

Ecological studies of soil conditions in wet-heaths

with particular reference to aeration.

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ABSTRACT

Four wet-heath sites were selected for study at Bramshill Forest. One was a Valley-bog with Erica tetralix L. as dominant species; another had Molinia caerulea (L.) Moench and Calluna vulgaris (L.) Hull as co-dominants, with Erica tetralix L. abundant (Central associates); the third was a drier Molinietum and the fourth a wetter Molinietum.

Field studies of performance of these three species showed that Valley-bog was poorest for their growth.

A quantitative study of root distribution of Molinia and Erica demonstrated the shallow-rooting habit of Erica. Root anatomy was also investigated.

A field experiment on competition between young plants of Molinia and Erica showed that, in drier Molinietum, Molinia significantly reduced the growth of Erica.

Application of nutrients in the field increased the growth of Molinia and eliminated the site differences for this species, but reduced the survival and growth of Erica. Water culture experiments demonstrated the low nutrient requirement of Erica.

Probes for sampling soil air and soil water were designed. Concentrations of gases dissolved in soil water were very different (lower O₂ and higher CO₂) from those in soil air at the same depths.

Root distribution relative to pore sizes was studied in soil sections. Roots of both Molinia and Erica were confined to pores > 150 μ in diameter. The response of the soils to drainage was investigated by "moisture-tension" and "micrometric" methods, and was concluded that a high proportion of pores > 150 μ diameter retain water in the drainage conditions of the sites studied.

In experiments each lasting fifteen days, Molinia and Erica were grown separately in water cultures supplied with factorial combinations of four concentrations of O_2 with four of either CO_2 or H_2S . . Molinia proved more tolerant of poor aeration than Erica.

The distribution and performance of Molinia and Erica in these sites has been discussed in relation to soil conditions and competitive relationships.

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I INTRODUCTION

a. The study area and its vegetation

The vegetation investigated in this work is found in an Ecological Reserve set aside by the Forestry Commission in 1946 in Bramshill Forest situated on the border between north-east Hampshire and Berkshire. The forest lies on two plateau areas, Hartford Bridge Flats and the high ground north of Crowthorne. The river Blackwater has formed a 3 mile wide valley between the two. While the tops of the plateaux are dry and well drained, the valleys and lower margins of the forest generally are poorly drained though the agricultural land which lies still lower is not so wet.

The geology of this area has been thoroughly described by White (1909). The Pleistocene Plateau Gravel caps the summit of a plateau, about 330 feet high, known as Hartford Bridge Flats. This gravel has sandy lenses and bands and does not hold water. Below this are the Eocene Barton sands (Upper Bagshot beds) whose lower limit roughly corresponds to the 300 feet contour to the south of the Blackwater valley. As with Pleistocene Plateau Gravel, water drains through these beds which are almost pure sand with some flints and a little clay towards the bottom. Frequently on steep slopes the middle Bagshot Beds (the Bracklesham Beds) outcrop below the Barton sands. They are 50 to 60 feet thick at Bramshill and have a complex series of clay and sand bands and seams of pebbles.

As mentioned above, water drains freely through the Plateau Gravel and Barton sands but on reaching the impermeable clays of the Bracklesham Beds it is thrown out near their top. White (1909) states that the Bracklesham Beds "furnish a few well marked springs, their water held up by beds and seams of sandy clay at various horizons, leaks out at innumerable points on the slopes, so forming small patches of boggy ground." These wet slopes are of greatest extent on the southern edge of Hartford Bridge

Flats. The forest compartment (No. 72) studied in this work is situated on one of these wet slopes. It has also been the subject of study by Rutter (1955), Reynolds (1956), Webster (1962a and b) and Loach (1964). Rutter (1955) has shown that the ground water rises almost vertically in the soil under an artesian pressure and flows away down the slope through the upper horizons.

Vegetation:

Rutter (1955) has described the vegetation of this area as a stable wet-heath community of south-eastern England. He recognises a "Central associates" in which Calluna vulgaris and Molinia caerulea are dominant with Erica tetralix usually abundant. Dead Molinia shoots decay rather slowly in wet habitats and this results in the building up of tussocks of varying heights which are an important rooting medium both for Molinia itself and Calluna and Erica.¹⁸

The distribution and relative proportions of these species may vary according to local conditions of soil and drainage. Thus under wetter conditions this associates may grade into a vegetation resembling a "Valley-bog" dominated by Sphagnum spp. in which Erica tetralix is an important constituent, whereas Molinia and Calluna are sparsely distributed. Here Molinia does not show markedly tussocky habit. In other wet situations Molinia assumes complete dominance and forms tall tussocks, reaching 30cm. or sometimes more in height. Myrica gale is often abundant in this "wet Molinietum" and Salix species, mainly S. repens and S. atrocinerea often occur.

Transition of the "Central associates" to a rather drier type of Molinietum also occurs at Bramshill. It has a herbaceous layer of almost pure Molinia with only a little Calluna vulgaris and hardly any Erica tetralix. Here the

¹⁸The three species constantly referred to in this thesis are: Molinia caerulea (L.) Moench, Calluna vulgaris (L.) Hull, and Erica tetralix L. Where only a generic name is given, the specific epithets given above should be understood.

tussock building of Molinia is less pronounced than it is in the wet type of Molinietum. Drier Molinietum is readily colonised by tree species, particularly Betula pubescens and some Frangula alnus and Quercus robur and cannot be regarded as a stable community in contrast to the wet Molinietum which apparently forms a stable community which is not readily invaded by Betula sp. It may be mentioned here that very often there is no marked distinction between the drier and wetter types of Molinieta and they grade imperceptibly into one another.

Dry conditions may, under other circumstances, favour the development of Calluna, and Erica tetralix then becomes less frequent than it is in the "Central associates". The rate of decomposition of dead remains of Molinia is rapid and this results in small Molinia tussocks. This community may grade into "Callunetum." A typical dry Molinietum, a distinct community in which there is no accumulation of dead shoot bases, may also dominate considerable areas of dry heath. It has a variety of sub-ordinate species typical of dry soil. A true Callunetum and a dry Molinietum are not found in the present study area.

It can be seen from the account given above that wet-heath is a very variable association of three major species. A search through the literature brings forth many descriptions of one or the other of its many facies. The aerial survey of Robbins(1931) in the north of Bramshill Forest shows that the wet-heath vegetation stretched over this area before most of the trees were planted. Rankin (1911), Fritsch and Parker (1913), Summerhayes, Cole and Williams (1924), Summerhayes and Williams (1926), Benson and Blackwell (1926), Fritsch (1927), Bright (1928), Petch (1944), Newbould and Gorham (1956) and Newbould (1960) have described some of the various facies of the wet-heath community in different parts of south-east England.

A comprehensive general survey of the British lowland bogs in the south and east of England has been made by Rose (1953). He describes wet- and damp-heaths as two of the eight zones typically found in lowland valley bogs. He regards the wet-heath zones of the type studied in the present work as a smaller type of soligenous bog where the ground is much dissected. He calls it the "spring" or "flush" bog which is present on a steep slope where the water-table reaches the surface as the seams of clay and harder sandstone often throw out springs well above the floor of the older valleys. . .

There appears to be some extension of the wet-heath vegetation towards the south-west of England. On the old red sandstone of Somerset, Heath and Luckwill (1938) described a damp Molinietum, and Watson (1915) a very wet and tussocky Molinietum with Myrica gale, Alnus glutinosa and Sphagnum spp.

In the descriptions of the vegetation of northern and western parts of the British Isles (Tansley, 1939; Pearsall, 1950), strictly speaking, there is found nothing corresponding at all closely to the wet-heath associates of south-eastern England. Molinieta of these parts differ from those of the south-east England in that they occur mainly on deep peats and particularly along the sides of moorland streams where the water-table is moving (Jefferies, 1915; McVean, 1959) or in the raised bog communities (Pearsall, 1950; Davies, 1944). Calluna and Erica tetralix may be present in the northern and western parts but are always with a number of species other than those of the heath communities of the south-east.

Dimbleby (1962) reports results of pollen analysis in many heathland soils over the Eocene Bagshot Beds both in the Bramshill Forest area and elsewhere. It has been suggested that natural woodland has been considerably more extensive in

the past, and the present wet-heath communities must owe their existence to anthropogenic influences, particularly frequent burning, as indeed does most of the present-day heathland in England.

From the fore-going it is clear that the wet-heath vegetation is essentially a community of south-eastern England. Various facies of this community are present in the Ecological Reserve in Bramshill Forest and are described in detail in Section II.

b, Previous investigations:

Rutter (1955) investigated the relation between the composition of the vegetation and the depth of the water-table in this area. He found that the proportion of Molinia caerulea in the vegetation increased both with mean summer water-table depth and mean tussock height, and was related to these measures by a significant multiple regression. Tussock height, which is determined by the difference between the rate of growth of the species and the rate of decomposition of its dead remains, was shown to be positively related to water-table fluctuation. This relation was interpreted in terms of the improved aeration as a result of water-table fluctuation which favoured the growth of Molinia.

The proportion of Erica tetralix was negatively related to the water-table depth and tussock height, i.e., it increased where the water-table was consistently high and the tussocks were small. Calluna vulgaris showed little relation to water-table depth and fluctuation, but was inversely related to tussock height.

Reynolds (1956) investigated the relation between growth of four conifer tree species, water-table depth and soil porosity on wet-heath sites in Bramshill and Crowthorne areas in the counties of Hampshire and Berkshire. Tree growth

increased with the proportion of Molinia in the vegetation and at a given percentage of Molinia, it increased with increasing water-table depth up to an optimum of about 30 - 60 cm. and decreased thereafter. He found that in the case of Pinus sylvestris (the only species investigated from this point of view) mean tree height could be related to the volume of air-filled porosity in the soil by a highly significant simple regression. He suggested that some of the residual variation in tree growth about this regression line could be due to the differences in the nutrient status of the sites. Since the highest air-filled porosities were usually found under Molinia it would be unjustified to interpret the correlation between tree growth and air-filled porosity of the soil in terms of a simple causal relationship, for the effects of air-filled porosity on tree growth could not be separated from those due to the higher nutritional levels of soils under Molinia, which were found by Loach (1964).

Loach (1964) studied inter-relations between soil nutrients and vegetation in three adjacent sites at Bramshill Forest. These were a Valley-bog of small extent, a Molinietum and a site with Molinia and Calluna as co-dominants and Erica tetralix abundant (Central associates). Soil analyses for N, P, K, Ca and Mg and the ability of these sites to supply nutrients to Molinia, Calluna and Erica, when grown in them in conditions in which they did not compete with one another, showed that the Molinietum was most nutrient rich whereas the Valley-bog had the lowest nutrient content. Experiments with Molinia showed that in these soils it was most sensitive to variation in supply of phosphate. The availability of the nutrients to the species in the field could not be separated from such site factors as aeration and competition from other species.

Webster (1962 a, b) examined the relation between the composition of the wet-heath vegetation and the gaseous

composition of the ground-water and of the soil air above the water-table in wet-heath vegetation at Bramshill. Ground-water samples were obtained from depths of 12 and 24 inches and air was sampled from a depth of 6 inches. The highest percent cover of Molinia was associated with the lowest concentrations of CO_2 and H_2S in the ground-water, whereas at higher concentrations of these two gases the proportion of Molinia decreased and that of Calluna and Erica increased.

In controlled experiments lasting 24 hours only, Webster (1962, b) found that the root and shoot extension in Molinia were significantly reduced by concentrations of CO_2 and H_2S in the soil air in the same range as those found dissolved, under summer field conditions, in ground-water of wet-heaths. However, these experiments were performed in the presence of considerable amounts of O_2 . Thus the effects of high levels of CO_2 and H_2S combined with extreme O_2 deficiency, as they are in the field, cannot be judged from the results of Webster's experiments.

The effects of moving and stagnant ground-water on the growth of Molinia were also investigated experimentally and the growth was significantly reduced in stagnant water as compared with flowing ground-water.

c, Present work:

As mentioned above, Webster (1962 a) had related the distribution of Molinia, Erica and Calluna to the gaseous composition of the ground-water sampled from depths of 12 and 24 inches. Only a limited proportion of roots of Molinia reach these depths and the roots of heath species hardly penetrate so far (Rutter, 1955). In view of this it was realised that detailed studies of aeration conditions at shallower depths, coupled with a quantitative study of root distribution, would be necessary for assessing the response of the component species of

the wet-heath vegetation to aeration.

The importance of competition between Molinia and Calluna and Erica as a factor controlling the distribution of these species in different sites had been suggested by previous workers (Rutter, 1955; Webster, 1962 a, b; Loach, 1964), and clearly required investigation.

In the light of these previous investigations, the object of the present work was to study the soil conditions in wet-heaths at Bramshill with particular reference to aeration. With this end in view, four contrasted sites were selected. The descriptions of these sites appear in the next Section (Section II, a). The problem was approached by studying the performance in the natural communities of the component species - Molinia, Erica and Calluna. It was soon decided to confine further studies to Molinia and Erica partly because of their marked contrast in behaviour and also because of the difficulty of including all three species in a single investigation on the scale contemplated.

Soil profiles in the four sites were described and the root distribution of Molinia and Erica on these sites was studied. This study was continued by investigating the relation of porosity to depth and the distribution of roots in relation to pore sizes.

Probes were designed to sample soil air and soil water from different depths down the profile and the soil air samples obtained were analysed for O_2 and CO_2 , the water samples for O_2 , CO_2 and H_2S . The response of Molinia and Erica to different concentrations of O_2 , CO_2 and H_2S was then studied by growing them in culture solutions aerated with different concentrations of these gases. These gas concentrations covered the range of concentrations found dissolved in the soil water.

The competitive ability of young plants of Molinia and Erica was investigated in the field on three of the four sites, in enclosures from which native vegetation had been removed. Nutrients were applied to these transplants to see their response to the availability of nutrients in these otherwise nutrient-deficient sites, and nutrient requirements of Erica were also investigated in water-culture experiments.

All these observations and experiments were then combined with those which were made by Loach (1964) on the nutrient status of the sites and the nutrient requirements of Molinia, and an explanation of the variation in composition of the vegetation studied in terms of the interacting effects of drainage, aeration and nutrition and the competitive relations between the species, was attempted.

II. VEGETATION STUDIES IN THE FIELD

a. Sites and their vegetation.

Four contrasted sites, representing different facies of the wet-heath vegetation, were selected at Bramshill in the compartment 72 of the Ecological Reserve (Map Ref.SU805576). A plantation of Picea sitchensis at one time occupied the whole compartment but it was largely destroyed by fire in 1944 and was replanted in 1945. Three of these four sites have been the subject of study by Loach (1964) in his investigations of the nutrient status of wet-heath soils. The fourth site lies a few hundred yards away to the east of these sites. Following Rutter's (1955) classification these sites correspond to Valley-bog, Central associates, drier Molinietum and wetter Molinietum.

Valley-bog: This lies in the north-west of the compartment and is a soligenous valley bog of small extent. Rutter(1955) has shown that here ground water rises almost vertically towards the surface under an artesian pressure. Erica is the dominant species here and Molinia and Calluna are sparsely distributed. Sphagnum spp. (S.papillosum, S. cymbifolium and S. rubellum) form patches alternating with masses of Molinia shoot bases (very small tussocks). It was planted with Pinus contorta, Picea abies and Picea sitchensis. The tree growth is very poor, particularly in the spruces. In 1964 a few trees exceeded five feet in height (Loach,1964). Other species present here include:

Frequent: Eriophorum angustifolium Juncus acutiflorus
 Potentilla erecta

Occasional: Carduus dissectum Carex panicea
 Drosera rotundifolia Juncus kochii
 Narthecium ossifragum Succisa pratensis

Rare: Dactylorhiza maculata ssp. ericetorum
 Ulex europaeus

Very Rare: Potamogeton polygonifolius (in a pool of water).

Central associates: This lies in the centre of the compartment. Calluna and Molinia are the main component species of the ground flora but Erica is also present. Planted tree species are the same as in Valley-bog and tree growth is intermediate between Valley-bog and drier Molinietum, being, on average, approximately eight feet in height (Loach, 1964). Spruces are very small, seldom exceeding three feet in height. Other species present include:

Occasional: *Juncus acutiflorus* *Juncus kochii*
 Rare: *Betula pendula* *Betula pubescens*
 Frangula alnus *Quercus robur*
 Rubus fruticosus *Salix repens* (ditch bank)
 Sphagnum spp.

Drier Molinietum: This lies on the southern boundary of the compartment at the bottom of the slope. It had been left unplanted as a ride but has never been used as a thoroughfare and since 1945 Betula pubescens, B. pendula, Frangula alnus, and Quercus robur have invaded the area. The ground flora consists mainly of Molinia which forms tussocks up to 25 cm. high. Very few plants of Calluna and a few Erica are present along the banks of a ditch which runs in the east-west direction. Other species present here are:

Occasional: *Juncus acutiflorus* *Juncus kochii*
 Potentilla erecta
 Rare: *Gnaphalium uliginosum* *Luzula multiflora*
 Rubus fruticosus *Salix atrocinerea*
 Ulex europaeus
 Very rare: *Polytrichum formosum* *Sphagnum* spp.

Growth of Pinus contorta on the adjacent planted portion is better than anywhere else in the compartment. Loach (1964) records an average growth of about 20 feet since 1945.

Wetter Molinietum: This lies a few hundred yards to the east of the Central associates site. Here Molinia is markedly tussocky (tussock height: 30-40 cm.) Myrica gale is abundant with its rhizomes ramifying between and within Molinia tussocks. Calluna and Erica are present in small amounts - less than in the Central associates. There is more Calluna than Erica. Sphagnum spp. is locally abundant in some places, particularly in the vicinity of a drain which runs in the north-south direction. Other species present are:

Frequent: *Betula pubescens*

Occasional: *Potentilla erecta* *Salix atrocinerea*
 Ulex europaeus

Rare: *Juncus acutiflorus* *Juncus kochii*

Tree growth is better than in the Central associates but it is poor as compared to the planted portion adjacent to the drier Molinietum.

b. Performance of the species on different sites

Webster (1962) used a point quadrat method for describing the Bramshill vegetation. He made cover estimates by recording the species that touched a pin of 3 mm. diameter regardless of the number of times the pin touched a species. Loach (1964) used the same method and found that the cover estimate did not adequately show the differences in the amount of foliage between either species or sites. The number of touches per pin for Molinia was often greater in Molinietum (drier Molinietum of present work) than in the Central associates. So he made a cover repetition estimate by recording the number of touches made by each species on a pin. The results are presented in Table 1.

TABLE 1. COVER REPETITION ESTIMATES
 SEPTEMBER, 1963 (From Loach, 1964)

	Total number of touches per 100 pins			
	<u>Molinia</u>	<u>Calluna</u>	<u>Erica</u>	<u>Site means</u>
VALLEY-BOG	156	137	122	138
CENTRAL ASSOCIES	323	204	24	184
DRIER MOLINIETUM	536	3	11	183
Species means	338	115	52	

The differences in the standing crop of the species as they grew on different sites, which were apparent to the eye, became clear.

Cover repetition is an indirect measure of the standing crop and will be affected not only by growth of individual plants but also by factors affecting colonization and spread, including the effects of former fires. Strictly speaking it cannot be regarded as a measure of the performance of the species (cf. Greig-Smith, 1964; Kershaw, 1964). It was desired to have information about the performance - the vigour of growth - of the species on different sites and it was obtained from randomly chosen branches of each species, since an individual plant was too difficult to define and measure.

i) Sampling of the species:

On each site a transect of 50 feet length was laid at random. Sampling units, a tiller in the case of Molinia and an erect branch in the case of Erica and Calluna, were sampled at one foot intervals along this transect. In a circle of 45 cm. diameter around each sampling point a tiller or branch of the species present was selected at random by using a suitable point quadrat frame. While sampling Erica and Calluna it was recorded as to whether they were rooted in Molinia tussocks or not. The samples were kept in polythene bags prior to study.

ii). Measures of performance.

Depending on the growth form of Molinia, Erica and Calluna different characters were used as measures of their performance. In Molinia the length and maximum breadth of the leaf blades of the leaves of the upper series were measured to the nearest mm. and were multiplied to get an approximate measure of the leaf area. The leaf areas were added for the leaves on a tiller to get the leaf area per tiller. The scale leaves and leaves of the lower series were either dead or dying at that time of the year and were discarded. The number of buds, present at the base of the "basal internode" of a tiller, was counted. The dry weights of the leaves, basal internodes and buds of each tiller were obtained. The samples were dried at 80°C.

In the branches of Erica, the length of the longest shoot, the total length of the current year's shoots, and their total dry weight were determined. The diameter of the stem immediately below third year's growth was measured.

In Calluna the current year's "short shoots" and "long shoots" (Gimingham, 1960) were separated from the branch. The length of the longest "long shoot" and their total length was measured. The number of short shoots was counted, and, being very small in size, were not measured in length. The total dry weights of both types of shoots were taken. The diameter of the stem just below the lowest fork was measured.

The age of the branch, both in Erica and Calluna, was determined by following a field method. The method was obtained from a student's report of Miss C. J. Bryant which was lent by Dr. J. M. Lambert of the University of Southampton, to whom grateful acknowledgement is made. The method is summarised below.

The method is based on the annual growth pattern

of the species. In Calluna in the younger part of a branch the age can be determined by observing the following characters:

i, The occurrence of a number of "long shoots" close together at the apex of each year's growth which bear "short shoots", or laterals of limited growth. In cases where the apical bud dies one (or more) of the "long shoots" develops more strongly than the rest and acts as a leading shoot.

ii, The occurrence of more persistent leaves and of closely set leaf and branch scars marking the previous year's growth.

In Erica a dead terminal stump is left at the end of each year's growth, and around this develop a group of current year's shoots one (or sometimes two) of which acts as a leading shoot while others die after a few years. More persistent leaves and closely set leaf and branch scars mark the previous years growth, as in Calluna.

In the older parts of the branches of both Calluna and Erica many of the shoots die and break off, so that a bend in the stem or a fork, associated with branch scars, indicates the end of a year's growth.

As a check on this method of age determination, transverse sections of the stem at the level of second, third, fifth and seventh year's growth (age determined by the field method) were cut and double-stained with Safranin-Fast green combination. The count of the annual bands of wood (not annual rings) made on these sections revealed 2, 3, 5 and 7 of them, respectively. This speaks for the reliability of the field method of age determination in Erica and Calluna. It must be realised that the section method (counting of annual bands of wood or annual rings) will not be entirely accurate in very old stems because the bands (or annual rings) are not always clear and complete so that such counts may sometimes underestimate age by a year or two (Watt, 1955).

iii) Results:

The number of sampling units of the three species sampled on different sites are given in Table 2.

TABLE 2 NUMBER OF UNITS SAMPLED

October, 1963

Number of units of a species that could be sampled = 50

	<u>MOLINIA</u>	<u>CALLUNA</u>	<u>ERICA</u>
VALLEY-BOG	50	50 (35 rooted in <u>Molinia</u> , 15 in <u>Sphagnum</u>)	50 (19 rooted in <u>Molinia</u> , 31 in <u>Sphagnum</u>)
CENTRAL ASSOCIES	50	50 (All rooted in <u>Molinia</u>)	42 (All rooted in <u>Molinia</u>)
WETTER MOLINIETUM	50	50 (All rooted in <u>Molinia</u>)	27 (All rooted in <u>Molinia</u>)
DRIER MOLINIETUM	50	0	0

Performance of the species:

The differences between performance on various sites were subjected to analysis of variance. In the case of small whole numbers, e.g., number of buds in Molinia and age of the branch in Erica and Calluna, the data were transformed, using a square-root transformation, in order to remove the skewness. The numbers being small (all or majority were less than 10) $\frac{1}{2}$ was added to each observation before taking its square-root (Bartlett, 1936; Cochran, 1938). The performance of Molinia, Erica and Calluna on different sites with their least significant difference are given in Tables 3, 4 and 5.

MOLINIA: TABLE 3 PERFORMANCE OF MOLINIA ON
DIFFERENT SITES

Mean values of 50 figures

SITES	LEAVES		BASAL INTERNODES		BUDS	
	Leaf area per tiller cm ²	Leaf dry weight per tiller gm.	Dry weight per tiller gm.	Number per tiller n	$\sqrt{n + \frac{1}{2}}$	Dry weight per tiller gm.
VALLEY- BOG	16.89	0.058	0.057	2.14	1.618	0.0062
CENTRAL ASSOCIES	21.62	0.072	0.062	2.72	1.787	0.0069
WETTER MOLINIETUM	29.44	0.094	0.073	3.30	1.945	0.0076
DRIER MOLINIETUM	25.93	0.084	0.066	3.46	1.983	0.0086
L.S.D						
P = 0.05	6.50	0.025	N.S.		0.057	0.0013

N.S. = Not significant

The performance of Molinia in the Valley-bog was poor and differed significantly from that in the wetter and drier Molinieta in all the characters used as its measure except the weight of the basal internodes. Its performance in the Central associates seemed to be better than in the Valley-bog, though it differed significantly from the latter only in having a larger number of buds. The leaf area and leaf weight, though they gave higher values in the drier Molinieta than in the Central associates, did not differ significantly between the sites, but the former differed from the latter in having a significantly higher number and weight of buds. There was no significant difference between the wetter Molinieta and the drier Molinieta in any of the characters studied, but the figures for leaf area and leaf weight were higher in the wetter Molinieta whereas those for number and weight of buds were higher in the drier Molinieta.

ERICA: Table 4.

The performance was poor on the Valley-bog and differed significantly from that on the wetter Moliniatum in the total length of current year's shoots, and their weight. There was no significant difference between the Valley-bog and the Central associates though the latter gave higher values for the different characters studied. Central associates did not differ significantly from the wetter Moliniatum.

TABLE 4 PERFORMANCE OF ERICA ON DIFFERENT SITES

October, 1963

o = Mean values of 50 figures. ⊕ = Mean values of 42 figures.

+ = Mean values of 27 figures.

SITES	Current year's growth					
	Length of longest shoot	Total length of shoots	Dry weight of shoots	Diameter of stem immediately below third year's growth	Age, years	
	cm.	cm.	gm.	mm.	n	$\sqrt{n + \frac{1}{2}}$
VALLEY BOG ^o (I)	7.9	33.7	0.1663	1.07	5.28	2.38
CENTRAL ASSOCIATES ⁺ (II)	9.4	51.0	0.2405	1.02	5.85	2.50
WETTER MOLINIETUM ⁺ (III)	10.2	67.0	0.2976	1.09	5.88	2.51
L.S.D. (P = 0.05)						
I and II	2.23	21.67	0.0950	N.S.		N.S.
I and III	2.52	24.47	0.1089	N.S.		N.S.
II and III	2.62	25.41	0.1128	N.S.		N.S.
N.S. = Not significant						

CALLUNA: Table 5.

This species also showed poor performance on the Valley-bog. The Central associates and wetter Molinietum differed significantly from Valley-bog in the weight of the "short shoots," and the diameter of the stem below the lowest fork. The Central associates gave a little higher value than the wetter Molinietum but there was no significant difference between the two. There was no significant difference between the sites for the length and weight of the "long shoots" though the values for these measures were highest for the Central associates.

TABLE 5 PERFORMANCE OF CALLUNA ON DIFFERENT SITES

October, 1963

Mean values of 50 figures.

SITES	<u>Current Year's growth</u>					Diameter of stem below lowest fork mm.	Age, years	
	<u>Short Shoots</u>		<u>Long shoots</u>				n	$\sqrt{n + \frac{1}{2}}$
	Number	Total dry weight gm.	Length of longest shoot cm.	Total length cm.	Total dry weight gm.			
VALLEY- BOG	40.96	0.0354	5.69	11.30	0.0290	6.80	13.6	3.75
CENTRAL ASSOCIES	50.86	0.0553	6.76	13.91	0.0396	10.40	14.1	3.81
WETTER MOLINIETUM	50.08	0.0524	6.64	13.22	0.0353	9.30	13.0	3.68
L. S. D. (P = 0.05)	N.S.	0.0161	N.S.	N.S.	N.S.	1.19		N.S.

N.S. = Not significant.

iv), Discussion:

It became clear that the Valley-bog was very poor for the growth of the three species including Erica which was dominant here. The Central associates was poor as far as Molinia was concerned but it was best for the growth of Calluna which was the dominant species here. Molinia gave best performance on the drier and wetter Molinieta. The slightly smaller leaf

area and leaf weight on the former as compared to the latter might have been due to a more severe intraspecific competition because it was a pure stand of Molinia. The largest number of buds and their weight on this site were a reflection of the higher density because the larger the number of buds the larger the number of tillers in the next season.

Loach (1964) in his experiment on the growth and nutrient uptake of the three species under field conditions, grew them, without interspecific competition, for two growing seasons in small enclosures on the sites from which the native vegetation had been removed. He measured the growth rate of the species as they grew on different sites, and found Molinietum (drier Molinietum of the present work) as the best site for the growth of Molinia and Erica whereas Calluna grew best in the Central associates though its growth did not differ significantly from that on the Molinietum. The growth of the three species was very poor in the Valley-bog and differed significantly from the other two sites (the Central associates and the Molinietum). The growth rate of Molinia though higher in the Molinietum did not differ significantly from that in the Central associates.

These results, obtained in conditions which excluded interspecific competition, correspond closely with those obtained in the present work on the performance of the species in the natural communities.

At this stage of the work it was decided to limit further studies to Molinia and Erica.

c. Root studies:

It was realised that the root studies of the species (Molinia and Erica) formed a necessary prelude to further work on their growth on, and the studies of the soil conditions, particularly aeration, in the different sites.

1. Root distribution:

Roots of Molinia and Erica were sampled to study their distribution at different depths down the profile and see the differences, if any, as the species grew on different sites.

i. Root sampling:

On each site a permanent transect of 70 feet length was laid at random. On the Valley-bog, Central associates and drier Moliniatum the transects were laid quite close to those laid before for the sampling of the species for their performance studies (Section IIp19), but in the wetter Moliniatum this transect happened to lie a little distance away to the east of the previous transect and here it was a little more wet. (The probes for sampling soil air and water, described in Section IV, were sited along these transects.) A "nail-board" (Plate 1) was used to take root samples at monthly intervals from June - September, 1964. The "nail-board" was a rectangular board of wood, 1 foot wide and 1.5 feet long through which 3 inch long nails projected on one side at right angles to the major plane of the board. The sampling spots along the transects were places where Erica and Molinia were growing together to the exclusion of Calluna. There being no Erica present on the drier Moliniatum only Molinia roots were sampled, whereas on the other 3 sites both the species were sampled.

A small trench was dug on one side of the sampling spot and the board was inserted into the side of it so that the nails penetrated into the soil. The soil around the board was then cut away so that a soil monolith remained on the board held by the nails. A rectangular wooden board of the same size as



Plate 1. "Nail-board" for root sampling.

the nail-board was secured to the latter at the four corners, above the soil monolith, using long nuts and bolts. This checked the loss of soil from the nail-board during transportation to the laboratory. These monoliths were used to describe the soil profiles on the different sites. pH determination of the soil in different horizons was made on a stiff paste of soil and distilled water, using a Pye portable pH meter and Pye-Ingold electrode.

Using a sharp knife, the soil monolith was cut into horizons along the nails. The top and the bottom horizons of the soil thus obtained were 1.5 inches deep (54 cu.in. vol.) while the remaining five horizons between them were each 3 inches deep (108 cu. in. vol.). The soil horizons were washed with a jet of water. The water used in the washing process drained away through a fine-meshed sieve (60 B.S.S.) which retained the roots and large soil particles and flint. These were separated by decantation, the roots tended to float while the soil and flint sank. Using this method of soil washing even very fine roots were not lost, whereas it was found that if the soil monolith was washed in one piece, though the roots were retained in their natural position, a large number of fine roots became detached and got washed away with the jet of water.

The underground parts thus obtained in different soil horizons were air dried. In each horizon the roots of Molinia and Erica were hand-sorted from the rest of the underground material. Because of their distinct colours (Erica roots were black while those of Molinia were creamish-white) the sorting was fairly easy. The tussocks were broken open and the roots of Molinia and Erica were separated from the tussock material (basal internodes, etc.). In the samples obtained from the Valley-bog every effort was made to carefully sort out the roots of the two species from the peat. Erica roots

and root-stocks were separated. Notes were made on the physical appearance of the roots present at different depths. The air-dry weights of the roots obtained at different depths were taken. No attempt was made to separate the living roots from dead ones, and the root weights reported here include living roots and dead ones not sufficiently decomposed to be unrecognisable.

ii, Results:

Descriptions of soil profiles:

General descriptions of the soil profile in the different sites are given below (Tables 6 to 9). These descriptions are based on the studies of soil monoliths sampled on four occasions (June - September).

TABLE 6 SOIL PROFILE IN THE VALLEY-BOG

Depth (cm.)	Colour, structure and texture	pH
	A surface matting of <i>Sphagnum</i> spp; ± consolidated, in places, by soft decaying <i>Molinia</i> shoot bases, 7.5 - 12 cm. thick.	4.0 - 4.20
0 - 14	Loose amorphous peat, dark brown, bound by many roots.	4.30
14- 18	Loose amorphous peat, lighter in colour (grey-brown) than above.	4.40
18- 30	Dense, black peat, greasy	5.20
> 30	Pale green, fine, quaking sand with occasional flints.	5.45

TABLE 7 SOIL PROFILE IN THE CENTRAL ASSOCIATES

Depth (cm.)	Colour, structure and texture	pH
	<i>Molinia</i> tussock, 12 - 15 cm. high and heather litter.	3.90
0 - 13	Black, dense, greasy with occasional admixture of sand.	4.20
13 - 30	Greyish brown to buff grey sand, with occasional orange mottling, orange streaks along root channels, a few flints.	4.60
> 30	Green sand with orange mottling, occasional flints.	5.20

TABLE 8 SOIL PROFILE IN THE WETTER MOLINIETUM

Depth (cm.)	Colour, structure and texture	pH
	<u>Molinia</u> tussock, 30 - 35 cm. high	4.20
0 - 15	Dark brown, friable, organic loam, crumbs 1 - 4 mm. diameter, many roots.	4.40
15 - 22	Light brown, clayey sand with orange mottling, orange streaks along root channels.	4.50
22 - 30	Light greenish fine sand, a few orange specks, occasional flints.	4.95
> 30	Greenish white to green clayey sand with a little orange mottling.	5.70

TABLE 9 SOIL PROFILE IN THE DRIER MOLINIETUM

Depth (cm.)	Colour, structure and texture	pH
	<u>Molinia</u> tussock, 20 - 25 cm. high	4.20
0 - 15	Black, friable, organic loam, crumbs 1 - 4 mm. diameter, many roots.	4.30
15 - 24	Dark brown, dense, clayey with occasional orange mottling, orange streaks along root channels, occasional flints.	4.50
24 - 28	Buff, sandy clay merging into	5.0
> 28	Light green clayey sand with frequent orange mottling; flints	5.35

Production of roots at different depths:

The sampling at different times of the year could not be expected to show temporal variations in the amount of roots produced by the species because of its limited nature, only one sample having been taken from each site every month from June to September. The four samples thus obtained on each site have been treated as replicates. The absolute weight of roots in the samples varied widely because different amounts of above-ground parts of a species were present on the samples. Consequently, before means were calculated the weights at

different depths were expressed as percentages of the total root weight in each sample.

The amounts of roots of Molinia and Erica found at different depths on different sites are shown in Figs. 1 and 2, respectively. A few points need clarification. 1, As mentioned earlier (p.29) the top and bottom soil horizons were only 1.5 inches deep while the remaining were each 3 inches deep. In order to express the air dry weight of roots as a percent of the total root system found at successive 3 inches soil depths, for the sake of clarity and uniformity of expression, the percentage weights of roots present in the 1.5 inches soil horizons have been doubled and the width of the histogram, in these parts, has been halved with the result that the total area has remained the same.

2, The "surface" refers to the horizons of recognisable plant remains (see descriptions of soil profiles, pp.30 and 31) above the nail-board, above general soil level and was of different height in different samples.

Expressed as their percent, the means of four replicates had fairly low standard errors (below 10%) down to 7.5 inches soil depth in Erica and 10.5 inches in Molinia, while below these depths the values were fairly high (20 - 40%), presumably because of very small proportions of roots present at these depths. (The data on which Figs. 1 and 2 are based are given in Appendix A.)

In Erica the proportion of roots present at corresponding soil depths did not differ significantly between sites. The same was true for Molinia. Erica had almost one-third of its total root system at the surface and the amount decreased with soil depth and below 7.5 inches there were very few roots present. There was hardly any evidence for the rooting of this species below 13.5 inches (on the wetter Molinietum only traces were found in 13.5 - 16.5 inches soil horizon).

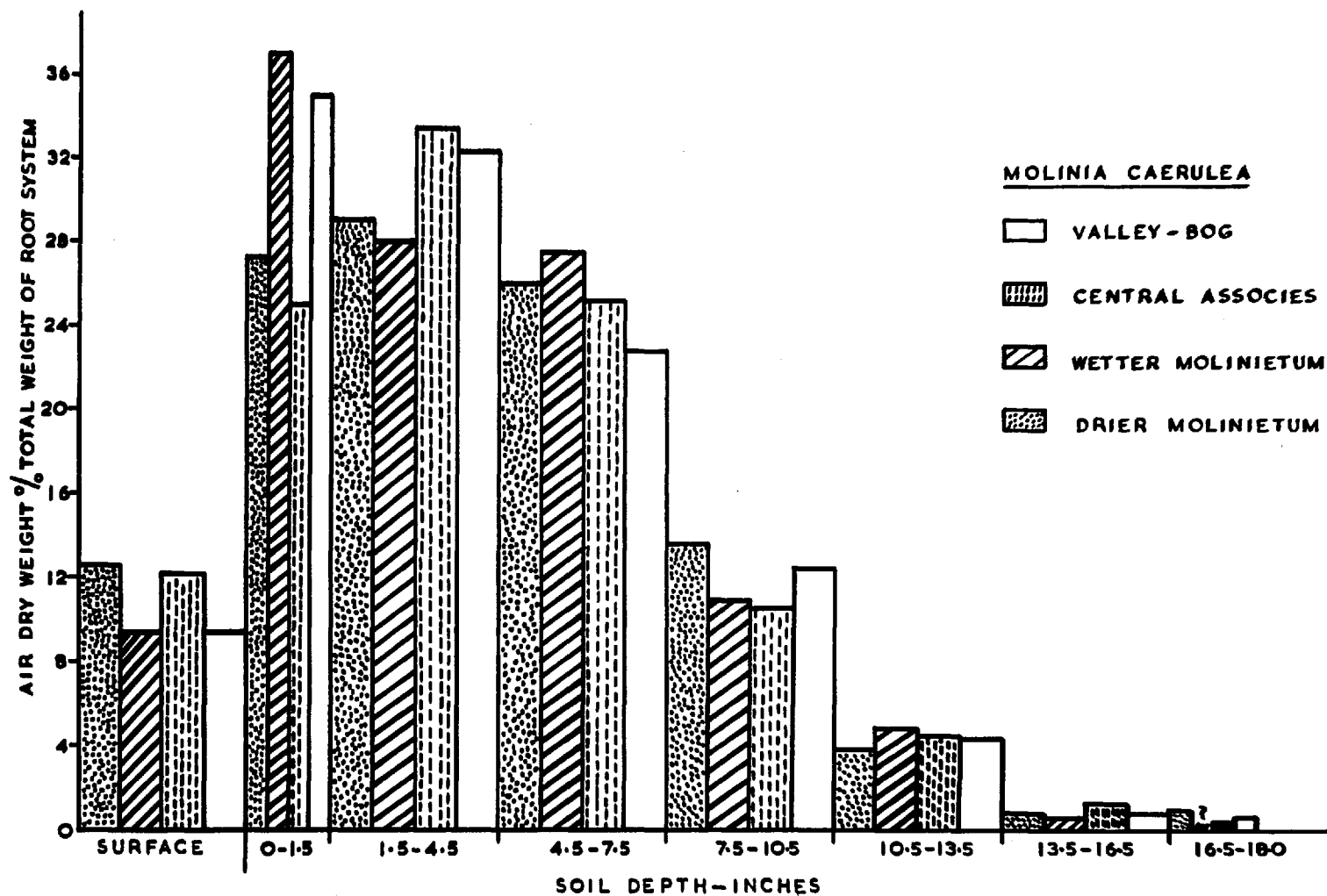


Fig. 1. *Molinia caerulea*: Percentage of total root system, by weight, found at successive 3 inches depths. (For explanation see text.)

In Molinia the amount of roots increased with depth to 4.5 inches and then there was a very slight fall to 7.5 inches but the decrease was very pronounced below this depth. Roots were present, though very few, down to the maximum depth of sampling (18 inches).

Erica should be regarded as a shallow-rooting (surface-rooting) species whereas Molinia is intermediate between surface-rooting and deep-rooting species (Boggie, Knight and Hunter, 1958).

The young roots of Erica which were near the surface and the adventitious roots on the prostrate stems were reddish brown and slightly shiny whereas the older roots were dull black.

As is clear from Fig. 1 there was hardly any difference in the rooting habit of Molinia sampled on different sites, but the roots showed some differences in their morphology. The roots present below 7.5 inches in the Valley-bog had a very loose cortex which was in various stages of sloughing off and in the roots below 10.5 inches it was mostly sloughed off and the bare white stele was to be seen. But on other sites the cortex, though loose at lower depths, was intact even up to a depth of 18 inches and no bare stele was observed. By applying a very slight pull it was very easy to break the bare stele from the Valley-bog site as compared to the stele which was dissected out of a root in which cortex was intact. The former did not possess an endodermis and the differential staining failed to stain the phloem elements whereas the latter had a distinct endodermis and the phloem elements stained deeply (Plate 2).

On all the sites except the Valley-bog, some of the roots below 4.5 inches and a majority below 7.5 inches had an orange-brown deposit on their surface.

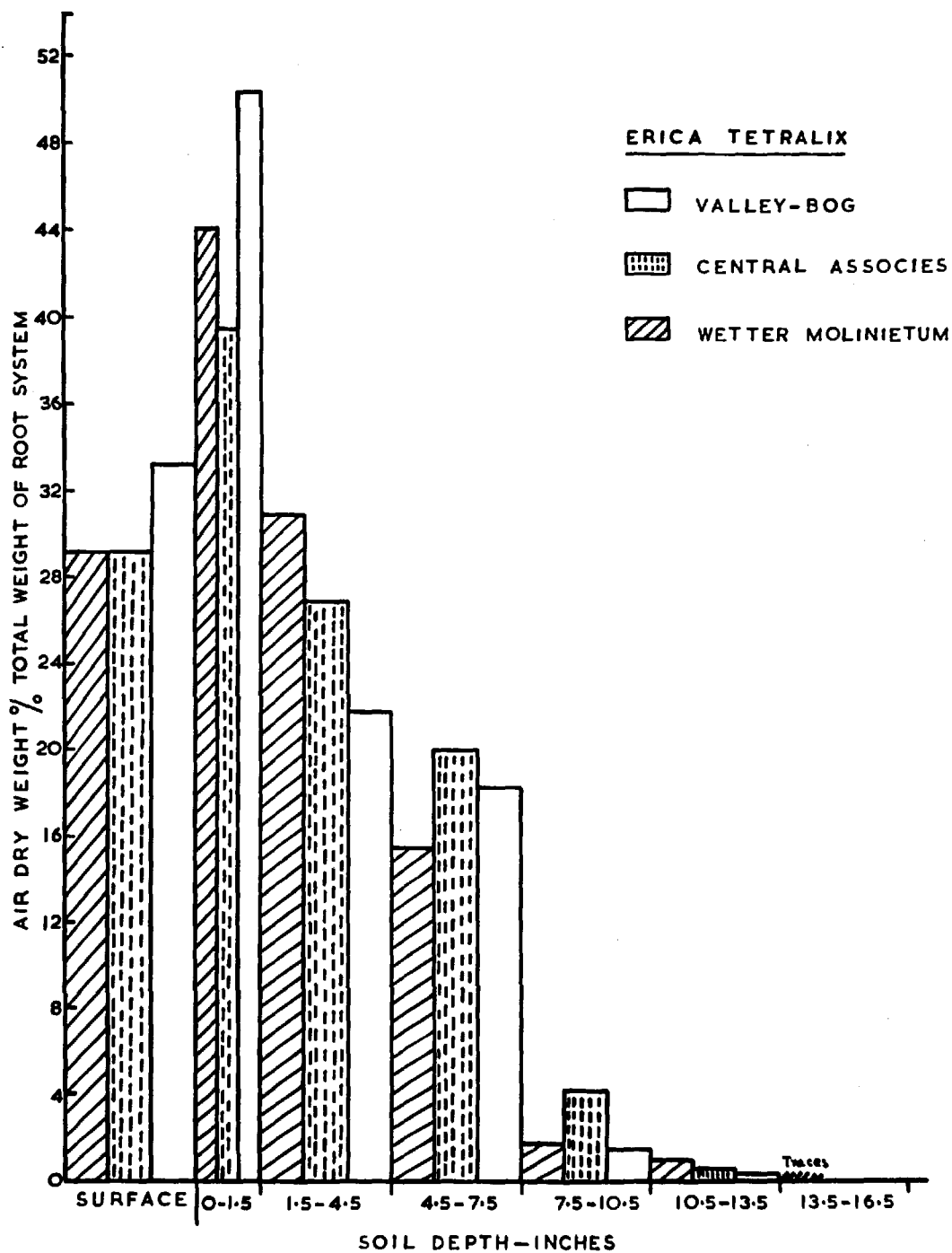
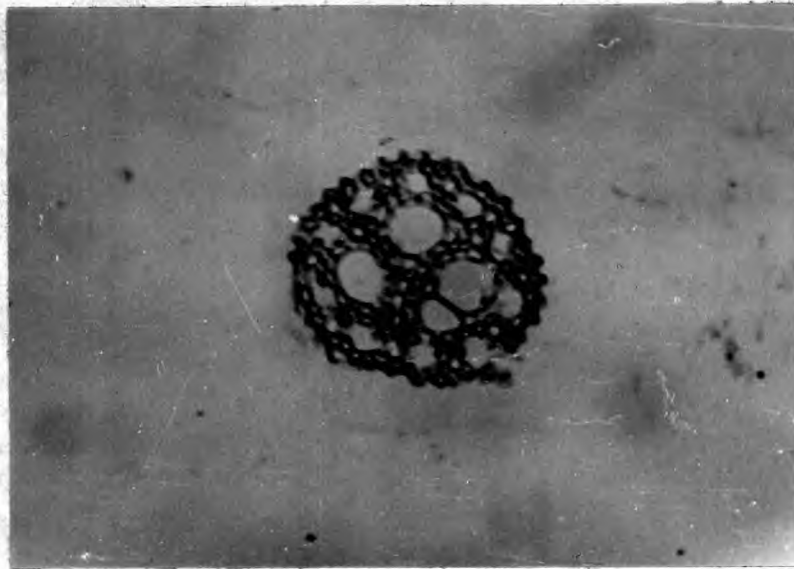
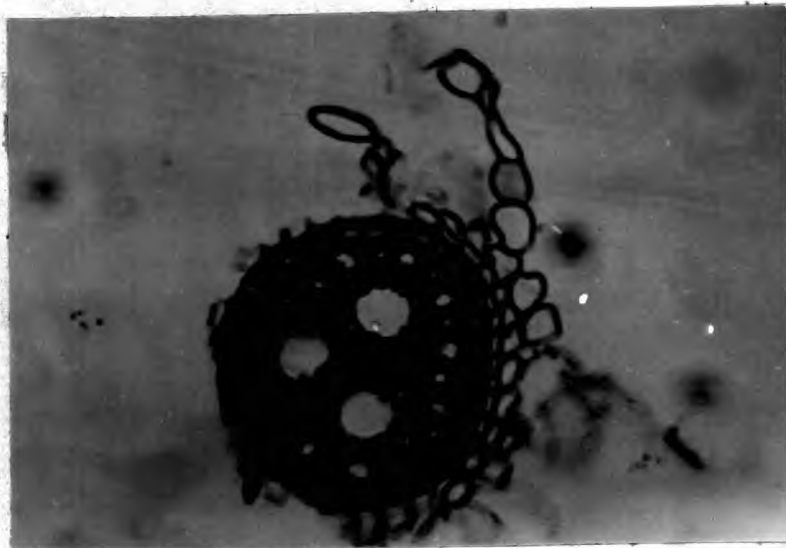


Fig. 2. *Erica tetralix*: Percentage of total root system, by weight, found at successive 3 inches depths. (For explanation see text.)



a



b

Plate 2. Molinia caerulea: Transverse sections of stele from the Valley-bog.

a: Bare stele. X225

b: Stele dissected out from a root with intact cortex. X225

iii, Discussion:

The "nail-board" method of root sampling has been used fairly widely and the size of the board and the size and position of the nails have varied greatly between workers (Blaser, 1937; Goedewaagen, 1948, 1949; Salonen, 1949; Schuster, 1964).

Heath and Luckwill (1938) found 18 cm. (≈ 7 inches) and 33 cm. (≈ 13 inches) as the maximum depths of penetration for Erica and Molinia, respectively. Rutter (1955) found roots of Erica penetrating up to 30 cm. (= 12 inches) in the Central associates while, in the same site, those of Molinia penetrated to a depth of about one meter. Boggie, Knight and Hunter (1958) used radioactive tracers for studying in situ the rooting habit of 25 species including Erica and Molinia. In Erica the evidence for rooting below 6 inches was inconclusive. Molinia showed high activity to a depth of 12 inches, an appreciable amount at 18 inches while the activity at 24 inches was very low or perhaps absent.

In the present work the maximum depth of penetration of Erica roots has been found to be 13.5 inches (only traces up to 16.5 inches in the wetter Molinietum). The maximum depth of penetration of Molinia roots has not been studied but the distribution of the amounts of roots at different soil depths suggests that though the roots may penetrate as deep as 40 inches (Rutter, 1955) the amount of roots at such depths would be negligible.

Various techniques have been used by various workers to distinguish living roots from dead ones. Vital stains have been used to distinguish between "active" and "non-active" roots. Goedewaagen (quoted by Troughton, 1957) used tetrazolium chloride and Schwass and Jacques (quoted by Troughton, 1957) have used 2, 3, 5 - triphenyl tetrazolium bromide. But these stains have not been found suitable for

older roots. No technique is yet available for distinguishing, with certainty, living roots from dead ones.

The process of decay in a root apparently starts in the cortex and later spreads to the stele (Troughton, 1957, Gadgil, 1965). Molinia has an early deciduous cortex whose decay leaves a bare stele surrounded by the endodermis. In the Valley-bog some of the roots below 7.5 inches and most of them below 10.5 inches had their cortex sloughed off. The ease with which the bare stele could be broken and the lack of endodermis and, most probably, functional phloem elements (see p. 34) suggested that it was either dead or in a very advanced stage of death and decay. In view of this the amount of roots below 7.5 inches in the Valley-bog must be regarded as including a large majority of dead or decaying roots which were still recognisable presumably because of a very slow rate of breakdown due to such site factors as high water-table and poor aeration, etc.

2. Seasonal production and longevity of *Molinia* roots:

Jefferies (1916) termed the main roots of *Molinia* "cord" roots and their branches "fibrous" roots. A study of the seasonal production and longevity of the cord roots was made by growing plants in Silwood soil. Such a study would have been too difficult in the field on the selected sites at Bramshill, unless a great deal of time and labour were given to it.

i, Method:

Wooden boxes 6 x 6 inches in inside width and 24 inches deep were used. Each box had two rows of 16 holes, 1.5 inches apart, on one side. After filling the boxes with soil, 6 inches long nails were pushed through these holes to support the roots in position when the time came to wash them out.

24 boxes were put in a trench at Silwood Park and were kept level with the general ground level (Plate 3). They were filled with the soil which had come out of the trench. The soil was a rather sandy brown earth of a highly leached nature with unstable structural development. In early November, 1964 (nearly the end of the growing season for *Molinia*) plants were collected from a forest ride in Bramshill Forest taking care to get the entire root system intact. The old cord roots were removed using a pair of scissors and the current year's cord roots were tagged and numbered by using a rust-resistant, galvanised soft iron wire (0.45 mm. diameter) which was twisted loosely round the root near its distal end - away from the root tip - and the number of twists indicated the root number. These plants were photographed before transplantation into the boxes. Of the 24 transplants only two did not grow in the next season. Two boxes were dug up every month from April to October, 1965 and from April to



Plate 3. Molinia caerulea growing in wooden boxes used
for the study of seasonal production and longevity
of roots.

July, 1966 (22 boxes in all). One side of the box was removed and the roots were washed free from the soil.

ii, Results:

The galvanised soft iron wire proved a very useful material for marking the roots and was found intact on all the marked roots. The results reported for a month are based on the study of two plants.

The first series of leaves, consisting of scale and functional leaves, started to expand in April, 1965. The previous year's cord roots did not increase in length but they produced a few small, new laterals. They produced more lateral branches (fibrous roots - Jefferies, 1916) in May and June and these branches were further branched having very fine roots. A few of these lateral branches were very profusely branched and were thicker in diameter than the branches they had produced, though they were thinner than the mother cord roots. Up-to this time no new cord roots had appeared, except for a few initials (small protuberances) at the base of the new shoot (Table 10). But in early July, when the second series of leaves had expanded, new cord roots had extended, and together with the branches from the old cord roots, some of them at least, had reached a depth of 12 inches. In August and September, there was an increase in the number of new cord roots and the branching of the roots and the root system was very well developed and some of the roots were rooting to 18 inches.

TABLE 10 SEASONAL PRODUCTION OF NEW CORD ROOTS

1965														
PLANT	APRIL		MAY		JUNE		JULY		AUGUST		SEPTEMBER		OCTOBER	
NO.	I	II	I	II	I	II	I	II	I	II	I	II	I	II
NUMBER OF NEW ROOTS	0	0	0	0	2	1	3	5	6	7	7	7	12	11
					(small protub- erances)									

The current year's cord roots were slightly lighter in colour as compared to the previous year's cord roots. The plants obtained from the boxes in April to July, 1966 showed that the old cord roots, which were now in their third year, were still living and, at least some of them, were profusely branched. The cortex appeared to be rather loose on these cord roots in comparison with those of the current or previous year's cord roots. But there was no sloughing of the cortex and there was no difference in the tensile strength of the old and the new cord roots.

iii, Discussion:

The increase in the number of new cord roots from April to October, 1965, though based on the study of different plants at different times instead of being confined to a single plant (which would have been the ideal situation) was consistent and the two plants sampled in a month agreed very well.

Stoddart (1935) and Weaver and Zink (1946) followed the life of individual roots by banding them with small pieces of metal. They have shown that the length of life of the roots of the same species was not uniform and considerable differences existed between the species. Stoddart (1935) found that both seminal and nodal roots of prairie grasses, even under adverse conditions, may live longer than two years.

Jefferies (1916) has casually mentioned that the cord roots in Molinia commonly function through 3 seasons. The present work has shown that they were functioning up to the third season. Unfortunately this study could not be prolonged to see if they would function any longer. The old cord roots did not increase in length in any of the 22 plants examined though they produced a number of branches which permeated the soil to great depths. The possibility of damage to the tips of the cord

roots, during transplantation, cannot be ruled out. But it is difficult to accept, particularly when the photographs of the plants taken before putting them into the boxes showed the root tips intact, that all of them were damaged while planting them in the boxes. However, the observation that the old cord roots did not increase in length cannot be regarded as a conclusive evidence and more detailed work, perhaps starting with germinating seeds grown in large transparent containers with the observations spread over a longer period of time, is needed.

3. Root anatomy:

i, Molinia caerulea:

A transverse section of the root (Plate 5) shows that the cortex is divisible into three zones: an outer zone of circular cells of various sizes which increase in size towards the interior of the root, a middle zone of almost circular cells becoming separated by their tearing and dissolution into radial rows with large air spaces between them, and an inner zone of radial rows of closely placed cells which become smaller in size as the endodermis is approached. The stele has a sclerenchymatous ground tissue and is responsible for the remarkable tensile strength of the root.

The cord roots present at different soil depths were studied quantitatively with particular reference to the amount of intercellular spaces in the cortex. A few cord roots were selected at random from those obtained from horizons of the soil monoliths sampled from the four sites (see p. 29). Transverse sections of these roots were cut with a microtome and were double stained using Safranin - Fast green combination. For each soil horizon, one of these sections was selected at random and a camera-lucida drawing of it was used for measuring the areas of the root, cortical spaces, stele and the large vessels in the stele. A planimeter was used for making these measurements.

Results:

The results are given in Tables 11 to 14 The values for the characters measured have also been expressed as a percent of the root area because of the different sizes of the roots obtained from different depths. The amount of the cortical spaces, expressed as a percent of the total root area, increased with increasing soil depth and beyond 4.5

TABLE 11.

VALLEY-BOG

SOIL DEPTH	AREA OF ROOT	AREA OF STELE	AREA OF CORTICAL	LARGE VESSELS	AREA OF	CORTICAL SPACES,	
inches	mm. ²	mm. ²	SPACES ² mm. ²	IN STELE	STELE, % Root	% Root Area	
				Number	Area ² mm. ²	Area	% Root Area
Surface	167.42	18.18	1.34	13	0.97	10.85	0.80
0 - 1.5	114.52	13.22	11.65	7	0.87	11.54	10.17
1.5 - 4.5	154.83	11.23	34.38	6	0.87	7.25	22.20
4.5 - 7.5	100.23	9.75	40.74	7	0.85	9.72	40.64
7.5 - 10.5	213.42	13.55	98.09	5	0.96	6.34	45.96
10.5 - 13.5	55.02	2.80	35.86	3	0.33	5.08	65.17
13.5 - 16.5	-	2.06	-	4	0.35	-	-

TABLE 12. CENTRAL ASSOCIES

SOIL DEPTH	AREA OF ROOT	AREA OF STELE	AREA OF CORTICAL SPACES	LARGE VESSELS IN STELE		AREA OF STELE,	CORTICAL SPACES,
inches	mm. ²	mm. ²	mm. ²	Number	Area mm ²	% Root Area	% Root Area
0 - 1.5	235.66	24.13	18.40	9	1.85	10.23	7.80
1.5 - 4.5	216.90	16.36	41.73	8	1.11	7.54	19.23
4.5 - 7.5	90.21	4.46	36.19	5	0.47	4.94	40.58
7.5 - 10.5	58.42	1.65	23.71	2	0.21	2.82	39.65
10.5 - 13.5	92.34	5.61	37.04	6	0.75	6.07	40.11
13.5 - 16.5	38.80	1.90	24.87	3	0.32	4.89	64.09

TABLE 13 WETTER MOLINIETUM

SOIL DEPTH	AREA OF ROOT	AREA OF STELE	AREA OF CORTICAL SPACES	LARGE VESSELS IN STELE		AREA OF STELE,	CORTICAL SPACES
inches	mm. ²	mm. ²	mm. ²	Number	Area mm. ²	% Root Area	% Root Area
0 - 1.5	179.78	14.29	20.99	8	1.15	7.94	11.67
1.5 - 4.5	202.61	16.69	49.50	6	1.61	8.23	24.43
4.5 - 7.5	79.12	4.29	32.47	4	0.71	5.42	41.03
7.5 - 10.5	112.18	4.13	52.14	5	0.65	3.68	46.47
10.5 - 13.5	31.98	1.07	21.48	2	0.16	3.34	67.16
13.5 - 16.5	61.84	2.47	37.93	3	0.37	3.99	61.33

TABLE 14 DRIER MOLINIETUM

SOIL DEPTH	AREA OF ROOT	AREA OF STELE	AREA OF CORTICAL SPACES	LARGE VESSELS IN STELE		AREA OF STELE,	CORTICAL SPACES,
inches	mm. ²	mm. ²	mm. ²	Number	Area mm. ²	% Root Area	% Root Area
0 - 1.5	144.17	17.76	19.00	7	1.40	12.31	13.17
1.5 - 4.5	309.46	26.85	34.66	7	2.33	8.67	11.20
4.5 - 7.5	121.14	10.16	47.93	6	0.81	8.38	39.56
7.5 - 10.5	75.45	4.95	32.89	2	0.57	6.56	43.58
10.5 - 13.5	200.04	13.14	88.28	4	2.13	6.56	44.13
13.5 - 16.5	22.06	0.98	13.22	1	0.16	4.44	59.92
	64.40	4.21	37.85	3	0.62	6.53	58.77

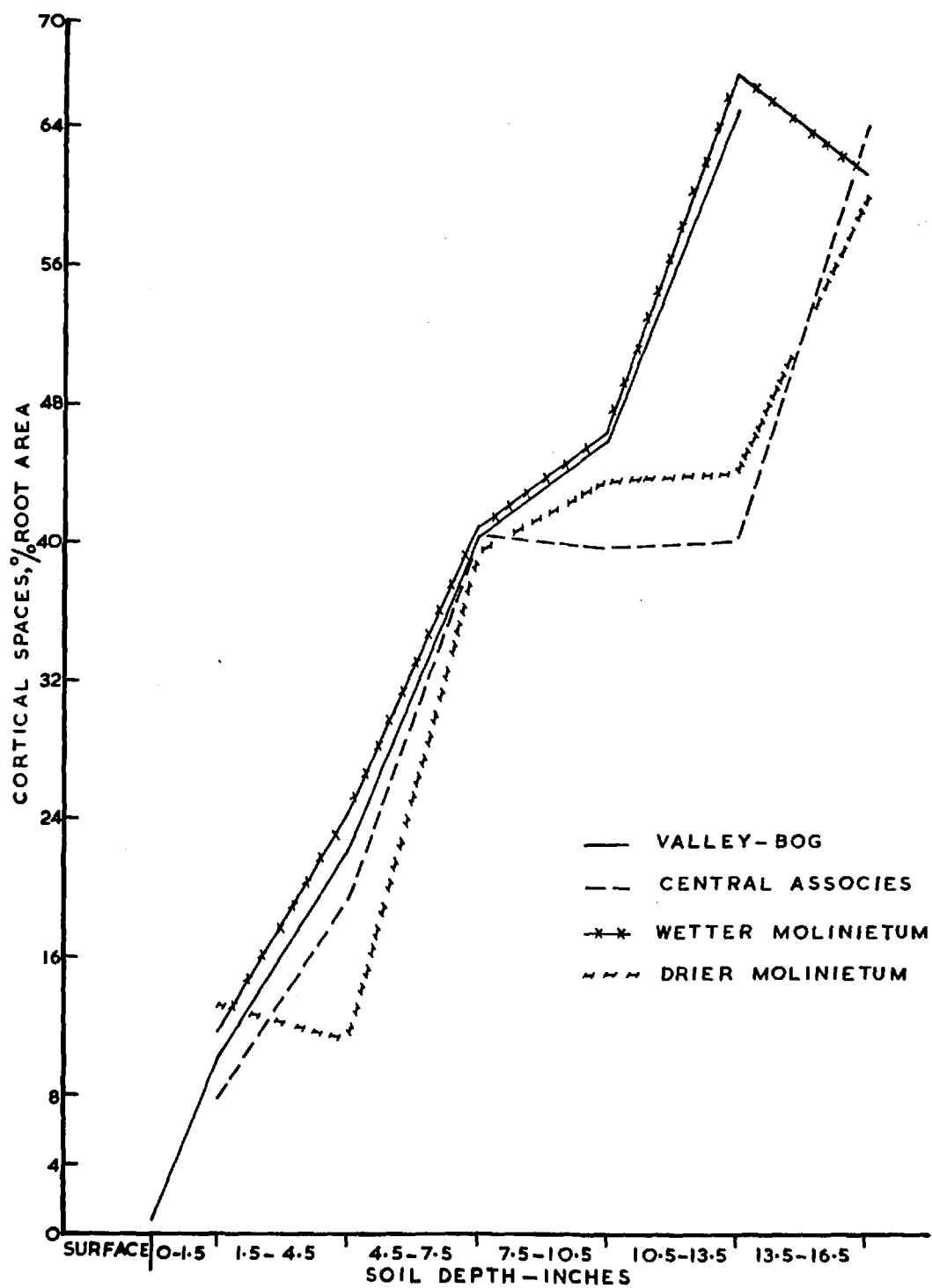


Fig. 3. *Molinia caerulea*: Cortical spaces, % root area, in old cord roots from different soil depths on different sites.

inches there was a marked increase (almost twice the amount at 1.5 - 4.5 inches horizon) (Fig. 3).

There were no significant differences, for the measures studied, between the roots from different sites for the same soil depth.

Sections of the old cord roots obtained from 4.5 - 7.5 inches horizon from the Valley-bog and 13.5 - 16.5 inches horizon from the wetter Molinietum showed, that, in spite of the enormous development of the cortical spaces, the roots were living and producing lateral branches (Plate 4).

It was realised that a study of the sections obtained from different depths on a single cord root would give more direct information than that obtained from the sections of the randomly selected pieces which most probably belonged to different cord roots.

Old cord root:

A cord root was carefully separated from the soil to its maximum depth of penetration which in this case was 13.5 inches. It did not have a growing tip and was of cream colour. It had a number of lateral branches which were white in colour, like the current year's cord roots. For each soil horizon one transverse section was selected at random from those obtained from a root piece and a camera-lucida drawing of it was used for the different measurements (see above, p.44). The results are given in Table 15 (Plate 5, Fig. 4). The results agreed with those obtained from the root pieces selected at random from the roots obtained in a soil horizon. Up-to a depth of 7.5 inches, in spite of a reduction in the root area (size), there was an increase in the amount of cortical spaces. But the decrease in area below 7.5 inches was not accompanied by an increase in the area of the cortical spaces and the latter remained more or less the same down to the maximum depth of penetration (13.5 inches).

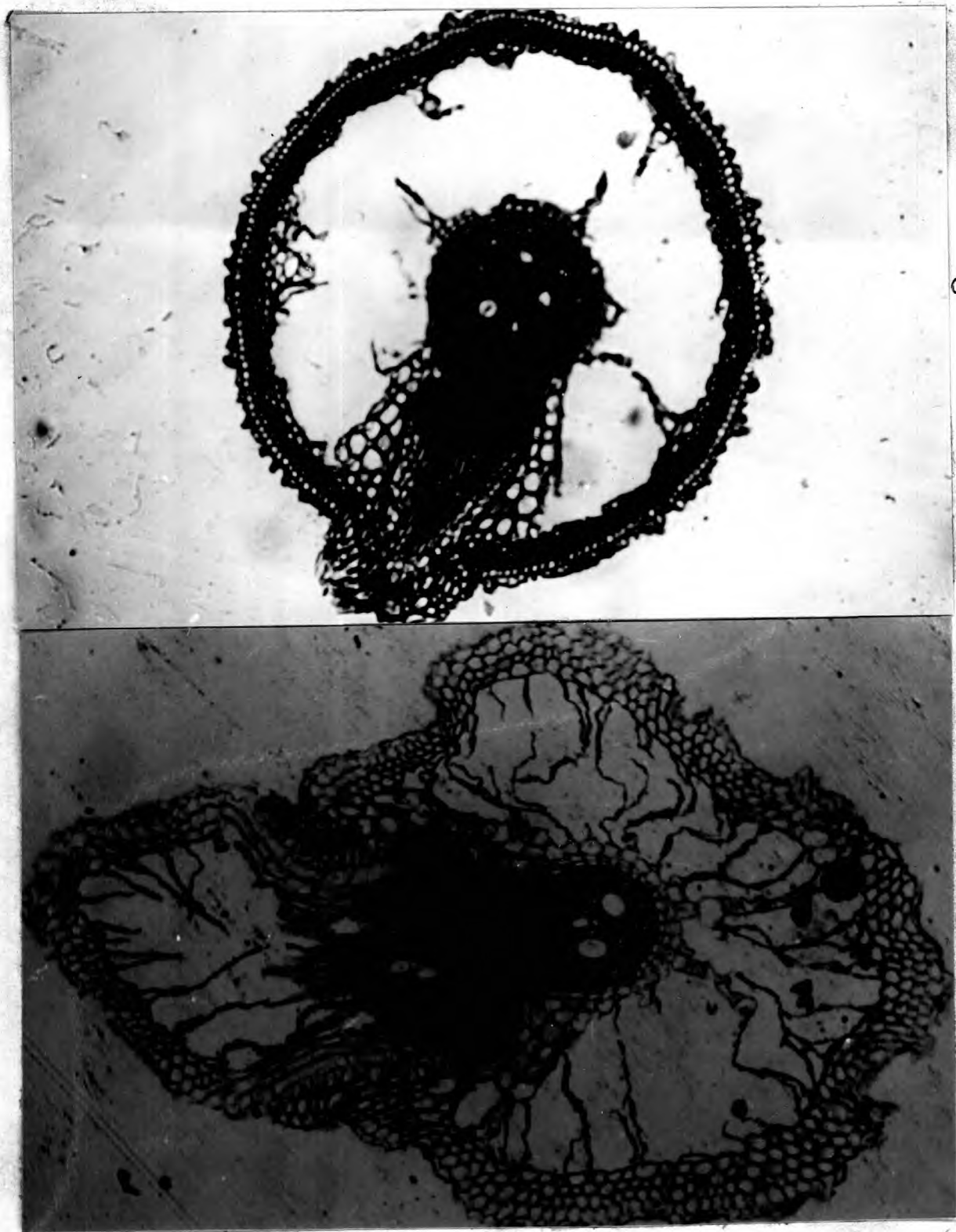
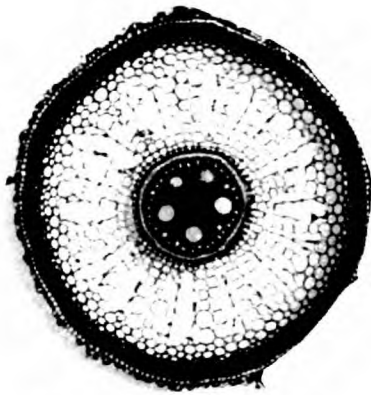


Plate 4. Molinia caerulea: Transverse sections of old cord roots.
 a: 4.5 - 7.5 inches soil depth from the Valley-bog. $\times 82$
 b: 13.5 - 16.5 inches soil depth from the wetter
 Molinietum. $\times 82$

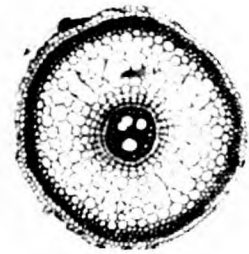
TABLE 15.

OLD CORD ROOT

SOIL DEPTH	AREA OF ROOT	AREA OF STELE	AREA OF CORTICAL SPACES	LARGE VESSELS IN STELE	Area	AREA OF STELE, % Root Area	CORTICAL SPACES, % Root Area
inches	mm. ²	mm. ²	mm. ²	Number	mm. ²		
0 - 1.5	78.92	6.86	8.26	4	0.44	8.69	10.46
1.5 - 4.5	77.68	6.19	14.62	2	0.49	7.96	18.82
4.5 - 7.5	73.55	5.38	22.99	2	0.42	7.37	31.25
7.5 - 10.5	52.06	4.13	21.23	2	0.33	7.93	40.77
10.5 - 13.5	43.47	2.97	20.82	1	0.24	6.83	47.89



Surface



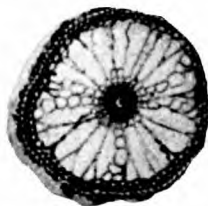
0 - 1.5 inches



1.5 - 4.5 inches



4.5 - 7.5 inches



7.5 - 10.5 inches



10.5 - 13.5 inches

That is to say the large increase in the area of the cortical spaces at lower soil depth, when expressed as a percent of the root area, is due to the decrease in the root area rather than an actual increase in the former.

New (current year's) cord root:

Results obtained from the anatomical studies of a current year's cord root are given in Table 16 (Fig. 4). The area of the cortical spaces increased to a depth of 4.5 inches and below this it decreased until near the root tip (0.5 inch short of it) the spaces were almost negligible (Note the reduction in root area).

Discussion:

Jefferies (1916) regarded the cortical spaces of Molinia roots as schizogenous in origin, but the present work shows that occasionally remains of the cell walls can be seen projecting into the spaces (Plate 5). This suggests that these spaces arise by the tearing or dissolution of the cells (lysigenous) rather than by the separation of adjoining cells (schizogenous). Intercellular spaces in the cortex of the roots of corn and rice have been reported to be lysigenous in origin (McPherson, 1939; and Katayama, 1961, respectively).

With increasing soil depth, there was a reduction in the area of the stele and the number of the large vessels in it.

The results obtained from the study of the new cord root show an increase in the amount of spaces with an increase in the distance from the root tip until a maximum is reached 1.5 - 4.5 inches below the soil surface. Katayama (1961) has found an increase in the amount of spaces with an increase in the distance from the root tip in the roots of upland rice and corn (Table 17).

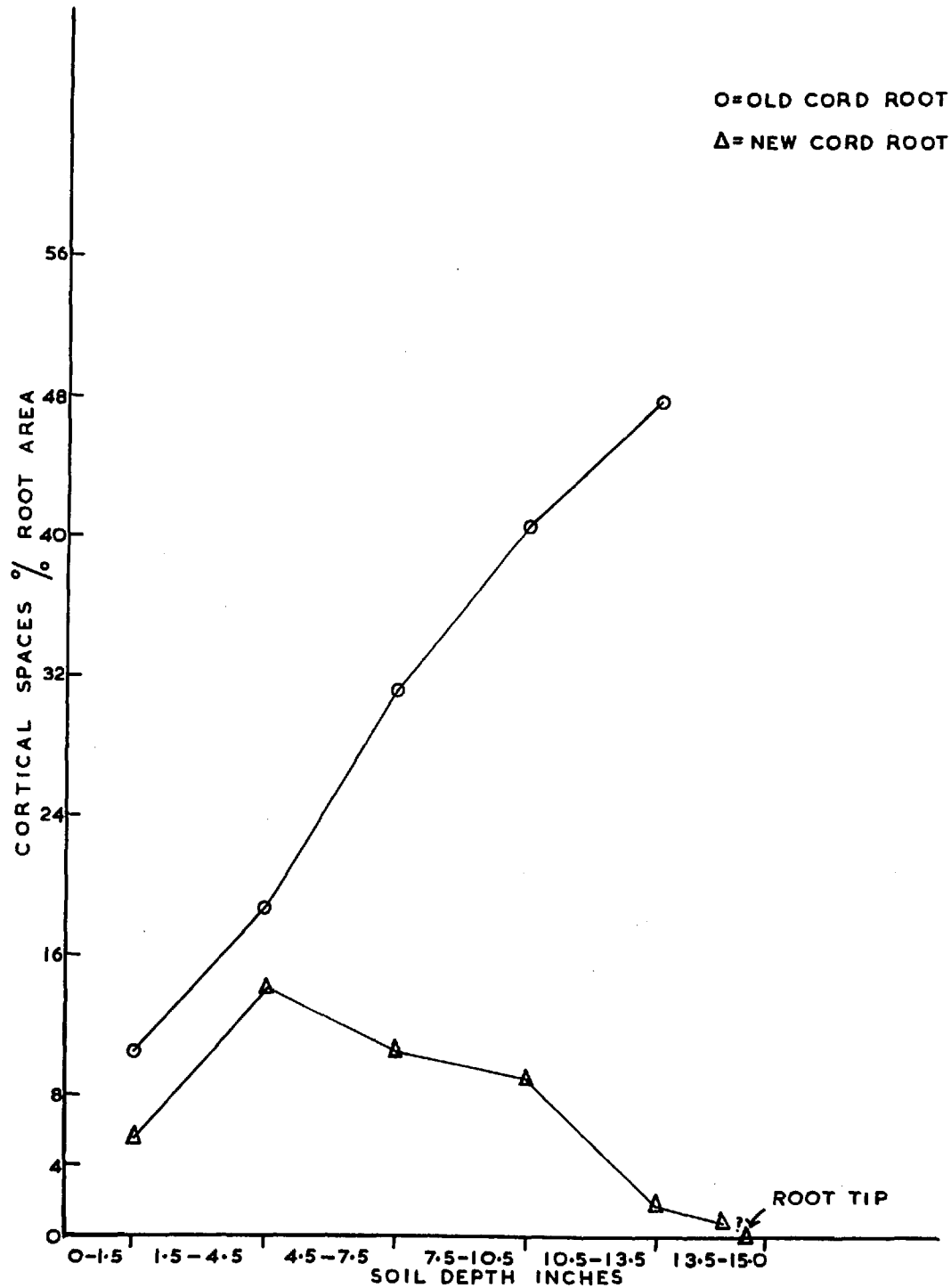


Fig. 4. *Molinia caerulea*: Cortical spaces, % root area, in a single cord root.

TABLE 16 NEW CORD ROOT

SOIL DEPTH	AREA OF ROOT	AREA OF STELE	AREA OF CORTICAL SPACES	LARGE VESSELS IN STELE		AREA OF STELE,	CORTICAL SPACES,
inches	mm. ²	mm. ²	mm. ²	Number	Area mm. ²	% Root Area	% Root Area
0 - 1.5	192.93	13.13	10.73	11	0.85	6.80	5.56
1.5 - 4.5	131.33	9.33	18.60	6	0.68	7.10	14.16
4.5 - 7.5	120.63	7.11	12.60	6	0.60	5.89	10.44
7.5 - 10.5	99.56	6.52	8.98	6	0.42	6.54	9.01
10.5 - 13.5	53.60	2.66	0.93	5	0.18	4.96	1.73
13.5 - 15.0	42.50	1.61	0.33	4	0.09	3.78	0.77

TABLE 17. INTERCELLULAR SPACES IN ROOTS

(From Katayama, 1961)

Distance from root tip, cm.			Amount of intercellular spaces, % root volume.	
			<u>Upland rice</u>	<u>Corn</u>
0	-	1	0	1.2
1	-	2	15.5	3.3
5	-	6	21.7	3.9

It may be argued that in the old cord roots the increase in the cortical spaces with an increase in the soil depth was probably due to the process of decay which, on the Valley-bog, left only a dead bare stele (see elsewhere, p. 34). Weaver and Zink (1945) found that the process of degeneration of the root cortex of the grasses they studied progressed regularly from the proximal to the distal end of the main root, and near the root tip usually 1 to 2 inches of cortex remained intact. This means that the older part of a root, i.e., that near the surface, would be the first to lose its cortex and, if the increase in the cortical spaces is due to the decay process, should have more cortical spaces than those in the deeper horizons of the soil. So the increase in the cortical spaces in the old cord roots from the deeper soil horizons cannot be explained satisfactorily as being a result of the decay process. Some edaphic factors (excess moisture and poor aeration) perhaps warranted a decrease in the living tissue without curtailing the normal life activities of the root, hence the increase in the cortical spaces. A discussion of the functional significance of these spaces is given in Section VII.

ii, Erica tetralix:

A transverse section of Erica root did not show any intercellular spaces. The root showed lenticel formation (Plate 6).

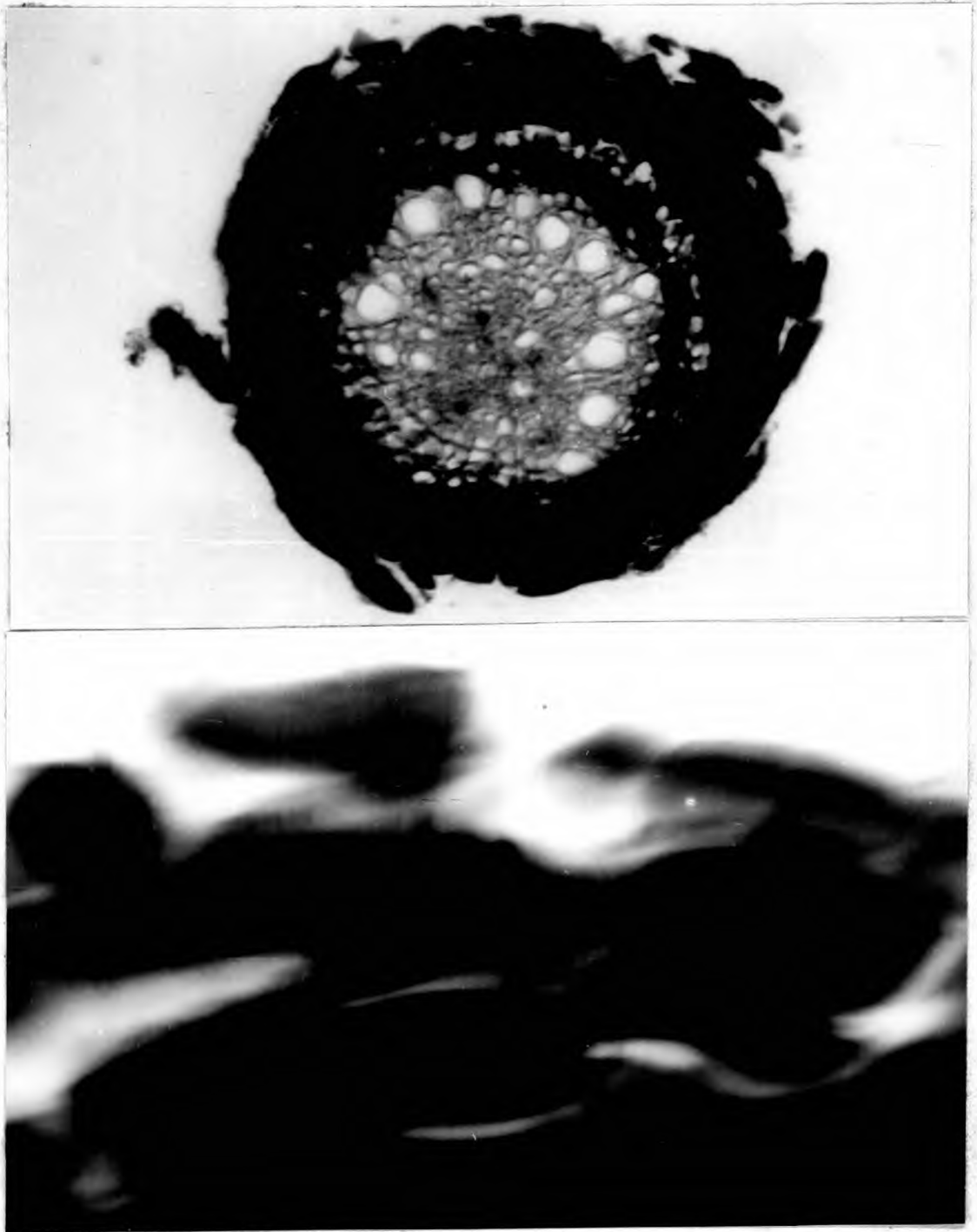


Plate 6. Erica tetralix: a, Transverse section of root showing lenticels. $\times 185$
b, A part of a, highly magnified. $\times 1850$

The lenticels were particularly clear on the roots near the soil surface.

Hahn, Hartley and Rhodes (1920) have described the occurrence of hypertrophied lenticels on the roots of young conifers in the presence of excess moisture. McVean (1956) has described water lenticels on stem, root and nodules of Alnus glutinosa. The lenticels are regarded as an aid to increase the efficiency of the aeration system of a plant.

III. COMPETITION BETWEEN MOLINIA AND ERICA IN THE FIELD WITH AND WITHOUT APPLICATION OF NUTRIENTS

The poor performance of the species on the Valley-bog (Section II. p25) may be due to either deficient nutrition or deficient aeration, or both. Loach (1964) has shown that this site has the lowest nutrient content in the soil. The drier Molinietum site was most nutrient rich, particularly in its upper horizons. The Central associates soil was intermediate between these two. Comparison of the soil analyses with others in the literature suggested that even the drier Molinietum was phosphorus deficient. Table 18 shows the amount of total nitrogen, total phosphorus and exchangeable potassium in the soils of different sites, expressed as mg/l. The data has been calculated from the figures given by Loach (op. cit.). It would have been very interesting to study the nutrient distribution in the wetter Molinietum soil, but such analyses were beyond the scope of the present work.

TABLE 18 TOTAL NITROGEN, TOTAL PHOSPHORUS AND EXCHANGEABLE POTASSIUM IN THE SUCCESSIVE LAYERS OF SOILS FROM DIFFERENT SITES (VOLUME BASIS) mg/l. [±]

SITES	SOIL DEPTH cm.	PIT I			PIT II		
		N	P	K	N	P	K
<u>VALLEY-</u> <u>BOG:</u>	0 - 20	841	34	58	1360	58	102
	20 - 40	1181	79	75	1256	80	106
	40 - 80	628	137	145	231	80	128
<u>CENTRAL</u> <u>ASSOCIES:</u>	0 - 20	1389	115	75	1341	84	73
	20 - 40	373	80	83	541	108	102
	40 - 80	268	79	134	134	68	69
<u>DRIER</u> <u>MOLINIETUM:</u>	0 - 20	3915	321	155	2978	207	131
	20 - 40	1215	116	137	1088	111	75
	40 - 80	200	62	61	178	64	64

[±]Calculated from data of Loach (1964).

One possible explanation of the dominance of Erica on the Valley-bog site (section II, p.16) is that the poor performance of Molinia and Calluna on this site renders them less strong competitors and allows Erica to spread. The absence of Erica from the drier Molinietum and yet its best performance on this site when grown in cleared enclosures (Loach, 1964) suggested that competition offered by Molinia is an important factor in the distribution of the species. Molinia growing poorly on the Valley-bog site appeared not to offer a strong competition to Erica which thus took the advantage. The validity of this suggestion was tested by performing an experiment on competition in the field between Molinia and Erica with and without application of nutrients, and is described below.

i, Method:

In his experiment on the growth and nutrient uptake of the three species - Molinia, Erica and Calluna - on the three sites - Valley-bog, Central associates and drier Molinietum - Loach (1964) had used small enclosures, 7 feet X 6 feet, in which the standing vegetation had been removed. There were 6 such enclosures on each site. Each enclosure had a four feet high wire fence to keep the animals (deer) out. In the present work these enclosures have been used for the experiment now described.

Planting pattern:

A 2 ft. X 2 ft. plot was established in the centre of the enclosure. It was divided into four sub-plots, each 9 inches X 9 inches. These sub-plots were 6 inches apart from each other. Of the four sub-plots in a plot one was planted with Molinia alone, another with Erica alone and the remaining two had equal numbers of the two species growing in competition with each other. By using a square metal frame with cross wires at 1.5 inches intervals, it was possible to plant equally

spaced seedlings of Erica and cuttings of Molinia. The species were planted in a 7 X 7 arrangement thus giving 49 plants of a species in "without competition" [‡] sub-plot. In a "with competition" [‡] sub-plot the plants of the two species alternated with each other (see Figure 5).

Erica tetralix seedlings were collected from recently burnt areas at Albury Bottom, Chobham Common, in early May, 1964, and were sorted into 3 size classes: a, b and c (a = 3.5 - 5.0 cm., b = 5.1 - 6.6 cm., c = 6.7 - 8.2 cm. high).

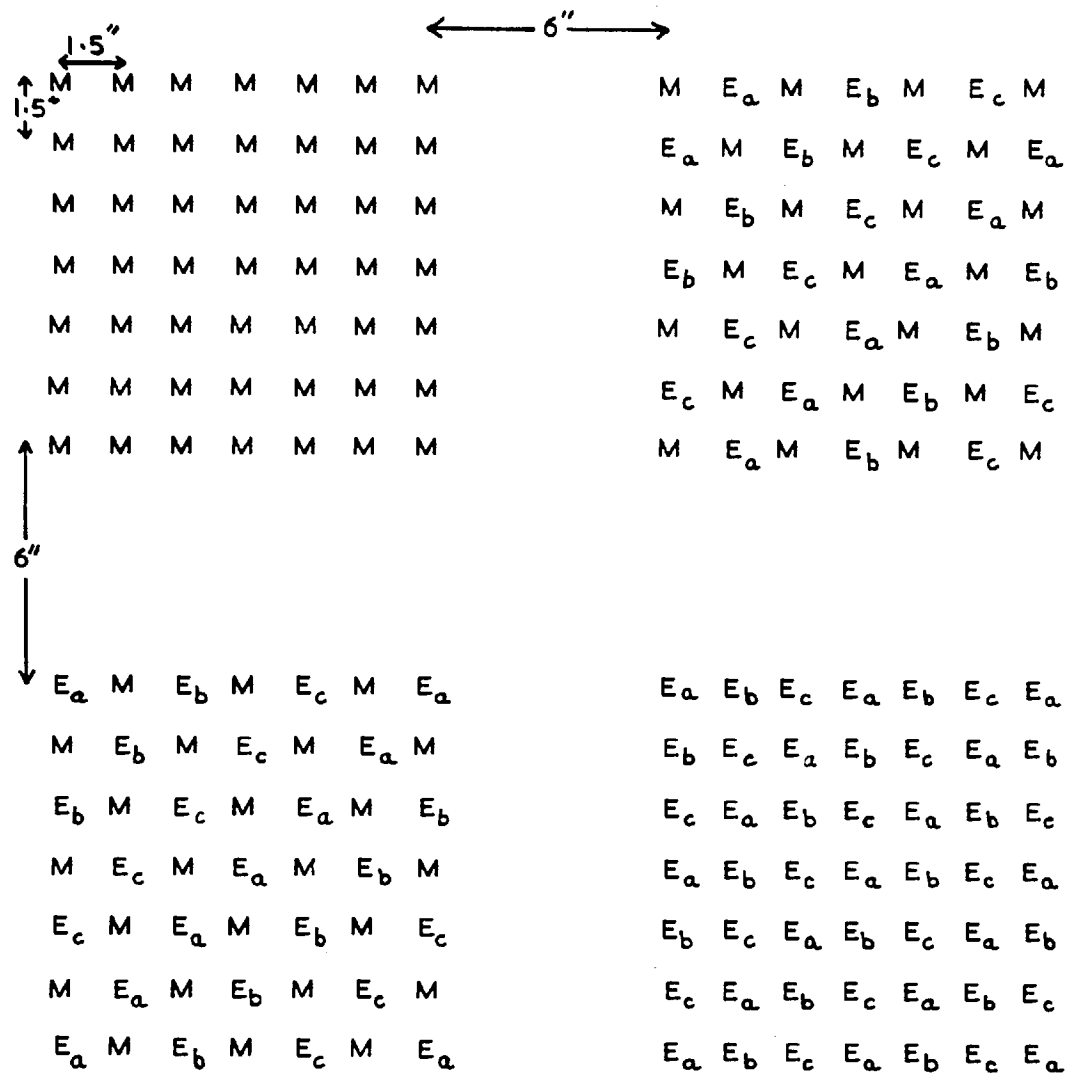
Molinia caerulea tussocks of similar size and appearance were dug from a flourishing "Molinia flush" at Crowthorne Forest in early May, 1964. They were opened up to separate the new basal internodes with their newly developed leaves and the nodal (adventitious) cord roots. Basal internodes (cuttings) with cord roots smaller than two inches were rejected. A large number of cuttings with two green basal leaves (leaves of the first series) were available and were selected for transplantation. The leaf length of the selected cuttings varied from 5 - 6 inches. Visual observation also enabled selection of only those cuttings whose basal internodes were approximately of equal length and diameter.

From Molinia cuttings and each size class of Erica seedlings - a, b and c - 10 groups of 12 plants each were selected at random. They were dried at 80°C. for 24 hours and were weighed to determine the initial weight at planting. In the case of Molinia the roots and shoots were weighed separately. This information was obtained partly to see the initial variability in weight and partly to provide data for comparison with final dry weights at harvest.

‡

Note: In these pages "with competition" refers to interspecific competition and "without competition" refers to the lack of interspecific competition and does not exclude intra-specific competition.

Fig. 5. Planting pattern. M = Molinia; E_a = Erica, size class a;
E_b = Erica, size class b; E_c = Erica, size class c.



Planting was carried out between 10th and 22nd May, 1964. In a sub-plot where Erica was planted "without competition" there were 17 a, 16 b and 16 c seedlings and in a "with competition" sub-plot there were 8 a (or 9 a), 8 b and 8 c Erica seedlings. The edge plants, those occupying the periphery of a sub-plot, were to be discarded at the time of harvest because they did not experience competition (interspecific or intraspecific) from all sides. Of the 49 plants of a species growing in a "without competition" sub-plot 25 were to be harvested, and of the 25 (or 24) plants of a species growing in a "with competition" sub-plot 13 (or 12) were to be harvested, thus giving, for one plot, equal number of plants (25) of a species which had grown with and without competition.

Dead plants of Erica and Molinia were replaced with fresh ones until 10th June, 1964 and after this no replacement was made. There was no indication of any site differences in the number of these replacements made, but far more Erica plants had died than Molinia. The death at this stage was related to the degree of root damage they suffered in transplanting. Molinia cuttings with their stronger and longer cord roots survived the handling during transplantation better than the fine and small roots of Erica seedlings.

Application of nutrients:

Of the 6 plots on a site (one in each enclosure) 3 randomly chosen plots were sprayed with nutrients while the other 3 did not receive any nutrients. Nitrogen, phosphorus and potassium were applied as Ammonium nitrate, Potassium chloride and Sodium di-hydrogen orthophosphate, respectively. Each nutrient was applied at the rate of 1.44 gm. per plot (4/9 sq. yd.), equivalent to 35 lbs. of each of nitrogen, phosphorus and potassium/acre.

The nutrient solution was prepared by diluting the salts in water obtained from the site where it was sprayed. A spray pump with an adjustable nozzle provided a uniform spray of the solution. Nutrients were applied on 3 occasions, namely 15th June, 1964, 1st August, 1964 and 28th June, 1965.

The plants were left in the field for two growing seasons, were weeded regularly, and were harvested in October, 1965. The plants occupying the periphery of a sub-plot were discarded. In Erica, the plants of different size classes were kept separate. It was fairly easy to locate them precisely by referring to the initial planting pattern. It was easy to extract the entire root system of Erica plants from the soil because of their being rooted near the surface. Molinia plants were deep rooted and it was not possible to extract the entire root system. The harvested plants were dried at 80°C. for 24 hours and their dry weights were determined (whole plant in the case of Erica and shoots only in Molinia).
Light measurements:

Light measurements were taken above Erica plants growing with and without competition with Molinia. A small rectangular photo-cell (1.5 " X 0.5"), which was held in a perspex frame (1.75" X 0.75"), was used for these measurements. It was mounted on a rectangular piece of brass metal which was soldered to the end of a long metal rod, which made it easy to push the photocell into the vegetation from a distance. The small size of the photo-cell reduced the disturbance of vegetation to a minimum.

The photo-cell was standardised against a standard photo-cell under different light intensities. An EEL portable "Lightmaster Photometer" was used for taking measurements with this photo-cell. On an overcast day in August, 1965 five

random readings were taken in each sub-plot (with and without competition) of a plot and on all the plots on the 3 sites. Full daylight was measured in the open where there was no shading from trees or other vegetation.

ii, Results:

Survival of the species:

Counts of the number of plants of a species that survived, after transplantation and initial replacement of the dead ones, were made on three subsequent occasions. Plants which were at all green were counted as living and missing plants were counted as dead, since it was assumed that they died and got blown away.

First count: July 10th, 1964 - 7 - 8 weeks after planting.

Second count: October 23rd, 1964 - nearly towards the end of the first growing season.

Third count: October 7th, 1965 - at the time of harvest.

Table 19 shows the results of these counts expressed as a percent of the number planted. The figures are means for 3 plots for the particular treatment (with or without nutrients and with or without competition) except in the case of Erica on the Valley-bog where one of the three plots, on which nutrients had been applied, had a cushion of living Sphagnum as the rooting medium for the species. With the application of nutrients Sphagnum showed a very luxuriant growth and the survival of Erica was very high on this plot as compared to the other two which had received nutrients but did not have a living Sphagnum cushion as the rooting medium. Molinia did not show any difference in its survival on this plot when compared with the other two plots on this site which had received nutrients. The survival figures for Erica on this plot have been kept separate from those for the other two plots which had received nutrients and thus the figures given in the

TABLE 19 PERCENTAGE SURVIVAL OVER TWO GROWING SEASONS

		1964								1965			
		JULY				OCTOBER				OCTOBER			
		With nutrients		Without nutrients		With nutrients		Without nutrients		With nutrients		Without nutrients	
		<u>$\bar{x}$ + C</u>	<u>- C¹</u>	<u>+ C</u>	<u>- C</u>	<u>+ C</u>	<u>- C</u>	<u>+ C</u>	<u>- C</u>	<u>+ C</u>	<u>- C</u>	<u>+ C</u>	<u>- C</u>
M	VALLEY-												
O	BOG	90	89	89	88	90	94	91	92	90	88	72	79
L	CENTRAL												
I	ASSOCIES	82	78	72	78	81	79	72	81	81	79	80	78
N	DRIER												
A	MOLINIETUM	97	92	98	100	98	98	88	90	93	98	87	88
E	VALLEY-												
R	BOG	81	88	80	81	49	42	81	76	28	11	52	39
I	(On <u>Sphagnum</u>)	94	86			90	80			76	76		
C	CENTRAL												
A	ASSOCIES	77	79	72	82	26	14	54	63	12	5	48	44
	DRIER												
	MOLINIETUM	82	92	87	88	24	11	61	55	16	14	46	42

^xWith competition¹Without competition

Valley-bog for survival of Erica plants with the application of nutrients are means of two instead of three plots.

The first count (July, 1964) showed hardly any differences in the survival of Erica on the plots with and without the application of nutrients on the different sites. But the second count (October, 1964) showed marked differences. By this time the Central associates and the drier Molinietum plots, which had received nutrients, had lost, on an average, about 80% of Erica plants, whereas "with nutrients" plots on the Valley-bog had lost about 55% of these plants. The third survival count (October, 1965) showed extremely low survival of Erica on all the sites on the plots on which nutrients had been applied. On the whole, even in plots which did not receive any nutrients the percentage survival figures for Erica in October, 1965 are half of those in July, 1964.

The figures for survival of Erica plants were slightly higher when growing in competition with Molinia than when growing without competition, particularly so in the plots on which nutrients had been applied.

The data for the percentage survival of the two species at the time of harvest (October, 1965) has been analysed separately by using an analysis of variance. An angular transformation was used to remove the skewness of the percentage survival data (Cochran, 1938). In the data for the survival of Erica on the Valley-bog the plot which received nutrients and had a cushion of living Sphagnum as the rooting medium, was not included in the analysis.

Table 20 shows the form of analysis of variance used for the data for survival (October, 1965) and for dry weight of Erica plants and Molinia shoots at the time of harvest (October, 1965). Levels of significance of various factors are also shown.

TABLE 20 SHOWING THE FORM OF ANALYSIS OF VARIANCE
USED FOR DATA FOR SURVIVAL AND DRY WEIGHT
OF MOLINIA AND ERICA AT HARVEST.

FACTOR	VARIANCE RATIO (F)			
	SURVIVAL		DRY WEIGHT	
	<u>ERICA</u>	<u>MOLINIA</u>	<u>ERICA</u>	<u>MOLINIA</u>
Sites		XX	XXX	
Nutrients				
(Competition)	XXXX	X	(X)	XXXX
Sites X Nutrients				
(Sites X Competition)			(X)	X
<u>Error (i)</u>				
Total (i)				
Competition				
(Sizes)	•		(XXXX)	
Sites X Competition				
(Sites X Sizes)			(X)	
Nutrients X Competition				
(Competition X Sizes)				
Sites X Nutrients X				
Competition (Sites X				
Competition X Sizes)				
<u>Error (ii)</u>				
Total (ii)				

Factors and symbols in brackets refer to Erica dry weights only because in this analysis the data for dry wt. of plants of different sizes was included, whereas that for the surviving plants from plots which had received nutrients was not included.

• F value significant at $P = 0.1$
 X " " " " $P = 0.05$
 XX " " " " $P = 0.01$
 XXX " " " " $P = 0.001$

Survival of Erica Table 21.

There was a highly significant ($P = 0.001$) effect of the application of nutrients on the survival of Erica, the survival being extremely poor on the plots on which nutrients had been applied. There were no significant site differences for the survival of the species. There was a slight indication ($P = 0.1$) of a higher survival when the species was planted in competition with Molinia as compared to that in the absence of competition.

TABLE 21 SURVIVAL OF ERICA

	Valley-bog	Central associates	Drier Molinietum	Means for nutrients
With nutrients	19.2 (23.53)	3.3 (15.21)	15.0 (20.90)	14.1 (19.88)
Without nutrients	45.2 (42.05)	46.0 (42.68)	43.8 (41.12)	45.0 (41.95)
L.s.d. means for nutrients ($P = 0.001$) = (15.13)				
	Valley-bog	Central associates	Drier Molinietum	Means for competition
With compet- ition	39.5 (38.62)	29.5 (31.57)	30.7 (32.07)	33.2 (34.08)
Without compet- ition	24.8 (26.96)	24.8 (26.33)	28.2 (29.95)	25.9 (27.75)
L.s.d. means for competition ($P = 0.1$) = (5.59)				

Unbracketed figures = % survival, means for 3 plots (except on the Valley-bog with nutrients).

Bracketed figures = Angular transformed data.

Survival of Molinia: Table 22.

There was a significant difference ($P = 0.01$) for the survival of the species between the drier Molinietum and the other two sites, though the latter did not differ significantly between themselves. Application of nutrients resulted in a

significantly higher ($P = 0.05$) survival rate but there was no site X nutrients interaction. Competition from Erica did not effect the survival of this species.

TABLE 22 SURVIVAL OF MOLINIA

	Valley-bog	Central associates	Drier Molinietum	Means for nutrients
With nutrients	89.0 (71.24)	80.0 (63.59)	95.0 (78.42)	88.0 (71.08)
Without nutrients	75.8 (60.86)	79.5 (63.35)	87.5 (70.56)	80.9 (64.92)
Means for sites	82.4 (66.05)	79.7 (63.47)	91.2 (74.49)	
	L.s.d. means for nutrients ($P = 0.05$) = (4.87)			
	L.s.d. means for sites ($P = 0.01$) = (8.37)			

Unbracketed figures = % survival, means for 3 plots.

Bracketed figures = Angular transformed data.

Competition and the growth of Molinia and Erica:

Table 23 shows the mean dry weight per group of 12 plants and per plant of Molinia and Erica at the time of planting.

TABLE 23 MEAN DRY WEIGHT PER GROUP OF 12 PLANTS AT PLANTING, mg.

<u>MOLINIA</u>		<u>ERICA</u>		
Roots:	364 ± 16	Sizes:	a	b
Shoots:	1,663 ± 29	Roots + shoots	115 ± 6	208 ± 9
				380 ± 11
<u>MEAN DRY WEIGHT PER PLANT AT PLANTING, mg.</u>				
<u>MOLINIA</u>		<u>ERICA</u>		
Roots:	30.3	Sizes:	a	b
Shoots:	138.6	Roots + shoot:	9.6	17.3
				31.7

the data for the dry weight of plants at the time of harvest was transformed ($\log_{10} x$) in order to remove its skewness. The data for Erica and Molinia was analysed separately.

Erica: Table 24.

Because of the extremely low survival on the plots on which nutrients had been applied, only the data obtained from the plots which did not receive nutrients were examined.

The growth of Erica was significantly poorer ($P = 0.001$) on the Valley-bog as compared to the Central associates and the drier Molinietum, and the latter did not differ significantly from each other. Competition from Molinia had a significantly depressing effect on the growth of Erica ($P = 0.05$).

TABLE 24 DRY WEIGHT OF ERICA AT HARVEST

	Valley-bog	Central associates	Drier Molinietum	Means for competition
With competition	47.2 (1.572)	99.7 (1.854)	84.5(1.768)	77.1 (1.731)
Without competition	53.5 (1.613)	109.8 (1.878)	113.6(1.920)	92.3 (1.804)

Means for
sites

50.3 (1.592) 104.7 (1.866) 99.0(1.844)

L.s.d. means for competition ($P = 0.05$) = (0.068)

L.s.d. means for sites ($P = 0.001$) = (0.166)

L.s.d. means for sites X competition ($P = 0.05$) = (0.119)

Unbracketed figures = Mean dry weight, mg.

Bracketed figures = $\log_{10} x$ transformed data.

The growth of Erica plants growing in competition with Molinia on the Valley-bog and the Central associates did not differ significantly from those growing without competition on these sites, but on the drier Molinietum competition offered by Molinia resulted in a significant decrease in the growth of Erica.

As expected, there were highly significant differences ($P = 0.001$) for the different sizes. There was no interaction of size with competition, but there was a significant ($P = 0.05$) sites X size interaction.

Mean dry weight at harvest of Erica plants surviving in the plots on which nutrients had been applied are given in Table 25. As mentioned before, this data was not included in the analysis of variance for the growth of Erica.

TABLE 25 MEAN DRY WEIGHT OF PLANTS AT HARVEST, mg., SURVIVING IN THE PLOTS ON WHICH NUTRIENTS HAD BEEN APPLIED.

Size	Valley-bog		Central associates		Drier Molinietum	
	$\bar{x}$ + C	- C	+ C	- C	+ C	- C
a	16.6	- $\frac{1}{2}$	23.5	-	19.1	25.9
b	31.4	42.3	43.8	57.5	35.1	57.0
c	83.3	90.5	104.3	163.4	114.1	182.6

$\bar{x}$ + C = With competition

- C = Without competition

$\frac{1}{2}$ = No survival

Molinia: Table 26.

Only the data for shoot weights was used. Root weights were not included because of the variability in the extent of root recovery on different sites. There was a highly significant ($P = 0.001$) response to the application of nutrients

TABLE 26 DRY WEIGHT OF MOLINIA SHOOTS AT HARVEST

	Valley-bog	Central associates	Drier Molinietum	Means for nutrients
With nutrients	1375 (3.133)	1253 (3.083)	1318 (3.103)	1315(3.106)
Without nutrients	453 (2.648)	643 (2.800)	768 (2.883)	621(2.777)

Means for sites 914 (2.891) 948 (2.942) 1043 (2.993)

L.s.d. means for nutrients ($P = 0.001$) = (0.202)

L.s.d. means for sites X nutrients interaction ($P = 0.05$) = (0.143)

Unbracketed figures = Mean dry wt., mg.

Bracketed figures = $\log_{10} X$ transformed.

and there were no differences between the sites for the growth of Molinia with the application of nutrients (Plate 7). The significant sites X nutrients interaction showed that without the application of nutrients the growth of Molinia was significantly ($P = 0.05$) poorer on the Valley-bog as compared to the other two sites between which there was no significant difference, though the figures for the drier Molinietum were higher than those for the Central associates. There was no significant effect of competition from Erica on the growth of this species.

Light measurements:

The mean values of light measurements above Erica plants, expressed as a percent of full daylight, are given in Table 27.

TABLE 27 LIGHT INTENSITY ABOVE ERICA PLANTS, % FULL DAYLIGHT

VALLEY-BOG				CENTRAL ASSOCIATES				DRIER MOLINIETUM			
+ N ⁰		- N		+ N		- N		+ N		- N	
+ C [±]	- C	+ C	- C	+ C	- C	+ C	- C	+ C	- C	+ C	- C
55.6	82.5	86.0	88.3	61.8	83.5	78.6	88.2	60.2	88.2	66.0	88.6
0 + N = With nutrients				± + C = With competition							
- N = Without nutrients				- C = Without competition							

iii, Discussion:

The significantly higher survival figures for Molinia on the drier Molinietum as compared to the Valley-bog and the Central associates, and the highest dry weight of plants (shoots) from this site, without the application of nutrients, were in agreement with the dominance and better performance of this species on this site (see Section II).

Strikingly low figures for the survival of Erica in October, 1965 on all the sites, even without the application of nutrients, are difficult to explain.



Plate 7. Molinia caerulea: Plants grown in enclosures on different sites.
 A: With the application of nutrients.
 B: Without the application of nutrients.

The growth of both Molinia and Erica was very poor on the Valley-bog but the application of nutrients resulted in equally good growth of Molinia on all the sites. Soil analyses (Table 18 , p. 60) showed that the drier Molinietum had higher nutrient content than the Valley-bog and the Central associates, but the improved growth of Molinia as a result of the application of nutrients even on this site suggested that it was nutrient deficient (see also Loach, 1964)..

Better growth of Erica on the Central associates and the drier Molinietum may be because of a higher nutrient content (Table 18 , p. 60) and better aeration (see Section IV) of these sites as compared to the Valley-bog where it was very poor. Very high mortality of Erica on all the sites as a result of the application of nutrients (Table 19) suggested that the species was very sensitive to a high level of soluble nutrients. This high mortality might have been achieved by a nutrient not normally found in high (soluble) concentrations in the soil and the effect found here may be an artefact. Conductivity measurements of the water samples obtained from these sites were made and experiments were carried out to study the effects of different levels of nutrition on the growth of Erica. These experiments are described in Section VI.

Molinia proved a strong competitor and significantly reduced the growth of Erica on the drier Molinietum. Competition results from a change in one or more factors of the local environment of a plant. Light and mineral nutrients are the two components most likely to be involved. Water was plentiful on these sites and cannot be regarded as a factor involved in the competition between Molinia and Erica.

There was no significant effect of competition on the growth of Erica on the Valley-bog and the Central associates sites. Molinia was growing poorly on these sites and the

light intensity above Erica plants growing in competition with it (plots without nutrients) was not markedly reduced as compared to that incident above the plants growing without competition. The significant decrease in the dry weight of Erica growing in competition with Molinia was found only for the drier Molinietum site. Of the three sites, this had the highest amount of soil nutrients (Table 18), so the significant depressing effect on the growth of Erica could not be ascribed to a competition for soil nutrients. However, light intensity was a factor which seemed likely to be important. Light intensity, in the drier Molinietum site, above Erica plants growing in competition with Molinia, on plots which had not received nutrients, was reduced, on an average, from 89 to 66 per cent of full daylight. Blackman and Wilson (1951) have shown that the relative growth rate of most plants is reduced by shading when the light intensity falls to 50 - 60% of daylight.

A greater amount of nutrients accentuated the effect of competition by promoting the growth of Molinia. Because of the limited nature of the data for Erica grown on plots which had received nutrients, a statistical comparison could not be made between its growth on plots with and without the application of nutrients. However, the mean dry weights of Erica plants, grown in competition with Molinia, which survived in the plots which had received nutrients, were lower than those grown in plots on which there was no application of nutrients (Tables 24 and 25.)

This experiment showed that low soil nutrient content of the Valley-bog could not account for the poor growth of Erica on this site, whereas this provided an explanation for the poor growth of Molinia since differences between sites almost disappeared after the application of nutrients. Aeration could be a factor of significance for the growth of plants on these wet soils. Studies of soil aeration were carried out and are reported in Section IV.

IV. SOIL AERATION STUDIES

Russell (1952) has emphasized the need of characterising soil aeration in parameters that are of significance to plant growth. Parameters that describe the environment at the interface between the plant root and the soil system are an excellent means to this end.

In soil the active plant roots are probably covered by a film of water. This is particularly true in the case of the roots growing in wet soils like these studied in the present work. The concentration of gases at the root surface will depend upon the composition of the soil air, the transfer of gases across the gas-liquid interface, the movement of gases both in the gaseous and liquid phases, and the presence of chemical and biological processes involving these gases in the soil. The effects of these various factors should be reflected in a measurement of the gases dissolved in the liquid phase. It would seem, therefore, that a quantitative measurement of the gases in the liquid phase, along with those in the gaseous phase, should be of considerable value in characterising the aeration status of a soil.

Webster (1962a) examined the relation between the composition of the wet-heath vegetation and aeration conditions in the ground-water sampled from depths of 12 and 24 inches. Root studies (Section II) showed that Erica was a shallow-rooting species and in the case of Molinia though the roots penetrated to deeper depths in the soil, only very small amounts were present below 10 inches soil depth. In view of this it was realised that the analyses of gases present in the soil air and dissolved in the water at soil depths where majority of the roots of Erica and Molinia were present, in addition to the analyses of water samples from deeper soil depths, would be of direct relevance to the studies of soil aeration in relation to the growth of these species in the sites studied in the present work.

i, Sampling of soil water:

Samples of water from a depth of 24 inches were obtained by using the ground-water sampling probes designed by Rutter and Webster (1962). A method was devised for sampling the water from different depths in the soil free from soil particles and without any gain or loss of dissolved gases.

Water can be obtained from a wet soil by applying a low suction. The soil water^{xx} sampling probes work on this principle. The details of the construction of a probe are given below.

The probe was a perspex cylinder (inner diameter = 1.75 inches) with a perforated perspex disc sealed to it at the lower end. The perforated disc was slightly recessed so that a disc of a porous plastic material, PORVIC,^{xxx} when sealed on to it with Araldite, became level with the end of the perspex cylinder. The Porvic (grade M) was kept saturated with liquid paraffin. It allowed water but not air to enter when pressure was reduced inside the probe. The probe had a tight fitting rubber bung with two glass tubes: one (A) for reducing the pressure inside the probe and the other (B) for introducing liquid paraffin, streptomycin solution and withdrawing the water sample (Fig. 6).

^{xx}Strictly speaking, soil water refers to the water from above the water-table and ground-water to that from below it. But in this section "soil water" refers both to the water from above and below the water-table.

^{xxx}Porvic is a porous plastic manufactured by POROUS PLASTICS LTD., Essex, England. It is obtainable in sheets, 0.125 cm. thick, with a maximum pore size of 2μ and can withstand a pressure equivalent to 1/5th of an atmosphere before the air-water interfaces in the pores breakdown. Water flows through it with great rapidity.

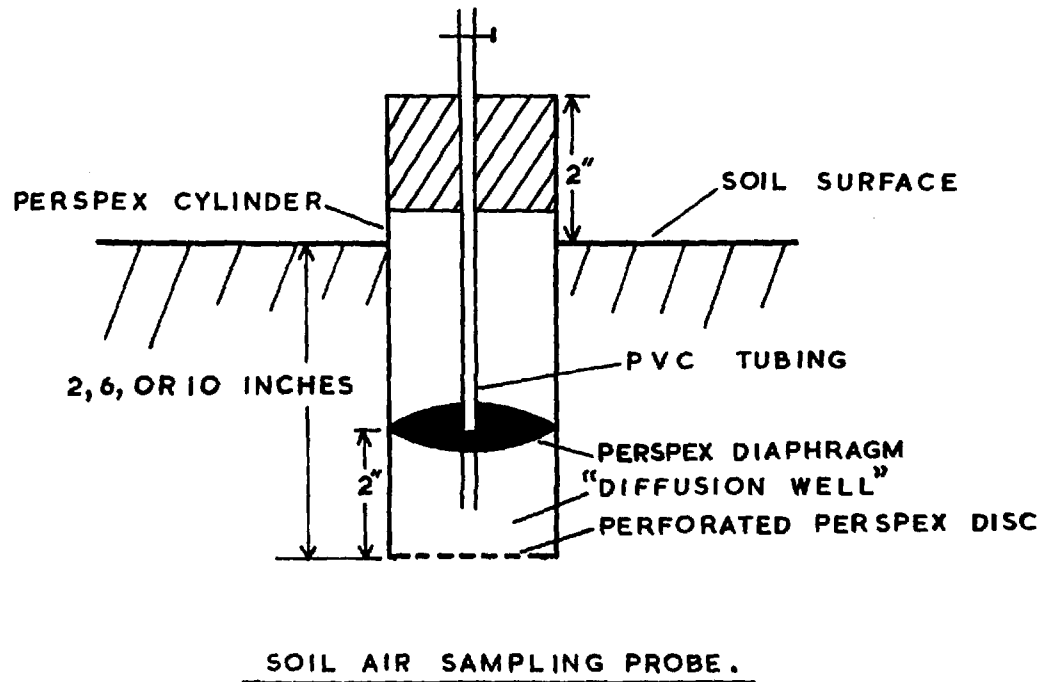
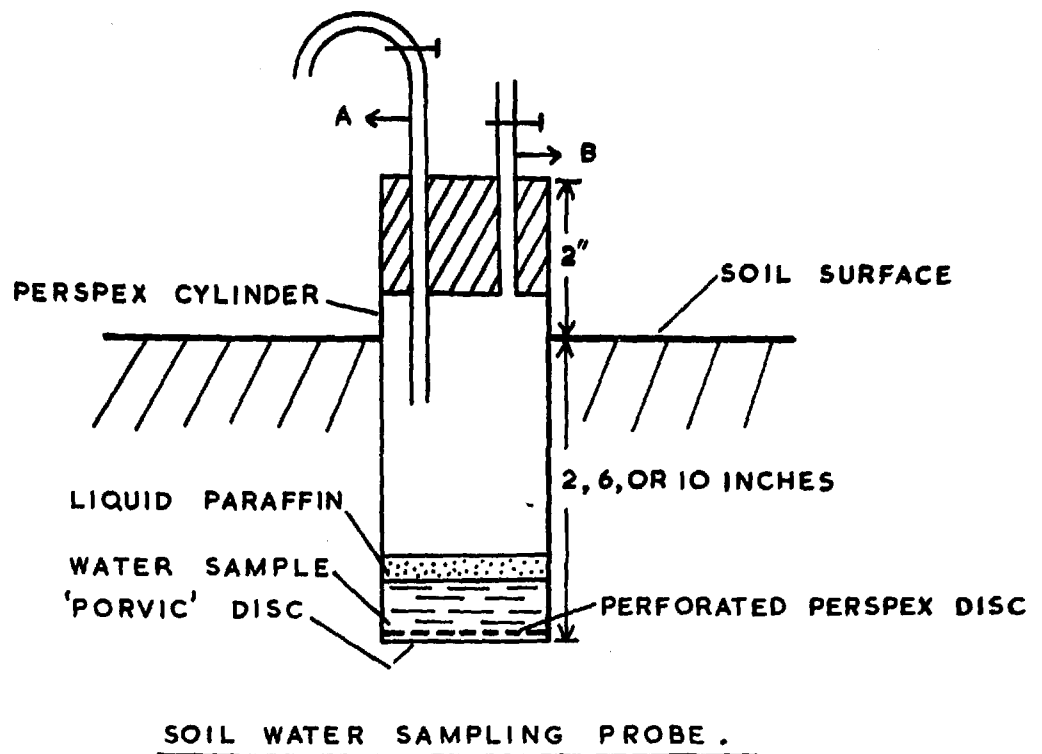


Fig. 6. Soil water and soil air sampling probes.

The probes were of three different lengths: 4, 8 and 12 inches, and were set in the soil for sampling water from 3 different depths, namely 2, 6 and 10 inches, respectively. A hole was augured into the soil to the required depth and the probe was thrust into position making sure that the "Porvic" disc was making a good contact with the soil. A small amount of liquid paraffin (5 ml.) and a drop of streptomycin solution were introduced into the probe through B. A suction equivalent to 10 cm. mercury was applied through A with the help of a large polythene syringe, and was measured with a manometer. The suction applied, on the one hand, did not let the paraffin run out of the probe into the soil through the "Porvic" and, on the other, sucked water out of the wet soil. The water collected under liquid paraffin which acted as a seal against the air in the probe. The streptomycin solution checked the activity of micro-organisms (Appendix B). Once the suction was applied, the time taken by water to collect in the probe depended upon the texture and water status of the soil.

Experimentation showed (Appendix B) that liquid paraffin acted as an effective seal against the gaseous exchange for four days at least, so the water sampled within four days of the application of suction was accepted as a reliable sample.

The water collected in the probe was sampled with a long-stemmed pipette which had a little liquid paraffin in it and was drained into a collecting bottle containing some liquid paraffin and a drop of streptomycin solution. This ensured that the water sample was not exposed to the air at any stage. The samples were stored in a refrigerator prior to analyses. The analyses were carried out within 72 hours of taking the samples.

It was easy to detect a probe which was not working properly (damaged "Porvic" or some leakage) because

the mercury in the manometer did not stay steady when the suction was applied.

The method was fairly simple and satisfied all the requirements. Once the probe was set in position there was no more disturbance of soil or vegetation and it was left in situ for subsequent samplings.

ii, Sampling of soil air: Fig. 6.

A perspex cylinder (inner diameter = 1.75 inches) was closed at the lower end with a perforated perspex disc. Two inches above this disc there was a perspex diaphragm with a hole in the middle with a transparent PVC tubing passing through it. At the upper end, the perspex cylinder had a tight fitting rubber bung with one hole through which passed the upper end of the PVC tubing. The PVC tubing was kept closed with a screw clip. This arrangement formed a "diffusion well" into which the soil air diffused.

Air sampling probes, like soil water sampling probes, were in three different lengths, viz., 4, 8 and 12 inches. To instal the probe in the soil a hole was augered into it about 1/4 inch deeper than the desired depth of the probe. The extra 1/4 inch was to provide a large surface area for diffusion into or away from the lower end of the probe. The probe was put into position making sure that it was a tight fit in the soil. The air in the probe ("diffusion well") was allowed to equilibrate with the soil air.

The air sample was collected in a glass tube with a tap at each end by connecting one end of the glass tube to the PVC tube and applying a slight suction with a polythene syringe. The glass tube had been evacuated before-hand. Air samples were stored in a refrigerator and were analysed within 72 hours of their sampling.

iii, Lay-out of the probes in the field:

On each site a 70 feet long transect was laid at random. Two ground-water sampling probes (Rutter and Webster, 1962) were put at random at 24 inches depth along the transect. Soil water and soil air sampling probes were put in the soil at 3 different depths, viz., 2, 6 and 10 inches. Two replicates of these were put at random along the transect in August, 1964. Three probes of a replicate (water or air sampling probes) were spaced 6 inches from each other along the transect. The two sets of sampling probes (water and air) were 9 to 12 inches apart from each other in such a manner that 2, 6 and 10 inches water sampling probes faced 2, 6 and 10 inches air sampling probes, respectively. This made the water and air samples obtained from the same depth very closely comparable. The distance between the two sets of probes could not be reduced further except at the cost of disturbing them.

iv, Methods of analysis:

Water samples:

Samples were analysed for dissolved carbon dioxide, oxygen and hydrogen sulphide.

Carbon dioxide:

The method was based on that described by Conway (1962) for the determination of CO_2 content of blood by using "Conway units." The total CO_2 dissolved in the sample was set free by acidification in the outer chamber and the free gas

diffused into barium hydroxide solution in the central chamber where it precipitated an equivalent amount of barium carbonate.

"Conway units" with perspex lids with three holes, instead of the standard ground glass ones, were used (Plate 8). Of the 3 holes in the perspex lid the middle led to the central chamber of the "unit" and the two side ones opened into the outer chamber. These holes carried small perspex tubes (inner diameter = 4 mm.) through which sample and different reagents were introduced. Vaseline was applied to the underside of the perspex lid to give a perfect seal to the "unit". The 3 openings to the "unit" were closed with tight-fitting neoprene stoppers. CO_2 -free air was passed through the "units" which were connected in series by small pieces of rubber tubing. The middle opening in each lid was kept stoppered. After 15 minutes the other two openings in the lid were stoppered and the "units" were now ready for subsequent handling. 2 ml. water sample were introduced into the outer chamber of the "unit". 0.5 ml. mercuric chloride and a drop of methyl orange were added to the sample (The addition of mercuric chloride prevented hydrogen sulphide coming off with CO_2 when dilute sulphuric acid was added to the sample). From a self-filling burette, 2 ml. N/50 barium hydroxide solution were introduced into the central chamber of the "unit". Dilute sulphuric acid (1 : 1) was introduced into the outer chamber until the methyl orange end point was reached when a little was added in excess. This liberated CO_2 from the outer chamber which diffused into barium hydroxide solution in the central chamber. The amount of barium hydroxide solution left unused was determined by titrating it against N/50 hydrochloric acid using phenolphthalein as an indicator. With each set of determinations at least two controls were also run, and the corrections (if there was any precipitation of barium carbonate in the control), wherever needed, were allowed for in the final results.

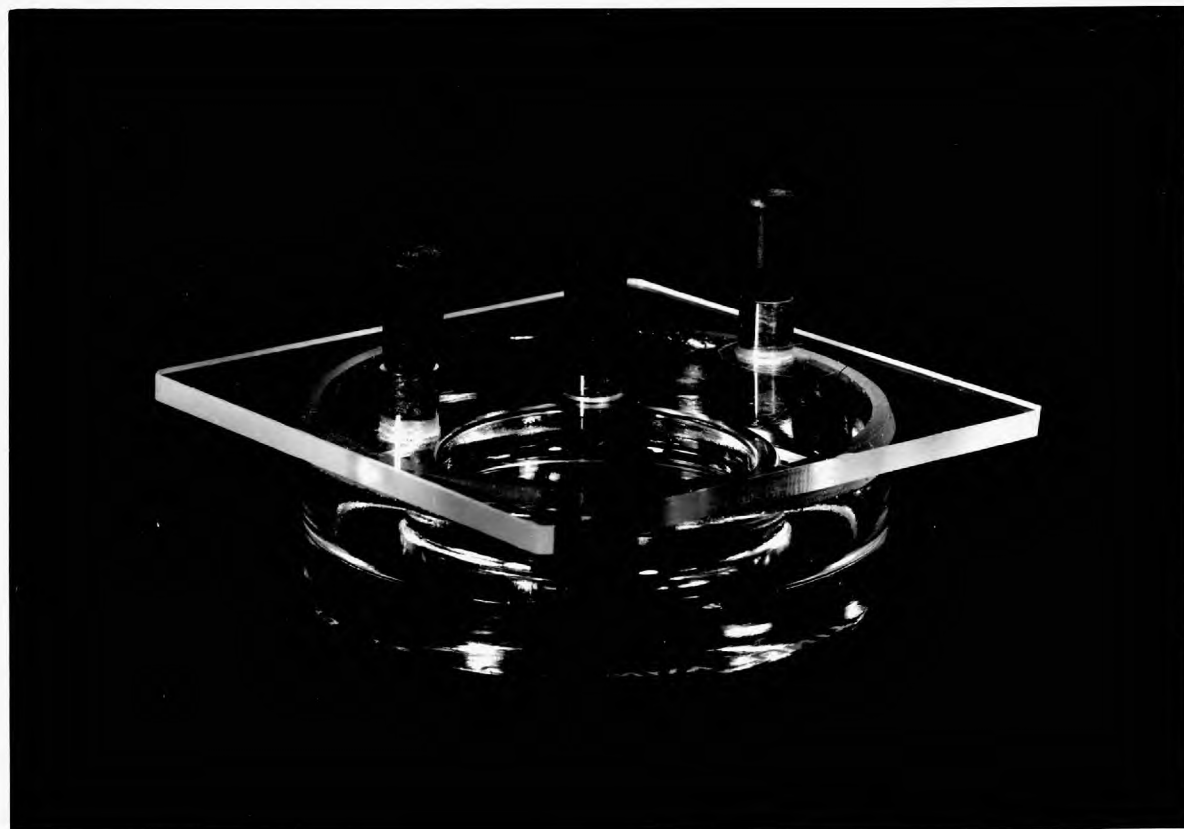


Plate 8. "Conway unit " with modified perspex lid .

the method was checked by liberating CO_2 from a known amount of sodium bicarbonate. In no case did the estimated result differ from the expected by more than 1%. Results given in Table 28 show that there was a complete recovery of CO_2 in $1\frac{1}{2}$ hours. However, to provide a margin of safety the units were left for two hours before the titration.

TABLE 28 RECOVERY OF CARBON DIOXIDE

0.1 gm. sodium bicarbonate in 100 ml. distilled water

Expected value of CO_2 in solution = 523.8 ppm.

Estimate value:	ppm.	Error, %
after 30 minutes	440.0	- 16
" 60 "	489.2	- 6.5
" 90 "	525.7	+ 0.37

This method made it possible to analyse a number of samples at one time. The use of the lids with holes in them made it possible to flush the unit with CO_2 - free air and eliminate the error due to the formation of barium carbonate by the carbon dioxide of the atmosphere which would be attendant upon the use of the standard ground glass cover which has to be removed for the introduction of sample and reagents into the "unit."

Oxygen:

Oxygen was analysed by using the Winkler method with the Rideal - Stewart (1901) or permanganate modification as described in the report of the committee on the Methods of Chemical Analysis As Applied To Sewage and Sewage Effluents (1956).

When the samples were analysed by using the Winkler method, involving the oxidation of iodine in the water sample and titration with thiosulphate using starch as an indicator, the values obtained for dissolved oxygen were found to be lower than those obtained by using the method with Rideal - Stewart modification. This showed that some interfering substances were present in the samples (ferrous salts - Rideal and Stewart, 1901), thus necessitating the use of the modification.

The analyses were carried out on a micro-scale. A small amount of liquid paraffin was added to a flat-bottomed glass tube and 2 ml. water sample were introduced into it by keeping the tip of the pipette dipping into the liquid paraffin. A magnetic stirrer was used to ensure thorough mixing of the reagents. For titration, thiosulphate solution was dispensed from a micro-syringe. The method was checked by determining the dissolved oxygen content of distilled water kept in the laboratory in open dishes and the results obtained did not differ from the expected by more than 1%.

Hydrogen sulphide:

"Conway units" with perspex lids with 3 holes in them, like those used in the CO_2 analysis, were used. 2 ml. water sample were introduced into the outer chamber and 0.5 ml. 2% zinc acetate solution in the central chamber. Addition of 1 ml. 5N hydrochloric acid liberated hydrogen sulphide which was absorbed and retained in the central chamber as zinc sulphide. This absorption was allowed to continue for 1 hour. 0.5 ml. N/80 iodine and 0.5 ml. 5N hydrochloric acid were introduced into the central chamber, the contents were thoroughly mixed and were allowed to stand for ten minutes. Iodine reacted with zinc sulphide and the excess unused was titrated against N/80 thio-sulphate solution using starch as an indicator. Like CO_2 analysis, two controls were run with each set of determinations.

The method was checked by liberating hydrogen sulphide from a solution of a known amount of antimony sulphide and using the above mentioned method for its determination. The results did not differ from the expected by more than 1.5%.

Air samples:

Air samples were analysed for oxygen and carbon dioxide. A Bonnier and Mangin gas analyser in the modified form described by Thoday (1913) with later adjustments by Vallance and Coult (1951) was used for these analyses. Absorption of CO_2 was carried out in 10% potassium hydroxide and that of oxygen in alkaline tri-acetyl-pyrogallol. No suitable method was available for a quantitative estimation of the hydrogen sulphide present in the air samples.

The method of transference of air samples into the gas analyser is described below.

A transparent PVC tube was slipped on to one end of the glass tube containing the air sample. The small space above the tap of the glass tube and the transparent PVC tube were filled with a mixture of equal parts of glycerine and a saturated salt solution (oxygen and carbon dioxide are insoluble in this mixture), and the system was closed with a screw clip. The tap of the sample tube, close to the PVC tube, was opened and the tube was gently tapped on a piece of cardboard. The glycerine - salt mixture moved down into the glass tube and displaced the air in it which now collected in the PVC tube. The air was obtained from the PVC tube with a hypodermic syringe whose dead space was filled with glycerine - salt mixture. A small quantity of air in the syringe was expelled at the surface of the beaker of mercury prior to its introduction into the gas analyser.

V, Results:

Water and air samples were sampled in October, 1964 and April and June, 1965. It proved practically impossible to sample the replicate sets each time but occasionally the samples obtained from some of the two replicates of the sets of probes on a site were analysed to see the variability in gaseous composition within a site. A complete set of analysis for dissolved carbon dioxide in water samples from the two replicates from all the sites was made in April, 1965. Wherever analyses

of the samples from the two replicates have been made the mean values along with the errors of the two determinations (not standard errors) are shown in Figs. 7 to 10. The results showed that there was not a great deal of variation within a site and the errors, though large in some cases, did not overlap. The results of the analyses of the water samples are expressed as ppm. and their equivalent values in air, as a percent, calculated from the solubility of these gases in water (data obtained from the Handbook of Chemistry and Physics, 1953) at 9°C - the mean temperature of the sampled water - and 760 mm. pressure. The results of air analyses are expressed as a percent of air volume.

Sampling in October, 1964 and April and June, 1965 was made to cover the different times of the growing season of the plants. Results of other workers on the annual cycle of fluctuations of gases dissolved in water (Webster, 1962) and those present in the soil air (Russell and Appleyard, 1915; Boynton and Reutner, 1939) helped in deciding the times of sampling. For the sake of clarity of expression for changes in gaseous composition with time, in Figs. 7 to 10 the data obtained from sampling in October, 1964 have been plotted after those for April and June, 1965.

Air samples:

Air samples were obtained from 2 and 6 inches soil depths on the three sampling dates from the four sites except the Valley-bog where in April and October no air could be obtained from 6 inches soil depth. No air samples were obtained from 10 inches depth from any of the sites since the probes contained water instead of air.

Figs. 7 and 8 show that the amount of carbon dioxide was highest in June as compared to April and October and the samples obtained in October had the lowest amount of this gas.

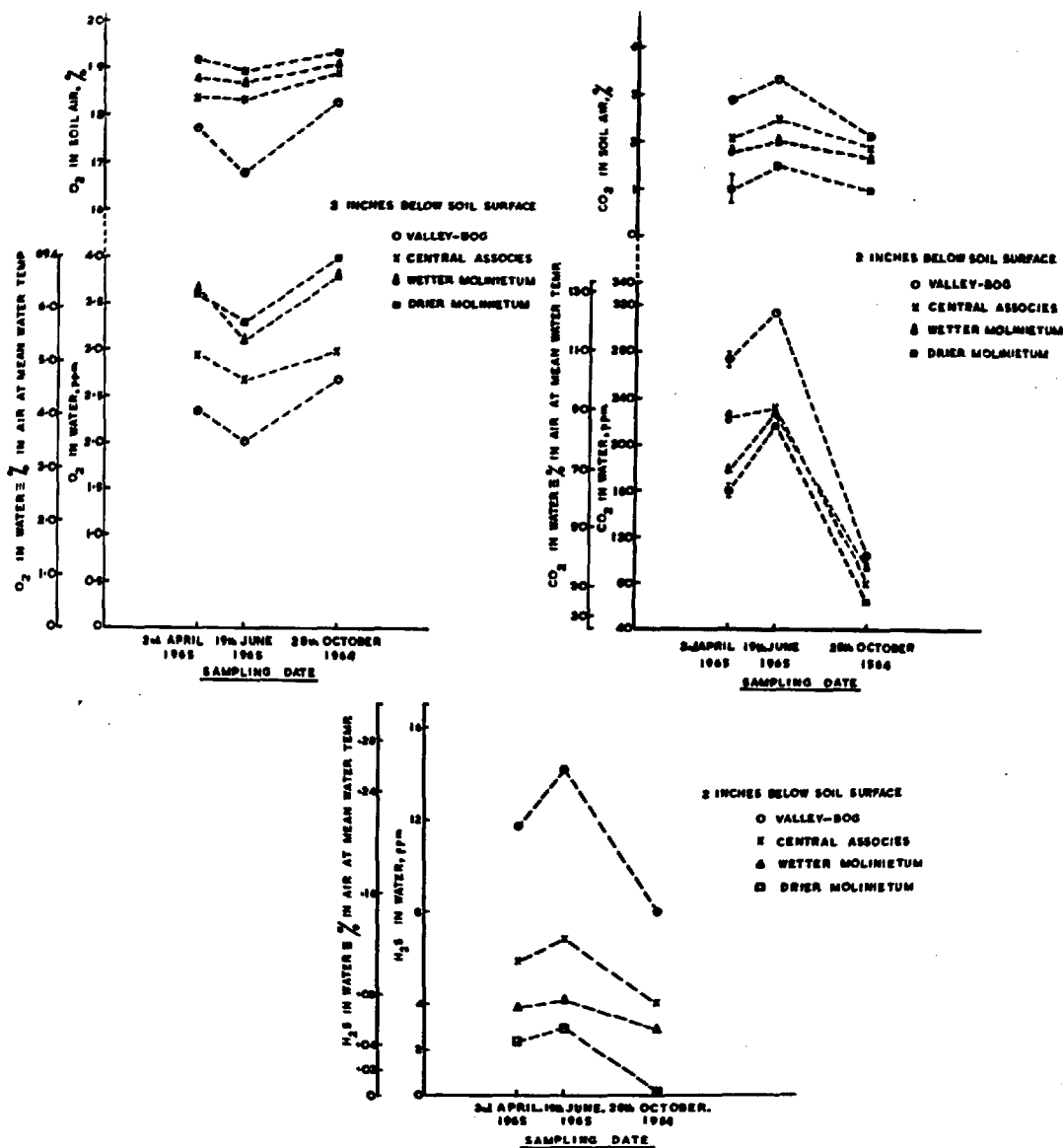


Fig. 7. Samples from 2 inches below soil surface from different sites. Concentrations of O_2 , CO_2 and H_2S in soil air and soil water (see text.)

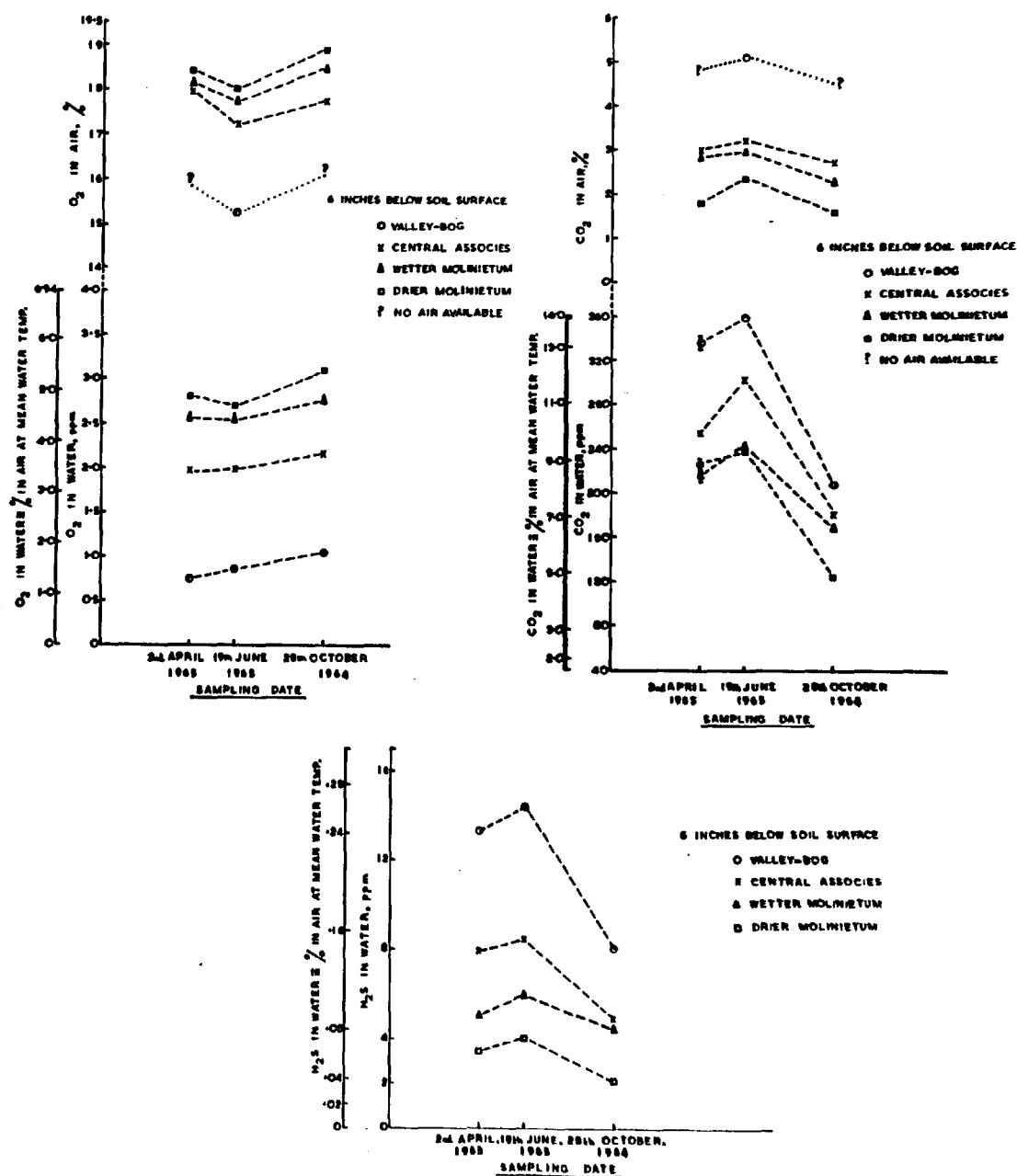


Fig. 8. Samples from 6 inches below soil surface from different sites. Concentrations of O₂, CO₂ and H₂S in soil air and soil water (see text.)

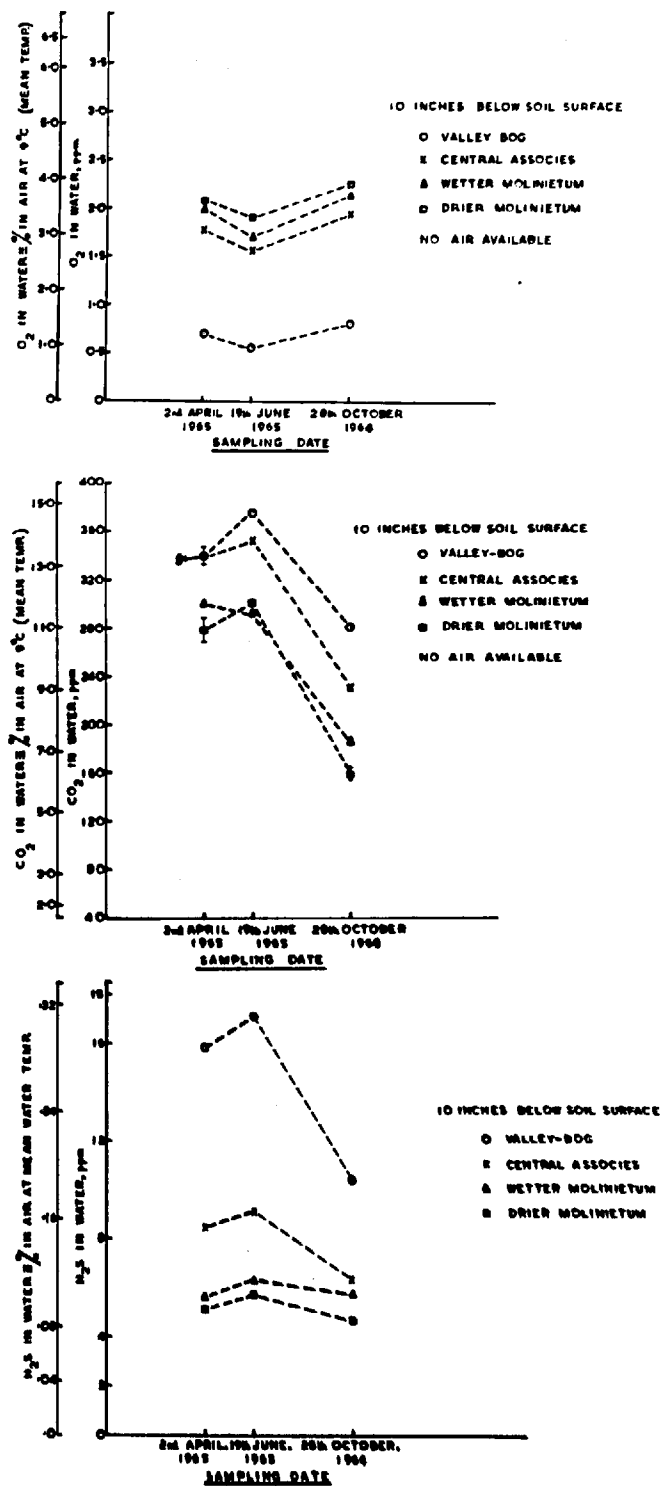


Fig. 9. Samples from 10 inches below soil surface from different sites. Concentrations of O_2 , and CO_2 and H_2S in soil air and soil water (see text.)

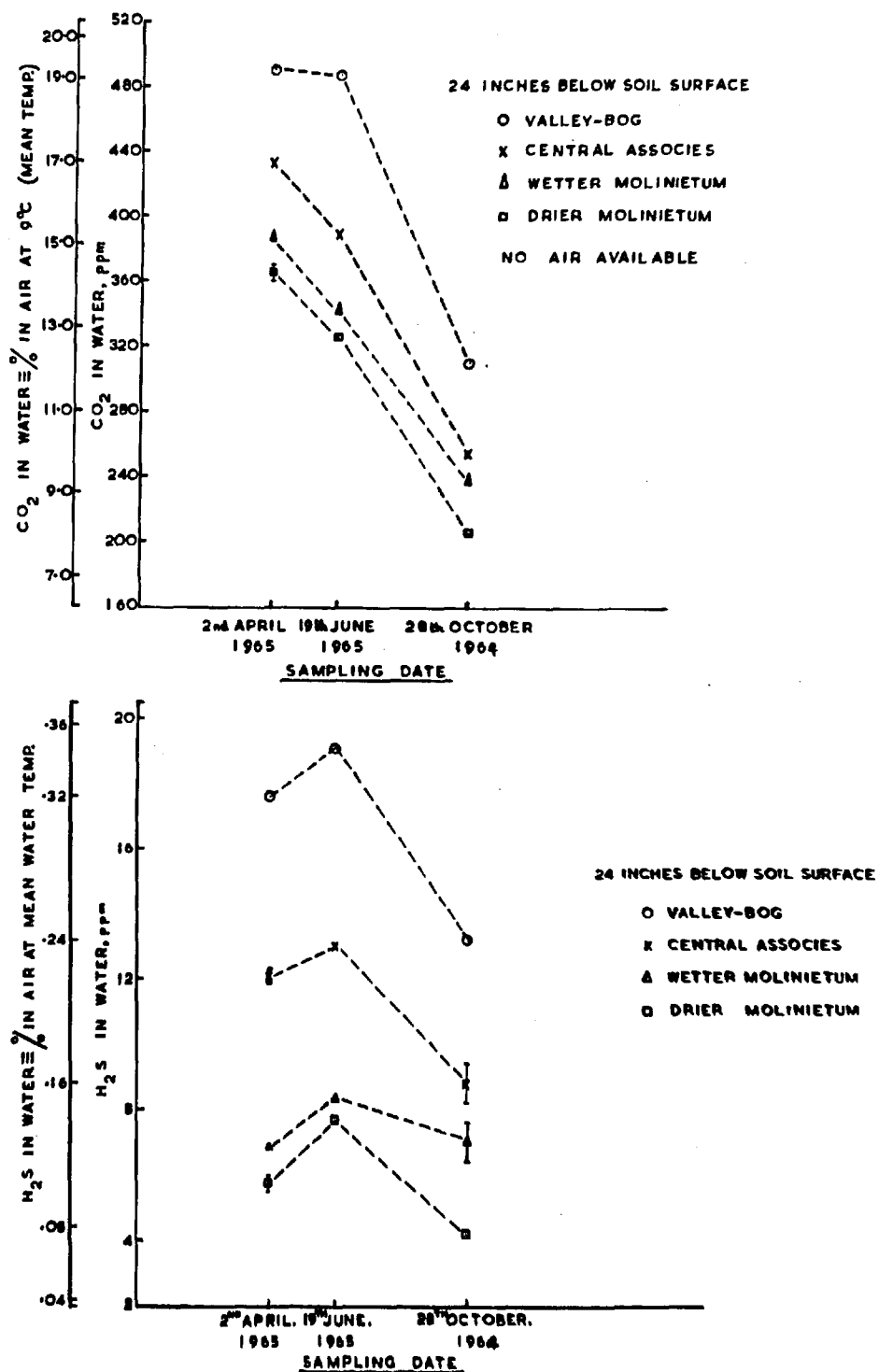


Fig. 10. Samples from 24 inches below soil surface from different sites. Concentrations of CO₂ and H₂S in soil water and soil air (see text.)

Oxygen followed the opposite course, viz., high in April, lowest in June and highest in October. On all the sites there was an increase in the amount of carbon dioxide and a decrease in the amount of oxygen with an increase in the depth of sampling. The total of oxygen and carbon dioxide did not diverge much from 21% (20.4 - 20.9%).

Water samples:

Figs. 7-10 show the results of the analyses of water samples for oxygen, carbon dioxide and hydrogen sulphide. Like the air samples, water samples obtained in June gave the highest figures for carbon dioxide and hydrogen sulphide and lowest for oxygen. On all the sites there was an increase in the amount of carbon dioxide and hydrogen sulphide and a decrease in oxygen with an increase in the depth of sampling.

Oxygen was not found in the water samples obtained from 24 inches depth from these sites except traces of it in the samples collected in October from the wetter and drier Molinieta.

There were distinct differences amongst the sites for the gases present both in the soil air and dissolved in water. Valley-bog gave highest figures for carbon dioxide and hydrogen sulphide and lowest for oxygen than the wetter and drier Molinieta. Central associates occupied an intermediate position between the two groups. Of the wetter and drier Molinieta, the latter was slightly better aerated.

The amounts of gases dissolved in water, when expressed as the equivalent concentration in air at a mean water temperature of 9°C and 760 mm. pressure, showed that the concentrations were much higher for carbon dioxide and much lower for oxygen than those in the air at the same depth. This was true for all the depths of sampling and all the sites. The differences between the amount of oxygen and carbon dioxide dissolved in soil water, expressed as a percent in air, and that present in soil air showed a variation with the time of sampling (Table 29). In the case of carbon dioxide the magnitude of the difference was least in October.

TABLE 29 DIFFERENCES BETWEEN THE PERCENTAGE OF O₂ AND CO₂
PRESENT IN SOIL AIR AND SOIL WATER

(For explanation see text.)

SITES	DEPTH OF SAMPLING, inches	<u>APRIL</u>		<u>JUNE</u>		<u>OCTOBER</u>	
		O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂
VALLEY- BOG	2	± - 13.67	+ 7.52	-13.29	+8.72	-13.68	+1.67
	6	° -	-	-13.77	+8.92	-	-
CENTRAL ASSOCIES	2	-13.28	+6.68	-13.68	+6.63	-13.65	+1.24
	6	-14.55	+6.99	-13.76	+8.68	-14.10	+4.43
WETTER MOLINIETUM	2	-12.48	+5.18	-13.30	+6.96	-12.50	+2.03
	6	-13.71	+5.74	-13.34	+6.52	-13.78	+4.26
DRIER MOLINIETUM	2	-12.95	+4.99	-13.26	+7.02	-12.39	+1.39
	6	-13.58	+7.08	-13.38	+6.95	-13.59	+3.26

± - amount in water is less than in air.
+ " " " " more " " "

° - No air samples available.

vi, Discussion:

The results for the analysis of soil air are similar to those obtained by Webster (1962a) who analysed samples obtained from sites at Bramshill, and other workers elsewhere. In the present work the highest value of 5.13% carbon dioxide was found in the soil air sampled from a depth of 6 inches from Valley-bog and the total of carbon dioxide and oxygen was 20.37%. Conway (1937) found that carbon dioxide in the soil air at Wicken Fen rose to as much as 9% in summer although figures closer to 7% were more frequently obtained and that even where large amounts of carbon dioxide occurred the total of carbon dioxide plus oxygen approached 21%. Russell and Appleyard (1915) found carbon dioxide rising to 7.6% in early May in badly drained soil at Rothamsted and in this case oxygen was only 8.6%. Boynton and Reutner (1939) found maximum amount of carbon dioxide in summer.

Webster (1962) found that in Erica dominated sites at Bramshill (like the present Valley-bog) the ground-water obtained in summer from a depth of 24 inches had 1200 - 1300 ppm. carbon dioxide dissolved in it (equivalent to 47 - 51% in air at 9°C and 760 mm. pressure). In the present work the highest figure for carbon dioxide dissolved in the water obtained from the same depth from the Valley-bog was 480 - 490 ppm. (equivalent to about 20% in air at 9°C and 760 mm. pressure). His results for hydrogen sulphide dissolved in the ground water were also much higher (a maximum of 50 ppm. = 0.9% in air at 9°C and 760 mm. pressure) than those found in the present work (a maximum of 20 ppm. = 0.37% at 9°C and 760 mm. pressure).

With an increase in the amount of oxygen dissolved in water there was a decrease in the amount of carbon dioxide and hydrogen sulphide. Production of hydrogen sulphide is a result of reducing conditions. Thus in the presence of a relatively higher amount of oxygen there was a relatively lower amount of hydrogen sulphide in the water.

A large decrease in the magnitude of the difference between the carbon dioxide dissolved in soil water and that present in soil air, at the end of October, could be related to the activity of micro-organisms in the soil. Mitchell, Adams and Thom (1941) found that the soils studied by them showed a marked increase in the microbial population during April and May. The fungal counts were highest in April, they stayed at this level till June when the numbers started to fall rapidly and reached the low levels from July onwards till February next year when they started to rise again.

At any depth in the soil the concentration of oxygen dissolved in the water was considerably less than that which would be in equilibrium with the concentration in the air at the same depth, and the concentration of carbon dioxide was much higher. This suggested that the main sites of oxygen consumption were in the water and that the low rates of gaseous diffusion in water limited the exchange of gases between the water-filled and gas-filled spaces in the soil. Russell and Appleyard (1915) have also reported that besides the free air there is another atmosphere which they assumed was dissolved in the water and colloids of the soil. They obtained the gases present in the latter atmosphere by evacuating the soil under a very high vacuum. The analysis of air obtained by this method showed that it was almost devoid of oxygen and consisted mainly of carbon dioxide and some nitrogen.

There is likely to be a falling oxygen concentration from the larger to the smaller air-filled spaces (see Hack, 1956) and possibly also from the larger to the smaller water-filled spaces. The concentrations of oxygen and carbon dioxide in the soil air reported here were based on the analyses of samples obtained by diffusion and represent a kind of mean for the concentration in the larger and smaller spaces in the soil. But due to the low level of suction applied in sampling the soil water, it is

likely that the water obtained mostly came from the larger spaces in the soil from which it moved more readily than from the smaller ones (Poiseuille's Law). The gaseous composition of the water present in the smaller spaces may be different from that reported here.

The various levels of the diffusion gradient of oxygen (and carbon dioxide) could not be separated but, at least, it was shown that the concentrations of the gases dissolved in the water were different from those present in the air at any depth in the soil. It was, therefore, relevant to discover in what sort of spaces the roots of Molinia and Erica were present and whether these spaces were water - or air-filled. These studies are reported in the next Section (Section V).

V - ROOT DISTRIBUTION AND SOIL POROSITY

Thin sections of soil can be used for the study of the root distribution in relation to the pore sizes and the evaluation of the soil porosity.

a, Soil sectioning:

Delage and Lagatu (1904) were the first workers to prepare thin sections of soils. In their technique the soil had to be crushed before being mixed with the hardening substances, and consequently, the natural fabric of the soil was destroyed. An advance on such a technique was put forward independently by Ross (1924) and Kubiena (1938). They carried out successful impregnations of blocks of soil with "kollolith" without breaking them. But these methods required the application of heat in the drying of soil prior to impregnation and during the subsequent hardening of "kollolith". The subjection to heat would have resulted in severe distortion of soil structure by uneven drying and shrinkage of its components. An advance was made by Haarløv and Weis-Fogh (1953), who used agar-agar as the impregnating material, and Minderman (1956) who used gelatin. These substances are miscible with water and thus did not require the preliminary drying of soil prior to impregnation. But the use of these soft impregnating agents necessitated the sectioning of the impregnated soil on a microtome, and this imposed a strict lower limit on the thickness of the sections that could be obtained, especially in mineral soils where the microtome knife must either "tip out" or "push in" the mineral grains which came in contact with the blade.

The natural or synthetic resins are totally immiscible with water. Their use provided a very hard block of soil from which thin sections could be cut by following the ordinary geological procedure. Consequently, in techniques developed by later workers, in which resins were used as the impregnating materials, attempts were made to reduce the distortion caused

by the drying process. Thus Bourbeau and Berger (1948), Day (1949) and Hepple and Burges (1956) air-dried the soil prior to its impregnation with resin. The air-drying of soil reduced the amount of distortion and disturbance as compared with drying in an oven. However, a more important advance in this technique was made by freeze-drying the soil samples (Alexander and Jackson, 1955; Burges and Nicholas, 1961; Nicholas, 1962), which minimised any distortion of soil structure during the drying process.

There has been a parallel development in the avoidance of heating during the hardening of the resins. Instead of resins which required "curing" by heat (Frei, 1947; Mochalova, 1956) a large number of synthetic resins which set irreversibly under the action of a catalyst, have come into use (a, "Castolite" - Bourbeau and Berger, 1948; Day, 1949; b, "Bakelite" - Hepple and Burges, 1956; Burges and Nicholas, 1961; c, "Polestar" - Altemüller, 1956; and d, "Marco" - Alexander and Jackson, 1955; Nicholas, 1962; Gadgil, 1965).

This brief survey shows that satisfactory techniques are available for the preparation of thin soil sections without any marked disturbance or distortion. These sections can be studied only by using a petrographic microscope or a polarising microscope with crossed nicol pieces. The difficulties of distinguishing pore spaces from the mineral matter and the ease with which the "artefacts", developed during grinding and polishing of sections, may be mistaken for pore spaces, can be obviated by the use of a resin containing a pigment. The method described below provides such a technique.

A methacrylated polyester resin, "Crystic 195", manufactured by Scott, Bader and Co. Ltd., Northamptonshire, U.K., was used in conjunction with a blue pigment. The coloured resin mixture occupied the pore spaces in the soil and it was very easy to distinguish them from the rest of the soil components, and

the sections could be studied with the aid of an ordinary microscope. The method involved the following operations:

i, Collection of undisturbed soil samples:

Soil samples were obtained from the four sites from 2, 6 and 10 inches soil depths (soil aeration studies were made at these depths - Section IV) from the pits dug for root sampling of Molinia and Erica (Section II, p. 27). At each sampling depth, two replicates were obtained from the opposite facing sides of a pit. A sample was collected in an undisturbed condition using an open-ended metal cylinder (10 cm. diameter and 5 cm. deep, approx.) which had a sharp cutting edge. Another metal cylinder of the same internal but greater external diameter as the sampling cylinder, which fitted snugly over the sampling cylinder, was placed over the latter and the two were driven into the soil using a block of wood and a heavy hammer. Every care was taken to keep the cylinder vertical to avoid any distortion. The cylinder was then dug up. Using a sharp knife, the soil was cut level with the top and bottom of the cylinder. The samples were transported to the laboratory in polythene bags and were stored in deep-freeze.

ii, Freeze-drying:

The samples, still contained in the metal rings, were plunged into liquid nitrogen to get a thorough freezing of the water in them before being subjected to freeze-drying. Three to four samples were placed in a polythene dish in a large desiccator and were connected to the freeze-drier.

Freeze-drying equipment in the Chemistry Department of Royal Holloway College, Surrey, was used and acknowledgement is made here to Prof. E. J. Bourne for the permission to use the equipment and to Dr. N. A. Soofi for his help in its use.

iii, Impregnation with the resin mixture:

"Crystic 195" resin to which a blue pigment was added, was mixed with the catalyst and the accelerator according

to the following formulation:

	<u>Parts by weight</u>
Crystic 195	100
Catalyst Paste H	4
Accelerator E	2
Blue pigment	Sufficient amount to give a reasonable colour.

The "setting" time of this mixture was 90 minutes at 20°C.

The metal rings around the soil samples were removed. Freshly prepared resin mixture was poured into the polythene dish containing the dried samples, and using a vacuum pump, pressure inside the desiccator was slightly reduced. This resulted in withdrawal of air out of the sample. The pressure was reduced to 15 cm. Hg in about half an hour. If the pressure was further reduced, the resin mixture started to boil. The resin mixture rose into the soil sample and filled the pore spaces. The system was maintained at the reduced pressure of 15 cm. Hg for about half an hour. By gradual opening of the bleed on the desiccator, the vacuum was slightly reduced over a period of twenty minutes so that the samples returned to normal atmospheric pressure well before any marked change in the viscosity of the resin mixture had occurred. The samples were taken out of the desiccator and left in the open for about three weeks when the resin became fully mature and the samples were hard like a rock.

iv, Sectioning:

In the interest of economy and labour, it was decided to prepare only one transverse section from one of the replicate soil cores from a sampling depth for a site, except in the case of the drier *Molinietum* where a section was obtained

from each of the two replicate soil cores from 2 inches depth. The section was cut from near the middle of the core because the sides may have suffered some disturbance at the time of sampling and subsequent handling.

Thin sections ($30 - 40\mu$) of the hard blocks of soils were cut following the usual geological procedure of cutting, grinding and polishing. The sections were mounted on glass slides in "Lakeside 70". Each slide was 3" X 3" and the sections were approximately 2.5" X 2.5".

Mr. J. Blount of the Geology Department of this College prepared the soil sections to whom grateful acknowledgement is due.

b, Pore sizes and root distribution.

An ordinary microscope with a mechanical stage was used for the study of the soil sections. Because of the distinct colour and structure it was easy to distinguish the roots of Molinia from those of Erica. Molinia roots were much more plentiful than Erica roots. Each slide was thoroughly studied in order to get measurements for 20 to 25 roots of each of the species. This was about the maximum number of Erica roots which could be found, and a similar number of Molinia roots were selected at random. For each root selected, the diameter was recorded and also the diameter of the pore in which it was found.

There were no Erica roots in the sections obtained from soils sampled from 10 inches depth. In the case of Molinia there were very few roots in the soil sections from this depth (see also Section II, p. 37).

Figs. 11-12 show the frequency distribution of pore diameters in which roots occurred, and Figs. 13-14 the frequency distribution of root sizes. No clear differences between sites could be detected and so these Figs. 11-14 show the data for species and depths, averaged over all sites.

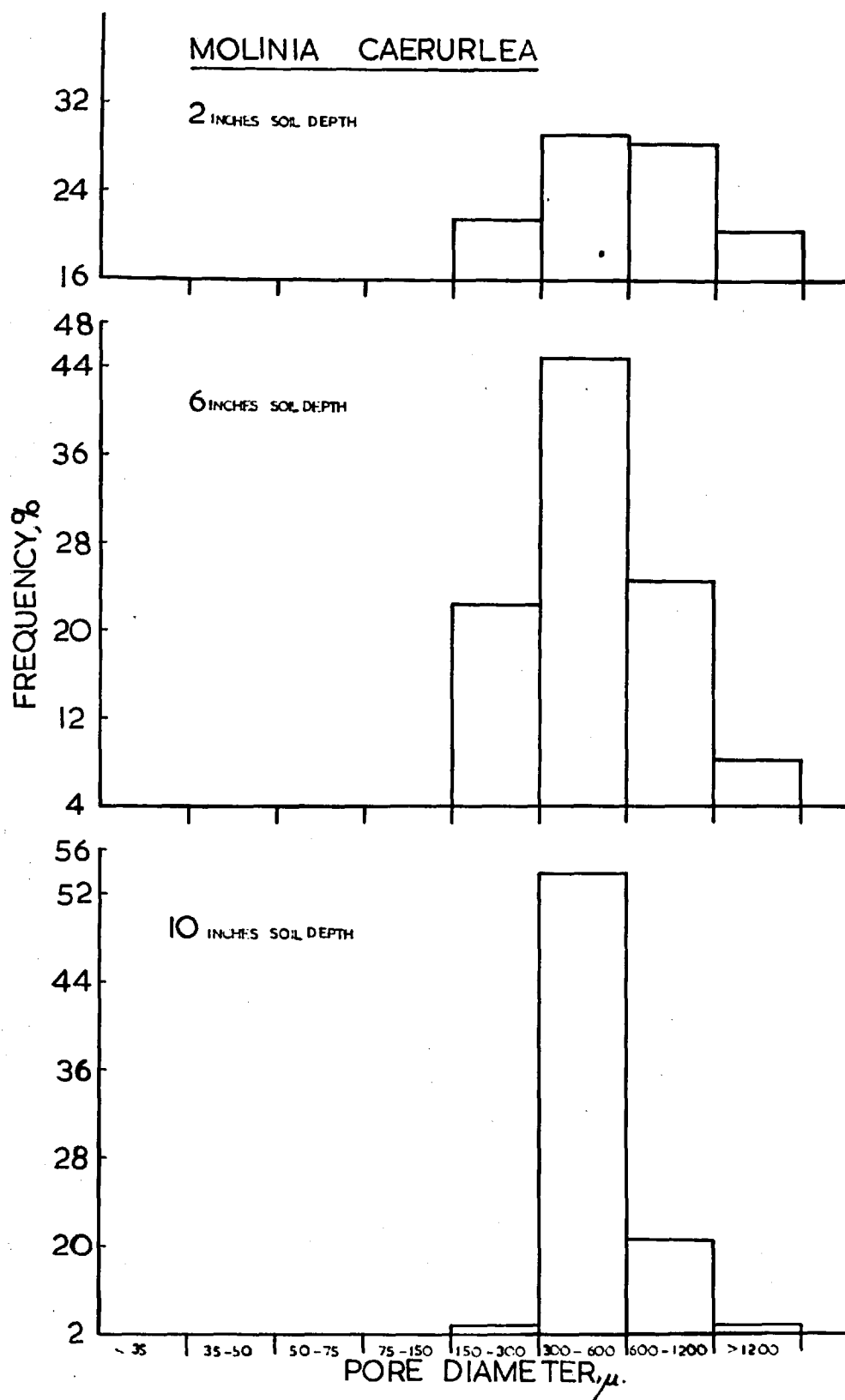


Fig. 11. Molinia caerulea: Frequency distribution of pore sizes in which roots were found.

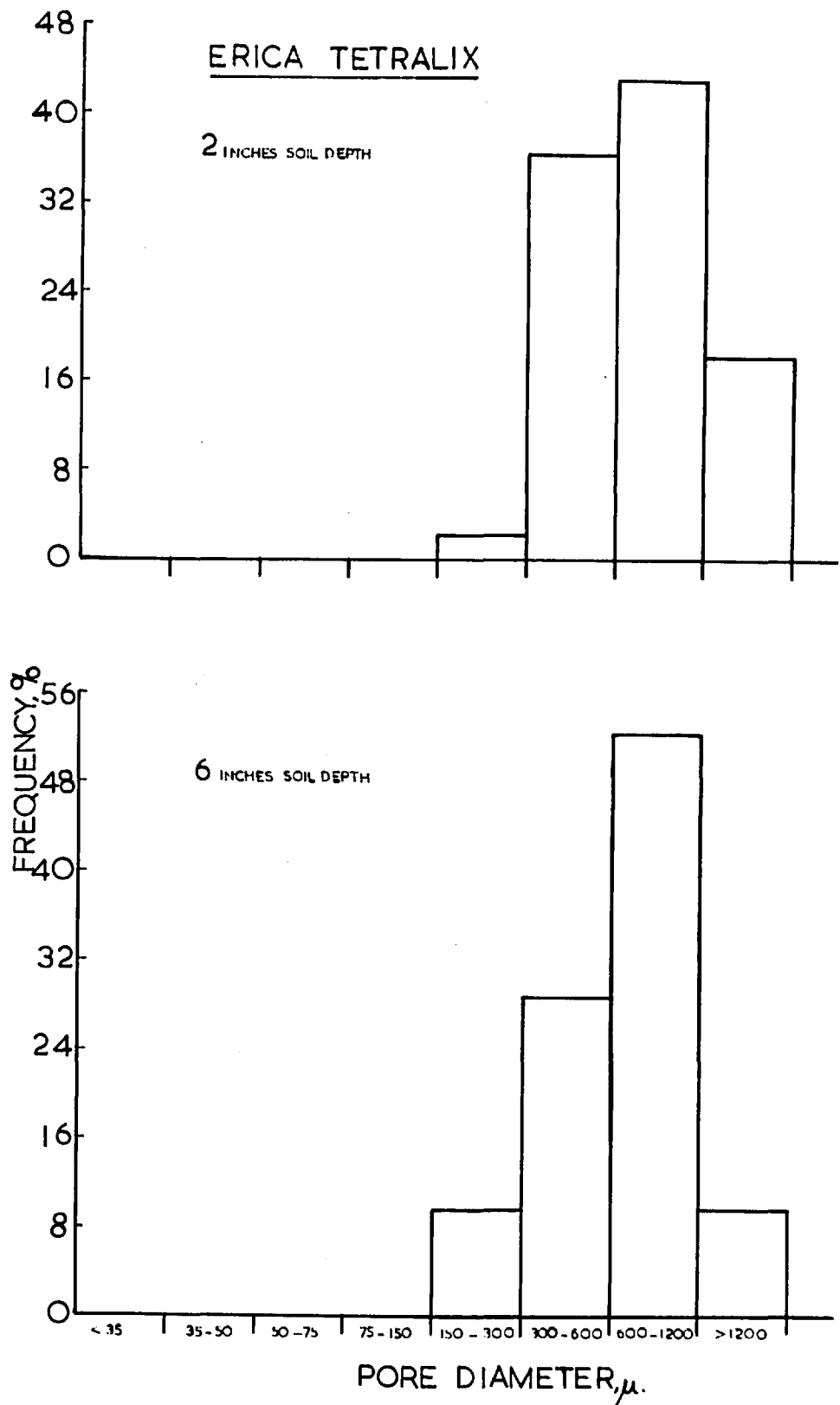


Fig. 12. Erica tetralix: Frequency distribution of pore sizes in which roots were found.

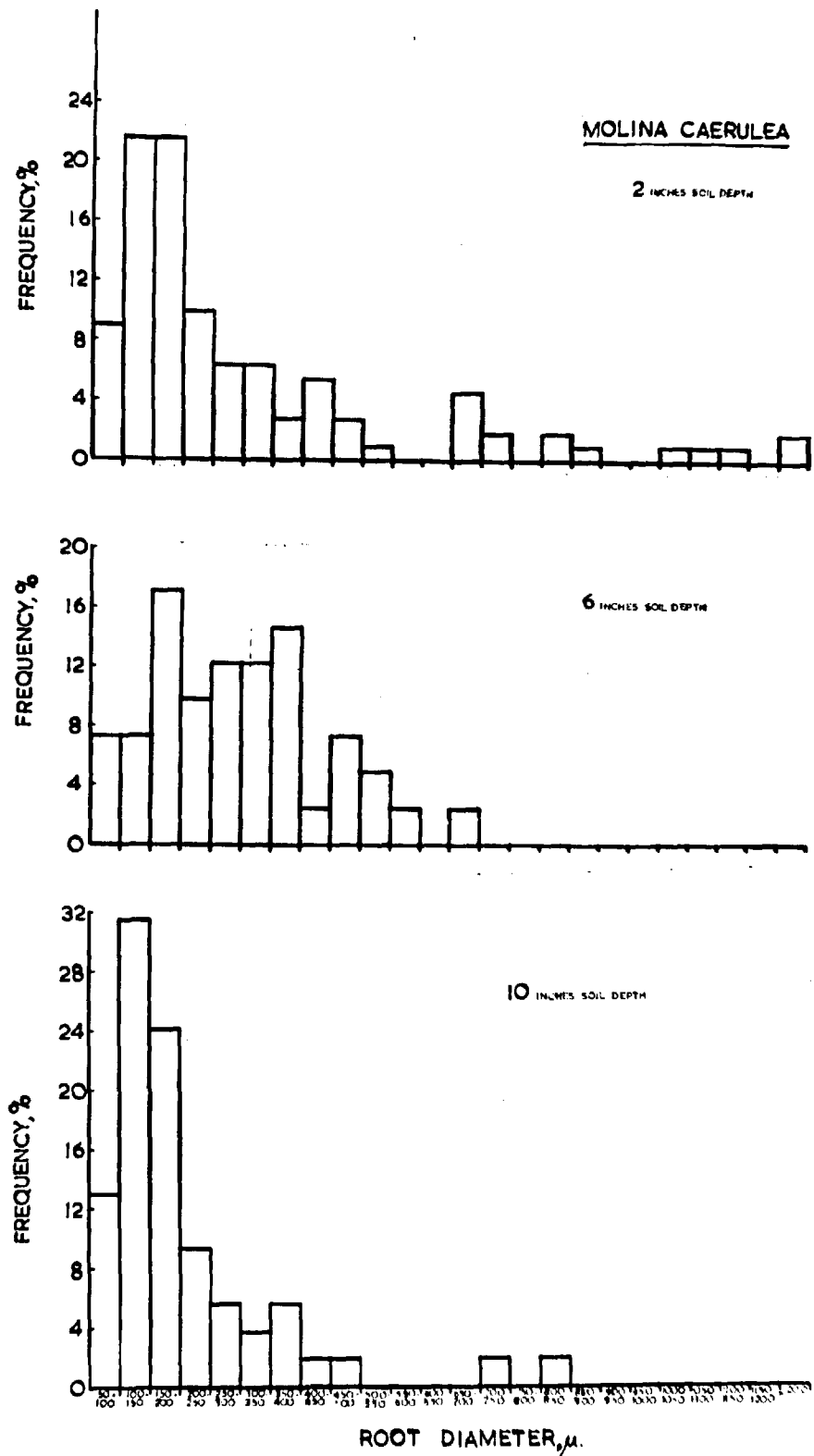


Fig. 13. Molinia caerulea: Frequency distribution of root sizes.

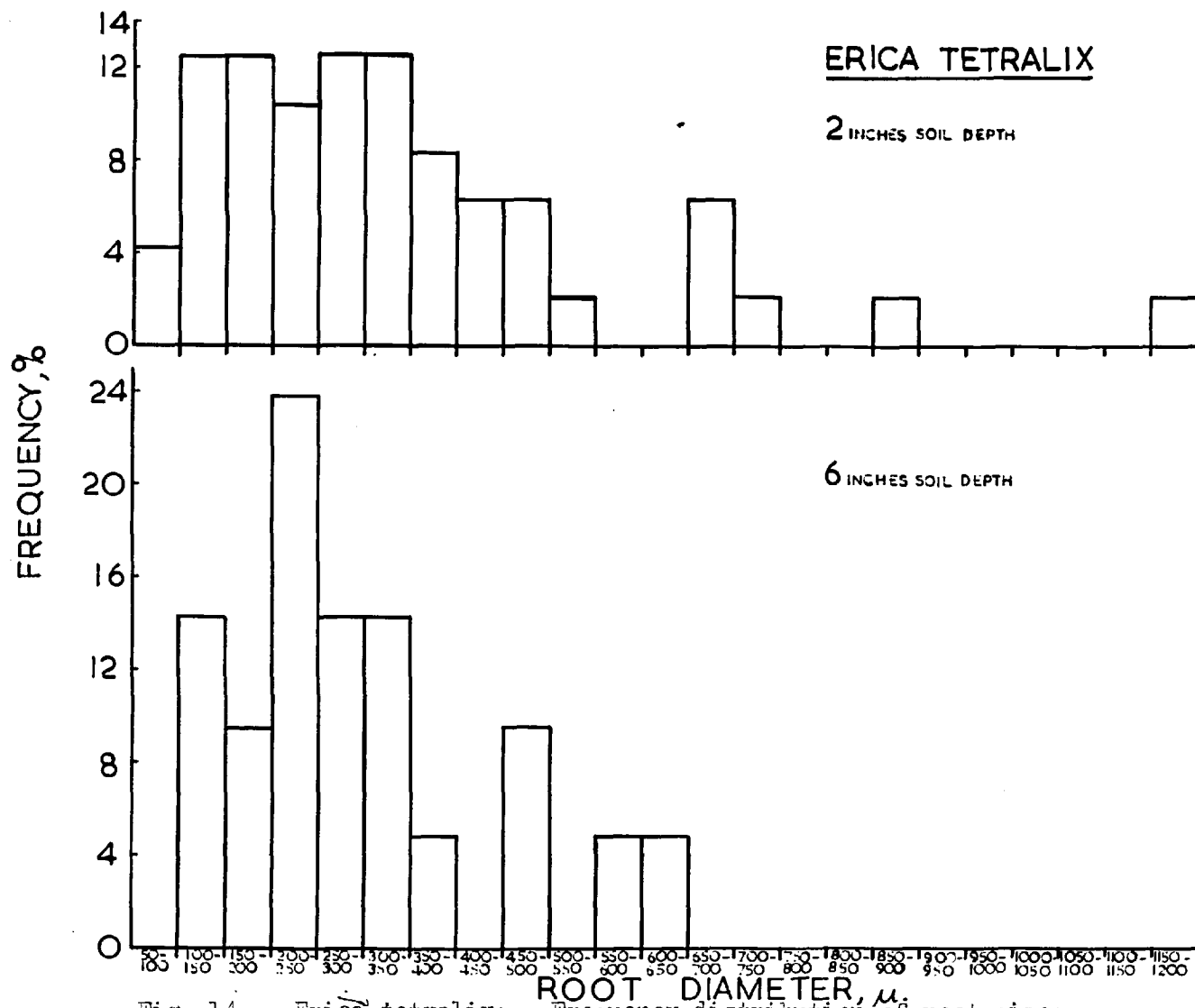


Fig. 14. Erica tetralix: Frequency distribution of root sizes.

The roots of both the species were present only in soil pores of diameters greater than $150\ \mu$. In Molinia the root distribution showed a maximum in the $300 - 600\ \mu$ pore diameter class, whereas in Erica the maximum was reached in pores with diameters of $600 - 1200\ \mu$.

Figs.13-14 show that both in Molinia and Erica the proportion of roots of smaller diameters increased with an increase in soil depth. This might be of significance in the adaptation of the roots to reduced aeration at greater depths, because it has been calculated (Lemon and Wiegand, 1962; Kristensen and Lemon, 1963) that the critical oxygen concentration for root activity varies more or less proportionately with root diameter. The critical oxygen concentration is that below which oxygen uptake by the roots is restricted.

It was found that the diameters of the roots were much smaller than those of the pores in which they were present, and, on an average, the ratio of pore diameter to root diameter was above 2 (Table 30).

TABLE 30 AVERAGE VALUES OF RATIO OF PORE DIAMETER
TO ROOT DIAMETER

<u>SOIL DEPTH</u>	<u>ERICA</u>	<u>MOLINIA</u>
inches		
2	2.40	2.68
6	2.79	2.65
10	× -	2.72

*Roots absent.

Although the roots are appreciably smaller than the pores in which they occur, their restriction to the larger pores might still be due to mechanical causes, for pores of a given diameter do not continue for much vertical distance

without constriction (See Fig. 21, p. 135). It seems unlikely that roots are excluded from smaller pores by poor drainage or aeration, since there is no marked change in root distribution relative to pore sizes with increasing depth or change in site (Figs 11-12). However, in case of Molinia there is some suggestion that at a depth of 2 inches more roots enter pores of 150 - 300 μ diameter as compared with 10 inches depth.

Wiersum (1957) found that in a rigid system (e.g., densely compacted soil) a root is able to penetrate only the pores which have diameters exceeding that of the young root and that although the young root tip is plastic, it cannot pass through a narrow pore by means of a short constricted zone. Aubertin and Kardos (1965) have also reported a definite influence on root growth of both the rigidity of the system and the size of the pores present in it. They found that maize roots did not grow into rigid porous systems which had pore diameter smaller than approximately 140 μ .

c, Soil Porosity

It was necessary to discover whether the roots occurred mainly in water-filled or air-filled pores, and investigations of soil porosity were undertaken to provide a basis for calculating the distribution of water- and air-filled pores in the soils under different conditions.

i, Micrometric method:

A micrometric method adapted from the Rosiwal method (Holmes, 1930) for determining the volume-percentages of minerals in thin sections of rocks was used for the quantitative expression of the soil pore space as revealed in thin sections of soils. This method is based on the principle that in any surface of adequate area a , the ratio of the sum of the areas of any given mineral to the total area of the measured rock surface

is approximately equal to the volume-percentage of that mineral in the rock, and b, that along any line of adequate length drawn on a plane surface, the ratio of the sum of the linear intercepts of any given mineral to the total length measured across the rock surface is approximately equal to the volume-percentage of that mineral in the rock. Instead of making measurements on a single line which would have to be very long and would, therefore, require an extensive surface to contain it, a series of random lines may be measured on a much smaller surface.

The applicability and the accuracy of this method in the determination of the volume-percentages of minerals in rocks, have been established by geologists (Johansen and Stephenson, 1919; Alling and Valentine, 1927). Swanson and Peterson (1942) have used this method for the study of the pore-size distribution in the sections of soils.

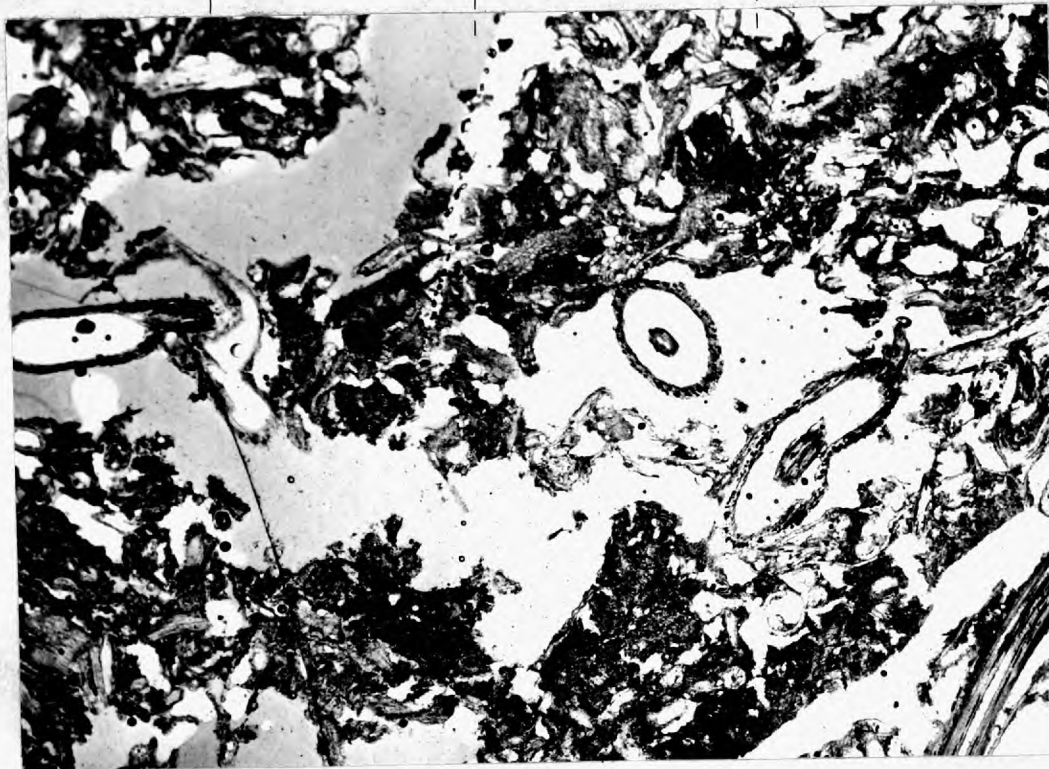
The structure (porosity, mineral matter and organic matter) of the soils from depths of 2, 6 and 10 inches from the four sites was studied from the soil sections. Only one section was studied for each soil depth for a site. Using the mechanical stage of the microscope, a transect of a measured length (usually 30 - 35 mm.) was studied. The micrometer scale was positioned along the line of travel of the mechanical stage (transect). The intercepts of pore space and mineral matter were measured along the transect. The organic matter was obtained by subtracting the total of intercepts of pore space and mineral matter from the total length of the transect. The results were expressed as a percent of the transect of a standard length (= 100 mm.). In each section five randomly placed transects were studied.

Plates 9 to 11 show macrophotographs of sections of soils sampled from 2, 6 and 10 inches depths from the Valley-

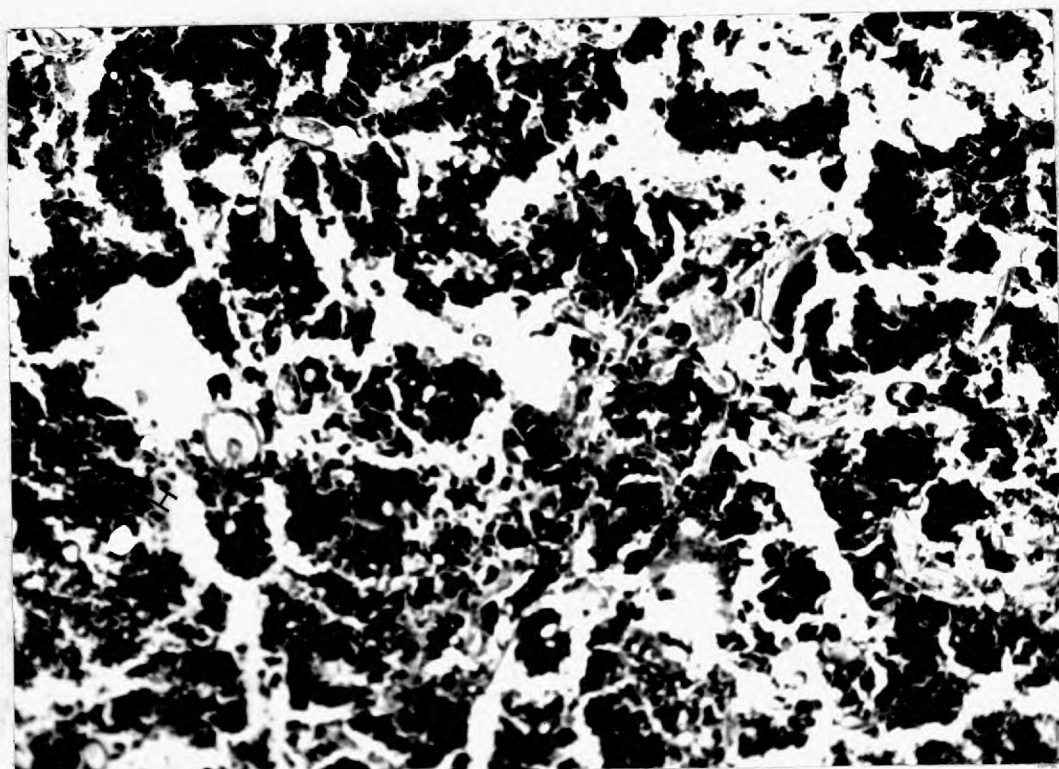
ORGANIC ¹¹¹
MATTER

PORE
SPACE

MINERAL
MATTER

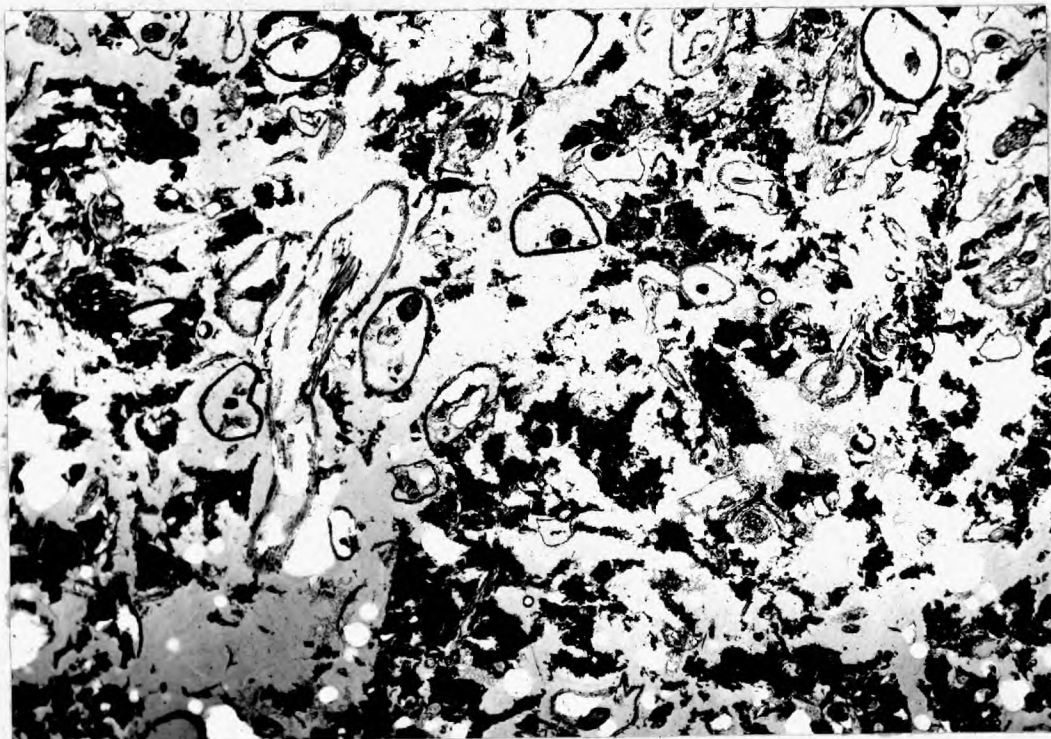


a

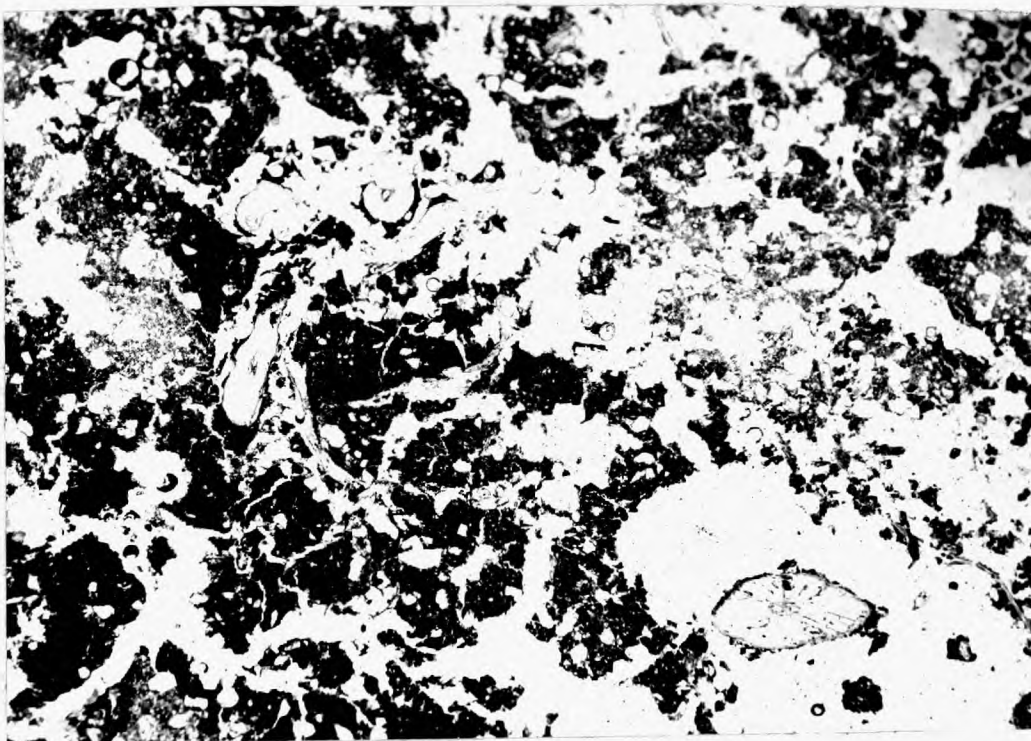


b

Plate 9. Macrophotographs of transverse sections of soils
from a depth of 2 inches.
a, Valley-bog.
b, Drier Molinietum.

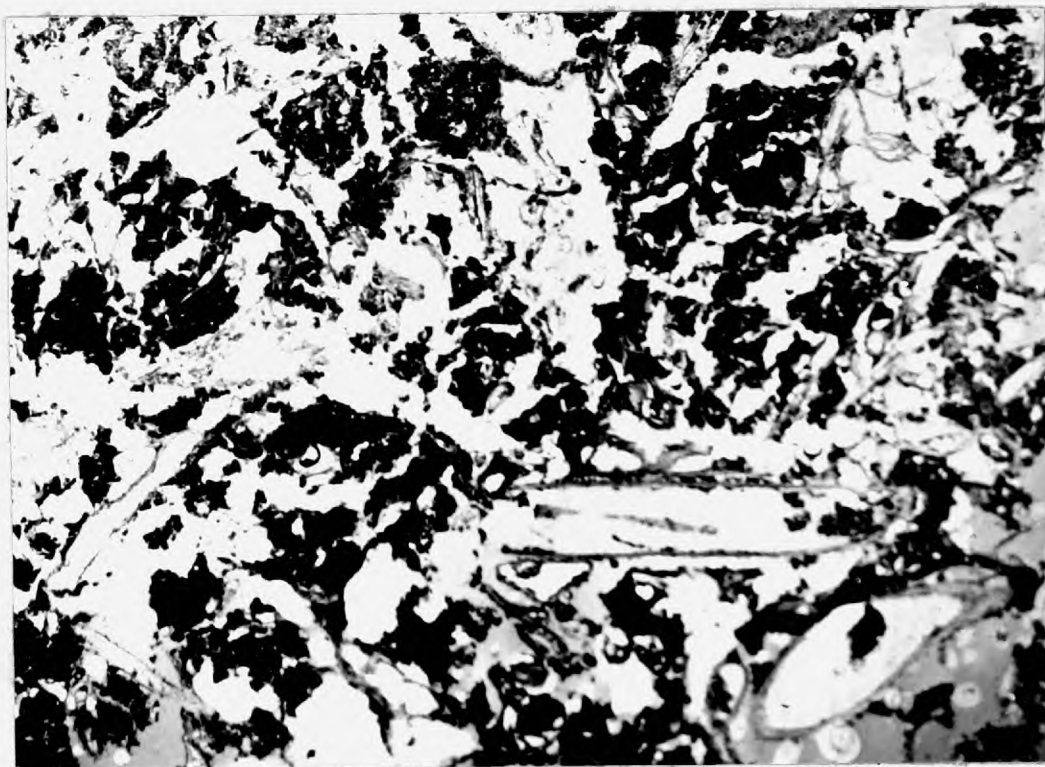


a

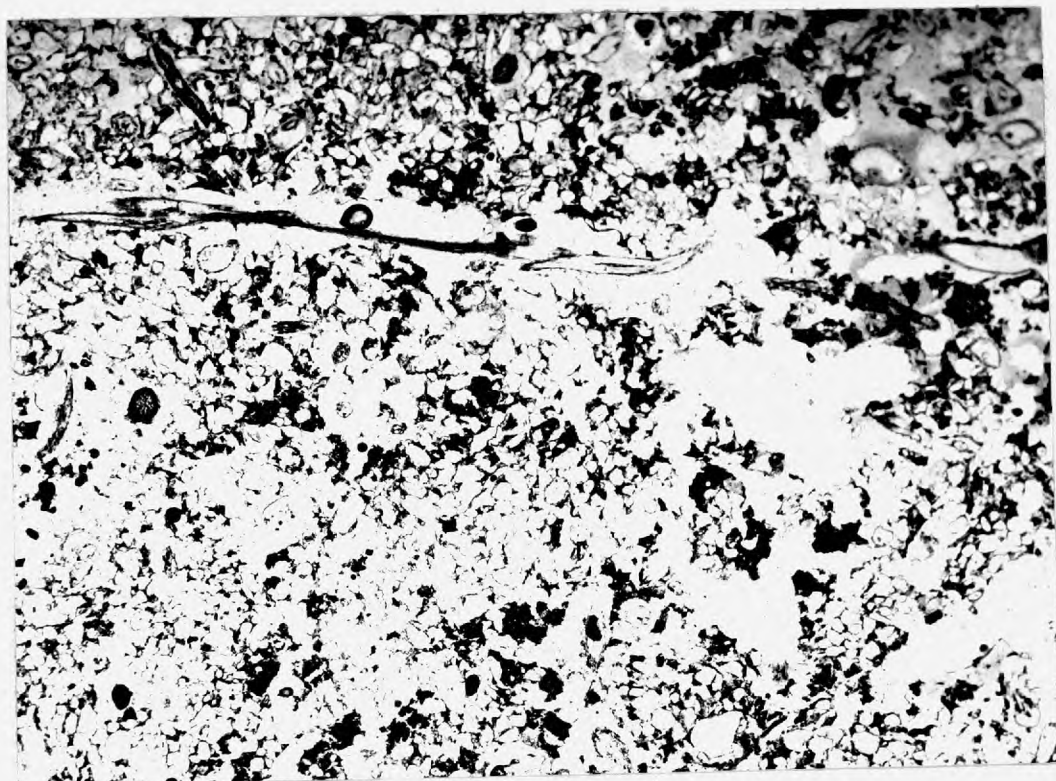


b

Plate 10. Macrophotographs of transverse sections of soils
 from a depth of 6 inches.
a, Valley-bog.
b, Drier Molinietaum.



a



b

Plate 11. Macrophotographs of transverse sections of soils
from a depth of 10 inches.
a, Valley-bog.
b, Drier Moliniatum.

bog and the drier Molinieta, the two most contrasted sites. These macrophotographs were taken using a camera with a lens of a short focal length (4.8 mm.).

Table 31 gives the values of total porosity, organic matter and mineral matter (volume-percentages) for different soil depths (2, 6 and 10 inches) from the four sites. These values are means of those based on the study of five transects. The standard errors of the means of these five determinations are also given. In the Valley-bog there was an increase in the amount of organic matter and to a lesser extent of mineral matter with an increase in soil depth and the total porosity declined correspondingly. In the Central associates the amount of organic matter at 6 inches was greater than at 2 inches depth, but it decreased markedly at a depth of 10 inches. The amount of mineral matter showed a consistent increase. In the wetter and drier Molinieta with an increase in soil depth, there was a marked decrease in the amount of organic matter and a pronounced increase in that of mineral matter (see also descriptions of soil profiles, Section II, pp.30-31). On all sites, on the whole, there was a decrease in total porosity with an increase in soil depth. The drier Molinieta soil showed the least variation in total porosity at different depths.

In order to see the variability between the two replicates obtained from one sapling depth, two transverse sections, one from each of the two replicates from two inches depth from the drier Molinieta, were studied. The results for total porosity are given in Table 32. The difference between the mean total porosities of the two replicate samples was hardly greater than the standard error of either mean.

TABLE 31 SHOWING TOTAL POROSITY, ORGANIC MATTER AND
MINERAL MATTER IN SOIL SECTIONS FROM DIFFERENT
DEPTHS FROM THE FOUR SITES (VOLUME-PERCENTAGES).

Means of five transects per section.

SOIL DEPTH, Inches		VALLEY-BOG	CENTRAL ASSOCIES	WETTER MOLINIETUM	DRIER MOLINIETUM
2	TOTAL POROSITY	54.60 $\pm$ 2.33	58.18 $\pm$ 5.10	63.24 $\pm$ 5.36	35.87 $\pm$ 2.71
	ORGANIC MATTER	33.35 $\pm$ 1.56	36.39 $\pm$ 5.00	31.80 $\pm$ 5.40	60.38 $\pm$ 2.64
	MINERAL MATTER	12.05 $\pm$ 1.42	5.43 $\pm$ 0.97	4.94 $\pm$ 0.83	3.74 $\pm$ 0.50
6	TOTAL POROSITY	38.85 $\pm$ 3.67	34.49 $\pm$ 3.06	47.68 $\pm$ 2.51	36.01 $\pm$ 2.17
	ORGANIC MATTER	42.34 $\pm$ 2.78	45.59 $\pm$ 1.97	17.83 $\pm$ 1.14	49.43 $\pm$ 1.49
	MINERAL MATTER	18.81 $\pm$ 2.91	19.92 $\pm$ 1.37	34.47 $\pm$ 2.51	14.60 $\pm$ 1.00
10	TOTAL POROSITY	32.78 $\pm$ 1.67	43.99 $\pm$ 2.31	30.37 $\pm$ 2.69	29.44 $\pm$ 1.33
	ORGANIC MATTER	50.01 $\pm$ 2.70	19.99 $\pm$ 2.84	10.36 $\pm$ 1.95	39.03 $\pm$ 3.12
	MINERAL MATTER	17.21 $\pm$ 1.17	36.00 $\pm$ 1.39	59.25 $\pm$ 1.92	31.52 $\pm$ 3.31

TABLE 32. COMPARISON OF TOTAL POROSITY MEASUREMENTS
BASED ON THE STUDY OF 5 TRANSECTS FROM
EACH OF THE TWO REPLICATE SOIL SAMPLES.
(VOLUME-PERCENTAGE)

Replicate samples from 2 inches soil depth from
the drier Moliniatum.

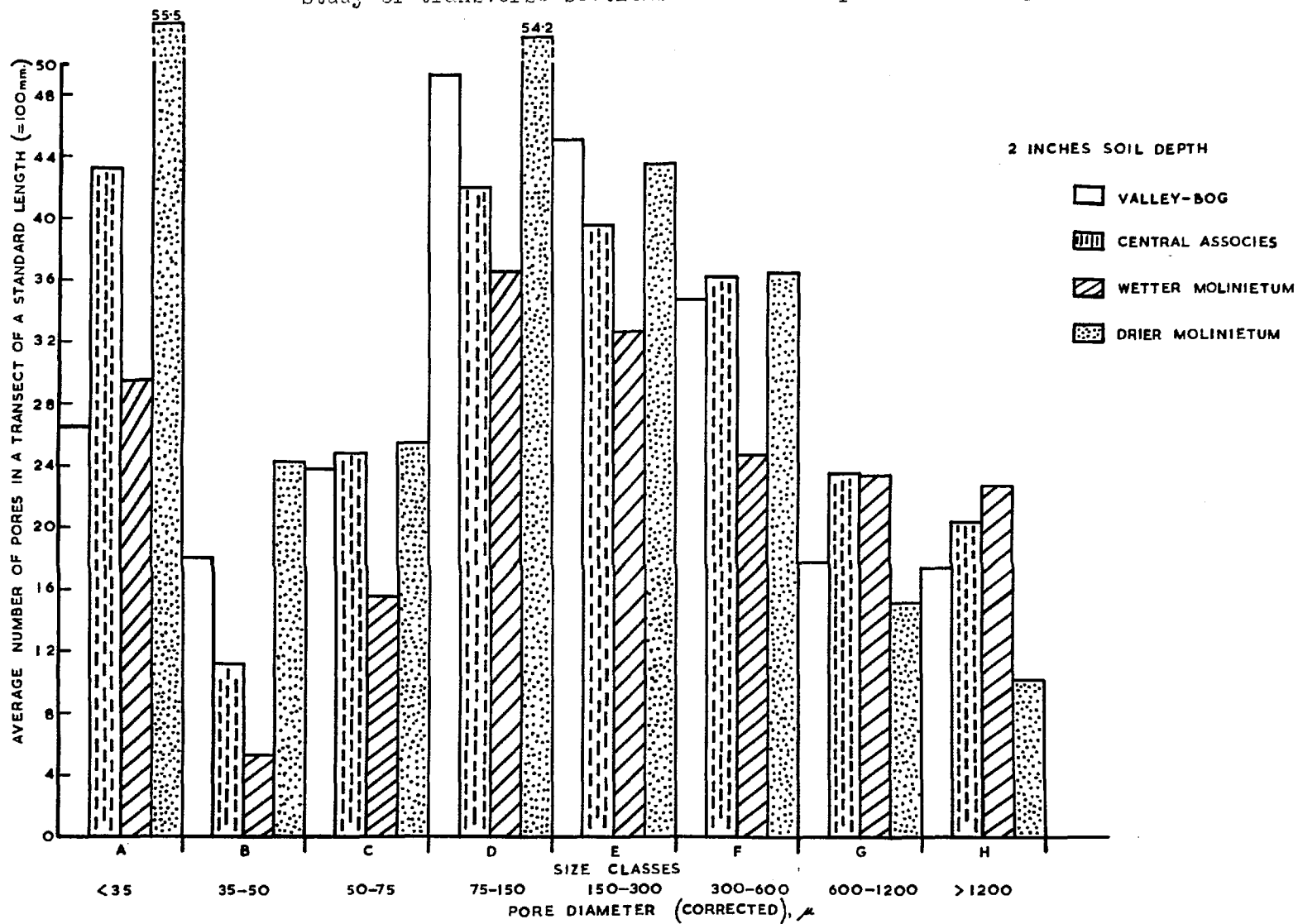
TRANSECT NO.	SAMPLE	
	I	II
1	30.62	31.40
2	33.49	30.19
3	31.66	32.00
4	45.36	36.27
5	38.24	34.86
MEAN	35.87 $\pm$ 2.71	32.94 $\pm$ 1.15

Pore-size distribution:

The pore intercepts measured along the transects do not represent actual pore diameters but will be under-estimates except when the transect passes through the centre of the pore. In view of this a correction had to be applied to the pore intercepts in order to obtain a frequency distribution of pore diameters. (see Appendix C).

Figs. 15, 16 and 17 show the average number of pores of different diameters as revealed by the study of sections of soils from different sites from depths of 2, 6 and 10 inches, respectively. It should be mentioned here that in these Figs. the height of the histograms rather than their area is meaningful because the horizontal axis is not sub-divided on a linear scale of pore diameter.

Fig. 15. Frequency distribution of pores of different diameters as revealed by study of transverse sections of soils sampled from a depth of 2 inches.



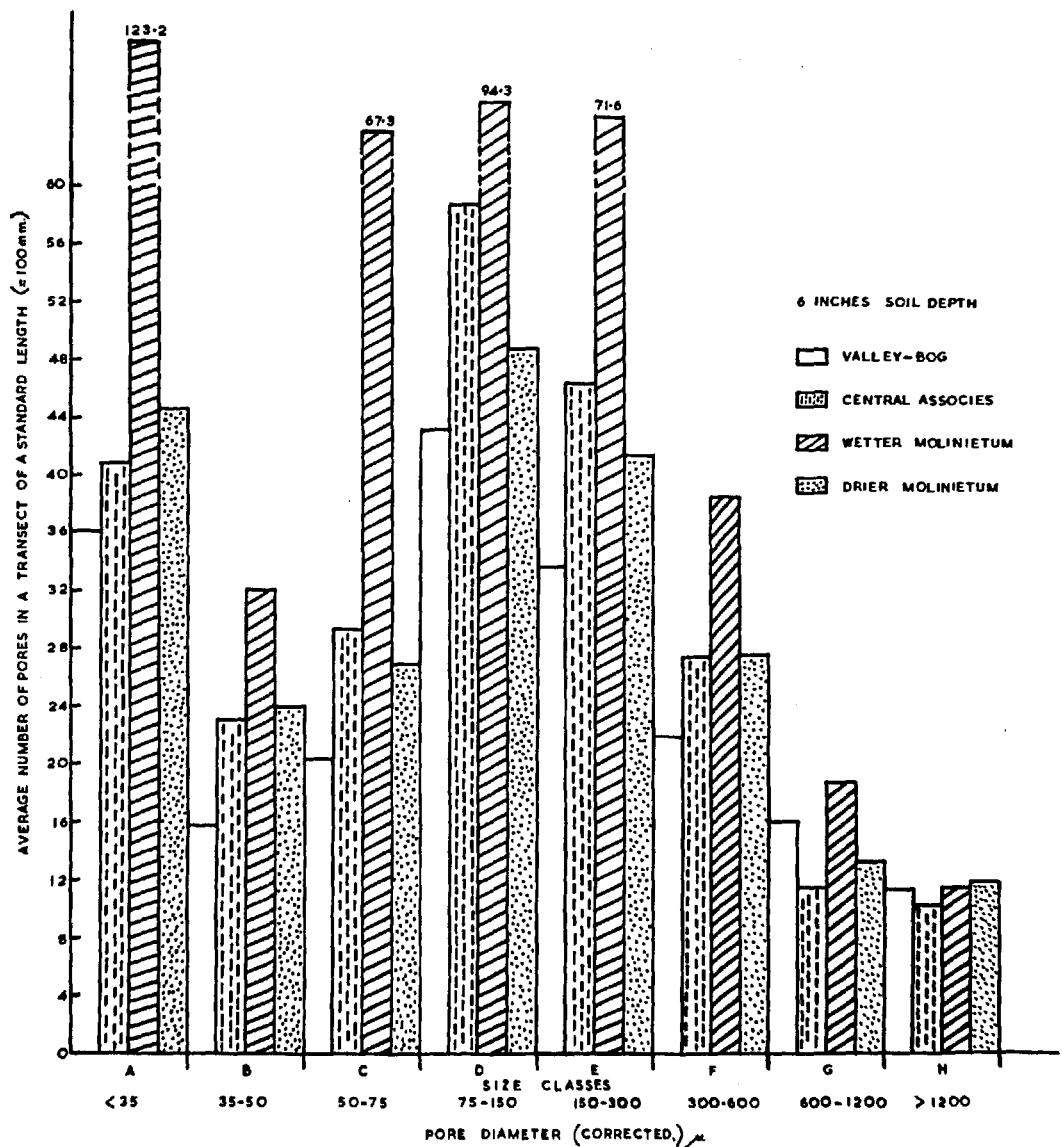


Fig. 16. Frequency distribution of pores of different diameters as revealed by study of transverse sections of soils sampled from a depth of 6 inches.

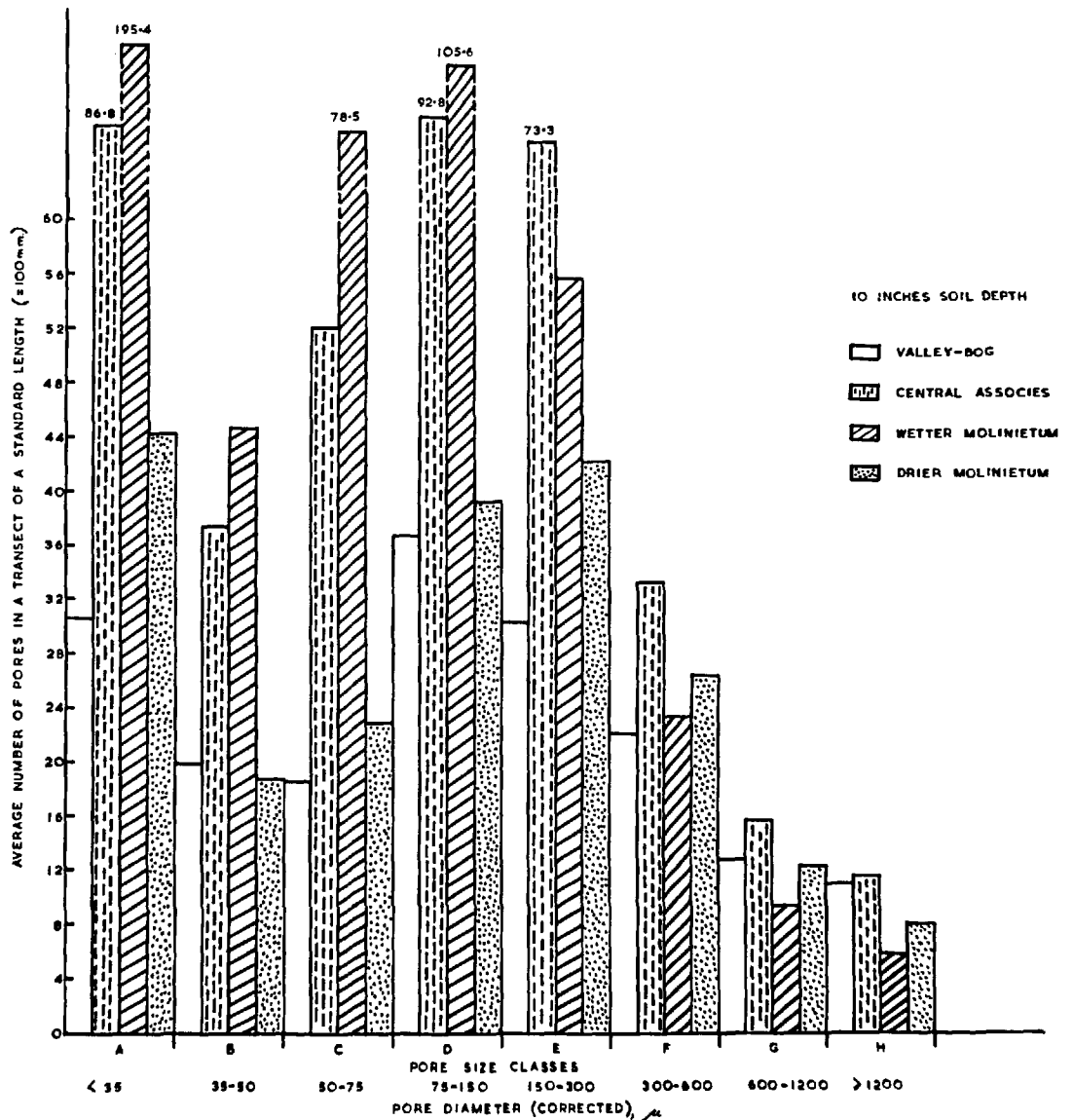


Fig. 17. Frequency distribution of pores of different diameters as revealed by study of transverse sections of soils sampled from a depth of 10 inches.

In the Valley-bog, with increasing soil depth, the number of pores in size class A ($< 35 \mu$) showed a slight increase whereas there was a consistent fall in the number of pores in the remaining size classes (B to H, $> 50 \mu$).

The soils of the Central associates and the wetter Moliniatum showed distinctly marked increase, with depth, in the number of pores in size classes A to E ($< 300 \mu$), whereas the number of pores in classes F to H ($> 300 \mu$) showed a consistent decrease. At 10 inches depth, the number of pores in size class A in the Central associates was twice of that at 2 inches whereas in the wetter Moliniatum it was 7 times of that at 2 inches depth.

With increase in soil depth, the drier Moliniatum soil did not show a very marked variation in the number of pores in size class A ($< 35 \mu$) though there was a regular fall in the number of pores in the remaining size classes (B to H, $> 35 \mu$) and this fall was particularly marked in the larger size classes (D to H, $> 75 \mu$).

In general, the change with depth was an increase in the number of smaller pores and a decrease in the number of larger pores. Comparing sites, at two inches depth the drier Moliniatum had the highest number of pores in class A ($< 35 \mu$), and at all depths the Valley-bog had the least number of these small pores.

ii, Moisture-tension method:

Method:

A modification of the moisture-tension methods described by Jamison (1958) and Rutter and Sheikh (1962) was used. A large drum was used for applying a variety of moisture-tensions on the soil samples. The details of construction and use are given below.

The drum (90 cm. tall, 60 cm. diameter) had a circle of 6 equally spaced holes of $5/16$ " diameter drilled in its

sides at each of three levels, viz., 25, 45 and 85 cm. below the top. The holes were plugged with rubber bungs. The bottom of the drum was covered with gravel to a level just below the lower-most holes (85 cm.). A length of drain pipe was stood in the centre of the drum which was then filled to within 5 cm. of the top with a very fine, water-sorted sand. A tensiometer was installed at the surface of the sand. The sand was saturated by running water into the drain-pipe until the water-table was brought to the surface of the sand. It could subsequently be drained to 20, 40 and 80 cm. depths by removing the appropriate circle of bungs. The tensiometer indicated the attainment of equilibrium between the artificial water-table and the surface sand.

The method of soil sampling and sampling depths were the same as in the case of sampling for soil sectioning (see above, p.101). In this case sampling was spread over three months, viz., June, July and September, 1964, and altogether there were six replicate cores for each depth at each site.

Saturation of the samples:

The lower end of the metal cylinder containing the soil sample was covered with a hard filter paper (Whatman No.50) taped in position with a water-proof adhesive tape ("Lassotape"). The samples were stood in deep trays of water for 48 hours, the depth of water being about 2 cm. in the beginning but slowly increased until nearly level with the top of the cylinders. This saturated the soil pores (by capillarity) with water, and soil and cylinders were now weighed after being allowed to drain for a minute to allow superficial water to drip off. This weighing gave the weight at saturation.

Application of moisture-tensions:

The saturated and weighed soil cores in the cylinders were stood on the surface of the saturated sand with only the filter paper to interrupt the contact between soil and

sand. Each sample was covered with a loosely fitting polythene bag to prevent evaporation and the whole of the drum was also covered with a polythene sheet tied around its rim.

The rubber bungs were removed at 20 cm. level. The steadiness of the tensiometer indicated the attainment of equilibrium tension conditions. The samples were weighed every day, and when they did not show any change in weight for three consecutive days, they were taken to be in equilibrium with the applied tension. The weight of the samples, when in equilibrium with 40 and 80 cm. water-tables (tensions), was also found in a similar manner.

After the final weighing at 80 cm. tension, the soil was removed from the cylinders and was dried at 105°C. for 24 hours and then reweighed. From this the water content retained at 80 cm. tension and the bulk density (or apparent density) of the soil was calculated.

The amount (volume) of water lost at a given tension (gm. or cc.), when expressed as a percentage of the total soil volume, represented the porosity (air-filled) of the soil at that tension,

i.e., Porosity at a particular

$$\text{moisture-tension, } h \text{ cm.} = \frac{\text{Volume of water lost at } h}{\text{Total soil volume}} \times 100$$

Results:

Bulk density, and water content, % of soil volume, at saturation and that retained at 80 cm. tension, are given in Table 33.

TABLE 33 MEAN BULK DENSITY AND WATER
CONTENT OF SOIL SAMPLES.

	Sampling depth,	Bulk density,	Water content, % soil	
	inches	g/cc.	At saturation	At 80 cm. tension
VALLEY- BOG	2	0.12 ± 0.01	93.3 ± 2.3	63.4 ± 3.0
	6	0.27 ± 0.06	89.4 ± 3.4	70.6 ± 2.2
	10	0.34 ± 0.03	86.2 ± 1.0	74.7 ± 1.6
CENTRAL ASSOCIES	2	0.43 ± 0.03	76.7 ± 2.1	58.7 ± 2.2
	6	0.71 ± 0.05	72.5 ± 2.1	61.8 ± 1.6
	10	1.14 ± 0.16	60.4 ± 5.4	53.9 ± 4.3
WETTER MOLINIETUM	2	0.52 ± 0.08	74.3 ± 3.6	57.7 ± 3.1
	6	1.16 ± 0.04	53.4 ± 1.3	46.6 ± 1.3
	10	1.54 ± 0.06	44.2 ± 1.3	39.2 ± 1.3
DRIER MOLINIETUM	2	0.56 ± 0.04	74.7 ± 2.1	61.9 ± 1.6
	6	1.20 ± 0.06	56.0 ± 2.2	52.5 ± 2.7
	10	1.53 ± 0.06	43.8 ± 1.2	41.3 ± 1.7

Figs. 18-20 show the mean porosity at different tensions for the four sites for soil samples from depths of 2, 6 and 10 inches, respectively. The standard errors of the means (of 6 replicates) are represented by vertical lines on either side of the points. The results were subjected to an analysis of variance after an angular transformation of the data. At 2 and 6 inches soil depths the Valley-bog soils had very significantly ($P = 0.001$) greater porosity than the other 3 sites and the drier Moliniatum soil had the lowest porosity. The Central associates

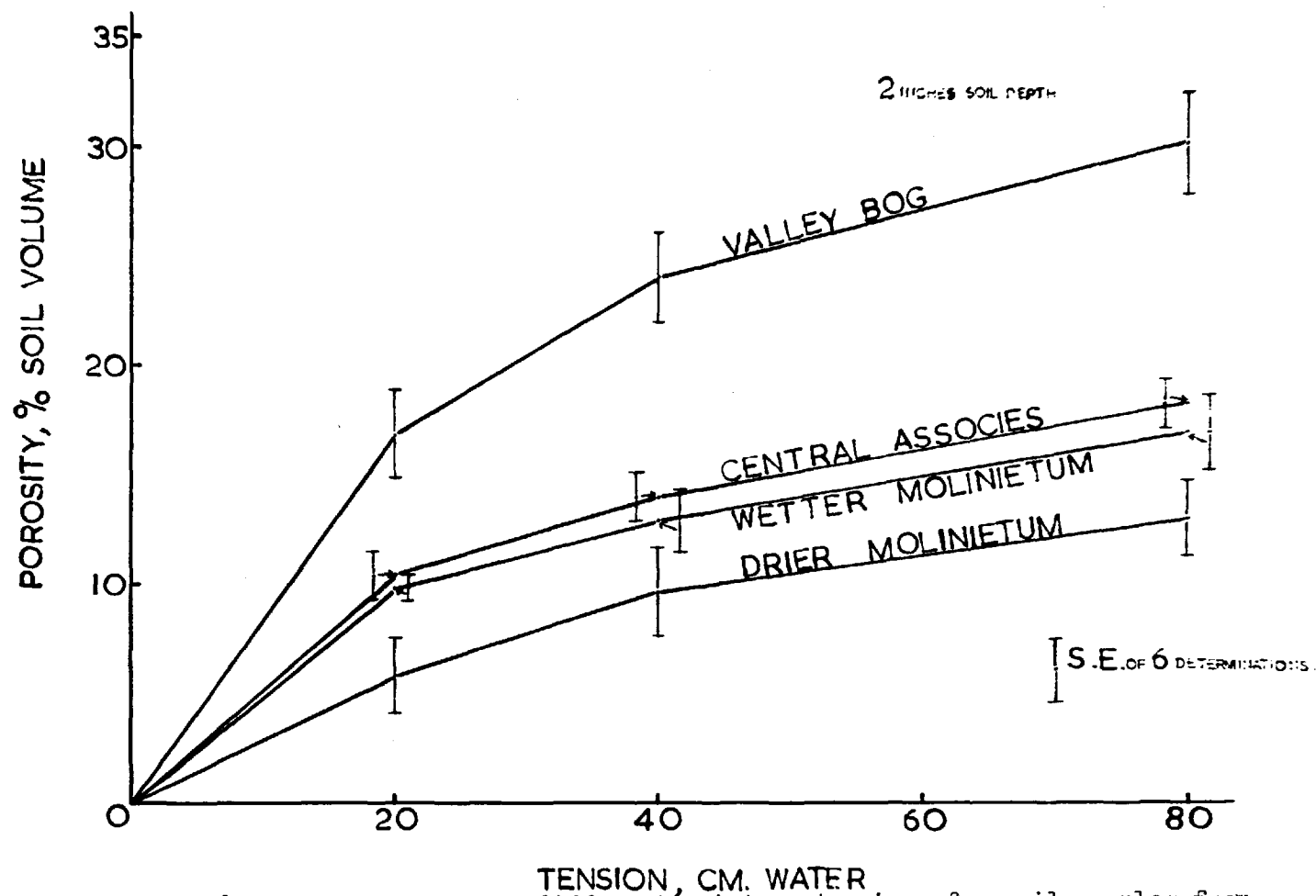


Fig. 18. Mean porosity at different moisture-tensions for soil samples from depth of 2 inches.

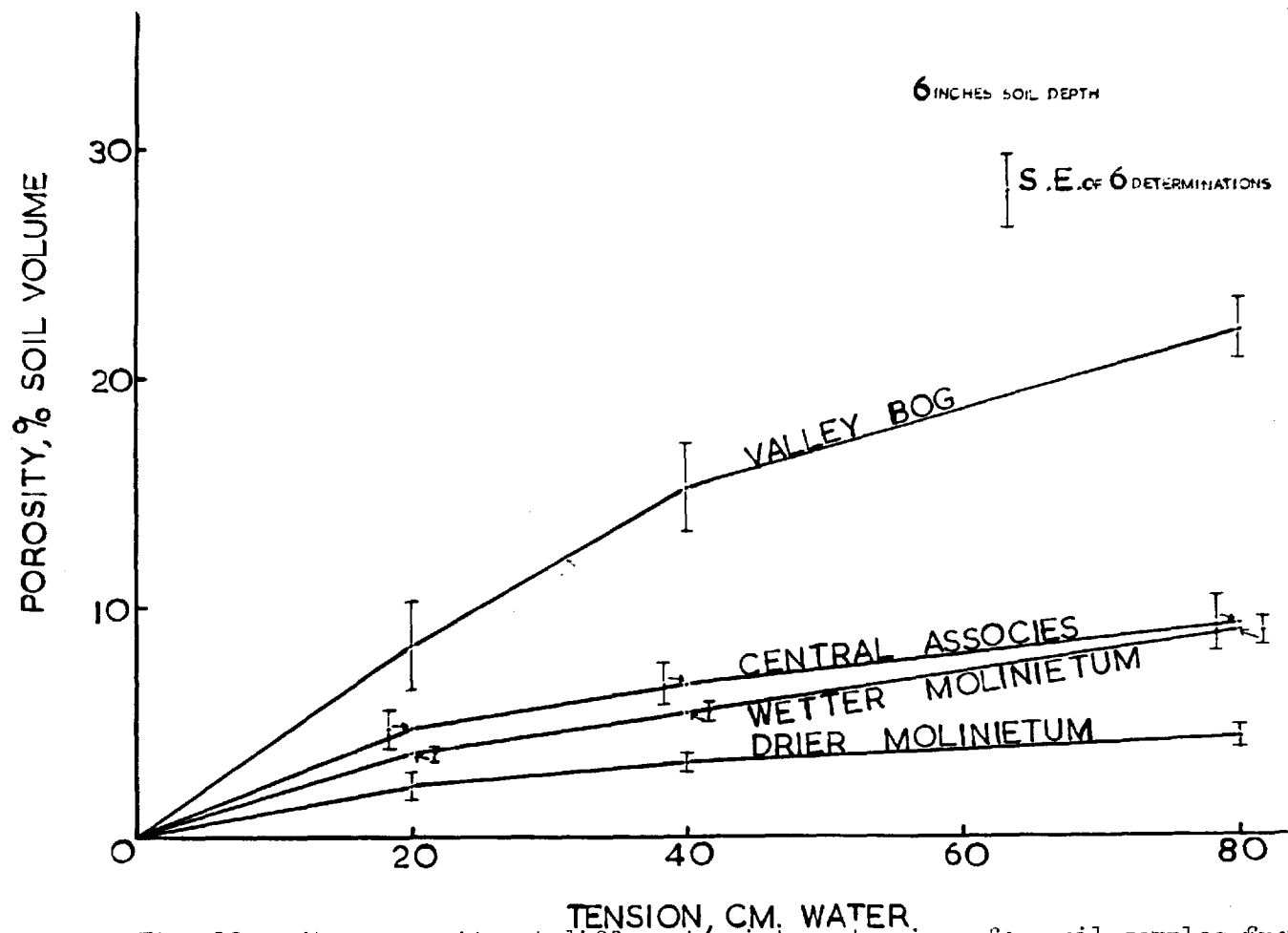


Fig. 19. Mean porosity at different moisture-tensions for soil samples from depth of 6 inches.

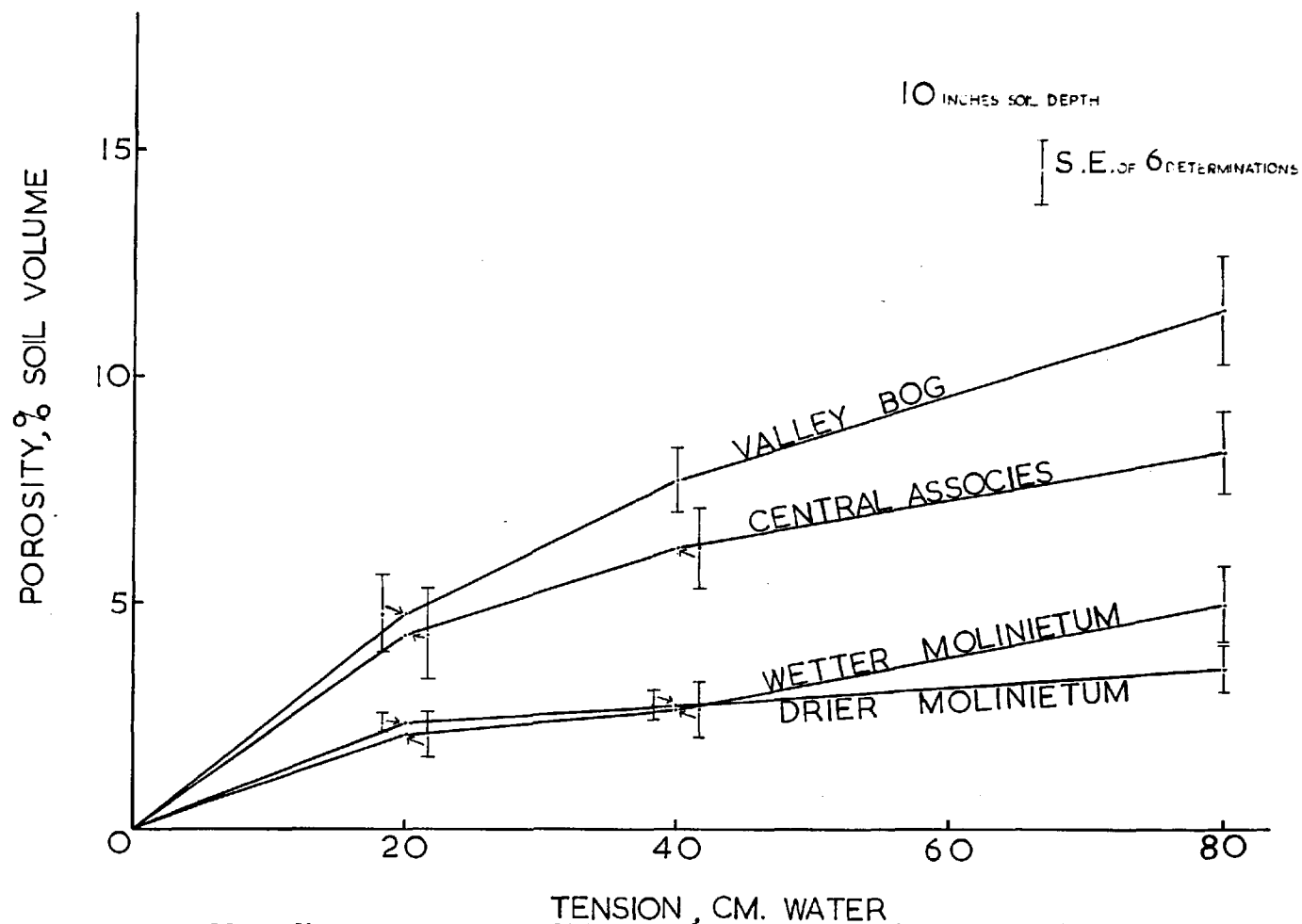


Fig. 20. Mean porosity at different moisture-tensions for soil samples from depth of 10 inches.

and the wetter *Molinietum* soils at these depths had intermediate values between these two extremes and were significantly different from both of them but they did not differ significantly between themselves. At 10 inches soil depth, the Valley-bog soil had significantly ($P = 0.05$) higher porosity than the Central associates and these two sites differed highly significantly ($P = 0.001$) from the wetter and the drier *Molinietum* which did not differ significantly between themselves.

The bulk density values given in Table 33 serve a useful guide to the differences in the porosities of soils.

Soil shrinkage:

The retention of soil samples within the metal cylinders made it easy to observe the shrinkage of soil sample, if any, as they were drained at different tensions. Only very approximate values of this shrinkage were obtained for the two replicate sets of samples taken in September, 1964.

Only the Valley-bog soils underwent a perceptible shrinkage (both vertical and horizontal). Table 34 shows the volume of soil at different tensions expressed as a percent of the initial volume of the soil. The amount of shrinkage increased

TABLE 34. VOLUME OF SOIL AT SHRINKAGE,
% ORIGINAL SOIL VOLUME

		Valley-bog soil.		
		Means of two replicates only.		
		Tension, cm.		
		20	40	80
Soil depth, inches	2	93.13	91.63	89.64
	6	96.27	89.91	88.95
	10	97.28	94.78	92.33

with an increase in the tension applied. Soil sampled from a

depth of 10 inches showed the least shrinkage, as compared with the other two soil depths (see also Table 33 for bulk densities of these soils).

The loss of soil volume at a particular tension was much less than the loss of water at that tension (see Figs.18-20) which showed that in the soil there were pores which allowed air to enter as water was withdrawn from them (c.f. Lauritzen and Stewart, 1941; Lauritzen, 1948; Stirk, 1954). This type of shrinkage has been termed "structural" shrinkage (Stirk, 1954).

The porosities for the Valley-bog soils shown in Figs.18-20 should be reduced by the percent diminution in volume due to shrinkage. This correction has not been applied because of the limited nature of shrinkage studies.

Effect of entrapped air on soil saturation and subsequent porosity determinations:

In the present work the soil samples were saturated by capillarity. Keeping in view the findings of Christiansen (1944) on the incomplete saturation of soils due to entrapped air and the resultant low soil permeability, the idea suggested itself that in the present studies the soils may not have been completely saturated to start with, perhaps due to the presence of entrapped air. To test this possibility 4 replicate soil samples were collected from each of the Valley-bog and the drier Molinietum from a depth of 2 inches. Two replicates of each soil were saturated by capillarity and the other two were saturated under a reduced pressure of 15 cm. of Hg. The pressure was reduced slowly over a period of half an hour in order to prevent any swelling of the soils which would have been attendant upon its sudden reduction in one step. The samples were left to saturate for 48 hours. A suction-plate method, modified by Reynolds (1956), was used to apply different tensions. The total

volume of water removed at each tension represented the air-filled porosity of the soil at that tension. The porosity at 80 cm. tension, expressed as a percent of the soil volume, for the soils saturated by the two methods is given in Table 35.

TABLE 35 SHOWING POROSITY, % SOIL VOLUME,
 AT 80 cm. TENSION

Samples from 2 inches soil depth.

	<u>Replicate</u>	<u>Saturated under reduced pressure</u>	<u>Saturated by capillarity</u>
VALLEY- BOG	a,	34.55	28.13
		Mean = 34.31	Mean = 33.61
	b,	34.08	39.09
	a,	16.08	13.32
DRIER MOLINIETUM		Mean = 17.93	Mean = 14.63
	b,	19.79	15.94

The Valley-bog soil did not, on average, show any difference in the porosity of the soils saturated by the two methods though the results are too variable to be conclusive. In the drier Molinietum soil the mean porosity of the samples saturated by capillarity was less by 3.3% than those saturated under reduced pressure, i.e., those in which entrapped air had been removed. Because of the low replication and the high variability between the two replicates in a group, this point cannot be emphasized any further.

iii, Comparison of "micrometric" and "moisture-tension"

methods of porosity determination:

As the tension is increased water is drawn from successively finer and finer pores, and the size of the pores that will be emptied by any given tension is calculated from the

height-of-the-capillary-rise equation:

$$h = \frac{2\sigma}{rDg} \text{ (see Keen, 1931)}$$

where h = tension expressed in cm. of water with which the soil is in equilibrium,

σ = surface tension of water,

D = density of water,

g = acceleration due to gravity

and r = radius of the capillary tube,

which at 20°C. becomes

$$d = \frac{3000}{h}$$

where d is the diameter of the tube (pore) in microns.

If the pores in the soil were parallel-sided then the tension required to empty pores of given diameters observed in a transverse section, can be calculated. But if pore diameters are not continuous and larger cavities are connected with one another through smaller necks, the emptying of larger pores will be controlled by the higher tension needed to empty the smaller necks. From the data on which the frequency diagrams of pore sizes shown in Figs. 15-17 are based, it is possible to calculate the volume of air-filled porosity at given tensions, assuming that the pores observed in sections are parallel-sided. Comparison with the volumes of water removed at given tensions will then show how far the calculations made from pore diameters are in error. This comparison is made in Tables 36, 37 and 38.

In Tables 36, 37 and 38 the most striking result is that the volume of pores $> 150\mu$, determined by micrometry, in which roots are found (see p. 108), is three to five times as great as the volume of water removed at 20 cm. tension, a tension

COMPARISON OF MICROMETRIC AND MOISTURE-TENSION METHODS FOR THE DETERMINATION OF SOIL POROSITY (TABLES 36, 37 and 38.)

TABLE 36 2 INCHES SOIL DEPTH: POROSITY, VOLUME-PERCENTAGE, AT DIFFERENT MOISTURE-TENSIONS
ASSUMING A RELATIONSHIP BETWEEN TENSION AND PORE-DIAMETER.

$$(d = \frac{3000}{h} \quad d = \text{pore-diameter in } \mu. \quad h = \text{tension in cm. of water})$$

^o Mean of 5 transects. [Ⓢ] Mean of 6 samples. ± Not determined.

SITES

TENSION VALLEY-BOG CENTRAL ASSOCIATES WETTER MOLINIETUM DRIER MOLINIETUM
cm. water

	^o Micrometry [Ⓢ] Moisture-tension		Micrometry Moisture-tension		Micrometry Moisture-tension		Micrometry Moisture-tension		131
20 (>150μ)	44.42 ± 2.67	16.84 ± 2.06	49.79 ± 6.20	10.43 ± 1.11	56.38 ± 3.83	9.79 ± 0.63	24.46 ± 3.13	5.75 ± 1.78	
40 (75 - 150 μ)	5.61 ± 0.62	7.05 ± 1.04	4.21 ± 0.70	3.45 ± 0.57	3.98 ± 1.16	3.03 ± 0.27	6.05 ± 0.92	2.39 ± 0.38	
80 (35 - 75 μ)	3.36 ± 0.49	5.97 ± 0.96	2.50 ± 0.50	4.16 ± 0.45	1.46 ± 0.60	5.09 ± 0.52	3.52 ± 0.20	4.72 ± 0.68	
>80 (<35 μ)	1.20 ± 0.16	± -	1.68 ± 0.26	-	1.41 ± 0.29	-	1.83 ± 0.28	-	

TABLE 37

6 INCHES SOIL DEPTH:

POROSITY, VOLUME-PERCENTAGE, AT DIFFERENT MOISTURE-
TENSIONS ASSUMING A RELATIONSHIP BETWEEN TENSION
AND PORE-DIAMETER.

$$(d = \frac{3000}{h} \quad d = \text{pore-diameter in } \mu. \quad h = \text{tension in cm. water})$$

^o Mean of 5 transects.^h Mean of 6 samples.

± Not determined.

SITESTENSION,
cm. water

VALLEY-BOG

CENTRAL ASSOCIES

WETTER MOLINIETUM

DRIER MOLINIETUM

^o Micrometry^h Moisture-
tension

Micrometry

Moisture-
tension

Micrometry

Moisture-
tensionMicrometry Moisture-
tension

132

20 (>150 μ)	29.76 ± 4.51	8.34 ± 1.88	22.26 ± 2.91	4.66 ± 0.83	26.87 ± 2.38	3.58 ± 0.33	25.70 ± 2.47	2.19 ± 0.56
40 (75 - 150 μ)	5.02 ± 0.75	6.81 ± 0.93	6.39 ± 0.90	1.96 ± 0.36	9.38 ± 0.74	1.84 ± 0.45	4.74 ± 0.90	1.00 ± 0.31
80 (35 - 75 μ)	2.71 ± 0.58	6.68 ± 1.17	3.97 ± 0.35	2.59 ± 0.26	7.55 ± 0.49	3.45 ± 0.25	3.65 ± 0.28	1.08 ± 0.08
>80 (<35 μ)	1.34 ± 0.13	± -	1.85 ± 0.36	-	3.88 ± 0.64	-	1.91 ± 0.11	-

TABLE 38

10 INCHES SOIL DEPTH:POROSITY, VOLUME-PERCENTAGE, AT DIFFERENT MOISTURE-TENSIONS
ASSUMING A RELATIONSHIP BETWEEN TENSION AND PORE-DIAMETER. $(d = \frac{3000}{h} \text{ where } d = \text{pore-diameter in } \mu. \text{ } h = \text{tension in cm. water}).$ ^o Mean of 5 transects.^b Mean of 6 samples. $\pm$ Not determined.SITES

TENSION, cm. water	VALLEY-BOG		CENTRAL ASSOCIES		WETTER MOLINIETUM		DRIER MOLINIETUM	
	^o Micrometry	^b Moisture-tension	Micrometry	Moisture-tension	Micrometry	Moisture-tension	Micrometry	Moisture-tension
20 (>150 μ)	25.15 $\pm$ 1.64	4.75 $\pm$ 0.86	24.71 $\pm$ 2.50	4.34 $\pm$ 0.99	7.71 $\pm$ 1.29	2.12 $\pm$ 0.49	20.81 $\pm$ 1.78	2.36 $\pm$ 0.24
40 (75 - 150 μ)	3.50 $\pm$ 0.37	2.94 $\pm$ 0.49	9.74 $\pm$ 0.61	1.83 $\pm$ 0.49	8.84 $\pm$ 1.38	0.53 $\pm$ 0.31	4.25 $\pm$ 0.56	0.39 $\pm$ 0.12
80. (35 - 75 μ)	2.70 $\pm$ 0.22	3.75 $\pm$ 0.57	6.52 $\pm$ 0.48	2.14 $\pm$ 0.16	9.04 $\pm$ 0.67	2.29 $\pm$.22	3.00 $\pm$ 0.61	0.81 $\pm$ 0.24
>80. (<35 μ)	1.42 $\pm$ 0.18	$\pm$ -	3.02 $\pm$ 0.28	-	4.78 $\pm$ 0.31	-	1.38 $\pm$ 0.40	-

which should break air-water interfaces down to $150\ \mu$ diameter. This means that this tension has left a high proportion of these pores still filled with water, presumably because they are connected with one another by much smaller necks. (Hysteresis is related to this type of structure, Haines, 1930; Nelson and Baver, 1940). There is a closer correspondence between the volume of pores of diameters between 150 and $35\ \mu$ and the volume of water removed by the appropriate tension, but there is still an indication that the removal of water is less than expected from the micrometric method.

Detailed study of a vertical section of soil:

The results obtained from a detailed study of a vertical section of a soil sample obtained from a depth of 2 inches from the wetter Molinietum will help in explaining the discrepancy found between the results of the "micrometric" and "moisture-tension" methods. Using an "epidiascope" the section was projected on to a large sheet of paper supported on a board. A faithful tracing of a randomly selected part of the section was made on this paper. A rectangular area was delimited in the middle of the drawing. Assuming the relationship between tension and pore diameter (d in $\mu = \frac{3000}{h}$) and assuming the upper part of the rectangle as representing initially an air-water interface in a fully saturated sample, the expected response of the sample to drainage was investigated by the following method.

Imagining a 20 cm. tension to be applied, pores were traced from the top surface and throughout the rectangle along all paths which were at no point restricted by diameters less than $150\ \mu$. This continuous pore system is represented by appropriate symbol in Fig. 21. Imagining the tension then raised to 40 and 80 cm., the further system of pores which would be emptied by the respective tensions was followed and marked.

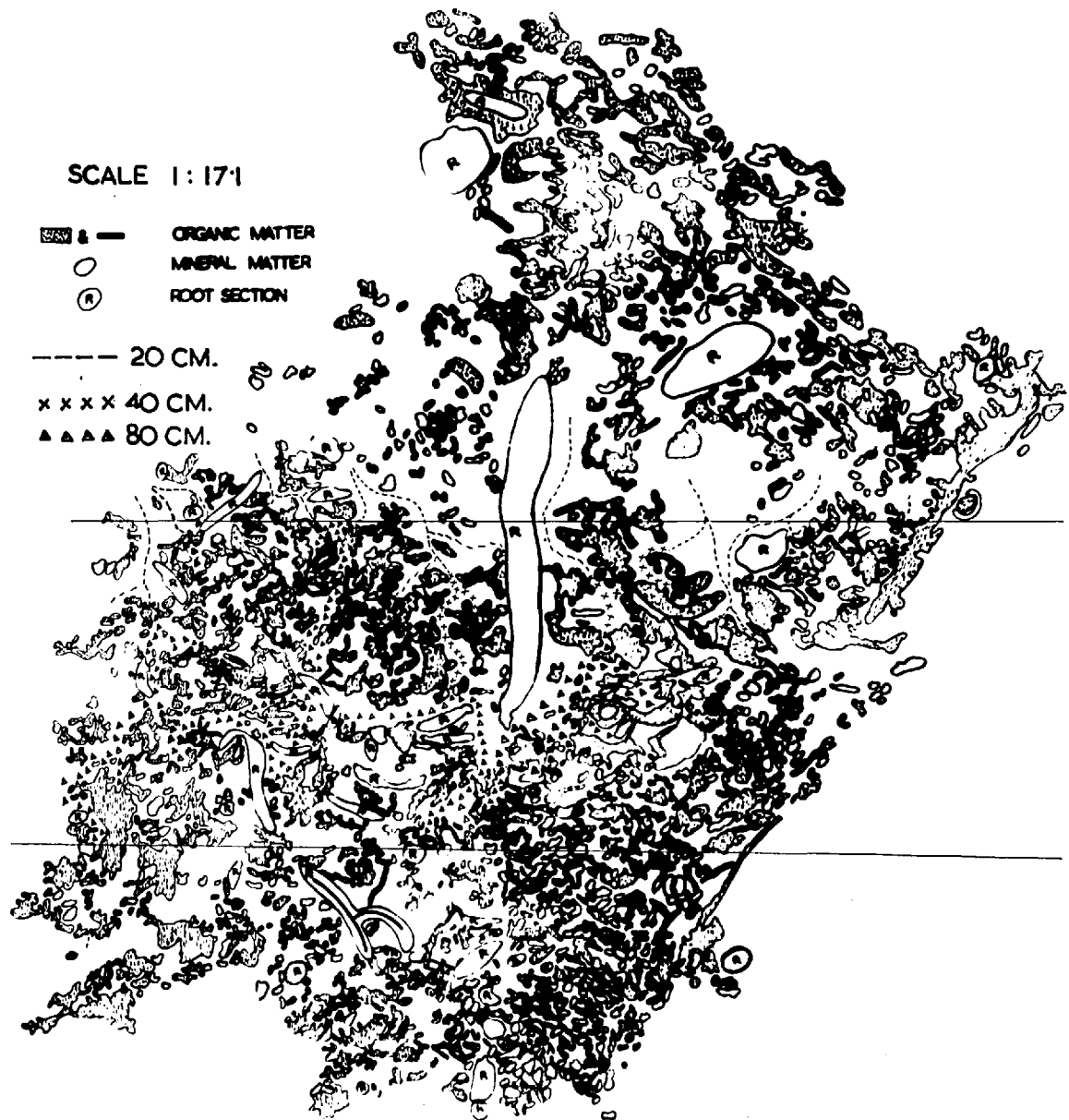


Fig. 21. A part of a vertical section of soil sample from a depth of 2 inches from the wetter Molinietum.

Ten transects were then laid at random in this area and the intercepts of the pores were measured along these transects. This gave a measure of the total porosity and its distribution between different pore sizes (volume-percentage). Then the volume-percentages of pores which were to drain at different tensions (20, 40 and 80 cm.) were measured along these transects. This porosity was termed the air-filled porosity. The results for the "total porosity" and "air-filled porosity" of these ten transects are given in Table 39.

TABLE 39 TOTAL POROSITY AND AIR-FILLED POROSITY (VOLUME-PERCENTAGES) AT DIFFERENT TENSIONS AS CALCULATED FROM THE VERTICAL SECTION OF SOIL ASSUMING A RELATIONSHIP BETWEEN TENSION AND PORE-DIAMETER.

soil from 2 inches depth from the wetter Molinietum.

<u>TENSION, cm.</u>	<u>TOTAL POROSITY</u>	<u>AIR-FILLED POROSITY</u>
20 (> 150 μ)	44.57 $\pm$ 3.00	6.05 $\pm$ 3.90
40 (75 - 150 μ)	4.00 $\pm$ 0.70	1.64 $\pm$ 1.00
80 (35 - 75 μ)	2.11 $\pm$ 0.10	13.61 $\pm$ 3.49
> 80 (< 35 μ)	0.42 $\pm$ 0.13	$\equiv$ _____

$\equiv$ Not calculated.

Calculated data show discrepancies between total and air-filled porosities similar to those found by direct drainage (see Tables 36-38) and the discrepancy is especially marked in the pores exceeding 150 μ . Furthermore, the calculated air-filled porosity is

very similar to that revealed by moisture-tension method. Closer agreement could hardly be expected in view of the fact that these calculations have been made on a single small section whereas the results obtained by the moisture-tension method are based on 6 replicate soil samples.

The large number of pores of smaller diameter in the soils of the Central associates and the wetter Moliniatum as compared to the Valley-bog soil, and their enormous increase at lower soil depths in the Central associates and the wetter Moliniatum (see pore-size distribution, Figs.15-17) explains the significant differences in the "air-filled porosity" determined by the moisture-tension method (Figs.18-20), though the total porosity values for these sites, as determined by micrometry, were, more or less, of the same magnitude (see Table 31, p.115). The higher proportions of smaller pores will themselves require high tensions to drain and will interfere with the drainage of large pores, the effect of which will be that the drainage of many large pores will be restricted because they empty only through smaller pores.

A search through the literature reveals only one investigation, by Swanson and Peterson (1942), in which the "micrometric" method of porosity determination has been compared with the commonly used methods, including the moisture-tension. Swanson and Peterson (1942) found a reasonable agreement between the two methods ("micrometric" and "moisture-tension" methods). However, they made their micrometric studies on sections of soils which had been air-dried prior to impregnation with "kollolith." The air-drying of the soil can be expected to have led to some distortion and disturbance of the soil fabric. Moreover, they did not include pores of more than 1200 μ diameter in their measurements. This would have excluded a considerable number of pores, root-channels and worm-channels ("non-capillary porosity") in the soil which would have increased the "micrometric" measure-

ments to a considerable extent.

d. Water-table depths and air-filled porosity in the field:

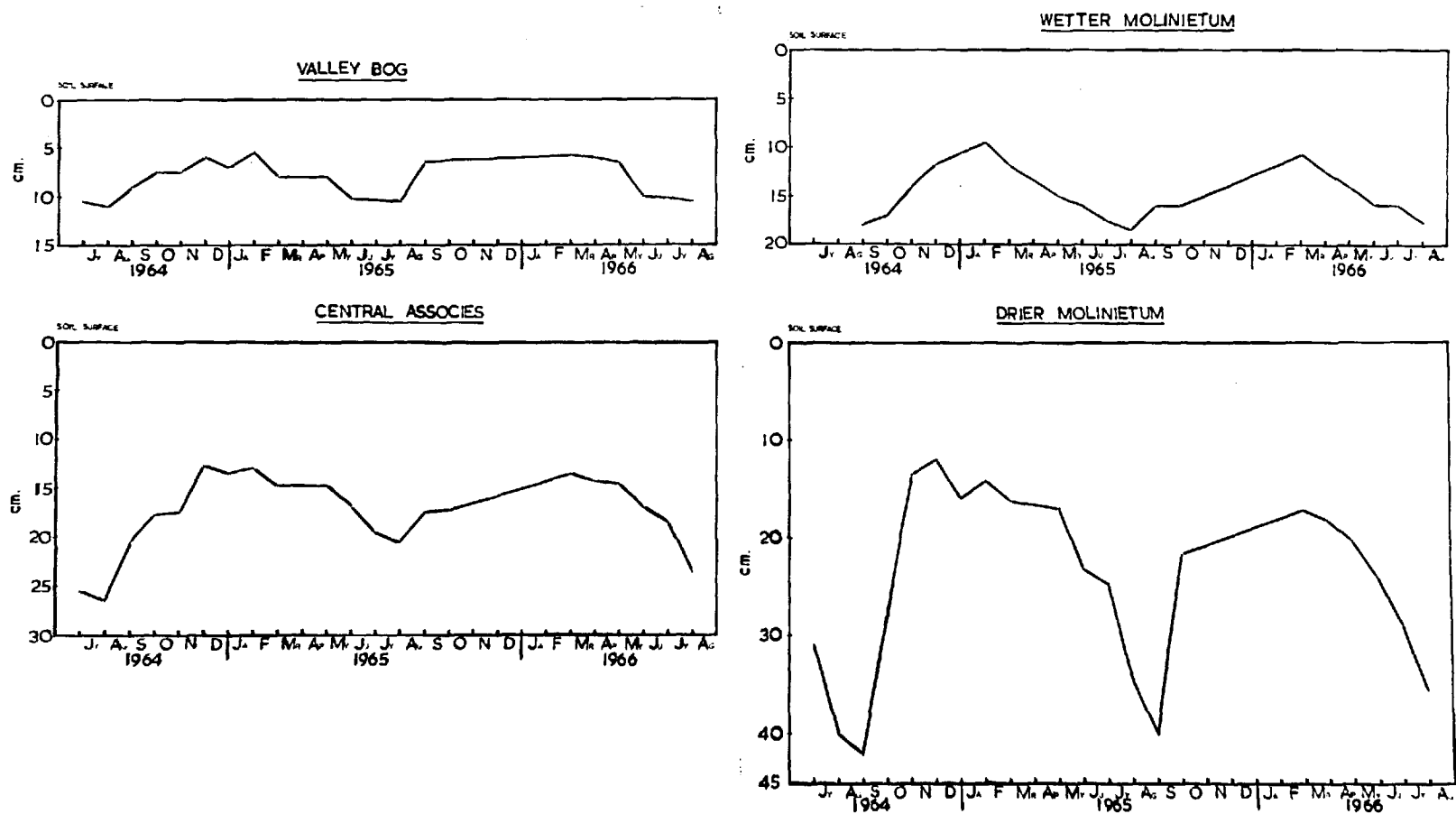
The depths of water-table in the four sites were recorded from July, 1964 to August, 1966 in order to follow the seasonal fluctuations. An auger hole was bored outside each of the experimental enclosures (see Section III, p.61), making a total of 6 in the Valley-bog, Central associates and drier Molinietum, and at 6 random positions, close to the transect (Section IV) in the wetter Molinietum. The depth of the holes was that which was considered sufficient to reach below the water-table at all seasons of the year. The data of Rutter (1955) and Loach (1964) for the water-table depths in the sites at Bramshill, provided a useful guide. A wooden stake was sunk level with the ground at a point on the rim of each hole, and water-table depths, which were recorded every month during summer and less frequently during winter were determined with reference to the top of this stake. The water-table measurements for each hole in a site were allowed for the variation in the position of the hole as measured with reference to the general soil surface and the top of the stake. The water-table depths shown in Fig. 22 are those below the general soil surface in each site. Each point in Fig. 22 is a mean of 6 replicates.

The mean water-table depths in the four sites in summer and winter are given in Table 40. They were calculated as means of the depths recorded from April to October, and November to March, respectively.

TABLE 40 MEAN DEPTHS OF WATER-TABLE IN SUMMER AND WINTER

	cm.			
	Valley-bog	Central associates	Wetter Molinietum	Drier Molinietum
Summer	8.7	18.5	16.2	28.6
Winter	6.6	14.2	11.3	14.8
Difference	2.1	4.3	4.9	13.8

Fig. 22. Water-table depths in the four sites.



The Valley-bog site showed the highest water-table and for a brief period only in summer (June - August) the water-table was slightly below 10 cm. of the soil surface. The water-table depth varied very little during the year, the difference between mean summer and winter water-table depths was only 2.1 cm. Water-table in the drier Moliniatum, during most of the summer was considerably below 30 cm., and showed a large seasonal variation, the difference between mean summer and winter water-table depths was 13.8 cm. The Central associates and the wetter Moliniatum sites fell between these two extremes, and the water-table in the wetter Moliniatum was higher than in the Central associates.

The studies of soil porosity reported above showed that the Valley-bog soil is most porous (see Figs.18-20, pp.124-26) but this advantage is reduced by its permanently high water-table so that the total volume of air-filled porosity above the water-table is relatively small. Of the four sites, the drier Moliniatum soil is least porous, but because of the deep water-table it may gain an advantage through the development of high tensions resulting in greater air-filled pore space above the water-table. Table 41 shows the air-filled porosity (calculated from Figs.18-20, pp.124-6) at different soil depths corresponding to the tensions resulting from the respective mean summer water-table depths.

From the calculated air-filled porosity, the rates of diffusion

TABLE 41 AIR-FILLED POROSITY AND GASEOUS DIFFUSION RATES AT DIFFERENT SOIL DEPTHS CORRESPONDING TO MEAN SUMMER WATER-TABLE DEPTHS.

Air-filled porosity - Calculated from Figs.18-20, % soil volume.				
Gaseous diffusion rates - Calculated from $D/D_0 = 0.6 S$ (Van Bavel, 1952)				
Soil depth inches	Valley-bog	Central associates	Wetter Moliniatum	Drier Moliniatum
air-filled				
porosity	3.2	6.8	5.4	6.4
D/D ₀	0.019	0.040	0.032	0.038

Soil depth, inches		<u>Valley-bog</u>	<u>Central associates</u>	<u>Wetter Molinietum</u>	<u>Drier Molinietum</u>
6	air-filled porosity	0	0.8	0.4	1.4
	D/Do	0	0.005	0.002	0.008
10	air-filled porosity	0	0	0	0.7
	D/Do	0	0	0	0.004

of gases through these soils was calculated by using the relation

$$\frac{D}{D_o} = 0.6 S \text{ (Van Bavel, 1952)}$$

where D = coefficient of diffusion through soil

D_o = coefficient of diffusion in air

S = air-filled porosity

The results are given in Table 41. The drier Molinietum soils showed higher air-filled porosity and consequently, higher values for the rates of diffusion of gases as compared to the other three sites. Of the latter, the Valley-bog showed lowest values for these measures.

Air-filled porosity values, even for the drier Molinietum soil from a depth of 2 inches, are low and Baver (1956) quotes Kopecky that artificial drainage is necessary if the air-filled porosity is below 10%.

e, General conclusions:

The main points that emerge from the present study are: a, that the "moisture-tension" method gives a measure of the air-filled porosity as distinct from the "micrometric" method which provides information on the frequency distribution of pore diameters but cannot be readily used to assess the

tension required to drain the particular pore sizes, and
 b) that at a particular tension all the pores that are expected to drain at that tension, on the basis of the generally accepted relationship between tension and pore diameter, will not be air-filled (drained). Only a proportion of these pores will be air-filled and the remainder will be water-filled. Especially of the pores of diameters greater than 150μ only 1/3rd to 1/5th will be air-filled at 20 cm. tension. Even at 80 cm. tension the total volume of water removed ("moisture-tension" method) does not, in any sample, equal the volume of pores exceeding 150μ (Tables 36 - 38). It must be concluded that these pores are mostly water-filled when the tension is no greater than 20 cm., and that many of them remain water-filled even at much higher tensions.

The question arises as to whether, within the pores exceeding 150μ in diameter, the roots tend to select those which are drained, or that they grow also in water-filled pores. In the case of Molinia 15 - 20%^{*} of the pores exceeding 150μ in diameter contained roots and it seemed probable that a high proportion of these roots were in water-filled pore spaces, at least, in the surface soil of the Valley-bog site and at lower depths on all the sites (compare the data for air-filled porosity, Table 41, p. 140, with the volume of pores exceeding 150μ as revealed by micrometry, Tables 36-38, pp. 131-3). No such data could be obtained for the roots of Erica (see footnote). One-third of the entire root system of this species was at the surface and the amount decreased with depth (see root distribution studies, Section II, Fig. 2, p. 35), and it was possible that

*Calculated from the total number of pores and the numbers of pores which contained roots, as revealed by the studies of 5 transects from each soil section. In the case of Erica no such calculations could be made because very few pores containing roots of this species were found along these transects. This had necessitated the thorough studies of sections to select the pores which contained roots, in order to relate the root distribution to pore sizes (see p. 103).

they developed mainly in air-filled spaces but no precise information on this point could be obtained from these studies. However, it could be expected that in the Valley-bog, at least, a large proportion of the roots at 2 inches and all the roots at lower depths were in water-filled pores (see air-filled porosities corresponding to mean summer water-table depth, Table 41, p. 140).

VI. WATER CULTURE EXPERIMENTS

NUTRIENTS AND ERICA TETRALIX

Experiment described in Section III showed that Erica was extremely sensitive to the application of nutrients in the field. To investigate the response further, the experiments described below were carried out.

Source of plants:

Seeds of Erica germinate easily at room temperature within two weeks of sowing, but the growth of seedlings is extremely slow. In an experiment lasting approximately 9 months, Bannister (1964) found a mean height of 23.7 mm. of the above-ground parts of a seedling and a mean dry weight of 2.5 mg./seedling. In view of this a large number of two to three years old plants were collected from the field and were used in the experiments described below.

Erica plants were collected on 10th August, 1965 from a wet-heath near Lightwater, Surrey. They were transplanted in sand in large metal trays and were watered with tap water.

a, Experiment I: Growth in nutrient solutions of different concentrations:

Plants were grown in plastic boxes in nutrient solutions of five different concentrations: 2 normal, 1 normal, 1/2 normal, 1/4 normal and 1/8 normal. There were four replicates and 7 plants per box. The pH of the solution was 4.0.

The normal nutrient solution used had the following composition:

<u>Nutrient element</u>	<u>Source</u>	<u>ppm. of element</u>
N	$\text{NH}_4 \text{ NO}_3$	50
P+K	$\text{KH}_2 \text{ PO}_4 + \text{KCl}$	2 P + 22K
Ca	$\text{Ca SO}_4 2\text{H}_2\text{O}$	20
Mg	$\text{Mg SO}_4 7\text{H}_2\text{O}$	6
Fe	Fe - EDTA	1.0
Mn	$\text{Mn SO}_4 4\text{H}_2\text{O}$	0.5
Cu	$\text{Cu SO}_4 5\text{H}_2\text{O}$	0.01
B	$\text{H}_3 \text{ BO}_3$	0.14

<u>Nutrient element</u>	<u>Source</u>	<u>ppm. of element</u>
Zn	Zn SO ₄ 7H ₂ O	0.04
Mo	(NH ₄) ₂ MoO ₇ 24 H ₂ O	0.005

This solution was weak compared with such solutions as Rothamsted and Long Ashton solution (Hewitt, 1966). Loach (1964) used this solution in his water culture experiments and found it suitable for the growth of Molinia.

Plastic boxes of 600 ml. capacity with perforated lids were used. The lids did not fit the boxes but rested on small pieces of polystyrene fixed to the inside of the boxes with "Durofix." The boxes and lids were painted black. Erica plants which had established themselves in sand culture, were washed free from sand in tap water and dried between soft tissue paper. Using a torsion balance, the fresh weight of each plant was taken to the nearest mg. The roots of the plants were carefully pushed through the holes in the lids of the boxes to reach the solution. The boxes were placed at random in the greenhouse on 17th August, 1965. The plants were allowed to grow for two weeks and were given additional artificial illumination during a 12-hour day. The position of the boxes was re-randomised twice a week. Solutions were renewed three times a week. The frequent changes of the solutions and the loose fitting lids with large number of holes in them, did not warrant an artificial aeration of the solutions.

At the end of the experiment, the plants which had dead spring shoots were counted as dead. The living plants were dried between soft tissue paper and using the torsion balance, the fresh weight of each plant was determined.

Results:

Table 42 shows the mortality as a percent of the number planted in a treatment. There was a marked reduction

in mortality with a reduction in the concentration of the nutrient

TABLE 42 %-AGE MORTALITY OF ERICA

<u>2 normal</u>	<u>1 normal</u>	<u>1/2 normal</u>	<u>1/4 normal</u>	<u>1/8 normal</u>
53.6	42.9	28.6	17.9	3.6

solution used, and the plants grown in 1/8 normal solution suffered the least mortality.

Because of the initial variation in plant weights, the increase in the fresh weight of each plant was expressed as a percent of the initial fresh weight. The analysis of variance was performed on the square root transformed data (Cochran, 1938). Table 43 shows the mean percentage increase in fresh weight.

TABLE 43 MEAN INCREASE IN FRESH WEIGHT,
% INITIAL FRESH WEIGHT

<u>2 normal</u>	<u>1 normal</u>	<u>1/2 normal</u>	<u>1/4 normal</u>	<u>1/8 normal</u>
15.8(3.96)	16.9(4.09)	16.6(4.05)	16.8(4.17)	25.8(5.08)

L.s.d. (P = 0.01) = (0.70)

Unbracketed figures = Original data, means of 4 replicates.

Bracketed figures = Square root transformed data.

1/8 normal solution proved to be the best for the growth of the species, and the growth was significantly higher (P = 0.01) at this concentration compared with the rest of the treatments (concentrations) which did not differ significantly amongst themselves.

There was a white deposit on the leaves of most of the plants growing in solutions of all concentrations, but this deposit seemed to be rather less on the leaves of the plants grown in 1/8 normal solution. The white substance appeared in small amounts along the whole of the leaf though it seemed to be rather more abundant near the leaf margin.

b, Experiment II: Growth in complete nutrient solutions with N, P, K and Ca at different levels:

The object of this experiment was to find out whether any of the particular nutrients N, P, K or Ca was toxic to Erica when provided in solution at a concentration higher than in 1/8 normal solution. A combination of N, P and K had proved toxic when applied in the field at the usual rate of fertiliser application (Section III). Ca was included because very low levels of this cation are present in acid soils.

N, P, K and Ca were factorily combined at two levels, viz., 1 normal and 1/8 normal, giving 16 treatments. 16 treatments were:

N P K Ca	N/8 P K Ca	N P/8 K Ca	N P K/8 Ca
N P K Ca/8	N/8 P/8 K Ca	N/8 P K/8 Ca	N/8 P K Ca/8
N P/8 K/8 Ca	N P/8 K Ca/8	N P K/8 Ca/8	N/8 P/8 K/8 Ca
N/8 P/8 K Ca/8	N/8 P K/8 Ca/8	N P/8 K/8 Ca/8	N/8 P/8 K/8 Ca/8

The number of treatments was then doubled by using K and Ca as either chlorides or sulphates. Nutrients other than N, P, K and Ca were used at 1/8 normal concentration. Sources of nutrients were the same as given on pp. 144-5 except in the case of K and Ca, as explained above. Where K and Ca were used as their Cl salts, the concentration of Cl in normal solution (K Ca) was 53 ppm. and in 1/8 normal solution (K/8 Ca/8) it was 6.6 ppm. Where they were used as SO_4 salts, the corresponding concentrations of SO_4 were 97.8 ppm. and 34.9 ppm., respectively. There were two replicate boxes in each treatment and 5 plants per box. The pH of the solution was 4.0.

Erica plants which were growing in sand culture (see above) were used in this experiment. (From 5th September, 1965 onwards the sand culture was watered with 1/8 normal solution). Each of the five plants in a box was weighed on a torsion balance to determine its fresh weight.

The plants were grown in a heated green-house for two weeks from 7th to 21st November, 1965. They were artificially illuminated and were given a 14-hour day. The position of the boxes was randomised twice a week. Solutions were changed three times a week. At the end of the experiment the fresh weight of each plant was determined using a torsion balance.

Results:

There was no mortality in N/8 P/8 K/8 Ca/8 treatment. In N P KCa and N P K Ca/8 treatments the mortality was 30 - 40 % and in the rest of the treatments it ranged from 20 to 30% of the number planted.

An analysis of variance was performed on the data for the increase in fresh weight expressed as a percent of the initial fresh weight. There was no significant effect of changing the anions, Cl and SO₄, on the growth of Erica. N, P, K and Ca each had a highly significant ($P = 0.001$) depressing effect when supplied at 1 normal concentration. There were significant first order interactions for N X K ($P = 0.001$), P X K ($P = 0.001$) and K X Ca ($P = 0.05$). N X P, N X Ca and P X Ca were not significant, but there were some highly significant ($P = 0.001$) higher order interactions. Tables 44 and 45 show the main effects of N, P, K and Ca, and their interactions, respectively.

TABLE 44 MAIN EFFECTS OF N, P, K and Ca.

Means for increase in fresh weight, % initial fresh weight.

Nitrogen		Phosphorus		Potassium		Calcium	
N/8	N	P/8	P	K/8	K	Ca/8	Ca
31.3	22.7	31.0	23.0	30.3	23.7	28.8	25.2
L. s. d. (P = 0.001) = 2.0							

TABLE 45 FIRST ORDER INTERACTIONS: N X K, P X K, K X Ca

Means for increase in fresh weight, % initial fresh wt.

	Nitrogen		Phosphorus		Calcium	
	N/8	N	P/8	P	Ca/8	Ca
K/8	33.1	27.4	32.8	27.7	33.0	27.5
Potassium						
K	29.6	17.9	29.0	18.4	24.6	22.8

L. s. d interaction means ($P = 0.001$) = 2.8L. s. d interaction means ($P = 0.05$) = 1.6

N, P, K and Ca when used at 1 normal concentration significantly reduced the growth of Erica as compared to when they were used at 1/8 normal concentration. The depressing effect of high concentration of K was increased in the presence of high concentrations of N and P, but was reduced in the presence of high concentration of Ca, though the last effect was not very significant.

White deposits on the leaves, like those seen in the first experiment, were also seen in this experiment and were present in varying amounts in all the treatments. These were presumably guttated substances. Kramer (1959) has suggested that such methods are used by plants to deal with excess supply of nutrients and that calcium often features in the contents of guttated liquids. Hackett (1962) found white deposits on the leaves of Deschampsia flexuosa when grown in culture solution and suggested that the cation supply was the factor concerned. In the present work the appearance of these deposits could not be related to any particular nutrient or concentration. The absence of such deposits on the leaves in the field and their appearance on the leaves of plants grown in culture solution may be due to a greater amount of available nutrients in the solution. This phenomenon needs a closer examination.

c, Conductivity measurements:

The total concentration of mineral elements in a solution can be roughly estimated from a measurement of the specific conductivity of the solution. Specific conductivities of the solutions were measured by using the "Dionic" conductivity meter which was very kindly loaned by Dr. P. J. Newbould of the University College, London, to whom grateful acknowledgement is made here. The specific conductivity values (abbreviated as K_{corr}) represent the total conductivity corrected for temperature at 20° C, less that due to hydrogen ions (cf. Sjörs, 1950) and are thus an estimate of the total electrolytes in solution apart from hydrogen ions. They are expressed as mhos per cm. $\times 10^6$ (reciprocal megohms).

An approximate measure of the osmotic pressure, in atmospheres, of the solution was obtained from conductivity measurements by using the relation $\text{O.P.} = 0.036 \times K$ mhos per cm. $\times 10^6$; given in U.S. Department of Agriculture Handbook 60, edited by Richard (1954).

Two replicate samples of soil water were obtained from a depth of two inches (soil water sampling probes - Section IV) from the Valley-bog and the drier Molinietum, the two most contrasted sites. Specific conductivity and pH measurements and the approximate values for osmotic pressure of these samples are given in Table 46 along with those of the different solutions used in Experiment I. The values for these measures obtained by other workers in wet-heaths (approximate values for osmotic pressure have been calculated by the writer), with Erica tetralix as the abundant species in them, are also included for the sake of comparison.

Table 46 shows that the specific conductivity values of the soil water samples from the Valley-bog correspond very closely with that of 1/8 normal solution used in Experiment I. Low values of specific conductivity of water from the Valley-bog

TABLE 46 pH, SPECIFIC CONDUCTIVITY AND OSMOTIC PRESSURE VALUES

	<u>Sample</u>	<u>pH</u>	<u>K_{corr}</u>	<u>O.P., atm.</u>
Nutrient solutions	Expt. I			
	2 normal	4.0	850	0.30
	1 normal	4.0	460	0.16
	$\frac{1}{2}$ normal	4.0	275	0.09
	1/4 normal	4.0	155	0.05
	1/8 normal	4.0	85	0.03
Soil water:				
	Valley-bog:			
	i,	4.80	96	0.03
	ii,	4.75	91	0.03
	Drier Molinietum:			
	i,	4.15	134	0.04
	ii,	4.10	128	0.04
	Wet-heath:			
	(Newbould and Gorham, 1956)	4.61	101	0.03
	(Clymo, 1960)	4.0	94	0.03

site agreed with those obtained by other workers in wet-heaths (Newbould and Gorham, 1956; Clymo, 1960).

Table 47 shows the increase in fresh weight, percent of initial fresh weight (means for Cl and SO₄ treatments) along with the specific conductivity values (means for Cl and SO₄ treatments) of the solutions used in Experiment II. If the treatments N PK Ca, N P K Ca/8 and N/8 P/8 K/8 Ca/8 are excluded, there is no discernible relationship with the conductivity of the solution, and consequently, the effects of particular elements cannot be related to their effects on the conductivity of the solution.

TABLE 47 MEAN VALUES OF SPECIFIC CONDUCTIVITY AND INCREASE IN FRESH WEIGHT, % INITIAL FRESH WEIGHT.

Treatment	K _{corr}	Increase in fresh wt., % initial fresh weight
N P K Ca	430	5.3
N P/8 K Ca	388	26.9
N P/8 K/8 Ca	353	24.9
N P K/8 Ca	330	25.3
N P K Ca/8	318	13.3
N P/8 K Ca/8	312	26.1
N P K/8 Ca/8	245	29.0
N P/8 K/8 Ca/8	240	30.2
N/8 P/8 K Ca	218	32.9
N/8 P K Ca	209	26.3
N/8 P/8 K/8 Ca	185	31.0
N/8 P K/8 Ca	148	28.8
N/8 P K Ca/8	142	28.8
N/8 P/8 K Ca/8	133	30.3
N/8 P K/8 Ca/8	100	27.5
N/8 P/8 K/8 Ca/8	85	45.2

The work of Sjörns (1950), Gorham (1950), Gorham and Pearsall (1956) and Newbould and Gorham (1956) has shown that the effect of mineral waters on the vegetation is not necessarily or intimately related to the specific conductivity values.

d, Discussion:

It is usually assumed that much of the nutrients taken up by plants are absorbed from the soil solution and that as nutrients are removed from the liquid phase of the soil complex they are replenished by their release from the solid phase.

In order to relate the results of these water culture experiments with Erica to the amount of nutrients present in the soil water, the analyses of soil water from the sites studied would have been very instructive. But such analyses were not possible in the present work. However, Clymo (1960 and 1962) gives analyses of soil water samples collected from a wet-heath in which Erica tetralix and Calluna vulgaris were abundant and Molinia caerulea showed a frequent distribution. Table 48 shows the concentration of different elements, expressed in ppm., which have been calculated from his data. The concentrations of these elements present in 1 normal and 1/8 normal solutions used in the experiments described here, and those used in Long Ashton Solution (Hewitt, 1966) are also included in this Table.

It can be seen from Table 48 that the concentrations of the different elements in 1/8 normal solution agree fairly well with those present in the water samples from a wet-heath.

TABLE 48 CONCENTRATIONS OF IONS IN SOIL WATER FROM A WET-HEATH AND IN CULTURE SOLUTIONS.

	ppm.						
	N	P	K	Ca	Mg	Fe	Mn
Wet-heath (Clymo, 1960 and 1962)	4.8	0.16	1.8	7.0	0.93	1.26	0.27
1/8 normal solution (Present work)	6.25	0.25	2.7	2.5	0.75	0.12	0.06
1 normal solution (Present work)	50	2.0	22	20	6	1.0	0.50
Long Ashton Solution (Hewitt, 1966)	140-284	41	130- 295	134- 300	36	2.8 or 5.6	0.55

These experiments showed that Erica was very sensitive to a high concentration of nutrients, and had a very low nutrient requirement. The harmful effect of concentrations of nutrients higher than those present in 1/8 normal solution could hardly be ascribed to osmotic phenomena, because even the 2 normal solution had an osmotic pressure of only a fraction of an atmosphere (= 0.30 atm., Table 46 , p. 151).

In the field Erica grew very well in the drier Molinietum when Molinia had been removed and the growth was significantly better than in the Valley-bog (Section III). The drier Molinietum had more nutrients than the Valley-bog (Section III), and its specific conductivity was somewhat higher than that of the 1/8 normal culture solution in which Erica grew best. Specific conductivity is not, however, a very close measure of the concentration of nutrients and the possibility that the concentration of nutrients in the soil of the drier Molinietum was supra-optimal for Erica could only be satisfactorily tested by the addition of further nutrients in low concentration. Though the addition of nutrients in higher concentration had shown that the Valley-bog was sub-optimal in nutrition for Molinia, it seems unlikely that it was so for Erica. In view of this the better growth of Erica planted in the soil of the drier Molinietum and its poor growth in the Valley-bog and the poor performance by the established plants in this site (Sections II and III) may be due to some factor other than the low nutrient content of the Valley-bog. Aeration was the obvious choice as a factor of which the effects should be investigated and experiments were performed to study the effects of different levels of O_2 and CO_2 and H_2S on the growth of the two species, Erica and Molinia.

It may be pointed out here that the experiments described did not establish the optimum levels of the various

elements for the growth of Erica, and that they may be lower than the lowest concentrations employed. The effects of elements such as Al and Mn, which may act as micro-nutrients or toxins according to concentration and which are found in high concentrations in acid soils, have not been tested and their importance must not be under-rated. The value of these experiments lies in their help to explain the high mortality of Erica obtained as a result of the application of nutrients in the field, compared with Molinia which grew better when nutrients were applied. Moreover, the results of these experiments provided a suitable culture solution ($1/8$ normal) for growing Erica in aeration experiments described hereafter.

Effects of different gas concentrations
on the growth of Molinia and Erica:

Studies of root distribution of the species in relation to the sizes of the soil pores (Section V) showed that the roots of both Molinia and Erica were present in large soil pores ($> 150\mu$). Depending on the sites, in these wet soils a majority of these large pores were occupied by water for most of the year. Therefore, the concentrations of the gases dissolved in soil water were of direct importance for the growth of the species in the field. Experiments described below were carried out to study the effects of different concentrations of gases, covering the range of concentrations found in the soil water samples (Section IV), on the growth of both Molinia and Erica in water culture.

a, i, The attainment and maintenance of different mixtures of gases (Oxygen, carbon dioxide and hydrogen sulphide):

Four concentrations of oxygen were factorially combined with either four concentrations of carbon dioxide (1st series of experiments: O_2 and CO_2 - 16 treatments), or four concentrations of hydrogen sulphide (11nd series of experiments: O_2 and H_2S - 16 treatments). There were four replicates in each treatment. The concentrations used were:

O_2 concentrations	= 0, 2, 4 and 8 per cent by volume in pure nitrogen.
CO_2 "	= 2, 4, 8 and 16 " " " " " "
H_2S "	= 0.06, 0.12, " " " " " "
	0.24 and 0.48

Gas cylinders containing pure and water-free oxygen, carbon dioxide, hydrogen sulphide and nitrogen were used as sources of these gases. Mixtures of gases of different composition were obtained by using

Plaster of Paris resistances[ⓧ] to the flow of gases (Kohl, 1961). Each resistance was calibrated by measuring the amount of water displaced by the gas flowing through it in a unit time from a source under constant pressure. The rates of flow through resistances used for oxygen, carbon dioxide and nitrogen supplies, were measured by using the respective gases. In view of the high solubility of hydrogen sulphide in water, the rates of flow through resistance used for this gas were measured by using oxygen, as its molecular weight (32) is close to that of hydrogen sulphide (34).

The required mixtures of gases were obtained by passing the gases under a constant pressure (5 lbs/□") from gas cylinders through suitable combinations of resistances. An example will illustrate the method. For a gas mixture containing 4% O₂ and 4% CO₂ a line from the O₂ supply was led through a resistance to give a rate of flow of 4 ml./minute, and another from the CO₂ supply was led through a similar resistance to give the same rate of flow. These two streams were mixed in a wide-bore (7mm. i.d.) PVC tubing and were led into a stream of N₂ with a rate of flow of 92 ml./minute obtained by a suitable resistance. This mixture of gases (4% O₂, 4% CO₂ and 92% N₂) was passed into a glass manifold with four outlets. Plaster of Paris resistances were then used to reduce the rate of flow through each outlet to 5 ml./minute (7.2 l./day). These resistances were then connected by wide-bore (7 mm.i.d.) PVC tubing to the culture solutions to be aerated by this particular gas mixture (Fig.23).

ⓧ

Making of plaster of Paris resistances: Glass tubes of different diameters were plugged lightly at one end with a little cotton wool. They were filled with plaster of Paris of varying consistency and then stood on end till the plaster hardened and dried. After drying them in a desiccator for two days the tubes were cut into different lengths. Depending on the length and diameter of the tubes and the density of plaster of Paris contained in them, different resistances could be obtained.

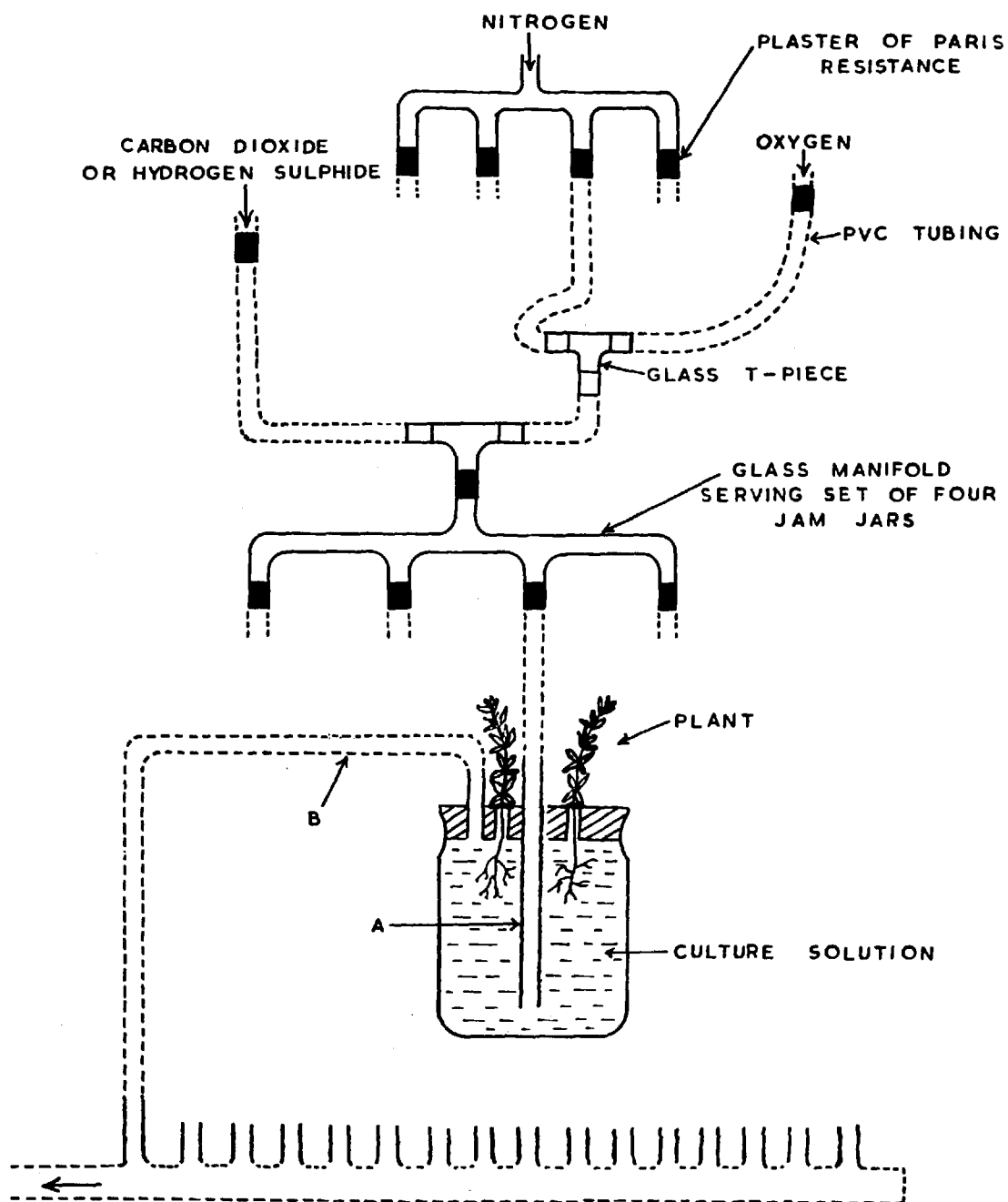


Fig. 23. Simplified version of the arrangement for the supply of gas mixtures to water cultures in the aeration experiments.

This arrangement provided a useful method of supplying the culture solutions with definite quantities of a gas of a definite composition. The rate of flow through plaster of Paris resistances was found to be constant under varying greenhouse conditions.

In order to check that the planned concentrations were actually being obtained, samples of the gas mixtures of O_2 and CO_2 were taken and analysed, and in the case of H_2S , samples of culture solutions were analysed (Section IV). Table 49 shows the results for the analysis of O_2 and CO_2 in some of the gas mixtures. For all practical purposes, the observed values

TABLE 49 CONCENTRATIONS OF O_2 AND CO_2 IN THE GAS MIXTURES
Per cent by volume.

<u>EXPECTED</u>		<u>OBSERVED</u>	
<u>O_2</u>	<u>CO_2</u>	<u>O_2</u>	<u>CO_2</u>
0	2.0	0	1.91
0	8.0	0	7.88
0	16.0	0	16.29
2.0	2.0	1.92	2.13
2.0	16.0	1.92	15.69
4.0	2.0	4.19	1.88
4.0	8.0	4.28	8.23
8.0	2.0	8.18	2.19
8.0	16.0	7.86	15.85

of O_2 and CO_2 concentrations in a treatment agreed with the expected values in that treatment.

Results for the concentrations of H_2S found in culture solutions are given in Table 50. Only H_2S concentration designated as 0.48% was higher than the expected, otherwise the remaining concentrations were the same as expected.

TABLE 50 CONCENTRATION OF H₂S IN DIFFERENT TREATMENTS

<u>EXPECTED</u>		<u>OBSERVED</u>
% by volume in air	ppm.	= % by volume in air at solution temp. = 22°C.
0.06	2.7	0.07
0.06	2.5	0.06
0.06	2.7	0.07
0.06	2.7	0.07
0.12	4.5	0.12
0.12	4.6	0.12
0.12	4.7	0.13
0.12	4.5	0.12
0.24	9.2	0.24
0.24	10.4	0.27
0.24	10.2	0.26
0.24	9.1	0.24
0.48	20.0	0.53
0.48	20.1	0.53
0.48	19.6	0.52
0.48	18.9	0.50

ii, Containers for growing plants:

The plants were grown in culture solution contained in "jam" jars (360 ml. capacity). Each jar had a tight fitting cork with two large holes. One of these holes had a glass tube (A) of 6 mm. inner diameter which ended 1 - 2 cm. above the bottom of the jar. The other hole supported a glass tube of the same diameter as A, which just reached the under-side of the cork (B).

There were 4 small holes in the cork, two on either side of the large ones supporting the glass tubes A and B, in which the experimental plants were planted (Fig. 23). Roots of a plant were carefully pushed through a hole making sure that they were touching the solution. These small holes were then sealed with plasticine. Plasticine proved an excellent sealing material and did not crush the plants. All the cracks in the system were sealed with molten paraffin wax of a high melting point (65°C).

The gas mixture was introduced into the jar through A where it came out in small bubbles into the solution. The slow but continuous supply of the gas mixture kept the solution supplied with different gases at the desired concentrations without causing any unnecessary turbulence in the solution. The gases escaped through B. The outlet tubes (B) from the four replicates of a treatment were led into an exhaust manifold and were then passed into a large tube (3 cm. i.d.) in which the exhaust gases from all the treatments were led out of the greenhouse.

Each jar was enclosed in a jacket of black paper to prevent light from reaching the culture solution. The position of four replicates in a treatment was randomised as far as possible, though the lengths of tubes and manifolds imposed some restriction on randomisation.

There was a "control" set of four replicates in which the solutions were supplied with ordinary air from a cylinder at 5 ml./minute.

iii, Composition of the culture solutions used:

In experiments with Molinia the plants were grown in "1 normal" culture solution, and in those with Erica the plants were grown in "1/8 normal" culture solution. The composition of the normal culture solution is given on pp.144-45. The plants were grown at a pH of 4.0.

b, Growth of the species at different concentrations of O_2 and CO_2 :

i, Molinia caerulea:

Source of plants: Seeds collected in October, 1964 from the drier Molinietum were stored over the winter in a refrigerator. In March, 1965 they were spread on the surface of a rigid glass-fibre matting resting on a frame of cork which was kept floating as a raft above 1 normal solution contained in baking trays painted with a pure bitumastic paint (Hackett, 1962). The trays were kept covered with glass and were kept in a heated green-house. The first appearance of shoots took from 14 - 21 days. These seedlings were grown in 1 normal nutrient solution for two months and the solution was changed every ten days. The floating raft arrangement encouraged most of the roots to grow vertically into the solution.

Seedlings of a more or less uniform size were selected. It was very easy to separate the roots from the glass-fibre. In order to see the initial variability amongst seedlings, 18 batches of four seedlings each were dried in the oven at $80^{\circ}C$ and the collective dry weight of the four seedlings in a batch was determined. The dry weight per seedling showed very little variation (4.01 ± 0.11 mg. per seedling).

After drying them between soft tissue paper, fresh weight of a batch of four seedlings going into a jar was determined on a torsion balance. The seedlings were planted in all the jars within 72 hours. The gas supplies were started on 23rd May, 1965 and the experiment lasted fifteen days (23rd May to 6th June, 1965).

Results:

Before taking the plants out of a jar it was noted whether the roots were in solution or not. Because of the small size of the root system, it was found that in a few cases

the roots were not in the solution. This was particularly true in all the replicates of two treatments: i, 2% CO₂, 2% O₂ and ii, 2% CO₂, 4% O₂. As a result, the four treatments for different concentrations of O₂ with 2% CO₂ were not included in the statistical analysis given below.

The pH of all the solutions, measured at the end of the experiment, ranged from 3.8 to 4.6.

The roots of the plants grown in solutions with 8 and 16% CO₂ and irrespective of the concentrations of O₂ (0, 2, 4 and 8%) had a few short branches while those grown in lower concentrations of CO₂ (2 and 4%) had a large number of long, white branches.

The plants from a jar were weighed together on a torsion balance for their final fresh weight. They were dried in the oven at 80°C. The final fresh weight was expressed as a percent of the initial fresh weight. The water content of the plants was expressed as a percent of their dry weight. The analysis of variance was performed on the log₁₀x transformed data (except dry wt. data) (Cochran, 1938) and the results are given in Tables 51, 52 and 53.

TABLE 51 MOLINIA: FINAL FRESH WEIGHT,
% INITIAL FRESH WEIGHT

		O ₂ concentration, %				Means for CO ₂
		0	2	4	8	
	2	295.6	-	-	306.5	
CO ₂	4	237.4(2.364)	303.5(2.477)	310.1(2.489)	286.1(2.453)	284.3 (2.446)
concen- tration, %	8	176.2(2.238)	216.6(2.320)	210.8(2.313)	233.8(2.367)	209.3 (2.310)
	16	113.4(2.053)	135.2(2.130)	147.0(2.167)	156.6(2.190)	138.0 (2.135)

Means
for O₂ 175.7(2.218) 218.4(2.309) 222.6(2.323) 225.5(2.337)

Control = 316.0 Un-bracketed figures = Means of four
(Air) replicates.

Bracketed figures = log₁₀x transformed data.
L.s.d. means for O₂ (P = 0.05) = (0.073) L.s.d. means for CO₂ (P = 0.001)
No significant O₂ × CO₂ interaction. = (0.1140)

TABLE 52 MOLINIA : FINAL DRY WEIGHT, mg.

		O ₂ concentration, %				Means for CO ₂
		0	2	4	8	
CO ₂ concentration, %	2	16.10	-	-	16.45	
	4	13.02	15.34	14.05	14.48	14.29
	8	10.85	13.35	12.90	11.58	12.17
	16	8.81	10.18	10.20	10.56	10.06
Means for O ₂		10.89	13.12	12.38	12.43	

Control (air) = 16.50

L. s. d. means for O₂ (P = 0.05) = 1.40

L. s. d. means for CO₂ (P = 0.05) = 1.38
(P = 0.001) = 2.16

No significant O₂ X CO₂ interaction.

TABLE 53 MOLINIA: WATER CONTENT, % DRY WEIGHT

		<u>O₂ concentration, %</u>				Means for CO ₂
		0	2	4	8	
	2	346.5	-	-	358.1	
CO ₂	4	317.9(2.497)	347.2(2.540)	370.9(2.569)	350.9(2.544)	346.7 (2.537)
concen- tration, %	8	314.4(2.491)	276.6(2.433)	260.7(2.403)	342.1(2.533)	298.4 (2.465)
	16	188.3(2.274)	205.7(2.313)	199.0(2.299)	236.4(2.372)	207.3 (2.314)

Means for

O₂ 273.5(2.421) 276.5(2.429) 276.8(2.423) 309.8(2.483)

Control (Air) = 369.1

L. s. d. means for CO₂ (P = 0.001) = (0.028)

Differences between O₂ concentrations, and O₂ X CO₂ interaction, not significant.

Un-bracketed figures = Means of four replicates.

Bracketed figures = log₁₀ x transformed data.

Tables 51, 52 and 53 show that an increase in CO₂ concentration resulted in highly significant decrease (P = 0.001) in growth (final fresh wt., % initial fresh wt. and final dry weight) and water content of the species. Reduction of O₂ from 8% to 2% did not significantly affect growth, but there was a significant reduction (P = 0.05) between 2% and 0% O₂. There was no

significant effect of O_2 on the water content though the water content of the plants grown at 8% O_2 was higher than of those grown in the remaining O_2 concentrations. There were no significant $O_2 \times CO_2$ interactions on growth or water content.

Though no statistical test could be made, growth and water content at 8% O_2 and 2% CO_2 , appeared not to differ from that in air.

ii. Erica tetralix:

Erica transplants grown for five weeks in sand culture watered with 1/8 normal solution (during the last two weeks) were used. The four plants for a jar were weighed individually on a torsion balance for their initial fresh weight. The plants were planted in all the jars within 72 hours. The gas supplies were started on 16th September, 1965 and the experiment lasted 15 days. The plants were grown under artificial illumination and were given a 14-hour day.

Results:

The roots of the plants grown at 2 and 4% CO_2 in the presence of O_2 and those of the "control" plants produced long, white lateral branches which penetrated deep into the solution and the shoots showed perceptible increases in length whereas those of the plants grown in the remaining treatments did not show any such responses.

The plants were weighed individually on a torsion balance, and Tables 54 and 55 show the results for final fresh weight, % initial fresh weight and water content, % dry weight, respectively.

There was a highly significant decrease in growth with increase in CO_2 concentration and at 8 and 16% CO_2 the plants lost in their initial weight and the weight at these concentrations did not differ significantly.

TABLE 54 ERICA: FINAL FRESH WEIGHT,
% INITIAL FRESH WEIGHT

		O ₂ concentration, %				Means for CO ₂
		0	2	4	8	
CO ₂ concen- tration, %	2	96.3(1.984)	109.2(2.037)	121.8(2.085)	121.9(2.086)	112.3 (2.048)
	4	96.2(1.983)	97.9(1.990)	118.2(2.072)	116.0(2.065)	107.0 (2.027)
	8	94.7(1.976)	95.4(1.980)	95.4(1.979)	96.7(1.985)	95.5 (1.980)
	16	90.8(1.958)	94.5(1.975)	95.1(1.978)	95.9(1.982)	94.0 (1.973)
Means for O ₂		94.5(1.975)	99.2(1.995)	107.6(2.028)	107.6(2.029)	

Control (Air) = 124.6

L.s.d. means for O₂ and CO₂ (P = 0.05) = (0.011)
(P = 0.001) = (0.020)

L.s.d. O₂ X CO₂ interaction means (P = 0.05) = (0.023)
(P = 0.001) = (0.040)

Un-bracketed figures = Means of four replicates.

Bracketed figures = log₁₀x transformed data.

TABLE 55 ERICA: WATER CONTENT, % DRY WEIGHT

		O ₂ concentration, %				Means for CO ₂
		0	2	4	8	
CO ₂ concentration, %	2	182.1(2.260)	209.2(2.315)	244.6(2.387)	250.3(2.397)	221.5 (2.340)
	4	171.2(2.232)	181.4(2.257)	227.0(2.355)	227.5(2.356)	201.8 (2.300)
	8	170.0(2.229)	173.8(2.240)	174.6(2.241)	173.6(2.238)	173.0 (2.237)
	16	165.4(2.218)	173.6(2.239)	174.1(2.240)	167.5(2.224)	170.1 (2.230)
Means for O ₂		172.2(2.235)	184.5(2.262)	205.0(2.306)	204.7(2.304)	

Control (Air) = 252.0

L.s.d. means for O₂ and CO₂ (P = 0.05) = (0.022)

(P = 0.001) = (0.040)

L.s.d. means for O₂ X CO₂ interaction (P = 0.05) = (0.045)

(P = 0.001) = (0.079)

Un-bracketed figures = Means of four replicates.

Bracketed figures = log₁₀ x transformed data.

An increase in O_2 concentration from 0 to 2% and 2 to 4% resulted in highly significant ($P = 0.001$) differences in growth but there was no significant difference in growth with an increase from 4 to 8%. There was a highly significant $O_2 \times CO_2$ interaction in that there was little response to increase in O_2 when CO_2 was high, or to decrease in CO_2 when O_2 was low.

The results for the water content of plants, % dry weight, followed the same pattern as those for final fresh weight, % initial fresh weight.

The growth and water content of the plants grown at 2% CO_2 plus 4 or 8% O_2 were nearly equal to those of the plants grown in solutions supplied with air (control).

c, Growth of the species at different concentrations of O_2 and H_2S :

i, Molinia caerulea: (Plate 12)

In the experiment on the growth of Molinia at different concentrations of O_2 and CO_2 , two months old seedlings were used. But because of the loss of two treatments due to the small size of the seedlings, it was decided to use plants of a larger size. Keeping in mind the different responses to be expected from seedlings and mature plants, reasonably small plants were collected in the beginning of June, 1966 from rides in Bramshill Forest. They were transplanted onto glass-fibre matting floating as a raft in metal trays containing 1 normal culture solution (p.162) of a pH of 4.0. The solution was changed frequently.

Plants which established themselves were selected for use in this experiment. Each of the four plants in a replicate jar was weighed individually on the torsion balance. The gas supplies were started on 22nd June, 1966 and the experiment lasted 15 days. The pH of the solutions was measured at the end of the experiment and ranged between 4.2 and 4.8.

Plate
12.



Results:

The roots of the plants grown at 0.24 and 0.48% H_2S produced only a very few, short branches which were of a creamish brown colour, whereas those of the plants in the rest of the treatments and the control produced a number of long, white branches.

Tables 56 and 57 show the results for the final fresh weight, % initial fresh weight and the water content, % dry weight, respectively.

TABLE 56 MOLINIA: FINAL FRESH WEIGHT, % INITIAL FRESH WEIGHT

		<u>O₂ concentration, %</u>				Means for H ₂ S
		0	2	4	8	
H ₂ S concentration, %	0.06	192.4(2.284)	205.9(2.313)	205.3(2.312)	202.4(2.305)	201.5 (2.303)
	0.12	168.5(2.226)	205.7(2.312)	193.5(2.286)	197.2(2.293)	191.2 (2.279)
	0.24	164.4(2.214)	165.1(2.220)	183.5(2.263)	193.1(2.284)	176.8 (2.245)
	0.48	124.6(2.094)	169.8(2.230)	176.1(2.243)	169.2(2.228)	159.9 (2.199)

Means for

O₂

162.5(2.204) 186.9(2.269) 189.6(2.276) 190.5(2.277)

Control = 208.0

L.s.d. means for O₂ and H₂S (P = 0.05) = (0.023)

(P = 0.001) = (0.040)

L.s.d. means for O₂ X H₂S interactions (P = 0.05) = (0.045)

(P = 0.01) = (0.060)

Un-bracketed figures = Means for four replicates.

Bracketed figures = log₁₀x transformed data.

TABLE 57

MOLINIA: WATER CONTENT, % DRY WEIGHT

		O ₂ concentration, %				Means for H ₂ S
		0	2	4	8	
H ₂ S concentration, %	0.06	333.4(2.522)	345.7(2.538)	336.0(2.526)	339.3(2.530)	338.6 (2.529)
	0.12	308.2(2.488)	314.7(2.497)	322.0(2.507)	319.2(2.503)	316.0 (2.499)
	0.24	292.9(2.465)	294.4(2.469)	310.5(2.491)	311.1(2.492)	302.2 (2.479)
	0.48	254.6(2.405)	293.6(2.467)	297.0(2.472)	291.7(2.465)	284.2 (2.452)
Means for O ₂		297.3(2.470)	312.1(2.493)	316.4(2.499)	315.3(2.498)	

Control = 358.9

L.s.d. means for O₂ (P = 0.05) = (0.021)

L.s.d. means for H₂S (P = 0.05) = (0.021)
(P = 0.001) = (0.038)

No significant O₂ X H₂S interaction.

Un-bracketed figures = Means for four replicates.

Bracketed figures = log₁₀ x transformed data.

There was a significant decrease in final fresh weight, % initial fresh weight, and water content, % dry weight, with an increase in the concentration of H₂S. The growth and water content in the absence of O₂ were significantly reduced compared with those in the presence of different concentrations of O₂ (2, 4 and 8%) which did not differ significantly from each other. There was a significant O₂ X H₂S interaction on the final fresh weight, % initial fresh weight but not on the water content of the plants.

The absolute figures for the growth of Molinia plants used in O_2 and CO_2 , and O_2 and H_2S experiments (e.g., compare the controls) differed greatly in spite of the fact that they were grown at more or less corresponding times, May - June and June - July, respectively in different years. This difference can be attributed to the differences in the age of the plants. In the case of " O_2 and CO_2 experiment" 2-month old seedlings were used, whereas in " O_2 and H_2S experiment" transplants had been used, and, in spite of the selection of small plants, they were much older than the seedlings.

ii Erica tetralix:

The source of plants and the setting up of the experiment were similar to the experiment with different concentrations of O_2 and CO_2 . Gas supplies were started on 25th March, 1966 and the experiment lasted until 8th April, 1966 (15 days). The plants were grown in a heated greenhouse under artificial illumination and were given a 14-hour day.

Results:

Tables 58 and 59 show the results for final fresh weight, % initial fresh weight, and water content, % dry weight, respectively.

TABLE 58. The species made some positive growth only at 0.06% H_2S and produced long, white lateral roots. Higher H_2S concentrations resulted in significant reductions in initial fresh weight. The growth in the presence of 8% O_2 was significantly better than in the rest of the O_2 treatments. There was no significant difference between 2 and 4% O_2 but they differed significantly from 0% O_2 . There was a significant $O_2 \times H_2S$ interaction in that the response to increasing O_2 concentration became less as the concentration of H_2S was increased.

TABLE 58 ERICA: FINAL FRESH WEIGHT,
% INITIAL FRESH WEIGHT

		O_2 concentration, %				Means for H_2S
		0	2	4	8	
H_2S concentration, %	0.06	98.0(1.991)	100.1(2.000)	101.4(2.006)	112.6(2.051)	103.0 (2.012)
	0.12	93.8(1.972)	98.5(1.993)	98.2(1.992)	103.2(2.013)	98.4 (1.993)
	0.24	92.5(1.966)	96.6(1.985)	97.4(1.988)	97.8(1.990)	96.0 (1.982)
	0.48	91.3(1.960)	93.3(1.969)	95.5(1.980)	95.8(1.981)	93.9 (1.973)

Means for
 O_2 93.9(1.972) 97.1(1.987) 98.1(1.991) 102.3(2.009)

Control = 113.9

L.s.d. means for O_2 and H_2S ($P = 0.05$) = (.008)
($P = 0.001$) = (0.014)

L.s.d. $O_2 \times H_2S$ interaction means ($P = 0.05$) = (0.016)
($P = 0.01$) = (0.021)

Un-bracketed figures = Means for four replicates.

Bracketed figures = $\log_{10}x$ transformed data.

TABLE 59

ERICA: WATER CONTENT, % DRY WEIGHT

		O ₂ concentration, %				Means for H ₂ S
		0	2	4	8	
H ₂ S concentration, %	0.06	141.5(2.150)	142.1(2.152)	137.9(2.139)	153.9(2.187)	143.8 (2.157)
	0.12	129.0(2.110)	128.7(2.109)	135.8(2.132)	139.2(2.143)	133.1 (2.123)
	0.24	124.3(2.092)	132.0(2.120)	139.3(2.143)	141.1(2.149)	134.1 (2.126)
	0.48	130.9(2.116)	131.2(2.116)	134.8(2.129)	137.9(2.139)	133.7 (2.125)
Means for O ₂		131.4(2.117)	133.5(2.124)	136.9(2.136)	143.0(2.154)	

Control = 156.2

L.s.d. means for O₂ and H₂S (P = 0.05) = (0.017)
 (P = 0.001) = (0.031)

Un-bracketed figures = Means for four replicates.

Bracketed figures = log₁₀x transformed data.

Water content in the presence of 0.06% H₂S was significantly higher than that in the presence of higher H₂S concentrations (0.12, 0.24 and 0.48%) and the latter did not differ amongst themselves. Water content at 8% O₂

was significantly higher than that in the rest of O_2 concentrations (0, 2 and 4%).

Water content and final fresh weight of plants at 0.06% H_2S and 8% O_2 were nearly equal to those of the plants grown in solutions supplied with air (control).

d, Discussion:

In experiments with Erica, transplants were used, whereas in the case of Molinia seedlings were used in one experiment (O_2 and CO_2) and transplants in the other (O_2 and H_2S). Moreover, the experiments were performed at different times. The results are, therefore, not completely comparable quantitatively, but the qualitative differences between the responses of the two species, at least in respect of fresh weight, are such that it can be concluded that Molinia is more tolerant of poor aeration than Erica.

In Molinia, both in the experiments with CO_2 and H_2S , reduction of O_2 down to 2% had little effect on growth and even at zero concentration of O_2 combined with the highest concentrations of CO_2 or H_2S employed, it gained in fresh weight during the course of the experiment. In Erica, on the other hand, reduction of O_2 below 8% caused a progressive reduction of growth and even at the lowest concentrations of CO_2 or H_2S , it lost fresh weight at zero concentration of O_2 . At high concentrations of CO_2 or H_2S it lost fresh weight whatever the concentration of O_2 , and hardly responded to increase in O_2 .

The growth of Molinia was progressively reduced by increase of either CO_2 or H_2S , but the highest concentrations of these gases still permitted some growth even in the absence of oxygen. In Erica, on the contrary, increase in CO_2 prevented growth unless the concentration of O_2 was kept above that of CO_2 and loss in fresh weight occurred with 8% and 16% CO_2 , whatever the level of O_2 ; increase of H_2S above 0.06%, the

lowest level employed, prevented growth in fresh weight and at the higher levels of H_2S , raising the level of O_2 had very little effect.

In these experiments the growth of both the species was measured in terms of final fresh weight only except in the case of first experiment with Molinia (O_2 and CO_2) where the data for the final dry weight are also given. In this experiment seedlings of a uniform size were used and there was very little variation in the initial dry weight (p.162). Because of the initial variability in the sizes of the transplants used in the rest of the experiments, no reliable measure of initial dry weight was available.

In the first experiment with Molinia (O_2 and CO_2) the changes in fresh weight were accompanied by changes in dry weight and the results for dry weight showed the same pattern as those for fresh weight. In view of this it can be safely accepted that in the second experiment with Molinia (O_2 and H_2S) the changes in fresh weight were also accompanied by changes in dry weight.

Erica showed a very slow relative growth rate of dry weight, viz., 3% per week, in the field conditions[‡], hence initial dry weights should have been known very accurately to show any treatment differences in dry weights at the end of these

[‡]Data given in Section III (p.71-2) was used for the calculation of the relative growth rate of dry weight of Erica in the field conditions.

$$\text{Relative growth rate (R)} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \quad (\text{Watson and Baptiste, 1938})$$

where W_2 = final dry weight (here mean for "without competition" sub-plots in the drier Molinietum = 113.6 mg)

W_1 = initial dry weight (here mean of 3 sizes: a, b and c = 19.5 mg.)

$t_2 - t_1$ = time interval over which the relative growth rate is measured (here 52 weeks: May, 1964 to October, 1964 and May, 1965 to October, 1965)

$R = 0.03 \text{ gm./gm./week}$ or 3 percent per week.

Relative growth rate of dry weight of Erica seedlings calculated from Bannister's (1964) data = $0.025 \text{ gm./gm./week}$ or 2.5 per cent per week.

experiments which lasted fifteen days only.²² In the best treatments the plants were growing visibly (production of roots and perceptible shoot growth) and this could be expected to be accompanied by a gain in dry weight. However, much of the fresh weight gain (or loss) was due to changes in water content, and in the absence of results from experiments of a much longer duration it has been assumed, with some reservation, that the responses of growth in fresh weight will be paralleled by responses in dry weight. (In the case of the response of Molinia to O_2 and CO_2 this has been shown to be the case).

Comparison with published work:

Oxygen:

The work of Cannon(1925), Vlamis and Davis (1943), Chang and Loomis (1945), Woodford and Gregory (1948) and Leyton and Rousseau (1958) suggests that the reduction of O_2 concentration in the rooting medium has little effect on respiration, salt uptake and growth of plants until it falls below 10%. In Erica the growth in the presence of 4 and 8% O_2 combined with 2 or 4% CO_2 was as good as in the plants grown in solution supplied with air (control). This suggests that this species can grow very satisfactorily in the presence of low levels of O_2 (~ 10%) so long as the concentration of CO_2 does not rise beyond a certain limit (p.169). Molinia was able to grow even in the absence of O_2 . A detailed discussion of this feature of Molinia appears in the next section (Section VII).

Carbon dioxide:

In both Molinia and Erica there was a highly significant decrease in growth and water content (uptake) with an increase in the concentration of CO_2 . High CO_2 levels have

²²The continuous supply of gases in these experiments set a limit on their duration. N_2 was used in very large quantities and each experiment needed 6 to 7 cylinders (165 cu. ft. each) of this gas.

been reported to inhibit root growth (Cannon, 1925; Girton, 1927; Vlamis and Davis, 1943; Erickson, 1946; Leonard and Pinckard, 1946; Porter and Thorne, 1955; Stolwijk and Thiman, 1957; and Webster, 1962b) and reduce the water absorption by plants due to the decreased permeability of the protoplasm (Kramer, 1938, 1940, 1945; Chang and Loomis, 1945; and Hagan, 1950) and the destruction of the semi-permeability of the cell membranes (Glinka and Reinhold, 1962).

An examination of previous work suggests that the influence of CO_2 is cumulative and depends largely on the duration of the treatment. Even saturated CO_2 solution when applied to roots for only a short time are tolerated and may produce a stimulating effect on plant growth (Geisler, 1963). The minimum levels of CO_2 cited in literature as producing toxic effects on plants vary greatly. The cumulative influence of CO_2 may explain the large differences found by Stolwijk and Thiman (1957) and Erickson (1946) in the CO_2 concentrations that inhibit root growth. CO_2 levels (1.5%) used by Stolwijk and Thiman (1957) over a period of ten days completely inhibited root growth whereas Erickson (1946) using six times greater CO_2 concentration (9.1%) over 24 hours found only reduced root growth.

In the present work, an increase in CO_2 concentration above 4% resulted in a highly significant decrease in growth and water content of Molinia and the growth at 16% CO_2 was nearly 1/5th of that at 4%. Webster (1962b) found that the rate of root extension in Molinia began to fall above a CO_2 concentration of 6% while shoot extension showed a similar fall only above 12% CO_2 . But the significant reductions in rates of root and shoot extension occurred only above 18% CO_2 . His experiments lasted only 24 hours and were carried out in the presence of 15 to 20% O_2 . The limited duration of his experiments prevents the acceptance of his results without reservations.

Several studies in which the gaseous composition of the rooting medium was carefully controlled indicate that CO_2 level must be as high as, or higher than, concurrent O_2 levels to produce a marked reduction in plant growth (Cannon, 1925; Leonard and Pinckard, 1946; Russell, 1952; Hammond, Allaway and Loomis, 1955; and Harris and Van Bavel, 1957). This was true in the present work in the case of Erica where at 2 and 4% CO_2 the plants made positive growth only when O_2 concentration was higher than CO_2 concentration. On the contrary, Molinia did not show any such effects and made some growth at all levels of CO_2 even in the absence of O_2 .

Hydrogen sulphide:

Okajima and Takagi(1953) have reported that H_2S inhibited respiration of roots and reduced the uptake of water and nutrients. H_2S is regarded as the inhibitor of the iron containing enzymes cytochrome oxidase, catalase and peroxidase (see Meyer, Anderson and Bohning, 1960).

A search through the literature did not reveal any work in which the study of the effects of H_2S on plant growth (alone or in combination with different O_2 concentrations) has been made over an extended period of time. In an experiment lasting 24 hours only, Webster(1962) found that the rate of root extension of Molinia showed a significant decrease at a H_2S concentration of 0.3%, whereas the rate of shoot extension showed a significant decrease at 0.5%. These H_2S concentrations at which Molinia showed significant decrease in growth were much higher than those found in the present work. This difference could be explained on the basis of a cumulative effect of H_2S , as was the case with CO_2 .

In Japan several investigations have been carried out on the effects of H_2S on the growth of rice (Mitsui, .

Aso and Kumazawa, 1951; Okajima and Takagi, 1953 and 1955; and Mori, 1955). In these experiments the effects of O_2 deficiency were not tested. In most of the cases the experiments lasted 48 hours and there was no rigid control on the supply of H_2S . The experiment started with 28.3 ppm. of sulphide and the concentration was reduced to about 5 ppm. at the end of the experiment (Okajima and Takagi, 1953 and 1955).

VII - GENERAL DISCUSSION AND CONCLUSIONS.

Three vascular species, Molinia caerulea, Erica tetralix and Calluna vulgaris are the dominant components of the wet-heath vegetation at Bramshill Forest. The relative proportions of these species vary considerably in different sites. In the past various studies have been directed towards relating the composition of the vegetation to the site factors, e.g., water-table depth and fluctuation (Rutter, 1955); gaseous composition of the ground-water (Webster, 1962 a,b) and soil nutrient status (Loach, 1964). The present work comprises field studies of soil conditions, with particular reference to aeration, in four contrasted sites which support different proportions of these species. Controlled experiments were designed to elucidate questions raised in the field studies. Most of the results have been discussed as they have appeared in different Sections (II - VI). In the present Section the information obtained from these studies has been brought together and some general points are discussed. The conditions of vegetation and environment on the four sites studied in the present work will first be summarised.

Valley-bog:

This is a soligenous valley-bog in which Erica is the dominant species and Molinia and Calluna are sparsely distributed. Planted tree species (Pinus contorta, Picea abies and Picea sitchensis) are growing very poorly. Sphagnum spp. have formed a mat of varying thickness (7.5 - 12.0 cm.) which is consolidated in places by soft, decaying Molinia shoot bases, 30 cm. of peat overlies a pale green, fine, quaking sand. The top 18 cm. of this peat layer consist of a loose, amorphous peat of a very low bulk density, followed by 12 cm. of dense,

greasy peat of a slightly higher bulk density. The mean summer water-table depth is about 9 cm. and it shows very little seasonal fluctuation. The soil has high porosity down the profile but this advantage is lost due to the permanently high water-table which results in very low air-filled porosity. Compared with the other sites, soil water samples obtained from different depths and air samples whenever available, contain very high concentrations of CO_2 and H_2S and very low concentrations of O_2 .

Loach (1964) has shown that the soil has a very low nutrient content.

Central associates:

Here Calluna and Molinia are the main component species of the ground flora and Erica is frequent. Planted tree species, though still poor by a forester's standards, are growing better than in the Valley-bog. Molinia forms small tussocks here (12 - 15 cm. high). Partly decomposed heather litter lies above about 13 cm. of black, dense, greasy humus with sand admixture. This layer has a low bulk density. Below this is pale brown-grey sand of high bulk density which shows orange mottling. This horizon extends to 30 cm. depth and below this lies green sand with a little orange mottling. The water-table is deeper than in the Valley-bog and it shows some seasonal fluctuation. The mean summer water-table depth is 18.5 cm. The total soil porosity is lower than in the Valley-bog. However, because of the deeper water-table the air-filled porosity in the field is higher than in the Valley-bog, but at greater depths it is lower than in the drier Molinietum. Samples of soil air and water obtained from different depths down the profile show lower concentrations of CO_2 and H_2S and higher concentrations of O_2 than in the Valley-bog.

Loach(1964) found that the amount of nutrients in the soil is intermediate between that of the Valley-bog and the drier Molinietum.

Wetter Molinietum:

Here Molinia is the dominant species and forms tall tussocks (30 - 40 cm. high). Calluna and Erica are present in smaller amounts than in the Central associates. Myrica gale grows here abundantly. Tree growth is better than in the Valley-bog and the Central associates. The soil profile shows about 15 cm. of dark brown, friable, organic loam of moderate bulk density, lying above a narrow zone (5 cm.) of light brown clayey sand of very high bulk density with orange mottling and orange streaks along root channels. Below this lies a fine sand with a few orange specks. The water-table is higher than in the Central associates (mean summer depth = 16.2 cm) and shows some seasonal fluctuation. The soil porosity is more or less the same as in the Central associates. As revealed by the analyses of soil air and soil water samples obtained from different depths, the soil is better aerated than the Valley-bog. No results are available for the nutrient content of the soil of this site since it was not included by Loach (1964) in his investigations.

Drier Molinietum:

In this site the ground flora consists mainly of Molinia which forms tussocks up to 25 cm. high. Calluna and Erica are restricted to the banks of a ditch. Formerly (Rutter, personal communication) this vegetation was fairly extensive in the area but the trees (planted in 1945) have grown so vigorously on it that the natural vegetation has been suppressed and the present study has been made on a ride which was left unplanted and has not been used as a thoroughfare. The soil profile is more or less the same as in the wetter Molinietum. The water-table is deep (mean summer depth = 28.6 cm.) in comparison with the other sites and shows a large amount of seasonal fluctuation.

The soil porosity is poorer as compared with the other sites, but due to the deeper water-table it gains an advantage through the development of higher tensions resulting in greater air-filled porosity. The analyses of soil air and water samples obtained from different depths show lowest concentration of CO_2 and H_2S and highest concentrations of O_2 as compared with the other sites.

Compared with the Valley-bog and the Central associates, this site is the most rich in nutrients (Loach, 1964), though still poor when compared with most agricultural and fertile forest soils.

In the light of the summaries of the soil conditions in the four sites, the results obtained for the growth of Molinia and Erica in these sites, will be discussed.

Field studies of growth and performance:

The performance of the main species in the existing vegetation was assessed by making different measurements (Section II, b, p.20) of a tiller in the case of Molinia and an erect branch in the case of Erica and Calluna. It was shown that the Valley-bog is very poor for the growth of the three species including Erica which is dominant here. Molinia performs best on the wetter and drier Molinieta. The Central associates and the wetter Molinietum do not show any significant differences for the growth of Erica and Calluna.

The growth of young plants of Molinia and Erica in the field in cleared plots, when grown with and without competition with each other and their response to the application of nutrients was studied only in three out of the four sites, viz., the Valley-bog, the Central associates and the drier Molinietum.

Erica, when grown in the absence of competition from Molinia, grows significantly better in the drier Molinietum and the Central associates than in the Valley-bog. The growth of Molinia is also significantly better in these sites. In the drier Molinietum Erica suffers a significant reduction in growth when grown in competition with Molinia, whereas no such reduction occurs in the Valley-bog apparently because of the poor growth of Molinia in this site. This provides an explanation for the dominance of Erica in the Valley-bog. Due to the poor performance of Molinia in this site, the species does not prove a strong competitor to Erica and the release from competition from Molinia enables Erica to dominate in the Valley-bog in spite of the fact that this site is not suitable for its best growth. The effects of competition from Calluna on the growth of Erica have not been tested in the present work. However, Bannister (1964) has shown that Erica tetralix is very sensitive to water loss and suggests that this puts the species at a competitive disadvantage with Calluna on soils where the latter can grow strongly. He has shown that Erica tetralix and Calluna are best suited for existence on moist soils but Calluna being the most efficient coloniser of the most soils, forces Erica to grow in water-logged places which are extremes for the growth of Calluna, and in these places Erica can successfully compete with it.

The application of nutrients (NPK) favoured the survival and growth of Molinia on all the sites and caused the differences between sites for the growth of this species to disappear completely. However, even on the drier Molinietum, Molinia responded to the application of nutrients, thus proving its nutrient deficiency for this species.

While the effects on Molinia in the Valley-bog have been overcome by the application of nutrients, these nutrients were applied to the surface and it is less certain

that Molinia would be so independent of aeration conditions if it had to obtain much of its nutrients from badly aerated horizons of the soil. This point needs further investigation.

The application of nutrients resulted in very high mortality of Erica on all three sites, except in one plot in the Valley-bog which had a cushion of living Sphagnum. The higher survival of the species in this plot may have been due to the removal of nutrients from the solution by Sphagnum spp. Since the work of Skene (1915) it has been known that Sphagnum can take up cations selectively from salt solutions, and Williams and Thompson (1936), Anschütz and Gessner (1954), Ramaut (1954) and Clymo (1963) have shown that other cations are exchanged for H ions. Clymo (1963) has found considerable uptake of anions by leaves of live Sphagnum but no detectable uptake by dead leaves. The nutrient application in this plot resulted in a luxuriant growth of Sphagnum which, presumably, favoured the survival of Erica by removing the nutrients from the solution.

The results of the water-culture experiments on the mineral nutrition of Erica show that "1/8 normal" culture solution (Section VI, p.146) gives maximum survival and growth of the species and the discussion of these results (Section VI, p.154) suggests that it is unlikely that the Valley-bog is sub-optimal in nutrition for Erica. Thus the low nutrient content of the Valley-bog cannot account for the poor growth of Erica in this site, whereas this factor seems important for the poor growth of Molinia.

Studies of soil aeration:

In the studies of soil aeration many workers have measured the rates of diffusion of O_2 in the soil solution by using the platinum micro-electrode method introduced by Lemon and Erickson (1952). The platinum micro-electrode is supposed to

simulate a plant root and O_2 flux to its surface is expected to provide a measure of the rate of diffusion of oxygen to a respiring root surface of similar area in the soil. Recently Van Doren and Erickson (1966) have reported the factors affecting the accuracy of the measurements of O_2 diffusion rates with the platinum micro-electrode. They have found that in water-logged soils the presence of 10 ppm. of manganese or iron can be sufficient to introduce a 25% error in the measurements of O_2 diffusion. In view of this the sampling of soil water, as described in the present work, and its subsequent analyses provides a useful approach to an understanding of the aeration status of water-logged soils. The soil water sampled is used for analysing the concentrations of other gases (CO_2 and H_2S) in addition to O_2 . However, in this method the various levels of the diffusion gradients of gases cannot be separated except in so far as the mean concentrations in the air-filled and water-filled spaces at any one depth are distinguished. The concentration of the gases found in the soil water cannot be expected to represent those at the root surface, but in these very wet soils they provide a better estimate than do the concentrations in the soil air.

Growth of *Molinia* and *Erica* at different concentrations of O_2 , CO_2 , and H_2S :

In these experiments the entire root system of the experimental plant was subjected to a particular gas composition, whereas in the field the part of the root system of the plant which is in upper horizons is, relatively speaking, in better aerated parts of the soil than the rest. In view of this the results of these experiments cannot be strictly translated to the field conditions. However, these experiments have shown the differential response of *Molinia* and *Erica* to the

different levels of aeration and they suggest that Molinia is more tolerant of poor aeration than Erica. The main reservation that must be made about this conclusion is due to the short duration of the experiments (15 days) though this is much longer than has been possible in most other investigations of this subject.

A comparison of results of these experiments with concentrations of O_2 , CO_2 and H_2S found in the soil water samples shows that not only in the Valley-bog but also in other sites the growth of Molinia would be reduced and that of Erica completely arrested because of the high concentrations of CO_2 and H_2S and low concentrations of O_2 . However, the roots of both species occur in the soil spaces exceeding $150\ \mu$ in diameter. It has been shown that a certain, though small, proportion of such spaces will contain air if they are 20 cm. above the water-table, though even if they are 80 cm. above a water-table not all these spaces will be air-filled. Some of the roots of both species will occupy air-filled spaces at least in the surface layers of the soil and the air-filled spaces have much lower concentrations of CO_2 and higher concentrations of O_2 than the water-filled spaces.

Erica:

The shallow rooting character of Erica no doubt allows it partially to avoid the very poor aeration conditions of the soil water, to which these experiments in water culture have shown it to be particularly sensitive. However, in the Valley-bog where the water-table is high and the air-filled porosity above the water-table is low, a high proportion of its roots even above the water-table must be in water-filled pores and conditions below the water-table are such as have been found to prevent its growth. The combination of the observed conditions in the Valley-bog and the response to particular conditions of aeration in the water-culture experiments provides a satisfactory explanation for the significantly poor growth of Erica on this

site as compared with the other sites.

Though Erica is less tolerant of poor aeration than Molinia, the species is capable of making good growth in the presence of low concentrations of O_2 provided concentrations of CO_2 and H_2S do not rise to a high level, e.g., growth in 4 and 8% O_2 combined with 2 or 4% CO_2 , or 8% O_2 and 0.06% H_2S is as good as in the control plants (grown in culture solution supplied with air). The results of Cannon(1925), Vlamis and Davis (1943), Chang and Loomis (1945), Woodford and Gregory (1948) and Leyton and Rousseau (1958) suggest that reduction of O_2 concentration in the rooting medium below 10% affects respiration, salt uptake and growth of many plants; but Erica is evidently tolerant of rather lower levels of O_2 than this. The development of lenticels on the roots of Erica is presumably a response shown by the species to poor aeration(see McVean, 1956).

Molinia:

In the Yorkshire moors Jefferies (1915) found Molinia to be associated with springs and slopes where ground-water was moving, but absent from places where water was stagnant. The association with moving ground-water was thought to be due to better aeration and lower acidity[≡] associated with these conditions. Smith (1918) and Fraser (1933) held the same view. On the other hand, Yapp, Johns and Jones(1916) found Molinia in rock outcrops round the salt marshes of the Dovey estuary in Wales growing apparently unrelated to any areas of improved drainage and placed more emphasis on the concentration of mineral elements rather than aeration. The present work shows that though Molinia

[≡]There were no marked differences in pH of the soils of the sites studied in the present work (c f. Pearsall, 1950; Newbould and Gorham, 1956).

is sensitive to high concentrations of CO_2 and H_2S , the differences found between its growth in the sites studied in the present work disappear with the application of nutrients. This suggests that, at least in these sites, mineral nutrition rather than aeration is the important factor governing its growth and distribution, though there may be an interaction of aeration on nutrition if nutrients have to be obtained from badly aerated horizons.

Tolerance of poor aeration by *Molinia*:

In *Molinia*, both in experiments with CO_2 and H_2S , the reduction of O_2 down to 2% had little effect on growth and even in the absence of O_2 and the presence of high concentrations of CO_2 and H_2S the species gained in weight. This ability of *Molinia* needs a closer examination at this stage.

Roots of *Molinia* possess a large volume of intercellular spaces, especially in the cortex of the old cord roots from deeper soil horizons and in the new (current year's) cord roots some distance away from the root tip (Section II). The development of a large volume of intercellular spaces may be regarded as an adaptation to growth in poorly aerated media. Many workers have found that the amount of intercellular spaces in the root cortex increases as the plants are grown in the presence of abundance of water or in poorly aerated media (Bryant, 1934; Goosens, 1936; McPherson, 1939; Lundkvist, 1955; Katayama, 1961; Kacperska - Palacz, 1962). This well-developed intercellular space system may not only provide a path for the internal diffusion of O_2 but also the O_2 requirements may have been reduced by reducing the amount of respiratory tissue.

Webster (1962a) found that even in the ground-water in which O_2 was deficient or undetectable and CO_2 concentration was high ($\approx 40\%$ in air at 9°C and 760 mm. pressure)

the air obtained from Molinia roots growing in this water, never contained less than 15% O_2 or more than 6% CO_2 , which suggested that the intercellular space system in the roots provided a path for the internal diffusion of O_2 into the roots from the shoots. However, aeration conditions within the roots were not independent of those in the soil. As O_2 decreased and CO_2 increased in the soil, there were corresponding, though far less pronounced, changes in the composition of the root air which suggested that there was some outward diffusion of O_2 from and inward diffusion of CO_2 into the root.

A system for the internal diffusion of O_2 has been found in many other plants, e.g., Cladium mariscus (Conway, 1937), Oryza sativa (Van Raalte, 1940, 1943; Barber, Ebert and Evans, 1962), Menyanthes trifoliata (Coult and Vallance, 1958), and Spartina alterniflora (Teal and Kanwisher, 1966). Barber, Ebert and Evans (1962) have shown that in rice the transport of O_2 from the shoots to the roots is consistent with the assumption that this was by diffusion through the intercellular spaces in the roots which they measured.

The outward diffusion of O_2 from roots of Molinia (Armstrong, 1964) and other plants (Oryza sativa - Van Der Heide et al., 1963; Eriophorum angustifolium and Menyanthes trifoliata - Armstrong, 1964; Spartina alterniflora - Teal and Kanwisher, 1966) suggests that the roots of some of the terrestrial plants can increase the diffusion of O_2 through the soil without causing changes in the air-filled porosity and that they are not entirely dependent upon the soil for their O_2 supply.

The occurrence of orange brown deposits on the roots of Molinia from deeper depths and orange streaks along root channels in the soil profile (Section II) have also been reported by other workers for other plants and soils (Lavrov, 1950 -

quoted by Bartlett, 1961; Mori, 1955). Iron is quite sensitive to change in oxidation-reduction potentials in soils (Merkle, 1955) and such deposits have been shown to be iron oxides (Bartlett, 1961). Their presence in the reduced medium indicates that conditions for oxidation are better near the root surface and is an evidence of the outward diffusion of O_2 from the roots.

Wet-heath sites and the growth of Erica and Molinia:

Erica:

The general picture that emerges from the present work is that in the sites studied Erica dominates the Valley-bog because it has a very low nutrient requirement (which may possibly be related to its very slow relative growth rate, Section VI) and can, therefore, tolerate conditions of nutritional deficiency which reduce the growth of its competitors, viz., Molinia (and Calluna?). Although Erica is very sensitive to high concentrations of CO_2 and H_2S , such as are found in the Valley-bog, it to some extent, evades this unfavourable aspect of the habitat because of its shallow root system. Its better growth in the Central associates and the drier Molinietum, when planted in cleared plots, is probably due more to the higher air-filled porosity in the top few inches of the soil than the somewhat higher content of nutrients. In nature the species does not dominate the Central associates because of the strong competition from Calluna (see Bannister, 1964b) and perhaps Molinia, although in this site no significant effect of competition from Molinia was found. In the drier Molinietum, Erica is almost absent except along the ditch banks. Here strong competition from Molinia coupled with the development of high moisture tensions during summer months, which may become accentuated when growing with actively growing Molinia, may be limiting the spread of the species. In the wetter Molinietum, Erica grows with

Molinia and Calluna, though the frequency of occurrence is less than in the Central associates. Here moisture conditions may be more favourable than in the drier Molinietum but due to the un-restricted growth of Molinia competition from this species is greater than in the Central associates. In the wetter Molinietum Erica performs better, though not significantly so, than in the Central associates. Here Molinia tussocks are much higher than in the Central associates and may be providing a better aerated^{*} medium.

It is concluded that the Valley-bog is a refuge for Erica rather than a site which provides optimum soil conditions for the growth of the species.

Molinia:

The growth of Molinia in the Valley-bog is significantly poorer than in the other sites, but the disappearance of site differences as a result of the application of nutrients suggests that the factor responsible for this is the low nutrient

*

In the wetter Molinietum and the Central associates all Erica and Calluna units sampled (Section II, b) were rooted in Molinia tussocks. Rankin (1911) and Rutter (1955) have also noted Molinia tussocks serving as a nidus for the roots of Erica and Calluna.

Molinia tussocks because of their loose nature would be better aerated than the wet soil around and below them. The possibility of the roots of Erica and Calluna growing in them because of their richer nutrient status does not seem to be very convincing. Loach (1964) has estimated that a Molinia tussock has only a small fraction (about 7%) of the total phosphorus in the top 20 cm. of the Molinietum soil (drier Molinietum of the present work). He did not measure the availability of nutrients in top soil and tussock material but this was shown that there were certainly more nutrients in the top soil than in the tussocks.

status of the Valley-bog and that Molinia grows better in other sites mainly because of their higher nutrient content. No information is available about the nutrient status of the wetter Molinietum soil, but in view of the results obtained for the performance of Molinia in this site (Section II, b) it seems likely that here too the soil nutrient content is higher than in the Valley-bog and perhaps in the same range as in the drier Molinietum.

Molinia seems to be a plant better adapted than Erica to grow with its roots in a poorly aerated medium if the medium also contains adequate nutrients. The performance of Molinia in habitats which are poorly aerated but richer in nutrients than the Valley-bog (e.g., fen peats) seems worthy of further study as does its response to changing combinations of aeration and nutrient concentrations in controlled solution cultures.

APPENDIX AMOLINIA CAERULEA ROOTS

DEPTH, Inches	Means of four replicates		Air dry weight of roots as percentage of total weights.	
	VALLEY-BOG	CENTRAL ASSOCIES	WETTER MOLINIETUM	DRIER MOLINIETUM
Surface	9.50 $\pm$ 0.54	12.20 $\pm$ 1.57	9.40	12.61
0 - 1 $\frac{1}{2}$	17.43 $\pm$ 2.71	12.52 $\pm$ 4.21	18.53 $\pm$ 2.10	13.64 $\pm$ 0.73
1 $\frac{1}{2}$ - 4 $\frac{1}{2}$	32.30 $\pm$ 1.98	33.44 $\pm$ 1.59	27.96 $\pm$ 2.70	29.00 $\pm$ 2.79
4 $\frac{1}{2}$ - 7 $\frac{1}{2}$	22.80 $\pm$ 2.27	25.20 $\pm$ 4.02	27.49 $\pm$ 1.87	25.98 $\pm$ 1.34
7 $\frac{1}{2}$ - 10 $\frac{1}{2}$	12.53 $\pm$ 0.70	10.60 $\pm$ 1.20	11.04 $\pm$ 1.03	13.60 $\pm$ 1.41
10 $\frac{1}{2}$ - 13 $\frac{1}{2}$	4.39 $\pm$ 0.96	4.50 $\pm$ 0.98	4.90 $\pm$ 0.68	3.91 $\pm$ 0.93
13 $\frac{1}{2}$ - 16 $\frac{1}{2}$	0.75 $\pm$ 0.23	1.33 $\pm$ 0.26	0.63 $\pm$ 0.30	0.77 $\pm$ 0.31
16 $\frac{1}{2}$ - 18	0.30 $\pm$ 0.10	0.20		0.54

ERICA TETRALIX ROOTS

DEPTH, Inches	Means of four replicates.	Air dry weight of roots as percentage of total weight.		
		VALLEY--BOG	CENTRAL ASSOCIES	WETTER MOLINIETUM
Surface	33.25 $\pm$ 4.12	29.12 $\pm$ 5.38	29.13 $\pm$ 1.64	
0 - 1 $\frac{1}{2}$	25.25 $\pm$ 2.56	19.75 $\pm$ 2.63	22.12 $\pm$ 1.95	
1 $\frac{1}{2}$ - 4 $\frac{1}{2}$	21.73 $\pm$ 1.57	26.81 $\pm$ 2.14	30.89 $\pm$ 2.59	
4 $\frac{1}{2}$ - 7 $\frac{1}{2}$	18.23 $\pm$ 1.68	19.96 $\pm$ 2.21	15.40 $\pm$ 3.35	
7 $\frac{1}{2}$ - 10 $\frac{1}{2}$	1.45 $\pm$ 0.74	4.18 $\pm$ 0.98	1.71 $\pm$ 0.68	
10 $\frac{1}{2}$ - 13 $\frac{1}{2}$	0.22	0.53	0.94 $\pm$ 0.65	
13 $\frac{1}{2}$ - 16 $\frac{1}{2}$	-	-	Traces	
16 $\frac{1}{2}$ - 18	-	-	-	

APPENDIX BUse of liquid paraffin and streptomycin solution in water sampling for gas analysis:Liquid paraffin:

It seems reasonable here to describe the method used for keeping the water under some liquid which should act as an effective seal against the entry or escape of gases during sampling or during storage prior to analysis. Simple experiments were carried out to test the efficiency of liquid paraffin as an effective seal against gaseous exchange.

Distilled water was boiled for 30 minutes and allowed to cool. After 1 hour the amount of oxygen present in it was determined by using the Winkler method. About 150 ml. of this water were put in a conical flask under a layer of liquid paraffin (about 5 mm. thick). Another 150 ml. of this boiled and cooled distilled water were kept under a layer of a 1 : 1 mixture of liquid paraffin and toluene (Toluene was tried because of its antiseptic properties). These flasks were kept in the open and 25 ml. water samples were taken from each at different times and analysed for their oxygen content. The results are given below:-

	<u>Time, hours</u>	<u>O₂, ppm</u>
Distilled water boiled, cooled and kept in the open:	1	2.15
	23	8.62
	48	8.80
Distilled water boiled, cooled and kept under liquid paraffin and toluene (1 : 1) in the open:	23	2.70
	48	2.98
	96	3.10
	120	3.54
Distilled water boiled, cooled and kept under liquid paraffin in the open:	23	2.24
	48	2.28
	96	2.30
	120	2.74

From these results it was evident that, for all practical purposes, liquid paraffin acted as an effective seal against gaseous exchange. Though with the passage of time there was a slight increase in the oxygen content of the water kept under it in the open, yet it could be used as a suitable seal for 96 hours at least. A 1 : 1 mixture of liquid paraffin and toluene did not prove as satisfactory a seal as liquid paraffin alone.

Streptomycin solution:

It was found that the addition of a drop of streptomycin solution to the water sample helped to maintain its gaseous composition presumably by checking the activity of micro-organisms. This was borne out by dividing a water sample, obtained from the Valley-bog from a probe in which no streptomycin solution was added at the time of setting it, into two parts and keeping the two in bottles under a thick layer of liquid paraffin. To one of the bottles one drop of streptomycin solution was added at the time of sampling while the other was kept as a control. The two bottles were kept in a refrigerator. Carbon dioxide content of the water was determined at different times and the results are given below:

Sampling day	<u>Carbon dioxide ppm.</u>	
	<u>With streptomycin</u>	<u>Without streptomycin</u>
1 day after sampling	290.55	314.95
2 days " "	287.21	317.80

This clearly showed that the addition of streptomycin maintained the initial concentration of carbon dioxide.

APPENDIX C

The correction applied to the pore intercepts (Section V, p.116) in order to calculate the frequency of true pore diameters, was obtained in the following manner.

The intercept of a pore will represent its true pore diameter only if it passed through the centre of the pore. Otherwise it will under-estimate it, depending on its distance from the centre of the pore, the intercept farthest away from the centre of the pore being the least representative of the true diameter. Ten equidistant lines (= intercepts) were drawn in a circle starting from its periphery and proceeding towards its centre. The results are given in Table I.

TABLE I :

True diameter of the circle = 16.4 cm.

<u>Intercepts, cm.</u>	<u>Proportionality factor (= True diameter / Intercept)</u>
1 = 4.9	3.35
2 = 8.5	1.93
3 = 10.7	1.53
4 = 12.4	1.32
5 = 13.6	1.20
6 = 14.6	1.12
7 = 15.3	1.07
8 = 15.8	1.04
9 = 16.1	1.02
10 = 16.3	1.01

Table I represents the frequency distribution of the factor diameter / intercept, i.e., in a large number of random intercepts about one-third of them will be within 5% of the true diameter, in about 7 intercepts in 10 the diameter will not be more than 50% greater than the intercept, but in 2 intercepts in 10 the

diameter will be more than twice the intercept.

The pore intercepts obtained along a transect of a soil section were classified into seven classes = < 35 , $35 - 50$, $50 - 75$, $75 - 150$, $150 - 300$, $300 - 600$, $600 - 1200$, and $> 1200 \mu$. Each class was divided into sub-classes of 0.1 of its ceiling limit, e.g., classes $300 - 600 \mu$ and $600 - 1200 \mu$ were divided into sub-classes as shown below.

Class: <u>$600 - 1200 \mu$</u>		Class: <u>$300 - 600 \mu$</u>	
	<u>sub-class mean</u>		<u>Sub-class mean</u> <u>Proportionality factor</u>
1200		600	
	1140		570 1.05
1080		540	
	1020		510 1.17
960		480	
	900		450 1.33
840		420	
	780		390 1.53
720		360	
	660		330 1.81
600		300	

The maximum diameter (ceiling limit) of the class was divided by the mean of each sub-class and the ratios so obtained were compared with the proportionality factors in Table I. Calculations could then be made, of which the following is an example.

In sub-class $540 - 600 \mu$, $0.3 n$ (n = total number of pores in a transect whose intercepts lie in this range: $540 - 600 \mu$) represented true diameter within 5%, viz.,

they were in the range $540 - 600 \mu$, whereas the remaining, $0.7 n$, were underestimates of pore diameters. They were transferred to the sub-classes of the class above or to the next class above according to the value of the proportionality factor, e.g., $0.3 n$ were transferred to the sub-class $600 - 720 \mu$ ($\frac{720}{570} = 1.26$), $0.1 n$ to sub-class $720 - 840 \mu$, $0.1 n$ to sub-class $1080 - 1200 \mu$, and lastly $0.1 n$ to the class representing pore-diameters of above 1200μ (This class was not sub-divided).

Based on the study of a transect, the number of intercepts falling into a given sub-class was expressed as their number in a transect of a standard length ($= 100 \text{ mm.}$), and these intercepts were then transferred in the way explained to give the frequency distribution of pore diameters.

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