Ecology of Woodland Plants in the Neighbourhood of
Huddersfield. (Figs. 1-70.) By T. W. WOODHEAD, F.L.S.*

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INTRODUCTION.

THE study of plant associations is being vigorously prosecuted in Britain at the present time, and several parts of the country have been surveyed. These surveys cover fairly extensive areas, and the results so far have been indicated on $\frac{1}{2}$ -inch or 1-inch to the mile maps.

The aim of the present investigation has been to pay special attention to a small area and examine in some detail features

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which had to be omitted altogether or only slightly dealt with in the primary surveys, and thus determine whether more detailed work would lead to profitable results. While the object of the primary survey was to illustrate the chief plant associations, the present paper rather attempts to bring out the dominant factors affecting the distribution and modifications of a limited number of the commonest species which form the undergrowth of our woodlands. The distribution of these has been traced in the uncultivated areas of a small portion of the West Riding of Yorkshire to the South and West of Huddersfield, a district included in the Survey by Smith & Moss (Leeds & Halifax District), and reference should be made to this for a general account of the vegetation of the district.

The area selected is favourable in that it affords considerable variation in altitude (1700 to 250 feet), in rainfall (50 to 32 inches), in temperature (42° F. to 47°·5 F.), in exposure to prevailing winds, in soil conditions—*e. g.*, deep ill-drained peat, shallow, relatively dry peat, humus, and soils derived from the denudation of coarse millstone-grit, fine-grained coal-measure sandstones, shales, and clays; and hence there are considerable differences in available water and inorganic salts for plant-food.

The study also throws light on the changes that have occurred in the vegetation of the district as a result of altered conditions.

The problems to be considered therefore were the investigation of the conditions affecting the distribution of the common plants of the undergrowth with reference to soil, moisture, exposure to wind, light, and shade, and to compare the tissues of the several species occurring under these various conditions. The species examined included, among others: Bracken (*Pteris aquilina*, Linn.), Bluebell (*Scilla festalis*, Salisb.), Quick or Creeping Soft Grass (*Holcus mollis*, Linn.), Wavy Hair-Grass (*Deschampsia flexuosa*, Trin.), Bilberry (*Vaccinium Myrtillus*, Linn.), Dog's Mercury (*Mercurialis perennis*, Linn.), Yellow Dead-nettle (*Lamium Galeobdolon*, Crantz), and Hog-weed or Cow-Parsnip (*Heracleum Sphondylium*, Linn.).

A very considerable amount of detailed work remains to be done in every branch of the subject, especially with regard to soils. The observations here recorded can, therefore, only be regarded as preliminary to more extensive work; and it is also important that similar examinations should be made of other selected areas and compared, for it is only by such comparisons that we can hope to arrive at the most satisfactory results.

Some of the observations contained in this paper were communicated to Section K (Botany) at the Southport Meeting of the British Association in 1903, and further results communicated to that Section at the Cambridge Meeting in 1904.

A prolonged absence from England has occasioned delay in the publication of this paper. Since its completion several important contributions have appeared or have come to my notice, and I have taken the opportunity to include references to many of them. In this connection I wish to thank Prof. Hans Schinz of the University of Zürich, and Prof. C. Schröter of the Polytechnicum, Zürich, for their kindness in granting me permission to use the excellent libraries connected with these and other institutions.

ECOLOGY IN BRITAIN.

In 1836 Hewitt Cottrell Watson contributed a short paper (98) to a discussion, initiated by R. B. Hinds (48) the previous year, on the construction of Maps illustrating the distribution of plants. The ideas in the minds of botanists at the time were concerned chiefly with mapping species. Watson's knowledge of the distribution of plants, however, led him to see that two methods were possible. Not only could the distribution of species be thus indicated, but maps of a very different type could be produced which would indicate vegetation. Although this idea was in Watson's mind, it was eventually crowded out in a statistical study of the distribution of species (100).

The present study of Plant Associations and Ecology in Britain, as elsewhere, has been based upon and greatly influenced by the admirable work of Warming (102), about which it is impossible to speak too highly. The works of other Continental botanists have also had a marked effect, especially those of Beck (4), Drude (25), Flahault (29), Graebner (36), Kerner (52), Schröter (84), and Schimper (83). Running close upon these are the researches of American Ecologists, who have recently shown great activity in this direction; and the publications of Pound and Clements (79), Cowles (18), Harshberger (44), Ganong (33), MacMillan (63), and others have taken a permanent place amongst the contributions to this subject. For a more extended bibliography a recent paper by Clements (14), also his excellent 'Research Methods in Ecology' (15), may be usefully consulted, as well as numerous papers during recent years in the 'Botanical Gazette.' Although these deal often with areas

widely removed from the one under consideration, they contain abundant observations capable of general application, and I have profited much by their perusal.

But the influence, direct and indirect, of Flahault is especially noteworthy, for it was through his pupil Robert Smith that the study of plant associations first gained a permanent footing here.

Smith applied Flahault's system in Scotland, and in this new area found it necessary to somewhat modify it, and eventually he produced the first vegetation map in Britain, dealing with the Edinburgh district (86). Unfortunately, on the eve of publication of a second map dealing with Northern Perthshire (87) he died, and the study of Plant Geography was much the poorer by the loss of an able and most enthusiastic worker. However, the subject was at once taken in hand by his brother, William G. Smith, who has since actively continued the work, not only in Scotland, where other maps dealing with Forfar and Fife have been published (87), but two areas in West Yorkshire (88, 89) have also been mapped with the assistance of C. E. Moss and W. M. Rankin, and other areas in the North of England by F. J. Lewis (57); while in the 'Flora of Halifax' an interesting account of the vegetation of the parish is given by W. B. Crump (20). To all these I am indebted in many ways, and to the suggestions of Dr. W. G. Smith; whilst to Prof. C. Schröter I am especially indebted for much help in connection with the literature dealing with the various branches of the subject, and I have profited much by his kindly criticisms.

I.—WOODLAND VEGETATION MAPS.

a. *A typical Mixed Deciduous Wood in the Coal-Measure Area.*

The broad features of the vegetation having thus been studied, it has been my endeavour to carry the problem a step further by paying special attention to a very limited area.

The first attempts were made to map in detail the dominant plants in a small wood, and Birks Wood (a portion of the somewhat extensive Woodsome Woods near Huddersfield) was selected, as being most accessible. For this purpose several tracings were made from the 25-inch survey map, and on these the distribution of the commonest species was indicated. The

first map (fig. 1, p. 338) indicates the distribution of the dominant trees, the dotted areas showing the distribution of shade trees, chiefly Sycamore (*Acer Pseudo-platanus*), Elm (*Ulmus montana*), and Beech (*Fagus sylvatica*). The lines show the distribution of Oak. A few other species are indicated by signs.

In making a primary examination to determine the shade-areas, photographic printing-paper was used.

A piece of printing-paper was exposed to bright light for ten seconds and this was used as a standard. This shade (as seen through the glass to be used) was copied as carefully as possible in oil-colour and then cut up into small pieces. Printing-frames were made of 3×1 inch glass slips backed with opaque paper in such a way as to form envelopes or pockets with glass fronts. A piece of the standard colour was pushed down to the lower end of the pocket, the upper half receiving a strip of printing-paper. The frames when filled were taken into the wood and a preliminary test made in the open; then a set was exposed simultaneously in the area to be examined, and a record taken of the time required to print to the depth of the standard. A somewhat similar but more elaborate method was devised by Wiesner (197), but his paper did not come to my notice until after these observations were made.

Considerable differences were found under the same species of tree in different parts of the wood, owing to the condition of the tree, the mode of its growth, closeness of planting, and the like. Again, the "Mosaic" of illuminated and shaded areas under the tree introduced another disturbing element and made it difficult to indicate in numbers the precise amount of shade produced for a given species; but so obvious was the difference between groups of trees composed of *Acer*, *Ulmus*, and *Fagus* on the one hand, and those consisting of *Quercus* and *Betula* on the other, and so frequently did these species occur in masses together, that to indicate the former as a "shade"-area and the latter as a "light"-area gave a useful working basis.

Cieslar (12) has shown, by using Wiesner's method, how great is the effect of shade on the production of humus and in influencing the number of species occurring under a given tree. He was, however, working under the very uniform conditions of planted Beech forests of determined "Durchforstungsgrad," and numbers under these conditions could more easily be given.

The next step was to map the undergrowth, and after several

unsuccessful attempts to show the distribution of the various species on one map, it was decided to map the more abundant species separately. The commonest and most striking plant is the Bracken (*Pteris aquilina*), and it was therefore taken first. Fig. 2 shows its distribution. A comparison of the tree-map with this suggested unmistakably that the distribution of Bracken was determined to a considerable extent by the dominant tree: that under trees with an open canopy like Oak and Birch, which, while affording much protection, admit a large amount of light, the Bracken flourishes; but under trees

Fig. 1.

BIRKS WOOD.

Map showing the distribution of Trees.

with a close canopy, such as Sycamore, Elm, and Beech, much light is cut off; and a comparison of figs. 1 and 2 will show that in these areas Bracken is almost or entirely absent—that is, the shade produced is evidently an important factor in limiting its distribution.

Thirty years ago little or no Bracken occurred here, but at that time there was an extensive shrubby undergrowth, especially of Hazel. The depredations of rabbits, however, was such

as to practically exterminate the shrubs, and the increased light thus admitted favoured the development of Bracken, until at the present time its distribution is limited, as shown in fig. 2. Similar changes have taken place over extensive areas in the adjoining Woodsome Woods.

Another interesting illustration of the effect of trees on the distribution of plants is found in the Woods at Honley.

Twenty years ago the thickly planted Pines produced such a dense shade that the ground beneath was practically devoid of

Fig. 2.

BIRKS WOOD.

Map showing the distribution of *Pteris aquilina*, Linn.

vegetation, the deep shade favouring the accumulation of considerable humus. Since then, thinning has taken place in a portion of the wood to the west, thus exposing the remaining pines to the prevailing winds. This, together with the ravages made by the pine-bark beetle and some felling of the pines, has gradually admitted light, thus favouring the development of Bracken. It has made inroads from the adjacent wood, slowly pushing its way, until at the present time it forms a dense sheet in the

Fig. 3.

BIRKS WOOD.
Map showing the distribution of *Scilla festalis*.

Fig. 4.

BIRKS WOOD.—Soil Map.

lighter part of the wood, thinning out under the deeper shade of the less injured pines.

The Bracken must have long been a characteristic plant in this zone, as the peat, in places a foot in thickness, consists so extensively of the remains of this plant that we might fairly call it Bracken peat.

It has, as associates, the xerophytes of the plateau, *Deschampsia flexuosa*, *Calluna Erica*, *Vaccinium Myrtillus*, &c.

We will now apply this method to another species.

Fig. 3 shows the distribution of *Scilla festalis* in Birks Wood. Here we see that its occurrence is only partially influenced by the dominant trees. It is abundant under Sycamore and Oak in certain areas, thinning out in others. Light was evidently not the only factor, so other conditions were examined. In certain parts of the wood, changes of soils being pretty well marked, an attempt was made to construct a soil-map. In fig. 4 we have the result. The details were obtained by means of an augur $1\frac{1}{2}$ inch in diameter and with a 6-inch thread to which iron rods were screwed. A similar borer is figured by Hall (43). The area was paced and borings made at intervals of 10 yards. The sketch-map was ruled in corresponding squares and results added*. As will be seen, the soil along the northern half of the wood consists of a shallow sandy loam resting on a bed of Elland flagstone quarried at the two extremities A and B. This area therefore is well drained, relatively dry, and the soil covered with only a thin layer of sandy humus; while the soils over the rest of the area consist of firmer, more clayey loam resting on a bed of clay, and in the parts indicated it is covered by 6 inches or more of humus. The well-known spongy properties of humus, coupled with the fact that such fine-grained soils as occur here are able not only to retain, but even raise water above the underground level, renders this area relatively moist.

On comparing this with the *Scilla* map, it will be seen that the plant is most abundant in a loamy soil covered by six inches or more of humus. The overshadowing trees are Oak with a considerable admixture of Sycamore, and it is thus an area of moderate shade. Along the northern edge of this the humus is very thin, on a dark sandy loam, the trees are Elm and Beech,

* Oliver & Tansley (75) have recently given an interesting account of a method of surveying vegetation by means of squares, adopted by them in the survey of the Bouche d'Erquy.

and notwithstanding the deep shade of the latter the plant is still common. To the north-east humus is absent altogether, the soil consisting of a clayey loam resting on stiff clay, becoming slightly more sandy, with humus in patches to the extreme east. In the stiff clayey soil the Bluebell distinctly thins out, and here it competes with Yellow Dead-nettle (*Lamium Galeobdolon*), Dog's Mercury (*Mercurialis perennis*), and *Arum maculatum*, together with numerous root-branches of small trees, between which the bulbs of *Scilla* are often tightly packed, though they

Fig. 5.

BIRKS WOOD.

Map showing the distribution of *Holcus mollis* and *Deschampsia flexuosa*.

not uncommonly escape this competition by penetrating more deeply in spite of the stiffness of the soil. Another determining factor is the deep shade of the trees in this area, consisting of Beech, Elm, Sycamore, and Elder. The remainder of the wood to the north and west has a shallow sandy soil mixed with humus, there being little or no humus as a distinct layer on the surface, hence its power of holding water is greatly reduced. This soil lies immediately above a bed of Elland flagstone quarried at A and B (fig. 4). In this area *Scilla* only occurs in small straggling patches. Its chief competitor here

is *Deschampsia flexuosa*, the dense, dry, wiry tussocks of which form an unfavourable medium for the germination of the seeds of *Scilla*; and although the two species are frequently found together, *Scilla* very rarely forms those unbroken sheets so characteristic of the moist areas and when associated with *Holcus mollis*. The thinning-out of this species in woods with a very shallow sandy soil, as in many of the woods in the gritstone area, is very striking.

A comparison of the soil-map with the bracken-map shows that a change of soils and accompanying conditions do not offer here a barrier to this species.

Fig. 5 shows the distribution of common grasses. The grass vegetation is composed mainly of two species. In the moister parts, where the soils consist of fairly thick humus over loam, is *Holcus mollis*. In the drier parts to the north, especially where the ground is in rounded mounds with shallow, well-drained, sandy soil mixed with humus, *Deschampsia flexuosa* dominates. Along with this are scattered such xerophytes as *Galium saxatile*, Linn., *Vaccinium Myrtillus*, Linn., *Calluna Erica*, DC., and *Teucrium Scorodonia*, Linn. Here and there *Holcus* makes deep inroads into this area, occupying chiefly the moister humus-covered hollows.

It will be seen, on comparing maps 2, 3, and 5, that *Holcus mollis*, Bracken (*P. aquilina*), and Bluebell (*S. festalis*) often occupy the same area and appear to be in competition with each other, but closer examination shows this is not the case. We have here a well-marked society or sub-association, the species of which are admirably adapted to each other's requirements. *Holcus* is a surface-plant (fig. 6, p. 344), its long rhizomes running in the loose leaf-mould, as may be determined by the ease with which it is uprooted. Beneath this in the deeper humus are the rhizomes of the Bracken, often running along the upper surface of or just within the loam, forming a distinct Bracken layer, the decay of its fronds contributing an annual quota for its higher associates; while in the firm loam below are the bulbs of *Scilla*, though often we find in the *Holcus* and Bracken layers young bulbs on their way downwards. Their soil requirements, their modes of life, their periods of active vegetative growth, their times of flowering and fruiting, are for the most part different. The unbroken sheets of blue when *Scilla* is in flower in early spring, followed in the summer by equally continuous sheets of *Pteris*, form the most striking features in the woodland vegetation

of this district. Thus, in many respects, each species is not within the sphere of influence of the other, and they flourish accordingly. Competition such as it is goes on between individuals of the same species. When, however, *Pteris* increases in density, the tendency is to markedly reduce the flowering activity of *Holcus*. Its tips early show signs of withering, its period of vegetative growth is limited, and eventually its distribution becomes stricted. In the late winter and early spring, however, it grows apace and makes great headway before the Bracken develops.

Fig. 6.

Vertical Section of Soil in dense *Scilla* area : *Holcus*,
Pteris, and *Scilla* layers.

The chief elements in the Meso-pteridatum of the moist Coal-Measure
Oak Woods, showing their relations to each other in the soil.

These observations support those of Areschoug (1), Rimbach (81), P. E. Müller (72), and others, a very useful summary of whose work has been given by Oliver (74), and more recently, with further interesting results, by Massart (65).

This association or Meso-pteridatum is very characteristic of

the moist Coal-Measure Oak woods in the West Riding of Yorkshire, and forms what we may call a *complementary association*; the subaerial parts, as we have seen, are edaphically complementary, the aerial parts being seasonally complementary.

Macdougall (62) recently made a study of temperatures at different depths, with the view of showing the extremes to which the different parts of plants are subjected, and found a considerable range. He records that in New York during the months of October, November, and December, 1902, the ground was at times frozen at a depth of one foot. Mr. Charles Brook has kindly supplied me with readings for a corresponding period taken by him at Harewood Lodge, Meltham, which will serve to indicate the variations in this district. Rarely is the ground frozen here to a depth of a foot, but this, however, did occur in February 1895, when the ground was frozen to a depth of 20 inches for 13 days. Probably not since 1809 has so low a temperature been recorded here. Maximum temperatures on the grass were not taken, but I give the maximum and minimum at 4 feet above the grass.

The relatively slight variations seen to occur at one foot, and still less at two feet, below the surface will obviously be an advantage to deep-rooted plants, especially to those vegetating early in the year. In this connection it is interesting to note that of the three plants of this association, the first to make its appearance (*Scilla festalis*), and therefore most likely to be injured by early frosts on account of its early vegetative growth and flowering, is the one most deeply rooted and also, as we shall see, possesses for all practical purposes an unfreezable sap.

Temperatures (° F.) recorded at Harewood Lodge, Meltham.

Altitude 510 feet.

Absolute monthly maximum and minimum temperatures
at 4 feet above the grass.

1902.								1903.				
June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.		Jan.	Feb.	Mar.	Apr.	May.
79.9	76.3	70.0	73.5	60.9	54.9	54.8		51.7	54.9	62.0	58.7	75.9 Max.
33.0	37.4	38.7	34.2	33.0	27.9	16.4		18.0	29.8	30.5	26.6	32.0 Min.
46.9	38.9	31.3	39.3	27.9	27.0	38.4		33.7	25.1	31.5	32.1	43.9 Diff.

Absolute minimum temperatures recorded on the grass.

Maximum temperatures not taken.

27.0 32.3 32.5 28.9 27.5 20.1 14.1 | 16.0 23.7 23.0 18.7 27.0

Maximum and minimum temperatures recorded at 9 A.M.

One foot below the grass.*

1902.								1903.				
June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.		Jan.	Feb.	Mar.	Apr.	May.
60.7	60.1	56.2	57.2	51.2	47.8	43.2		40.8	43.5	44.7	44.8	53.6 Max.
49.7	54.0	53.1	50.5	46.3	38.7	36.0		34.5	37.7	38.6	39.2	43.8 Min.
11.0	6.1	3.1	6.7	4.9	9.1	7.2		6.3	5.8	6.1	5.6	9.8 Diff.

Maximum and minimum temperatures recorded at 9 A.M.

Two feet below the grass.*

59.0	58.7	55.5	55.9	51.3	47.9	43.5		40.5	43.5	44.2	44.5	52.4 Max.
49.2	53.9	53.4	51.2	47.3	40.7	38.0		35.7	38.7	39.6	40.8	44.6 Min.
9.8	4.8	2.1	4.7	4.0	7.2	5.5		4.8	4.8	4.6	3.7	7.8 Diff.

For purposes of comparison, woods in other parts of the district were examined and similar maps prepared on the same scale; these were Molly Carr Woods and Haigh Spring Wood in the Coal-Measure Area, and Armitage Bridge Woods, Honley Woods, and Hagg Wood, on the edge of the Millstone-Grit Plateau. These gave the same results, except that in some areas indicated as Sandstone on the Geological Map it was found, on examining the soils, that these beds were overlaid in great part by moist clayey loam and considerable humus, and not by a dry sandy soil as in Birks Wood. The trees, too, in these parts of the woods are frequently shade-trees, hence in areas which from a Geological map might be expected to produce xerophytic grasses and their associates, the ground was dominated by mesophytes. These features occur not uncommonly throughout the Coal-Measure area. The detailed study, even of a small area, shows the importance, not only of the edaphic influences in determining the composition of the flora, but also that the distribution of the dominant species is the result of many interacting and complex forces.

* These do not represent absolute Maxima and Minima; the readings are taken at 9 A.M., which is the coldest hour of the day for Earth Temperatures. In the six summer months the absolute Maxima are perhaps one or two degrees higher; the Minima are probably not far from absolute Minima. In some respects the results are unusual. February and March were both very mild months, and April was abnormally cold, so that it was actually a trifle colder than both the preceding months.

b. *A typical Mixed Deciduous Wood of the Plateau and Slopes of the Millstone-Grit Area.*

Figs. 7 and 8 (pp. 348, 349) of Armitage Bridge Woods illustrate the characteristic features of the woods skirting the edge of the Gritstone Plateau.

The three portions of this woodland are known by distinctive names, as is common in the woods of the district generally. They surround that portion of the plateau known as Netherton Moor, cut off from the main tableland by the stream in Dean Clough to the north, by Mag Brook to the south, this stream joining the River Holme, which forms the eastern boundary. The plateau is under cultivation, but skirting the margin and covering the slopes are the relics of the primitive vegetation. As shown by the contour-lines, the altitude at the edge of the plateau is 550 feet. It then suddenly drops to 375 ft., or about 2 in 5. The upper portion has a very shallow sandy soil covered with a thin layer of peat, and succeeded below by shales and clays overlaid with deeper moister soils. The distribution of trees is shown in fig. 7. In Old Spring Wood and Spring Wood the dominant tree is Oak, with an admixture of Birch and Pine, and while Oak is the dominant tree in Mag Wood, areas to the north and east are occupied by shade-trees, Sycamore (*Acer Pseudo-platanus*, Linn.), Elm (*Ulmus montana*, Stokes), and Beech (*Fagus sylvatica*, Linn.). The characteristic plants of the undergrowth are shown in fig. 8, and they are *Deschampsia flexuosa*, *Pteris aquilina*, *Calluna Erica*, *Vaccinium Myrtillus*, and *Holcus mollis*. A reference to this map will show clearly the effect on the vegetation of the changed conditions in a very short distance. While the distribution of Bracken seems to be limited to a large extent by the shade-trees, obviously other factors come into play to limit its distribution in the Oak areas. In the higher parts of the wood, where the soil is shallow, sandy, and covered with a thin layer of peat, Bracken occurs in patches and is in competition with Ling and Bilberry; their rhizomes must of necessity occupy practically the same layer, and frequently we find them interlacing. Here we have a Xeropteridatum, the elements of which are not complementary; they form what we may term a competitive association, sometimes one, sometimes the other species dominating. Below this is a transition region, from the sandstones to the shales and clays;

the steep slopes are covered with fallen blocks of stone, the soil contains a considerable admixture of sand and is well drained and relatively dry. The Xerophytes are thus carried over the shales a considerable distance, thinning out in the moister lower parts of the wood. Here, in deeper soil, Bracken no longer

Fig. 7.

competes with rhizomatous plants, and thus forms an unbroken sheet with mesophyte associates, e.g. *Holcus mollis*, *Scilla festalis*, *Lamium Galeobdolon*, &c., a complementary association or Meso-pteridetum. This is well seen in Spring Wood. In Mag Wood, where the soil conditions are favourable to the

development of Bracken, it is, except for a few patches, cut out to the north by deep shade. Here, with deeper humus and therefore with increased moisture, the tendency is for the Mesophytes to ascend above the limit of the shales, and in the area indicated, where normally we might expect a xerophytic undergrowth, the deep shade of the beeches is such that *Scilla*

Fig. 8.

(a very attenuated form) is the only plant in possession of the ground.

Old Spring Wood has been greatly disturbed by quarrying operations &c., but in spite of great interference by man the dominant plants are those characteristic of the plateau.

*Distribution of Dominant Woodland Trees and Plants of the
Undergrowth in the Huddersfield District.*

Having determined some of the chief factors influencing the distribution of woodland plants in typical areas, it remained to extend the observations over a wider area, and so discover to what extent the results were capable of more general application. Consequently similar observations were carried on over an area of 66 square miles and the results recorded on maps of 6-inches to the mile scale.

This area is included in sheets 259 N.E. and S.E. 260, 261 N.W. and S.W., 271 N.E., and 272 N.W. and N.E. of the 6-inches to the mile Ordnance-Survey maps.

The two maps (figs. 9 & 10, pp. 352-3) show these details on a greatly reduced scale. This reduction, however, made it impossible to indicate the many small details studied; this will be easily understood if they are compared with the sketch-maps, figs. 1-5 and 7 & 8*. The map (fig. 9) shows the distribution of the dominant trees, viz.:—Coniferous trees, chiefly *Pinus sylvestris*, Oak (*Quercus Robur*, Linn.), and Birch (*Betula verrucosa*, Ehrh.); and shade-trees, chiefly Sycamore (*Acer Pseudo-platanus*, Linn.), Elm (*Ulmus montana*, Stokes), and Beech (*Fagus sylvatica*, Linn.). Areas are also indicated where trees occur buried in peat, these are chiefly Birch.

On comparing this with the undergrowth map (fig. 10) we see that the area covered by trees is relatively limited, while that covered by plants which are common in the undergrowth of the woodlands is much greater, especially to the west—i. e., species like Bracken (*Pteris aquilina*, Linn.), *Deschampsia*, Ling (*Calluna Erica*, DC.), and Bilberry (*Vaccinium Myrtillus*, Linn.) cover large tracts in a comparatively treeless region. We also see that while Bracken is absent commonly under shade-trees, it is not infrequently found there, and, on the other hand, it is not uncommonly absent under trees with an open canopy.

The distribution of *Vaccinium Myrtillus* is very interesting, especially when considered in the light of observations on its distribution elsewhere and the history of the vegetation in this

* In working out these details in the field I found it necessary to have a number of duplicate maps on which to record preliminary observations and build up the facts. To avoid the cost of many Survey Maps, tracings of the necessary areas were prepared and these were used as "negatives" from which the required number of prints were made on Thornton's Universal Photo-paper; these proved very useful.

district. It is primarily a humus plant, and its distribution depends on the presence of humus. As I have previously shown (109), and as Stahl (93) has since independently observed, the plant has Mycorrhiza on its roots. Stebler & Volkart (94), in their study of the "Matten und Weiden der Schweiz," made a statistical analysis of the species composing the several formations there, together with the influence of shade on their distribution. With reference to the occurrence of this species, they say: "Im Tieflande in Wäldern, in den Alpen im lichten Alpenwalde." We also find it in such situations in the Huddersfield district, but we see, on reference to the map (fig. 10), that there is a very considerable development also in open moorland areas outside our present woodlands. In Switzerland, however, it avoids the open sunny situations to such an extent that Stebler & Volkart apply to it the term "lichtfürchtend." This, however, seems too sweeping, for on p. 29 of the same contribution they say "Sie kommen in den Alpen im Freien vor, weil hier die Bildung des ihnen unumgänglich notwendigen Humus unter günstigen Bedingungen auch im Freien stattfindet." Still, as I have also observed, in Switzerland and elsewhere it reaches its greatest development in the open woods. In this connection, the observations of Wiesner (107) are of interest. In a brief reference to the dwarf form of this species (mentioned below, p. 388) which he often found in the Yellowstone district of North America, he says it occurred "in der Höhe von Thumb Bay im Schatten des Waldes und ich verfolgte es so weit, bis es zu verkümmern begann, also das Minimum des Lichtgenusses aufsuchte, welches ich = $\frac{1}{16.6}$ gefunden habe." It is very characteristic of the species in the Huddersfield district to avoid the deep shade of the sycamore-elm-beech woods, even though the necessary humus is available.

In view of the considerable evidence of the former occurrence of forest on the Moors of the Huddersfield district, as indicated below, can it be that its present distribution represents, to some extent at any rate, the position of previous open forest? In this connection successful attempts have been recently made, by Flahault (31), Eblin (27), Schröter (84), and others, to determine the limit of previous forest by means of the present distribution of species typically occurring in woods, and, as Früh and Schröter (32) have pointed out, extensive deposits of peat nowhere occur outside the tree limit.

10. MAP OF THE HUDDERSFIELD DISTRICT SHOWING THE DISTRIBUTION OF UNDERGROWTH & MOORLAND PLANTS IN THE HUDDERSFIELD DISTRICT.

This suggested a more extended examination of soils. The whole area under consideration lies on the Lower Carboniferous formations. Glacial deposits are entirely absent, and, except for deposits of peat to be mentioned below, the soils owe their origin chiefly to the direct denudation of the rocks. Lees (55) has given an interesting account of the "Lithology" of West Yorkshire, giving lists of species characterizing the several soils. In this he follows Thurman (96) and Baker (2), and finds that the soils exert a profound influence on the flora, due largely to their "mechanical" properties and to a much less extent to their chemical composition. Much has of late been written on this subject, an interesting summary of which has recently been given by Solms-Laubach (90). In the present study the works of Roux (82) and Hall (43) have been found very helpful.

Numerous analyses have been made of the soils in the different areas treated of in this paper, but the results are as yet too incomplete to be satisfactorily dealt with here, but they indicate that physical factors, especially those affecting available water, here play a more important part than the chemical, and the question of the influence of lime on vegetation is excluded by the total absence of these deposits in the district.

On the maps (figs. 9 & 10) the various features considered are shown only in the areas not under cultivation, from which it is clearly seen that while the distribution of certain species is influenced profoundly by the dominant tree, other factors are strikingly brought out. The extensive development of *Pteris*, ericaceous plants, and other xerophytes to the west is in remarkable contrast to their relative scarcity towards the east, where, however, they were somewhat better developed formerly than now, their reduction being due largely to cultivation.

The vegetation of this district will be seen to consist of 3 zones, using the term zone in the sense applied by Flahault (30), to indicate the successive stages of vegetation from the base to the summit of a mountain:—

(1) THE MOSS MOOR, which is high, wet, cold, and covered by deep deposits of peat, the dominant plants being cotton-grasses (*Eriophorum vaginatum* and *E. angustifolium*), and the more elevated and drier ridges being clothed with *Vaccinium Myrtillus*, *Empetrum*, &c. Bracken-covered slopes, with xerophytic associates, connect this zone with No. 2.

(2) MILLSTONE-GRIT PLATEAU.—An ericaceous zone of medium

altitude; soils shallow, sandy, dry, in places covered by shallow peat and exposed to the prevailing winds; the dominant plants are xerophytes, such as *Calluna Erica*, *Vaccinium Myrtillus*, *Deschampsia*, &c.

(3) LOWER COAL-MEASURE AREA.—A lower lying zone with soils deep, often covered by much humus and generally moist; the vegetation less exposed and mesophytic in character. The dominant plants of the undergrowth of the woodlands are *Holcus mollis*, *Pteris aquilina*, *Scilla festalis*, &c. If we keep strictly to the geological divisions, we find that the more elevated portions reach upwards of 1100 ft., and have soil conditions and climate favouring the development of xerophytes, and so bringing it within the ericaceous zone.

These three zones correspond nearly, but not quite, to the Moss Moor and the regions of Oat and Wheat cultivation respectively, indicated by Smith & Moss (88). The lower part of the Millstone-Grit plateau lies within the region of Wheat cultivation, while the elevated parts of the Coal-Measure area are in the region of Oat cultivation; though it is interesting to note that here Wheat cultivation is frequent though very much less so than formerly, economic conditions being in no small degree responsible.

As already stated, the rainfall and temperature vary considerably in the three zones, and below are given such observations as are available.

Rainfall.

Records of rainfall for a long series of years are not available for the exact areas required for our purpose; but for a limited period (1890-1901) records are published for several parts of the Moss Moor:—

Wessenden Head	1270 feet.	45·94 inches.
Harden Moss	1212 „	46·77 „
Deerhill	1149 „	44·77 „
Butterley (11 years) ..	1110 „	41·58 „

No records are available for the higher altitudes.

For the upper part of the Millstone-Grit area, three miles to the east of the Moss Moor, the averages are:—

Blackmoor Foot	800 feet.	42·16 inches.
Meltham Grange	850 „	40·31 „

For the Coal-Measure area the available records are just

beyond the northern boundary of our area. Here records have been regularly made for upwards of thirty years. For this period, after deducting the rainfall for abnormal years, the averages are :—

Huddersfield Cemetery....	400 feet.	33·00 inches.
Dalton, Huddersfield	350 „	32·19 „

Although from lack of records these cannot be compared with exactness, they serve to illustrate the fact that of the three regions the Coal-Measure area has the lowest rainfall, and, as stated in a letter to me by Mr. Joshua Robson, “every mile you go westward the total increases.” In passing over the Gritstone area the average rises steadily to about 42 inches, while the average to the extreme west on the Moss Moor is over 45 inches, while Lees (55) gives the rainfall of the Pennines generally as about 55 inches.

Mean Temperatures (° F.) at Harewood Lodge, Meltham, in the Millstone-Grit Area.

Altitude 510 feet. Lat. 53° 36' N., long. 1° 50' W.

	Jan.	Feb.	Mar.	April.	May.	June.	Year's mean.
At 4 feet above grass...	36·6 July.	37·5 Aug.	39·7 Sept.	44·0 Oct.	49·2 Nov.	55·7 Dec.	46·7 for 26 years 1879-1904.
On grass	58·5	57·8	54·1	46·6	42·2	37·6	
	27·9	27·3	29·4	32·1	37·2	43·5	35·9 „ 19 „ 1886-1904.
	46·7	46·1	42·1	36·1	32·8	28·5	
At a depth of 1 foot ...	37·0 57·7	37·1 56·9	38·5 53·8	42·8 47·5	48·5 43·0	54·6 38·9	46·4 „ 20 „ 1885-1904.
At a depth of 2 feet ...	38·0 56·9	38·0 56·6	39·0 54·1	42·8 48·6	48·0 44·2	53·6 40·2	46·7 „ 20 „ 1885-1904.

WARMEST MONTH.

At 4 ft. above ...	July 1901, 63°·2
On grass	July 1899, 49°·8
At 1 ft. below ...	July 1901, 60°·0
At 2 ft. below ...	Aug. 1899, 59°·3

COLDEST MONTH.

At 4 ft. above ...	Feb. 1895, 27°·8
On grass	Feb. 1895, 14°·9
At 1 ft. below ...	Feb. 1895, 32°·2
At 2 ft. below ...	Feb. 1895, 33°·6

The absolute highest temperature recorded at 4 feet above grass was 86°·9 on July 18th, 1901.

The absolute lowest temperature recorded at 4 feet above grass was +0°·5 on Feb. 8th, 1895.

The absolute lowest on the grass (*i.e.* on snow), Feb. 8th, 1895, -8°·9.

The only time the one-foot thermometer has been below freezing-point was from Feb. 11th to Feb. 23rd (inclusive), 1895. Lowest 31°·2, on Feb. 15th, 1895.

Lowest temperature of two-foot thermometer from Feb. 19th to 26th, 1905, 32°·9.

Mean Temperatures (° F.) taken at Huddersfield Cemetery in the Coal-Measure Area for the 28 Years 1877-1904.

Altitude 400 feet.

	Jan.	Feb.	Mar.	April.	May.	June.	Year's mean.
At 4 feet above grass.....	36.7	37.7	40.1	44.2	49.7	56.3	46.9
	July.	Aug.	Sept.	Oct.	Nov.	Dec.	
	59.4	58.4	54.5	46.8	41.7	37.7	

For the last eight years, 1897-1904, owing to the relatively high temperature of the winter months, the yearly average was 47°·8 F.

WINTER AVERAGE.

Dec.-Feb..... 37°·3

SUMMER AVERAGE.

June-August 58°·0

No records of temperature are available for the Moss Moor, but estimating the decrease at the rate estimated by Dalton, viz., 1° Fahr. for each successive ascent of 100 yards, we may give the temperature of the Moss Moor at 44° F., and for the highest points probably 42° F., while that of the lowest levels would be 47°·5 F.

I am indebted to Mr. J. Firth for details of rainfall and temperature taken at the Huddersfield Cemetery, to Mr. Joshua Robson for the records at Dalton, and for the remainder to Mr. J. W. Schofield, Waterworks Manager to the Huddersfield Corporation; while Mr. Charles Brook has kindly supplied me with the interesting records of temperature taken at Harewood Lodge, Meltham.

(a) *Cotton-Grass Zone of the Moss Moor.*

The term Moss Moor has been adopted by W. G. Smith (88) as the equivalent of the German "Hochmoor" or "Moosmoor," a term especially suitable as these moors are often known locally as "Mosses"—e. g., Harden Moss, Holme Moss, and Featherbed Moss, the latter being a very suggestive name when the cotton-grasses are in fruit.

This region is to the extreme west of the district and is a portion of the Pennines. The hills run from N. to S. with an altitude of from 1700 to 1100 feet. The rainfall is high (45 inches or more), and this is therefore an important catchwater area for the manufacturing towns and villages in the valley below. The geological formations here are the Kinderscout grits, and above them extensive deposits of shales and clays. Developed on these are large beds of deep ill-drained peat covered almost entirely with cotton-grasses, chiefly *Eriophorum vaginatum*, L., and to a much less extent *E. angustifolium*. These stretch for miles in monotonous characteristically

rippled sheets with very few associates. The saddle-backed ridge extending from West Nab to Shooter's Nab is an outlier of rough rock, the eastern slopes of which are covered with fallen blocks due to the denudation of the shales beneath. In the drier parts and hill-summits the cotton-grasses are replaced by Bilberry (*Vaccinium Myrtillus*), *Empetrum nigrum*, Linn., *Vaccinium Vitis-idaea*, Linn., and Cloudberry (*Rubus Chamæ-morus*, Linn.). The cotton-grasses play a very insignificant part in the flora of our present woodlands.

There is considerable evidence which points to the cotton-grass being of recent development, at any rate over certain parts of this moorland. Borings and excavations made at Deerhill, Good Bent, and Wessenden Head reveal a layer of buried heath-stems beneath the present cotton-grass, and persons now living (gamekeepers, &c.) can remember large tracts being covered with ling (*Calluna*) which are now dominated by cotton-grass (*Eriophorum vaginatum*, Linn.). At Wessenden Head considerable changes have taken place in this direction even within the last eighty years. This is attributed to interruption with drainage. During the last few years attempts have been made to improve the drainage by cutting long "grips" in the peat. This has already had a very marked effect, the cotton-grass shows evident signs of deterioration, while young shoots of ling are appearing in myriads over the area and its re-establishment is only a question of time.

Although now a treeless zone, forests were formerly extensive, and much buried timber is found here. An extensive deposit exists at Deerhill, chiefly of Birch (*Betula*) and a little Oak and Hawthorn (*Crataegus*). Buried trees (chiefly Birch) are also to be seen at Butterley Hill and Wessenden Head, and during excavations for a reservoir near Meltham a number of buried trees were found consisting of Oak, Birch, and Hazel (49). The position of these deposits is indicated on the District Tree Map.

I have not found the Scotch fir (*Pinus sylvestris*) in the peat of these moors, but Hughes (50) says:—"The immense quantities of fir and oak wood, more particularly the former, dug out of the moors surrounding Meltham give abundant proof that . . . extensive forests of these trees must have covered the hills . . . This fir wood, afterwards dug up out of the moors in hundreds of cart loads, was used as torches by the cottagers

within the last 70 years. They cut it into long splinters and made it serve for candles." In Switzerland and elsewhere on the continent, such pine splinters (or "Kienspähne") are still frequently used for this purpose. The altitude of these moors ranges from 800 to 1100 feet. This succession of deposits is well seen in section at Wessenden Head and Deerhill, where the series has been cut through by moorland streams. At the base is a thick bed of bluish clay which is permeated by numerous root-fibres. Above this is the moor pan, a layer of only a few inches in thickness, which can be easily detected by the peculiar grating sound produced when the blade of a knife is pushed into it. Resting on this is a thick bed of peat from four to six feet in thickness, while in some parts it very greatly exceeds this. At the base of the peat, remains of birch are abundant, especially at Deerhill, where the overlying peat, having been denuded, a very large number of birch remains are to be seen. We have here just those conditions necessary for the accumulation of peat, as indicated by Hall (43), Livingstone (60), and others, viz., considerable rainfall and an impermeable stratum, which result in a waterlogged soil, cutting off access of air and so checking the process of oxidation and the development of aerobic bacteria. These conditions, together with the poverty of the soil in mineral salts, especially carbonate of lime, favour the accumulation of humus and of humic acid; this in turn affects the osmotic action of the roots, with the result that, even in permanently wet places, xerophytes only can exist, and these are also favoured by the general climatic conditions of this zone. A general account of these peat-moors has recently been given by C. E. Moss (71).

On the steep hill-slopes peat is either very thin or absent, the soils being formed by denudation of the grits, shales, and clays, and forms a transition region to the Heather Zone of the Millstone-Grit Plateau.

These slopes are clothed with a very characteristic vegetation. *Pteris* is the dominant plant, and its associates are Bilberry (*Vaccinium Myrtillus*), Ling (*Calluna*), *Deschampsia*, *Nardus stricta*, and *Festuca ovina*, forming a Xero-pteridetum. These may be traced ascending the deep cloughs in gradually narrowing strands, the Bracken becoming reduced in size (sometimes not more than a few inches in height) until on the exposed summits it is practically absent. A map showing the distribution of

Bracken, therefore, gives us a very good outline of these slopes of the moorland valleys and cloughs, and up these it ascends to a height of 1700 feet. (Fig. 10, p. 353.)

To the east it descends along the valley-slopes in broken strands to spread out in sheets on the plains when protected by trees, to be again cut out by the deep shade of Sycamore, Elm, and Beech.

The woodlands of the hill-slopes consist chiefly of Oak, Birch, and Pine. All are planted, but are often on the sites of primitive forest or scrub, and none of the woods in this or the two other zones considered is now primitive. They are given up rather to the preservation of game than to the growth of timber. Not much felling or pruning is done, and thus they remain practically undisturbed for long periods. The Oak ascends to 1200 feet, but dies out above that limit, and the undergrowth is essentially that of the adjacent moorlands. In the neighbourhood of Harden Moss are Pine-plantations from 1500–1100 feet, and again at Black Moor from 1000–800 feet; but here they are fully exposed to the prevailing winds, thrive badly, and in several areas all the trees are dead. The undergrowth is chiefly Bilberry (*Vaccinium Myrtillus*).

(b) *Heather Zone of the Millstone-Grit Plateau.*

The central portion of the district is sharply marked off from the western, and consists of a magnificent Millstone-Grit plateau, through which deep narrow valleys have been cut into the shales below by the tributaries of the river Holme. Though now highly cultivated, it was formerly a heather moorland, and the several portions are known as Thickhollins Moor, Melthan Moor, Black Moor, Honley Moor, Netherton Moor, and Crosland Moor. This plateau dips gently to the S.E. from 1000 to 450 feet. The soils are shallow, sandy, well drained, and in places covered with a thin deposit of peat usually not more than 6–12 in. deep. In contrast to the Moss Moor, the conditions here are such as to be unfavourable to the formation of deep ill-drained peat. Some of this, as at Honley Woods, is Bracken peat, being composed almost entirely of the remains of this plant, and though this species is still present and in places abundant, the Ling and Heath associates are now dominant. This area is swept by the prevailing west winds, and in the spring by the dry east winds, which, together with the soil-

conditions, favour the development of Xerophytes. It is a typical physiologically dry area. Although the unreclaimed heather moors are now small in extent and somewhat widely separated, the roadside vegetation often consists of the relics of the original moorland, and is of the heather moorland type, and this indicated on the large-scale maps shows the present moorlands to be joined by a network of heath-plants. This primitive vegetation is only kept in check by heavy manuring, and if that is neglected the fields soon revert. Many acres which formerly produced rich crops have now "gone back" to moor. This type of vegetation extended formerly over the whole of the Gritstone area. The features thus brought out help us in great part to reconstruct the former vegetation of the Moss Moor and Millstone-Grit plateau.

Although the rainfall in the latter area is considerable, the soils are so permeable and poor in humus that they retain little water. Heavy manuring in a great measure corrects this, but when this is discontinued the less resistant cultivated plants give way to xerophytes, which alone can withstand the drier conditions and the sudden changes of temperature to which such soils are liable.

As Graebner has shown, the effect of rich nutrition on heath-plants, while it favours increased growth, renders them less able to withstand the extremes of drought and cold.

Oak is the dominant tree, but prior to cultivation, as shown by Moorhouse (69) and in ancient records, it was much more extensive in this area. Along the edges of the plateau, Birch (*Betula verrucosa*, Ehrh.) is abundant and at Honley Moor are plantations of Pine, while Holly (*Ilex Aquifolium*, Linn.) is common on the slopes of Honley Wood. The tendency in recent years has been to replace Oak with Sycamore, Elm, and Beech. Woodlands are developed chiefly along the valley-slopes, and on the map they give a general idea of the contour of the country, and appear much narrower than they really are. The eastern boundary of the Gritstone plateau is well marked by these woods, the woods on the plains being characterized by their broader (squarer) outlines.

The prevailing west winds sweep across these plains, and a reference to the map will show that plants growing in the open oak-birch woods, along the edge of the plateau, are placed under conditions of drought and exposure (especially when we

remember the shallow sandy nature of the soil here) in strong contrast to species in the same wood growing on the steep, moist, sheltered slopes. The trees, too, on the exposed parts are generally stunted, being little more than tall shrubs.

(c) *Coal-Measure Area.*

The river Holme forms a well-marked boundary between the Millstone-Grit plateau and the Lower Coal-Measures. The rocks here consist of shales, clays, and fine-grained sandstones often in rapid alternation. The soils offer a striking contrast to those of the west; they are generally deeper and consist of more or less clayey loam, and therefore moisture is more constant. The general altitude of this area ranges from 450 to 200 feet, though to the south-east the hills rise to 1200 feet. In parts (usually the higher level) the soils, where they lie immediately above the sandstones, are not uncommonly shallow, well-drained, relatively dry, and yield a flora distinctly xerophytic. It is on these soils that the heath-plants—Bilberry, Ling, *Deschampsia*, and others—are carried, often in small patches, to the east. In the days prior to high cultivation there is evidence that these tracts were much more extensive than at present, and yielded species now extinct, such as *Listera cordata*, R. Br., &c. While Oak is still the dominant tree, there is a greater development of Sycamore, Elm, and Beech. With the deeper soils, increased moisture, lower altitude, and less exposure the trees thrive better and attain much greater dimensions than in the higher regions to the west. But in both areas, though more especially to the east, tree-growth is handicapped by the smoke-cloud from the manufacturing towns and villages in the district. The undergrowth consists largely of mesophytes, the three characteristic plants being Bracken (*Pteris aquilina*), *Holcus mollis*, and *Scilla festalis*, forming a Meso-pteridetum. To the south-east, in the neighbourhood of Cheese Gate Nab and Pike Lowe, however, the hills ascend to 1200 feet. They are capped with Grenoside Sandstone, and here, as well as on their steep and exposed shaly slopes, we get a repetition of the xerophytes noticed on the slopes to the west, viz., *Vaccinium Myrtillus*, *Calluna Erica*, DC., *Erica cinerea*, Linn., *E. Tetralix*, Linn., *Pteris*, and xerophytic grasses; these plants also form the characteristic vegetation of the undergrowth of the woods on these hill-slopes.

*Distribution of the Plants of the Millstone-Grit and
Coal-Measure Areas, as affected by Soils.*

It is evident from the above observations that a change of geological formations and soil-conditions is accompanied by a change of plant formations.

In illustration of this we will take the upper central portion of the district shown on the maps figs. 9 & 10 (pp. 352-3), that is, the part covered by sheet 260 of the 6-inch Ordnance-Survey map. Here the two well-marked biological types occur, xerophytes and mesophytes, and their distribution has been worked out on the 6-inch map, special attention being paid to the transition region from the Millstone-Grits to the Coal-Measures. On the map fig. 11 (p. 364) the results are shown reduced to the 1-inch scale.

Fig. 12 shows the geology of the same area, the details being taken from sheet 260 of the 6-inch Geological-Survey map, and, as in fig. 11, reduced to the 1-inch scale. Glacial deposits are entirely absent, and, except for the formations of peat already referred to, the soils owe their origin mainly to the denudation of the underlying rocks, and therefore a comparison may, I think, be fairly made with the solid geology map.

If we now make a comparison of the two maps figs. 11. & 12, we find them both instructive and suggestive. *Pteris*, as we have seen, is abundant in both areas, but its associates differ considerably as we pass from one formation to the other. The xerophytes are seen to follow pretty closely the Millstone-Grit and Coal-Measure sandstones, except in the exposed, elevated regions; while the mesophytes indicate as clearly the shales and clays.

To render comparison easy, the same signs are used on the two maps: the blackened areas indicate shales and clays on the geological map and Mesophytes on the vegetation map; the other sign indicates respectively sandstones and Xerophytes, a small semi-xerophytic area is indicated by dotting.

Considerable differences occur in the physiological water in soils over beds indicated by the general term shales, and a more detailed study of these is in progress on lines similar to those followed by Hedgecock (45).

In some instances, Xerophytes are absent over areas indicated as sandstone on the Geological Map, as in Woodsome and

between the two, there is not infrequently an overlap—the Xerophytes being carried further down the slopes, due partly to the surface being strewn with fallen blocks of sandstone and soils resulting from their denudation. As we have seen, the more resistant sandstones usually occupy the higher ground, and the conditions of soil and climate there favour Xerophytes; while shales occupy the lower levels and sheltered slopes, where soils and climatic conditions favour the development of Mesophytes.

As we follow the species over the escarpments, we find that, on reaching the shales and clays, Ling is the first to die out, which it does very quickly. The Bilberry often extends further down the slope, but, as with Ling, it dies out as the humus becomes deficient, while *Deschampsia* holds on when both its usual associates have disappeared. These features can be well shown in a limited area, as in the case of the Armitage Bridge Woods (fig. 8, p. 349) or other woods skirting the Millstone-Grit Plateau, where, on the steep slopes, we get a rapid transition from the dry exposed grit area above to the moist sheltered slopes of the shales and clays below. These results fully bear out Warming's observations that the distribution of plants is determined largely by available water.

A comparison of the four maps (Trees, Undergrowth, Geology, and Xerophytes and Mesophytes) will show the effect of the dominant factors on plant-distribution in this area, viz.: soils, moisture, exposure, light, and shade.

In the field I found it very convenient to use special terms for these soil types, and had intended suggesting names which seemed to express well the associations in relation to soil-conditions; but, considering the unsettled state of Ecological Nomenclature, and that it will soon be considered by an international committee, I have withheld them. As one may gather from a perusal of Clement's paper (16), the study of ecology may very easily be burdened with many cumbrous names which to me it seems well to avoid if possible. The terms I have used, Xero-pteridetum and Meso-pteridetum, are easily understood, and indicate sufficiently well the two important associations determined by soil-conditions in this district.

Livingstone (60) has evidently been working on similar lines in a glaciated area in Michigan, but paying special attention to the distribution of trees, and has obtained corresponding results.

II.—EFFECT OF ENVIRONMENT ON STRUCTURE.

From what has been said, it is clear that these common species must frequently grow under very dissimilar conditions, and in examining the plants in the transition zone, or zone of tension as Cowles terms it, it is at once obvious that a change of conditions, while not immediately limiting their distribution, produces a marked effect on their habit and structure. We find that as the Mesophytes invade the region of the Xerophytes, and come under the influence of drier and more rigorous conditions, they develop xerophytic characters. On the other hand, as the Xerophytes encroach on the Mesophytes, and come under the mellowing influences of moisture and shade, they tend to lose xerophytic characters and take on mesophytic characters. The more plastic or adaptable a species is, the wider its range of variation and distribution; the less plastic or adaptable species show a narrow range of structural variation and a more restricted distribution. Between these extremes we find every degree of modification. My object has been, therefore, to ascertain the region of maximum development of a few common species, study their conditions of growth, and determine to what extent a change in one or more of these conditions has upon their structure.

Judging from a summary of the investigations made by Chrysler (13), similar changes have been noted in the strand-plants occurring on the Atlantic Coast in the vicinity of Woods Hole, Mass., and also near Lake Michigan near Chicago, Ill.; and Hesselman (47) has recently published the results of his investigations of the plants of the "Laubwiesen" of Sweden, and they agree closely with mine.

The study of Plant Biology has of late received considerable attention, and the works of Schimper, Goebel, Wiesner, Stahl, Haberlandt, &c. provide us with a useful foundation on which to build further investigations into the complex relations and life-histories of the plants forming these associations.

There is perhaps a danger, when studying the structure of a plant in relation to its environment, to assume on insufficient grounds direct adaptation. A useful and timely corrective in this direction is the recent excellent criticism by Detto (23). The point of view adopted by Küster (54) is also worthy of careful consideration in this connection. Many of the modi-

fications usually attributed, for example, to the direct influence of light, mechanical forces (as strain), &c., he would consider rather as pathological states due to insufficient nourishment, lowered transpiration, and the like.

Again, the results obtained by the examination of the tissues of plants exposed to sun or shade are sometimes contradictory. It is generally admitted that what are known as "sun-leaves" are developed in situations exposed to intense sunlight, as on sand-dunes, moorlands, Alpine regions, as well as under less rigorous conditions.

Leist (56), however, in examining the leaves of Alpine plants, came to the conclusion that they showed mesophytic rather than xerophytic, shade rather than sun, structures, and gave as an explanation the considerable period during which the mountains are enveloped by clouds.

Wagner (97), on the other hand, came to the opposite conclusion, and found that the "sun" type and xerophytic structures became more pronounced with increased altitude and the accompanying xerophytic conditions. This accords with the observations of Bonnier (7) and others, and also that transpiration and assimilation are augmented at high altitudes.

Wiesner's observations on transpiration (104) show that under the same conditions shade-leaves transpire more than sun-leaves. Bergen (5), however, in his study of the evergreens of the Mediterranean region, concluded that sun-leaves transpired more than shade-leaves under the same conditions.

The investigations of Ball (3) as to the value of stresses in the development of mechanical tissues has considerably modified our views on this subject; from his results we are no longer able to give such an important place to the effects of the stimulus of stresses as we were led to do by the earlier experiments of Hegler (46).

These instances will be sufficient to show that so-called adaptive structures will require in the future re-investigation, and that we are scarcely justified, in spite of the considerable work that has already been accomplished, in attributing dogmatically these modifications to particular factors. We may record the modifications and observe the conditions under which they are produced as far as we can discern them, but prolonged study, not only in the laboratory, but also in the field, will be necessary before satisfactory conclusions can be drawn.

We will now consider some of the modifications noted in the more important species characterizing the several associations of the Huddersfield district.

(a) DOMINANT SPECIES.

PTERIS AQUILINA, LIND. (*Pteridium aquilinum* Kuhn).

Bracken.

It has been already shown that the distribution of Bracken is extensive in this district. It is the dominant plant of the undergrowth in the Coal-Measure Oak woods, where it forms large and characteristic masses, but when the dominant trees are Sycamore, Elm, and Beech, or a dense shrubby undergrowth of Hazel or Elder, their deep shade tends to restrict its distribution. Outside these woods, it is confined mainly to the hedgerows, perhaps a relic of a former more extended distribution. It ascends into the Gritstone area, where, in the dry shallow soils, it is limited by competition with rhizomatous plants such as Ling and Bilberry. In the open Birch-Oak woods along the edges of the Gritstone Plateau many observations were made to determine the positions these rhizomes occupy with relation to each other. It was found that, in 95 per cent. of the plants examined, the rhizomes of Bracken were from four to six inches nearer the surface than was found to be the case in a corresponding number of observations in the Coal-Measure Oak woods. In areas where Bracken is associated with Ling and Bilberry, its rhizomes were found to be distinctly below those of the latter; while the rhizomes of Ling, though generally two to three inches above those of the Bracken, were not uncommonly found at the same level, and often they were distinctly interlaced. Here Bracken rarely forms continuous sheets, but is broken up into more or less isolated patches, as shown in the Heather area in the map of Armitage Bridge Woods (fig. 8, p. 349); and this is a characteristic feature in all dry Oak and Birch woods wherever these plants are associated; they form, as we have seen, a competitive association, and sometimes one, sometimes the other species dominates. In such situations, therefore, Bracken is much more exposed to adverse conditions, such as higher level, dry shallow soils, strong winds, much less protection by trees; and the rhizomes being more superficial, they are more likely to suffer injury through cold. As might naturally be expected,

it is in the open, more exposed parts of this area that xerophytic characters reach their greatest development. In the treeless hill-region to the west it is a characteristic plant of the steep hill-slopes, where it is a striking feature in the landscape. These slopes offer it considerable protection, but the species dies out above as the exposure increases. The leaves here do not exhibit as a whole such strongly marked xerophytic characters as those of the Gritstone Plateau, for, although the plants are exposed throughout a considerable period to intense sunlight, the soil-conditions as regards moisture are on the whole more favourable.

Growing in such diverse habitats and under such varying conditions, the plant shows extreme modifications in structure. Very numerous specimens have been collected and examined, and my observations on the structure of the leaf bear out fully those of Boodle (9), and his suggestion that "light is not the all-important factor determining the structure of the sun and shade leaves," is supported by my observations of plants in natural habitats in this area. I should, however, say that light is only one of the factors, the other chief ones being wind and available moisture; for we find extreme shade-structures in sheltered moist situations under the shade of Beech and Elm, and the maximum sun-form in bright, illuminated, windy, dry situations on the Gritstone Plateau.

The admirable pioneer work of Stahl (92), also of Haberlandt (42) and Schimper (83), laid the foundations for observations of this kind, and they have been since extended in many directions by numerous observers. For a more extensive bibliography on leaf-structures and functions, reference may be made to Karsten (50 A) and Burgerstein (10).

Figs. 13-16 (p. 370) show transverse sections of corresponding pinnæ from plants growing under different conditions.

Fig. 13 is a section of a leaf from an open Birch wood on the Gritstone Plateau. Here the fronds are from 12 to 18 inches in height, are dark green in colour, and leathery, the plants barely overtopping the plants of *Ling* among which they grow. The epidermis has a thick cuticle, the cells of which are devoid of chlorophyll; beneath this is a nearly continuous hypoderm consisting of thick-walled colourless cells forming an aqueous layer. Between these are occasionally thin-walled cells which contain few or no chlorophyll granules. Below this is a well-

developed palisade about three cells deep, followed by a reduced spongy tissue with relatively small air-spaces.

Fig. 14 is a section of a pinnule from the leaf of a plant grown in an Oak wood. The cuticle of the epidermis here is thinner, the cells contain few chlorophyll grains, and the hypodermis is developed only over the veins. The palisade, though well defined, consists only of two layers, and between these cells small air-spaces are frequent. In the spongy tissue the air-spaces are large.

Figs. 13-16.

Fig. 13. Trans. sect. of a pinnule of *Pteris aquilina* from a plant growing under xerophytic conditions on the Gritstone Plateau.

14. Trans. sect. of a pinnule from a plant growing in the medium shade of an Oak wood.

15. Trans. sect. of a pinnule from a plant growing under the shade of Sycamore.

16. Trans. sect. of a pinnule from a plant growing under the deep shade of Beech.

Fig. 15 is from a frond growing in the shade of a Sycamore wood. In this case the cuticle is very thin, palisade greatly reduced, a spongy parenchyma occupying a very considerable part of the mesophyll. Chlorophyll corpuscles more frequent in the epidermis than in fig. 14. The leaf is therefore much thinner.

Fig. 16 shows the section of a leaf from a plant growing in a moist situation under the shade of Beeches. It is exceedingly thin, the epidermal cells are very thin-walled and contain numerous chlorophyll granules, while the mesophyll is reduced to two or three cells in thickness.

All these variations in structure may be found within a very limited area; *e. g.*, the woods at Armitage Bridge, as they afford all the necessary conditions. These woods skirt the edge of the Gritstone Plateau and extend over the steep slopes. Their higher parts are dry and sandy, and the soil is covered with a shallow peat, and the plants are exposed to the adverse conditions of the plateau generally. Bracken occurs in patches among the ericaceous undergrowth, and in the less protected parts develops extreme xerophytic characters. Over the moister, more sheltered slopes, protected by the Oak, it becomes more mesophytic in structure; while in the deep shade area in the slope, under Beech and Elm, it becomes extremely attenuated and eventually dies out.

The amount of shade produced by a given species of tree is not always the same; consequently we do not necessarily find shade-structures developed in herbaceous plants under shade species. Closeness of planting, age of tree, and the condition of its growth have to be considered.

Pteris aquilina. Leaf-stalk.

The examination of leaves from these different habitats showed that not only was the leaf-blade modified in structure according to environment, but also the leaf-stalk. For purposes of comparison, transverse sections were made in each case $1\frac{1}{2}$ in. below the lowest pair of leaflets. These are shown in outline in figs. 17, 19, 21, 23, 25, 27 (p. 372). Portions of these are shown $\times 150$ diam., taken through the tissues of the same region in each case. Fig. 17 is a section from a plant growing in a dry windy situation in an open Birch wood on the Gritstone Plateau. Here we see (fig. 18) the stereom is very strongly developed, and the cavities of the fibres are reduced to minute pores. This band is 13 or 14 cells deep, encroaching closely on the outer steles, and the thickening is continued into the ground-tissue still further. If portions of these leaf-stalks are cut off and tapped together, they ring like dry bones. The stereom as here developed

Figs. 17, 19, 21, 23, 25, & 27.

Fig. 17. T. S. leaf-stalk from exposed situation of Gritstone Plateau.

18. T. S. portion of the same; $\times 150$ diam.

19. T. S. leaf-stalk, Oak-wood form.

20. T. S. portion of the same; $\times 150$ diam.

21. T. S. leaf-stalk from a very large frond from a moist Oak wood.

L = lacunæ.22. T. S. portion of 21; $\times 150$ diam.

23. T. S. leaf-stalk of an immature shade-form.

24. T. S. portion of 23; $\times 150$ diam.

25. T. S. leaf-stalk, mature shade-form.

26. T. S. portion of 25; $\times 150$ diam.

27. T. S. slender leaf-stalk, Oak-wood form.

28. T. S. portion of 27; $\times 150$ diam.

Figs. 18, 20, 22, 24, 26, & 28.

Leaf-stalks of *Pteris aquilina*, showing variations in the development of stercom in plants growing under different conditions.

will be of service in resisting strain in every direction. The stem is further strengthened by the development of well-marked stereom-strands between the steles (fig. 17).

Bracken Leaf-stem. Oak-form.

The leaf-stalk of a plant growing under moderate conditions of light, moisture, and wind in a Coal-Measure Oak wood shows in transverse section a somewhat cylindrical outline (fig. 19), flattened or slightly depressed, along the upper and lower surfaces. The sclerenchyma forms a firm but narrow band, often not more than four to five cells deep, with a slight tendency to increase along the upper surface (fig. 20). The supporting mechanism is that of a pillar or strut, and the great majority of specimens examined showed very little specialization beyond this, even in cases of very large fronds with leaf-stalks $\frac{3}{8}$ in. or more in diameter. In these the tendency is to develop one or more fairly large lacunæ (figs. 21 & 22).

Leaf-stalk. Shade-form.

If we now examine plants growing in the deep shade of Elm or Beech, we find the leaf-stalk strikingly reduced, often less than $\frac{1}{8}$ in. in diameter. Relatively large, very thin fronds are developed, but the leaf-stalk is too weak to support the weight of the blade, and the general habit of the plant is drooping or more or less prostrate. Fig. 23 is a transverse section of the leaf-stalk of a young frond, which had grown about a foot above the surface of the ground and before the blade had expanded. The outline is somewhat circular, but with a distinct tendency to flatten on the upper side. The sclerenchyma is slightly developed peripherally, forming a very narrow band two or three cells deep (fig. 24). As the leaf-stalk matures and the frond unfolds, it will be under the stimulus of slight but continuous stress, and a comparison of this with the mature form shows striking changes to have taken place (figs. 25 & 26). The outline becomes less circular, and a well-marked girder-form is developed; the tension-flange is narrow but considerably thickened, with a distinct wedge of sclerenchyma in the centre. The compression-flange is broadened considerably and develops lateral wings, which not only serve to withstand compression, but stiffen it for resisting lateral stresses, just as girders are

sometimes stiffened by side-pieces to resist lateral vibrations. In addition we find lateral stereom strands developed in the ground-tissue between the steles. These might be compared to the similar strands found in the exposed form. Fig. 26 shows these outer tissues with the much thickened stereom-band. Under these conditions and in such habitats, this form frequently recurs throughout the district.

Frequently we find leaf-stalks of a similar diameter in the Bracken of an Oak wood, but they are erect, not drooping. They are subjected mainly to compressive stresses, and the tendency of the stalk is to form the strongest strut or pillar. A transverse section (fig. 27) of such a slender-stalked form, therefore, shows a distinct pillar-mechanism with the strengthening material as far from the centre as possible. The outline is somewhat circular, with a uniform band of much-thickened sclerenchyma nine to ten cells deep (fig. 28), the fibres of which are more brittle than in the deep-shade form. In this the strands between the steles are often not developed.

The Bracken thus affords an interesting example of the development of mechanical tissues apparently as a result of tensile and compressive stresses. In the shade-form the stresses are small but continuous, due to the weight of the relatively large frond. Under opposite conditions in dry, open, windy situations, although the plants are dwarfed and thus relatively protected, the stalk is affected by varying stresses in all directions, and here we find the development of the stereom to be enormously increased. Under medium conditions, in the shelter of an Oak wood, the leaf-stalk is tall, erect, and pillar-like. Every gradation between these forms is found under intermediate conditions. Many of the specimens first examined showed these features to recur so often as to give support to Hegler's results (46). But forms were found which introduced an element of uncertainty; and it is obviously impossible to judge of all the conditions influencing these structures in the field. The exceptions were frequent enough to show that although the stimulus of stresses might be a contributory cause, evidently other influences were at work as yet undetermined. The evident pliability of this species recommends it as suitable for experiments in this direction, but the results are as yet too incomplete to be dealt with here. Ball (3), who has recently repeated Hegler's observations, contends, as the result of numerous interesting

experiments, that the development of mechanical tissues is not so induced; and he failed to produce either increase in the ability to resist mechanical pulling, or any thickening of the tissues, as the result of a gradual increase in the pull exerted upon young stems. The results he produced were inconstant—sometimes a thickening was produced, sometimes not. We must look, therefore, to some other (probably a series of interacting) causes for a full explanation of the development of stereom.

Pteris aquilina. Rhizome.

Many observations have been made and much has been written on the presence or absence of *Pteris* on calcareous soils, and the influences of the physical and chemical nature of the soil on its distribution and structure. In West Yorkshire it shows a distinct preference for sandstone soils, but, as indicated by Lees (55) and others, it is by no means absent from limestone; while More (70) includes it in the group "Calcifuge B," that is, not infrequent on lime soils, but invariably in greater abundance and luxuriance on soils from which lime is absent. More recently its distribution from this point of view has been dealt with by Gillot & Durafour (34). In the Huddersfield district calcareous soils are absent, therefore lime cannot be one of the factors influencing its distribution within this area.

Masclef (64) examined the rhizomes of Bracken growing respectively in clayey and calcareous soils on the escarpments at Rogerville and Harfleur and also on the granite rocks at Cezembre. He found that in siliceous soils they present the normal structure; in soils impregnated with lime the sclerenchyma was greatly developed, the outer band of reserve conjunctive tissue being reduced to half its normal diameter; whilst in pure chalk the sclerenchyma was increased to such an extent as to reduce the reserve tissues to a very narrow band. These changes he attributes to the chemical influence rather than to the physical nature of the soil. He found that specimens collected on soils containing 5 to 7 per cent. of lime showed structures between those growing on pure chalk and those growing on exclusively siliceous soils. No such quantity of lime could be expected in the soils in the Huddersfield district, and careful analyses of many samples showed them to contain from '02 to '04 per cent. of lime; yet an examination

of the rhizomes of plants growing in sandy soils containing .03 per cent. of lime on the Gritstone Plateau showed modifications exactly similar to those attributed by Masclef to the chemical influence of lime. I can find nothing in a chemical analysis of these soils which helps to account for these striking variations, but would rather attribute them to physical and climatic conditions. Certainly here the modifications cannot be attributed to the chemical influence of lime. The study of vegetation in this region tends to support the conclusions and experiments in this direction of Warrington (103), Hedgecock (45), and others.

In the moist sheltered situations over clays and shales of the Coal-Measures and under the shade of Beech, the rhizomes lie in the loose humus near the surface and may be very easily uprooted. Here they are relatively slender, easily break, and are scantily covered with brown hairs.

Fig. 29 (p. 378) is a diagram of a transverse section of such a rhizome, and fig. 30 shows in detail the structure of the mechanical tissues. The epidermis consists of thin-walled and wrinkled cells, and beneath this is a single line of dark brown cells whose outer and radial walls are strongly thickened and pitted. This is succeeded by a band 3-4 cells deep with yellowish, very slightly thickened walls, these cells containing a small number of starch-grains. The two bands of sclerenchyma between the outer and inner rings of steles, consist of cells with pale brown, slightly thickened walls, and contain numerous starch-grains.

In striking contrast to this, the rhizomes of Bracken growing in sandy soil in an Oak-Birch wood on the Gritstone Plateau show an enormous development of stereom (fig. 31). The epidermis produces abundant hairs forming a thick felt-like covering. Beneath this is a band 2-3 cells deep with dark brown, greatly thickened and pitted walls, succeeded by a broad yellowish-brown band 9-10 cells deep, and with strongly thickened walls forming a well-marked stereom-band containing little starch (fig. 32). Between this and the outer steles are several few-celled stereom groups. The stereom between the outer and inner steles forms often a complete ring and extending outwardly between them. The walls are dark brown, very strongly thickened and pitted, the cavities greatly reduced and containing few or no starch-grains. In addition to this, each of the outer steles is bounded on its outer side by a well-marked

Figs. 29-32.

Fig. 29. T. S. rhizome of *Pteris aquilina* growing under the shade of Beech.

30. T. S. portion of 29 $\times 150$ diam. showing weakly-developed stereom.

31. T. S. rhizome of *P. aquilina* from a plant growing in an exposed situation in dry sandy soil.

32. T. S. of 31 showing strongly-developed stereom. $\times 150$ diam.

stereom-band 2-3 cells deep, and an almost complete stereom-plate is formed in the centre between the inner steles. On the steep slopes in the transition region every gradation between these extremes is found as we pass from the dry exposed gritstone summit over the moister sheltered areas of the shales and clays, the rhizomes reaching their maximum development and possessing the greatest storage capacity in the moist Oak woods in moderate shade. The observations of Blackman (5 A), Brown (9 A), and others show that shade-leaves assimilate more in the shade than sun-leaves in the shade. Under these circumstances, much starch will be produced by the shade-plants and a considerable storage-tissue required. A comparison of the rhizomes of *Pteris* growing under different conditions shows, as we have seen, that under moderate shade the rhizomes attain their greatest development and possess the greatest amount of storage-tissue; while plants growing under xerophytic conditions have on the whole thinner rhizomes, but a great development of stereom, and therefore a correspondingly reduced starch-storage tissue. The maximum of storage-tissue, *in proportion to the diameter of the rhizome*, I found in plants growing in deep shade.

SCILLA FESTALIS, Salisb. Bluebell or Wood Hyacinth.

This species obtains its maximum development in this district in the moist Oak and Sycamore woods on the Coal-Measure shales and clays. A typical leaf of a plant from these woods (fig. 33, p. 380) is clear green, and characterized by the cuticle of the upper epidermis being fairly well developed and very slightly corrugated (fig. 34). Beneath this are two rows of cells with abundant chlorophyll corpuscles, and in the remaining cells the corpuscles are very few or absent, except a single layer beneath the lower epidermis where they are abundant. Air-spaces are well developed in the mesophyll, and running through the centre of it is a nearly continuous line of clear rounded cells. Between the three bundles, on either side of the midrib, are lacunæ. The position of each lacuna is indicated at an early stage in development by a colourless rounded cell. This increases considerably in size, is very thin-walled, and eventually breaks down; in some cases, especially adjacent to the midrib, some of the neighbouring cells are involved.

Plants growing in the deep shade of a Beech wood present a sickly appearance, often showing traces of partial etiolation.

Figs. 33-40.—Leaves of *Scilla festalis* from plants grown under different conditions.

Fig. 33. T. S. of a typical leaf from a moist Oak wood.

34. T. S. of ditto $\times 150$ diam.

35. T. S. of leaf growing under shade of *Fagus*.

36. T. S. of ditto $\times 150$ diam.

Fig. 37. T. S. of leaf grown in a sunny situation.

38. T. S. of ditto $\times 150$ diam.

39. Showing formation of hypodermis.

40. Showing much thickened epidermal cells of midrib.

The leaves are much narrower and thinner (fig. 35) than in the typical form and yellowish green in colour. The cuticle is very thin and not corrugated; a single layer of green cells is developed beneath each epidermis (fig. 36), chlorophyll granules being few and scattered in the remaining cells. A clear rounded cell is seen between the vascular bundles, but lacunæ are not developed. The inflorescence, too, is weak, the scape being slender and few-flowered, and these are of a pale blue colour.

Outside the woods the plant nowhere forms extensive masses in this area, occurring chiefly on the sites of previous woods and hedges and in hedgerows. Here the leaves are much darker in colour, broader and thicker than in the woodland forms (fig. 37). The epidermis has a thick lamellated cuticle and is distinctly corrugated (fig. 38). Occasionally leaves were found where the epidermis was locally two cells deep (fig. 39), the lower ones forming a large-celled aqueous hypodermis. The stomata are usually deeply sunk. The mesophyll is better developed, with fewer air-spaces, and two rows of cells beneath each epidermis contain abundant chlorophyll corpuscles. In the region of the midrib the lacunæ are very large, and occur between the bundles on either side up to the fourth or sixth bundle: here the cuticle is greatly thickened (fig. 40).

Leaves collected on April 7th showed the first division of cells to form an absciss-layer. This is found just where the leaf thickens to form the bulb-scale, and is easily seen with the naked

Figs. 41 & 42.

Fig. 41. Base of leaf of *Scilla festalis*, showing absciss-layer.

42. Absciss-layer of *Scilla festalis*. Longitudinal section.

eye as a well-defined dark line along which the leaf readily breaks (fig. 41). A longitudinal section through the absciss-layer is shown in fig. 42. Its development proceeds slowly and is accompanied by the decay of the leaf; the first evidence of this

is seen at the tip, which turns yellow and gradually extends to the base. Eventually it is cut off by a thin line of cells with corky walls, and thus decay below the absciss-layer is arrested. In the meantime its base has become swollen with reserve materials and forms a bulb-scale, the contents of which are practically unfreezable. With the means at my command I was unable to secure the freezing of these cell-contents; this is a feature of some interest in species producing leaves and flowers at such an early season. Comparatively few observations seem to have been made on the absciss-layer of Monocotyledons, but the details in *Scilla* agree very closely with those observed by Parkin (77) in leaves of *Narcissus*, *Galanthus*, and *Leucojum*.

As I have previously shown, the bulbs of *Scilla* are often curiously elongated, and a number of experiments have been carried out and observations made with a view to determine their fate. The results of one series of experiments are illustrated in fig. 43, which shows three bulbs in three stages of

Fig. 43.

- A, B, C. Three elongated bulbs of *Scilla*, March 2nd.
 D, E, F. The same bulbs as they appeared on April 11th.
 G, H, I. Ditto on April 26th.

development. A, B, & C represent their appearance at the commencement of the observations on March 2nd. These were placed in moist cocoanut fibre and examined at short intervals. By April 11th, changes indicated at D, E, F had occurred.

The foliage leaves had grown considerably in each case, the outer fleshy scale-leaf deprived of its nutrient materials had collapsed, the bases of the inner leaves had thickened, and at E had burst the base of the wrinkled outer scale. These changes continued, and by April 26th, as seen at G, H, I, the outer scale had almost disappeared, leaving behind the usual oval bulb. At the base of each bulb, roots of two kinds were now formed—(a) several slender fibrous roots, and (b) thicker more fleshy roots; two of the latter are shown in G, one each in H and I. These elongate and thicken considerably, and become eventually contractile.

DESCHAMPSIA FLEXUOSA, Trin.

This is a characteristic grass of the dry Oak woods in the Millstone-Grit area and in the Coal-Measure woods over sandstone. With *Festuca ovina* and *Nardus stricta* it dominates the dry grass-heaths, and in such exposed sunny situations forms dense wiry tussocks. It is much less abundant, giving place to *Holcus mollis*, on the Coal-Measure shales, and occurs, but very sparingly, even on stiff clay. It is the most extremely modified of our xerophytic grasses, and an excellent account of it and other xerophytic forms has been given by Miall (67). Its leaves are relatively short, wiry, permanently inrolled and nearly circular in transverse section, with only a narrow groove along the upper surface (fig. 44, p. 384). The epidermal cells of the lower surface are large and covered by a thick cuticle with distinct ridges over the wedge-shaped lateral walls (fig. 45). Beneath this epidermis is an almost continuous stereom, being two or more cells deep along the angles, the fibres of which are thick-walled with only a small cavity. The cells of the upper epidermis within the groove are slightly thickened, the stereom beneath this being confined to a narrow band in the central ridge over the midrib. Two or more layers of the cells of the mesophyll are also thickened and pitted. The inner and radial walls of the endodermis are very strongly thickened, especially beneath the phloem, where a band for a distance of 2 or 3 cells on either side of the median line is two cells deep.

When growing in the medium shade of an Oak wood this species has a characteristic habit. Its leaves are longer, arching and interwoven in such a way that the plants produce nest-like hollows in which humus collects. In structure (fig. 46) the

leaf differs from the heath-form in that the epidermis has rather thicker walls, the stereom beneath is discontinuous, the fibres are smaller with a tendency to form chiefly under the lateral epidermal walls, being continuous only at the angles. Similarly, the walls of the mesophyll and endodermis are thinner.

When growing in moist situations in the deep shade of Elm and Beech, as it frequently does on the wooded hill-slopes, its

Figs. 44-47.

Leaves of *Deschampsia flexuosa* from plants growing under different conditions.

Fig. 44. Diagram of Transverse Section.

45. Portion of Trans. Sect. Sun-form.

46. Portion of Trans. Sect. Oak-wood form.

47. Portion of Trans. Sect. Under shade of *Ulmus* and *Fagus*.

leaves are more slender, limp, and all tend to droop in one direction. In transverse section (fig. 47) the epidermal cells are seen to be smaller, with a thin cuticle, the stereom is discontinuous, the fibres are only slightly thickened, and the cells of the mesophyll are thin-walled. In the endodermis a cell

beneath the phloem has strongly thickened inner and radial walls, in sharp contrast to the remaining endodermal cells.

HOLCUS MOLLIS, Linn.

Quick or Creeping Soft-Grass.

This species, one of many studied by Lewton-Brain (59), is given by him as characteristic of waste and sandy places, but in the area under consideration, while it does occur in such situations, it reaches its maximum development in the moist Oak woods of the Coal-Measures, being a common associate of *Scilla* and *Pteris*. It extends into the Gritstone woods, where it competes with *Deschampsia flexuosa*, giving place to it in the drier woods and at higher levels. It is also common in open, sunny, dry situations such as roadsides and waste places.

In these varied habitats it differs strikingly in form. In moderate shade in the moist Oak woods its leaves are broad, gently curved, limp, and slightly hairy; in dry sunny spots they are erect, much shorter, narrower, more acuminate and hairy, the plant also flowers much more freely than when in the shade. On the steep wooded slopes when overshadowed by a close canopy of Sycamore or Elm, and thus brought under the influence of oblique or horizontal light, its leaves become longer, broader, thinner, much less hairy, and sharply reflexed at the base of the blade, the young shoot above showing a tendency to die early and flowers are not developed.

Fig. 48 (p. 386) is a transverse section of the erect-leaved sun-form. The epidermis has a firm cuticle, short stiff hairs are frequent, the stomata are deeply sunk, and motor cells are well developed. The cells of the mesophyll are closely packed and contain abundant chlorophyll granules.

Fig. 49 shows a portion of the lower epidermis, where the hairs are seen to alternate with relatively short epidermal cells.

Fig. 50 shows a similar section of a reflexed shade-leaf. The epidermal cells are smaller and thin-walled, the stomata are not sunk, the chlorophyll granules are less abundant in the mesophyll, and the motor cells are not so well developed.

Fig. 51 shows a portion of the epidermis of this form. The epidermal cells are elongated to such an extent that the hairs are separated by considerable intervals; this, together with the fact that hairs are less frequently produced, accounts for the very perceptible difference with regard to hairiness in the two

forms. Stomata (fig. 52) are more abundant and are not sunk as in the sun-form.

A comparison of longitudinal sections through the base of the

Figs. 48-55.

Leaves of *Holcus mollis* growing under different conditions.

Fig. 48. Sun-form leaf in Trans. Sect.

49. Lower epidermal cells of ditto.

50. "Shade"-leaf of *Holcus mollis*, reflexed form. Trans. Sect.

51. Lower epidermal cells of ditto.

52. Stomate of ditto.

53. Longitudinal Sect. base of blade of erect leaf-form.

54. Thickened cells of ditto.

55. Longitudinal Sect. base of blade of reflexed leaf-form.

blade at the point where it joins the sheath shows interesting modifications in the two forms.

Fig. 53 is such a section of the erect sun-form. The cells of the base are clear and transparent, and stand out sharply from

the chlorophyllaceous cells above and below. Towards the lower surface the cells are small, four- or five-sided in section, and for about four rows in depth distinctly thickened (fig. 54), forming a shield-like stereom-plate. Towards the upper surface the cells are thinner-walled and rather larger.

Fig. 55 is a section through the base of the blade of the reflexed shade-form. In this we see that the blade has been bent over by the great elongation of the cells of the upper surface, many of which show distinct collenchymatous thickening.

As Schimper points out (83), a plant strives in various ways to obtain an ecological optimum of light. *Holcus mollis* affords an interesting example of this. In sunny situations it assumes an erect sun position. In the somewhat diffuse light of an Oak wood its leaves curve in such a way as to expose their flat surfaces to light; and when growing under trees where the light above is practically cut off, but strikes the plant obliquely or horizontally, its blades become strongly and permanently reflexed, and their flat surfaces exposed to the direction of the incident rays.

VACCINIUM MYRTILLUS, Linn. Bilberry.

This species is especially abundant in the open Pine woods* of the Millstone-Grit area, and in the dry Oak and Birch woods it forms, together with *Calluna* and *Deschampsia*, the dominant vegetation of the undergrowth. It quickly dies out over the Coal-Measure shales and clays, and under the deep shade of Sycamore, Elm, and Beech, being confined in this area mainly to the drier soils over sandstone. To the west, it extends beyond the limit of the woods, is abundant along the dry mooredges and slopes, but is displaced to a large extent by cotton-grass (*Eriophorum vaginatum*) on the deep ill-drained peat, to reappear again in somewhat extensive masses on the hill-summits at 1600 feet and upwards.

* During a recent tour in the Eastern and Swiss Alps, I was much struck by the habit of this species in the Spruce forests. Here it grows in forests of such density as appear to be fatal to it in the Huddersfield district, probably owing to the density of the smoke-cloud characteristic of this part of West Yorkshire; whereas the intense sunlight of the Alps penetrates the forests sufficiently to favour its development, but it assumes a very characteristic habit: it forms flat branched plates, all the leaves exposing their upper surfaces to the light, being a very striking shade-type. While the plants growing in the open have their branches more erect, the leaves are erect and parallel to the stems and so expose their edges to the light, a typical sun-habit,

In these different situations the plant varies much in size. Typically from one to two feet in height, it may, in exposed windy situations and in a shallow soil deficient in humus, be not more than two to three inches in height, as on the western grassy slopes of Meltham Cop and at Cheese Gate Nab. Here the stem is much branched, very thin and wiry, and the cuticle of the epidermis much thicker than that of the taller larger plants. The internodes are greatly reduced, and in consequence the leaves, though very small ($\frac{3}{8} \times \frac{1}{8}$ inch), become much crowded together, so offering mutual protection. This dwarf form is of frequent occurrence in places where the soil is relatively dry and deficient in humus. Schröter (84) figures similar differences in *V. Vitis-idæa* and *V. uliginosum*, the small-leaved form of the latter species having received the name var. *microphyllum*.

Plants growing in very exposed situations frequently develop brown or red pigments, which, as Kerner (52) and others have pointed out, is a common feature in leaves exposed to cold and intense light. Overton (76) has shown that these red pigments were produced under the influence of cold; and Stahl (91) previously made the interesting observation that portions of leaves containing such pigments had, when illuminated, a higher temperature than parts not so coloured; and Rathay (80), Wiesner (104), and others have shown that transpiration is less in red than in green leaves. This sequence of events is interesting: that cold produces in leaves pigments which, under the influence of light, occasion compensatory warmth, and such leaves have also a reduced transpiration, all features of great value to a plant exposed to xerophytic conditions. In different species these pigments are produced under various, even opposite conditions, as shown by Katić (51), to whose paper, also to Buscalioni & Pollacci (11) and Czapek (21), reference may be made for literature and full consideration of the subject.

Fig. 56 shows a transverse section of a leaf of the high Moorland-form; the epidermis is strongly cuticularized, and the double row of palisade-cells well developed, the upper ones being much elongated and occupying nearly half the thickness of the leaf. Stomata are abundant on the under surface, but very few on the upper surface, and here they occur chiefly in the neighbourhood of the veins. In extreme forms from very exposed, sunny and dry situations no stomata were found on the upper surface, while they were numerous on both surfaces in the shade-forms.

Fig. 57 is a section of a very small leaf from the dwarf form, which scarcely rises above the short grass among which it grows. The leaf is thinner than the previous type, but has a very compact mesophyll—a feature of importance in reducing transpiration.

Figs. 56-60.

Leaves of *Vaccinium Myrtillus* growing under different conditions.

Fig. 56. T. S. leaf of typical Moorland form.

57. T. S. leaf of dwarf small-leaved form.

58. T. S. leaf of Woodland shade-form.

59. Hair of leaf.

60. Multicellular gland of leaf.

Fig. 58 is a section of a leaf from the form growing in a sheltered Oak wood on the Millstone-Grit escarpment. The leaf is much larger but thinner than the previous forms; the upper epidermis is very slightly cuticularized, air-spaces are

frequent in the palisade-layer and large in the spongy parenchyma. The chlorophyll granules are less abundant than in the two previous forms, and the leaf is distinctly paler, and, as above stated, stomata occur abundantly on both surfaces.

The leaf of the Bilberry is usually described as glabrous, but close examination shows that on both surfaces, especially on the upper surface, are numerous unicellular hairs with thick and warted walls (fig. 59). In addition to these, each tooth of the leaf-margin is terminated by a clavate multicellular hair with thin walls, and, when young, filled with finely granular contents (fig. 60). At the base of each hair ends a fine veinule. In an old leaf the contents turn brown and the hairs become shrivelled. These hairs are usually curved in such a way as to apply their apices to the upper surface of the leaf. A few are also found on both upper and lower surfaces chiefly over the veins; they also occur on the margin and near the base of the slightly channelled petiole. The contents are readily plasmolysed by a solution of sodium chloride, and they soon regain turgidity in water, showing their walls to be permeable. Experiments similar to those described by Pfeffer (78), Gregory (39), and others suggest them to be capable of absorbing water. Hairs occur on the under surface and on the leaf-margin of *Vaccinium Vitis-idaea*, and are stated by Lundström (61) and Kerner (52) to be absorptive. Lundström described many absorptive hairs, and in a list he gives the Bilberry is included. Wille (108) has shown, by means of a 1-per-cent. solution of lithium chlorate and subsequent spectroscopic examination, that many are capable of absorbing, but he sharply criticises Lundström's contention that they are "adaptive" structures; while Gregory (39), Schimper (83), and others have given numerous illustrations of hairs functioning as absorptive organs, some performing the double function of absorption and excretion. Drabble and Lake (24) have recently made some useful observations which bear directly on the point under consideration. In comparing the strength of the cell-sap of the epidermis of several species of plants growing under different conditions, they find, for example, that the cell-sap of *Geranium Robertianum* growing under moist conditions has a strength equal to a solution of sodium chloride having a concentration in gram-molecules of $\cdot 11$, while the same species growing on rocks under xerophytic conditions had a cell-sap equal to $\cdot 18$.

Vaccinium Myrtillus was one of the species they examined, and its sap had a density represented by .23. Their assumption is a reasonable one, that a relatively high concentration of the cell-sap will favour the rapid absorption of water, and so be of service to plants growing under xerophytic conditions.

(b) SECONDARY AND SUBORDINATE SPECIES.

Other species have been examined whose distribution is more restricted; three of these, *Heracleum Sphondylium*, *Lamium Galeobdolon*, and *Mercurialis perennis*, are often locally abundant in the moist Oak woods of the Coal-Measures, and they show well-marked structural differences in different habitats.

HERACLEUM SPHONDYLIIUM, Linn. Hogweed; Cow-Parsnip.

This species is of common occurrence in the moist Oak and Sycamore woods, especially in parts where the ground has been disturbed. It is also frequently met with in open sunny places, as in fields and banks. In the more exposed situations it is often less than a foot in height. Its leaves are much reduced in area, and are thick and hairy. Fig. 61 (p. 392) is a transverse section of such a leaf from a plant growing on the sandy soil of the Gritstone Plateau; the epidermis is seen to be strongly cuticularized and distinctly corrugated. In surface view the cells are oval or rounded and slightly wavy in outline (fig. 62). The cells of the palisade are very long and narrow, and consist of a single layer only, occupying more than half of the mesophyll. Below this is a layer of more rounded cells followed by two rows which are much elongated, and united in such a way as to form a characteristic network when seen in surface view.

Plants growing in the shade are not only taller, but the area of the leaf is greatly increased and is less hairy and very thin. The epidermal cells are larger and much more wavy in outline than in the sun-form (fig. 63), and they are very thin-walled. The cells of the palisade (fig. 64) are greatly reduced and are pear-shaped, exposing their broad upper surfaces to the light, and the air-spaces between them are large. Below this is a network formed by two layers of spongy tissue, and the cells of the lower epidermis are thin-walled and the stomata raised.

It has been shown by Noll (73) and Schimper (83) that plants growing in deep shade exhibit lens mechanisms in their epidermal

and other cell-walls. While examining sections of the shade-form of *Heracleum*, it appeared that the curvature of the upper wall of the epidermal cell seemed to be directly correlated with the form of the palisade-cells below it. The general effect of this curvature is to produce a central area of increased, but not uniform, light intensity, which is bounded by a shadow; and as a consequence of this differential lighting the modifications in the palisade-cells seemed attributable. In the sun-form this boundary

Figs. 61-64.

Fig. 61. T. S. "Sun"-leaf of *Heracleum Sphondylium*.
 62. Surface view upper epidermis of ditto.
 63. T. S. "Shade"-leaf of *H. Sphondylium*.
 64. Surface view upper epidermis of ditto.

of shadow may be of service in protecting the chlorophyll corpuscles from the injurious effects of intense light, as the mechanism is such that the chlorophyll corpuscles may circulate in an area of relative shadow.

One of my students (Mr. J. W. H. Johnson), while kindly preparing sections for me, worked out in detail several interesting points with reference to these modified lens mechanisms, the results of which will be shortly published. Haberlandt's recently published monograph (41) gives an excellent exposition of the lens mechanisms of epidermal cells. The form in *Heracleum* is of a somewhat different type to those figured by Haberlandt, and more recently by Guttenberg (40) in *Adoxa*, &c.

Figs. 65-68.

"Sun" and "Shade" leaves of *Lamium Galeobdolon*.

Fig. 66. Trans. Sect. of 65. From an open Oak wood.

68. Trans. Sect. of 67. From a plant growing under shade of Beech (*Fagus*).

LAMIAM GALEOBDOLON, Crantz. Yellow Dead-nettle.

The effect of shade is very strikingly shown in both stem and leaf of this species. Fig. 65 shows in outline (reduced) a

leaf from a plant growing in a moist open Oak wood. Fig. 66 is a transverse section of this leaf. The epidermal cells are strongly cuticularized in both outer, lateral, and to a less extent on their inner walls. The lower epidermis is slightly cuticularized on its outer wall; the palisade consists of large elongated cells frequently containing raphides. The cells of the spongy parenchyma are large and air-spaces are numerous. Fig. 67 shows in outline a leaf from a patch growing under the deep shade of Sycamore and Beech; the stems are long, very slender, and the plants prostrate, the leaves are very small and exceedingly thin. Fig. 68 shows a section of one of the leaves in which the cuticle is very thin and the cells of the mesophyll, although consisting of three layers, are exceedingly small and contain few or no raphides, while the stomata on the under surface are distinctly raised.

MERCURIALIS PERENNIS, Linn. Dog's Mercury.

This species not only occurs abundantly in damp woods, where large patches are developed due to its vegetative mode of increase, but is also a common plant of the hedgerows. Fig. 69 is a transverse section of a leaf from a shade-area of Sycamore

Figs. 69 & 70.

Transverse sections. Leaves of *Mercurialis perennis*.

Fig. 69 from a leaf growing in a sunny situation.

Fig. 70 „ „ in shade of *Acer* and *Ulmus*.

and Elm on a damp, clayey soil. The epidermis is thin-walled; mesophyll reduced to three rows of cells; air-spaces relatively large, with frequent crystal sacs beneath the upper epidermis. The leaf is very thin.

Fig. 70 is a section of a leaf of the sun-form from a hedgerow. The upper epidermis is distinctly cuticularized; palisade-cells much elongated, displaced at intervals by crystal sacs; spongy parenchyma in three layers; air-spaces relatively small. The leaf is distinctly thicker and firmer than the shade-form.

SUMMARY.

The vegetation of the Huddersfield district is naturally divided into three parallel zones:—

(1) THE MOSS MOOR, a part of the Pennines ranging in altitude from 1700 to 1000 feet. Of the three zones it is the most exposed, the climatic conditions are extreme, the soil consists chiefly of deep ill-drained peat, on which *Eriophorum vaginatum* dominates with very few associates. On the higher, drier ridges and moor-edges, *Vaccinium Myrtillus* with ericaceous plants are dominant. Though now practically a treeless region, there is much evidence that forests of *Betula* &c. extended over a considerable part of it, and much buried timber is found at the base of the peat. At the present time *Quercus* dies out at 1200 feet. A characteristic vegetation of *Pteris aquilina* with xerophyte associates covers the hill-slopes and forms a transition region to Zone 2.

(2) THE MILLSTONE-GRIT PLATEAU occupies the central portion of the district, and the altitude ranges from 1000 to 500 feet. In contrast to the Moss Moor, it consists of a series of fine plateaus with a general dip to the south-east. The rocks consist mainly of coarse-grained, jointed sandstones, overlaid by shallow pervious soils and in parts by thin, relatively dry peat. It is fully exposed to the sun and drying east winds, and although the rainfall is moderately high (42 inches), water so readily percolates or is drained off that it is a typical, physiologically dry area, and the vegetation is consequently xerophytic; ericaceous plants and xerophytic grasses dominating. Oak is the dominant tree, with Birch and Pine. All the trees are planted, but often on the sites of primitive forest, and Oak was formerly much more abundant than at present in this zone.

(3) THE COAL-MEASURE AREA.—In general the altitude ranges from 500 to 200 feet, except to the south-east, where it

rises to 1200 feet. The rocks consist of fine-grained sandstones alternating with extensive deposits of shales and clays. The soils are often deep, frequently covered with much humus, and retain much water. Climatic conditions are medium, and although the rainfall is much lower (33 inches) than in Zone 2, owing to the nature of the soil water is more constant and the vegetation is mesophytic, except on soils over sandstone and in the higher parts, where xerophytes extend from the Gritstone Plateau.

In a district like the one under consideration, where Glacial deposits are absent, and soils owe their origin largely to the denudation of the underlying rocks, a solid-geology map is of great value when making a primary analysis. It has here been shown that a comparison between such a geological map and a vegetation map is very instructive and suggestive; that a change in geological formations and soil-conditions is accompanied by a change in plant-associations.

It has been shown that carefully selected small areas studied in detail, and the results shown on lines such as the present Wood-maps, help considerably to bring out the main factors affecting plant-distribution; and it is believed that such maps could be usefully introduced in connection with larger surveys to supplement the features illustrated in small-scale maps. The results indicate that the study of small associations will materially aid the study of plant-geography, and bring to light many interesting points in the life-histories of the species.

The present study indicates that, in this district, the physical properties of the soil and accompanying conditions play a more important part in determining the character of plant-associations and the distribution of species than the chemical composition of the soil.

The dominant elements of an association tend to form a biological unit, and in the case of the Meso-pteridetum (*Scilla*, *Holcus*, and *Pteris*) dealt with we have a *complementary association*, the subaerial parts being in, or tending to occupy, definite and different layers, *i. e.* edaphically complementary, and the aerial parts are seasonally complimentary.

On the other hand, in the Xero-pteridetum an association where the dominant species (*Vaccinium*, *Calluna*, *Pteris*, and

Deschampsia), owing to soil-conditions, occupy the same layer; and after we have made allowance for differences in food requirements, they still form a *competitive association*, and sometimes one, sometimes the other species gains the upper hand. In this connection very little work seems to have been done, and further study will doubtless lead to interesting results.

In studying the vegetation in the transition region from the relatively dry Millstone Grits to the moister Coal-Measures, we find that the line of demarcation, though evident, is not sharply drawn between the two biological types; but as the xerophytes invade the region of the mesophytes, and come under the mellowing influences of moisture and shade, increased temperature and greater protection, they tend to lose their xerophytic characters and take on mesophytic characters. The reverse also holds good—that as the mesophytes encroach on the xerophytes, and come under the influences of drier and more rigorous conditions, they develop xerophytic characters.

These changes in soil and other conditions act more completely as barriers to some species than to others, but in the case of species not so restricted in their distribution, differences in physiological water and food-supply, presence or absence of peat or humus, produce striking modifications in their form and structure (e. g. *Pteris* and *Vaccinium Myrtillus*).

The influence of the dominant tree determines in a varying degree the distribution of the species (e. g. *Pteris*), and not only affects the amount of transpiration in the plants of the undergrowth, but also brings about modifications in structure, resulting from the amount of shade produced and accompanying conditions, e. g. *Pteris*, *Scilla festalis*, *Deschampsia flexuosa*, *Holcus mollis*, *Heracleum Sphondylium*, *Lamium Galeobdolon*, and *Mercurialis perennis*—each showing well-marked sun and shade, xerophytic and mesophytic structures according to environment.

Variations in light-intensity or the direction of the incident rays not only affect the structure, but also the habit of the plant, e. g. *Holcus mollis* and *Vaccinium Myrtillus*.

The several species of an association vary considerably as to their power of adaptability, and therefore in their range of distribution, e. g. *Pteris* as compared with *Calluna*. In general the less plastic a species is, the narrower is its range of structural variation and the more restricted is its distribution.

Changes in structure are produced by varying degrees of exposure to which the species are subjected, the modifications being concerned largely with conserving water by checking evaporation, *e. g.* thick cuticle, reduced number of stomata, more compact mesophyll and hairiness; or the development of water-storage tissues. In some cases, hairs may function as water-organs, *e. g.* *Vaccinium Myrtillus*; or the modifications may be such as to provide a means of eliminating excess of water, *e. g.* thin cuticle, increased number of stomata, increased leaf-surface, larger intercellular spaces in the mesophyll, &c.

The tissues most susceptible are the epidermal and ground-tissues, and not only are those of the leaf-blade affected, but also those of the petiole and rhizome, *e. g.* *Pteris*.

Modifications occur which are of mechanical advantage to the plant in aiding it to resist stresses due to wind in exposed situations. Others are of advantage in supporting relatively large leaves on slender leaf-stalks developed in sheltered situations in deep shade, *e. g.* *Pteris*.

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