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ON THE DEER-GRASS, *TRICHOPHORUM CAESPITOSUM* (L.) HARTMAN

by

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CONTENTS

ON THE DEER-GRASS, TRICHOPHORUM CAESPITOSUM (L.) HARTMAN

by H.A.P. Ingram.

Abstract

The species has been examined from an ecological standpoint, by comparing it with *Molinia caerulea* (L.) Moench, an alternative dominant of Scottish "blanket bog".

Of the two recorded subspecies, only ssp. *germanicum* and intermediates of uncertain status appear to survive in Britain.

A floristic description is given of the transition from dominant *Trichophorum* to dominant *Molinia* in an area typical of the N-W Highland region. Following "muirburn", both species reproduce from seed. The successful establishment of a *Trichophorum* seedling eventually produces a single tussock.

Edaphic factors appear to control the distribution of the two species. An account is given of a polarographic survey of soil oxygen, and a survey of groundwater movement based on applications of Darcy's law. The transition from *Trichophorum* to *Molinia* is accompanied by a striking increase in the rate of horizontal water movement.

An hypothesis is advanced whereby the groundwater acts as a vehicle of mineral nutrition. Productivity studies show that the rate of uptake of nutrients by adults is similar in the two species. A stagnant body of groundwater, supplying nutrients slowly, limits the early development of the relatively large *Molinia* seedlings, allowing successful establishment of the much smaller seedlings of *Trichophorum*. Moving groundwater, enhancing the mineral supply, permits luxurient development of *Molinia* seedlings, whose shade limits the development of *Trichophorum*. Ion exchange sites in the peat may form an intermediate nutrient reservoir.

Experiments to examine this hypothesis included one in which seedlings of *Trichophorum* were grown in competition with those of *Molinia*. The growth of *Molinia* was limited more by nutrient availability than by plant density. The growth of associated *Trichophorum* varied inversely with nutrient availability, due apparently to competition from *Molinia*. Other experiments and observations suggested light as the limiting factor for *Trichophorum*. The effects of soil aeration were not significant.

Some suggestions are included for improving techniques for the *in situ* estimation of soil oxygen.

September, 1964.

NOTE ON NOMENCLATURE

Except in the taxonomic discussions of Chapter I, authorities for the plant names mentioned here have been omitted. The names conform to usage in the following works:-

CLAPHAM, A.R., TUTIN, T.G. and WARBURG, E.F., 1952
"Flora of the British Isles"
London, Cambridge University Press.

PROCTOR, M.C.F., 1955
A key to the British species of *Sphagnum*.
Trans. Brit. Bryol. Soc. 2, 552-560.

WATSON, E.V., 1955
"British Mosses and Liverworts"
London, Cambridge University Press.

INTRODUCTION

The principal concern of the plant ecologist is to arrive at an understanding of the processes which have led to the presence of a particular growing plant in a particular place. It is a fact of common experience that the various species of our flora are not randomly distributed, but that there exists a definite relationship between the flora and its environment which manifests itself in a limitation of any given species to a particular, more or less easily defined set of habitats. The situation is complicated by the fact that a species is rarely found growing in pure stands. Instead, vegetation is normally an aggregation of species, but even so, these species are normally grouped together in particular combinations to form communities, often recognisable over a wide area and providing further evidence of a definite relationship between flora and environment.

The composite nature of vegetation makes the analysis of the distribution of plant communities a difficult undertaking. For this reason it is often found convenient to study instead the distribution of single species or of single ecotypes within a species. The approach to be adopted in such an autecological study depends upon the species concerned. Questions which it may be relevant and fruitful to ask about the ecology of *Polemonium caeruleum* in Britain may not necessarily be the same as those which should be asked about *Quercus* or *Calluna* which are much more common.

An autecological investigation frequently starts as an exercise in correlation. At this stage the investigator attempts to decide what features of the environment are distributed in the same way as the populations whose distribution he is attempting to understand. The demonstration of a correlation, however close, does not in itself imply a causal connection between the factor concerned and the population in question. The establishment of such a connection is usually a matter for experiment.

Experimental autecology has usually confined itself to an analysis of the development of plants* either in isolation or in pure stands, under varying incidence of the factor or factors which correlations have shown to be most probably controlling their distribution. The implication behind this type of experiment is that it attempts to answer the question, "Under what circumstances does the plant P attain its optimal development?" "Optimal" development may not be easy to define: the greatest dry weight may not produce the largest number of seeds, and it is not always easy to see whether these quantities aught to be evaluated per plant or per unit area. Granted a suitable definition of this term, however, it frequently remains difficult to see the relevance of such experiments, interesting though they may be to the

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* The word 'plant' is here used in the sense of the particular species or genetic race whose ecology is being investigated.

physiologist or the agronomist, in the context of natural and semi-natural vegetation. It is well known that a wild plant, transplanted to the garden or greenhouse, grown in fertilised compost, weeded and watered by a skilled gardener, may flourish as never before. Under natural conditions, plants frequently never attain optimal development, and may never be found under conditions in which such development would be possible.

The reason for this seems to be that a plant is frequently excluded from the habitat in which it could attain optimal development by competition from other plants. Tansley (1917) showed that competition played a vital part in determining the distribution of _Galium hercynicum_ and _G. pumilum_, and the point has since been emphasised by Lazenby (1955), Clapham (1956), and Clymo (1960, 1962). On a consideration of this work, it appears to be more ecologically relevant to ask the question "How does the environment act to control the replacement of the plant P by the plant Q?" The question now becomes one of comparison between the ecological behaviour of two or more species, ecotypes etc. and the method must be to determine how a varying incidence of the relevant factors affects the outcome of competition between them. De Wit (1960) has shown that, while the competitive behaviour of plants in general may be satisfactorily understood and described by suitable theoretical models, it is impossible to predice the outcome of competition in any particular case by means of experiments on pure stands alone. P and Q must be grown together in mixtures.

What of the choice of material? Our understanding of the ecology of Quercus in Britain is hardly likely to be much improved by comparing it with Juncus trifidus or even with Endymion non-scriptus, but we shall gain much from a comparison between Quercus and Fagus, or between Quercus robur and Q. petraea. The comparison must be relevant, made between pairs of forms which play a similar part in plant communities, which replace each other as the environment changes and which may truely be described as "ecological alternatives".

The present study concerns Trichophorum caespitosum. In Britain this species is found in the most oligotrophic mires. It is a widespread species, behaving as a physiognomic dominant in certain areas of Scotland and Ireland. In these areas it invites comparison with a number of other species of similar sociological status whose populations march with it. On drier soils it gives way to Nardus and Festuca. On wetter soils it is replaced by various species of Carex and by Eriophorum vaginatum. On more eutrophic soils Molinia becomes more abundant. In the belief that its ecology may be defined in terms of its relationship with such comparable species, attention has been directed towards the manner in which the environment controls its replacement by the latter two species, especially by Molinia.

CHAPTER I

Observations on the biology, taxonomy and variation of Trichophorum caespitosum in Britain

Although the present account is chiefly concerned with aspects of the ecology of Trichophorum, the species presents a number of other features which are both interesting in themselves and relevant to an understanding of its distribution.

Life history and general biology.

As its specific epithet implies, Trichophorum caespitosum is, in common with a number of other monocotyledonous mire plants, generally found to form tussocks. The origin and construction of these does not appear to have been described in detail, possibly on account of their compactness and apparent complexity. Metsävainio (1931) merely mentions the existence of a rhizome, but does not elaborate. A brief description is given by Heath and Luckwill (1938). The description which follows is based upon some material from Abernethy Forest in Strath Spey which was of exceptional luxurience, with rhizome internodes of sufficient length to enable the structure to be understood.

Fig. 1.1 is a diagrammatic representation of a rhizome apex as it appears in March. Seven internodes comprise one seasons' growth. The three lowest nodes bear short, rather broad, leaf-like scales whose insertions do not completely encircle the rhizome. There follows a series of progressively longer cylindrical sheathes with annular insertions. Initially each sheath is entire up to the membranous distal margin, but

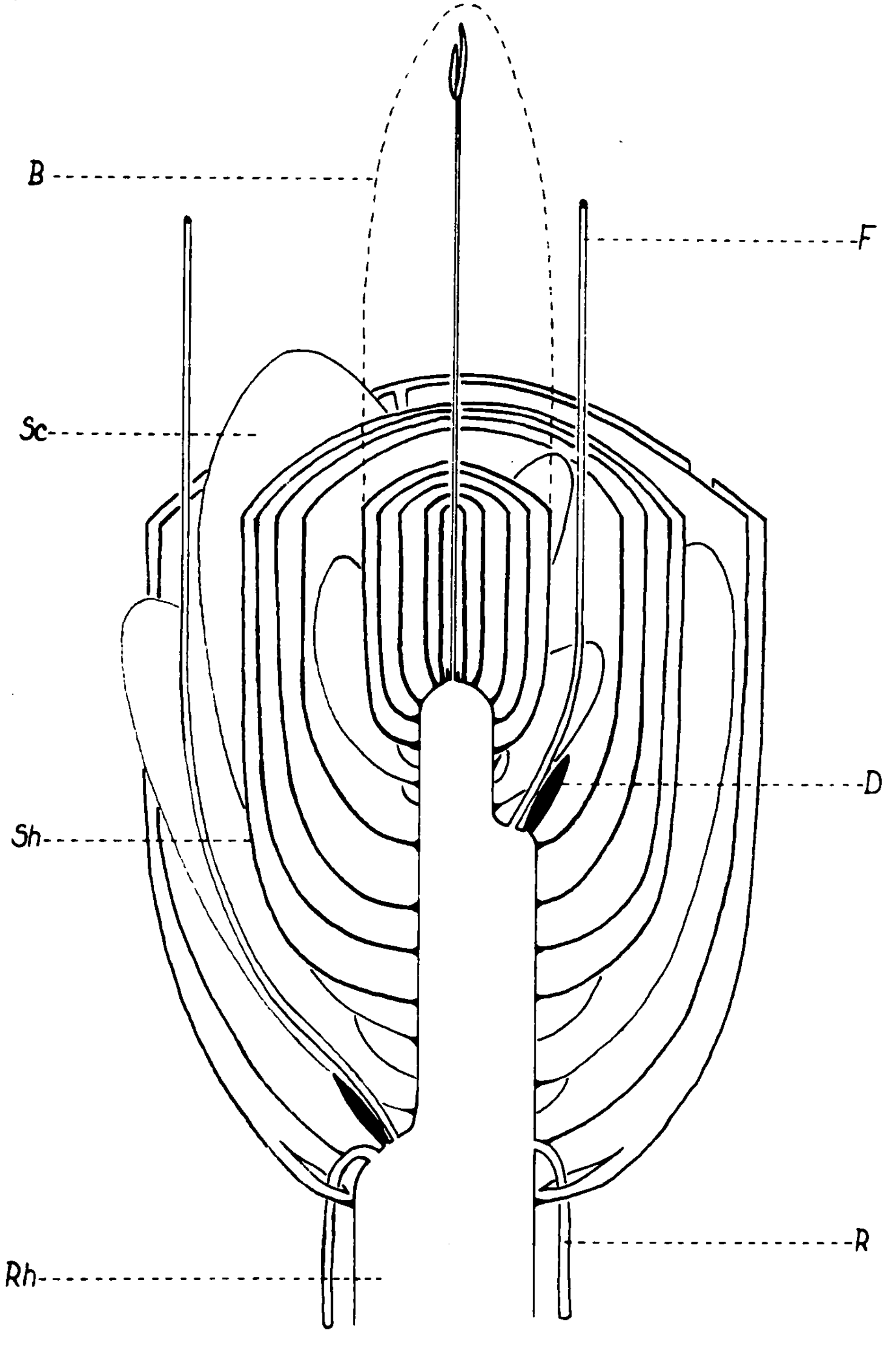

Fig. 1.1 Diagram to illustrate the distal portion of an overwintering rhizome (Rh) of Trichophorum caespitosum, showing the roots (R), scales (Sc), sheathes (Sh), and flowering stem (F) of one season's growth and the overwintering bud (B) from which next seaso's growth arises.

eventually a split develops down the side opposite the leaf rudiment. The leaf rudiment of the topmost sheath is a conspicuous peg-like structure. This sheath subtends the flowering stem and two buds. During the winter, one of these buds (Fig.1.1) develops slowly to form one of the hard green, pointed structures which cover the tussock in early spring. The following season's growth is accompanied by the extension of the internodes of this bud. The other bud usually remains dormant (Figs. 1.2, 1.3) but occasionally both may develop, in which case the rhizome branches (Fig.1.4). It is not known how long this second bud remains viable if branching does not take place, but it is possible that the prolonged survival of such growing-points, situated deep within the tussock, may be a factor contributing to the resistance of the species to "muirburn".

Roots arise adventitiously from the base of the elongating rhizome (Figs. 1.2, 1.4). Usually, two roots are produced annually, appearing near the junction between flowering stem and rhizome. They grow closely appressed to the rhizome, splitting each successive sheath of previous years near its insertion, until eventually they emerge from the base of the tussock into the underlying peat, which may well comprise the remains of the older portions of the plant. The interwoven strands of the rhizome, branching vertically upwards, and the roots, penetrating vertically downwards, form a coherent cable-like structure of very considerable strength, which, unlike tussocks of *Molinia* or *Eriophorum*

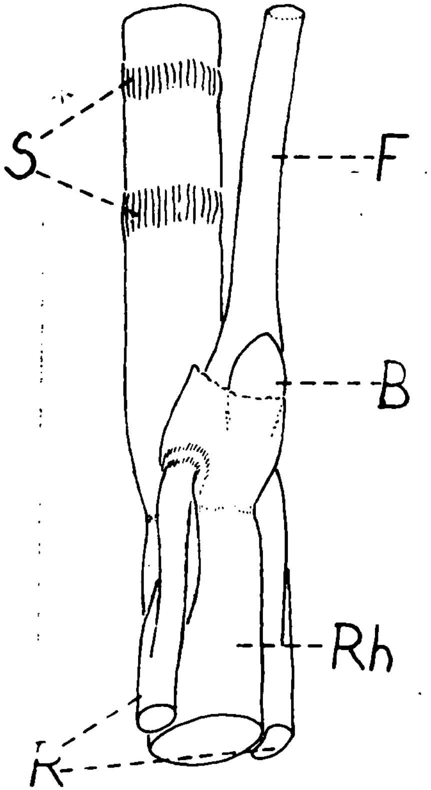

Fig. 1.2 Rhizome (Rh) of *Trichophorum caespitosum* with scales and sheathes(insertions at S) removed to reveal adventitious roots (R), dormant bud (B) and base of flowering stem (F).

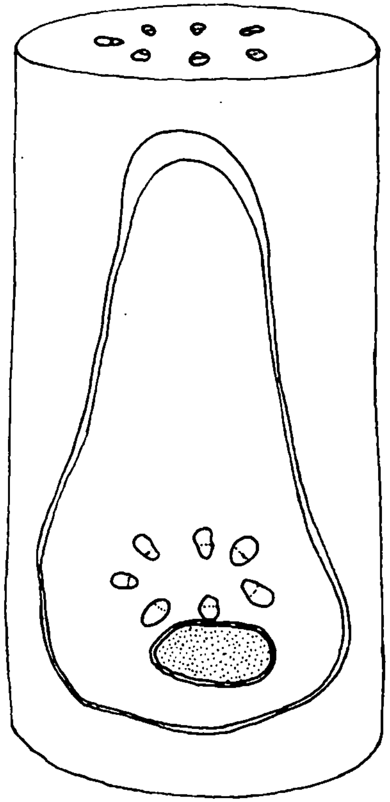

Fig. 1.3 Rhizome as Fig. 1.2, but with flowering stem cut out to show its vascular tract(stippled) together with the seven vascular bundles of the rhizome.

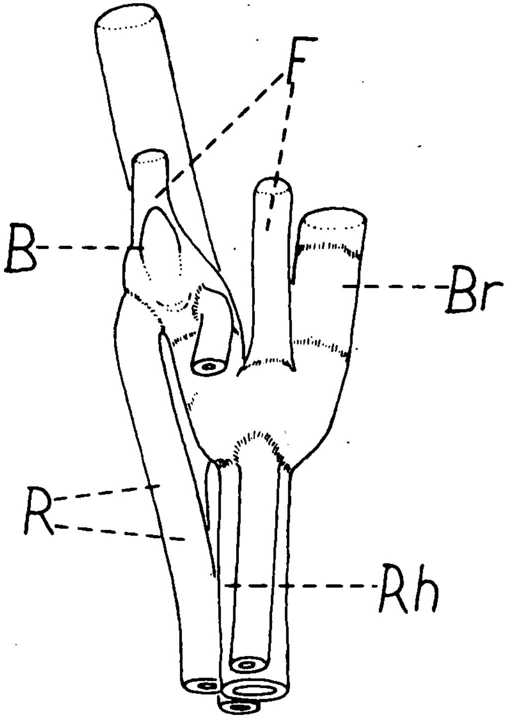

Fig. 1.4 Rhizome of *Trichophorum caespitosum* with scales and sheathes removed to reveal branch (Br) consequent upon the development of a bud such as that shown in Fig. 1.2. Other lettering as Fig. 1.2.

vaginatum of similar size, is almost impossible to uproot by pulling alone. The structure of the roots was described by Metsävainio (1931) from whose account they appeared very similar in anatomy to those of Eriophorum vaginatum. They are abundantly provided with "aerenchyma". This author found "mycorrhiza" in the roots of second and higher order of some specimens from Finland. Heath and Luckwill (1938) report a similar observation, presumably on British material, but since Metsävainio's very detailed observations suggested that the presence of fungi was by no means universal, and since none of the symptoms associated with the absence of an obligate mycorrhizal association have been met with during the course of experiments on such artificial media as Vermiculite, the ecological significance and true nature of these associations remain obscure.

Flowering occurs almost immediately after the spike has emerged from the overwintering bud at the beginning of the annual period of vegetative growth (Mid-April in North Wales, Mid-May in North West Scotland). The florets, of which there are normally six to seven per spikelet, are markedly protogynous. Occasionally some clones have been observed to be functionally dioecious but these have been kept under glass or polythene and the condition is not thought to occur in nature. In North West Scotland the nuts are ripe by early August, by which time the glumes have fallen from the fertile infructescences. At this stage it is usually found that the lowest one or two florets of a spike are infertile, bearing only the whitish remnants of the scarcely swollen ovary, but in exceptional cases a single spike may yield ten or more ripe nuts. The nuts are generally shed in late August or September, but in sheltered places they may remain attached to the infructercence axis as late as November. The agitation produced by wind may finally be responsible for dislodging the nuts. The perianth bristles are persistent, remaining attached to the base of the nut for more than a year after it has fallen. They are beset with minute papillae and cause stored seeds to form somewhat cohesive masses. It is tempting to suppose that their adhesion to sheep's wool etc. may bring about dispersal of the nuts by animals. No direct evidence supports this theory, but it presents a possible explanation of the frequently observed concentration of <u>Trichophorum</u> along tracks across English and Welsh bogs, where the species is otherwise scarce.

Germination occurs, in the greenhouse, during the last week in April or the first week in May of the year following dispersal. The dormancy mechanism has not been investigated in detail but nuts stored dry at room temperature show poor germination, while those exposed to hard frosts while moist may show 80-90% germination (percentage of nuts selected on the basis of size, colour etc. as being likely to be viable). No germination took place when nuts were kept in the dark under otherwise favourable conditions.

The appearance of a seedling at the five-leaf stage, which is

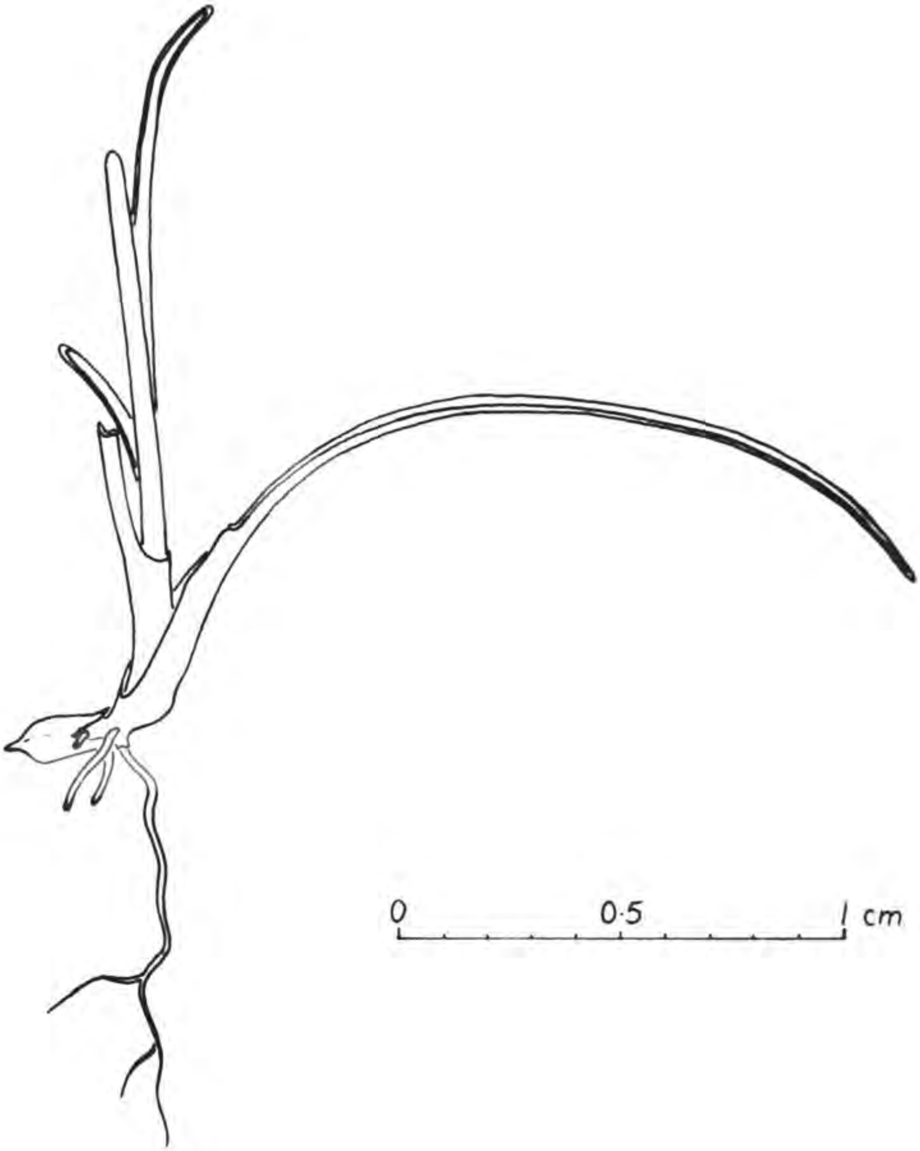

Fig. 1.5 Seedling of Trichophorum caespitosum, 1½ - 2 months after germination. Roots largely omitted.

Fig. 1.6 Seedling of Trichophorum caespitosum at 10 months (i.e. during first winter). Roots largely omitted. This plant already has 4 overwintering buds. The luxuriance of this plant may be ascribed to growth in garden comfort in a greenhouse.

attained by Mid-June, is shown in Fig. 1.5. The seedlings differ from adult plants in the possession of distinct leaves with sheathing bases later splitting on the adaxial side, and laminae which are flattened proximally somewhat triangular distally, and channelled on the adaxial side. From Fig. 1.6, it may be seen that, by the first winter, the juvenile rhizome already possesses several growing points and that overwinteringbuds of similar appearance to those of the adult have been produced. In an unheated greenhouse the structures which emerge from these buds during the second year are similar to those of the first year, namely foliage leaves, although the lowest internodes bear scales as in the adult. In the third year some stems may be produced bearing rudimentary inflorescences, but the plants do not bear normalspikes until the fourth year, by which time the leaf laminae of the juvenile are reduced to the peg-like structures born on the uppermost leaf sheathes. At this stage the plants have assumed the caespitose habit of the adult, and may have thirty or more stems.

From the life history of the juveniles and the sympodially branching rhizomes of the adult one may conclude that the tussock of Tricophorum is normally a clone, derived from a single seedling. Tussocks do not generally show any tendency to depart from an approximately circular shape, or to die off in the centre, and, although a single very large clone may occasionally become split into two distinct daughter tussocks, reproduction by vegetative spread and fragmentation is not the normal method of colinisation in Trichophorum.

It is naturally somewhat difficult to obtain reliable data on the longevity of a Trichophorum tussock. Under present conditions it is likely that the life of Scottish populations is limited by the length of time elapsing between successive severe 'muirburns' rather than by 'natural' factors. The largest tussocks so far encountered were growing in a bog south of Loch Mallachie in Strath Spey. A typical example measured 33cm. x 22 cm. across the base, and was estimated to have borne just over 4,000 stems during 1962. A local farmer thought that the area had last been burned in about 1940. The presence of Calluna stems with 26 annual rings suggests that it is unlikely to have been burned since that date but was probably burned earlier, and gives some idea of the probable date of establishment of the larger Trichophorum tussocks. Tussocks of such size and presumed longevity are not found in the North West Highlands, where it appears to be rare for ten years to elapse between intensive muirburns.

The two subspecies

Palla (1897) divided Trichophorum caespitosum into two species, which he called Tr. austriacum and Tr. germanicum. Later opinion has reduced these taxa to the rank of subspecies. Palla was led to the view that Tr. caespitosum comprises two distinct taxa on the basis of a study of the anatomy of the flowering stem in transverse section, but he also noted certain distinctions in external morphology which were often correlated with anatomy. The distinctions may be summarised as follows:-

Ssp. caespitosum (Ssp. austriacum (Palla) Hegi)	Ssp. germanicum (Palla) Hegi.
Chlorenchymatous sectors of stem cortex appearing entire and homogeneous in T.S. Tannin cells absent. Sub-stomatal air spaces conspicuous, 20-26µ.	Chlorenchymatous sectors each traversed by 'usually two) longitudinal strands of 'aerenchyma'* consisting of rather larger cells with thin, evanscent walls resembling those of the inner medulla. Conspicuous darkly pigmented tannin cells present in the chlorenchyma. Sub-stomatal air spaces small, 6-6.5µ.
Usually shorter and more delicate. Opening of uppermost sheath only slightly oblique, scarcely more than 1 mm. lower on the adaxial side than at the insertion of the lamina, the hyaline margin narrow, pale yellow or yellowish-brown, rarely pale red, tightly embracing the stem. Spikes smaller, with fewer flowers, Distal portion of perianth bristle generally smooth.	Generally taller and more robust. Opening of uppermost sheath markedly oblique, up to 3 mm. lower adaxially than at the insertion of the lamina, the hyaline margin broad, conspicuous tinged with red flecks, clasping the stem loosely or completely free from it. Spikes rather large, many flowered. Distal portion of perianth bristle distinctly papillose.
European mountain chains and North America.	Lowlands of Central and Northenn Europe.

Palla regarded the anatomical distinctions, which are very striking in typical material, as being of primary importance. The other features are less obvious, less clear cut and less consistent. There has been an unfortunate reluctance on the part of some taxonomists to recognise the subordinate character of the morphological criteria, and their use

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* In the account which follows, these are referred to as 'cortical lacunae'.

in isolation has led to a certain amount of confusion. For instance Ostenfeld (1912) reported finding two populations of Ssp. *caespitosum* in Britain and Ireland, but when his specimens were recently examined anatomically, both appeared typical of Ssp. *germanicum*. S.M. Walters examined various collections from the British Isles during the years following the second World War. He concluded that most British material was referable to Ssp. *germanicum*, but that Ssp. *caespitosum* occurred on Ingleborough and Ben Lawers, a finding quoted by Clapham *et al* (1952).

At an early stage of this investigation, it became clear that a complete analysis of the status of the two subspecies would form a major project in itself, neccessitating an extensive collecting programme which would have been incompatible with the ecological objectives. It was, therefore, decided to confine this aspect of the work to the examination of readily available herbarium specimens, together with material collected during the course of the ecological work. For this purpose, short lengths of flowering stem were softened and transverse sections cut by hand from the region opposite the tip of the leaf-rudiment on the uppermost sheath. The results of examining these sections may conveniently be summarised in terms of the appearance of (i) the sub-stomatal spaces, (ii) the cortical lacunae, (iii) the tannin cells. With regard to these features, the material could be classified into three categories:-

(1)	Typical Ssp. *caespitosum*	3 collections
(2)	Intermediate	14 collections
(3)	Typical Ssp. *germanicum*	130 collections

Of the typical Ssp. *caespitosum*, two collections were from near West Felton, Shropshire, by Babington (1834) and Leighton (1840) and the third was from Balerno, Midlothian, by Evans (1878) Subsequent search of moorland near Balerno has so far failed to reveal any *Trichophorum*. The intermediate forms are of considerable interest showing features typical of Ssp. *caespitosum* as follows: all had large sub-stomatal spaces; in 9 the cortical lacunae were weakly developed or absent; in 4 there were no tannin cells. Their distribution may be summarised as: Co. Kerry, 1; Lancashire 2; Lanarkshire 1; Midlothian 1, Arran 2; Aberdeenshire 1; Perthshire 6;. Many showed an approach to Ssp. *caespitosum* in external morphology, having previously been identified as that subspecies by Walters, but whatever may be the situation on the Continent, British material which, on anatomical grounds, is clearly referable to Ssp. *germanicum* shows so much variation in the relevant details as to make the external morphology totally unreliable when used alone.

The concentration of intermediate forms in Perthshire, which was, despite its great botanical interest, not noticeably over represented in the collections examined, may be significant. The Continental regions from which Ssp. *caespitosum* is recorded are particularly well represented floristically in this area and it is possible that we are here witnessing the results of introgression from some extinct or hitherto undiscovered populations of this subspecies.

This investigation has tended to confirm the conclusions of Walters in regard to the predominence of Ssp. germanicum in Britain, but has not produced direct evidence of the survival of Ssp. caespitosum into the present century. The ecological work described here should be taken as referring to Ssp. germanicum.

Chromosome number

Clapham et al (1952) quote 2n = 104 for Trichophorum caespitosum Ssp. caespitosum . This appears to be based upon the work of Sheerer (1940). Sheerer made no mention of the two subspecies in his paper, so there appears to be no justification for supposing that the count referred to Ssp. caespitosum. In view of the fact that the material came from Schleswig-Holstein, on phytogeographical grounds it is more likely to have been Ssp. germanicum.

Due to the presence of a tough root cap sheath, it has proved impossible to obtain favourable material of mitosis. Flower buds have been fixed at various times of the year, but [illegible] attempts to observe meiosis have been frustrated by the fact that it apparently occurs very quickly, so that for a long period even the correct time of the year remained obscure. Eventually, however, meiosis was observed in pollen mother cells from material of Ssp. germanicum collected from near

Roundstone, Connemara and fixed in acetic alcohol on 4th May 1963. A preparation stained by the Feulgen technique showed n = 52, thus confirming Sheerer's observations.

Variation

Apart from some of these features of its external morphology and internal anatomy which have been discussed in connection with the subspecies problem, Trichophorum caespitosum does not present many features which lend themselves to exact quantitative description. Nevertheless it is apparent that under natural conditions the stature of the flowering stems varies considerably, and the possibility arises that this variation may not be due entirely to the effect of the habitat, but that even within material clearly referable to Ssp. germanicum there may be appreciable genetic variability. At an early stage of these investigations, material of widely differing stature (flowering stem from tip of leaf rudiment to base of spikelet varying in length between 5 and 41 cm.) was transplanted to a mixture of one part John Innes Potting Compost to one part garden peat. It was found that the best establishment took place when a portion of a tussock bearing about one dozen flowering stems was used. This experiment was of an exploratory nature only, since time could not be spared to collect large quantities of material from numerous localities. All the transplanted stocks were kept in a single large seed box, ensuring the maximum environmental uniformity. After three seasons' growth stocks had converged, judged on the basis of length of flowering stem, suggesting that wild populations may exhibit a considerable degree of phenotypic plasticity. On the other hand, stocks of initially similar stature did not necessarily react in the same way to the "standard" environment: while some increased in stature, similar stocks from different localities decreased. This suggests that the phenotypic plasticity is superimposed upon genetic variability, as might be expected in an abundant species with a wide geographical range. This conclusion, introducing as it does the possibility of ecotypic differentiation, is the principal reason why the ecological investigations have been confined to a comparatively small area and to a limited aspect of the ecology of the species.

CHAPTER II

The Phytosociology of Trichophorum, Molinia and Eriophorum vaginatum with special reference to North West Scotland

A detailed and extensive phytosociological survey of all the associations* in which Trichophorum caespitosum is found is beyond the scope of the present enquiry. We are here concerned only with those associations in which the species occurs as a dominant, and with the associations most closely related to these. Before describing the communities upon which this study is mainly based, it therefore seems particularly advisable to give a brief résumé of other work on similar vegetation.

The earliest British description of communities dominated by Trichophorum caespitosum appears to be that of Pethybridge and Praeger (1935) who worked in the Wicklow Mountains. The vegetation of part of this area has recently been described again by Moore (1960) and will be discussed below. Hardy's survey (1905) of Scottish vegetation can scarcely have omitted some reference to Trichophorum, but this work is not readily available and is rarely quoted. Lewis (1908) briefly mentioned that an association similar to that of Pethybridge and Praeger occupied large areas in the Northern and Western highlands and islands

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* In this dissertation, the term 'association' is used in the sense of Tansley

of Scotland, but according to the account which he and Moss contributed to Tansley (1911) no descriptions of the Scottish communities were available at that date.

In the North Yorkshire Moors, Elgee (1912, 1914) found that dominant *Trichophorum* was confined to wet heaths on a small portion of the Cleveland watershed near Kildale. Recent observation suggests that such communities are now more widespread, but no detailed description has been published. Moss (1913) listed the *Trichophorum* association among the vegetation types of the Peak District, but made no further reference to them, beyond mentioning that *Trichophorum* is locally abundant in the retrogressive moor forming the Transitional association of the heather moor and cotton-grass moor at the edges of the Peak plateau.

Frazer (1933) gave the first detailed description of North West Scottish blanket bog communities. He worked in the district known as Inverleiver, situated on the northern side of Loch Awe in Argyll. This area lies some 130 miles South of the study-area of this dissertation, and is mainly underlain by the Loch Awe epidiorite series and by glacial drift. The topography is very rugged, the climate moist and the drainage impeded, and the vegetation of the area, as Fraser described it, resembles that of Inverpolly in many respects. Of recent years, Inverleiver has been considerably altered by afforestation and it would no longer be a convenient area for such studies. Fraser described a number of plant associations on peat soils. He regarded the Trichophorum-dominated communities as forming a climax vegetation which he named the 'Scirpus High Moor Type', and described a number of stages of development through which other associations progressed until the climax was produced. He also considered the effects of long-continued burning and grazing of the vegetation in accelerating these trends.

The plant lists given by Fraser show a close resemblance to those from similar communities at Inverpolly, though in general a comparable list from Inverpolly would contain fewer species. For instance, his list for 'Scirpus High-Moor' includes Empetrum nigrum and Deschampsia flexuosa, together with a long list of Sphagna. At Inverpolly the equivalent communities would not normally include the first two species, while the list of Sphagna would in general be much shorter. However, it should be remembered that many of Fraser's descriptions refer to sites which had been enclosed for afforestation some years previously, while most of Inverpolly has been subject to grazing and frequent burning right up to the time of writing (1963).

Tansley (1939) drew attention to the importance of Trichophorum as a physiognomic dominant of the raised bogs of Central Ireland, especially on the drier areas of the 'pool and hummock complex', and on the less undulating margins. He regards Trichophorum as "a true blanket bog dominant", in a sense in which Calluna is not. His treatment includes some valuable lists of 'Scirpetum caespitosi' from several blanket bogs in Argyll, Inverness-shire, Sutherland and Caithness. They closely resemble lists from Inverpolly, except for the presence of Juncus squarrosus in some of the less typical sites.

Godwin and Conway (1939) described a zone of dominant Trichophorum from the Cors Goch complex of raised bogs of the Teifi valley in Cardiganshire. This zone appears to resemble the vegetation occupying the surface of many raised bogs in Strath Spey, and is associated with the cessation of active bog growth and possibly also with extensive burning in the past. The size of the Trichophorum tussocks suggests long establishment, which would also account for the longer species lists, compared with Inverpolly.

Osvald (1949) described two types of British bog community in which Trichophorum played an important part. His 'Calluna-Scirpus caespitosus-Rhacomitrium Sociations' were characteristic of the most exposed dry areas of blanket bog. They appear to be an even more species-poor variant of the 'Scirpus caespitosus-Eriophorum-vaginatum Sociations' which he regarded as the typical vegetation of blanket bogs.

Pearsall (1950) discussed the distribution and importance of Trichophorum as a dominant. He drew attention to its increasing importance in bog vegetation as one proceeds northwards and westwards from the South Pennine massif into the Scottish Highlands. The account includes a list from a Trichophorum - Calluna bog on the Moor of Rannoch and diagrams of the topographical relationship of Trichophorum to other North West Highland dominants. In an account (1956) of blanket bogs in

Sutherland, this author gave lists in which Trichophorum was important, and discussed the relationship of the various vegetation types to the microtopography of the bog surface. These descriptions are of some interest in that the area concerned lies only about 50 miles North-East of Inverpolly, but the topography of the latter area does not generally permit the development of such large expanses of deep peat.

Moore (1960) gave an account of a re-survey of the vegetation of the Wicklow Mountains, fifty years after the date of the original survey of Pethybridge and Praeger (1905). Considerable areas of these mountains are covered by bog vegetation and most of this was ascribed to the Trichophorum-Sphagnum nodum which is floristically similar to the Trichophorum-dominated communities at Inverpolly. From the point of view of the present work, this community is principally of interest because, firstly it is developed at much higher altitudes than in Scotland (Moore's stands lie between 1500 and 2120 ft. OD. whereas at Inverpolly the community attains its principal development at altitudes below 1000 ft.) and secondly it has remained virtually unchanged during the past 50 years, although there is no evidence of the heavy grazing and frequent burning which appear necessary in order to maintain the dominance of Trichophorum in North West Scotland. Moore also included a valuable table in which the classification of bog vegetation proposed by various authors was compared.

The most complete floristic analysis of Scottish blanket bog by modern methods was recently completed by McVean and Ratcliffe (1962).

Their treatment, which is based on extensive experience and on data from many parts of the Highlands, agrees closely with the present author's views, and it is principally for this reason that the usual plant lists have been omitted here.

The communities to be considered in this dissertation were classified by McVean and Ratcliffe into the following noda:-

(i) Trichophoreto-Eriophoretum typicum (Western blanket bog)
(ii) Calluneto-Eriophoretum (Pennine blanket bog)
(iii) Trichophoreto-Callunetum (*Trichophorum*-*Calluna* bog)
(iv) Molinieto-Callunetum (*Molinia*-*Calluna* bog)
(v) Trichophoreto-Eriophoretum caricetosum (*Trichophorum*-*Carex* mire[*])
(vi) *Molinia*-*Myrica* nodum.

Of these, (i) - (iv) are regarded as true ombrogenous bog communities whila (v) and (vi) are classified as soligenous mires. Their floristic features may best be summarised by a table showing constant species and average number of species present in the stated number of stands (Table 2.1).

These six noda intergrade with each other and together account for the larger part of the mire vegetation of Inverpolly. They are all

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[*] The present author disagrees with the use by MdVean and Ratcliffe of the term 'mire' to denote the communities of waterlogged soils whose nutrient régime is topogenous, in contrast to, e.g. 'bog'. The word 'mire' is here used in the generally accepted sense to denote any vegetation of waterlogged soil, whether bog, fen, or marsh.

Table (2. 1).

Constants of certain Scottish mire communities (i - vi see text). From McVean and Ratcliffe, 1962. "X" indicates that the stated species was present in 81 - 100% of the stands.

	(v)	(i)	(ii)	(iii)	(iv)	(vi)
Average number of species present	28	23	22	17	18	18
Number of stands examined	9	12	10	12	9	9
Calluna vulgaris	X	X	X	X	X	.
Erica tetralix	X	X	.	X	X	.
Empetrum hermaphroditum	.	.	X	.	.	.
Myrica gale	.	X	.	.	.	X
Vaccinium myrtillus	.	.	X	.	.	.
Molinia caerulea	X	X	.	.	X	X
Carex echinata	X	.	.	.	.	.
Carex panicea	X	.	.	.	.	.
Eriophorum angustifolium	X	X	.	.	.	.
Eriophorum vaginatum	.	X	X	.	.	.
Narthecium ossifragum	X	X	.	.	.	.
Trichophorum caespitosum	.	X	.	X	.	.
Drosera rotundifolia	X	.	.	.	.	.
Rubus chamaemorus	.	.	X	.	.	.
Potentilla erecta	X	.	.	X	X	X
Hylocomium splendens	.	.	X	.	.	.
Hypnum cupressiforme	.	X	.	X	.	.
Sphagnum papillosum	.	X	X	.	.	.
Sphagnum rubellum	.	X	.	.	.	.
Pleurozium schreberi	.	.	X	.	.	.
Cladonia uncialis	.	.	.	X	.	.

characterised by a varying abundance of four species, namely

Calluna vulgaris
Eriophorum vaginatum
Trichophorum caespitosum
Molinia caerulea

each of which may attain dominance or co-dominance.

The status of *Calluna* can be considered apart from that of the other three. This species may, in some circumstances be an important member of most of the Inverpolly mire communities, though it is generally absent from, on the one hand, the wettest *Eriophorum* bogs and, on the other hand, the densest stands of *Molinia* where this is almost the only species present. The amount of *Calluna* present in all other situations appears to be controlled by burning. In certain parts of the reserve, which are situated above cliffs or in the vicinity of other places which present danger to sheep, it has been customary to allow *Calluna* to flourish unchecked, so that it presents an impenetrable barrier of old, dense bushes up to one metre in height. There is, as a rule, no intrinsic difference between these places and the remainder of the reserve, except that the latter areas are frequently subjected to 'muirburn'. This is the name given to the practice of setting fire to the vegetation, which is carried on everywhere in the North West Highlands as an aid to sheep husbandry. The emergent parts of most species of the monocotyledons of these mires die in the Autumn, and growth is not resumed until the following May. The resultant mass of straw, dried in the period of rainless weather which frequently occurs in the early part of the year, is easily burned in March or April. At the same time, any associated Calluna is either killed completely or burned back to the basal branches which may be protected by a deep layer of litter. Under the strict systems of management which formerly prevailed in the North West Highlands, muirburn was made on a system of rotation, every five to ten years. Each burned area would be carefully confined, and burned always with the wind. Recently, however, it has become the practice to burn more frequently than this, sometimes even anually, and often simultaneously over several square miles. Moreover, in the ensuing absence of careful supervision, it often happens that the fire advances into the wind and higher temperatures prevail for longer than would otherwise be the case. As a result of these tendencies, the protecting litter layer is rapidly removed, the Calluna plants are destroyed completely and bare peat is exposed. There is at the present time considerable controversy about the long- and short-term advantages and disadvantages of muirburn from the standpoint of animal husbandry, and the matter is being actively investigated by various workers. The question is discussed by Fraser Darling (1955), Fraser (1933), Gimingham (1960), Whittaker and Gimingham (1962) and in the reports of the Scottish Hill Farm Research Committee and the Hill Farming Research Organisation.

It will be apparent from the above that, in the communities under consideration we have to deal not with truely natural vegetation, but with a type of vegetation which may be described as 'semi-natural', in the sense that it is nearly always in process of recovery from human interference by burning. Since Calluna is largely destroyed by burning and may take five or six years to re-establish itself from seed, while the associated monocotyledons either escape destruction because of their hemicryptophyte life-form, or recolonise more rapidly from seed, the degree of co-dominance or dominance shown by Calluna varies from place to place and from time to time. This varying abundance of Calluna must, throughout the forthcoming account, be imagined to be superimposed upon the variations in abundance of the other three species, with which we are more particularly concerned.

At the beginning of the work at Inverpolly, it was hoped to investigate the ecology of Trichophorum, from a comparative standpoint, by examining its relationship, as a dominant, with Molinia on the one hand and with Eriophorum vaginatum on the other. The theoretical reasons for adopting this approach are set out elsewhere. Unfortunately, however, it has not been possible to carry the comparison with Eriophorum very far. The reasons for this are as follows.

Dominant Eriophorum vaginatum tends, in North West Scotland, to be confined to peat-covered plateaux, usually at an elevation of 1000 or more feet, OD, where it is a constituent of the Calluneto Eriophoretum of McVean and Ratcliffe (1962). This association is extensively developed on the schists east of the Moine thrust zone, which typically exhibit a plateau topography. The author has examined several examples round the head of Glen Docherty in the Kinlochewe Forest, and an example of the shrub-rich fascies in the Braemore Forest, South of Beinn Dearg. But while suitable conditions exist in the Inverpolly reserve, they are by no means widespread there. The only typical example so far investigated lies at 1000 ft. OD. near the summit of Creag nan Dearcag, a spur of Torridonian sandstone projecting westward from Stac Polly. It so happened that, in 1962 when the intensive investigations at Inverpolly began, Creag nan Dearcag had not been burned for many years. There was, therefore, an absence of the bare patches on which it has been possible to observe seedling establishment elsewhere. Moreover, seedlings of Eriophorum vaginatum resemble the adults so closely that they rapidly become undetectable as a complete cover develops. Since much of the forthcoming argument turns upon seedling establishment, it may be understood that restriction of the sites at which this process may be observed makes progress most difficult. A further difficulty arose in 1963 when an unauthorised muirburn took place over most of Stac Polly. The early months of that year were particularly dry, and this fire burned against the wind. Consequently most of the emergent vegetation including even the Eriophorum bog, which was saturated up to ground level, was completely destroyed. While this event may ultimately provide an opportunity to examine the re-establishment of the community its timing; was most unfortunate for the present purpose.

For three reasons, therefore, detailed investigations of the *Trichophorum*-*Eriophorum vaginatum* transition *per se* are omitted here, except in so far as they bear upon the *Trichophorum*-*Molinia* transition.

In contrast to the scarcity of dominant *Eriophorum vaginatum*, dominant *Trichophorum* and *Molinia* are everywhere in evidence on the reserve. This being so, a far greater range of stages of recovery after muirburn is available to the investigator of these communities and it has, therefore, been possible to select examples in which the process of establishment is most clearly shown, at sites where a transition from the dominance of one species to that of the other occurs.

Large areas of blanket bog vegetation dominated either by *Molinia* or by *Trichophorum* were examined during the early part of 1961. The districts visited included Inverleiver Forest (the area described by Fraser, 1933) Beinn Cruachan, Glen Orchy and the Black Moor of Rannoch, in Argyll, and the following areas in Ross-shire: Applecross Forest, Glen Shieldaig and Kishorn, Glen Carron and Lochrosque Forest, Kinlochewe Forest, Coulin Forest, Glen Torridon and Diabeg, Flowerdale Forest and Letterewe Forest, Strathnashellag Forest, Dundonell Forest and Braemore Forest. In general it was found that each dominant covered so large an area that it was difficult to form a clear idea of the factors which might determine their distribution.

The mosaic of *Trichophorum* and *Molinia*-dominated communities at

Inverpolly, was first examined in August, 1961. It then became apparent that

a) Places where transitions between these communities could be examined were very numerous.

b) Each community was typical of associations dominated by Trichophorum and Molinia respectively, but which had been found to form the continuous cover of much larger areas elsewhere.

c) The aerial portions of the adult plants were too well developed at this season to permit seedlings to be easily seen.

A more extensive reconnaisance of the reserve was carried out in 1962 in April and May. At this season, the ground surface is probably least obscured by vegetation or its remains since last year's litter has either partly decayed or been blown away, while the current season of vegetative growth has not begun. It was, therefore, easy to see the extent of each clone of Molinia and the more important Cyperaceae, and to distinguish seedlings which became established during the previous year. As a result of this reconnaisance, the decision was taken to concentrate these studies on the area known as Tarraigheal. This is situated between Loch Buine Moire, Loch Call an Uidhean and the two most westerly inlets of Loch Sionascaig, and is conveniently close to the road which runs through the reserve from Strath Polly to Inverkirkaig. It provides examples of blanket bog dominated by both Trichophorum and Molinia. According to Mr. Fraser, the sheep factor on the Inverpolly estate, most of the vegetation was burned here in 1957 and 1958, which means that in 1962 it had had four or five seasons in which to recover.

Some general idea of the vegetation with which we are concerned may be gathered from Table 2.2. This table is based on 19 lists which were made in the summer of 1963 (i.e. when the aerial parts of all species were fully developed). In each column is recorded the presence or absence of each of 34 species (26 phanerograms and 8 bryophytes) in a square quadrat of side 16". The quadrats were placed so as to sample the greatest possible variety of vegetation at each of four sites as follows:-

(i) M.G.1-4 Flush. *Molinia* dominant, in tussocks. Cover virtually complete.

(ii) B.T.1-5 Sloping bog. *Molinia* dominant, in lawns*. Cover incomplete (about 75-80%)

(iii) T.T.1-5 Flat bog. *Trichophorum* dominant, in lawns. Cover incomplete (about 75-80%)

(iv) N.R.1-5 Flat bog. *Trichophorum* dominant. Cover complete.

The rows of the table have been rearranged so as to facilitate comparison between the columns, and the columns have been rearranged so as to bring those with similar floristics together. It will be noted that, with the exception of List T.T.1, lists from the same site remained together. This implies that the lists were comparatively homogeneous,

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* The term 'lawn' is here used in the sense of the Scandinavian ecologists.

Table (2.2).

Species lists from four sites at Tarraigheal, Inverpolly. 29 August, 1963.

X : presence; — : absence.

Melampyrum pratense, *Carex nigra* and *Drosera anglica* occurred on Transect "A" between sites BT and TT.

	MG 3	MG 2	MG 1	MG 4	BT 2	BT 4	BT 3	BT 1	BT 5	TT 3	TT 2	TT 4	TT 5	NR 1	NR 4	NR 5	NR 3	NR 2	TT 1
Sphagnum papillosum	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Hylocomium splendens	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Campylopus flexuosus	-	-	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-
Erica cinerea	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agrostis stolonifera	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Hypericum pulchrum	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Selaginella selaginoides	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus bulbosus	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix repens	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex nigra	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nardus stricta	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex echinata	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plagiothecium undulatum	X	X	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-
Pseudoscleropodium purum	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Viola palustris	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Succisa pratensis	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Festuca ovina	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-
Carex panicea	X	X	X	X	X	X	-	-	X	-	-	-	-	-	-	-	-	-	-
Myrica gale	-	X	-	X	X	X	X	X	X	-	-	-	-	-	-	-	-	-	-
Eriophorum angustifolium	-	X	-	-	-	X	X	-	X	X	X	X	X	X	-	-	-	-	X
Hypnum cupressiforme	-	-	-	-	X	X	-	-	X	X	-	X	X	X	X	X	X	-	-
Sphagnum rubellum	-	-	-	-	-	-	-	X	X	X	X	X	X	X	X	X	X	-	-
ERIOPHORUM VAGINATUM	-	-	-	-	-	-	-	X	X	X	X	X	X	X	X	X	X	X	-
Potentilla erecta	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	-
MOLINIA CAERULEA	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Calluna vulgaris	-	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Erica tetralix	-	X	-	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Narthecium ossifragum	-	-	X	X	-	-	X	X	X	X	X	X	X	X	X	X	X	-	X
TRICHOPHORUM CEASPITOSUM	-	-	X	-	-	-	X	-	-	X	X	X	X	X	X	X	X	X	X
Drosera rotundifolia	-	-	-	-	X	-	-	-	X	X	X	-	-	-	-	-	-	-	-
Polygala serpyllofolia	X	X	X	-	-	-	X	X	X	X	X	-	-	-	-	-	-	-	X
Rhytidiadelphus squarrosus	X	X	X	X	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Riccardia pinguis	-	-	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Pleurozia purpurea	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	X	-

despite the deliberate attempt to compile them from the greatest diversity of stands within the site. It also implies that certain floristic differences exist between sites, which might enable one to distinguish their vegetation if dominance data were not available. At the same time, while only *Molinia* occurs in every stand, six other species, namely *Eriophorum angustifolium*, *Potentilla erecta*, *Calluna vulgaris*, *Erica tetralix*, *Narthecium ossifragum* and *Trichophorum caespitosum*, occur in every site, and *Hypnum cupressiforme*, *Sphagnum rubellum*, *Eriophorum vaginatum* and *Drosera rotundifolia* are common to three of the sites while another eight species are common to two of them. It is therefore, clear that although these four sites are distinguished sharply by differences of dominance and of overall vegetation cover, their floristic affinities are very strong, and it is here that the value of this vegetation chiefly lies, in regard to autecological studies.

Comparison of Table 2.2 with Table 2.1 shows that all the constants listed by McVean and Ratcliffe (1962), except, of course *Cladonia uncialis* and certain constants peculiar to their Calluneto-Eriophoretum, appear in Table 2.2.

Having thus briefly summarised the relevant aspects of the floristics of the Inverpolly mire communities, it is now necessary to consider quantitatively the contributions made by the more important species. For communities composed predominantly of forbs with erect leaves it is notoriously difficult to obtain an objective quantitative estimate of the abundance of the various component species, without resorting to the use of Levy pins or some other laborious method scarcely practicable under these circumstances. In the present work, any such conventional estimate of foliage cover is open to the further objection that Trichophorum, the species upon which this study is based, has no foliage in the adult state. Consequently a Trichophorum tussock which may occupy an appreciable area of ground surface, to the virtual exclusion of all other species, may in fact contribute far less aerial material per unit area of ground than a species such as Molinia, in which stems occupying a much smaller area of ground surface may carry a considerable area of leaf. The leaf-area index (Watson, 1956) or its equivalent in the case of a leafless species such as Trichophorum, is likely to be of considerable importance in so far as it affects interference between those different components of a community which are in competition for light. The aerial biomass is likewise important where questions of yield are concerned, and this aspect will be discussed more fully below. However, while these parameters provide important information, it was considered that the relative contributions of the various species could be most conveniently assessed by an estimate of the basal area occupied. Basal area may be defined as the area of ground surface through which the aerial parts of a plant emerge. (Greig Smith, 1957, 6-7). Such an estimate, being independent of the morphology of the aerial parts, gives a more reasonable basis for comparisons between the monocotyledons concerned. It also happens to afford a satisfactory comparison with the Ericaceous shrubs, since these were, at the time, in the early phase of growth in which they form compact masses of parallel ascending branches not more than 6 cm. in height. Attention has already been drawn to the ease with which such features may be observed in vegetation whose chief components have aerial parts which die off in the autumn, if it is possible to make the observations in early spring.

Data on basal area were collected in May, 1962 from Tarraigheal and from Creag nan Dearcag, the latter being included here for purposes of comparison. The method involved the use of a 6" x 6" grid of 36 1" squares, and the basal area was estimated by counting the number of 1" squares through which the aerial parts of the species concerned passed when the grid was placed flat on the surface of the peat or Sphagnum. For the Sphagna, the number of squares occupied by a vertical
n/ projection of the conal tufts was recorded. The results for thirteen of the most abundant phanerograms and for the Sphagna, are presented as Table 2.3.

Before considering these results, it is necessary to mention certain difficulties.

The number of squares recorded for a species is a better estimate of basal area if the species occurs in large clones than in small ones,

Table (2. 3).

Inverpolly. 2-3 May, 1962. Distribution of certain important species, recorded as the number of 1" squares of a 6" by 6" grid in which the base of the aerial portion of a species occurs. ("-" denotes no search made for the species).

(Data for Drosera, Polygala and Potentilla untrustworthy. See text.)

	Tarraigheal. Transect "A". Numbered positions															
	1				1a				2				4			
Myrica gale	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0
Calluna vulgaris	0	0	5	3	1	5	0	0	2	8	8	7	9	8	7	1
Erica tetralix	8	2	7	4	4	4	8	7	12	11	5	6	6	9	1	6
Molinia caerulea	9	5	9	4	3	9	7	4	11	4	9	9	19	13	11	9
Trichophorum caespitosum	7	29	20	24	20	22	21	26	11	13	10	8	1	2	15	12
Eriophorum vaginatum	3	1	2	8	2	1	3	1	4	2	4	0	0	0	0	0
Eriophorum angustifolium	0	0	0	3	6	1	4	3	0	0	0	0	0	0	3	0
Carex panicea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Narthecium ossifragum	11	6	16	10	20	26	15	11	16	9	19	21	10	0	0	0
Drosera anglica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drosera rotundifolia	0	0	0	0	0	0	2	3	0	0	1	2	0	0	0	0
Polygala serpyllifolia	0	0	0	0	0	1	3	0	0	0	0	1	0	1	1	0
Potentilla erecta	0	0	0	0	0	0	0	0	1	2	3	3	1	0	1	0
Sphagna	0	0	0	9	0	7	12	0	8	17	3	8	7	0	0	0
Total plant-squares	38	43	59	65	56	76	75	55	65	66	64	65	53	33	41	28
Total Mo.,Tr.,& Eri.vag.	19	35	31	36	25	32	31	31	26	19	23	17	20	15	26	21

continued overleaf:-

Tarraigheal. Transect"A". Numbered positions

	5				6				7			
Myrica gale	2	0	1	1	1	0	1	0	0	0	1	2
Calluna vulgaris	9	13	9	18	6	7	3	8	6	3	2	2
Erica tetralix	4	7	11	10	15	7	3	2	2	3	2	2
Molinia caerulea	26	24	13	24	27	31	28	24	19	32	27	22
Trichophorum caespitosum	0	0	0	0	3	4	2	1	0	0	0	1
Eriophorum vaginatum	0	0	0	0	0	0	4	0	5	0	0	0
Eriophorum angustifolium	0	0	0	0	1	0	0	3	6	3	8	6
Carex panicea	0	0	0	3	0	1	2	0	4	3	1	0
Narthecium ossifragum	1	0	2	4	5	0	0	0	0	0	0	0
Drosera anglica	0	0	0	0	0	0	0	0	0	0	0	0
Drosera rotundifolia	0	0	0	0	0	0	0	0	0	0	0	0
Polygala serpyllifolia	0	1	0	0	0	0	0	0	0	0	0	0
Potentilla erecta	0	0	4	2	1	0	0	2	7	6	1	4
Sphagna	7	0	2	7	14	11	11	10	0	2	1	7
Total plant-squares	49	45	42	69	73	61	54	50	49	52	43	46
Total Mo.,Tr.,& Eri.vag.	26	24	13	24	30	35	34	25	24	32	27	23

Creag nan Dearcag

Myrica gale	0	0	0	0	0	0	0	0
Calluna vulgaris	1	0	1	0	0	0	0	5
Erica tetralix	4	3	0	0	0	2	1	3
Molinea caerulea	8	7	6	1	5	4	4	3
Trichophorum caespitosum	3	0	9	0	5	0	7	0
Eriophorum vaginatum	20	24	20	26	25	16	17	16
Eriophorum angustifolium	1	3	5	4	4	3	1	5
Carex panicea	-	-	-	-	-	-	-	-
Narthecium ossifragum	4	0	1	2	0	1	0	3
Drosera anglica	0	1	1	0	0	0	0	0
Drosera rotundifolia	0	0	0	0	0	0	0	0
Polygala serpyllifolia	0	0	0	1	0	1	0	1
Potentilla erecta	0	0	0	0	0	0	1	0
Sphagna	34	36	27	31	34	36	36	32
Total plant-squares	75	74	70	65	73	63	67	68
Total Mo.,Tr.,& Eri. vag.	31	31	35	27	35	20	28	19

the latter tending to be over represented in the count. If there is reason to suppose that clone size is distributed in a similar manner in two species, then the count of squares affords a good basis for comparison of their basal areas. If, however, one of the species has an appreciably greater number of, for example, larger clones than the other, the latter species will be over represented compared to the former, and comparison of the counts of squares will be a less satisfactory estimate of their relative basal areas. When the present data are analysed, it should be remembered that in the places where it is abundant, Trichophorum may occur as somewhat larger clones than any other species. This difficulty was not apparent when it was decided to use this method of recording. In some ways the point quadrat method might have been more appropriate, as suggested by Greig-Smith (1957). A difficulty which is of less importance to the present study lies in the possible unreliability of records for Drosera anglica, D. rotundifolia, Polygala serpyllifolia and Potentilla erecta. The aerial portions of these species die away so completely in Winter that the individuals are not always easy to detect in early Spring.

The principal interest of these results lies in the comparison they afford between the basal areas of Molinia and of Trichophorum along the length of Transect 'A' at Tarraigheal. The vegetation of the area around position 1 is fully recorded in the columns headed 'T.T.' in Table 2.2, while that of the area around position 7 is also represented

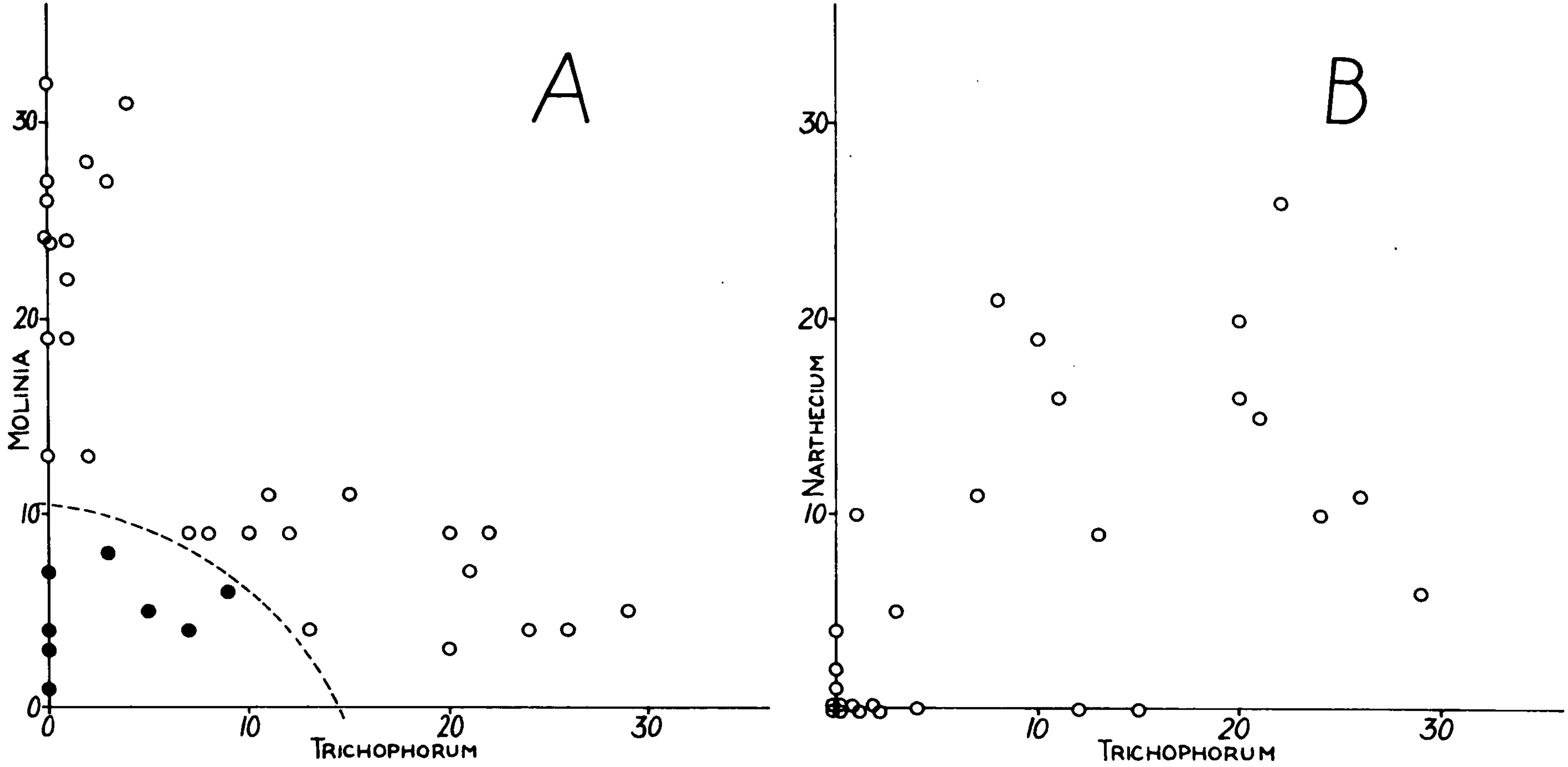

Fig. 2.1 The association between Trichophorum caespitosum and four other species, recorded as the number of one-inch squares in a 6" 6" grid in which the base of the stated species occurred. Inverpolly. 2-3 May, 1962. Data from Table (2. 3). Open circles : Tarraigheal. Closed circles : Creag nan Dearcag.

A. Trichophorum caespitosum with Molinia caerulea. Broken line encloses data from Creag nan Dearcag (Eriophorum vaginatum dominant).

B. Trichophorum caespitosum and Narthecium ossifragum. Tarraigheal.

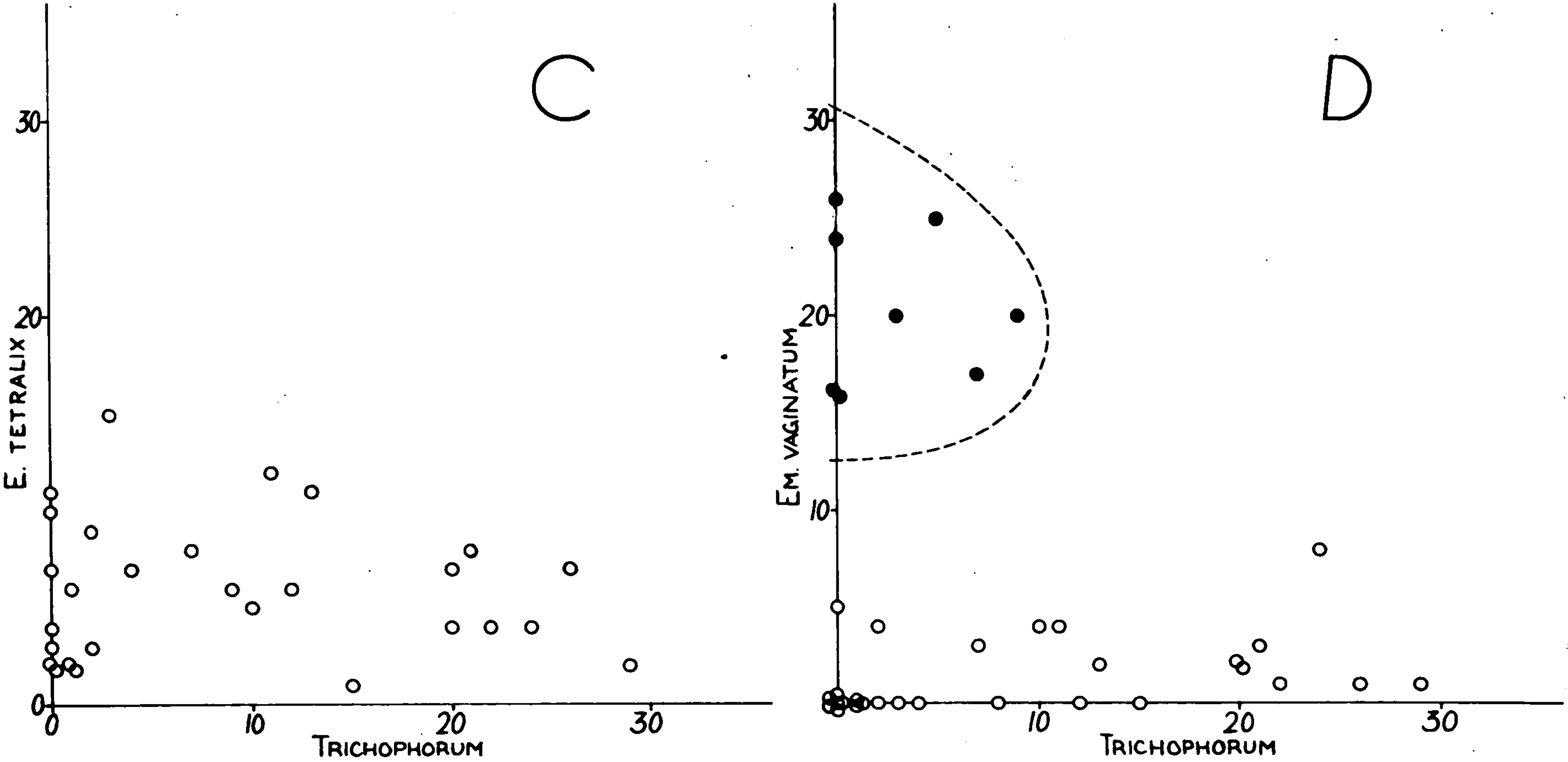

Fig. 2.1 (Continued).

C. Trichophorum caespitosum and Erica tetralix. Tarraigheal

D. Trichophorum caespitosum and Eriophorum vaginatum . Tarraigheal and (enclosed by broken line) Creag nan Dearcag.

by the 'B.T.' columns of Table 2.2.

The data for Transect 'A' whose other features are described elsewhere, are set out as the first 28 columns of Table 2.3.

The variations in basal area of Trichophorum are compared with those of four other species by means of the scatter diagrams presented in Fig. 2.1. In these diagrams, each 6" quadrat is represented by a point, whose position is defined, with respect to the two axes, by the number of 1" squares containing each of the two species concerned. Fig. 2.1A shows that quadrats in which Molinia is well represented generally have a poor representation of Trichophorum, while those with most Trichophorum have least Molinia. It confirms the subjective impression of an inverse relationship between the basal area of Trichophorum and Molinia. The points on this diagram which indicate simultaneous low values for both species all represent quadrats from the bog on Creag nan Dearcag where both species are subordinate to Eriophorum vaginatum. A contrasting situation is represented in Fig.2.1B, where the occurrence of Narthecium along the transect is seen to be positively correlated with that of Trichophorum. In Fig. 2.1C and D is seen the third possible situation, in which there is no apparent correlation between the occurrance of either Erica tetralix or Eriophorum vaginatum and that of Trichophorum.

It is, of course, to be expected that the most important species of two neighbouring communities, namely their dominants, should show the kind of inverse correlation in development which is indicated for *Molinia* and *Trichophorum*. This follows from the purely geometrical fact that occupation of any 1" square by one species necessarily reduces the chances that the same square will also contain the other. However, the existence of the type of relationship exhibited by *Trichophorum* and *Narthecium* suggests that geometrical considerations of this kind are not the only factors governing the co-existance of two species. Furthermore the simultaneous existence of the relationships between *Trichophorum* and *Erica tetralix* and between *Trichophorum* and *Eriophorum vaginatum*, serves to confirm the view that, in this instance at least, the tendency to mutual exclusiveness is primarily characteristic of the dominant species. At the same time, of course, such relationships occur between species showing a positive correlation with the dominants, for example between *Narthecium* and *Molinia*, but a situation of this kind is of less immediate ecological significance, since these two species are not analogous components of the communities in which they are respectively abundant, in the sense in which we may suppose an analogy between two dominants.

The data on basal area of *Molinia* and *Trichophorum* at points along Transect A are summarised in Fig. 2.2, for convenience of comparison with the factors discussed in Chapter III.

In addition to assessing the abundance of the adults by estimating their basal area, a further assessment was carried out by harvesting

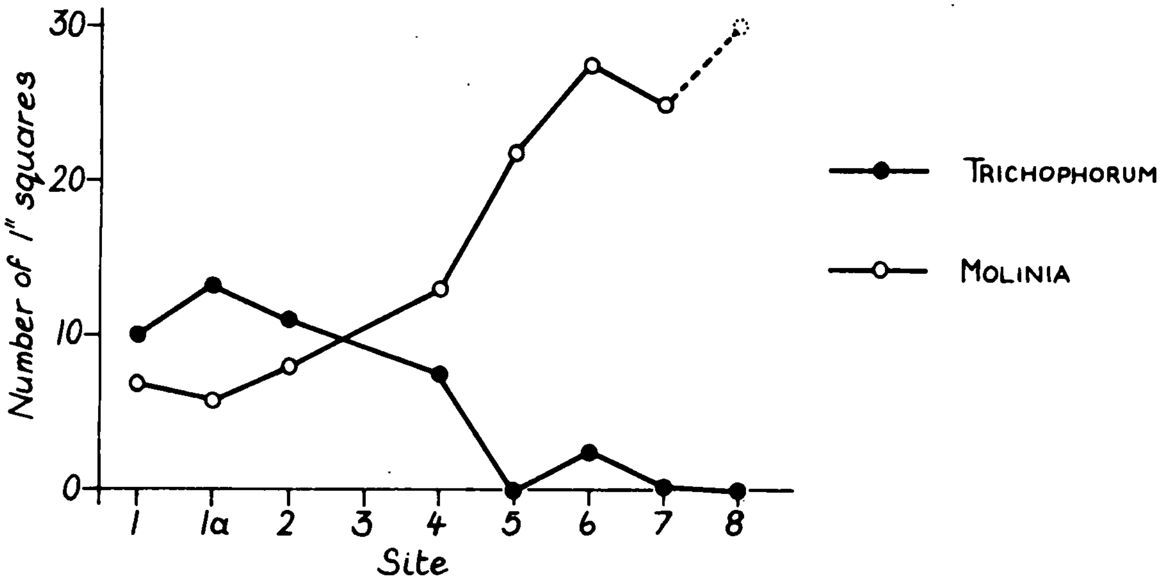

Fig. 2.2 Distribution of Trichophorum and Molinia along Transect "A". Tarraigheal. 2-3 May, 1963. Number of 1" squares from a possible 36. Data of Table (2. 3). Final point for Molinia estimated visually because here the plant forms tall tussocks.

the aerial parts of the plants. The object of this procedure was firstly to enable some comparison to be made of the annual dry-weight productivity of these communities and secondly to determine the manner in which the various components of the communities contributed to these annual totals.

The harvesting was carried out in August, 1963. At this time most of the species concerned were in fruit, and it was hoped, by harvesting them in that state, to catch them at or near their annual peak of development. It would presumably have been possible to determine for each species the exact time at which the dry weight of its aerial parts attained a maximum value, as a result of the season's growth, and before the onset of the autumnal movement of translocates, minerals etc. from the stems or leaves to over-winter storage (e.g. in the leaf-bases of Molinia) and the dispersal of fruits and seeds had begun to diminish its dry weight and to alter its chemical composition. However, this would have been a major undertaking in itself so that it was necessary to decide on the harvesting date on the basis of subjective observation of dispersal, leaf browning etc. The date chosen was a compromise between the optimum for Trichophorum, whose fruits begin to ripen in mid-August, and Molinia, which reaches the same stage about one month later in this district. Thus, in late August, while some Trichophorum fruits had already been shed and some stems were beginning to change colour, the fruits of Molinia were still dark-green to purple.

At each place where a harvest was to be taken, a careful reconnaisance was first carried out to determine which square metre of vegetation best represented the area as a whole. This procedure was somewhat subjective in the instance of the 'RL' site (see below), where no other phytosociological work had been carried out, but since the vegetation there was particularly uniform no great error is likely to have arisen. Elsewhere the selection was based upon the previous phytosociological surveys. It was necessary to select the harvesting point in this way because insufficient time was available to deal with the much more numerous harvests which would have been necessary in order to determine mean productivities for the various vegetation types in the most acceptable manner. There was no evidence of grazing at any of these sites.

The vegetation at each selected point was removed from a metre square quadrat, the stems being cut with a knife as close to the peat surface as possible. Some of the leaf-bases of Molinia stood too low to be harvested, but since they had not begun to swell, their omission was not considered to be very important. Most of the bryophytes were also omitted, together with major portions of certain species of angiosperms (e.g. the rosettes of Drosera), but these were not important components of the vegetation.

The dead material of previous years was removed in the field at site 'RL' but otherwise it was included with the living part of the harvest.

Each harvest was placed in several paper bags which constituted, in effect, a series of sub-samples from each quadrat. The bags were transported to Durham where drying was begun one to three days after harvesting. The error thus introduced, due to respiration after harvest, was unavoidable. After a preliminary period of drying, the contents of each bag was divided into five more or less equal portions and a further sample, amounting to between 10% and 20% of the whole, was collected as a series of approximately equal contributions from each portion. This sample was then sorted into four categories, namely:-

1. Material, dead on harvesting, which had grown in previous years.
2. The dominant)
)
3. The shrubs) grown during 1963.
)
4. The remainder)

After sorting, both sorted and unsorted material was subjected to a final drying for 14 hours at 60°C in a forced draught oven and weighed on cooling. From the sorted material, the proportional contribution of each category was computed for each bag, and averaged between the bags from each quadrat. These averages were then used to compute the contribution of each category to the total dry weight from each quadrat The results are shown in Table 2.4, where the site codes used correspond to those given for Table 2.~~1~~ 2, but with the addition of RL. This latter

Table (2.4).

Productivity data for Inverpolly, expressed as dry weight of living material(excluding roots) per square metre of ground surface. Estimates rounded to nearest integer. 27-29 August, 1963.

Site code	Total material (gm.)	Shrubs (gm.)	Herbs (gm.)	Dominant (gm.)	contribution of dominant (%)	Dominant
MGA	165	3	163	100	61	Molinia
MGB	194	1	193	111	57	Molinia
BT	221	82	138	106	48	Molinia
TT	192	68	124	92	47	Trichophorum
NR	277	51	226	181	65	Trichophorum
RL	264	none	264	260	98	Molinia

site is $\frac{3}{4}$ mile N.W. of Tarraigheal (NC090162), in the valley of the Allt Gleann an Strathain. The flat floor of this valley is largely covered with dense stands of almost pure Molinia, growing to a height of about one metre. It was considered probable that this well developed, mature community would show the highest productivity of all those examined.

Before discussing these results it is necessary to take note of two possible difficulties in their interpretation. The first is that the figures for total dry weight of living shrubs do not refer to one season's growth alone, because it was impossible to estimate the annual increment in these small, woody perennials. At M.G. A and B and at RL, this scarcely affects the issue, but at B.T., T.T. and N.R. the shrubs constitute 37%, 35% and 18% of the total dry weight respectively. Of these three sites, therefore, the true total for one year's growth should be less and the % contribution of the dominant greater than the figures given. B.T. and T.T. are communities at a similar stage of recovery after muirburn, so that comparisons between them are valid despite the large proportion of shrubs. The second difficulty is that these results refer only to that part of the productivity which is manifest above ground. The rhizome and root systems are omitted. The task of obtaining reliable data for the underground parts is formidably difficult when so little is known about the active life of the roots of these species. It has, therefore, been thought preferable to assume that the development of the plant below the ground is proportional to its development above ground. In view of the intimate physiological interdependence of these two portions of a plant, this seems to be a more realistic assumption than any which can at present be made about the biology of the root systems.

Bearing in mind these reservations, we may now turn to a detailed examination of Table 2.4. With the exception of RL which is almost pure Molinia, it is apparent that the dominant is responsible for between 47% and 65% of the total dry weight. If we make an assumption, for the sake of argument, that two-thirds of the weight of shrubs was produced in previous years, the % contribution of the dominant in B.T., T.T. and N.R. becomes 64%, 63% and 75% respectively. At all events we are clearly justified in regarding the physiognomic dominant as that member of the community which contributes most to its annual productivity, and we may again note the replacement effect shown by Molinia and Trichophorum between the lower and upper ends of Transect A (i.e. between B.T. and T.T.). It is again evident, from the similarity in the percentages for all sites except RL, that the two dominant species play comparable roles in their respective communities.

If we consider the estimates of total dry weight per square metre, a most interesting fact emerges. Despite the subjective impression that the productivity of areas dominated by Molinia is greater than that of areas dominated by Trichophorum, we find that the figures for the more recently burned areas of Tarraigheal (i.e. for M.G.A., M.G.B, B.T. and T.T.) are comparable, being 165 gm., 194 gm., 221 gm. and 192 gm. as they stand, or 163 gm., 193 gm., 165 gm. and 147 gm. if we make the above assumption about the shrub contribution. The similarity is even more striking if we consider the mature closed communities represented by N.R. and RL, for which the figures are 277 gm. (243 gm. with shrub adjustment) and 264 gm. respectively. These estimates lend no support to our subjective impression.

Data on the distribution of seedlings of Trichophorum and Molinia were collected in April, 1962 at Tarraigheal. The morphology of Trichophorum seedlings had previously been ascertained from seeds germinated at Durham (see Chapter 1). The seedlings are so unlike the adults that such an investigation was a necessary preliminary to the collection of the data which follows.

Seedling distribution was observed in a small number of 11" x 18" plots. Each plot was divided into three sub-plots, each comprising 11" x 6" rectangles. The number of seedlings of each species present in each rectangle was recorded together with the presence or absence of at least part of the base of adults of each species. The plots were placed so as to sample an area dominated by Trichophorum, and one dominated by Molinia, and within each area one plot was placed in a position chosen as having approximately half the peat surface bare of adult vegetation or its remains, and another in a position where the bare peat occupied about one quarter of the total area. The results of the seedling counts are presented as sets of three figures, each referring to one of the three groups of eleven contiguous 1" x 6" rectangles, which together made up the plot.

The total numbers of seedlings in each sub-plot appear in the body of Tables 2.5 (Trichophorum) and 2.6 (Molinia). It seems reasonable to suppose that the proportion of bare ground present at each site is an indication of the suitability of that site for seedling establishment. This would account for the reduction in seedling numbers of Trichophorum between the 50% bare and 25% bare sites, but it is of interest that Molinia does not show this relationship. This is thought to be a reflection of comparative intolerance of Trichophorum seedlings to shading. It is clear that there are more Molinia seedlings in sites where Molinia is dominant, and conversely more Trichophorum seedlings in sites where Trichophorum is dominant, though not significantly more in the 25% bare site. The latter inconsistancy is again thought to be a reflection of the comparative intolerance of Trichophorum seedlings to shading. It appears that effective colonisation by Molinia seedlings may take place in a habitat where the degree of cover is sufficient to inhibit colonisation by Trichophorum seedlings. The response of Trichophorum to shading is further discussed in Chapter V.

In the previous paragraph, discussion centered upon the relative seedling densities within each of two species at two sites. From a

Tables (2. 5).&(2. 6).

Seedling counts at Tarraigheal, 1962. The plots are identified by the numbers in brackets.

	50% bare		25% bare
Trichophorum dominant	40 40 49 (1)	(1) > (2) (P< 0.1%)	10 5 2 (2)
	(1) > (3) (P < 1%)		(2) >(4) (Not Sig.)
Molinia dominant	0 9 15 (3)	(3) >(4) (Not Sig.)	7 1 2 (4)

Table (2. 5) *Trichophorum* seedlings at Tarraigheal

	50% bare		25% bare
Trichophorum dominant	0 1 0 (1)	(1) = (2)	1 0 0 (2)
	(1) < (3) (P <5%)		(2)< (4) (P <5%)
Molinia dominant	2 5 3 (3)	(3)<(4) (Not Sig.)	3 3 7 (4)

Table (2. 6) *Molinia* seedlings at Tarraigheal comparison of Table 2.5 with Table 2.6 it appears that the overall densities of seedlings differ markedly between the two species, Trichophorum having in general the higher number per plot. The comparison of seedling densities between species is not valid in this case, because the data were not collected with that object in view. From Chapter 1 it will be evident that young Trichophorum plants may remain recognisably distinct from the adults until the fourth season. Juvenile Molinia may, however, become indistinguishable from the adults during the second winter. Thus 'seedlings' of Trichophorum here implies all plants one, two or three years of age, whereas the 'seedlings' of Molinia here comprise only one-year-old plants. The seedling numbers of the two species cannot therefore be compared on a per unit area per year basis.

There is no evidence that individual clones of either Molinia or Trichophorum fragment during the course of their vegetative enlargement. One is, therefore, obliged to conclude that on the Inverpolly reserve, these species became established by seed alone. The data of Tables 2.5 and 2.6 confirm this view, though more extensive data are desirable. It is important to notice that, in interpreting these data, no question arises as to whether the relative abundance of seedlings of either species, in sites where it is dominant, is due to the relatively greater suitability of the site or merely to the proximity of a relatively liberal seed scource. The data merely demonstrate the importance of seedlings as the essential precondition of a species attaining dominance.

CHAPTER III

The Physical and Chemical Environment

In the previous chapter, the phytosociology of Trichophorum and other mire dominants was discussed so far as possible without reference to the background of physical and chemical conditions which is thought to control the distribution of the various communities in question. The species concerned may attain dominance in a wide variety of habitats in different parts of the British Isles. In the Introduction, and again in Chapter I, it was emphasised that, particularly where abundant and widely ranging species are concerned, it cannot be assumed that material from different habitats or from different areas has similar genetic constitution. In this chapter, interest centres on the habitats most generally available to Trichophorum in North West Scotland. It must not be assumed that the conclusions drawn for this area are valid elsewhere.

In Chapter II the phytosociological reasons for selecting the Inverpolly Reserve as a study area were discussed. The area was held to be representative of the North West Highlands as a whole. Communities which elsewhere cover very large areas, here form a mosaic on a scale where the factors governing their distribution can be comprehended easily. In this chapter, environment is discussed with special reference to the Inverpolly Reserve.

Climate

Climatic records for the Inverpolly area are very incomplete. The Scottish Hydro-Electric Board have maintained a monthly rainfall gauge at about 400ft. O D. at the foot of Fionn Loch on the northern edge of the Reserve since September 1960. I am indebted to the Board's observer, Mr. Angus MacLeod of Inverkirkaig, for the records over the period up to April, 1962. In 1963 the Nature Conservancy established a Meteorological station at Strath Polly, almost at sea level, and are continuing to maintain complete records there. Mr. F.H.W. Green, the Conservancy's chief meteorologist, has kindly supplied me with data from this station for the whole of 1963. Strathpolly and Fionn Loch lie about two miles South West and North East of Tarraigheal respectively, and the study area there lies at an altitude mid-way between them. The total annual rainfall at Fionn Loch in 1961 was 54.25" and at Strathpolly in 1963 the corresponding figure was 39.56". The Spring of 1963 is known to have been particularly dry, but the rainfall data as a whole suggest that, whereas comparatively dry weather with monthly rainfall totalling under 2" may generally be expected at some period between February and June, the months between July and October usually experience totals lying between 5 and 7" so that the principal period of plant growth is exceedingly wet. The lysimeter at Strathpolly recorded a potential water surplus very close to the rainfall for this period of the year, indicating only small losses of water through transpiration and evaporation, and confirming the generally humid impression of this season.

Temperature conditions for plant growth appear to be very favourable, the mean temperature in the Stephenson screen at Strathpolly having exceeded the accepted threshold value of 5°C in every month of 1963 except January, February and December. A closer correspondence is found between the observed period of plant growth and the period without air frost, which extends from May until September. The climate is, however, in general rather cool, with an average value for half (maximum + minimum) of only 7.9°C for the year, varying between 0.1°C for January and 13.7°C for June.

There is no pyroheliometer at Strathpolly so that not even the crudest estimate of solar radiation is available as yet. In view of the limiting effect of light on plant productivity, about which more will be said later, this omission is unfortunate.

Solid Geology

Most of the Inverpolly Reserve lies within the zone of pre-Cambrian rocks which forms the North-Western seaboard of the Scottish mainland. Two formations are involved, namely the Lewisian Gneiss and the Torridonian sandstone. The Lewisian Gneiss is the older formation. In this district it consists of acidic orthogneisses, typically pyroxene-gneiss (Phemister, 1960). A series of long, broad basic dykes is intruded into the gneiss. The dykes have a North West - South East strike. The Torridonian Sandstone overlies the gneiss in the Eastern part of the reserve. In this district the sediments are referred to the Applecross Group, comprising dark brown or red arkoses with conglomeratic layers, the grits and pebbles of which also consist of silicious material. Extensive weathering of the Lewisian appears to have taken place before the deposition of the Applecross Group, which lies unconformably on a 'buried landscape' of Gneiss. Further weathering and glacial activity have now reduced the gneiss to a wilderness of rounded knolls with summits at 500'-600' O.D. interspersed by narrow gulleys, frequently occupied by lochans. The dykes have been less resistant to erosion than the surrounding rock, and few traces of them now remain. Their positions are marked by a series of greatly elongated troughs. The Torridonian Sandstone has been eroded away from the North-Western part of the reserve, but in the East and South forms a series of mountains with summits lying between 2,000' and 3,000'. The topography of these features is very variable, comprising, on the one hand, gently rounded ridges and plateaux, and on the other the chimneys and pinnacles of Stac Polly.

Pockets of morainic material occur on the reserve but these are of small extent and unimportant for the present purposes.

Both the Lewisian Gneiss and The Torridonian Sandstone are very hard rocks, and under present-day conditions they appear to weather extremely slowly. In the case of the acidic gneiss, the weathering process consists of hydrolysis of the felspathic components to produce silicates or carbonates of potassium, which, being extremely soluble, are immediately removed. The remaining components of the feldspars form clay. This process releases the less readily hydrolysed components notably quartz, and it frequently happens that the only mineral particles to be found in the peat on the steep sides of the knolls are quartz grains. The sandstone is weathered by destruction and removal of the cement again releasing quartz grains (Hatch, Rastall and Black, 1938). Both these rock formations are highly impervious to water. The result is that such plant nutrients as are released by weathering are immediately leached away under the influence of the high rainfall and accumulate in the waterlogged depressions. Meanwhile such mineral matter as remains in the potentially better-drained sites is almost devoid of plant nutrients.

Soils

With the exception of the morainic pockets, virtually all the land surface of the reserve below an altitude of about 1,500 feet is covered by peat deposits of one kind or another. The detailed history of these deposits has never been investigated, but from the abundance with which tree remains occur towards the base of the peat it appears that much of the area was originally occupied by woodland. Some authors (e.g. Fraser Darling, 1947, 1955) give the impression that the replacement of this woodland is largely due to human influence, especially during the period leading up to the Highland Clearances, which reached their height between 1750 and 1850.

The system of land use which led to the clearances, based as it was upon burning and grazing by sheep, does not at the present day encourage peat-forming vegetation. This is particularly true of the areas now dominated by Trichophorum and Molinia, where the impression is of wastage rather than accretion. Although it is known that parts of the Reserve (whose population has varied between 0 and 2 during the period of this work) were formerly quite densely populated, it therefore seems most unlikely that the changes leading to the replacement of woodland by peat deposits were primarily anthropogenic in origin. However, a final solution of this problem must await detailed examination of the peat by modern analytical methods.[*]

The principal peat deposits of the Highlands occur in the form of 'blanket bog'. This term is used by Tansley (1939), Osvald (1949) and

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[*] Since the above paragraph was written, I have been informed by Mr. Neville Moor of the Sub-Department of Quaternary Research, Cambridge, of the salient results of his recent investigations in North West Ross-Shire and West Sutherland. Mr. Moor has carried out palynological analyses and radio-carbon dating of the deposits in an infilled rock basin South of Loch Duartbeg, which lies near the coast and about 15 miles North-North-East of the present study area. He finds that the decline in Ulmus pollen, characteristic of the Zone VII A - VII B transition, took place in this area as recently as 3860 B.P. Shortly after this date, at 3690 B.P., there occurs a pronounced rise in the frequency of pollen of Calluna, Gramineae, Cyperaceae and of Sphagnum spores. From this it seems probable that, while the widespread development of the vegetation types now associated with blanket bog took place within the period of human occupation, it preceded the highland clearances by at least 35 centuries.

Fraser (1954) to describe the result of peat formation in conditions of high rainfall and atmospheric humidity, where the extension of peat-forming vegetation may take place in entire dependence on meteoric water, to form deposits which are not confined to basins, but which may cover terrain with an appreciable slope. It is often implied that such bogs are entirely and uniformly oligotrophic, due to their exclusive dependence on rainwater, but the studies of Gorham (1958) have shown that in the oceanic regions where these bogs occur, the rain may often be appreciably contaminated with mineral salts derived from sea-spray. Furthermore, it is by no means certain that the water of these bogs never comes in contact with the mineral substratum. Tansley himself emphasises the need for impeded drainage, which implies that some of the water must come in contact with the underlying rock. While it may happen that none of the water ever enters the rooting zone in completely flat bogs, wherever a slope induces lateral water movement through the peat, there remains a possibility of soligenous influence. The importance of laterall movement is discussed later.

The classification of peat as a soil, i.e. a substrate for plant growth, has received most attention from silviculturalists (e.g. Fraser, 1933, Zehetmayr, 1954). So far as the blanket bogs of Western Scotland are concerned, Fraser's classification is generally employed, and may be summarised as follows.

(A) Psudo-fibrous Peat. Fibrous in appearance only. When squeezed in the hand it does not lose water but exudes between the fingers and the fibrous appearance is lost. Thixotrophic, with a highly hygroscopic gelatinous matrix. Colour when fresh, yellowish-brown, becoming dark brown or black on exposure to air. Shrinks on drying.

(B) Fibrous peat. Fibres persistant. When squeezed in the hand, water is removed and the mass regains its original shape when released. Elastic and not easily penetrated by a spade. Colour depends on origin, and alters only slightly on exposure to air. Does not shrink appreciably on drying.

(C) Amorphous Peat. No fibres apparent. The material aggregated into dense, black granules forming a spongy structure. Colour not altering on exposure to air. On drying forms hard, black lustrous particles.

Pseudofibrous peat characteristically underlies vegetation in whibh *Trichophorum* is dominant, and the pseudofibrous condition is assumed at about 10 cm. below the surface.

Fibrous peat is formed by the growth of *Sphagna* or *Eriophorum vaginatum*. It differs very little in texture from a turf of these plants. It alters with depth, and below about 1 metre from the surface it may come to resemble pseudofibrous peat. It is the characteristic peat type of the *Calluna*-dominated bogs of Eastern Scotland.

Amorphous peat is generally associated with the dominance of *Molinia* or *Juncus effusus*.

These soil types occur, in association with the vegetation we have mentioned, in most regions of the British Isles. In particular the pseudofibrous soil texture is associated with Trichophorum in all its lowland habitats. The question arises as to whether Trichophorum is itself responsible for the development of this texture, or whether such characteristics develop in response to some other factor, with which the growth of Trichophorum is also associated. So far no conclusive answer to this problem has been forthcoming. Plants grown from seed on a soil very rich in peat have not produced this condition over a period of three years, but it is quite probable that considerably longer periods may be involved under natural conditions, so no great importance can be attached to this negative result.

Distribution of soils and vegetation.

From the foregoing remarks it will be apparent that soil and vegetation type are intimately related. When we come to consider their distribution with respect to the topography of Inverpolly, it is convenient to consider the following pairs of soil type with physiognomic dominant as units:

Soil type	Physiognomic dominant
I Pseudofibrous peat	Trichophorum
II Fibrous peat	Eriophorum vaginatum
III Amorphous peat	Molinia

For the reasons stated in Chapter II, no further attempt will here be made to discuss the conditions accompanying the transition from dominant *Trichophorum* to dominant *Eriophorum vaginatum*. Attention will, therefore, be concentrated upon the transition from *Trichophorum* to *Molinia*.

A sketch plan of Tarraigheal, showing the area in which most of the field work was carried out, is shown in Fig. 3.1. This plan is intended to be studied in conjunction with the two sketch sections of Fig. 3.2, in which the vertical scale has been exaggerated approximately six-fold with respect to the horizontal scale. In addition to the areas of dominance of *Molinia* and *Trichophorum*, the plan shows the distribution of woodland, of the *Trichophorum*-*Carex* mire nodum (McVean and Ratcliffe, 1962) and of *Calluna* as a co-dominant or dominant, in 1962-3. The *Trichophorum*-*Carex* mires occupy depressions in areas of peat, with a water-table at, or near, the surface, which otherwise support dominant *Trichophorum*. They are associations of greater sociological complexity than the others considered here, and for this reason they have not been examined in detail. The distribution of dominant or co-dominant *Calluna* varies from year to year, depending upon the time which has elapsed since the last muirburn.

Mires dominated by *Trichophorum* occupy the greater part of the treeless area, where the peat surface is either horizontal or slightly convex. Mires dominated by *Molinia* occur on the more steeply-sloping peat surfaces, notably where knolls of gneiss covered by thin peat

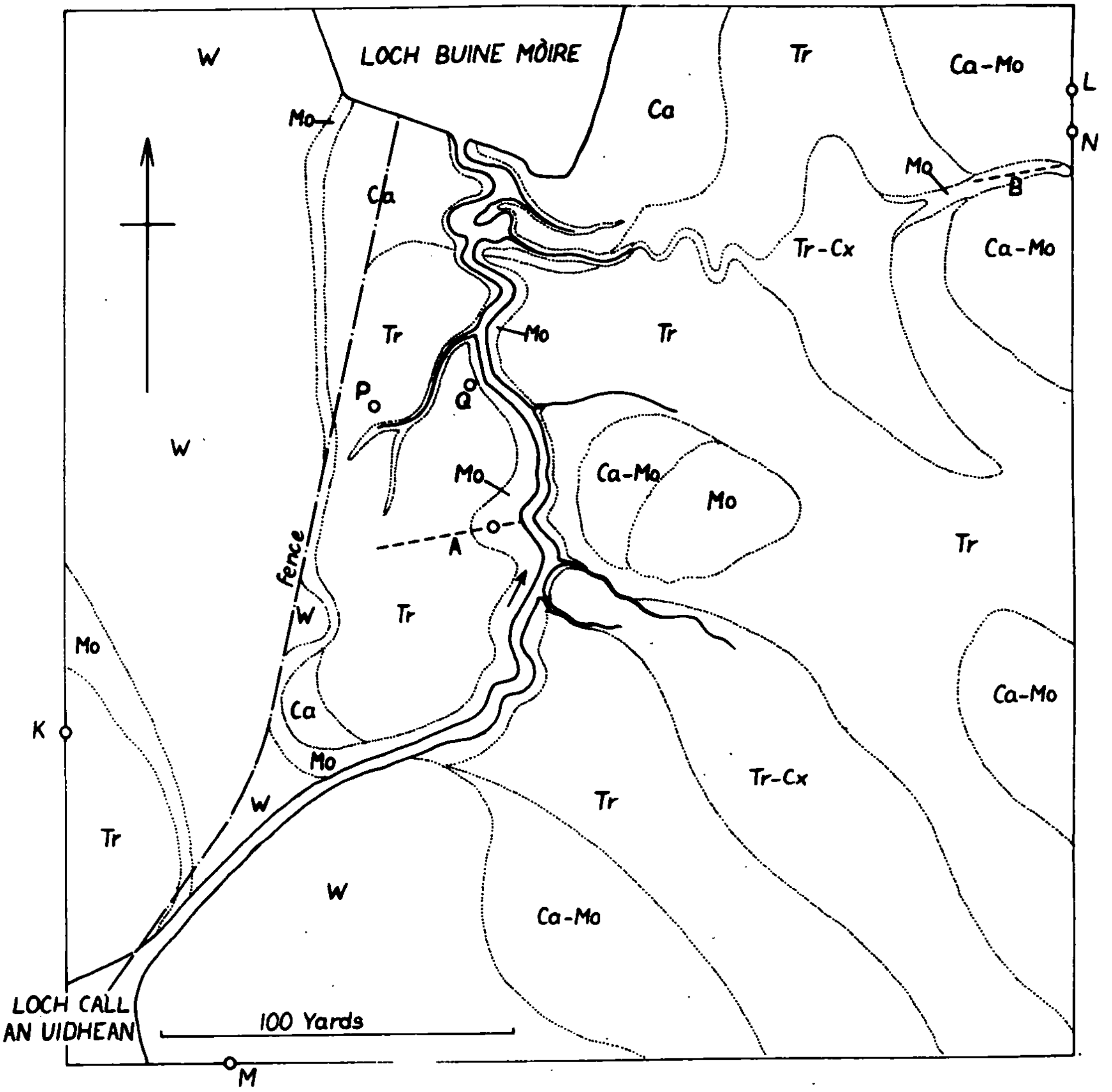


Fig. 3.1 Sketch plan of the study area at Tarraigheal, showing approximate boundaries of the principal types of vegetation. Abbreviations: W - Woodland; Tr - *Trichophorum*; Mo - *Molinia* C - *Carex* spp.; Ca - *Calluna*. The positions of Transects "A" and "B" and of sites P and Q are also shown.

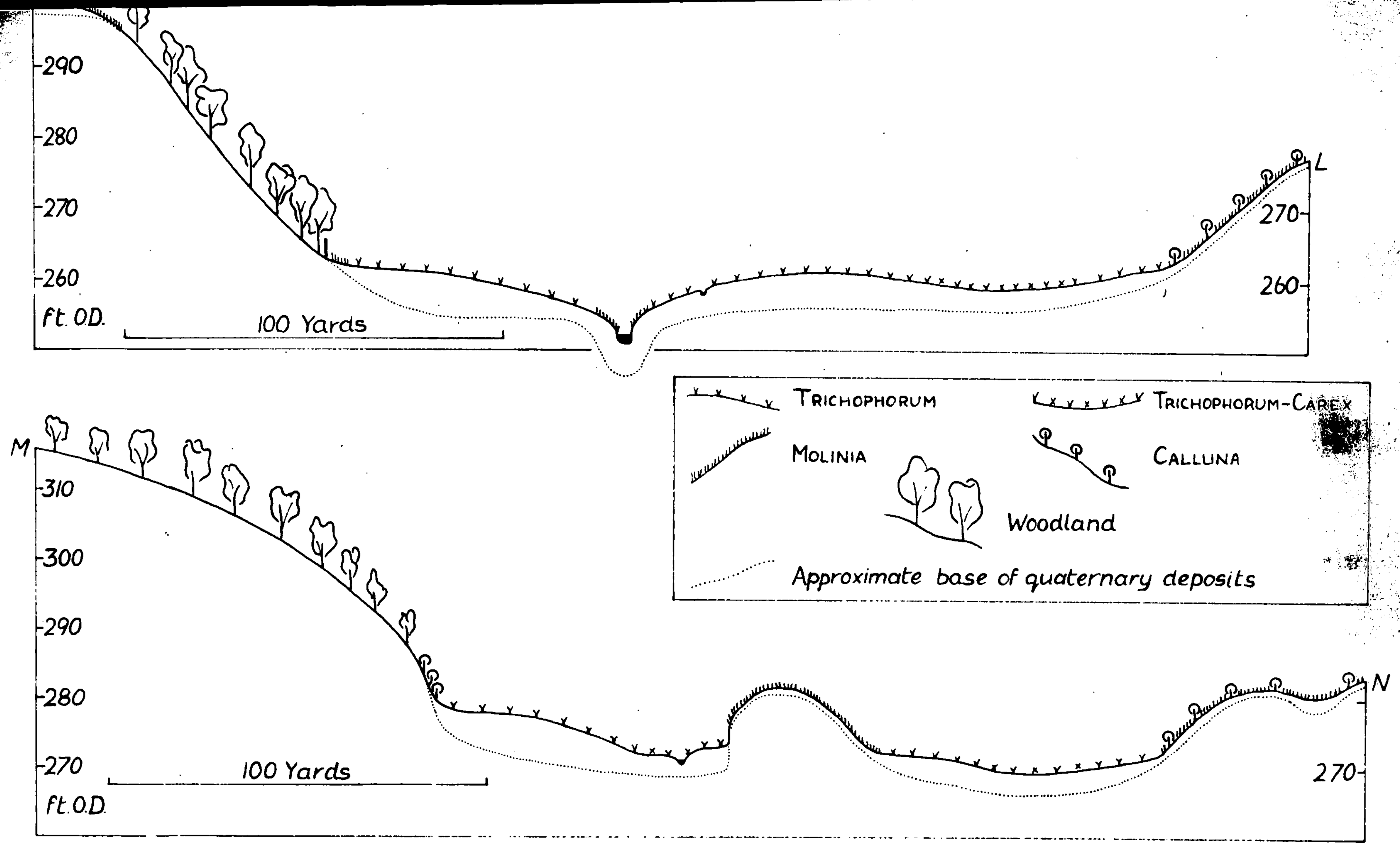


Fig. 3.2 Sketch sections across the area represented in Fig. 3.1, along the lines K - L and M - N.

project out of the general covering of blanket bog, and around the margins of the *Trichophorum* areas, particularly in association with drainage axes.

Fig. 3.2 also attempts to show the approximate base of the peat at Tarraigheal. The position of the contact between peat and solid rock has not been examined as extensively as one would wish, so this portion of the sketch is extrapolated from data collected in the course of the present work. The results of some soundings made in two sites are included as Figs. 3.3 and 3.4. Fig. 3.3.shows the depth of peat deposits along Transect "A". It may be seen that at this site we have to deal with a semi-cupola of peat resting for the most part on a horizontal surface, and varying in thickness from about 50 cm. beside the burn to just over 300 cm. near the apex. The figure clearly shows that the course of the burn is determined by a buried channel in the gneiss, now largely filled in with mixtures of sand and peat. This transect runs in a straight line along an axis of maximum slope, from the area surrounding the apex of the cupola, over which *Trichophorum* is dominant, to an area where a broad gully runs down to the bank of the burn, and in which *Molinia* is dominant. The surface profile of this gully is also shown in Figs. 3.5 and 3.6. Fig. 3.4 shows a linear section (Transect "B") along the axis of a second gully in which a comparatively shallow infilling of peat supports a luxurient growth of *Molinia* tussocks. The series of sections at rightangles to this

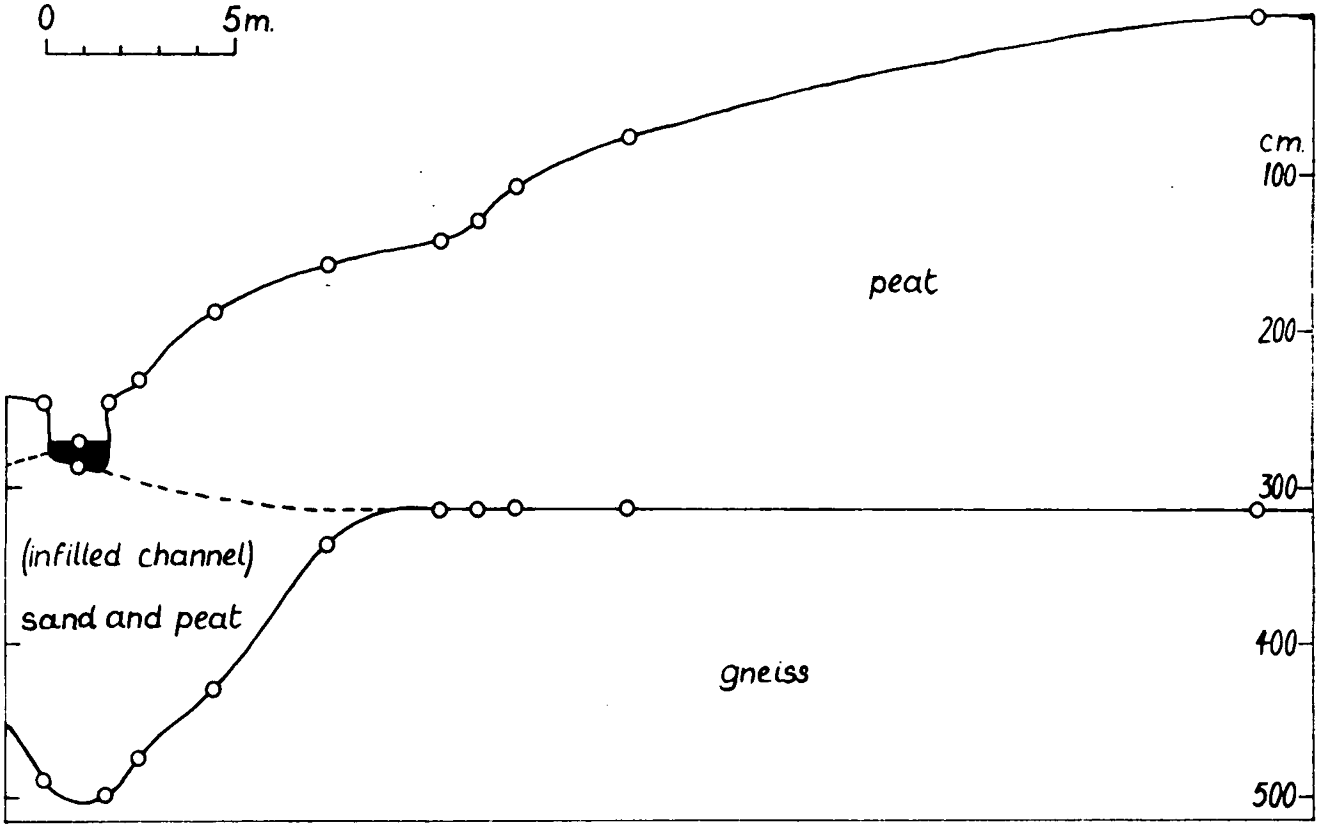
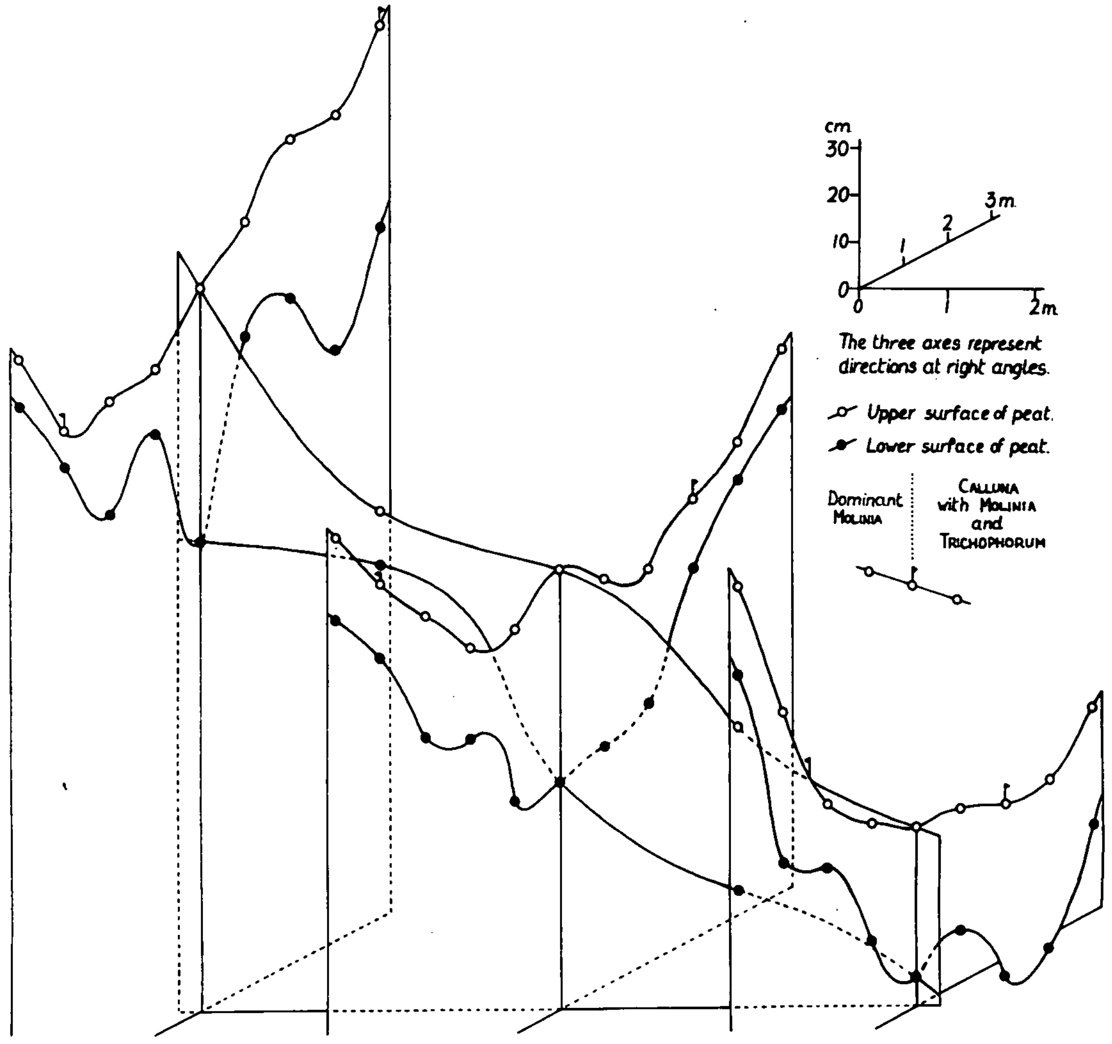


Fig. 3.3 Section through peat deposit at Tarraigheal, following the line of Transect "A". Levelled April 1963.

Fig. 3.4 Four profiles in the peat infilling of a rock channel at Transect "B". Levelled April 1963.



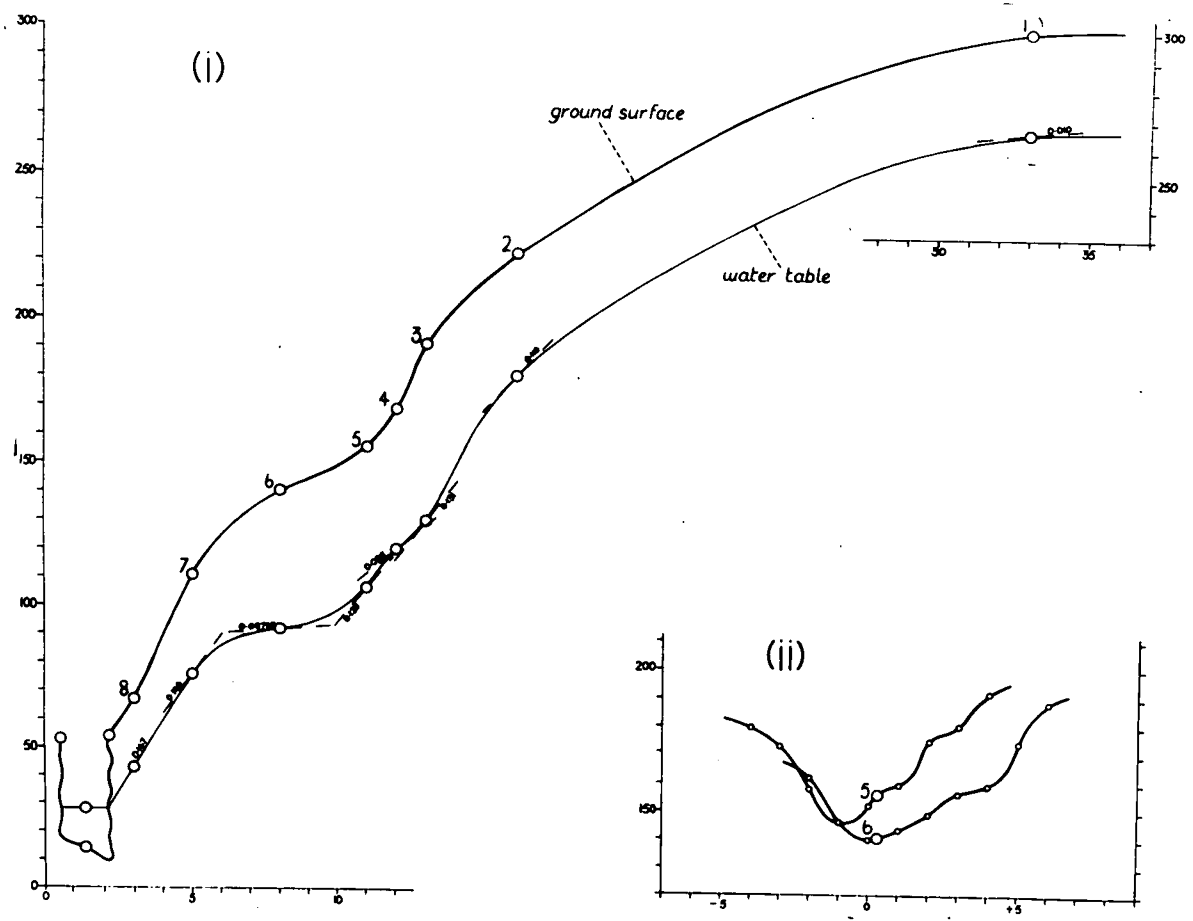


Fig. 3.5 (i) Surface profile (thick line) of peat at Transect "A". Levelled 27 April 1962. Thin line shows position of water-table determined for 4 May 1962. Broken lines are constructions for estimating the slope of the water-table. Vertical scale : cm. Horizontal scale : m.

Fig. 3.6 (ii) Surface profile at right-angles to Transect "A". Levelled 5 May 1962. Vertical scale cm. Zero as Fig. 3.5.

transect shows the Molinia giving way to Trichophorum and Calluna on the shallower peats on the sides of the small valley in which the gully lies.

From these two transects it is evident that the transition from Trichophorum to Molinia is associated with the canalisation of drainage, Trichophorum being found in areas whose profile suggests that such horizontal water movement through the peat as may occur is diffused over a wide area, while Molinia is found on peat in which this horizontal water movement has been concentrated along definite and restricted axes, where it is accordingly more rapid.

Hydrology

The influence of ground-water movement on the distribution of mire vegetation has recently come to be recognised as being of great importance. Despite this, comparatively little British work has yet appeared in this field, to which the most important contribution is still that of Kulczyński (1949). This study, which was carried out between 1928 and 1934, covered the whole of the Polesie area of Poland. This is a region of very low relief situated across the main Black Sea - Baltic watershed of Central Europe. Kulczyński showed that the distribution of the various types of mire was determined by minute differences in level which controlled the circulation of the groundwater. He expressed his conclusions as follows (loc. cit. pp. 11-12)

"I. In peat-bog development, and for the formation of peat-bog types, the fundamental factors are of a hydrologic nature. In particular, the most important role belongs here to the movements of bog waters.

"The waters, under the influence of which peat-bog formative processes take place, may be divided into three systems:

"a) System I of absolutely immobile ground-water, deprived of all terrestrial inflow and regenerating, exclusively and directly, from rainfall. In this system are included, for instance: the water which in the Atlantic climate saturates the cupolas of raised bogs; the water of raised-bog pools, lakes etc; the ground-water saturating elevated water parting regions; also the water of lakes without inlet and outlet; etc.

"b) System II of mobile ground-water. This water is normally fed by the water of System I, and consumed by the water of System III. It constitutes a ground-water which is incessantly renewed. To this system appertains the water of easily permeable soils, which flows on sloping impermeable earth strata. Included here, among others, is such ground-water as filters through the peat masses of valley bogs posessing a unilateral declivity and a drainage area.

" c) System III of mobile surface water. I consider as belonging to this system: river-, stream-, and inundation- waters, as well as the water of lakes provided with inlet and outlet."

Kulczyński goes on to differentiate between raised bogs, which develop in the immobile ground-water of System I and 'valley bogs', which are equivalent to the fens of British authors (not to the valley bogs of, for example, the New Forest), which develop in the mobile ground-water of System II, or under the influence of System III. The former are said to be ombrophilous peat-bogs, while the latter are called rheophilous peat bogs.

Although from this résumé these distinctions appear to be clear cut, examination of the monograph as a whole shows that various types of transition-bog occupy sites intermediate between raised bogs and fens. While some of these have arisen from raised bog or fen by a change in the drainage relations of the area, such as may result from river capture or the silting-up of river beds, others appear to occupy zones of transition between raised bogs and fens, where the groundwater is not fully mobile as in System II, but may exhibit only sluggish or seasonal movement. Clearly for the fens to be "fed by the water of System I" implies perceptible water-movement, at least in the peripheral portions of that System. It, therefore, seems probable that the hydrological conditions which underly the phytosociological diversity of Polesie are differences of degree rather than differences of kind, and that the amount of water-movement may be more critical than its presence or absence in determining the floristics of a particular site.

At the present time there is no method whereby the rate of horizontal movement of ground-water through peat may be determined directly

In the investigations carried out so far an indirect method has accordingly been employed. This method is based upon the application of a relationship which was empirically determined by Darcy in 1856. "Darcy's Law" states that the volume v of water flowing across unit area of cross-section of soil in unit time is proportional to the hydraulic gradient:

$$v = k\frac{dH}{dl}$$

Where dH is the difference in head between two points at distance dl apart. The constant k is known as the hydraulic conductivity of the soil, and has the dimensions LT^{-1}. Its value varies not only with the properties of the soil but also with the viscosity and potential of the fluid concerned, but for water in soils, and over the range of temperature normally encountered in the field, the effects of the two latter parameters can be ignored (Marshall, 1959).

The value to be expected for the hydraulic conductivity varies considerably according to whether the soil is saturated or not. Generally speaking the hydraulic conductivity of a soil decreases on drying, and is so much greater in saturated than in unsaturated soil that virtually all the water movement in many soils may be assumed to take place below the water-table.

Where, as in the present systems, water enters the peat as rain, $\frac{dH}{dl}$, the hydraulic gradient, will be equal to the slope of the water-table and the direction of flow will be in general normal to the contour of of this slope. Rutter (1955) found that in some Hampshire heaths this condition did not obtain, but the situation was there complicated by an upwelling of ground-water from the underlying mineral soil which does not appear to take place on the Inverpolly bogs. Rutter studied the height of the water-table and the hydrostatic pressure at various points below it by means of batteries of tubes driven vertically into the ground. The same method was adopted in the present studies.

Ten sites were selected, and at each a battery of 1 m. lengths of electricity conduit (internal diameter 15 mm) was driven into the peat with a mallet. The tubes of each battery stood in a straight row, parallel to the contour of the bog surface, at 10 cm. intervals. A length of gas barrel (external diameter 14 mm.) whose lower end was kept flush with the lower end of the tube, was held inside each tube as it was driven into the ground in order to prevent peat from entering. A further 10 cm. was then cleared beyond the end of the tube by means of the gas barrel. The water level in the tubes was measured at intervals by lowering a weighted length of insulated copper wire down each in turn and recording the depth at which the bared end of the wire made electrical contact with the contents of the tube. The contact point was shown by connecting the other end of the wire to the negative terminal of the voltammeter, in place of the platinum electrode used for oxygen determinations.

The results of this investigation are set out in Table 3.1, and presented graphically in Figs. 3.5 - 3.8. The positions of the batteries of tubes are indicated as "P" and "Q" on Fig. 3.1, together with the eight numbered sites on Transect "A". Transect "A" is normal to the overall contour of the bog, and it is, therefore, probable that it is also normal to the water-table and parallel to the direction of flow of the ground-water.

The method of determining the level of the water-table is illustrated by the diagram at Fig. 3.7. It follows that of Rutter (loc. cit.). From the diagram it may be seen that the water-level attained in any tube declines as the depth of the lower end of the tube increases. It seems unlikely that the hydraulic pressure responsible for the rise of water in the tubes does not remain equal to the distance from the water table as depth increases. The most likely explanation of this effect would, therefore, seem to be that equilibration has failed to take place in the deeper tubes. At all events it is clear that the true level of the water-table is most nearly represented by the level of water in the shallowest tube in which contact was made. The water table on 4th May, 1962, would, therefore, appear to lie at 64.5 cm. at P and at 57.0 cm. at Q. Both are heights above an arbitrary zero.

The same principle has been used to determine the shape of the water-table along Transect 'A' on 4th May, 1962. The levels at each site, which are plotted in Fig. 3.5 have been determined by inspection of Fig. 3.8. In making these determinations, no value has been

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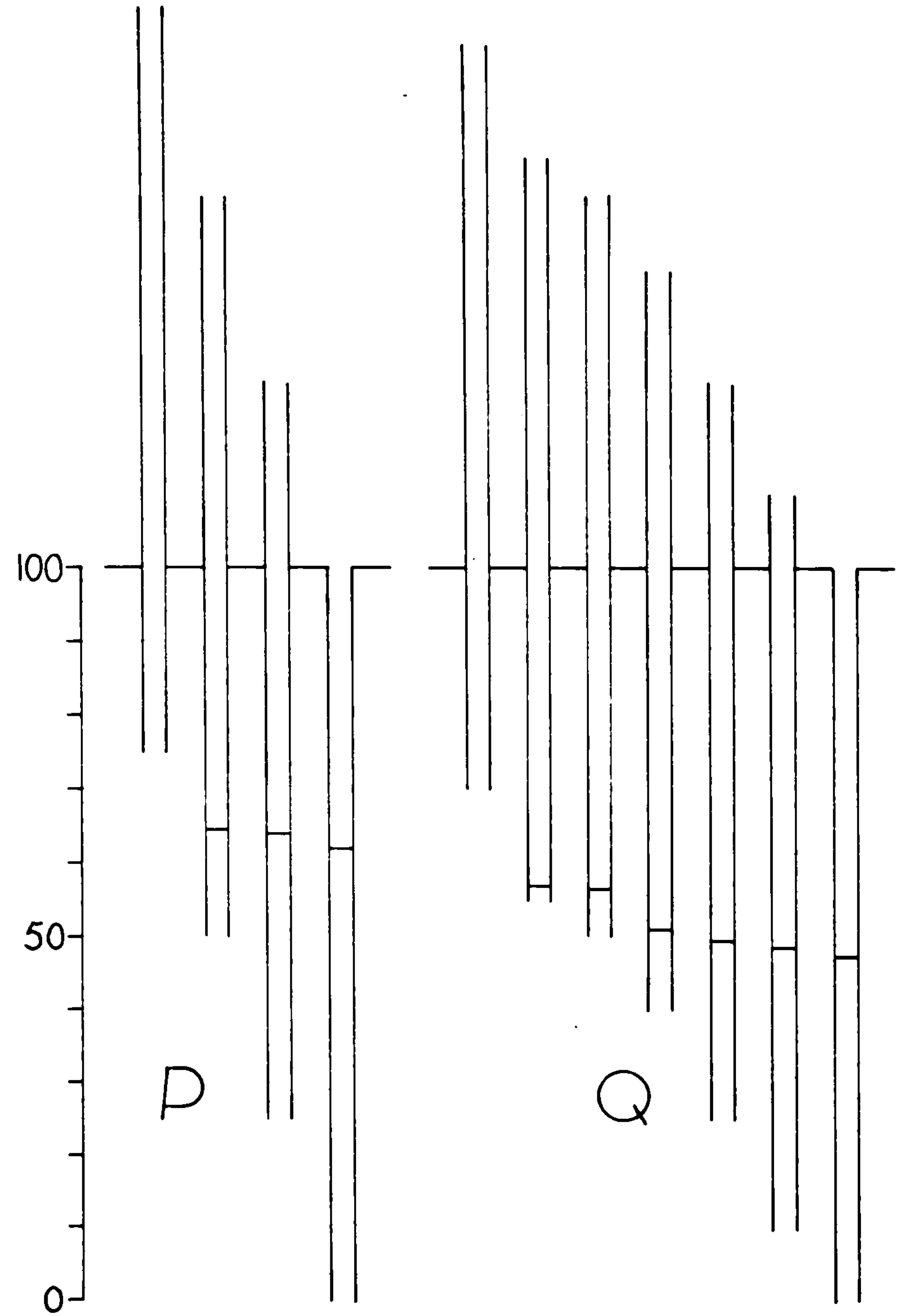
Fig. 3.7 Left.

Diagram of the arrangement of batteries of 1 metre tubes for determining position of water table at sites P and Q, Tarraigheal. Water levels in tubes as on 4 May, 1962.

Right.

Fluctuation in water levels recorded by electrical contact in the tubes shown at left. Zero of vertical scale as at left. April - May, 1962.


100
50
0
P
Q

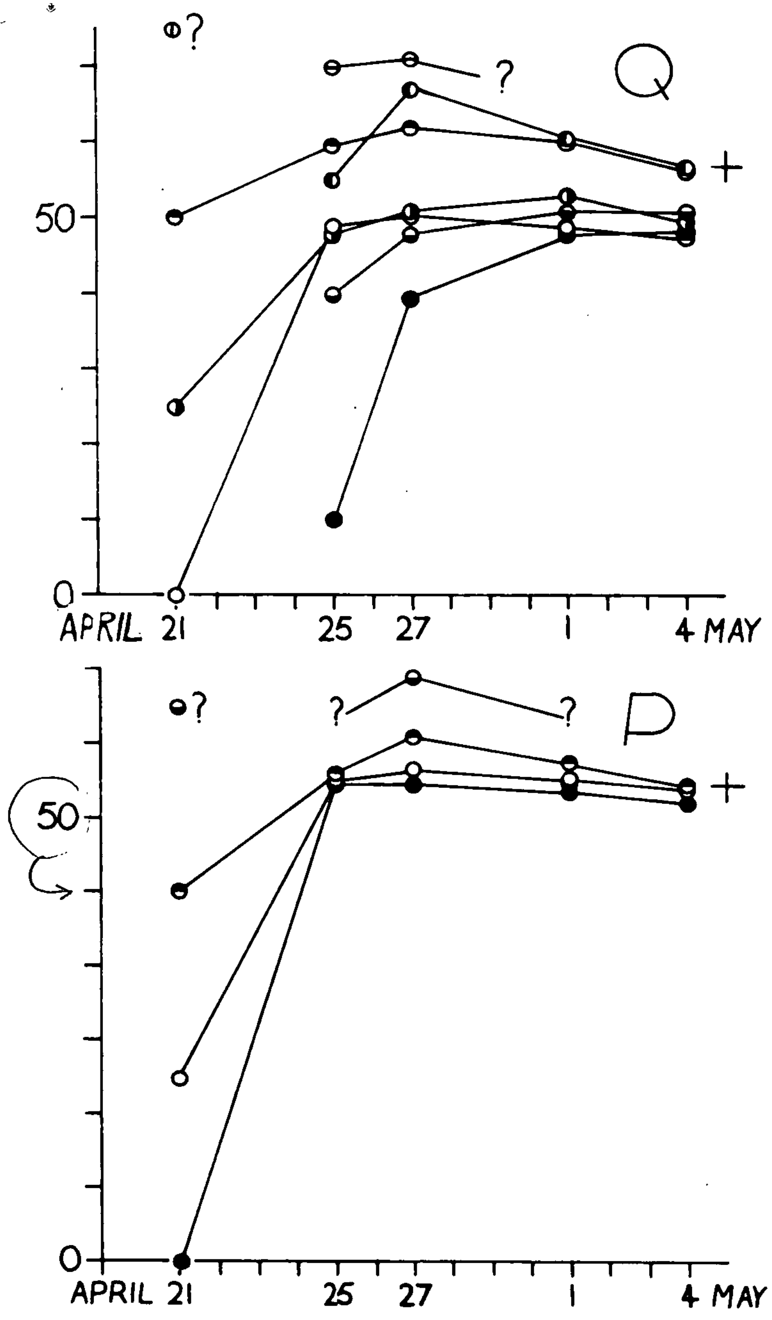

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Fig. 3.8 Fluctuation in water-levels recorded by electrical contact in batteries of tubes at sites along Transect "A", Tarraigheal. Vertical scale as Fig.3.5.Numbers to left of graph indicate level of peat surface at each site. Numbers to right of graph indicate level of water table on 4 May. Graphs summarise data of Table (3. 1). Points distinguished by separate symbol for each site , as shown by larger circles to the left. April - May, 1962.

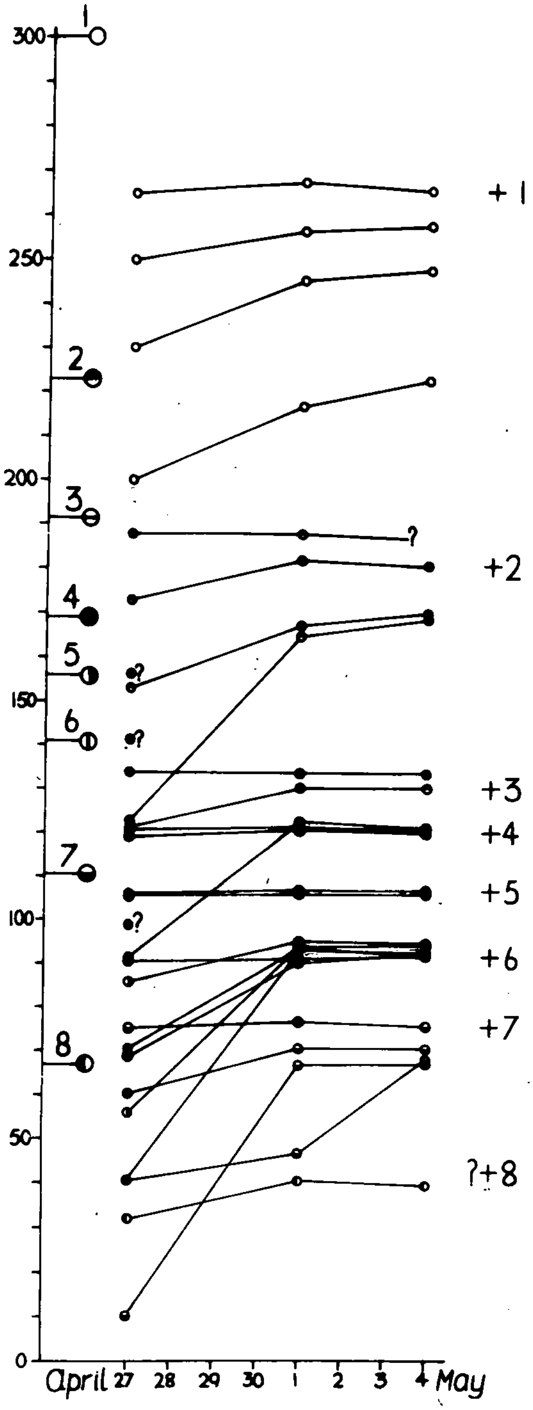

Table (3.1).

Tarraigheal, Inverpolly, 1962

Depths of water surface below upper ends of batteries of 1m. tubes at various sites, recorded by electrical contact. "-"indicates no contact. Values in cms.

The column labelled "Depth" records the distance from the peat surface to the lower end of the tube.

(The numbers in brackets refer to sites along Transect "A".)

Site code	Depth	21 April	25 April	27 April	1 May	4 May	
A.	25	in	-	96	-	-	out
	50	in	84	79	82.5	85.5	out
	75	in	60	58.5	59.5	61	out
	100	in	35.5	35.5	36.5	38	out
S.	25	in	-	- out			
	30		in	99	-	-	out
	45		in	88	94.5	98	out
	50	in	90.5	88	90	93.5	out
	60		in	92	89	89	out
	75	in	77	74	72	75.5	out
	90		in	70.5	62	61.5	out
	100	in	51	49.5	51	52.5	out
Transect A							
(1)	35			in	97.5	99	out
	50			in	93.5	92	out
	70			in	84.5	82	out
	100			in	83	77	out
(2)	35			in	100	-	out
	50			in	91	92	out
	70			in	85.5	82.5	out
	100			in	58	54	out
(3)	35			in	-	-	out
	50			in	-	-	out
	70			in	91	91	out
	100			in	68.5	70	out
(4)	35			in	100	100	out
	50			in	98	98.5	out
	70			in	-	107	out
	100			in	78.5	76.5	out
(5)	35			in	99.5	100	out
	50			in	99	99	out
	70			in	90.5	91	out
	100			in	62	61.5	out
(6)	35			in	99	99	out
	50			in	99	98.5	out
	70			in	77	78.5	out
	100			in	47.5	48	out
(7)	35			in	98.5	99.5	out
	50			in	89.5	89.5	out
	70			in	93.5	72	out
	100			in	43.5	43	out
(8)	35			in	91	92	out

cleared to 10 cm. below end of tube.

accepted unless a rise of 1cm. was recorded in that tube, since some of the apparent rises of less than this may have resulted from the contact becoming fouled by debris at the lower end of the tube. It will be apparent from the diagram that the water-table is in general parallel with the overlying ground surface - an effect also noted by Rutter (loc. cit.). This suggests that values for $\frac{dH}{dl}$ derived from water-table determinations at one date are likely to remain valid for another date, upon which, for example, the water-table as a whole lies at a higher level, or that alternatively if no water-table data are available, that the slope of the ground surface may be substituted without appreciable loss of accuracy. Values for $\frac{dH}{dl}$ have been obtained for Transect "A" by constructing tangents to the water-table profile at each point, and are given in Table 3.2. The validity of inserting these values in the formula for Darcy's Law depends on the assumption that the transect runs parallel to the axis of maximum slope, a point discussed above.

In Table 3.3 are set out all the available data on the variation of hydraulic conductivity (k) from point to point on the transect, computed according to the method set out in Appendix IIIb. It will be noted that there is a considerable degree of variation in conductivity with depth, and that in most cases this takes the form of an increase with depth. In the absence of any information on the repeatability of these data, it is difficult to be certain of the reality of this increase, but on the information provided by Luthin and Kirkham (1949) which is discussed in Appendix IIIb it is to be expected that probable

Table (3. 2).

Tarraigheal. 4 May 1962

Depth and slope of water table. TransectA.

Site No.	1	2	3	4	5	6	7	8
Depth below surface(cm.)	34.0	42.0	51.0	48.5	49.0	48.5	35.0	24.0
Slope($\frac{dH}{dl}$)	0.010	0.110	0.131	0.085	0.120	0.008	0.140	0.167

Estimated value. See Appendix IIIb

Table (3. 3).

Hydraulic conductivity. Transect A

Depth below surface / Site No.	1	2	3	4	5	6	7	8
35 cm.	-	-	-	-	-	NOT COMPUTED	-	2.4×10^{-2}
50 cm	7.6×10^{-3}	-	-	-	-		1.7×10^{-2}	-
70 cm.	9.1×10^{-3}	1.2×10^{-2}	-	-	1.1×10^{-2}		-	-
100 cm.	5.1×10^{-3}	1.9×10^{-2}	2.9×10^{-2}	9.4×10^{-3}	2.5×10^{-2}		3.2×10^{-2}	-

Body of table : K (cm. cm.$^{-2}$ days^{-1})

Table (3. 4).

Velocity of flow of ground water. Transect A.

Depth below surface / Site No.	1	2	3	4	5	6	7	8
35 cm.	-	-	-	-	-	NOT COMPUTED	-	4.0×10^{-3}
50 cm.	7.6×10^{-5}	-	-	-	-		2.4×10^{-3}	-
70 cm.	9.1×10^{-5}	1.3×10^{-3}	-	-	1.3×10^{-3}		-	-
100 cm.	5.1×10^{-5}	2.1×10^{-3}	3.8×10^{-3}	8.0×10^{-4}	3.0×10^{-3}		4.5×10^{-3}	-

Body of table: v (cm. days^{-1})

errors would not amount to so much as to render this effect not significant and it is of interest that the soils examined by these authors showed the same tendency. It will also be noted that there is a tendency for the conductivity to increase from values of between 9.1 x10^{-3} and 5.1 x10^{-3} cm./cm^2/day at the upper end of the transect (under Trichophorum) to between 1.7 and 3.2 x10^{-2} cm./cm^2/day at the lower end (under Molinia). This tendency is compatible with what has already been said about the physical consistancy of the pseudo~~phil~~fibrous and amorphous peat types.

It is now possible to consider the crucial question of the magnitude of differences in the rate of ground-water flow at different points along the transect. The values given in Table 3.4 have been computed by multiplying the values for hydraulic gradient, set out in Table 3.2 by the values for hydraulic conductivity of Table 3.3 according to Darcy's Law:

$$v = k \frac{dH}{dl}$$

Comparison of the results for the upper and lower ends of the transect shows that the velocity of flow under dominant Molinia may be between 50 and 100 times greater than that under dominant Trichophorum. It is, in retrospect, most unfortunate that so few of the sites investigated on Transect "A" lay within the area of absolute dominance of Trichophorum and that of these only one (Site 1) was investigated with regard to the ground-water flow rate. Had the magnitude of differences in velocity to be expected been appreciated at the time, it might have been possible to make an assessment of the critical value associated with the transition in dominance from one species to the other.

In the above argument it is assumed that all the horizontal flow takes place below the water-table. In many agricultural soils the validity of this assumption follows from the very great reduction in hydraulic conductivity when a soil becomes unsaturated, and from the small depth of the "capillary fringe" i.e. the region in which the soil is wholly or almost wholly saturated, but with water having a pressure less than atmospheric (van Schilfgaarde, 1957). In the present peat soils, the "capillary fringe" probably occupies almost the whole of the region above the water-table. Nevertheless, since no hydraulic gradient exists in this region in dry weather, there is no source of potential energy to induce flow. During rain, however, the relatively great conductivity in this region presumably permits rapid downward percolation, and the peat above the water-table may well be so nearly saturated that the water-table rises swiftly in response to a very small accession of water from above. Thus parts of the soil which previously contributed little to the horizontal component of flow now transmit water horizontally by vitue of their submergence beneath the water-table whose inclination to the horizontal provides the necessary energy. If the rain is sufficiently heavy, the water-table will approach the surface more and more closely, while water-table and soil surface remain approximately parallel, until eventually the whole soil profile is involved in the horizontal transmission of water. The parallelism of water-table and soil surface implies that the hydraulic gradient is likely to remain approximately constant as the soil "fills up". If the vertical variation in hydraulic conductivity is not great, and the present results suggest that it is small in comparison to the horizontal variation, we may assume that the same overall differences in velocity will prevail at different points on the transect regardless of the height of the water-table, but that the length of time during which a soil zone of given depth is subjected to horizontal water-flow will depend upon how deep it lies. We may imagine the soil profile to comprise a series of such zones, arranged as layers, parallel with the surface, each layer transmitting water horizontally for a shorter time than the layer below and for a longer time than that above.

The possible implications of these results from the point of view of plant distribution will be discussed in the next chapter.

Soil Oxygen

Several authors have suggested that differences in the oxygen regimes of the moister kinds of soil may have a bearing on the distribution of vegetation. Jefferies (1915) considered that *Molinia* was associated with flushing by well-aerated water, but this appears to have been a purely subjective impression. Soil oxygen was one of the features of the peat soils at Inverliever which were investigated by Fraser (1933). Fraser considered that oxygen defficiency, manifested by an ability to take up oxygen on exposure to the atmosphere, was a factor contributing to the poor development of planted trees. He determined a quantity which he called the "Oxygen-requirement" for a number of peat types, by using fresh peat samples to reduce an acid solution of ferric ammonium sulphate. He pointed out that the oxygen-requirement was not a direct measure of the degree of aeration, which is presumably the factor responsible for the success or otherwise of tree establishment, but that it reflected the extent to which anaerobic processes had been involved in peat formation. The results showed that, whereas the surface of amorphous peat with Molinia dominant had an oxygen requirement comparable to that of an ordinary mineral soil, the oxygen-requirement at the surface of pseudo-fibrous peat with Trichophorum dominant was approximately nine times as great. The values increased with depth, but to a smaller extent in pseudo-fibrous peats than in amorphous types. These results tend to confirm the opinion of Jefferies (loc. cit.).

Pearsall (1938) determined the redox potentials of several peat soils in Britain. This is also a measure of the capacity of the peat to bring about oxidation or reduction, and its effects on vegetation would again appear to be largely indirect. Since oxidation in organic systems frequently gives rise to acidity, the interactions of redox potential and pH are of interest. Molinia was found to be prominent on reducing soils with a pH greater than 4.4, and on oxidising soils with a pH less than 3.9, and it was suggested that this species may not tolerate high acidity except where oxygen is present. Trichophorum- dominated bogs were not included in this investigation.

Poel (1960 a and b, 1961) used a polarographic technique to estimate the "oxygen diffusion rate" in various soils. (Detailed comment on this method will be found in Appendix III (a)). He concluded that the rate measured under Pteridium growing in the exceptionally well-drained conditions of the buried base of an old wall in the Wyre Forest was approximately five times that measured under Juncus conglomeratus in a waterlogged soil. On hill-grazings in Perthshire the highest value measured was in well-drained soils, beneath Molinia-Nardus sward. This value was again about five times as great as the lowest, which was encountered on waterlogged, poorly-drained soils beneath a Juncus-Carex-Sphagnum vegetation which also included Molinia, which, it was implied, formed tussocks. More detailed investigations into the distribution of Pteridium aquilinum, whose rhizomes are known to require a well aerated soil, showed that in some instances at least the transition from a community dominated by Agrostis, Festuca and Pteridium to one dominated by Juncus acutiflorus was accompanied by a marked decrease in "oxygen diffusion rate", though the value at which this transition occurred varied somewhat widely and the suggestion of a particular limiting value was thought to be unjustified. This work also did not include any soils supporting dominant Trichophorum.

In April and May of 1962 a considerable number of polarograph readings was taken at Tarraigheal. On this occasion a stationary platinum microelectrode was used, in the manner of Poel, but a correction for soil temperature was applied to the readings of current, which are proportional to the oxygen diffusion rate in the soil. This temperature correction is not considered to be very satisfactory for reasons discussed in Appendix IIIa, and at this date no method was available whereby a correction for conductivity could be applied. For technical reasons, also discussed in Appendix IIIa, it was not thought justifiable to convert the corrected readings of current to absolute values of oxygen diffusion rate. However, since such a conversion would have implied multiplying all the values by a constant factor, their relative magnitude would have remained unaltered, and they are accordingly presented here as estimates of the relative oxygen diffusion rates.

It was considered that the best use could be made of the somewhat questionable stationary electrode technique by taking advantage of the very small volume of peat which surrounds the electrode, and of the fact that the electrode assembly maybe made small enough for its weight to be entirely supported by the platinum wire. The electrode was accordingly inserted carefully into the peat until the lower end of the glass insulation entered the surface. In this way the exposed portion of wire was embedded to its full length, but in the topmost three centimeters of the soil only. The intention was to simulate, so far as possible, the condition of a small Trichophorum or Molinia seedling root, and accordingly the positions chosen for inserting the electrode were all either in the neighbourhood of such seedlings or in sites where experience showed that their establishment could occur.

The results for Transect "A" are set out in Table 3.5 and Fig. 3.9, together with their standard deviations. The results are in general agreement with the suggestions of Jefferies and Fraser, in so far as there is a progressive rise from a mean of 11-12 μA at the upper end of the transect (Trichophorum dominant on pseudofibrous peat) to a mean of about 25 μA at site six (Molinia dominant on amorphous peat). There is, however, an abrupt decline between sites six and seven. Because there was little evidence of seedling establishment at site eight, no readings were taken there.

It will be apparent that these results show considerable variability. Poel found this tendency in his work, and ascribed it to heterogeneity in the soil on a scale which was large compared with the size of his electrode. It seems very probable that a similar explanation would be valid here, but the present results show no clear evidence of the other tendency noted by Poel, namely a decrease in the variability with decreasing oxygen diffusion rate.

A further series of polarograph readings was made in April, 1963, using the rotating electrode described in Appendix IIIa. This electrode assembly is much more massive than that with which the previous results

Table (3.5).

Tarraigheal. April-May 1962.

Polarograph readings and position. Transect A.

Stationary platinum microelectrode in surface 3 cm. Current after 5 minutes polarisation at -0.4 volt. Temperature correction : $q_t = 3.18\%/$ C°; t = 25 C°.

Site no.	1	1a	2	3	4	5	6	7	8
Number of readings	10	10	10	10	10	10	8	10	-
Mean current (μA)	11.7	11.2	17.1	16.5	21.8	22.6	25.4	20.4	-
Standard deviation (μA)	9.8	5.7	4.2	7.2	6.1	9.1	9.2	7.4	-

"-" indicates not investigated.

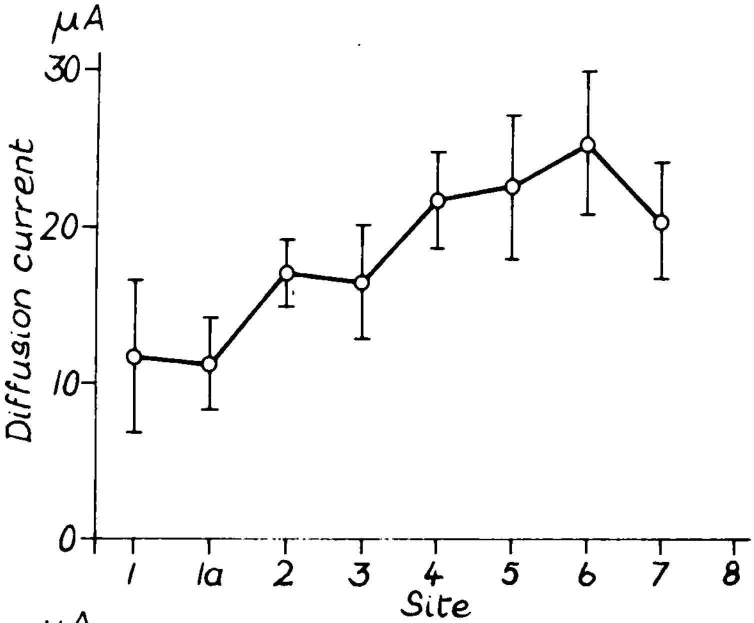

Fig. 3.9 Polarograph readings (with standard deviations) at sites along Transect "A", Tarraigheal. Stationary electrode in surface 3 cm. of peat. Corrected to 25°C. Data of Table (3. 5). April - May 1962.

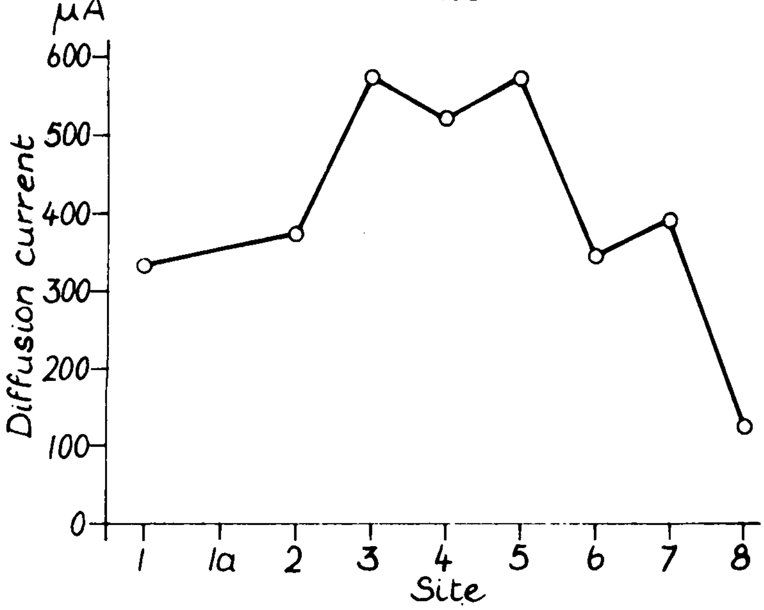

Fig.3.10 Polarograph readings (with standard deviations) at sites along Transect "A", Tarraigheal. Stationary electrode at 22-23 cm. below peat surface. Corrected to 25°C and 100umho. Data of Table (3. 6). April 1963.

Rotating

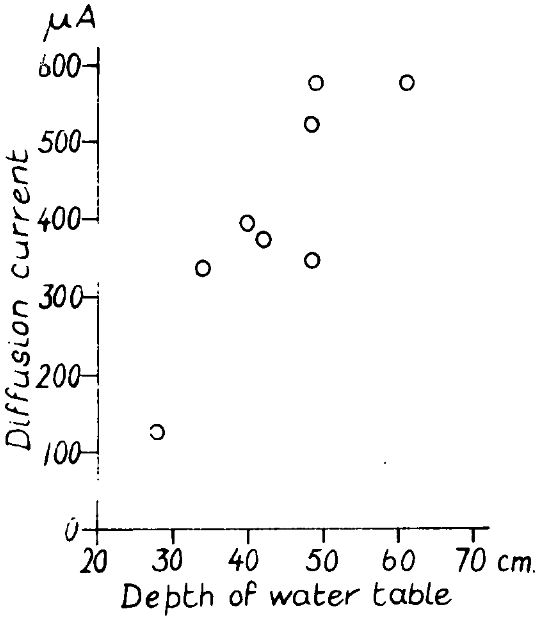

Fig. 3.11 Variation of polarograph readings (from Table 3.6) with depth of water table.

were obtained, and does not lend itself readily to the making of observations near the soil surface. It was, therefore, necessary to take the present series of readings at depths of between 22 and 23 cm. In the one case where a reading was carried out at 18 cm. it was found to be identical with that obtained at 22.5 cm. at the same place. The soil temperature was recorded as before, and the conductivities of soil water samples from the same positions were later obtained, using a Lock portable conductivity bridge Type B C.1 together with a Lock conductivity cell, Type 7407 having black platinum plate-electrodes. The readings were corrected to a temperature of 25°C, as before, and to a specific conductivity of 100 µmho. There was no time to make repeat determinations to test the variability of results at any site and depth, but it should be noted that, with this electrode, the volume of peat sampled is considerably greater than in the previous case, since we are here effectively determining the relative oxygen concentation in a sample of not less than 10 ml. of water expressed from the peat following the insertion of the probe.

The results of this second investigation are presented in Table 3.6 and Fig. 3.10. In comparing them with those of Table 3.5 and Fig. 3.9 it should be remembered that a rotating electrode in open solution passes a much higher current than a stationary electrode in an impeded solution having the same oxygen concentration. It is, therefore, necessary to consider, as before, the relative magnitude of the values only.

Table (3. 6).

Tarraigheal. April 1963.

Polarograph readings and position. Transect "A.

Rotating platinum electrode. Applied P.D. -0.8 volt.Temperature correction : $q_t = 4.9\%/^\circ C.$; $t = 25^\circ C.$ Conductivity correction:$q_c = 170\%/^\circ C \times 10$; $c = 100 \mu mho$

Site number	1	1a	2	3	4	5	6	7	8
Current(uA)	336	-	375	577	522	578	347	393	129
Electrode depth(cm.)	22.5 &18.0	-	22.0	22.0	22.0	22.0	23.0	22.0	22.5

"-" indicates not investigated.

The second series of readings of current behaves similarly to the first, in that there is a considerable rise between the upper Trichophorum dominated, end of the transect and the neighbourhood of sites 3-5, the latter of which is clearly within the area of dominant Molinia. Following this, however, there is a very steep decline in the readings, those for sites 6 and 7 being approximately equal to those for 1 and 2, and that for site 8 being little more than one third the value at site 1. It is very difficult to decide whether the general pattern of these determinations follows that of the 1962 series for the lower end of the transect, and in this light the absence from the latter series of any values for site 8 appears most unfortunate. However, the general similarity over the upper part of the transect, together with the decline previously recorded between sites 6 and 7 suggests that had a value for site 8 been available it would probably have shown a similar decline to that of Fig. 3.10.

Comparison of the 1963 results with the water-table profile of 4th May, 1962 (Fig. 3.5) suggests that the oxygen regime may be related to the water-table. No series of measurements of water-table depth exists for the period when these results were obtained but in view of the foregoing remarks about the nature of water-table fluctuations there is every reason to suppose that, while its over-all depth may fluctuate, the water-table must always lie approximately parallel to the surface so that the effect of rainfall and dr~~a~~ught is to raise or lower the o/

profile bodily, without appreciably altering its shape. The series of points in Fig. 3.11 are the result of plotting the water-table depth in May, 1962 against the polarograph readings of Fig. 3.10. This diagram suggests a strong positive correlation between these two parameters.

It is generally considered that waterlogging is the principal cause of poor aeration in soils. If this is the case in the present soils, the above correlation may readily be understood in terms of the argument previously set out. The duration of waterlogging at any point in the profile must depend upon the position of that point, relative to the water-table. If, as in the intermediate sites on Transect "A", the water-table on a given occasion lies relatively deep in the peat at a given depth, the peat will relatively rarely be submerged beneath it. If, on the same occasion, the water-table lies, as at the ends of the transect, relatively shallowly, peat at the same depth will be submerged relatively more often and will be relatively less well aerated.

The presence of this correlation and of a mechanism to account for it, are both considerations which suggest that soil oxygen concentration or soil oxygen diffusion rate are not in this case, to be regarded as primary characteristics of the environment. Their effect on plant distribution cannot be considered independently of the mire hydrology of which they are a secondary manifestation.

CHAPTER IV

The impact of the environment on the distribution of Trichophorum and Molinia

In Chapters II and III the transition from dominant Trichophorum to dominant Molinia was examined phytosociologically, and some information was given on certain changes in the soil environment which accompany the transition. The present chapter is an attempt to draw together the material of these two previous chapters so that some conclusions can be formed about the way in which the transition arises.

In view of the absence of trees from the mires described here and the uniformity of treatment as regards burning, grazing and other influences to which they have been subjected, the transition in dominance from Trichophorum to Molinia, which is so frequently repeated at all aspects and over such comparatively short distances at Inverpolly, can only be due to differences in the soil. Of the various edaphic properties of the Inverpolly peat deposits which might be concerned, water movement and oxygen supply have been selected as likely to be of greatest importance. We have seen that a transect which traverses the side of a cupola of saturated peat from an apical area dominated by Trichophorum to a peripheral zone dominated by Molinia also traverses soils with a great range of velocity of ground water movement and with considerable variation in the concentration of dissolved oxygen.

Before attempting to decide which, if either, of these two factors is responsible for the transition, it is necessary to form some idea of the way each may affect the species concerned.

I. Movement of Ground-Water

In previous ecological work where ground-water movement has been studied, there has usually been an implication that the effect of such movement upon plant life is due to the presence in the ground-water of dissolved inorganic nutrients. The ground-water is held to be chiefly important as a vehicle by means of which such nutrients are conveyed to the neighbourhood of plant roots and from which they may be absorbed. It is also possible that in some soils its movements may remove metabolites such as hydrogen ions from the roots so that the metabolites do not attain toxic concentration, but the importance of this is less certain. The literature dealing with vegetation on oligotrophic habitats such as moorlands (Pearsall 1950, McVean and Ratcliffe, 1962) and bogs (Malmer and Sjors, 1955) is full of feferences to "flushes" and "soaks", which are zones where the nutritional status is enhanced by the movement of ground-water. In this country it is customary to regard bogs and fens as arising through the waterlogging of their habitats with waters which are respectively poor and rich in mineral nutrients, but it was shown by Kulczyński (1949 and see Chapter III) that in Poland these two extreme types of mire were associated simply with the differences in rate of flow from place to place in a continuous body of ground-water.

A large number of determinations of the mineral nutrient content of mires has been carried out in Britain in recent years, notably by Gorham (1950, 1953 a and b, 1956 etc.). These determinations have in general been confined to samples collected at one particular point in time. Similar determinations have also been carried out in South Sweden by Malmer (1962 a, b, c), but in this case the fluctuations in concentration were followed throughout the year. The results may best be understood in the light of the distribution of the various nutrient elements between the different physical constituents of the soil. Malmer concluded that for this purpose it was convenient to distinguish between three different parts of the substratum, namely:

(i) the open water on the surface of the mire;

(ii) the water in close contact with the dry matter of the peat, from which it could be removed with a filter-pump or pressure membrane apparatus;

(iii) the dry matter together with such residual water as could not be removed with a pressure membrane apparatus.

It was found that in general more than 90% of the total content of the elements examined was present in part (iii). Na and Cl were exceptions, being sometimes found predominantly in solution in parts (i) or (ii). The concentration of elements in (i) and (ii) was found to fluctuate considerably according to the weather, becoming gradually greater during a dry period and decreasing abruptly on dilution by rain. There were parallel fluctuations in pH and specific conductivity.

In addition to these short-term changes, the concentration of elements in the peat fraction (i.e. part (iii) above) underwent seasonal variations. Nutrients such as K, Mn, N and P tended to disappear from the substrate in Spring. At the same time the amount of these elements present in the growing plants was shown to rise, suggesting that the seasonal fluctuations were due to "biological demand". The extent to which the substrate was depleted depended upon its hydrological situation. If it lay near a drainage axis the fall in nutrients was less evident, suggesting that the supply was to some extent replenished from the ground-water.

Malmer's results provide considerable insight into the mechanism of the mineral nutrient supply to mires. They suggest, in the first place, that very little importance can be attatched to the results of analyses of samples of peat collected at one point only in time, especially if only the water in the peat is studied. Secondly, they suggest that the water and the peat together form a complex avenue through which nutrients are supplied to the plants. The influx of nutrients reaches the mire dissolved either in rain (Gorham 1955, 1958) or in horizontally-flowing ground-water. The nutrients are then adsorbed, presumably by a process of ion exchange, on to the peat particles which form the reservoir exploited by the plant roots. The effective capacity of the reservoir depends ultimately upon the rate of the influx.

From this argument we may understand how the ground-water exercises its ecological influence, even though the concentrations of the nutrients dissolved in it are small compared with those in the dry matter which it permeates. We may understand how, through the action of this dry matter as a reservoir, this influence extends to the most shallowly-rooted plants whose absorptive organs may only lie within the zone of horizontal water movement during wet weather (Chapter III). Finally, we may understand that the influence of the ground water depends upon the amount of the nutrient elements which it supplies to the dry matter reservoir.

The amount of any mineral nutrient supplied by the ground water is a function of the product of its rate of flow and the moment-to-moment concentration of that nutrient within it, integrated with respect to time. In the present study we have shown that the transition from dominant *Trichophorum* to dominant *Molinia* is accompanied by at least a fifty-fold rise in the rate of flow, but we have no evidence about mineral nutrient concentration. This omission may seem as inexcusable as it is regrettable, but there are several reasons for it. The most important of these arises from the need to integrate concentration and rate of flow continuously during at least one entire growing season. As suggested above, determinations at a single point in time do not fulfill this requirement. To be adequate, determinations made by conventional methods would need to be carried out sufficiently frequently to take account of all possible variations due to precipitation and seasonal conditions, and for this purpose a laboratory would have had to be set up near the study area. This was not practicable. Some interesting possibilities are, however, offered by the recent introduction of electrodes akin to those used to determine pH, but which are sensitive to metallic cations. It seems very probable that, by this means, it may shortly be possible to devise methods of continuously recording at least the potassium concentration in mire waters, with minimum disturbance to the habitat.

In the absence of the continuous record which we think desirable, it is pertinent to enquire whether any assumptions may usefully be made about the concentration of mineral nutrients in the ground-water. We have shown in Chapter III that a continuous body of ground-water underlies the phytosociological transition of Transect "A" at Tarraigheal, and it is clear that during the course of its horizontal flow down the transect from Site 1 towards Site 8, this water encounters no rock outcrop or other contingency which might augment its mineral nutrient content, other than such slight additions of meteoric minerals (mainly Na and Cl, neither of which is an important plant nutrient) as must inevitably occur as it traverses a catchment. To what extent are we justified in assuming that, at any given time, the concentration of any nutrient ion in this body of water remains similar throughout? Since there is no significant source of nutrient ions along the transect, and the vegetation itself appears to be the only sink, it is to the vegetation that we must turn for an answer to this question.

Thomas and Trinder (1947) published a series of analyses of the ash of the above-ground parts of certain moorland plants, including Trichophorum and Molinia. The material of these two species was collected at intervals of one or two months, from February to September, from an ungrazed area in the North Tyne valley. Their results showed that the percentage of dry weight contributed by the various components into which they divided the ash fluctuated considerably during this period, but the average values for the whole season were remarkably similar in Trichophorum and Molinia, though Silica was appreciably higher in the grass. The average values for some of the components, together with the month during which the maximum value for each was recorded, are given in Table 4.1. The data of Thomas and Trinder do not permit any assessment of the total quantity of the various nutrient elements taken up into the stems and foliage during the year, because the actual dry weight of the plants concerned is not given. Neither do they permit an assessment of the time of year at which the amount of these elements so incorporated reaches its maximum, since a fall in the percentage content may be more than offset by the increase in total dry weight during the growing season.

It was not possible to obtain a similar series of values together with productivity data from Inverpolly, but on the assumption that the ash components in the above-ground parts reach their maximum towards the

Table (4. 1).

Some ash components of Trichophorum and Molinia, expressed as percentage of dry weight (roots excluded). Smale Forest, Northumberland. (Based on Thomas and Trinder, 1947)

	Molinia		Trichophorum	
	Mean	Month in which max.	Mean	Month in which max.
SiO_2 free ash	2.967	May	2.83	May
SiO_2	1.073	February	0.60	September
CaO	0.210	September	0.225	September
P_2O_5	0.443	May	0.373	May
K_2O	1.63	May	1.43	May
Na_2O	0.043	June	0.047	September
MgO	0.237	September	0.239	May
Cl	0.318	May	0.255	September
S	0.203	May	0.205	September

end of the growing season, analyses of data for some components of the ash of the productivity harvests (see Chapter II) were obtained. A part of these data is shown in Table 4.2. Here again there is a very striking uniformity in the percentage contributed by any particular component to the dry weight of Trichophorum and Molinia. The results for phosphorus are an exception, and show an extraordinary variability even between two samples from the same harvested plot at RL, a variability for which there is no obvious explanation.

We may now consider these similarities in the constitution of the ash in conjunction with the similarities already noted in Table 2.4. between the amount contributed by the dominant to the total dry weight productivity per unit area at most of these sites. If we are correct in supposing that the conditions revealed by chemical analysis of the above-ground portions of the plants are a good guide to the chemical constitution of the plant as a whole, it becomes apparent that the dominants, at least, are not in general removing widely different quantities of nutrient elements from the peat.

An attempt has been made to compute the total annual uptake per unit area of certain elements by the vegetation at sites T.T and B.T. which represent respectively the upper and lower ends of Transect "A". For this purpose representative samples of the vegetation remaining after removal of the dominant were analysed chemically, and these results are included in the left-hand columns of the computation which appears in Table 4.3. In the centre columns of this table are shown

Table (4. 2).

Some ash components of *Trichophorum* and *Molinia*, expressed as percentage of dry weight (roots excluded). Inverpolly, 27-29 August 1963. Analyses by courtesy of D.E.Morgan, Esq., N.A.A.S., Bryn Adda, Bangor.

	Site code	N	P	K	Ca	Mg	Cl	Na
Molinia	MGA	1.57	0.102	1.19	0.25	0.19	0.46	0.044
	MGB	1.57	0.090	1.04	0.26	0.17	0.44	0.044
	BT	1.64	0.097	1.01	0.20	0.13	0.39	0.037
	Rh	1.61	0.004	0.82	0.21	0.14	0.46	0.048
	Rh	1.46	0.104	0.87	0.21	0.19	0.48	0.051
Trichophorum	TT	1.05	0.003	0.78	0.18	0.13	0.35	0.050
	NR	1.07	0.102	0.96	0.17	0.16	0.46	0.072

Table (4.3)

Uptake of some nutrient elements at Tarraigheal, Inverpolly, during 1963.

Site code	Component	Analysis of component (% of dry weight)				Weight (gm.) per square metre									
						Including all shrubs					Including 1/3 shrubs				
		N	P	K	Ca	Dry matter	N	P	K	Ca	Dry matter	N	P	K	Ca
TT	*Trichophorum*	1.05	0.003	0.78	0.18	92	0.97	0.003	0.72	0.16	92	0.97	0.003	0.72	0.16
	Shrubs					68					23				
		1.06	0.099	0.50	0.44	100	1.06	0.099	0.50	0.44	55	0.58	0.054	0.27	0.24
	Remainder					32					32				
	TOTAL					192	2.03	0.102	1.22	0.60	147	1.55	0.057	0.99	0.40
BT	*Molinia*	1.64	0.097	1.01	0.20	106	1.74	0.104	1.07	0.21	106	1.74	0.104	1.07	0.21
	Myrica	2.06	0.075	0.56	0.24	30	0.62	0.023	0.17	0.07	10	0.21	0.008	0.06	0.02
	Other shrubs					53					18				
		1.22	0.071	0.75	0.36	85	1.04	0.060	0.64	0.31	50	0.61	0.036	0.38	0.18
	Remainder					32					32				
	TOTAL					221	3.40	0.187	1.88	0.59	165	2.56	0.148	1.51	0.41

the results as they appear when the whole of the living shrub material is included in the total. The results in the right-hand columns of the table have been adjusted on the assumption, made in Chapter II, that only one third of the dry weight of the shrubs was produced during the 1963 growing season. From this table it appears that the relative uptake by one square metre of vegetation at either end of the transect differs according to which element is considered. For calcium the figures are almost identical. For phosphorus they differ by a factor of as much as 2.5. The figures for potassium and nitrogen differ to a smaller extent, the larger uptake being shown at the lower end of the transect, which is scarcely surprising in view of its somewhat larger productivity.

The observations of Malmer (1962.b) quoted above suggest that in oligotrophic mires the annual "biological demand" is mostly satisfied by the nutrient reservoir adsorbed on the peat particles, and that it is generally replaced during the period of over-winter decay. This conclusion is in conformity with the views of Goodman and Perkins (1959) who studied mineral uptake and retention in <u>Eriophorum</u> <u>vaginatum</u>. It also follows from an observation which can be verified in almost any upland district of the British Isles: namely that the vegetation of flat but sloping blanket-bogs does not change progressively in a direction normal to the contour, as might be expected if the percolating ground-water was the principal source of nutrients which became progressively depleted, as it passed successive absorbing roots in its passage down the slope. Since, therefore, the Trichophorum- and Molinia-dominated vegetation at the upper and lower ends of Transect "A" make similar seasonal demands upon the local mineral reservoir adsorbed onto the peat, it seems unlikely that the vegetation of either of these maturing communities (cover 75%-80%, see Chapter II) will greatly influence the mineral content of the ground-water.

In the light of the above arguments, we may, therefore, tentatively adopt as a working hypothesis the view that the mineral content of the body of ground-water underlying Transect "A" is probably not greatly altered as the water flows from the top to the bottom of the transect, or that any such alteration as may occur will be relatively small compared with the very large change in the rate of flow between the two ends of the transect. From this it follows that the rate at which nutrients in the ground water are made available at a given point depends very largely upon the rate of flow.

At the beginning of this chapter it was suggested that there might be a causal connection between the difference in the rate of flow of ground-water and the difference in vegetation on Transect "A". It was also suggested that the connection might have to do with the supply of mineral nutrients to the plants. We have, however, now shown that the mature vegetation at both ends of this transect, and indeed in other places at Inverpolly, has a similar dry weight productivity per unit area, a similar above-ground mineral content, and, therefore, a similar demand for mineral nutrients. We have also suggested that most of this seasonal demand is probably satisfied by the local reservoir.

The growth of plants in established mire communities at Inverpolly appears, therefore, not to be limited by mineral nutrient supply, but by some factor, such as light, whose incidence is similar over the whole area. We suggest that nutrient supply is principally effective before these communities become fully established, and that it limits the growth of seedlings rather than that of adults.

In Chapter II we concluded that the Trichophorum and Molinia populations at Tarraigheal had become established from seed. Extensive field observations, both here and elsewhere, suggest that the seedlings of Trichophorum attain, during the first year, a much lower stature (in general between 1.5 and 2 cm) than do those of Molinia at the same stage (10-15 cm). These observations are confirmed by the experimental evidence reported in the next chapter. This suggests that, while the adult populations of these two species may make similar demands on the mineral reserves of the habitat, the demand per unit area of a stand of Molinia seedlings may exceed that of an equally dense stand of Trichophorum seedlings by a factor proportional to the difference in their size. (This assumes that seedlings and adults have similar mineral composition). Williams and Barber (1961) emphasized the importance of establishing a quantitative equivalence between a biological effect and its presumed cause. It appears likely that, in the ratio between the rates of ground-water flow at the upper and lower ends of Transect "A" and the ratio between the productivities of the seedlings of adults becoming established at these two ends, we have the two quantities of comparable order of magnitude which we require in order to postulate a causal connection. It seems most unlikely that seedlings becoming established after burning are able to make use of the same mineral reservoir as was demonstrated (Malmer 1962.b) to be available for the adults. Mr. J.B. Kenworthy has recently demonstrated that muirburn is followed by appreciable losses of nutrients from the plant litter and surface peat which it affects. For instance the potassium may be removed virtually completely during the month following muirburn. (Forthcoming Ph.D. dissertation - St. Andrews). At this most critical stage, therefore, the supply available from the ground-water solutes assumes over-riding importance.

To suggest that pure stands of seedlings of Molinia and Trichophorum became established over quickly- and slowly-flowing ground-water respectively is an oversimplification. The situation is in reality one of competition between these two species for nutrients and light. Such a situation was found by Lazenby (1955) where the degree of soil waterlogging interacted with competition for light in governing the establishment of Juncus effusus seedlings in grass-clover mixtures. In Chapter II it was suggested that Trichophorum seedlings are comparatively intolerant of shade, and that their growth could be inhibited by a dense cover of Molinia seedlings. Where there are nearby sources of an abundant supply of the seeds of both species, it seems probable that Trichophorum seedlings will be suppressed in places where the nutrient supply is sufficient to support a dense population of seedlings of Molinia. Where, however, the nutrient supply is much reduced and the growth of Molinia seedlings is consequently restricted, the Trichophorum seedlings will be more adequately illuminated, larger, and better able to exploit the substrates limited nutrient supply.

Some preliminary experiments to test this hypothesis will be described in the next chapter.

II. Soil oxygen

In Chapter III it was shown that the distribution of soil oxygen at Tarraigheal has a closer relationship to the mire hydrology than to the vegetation. Nevertheless in view of the connection previously suggested by other authors it is useful to consider whether the oxygen status of the peat may have an effect on vegetation, albeit an effect of secondary importance compared to that of the nutrient status.

It is generally considered that the roots of all plants of waterlogged soils are subject to shortage of oxygen. This may affect their growth either directly, through their respiratory demand, or indirectly through its effect on the availability of mineral nutrients.

With regard to the direct effects of oxygen shortage on root respiration, Metsävainio (1931) showed that a large part of the root tissue of many mire plants, including Molinia and Trichophorum is composed of thin walled canals with few associated living cells. Such tissue is called aerenchyma. It has long been assumed that its function is to provide a pathway for gas exchange between the roots and the open atmosphere, and the experiments of Conway (1937) showed that in Cladium such a pathway exists. Van Raalte (1941) showed that the oxygen requirement of the meristems can be fully met by gaseous diffusion down the root in rice, and that the gas also diffused out into the surrounding medium. Studies using ^{15}O have confirmed the high rate of gaseous diffusion down the roots of rice, but have also shown that oxygen diffuses at appreciable speed down the roots of Vicia faba and barley (Evans and Ebert, 1960, Barber, Ebert and Evans, 1962). This latter finding is in conformity with the views of Williams and Barber (1961) who pointed out that as a supply pathway and reservoir for oxygen, the provision of aeranchyma is usually excessive. They suggested that its probable function was to provide a sufficiently large surface area of root for mechanical and absorptive purposes, while greatly reducing the content of living material, and hence the oxygen requirement. Webster (1962 a and b) showed that the growth of tillers of Molinia was significantly reduced by high concentrations of carbon dioxide and hydrogen sulphide in the ground-water and suggested that this was the reason for the reduced cover shown by this species under comparable conditions in the field. He also showed a significant reduction in the growth of Molinia in stagnant as compared with moving ground-water and ascribed this to the build-up in carbon dioxide, though there seems no clear reason why his results should not have been due to the nutritional effect of water movement. His work suggests that aeration of the roots was effected through the intercellular spaces, but although the oxygen content of these was reduced if the roots were placed in soils deficient in oxygen no ecological effect was demonstrated which could clearly be ascribed to soil oxygen alone. On the evidence currently available, it would appear difficult to account for any direct effect of soil oxygen in controlling the distribution of Trichophorum and Molinia unless it can be shown that one species is markedly less well equipped to withstand a shortage. The anatomical evidence presented by Jefferies (1915) and Metsävainio (1931) suggests that this is unlikely, but only ^{15}O techniques would provide a conclusive demonstration, and these require a cyclotron.

A certain amount is known about the indirect effects which soil oxygen may have upon plant growth. These effects arise mainly through changes of various inorganic nutrients.

A large part of the available nitrogen supply of some soils is in the form of nitrate produced by microbial activity. The process of nitrification may be studied by suitable "storage experiments". In this way Persson (1961) showed that fen peat soils in North Sweden were much more weakly nitrifying than spring and meadow soils, and he considered that this might be due to low temperatures and lack of oxygen in the fens. Fraser (1933) carried out similar experiments with various

West Highland peat types and concluded that n~~y~~trification takes place i only in some Juncus and Molinia flush peats.

Mandal (1962) analysed the effect of varying soil oxygen regime on the dry-weight yield of rice grown under "paddy" conditions in bottles of waterlogged soil aerated with different mixtures of N_2 and O_2. He found that yields were higher with a mixture containing 10% O_2 than with mixtures containing more or less oxygen, and that the percentage incorporation of Ferric and Manganic oxides were also maximal under these conditions. His explanation was that at low oxygen concentrations the equilibrium

$$SO_4'' \rightleftharpoons S'' + 2O_2$$

shifts to the right so that the transition elements are precipitated as their insoluble dibasic sulphides, whereas at high oxygen concentrations where these elements are present in the trivalent form they are precipitated as their tribasic hydroxides,. Mandal also showed that the nitrogen content of the plants attained a maximum at intermediate oxygen concentrations.

From these examples we may appreciate how complex the interactions between soil oxygen and the availability of both macro- and micronutrients may be. It seems probable that if an effect of oxygen on plant growth could be clearly demonstrated, the mechanism should be sought here, rather than in the direct effects of oxygen shortage on biological activity. In the next chapter we hope to show the results of some aeration experiments, but we have already suggested that, so far as the Trichophorum - Molinia transition is concerned, oxygen is of secondary importance to nutrient supply.

CHAPTER V

Experimental

In previous chapters it has been suggested that the transition from dominant Trichophorum to dominant Molinia is accompanied by an increased availability of plant nutrients, and possibly also by a more plentiful supply of soil oxygen. It has also been suggested that the effect of these factors may best be understood by supposing that they act upon the competitive relationships between the seedlings of the two species. For a further understanding of this mechanism it is necessary to describe some experiments which were carried out during the course of this work. In an investigation of this kind, an experiment may have value from various points of view. The correlations between vegetation and habitat have here only been investigated with regard to some of the most salient habitat factors. In order to demonstrate a causal connection between the vegetation and these factors, it is necessary to show by experiment that the vegetation may be controlled in the manner postulated by these factors alone, otherwise, there remains the possibility that other factors, whose correlation with the vegetation was not investigated, might be implicated. Where, as in the case of mineral nutrient supply rates, the environmental factor may be difficult to measure precisely, such experiments may afford a check on the correctness or otherwise of the determinations. Finally, it is very probable that various features of the situation which have been overlooked in the relative complexity of the field may be revealed during the course of an experiment.

In many respects, the most satisfactory ecological experiments are those performed in the field (e.g. Tamm, 1954, 1956) Nagy (unpub. 1964), but difficulties of both execution and interpretation render them most useful for providing confirmatory evidence. In this work there was insufficient time for field experiments on a useful scale so it was necessary to have recourse to greenhouse experiments.

Material

The fruits used in these experiments were collected in the wild from typical *Trichophorum* and *Molinia* habitats in the North-West Highlands. It was not possible to obtain a sufficient supply from Tarraigheal itself, but collections were made from uniform mature stands in the immediate neighbourhood. In this area, the achenes of *Trichophorum* ripen by early August and the caryopses of *Molinia* about one month later. The method of harvesting consisted in simply gathering a bunch of inflorescences in the hand and cutting them off with a knife. The inflorescences were then spread out on newspaper to dry in a warm room, and the fruits removed and cleaned.

The cleaned fruits were lightly dusted with D.D.T., after it was found that large quantities of *Molinia* caryopses attract the unwelcome attention of various anthropods. They were stored in a dessicator over anhydrous Calcium Chloride in the dark, then washed and soaked in distilled water for 24 hours before transfer to the germinators.

Various combinations of warm and cold treatments were unsuccessfully tried in an attempt to overcome dormancy in the achenes of Trichophorum. The effect of frost and light in stimulating germination was referred to in Chapter I. The seedlings used in this experiment were obtained from achenes which had remained in germinators* in an unheated greenhouse throughout the severe winter of 1962-3. Germination occurred mainly during the last week in April and the first week in May. Between 80% and 90% of those Trichophorum achenes which lay within 5 cm. of the edge of the germinating surface were found to have germinated by mid-May. Many fewer seedlings of Molinia were obtained, but since the proportion of glumes subtending fruit could not readily be assessed the same crude estimate of percentage germination could not be made for this species. While they remained in the germinators, Molinia seedlings were subject to attack by Botrytis. When the seedlings could not be removed from this humid atmosphere immediately, these attacks were controlled by spraying with the non-metallic fungicide 'Karathane'. Trichophorum seedlings appeared to resist such fungal attacks. This may be a significant aspect of the paludal habit of this species.

As soon as possible after germination, the seedlings were transfered to the surface of vermiculite in the culture vessels

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* For design of germinators, see Appendix Va.

described in Appendix Vb (Design C). The small amount of root which had grown before transplanting had spread horizontally over the moist paper and acted as a support to maintain the transplanted seedlings upright. The roots of Molinia seedlings (but not those of Trichophorum) showed a tendency to penetrate the chromatography paper, and this occasionally made them difficult to remove from the germinator. During and after transplanting, and until the nutrient supply apparatus, was connected, the Vermiculite was kept saturated with distilled water by means of a Mariott bottle constant-head device (Hewitt, 1952).

The seedlings were arranged on the Vermiculite in an hexagonal pattern, as shown in Fig. 5.1 in which the distance from a plant to its nearest neighbour was 1.05 cm., and the planting density was 1.1 plants/ $cm.^2$. Thirty-six plants were transferred to each beaker, the completed pattern having the shape of an elongated hexagon, the positions being allocated to the two species as shown in Fig. 5.1. It was originally intended to subject five vessels to each of the seven treatments, making a total of 35 vessels in all, but to plant two vessels entirely with Trichophorum seedlings, two with 27 Trichophorum and 9 Molinia seedlings and one with 18 Trichophorum and 18 Molinia seedlings. A shortage of beakers prevented the early transplanting which is apparently necessary for successful establishment, so that the majority of "all Trichophorum" and one of the 3:1 Trichophorum : Molinia mixtures failed to provide good quantitative results. This delay also meant that the different nutrient and aeration treatments could not be applied until July 3rd. Since the experiment was dismantled on 4th September, there were only nine weeks in which the effects of the treatments could be observed.

From what has been said in Chapter IV it is clear that the concentrations of ions in mire water or peat may bear little relationship to their availability for plant growth, and cannot therefore be used as a guide to the composition of nutrient solutions. In view of this it was decided to make use of a standard nutrient medium of proved worth in the present experiment. The formulation selected was one of those used at Long Ashton, as described by Hewitt (1952). The method of making up the medium is shown in Table 5.1. Stock solutions of all the ingredient salts were prepared, using recrystallised grade reagents and single glass distilled water. The composition of these solutions is shown in the third column of Table 5.1. The macronutrient stocks were stored in dark glass winchesters connected to automatic burettes. It was found convenient to combine equal volumes of the stocks of micronutrients into a single mixture. A second mixture was similarly prepared from the trace element stocks. When required, stocks of the nutrient medium were prepared by diluting, in one litre of distilled water, the volumes of stock solutions given in the fourth column of Table 5.1, 50 ml. and 10 ml. of the micronutrient and trace element mixtures respectively, being added. The calcium nitrate solution was diluted separately to avoid precipitation. The two mixtures were placed

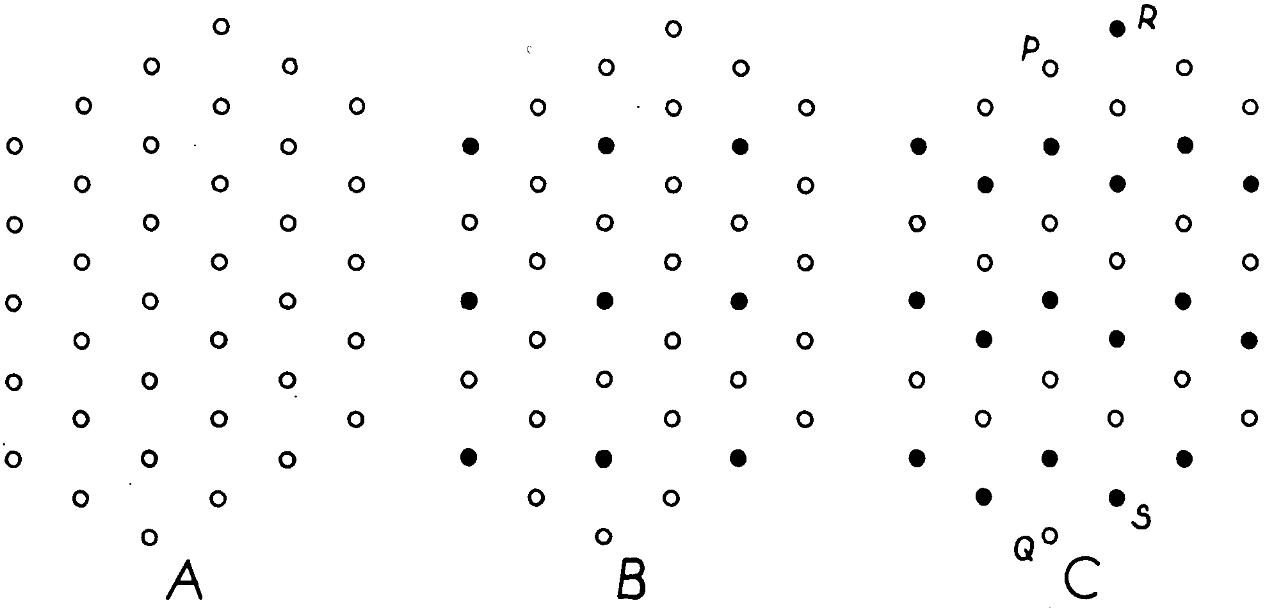


Fig. 5.1 Arrangement of seedlings of Trichophorum caespitosum and and Molinia caerulea in the sub-irrigated cultures.
Open circles - Trichophorum. Closed circles - Molinia. Plant to neighbour distance 1.05cm.
A - all Trichophorum. B - 3 Trichophorum : 1 Molinia. C - 1 Trichophorum : 1 Molinia.

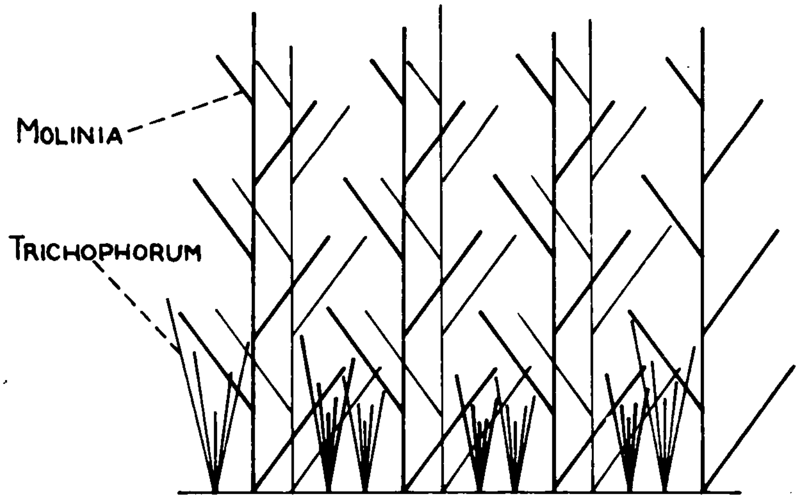


Fig. 5.2 Diagram of the appearance, at the time of harvest, of the two centre rows from a culture vessel planted with equal numbers of Trichophorum and Molinia seedlings.
C.f. Fig.5.1 C: foreground, row S - R (thick lines); background, row Q - P (thin lines).

in the reservoirs on the left hand side of the supply apparatus described in Appendix Vc. A third mixture was prepared, using one tenth of the volumes of stocks shown in Table 5.1, and this was placed in the reservoir on the right-hand side of the supply apparatus. Precipitation of calcium sulphate does not occur in this more dilute mixture, so it was not necessary to dilute the calcium nitrate to a separate solution. The supply apparatus diluted the mixtures a further 100-fold, so that the left-hand side produced a medium of the standard concentration suggested by Hewitt (= 10c), while the right-hand side produced a medium at one tenth of this concentration (=c).

It was found that if the dilute mixture remained in the right-hand side of the apparatus for more than one week before dilution and use, a growth of microorganisms became apparent in the reservoir. To prevent this, some ethyl mercuric chloride, recrystallised from ethyl alcohol, was placed in the reservoir, enclosed in a small sachet of polythene fabric. Hewitt (1952) recommends the use of this substance under such circumstances, since it is alleged to be too insoluble in water to render it harmful to plant growth. However, this may be, plants growing in those culture vessels through which the treated medium flowed at the "fast" rate (see below) became chlorotic shortly after the treatment was begun, and eventually died while the rest remained healthy.

The culture media were diluted with single glass-distilled water,

Table (5. 1).

Composition of stock solutions and concentrated mixed nutrient medium.

Description	Formula	gm./L.of stock	ml.stock /L.mixture
Potassium nitrate	KNO_3	202	100
Anhydrous calcium nitrate	$Ca(NO_3)_2$	328	200
Monosodium dihydrogen orthophosphate	NaH_2PO_4: $2H_2O$	208	100
Magnesium sulphate	$MgSO_4 \cdot 7H_2O$	184	200
Ferric citrate	$FeC_6H_5O_7 \cdot 3H_2O$	29.9	100
(MICRONUTRIENTS)			
Manganous sulphate	$MnSO_4 \cdot 4H_2O$	22.3	10
Cupric sulphate	$CuSO_4 \cdot 5H_2O$	2.5	10
Zinc sulphate	$ZnSO_4 \cdot 7H_2O$	2.9	10
Boric acid	H_3BO_3	18.6	10
Ammonium molybdate	$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	0.35	10
(TRACE ELEMENTS)			
Aluminium sulphate	$Al_2SO_3 \cdot 12H_2O$	7.44	2.5
Galium nitrate(1% solution of $Ga^{\cdot\cdot}$)	$Ga(NO_3)_3\ nH_2O$	20(ml.)	2.5
Cobaltous sulphate	$CoSO_4 \cdot 7H_2O$	1.12	2.5
Nickel sulphate	$NiSO_4 \cdot 7H_2O$	1.12	2.5

which was conducted directly from the still to polythene aspirators. Each aspirator contained sufficient Liquid Paraffin B.P. to form a continuous layer over its contents, so that contact with the atmosphere was prevented while the temperature of the water was still 70° - 80°C; thus ensuring that very little oxygen became dissolved in it. Part of each diluted medium was used directly for the unaerated treatments. The remainder passed through the aerating columns described in Appendix IVa and was saturated with oxygen at the point of departure from the supply apparatus. This was used for the aerated treatments.

Two rates of inflow to the culture vessels were maintained, a "slow" rate (v) nominally at 141 ml/day/vessel (2 drops per minute in the rate monitor - see Appendix IVa) and a "fast" rate (10v) ten times as great, at 1.41 l/day/vessel (20 drops per minute). The object of this was to subject the plants to a tenfold increase in nutrient supply by increasing the flow-rate as well as by increasing the concentration, but the poisoning of the plants growing in the more rapidly flowing medium prevented this comparison from being made.

In addition to the treatments mentioned above, one series of culture vessels was connected to a Mariott's bottle device, arranged so as to maintain the Vermiculite saturated with unaerated distilled water so that neither nutrients or oxygen were supplied to these plants. This treatment is, therefore, referred to as "stagnant". The treatments are summarised in Table 52.

Table (5. 2).

Plot numbers, mixtures, treatments and their fate in the sub-irrigated culture experiments.

			I 36 Tr.	II 36 Tr.	III 27 Tr. with 9 Mo.	IV 27 Tr. with 9 Mo.	V 18 Tr. with 9 Mo.
	Stagnant	A	(1)	(2)	3	4	5
	c x v = r unaerated	B	6	(7)	8	9	10
	c x v = r aerated	C	11	12	13	14	15
	10c x v = 10r unaerated	D	(16)	(17)	18	19	20
	10c x v = 10r aerated	E	(21)	(22)	23	24	25
	c x 10v = 10r unaerated	F	26	(27)	28	29	30
10r	c x 10v = r aerated	G	31	(32)	33	34	35

"( )" : Seedling failure "_" : Treatment failure

Tr. : Trichophorum Mo. : Molinia

At the end of the experiment it was found that while those Trichophorum seedlings which were growing without accompanying Molinia were of similar size in any given culture vessel, the presence of Molinia caused a considerable depression in the stature of the central Trichophorum plants, while no such "edge" effect was apparent in Molinia. The appearance of the two controls rows of plants (e.g. rows P-Q and R-S, Fig. 5.1) in a vessel with equal numbers of either species is shown diagramatically in Fig. 5.2.

The plants were harvested by cutting them off with fine scissors at the level of the nylon netting. They were subsequently dried in cellophane bags at 60°C in a forced draught oven for three days and weighed. It was considered that the individual plants, especially of Trichophorum, were too small to be weighed separately. The figures shown below, refer, in the case of Molinia, to sub-plots of 9, or of 4 and 5 plants, obtained by dividing the crop along a randomly orientated diameter. In the case of Trichophorum, the larger peripheral plants were separated from the 9 or 13 smaller, central plants to exclude the "edge effect" as far as possible.

Effect of the treatments on Molinia

The results for total plant dry weight per plot are shown in columns (v) and (x) of Table 5.3. Inspection of these results suggests that in general, they are affected more by the treatment than by the

Table (5.3)

Dry weights of Molinia seedlings (mg.).

Mixture / Treatment	27 Trichophorum : 9 Molinia					18 Trichophorum : 18 Molinia				
	Plot number	Mean plant weight (half plot)		Mean weight (whole plot)	Total weight	Plot number	Mean plant weight (half plot)		Mean weight (whole plot)	Total weight
A Stagnant	4	36.0	36.0	36.0	324	5	22.7	18.9	20.8	374
r B Unaerated	9	188.8	240.8	214.8	1933	10	69.7	56.6	63.2	1138
r C Aerated	14	114.2	113.0	113.6	1022	15	64.4	75.4	69.9	1258
10r D Unaerated	19	84,2	76.8	80.5	724	20	79.7	113.0	96.4	1736
10r E Aerated	24	173.6	178.8	176.2	1585	25	76.3	65.2	70.8	1276
Column numbers of this table	i	ii	iii	iv	v	vi	vii	viii	ix	x

density of Molinia. The totals for treatments A, C and E are of the same order at either density, while for treatment B, the lower density produced the larger weight, the converse being evident for treatment D. Assuming a completely plastic response to increasing density, the mean plant weight over a whole plot would be expected to be halved if the density is doubled, while the treatment remains the same. This expectation is represented by the continuous line drawn in Fig. 5.3, in which the mean plant weights at the two densities (columns (iv) and (ix) of Table 5.3) are plotted against each other for each of the five treatments. The points obtained for treatments A, C and E lie close to the expected positions, while the departure is greater for treatment B and D. Clearly the hypothesis of a plastic response is in closer agreement with these data than the alternative hypothesis that the mean plant weight is independent of density and affected only by treatment, represented by the broken line on Fig. 5.3. Since, therefore, the weight of an individual Molinia seedling would appear to vary inversely with density in this way, the weight per unit area of the crop as a whole is, within limits at least, independent of seedling density and controlled by other factors.

The significance of the effects of the various nutrient and aeration treatments was assessed after eliminating the density effects. For this purpose the mean plant weights in columns (vii) - (ix) of Table 5.3 were doubled, to convert them to those expected on the hypothesis

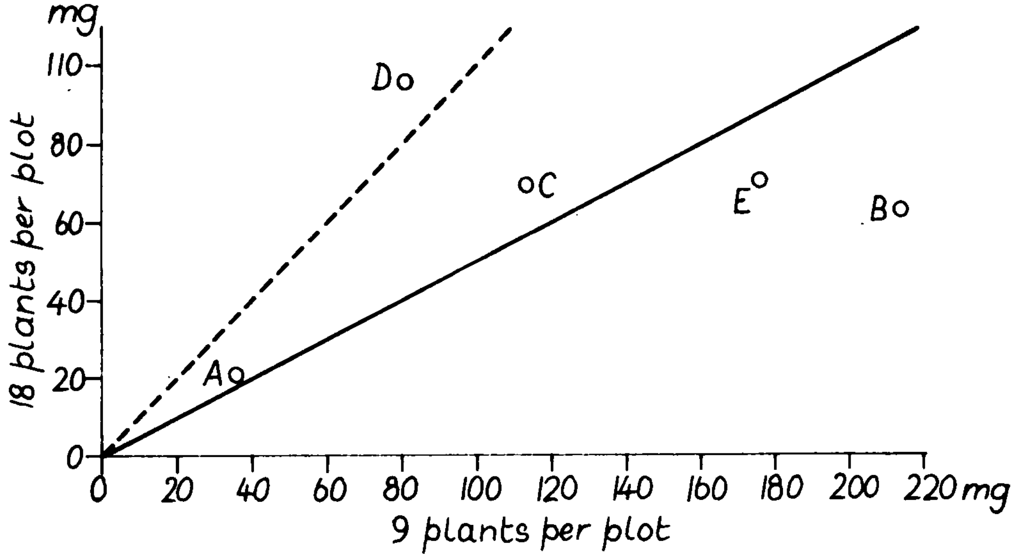


Fig. 5.3 Influence of density on mean plant weight of Molinia seedlings subjected to five treatments. Continuous curve : plastic response. Broken curve : no response to density.
Letters indicate treatments (c.f. Tables 5.3 - 5.5).

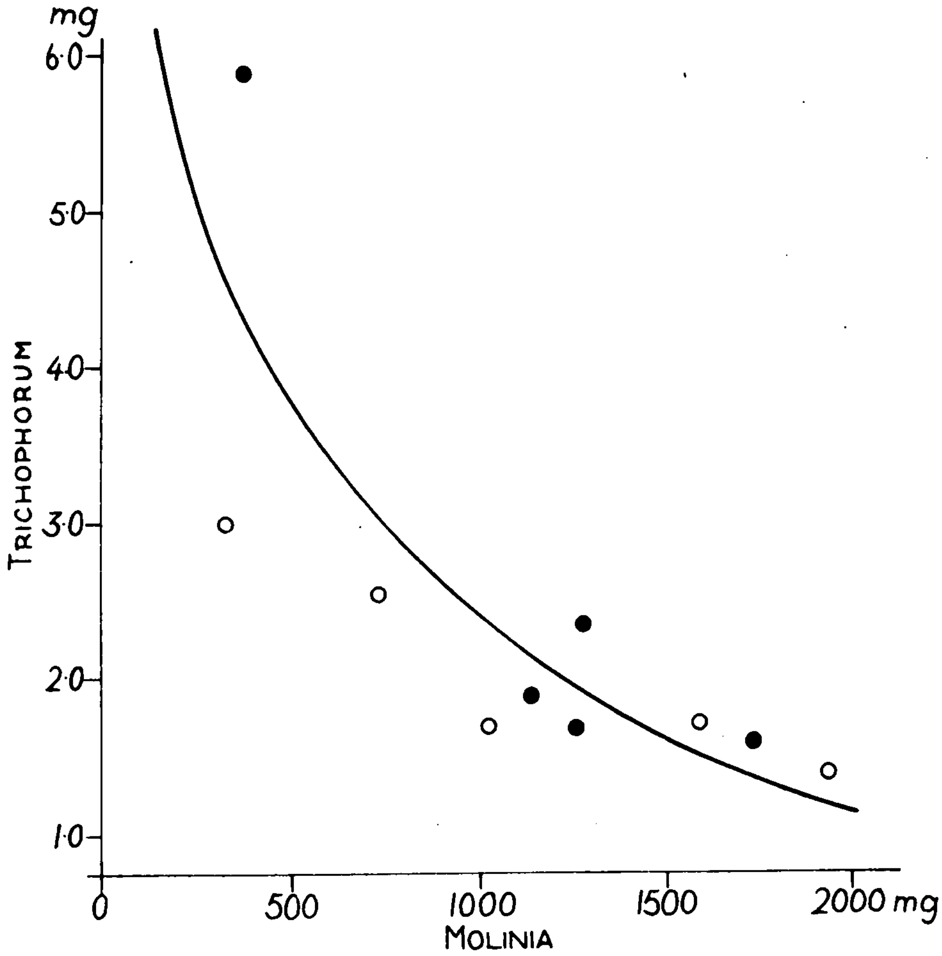


Fig. 5.4 Curve of mean dry weight of central plants of Trichophorum against the total dry weight of the accompanying Molinia crop.
Open circles : 27 Trichophorum with 9 Molinia. Closed circles : 18 Trichophorum with 18 Molinia.

of a plastic response, to a density of 9 plants per plot, in order to make them comparable with the results of columns (ii)-(iv). From the four independent estimates of individual plant weight so obtained, an overall mean was computed for each treatment. These means are set out in Table 5.4, together with the significances, where appropriate, of their differences on the basis of "Student's t-test". It is not to be expected that comparison between means based on four samples only will be a sensitive index of the effect of a treatment. Nevertheless it is clear that plants grown at the intermediate rate of supply of nutrient (r) were significantly larger than those from under "stagnant" conditions, although the further increase in dry weight at the highest rate of supply (10r) which was obtained from the aerated treatment (comparison C - E) was not significant. The corresponding comparison (B - D) between the unaerated treatments showed a non-significant decrease at the higher rate of supply. This is inexplicable, but in keeping with the behaviour already noted in Fig. 5.3 etc. for these treatments. Consideration of these results suggests that it would have been more profitable to have worked at lower rates of supply, since the response to nutrient supply which was evident at the lower rates falls off at the higher rates. This is presumably because growth is then limited by factors other than mineral nutrition. Due to the failure of treatments F and G it is not possible to draw any conclusions about the effect of ground-water movement <u>per se</u> on the response to nutrient

Table (5. 4).

Effect of nutrient supply and aeration on Molinia.

t - test on means computed from data of table (5. 3), as described in the text (pp. 98-99).

Treatment	Mean plant dry weight (mg.)	P(%)				
A Stagnant	38.8		I.			
r B unaerated	170.6	0.01			25(Not Sig.)	
r C aerated	126.7					Not Sig.
10r D unaerated	136.6			10(Not Sig.)		Not Sig.
10r E aerated	158.9					

supply. The relevant comparisons (B - C and D - E) show no significant effect of soil aeration, though since the suspect results of treatments B and D enter into both these comparisons, this conclusion is tentative only.

Effect of the treatments on Trichophorum

From the point of view of an interpretation of the results of this experiment, it is most unfortunate that the pure stands of Trichophorum did not become fully established. Had they done so, they would have been expected to show similar responses to increasing mineral nutrient supply to those shown by Molinia.

The results obtained for the dry weights of Trichophorum seedlings grown in competition with Molinia in the plots referred to in Table 5.3 are shown in columns (ii), (iii), (vi) and (vii) of Table 5.5. We have already noted that the Trichophorum seedlings showed a marked "edge effect" when grown with Molinia (Fig. 5.2). For this reason interest chiefly centres upon the central plants in each plot, whose mean dry weights are shown in columns (iii) and (vii). The largest values recorded were in the "stagnant" plots (treatment A). The weights obtained at the intermediate nutrient supply rate, r, (treatments B and C) were generally less than one half the values for treatment A. Plants grown at the highest supply-rate, 10r (treatments D and E) were on average slightly heavier than those grown at r, but did not approach the weight of those grown at the lowest supply-rate in the "stagnant"

Table (5.5)

Dry weights of Trichophorum and Molinia seedlings (mg.).

Mixture / Treatment	27 Trichophorum : 9 Molinia				18 Trichophorum : 18 Molinia			
	Plot number	Total weight of Trichophorum	Mean weight of 13 central Trichophorum	Total weight of Molinia	Plot number	Total weight of Trichophorum	Mean weight of 9 central Trichophorum	Total weight of Molinia
A Stagnant	4	87	3.00	324	5	118	5.88	374
B $\overset{r}{\text{Unaerated}}$	9	93	1.39	1933	10	43	1.78	1138
C $\overset{r}{\text{Aerated}}$	14	59	1.69	1022	15	46	1.67	1258
D $\overset{10r}{\text{Unaerated}}$	19	84	2.54	724	20	61	1.56	1736
E $\overset{10r}{\text{Aerated}}$	24	99	1.69	1585	25	61	2.33	1276
Column numbers of this table	i	ii	iii	iv	v	vi	vii	viii

plots. The total dry weights of *Molinia* have been repeated in columns (iv) and (viii) of Table 5.5. Fig. 5.4 shows the result of plotting mean dry weight of *Trichophorum* against total dry weight of the *Molinia* crop with which each *Trichophorum* crop was in competition. There is an inverse relationship between the size of the *Molinia* crop and the development of the *Trichophorum* beneath it. The relationship is apparently in the form of a hollow curve, but the points toward the upper end of this curve are few and scattered, so that it would be rash to speculate on the significance of its shape.

The *Trichophorum* and *Molinia* seedlings grown in this experiment responded differently to mineral nutrient supply rate. Whereas the *Molinia* crop increased in dry weight with increasing nutrient provision, the *Trichophorum* crop decreased in weight. For a complete explanation of this phenomenon, it is necessary to have evidence from pure stands of *Trichophorum*. Due to late planting and consequent failure of the pure stands of *Trichophorum* in this experiment to become fully established, such evidence is not available. The larger, peripheral *Trichophorum* seedlings from the mixed plots were by no means free from the competitive effects of *Molinia*, as is made clear by Figs. 5.1 and 5.2. However, if we consider firstly the absence of an "edge effect" from the late planted pure *Trichophorum* stands, and secondly the marked edge effect shown by *Trichophorum* in the mixtures, it seems reasonable to conclude that the decrease in weight in the

Trichophorum stands grown at higher rates of nutrient supply was due to the increased development of Molinia under these conditions and that the Trichophorum was suppressed by competition from Molinia.

The absence of marked edge effects from the Molinia crops suggests that the culture vessels achieved their objective of providing an even distribution of nutrients throughout the rooting medium. It seems probable, therefore, that the restriction in growth of Trichophorum was not due to nutrient deficiency but to a shortage of some other essential growth factor, brought about by the presence of Molinia. The most obvious factor would appear to be light.

Although no systematic investigation of the effect of light intensity on the growth of Trichophorum has yet been carried out, some relevant observations may be summarised below:-

(a) Young seedlings grown in a shaded greenhouse, or in a north-facing cold frame shaded from the sun, developed chlorosis which was not apparent in unshaded controls.

(b) Young seedlings grown beneath the dense shade cast by a stand of the much taller first-year seedlings of Eriophorum vaginatum developed pronounced chlorosis which was not apparent in controls grown in similar conditions, but without a cover of Eriophorum seedlings. The Trichophorum seedlings failed to survive the second growth season.

(c) Seedlings of Trichophorum growing in the shade of Calluna bushes or of luxuriant stands of Molinia or adult Trichophorum are chlorotic by comparison with specimens found nearby in open situations.

(d) Adult Trichophorum plants growing with Molinia or Eriophorum vaginatum became more chlorotic than the other two species when placed in low light intensities in the laboratory. After a fortnight of such conditions in May, the regions of elongation at the base of the flowering stem; and immediately below the flowering spike, were almost white, while the intervening region which had extended in full sunlight remained comparatively green. When the plants were returned to full sunlight, gradual recovery was apparent but the stems tended to lodge. The Molinia and Eriophorum vaginatum remained more healthy throughout the treatment.

(e) Adult Trichophorum is not found in woodland, even where adaphic conditions appear to be suitable. Cuttings transferred to woodlands in North West Scotland became chlorotic and etiolated and after two seasons' growth the number of stems per cutting had failed to increase. Controls transferred to open mire vegetation had become established after two seasons and were difficult to distinguish from neighbouring undisturbed Trichophorum clones of similar size. The number of stems per cutting had in some cases doubled.

The chlorosis recorded in (a) to (e) above appeared in each case to be due at least in part to shortage of light. When the present experiment is considered in regard to these observations, it seems probable that shortage of light was similarly responsible for the

p.105 →

chlorotic appearance of the central Trichophorum plants of the mixed stands. A rigorous demonstration of the nature of the competitive effect exercised by the Molinia plants would demand their replacement by screens, but the foregoing observations provide strong circumstantial evidence that Molinia suppresses Trichophorum by excluding light.

This experiment has numerous shortcomings. Nevertheless its results appear to support the hypothesis advanced in Chapter IV. The development of Molinia seedlings is increased under conditions of high nutrient supply rate such as were postulated to occur where rapid ground-water movement is found. The greater productivity per unit area of Molinia is independent, within limits, of the seedling density. The higher productivity results in the suppression of accompanying Trichophorum seedlings, probably through competition for light. The eventual outcome of this process could only be determined by a long-term experiment, but from sundry observations it seems unlikely that Trichophorum seedlings would long survive beneath luxurient young Molinia plants.

SUMMARY AND CONCLUSIONS

In this dissertation, an attempt has been made to study an aspect of the ecology of *Trichophorum caespitosum* ssp. *germanicum* in the North West Highlands of Scotland by comparing it with *Molinia caerulea*. Each paragraph below is numbered according to the chapter to which it refers.

I. The account begins with description of the relevant features of the life history of *Trichophorum*. The species reproduces from seed, each tussock being a single clone. A review of the status of the two subspecies reveals no clear evidence of the survival of ssp. *caespitosum* in Britain. Much of the apparent variability of ssp. *germanicum* is phenotypic but there is also evidence of genetic variability including some which may have originated from introgression with ssp. *caespitosum*.

II. There follows a summary of the history of research on plant communities which include *Trichophorum caespitosum*. The species becomes more abundant Northwards and Westwards in Scotland. In a study area selected as being floristically typical of the North-West Highland region, the transition from dominant *Molinia* to dominant *Trichophorum* is described floristically. The two species are not mutually exclusive. The communities concerned are frequently burned, whereupon the vegetation becomes re-established from seed. The factors that control this process of establishment and that determine which of the two species attains dominance are, therefore, unlikely to have operated so long ago that they cannot be evaluated, thus avoiding one of the chief difficulties presented by perennial vegetation. The annual dry weight productivity is similar in the two communities.

III. The environmental factors most likely to control the distribution of these mire communities are edaphic. Examination of the study area suggests that Molinia attains dominance in situations where the ground-water is more rapidly moving, and where the peat is on the whole better aerated, than in neighbouring situations where Trichophorum is dominant. The transition in dominance is, however, accompanied by changes in the rate of ground-water movement which are quantitatively far greater than the accompanying changes in availability of soil oxygen, and the vegetation shows a better correlation with the former than with the latter.

IV. Moving ground-water may increase the supply of nutrient ions to plant roots. In a root system with "aerenchyma", variations in soil oxygen supply may also chiefly affect the plants by restricting the availability of certain nutrients and by controlling the activity of nitrifying bacteria. Examination of their ash content shows that the mineral composition of Trichophorum and Molinia is similar. In view of the similar productivities of the two communities it follows that the quantities of inorganic nutrients required to sustain a seasons' growth is also similar in both species. It, therefore, appears that the nutrient supply rate does not act by limiting the growth of adult plants. On the other hand, a comparison of the size of first year seedlings suggests that the annual incorporation of nutrients into young Molinia may greatly exceed the annual incorporation into young Trichophorum occupying an equal area of ground surface. An equal curtailment of the nutrient supply to the seedlings of these two species would, therefore, suppress the growth of Molinia more than that of Trichophorum. Variations of soil aeration failed to affect either species significantly.

V. Confirmation of this hypothesis was sought in an experiment in which the seedlings of Trichophorum and Molinia were grown together. The growth of Molinia could be restricted by reducing the mineral nutrient supply, while the productivity per unit area of this species was to some extent independent of plant density. The growth of the associated Trichophorum varied inversely with that of Molinia, apparently due to competition for light. This competitive effect resulted in the greatest development of Trichophorum under conditions of lowest nutrient supply.

It is concluded that the establishment of dominant Molinia results from the greater capacity of the seedlings of this species to respond to the enhanced supply of mineral nutrients available where the ground-water flows more rapidly. In such situations Molinia seedlings suppress those of Trichophorum early in the period of recovery after muirburn, so that adult Trichophorum is a subordinate member of the community. Where, however, there is a tendency for the groundwater to stagnate, Molinia seedlings remain too small to restrict significantly the growth of Trichophorum, which eventually attains dominance.

APPENDIX IIIa

On the application of polarographic techniques to the study of oxygen in peat soils

(1) Introduction. Since the publication of two papers by Poel (1960a,b) British plant ecologists have shown considerable interest in the application of a polarographic technique to the study of the oxygen regime in soils. The studies described in this appendix arose from the author's interest in the oxygen regime of peat soils, since it was clear from Poel's description of the method, that polarography might offer a simple and rapid means by which this aspect of peat could be investigated. However, it soon became evident that the technique was not so simple as the descriptions had suggested, and that before valid conclusions could be drawn it would be necessary to undertake some fundamental research into the physics of the method. The present author does not consider himself qualified to carry these researches through to conclusions which a physicist could accept, but has merely attempted to point the way towards the development of more rigorous techniques, to indicate some of the ways in which the generally accepted methods fall short of his own expectations, and to try at the same time to use the modified apparatus to investigate the soils with which he has been concerned.

(1) Principle of the method

It is customary to regard the processes of chemical oxidation and reduction as being accompanied by a transfer of electrons to or from the substances concerned. Oxidation involves the loss of electrons, while reduction involves an addition of electrons. For example the oxidation of the ferrous ion to the ferric ion may be described thus:

$$Fe^{++} - e \longrightarrow Fe^{+++}$$

It is evident that the process of electron transfer involves an increase in potential of the substance oxidised, and a loss of potential of the substance reduced. The extent of potential loss, or potential gain, is characteristic of the substance concerned. Hence the potential at which one material can be oxidised or reduced may be lower or higher than that at which another substance can be oxidised or reduced. In a normal chemical oxidation or reduction, the necessary potential required to bring the reaction about is provided by a reagent of the correct "redox potential", but the reaction may also be brought about at the surface of an electrode maintained at a suitable potential difference with respect to a solution of the substance to be reduced or oxidised. The electrode is positive with respect to the solution if oxidation is required, or negative if reduction is to be carried out. Under these circumstances the electrode is the sink for electrons, during oxidation, or the source of electrons during reduction.

If a solution containing a reducible substance forms the electrolyte of a cell in which the anode is non-polarisable, while the cathode is composed of a substance such as mercury or platinum which can, by means of a potentiometer, be made more or less negative with respect to the anode, the current flowing in the circuit is found to vary in a characteristic manner as the applied potential difference is increased. The form of the curve of current against applied potential difference is shown in Fig.3.12, from which it will be seen that at first, increase in the potential makes little difference to the current which flows, but that as the potential necessary for reduction is approached, there is a sudden increase in current, after which further increase in potential again has little effect. The sudden increase is due to the onset of reduction, and the potential at which this occurs (conveniently measured at the mid-point of the rise and called the "half-wave potential", v) is, like the redox potential, characteristic of the substance concerned. The current c, ultimately attained when v is exceeded, is due to the transfer of electrons from the cathode to the substance being reduced, and is, therefore, limited by the availability of this substance at the surface of the electrode, which is a function of its concentration and rate of diffusion through the solution. The two quantities v and c form the basis of the methods of qualitative and quantitative analysis known as "polarography", since v indicates the presence of a particular ion or element in solution, while c is proportional to the amount which is present.

In common with many other substances, oxygen may be determined by polarographic reduction. The reduction takes place in two stages,

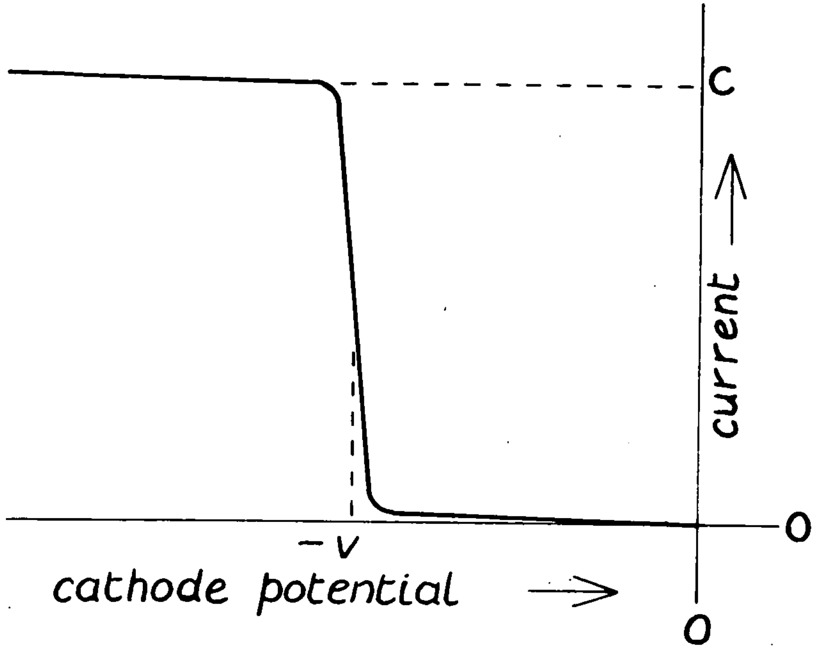


Fig. 3.12 Curve of current and applied potential difference. Polarographic reduction of a single ion species at the cathode

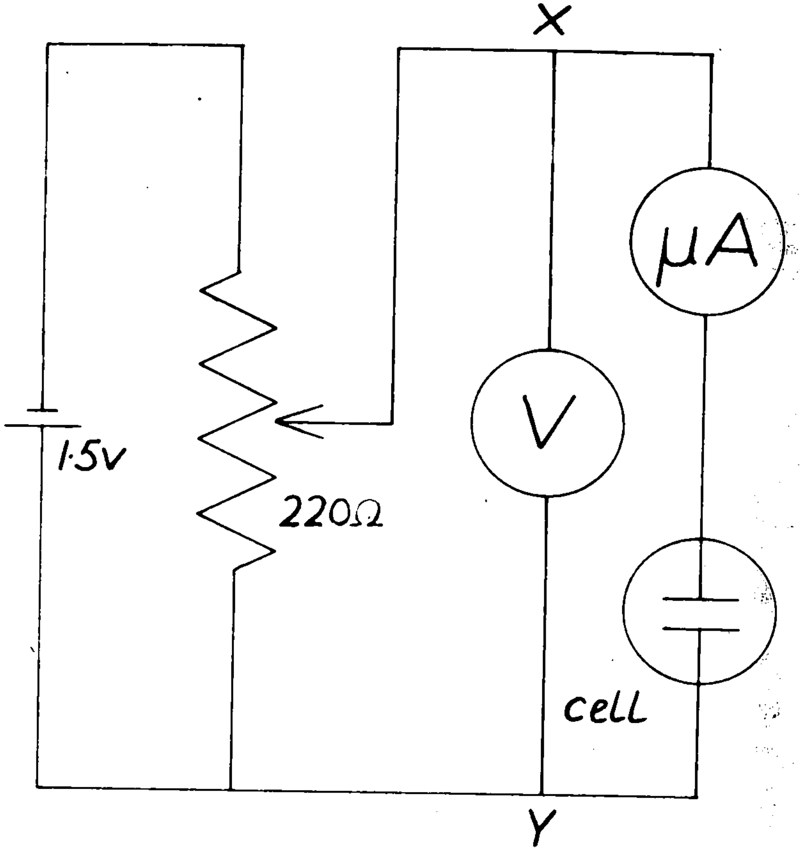


Fig. 3.13 Circuit showing essential features of L.W.Poel's voltammeter. (Based on Poel,1960,a)

whose precise nature is uncertain, but which are thought to be as follows (Kolthoff and Lingane, 1952).

Stage I

$$O_2 + 2H^+ + 2e \longrightarrow H_2O_2 \quad \text{(acid medium)}$$

$$O_2 + 2H_2O + 2e \longrightarrow H_2O_2 + 2OH^- \quad \text{(neutral or alkaline medium)}$$

Stage II

$$H_2O_2 + 2H^+ + 2e \longrightarrow 2H_2O \quad \text{(acid medium)}$$

$$H_2O_2 + 2e \longrightarrow 2OH^- \quad \text{(alkaline medium)}$$

Stage I occurs at a half-wave potential above -0.1 volt, which is so small that oxygen has to be eliminated from solutions of all other substances to be determined by polarographic reduction, since otherwise the oxygen wave obscures all the others. Stage II occurs at about -1.1 volts. There is a plateau between the two waves at about -0.7 or -0.8 volts, which may conveniently be used for quantitative determinations.

(2) Apparatus

It will be convenient to consider this in two sections. The first deals with the device used to provide the applied potential difference between the electrodes, and to measure the current which passes, this device being called a voltammeter. The second section considers the question of the choice of electrodes.

(a) Voltammeter The essential features of this instrument are firstly a reliable means of providing a repeatable, stable potential difference between the cathode and the anode, and secondly a reliable means of providing repeatable estimates of the current which passes between the electrodes. Fig. 3.13 shows the circuit proposed by Poel for this purpose. The potential difference applied to the two electrodes, shown here as though they were placed in a conventional electrolytic cell for measuring purposes, is obtained by connecting a 220 ohm potentiometer across the poles of a 1.5 volt dry battery. The current which flows through the cell is measured by means of a moving-coil microammeter, while a moving-coil voltmeter is provided to measure the potential drop between the slider and one end of the potentiometer. It will be noted that this potential difference is not applied directly to the cell, but is instead connected across the cell and microammeter, which are in series. The voltmeter does not therefore, actually measure the P.D. across the cell at all, since the cell is only a part of the total resistance between x and y, the other part being due to the microammeter. Unless the resistance of the microammeter is negligible compared with that of the cell, there will, therefore be an appreciable error in estimating the P.D. applied to the latter; an error which will vary in an imponderable manner with different soil oxygen values.

During the course of one reading, according to the method proposed by Poel, the applied potential is switched across the cell for about 5 minutes before a reading is taken. This delay is made necessary by the onset of polarisation at the cathode, which, in the present author's experience, may have the effect of increasing the resistance of the cell tenfold, with a corresponding decay in the current measured by the microammeter. If, when the reading is taken, the microammeter has an internal resistance of the order of 3% of that of the cell, the applied P.D. will be about 97% of the value shown by the voltmeter, but when polarisation begins, the value may only be about 75% of that shown. If results are to be comparable between different soils, it is essential not only to standardise the time taken from the moment of switching on until the reading is taken, but also to ensure that the history of the course of polarisation is as nearly as possible identical on each occasion. Since the degree of polarisation at any time after switching on is determined by the charge that has passed, which in turn depends upon the applied P.D. it is evident that polarisation can most easily be made to take a similar course on different occasions if the applied P.D. is kept at a nearly constant value while the process takes place.

For these two reasons, therefore, Poel's circuit was considered unsuitable for the present purposes.

At this point the reader may enquire whether these objections could be overcome by rearranging the components in the manner shown in Fig. 3.14, in which the voltmeter is connected directly across the two electrodes. It would, indeed, be possible to produce a workable instrument

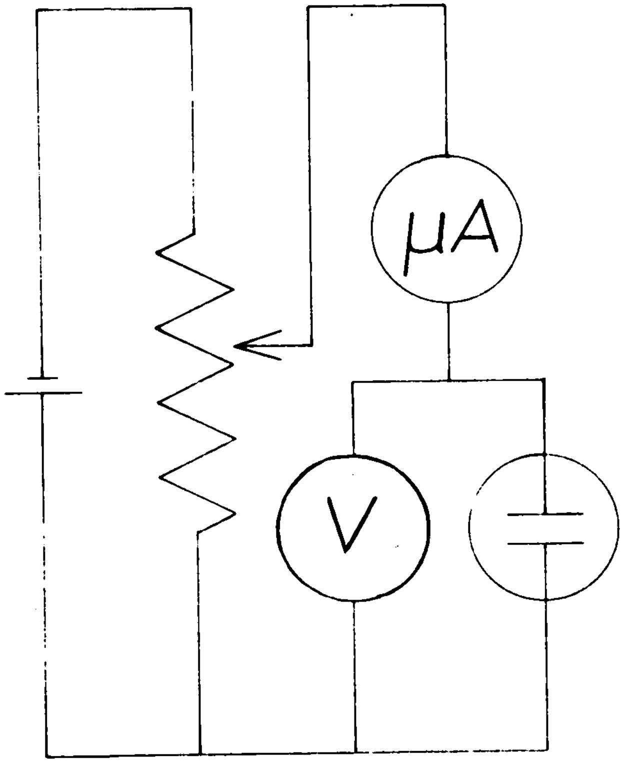


Fig. 3.14 Circuit showing essential features of voltammeter employing a vacuum tube electrometer.

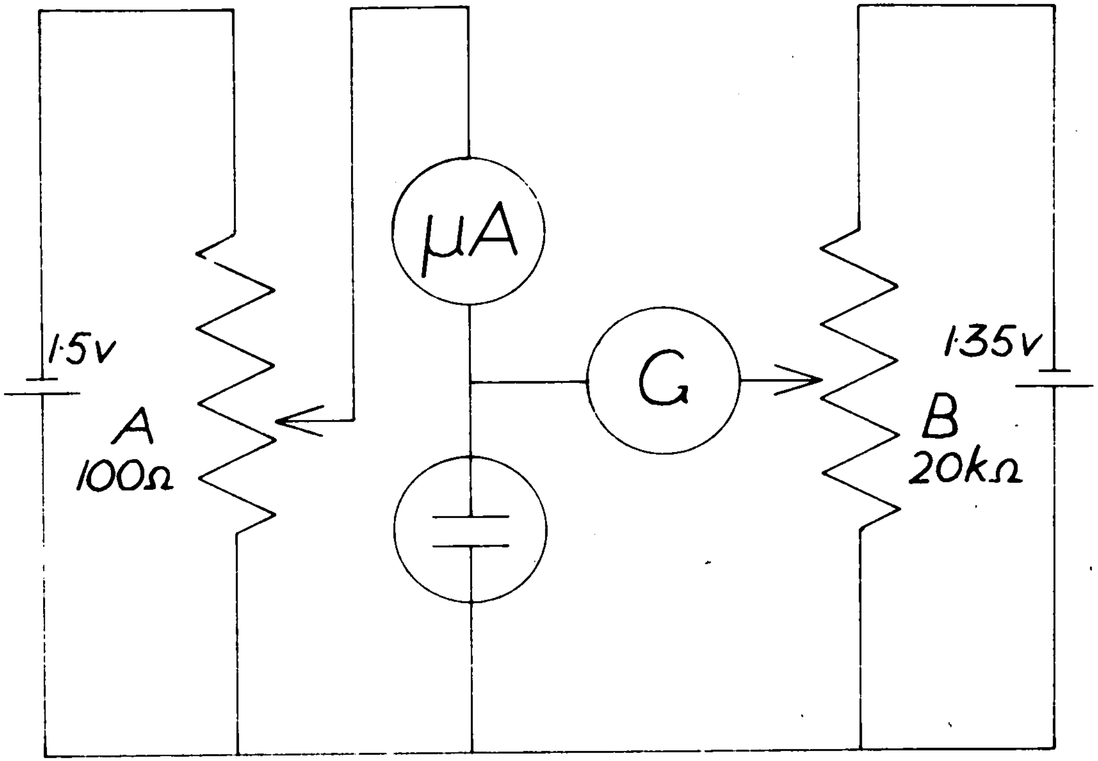


Fig 3.15 Circuit showing essential features of voltammeter employing a standard cell and potentiometer,

in this way, but an ordinary moving coil voltmeter is here not a suitable device for measuring potential because its internal resistance would be too low. Even the better instruments currently available have an internal resistance which is certainly no greater than the cell would have, under average conditions in peat, so that of the current indicated by the microammeter, appreciably less than half would flow through the cell, while the rest flowed through the voltmeter, and the error thus introduced would, as before, be imponderable because the resistance of the cell could not be determined. In order to make this circuit workable the resistance of the voltmeter must, therefore, be very much greater than that of the cell. It would, indeed, need to be of the order of 5×10^6 ohm. to reduce the error to below 1%. Suitable voltmeters exist. They are known as "vacuum-tube electrometers" or "valve voltmeters", and form the basis of the modern direct-reading pH meter. They are, however, both bulky and expensive.

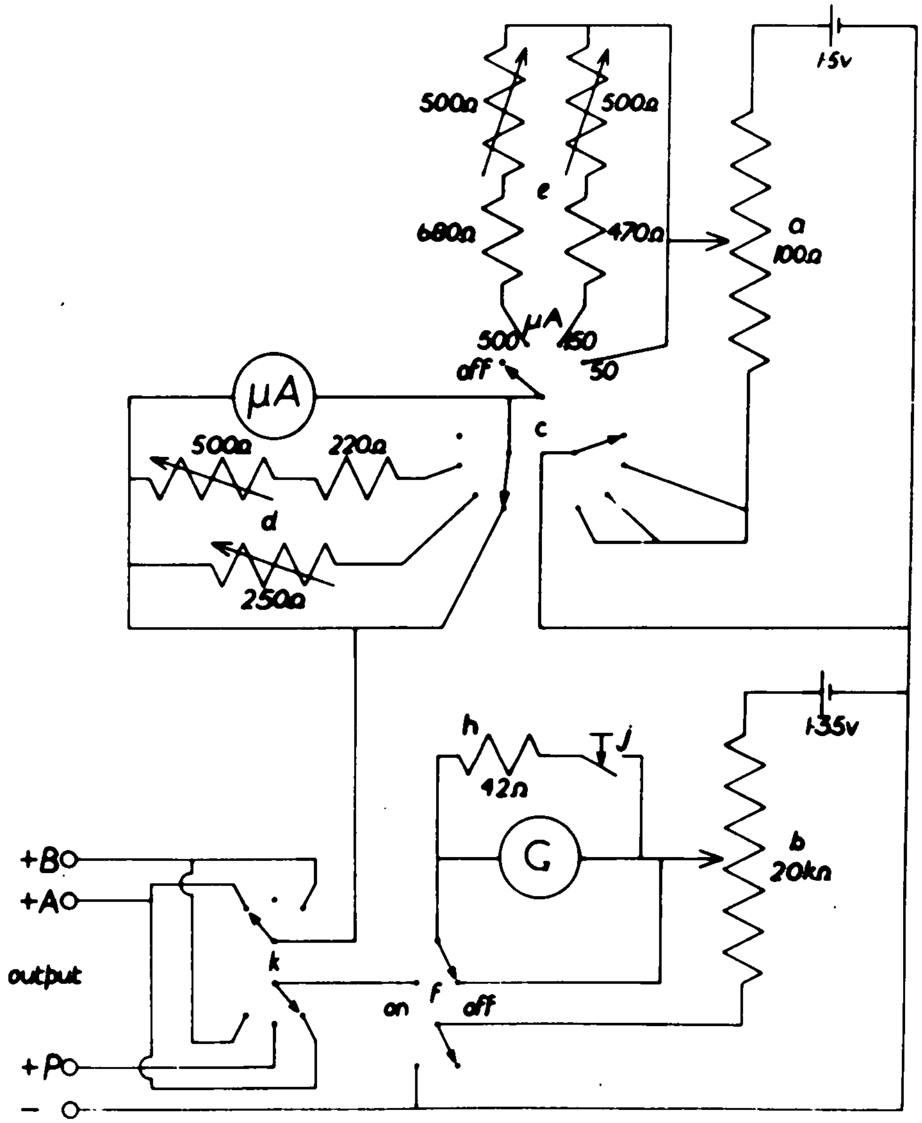
These difficulties can be overcome very simply by replacing the voltmeter of the circuit shown in Fig. 3.14 by a standard cell, a potentiameter and a null-point detector. The theoretical circuit is shown in Fig. 3.15. The standard cell used is a Mallory mercury battery, giving an e.m.f. of 1.35v $\pm \frac{1}{2}$%, and having a temperature coefficient which is negligible for the present purposes. A potentiometer (b) is connected across this battery. The type chosen has a resistance of 2×10^4 ohms., so that the current delivered by the battery is less than 7×10^{-5} amp., which is well within the load which can be imposed on batteries of this type without appreciably reducing their e.m.f. This potentiometer has a track arranged as a helical coil of ten turns, which facilitates the accurate setting of the slider necessary to take advantage of the linearity of the coil, which is better than 1%. A centre-reading microammeter was used to indicate the nüll-point, at which no current passes from the cathode to the slider of potentiometer (b), under which conditions the slider and the cathode are at the same potential with respect to the anode. In order to apply the required P.D. to the cell, therefore, the slider of the potentiometer (b), is set to a position corresponding to the required potential (which must, of course, be less than 1.35 volts with this arrangement), and the potentiometer (a) is adjusted until the nüll detector reads zero, when the cathode assumes the same required potential. It will be noted that when the nüll detector reads zero all the current indicated by the microammeter flows through the cell.

The value of the resistance of potentiometer (a) requires some comment. The life of the 1.5v battery will be prolonged by a high resistance, but if the resistance is too high, a large drift in the P.D. across the cell will occur during polarisation. The value chosen is, therefore, a compromise between preserving the life of the battery and preserving the similarity of polarisation history stipulated above. If an average value of cell resistance of 3×10^{4} ohm. is assumed, together with a ten-fold increase in resistance during polarisation from an initial value of 3×10^3 ohm., calculation shows that a resistance of 100 ohms. for (a) would produce a drift of 0.75% of a final applied P.D. of 0.8 volts. This is taken to be an acceptable variation while the resulting current of 1.5×10^{-2} amp. is not great enough to discharge a transistor radio battery inconveniently rapidly.

The dry cell chosen for use here was an Ever Ready A.D.4. This cell measures 2½" x 2½" x 3½" and is considered to be of ample size to withstand the requisite discharge current without becoming "noisy".

Fig 3.16 shows the full circuit of the voltammeter. The values of the components are shown on the diagram. The microammeter is controlled by a 3-pole 4-way rotary switch (c) which, by switching in a set of shunt resistors (d), provides three ranges of 0-50, 0-150 and 0-500 micro-amps. Because these shunts have the effect of lowering the resistance of the microammeter circuit as a whole, a set of series resistors (e) is included to restore the total resistance to that of the meter alone so that the P.D. across the cell is not increased by switching in the shunts. The shunt and series resistors have fixed and adjustable components in series to facilitate adjustment of the ranges. In the "off" position of (c) the 1.5 volt dry battery is disconnected on the positive side at the microammeter and at one end of potentiometer (a), while the microammeter is protected by short-circuiting its contacts. The voltage measuring circuit is controlled by a double-pole double-throw

Fig. 3.16 Complete circuit of standard cell voltammeter.



toggle switch (f). In the "off" position this short circuits the galvanometer (for protection) and isolates the positive side of the standard 1.35 volt mercury battery. In the "on" position it connects the potentiometer and galvanometer across the electrodes. The galvanometer is protected by a shunt (h) which can be switched out by depressing the microswitch (j) when carrying out a fine adjustment of the applied P.D. A 2-pole 3-way rotary switch (k) controls the three positive output terminals A, B and P. A and B were provided so that two alternative reference electrodes could be used to provide a check on each other's reliability. P provides direct access to the voltage measuring circuit for purposes of calibration.

In use, the reference electrode is connected to A and the platinum cathode to the negative terminal. After setting (b) to the required value, (k) is switched to B and (c) to 500 ohm., and with (f) to "on" (a) is adjusted until the galvanometer reads zero, after which (f) is switched to "off". The electrodes are now switched into the circuit by turning (k) to A, and the time is noted. As polarisation proceeds (c) is switched successively to the 150 and 50 microamp. ranges and, as the time for reading the current approaches, the applied P.D. is checked by switching (f) "on" and depressing (j). After the reading has been taken (c) and (f) are returned to "off" and (k) to P.

The components of the voltammeter are mounted on a 14 s.w.g. aluminium panel with a stub chassis at the rear bearing the preset adjustable resistors at (d) and (e), and housed in a waterproof steel junction box with a light aluminium lid. The list of electrical components is as follows:

Meters: A: 0-50 μA. moving coil, 800Ω impedance, ex W.D. s 145 SUB 18.

G: 50-0-50 μA, moving coil 250Ω impedance, ex W.D. v 3345

Potentiometers: a : 100Ω, $1\frac{3}{4}$" wire wound CLR.5237/263, by Colvern

b : 20KΩ , wire wound helix ("Helipot") by Beckman.

Pre-set variable resistors: 250Ω and 500Ω , 1", wire wound by Radiospares

Fixed resistors: wire-wound, high stability.

Switches: c, 3-pole, 4-way, rotary, by Radiospares.

f, 2-pole, 2-throw, toggle (heavy duty) by Radiospares.

j, microswitch, ex. W.D.

k, 4-pole, 3-way, rotary, by Radiospares.

Batteries: 1.5 volt Ever-Ready A.D.4 dry cell

: 1.35 volt Mallory Voltage Reference Battery. Type 303114.

(b) <u>Electrode systems</u> The calomel anode was the same as that described by Poel (1960a, p. 167 and Fig. 2), except that a larger cone and socket (B20) was used to improve the contact.

The correct functioning of this electrode depends on the maintainance of continuous layer of saturated KCl solution between the components of the ground glass joint, so that there is a complete circuit between the calomel and the soil. In practice it was found that the ground glass joint was such a good seal that the circuit was interrupted, so continuity was maintained by inserting a human hair in the joint, which then allowed the solution to leak away at an appreciable but not inconveniently high rate.

The cathode used by Poel was a modification of that described by Lemon and Erickson (1952). These workers used a stationary platinum micro-electrode made from a short length of platinum wire sealed into a glass tube and embedded in the soil at the requisite depth. Poel points out the similarity between such an electrode, which responds to the rate of diffusion of oxygen towards its surface, and the living plant root with its demand for respiratory oxygen. His own cathode was a more robust modification of that used by Lemon and Erickson, adapted for use in greater depths of soil.

Although the present author has used electrodes of the Lemon-Erickson pattern to investigate conditions near the surface, he feels that extreme caution is necessary in interpreting the results, expecially in terms of actual oxygen diffusion rate, as has been done by Poel. The reasons for these misgivings are set out below, They are not mentioned in Poel's papers.

The first difficulty arises from a misconception of the physical basis of the polarographic method. It will be apparent from what was said in section (1) above, that the phenomena on which the method depends take place in ionising solvents, such as water. They do not take place in solid or gaseous media. It will also be apparent that the current which passes must depend upon the area of the electrode over which the reduction of oxygen takes place. Since most soils are a mixture of solid, liquid and gaseous phases, it is evident that the platinum electrode will only be in contact with the aqueous soil solution over a part of its surface. Unless the porportion of surface which is thus wetted is the same in all the soils investigated, comparable results cannot be obtained. Lemon and Erickson (1955, p.390) recognised that in agricultural soils the results would depend upon the relationship between moisture tension and texture, which would control the availability of water to form a layer over the electrode. As a **rule, no such difficulties regarding water availability are** to be apprehended in a typical peat soil. Instead the most likely cause of results that are not comparable is that differences in texture of peat from different sites will result in the obstruction of different proportions of the electrode area by solid particles. Clearly, therefore, while there is every reason to encourage the use of polarographic methods in liquid media, such as are provided by aquatic habitats (Manning, 1940) or sewage (Ingols, 1941, Moore, Morris and Okun, 1948), their use in soils directly should be undertaken only with the greatest caution.

The second difficulty which must be considered is the question of the effect of temperature. All polarographic determinations are subject to considerable temperature coefficients. A figure of 1.5-2%/°C is quoted by Kolthoff and Lingane (1952) for the dropping-mercury electrode, but they state that platinum microelectrodes may be expected to show coefficients in excess of 4%/°C. Since the soil temperature varied between 6.9°C and 18.5°C during a series of determinations made by the present author during April, 1962, it was clearly important to determine the value of the temperature coefficient so that the necessary correction could be made. An attempt was accordingly made, using a sample of Durham tap water because of its moorland origin, which had been allowed to stand for 48 hours to absorb atmospheric oxygen. During the determinations, the sample was isolated from the atmosphere by a layer of medicinal paraffin and its temperature slowly raised in a thermostat bath from 0-28°C. The resulting curve is shown in Fig. 3.17. The slope of the curve indicates a positive temperature coefficient of 3.18% of the value at 25°C, per centigrade degree: a not inconsiderable figure. At the same time it will be noted that the points show a considerable scatter about the straight line of best fit. This scatter is due to failure of the system to yield a steady current, so that even after time has been allowed for polarisation to be completed the microammeter needle still drifts. The explanation of this lies in the effect of convection currents in the sample, and of vibrations in the laboratory, as the movement of the electrode relative to the sample. This relative movement in turn accelerates the rate at which oxygen molecules arrive at the surface of the electrode, so that the diffusion current resulting from their reduction is increased, giving the impression of an increased oxygen concentration or oxygen diffusion rate. This effect does not occur when the cathode is placed in a soil, since

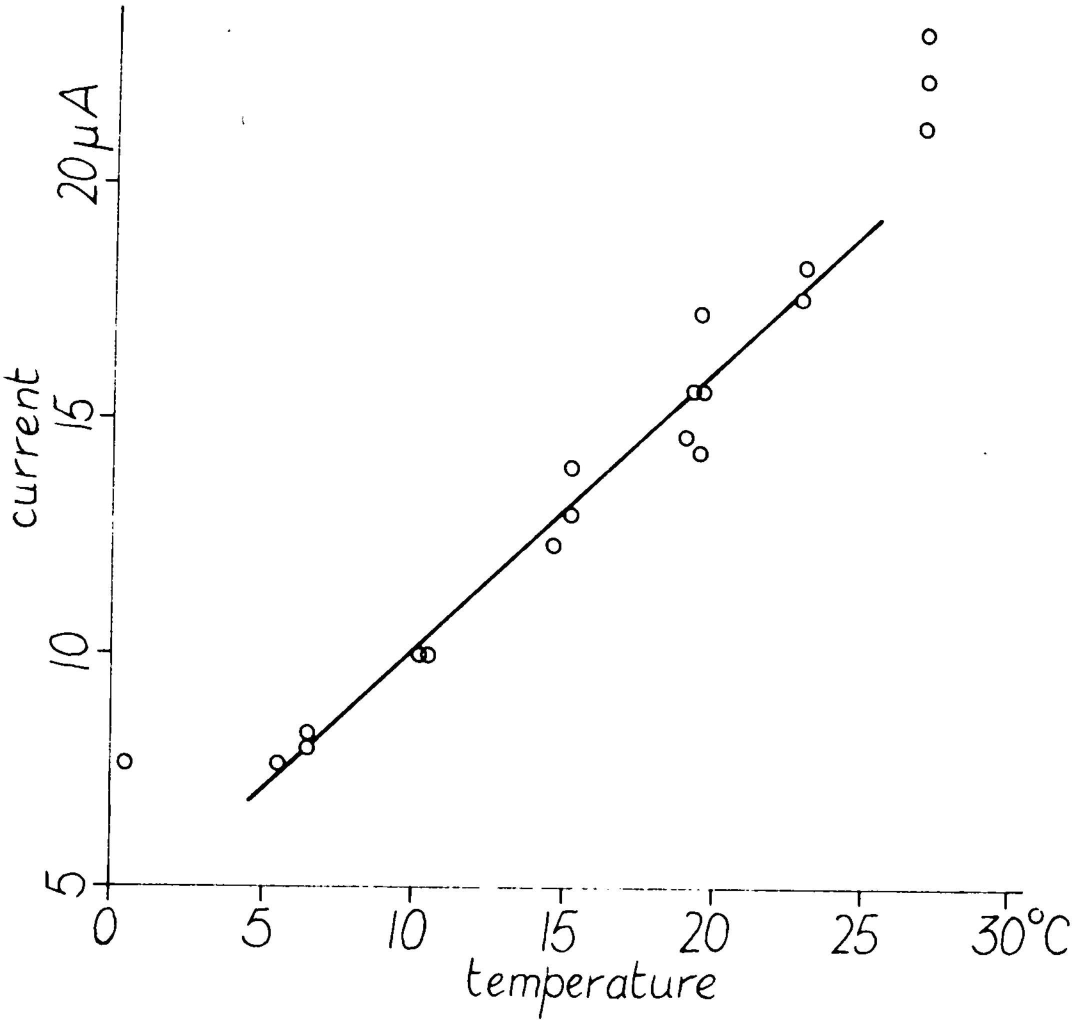


Fig. 3.17 Curve of diffusion current and temperature at constant oxygen concentration, without conductivity correction. Stationary electrode.

relative movement between the cathode and the soil water is prevented by the obstructive effect of the soil particles.

A third difficulty arises in connection with the effect of conductivity on the readings of current to be expected from the polarograph. If, in addition to oxygen, there is an ionisable solute present in the water of the test sample, this has the effect of increasing the current which passes at a given oxygen concentration. This effect is due to the decrease in the total resistance of the medium between the cathode and anode, which arises from the presence of the solute ions, and is without reference to any further polarographic reduction. If a sufficiently large quantity of electrolyte is present in the sample, the effect on the current of further additions becomes negligible. Use is made of this fact in standard polarographic practice by adding to the test sample a much more concentrated solution of "backing electrolyte" (usually Potassium Chloride) whose effect is to "exalt" the diffusion current (Kolthoff and Lingane, 1952) while preserving the linear relationship between current and concentration of the substance to be estimated. It is, of course, not possible to make use of this technique in work on soil oxygen <u>in situ</u>. Since, therefore, the differences in conductivity which occur from place to place in a soil cannot be masked in this way, it is necessary to determine their probable effect, to measure them, and then to adjust the results accordingly. The author has been unable to discover any means by which the effect of adding electrolyte can be measured in a soil directly, owing largely to the difficulty of ensuring an even distribution of the introduced ions. At the same time, it is clearly not possible to obtain reliable results in open solution, as was shown in the attempted temperature calibration. Nevertheless, it is clearly necessary to devise a method which works in open solution, since only then can the conductivity calibration be carried out.

Stationary platinum micro-electrodes are seldom used in polarographic laboratories, largely on account of the unstable currents which are obtained with them (Kolthoff and Lingane, 1952). The system most frequently employed is the dropping-mercury electrode, but it is hardly necessary to describe this device in detail before suggesting that it is not well adapted to use in situ in soils. A popular device for use in conditions where the presence of quantities of free mercury are unwelcome is the membrane electrode. Here a stationary platinum disc is enclosed with a suitable anode in a small volume of electrolyte solution behind a plastic membrane, through which oxygen can diffuse. After a period of equilibration, the oxygen concentration in the solution assumes a value which is related to the oxygen tension in the environment surrounding the membrane, and may be determined polarographically in the usual way. If the volume of solution enclosed by the membrane is sufficiently small, equilibration is rapid and relative movement between solution and cathode is much reduced. Moreover the solution acts as a "backing electrolyte" so that no adjustment is necessary for conductivity. Automatic temperature compensation is also possible. A third device is the rotating electrode. As in the case of the stationary microelectrode, the test solution here has direct access to the cathode surface. The effects of convection and vibration are, however, masked by sweeping the electrode through the sample at constant speed by rotating it mechanically.

The construction of a rotating electrode for use in the field raises several problems. For best results, the electrode must revolve at a constant speed in excess of about 300 r.p.m. In the laboratory this could easily be arranged by employing a synchronous motor with suitable gearing, but the requisite a.c. mains supply is not generally available in the field. Direct current motors are not reliable where a constant speed is required, so the absence of a mains supply cannot be compensated by the use of dry batteries or accumulators. In view of these difficulties it was decided to use a clockwork gramophone motor as the basis of the portable rotating electrode assembly. Such motors are of simple construction and their speed is accurately regulated by means of a centrifugal governor. They will runn for 4-5 minutes without rewinding.

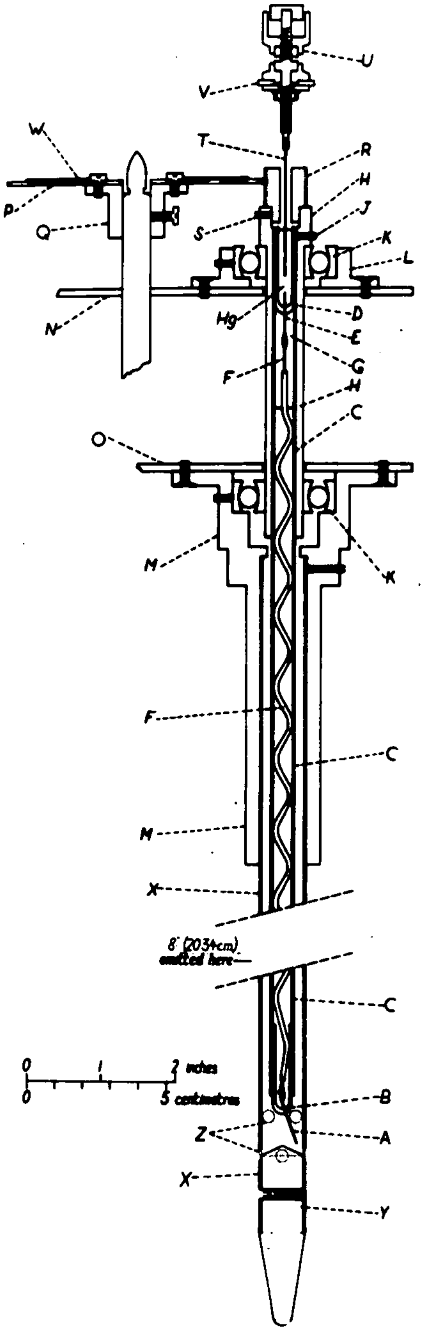
The motor used here was an H.M.V. model, purchased for 12/6d from a junk dealer in Durham market. The mechanism was mounted between two steel plates $5\frac{3}{4}$" in diameter. A spindle to carry the record turntable and a small lever for adjusting the governor projected through the upper plate.

A sectional elevation to illustrate the conversion of the motor to a rotating electrode assembly is shown in Fig. 3.18. Details of the motor mechanism have been omitted.

The platinum electrode A is a length of S.W.G. wire, sealed into the lower end of a glass tube B, which is in turn sealed, by means of "Araldite" resin, into the lower end of the stainless steel tube C. Into the upper end of C is sealed, also with "Araldite", a second glass tube D, filled with mercuty (Hg). This glass tube also has a length of platinum wire E sealed into its lower end. A and E are connected together by a length of copper wire F, insulated with p.v.c., the junctions being silver-soldered. The upper junction and the projecting part of E are protected and insulated by being enclosed within a plug of "Araldite" G, which was cast onto the lower end of D in a mould of rubber tubing, before D was sealed into the upper end of C.

The upper end of tube C is supported inside a hollow spindle H by three Allen grub-screws J, 120° apart. The spindle H is turned in brass, and revolves in two self-aligning steel ball races K, which are mounted in turned brass housings L and M. The flanges of L and M are screwed to the steel plates N and O, which form the upper and lower sides of the clockwork motor. Holes are bored in these plates to accommodate the spindle H. The entire construction and functioning of the assembly depends upon the correct positioning and alignment of these holes,

Fig. 3.18 Sectional elevation of clockwork rotating electrode assembly.



which therefore had to be bored in a lathe.

The gramophone turntable is replaced by a 3½" "Meccano" gear P, which is provided with a special brass bush Q of suitable size to accommodate the turntable spindle. The gear imparts motion to the electrode by meshing with the ½" "Meccano" pinion R, whose boss is secured in a recess at the upper end of the spindle C by means of three Allen grub-screws,, 120° apart.

Contact is maintained, while the electrode rotates, by means of the platinum wire T which passes through the pinion R to dip into the mercury in D. T is silver-soldered to the contact of an insulated terminal U, carried on an aluminium plate V, which is supported above the housing L by means of two lengths of brass studding (not shown). A threaded brass cone (also omitted) can be screwed along one of these studs to control the speed of rotation by altering the position of the lever which operates the centrifugal governor. The speed is adjusted with referance to a stroboscopic card W, carried on the gear P. The card has 90 radial lines drawn upon it at 4° intervals. When illuminated by means of the 50 c.p.s. public electricity supply, the spindle rotates at 467 r.p.m. after adjusting the governor until the lines appear stationary.

The electrode is protected by an outer shield constructed in the form of a probe. The shield is carried in a prolongation of the lower bearing housing M. It comprises a tube X of stainless steel carrying at its lower end a stainless steel plug Y which is retained by an Allen grub-screw. Two rows, of four holes (Z) each, allow soil water to enter the tube X and to immerse the electrode A.

The assembly was designed to enable the electrode and inner tube C and their outer tubular shield to be easily removed for maintainance or replacement.

The calibration of the rotating electrode was carried out in beakers of initially de-ionised water surrounded by the water of a thermostat bath. The water was allowed to stand at 25 ± 0.5°C for a period of 24 hours before use, to enable an appreciable quantity of oxygen to dissolve. During this period it was protected from dust by a suitable ventilated cover. Before calibration, the sample contained in each beaker was isolated from further contact with the atmosphere by covering with a $\frac{1}{2}$ cm. layer of medicinal paraffin. All apparatus subsequently introduced into the samples was first wetted with paraffin in order to prevent bubbles of air being carried down with it through the isolating layer.

The usual calomel anode was used. For this reason there occurred a continuous leakage of saturated potassium chloride solution into the sample. The effect of this upon the conductivity of the sample was measured with a Lock Portable Conductivity Bridge, Type B.C.1, used in conjunction with a Lock Conductivity Cell Type 7407.

Since no temperature calibration could be effected without applying a conductivity correction in respect of the KCl leak from the anode, the conductivity calibration was carried out first. For this purpose the temperature of a sample was maintained at 25°C, while its conductivity was allowed to increase, at first only through the addition of saturated KCl solution from the anode, but at a later stage by supplementing this with small amounts of saturated KCl solution introduced through a pipette. The quantities of solution added were considered to be negligible in comparison to the total sample volume, and, therefore, to have a negligible effect upon the oxygen concentration therein. The polarograph current with the cathode at -0.8 volts with respect to the anode was measured simultaneously with conductivity at various stages of the experiment, after stirring the sample to ensure an even distribution of the KCl.

The curve for current and conductivity is shown in Fig. 3.19, from which it may be seen that the current varies as the logarithm of specific conductivity up to about 500 μmho, which covers the range of conductivity normally met with in bogs. Hence over this range we have

$$I \propto \operatorname{Log} c \quad \text{(temperature and } O_2 \text{ constant)}$$

Where I is the current and c the conductivity

Correction for variations of conductivity between different test solutions may, therefore be made by introducing a conductivity coefficient, q_c, which relates the current I_{c_0} observed at conductivity c_0 to the current I_c which would have been observed in a solution of arbitrarily chosen "standard" conductivity c by

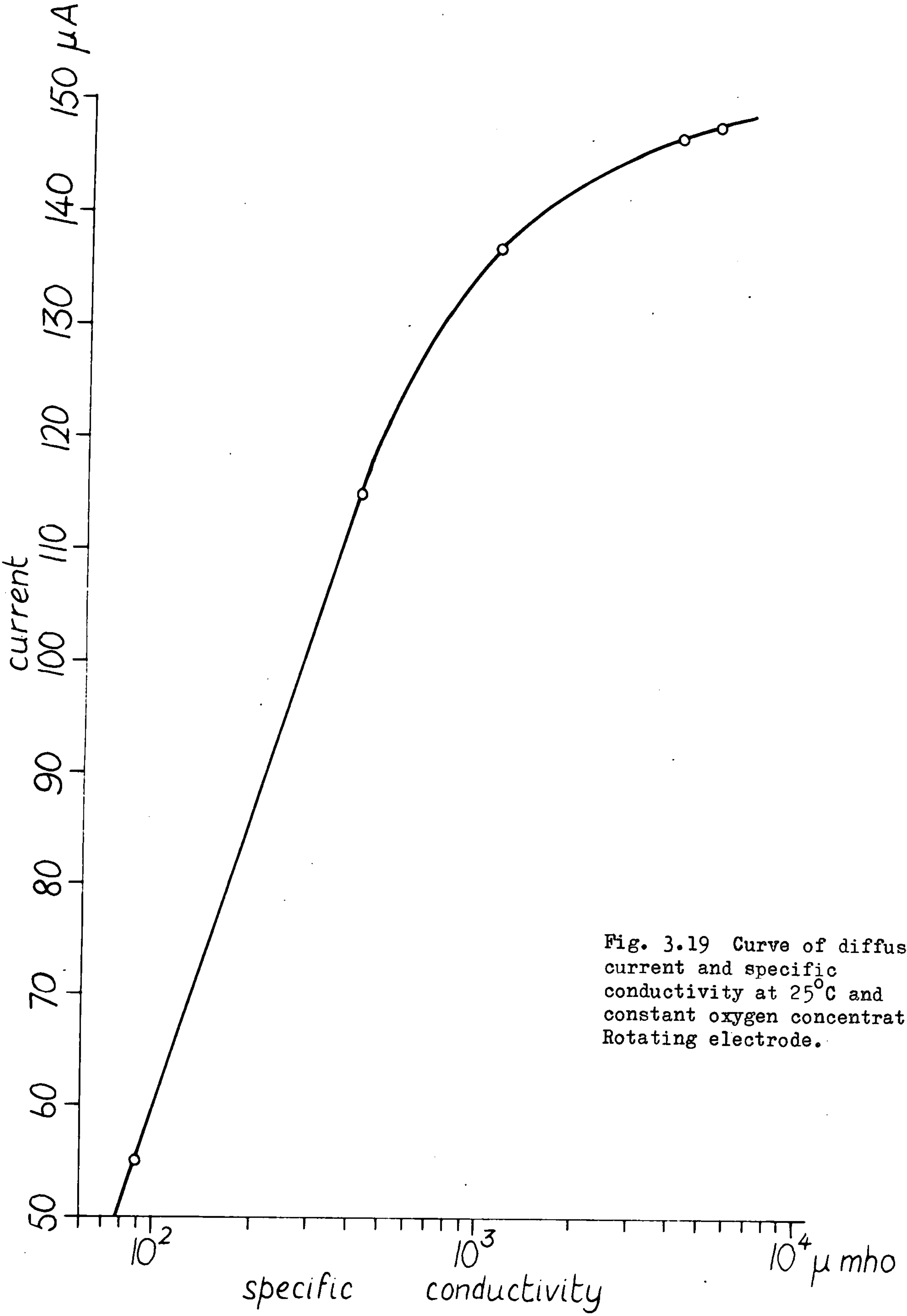


Fig. 3.19 Curve of diffusion current and specific conductivity at 25°C and constant oxygen concentration. Rotating electrode.

$$I_c = I_{c_o} \cdot \frac{100}{100-q_c(\log_{10} \frac{c}{c_o})} \quad \text{(temperature and } [O_2] \text{ constant)}$$

whence q_c may be defined as the fractional increase in current per tenfold increase in conductivity, expressed as a percentage of the value at the "standard" conductivity c.

In this work the value adopted for c is 100 µmho, and from the curve of Fig. 3.19 a value for q_c of 170% was determined for the rotating electrode.

The temperature coefficient was next determined, using a similar sample of de-ionised water. The procedure employed was exactly the same as in the case of the conductivity calibration, except that instead of holding the temperature of the thermostat bath at a constant 25 ± 0.5°C the thermostat was set at a range of values between ~~2~~7 and 28°C. Since the solubility of oxygen in water decreases with increasing temperature, there was a risk that raising the temperature might cause oxygen to come out of solution, so that its concentration would not remain constant. Accordingly the thermostat was first set at the highest temperature and left for about one hour before taking the first reading, after which the other temperature settings were obtained by cooling the bath. It will be seen from the plot of results in Fig. 3.20 that, despite this precaution, the readings of current obtained at the two lowest temperatures were anomalous. This might have been due to a leakage of air into the system.

/7°

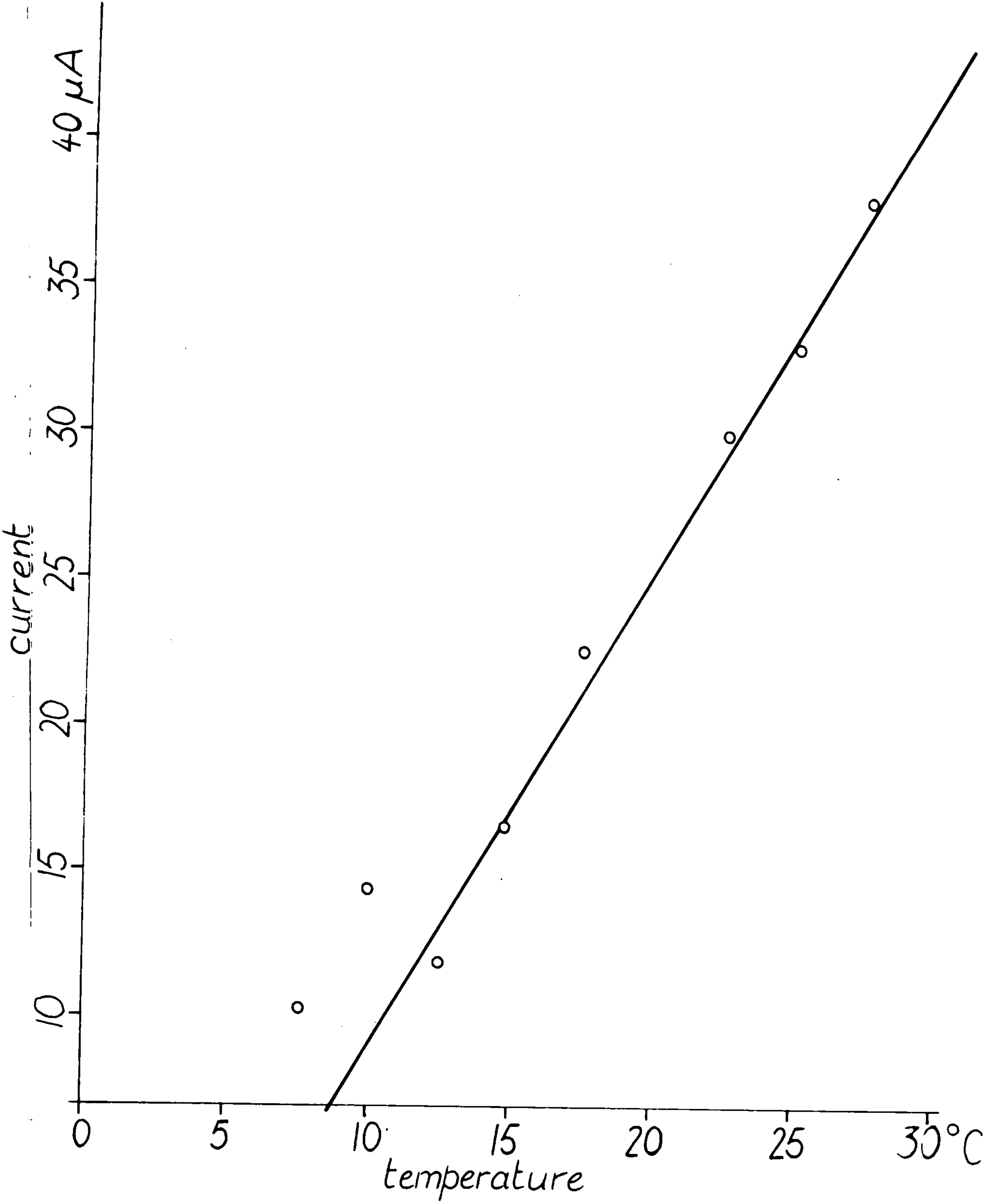


Fig. 3.20 Curve of diffusion current and temperature at constant oxygen concentration, the current corrected to 100umho. Rotating electrode.

The readings of current were corrected for conductivity, which increased steadily during the experiment (or would have done so had the temperature not been steadily reduced), the computation being set out in Table 3.7. The curve for current against temperature is shown in Fig. 3.20. If we ignore the two obviously anomalous results for 7.6°C and 10.0°C, the remaining values show a close approach to linearity, hence

$$I \propto t \quad \text{(conductivity and } [O_2] \text{ constant)}$$

We may, therefore introduce a temperature coefficient q_t analogous to the conductivity coefficient q_c, relating the current I_{t_o} observed at temperature t_o to the current I_t which would have been observed at an arbitrarily chosen "standard" temperature t by

$$I_t = I_{t_o} \cdot \frac{100}{100-q_t\ (t-t_o)}$$

whence q_t may be defined as the fractional increase in current per degree rise in temperature, expressed as a percentage of the value at the "standard" temperature t.

In this work the value adopted for t is 25°C and from the curve of Fig. 3.20 a value of 4.9% for q_t was obtained with this electrode.

The rotating electrode assembly has proved sufficiently robust and convenient for use in the field. For determinations in which the electrode lies at more than 20 cm. below the peat surface, the probe alone

Table (3.7)

Computation of I_c. ($c = 100\ \mu$ mho, $q_c = 169\%$.)

c_o (u mho)	$\frac{c}{c_o}$	$\log_{10}\frac{c}{c_o}$		$a = -q_c(\log_{10}\frac{c}{c_o})$	$b = a - 100$	I_{c_o} (uA)	$I_c = I_{c_o}\cdot\frac{100}{b}$ (uA)	t_o (^{o}C)
105.0	0.953	$\bar{1}.979$	-0.021	- 3.55	103.55	39.3	38.0	27.5
129.6	0.775	$\bar{1}.888$	-0.112	-18.93	118.93	39.3	33.0	25.0
131.6	0.760	$\bar{1}.881$	-0.119	-20.11	120.11	36.0	30.0	22.5
123.4	0.810	$\bar{1}.909$	-0.091	-15.38	115.38	26.0	22.6	17.5
114.7	0.872	$\bar{1}.941$	-0.059	-9.97	109.97	18.3	16.6	14.8
109.0	0.917	$\bar{1}.962$	-0.038	- 6.42	106.42	12.7	11.9	12.5
102.7	0.973	$\bar{1}.988$	-0.012	- 2.29	102.03	14.7	14.4	10.0
96.2	1.039	0.017	-0.017	- 2.87	97.13	10.0	10.3	7.6

is sufficient to support the weight of the assembly. The space within the shield is normally sufficiently full of water after two minutes in Inverpolly blanket peat to cover the electrode and to enable a determination to be made. Hitherto no provision has been made for excluding atmospheric oxygen from the sample thus obtained, but it is hoped later to cover the entry ports X with a thin sleeve which will retain a small quantity of medicinal paraffin within the shield while the probe is driven into the soil, and which can then be removed to enable the soil water to flow in beneath the paraffin. At present the agitation produced by rotating the electrode facilitates contamination of the sample from the atmosphere, and a slow rise in the oxygen diffusion current occurs. The values quoted in Chapter III were obtained as soon as the electrode was covered by the sample, thus obviating the effects of such contamination as far as possible.

APPENDIX III(b)

Summary of computation of values of hydraulic conductivity at various points below the water table on Transect "A"

These computations are based on the data of Fig. 3.8.

1) Computation of the A-function. (Luthin and Kirkham, 1949)

Cavity dimensions - $W = 10.0$ cm (= 3.94 inch)

$2r = 1.4$ cm (= 0.551 inch)

For a cavity of length 4", having the same proportions,

$$2r = 4 \times \frac{1.4}{100} = 0.56 \text{ inch}$$

For a cavity of dimensions $W = 4"$, $2r = 0.56$ inch

$A = 10.0$ inch (Luthin and Kirkham, 1949, Fig. 2)

Since A varies linearly with W when W is of this order of size (Luthin and Kirkham, 1949, Fig. 3), for the present cavity

$$A = 10.0 \times \frac{3.94}{4.00} \text{ inch}$$

$$= 9.85 \text{ inch} \quad (25.03 \text{ cm})$$

2) Computation of the permeability (k)

$$K = \pi R^2 \frac{(\ln(d-y_1)/(d-y_2))}{A\,(t_2 - t_1)}$$ (Luthin and Kirkham, 1949)

Where the quantities are defined by the accompanying diagram (Fig. 3.21). These definitions correspond to those given by Luthin and Kirkham, 1949, in their Fig. 1 (but not to those of their text) and Luthin, 1957.

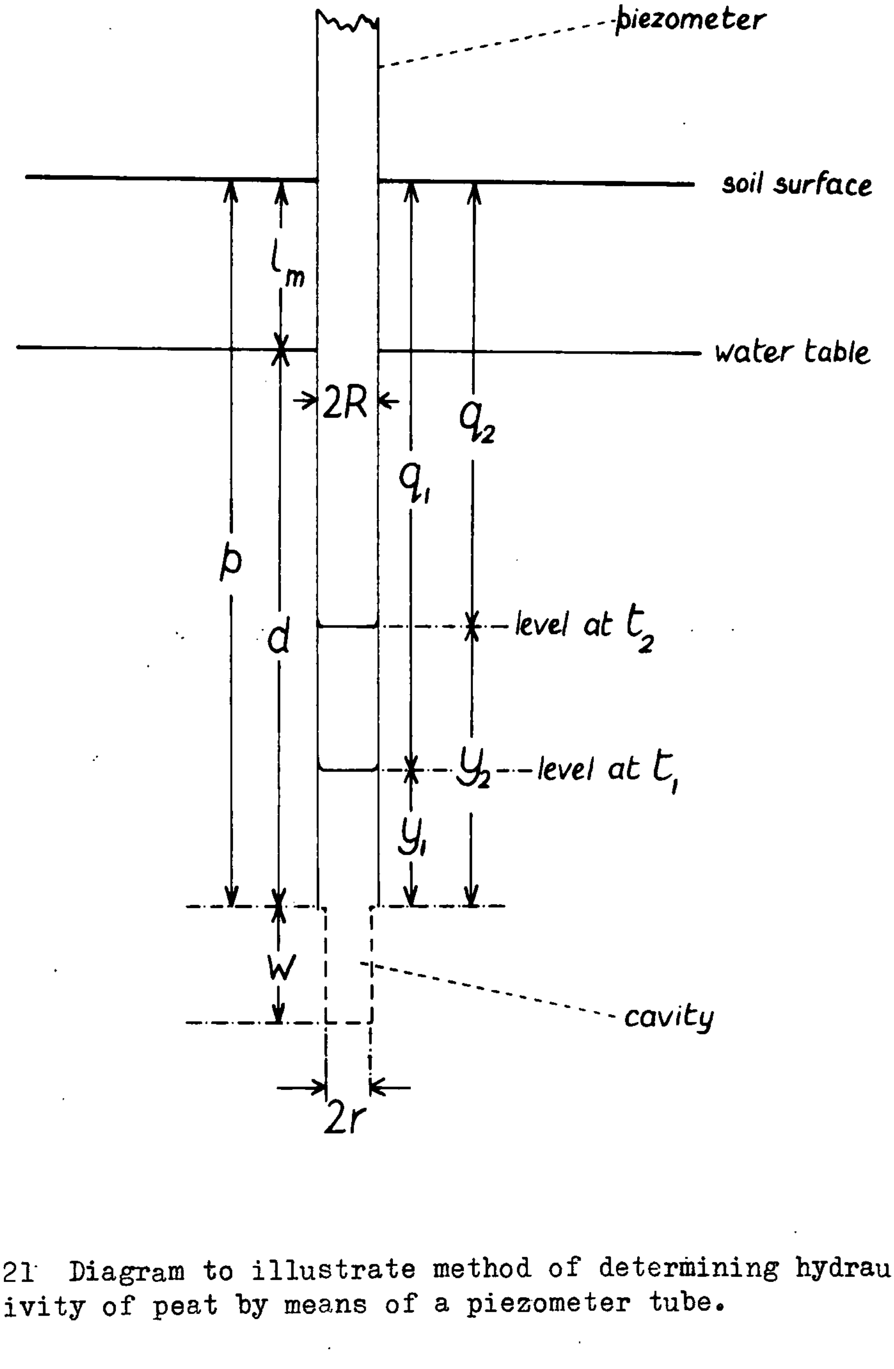


Fig. 3.21 Diagram to illustrate method of determining hydraulic conductivity of peat by means of a piezometer tube.

π

$$\therefore \quad K = \frac{\pi R^2}{A(t^2 - t_1)} \cdot \ln \left(\frac{d-y_1}{d-y_2} \right)$$

Internal diameter of piezometer = 15 mm. (=2R)

In the present system, A = 25.03 cm., R = 0.75 cm. and $t^2 - t^1$ = 4 days (the period from 27th April to 1 May, 1962).

π

$$\therefore \quad K = \frac{\pi \times 0.75^2}{25.03 \times 4} \cdot \ln \left(\frac{d-y_1}{d-y_2} \right) \quad \text{cm/cm}^2\text{/day}$$

$$= 1.77 \times 10^{-2} \ln \left(\frac{d-y_1}{d-y_2} \right) \quad \text{cm./cm}^2\text{/day}$$

This quantity is principally a measure of horizontal conductivity (Marshall, 1959). During the period 27th April to 4th May over which the piezometer observations were made, the weather remained predominantly dry. In consequence, the value of l (the distance between the water table and the peat surface) increased due to the rate of outflow of ground-water being greater than the rate of influx. This increase in l is recorded at most sites, during the period of three days (1-4 May) immediately following the period in question, as a decline in the water level in the pipe whose lower end lay just beneath the water table. (See section on the measurement of the depth of the water table in Chapter III) Assuming that the water table has declined at a constant rate over the whole 7-day period, we may extrapolate backwards, and so to determine a value for l (called here l_m) for 29th April, which is the halfway point of the period in question. This value may be used in the relation

$$d = p - l_m$$

to estimate the arithmetic mean for d for this period, and this value is used in subsequent calculations. From the form of the equation for K it is clear that K is a logarithmic function of d and that a logarithmic mean should strictly be used, but in relation to the error likely to be introduced by the assumption of a linear increase in l with time, the error involved in taking the arithmetic mean appears inappreciable.

The method of computing l_m and results for seven sites are shown in Table 3.8. No computation has been performed for site 6 because inspection of the graphs of Fig. 3.8 which apply to this site shows that on 1st May, the water in the deeper pipes had here attained the level of the water table. Since this did not occur elsewhere on the transect, and since it makes Luthin and Kirkham's formula unworkable, it has been assumed that the close proximity of the large body of free water in the recording hole at this site had disturbed the hydrology too much to allow the present technique to be used.

The computation of K for various points along Transect "A" is set out in Table (3.9). Possible error may arise in these results in four ways. Firstly, the value of the A-function may have been incorrectly determined. Examination of the paper by Luthin and Kirkham (1949)

Table (3. 8).

Computation of l_m. Transect "A". Tarraigheal. 1962

Site number	1	2	3	4	5	6	7	8(1)
Value of l on 1May	32.5	41.0	61.0	48.0	49.0	not computed	33.5	-
Value of l on 4May	34.0	42.0	61.0	48.5	49.0		34.5	24.0(2)
Increase in l, 1-4 May	1.5	1.0	0	0.5	0		1.0	-
Computed increase in l, 29 April - 4 May (= Increase 1-4 May × $\frac{5}{3}$)	2.5	1.7	0	0.8	0		1.7	1.1(3)
l_m (= value of l on 4May minus increase 29 April-4 May)	31.5	40.3	61.0	47.7	49.0		32.8	22.9

All lengths in body of table are given in cm.

(1) No pipe available for estimate of l.

(2) Value estimated from profile constructed in Fig.3.5

(3) Mean value for all other sites.

Table (3.9)

Transect "A", Inverpolly, April-May, 1962. Computation of K.

Site number		1			2		3	4
l_m	(cm.)	31.5	31.5	31.5	40.3	40.3	61.0	47.7
p	(cm.)	100.0	70.0	50.0	100.0	70.0	100.0	100.0
$d = p - l_m$	(cm.)	68.5	38.5	18.5	59.7	29.7	39.0	52.3
q_1	(cm.)	100.0	70.0	50.0	100.0	70.0	100.0	100.0
$y_1 = p - q_1$	(cm.)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
q_2	(cm.)	83.0	54.5	43.5	58.0	55.5	68.5	78.5
$y_2 = p - q_2$	(cm.)	17.0	15.5	6.5	42.0	14.5	31.5	21.5
$d - y_1$	(cm.)	68.5	38.5	18.5	59.7	29.7	39.0	52.3
$d - y_2$	(cm.)	51.5	23.0	12.0	17.7	15.2	7.5	30.8
$\frac{d - y_1}{d - y_2}$		1.33	1.67	1.54	2.91	1.95	5.20	1.70
$f = \ln \frac{d - y_1}{d - y_2}$		0.2857	0.5128	0.4318	1.0647	0.6678	1.6487	0.5306
$K = f\ 1.77 \times 10^{-2}$	(cm./cm.^{2}/day)	5.1×10^{-3}	9.1×10^{-3}	7.6×10^{-3}	1.9×10^{-2}	1.2×10^{-2}	2.9×10^{-2}	9.4×10^{-3}

(Table continued overleaf)

Table (3.9) continued.

Site number		5		6	7		8
l_m	(cm.)	49.0	49.0	NOT COMPUTED	32.8	32.8	22.9
p	(cm.)	100.0	70.0		100.0	50.0	35.0
$d = p - l_m$	(cm.)	51.0	21.0		67.2	17.2	12.1
q_1	(cm.)	100.0	70.0		100.0	50.0	35.0
$y_1 = p - q_1$	(cm.)	0.0	0.0		0.0	0.0	0.0
q_2	(cm.)	52.0	60.5		43.5	39.5	26.0
$y_2 = p - q_2$	(cm.)	38.5	9.5		56.5	10.5	9.0
$d - y_1$	(cm.)	51.0	21.0		67.2	17.2	12.1
$d - y_2$	(cm.)	12.5	11.5		10.8	6.7	3.1
$\frac{d - y_1}{d - y_2}$		4.08	1.83		62.2	2.57	3.91
$f = \ln \frac{d - y_1}{d - y_2}$		1.4061	0.6043		1.8278	0.9439	1.3635
$K = f\ 1.77 \times 10^{-2}$ (cm./cm.^{2}/day)		2.5×10^{-2}	1.1×10^{-2}		3.2×10^{-2}	1.7×10^{-2}	2.4×10^{-2}

suggests, however, that such error is likely to be small, because their data for the curves upon which the present estimate is based appear to be highly consistant. Secondly, error may arise through the measurement of water depths and pipe lengths. These measurements were made to the nearest 0.5 cm. and for this reason the final result has been given to two significant figures only. The third source of possible error arises from the fact that the Luthin and Kirkham equation for K is derived by assuming that the water table remains both constant in depth and horizontal during measurement (Luthin, 1957). A correction has been introduced in respect of movement of the water table, and the relative magnitude of this effect is in any case small. Apparently, no method exists as yet by which a correction in respect of a tilted water table may be applied, and the derivation of such a correction is felt to be beyond the scope of this enquiry. Fourthly, errors in the estimation of time may be involved. The measurement and recording of water levels in the fifty pipes which were involved in this part of the investigation occupied about two hours, a similar length of time to that required for installing all the pipes along the transect. These operations were carried out between 1400 and 1600 hours G.M.T., in the same sequence on each occasion, and it is not considered likely that an error of more than 1% could have arisen in this way. This error is very small in comparison to the others.

Luthin and Kirkham (1949) point out that estimations of hydraulic conductivity by means of piezometers are subject to large probable errors. This results from the fact that the conductivity being measured is that of a comparatively small region at the foot of the piezometer, and that considerable local variations in conductivity may be expected in most soils. On their results, that which approached the present estimates most closely, namely the one for Luton clay, was quoted to ± 8%. Unfortunately, time has not permitted the collection of sufficient data to estimate probable error in the normal way for the present peat soils, but it is clear from those instances in which more than one estimate is available for a single site (e.g. at Site 1) that considerable variation with depth may be expected.

APPENDIX Va

Apparatus for germinating seeds (Fig. 5.5)

The germinators used for raising the seedlings for the experiment described in Chapter V were made from polythene bowls measuring 35 cm. x 30 cm. x 12 cm. (depth). Holes were drilled through the longer sides of each bowl, through which passed two glass rods. These supported a sheet of greenhouse glass so that its surface lay about 0.5 cm. below the rim of the bowl. The sheet of glass was cut to a size such that when it was in position there remained a gap of about 0.5 cm. between its edges and the sides of the bowl. The glass sheet was covered with chromatography paper cut to the shape of a cross whose arms passed through the gap and dipped into a reservoir of distilled water contained in the bottom of the bowl. The bowl was covered with a sheet of transparent polythene, whose edges were retained beneath the rim by a length of aeroplane elastic and whose centre was supported on a short length of glass tubing held upright by a cork.

This type of germinator has the advantage that it will provide a moist surface for more than a year, if necessary, without needing to be refilled with water. It has the disadvantage that there is a moisture gradient from the edges to the centre of the horizontal sheet of paper, which may cause seedlings in the centre to dry out in fine weather. This gradient is due to the slope of the polythene sheet, a feature made necessary by the need to disperse the droplets of water which

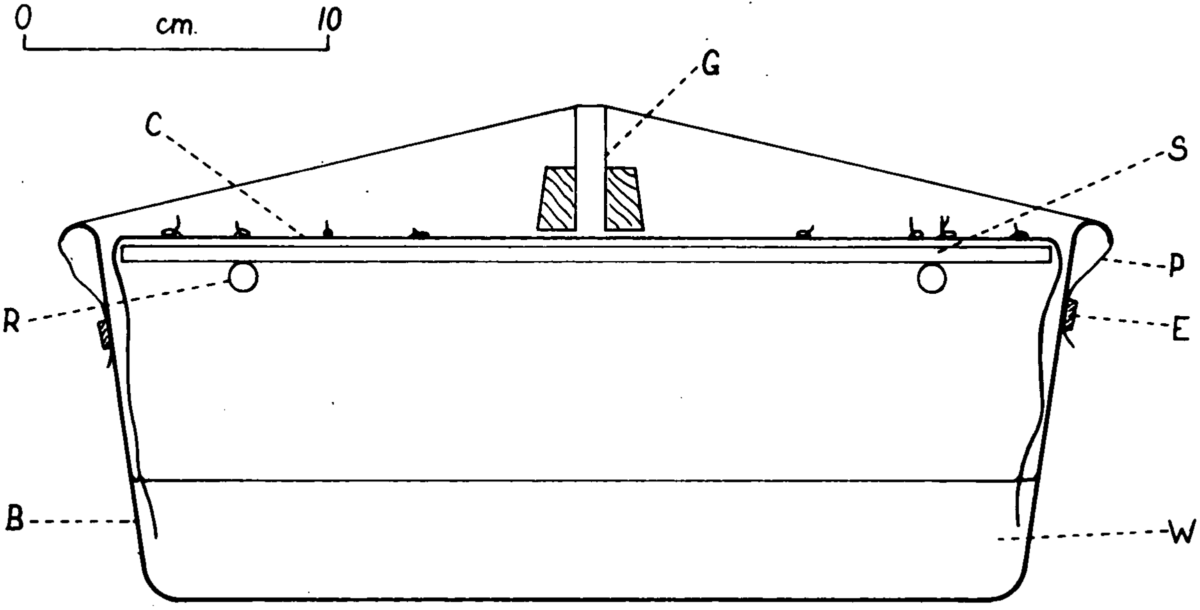


Fig. 5.5 Sectional elevation of seed germinator.

B, polythene bowl;
C, chromatography paper bearing seedlings;
E, elastic band;
G, glass tube and cork support;
P, transparent polythene cover;
R, glass rod;
S, glass sheet;
W, distilled water.

condense upon it, but if no fruits are placed further than 5 cm. from the edge, this difficulty may be avoided.

APPENDIX Vb

The design of apparatus for plant culture in continuously flowing nutrient solution

1. Theoretical considerations

(a) Velocity and direction of flow of the nutrient medium. In any experiment in which a number of plants, growing together, are to experience the same conditions of concentration, flow rate and aeration of the aqueous nutrient medium, it is necessary to devise apparatus in which the rate of flow does not vary appreciably from place to place in the vessel in which the plants are grown, and in which the presence of the plants themselves has a negligible effect on the over-all flow pattern. The vegetation pattern in the field suggested that, so far as the differentiation between *Trichophorum* and *Molinia* was concerned, the increased rates of flow of ground-water with which *Molinia* was associated took place mainly in a horizontal direction, or at least in a direction parallel to the surface of the peat. Apparatus in which the nutrient medium flowed more-or-less horizontally was, therefore, considered first. A practical difficulty in designing such apparatus is that of ensuring an even rate of flow over the whole area of wall through which the medium enters or leaves the vessel, due to the increase in hydrostatic pressure with depth. If this could be overcome there remain two further difficulties which seem inevitable under these circumstances. The first is that the growth of the roots of the plants themselves downwards into the medium must retard the flow in the upper parts of the vessel so that most of the medium would flow beneath them and a knowledge of the over-all rate of flow would be no guide to the experience of the plants themselves. The second difficulty is that the plants nearest to the inflow would have the benefit of the full concentration of nutrients and dissolved gases in the medium, while those further away would be bathed by nutrient progressively depleted by their neighbours "upstream".

Although the use of a design involving vertical flow is, in some respects, a less faithfull reproduction of the natural situation, it appears to overcome these difficulties. The essential features of such a design are: (a) Provision of an adequate resistance to distribute the flow evenly over the horizontal cross-section of the vessel. This is rendered much simpler than in the former apparatus because here the flow takes place parallel to the gradient of hydrostatic pressure in the vessel and not at right angles to it, so that the pressure over the whole of the diffuser will be equal. (b) The provision of adequate support for the plants.

(b) Aeration of the medium Many workers (e.g. Olsen, Mandal) have shown that the results of experiments on plant nutrition in hydroponic culture are considerably affected by the degree of aeration employed. It has, therefore, become the standard practice to aerate all such cultures very thoroughly and the air is usually either entrained in the nutrient inflow, in which case it may also supply the motive power which causes the nutrient to flow, or it may be supplied as a stream of small bubbles in the culture vessel itself. There are few published designs for experiments in which aeration has been controlled or varied, but since it was desired to investigate the effect of aeration on the growth of Molinia and Trichophorum seedlings, the apparatus had to be devised with this end in view. As in the case of the aqueous medium, it was important to ensure an even distribution of air throughout the culture vessel.

2. The development of culture vessels

In any culture experiment involving a number of treatments and replications, the design of the vessels used has to be a compromise between the theoretically desirable and the practically attainable. Three possible designs, A, B and C have been considered, differing in:

(i) The type of resistance employed to achieve an even horizontal distribution of medium and air.

(ii) The method used to support the seedlings

(iii) The method of aerating the medium

(iv) The arrangements for disposing of waste medium.

All three designs involved entry of the medium from below and subsequent upward flow. This method is known as "subirrigation", and is usually preferred to irrigation from above, because the rate of flow is easier to control, distribution arrangements need be less elaborate and continuous drainage is simpler to arrange. The necessity of not aerating some of the treatments was held to preclude irrigation from above.

A. (Fig. 5.6). This culture vessel was based on a 2 litre Pyrex beaker (diameter 14.5 cm., height 18.5 cm). in which a sharp constriction formed a shelf at about one-third of the total height. Distribution was intended to be achieved by the use of a sintered glass disc (pore size 100-300μ), cemented to the shelf with glassworker's pitch. A tubulure in the upper and lower portions of the vessel provided for inflow and outflow of the medium, and the plants were supported on nylon netting stretched over the mouth of the vessel, the spout of which was built up to the height of the remainder of the lip with glassworker's pitch. This design was abandoned. It was found that the sealing-in of the tubulures led to a high breakage-rate in beakers. The vessels were, therefore, expensive. The method of distribution was inadequate when aeration was employed, since the liquid medium only crossed the sintered plate in the central area above the air inlet, while passage of air was confined to the periphery of the plate (Fig. 5.6 A). The supporting net was found to interfere with the drainage, which worked only intermittantly so that the net heaved up and down.

B. This design made use of a one gallon Pyrex urn liner (diameter 21 cm. height 21 cm) (Fig. 5.6B). This vessel is very well suited to water-culture experiments, being made of thick (3 mm) glass, and

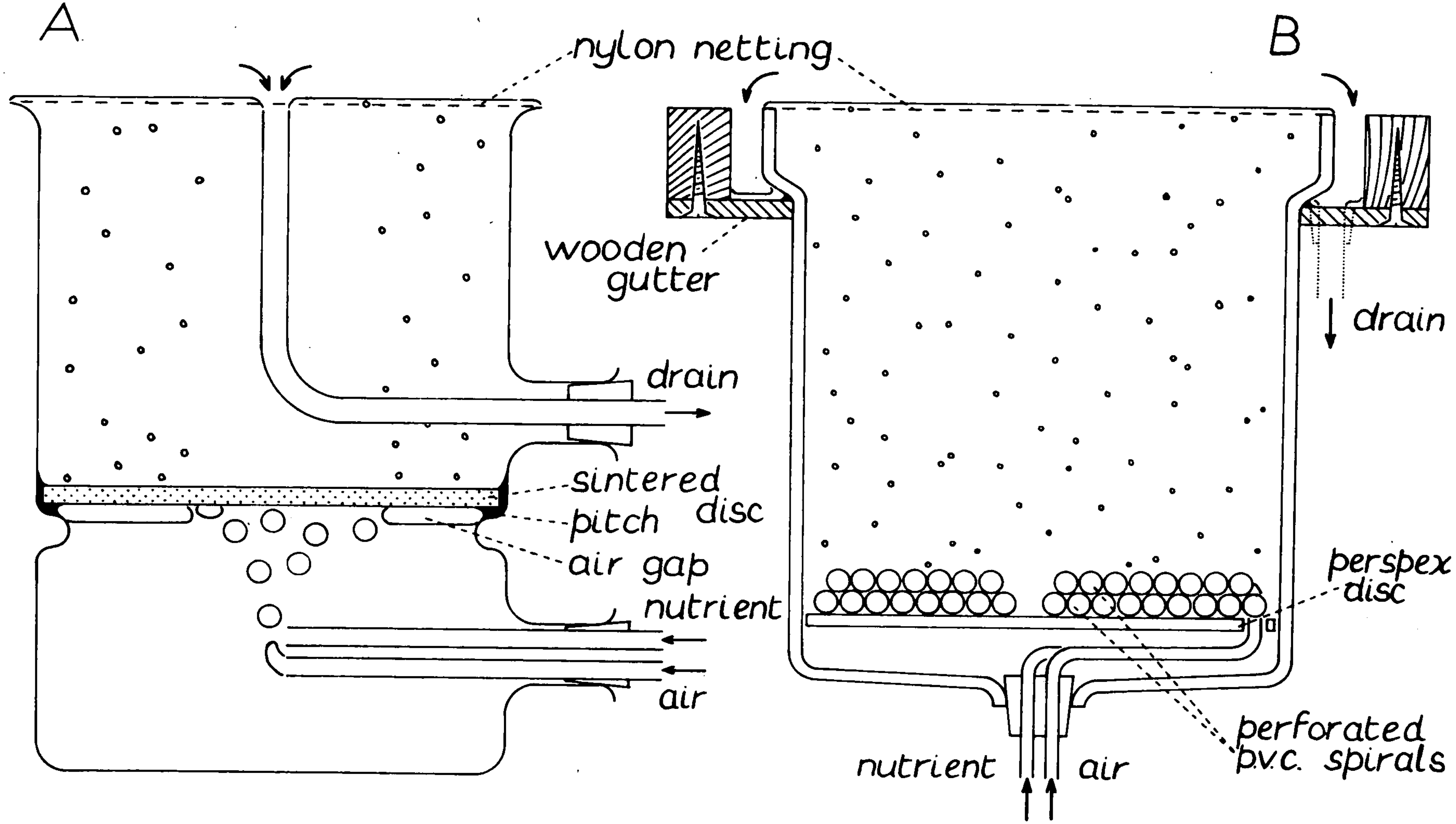


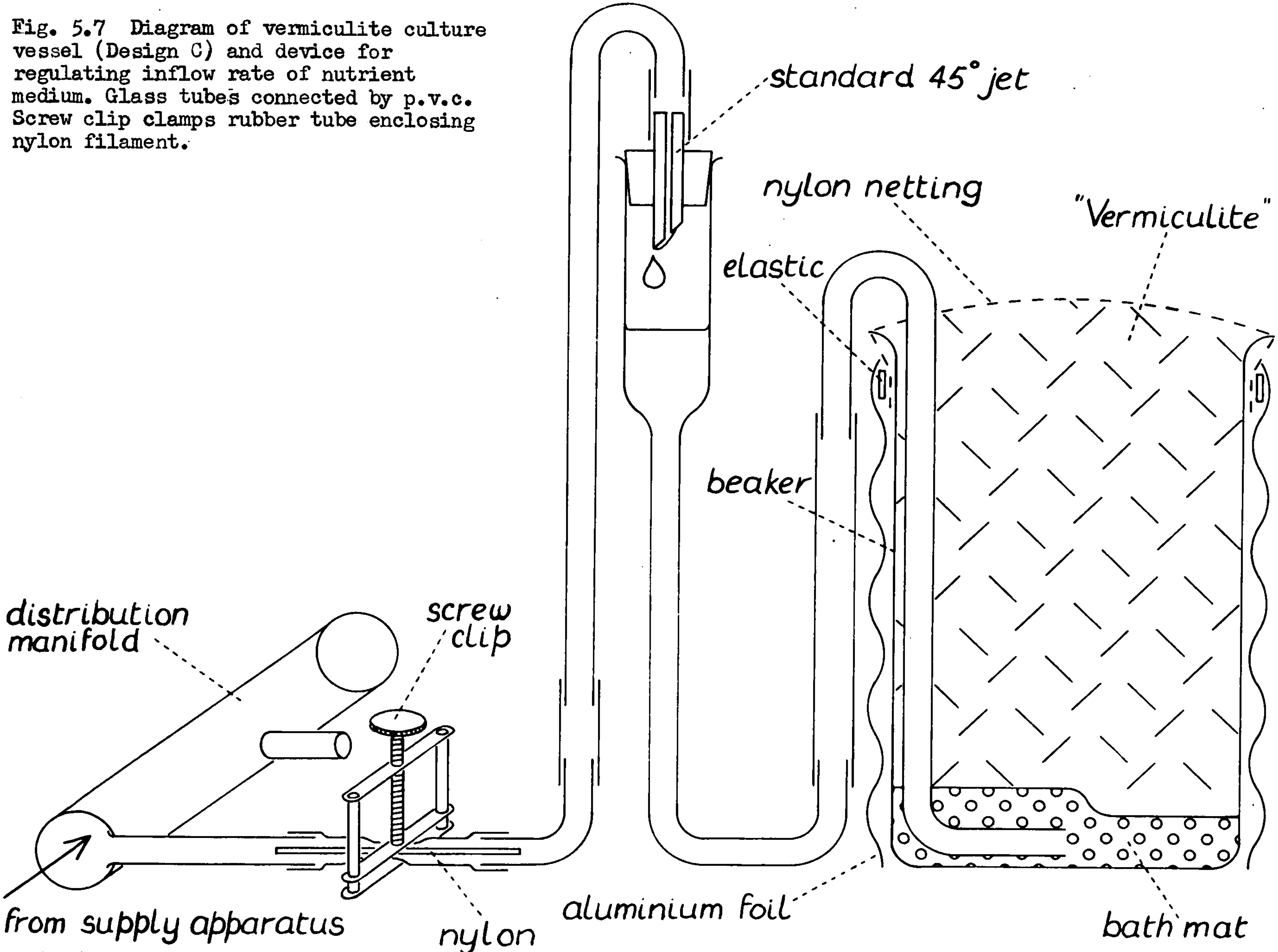
Fig. 5.6 Two designs for continuously-flowing water culture vessels
A, based on a 2-litre beaker.
B, based on an urn liner (nylon threads anchoring spirals to perspex and perspex to rubber bung omitted)
The nylon netting is attached by elastic bands (omitted).

having the upper lip ground flat and a hole in the base for the nutrient inflow. It was fixed with putty into a circular hole in a wooden stand waterproofed with bitumen and designed to catch the overflow from the lip. Distribution of air and liquid medium, which entered the vessel separately through a rubber bung in the basal hole, was achieved by two flat spirals of p.v.c. tubing (5 mm. internal diameter), wound one above the other on a circular perspex former which was ahchored to the bung. Each spiral tube had a row of holes punctured along its upper side with a sewing needle, and spaced at intervals of 1 cm. Air was distributed by the lower spiral, while the liquid medium was pumped into the upper one, which could more easily be removed for cleaning. Both tubes were tied to the perspex with single strands of nylon passing through carefully positioned holes. The plants were supported on nylon netting kept in place with elastic.

Although this apparatus was much more satisfactory than the last, and appeared to work well when wheat was grown in it, there was a tendency for the holes in the upper spiral to become blocked, which would have necessitated removing the growing plants for maintainance. The vessels were also rather expensive, which would have limited the possible number of treatments and replications.

C. The last design, which was eventually adopted, was much simpler and cheaper than the other two. The vessel employed (Fig. 5.7)

Fig. 5.7 Diagram of vermiculite culture vessel (Design C) and device for regulating inflow rate of nutrient medium. Glass tubes connected by p.v.c. Screw clip clamps rubber tube enclosing nylon filament.



was a 400 ml. Pyrex glass beaker (diameter 8.3 cm. height 10.8 cm.) of normal form. This was made possible by the discovery that bath mats sold by Messrs. Woolworth act as efficient distributors of nutrient medium. These mats are made of expanded polythene and are about 1 cm. thick when not compressed. The cellular network of bubbles of which they consist is very homogeneous (in contrast to, e.g. a bath sponge which has cavities of many different sizes), and is uniformly permeable to water provided all air is expelled from it. A circular pad cut out of a mat with scissors to a size slightly larger than that of the base of the beaker was placed under water in the beaker and squeezed against the bottom until no more air bubbles rose. A length of 5 mm. Pyrex tubing bent into a shape resembling a bacon hook was then inserted through a hole, cut near the periphery of the pad with a cork-borer, so that its lower end provided an entry point for the liquid medium below the centre of the pad. The rest of the beaker was filled with grade 3 "Vermiculite" sold by Messrs. Joseph Bentleys of Hull as an inert substrate for horticultural experiments. This grade of Vermiculite which consists of expanded flakes of mica about 3.5 mm. in diameter, is also permeable to water, when free of air. The Vermiculite used in this apparatus was soaked with distilled water under a vacuum before being placed in water in the beaker above the polythene pad, and packed down until the centre of the wet mass bulged 1 or 2 mm. above the lip of the beaker when the pressure of the hand was removed. It was then covered with nylon netting (mesh size 1.5 x 1.0 mm.). which was drawn tight and held in place by a band of aeroplane elastic.

When eosin solution was injected into the inflow, the red colouration appeared over the whole surface of the Vermiculite at the same time, so that it seemed reasonable to suppose that the distribution brought about by the combination of polythene pad and Vermiculite was effective.

The effect of air in preventing the flow of water through Vermiculite and expanded polythene has been mentioned above, and precludes the use of a separate air supply to this apparatus. Aeration was, therefore, arranged by bubbling air through the liquid medium before it entered the vessel. The necessary apparatus is described in section 4 below.

3. Control of flow rate

In constant-flowing culture experiments of this kind, it is usual to control the rate at which the medium enters the culture vessel by arranging for the "head" or hydrostatic pressure of the medium to be kept constant, and to employ a resistance to the flow in the form of a constriction in the duct, at the point where the supply to any particular vessel joins the main system feeding its neighbours. In the constricted duct, the medium dissipates the energy, which it possesses by virtue of its hydrostatic pressure, through friction with the walls of the duct, and it is, therefore, evident that in a system supplying several vessels the frictional losses at each constriction must be large compared with those which occur in the rest of the system of supply tubes, in order that variations in the rate of inflow to one vessel will not affect the others. Theoretically, the most satisfactory form of constriction is a length of capillary tubing. Unfortunately this could not be used here because, during the course of the experiments the resistance offered by the culture vessel slowly increases, due, it is thought, to the spread of algae and mosses over the upper surface of the Vermiculite, so that provision had to be made for adjusting the inflow rate every few days by widening the constriction. Even if this consideration had not been the overruling factor deciding the type of constriction, fine capillary tubing of constant internal diameter, known as "viridia", is so expensive as to debar its use in a fairly extensive series of replications and treatments unless a plentiful supply of broken thermometers is available.

The adjustable constrictions consisted of a 3 cm. length of 5 mm. rubber tubing, pinched by a screw clip. The adjustments were facilitated by threading through the constriction a solid nylon fibre about 0.2 mm. in diameter.

The experiments were designed to require a maximum flow rate of 2 litres per vessel per day. This rate of flow is too small to measure by conventional means. The principle adopted here was to time the fall of drops from a small jet (Fig. 5.7). For this method to be effective, one jet had to be provided for each vessel, and each jet had to form drops of the same volume. The problem of providing a set of closely similar jets was overcome by making them from 2.5 cm. lengths of capillary tube (external diameter 5.5 ± 0.05 mm., internal diameter 0.5 mm), which were too short to offer any appreciable resistance to flow. The actual surface on which the drops were formed was ground onto the end of the capillary tubes using the coarse and fine emery powder employed by geologists to grind rock sections. During the grinding process a slow flow of water had to be passed through each tube to prevent carborundum particles lodging in the capillary. The surface was intended to form an angle of 45° with the axis of the tubing, but since no special apparatus was made to hold the tubes and the angle was judged by hand, there was a variation of about 5° round the 45° value. Table 5.6 shows the number of drops in 10 ml, which were formed by the most acute and most obtuse of a sample of 40 tubes. It will be noted that the two means differ by 1.5, which is approximately 1.1% of the total number of drops, which appears to be an acceptable deviation.

It is now necessary to consider the principles involved in the construction of the nutrient supply vessels and apparatus for maintaining a constant head. Practical considerations make the layout rather complex, so the complete assembly is described in detail in Appendix Vc. Essentially, the apparatus was required to produce a large quantity of extremely dilute nutrient solution, some of which was to be aerated and some not. The unaerated condition was achieved by using water which

Table (5. 6).

Preformance of flow monitoring jets. Number of drops in 10 ml.

Approx. Angle		43° (most obtuse)	47° (most acute)
Trial	1	134.5	137
	2	135	136
	3	135	136
Mean		134.8	135.3

had been distilled straight into polythene aspirators where it was prevented from coming in contact with air by a floating layer of medicinal paraffin. It was felt that the stirring necessary to ensure the adequate mixing of the nutrients could only be accomplished with difficulty if this air-free condition was to be preserved and algal growth prevented. The distilled water was, therefore, stored without nutrients in large reservoirs under paraffin, and the nutrients were added as a constant proportion of a concentrated solution immediately before the medium entered the aerating and distribution apparatus. In this way the aeration of the concentrated solution which took place while it was being made up was rendered negligible, while suitable conditions for algal growth were restricted to a small part of the apparatus, from which light could easily be excluded with aluminium foil.

The mixing in constant proportions of a large volume of liquid from a large reservoir with a small volume from a small reservoir can be best be achieved by making use of the well known principal of Pascal's vases, whereby if a number of vessels of different sizes and shapes are connected together below, any liquid they contain will flow through the connecting tube until hydrostatic equilibrum is attained, which would usually imply the liquid assuming the same level in each vesselIf some liquid is now drained from the system by means of the tap shown in Fig. 5.8, it follows that the liquid declines the

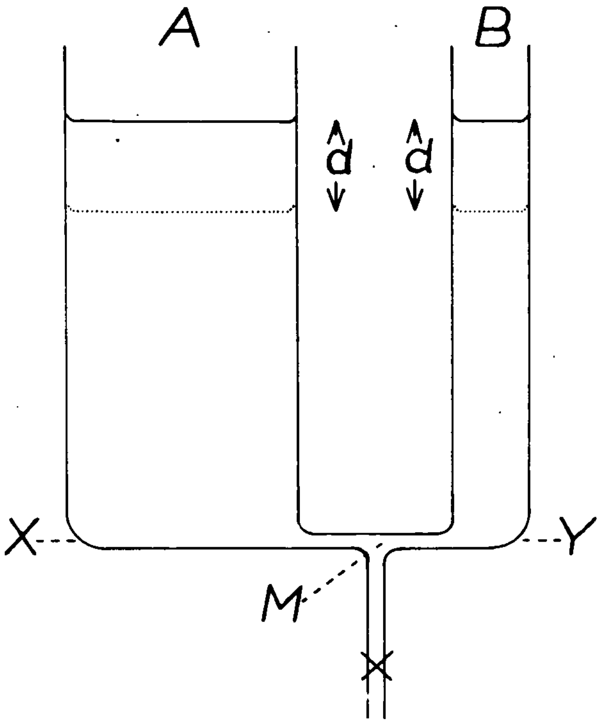


Fig. 5.8 Diagram illustrating principle of constant proportional mixing device

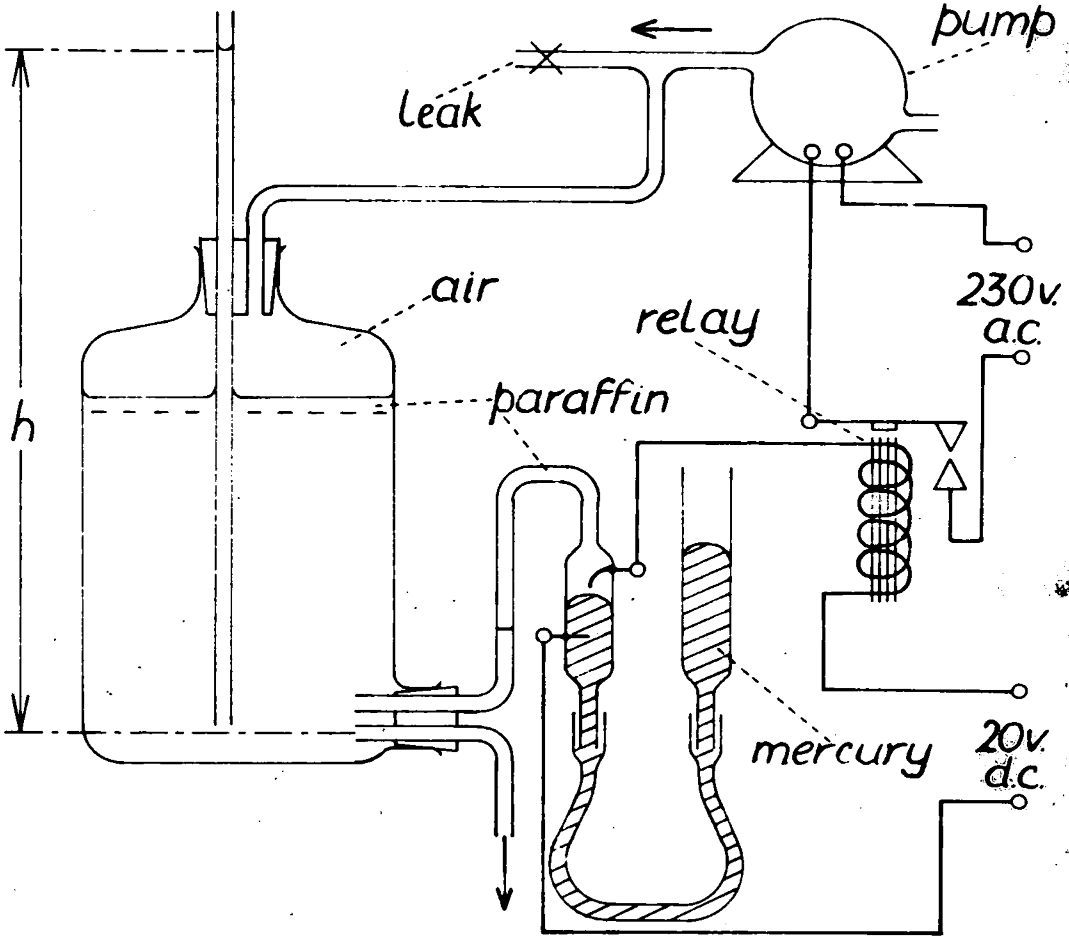


Fig. 5.9 Diagram of nutrient reservoir with device for maintaining a constant head while not aerating the medium.

same distance, d, in each vessel, provided the rate of flow through the tap is insufficient to bring frictional resistance into play. Furthermore, if the cross-sectional area of the two vessels does not alter with depth, their contents will mix in constant proportion at the point M, the proportion being dependent only on their relative cross-sectional areas. For instance in the present experiments, the apparatus was required to produce a dilution of one part in 100, The effective cross sectional area of B was, therefore, arranged to be $\frac{1}{99}$ x that of A.

The hydrostatic equilibrium of Pascal's vases is achieved when the pressure at level X exerted by the liquid in A is equal to the pressure exerted by the liquid in B at Y, which is at the same level as X and the two outlet tubes. This equilibrium results in an equivalence in level between the liquids in the two vessels only if they do not differ appreciably in density. If, however, the concentrated solution in B is appreciably more dense than the water in A, their levels cannot be used as a test of equilibrium when the vessels are filled, but instead a manometer has to be connected to the outlet tubes to show when the pressures are equal. (See Appendix Vc).

With regard to the maintainance of a constant head, the necessity to keep the water in the large reservoir free of air precludes the use of such simple devices as the Mariotte's bottle (Hewitt, 1952, p. 121, Fig. 5A(I)) in which air bubbles through the water as it leaves the vessel. Instead, the device shown schematically in Fig. 5.9 is used.

This is a simplification of the method published by Humphries (1950). A small electric pump is used to pump air into the space above the paraffin in the storage vessel until the head, indicated on the vertical tube, reaches the required value. At the same time, the head is registered at the outlet from the vessel by means of a mercury manometer. The mercury is isolated from the water in the vessel by a small volume of paraffin trapped in an upward curve of the fixed arm of the manometer, which is also provided with two platinum contacts. When the head falls due to water being withdrawn from the vessel, the circuit between the two contacts is completed by the rising column of mercury in the fixed arm. The precise pressure at which this takes place is determined by adjusting the height of the free arm. The completion of the circuit closes the contacts of a relay which switches on the pump, forcing air into the upper part of the reservoir until the head has been restored, when the declining mercury column breaks the circuit and the relay opens. If the valves on the pump are efficient and the outflow rate is very slow, a rise in temperature in the greenhouse may cause the air in the reservoir to expand at a rate faster than can be compensated by the outflow, in which case the head increases. In order to prevent this from occurring, a slow leak is fitted to the air inlet tube.

This method of maintaining a constant head has proved very reliable in use. It may be adapted to the "Pascall's vase" design by enclosing the air spaces in the smaller reservoirs and connecting them to the air space in the large reservoir. Details will be found in Appendix Vc.

5. Aeration

As mentioned above, the design of culture vessel employed in these experiments makes it imperative to aerate the medium, where necessary, before it enters the culture vessel. For this purpose the medium to be aerated is made to flow down a column of glass up which rises a stream of bubbles, produced by blowing air from an oil-free compressor through a sintered glass plate (Fig. 5.10). In the present experiments, the more concentrated nutrient medium enters the distribution manifolds at a lower rate than the less concentrated. If the same degree of aeration is to be achieved the effective length of the column must be adjusted so that the time spent by any particle of liquid inside the column is on average the same in either case. The effective column length (in Fig. 5.10) is adjusted by moving the central supply tube up or down through the cork at the base. The column is then set up so that the constant head device fills it with medium to a level slightly above the upper end of this tube.

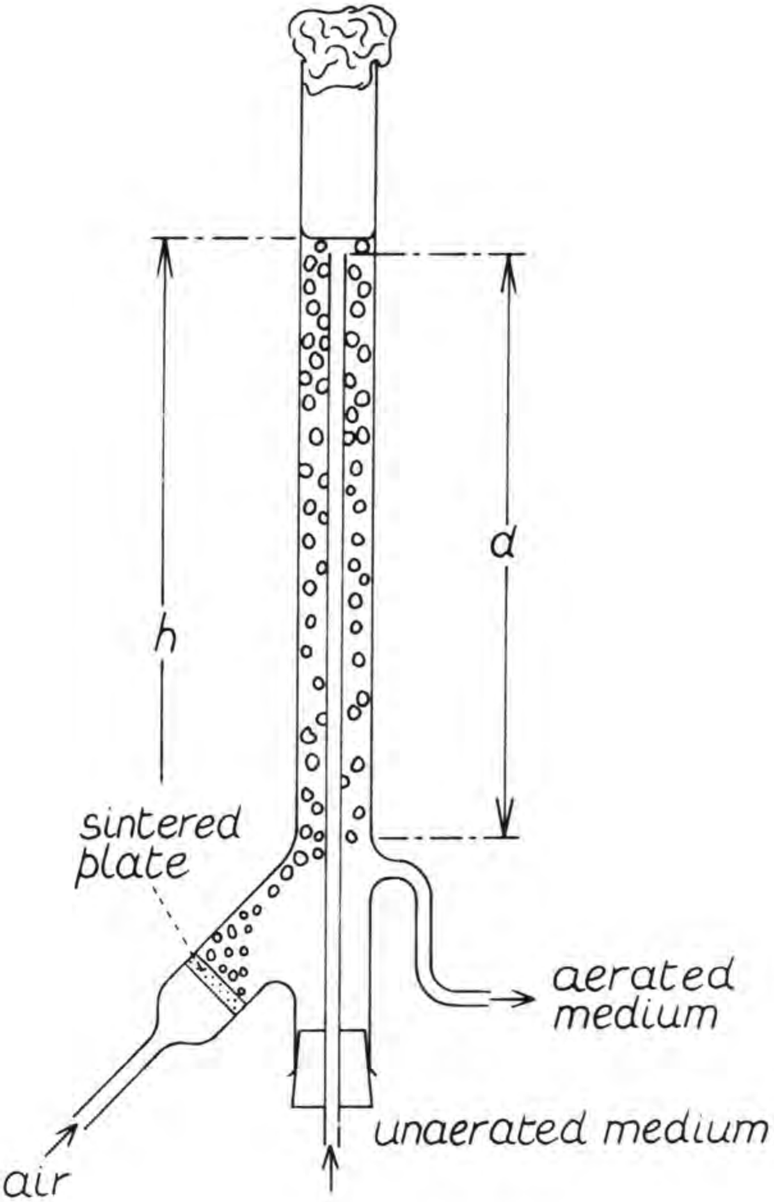


Fig. 5.10 Diagram of adjustable aerating column.

APPENDIX Vc

Description and method of operation of culture medium supply apparatus

(Fig. 5.11)

The 601 polythene aspirator bottle A contains distilled water under paraffin, which in use flows out through the basal tap into the 500 ml. wide-mouthed flask B whose function is simply to provide a connection between the six tubes which pass through its stopper. Tube G communicates with the mercury switch H which operates the small compressor J through the relay K, in order to maintain the constant head indicated in D. The level of water in A is indicated in E. The vessels L and M are filled with concentrated nutrient solution from the Winchester bottles P and Q through inlets controlled by the clothes pegs R and S. Each vessel consists of a legth of 4 cm. glass tubing, whose internal cross sectional area is adjusted to the required fraction of that of A by inserting a length of tubing of the required diameter (about 1 cm.) axially through both stoppers. This method has to be employed because a much finer gradation of diameters is available in the smaller sizes of tubing than in the larger. The air spaces above the liquid in A, E, L and M communicate through a series of tubes, ensuring that the same head is maintained in all the reservoirs. Y is a controlled air leak, preventing an increase in head if the temperature rises and Z is a pressure relief valve opened while filling the

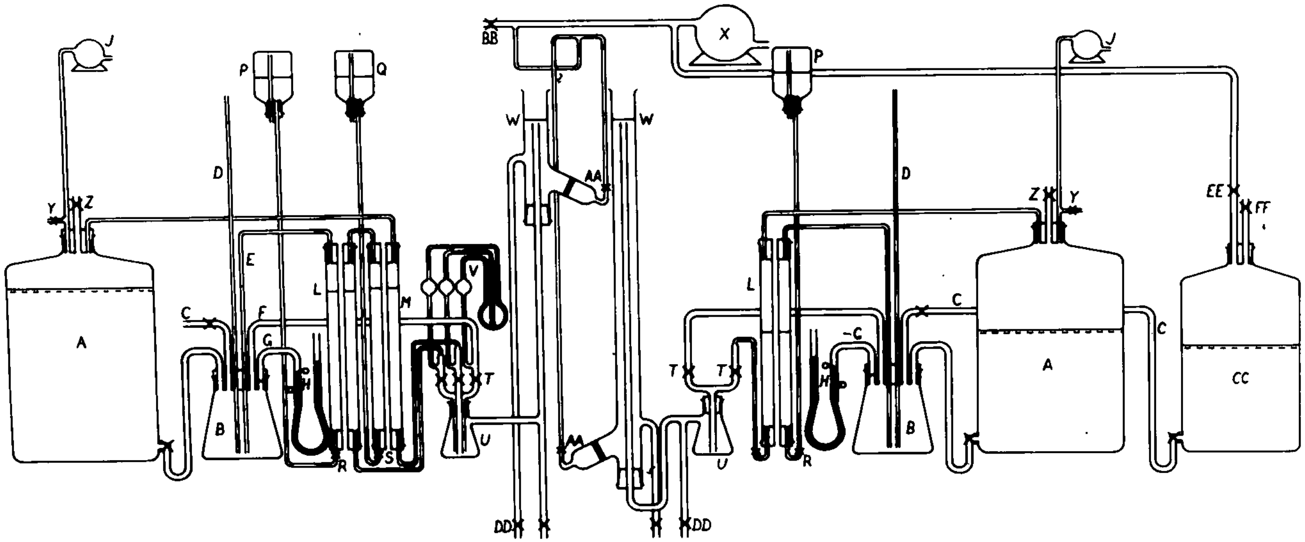


Fig. 5.11 Diagram of culture medium supply apparatus.

K not shown

reservoirs. The contents of B, L and M are discharged simultaneously into the mixing flask U (250 ml) through the taps T which are in close proximity and designed to be turned on or off together. The hydrostatic pressure in the vessels is brought to equality by means of the three-limbed manometer V in the left-hand half of the installation, in which the densities of the concentrated solutions differ appreciably from that of water. On the right hand side hydrostatic balance is attained by aligning the levels in E and L, which are mounted side by side. On the left-hand side the solution from L is first diluted with water at the Y-junction, and that from M, which contains calcium nitrate only, is added later towards the bottom of the flask. This avoids the precipitation of calcium sulphate. No such precipitation occurs at the ten-fold dilution used on the right-hand side. Half the outflow of diluted nutrient from V is aerated in the column W supplied with air from the compressor X. The flow of air is adjusted by means of the clip AA and the controlled leak at BB until the size and density of bubbles appears similar on either side. The air streams to each side divide at a point above the constant head level, to avoid the danger of mixing the nutrient solutions should X break down. The distilled water supply is renewed from a 35 litre polythene aspirator CC (shown here attatched to right-hand side) which is connected to B through the tube C. To fill A, the taps T and outlet controls DD are closed and Z and C are opened. Pressure from X is then applied to CC by opening EE. The controlled leak FF is adjusted until the pressure in B is equal to the height of E.

Except for the Winchesters P and Q, all glass used in the apparatus was Pyrex and the connecting tubes were of Pyrex and p.v.c., with short lengths of rubber at screw clips. The tubes were of 1 cm. and 0.5 cm. diameter, the difference being indicated conventionally on the diagram. The air-filled tube G was covered with aluminium foil to prevent an increase in volume of the air when the heat of the sun fell on the apparatus. All vessels were stoppered with rubber, except the aerating columns W where the basal stopper was of cork in order to facilitate adjustment.

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