ridge surfaces (a and b).
2. For some reason (discussed below) 'overflow sites' develop on the lowest parts of one ridge but not on others. Upward growth of the overflow sites is slower than that of the lowest parts of other ridges. It is also slower than that of higher parts of the same ridge (c).
3. Subsequent growth of ridge 1 will cause the water levels of the pools 1 and 2 to become continuous. This will effectively produce a fall of the water table in pool 2 relative to ridge 3. (d)
4. With further growth of ridges 1 and 3 the original overflow sites of ridge 2 will be submerged.

The process of flooding would therefore involve two phases. The first would be overflow of water across the lowest part of the ridge. The second would be inundation of these areas, due to their growth being retarded whilst the lowest parts of the next ridge downslope continued to grow. It can be expected that these two phases will produce rather different ecological conditions.

Several features of the study area are consistant with this sequence. In particular it has been shown that submerged peat ridges occur between islands (p. 19 and figure 14). The fact that these submerged ridges support dense stands of Eriophorum angustifolium is compatible with the sequence described above and it would be difficult to envisage any way in which these gaps in the ridges could be produced by erosion when they are colonised in this way. Another similarity is that where linkage has occurred on the study area the upslope pools are relatively shallow. In one case however it has been demonstrated (in the N.W. Pool Network) that this is due to an actual fall in water level (exposing bare peat edges) and in this case it appears that the level of the overflow sites has been lowered by some form of 'erosion'. It is reasonable to expect that this will occur where there is a pronounced difference in level between the pools concerned.

There appears to be no reason why initial development of overflow sites should occur on some ridges and not on others. It is more reasonable to assume that they would occur on all ridges, but that the relative degree of retardation might vary so that some would be more effective in linkage than others. In this respect the hypothetical sequence indicates a possible reason why linkage does not occur through every ridge. One effect of linkage is to increase the hydraulic gradient of the ridge above the pools which have linked (i.e. ridge 3 in the diagram). This is substantiated by the figures quoted earlier for differences in water level between certain pools forming the Eastern Pool Network. The difference between pools A and B was 7.8 cm. and between B and C 12.4 cm. (measured on one occasion). In terms of the developmental sequence outlined above pool B represents two previously separate pools (see map figure 13). According to Darcy's Law the rate at which water moves through the peat of a ridge will be proportional to the gradient, so it can be expected that some increase in rate of water movement will occur in the ridge where hydraulic gradient is increased. Depending on the hydraulic conductivity of the peat and the climatic regime of the area it can be expected that there will be a minimum hydraulic gradient in the ridge at which flooding of the surface will be precluded. Since linkage is considered to depend on flooding of the lowest parts of the ridge surface, the process appears to be self-regulating. There will be a limit to the number of pools which can link together to form a single unit. This will depend on the original frequency of ridges and the average gradient of the bog surface, as well as the intrinsic hydraulic conductivity of the ridges.

Another possibility is that linkage may be influenced by a gradual increase in climatic wetness. The resulting increase in rate of water movement through the system may be greater than can be accommodated by the hydraulic conductivity and gradient of the ridges. If the ridges were all equal in terms of gradient and hydraulic conductivity then overflow would take place on the lowest points of all the ridges, if their upward growth could not keep pace with the increasing climatic wetness. Slight differences in the thickness of the fresh Sphagnum layers and also width of the ridges (a component of gradient) might then determine those ridges which would be most liable to 'flooding'. This places the emphasis on overflow and movement of water across the lowest parts of a ridge, rather than on a gradually rising water table flooding these parts of the ridge. That is, on the first phase rather than the second phase described above.

Such a change in the hydrological regime is also consistent with the fact that linkage results in reduction of ridge frequences. After linkage the hydraulic gradient of each effective ridge is increased, whilst the average gradient of the bog surface remains constant, and this is consistent with an increased hydrological input.

The whole problem of flooding appears to hinge on relative growth rate of the bog surface. In the case of a ridge which is growing relatively rapidly the hydraulic gradient will be increased, thereby increasing the rate of water movement through the surface layers. At the same time rapid growth may result in a thicker layer of relatively permeable fresh Sphagnum peat at the surface. Both these features would restrict the 'flooding' of the lower parts of such a ridge.

I have suggested earlier that pattern initiation is due to differences in response to flooding, some areas showing retardation and others a resurgence of growth. In effect the lower parts of ridges, subject to flooding, represent an analogous situation. It is possible that the development of an overflow site is a gradual process of vegetational change. Chapman (1965) has shown that subtle vegetational differences exist in areas of blanket bog where there is pronounced water movement. The overflow sites of the north-west pool network (table 1 page 17) differ less from the normal ridge vegetation than do those of the Eastern Pool Network, which are subject to fairly continuous inundation.

It is appropriate to regard the overflow sites as small examples of 'water-tracks' in which the rather specialised vegetation may be due to greater availability of nutrients (Ingram, 1967), or to locally improved conditions of oxygen availability (Armstrong and Boatman, 1967). In contrast the continuously inundated areas, such as some of those in the Eastern Pool Network, have a preponderance of markedly hydrophilous species and a total absence of Ericaceous species and caespitose plants. It is suggested (Walker and Walker 1961, Boatman and Armstrong, 1968) that hummock formation may depend on the presence of suitable vascular plants. I have already emphasised that the difference in modal water level of sites dominated by Calluna and those dominated by 'hollow' species is only 5 cm. I suggest that waterlogging of the rooting zone of these species might be the most significant stage in the formation of overflow sites. An investigation of the ecological conditions of the overflow sites would be a rewarding study and might also indicate how the process of flooding operates in other situations.

Finally it is necessary to consider the development of Sphagnum dominated hollows. If the pool networks remain unvegetated due to the presence of algae, it is necessary to question why the narrow linear hollows are Sphagnum dominated and, that being so, why they do not become colonised by 'ridge' species. Stratigraphical evidence shows that pool phases have often been recolonised especially by associations of Sphagnum papillosum and Eriophorum angustifolium, and in a number of cases pool conditions have been re-established. This is true of the large linear hollows (figure 25) and is also indicated by many of the profiles below the Eastern Pool Network. I have suggested that colonisation of shallow steep-edged pools has been assisted by accumulations of wind-blow litter of Molinia caerulea, particularly in the peripheral regions of the bog. Examination of the process of pool colonisation by S. papillosum and E. angustifolium in association with Molinia litter indicates that these species require some support. This would help to explain the scarcity of such species in deep pools. In all cases examined colonisation was found to occur by lateral spread of S. papillosum over Molinia litter, possibly supported by the mat of Eriophorum angustifolium runners. Even in relatively small hollows (e.g. the small linear hollow figure 26) it is apparent that such colonisation has been restricted to the peripheral parts of the pool in the absence of a continuous mat of compact litter. The large linear hollows show an alternation of pool conditions and growth of Sphagnum papillosum. It is possible that recolonisation by S. papillosum is again dependent on a mat of Molinia litter and the lateral stems of Eriophorum angustifolium since both are abundant and even dominant in the pool phases.

On the other hand it is possible that the balance between pool phase and establishment of an E. angustifolium S. papillosum association can be swayed in either direction by quite small changes in conditions. There are strong indications that where pools have once formed, subsequent development is much more sensitive to changing conditions (presumably climatic) than on firmer areas where pools have never formed (e.g. figure 22, 23). I suggest that this is due to the pool deposits being capable of a greater degree of compaction. This provides one possible reason why such areas are not generally colonised by hummock species. Because of the nature of the vegetation of hollows upward growth will not be as pronounced as in hummocks.

This brings me to the final point concerning the perpetuation of hollows. It has been shown that the hydraulic conductivity of the surface layers of a hummock or ridge (fresh Sphagnum peat) is considerably higher than in the deeper more compact and amorphous horizons (figure 39b). Due to this the water level in a hollow is maintained at a more constant level than in the adjacent hummock. I consider this to be fundamental to the maintenance of hollows since it ensures that the water level requirements of both ridge and hollow are maintained. The greater degree of water table fluctuation in the ridge is sufficient to permit growth of Calluna and Eriophorum vaginatum which provide the support necessary for upward growth of the hummock-forming mosses such as Sphagnum rubellum. In contrast the narrow range of water level fluctuation maintained very close to the level of the bryophyte surface of the hollow will preclude the establishment of hummock forming species, and the hollows will therefore remain.

SUMMARY OF CONCLUSIONS

Strongly patterned surfaces on the study area occur where the peat is more than 2m deep. This often corresponds with hollows in the underlying mineral ground. Pattern is indistinct or absent where peat is less than about 1m thick and where the present gradient of the bog surface exceeds 1 in 37. Orientation of the pattern is directly related to present slope of the bog surface. Pools and ridges are elongated parallel to the contours even when the slope is only 1 in 100.

Stratigraphical studies show that the present large scale pattern has developed only within the upper layers of the peat (generally within 1m of the surface). It is superimposed on a relatively level surface with a small-scale hummock and hollow relief. A change from humified to fresher peat often accompanies this change. The small scale pattern shows vertical alternation of hummock and hollow in a number of places. In contrast the components of the larger pattern have remained constant once established, though some lateral oscillation of vegetation zones is demonstrated.

Range of water level fluctuation is least (15 cm.) in the pool networks on the crown of the bog and gradually increases towards the periphery (25 cm+). The upper limit of water level is a threshold above which run off occurs. This occurs repeatedly during winter and less often during the summer. Short periods of heavy rain in summer can cause the water table to rise to this threshold level, even after two weeks drought. On sloping areas with linear ridges and hollows the range of fluctuation is much less in the hollows than in the hummocks. (It can be three times greater in the hummocks). This difference is most marked during high water levels. It is considered that differences in ecological conditions between hummock and hollow are largely due to the different behaviour of the water table in these two situations. The importance of the differences demonstrated, is emphasised by the fact that water level modes for plants characteristic of hummocks and hollows differ by only 5 cm.

It is suggested that the growth of filamentous algae in bog pools during late summer inhibits the growth of aquatic _Sphagnum_ species and that this is important in maintaining the patterns of open pools. Where accumulations of wind-blown _Molinia_ litter occur in the pools then colonisation of the pools may occur, to the extent that a _Sphagnum papillosum_ carpet may be formed.

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Appendix 1: Survey Methods

As a basis for subsequent description of the study area a grid was marked out on the surface of the peat by means of stakes at 50' (15.2 m) intervals. The data for figure 3, showing the peat surface contours were obtained by levelling at 10 feet (3 m) intervals along the grid lines (using a Quicksett Level and levelling staff to 1/20 feet). In the case of large pool networks the level was taken on the peat surface at either side of the pools and on the surface of islands, where accessible. Contours were drawn at 3" (7.6 cm) intervals. Isolated tall hummocks were not included, nor was any attempt made to fit contours accurately around the edges of the deeper pool networks, even though the height of the edges often exceeded four contour intervals. The contours therefore indicate only the general height of the peat surface and do not show the major depressions which extend below the water table. The height of the bottom of the ppols was measured along the three grid lines, profiles of which are shown in figure 6.

Data for figures 4 - 7 were obtained by measuring the depth of peat at the same positions as the surface levelling. Additional measurements were made between grid lines where it was apparent that there was an abrupt change in height of the mineral ground. Owing to the steep slopes of the mineral ground it was only possible to draw contours at 1 ft. (30.4 cms.) intervals.

All figures obtained were related to the height of a mark chiselled on a granite rock (at point 519E 299N). This arbitary datum is represented by the contour line at 20 ft. on the maps but the relation of this height to O.D. is not known. Other measurements of height made during the course of hydrological investigations are also related to this datum. Similar methods were used in the case of the small pool networks near Long Loch.

Orientation of pools (figure 11) was measured in the field with a compass.

Appendix 2: Production of low-level aerial photographs

In order to record the present morphological features and vegetation of the pool networks and to produce accurate large scale maps of these, it was necessary to take low level aerial photographs since no existing photographs were suitable for this purpose.

The method adopted is an adaptation of that described by Edwards and Brown (1960). A camera was supported by means of a 700 g. rubber meteorological balloon, inflated with hydrogen to a diameter of 2 - 2.5 m. A single nylon line was attached to the neck of the balloon, by means of which the balloon could be guided from the ground. The camera, a 35 mm. 'Robot' automatic, was mounted, together with a solenoid, on the base of an aluminium frame suspended from the neck of the balloon, by a rigid aluminium rod about 50 cm. in length. A lightweight three-core electric cable was connected to the terminals of the solenoid and passed up to the neck of the balloon where it was attached, the main part of this cable descending to the ground. At the lower end the cable was plugged in to contacts on a box containing batteries, which was carried by the operator. The solenoid was operated by pressing a switch on the battery-box and the electric circuit incorporated a feed-back by means of which a light on the battery-box flashed when the camera shutter operated.

The 'Robot' automatic camera has a clockwork mechanism which winds on the film and re-sets the shutter after each exposure. When fully loaded 60 frames (24 x 24 mm.) can be obtained on a film. However, the mechanism is only sufficient to wind the film on about 40 times and it was therefore necessary to lower the balloon and rewind the mechanism at that point. The light on the battery-box was automatically operated and remained on when the film was finished. Total weight of the equipment lifted by the balloon, including the balloon material itself, was 14 - 15 lbs., which required over 150 cubic feet of hydrogen to ensure a sufficient lift. The apparatus was designed for the camera to operate at a height of 200 ft. (61 m.) above the peat surface. At this height the area included in the photograph was a square with sides 112 ft. in length (about 34 m.).

It was found that completely still air was necessary to position the balloon accurately and also to ensure that vertical photographs were taken. Any air movement caused lateral drift of the balloon and periodic loss of lift. Furthermore, movement of the balloon in this way caused the camera mounting to swing like a pendulum. In still air the camera mounting remained completely vertical. Suitable conditions on the Silver Flowe were found to occur rarely and the opportunity had to be taken whenever favourable conditions occurred during the course of other work.

Photographs obtained were printed at approximately equal scales (1 : 190), this being determined by the position of cords along certain grid lines of the study area which showed clearly on the photographs. The printed photographs were then examined on a Zeiss Aero-sketchmaster by means of which the outlines of pool networks could be drawn at any required scale and slight distortion due to deviation from the vertical was corrected. The two maps of the pool networks (figures 17 and 18) were compiled in this way.

Appendix 3: Extraction of peat cores

The solid peat of the ridges was sampled by means of a Hiller corer but the *Sphagnum papillosum* covered hollows and the deep open pools each presented difficulties in the extraction of peat cores.

Aluminium tube

Hollows dominated by *Sphagnum papillosum* could not be sampled by a standard peat corer owing to the fibrous texture of the fresh *Sphagnum* peat with *E. angustifolium*, which formed the upper layers. It was found that this vegetation could be extracted by means of an aluminium tube (8 cm. in diameter), sharpened at one end, which was pushed into the vegetation with a twisting motion so that a core of vegetation was cut. The core was then extracted by placing a hand under the lower end of the tube. In this manner cores of maximum length 50 cm. could be obtained, which was sufficient to investigate the fibrous horizons concerned. The peat core was removed from the tube by means of a plunger, and was pushed out of the upper end of the tube so that contamination was unidirectional. The core was then enclosed in a polythene sheet and was carried in a rigid plastic tube to prevent damage occurring during transportation.

Special sampler for pool sites

Since the chamber of a Hiller corer becomes water filled and does not operate successfully in the soft peat immediately below the deep pools it was necessary to design a corer suitable for such material. This incorporates two rigid plastic tubes, each about 1.2 m. long with diameters of 5 and 7.5 cm., which are placed one inside the other. Attached to the outer tube at the lower end is a bevelled cutting edge the inner margin of which is continuous with the inner plastic tube. By turning the inner tube against the outer one a number of teeth are made to close across the tube forming a diaphragm just above the cutting edge. A reverse movement causes the teeth to retract into the space between the two tubes. The corer is pushed into the soft peat (with the diaphragm retracted) to a maximum depth of 60 cm. The diaphragm is then extended thereby cutting and supporting the core and the instrument extracted. If necessary a plunger was used to remove the core, as in the case of the aluminium tube.

Appendix 4: Tables showing climatic data

TABLE 1

Monthly rainfall totals (inches) and % of average monthly rainfall at Loch Dee (25/479792) during the study period

	1966 Actual monthly totals	1966 % of average monthly rainfall	1967 Actual monthly totals	1967 % of average monthly rainfall
January	6.09	56	8.01	74
February	8.27	124	8.26	124
March	10.15	181	8.77	156
April	4.62	86	5.69	106
May	6.65	126	10.02	191
June	5.28	114	3.86	83
July	2.39	38	6.46	104
August	6.71	93		
September	7.94	102		
October	7.95	81		
November	8.83	96		
December	15.60	170		
Annual Total	90.48			

The annual total for 1966 is 103.5% of the estimated average annual rainfall 1916-50 (87.36 inches)

TABLE 2

Monthly rainfall totals (inches) and % of average monthly rainfall at Clatteringshaws. (25/554780)

	1966		1967	
	Actual monthly totals	% of average monthly rainfall	Actual monthly totals	% of average monthly rainfall
January	5.86	58	7.37	73
February	9.22	146	8.43	134
March	6.40	120	7.59	143
April	5.60	118	3.83	80
May	6.23	125	9.74	194
June	4.43	102	3.06	70
July	1.85	31	6.22	105
August	6.66	97		
September	7.11	100		
October	7.51	84		
November	8.35	98		
December	13.12	150		

Annual Total 82.34

The annual total for 1966 is 100.42% of the estimated average annual rainfall 1916-50 (81.99 inches)

TABLE 3

Rainfall totals and potential transpiration for monthly periods at Clatteringshaws

	1966		1967	
	Rainfall (inches)	Potential Transpiration for months concerned (inches)	Rainfall (inches)	Potential Transpiration for months concerned (inches)
January	5.86	0.0	7.37	0.0
February	9.22	0.3	8.43	0.3
March	6.40	1.2	7.59	1.2
April	5.6	1.7	3.83	1.9
May	6.23	3.35	9.74	2.65
June	4.43	3.13	3.06	3.46
July	1.85	3.32	6.22	2.7
August	6.66	2.29		
September	7.11	1.53		
October	7.51	0.8		
November	8.35	0.2		
December	13.12	-0.05		

TABLE 4

Actual and average monthly values for net water surplus or deficit at Clatteringshaws

	Net water surplus or deficit 1966 (inches)	Average water surplus (inches)	Net water surplus or deficit 1967 (inches)
January	5.86	10.09	7.37
February	8.92	6.01	8.13
March	5.2	4.13	6.39
April	3.9	2.75	1.93
May	2.9	1.85	7.09
June	1.3	0.95	-0.40
July	-1.47	2.80	3.52
August	4.37	4.49	
September	5.58	5.48	
October	6.71	8.14	
November	8.15	8.33	
December	13.17	8.82	

TABLE 5

Maximum rainfall, expressed as a percentage of average monthly rainfall, at which a net soil water deficit will just occur (based on average monthly values for rainfall and potential transpiration); to indicate those months when deficit is most likely.

	Percentage of average monthly rainfall	
	Clatteringshaws	Loch Dee
April	42.1	37.52
May	63.0	60.1
June	78.2	73.4
July	52.5	50.0
August	34.8	33.5
September	23.14	21.2

Appendix 5: Darcy's Law and Hydraulic Conductivity

If open tubes are inserted at two points in uniform saturated soil through which water is passing, the difference in the level of the water surface in the two tubes will give the difference in hydraulic head between these two points. Water will move from the point represented by the high level towards the low. The difference in head, ΔH, divided by the distance between the points, Δl, is the hydraulic gradient. It is known empirically from the work of Darcy in 1856, that the volume, V, of water flowing across unit area of cross-section of soil in unit time is proportional to the hydraulic gradient, i.e.

$$V = k. \Delta H/\Delta l$$

The constant k, from analogy with similar equations for flow of heat and electricity, has been termed the hydraulic conductivity (Richards 1952). It is commonly expressed in units of cm/sec or cm/day in mineral soils. The value k varies not only with the texture of the soil but also with viscosity and potential of the fluid, though for soil-water systems over the normal range of field temperatures above freezing point the effects of these two factors may be ignored. The value k can therefore be regarded as constant for soils of a given texture. It has been recommended (Richards 1952) that the word permeability should continue to be used qualitatively to represent the quality or state of a porous medium, relating to the readiness with which it conducts or transmits fluids.