THE ECOLOGY OF A WEST PERTHSHIRE HILL PASTURE, WITH STUDIES OF SOIL AERATION AND HYDROGEN ION CONCENTRATION AS FACTORS IN THE GROWTH OF BRACKEN (*PTERIDIUM AQUILINUM*, KUHN.) AND HEATHER (*CALLUNA VULGARIS*, SALISB.).

by

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PREFACE.

This thesis is founded on work carried out from 1943 to 1948, during the writer's tenure of the post of Bracken Ecologist at the West of Scotland Agricultural College. This appointment was under the auspices of the Bracken Eradication Committee of the Department of Agriculture for Scotland, and was primarily for the purpose of preparing large-scale vegetation maps of the Committee's experimental area. The production of these maps occupied three years (1943 to 1946). During the whole of the first year, the writer resided in the district. In subsequent years, the winter months were spent at the College, in Glasgow, where the field maps were traced. The field experiments occupied the summer of 1947, although some experiments had been laid down in 1946. The green-house experiments on soil aeration and hydrogen ion concentration were, for the most part, attended to when the weather was unsuitable for field work, at weekends, and in the evenings.

The prints of the maps were made by the writer, and also the negatives and prints for

the photographs in the text, with the exceptions of Figs3, 4, 6, 7, 8, 9, 12, 13, 24, 25, 37, 38 and 39.

The writer is indebted, first and foremost, to Professor K.W.Braid, of the Botany Department, West of Scotland Agricultural College, for his guidance and criticism at all stages of the work.

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The writer is grateful for the assistance of John R.Lee, Esq., in the identification of the mosses.

Acknowledgement for sources of methods and for work performed by others, is made in the text.

An outline of certain of the experiments on aeration has been published by the writer in Nature, Vol.162, p.115 (1948).

L. W. POEL.

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PART I

THE ECOLOGICAL SURVEY

I. INTRODUCTION.

The hill pasture area which the writer has studied is known locally as Ballochraggan and, until lately, was part of Portend Farm, Port of Menteith, Perthshire. In its vegetation, it is typical of many hill farms in the West of Scotland. Its position in relation to well-known centres is shown in Fig. I, which has been prepared from the One-Inch Ordnance Survey map. The district is on the southern border of the Highlands, the fault running along the northern side of the Menteith Hills.

Ballochraggan covers an area of 413 acres ascending from the Stirling-Aberfoyle road, which is, at that point, 148 feet above sea level, to the crest of the Menteith Hills, a height of 1150 feet. In Fig.40, a fence can be seen near the 400 feet contour. Below the fence are 110 acres; above, the land rises, gradually at first, very steeply later, to a grassy ridge at an approximate level of 700 feet, running more or less parallel to the fence. This ridge can be seen in Figs.37 and 38, and in the background on the left in Fig.39. On the northern side, the ridge falls gradually to a plateau, the average height of which is 600 feet. The area between the fence and the northern limit of the plateau is 142 acres. Beyond the plateau, the area

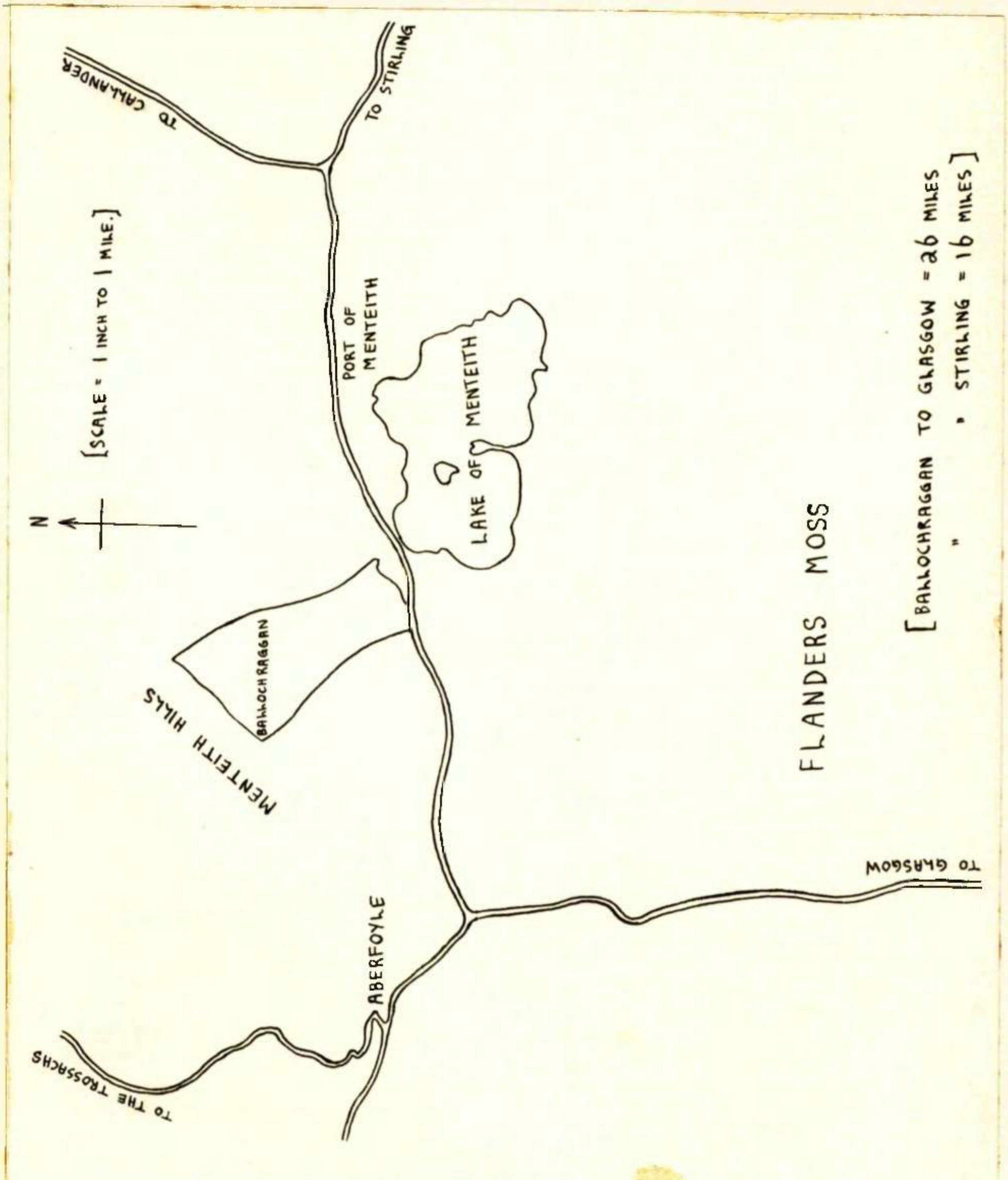


Fig.1. Map showing the location of Ballochraggan.

becomes very rocky and precipitous in many parts, and includes the conglomerate faces of the Menteith Hills. The northern boundary fence runs along the crest of these hills. Adjacent to Ballochraggan in the west are young plantations, mostly of larch and spruce, planted by the Forestry Commission.

It is convenient to divide Ballochraggan into four regions:

1) The lower region, between the road and the middle fence.
2) The middle region, between this fence and the top of the grassy ridge.
3) The plateau.
4) The upper region.

Geology: The predominant rocks of Ballochraggan are conglomerate and cornstone of the Old Red Sandstone series. In many cases, what were formerly believed to be rocky outcrops have been shown, in the course of drainage and ploughing operations, to be detached boulders and stones. The soils dominated by grasses and *Pteridium* are very stony. During the digging of a trench across part of the lower region for laying a water supply to a neighbouring farm, glacial drift was observed to the floor of the trench at a depth of four feet below *Agrostis-Festuca* grassland. No doubt, the layer extends far deeper than this. Incidentally, this excavation revealed a James VI twopenny coin about two feet down. Below the peaty soil of Calluna areas, boulder clay of unknown depth covers the rocks.

Former Cultivation and Activities: There is abundant evidence showing that much of Ballochraggan was at one time cultivated. Throughout the area, as reference to the large-scale maps will show, the grass-covered remains of old walls, now no more than ridges a foot or so high, are found. In Map Section 14, Square 6, appears the remains of a circular stone structure, possibly used as a sheep-fold in bygone days.

Many of the grass and Pteridium areas exhibit parallel grooves in their surfaces suggestive of former tillage. It is noteworthy that these relics of ploughing are found extensively on the grassy parts of the plateau area as well as on the lower zones. At present, there is one cottage inhabited on the area, but near it are the embedded remains of earlier buildings (Map Section 4, Square 6). John A. Stewart, on page 52 of his "Inchmahome and the Lake of Menteith" (1931) refers to persons occupying Ballochraggan in 1637 and towards the end of the 18th century. The descendants of the latter of these two tenants inhabit a neighbouring croft at the present day. More recently, Ballochraggan was part of a nearby farm, but sheep losses were so serious that the area became derelict from an agricultural standpoint. This was largely related to the great increase in bracken which has been general in the West of Scotland during the last fifty to a hundred years. Grouse and deer shooting on the higher parts, and that of woodcock and snipe on the lower parts, had become the sole activities on the area. In 1942, the control of Ballochraggan passed to the West of Scotland Agricultural College and, at that time, the land was heavily infested with bracken three or four feet in height.

Biotic Influences: At present, the area is subject to the influence of a considerable number of biotic factors arising from agricultural activities. Since 1942, the bracken on the lower, middle and plateau regions has been cut, some parts twice a year during the early years. Most of the middle and plateau regions were cut for the first time in 1943. The effect of this continued cutting has been a marked decrease in the size and number of the bracken fronds, this being particularly noticeable on the lower region. An improvement in the quality of the herbage has accompanied the reduction of the bracken. This improvement was favoured by increased grazing, and by manurial treatments applied to certain parts of the lower and middle regions. The colour of the grass is now so rich a green as to attract attention at a distance of some miles. Since 1942, several small areas below the middle fence have been ploughed.

Furthermore, many marshy parts have been drained.

Rabbits are very numerous on the grassy parts where they constitute an important factor in soil erosion, but are rarely encountered on the Molinieta and Callunetа. Farrow (1916) has drawn attention to the role of these animals in the dying-out of heather on Breckland. Further reference will be made in a later section to this aspect of rabbit infestation. The soils dominated by Agrostis-Festuca and Holcus mollis with or without Pteridium, contain many rabbit burrows, particularly on knoll-sides, and on the steep slope below the large Pinus sylvestris on the skyline to the right in Fig.39. In the latter situation, extensive soil erosion has taken place, exposing many of the tree roots. The undermining effect of rabbits appears to have been an important factor in this process of erosion.

2. THE BOTANICAL MAPPING.

Introduction.

The primary purpose of the botanical mapping of Ballochraggan was to provide an accurate record of the vegetation for assessing the changes in ground cover concurrent with and following bracken eradication. It was essential that, for such a purpose, the mapping should show as much detail of the vegetation as possible. Furthermore, from a purely ecological point of view, the preparation of a large-scale botanical map was a very desirable undertaking.

Gaut (1904) prepared a map of an eight acres field to a scale of 1 : 2,000. This is more than half the scale of the present mapping, but is not so detailed and only covers a small area. The writer believes that the map of Ballochraggan is on a larger scale and is more detailed than any hitherto attempted in the British Isles.

In Brittany, the Bouche d'Erquy was mapped to a scale of 1 : 240 (Oliver, 1907, and Oliver and Tansley, 1904) the area surveyed being about a square mile. The method of survey was similar to that employed at Ballochraggan, except that the squares into which the area was divided were of side 100 feet. The salt marsh vegetation was more uniform than the vegetation of Ballochraggan.

Moreover, large teams of workers took part in the survey. The outlines of the vegetation areas were sketched in by eye.

Method of Survey.

In 1942, the lower and middle regions were pegged out into squares of side 200 feet, using the straight portion of the southern boundary wall as base line. This preliminary work was carried out by Mr.C.Macquarrie, B.Sc. and later extended to include the plateau region by Mr.G.Murray, B.Sc. A series of letters was used to denote the vertical lines, and numbers for the horizontal ones. Before the present writer's appointment, Professor Braid had mapped Section 4 and the lower six squares of Section 7. For the remainder of the survey, the writer was responsible.

The mapping was carried out square by square to a scale of 1: 1,200, the field drawing being made on 1/10 inch graph paper. The end of a 100 feet chain was fixed to a corner of a square and arrayed out towards an adjacent corner. The outlines of vegetation could then be plotted by taking offsets from the chain. On completion of the first half of the side of the square, the chain was drawn up to the next corner, and so on along the other three sides, until all the details of the square were filled in.

Owing to the large scale of this

mapping, most of the recognised symbols of the British Ecological Society were unsuitable, and symbols had to be invented as required. A full list precedes the sections of the map in the Appendix.

After inking in, the squares were assembled in blocks of twelve, this being a convenient size for the sections of the complete map. Tracings were then prepared on tracing cloth and, from these, photographic prints (such as those in the present work) or "dyeline" copies for field use were produced.

Not only was the vegetation mapped, but also such features as streams, ditches, the remains of old walls, pathways and especially rocks, boulders and large stones were included. It was realised that the presence of the rocks, etc., made it possible to locate positions many years later, in the event of the loss of the corner pegs and tree landmarks. Incidentally, the smaller boulders have been found to be unsatisfactory for this purpose as observation showed that "new" stones and small boulders have appeared above the surface since the mapping was carried out. This is due to the dying-off of the vegetation and erosion of the soil which had concealed them. This phenomenon is particularly noticeable in Section 5, Square 6, where many more stones, some quite large, are now present. Conversely, it is to be expected that stones formerly in evidence at Ballochraggan are gradually being covered, but this has not yet been observed with certainty.

The sections of the map are numbered from 1 to 31, as in Fig.40. In each section, the four squares in the bottom row are numbered from 1 to 4, starting from the left. The next row is numbered 5 to 8, and so on. Thus, in referring to a square, the section and square numbers are specified. The corners of squares are denoted by the letter and number of the lines which intersect at that point. In fixing the position of any point within a square, the section and square numbers are given, followed by the co-ordinates of the point from the lower left corner.

The mapping by the writer extended over the summers of 1943 to 1946 inclusive. During the corresponding winters, the field maps were traced. The upper region is not included in the scope of the mapping as the time taken surveying such rocky ground would not be commensurate with its agricultural value.

3. THE PLANT ASSOCIATIONS OF BALLOCHRAGGAN.

LITERATURE: The most recent general account of Scottish acidic grasslands and heaths is that provided by W.G.Smith in "Types of British Vegetation" (Tansley 1911). According to Tansley (1939, p.751), "No recent intensive work, either floristic or ecological, has been done on the heaths of Scotland.....".

Between 1900 and 1906, Hardy, W.G. and R. Smith surveyed the vegetation of a number of Scottish counties, preparing maps on the basis of the ordnance survey. Having regard for the total area covered, and the small band of workers, the maps were necessarily on a small scale. The survey was never completed for the whole of Scotland. These valuable contributions included a few species lists and numerous observations on succession between the various forms of vegetation. In this series of papers were Lewis' studies on the strata of vegetation revealed in peat profiles, corresponding with glacial and interglacial periods.

Turning to the few pieces of intensive research carried out on the Scottish heaths, Crampton (1911) gave numerous lists of species for the plant associations of Caithness, and considered the vegetation in relation to such factors as geology, the drainage system, exposure, grazing, etc.
A section particularly relevant to an ecological study

of an area such as Ballochraggan is that relating to the effects of springs on moorland associations. In Caithness, "flushes" arose as a result of springs, and these Crampton divided into "dry" and "wet". The wettest flushes on peat soils were occupied by Sphagnum cuspidatum. At the margins, Juncus effusus and Carex spp. were found. The drier flushes were characterised by beds of Polytrichum commune. Where the margins were subject to periodical overflowing, Nardus became dominant. If a sudden change in gradient occurred on a slope, Molinietum developed. These species also came to dominate the dry acidic and neutral flushes. In the category of alkaline flushes, Juncus articulatus was dominant, being more abundant than J. effusus. The dry alkaline flushes were Nardeta or Cariceta. The reasons for changes in vegetation accompanying flushing were given as being probably hydrogen ion concentration, soil aeration, the rate of flow of water, and the constancy or otherwise of the flow.

A most notable contribution of more recent date is that of Fraser (1933). From the standpoint of the present section, Appendices II and IV in his paper are especially relevant. In the former, full species lists are given for the various moorland associations encountered. Appendix IV includes vegetation maps, quadrats and profile transects.

Asprey (1947) has made an ecological study of the Inverness-shire islands of Canna and Sanday. Most of the area is occupied by grassland of the bent-fescue type and by *Calluna* heath. He gives species lists in both cases. On the higher parts of Canna, and in small areas on Sanday, "moorland" is found. Floral lists are given for plant communities dominated by *Scirpus caespitosus* and *Calluna*, *Scirpus caespitosus* and *Molinia*, *Calluna*, *Molinia*, and, in the wettest situations, by *Sphagnum spp*. He encountered three kinds of flushes, namely, those dominated by *Philonotis fontana*, by *Hypnum cuspidatum* and by *Brachythecium rivulare*, respectively.

1. PTERIDIUM AQUILINUM ASSOCIATIONS.

Bracken, either alone or dominating other vegetation, occupies by far the most of Ballochraggan. As indicated previously, the fern was dense over much of the area in 1942, but as a result of continued cutting, the height and density of the fronds has been very much reduced over the lower and middle regions. In the former part, especially in Map Section 1, the fronds have become quite sparse and little more than a foot high. Bracken which has not been cut or otherwise restricted is to be found in small quantities in the land between the main stream and the western boundary wall, and much more extensively in the upper area. In such parts, the bracken grows to a height of five feet or so and is so dense as to render walking through it arduous.

a) Pure Pteridium.

When bracken is enjoying optimal conditions, it becomes so tall and dense, and casts so much shade when the fronds are fully expanded, that the ground vegetation is entirely suppressed. This is the state of affairs in most of the untreated bracken areas at Ballochraggan and, as can be seen from the maps, patches of pure, dense bracken occur in many of the parts which have been subjected to cutting. In the winter and spring, before the appearance of the fronds, such patches are represented by masses of brown litter and bare soil which, in the early spring and until the fronds are sufficiently large and numerous to shade, may be colonised by individuals of such species as Anthoxanthum odoratum, Carex panicea, Cnicus arvensis, Holcus mollis, Potentilla erecta, Scilla nutans, Veronica chamaedrys, and Viola canina. In due course, the fronds of the bracken appear and, if uncut, ultimately suppress the scattered ground flora.

When a pure Pteridietum is, by continued cutting, very much reduced in height and density, it is gradually converted into the second type of bracken association, namely:-

b) Pteridium in Holcusetum mollis.

Observations made in the summer of 1947 in Section 5, Square 4, showed that considerable changes had taken place in the extent of pure bracken in the four growing seasons which had elapsed since the maps were made. The patches of dense bracken are now almost gone, most of their area having reverted to Holcus mollis with bracken of normal density amd size. The original outlines of dense bracken can still be traced, however, because of the slightly different green of the new grass.

A Pteridietum in Holcusetum mollis is peculiarly poor in associated plants.

In one area at Ballochraggan, a transition from Holcus mollis to Festuco-Agrostidetum has been observed since the mapping (Section 5, Square 8, and Section 6, Square 5). At present, in what was formerly a Holcusetum mollis, about 50% of the surface is covered by patches of bent-fescue. This transition has only been observed so far in this one locality. Frequently, it does not occur, and the creeping soft grass appears to be stable. There is a need for permanent quadrat work in order to study the full course of the changes following continued bracken cutting.

c) Pteridium in Festuco-Agrostidetum.

This type of grassland occupies

most of the lower and middle regions. While being quite rich in species, it is very uniform in composition in different localities. The _Agrostis-Festuca_ association is frequently found in relatively small areas without the presence of bracken but, more usually, there is what one might call a "moderate" infestation by the fern. It is misleading to speak of the bracken as dominant in respect of the whole association as it occupies a different stratum from the grasses and other ground flora. The bent-fescue vegetation is vigorous, and is not adversely affected by the covering of bracken, unless the latter becomes so dense as to reduce the light seriously, and lead to the deposition of a thick layer of litter.

A general list of species found in the bent-fescue associations of Ballochraggan follows:

Dominant

Agrostis tenuis

Festuca ovina

(_Agrostis canina_ is co-dominant with Festuca on the higher ground.)

Abundant

Achillea millefolium	Potentilla erecta
Anthoxanthum odoratum	Pteridium aquilinum
Galium saxatile	Rumex acetosella

Trifolium repens

Locally Abundant

Carex vulgaris
Deschampsia caespitosa
D. flexuosa
Iris pseudacorus
Juncus acutiflorus
Juncus effusus
Nardus stricta
Thymus serpyllum
Triodia decumbens
Ulex europaeus

Frequent

Campanula rotundifolia
Carex panicea
Cerastium vulgatum
Cnicus arvensis
C. lanceolatus
Cynosurus cristatus
Digitalis purpurea
Euphrasia officinalis
Hieracium pilosella
Holcus lanatus
H. mollis
Luzula campestris
Plantago lanceolata
Prunella vulgaris
Ranunculus acris
R. repens
Rumex acetosa
Scabiosa succisa
Veronica chamaedrys

Locally Frequent

Calluna vulgaris
Juniperus communis
Poa annua
P. pratensis
Poa trivialis
Prunus spinosa
Scilla nutans
Urtica dioica
Vaccinium myrtillus

Mosses

Bryum pallens
Dicranella heteromalla
Dicranum scoparium
Hylocomium splendens
H. squarrosum
Hypnum palustre
H. Schreberi
Plagiothecium elegans
Rhacomitrium aciculare
Thuidium tamariscinum

The flora of the numerous sheep tracks which cross the Festuco-Agrostideta is usually very different from that adjoining. Triodia decumbens and Poa annua are plants typical of trodden pathways.

Increasing soil moisture in a Festuco-Agrostidetum involves two alternative courses of succession, depending upon whether peaty conditions develop along with the rising water-table or not. In the latter circumstances, Caricetum and Junceta replace the bent-fescue. If, on the other hand, peat accumulates, successions involving Nardus, Molinia, Calluna, Eriophorum and even Sphagnum may ensue.

2. CARICETUM VULGARIS.

Sedge areas are mostly dominated by Carex vulgaris, but at the edges of ditches, C.flava and C.echinata are very frequent species. Carex binervis is encountered in the drier situations. This type of vegetation seems to represent an intermediate stage between grassland and Juncetum acutiflori. Wherever water accumulates in a grassland, the dominant grasses which are characteristic of the drier soils, namely Agrostis tenuis, A. canina and Festuca ovina, die out. Grasses such as sweet vernal and Nardus are much more resistant. Potentilla erecta is also a plant which seems able to endure a wide variety of soil moistures.

3. JUNCETUM EFFUSI.

Except in certain areas which have been ploughed, Juncus effusus never occurs dominant over large areas at Ballochraggan. Many relatively small patches, or even isolated tufts, are found. It is prone to appear in any of the associations where a local condition of higher soil moisture obtains. In the middle and plateau regions, it follows the bases of the east and west boundary walls for considerable distances. It may be that the soil is slightly more moist close to a wall due to the running-off of rain-water. Juncus effusus also occurs locally in Juncetum acutiflori, very frequently in Cariceta, in moist parts of bent-fescue, in Molinia-Nardus areas and Eriophoretum vaginati. Occasionally, bracken is found in a patch of this rush. Many of the situations where Juncus effusus grows tend to be drier than those occupied by J. acutiflorus. Juncus conglomeratus is frequently present with the dominant species.

4. JUNCETUM ACUTIFLORI.

Marsh associations, mainly dominated by Juncus acutiflorus, are found extensively at Ballochraggan. The largest areas are situated where main channels of drainage have become obstructed as a result of neglect in bygone years. The largest Juncetum acutiflori begins in the east corner of

Section I, extending across the lower halves of Sections 2 and 3. This is the lowest part of the whole area, and drains most of the region below the middle fence. The marsh is divided into two sections, each having a main channel with its system of tributaries conducting the water across the southern boundary of the area, ultimately emptying itself into the Lake of Menteith. These two natural divisions are separated by a narrow neck of relatively dry land, in Section 2, Squares 4 and 8. The upper half of this barrier forms a steep knoll which is quite dry, bearing bracken in bent-fescue, with a few gorse bushes on the crest. The lower part, extending 140 feet north from the boundary wall, is also well raised above the level of the swamp; it is flat and shows signs of having been a small field at one time. It is of interest to note that the elevated parts of this barrier are bracken-ridden, whereas the bridge connecting them, only a few feet above the marsh, is devoid of the fern. This is one of the many observations demon:
:strating the necessity of adequate drainage and, therefore, good aeration, for bracken.

The stream which drains the western part of this Juncetum arises in Section 15, Square 3, on the line of the middle fence. Its course may be traced through numerous small areas of <u>Juncus</u> and <u>Carex</u>. On entering the main Juncetum, it first passes through a zone where Iris is dominant. Its point of exit from Ballochraggan, through the boundary wall between corners I.1 and J.1, is the lowest point on the area, and is very swampy. Before the College draining scheme was carried out, very few branch ditches remained, as can be seen from the map. A complete system now exists but, although the level of the water was lowered to a certain extent, thoroughly effective drainage was not provided. One of the causes of this would appear to have been the "tongue" of drier soil projecting more than half way across the marsh in Section 2, Square 2. Even the Juncetum beyond this is slightly raised above the general level and renders effective drainage of the swamp lying to the east very difficult. It so happens that the wettest zone is located between the tongue and the large, flat stone in Square 3. Consequently, although the level of water was reduced, this part remains very wet and unstable underfoot.

A list of the plants found in this Juncetum follows:

Dominant

Juncus acutiflorus

Locally Dominant

Iris pseudacorus

Juncus effusus

Abundant

Carex vulgaris	Hydrocotyle vulgaris
Holcus lanatus	Ranunculus repens

Locally Abundant

*Juncus bufonius	*Montia fontana
*J. bulbosus	*Potamogeton polygonifolius
J. lamprocarpus	Salix aurita
*Mentha aquatica	Spiraea ulmaria
*Menyanthes trifoliata	*Utricularia intermedia

Frequent

Agrostis alba	Cnicus palustris
A. tenuis	Lotus major
Anthoxanthum odoratum	Luzula campestris
Caltha palustris	Lychnis flos-cuculi
Cardamine pratensis	Nardus stricta
*Carex echinata	Narthecium ossifragum

Pinguicula vulgaris

Locally Frequent

*Carex leporina	*Myosotis scorpioides
Cynosurus cristatus	Pedicularis palustris
Drosera rotundifolia	*Potamogeton natans
*Equisetum sylvaticum	*Ranunculus flammula
Festuca ovina	Rumex acetosa

Triglochin palustre

Occasional

Agrostis canina	Geum rivale
Carex flava	Hieracium murorum

Occasional (Contd.)

Carex praecox	Orchis maculata
C. pulicaris	Parnassia palustris
Cerastium vulgatum	Plantago lanceolata
Epilobium palustre	Poa trivialis
Euphrasia officinalis	Polygala vulgaris
Galium palustre var. Witheringii	Sonchus oleoraceus

Rare

Cnicus lanceolatus	Hypericum pulchrum

Mosses

Atrichum undulatum	Mnium undulatum
Aulacomnium palustre	Philonotis fontana
Climacium dendroides	Polytrichum commune
Dicranella squarrosa	Rhacomitrium fasciculare
Eurhynchium Stokesii	Sphagnum contortum
Hypnum cordifolium	S. cymbifolium
H. cuspidatum	S. plumulosum

Thuidium recognitum

Those species marked * were usually encountered in, or on the edges of, ditches.

5. NARDETUM.

There is very little Nardetum, the most extensive patch being found in Section 19, Square 12. Nardus is encountered frequently in the marginal zone between bent-fescue and Caricetum or Juncetum acutiflori, in association with Molinia, *Calluna* and *Vaccinium myrtillus* and with *Deschampsia flexuosa.* Smith (1918) states that *Nardus* is marginal to peat and peat vegetation. He shows that flushing of Nardetum with spring water, especially when calcareous leads to the replacement of the *Nardus* by *Festuca ovina, Agrostis alba, Cynosurus cristatus, Holcus lanatus, Trifolium repens, Ranunculus repens,* etc. Conversely, irrigation of a neutral grassland with peat water causes a line of the moor mat grass to follow the course of the water. Smith takes the view that Nardeta have been derived from pre-existing Calluneta. Reference will be made below to the frequent occurrence of grasses dominated by *Nardus* fringing patches of *Calluna,* but it appears that, in general, the *Nardus* of Ballochraggan has developed from Festuco-Agrostidetum, by soil moisture increasing, and a thin layer of peat tending to accumulate.

6. MOLINIETUM.

Associations characterised by a high proportion of the purple moor grass (*Molinia caerulea*) cover much of the ground upwards of about 400 feet. The wet "Molinia bog" of Jefferies (1915) in which the plant grows in tall, dense tussocks, occurs but seldom, and then only in small areas, and poorly developed. By far the greatest amount of the *Molinia* exists as a more or less level grassland, where the soil would not appear to be wet enough to favour tussock development. In some cases, however, it may be kept level by the grazing of stock.

The associated flora of this type of Molinietum is not rich in species, in conformity with the general tendency of peat communities. A typical list is now given:

Dominant

Molinia caerulea

Abundant

Nardus stricta   Vaccinium myrtillus

Locally Abundant

Calluna vulgaris   Erica tetralix

Deschampsia flexuosa   Juncus squarrosus

Scirpus caespitosus

Frequent

Agrostis tenuis   Festuca ovina

Potentilla erecta

Locally Frequent

Juncus effusus

Occasional

Agrostis canina   Luzula campestris

Anthoxanthum odoratum   Pedicularis palustris

Rare

Erica cinerea   Galium saxatile

Polygala vulgaris

Mosses

Campylopus flexuosus	Hypnum Schreberi
Dicranum scoparium	Leucobryum glaucum
Hylocomium squarrosum	Polytrichum juniperinum

Sphagnum plumulosum

Molinia is very frequently associated with *Vaccinium myrtillus*, but the latter is invariably stunted, often tinted red, and never reaches such a development as to approach a Vaccinietum.

Nardus is sometimes co-dominant. This frequently led to difficulty in deciding upon the dominant plant during the mapping, so that, in such cases, the symbols for both were used. In other cases, *Deschampsia flexuosa* occupied a similar position as co-dominant.

In moister situations, one may find what is apparently a derivative of the normal *Molinia* vegetation and which is characterised by a development of *Sphagnum*, in which the lower parts of *Molinia* and other plants are embedded. This associa: :tion is symbolised on the maps by horizontal and vertical hatching. Because of the high water content of the soil, the Molinietum is in process of being ousted by *Sphagnum*. The associated species, in order of frequency, are:

Calluna vulgaris (of stunted size)

Vaccinium myrtillus

Juncus squarrosus

Nardus stricta

Erica tetralix

Scirpus caespitosus

Festuca ovina

Pteridium is absent from the Molinieta, and the zone of overlaps between Molinietum and Festuco-Agrostidetum containing bracken is, as a rule, even narrower than between the latter and Juncetum. The reason for this is not clear, especially as much of the Molinietum at Ballochraggan is of the relatively dry type. Furthermore, as a result of degeneration and fires, much of the former Callunetum on the plateau contains Molinia in abundance, and the fern is a vigorous invader.

In order to study the growth of bracken in a Molinietum, transplant experiments were laid down in Section 10, Square 3. Most of the Molinia vegetation is of the type containing a high percentage of Sphagnum. The experiments were of two kinds, namely, the planting of one-year-old sporelings, and the transference of sods containing bracken.

A. Sporeling Transplants.

The sporelings, three innumber,

were pot-bound at the time of transplanting. They were removed from the pots and planted in the positions indicated as 1, 2, and 3 on the transparent "flimsy" covering the map. This took place on May 10th, 1946, and at that time, no.1 had four very small fronds, no.2, one young frond expanding. No.3 also had one minute frond. In order to prevent grazing by animals, the transplants were covered by squares of wire netting, each supported on four wooden pegs, so arranged in height that the net was about nine inches above the vegetation.

On September 11th of the same year, two of the fronds of no.1 were dead, and the two remaining ones turning brown. No new fronds had been produced. No.2 had put up a second frond, but this was very small. The original frond was in a dying condition. As for no.3, no living fronds were present.

Re-examination on October 13th, 1947 showed that the strength of the transplants had declined further. Two fronds had arisen from no.1 during the summer, but had since died. There was no sign of no.2. No.3 bore one small dead frond.

On July 23rd, 1948, one minute frond was evident on each of nos.1 and 2. No fronds had been produced by no.3. By September 15th, only the frond on no.1 was alive.

B. Sod Transplants.

A square sod of side two feet and nine inches in depth was cut at (A), in Festuco-Agrostidetum with strong Pteridium. A sod was also taken from (B) in the Molinia zone. The bracken-containing sod was transplanted to the hole left at (B) and the Molinia one to that at (A). A duplicate interchange was made between (C) and (D).

The two Molinia-type transplants differed from each other in that the one at (A) had an extensive base of Sphagnum, less than a quarter of the area being free of the moss. Molinia and dwarf Calluna were co-dominant, with Vaccinium myrtillus sub-dominant. The bed of Sphagnum was absent from the transplant at (C) so that it appeared considerably drier.

At the time of transplanting, the sod at (B) bore the stumps of 16 fronds produced during the 1946 season. That at (D) had 14 fronds. Only the stumps remained for the most part as the bracken on the area had been cut during the summer.

One-yard quadrats were pegged out to include each transplant. Thus, the positions of fronds either outside or inside the transplants having been plotted initially, a means was provided for the accurate study of the invasion of bracken into the transplant, or from the transplant into the surrounding vegetation, as appropriate. Moreover, as vegetation charts of the transplanted sods were made at the start, recharting at a later date should reveal any changes which had taken place in the constitution of the flora in each case.

The transplants were re-examined on October 13th, 1947.

Transplant at (A): No invasion by bracken had occurred and, apart from being somewhat drier than before, the appearance of the transplant was little changed.

Transplant at (B): No fronds had been put up during the 1947 growing season.

Transplant at(C): There had been no invasion by bracken, but a tendency was noticed for the Festuco-Agrostidetum flora to enter the transplant. Galium saxatile was invading at one corner. The appearance of the transplant had not undergone any radical alteration, and it cannot be said that it had changed floristically, yet, nevertheless, a subtle difference was evident which was probably due to drying-out.

Transplant at (D): Only three fronds were present of which two were very small, the largest being but nine inches high. No change in the flora of the transplant could be perceived.

A further examination was made on September 15th, 1948.

Transplant at (A): One small frond was observed one inch within the margin of the transplant.

Transplant at (B): *Sphagnum* was invading from one side. Only one frond was present and this was dead. *Deschampsia flexuosa* was invading the transplant.

Transplant at (C): No invasion by bracken had yet occurred, but "drying-out" of the transplant was proceeding.

Transplant at (D): Three fronds, two of which were very small, were present. The heath vegetation appeared to be invading; *Deschampsia flexuosa* was entering at one side.

Both these sets of experiments demonstrated that the soil of this *Molinia-Calluna-Sphagnum* type of vegetation is a very inhospitable medium for bracken. In this area, the high water content of the soil makes the explanation on the grounds of deficient aeration the most acceptable. As has been stated above, however, such vegetation is not typical of the Molinieta of Ballochraggan, which are considerably drier. No transplants into the more usual type have yet been made by the writer, but such experiments were laid down by Mr. J. Reid at a hill farm known as Touchmollar, near Stirling. The writer had the privilege of examining, during the summer of 1947, the sods of bracken transplanted into Molinietum at this area in 1942. In most cases, no invasion of the

Molinietum soils had taken place. Two fronds were found seven inches outside one transplant. Most of the transplants bore few fronds, which were small. In two instances, however, large numbers of tall fronds occurred, thirty nine being counted on one transplant. There had been no invasion from these vigorous centres. On the other hand, the unfavourable characteristics of Molinietum soil had not been transmitted to the transplants. There is thus experimental evidence that even the drier types of Molinieta possess properties extremely hostile to the spread of bracken.

7. CALLUNETUM.

Although *Calluna* of stunted habit enters into the composition of Molinietum and even the bent-fescue in some localities, Callunetum is not encountered below the plateau, and its greatest development is attained on the upper region. The Menteith Hills are capped with a dense, knee-high growth of heather. Most of the field observations have, however, been confined to the lesser Calluneta of the plateau.

In 1942, when Ballochraggan was taken over for experimental purposes, most of the heather was old and "leggy". Counts of annual rings indicated ages ranging from 12 to 24 years. Considerable tracts of this moribund vegetation were burnt in 1943, and further quantities have been burnt in succeeding years. Much of this burning had already taken place before the commencement of the mapping, but the burnt patches are indicated as Callunetum on the maps in order to represent the initial vegetation of the area as nearly as possible. One of the few areas of young, vigorous heather within the scope of the mapping is that in Section 22, Square 4.

The heather on the plateau occurs as numerous relatively small patches, with the exception that the large Eriophoretum in Sections 30 and 31 had heather as co-dominant prior to burning in 1943. (It appears that in this case, the _Calluna_ was being ousted by the cotton grass.) It is noticeable that these patches are found on those parts of the plateau which are raised above the general level. This feature is strikingly evident when the plateau is viewed either from the top of the ridge or from the upper region. The heather is not dense. It is undoubtedly in an advanced stage of degeneration, being heavily mixed with _Molinia_. Frequently, many of the branches are dead and, in some parts, the heather rhizomorph disease, caused by _Marasmius androsaceus_, is prevalent. Intermediate stages may be found between the Callunetum and Molinietum; reference has already been made to _Molinia_ areas which contain scattered, straggly heather plants. There is also evidence that the heather patches are shrinking from the periphery inwards, in that many are fringed by a mixture of Molinia and Nardus, in which Calluna plants are scattered. This thinning-out of the Callunetum towards its edges has been reported at Breckland by Farrow (1916) who attributed the phenomonon to rabbit attack. At Ballochraggan, rabbits are few on the plateau. The writer believes that the degeneration of unburnt heather at Balloch:raggan is due to age and, possibly, grazing by sheep. Wire cages have recently been placed on Calluna areas at various points on the plateau and already, the absence of grazing is exerting its effect on the vegetation. The carpet of heather has become much more uniform, as a result of the growth of new shoots and of seedlings. A further point which was noted by Farrow has its parallel in this area, namely, the increased degeneration of Calluna where pathways enter and leave.

A species list now follows:

Dominant

Calluna vulgaris

Locally Co-dominant

Molinia caerulea

Frequent

Blechnum spicant	Molinia caerulea
Deschampsia flexuosa	Nardus stricta
Festuca ovina	Potentilla erecta

Vaccinium myrtillus

Locally Frequent

Erica cinerea	Juncus squarrosus
E. tetralix	Pteridium aquilinum (invading)
Eriophorum vaginatum	Scirpus caespitosus

Occasional

Carex panicea

Rare

Lycopodium clavatum	Polygala vulgaris

Thymus serpyllum

Mosses

Dicranum scoparium	Hypnum cupressiforme
D. scoparium	var. ericetorum
var. spadiceum	Leucobryum glaucum
Hypnum cupressiforme	Plagiothecium undulatum

Sphagnum compactum

Observations on the Recolonisation of Burnt Callunetum.

Heather-burning having taken place at various times since 1942 renders the area particularly suitable for a study of the recolonisation of Callunetum after a fire. Tansley (1939) states that no detailed investigations of the successions following burning have been made in Scotland.

W.G.Smith (1916 and 1918) has shown that the return of heather after a fire is slower when the plants are old. Brief mention was made of the main plants characterising the transitional stages. Erica cinerea appeared on the dry soils, and E. tetralix on the damper parts. Other plants typical of the recolonisation were given as being _Agrostis vulgaris_, _Galium saxatile_, _Juncus_, _squarrosus_, _Molinia caerulea_, _Nardus stricta_, _Pteridium aquilinum_ and _Vaccinium myrtillus_. Sometimes, these species dominated the heather permanently. According to Smith (1916) the most rapid return of heather to dominance after burning was in five years, but in the later paper, the period was given as from two to four years.

Jeffreys (1917b) gave in diagram form, the various courses of succession arising from heather-burning on Durham Coal Measure Fells. The area became dominated by either _Rumex acetosella_, _Vaccinium myrtillus_, _Empetrum nigrum_, _Nardus_ or _Molinia_, according to soil conditions. The Callunetum could be restored via the _Vaccinium_ or _Rumex_ as sub-seres; that is, _Calluna_ only returned to dominance on the drier soils. The _Rumex_ could, alternatively, give rise to a succession via _Holcus mollis_ culminating in Pteridietum.

Adamson (1918) found a different succession on the Southern Pennines. _Deschampsia flexuosa_ and _Nardus_ appeared promptly but were soon replaced by _Vaccinium myrtillus_. Subsequently, _Vaccinium vitis-idaea_, _Empetrum_ and seedlings of _Calluna_ entered. After a time, the _Calluna_ became dominant, assisted by its increasing shade in ousting the other species. *Vaccinium myrtillus* could be stable in some situations.

Fritsch (1927) made a study of the recolonisation of Hindhead Common. The fire occurred in the early part of 1924, and the observations were made in July of the same year. On the lower part of the area (the "Erica slope") the vegetation was dominated by *Calluna* and *Erica cinerea*, and was only seven years old at the time of the fire. Many *Calluna* and *Erica* plants were sprouting from the stool and only the older *Calluna* was dead. A few plants of the latter survived, but the subsequent growth was weak. Fritsch suggested that the controlling factors in determining whether the plants are killed by a fire or not, are the heat produced and the duration of the fire. With old, large heather, the total heat kills both old and young. He found poorer regeneration in the "old *Calluna-Ulex* zone" on the crest of the ridge, even though burnt at the same time. In this case, the degree of exposure might have exerted an effect on the rate of restoration of the *Calluna* and *Erica*. He discussed the effect of recurrent fires. These result in a progressively lower humus content, leading to invasion by bracken or mosses and grasses.

Heath, Luckwill and Pullen (1937) charted quadrats on Blackdown, Mendip, in studies of the stages in recolonisation. *Molinia* and *Erica tetralix* became abundant at first, but thereafter, the Calluna plants (by their increasing shading effect) gradually suppressed the other species, and the Callunetum was restored in s Observations at Ballochraggan.

Observations at Ballochraggan.

There are two methods open to the student of vegetation in tracing the story of succession after burning of an area. Firstly, permanent quadrats and transects can be laid down immediately after the fire and charted at fixed intervals over the years until stability is reached. By the second method, areas burnt in different years are studied, and a composite picture built which is assumed to represent the succession on one area. That this indirect method is inferior is indubitable, but frequently it has to be employed because of limited time. For this same reason, the indirect technique was the one adopted in the present researches. It should be stated that the work so far accomplished is of a preliminary nature. It is intended shortly to peg out permanent quadrats on the various areas, and thereby obtain more accurate data than has hitherto been possible.

The observations reported below were made during the summer of 1947.

<u>1943 burns:</u> (a) <u>Section 22 Square 8.</u>

Molinia caerulea	Co-dominant
Calluna vulgaris	Co-dominant
Deschampsia flexuosa	Abundant
Vaccinium myrtillus	Abundant
Festuca ovina	
Juncus squarrosus	
Nardus stricta	
Potentilla erecta	

The <u>Calluna</u> bore flowering shoots which were about six inches high. At midsummer, the dominant plant appeared to be <u>Deschampsia flexuosa</u>, due to the aspect produced by its flowering at that time.

(b) <u>Section 23, Square 2.</u> Part of a line transect passed through a 1943 burn and yielded the following data, plants being recorded at every six inches:

Molinia caerulea	39	plants
Calluna vulgaris	22	"
Nardus stricta	14	"
Scirpus caespitosus	8	"
Festuca ovina	6	"
Vaccinium myrtillus	5	"
Deschampsia flexuosa	3	"
Erica tetralix	2	"
E. cinerea	1	plant

Juncus squarrosus	1 plant
Luzula campestris	1 "
Potentilla erecta	1 "

It is clear in this case, and appears to be so elsewhere on the area, that Molinia can seize control of a former Callunetum as a result of a fire. The young Calluna seedlings arise in patches, not forming a complete carpet. Such patches are often in the shelter of the burnt stems of the old, dead plants. Heather at this stage readily produces flowers and, doubtless, the seeds help in increasing the density. Given sufficient time, during which the heather forms a more uniform carpet and begins to shade the grasses near to the soil surface, the proportion of Molinia may be very much reduced, and a vigorous Callunetum come into being once more.

Where Calluna had been dense prior to burning, an almost pure covering of young heather may result, with very little Molinia present.

1946 burns: (a) Section 23, Square 7 (near H.20).

This area is in the form of a small knoll, and, at the time of examination (which was about twelve months after the fire) the surface of the soil was covered by vegetation to the extent of approximately 50% of its area. A list of species for this part follows:

Agrostis tenuis	abundant
Deschampsia flexuosa	abundant
Festuca ovina	abundant

Anthoxanthum odoratum	Nardus stricta
Calluna vulgaris	Polygala vulgaris
Carex panicea	Potentilla erecta
Erica cinerea	Pteridium aquilinum
E. tetralix	Scirpus caespitosus
Molinia caerulea	Vaccinium myrtillus

In the north-west marginal zone, Molinia was dominant, and there was much more Nardus. It is possible that here the Calluna was sparse before burning, and that considerable quantities of the two grasses were already present. It has been shown above that the marginal sparseness of heather, attended by abundance of Molinia and Nardus, is of frequent occurrence at Ballochraggan.

In the most westerly part of this area, the dominant species was Vaccinium myrtillus. Bracken and tormentil were more frequent.

(b) Section 28, Square 1.

A similar type of flora but with fewer vascular plants, was obtained, with the addition of mosses and Cladonia spp. All of this patch, except the centre, had been invaded by vigorous bracken. Possibly, the bracken was present in the heather before burning, but the indications were that the *Calluna* had been denser than in the previous area described. If Fritsch's view is correct, the greater heat generated in the burning of the denser heather would involve more complete destruction of the flora, and hence, fewer species with mosses and *Cladonia*, which are often among the first plants to colonise after a fire. An important factor to bear in mind, however, when seeking to apply Fritsch's conclusions in this connection to heather moorland of the West of Scotland, is the difference of climate between the two districts. In the damp climate of West Scotland, the heather never really becomes dry enough to burn very fiercely. Indeed, fires are often most difficult to start and maintain. This is very different from the state of affairs in the South East of England, where raging fires may arise accidentally. Consequently, the intense heat experienced on Hindhead is probably of rare occurrence in the wetter counties. It cannot, therefore, be said that destruction of the original plants is usually at all complete; frequently, the roots and rhizomes of many of the plants remain unharmed, only the foliage being destroyed. Regeneration of plants such as *Molinia*, *Deschampsia flexuosa*, *Potentilla erecta*, etc., may be very rapid, and the moss-lichen phase be missed altogether. Thus, in a few square yards of heather burnt early in 1947, the following plants were found in the late autumn of the same year:

Agrostis tenuis
Deschampsia flexuosa
Festuca ovina
Molinia caerulea
Polygala vulgaris (one plant only)
Potentilla erecta

It is clear that the original flora had not been entirely killed. An estimate of the proportion of the surface colonised was 25%. Towards the west margin, the covering was almost 100%, but this part was burnt most ineffectively. It was dominated by Molinia, with Vaccinium myrtillus and Erica tetralix present. Fronds of Pteridium were common.

8. ERIOPHORETUM.

This association is the penultimate stage in the succession arising from stagnant water: :logging of acid peat. At Ballochraggan, the largest expanse of cotton grass bog is found in the north-east corner of the plateau, that is, in Sections 30 and 31, and extending a few hundred feet northwards of the limit of the mapping. This large area, and other, smaller patches, seem to have arisen as a result of neglected drainage in the past. Attempts at draining the large Eriophoretum have been made, but the area is in the form of a saucer and consequently, the necessary gradient could not be secured. The indications are that the boundaries of this area are extending into the adjoining Molinietum, for example, in Section 31, Square 6. This invasion is preceded by an increase in the _Juncus squarrosus_ in the Molinietum.

The main Eriophoretum was formerly co-dominated by Calluna, but the area was burnt in 1943 and the writer did not see the original condition of the heather. Judging from the dead stems remaining, the plants were very old and "leggy" and, undoubtedly, the heather was in an advanced stage of degeneration. Many _Calluna_ seedlings have developed since the fire, but it is unlikely that anything approaching a Callunetum will be restored. The latter was probably the association occupying the area before waterlogging and stagnation became serious.

At Ballochraggan, as on bogs elsewhere in Scotland, _Eriophorum vaginatum_ is the dominant species over most of the cotton grass areas, _E. angustifolium_ only assuming dominance in the wetter patches. In parts of England and Wales, the latter is the more extensive.

The list of species which follows indicates the poverty typical of Eriophoreta. The list is compiled from the relevant part of a line transect taken between R.23 and T.23, in which the plants were recorded at every foot:

Eriophorum vaginatum	81	plants (dominant)
E. angustifolium	28	"
Sphagnum spp.	26	"
Polytrichum juniperinum	24	"
Calluna vulgaris	14	"
Erica tetralix	8	"
Empetrum nigrum	2	"
Juncus acutiflorus	2	"
Narthecium ossifragum	1	plant
Vaccinium myrtillus	1	"
Vaccinium oxycoccos	1	"

The following mosses were found in Eriophoretum:

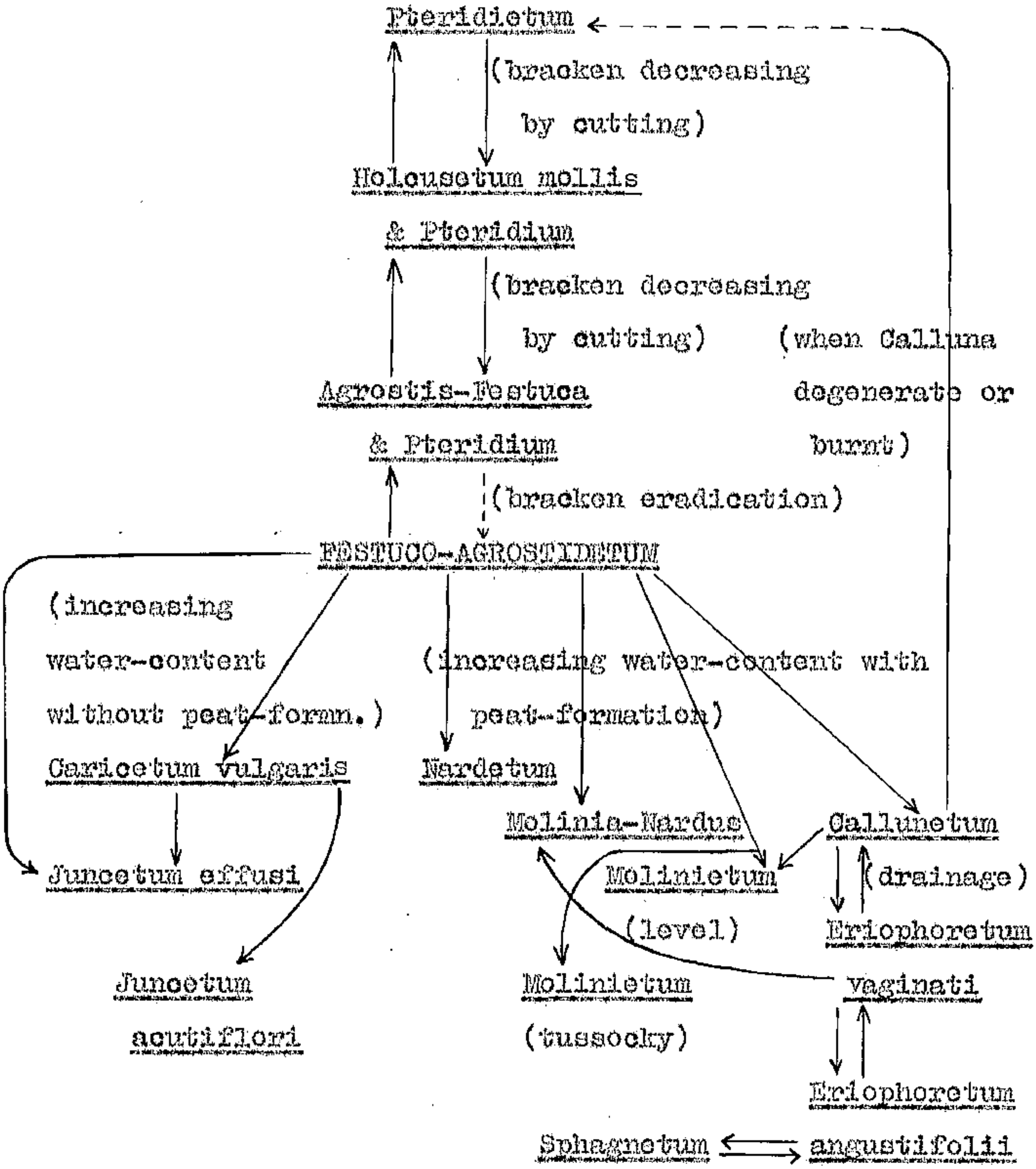
Aulacomnium palustre	* Polytrichum juniperinum
Campylopus flexuosus	* Sphagnum plumulosum
Dicranum scoparium	S. recurvum

(* - locally dominant)

The figures given show the over:whelming preponderance of Eriophorum vaginatum. Eriophorum angustifolium, Sphagnum plumulosum or Polytrichum juniperinum dominate the very wet parts. These wet patches frequently occur on the sites of former peat-cutting activities. The positions of such excavations are indicated by broken lines in Section 31, and are often angular in outline.

Fig.2

Diagram of Main Lines of Succession at Ballochraggan



PART 2

THE ECOLOGICAL FACTORS OF SOIL AERATION AND HYDROGEN ION CONCENTRATION IN RELATION TO BRACKEN AND HEATHER.

INTRODUCTION.

The experimental work on soil aeration arose out of observations made in the course of the survey of Ballochraggan, and from suggestions by Watt (1945) that this factor might be important in the relations between bracken and heather. The writer also considered the possibility of hydrogen ion concentration being a factor in this connection. As, however, he was employed as field ecologist, laboratory and greenhouse investigations were necessarily restricted. They have suggested a number of lines of physiological and ecological research, some of which the writer hopes to study in the future.

I. SOIL AERATION.

General Literature.

Even during the eighteenth century, Senebier (1791) had shown that the roots of plants died in stagnant water. Since then, many workers have demonstrated the necessity of adequate aeration for plant growth. Clements (1921) has provided a comprehensive account of the earlier work, and Miller (1938) gives a brief section on aeration in relation to the roots of plants, together with a full bibliography.

The study of soil aeration as a factor in plant growth owes much to the work of W.A.Cannon and his associates. It is to be regretted that the more recent work has been in the form of relatively small contributions from many investigators. Whilst these contributions have advanced our knowledge of this subject to some degree, no work compares with that of Cannon in volume or in devotion to detailed observation and experiment over a long period.

Livingston and Free (1915 and 1916) as co-workers of Cannon, studied the responses of a number of species to low oxygen concentrations and found wide variation in oxygen requirements. Attention was drawn to the ecological importance of this.

Cannon and Free (1917) confirmed

the variability of plants in response to this factor. In experiments on _Prosopis velutina_ and _Opuntia versicolor_, desert plants of Arizona, the plants were grown in glass tubes so that the soil atmospheres could be replaced by any gas or gas mixture, from cylinders. _Prosopis_ was found to be more tolerant of high partial pressures of carbon dioxide. Moderate aeration favoured branching of the roots and accelerated growth in _Opuntia_, but not in _Prosopis_. Experiments were also carried out on _Coleus_, _Heliotropium_, _Nerium_ and _Salix sp._. The soil atmosphere was replaced with mixtures of air diluted with nitrogen or carbon dioxide. It was found that resistance to low oxygen content increased in the order as given. Thus, in the case of _Coleus_, a small decrease in oxygen supply was speedily followed by injury and, ultimately, death, whereas _Salix sp._ grew normally in pure nitrogen for ten weeks. On this point, there is some disagreement in a subsequent publication (Cannon, 1920) where it is reported that _Salix_ continued to grow for more than seven days in commercial nitrogen (which was found to contain about 0.5% oxygen) but growth was arrested in pure nitrogen (obtained by passing the commercial product through alkaline pyrogallol). Rice, in this series of experiments, maintained growth for over thirteen days in commercial nitrogen. A species of

Juncus was the only plant to grow in pure nitrogen at all, yet it was one of the species inhibited in commercial nitrogen.

A full account of the experimental techniques has been provided by Cannon (1925) together with individual reports of the responses of many species to different conditions of oxygen supply. An account of work by Free on the use of helium in place of nitrogen as an inert gas for anaerobic experiments is also included.

The morphological changes in the root system attendant upon transference to different conditions of aeration have been studied by Cannon and Free (1920) and Weaver and Himmel (1930). The former worked on sunflower and maize. The result of transferring sunflowers previously grown in well-aerated soil, to soil treated with nitrogen was that the roots died and were replaced by new ones arising from the lower end of the stem. Such superficial roots were distinguished by being shorter, thicker, less branched and almost devoid of root hairs. The same type of root system developed when sunflowers were transferred to unaerated water culture. The significance of this in explaining the sparseness of root hairs in many swamp plants was noted. No morphological change occurred when maize was placed in soil treated with nitrogen, but the growth rate of the roots was reduced. Weaver and Himmel dealt with water plants (Typha, Scirpus, Phragmites and Spartina) grown in soils providing various degrees of aeration and water content, and found that in the poorly aerated cultures, superficial root systems developed from the lower ends of the stems. These were fine, white and greatly branching. In the cultures presenting the worst conditions of aeration, namely, the saturated, undrained ones, there was a depth of water standing above the surface of the soil, and, in this, the superficial roots ramified freely.

Bergman (1920) employed the experimental technique of submerging the pots containing the plants in water. The mesophytes so treated perished, but not if the water was aerated by a stream of air.

Beneficial effects of aeration in soil and water cultures were noted by Knight (1924). He also confirmed Bergman's observations that green algae in the light may produce sufficient oxygen for the requirements of the roots of plants growing in the water, or in culture solution.

Hall, Brenchley and Underwood (1914) and Allison and Shive (1923) also studied the effects of aeration on plants grown in water culture. They reported the superiority of the aerated plants in length and in profusion of the branching of the roots, in the rate of growth of roots and shoots, and in yield.

Bryant (1934) in experiments on barley, found that more roots were produced under unaerated conditions in water culture, but that they were much shorter and thicker than those of the aerated plants. There was an anatomical difference between the roots, the parenchyma of the aerated roots being distinguished by few air spaces. These were small compared with the large spaces of the unaerated plants. This anatomical effect of aeration has also been observed in maize by Beal (1918) and Andrews and Beal (1919).

Further information relating to the effect of aeration on the distribution of the root system in nutrient solution has been provided by Clark and Shive (1932) and Gilbert and Shive (1942). Once again, it was found that the unaerated roots were confined to the superficial layer of solution.

In studies on <u>Cladium mariscus</u>, Conway (1936) describes the development of cortical air spaces in roots growing in permanently waterlogged peat. Under such circumstances, the roots are thick, fleshy and little branching occurs. When in soil which is not permanently waterlogged, laterals are more frequent. If the roots reach the air, or grow in well-aerated water, the roots are no longer fleshy but fine with many laterals.

A valuable method of obtaining samples of soil atmospheres for gas analysis is also described.

The well-known view that the respiration of the underground parts of a hydrophyte is mainly supported by the passage of air down from the leaves and aerial stems, rested upon the assumption of continuity of the air spaces throughout the plant. Conway (1937) has been able to establish the fact of continuity by a technique involving the application of small suctions at various points. With regard to the resistance to the flow of air offered by the various plant organs, she concludes that, relative to their diameters, the roots offer less resistance than the rhizomes, because the stele in roots occupies a smaller proportion of the cross sectional area. The stele of the rhizome is large and, being mostly made up of fibres, plays very little part in the conduction of gases. Moreover, the old, withered leaves of Cladium are the main channels for the passage of air from the atmosphere to the roots and rhizomes for, in analyses of gas samples drawn from various tissues, Conway discovered that, providing the old leaf bases were irtact, a very much higher percentage of oxygen was present in the cortical spaces of the roots than in the external environment of the root system. In keeping with the essential role of the older leaves, if these were removed or blocked, low partial pressures of oxygen were encountered in the intercellular spaces of the roots, even when the medium of growth was well supplied with oxygen.

A useful review of the more recent trends in the study of soil aeration, is provided by Conway (1940). In this paper, attention is drawn to the probable importance of oxidation-reduction potentials and the consequent interdependence of aeration and hydrogen ion concentration.

(A) PTERIDIUM.

I. Review of Literature.

There are abundant examples at Ballochraggan of bracken overlapping marshes and swamps dominated by Juncus acutiflorus and Carex spp. This is a feature which can readily be observed in any area where bracken and badly-drained soils occur. The marginal zone is seldom more than about six feet wide. It is a fact that has long been known to the farmer as well as to the student of vegetation that bracken is prevented from spreading on encountering waterlogged soil.

R. Smith (1900a) reported that, in the Edinburgh district, bracken was much better developed on the sunny, dry, south sides of the Pentlands than on the ill-drained northern slopes.

Farrow (1915) stated that the fern

could advance anywhere except down the damper valleys. He suggested that, in the latter situation, the water-table would be high, and that, therefore, the bracken rhizomes would find themselves in stagnant water. In keeping with this view, it was noted that the vegetative advance was completely arrested by a small ditch. Incidentally, from this latter point, Farrow deduced that there is little reproduction by spores.

Jeffreys (1917a) also recorded the observation that bracken stops short at badly-drained soil. In the bed of a stream which was usually dry, he found the fern growing in Juncetum effusi, and he stated that the bracken could not have grown had the stream been permanent. Another aspect noted by Jeffreys was that bracken frequently failed to cross a footpath even when the latter was disused. The hardening of the soil by compression was given as the main cause, but it is relevant to a discussion of aeration that he suggested as a contributing factor the effect of lowering of the surface of the soil by continual trampling. He considered that the level of the path being lower than the surroundings would make the soil damper.

Braid (1934) has drawn attention to the frequent use of flooding in parts of Scotland in the past to check the spread of bracken. He considers the cessation of such practices, consequent upon the migration of rural populations to the towns and cities, to be a factor of importance in the great increase in bracken which has since occurred in the West of Scotland.

In the same paper, reference is made to bracken invading wet soil, when the outlying parts are maintained by connections with the adjoining Pteridietum. On drainage, such unhealthy bracken can become active and self-supporting. In other cases, an area of bracken may be "drowned out" by the raising of the water-table. When this condition is advanced, the fronds are very small, and juvenile in form. Excavation reveals the remains of rhizomes connecting the small, living fragment with what was once a large system. Attention is drawn to the fact that drainage will lead to the recovery of such vestiges, with subsequent invasion from those centres. Braid is unable to state with certainty that the "drowning out" he describes is due to poor aeration.

Watt (1945) states that on alkaline, waterlogged peat, all the bracken rhizomes may occur within two inches of the surface and, on such soils, the rhizome system is short. It frequently happens that rhizomes are limited in their downward penetration by purely physical barriers such as a layer of continuous hard rock, but often the obstacle is of a physiological nature, and aeration of the soil is probably an important factor in this connection. Watt also recalls that the fern is absent from heavy clays (especially if waterlogged in winter, even if only at long intervals) Nardeta, rush "flushes", and bogs. Rhizomes invading such soils are shallow.

2. Field Observations and Experiments.

(a) Excavations.

Many examples have been observed at Ballochraggan of small, apparently isolated patches of bracken in *Caricetum vulgaris* and *Juncetum acutiflori*. They are frequently associated with stones. The inference is that these patches were formerly part of the nearest mass of bracken, but that impeded drainage led to the margins of the Pteridietum becoming marshy, with subsequent encroachment of the *Carex* and *Juncus*. The bracken area became broken up into fragments by the dying-off of most of the rhizome system. The possibility existed that these fragments had not been derived from pre-existing Pteridieta, but had developed from spores. In order to gain conclusive evidence on this point, and to study the underground parts of such islands of bracken, an excavation was made of a typical example.

The site of the excavation is in Section 5, Square 4, 130, 80. The main mass of *Pteridium* in *Agrostis-Festuca* lies to the north and

Fig.3. The site of the excavation of <u>Pteridium</u> rhizomes in Section 5, Square 4. The underground sys: :tems were excavated between the walking stick and the spade handle.

east, forming a bay round very wet soil dominated by various species of _Carex_. The wetness of this area was aggravated during the summer of 1947 (when the excavation was made) by water overflowing from the nearby irrigation experiment. As will be seen from Fig. 3, the Pteridietum slopes down noticeably into the _Carex_ area. About six feet from the nearest point of the Pteridietum, is a small stone which, at the time, was covered almost completely by a felt of grass, mainly _Festuca ovina_. At the sides of this stone arose a few small fronds which seemed to indicate a very poor rhizome system below. The felt of grass was carefully removed and one or two short branch rhizomes were found growing against the upper surface of the stone. They were markedly flattened and lighter in colour than the rest of the system. The sides of the stone were embedded in the soil, which consisted of a malodorous mud. The rhizome system in the mud was found to be composed of a few compact clumps connected together. These clumps were closely pressed to the surface of the stone (the sides of the latter being flat) were in a healthy condition, and bore many branches and frond buds. Fig. 4 shows the clumps and Fig. 5 is a diagram of the whole system excavated.

Several rhizomes disappeared further into the swamp to the left of the walking-stick

Fig.4. Section 5, Square 4 excavation. Three clumps of Pteridium rhizomes from the sides of the largest embedded stone.

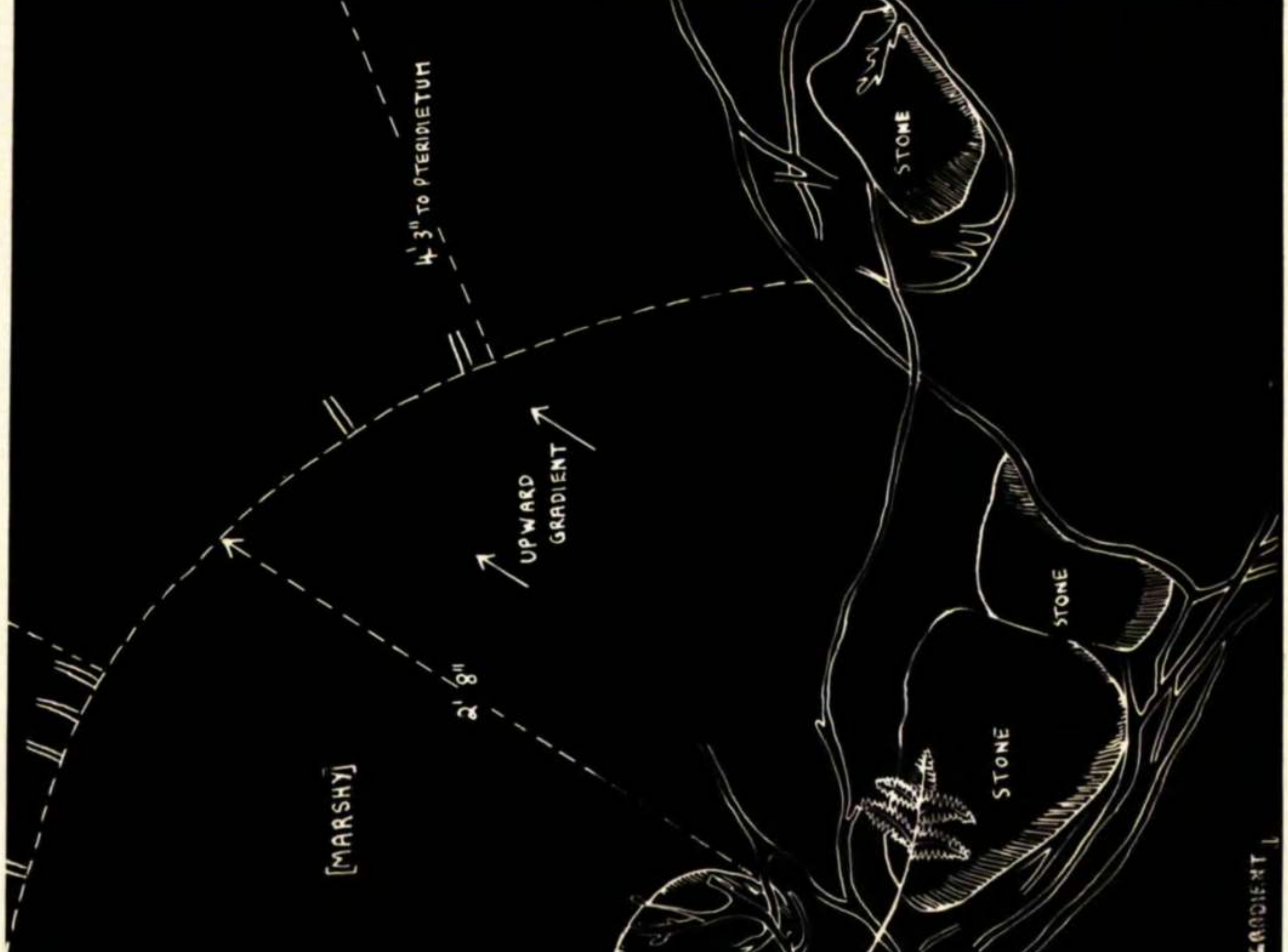


Fig.5. Diagram of the Section 5, Square 4 excavation.

in Fig.3. Lack of time prevented their courses being traced in full, but it is certain that only one penetrated any distance. The severed end of this was seen in the wall of a drain just off Fig.3 to the left.

Between the stone and the spade-handle in Fig.3, one or two smaller islands of bracken, each consisting of a few very minute fronds, were observed. The soil on this side is drier than elsewhere, and rhizomes were traced back from the clumps round the stone, linking up the tiny islands and continuing on to join the main Pteridietum. It is probably significant that each of the small patches was centred about an embedded stone.

In order to discover any other rhizomes connecting the main island with the Pteridietum, a semi-circular trench was dug. Six more rhizomes were revealed. All of these occurred in the drier half of the trench; no rhizomes, not even rotted remains, were found in the wetter part.

Two subsidiary excavations were made in other marshy situations. At Section 23, Square 2, 150, 193, a small clump of bracken was found in Juncetum acutiflori. The mature fronds arose from a low tussock of Molinia and Nardus. Excavation showed the base of this tussock to be composed of dead Sphagnum in which was embedded a profusely-branching rhizome system, rich in frond buds. This, presumably, had been derived by proliferation of lateral branches from the main leader rhizome connecting the patch, and other more distant patches, with the Pteridietum. A second leader existed, but this had rotted away at one point, thus breaking the connection.

In Section 10, Square 12, there is a Caricetum with small, scattered patches of bracken. The patches are slightly raised above the general level of the Carex. Similar examples of this were found elsewhere on Ballochraggan.

In each of the cases of small groups of Pteridium fronds apparently isolated in Juncetum or Caricetum investigated, it has been shown that a well-branched rhizome system frequently exists below ground level, that the branches are short, near the surface, and usually well supplied with developing and latent frond buds. These networks are invariably connected to the nearest Pteridietum by one or more rhizomes which tend to run at a lower level than the frond-bearing clumps. Furthermore, in one case, the clumps were associated with embedded stones; in another, the maximum rhizome branching and frond production was in a relatively dry, loosely-packed mass of dead Sphagnum. In the third case, the fronds always arose on slightly raised patches of ground. In short, the frond-producing rhizomes were found in those situations where one might expect better conditions of aeration. Crampton (1911, p.60) noted that the Calluna moor vegetation in Caithness underwent a change in composition in the neighbourhood of rocks isolated in the peat. The rocks were of such a nature that no chemical influence could have been involved, and he attributed the change to better drainage. Bracken was sometimes found to spread from such centres, the heather being subsequently destroyed by the fern.

It is evident that, far from being almost extinct, these small patches of bracken have great potentialities for growth, as judged by the number of frond and rhizome buds. Drainage of marshy areas could stimulate the buds to expansion and elongation with the result that a rapid spread of bracken from these centres could occur. The excavations made confirm the observations and conclusions of Braid referred to above.

(b) Irrigation Experiments.

Eradication of bracken by irrigation has been advocated (McTurk, 1837, and Murray, 1837) for upland pastures well-supplied with springs and streams. The effect of alkaline spring waters on hill pasture vegetation (but excluding bracken) has been reported by Smith (1916) and

Heddle and Ogg (1936). The raising of the soil pH, and superficial aeration were given as probably being the main factors involved. There have been no quantitative investigations of the effect of irrigation on soil aeration, in so far as the present writer is aware.

Ballochraggan is very rich in natural water supplies. The numerous springs and streams are a feature of the area which the maps show particularly clearly. A pH survey of these water supplies was carried out in 1947, and it was found that most springs and streams gave a reaction around pH 7.0-7.2. The range encountered was from pH 6.5 to 7.6.

The following experiments were carried out in the belief that the main effect of irrigation is on the oxygen supply in the soil. Puddling of soil involves the replacement of the soil air by water. If, however, spring water of high dissolved oxygen content flowed continuously through the soil, reasonably good conditions of oxygen supply might still exist. In point of fact, this does not occur except in the most porous types, and the latter are not found at Ballochraggan. Once the soil is puddled, most of the subsequent water flows freely over the surface, and movement of water lower down must be very slow. Thus, low values for dissolved oxygen result.

During the summer of 1947, two experiments were commenced to study the effects of irrigation on vigorous Pteridietum.

I. Section 5, Square 4 (by the stone at 110.90)

I. Section 5, Square 4 (by the stone at 110.90).

On May 15th, two one-yard quadrats were pegged out in Pteridietum. One of these was irrigated continuously with water from the nearby stream, conveyed by iron pipes and a shallow channel. The second quadrat was left untreated to serve as a control. Before commencing irrigation, the positions of the 1946 frond stumps (bracken on the area had been cut in 1946) were plotted for each quadrat.

Within a week, more young fronds were arising in the irrigated quadrat than in the control. They were also more advanced. This could be attributed to the temporary stimulus to growth of increased water supply.

After seven weeks, the lower side and centre of the irrigated quadrat was found to be almost devoid of fronds. The largest frond in the quadrat was broken at the isthmus, and was leaning over. This might have been due to crushing by animals, but there was no evidence of trampling nearby. The fronds showed signs of yellowing, although this was more marked and widespread in the area between the quadrat and the *Caricetum vulgaris* into which the water from the quadrat drained. Even clumps of bracken fronds round stones out in the marsh, formerly healthy, were dying. This effect may have been brought about by a general raising of the water-table in the Caricetum, caused by the continual flow of water from the quadrat.

By the middle of the 1948 growing season, the difference between irrigated and control quadrats had become even more pronounced. The former bore no fronds at all. Many of the grasses had disappeared, and it was noticeable that _Carex vulgaris_ had spread up from the marsh to within three feet of the quadrat.

The fronds were cut and the stumps plotted and counted in the Septembers of 1947 and 1948.

Table I. Comparison of Numbers of Fronds in Irrigated and Unirrigated Quadrats

Quadrat	No. of Fronds		
	1946	1947	1948
Irrigated	50	24	0
Unirrigated	55	48	37

Two factors may be involved in the decreasing number of the fronds in the control quadrat. In the first place, the area has been subjected to bracken cutting and secondly, the choice of site for the control was unfortunate in so far as, being at a lower level, it was liable to seepage of water from the channel serving the irrigated quadrat. The water supplied to the experimental quadrat was found to have a pH reaction of 7.2. It will be shown in a later section that such a reaction is not favourable to bracken, but a pH change of this order would not account for the rapidity with which the adverse effects of irrigation make their appearance.

Another factor which might explain the results is a difference in soil temperatures. It is to be expected that irrigation with spring water might lower the soil temperature considerably. Temperatures were accordingly measured at six inches below the surface. No difference was found, both soils being at 13 deg.C.

2. Section 18, Square 11(near the stone at 110.18).

The area was selected in the first place as an example of an overlapping zone of bracken and heather which was at such a level in relation to the nearby stream that the latter could be deflected on to the margin without difficulty. Between the heather area and the Agrostis-Festuca grassland dominated by Pteridium, is a strip about ten feet wide where Nardus and Deschampsia flexuosa are the dominant grasses, and where the bracken is sparse with denser patches of fronds occurring. Sparse bracken penetrates into the heather area to distances varying from six to ten feet along the line of invasion.

The stream water was led by a shallow channel into the easterly end of the zone of overlap. In cutting the channel, it was noticed that, in a small patch of marshy grassland, bracken rhizomes were present in the soil (no fronds being in evidence) and that such rhizomes were in most cases rotted and dead. In the drier soil to both sides of the marshy strip, the rhizomes were perfectly healthy. From its point of entry to the area, the water flowed westward through the marginal zone, and also through the adjacent Nardus-Deschampsia flexuosa containing bracken. It finally drained into the Juncetum acutiflori in Square 10.

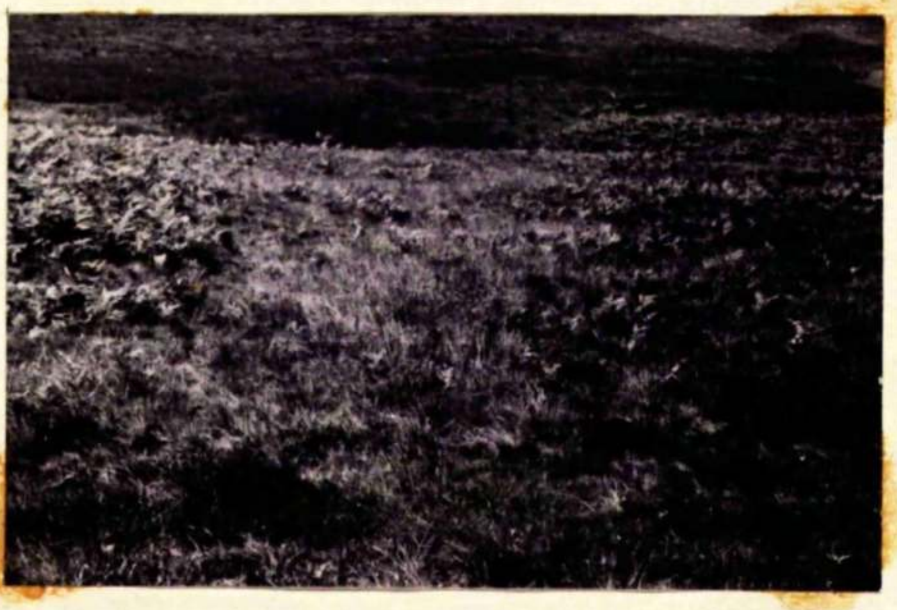


Fig.6. Irrigation experiment in Section 18, Square 11 from the stone at 110-18, looking westward. Irrigated Pteridium in the centre, irrigated Pteridium and Calluna on the right, unirrigated Pteridietum on the left. Juncetum acutiflori in the background.

Fig.7. Irrigation in Section 18, Square 11 from the _Juncetum_ _acutiflori_ area, looking eastward. Irrigated _Pteridium_ in the centre. Unirrigated Pteridietum in the left background.

Fig.8. Irrigation in Section 18, Square 11, showing the stunted form of new fronds arising in the irrigated zone.

Irrigation commenced on May 21st 1947. By July 14th, many fronds in the irrigated section were dead, and the line of demarcation between irrigated and unirrigated became progressively more clearly defined (Figs. 6 and 7). The area of dead fronds was far more widespread towards the Juncetum owing to the decreasing slope of the land with consequent spreading of the water. Fronds which arose after the commencement of irrigation were small (Fig.8).

Estimations were made of the oxygen dissolved in the soil water at several points, by means of the syringe pipette described later and shown in Fig.10. The method of collecting the water sample was, firstly, to cut off the water supply of the irrigation, and then to excavate a small hole at the point of sampling. This was allowed to fill by seepage from the soil. The results are shown below.

<u>Table 2. Dissolved Oxygen in the Soil Water after Irrigation.</u>

Site of Sample	Tempr. (deg.C.)	Dissolved Oxygen (ml/l. at N.T.P.)
1) Patch of dense fronds (nearly all dead)	11.0	5.51
2) Heather-bracken	-	6.89
3) Edge of *Calluna* area	10.6	4.58
4) *Nardus* area adjoining	11.0	5.85

These oxygen values are no doubt greatly in excess of the actual quantities of oxygen present in waterlogged soils, which are probably almost nil. The mode of collecting the sample is open to criticism on the ground that there is no guard against exposure to the oxygen of the air. Nevertheless, the figures indicate that irrigation does lead to oxygen values which are well below equilibrium. According to Winkler (quoted in the "Chemists' Yearbook") the figure for dissolved oxygen in equilibrium with the air at 11°C. is 7.69 ml/l. at N.T.P.

In making the sampling holes for the estimations in Calluna and Nardus soils, the writer was surprised to find that, whereas water appears to penetrate fairly freely into the bracken soil, the soil below the superficial two inches of peat was quite as dry as is usual for that type of soil, even though water had been flowing continuously over the surface for four months. It would thus appear that peat can act as an impervious layer. Low partial pressures of oxygen might be expected in the lower soil, although not saturated with water, as the layer of waterlogged peat and the stream of water on the surface will isolate the soil atmosphere from the air above.

Bracken rhizomes excavated from the irrigated zone showed that in four months, the underground parts did not appear to have been seriously affected. It seems that on irrigation, the bracken plant very quickly finds itself unable to maintain even a few fronds. These soon become diseased, and die off. The time required to produce signs of disease in the rhizome is not known, but it is certain that prolonged irrigation would be necessary to bring about complete eradication of the fern by this agency.

(c) Experiments involving Stagnant and Spring Water.

The irrigation experiments, while lending some support to the view that aeration is the main factor involved, did not enable the relative effects of water poor in dissolved oxygen and water containing oxygen in equilibrium with the air to be separated. A direct comparison of growth under these conditions was clearly desirable.

Two rectangular baskets of dimensions 18" X 8" X 3" were constructed of ½" mesh wire netting. Sods containing strong bracken were cut from the area on the west side of the main stream in Section 1. This bracken had never been cut, having been reserved as a control against which to assess the effects of bracken cutting. Care being taken to disturb the soil round the rhizomes as little as possible, the sods were transferred into the wire baskets. At this stage, expanding fronds about one foot high were present, but these subsequently died off, and the baskets were left in a shady, damp place until new fronds had been produced.

By this time, two rectangular holes had been dug in Section 2, Square 3, one in the centre of a spring, the other in boggy soil a few feet away where the water-level was at the surface. One basket was submerged in each of the holes. The one containing the more vigorous plant was placed in the stagnant water.

On July 9th, the date of submergence of the baskets, the plant in stagnant water bore three fronds, one of which was about twelve inches, the second, four inches and the third, one inch high. The latter two were totally submerged, as were a number of buds pushing above the surface of the soil. The large frond had a very small dead patch, probably caused by late frosting.

The bracken in running water possessed but two fronds, seven inches and three inches high. In addition, a few buds were appearing. The smaller frond was completely submerged.

The temperatures of the water in both cases were measured, and also those of the adjacent soil. The figures are shown in Table 3.

Table 3: Temperatures of Bog and Spring Water, and of Soils in Contact. (Measured 9/7/1947)

A) Water Temperatures (°C.)

Bog Water	Spring Water	Difference
15	8	7

B) Soil Temperatures (°C.) at 10 ins. depth

Adjacent to bog water	Adjacent to Spring Water	Difference
13	10	3

This difference in water temperatures is far greater than was anticipated and would have a marked effect on the quantities of dissolved oxygen, apart from any direct effect on the rate of plant metabolism.

On July 17th, the dead patch on the large frond of the plant in bog water was greatly extended, the frond showing a tendency to wilt. Submerged fronds were unhealthy in appearance. In the case of the plant in spring water, the larger frond was still perfectly turgid and, although submerged, the smaller frond was also quite healthy.

A week later, the browning of the frond in stagnant water was general. The larger of the submerged fronds was similarly affected. The plant in the spring was still healthy. The large frond was of a good green colour, and turgid, although there were a few dead pinnule tips near the forking. The small, submerged frond was covered with floating scum but, on clearing, was seen to be green and turgid, if somewhat translucent due to soaking with water.

By Aug. 7th, the plant in bog water was dead, and the larger frond in running water was dying. It was noted that the latter had become abnormally hard and rigid. The submerged frond was still alive and, indeed, had expanded slightly. Both fronds in the spring were found to be dead on Sept. 23rd.

On Sept.15th, 1948, the baskets were removed from the water and the rhizomes examined. In the case of the basket in bog water, relatively few rhizomes were found, and many of these were rotten. Numerous rhizomes occurred in the basket in the spring water, although no fronds had appeared during the 1948 season. The rhizomes in the upper levels were healthy, in general, but many of those lower down were rotten and fragmented.

Estimations of dissolved oxygen were made on Sept.23rd, 1947, by means of the "micro-Winkler" syringe pipette (Krogh (1935) and Fox and Wingfield (1938)).

Table 4: Oxygen Dissolved in Bog and Spring Water.

	Temperature (°C.)	Dissolved Oxygen (ml./litre at N.T.P.)
Bog Water	9.5	5.18
Spring Water	9.5	6.80

(Winkler's value for dissolved oxygen in equilibrium with air at 9.5°C. is 7.87 ml/l at N.T.P.)

It will be noticed that, on this date, the temperatures of the two waters were identical. It is possible that the marked difference recorded previously was largely attributable to heat given out in the catabolic processes of the roots of the bog plants being absorbed by the small volume of stagnant water. On this basis, the temperature of the bog water would fall with the approach of autumn, owing to the decline of plant activity. The abundance or otherwise of micro-organisms in the stagnant water might also have contributed to this effect. On both the days when temperatures were measured, cool, cloudy conditions prevailed, so that heating of the still water by the sun was precluded as a cause of the temperature difference.

With the temperatures equal, the difference in dissolved oxygen concentrations is considerable, although even the spring water is below the equilibrium value given by Winkler.

This latter fact may account for the failure of the plant in spring water to produce fronds in the second year. When there is a marked temperature difference between the two waters, the values for dissolved oxygen will be considerably more widely separated.

This experiment justifies the conclusion that a superabundance of water is only fatal to bracken when stagnation occurs. On the other hand, in spring water the oxygen dissolved, while sufficient to support life for some time, is inadequate for active growth of the fern. Thus, in several streams in the upper region, the writer has found rhizomes, which have penetrated from adjacent bracken areas, living in the gravel of the stream beds, or against submerged stones, and bearing a few fronds. Reference has been made to the observation of Farrow (1915) that a small ditch arrests the spread of bracken. When, however, the water flows rapidly, the rhizomes are able to enter. Although the present writer has not so far encountered a case, there appears no reason why, in some cases, they should not ultimately reach the opposite bank and, if the ground is devoid of bracken and soil conditions are suitable, become new centres of invasion.

3. Greenhouse Experiments.

Further inquiry into this problem demanded experimental work under more closely controlled conditions in the greenhouse. Preliminary experiments involving the growing of young *Pteridium* plants in water culture under conditions of aeration, absence of aeration, and passage of nitrogen had been carried out by the writer in the Botany Department, Glasgow University, during the 1946 season. Although these yielded much useful information regarding the problems of growing bracken in a watery medium, the results were inconclusive in assessing the role of aeration. Later experiments were performed in the greenhouse at the West of Scotland Agricultural College.

(a) Water Cultures.

Cultural Arrangements.

Young Pteridium sporophytes were grown in water culture. The solution in some of the jars was aerated, another set was left unaerated, and nitrogen was bubbled through a third group to provide low oxygen tensions.

The culture vessels used were earthenware or glass jars, mostly of 750 ml. capacity, although a small proportion of 350 ml. jars had to be employed because of shortage of the larger ones.

The glass jars were given two coats of black paint externally prior to use to exclude light.

Squares of sheet composition cork of 4 ins. side were used to support the plants, and to carry the glass aeration tubes. A half-an-inch diameter hole in the centre of the cork, and a smaller one towards one side, were bored for the plant and tube respectively, there being only one plant per jar. The cork squares were then impregnated and coated with paraffin wax.

The Growth of Sporelings.

The plants were very young sporophytes in their first year of growth, derived from spores sown late in 1946. The "moist pot" method, used with great success at Glasgow University, was adopted for the germination and subsequent development of bracken spores. Two unglazed pots, differing by an inch or two in diameter, are fitted one inside the other, and the space between packed with *Sphagnum*. The double pot is placed standing in a saucer of water and the mouth covered with a plate of glass. The inner wall thus becomes moistened, and the air saturated. Spores are sown on this moist surface by means of a brush. When the young sporophytes have produced a few small fronds, they are transplanted into good soil in individual pots. These pots must still be covered. Small perforated bell-jars, their upper apertures plugged with cotton wool, have been found most suitable, as they allow the fronds to develop upwards without hindrance. When the plants have a number of juvenile fronds two or three inches long, they are usually suitable for transference to culture solution. At this stage, they will possess a few roots, varying in size, the longest being one inch long. Great care is necessary in extracting the plants from the pots. Running water and a brush are required to remove soil clinging to the roots. It is essential that the soil be removed as completely as is consistent with the greatest care in keeping the roots intact, since slimy moulds are liable to develop in the early stages of growth in nutrient solution. This is most marked when many particles of soil have been left attached.

<u>Conditions for Successful Transference to Water Culture.</u>

The young sporophytes were carefully supported in the holes in the cork squares, by means of cotton wool. The level of solution in the jars was maintained very near the cork at first, as the roots were short. This was permissible at this stage as aeration was not commenced until the plants were well established, and had produced some new roots. During aeration, the level had to be lower so as to keep the cotton wool dry. Moistening of the cotton wool, in which are the expanding buds, greatly favours the development of algae and fungi. Botrytis and Trichothecium play havoc among these young plants under such conditions, and are encouraged by the saturated atmosphere which it is necessary to maintain around the juvenile fronds. The early fronds of the young sporophyte are very thin and, unlike the mature ones with their shiny upper surfaces, have no protection against the effect of contact with dry air. Most of the culture jars were placed in a "moist chamber" constructed of a suitable wooden framework with glass plates for walls and roof. This is shown in Fig.9, which is a general view of the water culture arrange: :ment. In this moist chamber, the aerated and unaerated series were accommodated; the nitrogen series had to be placed in a frame on the floor of the greenhouse. In both cases, a saturated atmosphere was maintained, and attempts to "harden off" the plants, by separating the plates of glass gradually, led to shrivelling.

Nutrient Solutions.

Several experiments were made in 1946 to arrive at a suitable nutrient solution for Pteridium. The first solution used was Tottingham's

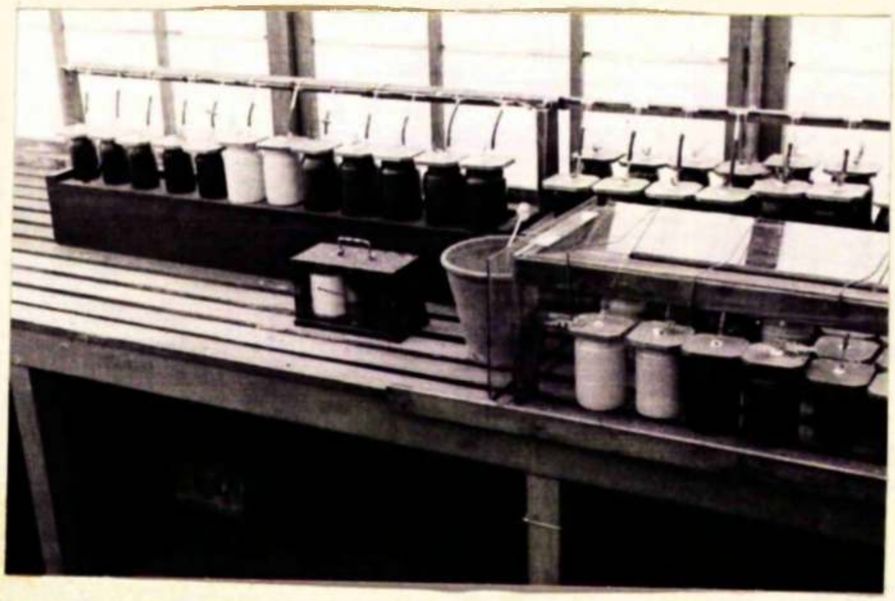


Fig.9. The arrangement of the water culture aeration experiments in 1947. The *Pteridium* cultures are in the glass cloche, the aerated series being in front. The aerated *Calluna* plants are immediately behind the cloche, with the unaerated *Calluna* series in the background. On the left is the *Calluna* series treated with nitrogen.

"T3RIS4" variant of Knop's well-known formula (Miller, 1938, p.242) used at one quarter strength. For ferns, a more dilute solution than for angiosperms is usually recommended. Iron was added in the form of a ferric phosphate suspension (Miller, 1938, p.242). In this solution, the fronds were chlorotic and, believing that this might be due to excessive calcium, various modifications of the original formula were made in the direction of decreasing the calcium nitrate. Proportionate increases in potassium nitrate compensated for loss of nitrate. The solution finally adopted was one in which the calcium nitrate was one quarter, and the potassium nitrate twice that in the original formula. Growth in this "1/4 calcium" solution, as it can be conveniently called, was good, and the chlorosis of the fronds not so marked as before. It appears, however, that the juvenile fronds of bracken growing in water culture are characterised by a tendency to a pale green colour. In a given set of cultures, some of the plants might exhibit this slight chlorosis, while others are normal in colour.

Arrangement for Aeration.

Each of the three series of cultures contained eight jars. Air was supplied to the jars in the aerated series via capillary tubes connected to a chain of T-pieces, and thence to an electric compressor pump. The quantity of air delivered by this pump was greatly in excess of that required to give a moderate rate of bubbling through the various jars, and the surplus was allowed to escape through the straight limb of a Y-piece, inserted close to the pump exit. The rate of bubbling could be adjusted by means of a screw clip on this escape tube, which also served to drain off the majority of the lubricating oil carried over from the pump. Further traces of oil were removed by passage of the air through a bottle packed with cotton wool, and cooled by immersion in a tank of water. Variations in the rates of bubbling from jar to jar could be levelled off by screw clips on the tubes to individual jars.

This method of controlling the air delivery from the pump, and removing excess oil and oil fumes, is the one employed at Glasgow University.

The Determination of Dissolved Oxygen.

Krogh (1935) and Fox and Wingfield (1938) have described apparatus whereby Winkler's method for the estimation of oxygen dissolved in water and aqueous solutions might be adapted for small samples. In these "micro" methods, the various chemical reactions take place inside the barrel of a syringe pipette, thus reducing contact with the atmosphere to a minimum.

The syringe pipette used in the present investigations was constructed by the writer, and is shown in Fig.10. Modelled on Krogh's instrument, it consists of a 20 ml. hypodermic syringe, with a rectangular brass framework securely attached to the barrel. A slot had been drilled in one of the sides of this attachment, and a small metal angle piece is held by means of screw and nut through this slot. It can be fixed tightly at any desired position within the length of the slot. The angle piece carries a short strip of metal attached by screw and nut, so that the strip can be moved in a plane at right angles to the framework. In position, the strip acts as a stop preventing further withdrawal of the ground-glass plunger. When this stop is swung to one side, the plunger can be drawn to the second stop, which is a relatively long screw fitted in the top of the framework. The final position of the plunger can be varied by means of this screw. A length of capillary tubing is attached to the syringe in place of the hypodermic needle.

The procedure (based on that of Krogh) is as follows. The "dead space" of the syringe (that is, the bore of the capillary tube plus the space between the bottom of the barrel and

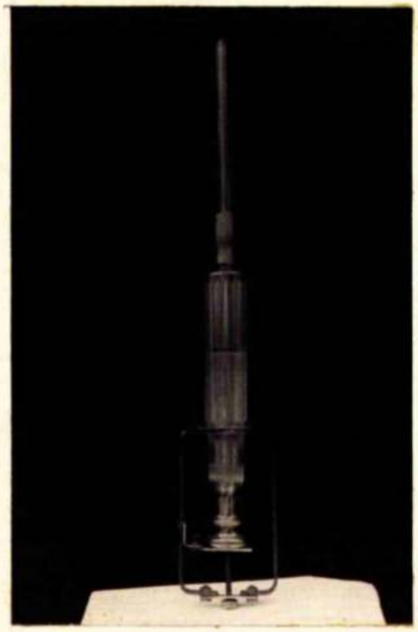


Fig.10. The writer's "micro-Winkler" syringe pipette, used in the determination of dissolved oxygen.

the end of the plunger when the latter is fully depressed) is filled with a 45% manganese sulphate solution. Taking care not to introduce any air into the end of the capillary tube, a sample of the solution is drawn in by raising the plunger to the first stop. This stop is then swung to one side and, with the tube dipping into a solution containing 33% caustic soda and 10% potassium iodide, the plunger is raised to the second stop, the latter being screwed down to its limit. The syringe is shaken and allowed to stand for a few minutes. Meanwhile, a few ml. of pure hydrochloric acid (free of chlorine) are placed in a 100 ml. beaker. After the period of standing, the end of the capillary tube is wiped and, by unscrewing the second stop three turns, the acid is drawn into the barrel. The syringe is shaken and, liberation of iodine being complete, the contents are discharged into the beaker containing the surplus acid. The barrel is then washed out twice with distilled water, and the iodine is subsequently titrated with standard sodium thiosulphate (approximately N/100) in a 2 ml. micro-burette. Exposure to the air after acidification has no effect, as the reaction with oxygen only occurs in the alkaline medium.

In order to calculate the quantity

of dissolved oxygen, it is necessary to know the precise volume of the water sample. The graduations on the syringe barrel are useless for this purpose. The volume of the sample is equal to the volume of the syringe with the piston at the first stop, minus the dead space. These quantities were determined by the writer for his syringe pipette according to the method described by Fox and Wingfield (1938) which is as follows. The syringe is filled with a standard potassium iodate solution, by drawing the piston to the first stop. The contents are discharged into a suitable vessel for titration, the syringe being rinsed out twice with distilled water. 1 ml. of 1% potassium iodide solution and three drops of phosphoric acid are added and the iodine liberated is titrated by means of standard sodium thiosulphate solution. The volume of the syringe barrel plus the "dead-space" is calculated from the titration result. The volume of the dead space alone is determined similarly. The dead space is filled with the standard potassium iodate, which is then drawn up into the barrel with distilled water and discharged into the titration vessel, with subsequent rinsings. The iodate is estimated by titration as before and the volume of the dead space calculated. The volume of the water sample is the difference between the two volumes determined.

In the later estimations of dissolved oxygen, certain modifications of the method were made. Because of the dead space containing manganese sulphate solution which would contaminate the culture solutions, the sample could not be drawn directly from the jars. It was necessary to siphon off a quantity into a small bottle first. The agitation and exposure of a small volume of water to the air are obvious sources of error. Dr. Bond, of Glasgow University, suggested the following procedure for overcoming this difficulty. The dead space is filled with water of known oxygen content. This is obtained by filling a trough with water, allowing it to stand for a day and measuring its oxygen content as above prior to each set of determinations. The sample can then be taken directly from the culture jar, drawing the piston up to the first stop. The manganese sulphate solution is introduced by drawing the piston to the second stop, and alkaline potassium iodide solution by raising the screw three turns. After the reaction is complete, a further three turns enables the acid to be drawn in.

Hydrochloric acid suffers from the disadvantages that firstly, it is difficult to obtain and keep it free of chlorine and, secondly, the fumes are troublesome. Fox and Wingfield (1938) used phosphoric acid. This has neither of the above drawbacks and was used in the more recent work, although its high viscosity necessitates caution in drawing it into the syringe to avoid leakage of air down the sides of the plunger.

It is necessary to apply a correction for the oxygen dissolved in the reagents, and this was calculated from the data given by Krogh (1935) that 3.4 ml. of oxygen are present per litre of reagents. The figures given in the various tables are the corrected ones.

In estimations made by the Winkler method, precautions must be taken to ensure that the solution to be sampled is free of nitrites. If nitrite is present, further iodine is liberated, and it is impossible to obtain a satisfactory end-point in the titration. In the earlier stages of the present work, nitrite was detected by acidifying a sample of solution from the jar with 1 ml. of concentrated sulphuric acid and adding sufficient N/10 potassium permanganate solution to give a pale pink colouration. Disappearance of this colour was taken to indicate the presence of nitrite. This test is not specific for nitrite, and would give a positive reaction in the presence of other reducing agents which the sample might contain.

More recently, the α-naphthylamine and sulphanilic acid method of qualitative test and quantitative estimation of nitrite (Cumming and Kay, 1945, p.469) was employed in some cases.

To remove the nitrite, potassium permanganate is added until a permanent pink colour is obtained. At this stage, all nitrite has been oxidised to nitrate. It is then necessary to destroy the excess permanganate and this is achieved by adding sufficient 2% potassium oxalate to decolourise the solution. This is the recognised method for ensuring a nitrite-free sample in the standard Winkler procedure (Cumming and Kay, 1945 p.465). The present writer did not attempt to introduce the oxidising reagents into the syringe but, if nitrite was present, the contents of the sampling bottle were treated.

No correlation was found between nitrite content and culture treatment. Within a series, wide variation occurred.

Standard sodium thiosulphate solution slowly decomposes on storage, especially at high dilutions, even when kept in a dark blue bottle. Initial and subsequent standardisations were carried out against standard cupric sulphate solution (Cumming and Kay, 1945, p.148).

Results for Aerated Series.

Aeration was commenced on July 18th,

1947, and was continuous thereafter. Three weeks later, rhizomes were developing in nos.1, 2, 3, 4, and 8. No.5 was dead due to evaporation having lowered the level of the solution below the very short roots. Luxuriant roots were present in nos.1 and 8.

On September 9th, that is, after the experiment had been running nearly nine weeks, the plants were harvested as both aerated and unaerated series were threatened by Botrytis and Trichothecium.

Table 5: Data relating to Root, Rhizome and Frond Lengths, and Number of Fronds for Bracken in Aerated Water Culture.

Plant No.	Max. Length of Roots (cms.)	Length of Rhizome (cms.)	Max. Length of Fronds (cms.)	No. of Expanded Fronds	No. of Buds & Developing Fronds
1	25.1	2.5	17.0	5	9
2	24.3	2.5	9.3	6	13
3	31.1	4.9	14.3	5	11
4	11.9	2.5	5.1 *	1 *	3 *
5	(dead)				
6	14.8	1.2	10.4	5	6
7	2.7 *	1.0	-	1 *	6
8	28.7	4.3	16.5	8	16
Means:	22.6	2.6	13.5	6	10

(* - omitted from mean)

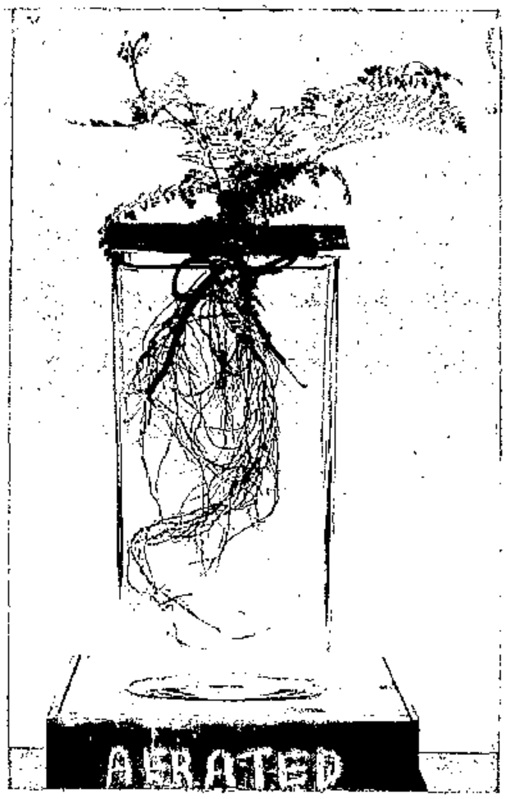


Fig.11. *Pteridium* plant from aerated water culture (1948).

Fig.11 shows the condition of an aerated plant. It is a photograph of a plant aerated in 1948, as the negatives of the 1947 series were unsatisfactory. The only difference in the conditions of growth was that in the more recent experiment, the plants were so orientated in the cork that the rhizomes developed in the culture solution. When below the cork and, therefore in the dark, elongation and branching of the rhizome system was considerable. In the 1947 plants, the rhizomes were short, as indicated by the appropriate figures in Table 5. The great development of the root system was the most notable feature of the aerated plants. There was no appreciable proliferation of roots at the surface of the solution, or in the moist air beneath the cork. The long roots produced in aerated nutrient solution were almost golden in colour, very different from the dark brown roots appearing under soil conditions. The main roots and branches terminated in swollen tips.

Further numerical data on the aerated series appear in Table 6 below:

Table 6: pH, Temperature and Dissolved Oxygen-Content of Solutions, and Dry Weights of Bracken in Aerated Water Culture.

Plant No.	pH of Soln.	Tempr. of Soln. (°C.)	Dissolved Oxygen(ml/l at N.T.P.)	Dry Wt. of Roots and Rhizomes (mgms.)	Dry Wt. of Fronds (mgms.)
1	6.23	11.5	7.67	58.4	164.2
2	6.31	11.2	7.31	49.8	83.0
3	6.48	11.2	7.72	148.8	181.4
4	6.62	11.4	7.89	37.8 *	7.2 *
5	(dead)				
6	6.36	11.3	7.96	36.8	64.5
7	6.42	11.2	7.80	15.6 *	8.3 *
8	6.70	11.2	7.63	115.8	244.3
Means:	6.44	11.3	7.70	81.5	147.5

(* - omitted from mean)

(Winkler's value for dissolved oxygen in equilibrium with air at 11°C. is 7.69 ml/l. at N.T.P.)

(Ratio of mean dry wt. of roots and rhizome to mean dry wt. of fronds - 1 : 1.8.)

Plants 4 and 7 were weakly at the start of the experiment and never really became established.

The figures for dissolved oxygen bear no relation to the maximum length and dry weight of roots. This is to be expected when aeration is continuous; the air supply is at all times ample to maintain the oxygen dissolved at the equilibrium level, while fulfilling the respiratory demands of the roots.

Results for Unaerated Series.

This series was also set up on July 18th, 1947. Three weeks later, the root systems were not so good as those of the aerated plants at the same stage.

Harvesting of this series took place on September 9th, 1947, and some of the results appear in Table 7.

Table 7: Date relating to Root, Rhizome and Frond Lengths, and Number of Fronds for Bracken in Unaerated Water Culture.

Plant No.	Max. Length of Roots (cms.)	Length of Rhizome (cms.)	Max. Length of Fronds (cms.)	No. of Expanded Fronds	No. of Buds & Developing Fronds
1.	9.6	2.7	17.5	3	8
2	5.0	4.3	9.5	4	6
3	3.4	1.3	7.3	3	8
4	7.9	2.8	13.0	4	7
5	3.0	1.0	6.0	1	3
6	4.7	4.1	11.5	3	11
7	9.4	4.0	6.6	2	12
8	10.8	2.5	7.4	7	17
Means:	6.7	2.8	9.8	3	9

As can be seen from Table 7, and from the plants depicted in Figs.12 and 13, the roots of this series were distinguished by being short and "bunched". Plant 4 was the best, as judged by dry weight of fronds, yet its roots, like those of the other plants in the series, did not penetrate more than a centimetre or so beneath the surface of the solution. The roots of the unaerated plants were dark-brown in colour and did not possess the swollen tips characteristic of those produced in aerated culture. The mean length of the rhizomes was slightly higher than in the aerated series and may, in fact, have been higher than indicated, as the lengths given for nos.7 and 8 were rendered inaccurate due to the tortuous form of the rhizomes in these cases.

Pteridium: Unaerated water cultures (1947).

Fig.12. Plant no.6.

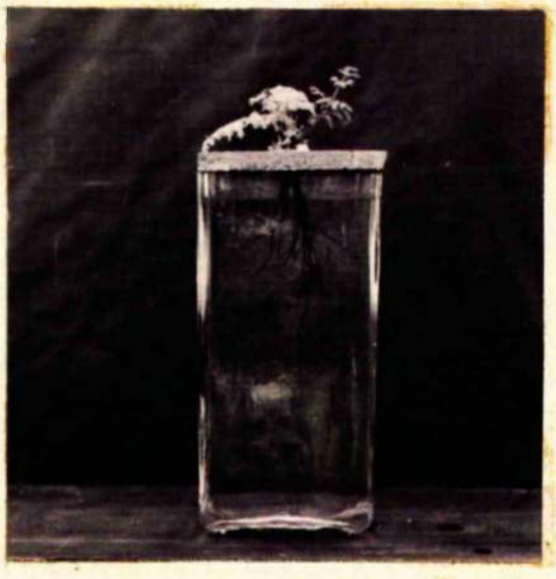


Fig.13. Plant no.8.

Table 8: pH Temperature and Dissolved Oxygen-Content of Solutions, and Dry Weights for Bracken in Unaerated Water Cultures.

Plant No.	pH of Soln.	Tempr. of Soln. (°C.)	Dissolved Oxygen(ml/l at N.T.P.	Dry Wt. of Roots and Rhizome (mgms.)	Dry Wt. of Fronds (mgms.)
1.	5.66	21.5	5.38	66.5	84.6
2	5.42	16.0 *	6.75 *	84.1	65.0
3	5.36	20.8	6.88	26.5	30.9
4	5.64	20.5	6.51	42.4	121.1
5	5.40	20.9	7.35	23.6	13.4
6	5.55	16.0 *	7.43 *	114.5	66.2
7	5.43	16.0 *	6.66 *	68.3	46.0
8	5.36	-	-	50.2	91.2
Means:	5.48	-	6.29	59.5	64.8

(* - measured one day later)

Ratio of mean dry wt. of roots and rhizome to mean dry wt. of fronds - 1 : 1.1

(Winkler's value for dissolved oxygen in equilibrium with air at 16°C. is 6.89, and at 21°C. is 6.23 ml/l at NTP).

The mean for dissolved oxygen is only slightly below equilibrium. The level will have been attained by downward diffusion from the surface and, therefore, although the figure represents an oxygen concentration little less than that obtaining under aerated conditions where numerous long roots developed, it could not be maintained in stagnant solutions in the presence of vigorously-respiring root systems. The writer suggests that attempts by the short roots to elongate would be frustrated by the rapid depletion of the oxygen supply.

A comparison of the pH values recorded for this series with those for the aerated solutions shows a difference of approximately 1 in favour of the latter. Various workers have shown that, not only does the blowing of air through a nutrient solution maintain the oxygen-content at a level adequate for the growth of most plants, but its function in removing toxic carbon dioxide is probably of equal importance. It might be suggested that, in the unaerated solutions, the difference of reaction was a factor involved in the poor growth of roots, but this is inadmissible in the light of the evidence discussed later that bracken exhibits a considerable tolerance with regard to reaction, and that its optimal level lies between pH 5 and pH 6.

Results for the Nitrogen Series.

Owing to shortage of sporelings of suitable size at the time of setting up the aerated and unaerated cultures, the nitrogen series could not be initiated until September 20th, 1947. The plants used were, on the whole, more robust than those of the other two series.

On October 6th, the plants were examined and, in several cases, a tendency to wilt was noted. Moreover, some of the fronds had become paler in colour. Plant no.1 was the most luxuriant member of the series, yet two of its fronds had wilted. Its foliage was paler than at the start of the experiment. The roots of this plant and the others were short.

The plants were harvested on November 18th. The data obtained are shown in Tables 9 and 10.

Table 9: Data relating to Root, Rhizome and Frond Lengths and Number of Fronds for Bracken in Walter Cultures through which Nitrogen was passed.

Plant No.	Max.Length of Roots (cms.)	Length of Rhizome (cms.)	Max.Length Of Fronds (cms.)	No.of Expanded Fronds	No.of Buds & Developing Fronds
1	6.6	3.0	26.0	12	0
2	3.3	2.0	8.3	8	8
3	3.1	2.5	11.2	11	9
4	6.7	4.8	10.3	5	19
5	7.8	2.7	15.8	9	14
6	12.7	8.5	16.0	12	12
7	3.3	-	3.0 *	4 *	4 *
Means:	6.2	3.9	14.6	9	12

(* - omitted from mean)

<u>Pteridium</u>: Nitrogen series of water cultures.

Fig.14. Plant no.1.

Fig.15. Plant no.4.

Fig.16. Pteridium: Nitrogen series of water cultures. Plant no.5, showing the mat of adventitious roots.

The final form typical of the plants of this series is shown in Figs.14 and 15. Except in no.6, the roots were short, arising from the rhizome in a thick clump, as in the unaerated plants. The rhizomes in most cases bore many adventitious roots and, in some, these were developed to such an extent as to produce a network on the damp cotton wool and on the surface of the cork. Fig.16 shows plant no.5 photographed on white glass, illuminated from behind, and the marked development of adventitious roots can clearly be seen.

Table 10: pH and Dissolved Oxygen-Content of Solutions and Dry Weights for Bracken in Water Cultures through which Nitrogen was passed.

Plant No.	pH of Soln.	Dissolved Oxygen(ml/l at N.T.P.)	Dry Wt.of Roots & Rhizome (mgms.)	Dry Wt.of Fronds (mgms.)
1	6.69	0.908	104.8	351.0
2	7.10	-	31.0	65.8
3	6.90	1.512	76.7	90.0
4	6.24	1.780	173.2	169.2
5	6.59	0.946	107.3	110.9
6	7.09	0.946	137.8	306.6
7	6.45	1.098	15.0 *	8.0 *
Means:	6.72	1.191	105.1	182.2

(* - omitted from mean)

Ratio of mean dry wt. of roots and rhizome to mean dry wt. of fronds - 1 : 1.7.

The temperatures of the solutions were not measured for this series and, consequently, Winkler's value for equilibrium dissolved oxygen cannot be given.

Several attempts were made to estimate the dissolved oxygen in the solution of plant no.2, but so much nitrite was present that an accurate figure was unobtainable.

Discussion of Water Culture Results.

Aeration of the solutions in which young *Pteridium* sporophytes were growing markedly favoured elongation of main roots and laterals, but the effect on the dry weight of the root system was not so great as might be expected. The long, golden roots of aerated plants elongated so rapidly that their bulk was large in proportion to dry weight. Elongation was restricted in unaerated solutions, but roots descending from the rhizome were more numerous. At the bottoms of some of the unaerated jars, fragments of roots were found; it would appear that roots attempting to establish themselves at lower levels in the solution tended to become unhealthy and break off.

The results of the nitrogen series

are difficult to interpret in relation to the other two sets because of their larger initial size. In length, the roots were more or less comparable with those in unaerated cultures, being almost invariably confined to the better oxygenated zone near the surface. A very low oxygen tension obtained in the nitrogen cultures, far below that of the stagnant ones, yet apart from a slight tendency to wilting of the fronds, the ability of the plants to maintain fronds of considerable stature, in some cases, was not impaired. In the light of field observations and of the results of soil cultures (to be described below) this apparent lack of response to low oxygen supply was unexpected. One notices, however, that the mean length of rhizomes was higher in this series than in either of the others. This may, of course, be referred to the greater advancement of these plants initially; indeed, this is more likely than that the increased rhizome development was a specific response to oxygen deficiency. In either case, the presence of the well-developed young rhizome with its two lateral lines of thin walled, loosely packed cells which are usually considered to be aeration tissue, may have enabled the plants to absorb an adequate quantity of atmospheric oxygen. There is actual evidence that, in young rhizomes, the peripheral ring of sclerenchyma has wider "aeration gaps" than in the older rhizomes. The latter are, presumably, able to absorb oxygen from the soil air by means of their aeration lines under natural conditions. Such absorption may be relatively greater in the young rhizome because of a proportionately more extensive area of aeration cells. The network of adventitious roots associated with the rhizomes in some of the plants in the nitrogen series may also have served to increase oxygen intake. It is possible that, had the rhizomes in this experiment been beneath the corks, in the solutions, collapse of the fronds might have occurred under unaerated and nitrogen conditions.

(b) Soil Cultures.

The method was based on that of Knight (1924) and, briefly, consisted of saturating with water the soil of a series of plants in pots, and aerating the resultant mud of some by means of tubes connected to a suitable air supply. Three 8½-inches-diameter unglazed pots were used. The drainage holes were plugged with corks and the pots coated internally and externally with paraffin wax. Two of the pots were fitted with glass aeration tubes ending in an inch depth of broken crocks. A layer of broken crocks was also placed in the third pot. All three were filled with good potting soil. The three clumps of rhizomes excavated from the marsh in Section 5, Square 4 (Fig.4) were planted, one in each of the pots. As has been indicated previously, these clumps bore many buds and thus appeared to have considerable potentialities for growth, given suitable conditions. The pots were moderately watered and fronds developed in due course.

On July 30th, 1947, water was added slowly to the three pots until the level stood at about a half inch below the rims. Under such conditions, the soil surface was under water. The pot containing the most vigorous rhizome network was selected to be the stagnant one. The two pots to be aerated were connected to the air supply from the electric compressor used in the water culture experiments, the flow being adjusted by screw clips to give a moderate rate of bubbling.

By August 14th, the aeration tube of one of the aerated pots had become blocked and, as efforts to clear the passage permanently were unsuccessful, this unit of the experiment was discontinued. At that time, the fronds were still turgid, although not to be compared in luxuriance with the second aerated culture. Aeration of the latter was stopped on September 2nd, when the plant was still growing luxuriantly. One of its fronds was large and spreading. The fronds produced a

Pteridium soil cultures

Fig.17. Final condition of unaerated and aerated plants.

Fig.18. Undersurface of frond from aerated plant, showing the exceptionally dense crop of sporangia. (Photographed under a wide-diameter hand lens.)

dense crop of sporangia, the great profusion of which can be seen in Fig.18. A germination test carried out on the spores after six months storage yielded 50% germination, so that the initial viability was possibly high.

The unaerated plant, despite its superiority before the commencement of the experiment, showed signs of failure even within twenty four hours of waterlogging. In that time, the lower pinnae had become slightly chlorotic. One was shrivelling from the tip. A film of algae subsequently developed on the surface of the water. This was removed from time to time so as to avoid any rise in the oxygen content of the water from that source (Bergman, 1920). On August 15th, the state of disease was far more advanced and, by September 2nd, all the fronds were dead; only one small bud was to be seen.

Table 11: Dissolved Oxygen in the Water of Aerated and Unaerated Soil Cultures. (Sept.16th, 1948)

	Tempr. of Water ($^{\circ}$C.)	Dissolved Oxygen (ml/l. at N.T.P.)
Aerated	16.3	7.31
Unaerated	16.2	2.11

(Winkler's value for dissolved oxygen in equilibrium with air at 16°C. is 6.89 ml/l. at N.T.P.)

In carrying out these estimations, the air supply to the aerated pot was turned off fifteen minutes before sampling. A cavity was made in the mud in each case and, after allowing time for the solid, abrasive matter to settle, the sample was taken with the end of the syringe pipette well below the surface layer. These figures do not necessarily represent the oxygen tensions in intimate contact with the roots and rhizomes. It is probable that the true figure for the unaerated mud would have been considerably lower than 2.11.

The underground systems were excavated in due course and it was found that the aerated plant possessed a good network of relatively long roots, whereas those of the unaerated plant were few and short, despite the initial superiority of the rhizome system in the latter.

<u>Discussion of Soil Culture Experiments.</u>

Although in the water cultures, lack of aeration or even the passage of nitrogen through the solution failed to bring about complete collapse of the plant, it has been shown that, when grown in soil culture, the fern was extremely sensitive to aeration, and the fronds succumbed rapidly in stagnant mud. The age of the experimental material was not the same in the two series of experiments and a direct comparison of the results cannot therefore be made. The suggestion is put forward that, in stagnant, waterlogged soils in the field and greenhouse, where available oxygen may be less than in unaerated solutions or even in those treated with nitrogen, the mature plant is unable to maintain numerous, large fronds. Aeration tissue, essential for the continued health and growth of a vast rhizome system, cannot function adequately under such conditions. Root respiration and, consequently, water absorption decline, followed by the collapse of the foliage.

(B) CALLUNA.

1. Review of Literature.

The work of Pethybridge and Praeger (1905), Crampton (1911, pp.68-70), W.G.Smith (1916) and Adamson (1918) has shown that *Calluna*, although requiring a layer of moist peat, does not flourish when the peat is waterlogged and drainage is bad. Under waterlogged conditions, the heather tends to be replaced by *Eriophorum vaginatum* and, where the water is at or very near the surface, *Eriophorum angustifolium*. Smith (1916) has drawn attention to the effect of irrigation of Callunetum by the deflection of streams arising from springs. The heather is, in time, replaced by grassland. This he attributed to such causes as the effect of alkaline water, possible mineral deposits and aeration of the superficial layer of the soil.

Heath and Luckwill (1938) have

made observations which show that the roots of *Calluna* are found in the comparatively well aerated surface peat, but Farrow (1915) did not find roots in the surface layer at Breckland. Instead, the great majority of heather roots occurred between 5 and 15 cms., and ramified horizontally. Some of the main roots extended as far as 40 cms. below the surface. Heath and Luckwill, in the same paper, state that, in a number of heath plants including *Calluna*, accumulation of humus leads to the gradual burying of the lower part of the stem, which, in consequence, gives rise to adventitious roots in the surface layer. This has also been observed at Ballochraggan.

From the literature and from observations at Ballochraggan, it would appear that although *Calluna* can flourish on soils of higher water content and lower oxygen content than *Pteridium*, waterlogging leads to its gradual replacement by Eriophoretum or moist grassland, according to whether the water is stagnant or running. The undernoted experiments were designed to obtain more precise information about the aeration requirements of the heather plant.

2. Water Cultures.

(a) 1946 Experiments (at Glasgow University).

As with bracken, preliminary

experiments were carried out in 1946. Two 4-litre glass troughs were used as culture vessels. The experimental plants were seedlings, approximately two years old, obtained from burnt areas at Ballochraggan. Large cork discs were used to support the plants, and there were six plants per trough. The nutrient solution was Tottingham's T3R1S4 variant of Knop, used at one quarter strength. The solution in one of the troughs was aerated by means of an electric compressor, the second culture being left unaerated.

The root systems in both developed well. A microscopical examination of portions of the roots showed that micorrhizal development was greater in the unaerated plants.

Growth of the shoots was likewise good, although the young tips became so chlorotic as to be almost white. This chlorosis was persistent and, as in the experiments on bracken, modifications were made in the proportions of the various constituents of the nutrient solution involving a reduction in the calcium content. Calcium excess seemed a possible explanation of the chlorosis in view of the calcifuge habit of *Calluna*. With the calcium nitrate reduced to one fifth and the potassium nitrate doubled (to compensate for loss of nitrate) some slight, but transitory, improvement was noted. A similar response followed the reduction of the calcium nitrate to one tenth with a corresponding trebling of the potassium nitrate. Work in 1947 indicated that the hydrogen ion concentration of the solution is in all probability the master factor governing the appearance of the chlorosis. This work is described in the section of this thesis on Hydrogen Ion Concentration. A reaction of pH 5 or above predisposes to chlorosis of the young shoot. Values of pH 4.98 and pH 5.08 were given by the "one fifth calcium" and "one tenth calcium" solutions respectively, when freshly made up.

(b) 1947 Experiments (at the Agricultural College).

Nutrient Solution.

Rayner (1915) used a solution containing potassium nitrate as the principal constituent, in her agar cultures. Crone's solution (Stiles, 1936, p.270) contains the same salts in approximately the same proportions, except that sodium chloride, present in Rayner's solution, is absent from Crone's. The latter has been shown to be particularly favourable to the production and elongation of roots (Bryan, 1922). It was therefore used in the present experiments, but at half-strength so as not to exceed Rayner's formula in total concentration of salts. The reaction of half-strength Crone's solution, freshly made up, was pH 6.9.

Cultural Arrangements.

The culture vessels were similar to those used in the bracken cultures. Three series of cultures were set up. One was aerated, another was left unaerated, and nitrogen was passed through a third series. Each jar contained only one plant, and there were twelve jars in each series. Jars nos.1 to 4 (inclusive) were of 350 ml. capacity, and the remainder 750 ml.

Plant Material and Problems of Transference to Water Culture.

The plants used were derived from the same source as those of the 1946 experiment. They were thus three or four years old seedlings. After transference from soil, all plants were allowed to become settled in the new medium before any treatments were applied. During this preliminary stage, a number of plants was lost owing to the appearance of crystalline deposits at the tips of the lower leaves. Whether this was due to a form of guttation or to the creeping of the nutrient solution up the stem and lower branches, with subsequent evaporation, is not certain. Once new water roots were produced, the plants seemed to go ahead satisfactorily.

In due course, many shoot tips became chlorotic, but after adjustment of the hydrogen ion concentrations in all cultures to approximately pH 4, the green colour was rapidly restored. No attempt was made to maintain the reaction at this level, subsequent adjustments only being made when the earliest signs of chlorosis reappeared in individual plants. Adjustment was made by means of N. sulphuric acid.

Results for Aerated Series.

Aeration commenced on June 29th, 1947, and was continuous. On August 5th, it was noted that the roots were much shorter than those of the unaerated plants. The shoots also were not nearly so good. The reactions of the solutions rose after adjustment much more rapidly, doubtless as a result of the removal of carbon dioxide in the air stream. In consequence, chlorosis was more frequent and more rapid in its appearance. The plants were harvested on September 29th, and the quantitative data are given in Table 12.

Table 12: Date relating to Temperature, Oxygen Content and Final pH of Solution, Root Length, Dry Weights of Roots and Shoots for Calluna in Aerated Water Culture.

Plant No.	Tempr. of Soln. (°C.)	Dissolved Oxygen(ml/l at N.T.P.)	Final pH	Length of Roots (cms.)	Dry Wt. of Roots (mgms.)	Dry Wt. of Shoots (mgms.)
1	15.8	7.10	6.48	5.7	54.7	141.7
2	15.8	7.06	6.78	5.8	77.9	257.0
3	15.8	7.15	6.71	10.0	65.9	126.8
4	15.5	7.24	6.93	6.7	73.8	153.5
5	15.8	7.02	6.98	10.9	128.1	294.5
6	15.7	7.00	6.58	7.7	128.8	382.0
7	15.6	7.35	6.03	7.8	76.8	186.8
8	15.7	6.88	7.20	6.9	61.3	163.9
9	15.7	6.88	6.97	10.4	110.6	445.7
10	15.8	7.12	6.94	8.7	136.3	436.5
11	15.8	7.00	6.76	10.1	69.8	169.9
12	15.9	7.02	6.81	6.7	88.9	354.5
Means:	15.7	7.05	6.76	8.1	89.4	258.6

Ratio of mean dry wt. of roots to mean dry wt. of shoots - 1 : 3.

Winkler's value for dissolved oxygen in equilibrium with the air at 16°C. is 6.89 ml./litre at N.T.P.

The final condition of four of the plants in this series is shown in Fig.19.

The roots of the aerated plants produced lateral buds in profusion, but elongation was poor. In some cases, branch buds near the tips of the roots imparted a "nodulated" appearance to the system. It is of interest to note the apparent discrepancy between the results of this experiment and the preliminary one in 1946. It will be recalled that good root growth was obtained in both aerated and unaerated cultures. The writer believes that the mean oxygen tension over twenty four hours was insufficient to inhibit growth in the earlier experiment, aeration being for only twelve hours per day.

Small pieces of root were cut from each plant at the time of harvesting and immediately fixed in alcohol-formalin-acetic acid fixative. The material was later stained in lactophenol cotton blue and mounted in glycerine jelly containing cotton blue. Such preparations were made from all three heather culture series. In those from the aerated plants, the mycorrhizal fungus was mostly intracellular and only occasionally were external hyphae found. The mycelium in the cortical cells was not dense and never filled the cells.

Calluna water cultures (aeration experiment).

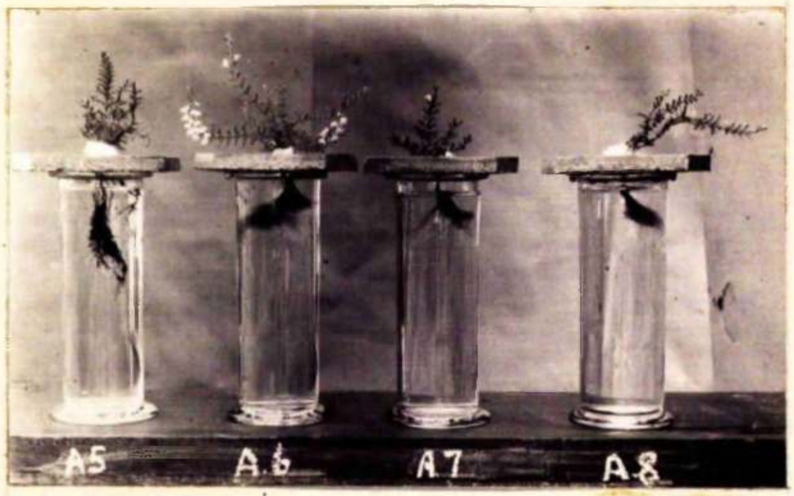


Fig.19. Aerated plants nos.5, 6, 7 and 8.

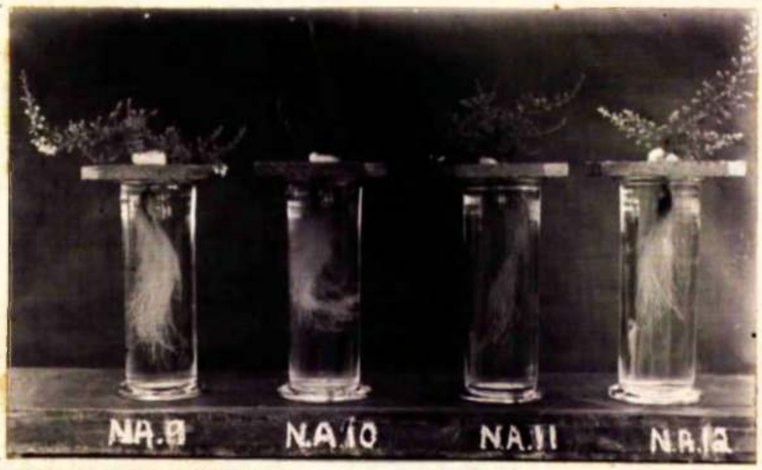


Fig.20. Unaerated plants nos.9, 10, 11 and 12.

Fig.21. Nitrogen series: plants nos.9, 10, 11 and 12.

The shoots had produced only a moderate amount of new growth, but this was for the most part healthy and turgid. Except for a few tips which were chlorotic, the leaves were of a good dark green colour.

Plant no.11 was remarkable in so far as nearly all its branches curved downwards in a "scorpioid" fashion.

Four of the plants in this series came to bear flowers, no.6 having as many as thirty four at harvesting.

Results for Unaerated Series.

This series was set up on the same date as the aerated one and, by August 5th, the plants were unquestionably superior. The roots were longer, whiter and free of slime. The shoots, particularly of plants 9 to 12 inclusive, were very good. The series was harvested on September 30th and the following numerical results were yielded.

Table 13: Data relating to Temperature, Dissolved Oxygen and Final pH of Solution, Root Length, Dry Weights of Roots and Shoots for Calluna in Unaerated Water Culture.

Plant No.	Tempr. of Soln. (°C.)	Dissolved Oxygen(ml/l at N.T.P.	Final pH	Length of Roots (cms.)	Dry Wt. of Roots (mgms.)	Dry Wt. of Shoots (mgms.)
1	16.5	7.46 *	4.76 *	4.5 *	-	-
2	16.8	5.64	5.94	17.8	52.8	188.4
3	16.8	5.35	6.12	18.8	66.2	182.5
4	17.0	5.35	6.38	10.1	80.0	284.2
5	16.8	4.76	6.36	18.6	145.4	381.8
6	16.9	5.29	6.80	16.0	103.8	336.8
7	17.0	5.68	6.31	14.7	72.2	402.4
8	18.1	5.75	6.40	16.4	60.9	175.0
9	18.2	3.94	6.37	16.3	121.5	505.5
10	18.2	5.82	6.44	20.0	95.4	492.2
11	18.2	5.66	6.75	16.6	138.5	543.4
12	18.5	5.17	6.60	13.4	118.7	425.5
Means:	-	5.15	6.41	15.3	96.0	356.1

(* - omitted from mean)

Ratio of mean dry weight of roots to mean dry weight of shoots - 1 : 3.7.

Winkler's value for dissolved oxygen in equilibrium with the air at 16°C. is 6.89, and at 18°C. is 6.61 ml./l at N.T.P.

Plant no.1 showed no signs of root growth at all, and the distal parts of most of the shoots were dead. For this reason, the values for dissolved oxygen, pH and length of roots were omitted from the means. The failure of this plant to establish itself was not without advantage, in so far as it provided an unaerated culture in which the oxygen content of the solution was undiminished by the requirements of an actively-growing root system. Thus a standard existed against which to assess the effects of the Calluna root respiration on the oxygen content of the medium. The dissolved oxygen value in this culture is seen to be approximately 2.3 ml. per litre above the mean for the rest of the series. Plotting of the values for dissolved oxygen against dry weight of roots did not indicate any relationship between the two for these cultures.

Fig.20 shows plants of this series immediately prior to harvesting, and the luxuriant development of roots and shoots as compared with the aerated series in Fig.19 is clear. The greater size of the root systems was, however, due to increase in length without much increase in dry matter. The shoots, on the other hand, showed an increase in dry weight of almost 100 mgm. over the aerated plants. Growth of shoots was, in most cases, extremely good. In some of the most luxuriant individuals, however, elongation had proceeded so rapidly that the new growth tended to be very straggly. This was noted in nos. 5, 7 and 9. Nos.6, 8, 10, 11 and 12, while not quite so luxuriantly elongated, were much firmer.

It is noteworthy that the shoots of nos. 2, 3 and 4 (which were in the small size of culture jar) while being perfectly healthy, were much smaller than the rest.

Only two plants of this series bore flowers. There were thirty four on no.9 and seven on no. 10.

The mean pH was only 0.35 below that for the aerated set. A greater difference might have been expected in view of the extensive root systems, the vigorous growth of roots and shoots, and the absence of aeration. Furthermore, it is difficult to understand why the reaction of no.1 should have been by far the lowest of the series, when no root growth whatever occurred.

Examination of the preparations of small pieces of the fine root branches showed little difference from the aerated plants in the amount and distribution of the mycorrhizal fungus. No.1 (the plant for which no growth was recorded) was an exception in that many of the cortical cells were packed with mycelium, and there were abundant external hyphae. The roots of this plant were evidently unhealthy as the cortical cells were stripped off in parts, leaving the stele exposed.

Results for Nitrogen Series.

The nitrogen series was not set up until July 22nd. The passage of nitrogen through the solutions was almost continuous. Harvesting took place on October 22nd.

Table 14: Data relating to Dissolved Oxygen and Final pH of Solution, Root Length, Dry Weights of Roots and Shoots for Calluna in Water Cultures through which Nitrogen was passed.

Plant No.	Dissolved Oxygen(ml/l at N.T.P.)	Final pH	Length of Roots (cms.)	Dry Wt. of Roots (mgms.)	Dry Wt. of Shoots (mgms.)
1	2.12	4.98	4.6	38.9	117.2
2	3.67	7.14	7.4	57.8	202.6
3	1.04	4.61	7.2	47.9	171.0
4	3.00	6.41	7.7	75.0	270.2
5	3.18	5.48	8.6	59.2	164.1
6	2.20	4.02	7.1	101.1	225.7
7	2.65	5.12	11.6	98.6	338.8
8	(dead)				
9	3.60	4.02	7.8	68.8	331.5
10	2.57	3.47	7.3	47.0	93.3
11	2.52	3.94	12.0	118.7	520.8
12	2.29	3.87	8.8	75.5	218.3
Means:	2.62	-	8.2	71.7	241.2

Ratio of mean dry weights of roots to shoots - 1 : 3.4.

Two quantities were very variable in this series, namely, dissolved oxygen and final pH of solution. No relationship was apparent between either of these quantities and the dry weights of roots. The temperatures of the solutions were not measured.

The final state of typical plants of the nitrogen series is depicted in Fig.21. The mean length of roots was almost the same as in the aerated set. The means of the dry weights of roots and shoots were somewhat lower. Many lateral root buds had been formed but, except in a few cases, these had not elongated. In some, the buds were swollen. The series was characterised by very little growth of shoots, although in one or two exceptional plants, good growth had occurred, but this was far from being of a luxuriant nature. Even in those plants which had only grown to a slight extent, the shoots were quite healthy in appearance, with the exception of no.1, in which the leaves were slightly wilted.

Examination of the roots for mycorrhiza showed that external hyphae were more frequent than in the other two series, but they tended to be short. Dense networks did not occur. In many cells, the mycelium appeared to be in an advanced stage of digestion. Rayner (1927, p.99) notes the "strong stainability" of the rounded, partly-digested balls of mycelium.

Conclusions from Water Cultures.

It would appear from the foregoing experiments that the optimal concentration of dissolved oxygen for young Calluna plants in half-strength Crone's solution is in the region of 5 ml. per litre at N.T.P. though it should be borne in mind that oxygen concentration may not be the sole factor operating in these experiments. It cannot be said that all conditions other than oxygen concentration were the same in the three series, because the unaerated plants were not subjected to the continual stirring of the medium involved in the passage of gases. It may be the absence of some factor associated with stagnation which limited growth in both aerated and nitrogen series. Alternatively, on the basis of oxygen concentration being the master factor, one must conclude that saturation with the oxygen in air provides a concentration of the gas which is toxic for Calluna. The limitation of growth under treat:ment with nitrogen would thus be due to a different cause, namely oxygen deficiency.

One would expect that a lower pH would be a feature of stagnant solutions and, consequently, reaction might be a factor involved in the difference in growth encountered between plants in stagnant and agitated solutions. In this experiment, however, it has been seen that pH was not affected to the extent anticipated. There was only a small difference between the means for the aerated and unaerated sets. Although widely varying, most of the pH values for the nitrogen series were below the means for the other two. The writer finds this inexplicable.

3. Soil Cultures.

As in the equivalent bracken experiments, there were aerated and stagnant cultures but, in addition, plants were grown in normal, peaty soil in unwaxed pots. Other differences between the bracken and the heather cultures were that, in the latter, the three sets of conditions were each represented by two cultures and the pots used were only six inches in diameter.

The peaty soil which had contained the *Calluna* seedlings from Ballochraggan used in the water cultures was utilised to fill the pots in this experiment. The largest seedlings were selected and one planted in each of the pots. The plants were set aside for a time to enable them to become established, during which time they were watered at intervals, care being taken not to waterlog the undrained pots.

On July 30th, 1947, water was added slowly to the waxed pots until the soils were completely waterlogged and the level stood about half an inch above the soil. The two aeration tubes were connected to the air line from the pump and the flow adjusted by screw clips.

By August 10th, it was noted that the plants in unwaxed pots were superior to those under both aerated and unaerated waterlogged conditions. These plants were watered periodically. The experiment was allowed to run for longer than the bracken soil cultures, the plants being harvested at the end of October, 1947.

Estimations of dissolved oxygen in the aerated and unaerated pots were made by means of the "micro-Winkler" syringe pipette as in the bracken soil cultures. The figures in Table 15 show the oxygen content of the aerated cultures to have been more than twice that of the stagnant ones.

Table 15: Temperature and Dissolved Oxygen in Aerated and Unaerated Waterlogged Soil Cultures of Calluna.

	Aerated		Unaerated	
	(1)	(2)	(1)	(2)
Temperature (°C.)	18.3	18.3	18.6	18.3
Dissolved Oxygen(ml/l at N.T.P.)	7.15	7.22	-	3.1
Max. Length of Roots (cms.)	10.0	12.5	8.5	4.0

In both of the aerated cultures, one shoot was very much elongated. The other shoots had been swamped by excessive bubbling of the mud. It was very difficult in the pot culture work in general to maintain a constant flow of air through the pots, partly because the delivery of the pump depends upon the time which has elapsed since lubrication. A few flowers were produced by both aerated plants. The root systems were fairly well-developed, though not by any means profuse. Adventitious roots were present, arising from the base of the stem and from the lower sides of the first lateral branches, which were submerged in the mud. Preparations were made of the roots for examination of the mycorrhiza. In the aerated roots, there were luxuriant external hyphae in parts and abundant intracellular mycelium in many of the finer sub-divisions of the system. Some of the external filaments were very broad and brownish in colour.

In one of the unaerated plants, many of the lower leaves had long been yellow and orange. Otherwise, it can hardly be said that it was very markedly inferior to either of the aerated specimens. The roots were a little shorter, but the degree of branching was comparable with that found under aerated conditions. Likewise, mycorrhizal development was very much the same. The second unaerated plant, on the other hand, was almost dead and there had been negligible growth of roots and shoots. The roots, under the microscope, appeared very woody. Young roots and mycorrhiza were very infrequent.

The plants under (as near as possible) normal soil conditions constituted a control on both aerated and stagnant cultures. They were most luxuriant in their vegetative development at the time of harvesting. In neither of the two plants were any flowers produced. Root growth was very similar to that of the aerated plants, lengths of 13.8 cms. and 11.5 cms. being recorded. Mycorrhiza was far less frequent, although clumps of external hyphae were occasionally encountered. The intracellular stage was confined to the cortical cells of some of the emergent lateral buds.

Conclusions from Soil Cultures.

The results of the soil cultures were in agreement with those of the water cultures. The dissolved oxygen in the aerated pots was of the same order of magnitude as that in the aerated solution cultures and, accordingly, the growth of the potted plants was restricted. Likewise, the unaerated soil cultures were unhealthy or dead, the dissolved oxygen of the water approximating to that in solution cultures through which nitrogen was passed. Indeed, as has been indicated above, the actual oxygen concentration in contact with the root systems was probably lower than the value obtained. The soil in the normal (unwaxed) pots was watered periodically, but it tended to solidify, shrinking from the walls of the pots. Nevertheless, as close an approach to optimal field conditions of the soil for Calluna as is possible in the green-house was obtained. The absence of the living roots of the associated flora must not be overlooked, however.

Without precise information of the oxygen-content of heather soils, both normal and water:logged, interpretation of the dying-out of heather in waterlogged soil on the basis of the experiments described must be made with caution. Tentatively, therefore, the view is put forward that the oxygen concentration in a soil bearing a vigorous growth of Calluna is of the same order as that in the unaerated water cultures and that when drainage deteriorates and the peaty soil becomes waterlogged, the oxygen concentration falls to a very low level, the actual value being, in all probability, well below that in the nitrogen series of water cultures. The heather plant, being somewhat resistant to the effects of low aeration, does not immediately succumb, and thus, the decline of the Callunetum is gradual. The degenerate heather is successfully invaded by Eriophorum spp., whose aeration requirements one assumes to be small.

2. HYDROGEN ION CONCENTRATION.

General Literature.

The literature relating to this subject is very extensive. It will be possible to review only a few of the main contributions here.

Olsen (1923) made a very comprehensive study of the hydrogen ion concentrations of the Danish soils in relation to the incidence and frequency of numerous species. From these investi:gations, Olsen concluded that the reaction of the soil is a major factor governing the composition of a plant community. Each species occurs between certain limits of pH. Within these limits, there is a narrower range where growth is greatest.

In the second section of his monograph, Olsen described soil and solution culture experiments in which various species were grown at different reactions. The two types of experiment did not yield the same result for a species. For example, in soil culture, *Deschampsia flexuosa* grew best at pH 5.2, but in water culture, the largest plant occurred at pH 4.0. A similar difference was found in *Senecio silvaticus*. *Tussilago farfarus* is a
found in *Senecio silvaticus*. *Tussilago farfarus* is a
plant of alkaline soils. In soil culture, it attained its best development at pH 7.6, but in solution culture, the maximum occurred between pH 6 and pH 7. No species from alkaline soil was found

to grow in an alkaline culture solution.

Experiments were also performed to study the effects of reaction on germination. The technique employed was to place the seeds in flasks containing a few millilitres of nutrient solution adjusted to different levels of reaction. It was found that the percentage germination was not affected by pH, but that an influence was exerted on the time taken for signs of germination to become evident, on the health of the radicle, and on the number of root hairs.

Arrhenius (1922) quoted figures from his own work and that of other investigators showing that, in certain crop plants, the percentage germination varies according to the pH. (Olsen's work was performed with wild species.) This publication is particularly valuable for the full bibliography of the earlier work, 250 references being listed.

A modern account of pH in relation to the growth of plants has been provided by Small (1946).

(A) PTERIDIUM.

1. Review of Literature.

Salisbury (1925) noted the tendency of plants growing in water culture to alter the pH of the solution, by the process of selective absorption. On the other hand, the pH of the soil remains more or less steady because of its buffering properties. Salisbury measured the pH of a large number of soils bearing certain species of which bracken was one. Most of his samples were taken from southern counties. For bracken, Salisbury took the pH samples from 200 localities. The results were shown graphically, number of localities being plotted against pH. Bracken soils ranged from pH 3.6 to 7.6, with maximum incidence at 5.5. The other species considered were <u>Vaccinium myrtillus</u>, <u>Scilla nutans</u>, <u>Psamma arenaria</u>, <u>Mercurialis perennis</u> and <u>Ranunculus ficaria</u>. The graphs for <u>Mercurialis</u> and <u>Ranunculus</u> were characterised by a well-marked double maximum, and a tendency to such a form was noted in <u>Vaccinium</u> and <u>Scilla</u>. The double peak was not apparent in the bracken curve. It has been suggested by Robbins (1923) that the minimum between the two modes may correspond with the "net" isoelectric point of the cell proteins.

Watt (unpublished data) found bracken growing on a wider range of alkaline soils than Salisbury, namely, as high as 8.2, the lower limit being the same as reported by Salisbury.

Heath and Luckwill (1938) found that the pH of soils dominated by several types of vegetation increased with the depth of the sample. The mean value they obtained for <u>Pteridium</u> was 5.4, which is in good agreement with Salisbury's figure for the mode.

It is thus clear, in so far as field conditions are concerned, that the bracken fern is able to grow on soils of widely divergent hydrogen ion concentration but, nevertheless, the sporophyte seems to prefer a decidedly acid reaction.

Very little work has been done on the growing of bracken in artificial media at different levels of pH. Workers at the National Institute of Plant Physiology carried out experiments (unpublished) at Rothamsted. These were mostly of a nutritional type, but also included initial experiments on the effect of irrigation with nutrient solutions adjusted to different reactions on bracken in sand cultures. As the experiments were only visualised as preliminary to a much larger investigation, only three reactions were tried, and none of these were on the alkaline side of the neutral point. No significant difference was observed between the plants at the three reactions (pH 4, 5.5 and 7). Unfortunately, the investigations have not been pursued further.

2. Water Cultures (at Glasgow University, 1946).

The work of Bryan (1922) was valuable as a guide to the experimental technique. Bryan first tried a number of nutrient solutions to determine that most favourable to nodule-production in soyabean.

From the point of view of root growth and branching, Mendota Lake Water gave the most satisfactory results, but Bryan adopted Crone's solution as a basis for his experiments, as nodule production was best in this medium. As a matter of fact, the proportions of the various salts in Bryan's recipe do not correspond with those of Crone. There appears to be a tendency in the literature relating to formulae of nutrient solutions for the older recipes to be modified, while still bearing the names of their originators. Knop's solution, for instance, appears in many forms not stated to be modifications. Miller (1938, p.242) misquotes Crone, but the correct version is given by Stiles (1936, p.270). The culture vessels used by Bryan were glass percolators, fitted with openings at the bottoms (guarded by clips) so that solution changes could be made without disturbing the plants. The solutions were adjusted to pH 3, 4, 5, 6, 7, 8, 9 and 10 approximately. The actual values were, in some cases, scarcely even approximate to the nominal figure. For example, pH 6.5 represented pH.7. The solutions were renewed daily. A good precaution which Bryan observed was the gradual adjustment of the solution to the prescribed level over a period of two days. In his main experiments, Bryan modified his original version of Crone's solution, substituting potassium chloride for the nitrate, the latter being unfavourable to nodule development. It was noted that the buffering of Crone is poor in the alkaline range and, in an attempt to stabilise the reactions, alkaline levels were obtained by first adding sodium carbonate (0.75 gm. per litre) and then sulphuric acid, as required. Even so, the alkaline solutions soon changed in reaction in contact with the growing roots. The solutions were filtered before adjustment. This, in the opinion of the present writer, was both ill-advised and unnecessary, as elements derived from the "insoluble" salts are likely to be soon exhausted, the solid residue not being present to maintain equilibrium with the small quantity in solution. Admittedly, Bryan changed the solutions daily and little depletion might be expected in so short a time as twenty four hours, but even the best of Bryan's plants, as shown by his photographs, were not very robust specimens. A colorimetric method was employed in the determination of the reactions, which was checked from time to time against the hydrogen electrode. Apart from his results relating to nodule formation as affected by pH (which are irrelevant to the present investigations) Bryan found that the pH of a solution will only remain constant when it happens to be the optimum for the species. The reactions of other solutions tend to be altered by the plant towards the optimum. According to Powers (1927) mint, which he found to have an optimum of pH 6 for growth in water cultures, tends to adjust the pH rapidly and, if it is not allowed to do so, dies. Miller (1938, p.264) quotes a table in which figures are given for the initial reactions of several well-known solutions and the reactions after wheat had been grown in them for 52 hours. The figures show that those solutions which are initially nearer neutrality remain unchanged. Crone and Sachs solutions, originally pH 6.6 and 6.7 respectively, were both 6.6 after 52 hours. The other types averaged 4.6 at the start and were raised by approximately a unit in the same time.

Cultural Arrangements.

The plants used in this experiment were young sporophytes, similar to those of the aeration cultures. Three plants were grown in each jar, suitably supported in cork plates by cotton wool. The jars were earthenware and were of 1400 ml. capacity. The writer's "one quarter calcium" solution was selected as the nutrient solution.

Adjustment of Reaction.

The plants were grown for a week after transferring to solution culture before any adjustments were made. The reactions were adjusted with N/4 sulphuric acid or N/4 caustic soda, according to the pH required. On August 24th, after the solutions had been changed, and the jars numbered B.3, B.4 and so on to B.10, B.3 to 5 (inclusive) were adjusted to pH 5 approximately. B.6 was adjusted to pH 6. Numbers 7, 8, 9 and 10 were brought up to pH 7. (All estimations of the hydrogen ion concentrations in the acid range were made by means of the B.D.H. "Capillator"; for the alkaline reactions, the Helliga Comparator was used. Buffering was negligible on the alkaline side and the Capillator was therefore unsuitable.) Two days later, all the solutions were adjusted to their appropriate levels of reaction.

It soon became clear that the reactions of B.3 to B.7 (inclusive) were remarkably steady over long periods, not requiring adjustment until the solutions were changed. (Changing of solutions took place at fortnightly intervals.) B.8 had to be levelled up from time to time, but during the whole course of the experiment, the pH of this jar never fell below 7.2. The solutions of B.9 and B.10, however, were extremely unstable in reaction. The alkalinity of these solutions was so great that some of the dissolved salts were precipitated on the addition of the caustic soda. In the case of B.9, values as low as 7.8 were reached in 48 hours, but it is suspected that the fall sets in much sooner, in fact shortly after adjustment. B.10 also fell as low as 7.8 on occasion and its average was little different from B.9 over the same period of time.

<u>Arrangement for Aeration.</u>

In the absence of an electric compressor as used in the aeration experiments, the writer employed a device suggested to him by Dr. G. F. Asprey, late of the Botany Department, Glasgow University, for the aeration of the cultures in the pH experiment. The apparatus consisted of an aspirator, the top opening of which was fitted with a stopper carrying two tubes. One of these was securely connected to the water exit of a filter pump. Internally, it was continued about half way down the aspirator. The second tube was short internally and formed the delivery tube for the air stream. The lower opening of the aspirator was fitted with a stopper and a large bore glass tube terminating in a short length of rubber tubing controlled by a screw clip. The filter pump was, in operation, connected to the water supply and, after the level of water in the aspirator had reached a depth of a few inches, the clip on the water exit tube was adjusted to maintain the water at a constant level. Under such conditions, the air carried by the incoming water was expelled through the delivery tube at a pressure adequate for the aeration of a considerable number of jars. Theoretically, aeration by this apparatus would be continuous, but in practice, the pressure of the water main supply was so variable that it was found impossible to keep the water level steady in the aspirator for more than a few hours. In the event of the level falling until the water exit was reached, the air escaped with the water: if the level rose, the aspirator was filled, and the culture jars had water injected into them. However, intermittent aeration was provided by this means and was adequate as judged by the penetration of the roots into the lower levels of solution in those of favourable reaction.

Results of the Experiment.

On October 2nd, 1946, after the plants had been growing for over five weeks under the conditions of pH difference, they were harvested, as some were beginning to show signs of succumbing to *Botrytis*. (The cultures were housed in a glass cloche, as in the aeration experiments.) The data obtained are summarised in Table 16.

Table 16: Data relating to Bracken grown in Water Cultures adjusted to Different Reactions.

	Fronds	Roots	Rhizome	Mean Length of Roots (cms.)	Mean Dry Wt. of Plant (mgms.)
pH 3:					
1.	xxx	xx	-	7.3	130.2
2	xxxxx	xxxx	2.5 cm.		
3	xxx	xx	-		

	Fronds	Roots	Rhizome	Mean Length of Roots (cms.)	Mean Dry Wt.of Plant(mgms.)
pH 4:					
1	xx	xxx	-		
2	xxxxx	xxx	5 branches	10.3	118.0
3	xxxx	xxxx	1 cm.		
pH 5:					
1	xxxxx	xxx	2 branches		
2	xxxx	xxxx	v. small	14.5	129.2
3	x	x	-		
pH 6:					
1	xxxxx	xxxxx	3 branches		
2	xxx	xx	-	11.5	178.9
3	xxxxxx	xxxxx	5 branches		
pH 7:					
1	xx	xx	-		
2	(dead)			5.1	19.3
3	xx	x	-		
pH 8:					
1	xxx	x	-	7.4	58.6
2	x	x	-		
3	xxx	xxx	-		
pH 9:					
1	-	xx	-	5.4	46.7
2	x	-	-		
3	x	xx	-		

	Fronds	Roots	Rhizome	Mean Length of Roots (cms.)	Mean Dry Wt. of Plant (mgms.)
pH 10:					
1	x	x	-	2.6	16.2
2	(dead)				
3	x	-	-		

xxxxx, very good; xxxx, good; xxx, fair; xx, poor; x, very poor.

The numerical data above are plotted against pH in Figs.22 and 23. The photographs (Fig.24 and 25) show the final condition of the series.

Discussion of Results.

In considering the results of this experiment, the most obvious point is the wide differences encountered between the three plants of a jar in certain cases. Among such divergences, the most outstanding was the appearance in the pH 3 culture of a plant of remarkable luxuriance. The other two plants in the same jar had possessed healthy foliage in the earlier stages of the experiment, but these fronds had given place to "bunched" growth which was permanently wilted to a slight extent. It is evident that root absorption (and, consequently, frond elongation) was being restricted in these plants. The pH of this solution remained steady within narrow limits, so that a reaction of pH 3 cannot be seriously detrimental

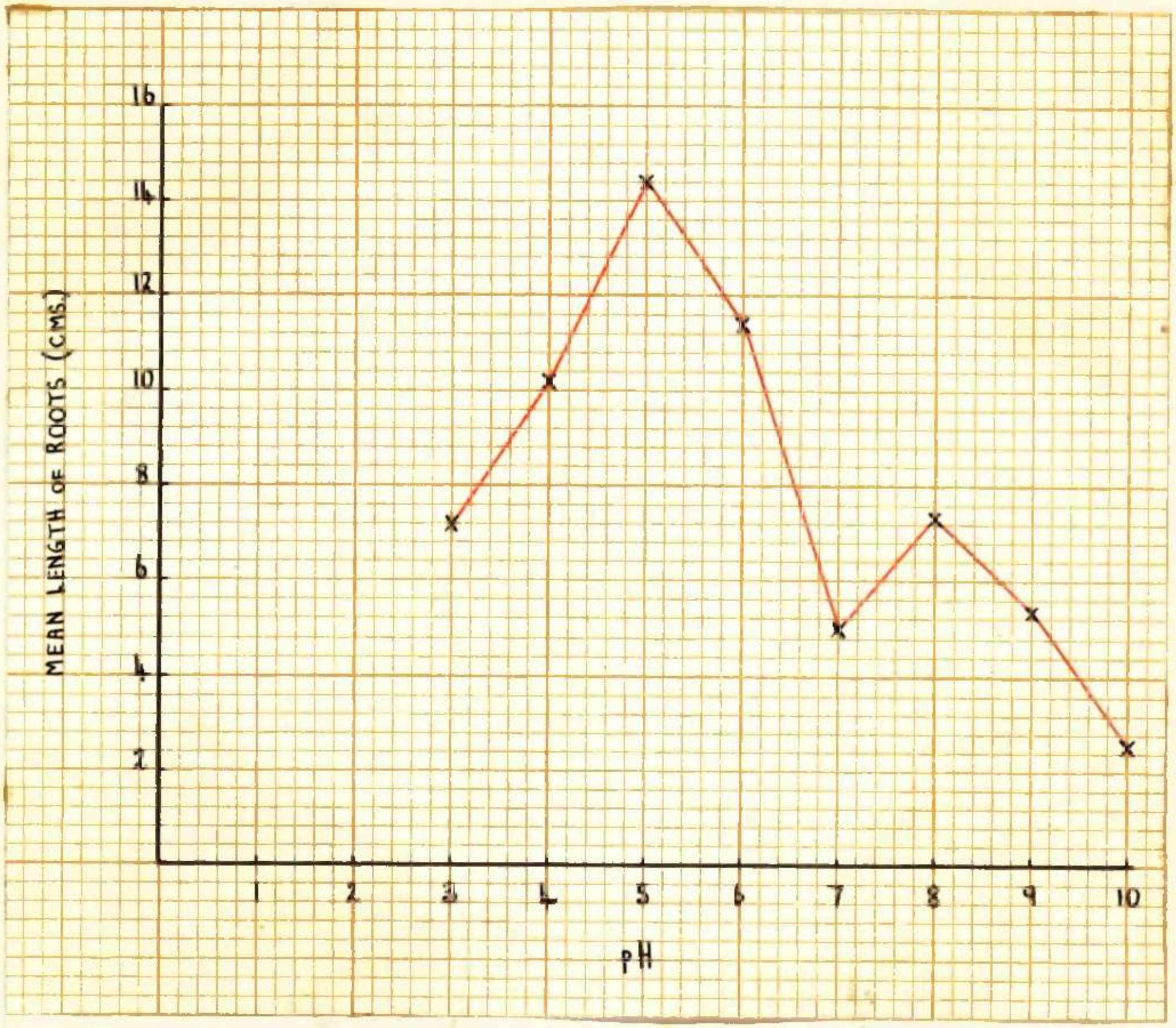


Fig.22. Graph showing the mean length of roots at each reaction against pH for <u>Pteridium</u> in water culture.

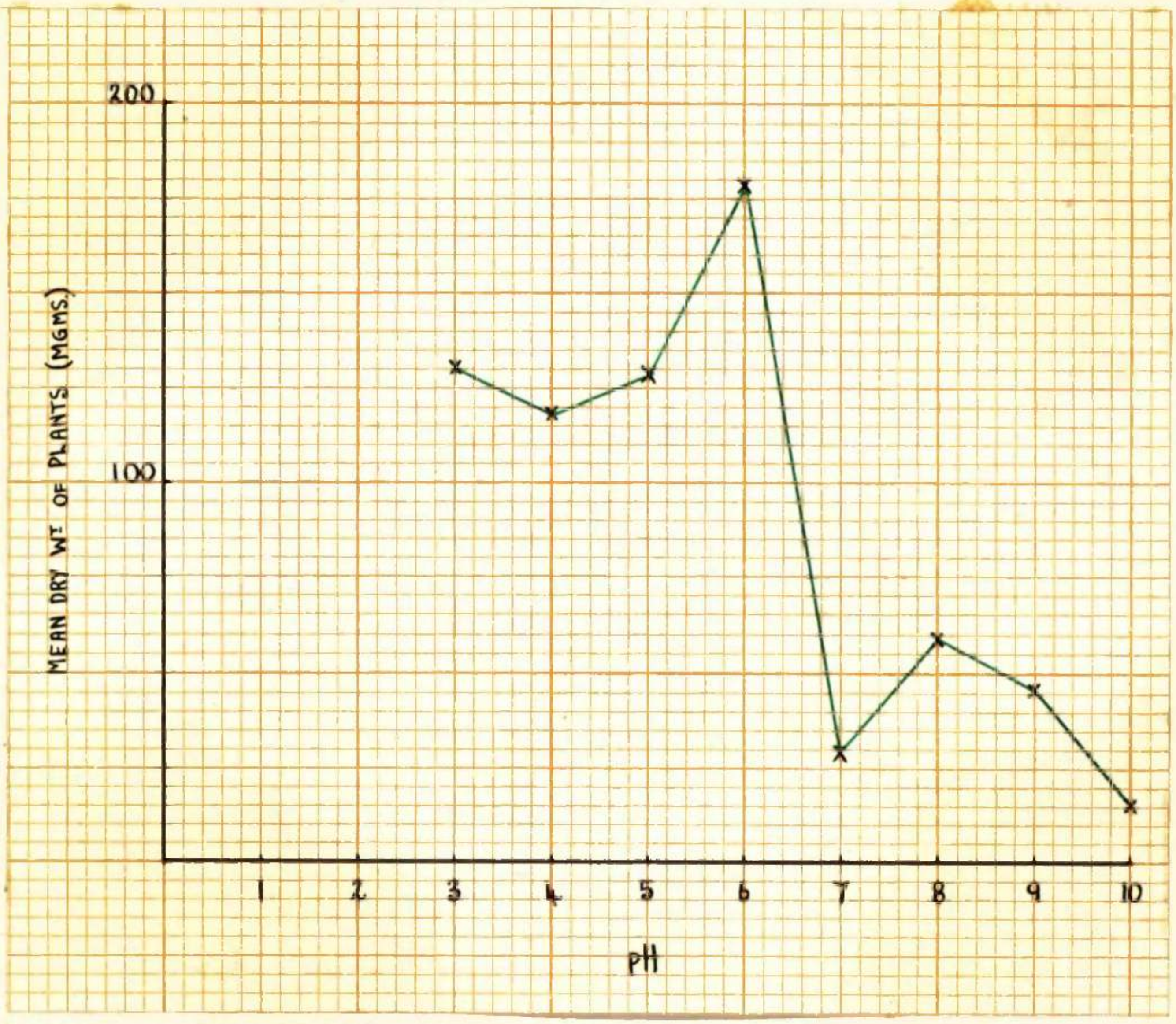


Fig.23. Graph showing the mean dry weight of plants at each reaction against pH for <u>Pteridium</u> in water culture.

Final condition of Pteridium in water cultures of various reactions.

Fig.24. pH 3 pH 4 pH 5 pH 6 pH 7

Fig.25. pH 8 pH 9 pH 10

to bracken sporophytes, at any rate under the artificial conditions of the experiment. Admittedly, the jars were not replicated and conclusions based on one culture are to be treated with due caution. It is a fact which cannot be gainsaid, however, that a bracken plant did become luxuriant in this very acid medium.

At none of the reactions tried was it found that Pteridium was speedily killed, though it is clear that a pH from 7 upwards is un:favourable for growth of the fern in water culture.

In considering the forms of the curves in Figs.22 and 23, the small scale of the experiment must be borne in mind, and it is likely that repetition on a much larger scale would erase some of the irregularities. Nevertheless, one is strongly tempted to attach significance to the presence of the double maximum in both graphs, in view of the work of other investigators referred to earlier in this section. In the curve for maximum length of root systems in relation to reaction, the peak occurs at pH 5, but this might be unjustified as one of the plants in this jar had only one root at the maximum length, all the others being very much shorter. The peak of the dry weight curve corresponds with pH 6, so that, on the basis of this limited experiment, it would seem that between pH 5 and pH 6 is the range of reaction most favourable to the general growth of *Pteridium* under the conditions of the experiment. A minimum is located in both curves at pH 7, with a second, but very much lower maximum at pH 8.

3. The Germination of the Spore and Subsequent Development on Agars of Various Reactions.

As a development of the experiment on the young sporophyte, and in view of the work which has shown that all stages in the life-cycle of the fern may not respond similarly to the factor of hydrogen ion concentration (Conway, 1947), it was clearly desirable to study the effects of different reactions on the germination of the spore, and on the growth and development of the prothallus.

A 1% British agar was prepared, using the "one quarter calcium" solution instead of water. As strong alkali is known to precipitate the mineral components of agar to an extent roughly dependent upon the amount of alkali added, it was necessary to test a sample of the agar with a good excess of caustic soda solution to find whether the medium at 1% strength set sufficiently firmly. It was found that, although the jelly was not so rigid as at lower reactions, it was firm enough to bear the prothalli. Strong sulphuric acid added to a sample did not affect the setting capacity of the agar to the same extent as the addition of alkali.

In experiments involving the growing of prothalli on agar, it is always advisable to have the agar as weak as is consistent with setting, as a rigid gel is penetrated with difficulty by rhizoids.

The initial reactions were measured by means of the Capillator, except that for estimations above 9.6 (the upper limit of the Capillator) the Hellige Comparator was used. The agar was poured into eight 250 ml. flasks, leaving about one ninth of the volume in the original flask. The contents of the latter were then divided between six boiling tubes, giving a depth of about one and a half inches in each. The tubes were plugged and the agar allowed to set. As the agar was found to have an initial reaction of pH 6.8, this series of six tubes provided the pH 7 cultures without adjustment. The contents of each of the eight flasks were adjusted to a different pH by means of N. sulphuric acid or N. caustic soda to give agars of approximately pH 2, 3, 4, 5, 6, 8, 8 and 10. The agar in each flask was divided between six tubes as described for the pH 7 set.

It was often necessary to make several additions of acid or alkali to arrive at the correct reaction and, after each addition, a sample had to be withdrawn into the micro-pipette for testing. It will be appreciated, therefore, that it was impossible to work under sterile conditions, and it is not surprising that moulds and bacteria were troublesome in some of the cultures.

After allowing the agar to set with the tubes in a vertical position, liberal sowings of spores were made with a brush. The tubes were supported in test-tube racks and kept in the greenhouse. Caps of cellophane were placed over the cotton wool plugs and held in position by elastic bands, to restrict loss of water from the tubes.

The experiment was started on March 10th, 1947. Sterile water in small quantities was added occasionally. The cultures ran for a long period, harvesting taking place on December 1st. The main results for two typical cultures at each reaction are summarised in Table 17.

Table 17: Data relating to the Germination of Spores and Development of Prothalli on Agars of Different pH.

Tube No.	No. of Prothal.	Size of Prothall.	Antheridia	Archegonia	Sporophytes
pH 2 to 5 (inclusive)	No germination.				
pH 6:					
B.S.6/1	209	Small e.g. 7 mm.	Usually none	Numerous e.g. 53	None
B.S.6/2	282	Mostly small	Few	Numerous	5 early stage

Tube No.	No. of Prothal.	Size of Prothall.	Antheridia	Archegonia	Sporo: :phytes
pH 7:					
B.S.7/5	6	Various	Numerous	Numerous	1 (see Fig. 27)
B.S.7/6	4	Various	Numerous	Numerous	None
pH 8:					
B.S.8/2	2	Large	None	Numerous e.g. 100	None
B.S.8/5	Groups of numerous, minute prothalli		Numerous	None	None
pH 9:					
B.S.9/3	1 (dead)	Large	None	Numerous	1 (see Fig. 29)
B.S.9/4	3	Large	Numerous	Numerous	None
pH 10:					
B.S.10/1	1	Small	None	20	None
B.S.10/5	Group of minute prothalli		Numerous	None	None

The large numbers of prothalli produced at pH 6 were rich emerald green in colour and were very uniform in size. The density was so great that the prothalli were, in general, orientated vertically to the surface of the agar. Two pH 6 cultures are shown in Fig. 26. At pH 7, the few large prothalli had turned brown and possessed remarkably thick, fleshy cushions.

Pteridium cultures on agar at different reactions.

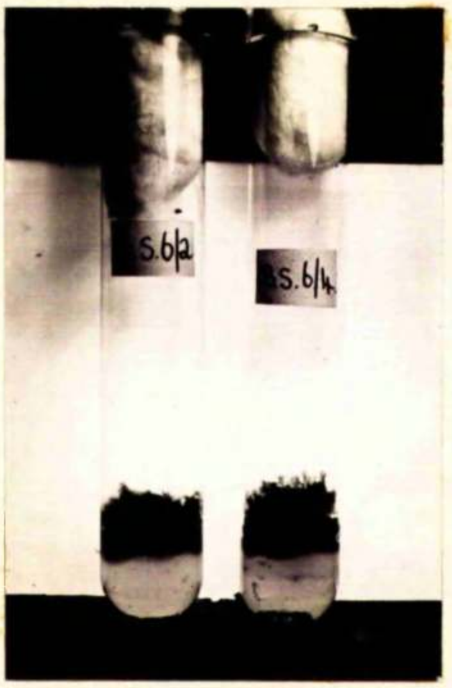


Fig.26. pH 6

Fig.27. pH 7

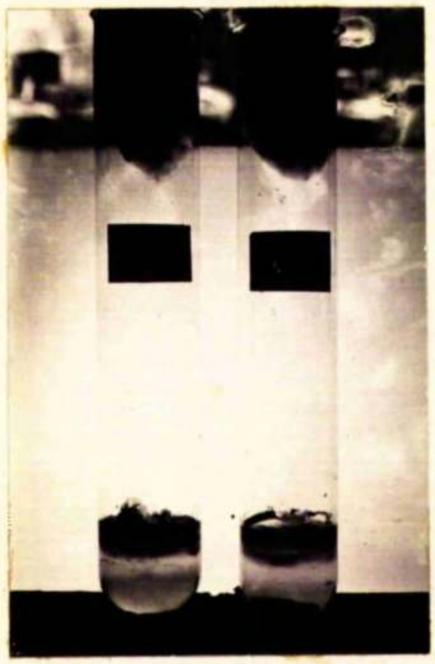


Fig.28. pH 8

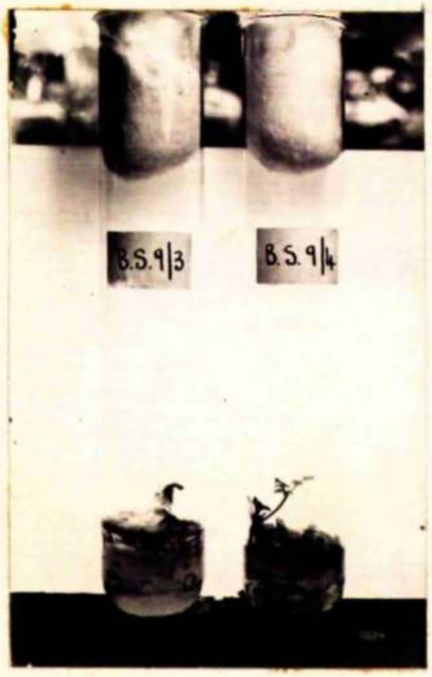


Fig.29. pH 9

Similar large prothalli occurred at pH 8 and pH 9, with the exception that certain of the former cultures bore clusters of minute prothalli, to which further reference is made below. In those pH 10 cultures not containing clusters of this type, the few prothalli were smaller than at pH 8 and pH 9.

The examination of the cultures microscopically began with the pH 6 series, and the most outstanding feature was the great profusion of archegonia. These were found not only near the growing point, but all along the midrib. This was the arrangement in the majority of the prothalli which were narrow in proportion to length. A few prothalli, however, were larger and more heart-shaped and, in these, a cushion was developed in which were embedded the large numbers of archegonia. The latter were at various stages of development, mature, brown ones being found on the older parts, immature ones nearer the apical cell. Antheridia were present in small numbers in a few prothalli (particularly those which were pale green in colour) and were usually confined to the margins. The sporophytes found were very young, appearing as spherical, green bodies embedded in the prothallus.

At pH 7, the numerous antheridia which the large prothalli bore were mostly ruptured. The large prothalli found at higher reactions either had no antheridia at all, or, if the latter were present, they were ruptured. Spermatozoids were observed in the water on the slide, and also in the necks of the archegonia in some instances. The clusters of very minute prothalli occurring at pH 8 and 10 were invariably pale green in colour. Antheridia were so profuse in some prothalli that almost every cell had developed into one. Certain of the prothalli were actually filamentous. Thus, in this experiment, male, female and hermaphrodite prothalli were encountered, the first strongly differentiated from the others morphologically. Apart from the fact that antheridia appear to be generally more numerous on the alkaline side of neutrality, it is difficult to see any correlation between the relative numbers of antheridia and archegonia, and hydrogen ion concentration. A complicating factor, for instance was the great difference in density between the pH 6 cultures and the higher reactions. The congested conditions in the former would have restricted the growth in size of individual prothalli.

The sporeling plant growing in B.S.7/5 (illustrated in Fig.27) possessed a root system which was spreading freely through the agar. When extracted, the root system measured about 10 cm. in length. The plant at pH 9 (Fig.29) had three small fronds, with a similar number of frond buds. Its root system was 6.1 cm. long.

The reactions of the agars were checked after harvesting, as any changes must be taken into consideration in assessing the results of the experiment. In estimating the final values, a portion of the agar was mixed in distilled water, care being taken to exclude prothalli, algae, etc. The reactions of the samples so prepared were measured with the glass electrode system. In certain cases, values were also obtained with the Capillator, in order to compare the latter against the standard method.

Table 18: Initial and Final Reactions of Agars in Bracken Germination Experiment.

Culture Number	Initial pH	Final pH (Glass electrode)	Final pH (Capillator)
pH 2:			
B.S.2/1	2.0	2.27	2.0(T.B.)
B.S.2/4	2.0	2.25	2.2 "
pH 3:			
B.S.3/1	3.1	2.48	2.6 "
B.S.3/4	3.1	2.51	2.6 "
pH 4:			
B.S.4/3	4.1	3.96	4.2 (B.P.B.)
B.S.4/6	4.1	3.81	4.1 "
pH 5:			
B.S.5/1	4.9	3.58	-
B.S.5/2	4.9	3.56	-

Culture Number	Initial pH	Final pH (Glass electrode)	Final pH (Capillator)
B.S.5/3	4.9	3.71	4.0 (B.C.G.)
B.S.5/4	4.9	3.72	4.0 (B.P.B.)
B.S.5/5	4.9	3.69	-
B.S.5/6	4.9	3.60	3.8 "
pH 6:			
B.S.6/1	6.0	6.59 *	-
B.S.6/3	6.0	6.41	6.6 (B.T.B.)
pH 7:			
B.S.7/5	6.9	6.67 *	-
B.S.7/6	6.9	6.88 *	-
pH 8:			
B.S.8/1	7.9	7.08	7.0 (B.T.B.)
B.S.8/2	7.9	7.83 *	-
B.S.8/4	7.9	7.40	7.4 "
B.S.8/5	7.9	6.58 *	-
pH 9:			
B.S.9/1	9.0	8.82	9.1 (T.B.)
B.S.9/3	9.0	8.40 *	-
B.S.9/4	9.0	6.64 *	-
pH 10:			
B.S.10/1	10.0	8.40 *	9.0 "
B.S.10/2	10.0	8.20	8.9 "
B.S.10/5	10.0	7.96 *	9.1 "

B.C.G. - Bromo-cresol green, B.P.B. - Bromo-phenol blue, B.T.B. - Bromo-thymol blue, T.B.- Thymol blue (alkaline range)

The cultures occurring in Table 17 are marked *.

Due, possibly, to fungal growth, the pH 5 cultures suffered a large fall of reaction, with the exception of B.S.5/2. This, in all probability, accounts for the complete absence of germination at pH 5, while one unit of pH higher, germination must have been near 100%. Conway (1947) carried out an experiment on somewhat similar lines, and she obtained prothalli in the pH 4 and pH 5 cultures. She did not, however, check the reactions at the end of the experiment. In view, therefore, of the disagreement between these experiments, a definite statement cannot at present be made concerning the lowest pH at which germination occurs. Undoubtedly, the optimum level is in the region of pH 6 to 6.5. Germination was not very rapid in any of the writer's cultures. Good germina:tion was observed in the pH 6 series after about seven weeks, when most were at the filamentous stage, emerging from the spore. The spores may have been somewhat stale at the start.

It is of interest to note that, in both of those cultures in which clusters of minute, male prothalli were found, the fall in pH was greater than in the other tubes of the same set, in which large prothalli had been growing. The writer is unable at present to hazard any explanation of this observation.

Readings taken with the B.D.H. Capillator show that, for a well-buffered medium such as agar, the colorimetric method is reasonably reliable.

<u>Conclusions from Bracken Experiments.</u>

The water cultures, in so far as one can draw conclusions from work on so small a scale, show a reaction of about pH 5 to be the most favourable for growth of the sporophyte. It is also clear, however, that the fern exhibits a fairly wide tolerance. This is well in keeping with the wide range of soil reactions on which bracken is encountered in the field. The tolerance is particularly marked on the acid side, where good plants were found at pH 3 (the lowest of the series) and this is portrayed in the relatively less steep decline below pH 6 of the curve in Fig.23.

The best germination of spores was at pH 6, so that the optimum in this experiment lay somewhat above that for the growth of young sporophytes in water culture. Allowing for the considerable fall in the reaction of the pH 5 cultures, but for which a certain degree of germination might have occurred, markedly acid media are inhibitory for spore germination. Although, however, germination was found at neutrality and at all the alkaline reactions tried, it was extremely low, and the writer finds no justification for the view that the spore prefers an alkaline or neutral medium for germination. The range for high percentage germination and production of prothalli of good colour and vigour is very narrow indeed, namely around pH 6. Although large sporophytes developed in two of the tubes at higher reactions, it is believed that this was more a result of adequate room for growth than a direct effect of pH. In the pH 6 tubes, overcrowding was severe, allowing no space for individual prothalli to increase in size. Even so, a few sporophytes in an early stage of development were found.

(B) CALLUNA.

1. Review of Literature.

Olsen (1923) gave the following data for the average frequency of *Calluna vulgaris* in relation to pH of the soil in Denmark:-

Soils	pH 3.5 to 3.9 ;	Frequency	20
"	pH 4.0 to 4.4 ;	"	47
"	pH 4.5 to 4.9 ;	"	10
"	pH 5.0 to 5.4 ;	"	20

Fraser (1933) found *Calluna* occurring on soils ranging from pH 2.6 to 4.8, with a maximum incidence at pH 3.9.

Heath and Luckwill (1938) measured the pH of the soil at various depths under *Calluna* and found the mean to be 4.7.

2. Water Cultures (at the Agricultural College).

Cultural Arrangements and Plant Material.

The culture vessels used were earthenware or glass jars, some of which were 750 ml. capacity, others holding only 350 ml. of solution. One plant was grown in each jar and there were four cultures at each reaction. The nutrient solution was half-strength Crone. The experimental plants were seedlings originating from the same source as those used in the aeration experiments.

Experimental Procedure.

The experiment was commenced on July 2nd, 1948. The cultures ranged from pH 2 to 10 in steps of one unit. All the determinations of hydrogen ion concentration were made with the glass electrode system. Adjustments of the solutions to the desired pH were effected by the addition of N. sulphuric acid or N. caustic soda, as appropriate. The adjustments to the more extreme levels were made in stages over two days. The reactions of the solutions were maintained within 0.3 of the nominal value by checking and, if necessary, adjustment, every two days. Although the reactions of the alkaline solutions were unstable, the instability was not so great as with the form of Knop's solution used in the equivalent bracken experiment. The strongly acid reactions remained almost constant throughout the course of the experiment. Once brought to the prescribed level, the pH 2 and pH 3 cultures, though checked regularly, did not require alteration. Adjustments were occasionally made to the pH 4, 5, 6 and 7 cultures. Thus, it can be said that fairly efficient buffering extended as far as pH 7. Above, pH 8 and 9 were extremely unstable, the reactions dropping as much as one unit in 48 hours. The pH 10 solutions only fell by about 0.5 in the same period, a second but less efficient buffer zone beginning around pH 9.5. Apart from the stability or otherwise of the solutions, the positions of these buffer ranges were indicated by the amounts of acid or alkali required to effect adjustment. In the unbuffered zones, one drop of the reagent exerted a profound influence on the pH whereas, elsewhere, relatively large quantities were necessary.

Results of the Experiment.

The results of this experiment were not entirely satisfactory in that wide variations occurred in the condition of the four plants at each reaction. One of the factors contributing to this inconsistency in the results was the initial variability of the plants in size and, possibly health, which is inevitable when young plants are taken from the field. The plants varied in the ease with which they adapted themselves to water culture. Another cause of failure in some cases was the appearance of crystalline deposits on the lower leaves and branches. This phenomenon has been referred to previously. Despite these discrepancies, however, this experiment yielded some indication of the effect of pH on young *Calluna*. A description of the final form of the experimental plants is given in Table 19.

Table 19: The Final Condition of Heather Plants grown in Half-Strength Crone Solution at Various Reactions.

Nominal pH of Solution.	Condition of Plants.
2	All dead.
3	One plant dead and very few living shoots on two others. Fourth plant green, but little root growth.
4	One plant very good, with branched root system 11 cms. long. Of the other plants, one was small but vigorous; another had many dead branches; the fourth was dead.
5.	Three plants dead. Fourth small and chlorotic.
6	One dead. Others dying, with chlorotic tips.
7	Marked chlorosis of tips. Profuse root branching in two plants, but poor elongation. One plant nearly dead.
8	Two dead. No shoot growth in remaining two. One very chlorotic. Some root branching but poor elongation.

Nominal pH of Solution	Condition of Plants.
9	Three dying. Chlorosis of living shoots. One dead.
10	Three dead. Remaining plant green and turgid, but no root growth.

Notwithstanding its limitations, this experiment is in accordance with the field evidence that a reaction of about pH 4 is most suitable for the growth of heather. Two of the pH 4 plants were growing vigorously. At no other reaction were the plants healthy. At pH 5, chlorosis became evident and was progressively more marked at higher reactions. Olsen (1923) found a similar chlorosis in alkaline solutions in all the species with which he dealt. An anomaly was the green plant occurring at pH 10. No growth took place, however, either in its root or stem.

3. Germination and Subsequent Development on Agars of Various Reactions.

The arrangement of this experiment was similar to that on the germination of bracken spores, with the exception that the agar was made up with half-strength Crone solution. Calluna seeds, collected from Ballochraggan, were sown as uniformly as possible on to the agar in each tube. Sowing took place on March 10th, 1947. Six weeks later,

<u>Calluna</u> cultures on agar at different reactions.

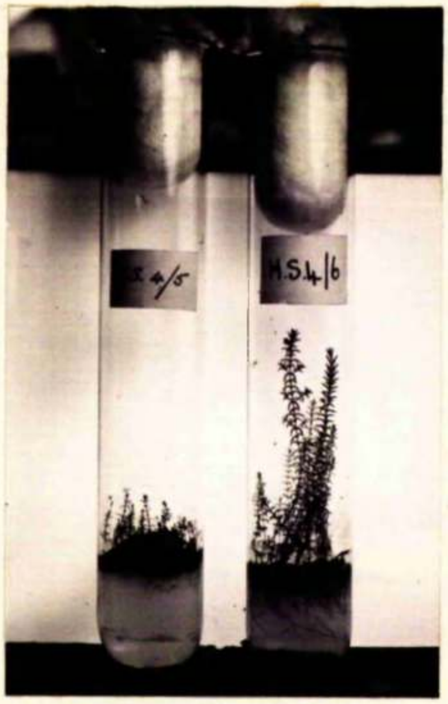


Fig.30. pH 4

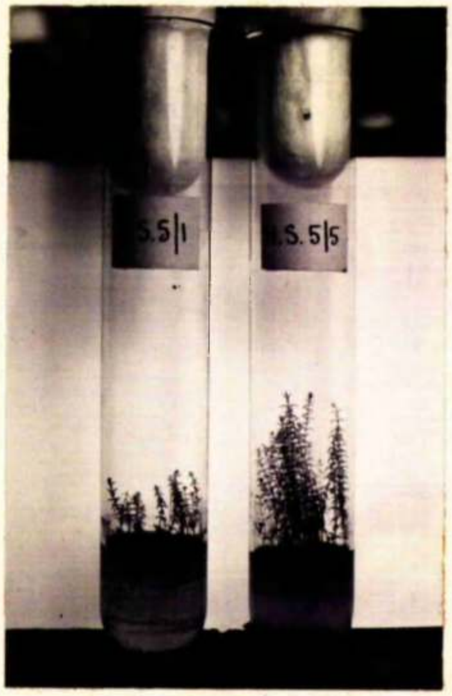


Fig.31. pH 5

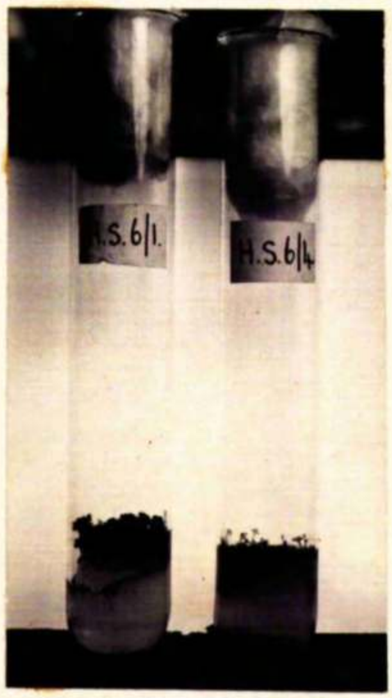


Fig.32. pH 6

the cultures were examined and germination to a greater or lesser degree was found to have occurred at all reactions. In most cases, the radicle was emerging, but in some at pH 4, 5, and 6, elongation of the hypocotyl had followed.

The final examination of the series of cultures was made on November 3rd, 1947. No seedlings or germinating seeds were present in any of the tubes at pH 2 and pH 3. A low degree of germination had occurred in the early stages of the experiment, but development had not proceeded beyond the emergence of the radicle. The seedlings had then died off. It appears, therefore, that the effect of reaction is less marked on germination itself than on the developmental processes succeeding germination.

Two typical examples at each reaction were photographed, and some of these appear in Figs. 30, 31 and 32. Although seedlings occurred at pH 7 and above, the photographs are not included as the seedlings cannot be seen clearly. The photographs show the wide variation in the development of seedlings among the six cultures at pH 4 and those at pH 5. The tubes selected for photographing were chosen to represent both the best seedlings and the poorly-developed ones in a given series. A feature which cannot be revealed in a photograph of this type is the severe chlorosis of almost all the tips which occurred

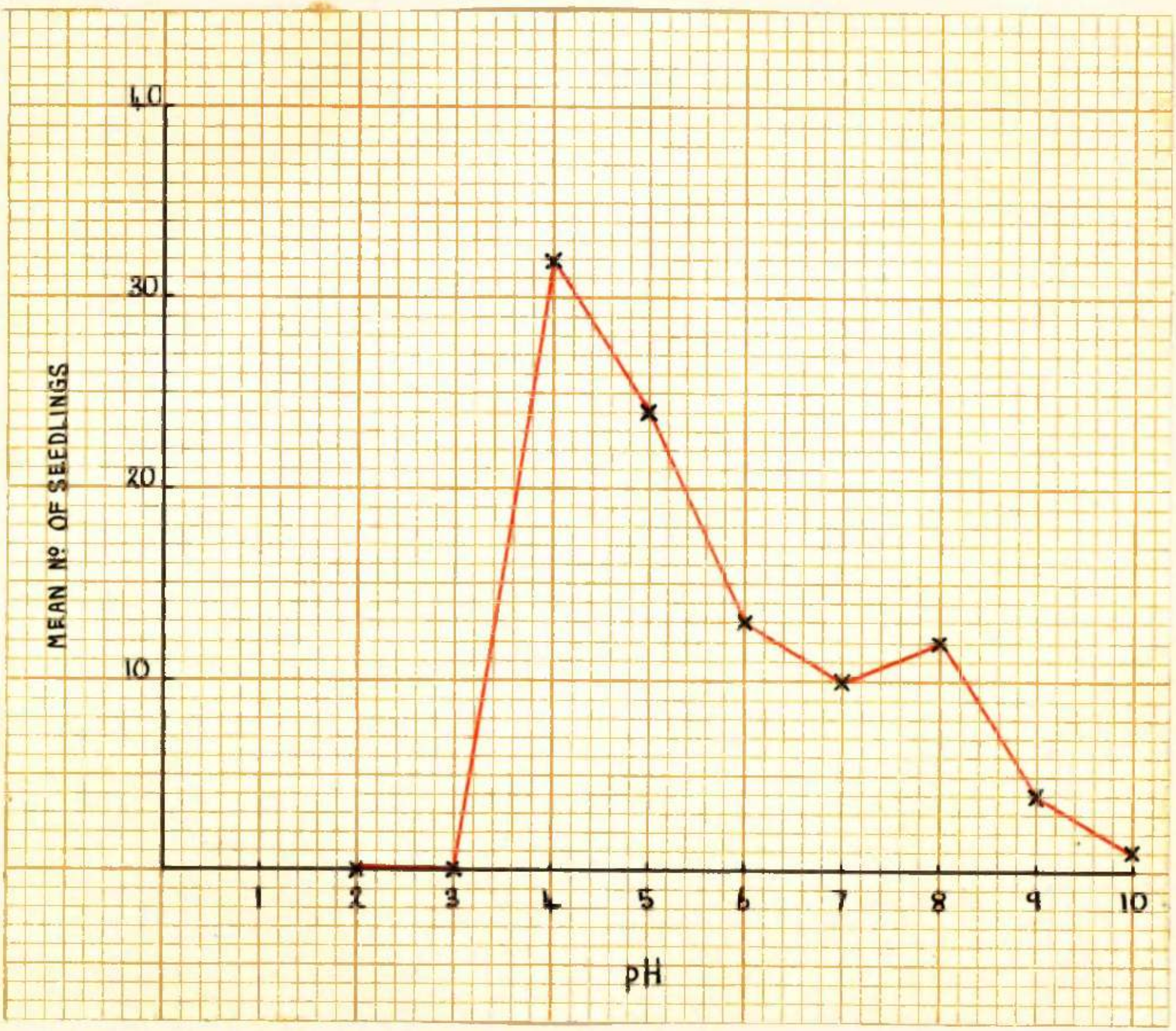


Fig. 33. Graph showing the mean number of Calluna seedlings at each reaction against pH in agar cultures.

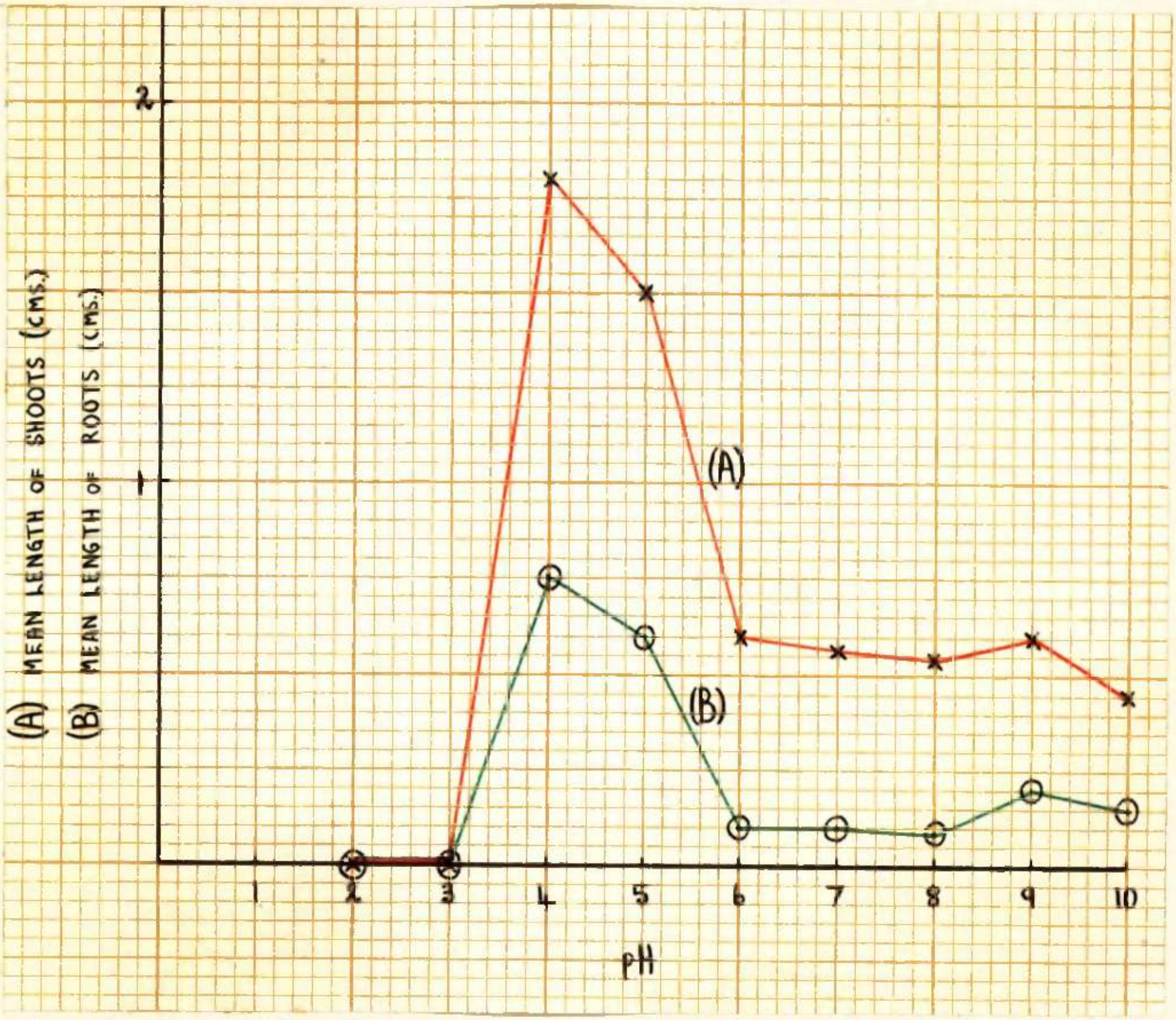


Fig. 34. Graph showing the mean length of shoots (A) and mean length of roots (B) against pH for <u>Calluna</u> in agar cultures.

in the pH 5 seedlings. In many plants, this had been followed by the death of the tips.

The numerical data are presented in graphical form. In Fig.33, the mean number of seedlings for each set of six tubes is plotted against pH. This is not a measure of the germination of Calluna seeds in relation to pH, but of those embryos attaining seedling status. The bimodal form of the curve is well-marked. Most seedlings are found at pH 4, with a second but very much lower maximum at pH 8. After counting, the lengths of the shoots and roots were measured for every seedling and the means plotted against pH in Fig.34. Greatest dimensions were found at pH 4 and, in these curves, the tendency to a double maximum is not so clearly defined.

Above pH 5, all the seedlings were very stunted and, in many cases, possessed no roots. A large proportion were dead.

As in the case of the bracken cultures, estimations were made of the final reactions of the agars, and it was found that considerable changes in reaction had taken place in those cultures in which seedlings occurred. The values obtained are given in Table 20.

Table 20: Initial and Final Reactions of Agars in Heather Germination Experiment.

Culture Number	Initial pH	Final pH (Glass electrode)	Final pH (Capillator)
pH 2:			
H.S.2/1	2.0	2.29	2.0 (T.B.)
H.S.2/6	2.0	2.14	
pH 3:			
H.S.3/1	3.0	2.42	2.6 "
H.S.3/6	3.0	2.50	
pH 4:			
H.S.4/3	3.9	5.92	6.2 (B.T.B.)
H.S.4/4	3.9	6.22	6.6 "
H.S.4/5	3.9	5.20	
pH 5:			
H.S.5/2	5.1	6.30	6.6 "
H.S.5/3	5.1	6.22	6.4 "
pH 6:			
H.S.6/2	6.2	-	6.5 "
pH 7:			
H.S.7/3	7.0	-	6.6 "
H.S.7/4	7.0	6.07	6.2 "
pH 8:			
H.S.8/2	7.9	6.65	6.8 "
H.S.8/5	7.9	6.52	
pH 9:			
H.S.9/1	9.0	6.85	6.8 "
pH 10:			
H.S.10/1	10.0	7.28	7.2 " 7.8 (P.R.)

(B.T.B. - Bromo-Thymol blue, P.R. - Phenol red, T.B. - Thymol blue (alkaline)).

Preparations were made of typical root systems in the cultures for microscopical examina:
:tion. The material was stained with cotton blue in lactophenol and mounted in glycerine jelly containing a small quantity of cotton blue. In the seedlings at pH 4, many cortical cells of the finer branch roots were packed with heavily stained mycelium. External hyphae of the mycorrhizal fungus were also present, especially round some of the root tips. At pH 5, however, external hyphae were far more profuse, but the contents of the cortical cells did not take up the stain. It was thus difficult to determine whether the intracellular mycelium was present but at a different stage from that at pH 4, or the deformed protoplasts of the cells were being observed.

3. SUMMARY AND CONCLUSIONS ON SOIL AERATION AND HYDROGEN ION CONCENTRATION.

A) SOIL AERATION.

1. Field Observations.

1) The advance of bracken is arrested by marshy ground.

2) Small groups of bracken fronds are frequently found apparently isolated in *Carex* and *Juncus* areas.

3) Such groups are invariably associated with a stone or other feature of the site whereby better conditions of aeration might be expected to obtain.

4) In all cases which the writer has examined, excavation of the underground parts revealed a compact rhizome system, connected to the nearest Pteridietum by one or more rhizomes.

2. Field Experiments.

5) Irrigation of bracken leads to the death of existing fronds and to a marked decrease in the number and size of subsequent fronds.

6) The effects of irrigation on the rhizomes are very slow to appear.

7) The fronds of rhizomes immersed in running water remain healthy longer than those of rhizomes in stagnant water.

8) Irrigation of Callunetum, while supporting the greater resistance of the plant,

has not yet indicated how long irrigation must be continued to produce signs of ill-health.

3. Solution Cultures.

9) Providing that oxygen supply is the critical factor in the water culture experiments and the effects are not due to some unknown factor arising out of the presence or absence of agitation, the oxygen requirement of bracken is considerably higher than that of heather.

10) With young bracken sporophytes, aeration has a more immediate effect on root development and distribution than on growth of fronds.

11) In *Calluna*, aeration and passage of nitrogen inhibit root and shoot development.

4. Soil Cultures.

12) With the mature bracken plant, waterlogging leads to rapid collapse of the fronds.

13) When a waterlogged culture is aerated continuously from the start, large fronds can be produced and maintained. These may produce spores of high viability.

14) Although the cultures for *Calluna* were inconclusive, the indications were that the heather plant is more resistant to stagnant waterlogging.

15) In both *Pteridium* and *Calluna*, root growth is favoured by aeration of waterlogged soil cultures.

B) HYDROGEN ION CONCENTRATION.

1. Pteridium.

1) The maximum growth of young sporophytes in nutrient solution occurs between pH 5 and 6.

2) Maximum germination of spores takes place at pH 6 on agar.

3) Although undifferentiated sporophytes were found at pH 6, subsequent development was recorded only at neutrality and pH 9.

2. Calluna

4) In nutrient solution, the optimal level of reaction appears to be about pH 4.

5) Above pH 4, chlorosis is progressively more marked.

6) In agar cultures, the maximum germination of seeds occurs at pH 4.

7). A reaction of pH 4 is also optimal for elongation of shoots and roots in agar culture.

8) At pH 5, severe chlorosis of the tips prevails.

9) Above pH 5, shoots and roots are very stunted.

4. THE COMPETITION BETWEEN BRACKEN AND HEATHER.

Aeration as a Factor.

Watt (1945) has drawn attention to the unsound foundation of the view that bracken is always successful in competition with heather. The outcome depends upon the age and vigour of the *Calluna* and, although the margin of a vigorous Callunetum may be invaded by bracken, the latter can be kept in check and may ultimately be ousted by the heather. The means by which heather suppresses bracken was thought by Watt to be the effect on soil aeration of the accumulation of heather humus. Such a layer, he believes, would so reduce aeration that fewer buds would be produced by the rhizomes.

Watt's hypothesis rests upon two assumptions, 1) that bracken is more sensitive than heather to reduced aeration, 2) that the superficial layer of heather humus restricts aeration of the soil beneath. The results of the experiments described above provide some experimental basis in favour of the first assumption. On the second point, there is the evidence that the surface peat of *Calluna* and *Nardus* areas at Ballochraggan were extremely resistant to the downward percolation of water during irrigation. It is very likely that it constitutes a similar barrier to gaseous exchange between the soil atmosphere and the air, under ordinary field conditions. If this is the case, the oxygen in the soil will rapidly

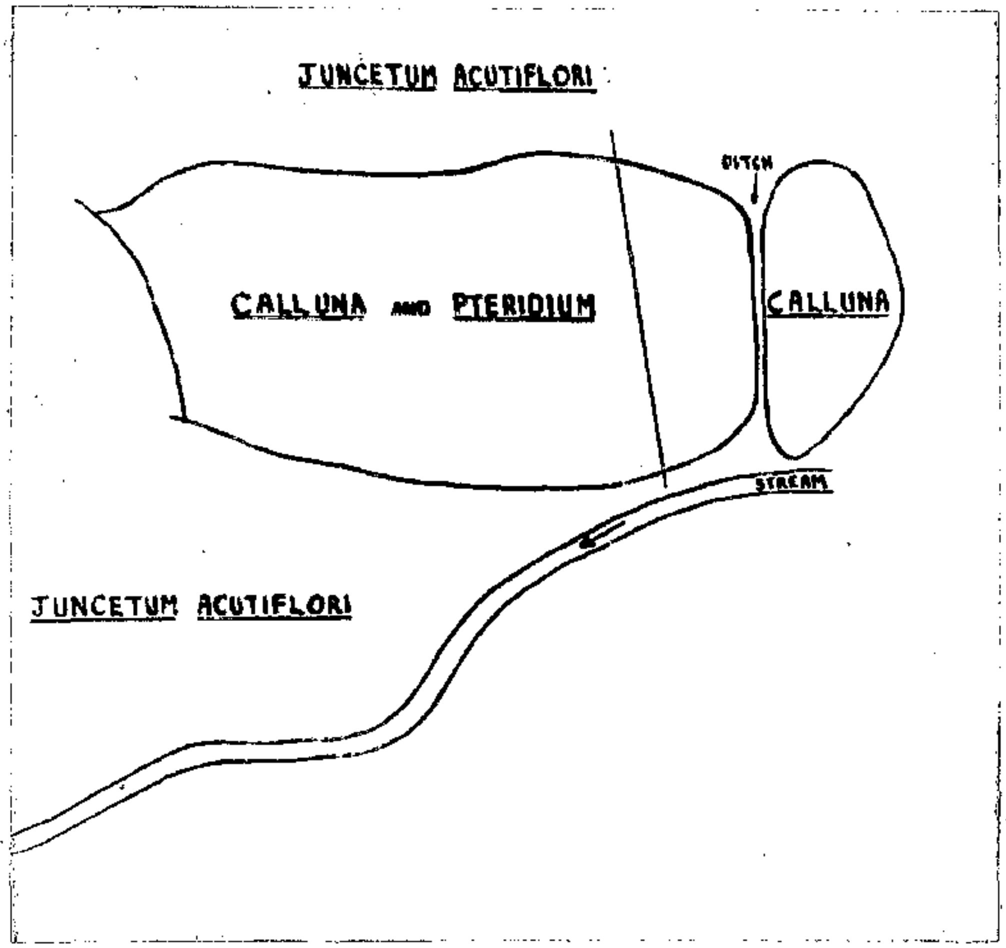


Fig. 35. The island of Calluna and Pteridium in Section 23, Square 2, showing the line of the profile excavation.

be exhausted by root respiration and low oxygen percentages will result.

Estimations of "air content", expressed as percentages of the soil by volume, were made by Heath, Luckwill and Pullen (1937). They found the Pteridietum soils to be well-aerated relative to those of Callunetum. Furthermore, the superficial two inches of the heather soils were moderately aerated, but the more compact sub-peat yielded very low values.

It is relevant at this stage to describe an investigation of the underground systems of these plants in an area where they occur together, particularly from the standpoint of the soil horizons occupied and, if possible, to correlate their relative positions with different conditions of aeration.

The site of the profile excavation was Section 23, Square 2, 155.180. The area is a small island of old, "leggy" Calluna, raised a few feet above the "flush" which surrounds it. On the southern margin, the fall is steep towards a stream. An outline diagram of the area (not to scale) is given in Fig. 35. A narrow ditch separates the eastern end from the rest. Whereas the larger, western part is dominated by a mixture of degenerate Calluna and vigorous Pteridium, the small, eastern section is devoid of the fern. This confirms Farrow's (1915) observation that a small ditch containing stagnant

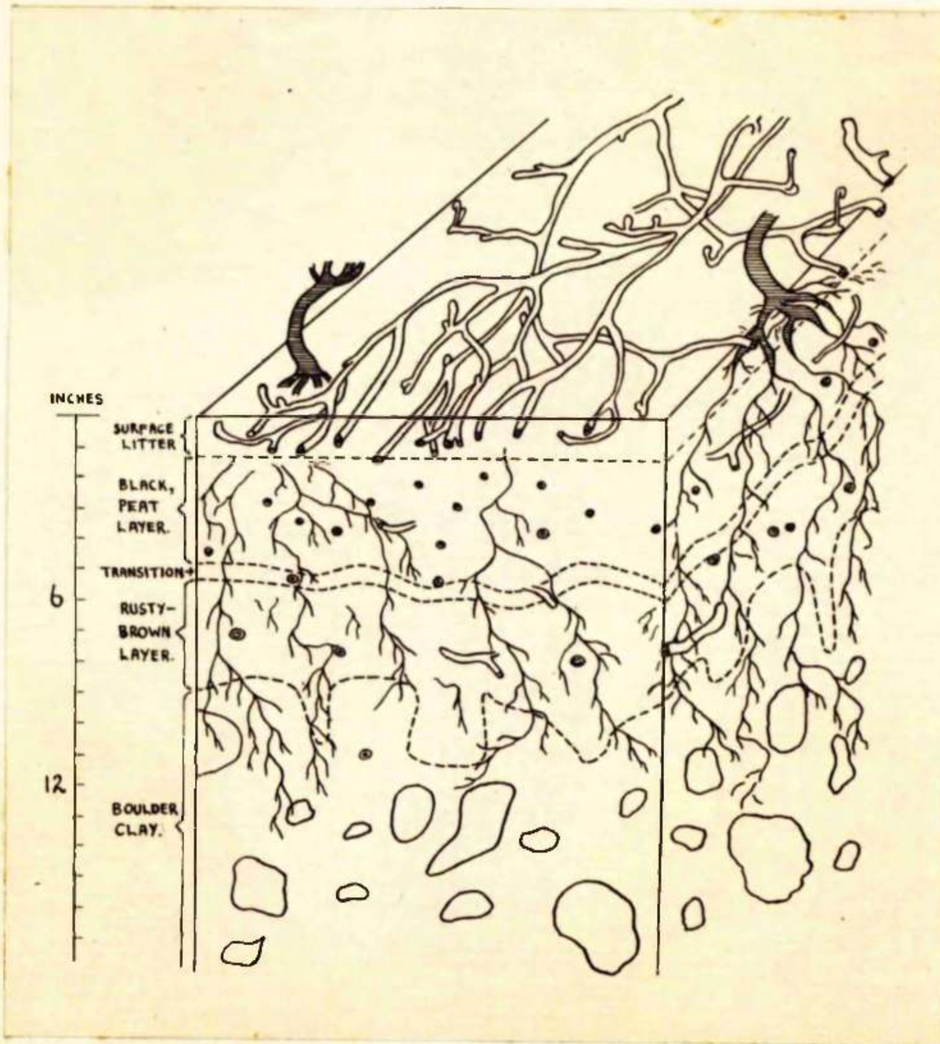


Fig.36. Diagram of the profile exposed in Section 23, Square 2, showing the positions of the under:
:ground parts of <u>Calluna</u> and <u>Pteridium</u> in relation to the soil layers.

water arrests the spread of bracken. The line of the profile is shown in red. A trench was dug to a depth of about three feet. Fig.36 is a diagram of the profile exposed and shows the distribution of the underground parts of the bracken and heather. The superficial layer of humus and litter was about one and a half inches in thickness. It was loosely packed and, in it, a complex system of frond-bearing rhizomes ramified. Thicker rhizomes were found in the black, peaty layer. Below this, a brownish region occurred, with downward projections into the boulder clay. The brown layer would appear to represent the iron zone of a podsol, but, in this case, podsolisation is at an early stage, there being only a suggestion of a bleached layer above. Even at so shallow a depth as six inches, that is, at the top of the brown zone, there were very few living rhizomes. Rotted remains were abundant in this zone and in the boulder clay. The lowest living rhizome encountered was at eleven inches below the surface. Healthy rhizomes of Juncus acutiflorus extended considerably lower. It is of interest to note that the bracken rhizomes were, in general, growing in an east-west direction, very few towards the Juncetum.

The roots of heather were frequently found in the iron zone and showed no tendency to be restricted to the surface humus or the upper peat layer. This is the reverse of the usual arrangement where bracken rhizomes run below the shallow-rooted Calluna.

Owing to the surrounding Juncus flush, the water table is high in the Calluna-Pteridium hummock. (The boulder clay was wet, and water collected readily on the floor of the trench.) In the writer's view, the Juncetum is of relatively recent origin, brought about by deteriorating drainage. It would seem that, previously, the boulder clay and iron zones of the Calluna hummock had been well-drained and strong bracken rhizomes, as judged by the diameters of the remains, had occupied these horizons. The Calluna roots present in bygone days thus bore their normal relationship to the deep bracken rhizomes. The progressive rise of the water table, consequent upon the failure of adequate drainage, would bring about conditions of oxygen deficiency in the lower horizons of the soil. Thus, the rhizomes would be killed off gradually until, at present, hardly any remain living in the iron zone and the boulder clay. Simultaneously, the surface of the soil would have been rising further above the level of the Juncetum by deposition of litter and humus and subsequent peat formation. Being "forced out" of the lower levels, rhizome development would be transferred to the more superficial, drier layer, where aeration is relatively good. The heather, being more tolerant of poor aeration and, further, being too old to maintain itself in competition with bracken in the zones which the latter has seized, occupies the lower peat and iron layers. Had the *Calluna* been vigorous, the bracken could never have attained such strength. On the basis of Watt's view, more humus and compact peat would have been produced by strong *Calluna* and conditions of aeration almost as poor as in the wet boulder clay would have resulted. The superficial network of frond-producing rhizomes could not have developed, and thus the *Calluna* might have suppressed the fern.

This hypothesis depends upon oxygen deficiency being the cause of death of the deep rhizome system. It is possible that increased water content has resulted in unfavourable changes in the chemical nature of the iron zone and boulder clay.

The writer has commenced studies of the respiration rates of bracken and heather roots under different conditions of oxygen supply. In the field, it is hoped to carry out estimations of oxygen in the various soils, and soil horizons. Experimental work on the porosity of the superficial layers of *Calluna* soils is also desirable.

Hydrogen Ion Concentration as a Factor.

The optimal levels of reaction for germination and growth of young plants are higher in *Pteridium* than *Calluna*. Furthermore, the bracken sporophyte exhibits a very much wider range of tolerance. Thus, one could visualise the *Calluna* being adversely affected by a rise in the soil reaction, the bracken being favoured. The writer believes that this factor may be important in explaining the growth of bracken after a fire, as well as the reassertion of dominance by the heather which may follow later. Burning results in the surface of the soil being overlaid by alkaline ash. Conway (1947) states that bonfire ash yields a pH reaction of 8.2 to 8.4. Whilst this ash is on the surface, conditions unfavourable to the regeneration of *Calluna* will obtain. In time, however, the ash will be washed gradually to the lower soil levels. The net reaction of the soil will be the resultant of the effects of the ash and the acid peat. This net value, very alkaline at the surface after the fire, will fall as the ash products penetrate lower into the soil, due to neutralisation by humus acids. It is thus possible that, by the time the soil occupied by the bracken roots and rhizomes is reached, a pH approaching the optimum value might exist for a period. This might give the impetus to growth of bracken observed so frequently after a fire.

At the surface, the alkaline components of the ash either having been neutralised or leached out, favourable conditions for heather seed germination, and development of the seedling plants, may be restored. In this way, Calluna may reassert its dominance after some years.

Much of what has been written in this section is frankly speculative. In an attempt to provide a factual basis, the courses of changes in soil reaction after a fire should be traced by systematic measurements until stability is regained.

Concluding Remarks.

In this section, hypotheses have been put forward tentatively in an effort to relate the experimental data obtained on the responses of bracken and heather to aeration and hydrogen ion concentration, to the problem of competition between these species under field conditions. Some aspects appear to be more easily explicable on the basis of soil aeration, others on soil reaction, being the governing factor. It may well be that the complete explanation is to be sought in the interaction of these and/or other factors. For instance, oxidation-reduction potentials of soils (themselves probably a measure of aeration) vary inversely with the hydrogen ion concentration. It is clear that there are numerous lines of experimental inquiry (some of which have been indicated above) which must be pursued, both in the laboratory and in the field, before the full story of competition will be known.

LITERATURE CITED.

ADAMSON, R.S., 1918: On the Relationships of Some Associations of the Southern Pennines. J.Ecol., 6; 97-109.

ALLISON, R.V., and SHIVE, J.W., 1923: Studies on the Relation of Aeration and Continuous Renewal of Nutrient Solution on the Growth of Soybeans in Artificial Culture. Amer. J.Bot., 10, 554-567.

ANDREWS, F.M., and BEAL, C.C., 1919: The Effect of Soaking in Water and of Aeration on the Growth of Zea mays. Bull. Torrey Bot. Cl., 46, 91-100.

ARRHENIUS, O., 1922: Hydrogen Ion Concentration, Soil Properties and Growth of Higher Plants. Ark. Bot., 18, 1-54.

ASPREY, G.F., 1947: The Vegetation of the Islands of Canna and Sanday, Inverness-shire. J.Ecol., 34, 182-193.

BEAL, C.C., 1918: The Effect of Aeration on the Roots of Zea mays. Proc. Ind. Acad. Sci., 1917, 177-180.

BERGMAN, H.F., 1920: The Relation of Aeration to the Growth and Activity of Roots, and its Influence of the Ecesis of Plants in Swamps. Ann. Bot., 34, 13-33.

BRAID, K.W., 1934: Bracken as a Colonist. Scot.J.Agric., 17, 59-71.

BRYAN, O.C., 1922: Effect of Different Reactions on the Growth and Nodule Formation of Soy Beans. Soil Sci., 13, 271-302.

BRYANT, A.E., 1934: Comparison of Anatomical and Histological Differences between Roots of Barley grown in Aerated and Non-aerated Culture Solutions. Plant Physiol., 9, 389-391.

CANNON, W.A., 1920: Effect of a Diminished Oxygen Supply in the Soil on the Rate of the Growth of Roots. Carnegie Inst. Wash. Yearbook, 19, 59.

———— 1925: Physiological Features of Roots, with Special Reference to the Relation of Roots to Aeration of the Soil. Carnegie Inst. Wash. Pub., No. 368.

———— and FREE, E.E., 1917: The Ecological Significance of Soil Aeration. Science, 45, 178.

————, ————, 1920: Root Adaptation to Deficient Soil Aeration. Carnegie Inst. Wash. Yearbook, 19, 62.

CLARK, H.E., and SHIVE, J.W., 1932: Influence of Continuous Aeration upon the Growth of Tomato Plants in Solution Cultures, Soil Sci., 34, 37-42.

CLEMENTS, F.E., 1921: Aeration and Air-Content. Carnegie Inst. Wash. Pub. No. 315.

CONWAY, E., 1947: A paper read before the Royal Society of Edinburgh on the autecology of bracken. (In Press).

CONWAY, V.M., 1936: Studies in the Autecology of Cladium Mariscus, R.Br. Part I. Structure and Development. New Phytol., 35.

————, 1937: Studies in the Autecology of Cladium Mariscus R.Br., Part III. The Aeration of the Subterranean Parts of the Plant. New Phytol., 36, 64-96.

————————, 1940: Aeration and Plant Growth in Wet Soils. Bot. Rev., 6.

CRAMPTON, C.B., 1911: The Vegetation of Caithness considered in Relation to the Geology. Comm. for Survey and Study of British Vegetation.

CUMMING, A.C., and KAY, S.A.: Quantitative Chemical Analysis. 13th Ed., Edinburgh, 1949.

FARROW, E.P., 1915: On the Ecology of the Vegetation of Breckland. Part I. General Description of Breckland and its Vegetation. J.Ecol., 3, 211-228.

————————, 1916: On the Ecology of the Vegetation of Breckland. Part II. Factors relating to the Relative Distribution of Calluna Heath and Grass Heath. J.Ecol., 4, 57-64.

FOX, H.Munro, and WINGFIELD, C.A., 1938: A Portable Apparatus for the Determination of Oxygen Dissolved in a Small Volume of Water. J. Exp. Biol., 15.

FRASER, G.K., 1933: Studies of Scottish Moorlands in Relation to Tree Growth. Bull. Forest. Comm., No. 15.

FRITSCH, F.E., 1927: The Heath Association on Hindhead Common, 1910-1926. J. Ecol., 15, 344-372.

GAUT, R.C., 1904: Botanical Survey of a Pasture. Naturalist, No.567, 105-113.

GILBERT, S.G., and SHIVE, J.W., 1942: The Significance of Oxygen in Nutrient Substrates for Plants. I. The Oxygen Requirement. Soil Sci., 53, 143-152.

HALL, A.D., BRENCHLEY, W.E., and UNDERWOOD, L.M., 1914: The Soil Solution and the Mineral Constituents of the Soil. J.Agric.Sci., 6, 278-301.

HARDY, M., 1906: Botanical Survey of Scotland (North of Mid Perth and Mid Fife). Scot.Geogr.Mag., 22, 229.

HEATH, G.H., and LUCKWILL, L.C., 1938: The Rooting Systems of Heath Plants. J.Ecol., 26, 331-352.

——————, ——————, and FULLEN, O.J., 1937: The Heath Association on Blackdown, Mendip, Somerset. Proc. Bristol Nat.Soc., 4th Series, 8, 348-364.

HEDDLE, R.G. and OGG, W.G., 1936: Irrigation Experiments on a Scottish Hill Pasture. J.Ecol., 24, 220-231.

JEFFERIES, T.A., 1915: Ecology of the Purple Heath-Grass (*Molinia caerulea*). J.Ecol., 3, 93-109.

JEFFREYS, H., 1917a: On the Vegetation of Four Durham Coal-Measure Fells. III. On Water Supply as an Ecological Factor. J.Ecol.5.

——————, 1917b: On the Vegetation of Four Durham Coal-Measure Fells. IV. On Various Other Ecological Factors. Ibid., 5.

KNIGHT, R.C., 1924: The Response of Plants in Soil and Water Culture to Aeration of the Roots. Ann.Bot., 38, 305-325.

KROGH, A., 1935: Precise Determination of Oxygen in Water by Syringe Pipets. Ind. and Eng.Chem., Anal. Ed., 7, 131-133.

LIVINGSTON, B.E., and FREE, E.E., 1915: The Relation of Soil Aeration to Plant Growth. Carnegie Inst.Wash Yearbook, 14, 60.

—————, —————, 1916: Relation of Soil Aeration to Plant Growth, Ibid., 15, 78.

McTURK, N., 1837: On the Extirpation of Ferns from Pasture Lands Where the Plough Cannot be Used. Prize Essays & Trans. High. Soc. Scot., 2nd. Series, II, 371-376.

MILLER, E.C., 1938: Plant Physiology. 2nd. Ed., McGraw-Hill Book Co., Inc. New York.

MURRAY, J., 1837: On the Best Means of Eradicating Ferns from Pastures. Prize Essays & Trans. High.Soc.Scot., 2nd.Series, II, 376-379.

OLIVER, F.W., 1907: An Experiment in Co-operative Field-work in Botany. Trans.South-Eastern Union of Scientific Societies.

—————, and TANSLEY, A.G., 1904: Methods of Surveying Vegetation on a Large Scale. New Phytol., 3, 228.

OLSEN, C., 1923: Studies on the Hydrogen Ion Concentra: :tion of the Soil, and its Significance to the Vegetation, especially to the Distribution of Plants. C.R.Lab. Carlsberg, 15, 1-166.

PETHYBRIDGE, G.H., and PRAEGER, R.L., (1905): The Vegetation of the District Lying South of Dublin. Proc.R.Irish Acad., 25, 124-180.

POWERS, W.L., 1927: The Effect of Hydrogen Ion Concentration on the Growth of Certain Plants. Soil Sci., 24, 1-4.

RAYNER, M.C., 1915: Obligate Symbiosis in Calluna vulgaris. Ann. Bot., 29, 97.

—————, 1927: Mycorrhiza. New Phytol. Reprint, No. 15.

ROBBINS, W.J., 1923: An Isoelectric Point for Plant Tissue and its Significance. Amer. J. Bot., 10, 412-440.

SALISBURY, E.J., 1925: Incidence of Species in Relation to Soil Reaction. J.Ecol., 13.

SENEBIER, J., 1791: Physiologie Vegetale. In Encyclopedie Methodique, I.

SMALL, J., 1946: pH and Plants.

SMITH, R., 1900a: Botanical Survey of Scotland. I. Edinburgh District. Scot.Geogr. Mag., 16, No.3, 385.

——————, 1900b: Botanical Survey of Scotland. II. North Perthshire District. Ibid., 16, No.8, 446.

SMITH, W.G., 1902: The Origin and Development of Heather Moorland. Scot. Geogr. Mag., 18, No.II, 587.

——————, Botanical Survey of Scotland. III and IV. Forfar and Fife. Ibid., 20, No.12, 617.

——————, 1905: III and IV (continued with map of Fife) Ibid., 21, No.1, 4.

——————, 1905: III and IV (continued with map of Forfar) Ibid., 21, No.2, 57.

——————, 1905: III and IV (concluded). Ibid., 21, 117.

——————, 1916: Utilisation of Northern Mountain and Heath Land. Brit.Ass. Rep., Sect. K, 498.

——————, 1918: The Distribution of Nardus stricta in relation to Peat. J.Ecol., 6, 1-13.

STEWART, J.A., 1931: Inchmahome and the Lake of Monteith.

STILES, W., 1936: Introduction to the Principles of Plant Physiology. Methuen, London.

TANSLEY, A.G., 1911: Types of British Vegetation. Cambridge.

————————, 1939: _The British Islands and Their Vegetation._ Cambridge.

WATT, A.S., 1945: Bracken versus Heather. (A paper read before the British Ecological Society.)

WEAVER, J.E., and HIMMEL, W.J., 1930: Relation of Increased Water Content and Decreased Aeration to Root Development in Hydrophytes. _Plant Physiol._, 5, 69-92.

WINKLER, L.W., 1904: quoted in " The Chemists' Year Book", 1947 Edition, p. 143.

APPENDIX

VIEWS OF BALLOCHRAGGAN (FIGS.37, 38 & 39).

SMALL SCALE MAP (FIG.40).

KEY TO SYMBOLS.

31 SECTIONS OF THE MAP.

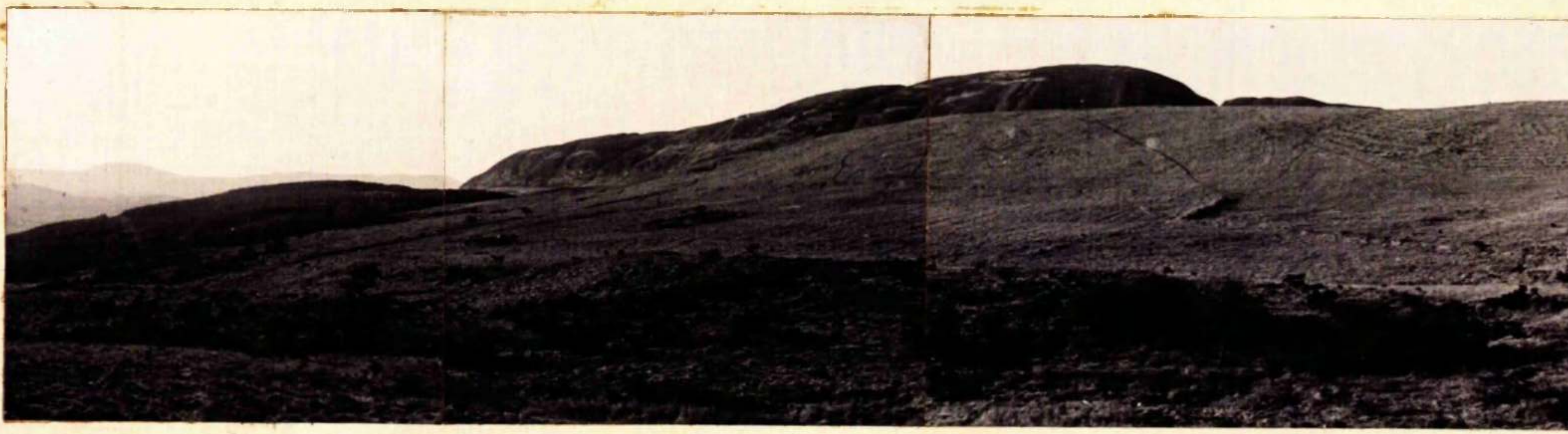


Fig.37. Ballochraggan: Part of the middle region, facing towards the north-west, including Sections 13 and 14. In the background are the Menteith Hills and, in front of these, the grassy ridge which is the upper limit of the middle region. On the slope of the ridge, the remains of the old wall and the cir:cular stone structure in Section 14 can be seen. The Forestry Commission plantations are in the background on the left.

Fig.38. Ballochraggan: Adjoining the right of Fig.37, and including parts of Sections 15, 16, 20 and 21. The rocky cleft in the grassy ridge in Section 20, Squares 8 and 12, can be seen, and also the eastern boundary wall. On the left is the group of <u>Betula</u> shown in Section 15, squares 5 and 9.

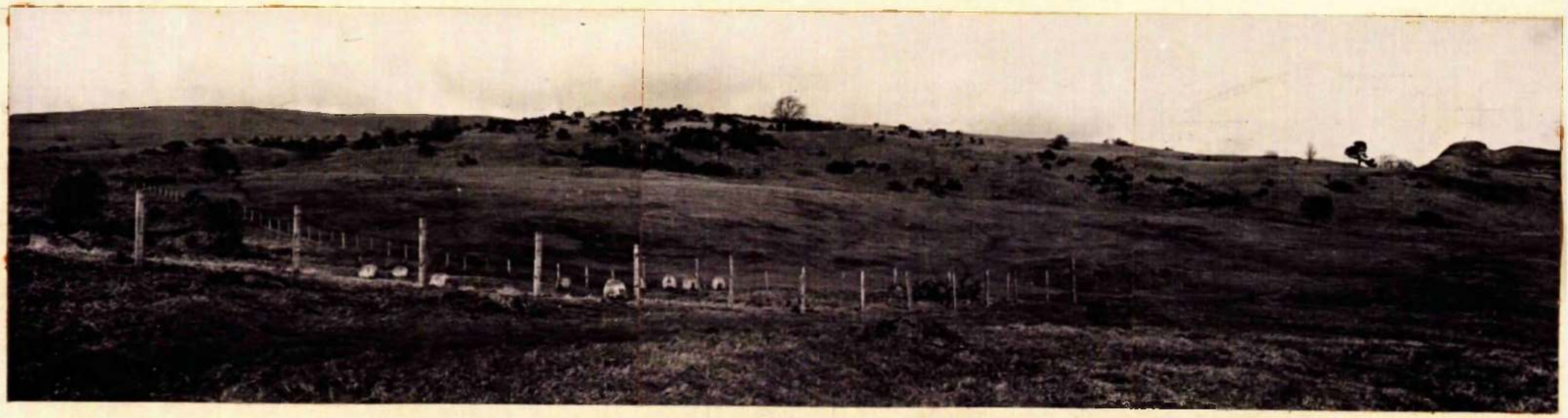
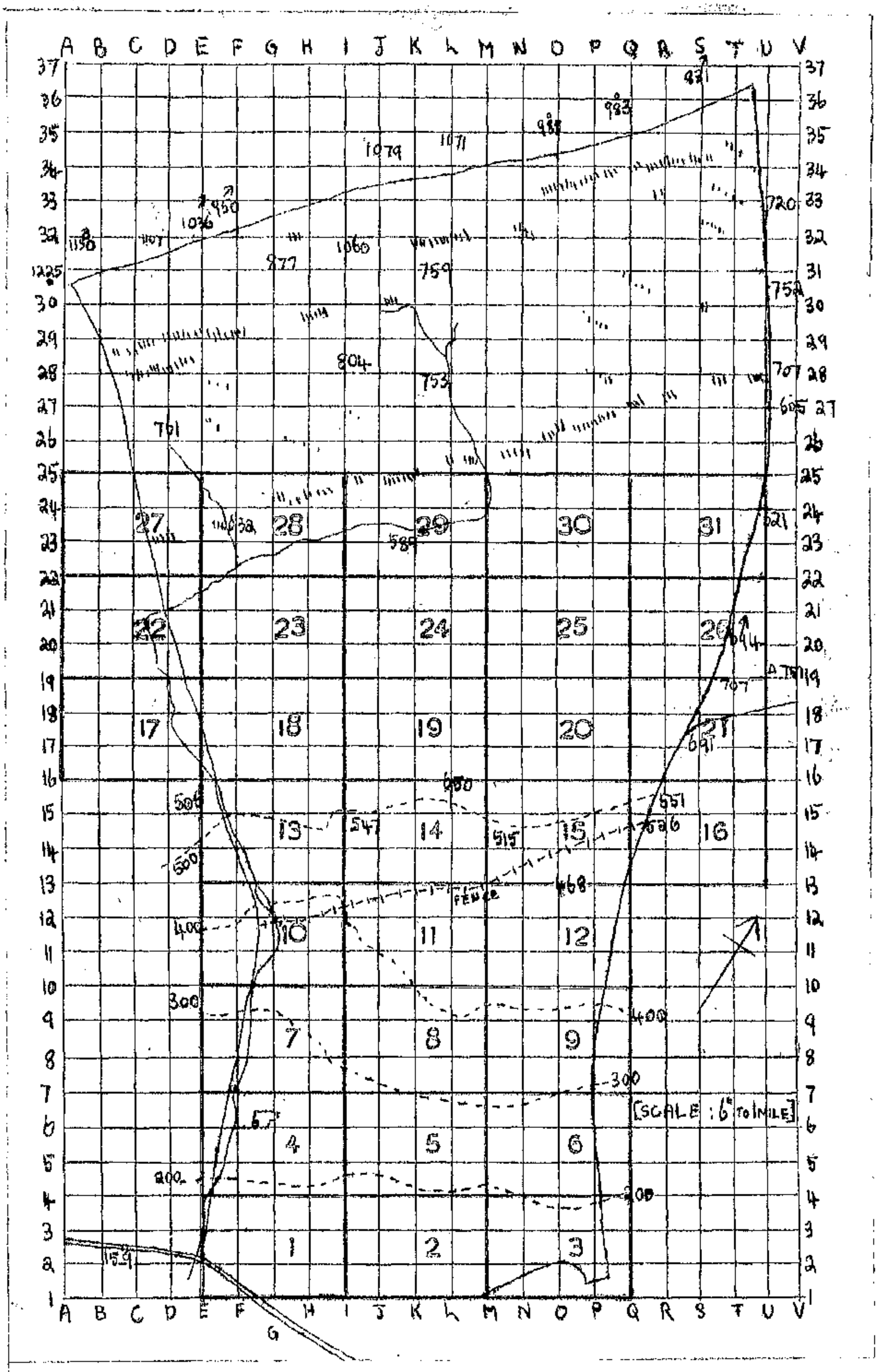


Fig.39. Ballochraggan: Part of the lower region, looking to the north-east, and including parts of Sections 5, 6, and 8. The fence in the foreground is the boundary of one of the ploughed areas. In the left background, the grassy ridge can be seen. On the right side of the photograph, the large *Pinus sylvestris* mentioned on page 5 is visible on the skyline.

Fig. 40.

Map of Ballochraggan, prepared from the Six-Inches Ordnance Survey, showing the system of squares into which the area was divided and the Sections of the botanical map. The altitudes at various points, and contours are as given on the Ordnance map



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589
521
644
707
691
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547
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515
551
526
500
468
FENCE
400
400
300
300
200
200
159
[SCALE : 6" TO 1 MILE]

KEY TO SYMBOLS EMPLOYED

Festuco-Agrostidetum	AF	Juncus articulatus (sparse)	J
Calluna vulgaris (sparse)	C	Juncetum articulati	- - - - -
Calluna vulgaris (not dense		Juncus effusus	
Callunetum		Juncus squarrosus	J_s
Caricetum	x x x x	Molinia caerulea	M
Deschampsia caespitosa	A_c	Nardus stricta	N
Deschampsia flexuosa	D_f	Narthecium ossifragum	ne
Erica cinerea	E_c	Polytrichum spp.	P
Erica tetralix	E_T	Pteridium aquilinum (sparse)	/ / / or ? ?
Eriophorum angustifolium		Pteridium aquilinum (moderate)	/ / /
Eriophorum vaginatum	o o o	Pteridietum	
Festuca ovina	F	Scirpus caespitosus	/
Holcus lanatus	H_L	Sphagnum spp.	S
Holcus mollis	H_m	Vaccinium myrtillus	V_m
Iris pseudacorus	v v v	Vaccinium oxycoccos	V_o

Molinia-Sphagnum-Juncus squarrosus

KEY TO SYMBOLS: (continued)

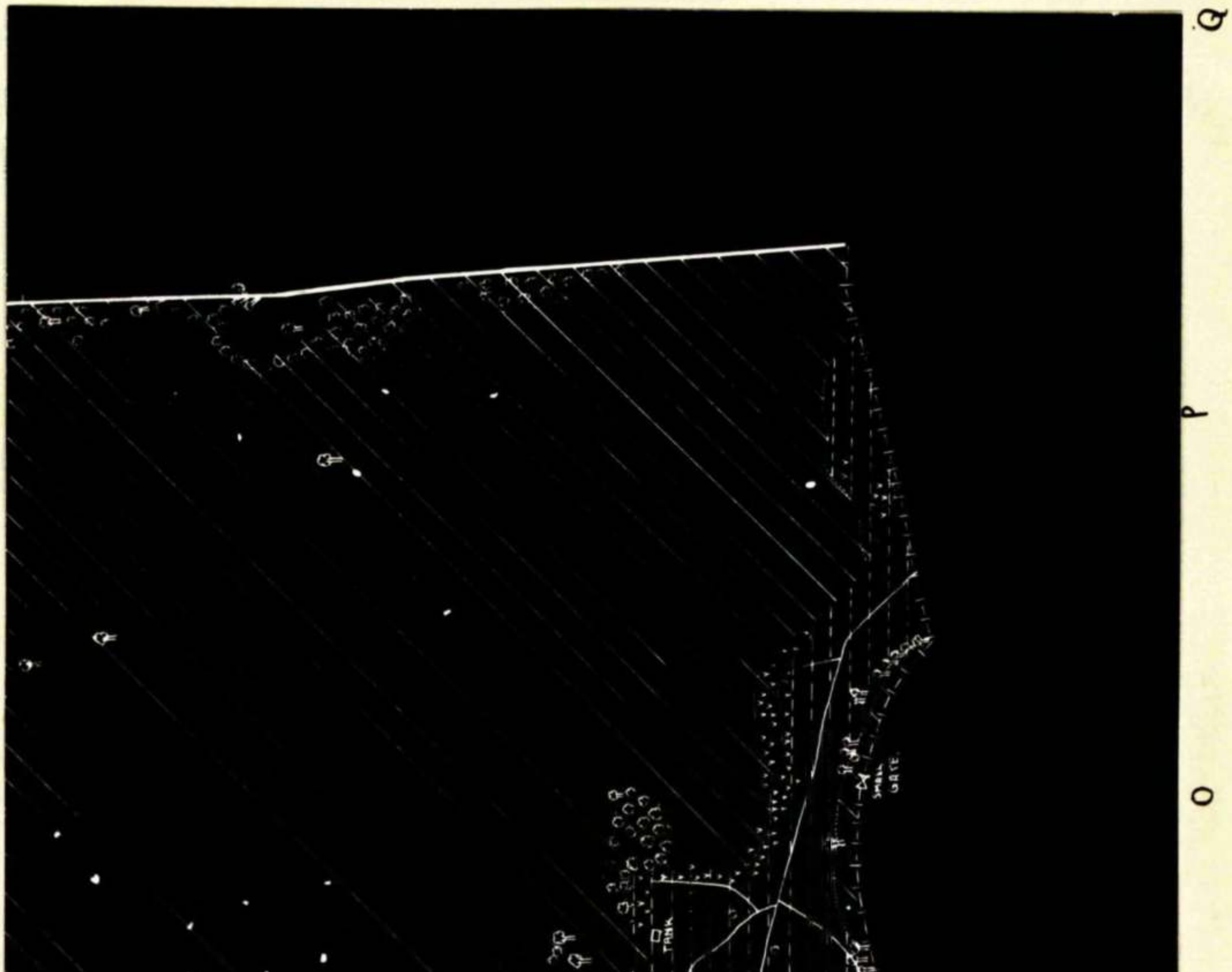
Bushes (Juniperus, Ulex, Prunus spinosa, etc.)	Standing Water
Coniferous trees	Steep banks
Deciduous trees	Small streams & ditches
Pathways	Wider streams

Rocks & boulders shown solid black

SECTION 1.

SECTION 2.

SECTION 3.



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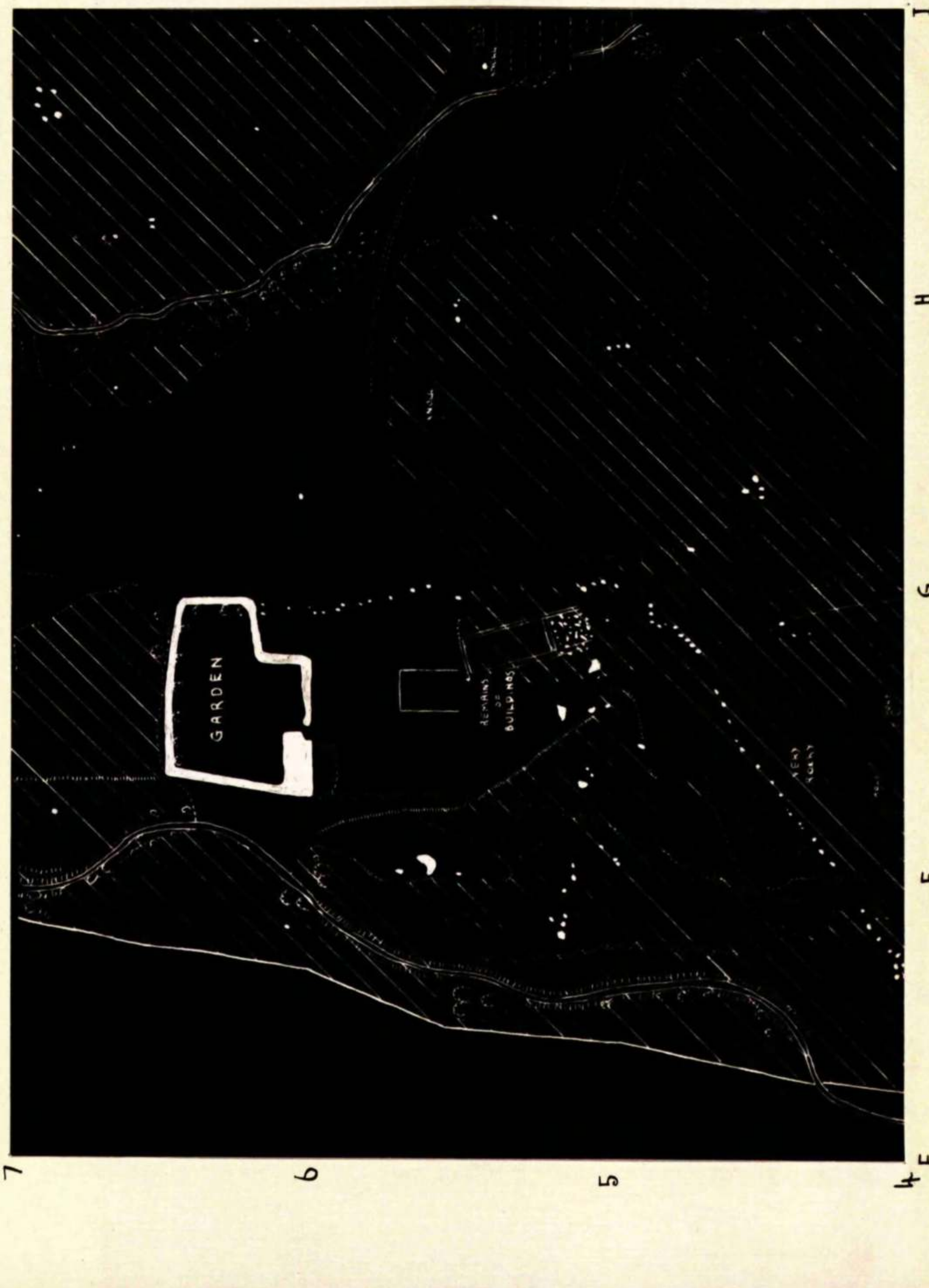
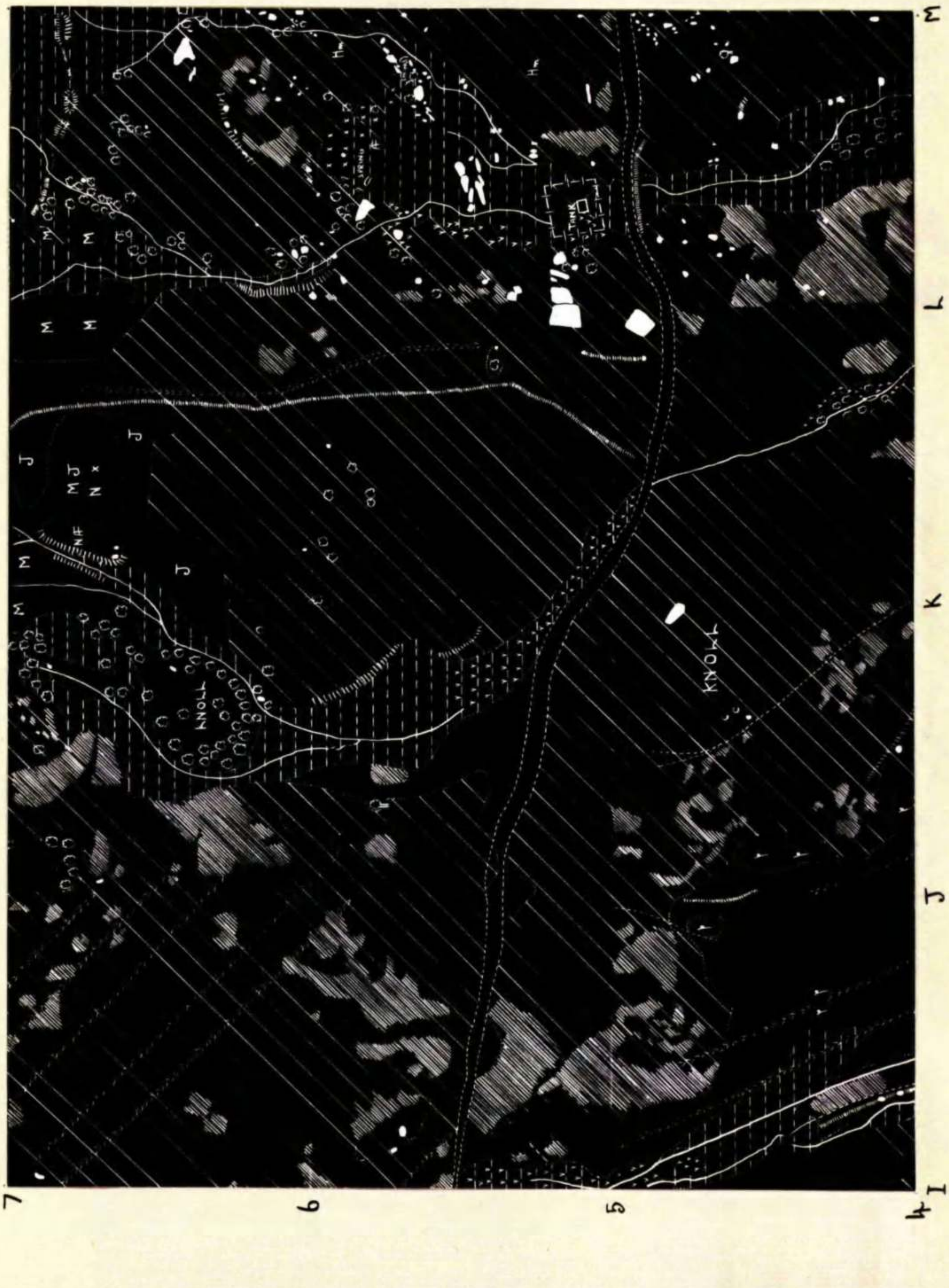
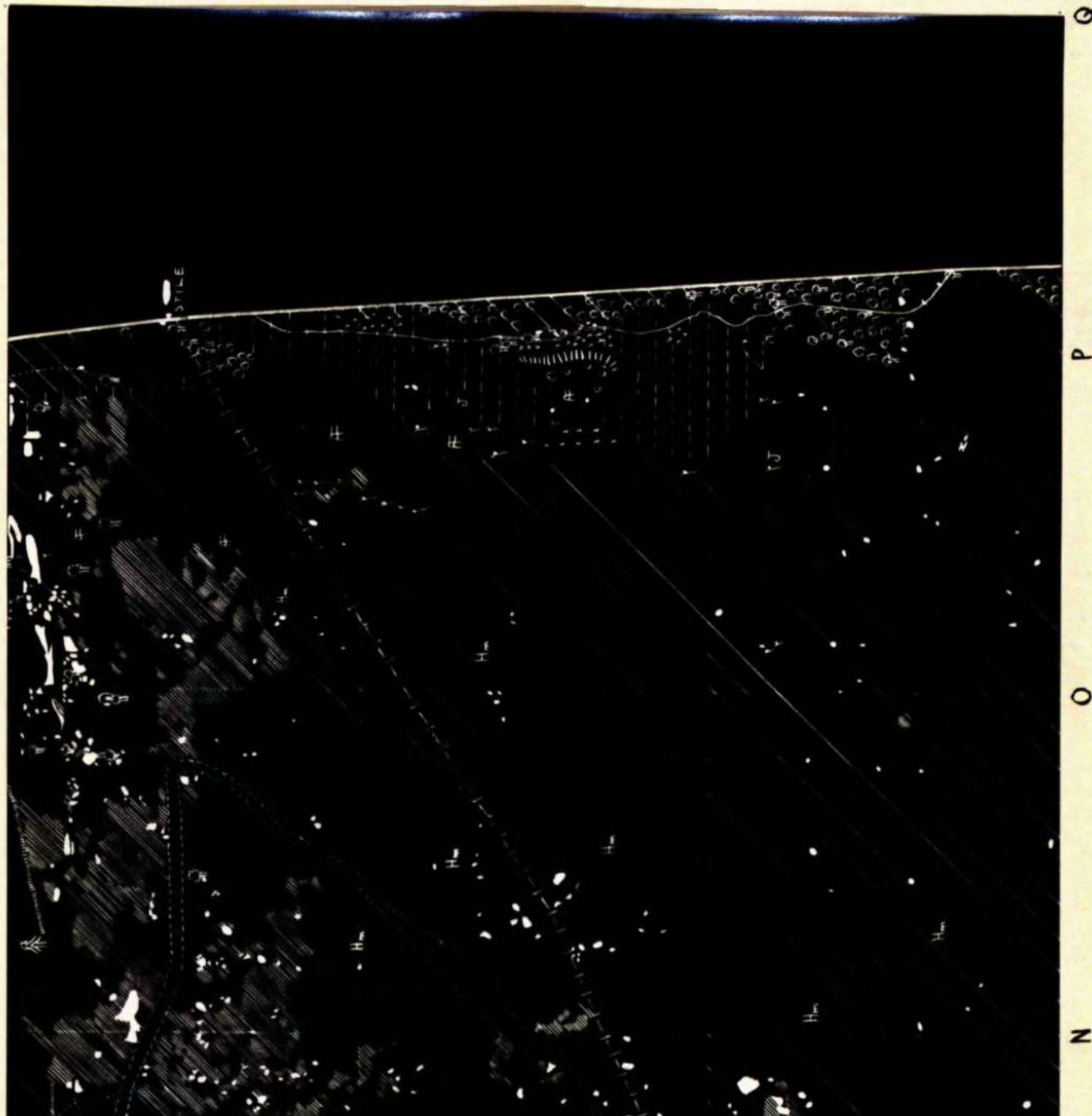


SECTION 5.



SECTION 6.



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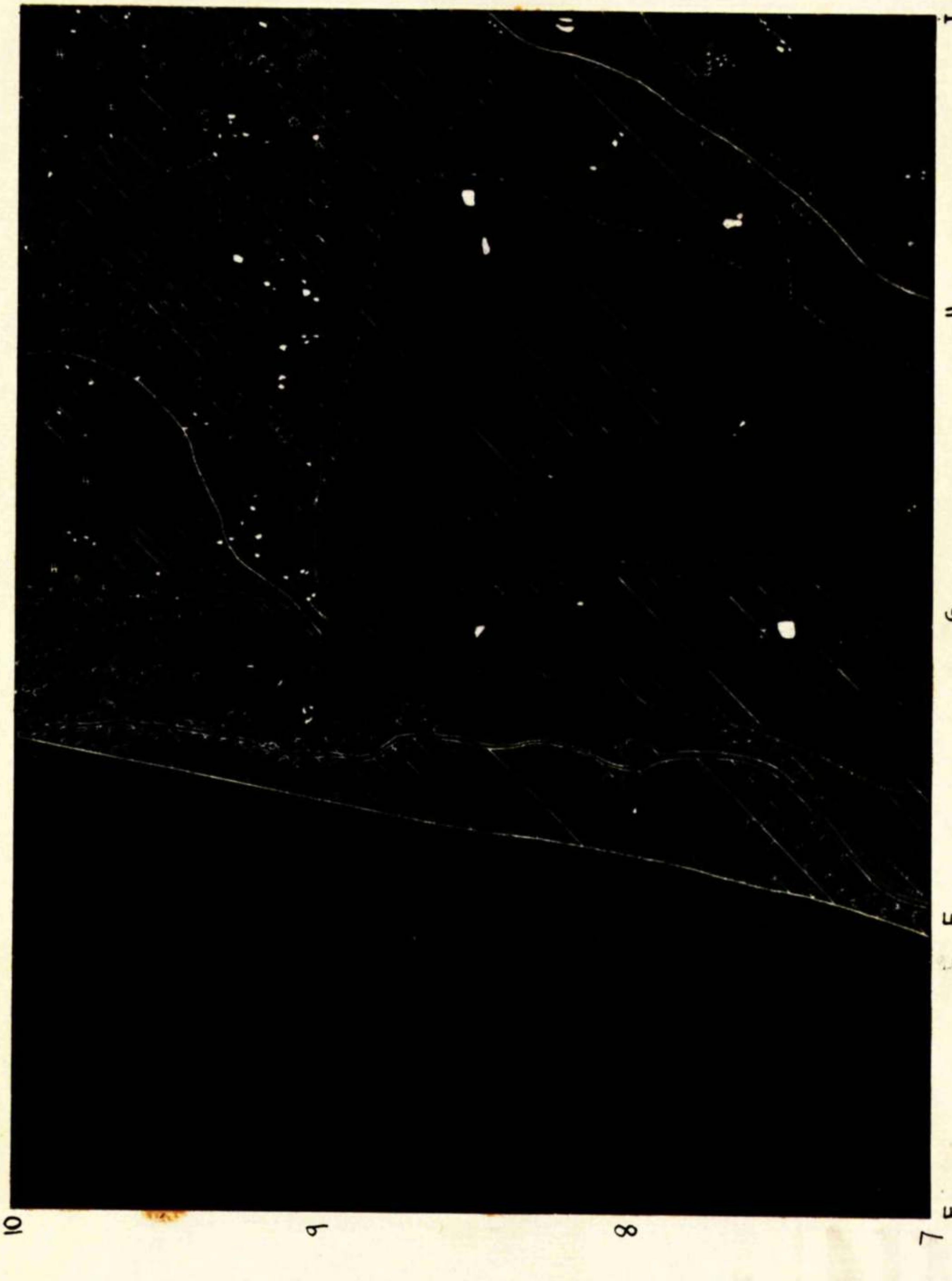

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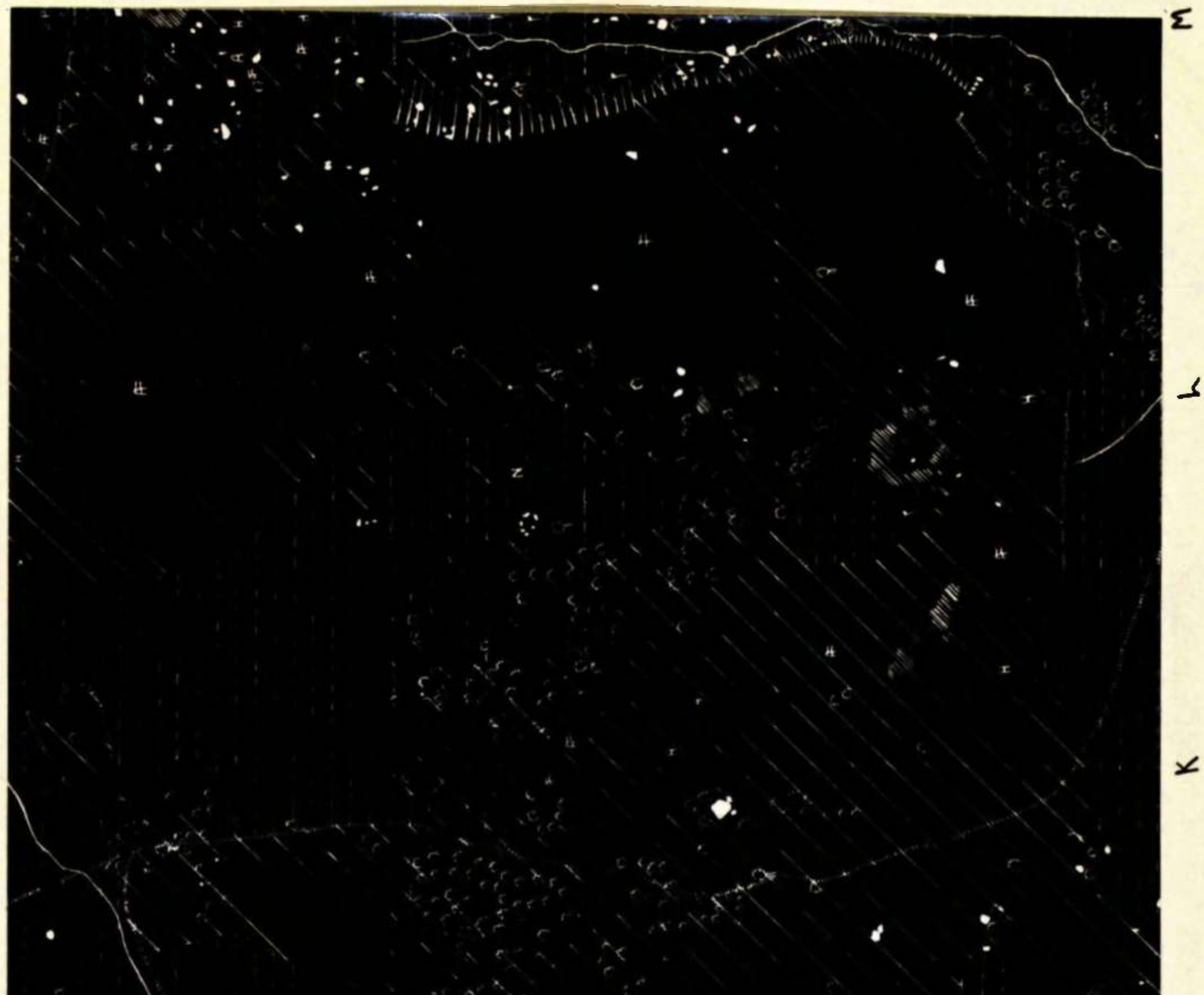

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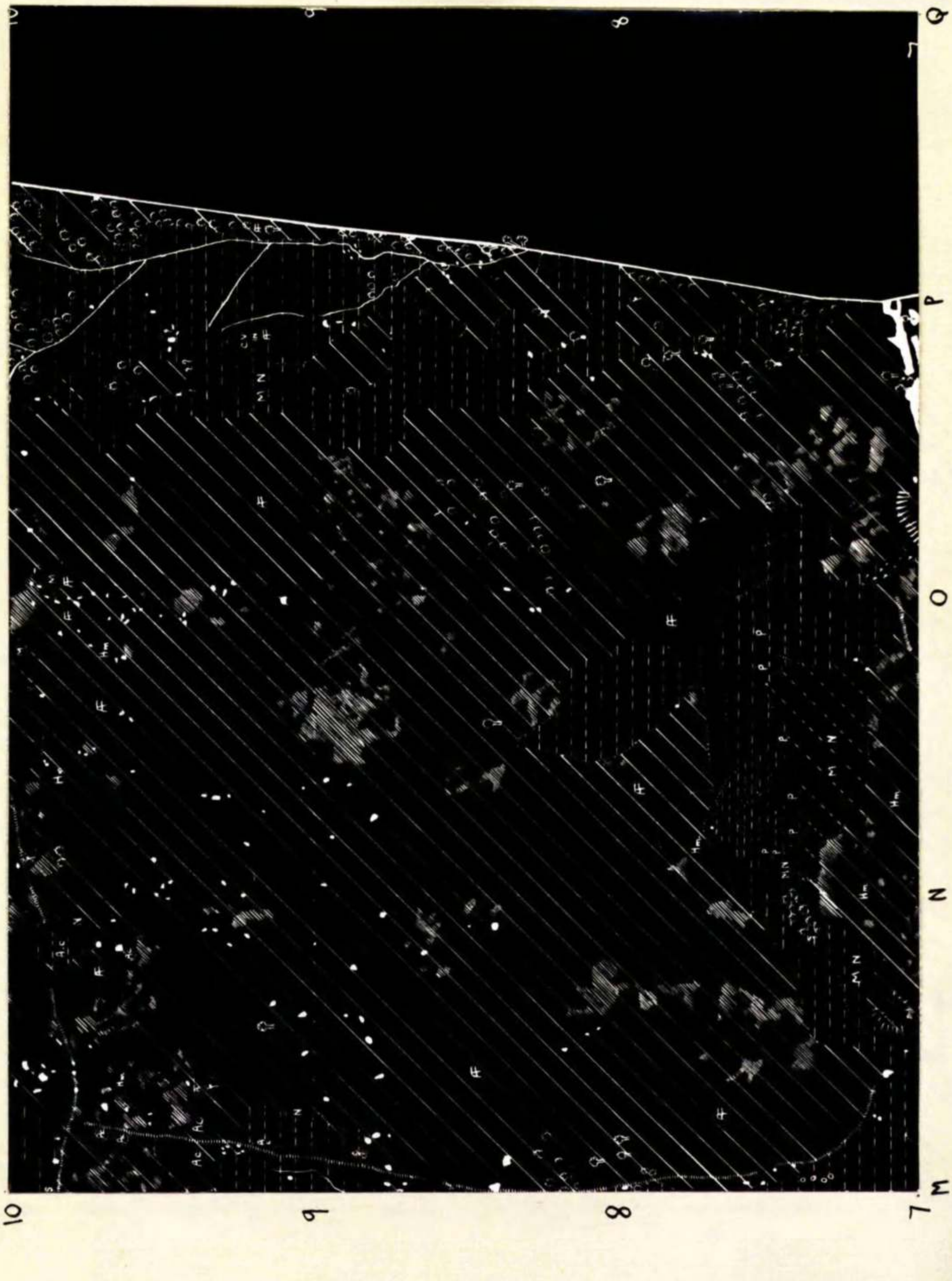

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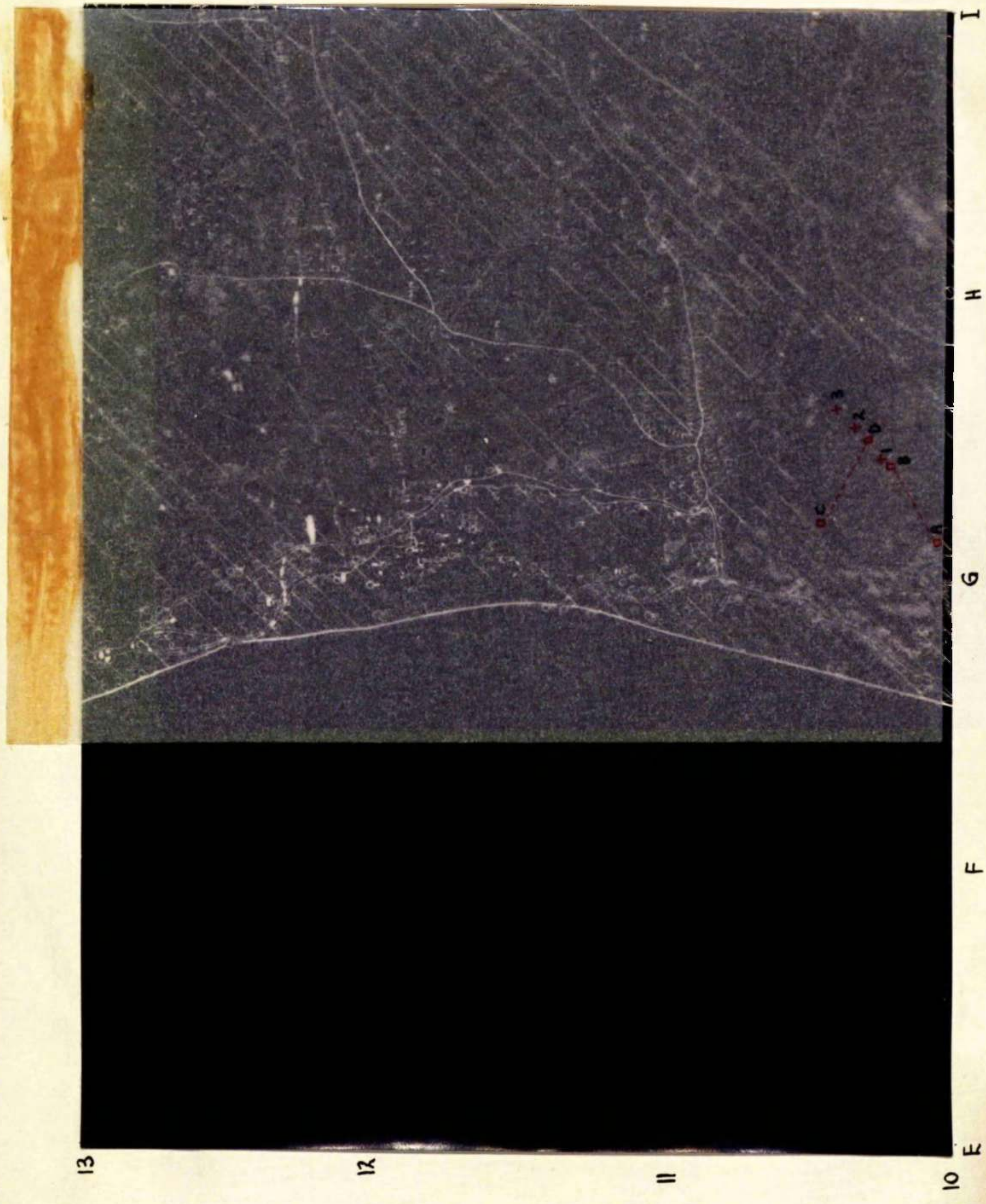

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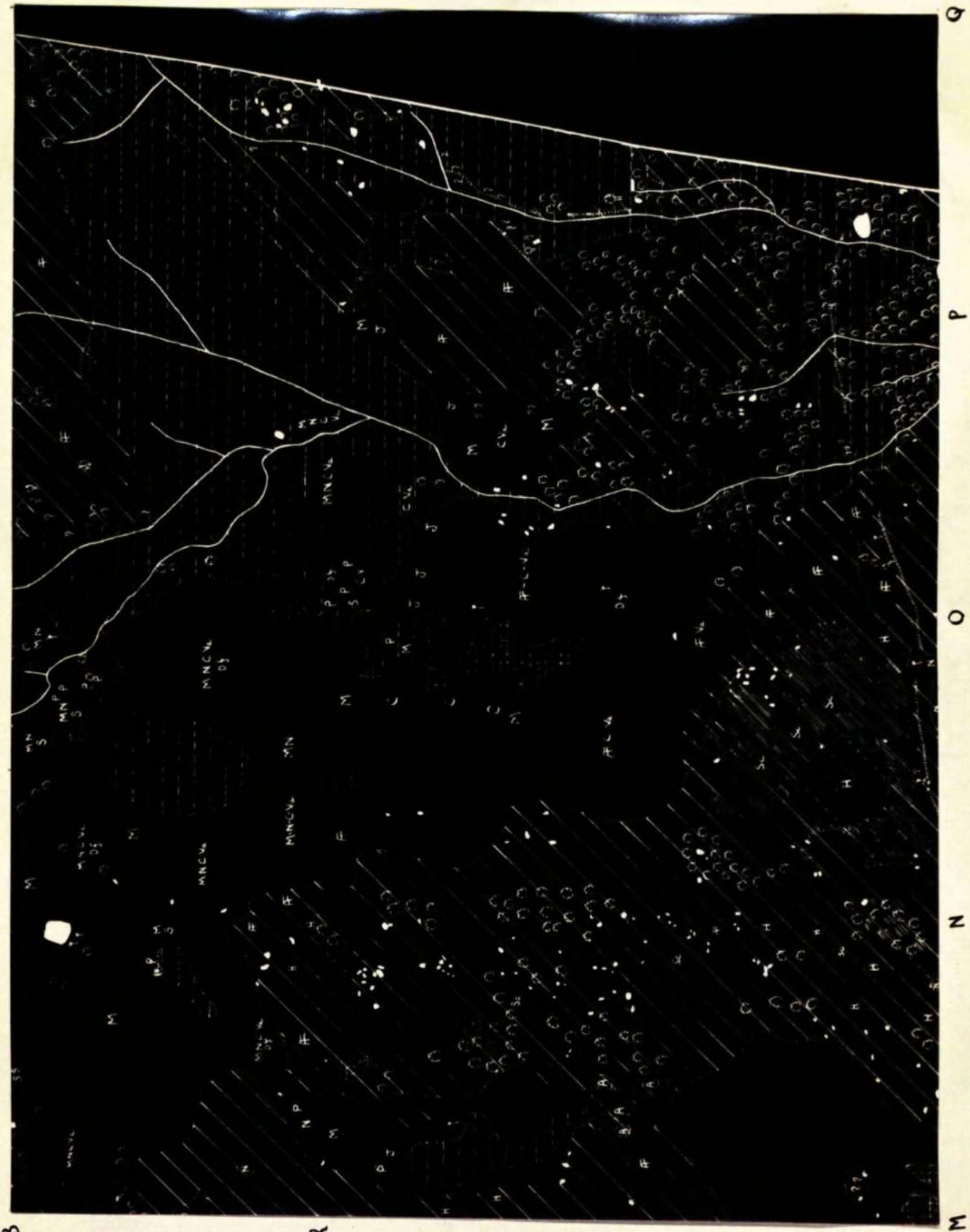

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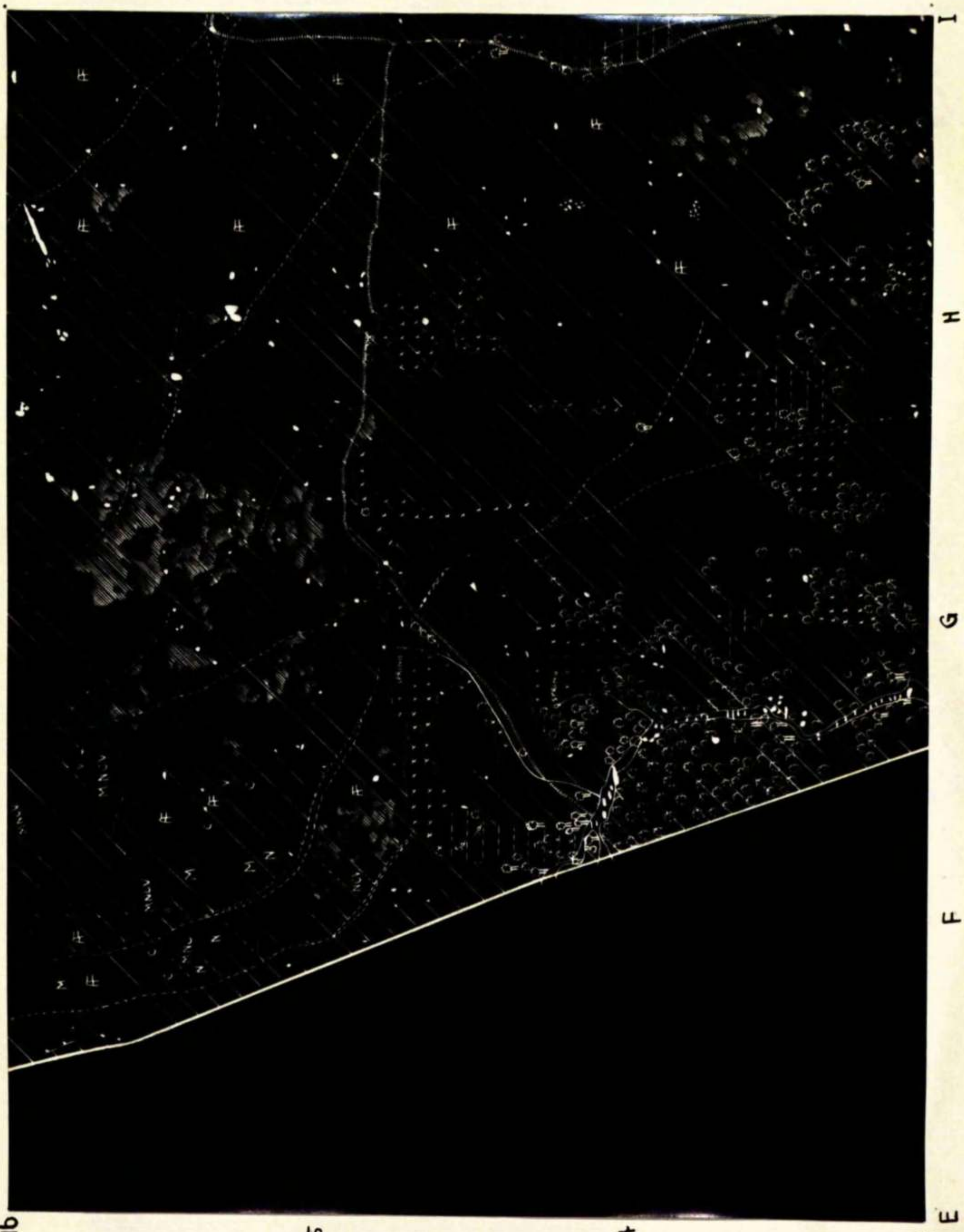

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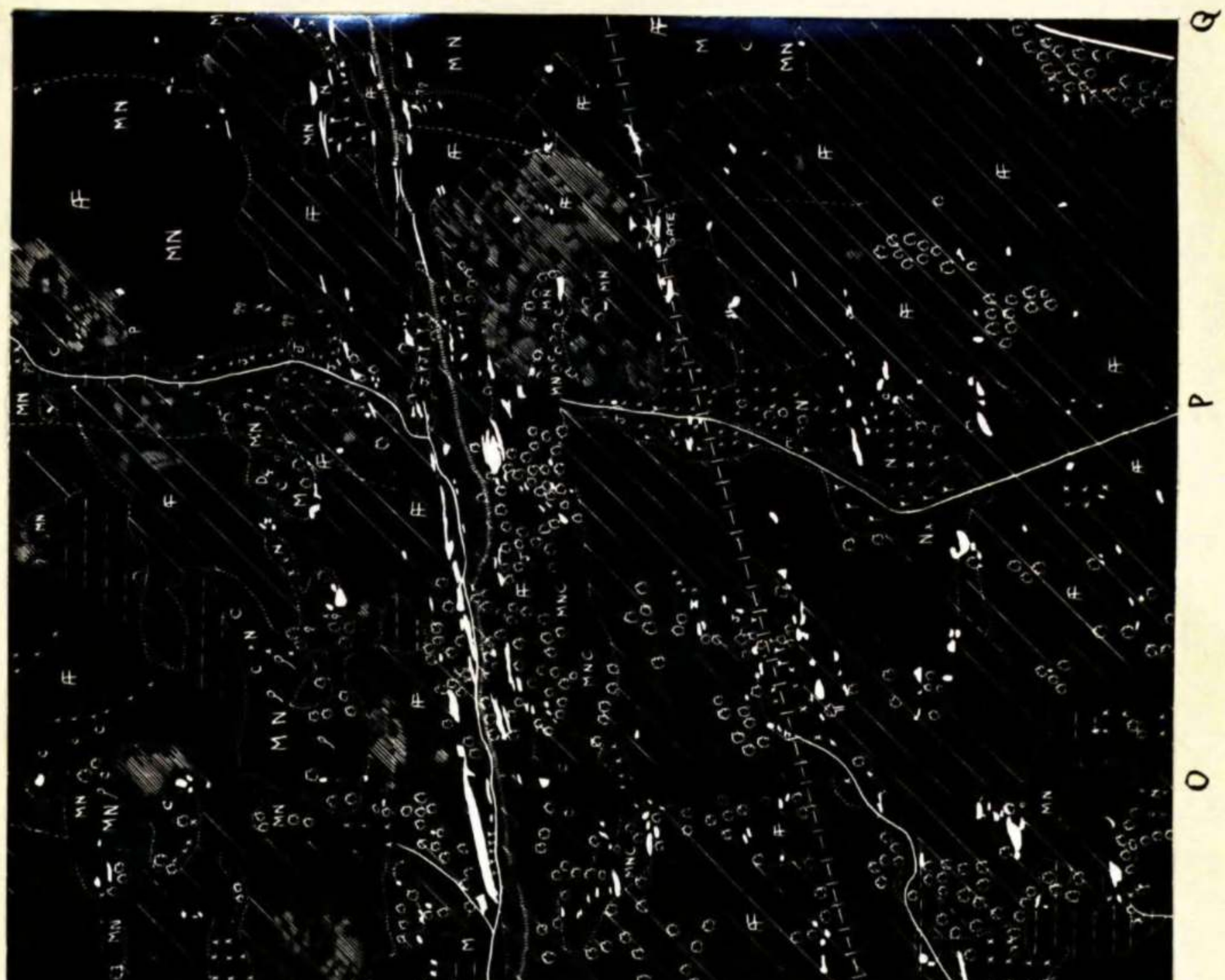

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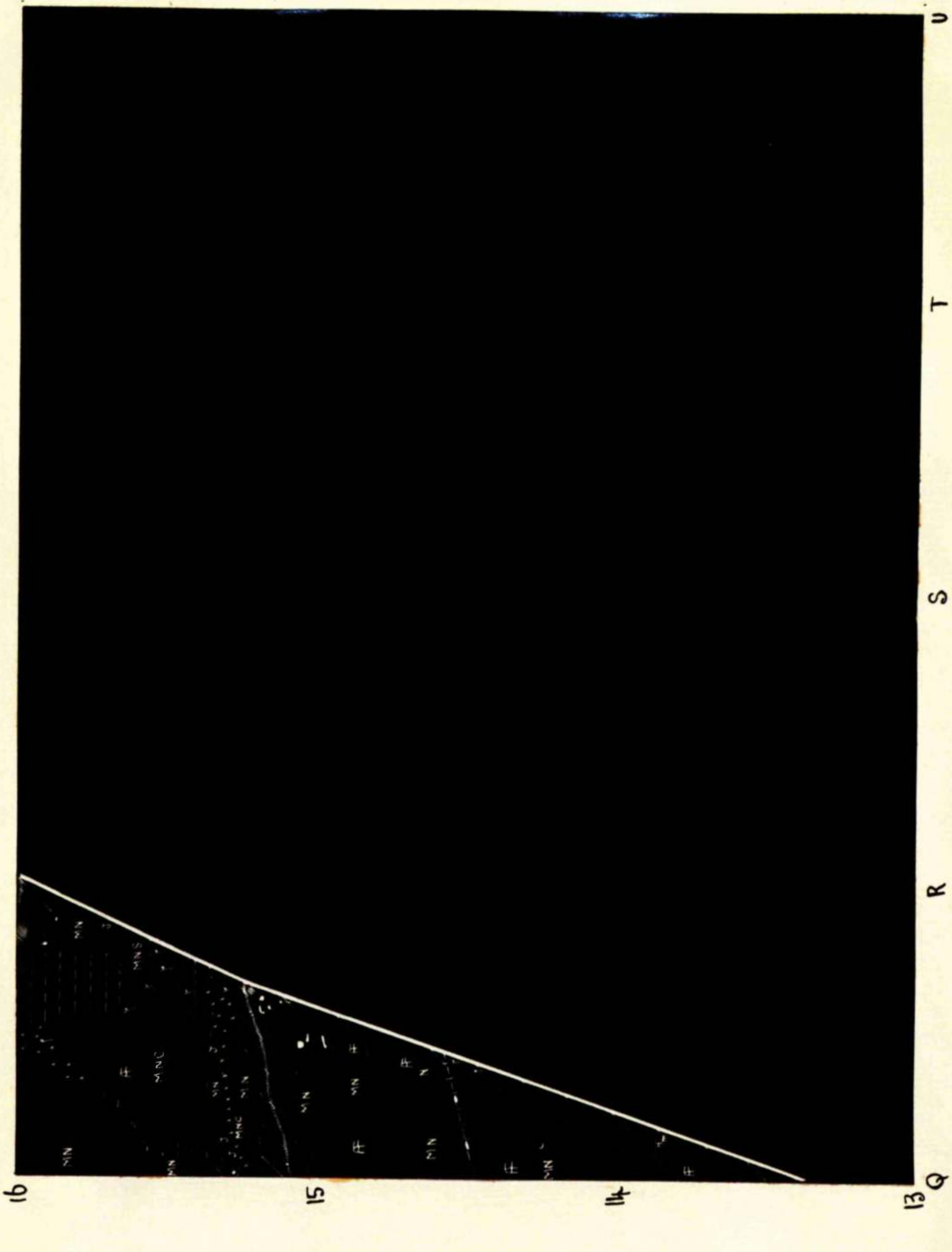

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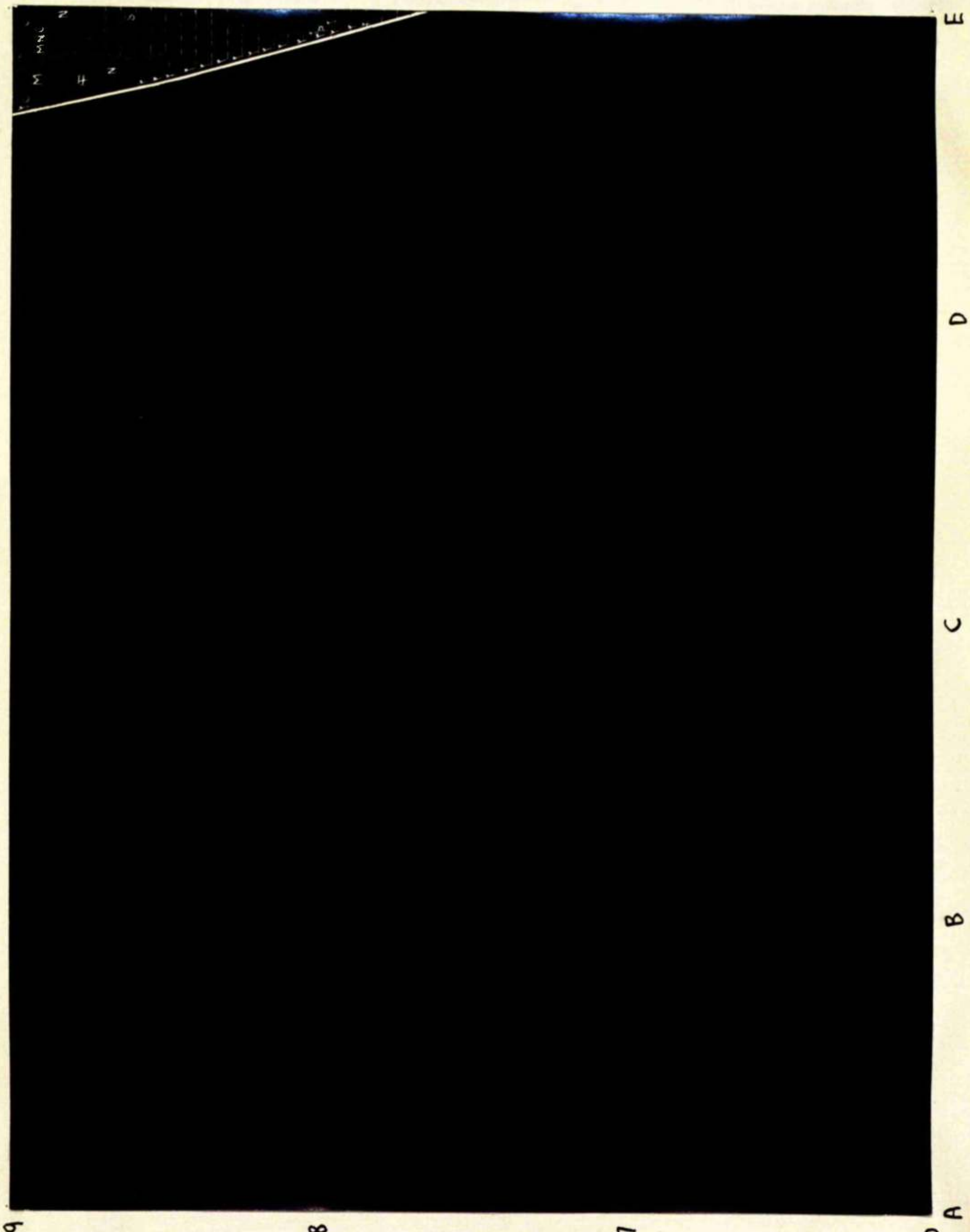

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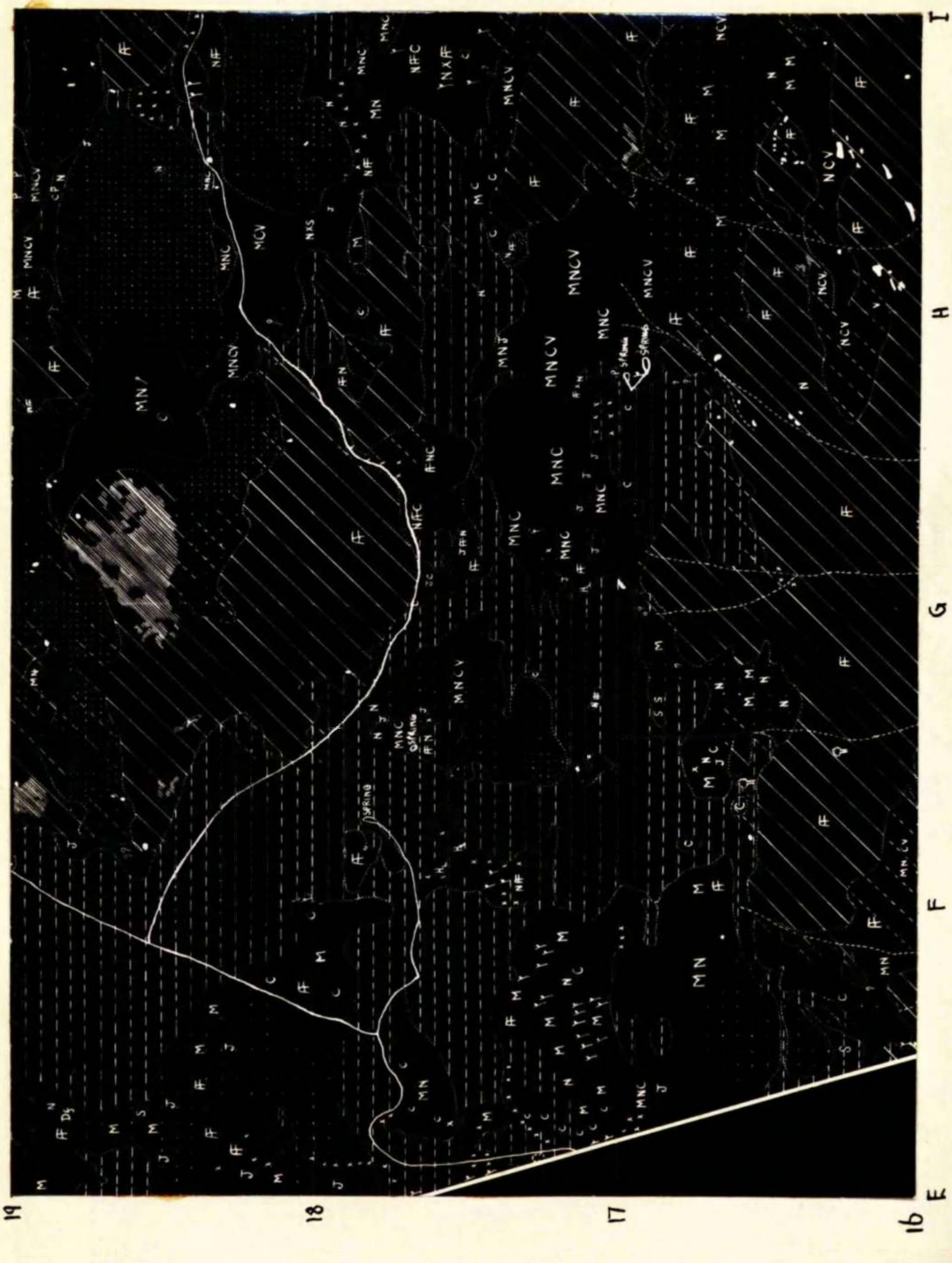

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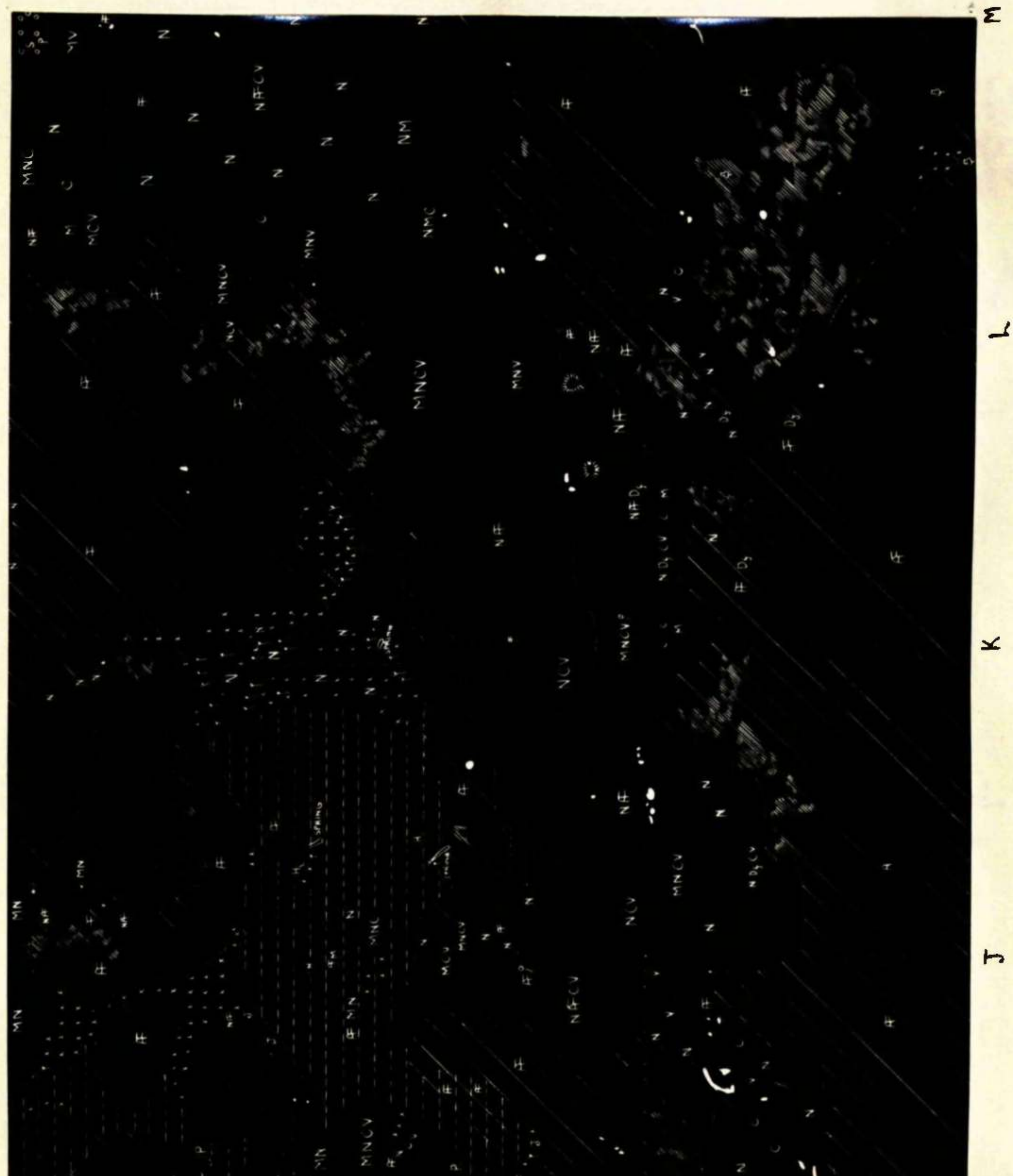

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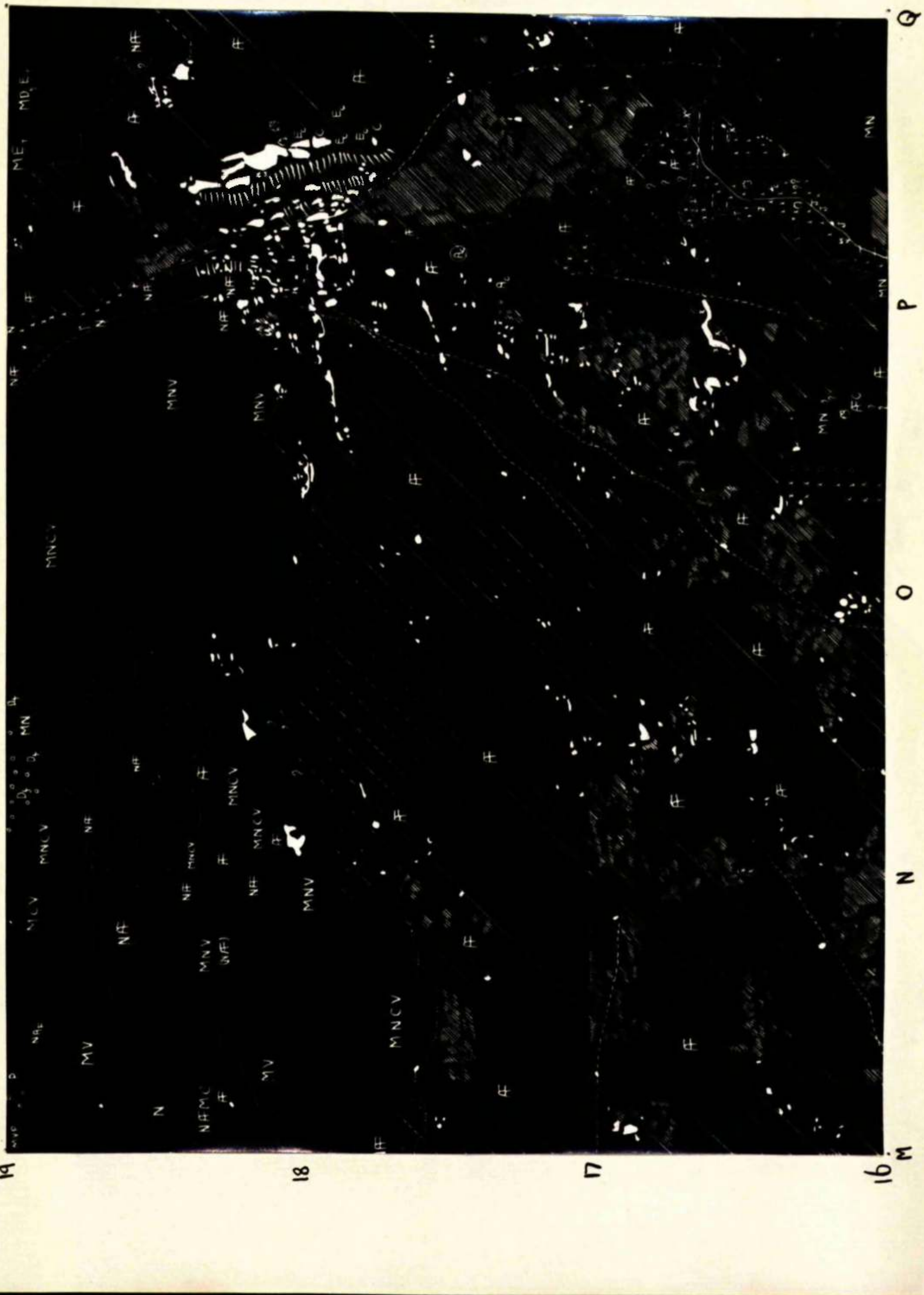

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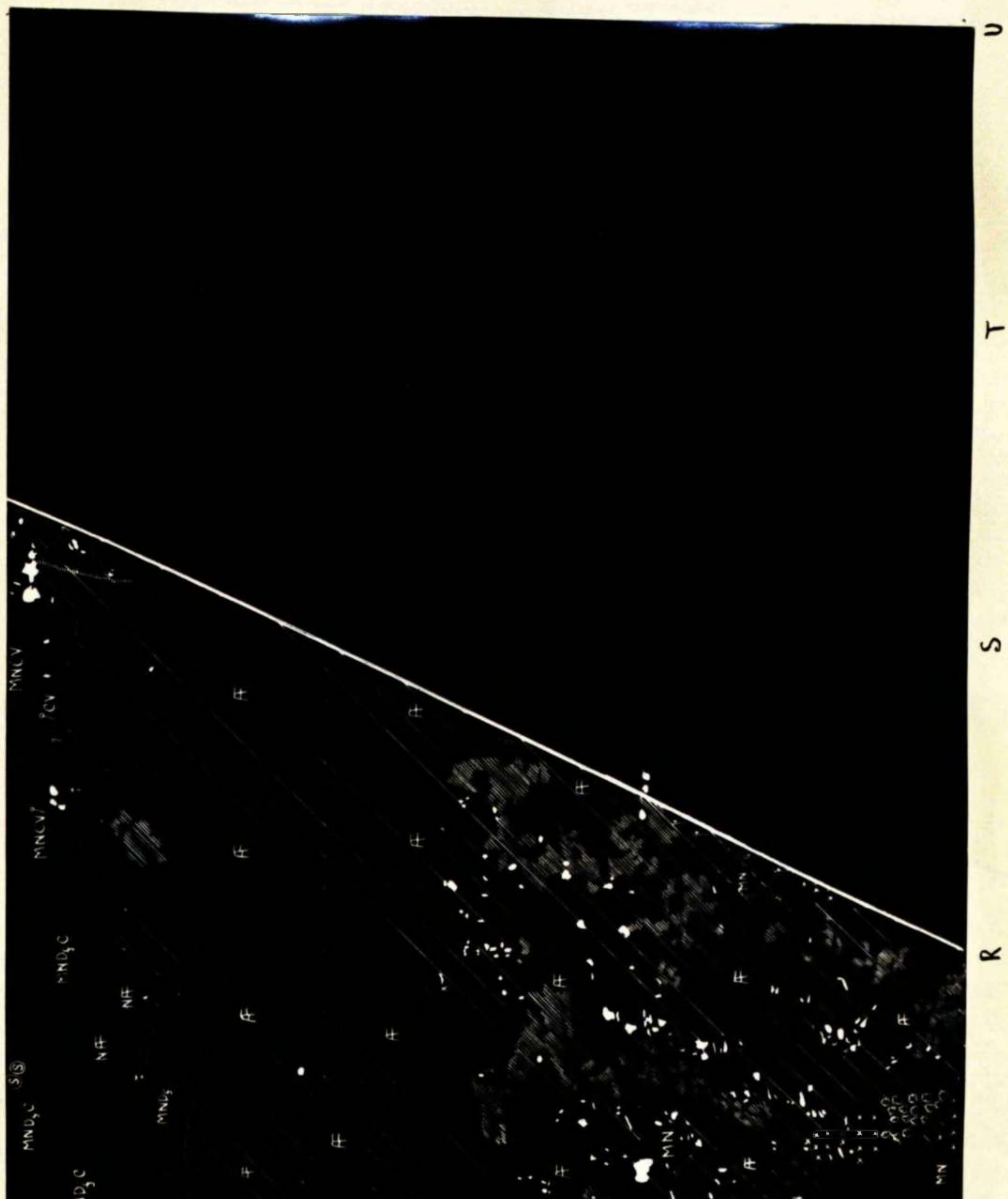

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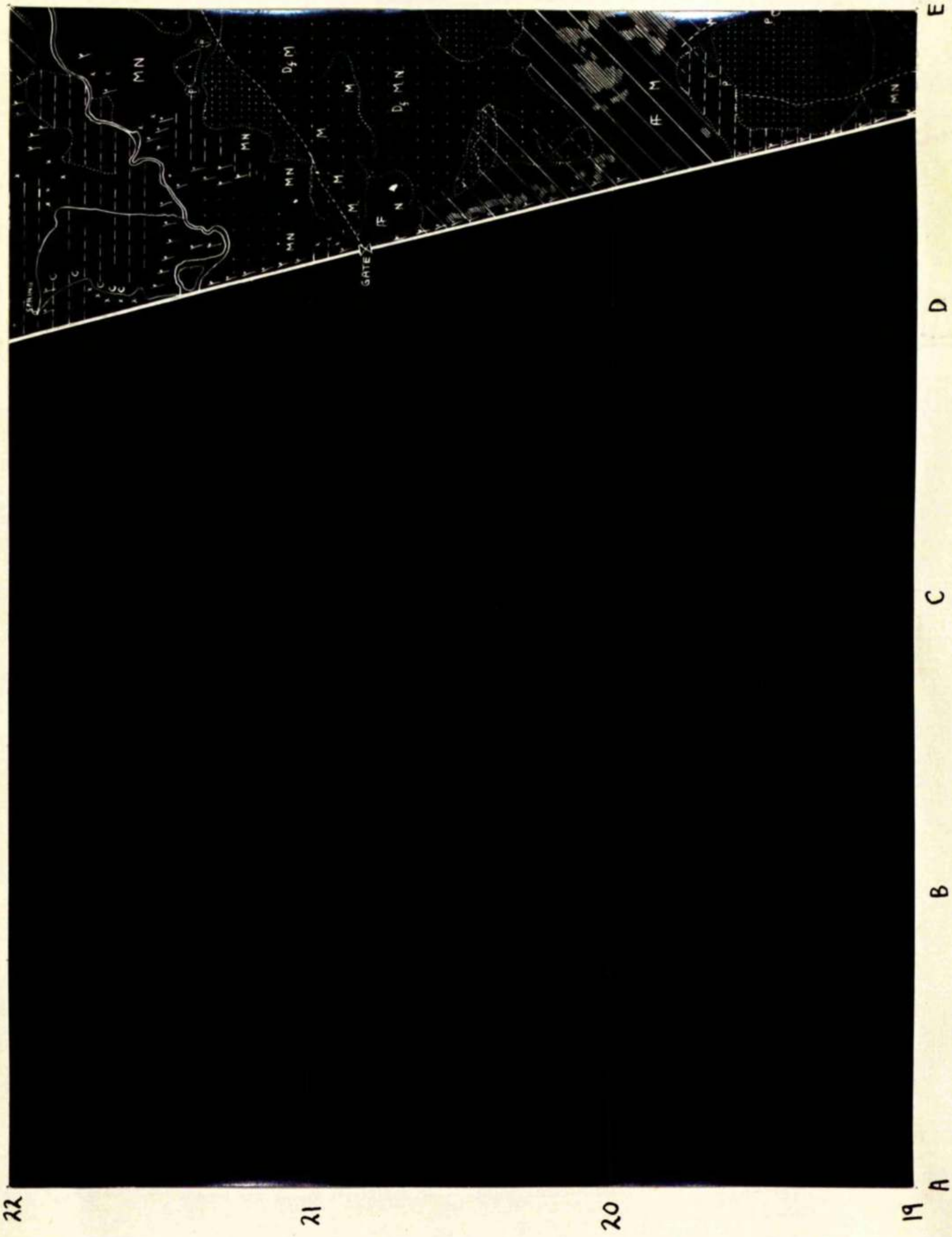

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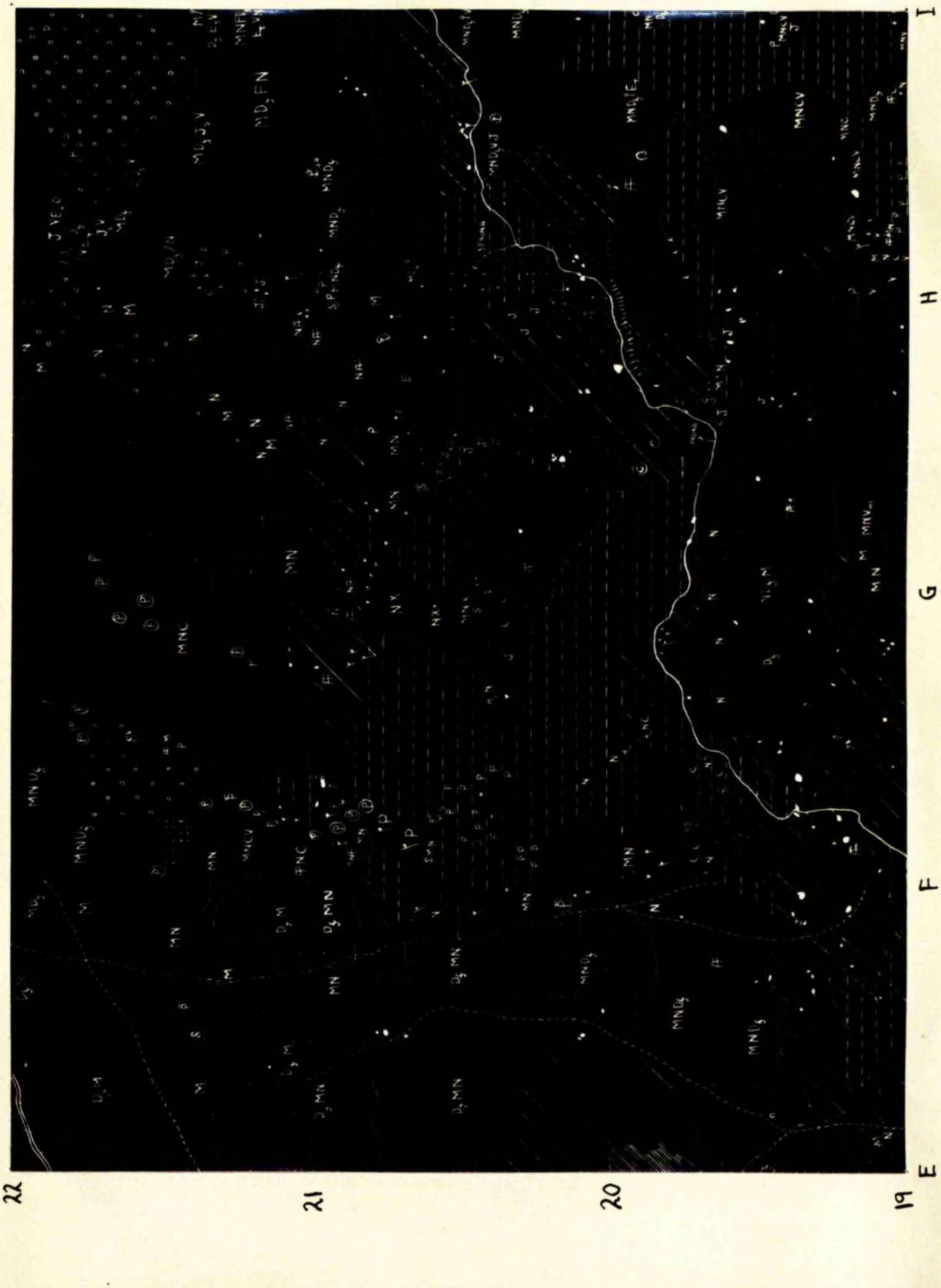

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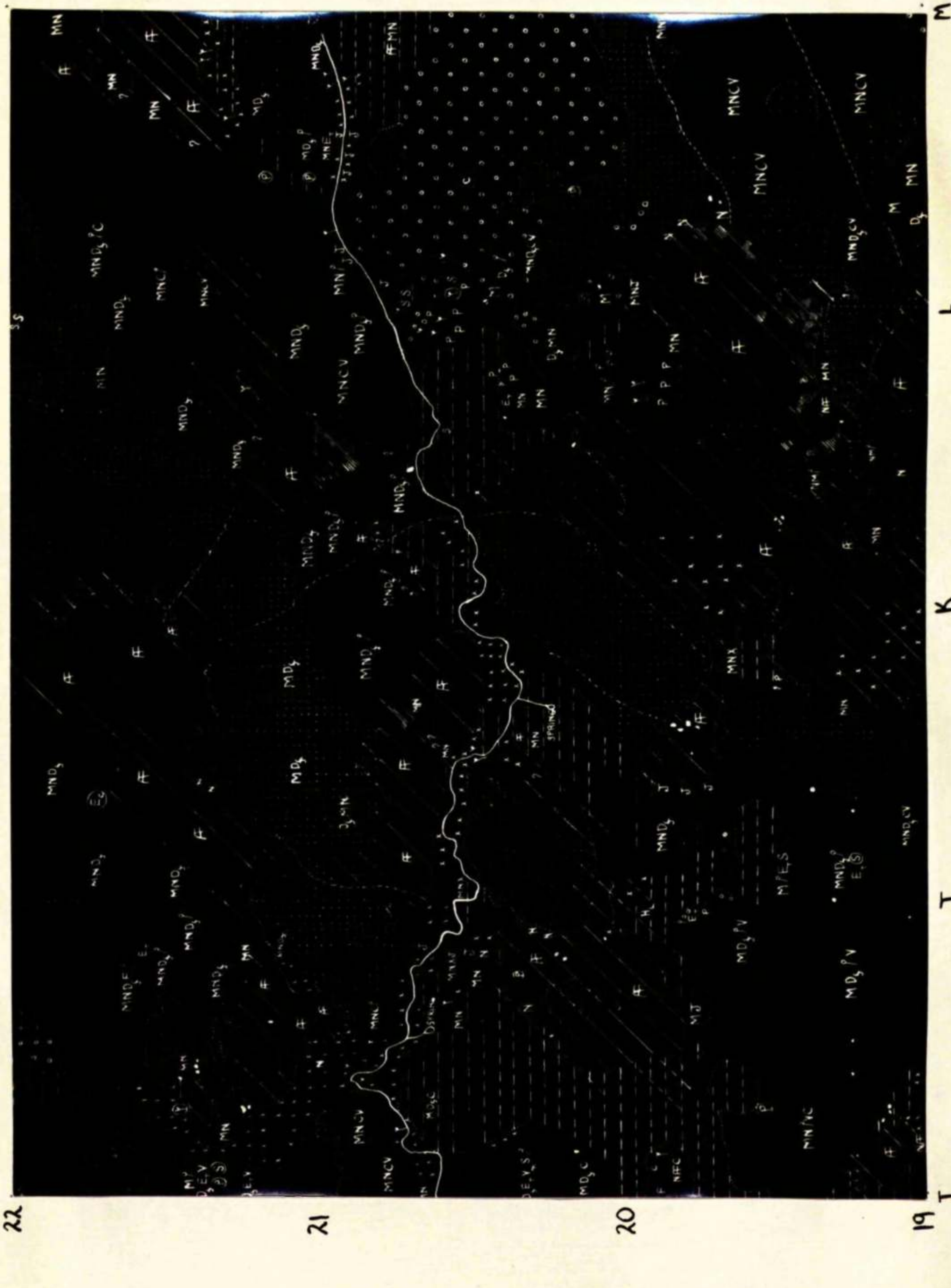

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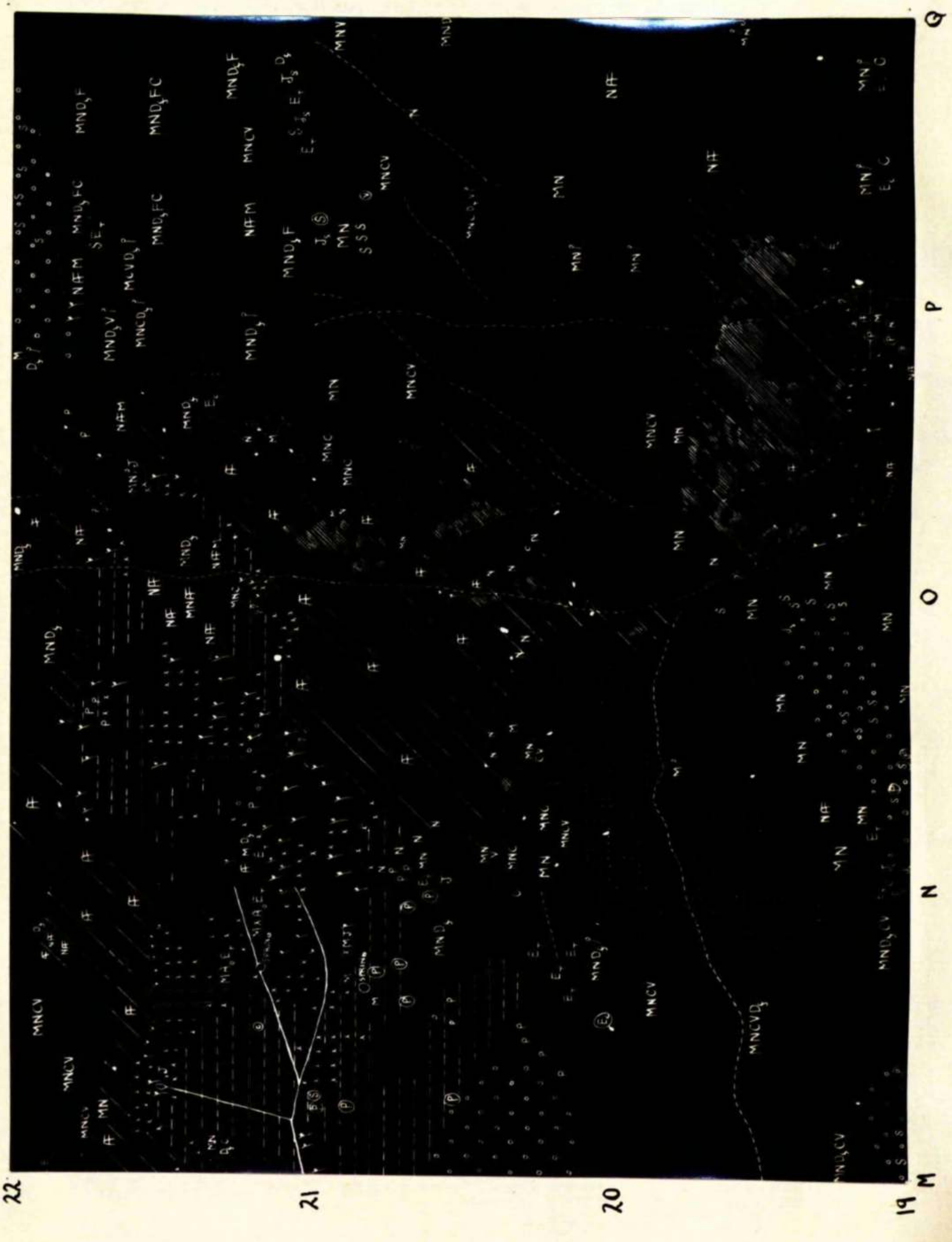

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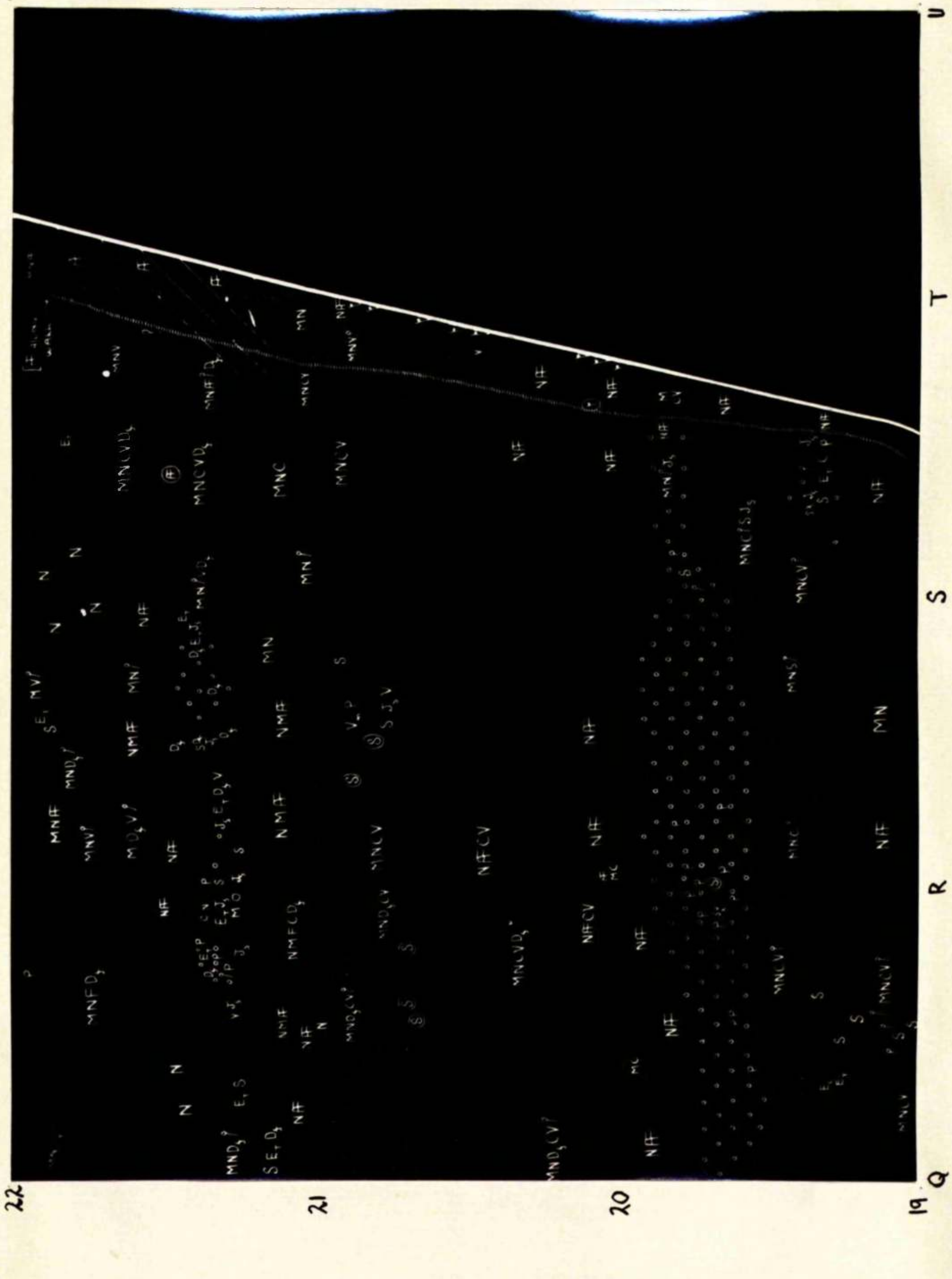

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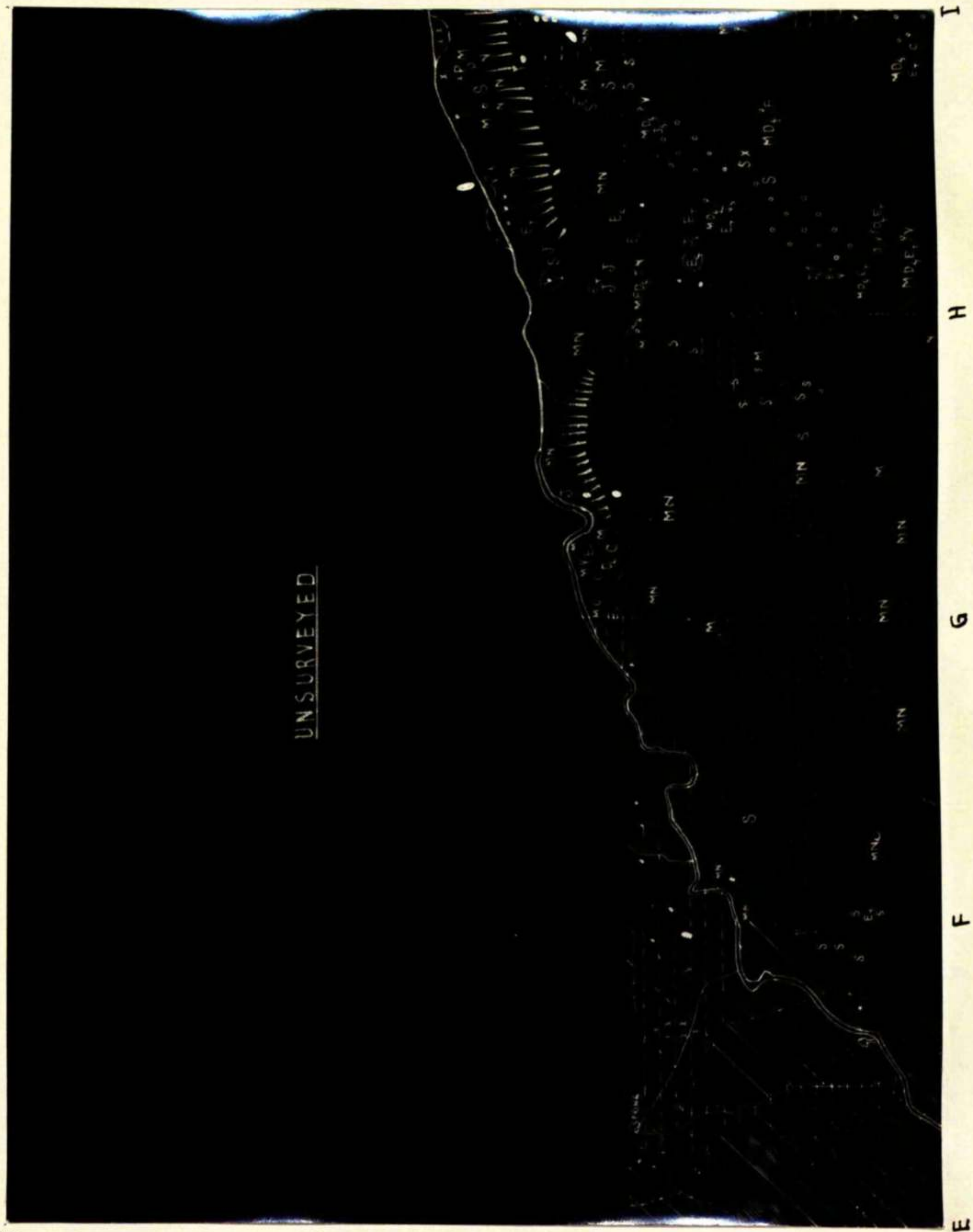

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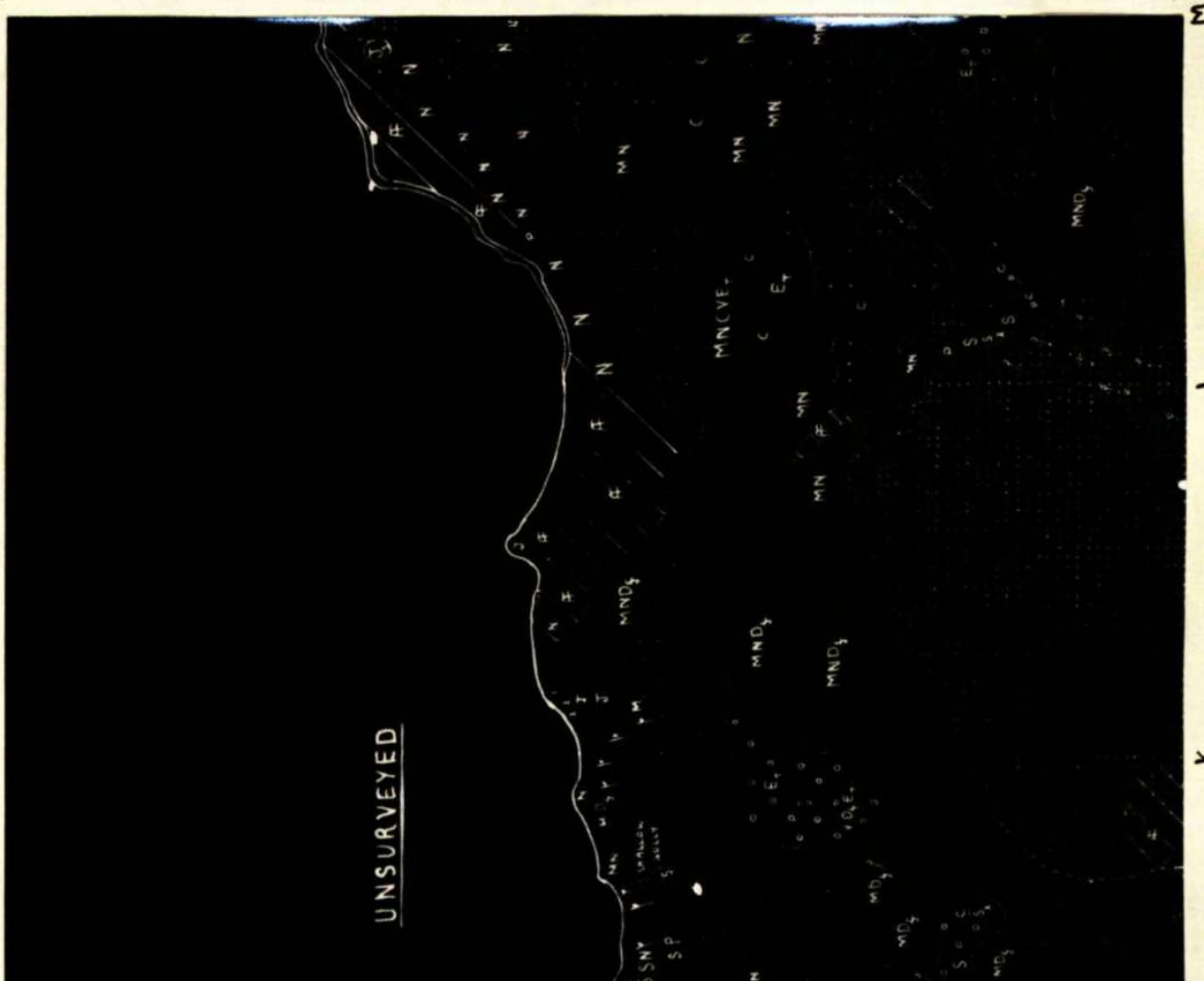

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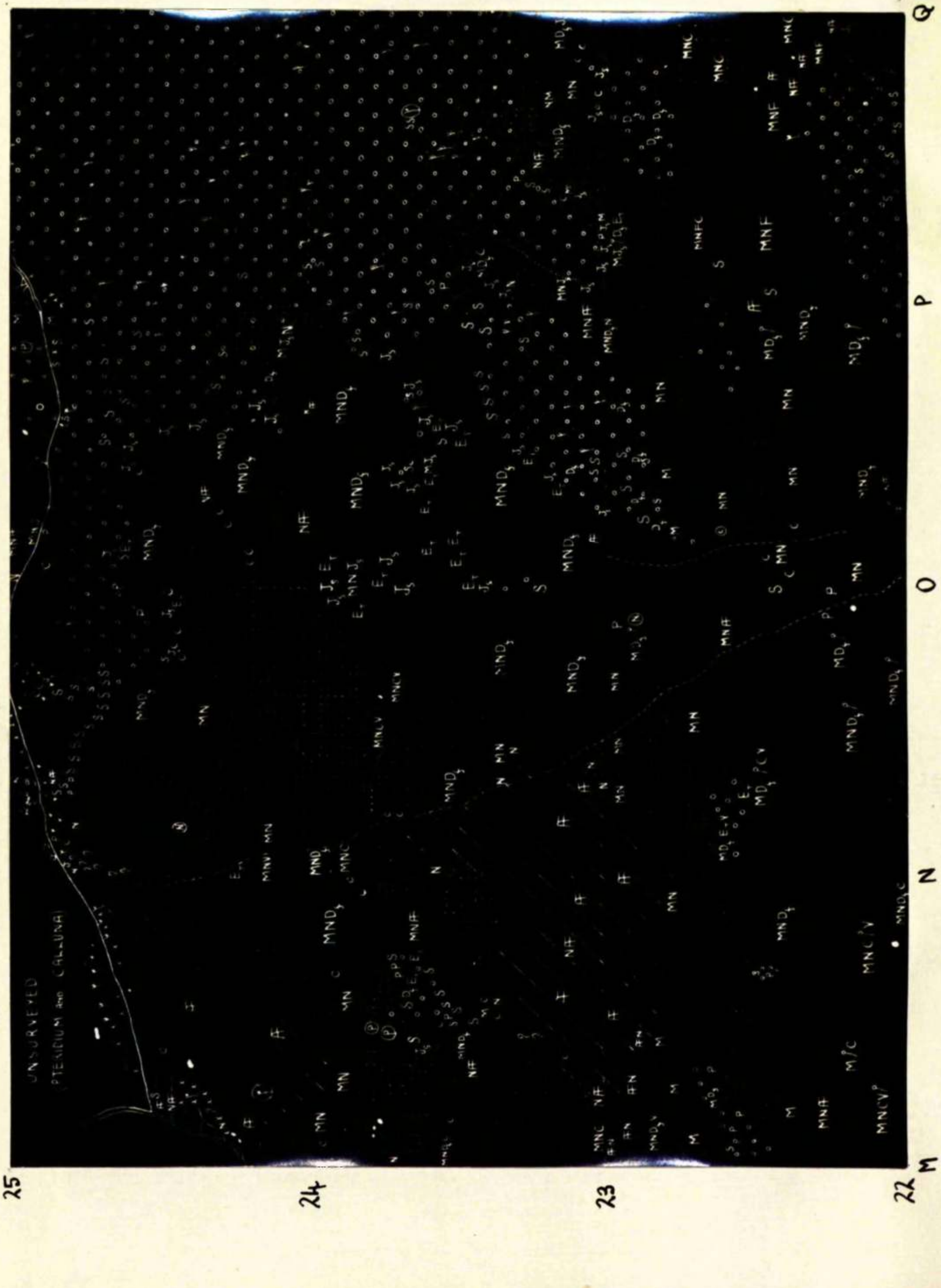

SECTION 31.