British Beechwoods.

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with 6 photographs and 3 figures in the text.

Introduction.

THE BEECH IN THE BRITISH ISLES.

The English beechwoods have a special interest in relation to European beechforest as a whole inasmuch as they are developed on the extreme north-western limit of the natural area of distribution of *Fagus silvatica* L. As is well known, the beech is not native in Ireland, though it grows well, sets seed, and can regenerate. There is no evidence that it is native in Scotland, the subspontaneous woods which occur, for example, in Aberdeenshire and Perthshire, being certainly derived from planted trees; but again, seed is sometimes ripened at low elevations as far north as Caithness, the northernmost Scottish county apart from the outlying islands. Similarly there is no good evidence of the existence of native beech in the extreme south-western counties of England (Somerset, Devon and Cornwall) though in Cornwall (the westernmost) the tree is freely subspontaneous in certain localities. The same is true of Wales and of the north and north midlands of England.

On the other hand, in the south-eastern and parts of the south midland counties of England the beech has all the appearance of a natural forest dominant (see map, fig. 1). Here it forms extensive woods on the chalk and oolitic limestones and associated soils. In this area and on these soils the beech springs freely from self-sown seed and beats all its competitors. The natural process of succession through grassland and scrub, and often through ashwood or ash-oakwood, has been followed out in detail up to the establishment of pure beechwood, which is naturally interpreted as the climatic climax. If a natural boundary to the distribution of native beech is to be drawn it would seem correct to draw it round this southern area illustrated in Fig. 1, excluding the west, the central and north midlands, and the north altogether, and to regard this boundary as representing the limit, not indeed of the climatic region in which beech can flourish, but of the region where it has actually established itself as a wood-forming tree without the aid of man. This is certainly more logical than to draw the boundary in northern England or in central Scotland, as is done in existing maps of continental origin. Such boundaries, as is evident from what has been stated, have no basis in any known facts.

But we have to recognise the possibility that beech is not native in Britain at all. The records of beech from pre-Roman and post-glacial deposits are too uncertain and unsatisfactory to be accepted. We have not succeeded in finding a single record which is not open to doubt. Julius Caesar records the absence of beech at the date of his invasion (B. C. 55) *) and he certainly traversed the region which it would have first colonised if it had previously entered the country without the aid of man, and in which it now behaves like a native tree. There is no certainly established fact which precludes the hypothesis that beech was introduced by the Romans themselves.

On the other hand, it may be native, and it may even have extended at one time beyond the southern areas where it is now dominant on chalk and oolite and associated soils. We can only hope for future evidence which will enable us to decide between these alternatives **).

For the present the line bounding the southern areas is the most natural which we can draw.

1. DISTRIBUTION (see Map. Fig. 1).

The three areas of extensive beechwoods in the South of England are, first, the Chalk fringing the Weald and forming the North and South Downs with a western connexion between them, in the counties of Kent, Surrey, Sussex and Hampshire; secondly, the Chiltern Hills in South Oxfordshire and South Buckinghamshire, extending eastwards into West Hertfordshire, with the slopes of the Thames valley, which breaches the chalk range to the South and separates

*) «Materia cujusque generis, ut in Gallia, est praeter fagum atque abietem» (*De Bello Gallico* V, 12, § 5).

**) Sice the above was written some, fresh evidence has been published of beech pollen grains in post-glacial (pre-Roman) peat in the north of England.

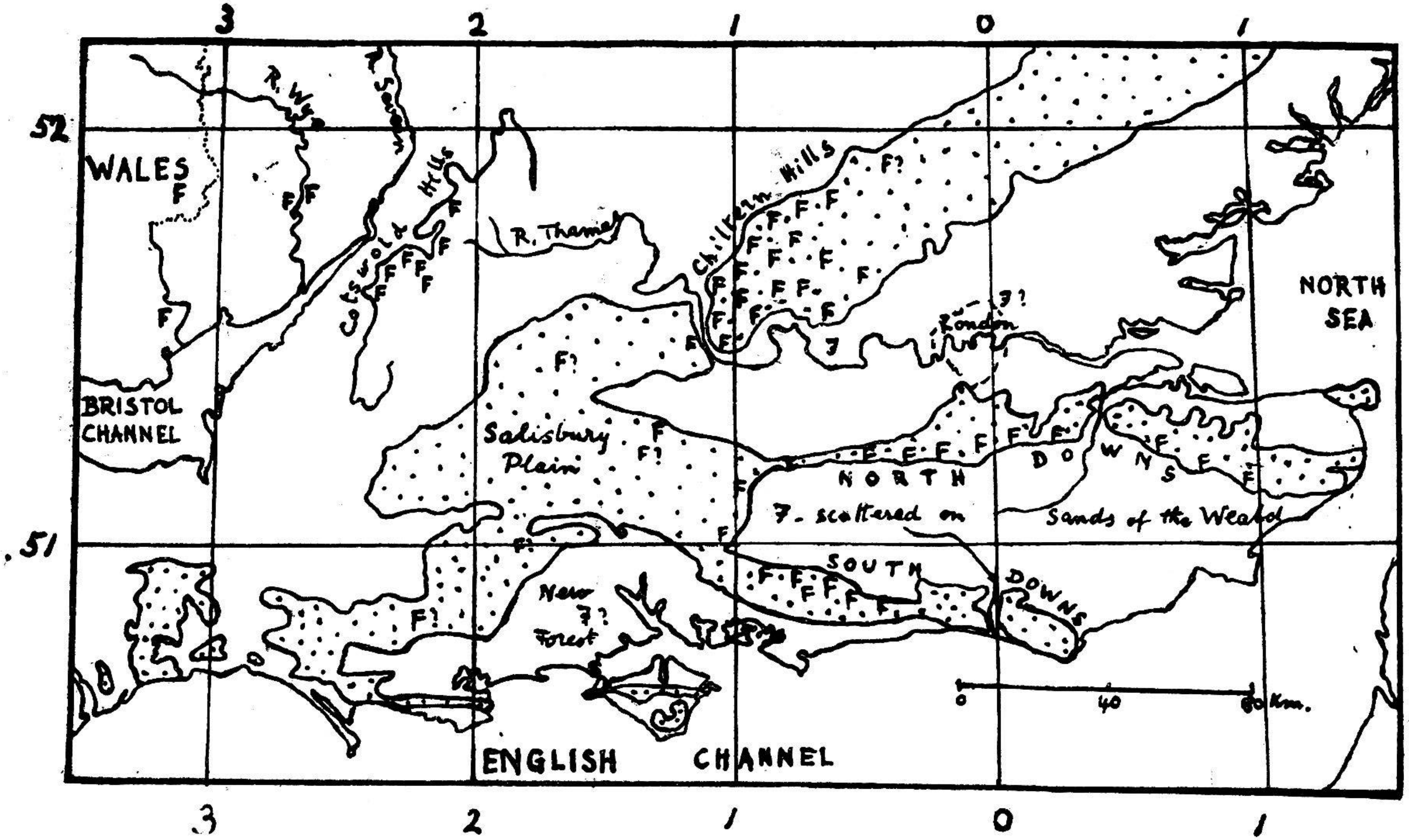

Fig. 1. Map showing distribution of semi-natural beechwood in Southern England, and its relation to the Chalk (dotted) and to the Inferior Oolite of the Cotswold Hills. The areas to the west of the Cotswolds are based on Carboniferous Limestone.

F = semi-natural beechwood apparently native. F? doubtfully native.

Ꟶ = semi-natural beechwood on sands and gravels.

the Chilterns from the Berkshire Downs; thirdly, the Cotswold Hills occupying the Inferior Oolite fomation in Gloucestershire. Besides these there is an extreme westward extension of beech on the Carboniferous Limestone of the Wye Valley, in the neighbourhood of Symonds Yat*) (Herefordshire and Gloucestershire), and a possible though rather doubtful extension through Hampshire into Dorsetshire and Wiltshire. In addition there is a certain amount of beechwood which appears to be spontaneous on some of the sandy soils of the Weald, enclosed by the chalk ranges first mentioned, and some smaller outliers on Tertiary sands around London. Such self-sown beech as exists in Somerset, Devon and Cornwall has almost certainly taken origin from planted trees. The general distribution of beech which may be considered as native is thus in England clearly south-eastern, with a westward extension just south of the 52nd. Parallel of Latitude.

The absence of a tension zone between beech and oak forest to the North and West of this area shows that the actual northern limit of apparently natural beechforest is not climatically determined: the existing limit is, in fact, considered by some to be the front line of advance of natural beechforest in its migration North and West in this country. It is quite possible however that in later post-glacial times the beech extended far to the North of its present limit, but the evidence of such northward distribution, derived from the preservation of beech pollen in the peat, is much too scanty to be conclusive. The line bounding the area described certainly separates the existing, possibly natural, beechwoods of the South from certainly planted or subspontaneous beech further to the North. Historical records are quite sufficient to show that the southern beechwoods are (historically) old and the northern recent.

It is a striking fact that all the three areas of southern beech described, together with the westward extension at Symonds Yat, and also those over the Welsh border (see footnote), are based

*) Mr. H. A. Hyde of the Cardiff Museum informs us that there is an area of beech on the Carboniferous Limestone about 6 miles north of Cardiff and 30 miles south-west of Symonds Yat, which he thinks may be native: also another area in rocky woods on the Carboniferous Limestone near Llangattock in Breconshire, 22 miles nearly due west of Symonds Yat. From Mr Hyde's notes it would appear indeed that these woods (which we have not seen) have a very good claim (see map, Fig. 1).

on lime-stone soils, no natural beechwood occurring on adjoining clays and only a little on sands. It cannot, however, be inferred from its distribution that the beech is naturally limited to calcareous soils in England, for it spreads over much of the non-calcareous loam covering the chalk plateaux and often lacking, or very poor in, calcium, and it also grows and rejuvenates here and there on the sands of the Weald and of the Tertiary beds of the London Basin. In the North, the beech, both as a planted tree and also where it is subspontaneous, likewise occurs both on lime-stone and siliceous soils which may be markedly deficient in calcium salts.

Most of the available information about the behaviour of beech in this country is derived from the study of its behaviour on the chalk and loams of the South Downs and the Chiltern Hills; to a less extent on the Cotswolds. All of these produce the climatic soil type known as «brown earth». Less intensive studies of beech on podsol, both in the South and the North, serve to show that on this soil type the behaviour of the beech is very similar to that on the podsols of the Continent within the known natural range of the species.

2. ALTITUDINAL RANGE, SLOPE, AND EXPOSURE TO WIND.

In the South the beech extends from near sea-level up to approximately 1000 feet or about 300 m., the greatest height of the highest hills within its area. Certainly it would reach a higher altitude were such available. In the rest of the country, that is where it was certainly originally planted, the maximum recorded altitude varies with the locality but is not directly connected with the height of the hill mass upon which it grows, as can be seen from the data given on p. 299.

The dependence of beech on man in the North deprives these records of any exact significance as limiting altitudinal values, and the potential maximum altitudes in some districts — e. g. Perthshire — are likely to be much higher. For example, in the Pennines, while the beech is recorded as reaching 1600 feet (about 490 m.), *Quercus robur* as reaching nearly 335 m., and *Q. sessiliflora* 400 m., in Perthshire the relative positions are reversed, with *Q. robur* reaching over 300 m. and the beech only 280 m. Nevertheless, at

Name of place or hill range		Latitude	Altitude to which beech grows	Maximum altitude of the hill mass
1. Southern Pennines		52° 23′	1600 feet (488 m.)	2088 feet (636 m.)
2. Central Pennines		54° 12′	1350 feet (411 m.)	2310 feet (704 m.)
3. Northern Pennines		54° 42′	1600 feet (488 m.)	2893 feet (882 m.)
4. Pentlands	Northern slope	55° 47′	800— 900 feet (243—274 m.)	1898 feet (579 m.)
	Southern slope	55° 47′	900—1000 feet (274—304 m.)	
5. Lomonds, Fifeshire		56° 15′	1000 feet (305 m.)	1712 feet (522 m.)
6. North Perthshire		56° 32′	over 900 feet (274 m.)	3984 feet (1210 m.)
7. Deeside, Aberdeenshire		57°	1100 feet (335 m.)	3786 feet (1150 m.)
8. Donside, Aberdeenshire	Southern exposure	57° 10′	1350 feet (411 m.)	2600 feet (793 m.)
Tomintoul, Banffshire	Northern exposure	57° 15′	1150 feet (350 m.)	
9. Caithness, Northern Scotland		58° 30′	150 feet (46 m.)	2313 feet (705 m.)

some of these altitudes the beech grows slowly and is small in size, only reaching 20 to 40 feet (say 6—12 m.) in height, and the higher figures probably approximate to the altitudinal limits — e. g. in the North of England something under 500 m.

Records of beech at high altitudes on contrasting exposures are few, but Smith puts the maximum altitude of «mixed deciduous woods» in the Edinburgh district at 100 feet (30 m.) higher on the south than on the north exposure. The trees on Donside and at Tomintoul grow on opposite slopes of the same hill mass at about the same altitude, and both are healthy, though not vigorous.

Of more significance are the records of maximum altitudes at which beech produces ripe seed. These are unfortunately very few. In favourable seasons on the Pennines ripe seed is set at 1500 feet (460 m.); on Donside, Aberdeenshire, at about 700 feet (213 m.). At low elevations ripe seed is produced as far north as Caithness (latitude approximately 58° 30').

S t e e p n e s s o f S l o p e. On the chalk escarpments of the South a slope of about 38° to 40° renders the surface soil too unstable for the development of a continuous carpet of herbaceous vegetation. Actually slopes of this steepness are seldom met with on the South Downs and on the Chilterns. Beechwoods occur on slopes of an angle of at least 35°, though in places trees have established themselves and held the soil with their roots where an artificially steep slope exceeding the natural angle has been brought about by man's activities.

W i n d. Although the effect of the prevailing westerly winds is registered in the crown forms of isolated and exposed trees even near the East Coast, no examples have been observed where the life-form is so altered that the tree becomes a bush (with «squirrel tail» or other forms such as are seen in Jutland) or where woodland gives way to beech scrub (Danish bogekrat). The maintenance of an erect leading shoot even in exposed situations to a height of about 15 feet (4.5 m.) secures the production of a main stem, although even at that height there is a perceptible lack of symmetrical disposition of the branches. This becomes accentuated in larger trees whose crowns are obviously lop-sided — an effect produced by strong winds both at low and high altitudes. In its physical and physiological resistance to wind the beech, with the sycamore *(Acer pseudoplatanus)* and the black Italian poplar *(Populus serotina)*, surpasses other trees commonly grown in this country, and its widespread use in shelterbelts, wind-breaks and as boundary trees, either in single rows or belts, to plantations of less wind-resistant conifers, demonstrates an early recognition of this quality by foresters. Its usefulness in this respect is seen also in mixture with other trees (e. g. *Larix decidua)* which are less liable to be upturned than if grown pure.

This quality of wind-resistance enables beech to invade successfully where many other trees find conditions hostile. Thus on the shallow chalk soil of exposed slopes of the South Downs beech is the pioneer invader of scrub, where under similar but sheltered conditions ash normally precedes it; and in Great Britain generally, where soil conditions are suitable, the direct action of the wind does not limit the spread of the tree.

Indirectly the regeneration of the beech may be temporarily hindered by wind. Through the blowing away of leaf litter the soil is left bare or covered by a low-growing carpet of mosses or (on acid soil) of *Deschampsia flexuosa*, rendering the conditions hostile to a germination of beech adequate to restock the ground (see also p. 321). This would lead to the withdrawal of the beech on the windward side: but at the same time, by this very withdrawal, the chief contributory cause of the unsuitable seed bed is removed and a ground vegetation appears in which seed can germinate. Thus re-invasion of the abandoned ground is made possible. A similar result would follow the colonisation of the abandoned ground by such species as birch and ash. In no observed instance has the return of the beech been prevented or a permanent loss of ground followed.

3. CLIMATIC LIMITS.

Exact limiting data for the growth and reproduction of beech are lacking. Beech survives under such extremes of annual rainfall as 21.8 in. (554 mm. — Cambridge) and 78.8 in. (2002 mm. — Fort William, W. Inverness). It easily tolerates the temperatures within the narrow ranges characteristic of our oceanic climate. It is satisfied with a July mean of 54.5° F (12.5° C — Wick) and survives (though it does not ripen seed) with a January mean of 34.3° F (1.3° C — Braemar). Much lower winter temperatures are of course endured without harm, and the northern latitudinal limit for beech certainly lies outside this country.

The existing altitudinal maxima are artificial and the temperature limits undetermined: but beech grows and ripens seed beyond the upper limit of the wheat zone with a July mean of 56° F (13.3° C).

Flowers are produced at lower temperatures than seem necessary for the setting of fertile seed, and the July means of 54.5° F (12.5° C) at Wick, where it ripens seed, and 54.8° F (12.7° C) at Braemar, where it does not, are probably in the neighbourhood of the minimum temperatures required. In this connection mean temperatures over long periods have little (if any) significance, as it is well known that good mast years constantly follow a year of low rainfall (and probably high summer temperature). The temperature during the period when the flower primordia are laid down is more likely to be critical— say the weeks from the end of May to the end of June. But flowering is not necessarily followed by seed maturation.

Seedlings are recorded at 1500 feet (457 m.) in Derbyshire and 700 feet (213 m.) in Aberdeenshire. The young seedling is sensitive to cold (it is killed by a temperature of 20.3° F = — 6.5° C) and is recorded as also sensitive to drought, but while both these factors may, and probably do, check the speed of beech invasion, they do not apparently set limits to the distribution of the species in this country.

4. SOIL.

In a country like Great Britain, whose surface has relatively recently been exposed to glaciation and subsequent redistribution and modification of glacial deposits by water and sub-aerial agencies, and in which the climate is not extreme, the soils are young and still retain many of the characteristics of the parent rocks and deposits. Consequently a great diversity of soils corresponding with the various geological formations is open to colonisation. The beech is found on soils derived from the newer and older rocks, from hard and soft rocks and from acidic and basic rocks: therefore on soils of very different origins and very different physical and chemical properties. Its wide range of accommodation does not, however, include the wet soils of fen and peat moor, nor is beech found in the «Alder-Willow-Association», although Allorge draws attention to the floristic affinities of wet hollows, paths etc. in beechwood with the Alnetum. Beech is generally reported as absent from clay soils, but while it is scarce on heavy soils, it does occur and can reproduce under conditions where earthworm activity produces a loose crumbly surface. On the other hand, where waterlogging deprives the soil of the beneficial work of the worms, beech rejuvenation is likely to fail.

While many of the soils of Great Britain are not the final expressions of the climate, yet certain major soil-types are recognisable, depending partly on geological formation, partly on climate. Below are described the soil types on which climax beechwood has been studied in Grat Britain.

Beechwood soil-types. As has already been stated, climax beechwood occurs on a fairly wide variety of soil-types. These may be grouped as I, Beechwoods on chalk; II, Beechwoods on the noncalcareous soils of the Chalk plateaus; III, Heath Beechwoods on acidic gravels, sandstones etc.; and IV, «Herbaceous» Beechwoods (Scottish) on soils derived from Old Red Sandstone (Devonian). (The numbering of the types and sub-types described here corresponds with that used in the classification of the beechwoods given in section 11, p. 322.)

I. Beechwood on Chalk. Fig. 2, I (a) and I (b). The soil here is kept immature by the rainwash erosion on relatively steep slopes.

(a) The Sanicle beechwood (see p. 338) commonly grows on steep slopes (up to an angle of 35°) where the soil is shallow (31 cm.). A typical profile shows the following strata. The litter is scanty, varying in depth from 0 to 2.5 cm. (1) The surface 6 in. (15 cm.) is dark in colour, fairly compact, with much humus and some small lumps of chalk (stones). (2) The next 5 in. (13 cm.) is brown-black in colour but is more «earthy» with fewer but larger rounded chalk stones. (3) The bottom 2 in. (5 cm.) consists of angular chalk stones with soft chalk between. At about 33 cm. solid chalk is reached.

Tests made on the surface 6 in. (15 cm.) show that the soil is highly alkaline (pH 8.5) with much $CaCO_3$ (59.5%) and a moderately high humus («loss on ignition») content (12.94%). Because of the slope, texture, and porous substratum the soil is essentially a dry one.

The Mercury beechwood (see p. 338) commonly occupies slopes of easier gradient with an average inclination of 22° and a maximum observed slope of 29°. Hence the soil is deeper (51 cm.). Here the litter is continuous and about 2.5 cm. deep. (1) The surface 7 to 8 in. (18 to 20 cm.) is very open and friable, with much humus and many small chalk stones. (2) The next 2 to 3 in. (5 to 7.5 cm.) consists of larger chalk stones and soil slightly coloured with humus between. (3) Angular chalk stones with soft chalk between them make up the bottom 10 in. (25.4 cm.). Underneath is solid chalk.

A surface 6 in. (15 cm.) sample yields the following data: pH = 8.5; humus («loss on ignition») = 23.33%; $CaCO_3$ = 33.32%. The soil is thus highly calcareous and highly alkaline, but owing to the gentler gradient and higher humus content, the moisture relations are more eustatic than those of the Sanicle type (a).

II. Beechwood on the «Chalk Plateau» covered by non-calcareous soil. Figs. 2 and 3, II (a), II (b) and II (c). The superficial deposits overlying the chalk of the South Downs plateau and of the Chilterns plateau do not have same origin. Those of the South Downs probably arose for the most part entirely by the leaching out of the chalk with the accumulation of the insoluble residue to form a loam. The thinner loams of the Chilterns plateau — they all contain many flints — probably also mainly arose in situ by the leaching out of the chalk, but the bulk of the deposits are deeper and are probably the redistributed remains of Eocene geological formations (Reading beds), mixed with leached soil by the action of glacial water. The result is a soil cover varying in physical composition from place to place, but fairly uniform over considerable areas: the soils investigated are loamy and are completely lacking in $CaCO_3$ down to a depth of at least 40 in. (1 m.). Differences in texture and profile serve as a basis for distinguishing three subtypes, the first of which is grouped with the plateau soils of the South Downs (a): the other two, (b) and (c), are described separately and complete a series with a «brown earth» soil type at one extreme and a degenerate «brown earth» at the other showing a definite approach to III (podsol).

(a) On the South Downs, depending on the degree to which leaching has taken place, a series of soils arises differing in total

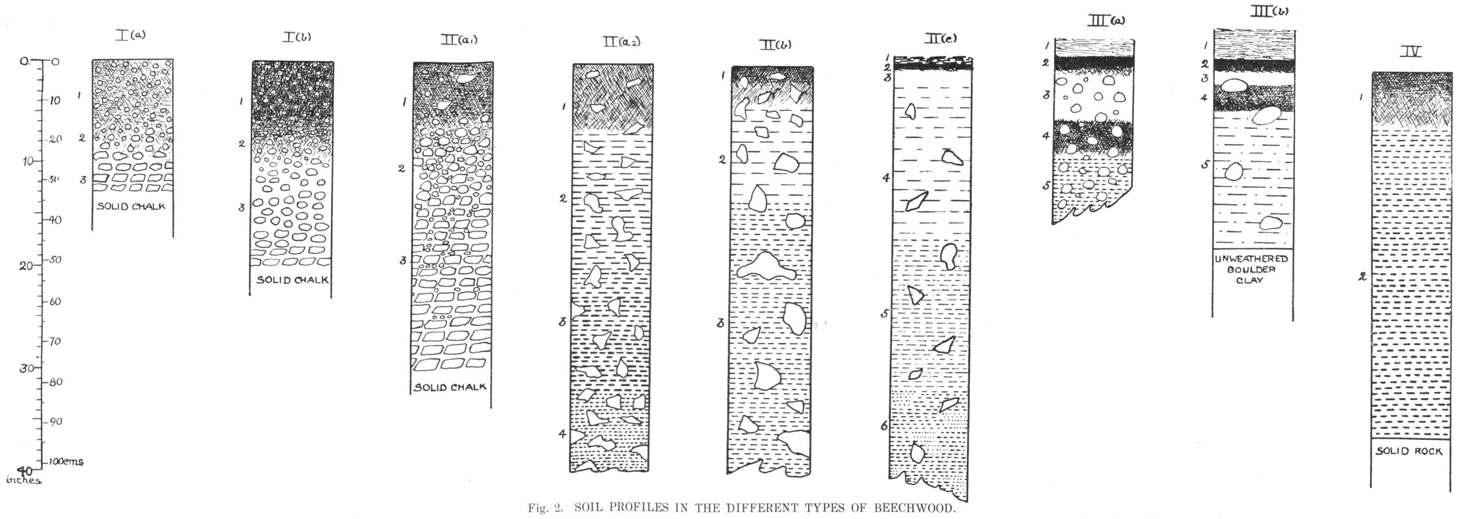

Fig. 2. SOIL PROFILES IN THE DIFFERENT TYPES OF BEECHWOOD.

The general line of the tops of the profiles is the line of surface of the soil containing mineral particles. The layers above this line (IIc, IIIa, IIIb) are compacted litter (broken lines) and raw humus or Trockentorf (black): loose leaf litter is not shown. Cross hatching in the surface layer indicates the approximate amount and distribution of humus: in IIIa and IIIb also the illuvial horizon (4). The broken lines in the lower parts of profiles IIa2 to IV represent the colour and texture of the deeper soil layers — the closer and thicker the lines, the closer the texture and deeper the colour (red to yellow) increasing with depth. Dots and short broken lines represent an obvious sand fraction (IIa2, IIc, IIIa, IIIb). IIa1 and IIa2 are two extreme examples of the «best» plateau soils (IIa), the first calcareous, the second extremely acid. For further explanations see text.

depth, from 30 in. (76 cm.) to over 48 in. (1.2 m.), in the thickness of the insoluble residue from 0 to 39 in. (1 m.), in the $CaCO_3$ content (from 1.16%, where the loam is 9 in. deep, to 0.00% where it is deeper), in the humus content (from 15.49% to 8.08%) and in the pH value of the surface 3 cm. (from 7.2 down to 6.1). The soils show a gradation from a friable, loose, open-textured, neutral soil to an acid, compact and sticky soil.

Profile II (a, 1) represents the shallowest and most calcareous of this series. (1) Dark, loose soil with much humus and small chalk lumps and flints (0 to 6 in.: 0 to 15 cm.), overlying (2) yellow-brown rubbly chalk (at 6 to 14 in.: 15 to 36 cm.) overlying (3) chalk stones with whitish soil between fragments (at 14 to 30 in.: 36 to 76 cm.). Solid chalk is found at 30 to 36 in. (76 to 92 cm.).

The Chilterns representative of this subtype resembles the deeper loams of the South Downs and includes examples where the loam is of unknown depth (certainly over 40 in.: 1 m.), besides others where the loam is relatively shallow (18 in.: 41 cm.). On the deeper loams (Profile II (a, 2) the litter is about 1 in. (2.5 cm.) thick, and shows no tendency to form raw humus. (1) The surface 6 in. (15 cm.) are friable and well mixed with humus. (2) Between 6 and 20 in. (15 and 51 cm.) the soil is paler, dirty coloured, flinty and relatively open textured. (3) Between 20 and 32 in. (51 and 81 cm.) the colour is reddish-brown, the texture very close, and the soil shrinks on drying to form hard prismatic lumps. (4) Below 32 in. (81 cm.) the soil is red-brown, very flinty, and with a large sand fraction. This layer extends to at least 45 in. (114 cm.). There is no free $CaCO_3$ down to a depth of at least 42 in. (107 cm.).

Surface 6 in. (15 cm.) samples from different woodlands on these deeper loams have an average humus content of 8.20% (range 7.41% to 9.11%). This humus is fairly evenly distributed (v. Table). The average pH value is 4.50 (range 4.2 to 4.9). Despite this high acidity the vegetation includes many species commonly regarded as characteristic of alkaline or only slightly acid soil, e. g. ***Asperula odorata*, *Bromus asper*, *Euphorbia amygdaloides*, *Fragaria vesca*, *Lamium galeobdolon***, etc.

The characteristic features of the S. Downs plateau soils and these deeper loams of the Chilterns are the presence of a surface layer well mixed with humus, an abundance of earthworms and burrowing mammals, making the soil loose and yielding under foot, and the absence of any tendency to form raw humus on the surface and of any visible bleached horizon.

(b). This subtype, profile II (b), is intermediate between (a) and (c). The leaf litter is for the most part loose, but here and there is distinctly matted below and in parts shows a tendency to form a thin layer of black peat. (1) The surface 1.5 in. (3.8 cm.) is a dark layer coloured with humus and loosened in part by the burrowing of mice. (2) Below, the humus colour disappears rapidly and the profile from 1.5 in. to 13 in. (4 cm. to 33 cm.) is occupied by a pale, yellowish soil. (3) Between 13 in. and 39 in. (33 cm. and 99 cm.) the soil is reddish in colour and very tenacious. The uppermost 0 to 8 in. (0 to 20 cm.) are very flinty, but below that the flints are few, though large. There is no free $CaCO_3$ down to a depth of 39 in. (99 cm.) and the pH in no part of the profile (except the surface 4 cm.) exceeds 5.2. The surface 6 in. contains only 6.19% humus which is unequally distributed, the amount decreasing rapidly from above downwards. (Table 1.) There is a slight trace of bleaching in the surface layer.

(c). The tendencies noted in (b) become definite features in subtype (c), profile II (c). The loose leaf litter is deeper (2 in.: 5 cm.), and below this the leaves are matted together, forming a continuous layer 0.5 in. (1.3 cm.) thick (1). This decomposes to a black peat (2) (Trockentorf) from 0.5 to 2 cm. thick. (3) The underlying mineral soil is definitely bleached to a depth of 3 cm.: the uppermost .5 cm. is dark with much infiltrated humus, the remaining 2.5 cm. being whitish grey, with a slight change in colour and a trace of consolidation below. (4) Between 1 in. and 16 in. (2.5 cm. and 40 cm.) the soil is pale yellow, compact when moist *in situ*, but powdery when dry. (5) Between 16 in. and 31 in. (40 cm. and 79 cm.) it is a stiff mottled grey-yellow-red clay-like soil; and (6) between 31 in. and 40 in. (79 cm. and 101 cm.) it is mottled grey-red with pockets of sand in a matrix of plastic soil. Flints are few compared with (a) and (b). Throughout the profile there is no $CaCO_3$ and the pH never exceeds 4.65.

A surface 6 in. (15 cm.) sample contains 6.20% humus which shows a very steep gradient from above downwards; the pH is 4.0.

TABLE 1.

Soil Type II: Plateau Beechwoods, Chiltern Hills.
«Loss on Ignition» and pH in the surface soil layers.

Depth in cm.	a		b		c		
	„Loss on Ignition"	pH	„Loss on Ignition"	pH	Soil layer	„Loss on Ignition"	pH
0— 3.8	9.57	5.11	11.25	5.43	Black peat (Trockentorf)	71.72	4.0
3.8— 7.6	8.31	4.95	5 66	4.93	Lower part of black peat	26.36	3.85
7.6—15.0	7.72	5.13	4.78	4.84	Upper 0. 5cm. bleached horizon	13.22	3.90
					0.5—3.0 cm. bleached horizon	5.72	4.19
					3.0—10 cm.	6.09	3.95
					10—18 cm.	3.97	4 22

The soil is firm under foot: there are few or no animal burrows and the few earthworms appear to restrict their activities to the surface peat.

Comparison of the pH profiles (Fig. 3) representative of the three subtypes on the Chilterns plateau shows that the general degree of acidity is least in (a), intermediate in (b), and highest in (c). Further, if we except the initial part of the curve for (c) we find that the general course of each of the curves is similar; an increase in acidity to a maximum is followed by a general fall, the zone of maximum acidity occurring at progressively lower levels as we pass from (a) to (c).

The depression in the initial part of the curve for II (c) may be attributed to a secondary leaching due, it is believed, to the slow decay of the leaves, the formation of matted raw humus and of black peat. The degeneration of soil brought about here is well known on certain soils in Denmark and in Sweden, and the following observations and data for the pH and «loss on ignition» (Table 2) support the view that beech has this effect on the Chiltern soils.

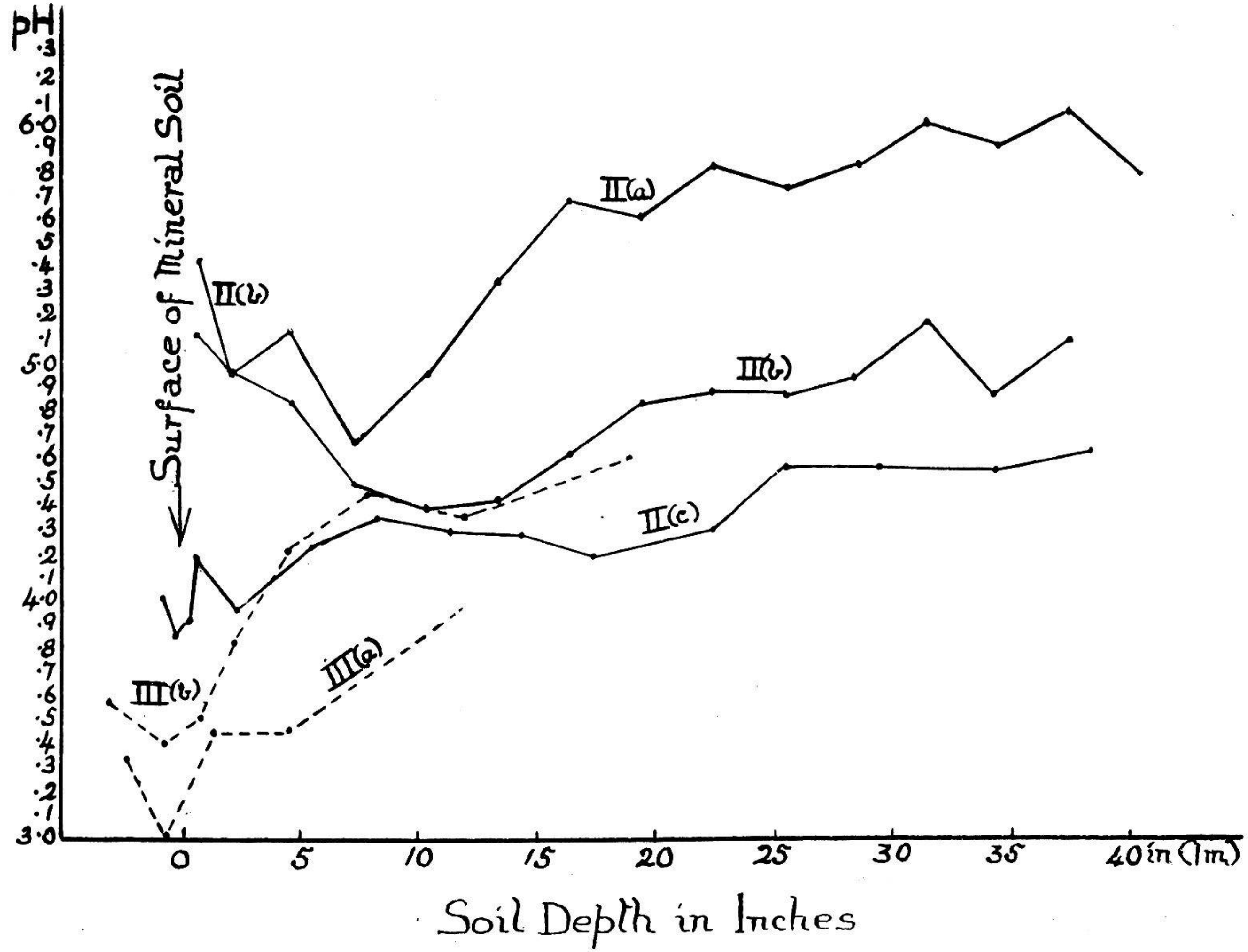

Fig. 3. Graphs of the pH profiles in Soil types IIa, IIb, IIc, IIIa, IIIb.

TABLE 2.

Comparison of pH and «loss on ignition» of surface soil under beech and under adjoining ash, oak, etc., in different localities on the Chiltern Hills plateau.

pH Values.

Locality	Ashridge		Ashridge		Ashridge		Ashridge	
Depth of Sample in cm.	Beech	Ash and Oak	Beech	Oak	Beech	Oak and Chestnut	Beech	Ash and Oak (felled)
5 cm. humus immediately above mineral soil	3.54	—	3.91	4.69	3.58	3.63	3.77	—
0—1 mineral soil	3.65	4.80	4.06	4.61	3.86	4.48	3.77	4.91
1—3,5 mineral soil	4.19	5.03	4.21	4.62	4.02	4.47	4.06	4.83

Besides the lowering of the pH under a canopy of beech as compared with one of ash or oak, there is also the distinct rise in the steepness of the humus gradient comparable with that already noted in the series II (a), (b) and (c). This steepness is due not only to the tendency of black peat to collect on the surface of the soil under a beech canopy, but also to the fact that the humus content in the surface layers of the mineral soil is lower. The humus under the canopy of ash and oak is well mixed with the mineral soil by earth-

pH and «loss on ignition».

Depth of Sample in cm. (mineral soil)		Hampden		Hampden	
		Beech	Ash	Beech	Ash-Hawthorn
0—3.8	pH	4.25	4.79	4.78	4.95
3.8—7.6	pH	4.38	4.74	4.57	4.95
0—3.8	Loss on Ignition	9 81	13.08	9.50	12.95
3.8—7.6	Loss on Ignition	8.06	10.98	7.41	10.36

worm activity, which is apparently depressed under beech. Further, the removal of the surface beech litter and humus reveals a network of depressions, the old and abandoned runs of burrowing animals.

III. *Heath Beechwoods.* The soils derived from acid geological formations (sandstones, gravels, etc.) show a diversity comparable with the series found on the chalk plateaux. At one extreme, and especially on well watered but well drained slopes, the mineral soil is well mixed with the humus: at the other, and almost entirely on flat soil, the litter decays slowly and accumulates on the surface, forming raw humus and causing bleaching of the surface mineral soil. All these soils are acid and coarse-textured. No study has been made of the more fertile sands and the following account deals only with those showing definite podsolisation. Two subtypes are recognised, the Southern Heath Beech woods (a) found in south-eastern England on sands and gravels, and the Northern (b) found in northern Scotland and studied mainly from drained glacial till overlying granite and metamorphic rocks (Fig. 2).

(a) The soil is infertile and very acid (Fig. 3). A profile, III (a), from the gravel in Burnham Beeches shows a layer of litter about 1 in. (2.5 cm.) thick. Decomposition is slow and (1) a layer (1.5 in.: 3.8 cm.) of partly disintegrated leaves overlies (2) a layer of the same thickness of brown-black friable peat. (3) The bleached horizon (3 to 6 in.: 7.5 to 15 cm.) is almost white above, but grades below to (4) an unconsolidated light brown illuvial horizon (3 in. : 7.5 cm.). (5) At 9 in. (23 cm.) from the surface of the mineral soil, the soil becomes light red. The whole is very pebbly. On the Lower Greensand in Sussex a definite iron pan is formed but details are lacking. As in II (c) the humus gradient is very steep.

(b) In contrast to (a) the soils contain considerable reserves of bases, although there is no free $CaCO_3$. Hence the general level of the pH curve is higher (Fig. 3) but shows the same general drift. The depth of the organic matter on the soil surface is greater, including (1) a 2 in. (5 cm.) consolidated layer of laminated beech leaves, 1.5 in. (3.8 cm.) of partly disintegrated leaves, and (2) .5 to 1 in. (1.7—2.5 cm.) of black-brown amorphous and moist peat. (3) The bleached layer is 1 to 1.5 in. (2.5—3.8 cm.) thick, the upper part containing much infiltrated humus; (4) the illuvial horizon is about 2 in.

(5 cm.) thick and shows a thin humus pan below, marking a sharp transition to (5) an open reddish-grey sandy-loamy layer from 9 to 11 in. (23 to 28 cm.) thick. This horizon overlies the compact unweathered glacial till at a depth of 15 to 20 in. (38 to 51 cm.). No roots penetrate this consolidated glacial till.

In both these subtypes animal activity is low so that little (if any) mixing of humus and mineral soil takes place by this means. Differences between the two subtypes appear to be of degree and not of kind, the northern podsols reflecting the lower temperatures of a higher latitude in the slower rate of leaf decay: the layer of laminated humus is thicker and the underlying peat wetter.

In the southern heath beechwoods no tests have been made to see what changes in humus content and in acidity are brought about when a beech canopy replaces one of oak or birch. But in the northern subtype no difference was detected either in the pH or the profile when comparison was made with the adjoining conifer wood. The fact that the northern beechwoods examined grow on soils containing large reserves of bases, and also that the subspontaneous beechwoods themselves have only existed for a short time, probably explains why there is as yet no detectable difference between the soils of the beech and those of the conifer wood.

On the southern sands (those of the Weald and of the Eocene beds of the London and Hampshire basins) of which the soils have been described (III a) in this section, the beech shows local but progressive colonisation. Most of these soils bear heath, birch and oakwood *(Betula alba* and *B. pubescens*, *Quercus robur* and *Q. sessiliflora)* and subspontaneous pinewood. In a good many places there is scattered beech, and in others locally pure beechwood, some at least of which has certainly arisen naturally from self-sown seed.

Similar soils in Denmark show a retrogressive vegetation due to soil degeneration under continuous beechwood canopy. A similar process of soil degeneration occurs here and it is probable that its rate would be faster because of the more «Atlantic» climate, so that the degeneration would be marked during the life of a single generation of trees. From this we may infer that, on the poorer sands at any rate, a mature beechwood could not regenerate in situ, and that though beech colonisation may be progressive on the sands as a whole, the mature wood cannot perpetuate itself after continuous cover has been established, since it rapidly brings about conditions prohibitive to its own regeneration. If this conclusion is sound no beechwood on these sands can be older than the period of life of the oldest trees. Even the brown earths of the chalk plateaux show evidence of the same soil degradation under beech canopy — a phenomenon apparently not recorded from central and southern Germany.

IV. «Herbaceous» Beechwoods (N. Scotland). The soils of this type are all derived from Old Red Sandstone. They have not been studied in detail, but they approximate in general character to the soils of II (a), with a relatively low acidity, and an absence of raw humus.

The profile produced (IV) is from a soil of this kind, and the following field note may be added. «Ash, sycamore and beech leaf-litter, .5 to 1.5 in. overlying variable (0 to .75 in.) depth of mull humus which gradually changes into (1) reddish-black humose soil 4 to 6 in. (10 to 15 cm.): overlying (2) purple-reddish soil extending to bed rock at 3 feet 6 in. (107 cm.). Surface soil an open friable loam becoming somewhat heavier, silty and containing a large quantity of mica below.»

The distribution of the beech roots in the different soil horizons with their varied physical and chemical properties has not been the subject of intimate study. But the structure of the root system as a whole is an expression of soil depth. On deep soils it is heart-shaped, with an even distribution of the larger roots running obliquely downwards: where there is a physical barrier in the form of solid or compact unweathered parent rock or an iron pan, the root system is entirely or almost entirely confined to the weathered zone, but with a definite concentration of the larger roots running near or on the surface of the mineral soil. The distribution of the finer rootlets is correlated with the distribution of the humus in the upper soil layers, i. e. in I, II (a) and II (b) they are numerous throughout the surface 6 to 8 in. (15 to 20 cm.) but in the podsols II (c) and III they become more and more restricted to the superficial raw humus and surface soil layer.

Since a loss in depth of the root system does not involve so great a sacrifice in the height of the beech as in deeprooting trees like oak, the root system is best described as «accommodating». The minimum soil depth observed is 9 in. (23 cm.) with single stemmed erect beech to 48 ft. (14.6 m.) in height. On the chalk escarpment of the South Downs a soil of 16 in. (40.6 cm.) bears beech of about 80 ft. (24 m.), and it may be stated generally that the greater the effective soil depth the taller the tree.

The soils described illustrate a range of texture from open loose soils to the compact silty soils of II (c). But the height growth of the beech increases as the extremes are left behind to a maximum on loam. The power of accommodation of the beech is further illustrated by its dominance on coarse sands (e. g. Lower Greensand in south-eastern England) and on gravel (Fluvioglacial gravel in Morayshire) and its local occurrence on clay (e. g. London Clay, Weald Clay).

The data given show that the nature, amount and distribution of the dead organic matter in soils bearing beechwoods vary much within wide limits. High values are obtained both in chalk soils and in podsols but, whereas in the former the humus is mixed with chalk, which counteracts any harmful physical or chemical effects, it accumulates as acid raw humus on the surface of the latter, causing a leaching of iron and bases. On non-calcareous soils there is a close correlation between the distribution of the humus in the surface soil and beech growth.

Corresponding with the facts just mentioned, the hydrogen-ion concentration shows a very wide range: from a pH of 3.01 for the surface black-brown friable peat of III (a) to a pH of 8.5 on chalk. Between the pH of the upper soil and beech growth there is no necessary connection, for trees of 100 ft. (30 m.) grow on soils whose surface 6 in. (15 cm.) has a pH of 4.2 (Chiltern plateau). High acidities also prevail in the lower layers of some of these soils, as the following data show for a soil bearing beech 80 ft. (24 cm.) high: surface 3 in. (7.15 cm.), pH 4.45: at 10 to 13 in. (25 to 33 cm.), 4.6: at 18 to 20 in. (46 to 51 cm.), 4.85: at 38 to 40 in. (96.5 to 101.5 cm.), 4.9. Similar values are also found for podsol, where it is known that the whole of the beech root system may be confined to horizons having a range of pH from 3.4 to 4.6 (III, b). In II (c) the bulk of the root system,if not the whole, is restricted to soil whose pH at no level exceeds 4.65.

The indifference of the behaviour of the beech towards $CaCO_3$ is well shown by its good growth in soils containing much or no free $CaCO_3$. The range is from soils with no $CaCO_3$ demonstrable down to a depth of 1 m. to a percentage of 59.5 in the surface 6 in. (15 cm.) of I (a). These results emphasise the fact that while beech can tolerate much $CaCO_3$ in the soil it does not require it.

In view of the power of beech to grow on soils of widely different textures and humus contents, data respecting soil water content are much to be desired. Unfortunately few determinations have been made and none at all to indicate the limits for beech growth. A series of 14 sets of 3 taken at different depths in the plateau beechwoods of the South Downs yield the following averages (with extremes in brackets). The samples were collected in August and September of the dry year 1921.

Soil layer.	*Moisture percentage of dry weight.*
0—2 in. (0—5 cm.)	31.9 (18.99—52.90)
6—8 in. 15—20 cm.)	25.6 (14.41—36.72)
18—20 in. (46—51 cl.)	20.4 (14.85—34.22)

The highest value for moisture content so far obtained is 81.60% from the top 2 in. (5 cm.) of an *Anemone* beechwood in Aberdeenshire on Old Red Sandstone. This sample was taken in June.

In most beechwoods the level of the water-table is not relevant. In the post-climax beechwoods on heath soils, III (b), the water-table is about 18 to 24 in. (46 to 61 cm.) below the surface of the mineral soil.

Determinations of the content of the soil in nutrient salts, including nitrates, and soil aeration are lacking, but field observations indicate that while the beech can grow on soils poor in all three, better growth is obtained where supplies of nutritive salts and oxygen are more abundant. Good beech growth is associated with an abundance of nitratophilous herbs.

5. GROWTH FORM. AGE.

As already stated, the beech is always a tree, never a shrub. The considerable variation in Great Britain in stem and crown form and bark surface raises the question of the existence of distinct races. No detailed studies have been made, but curvature of the stem (almost invariably) and rough bark, commonly although not exclusively, characterise trees of slow growth. How far this result is due to unfavourable soil conditions or to a system of management which eliminates the individuals belonging to the best strains, leaving those of slower growth and spreading crowns to restock the ground, is unknown. In some localities poor soil seems to be the cause of the poor growth as there has been no selective elimination of the best trees; but without definite information on the source of the seed and in the absence of experimental trial no decision can be made. Only smooth-barked trees have been seen on the South Downs, but on the Chiltern and Cotswold plateaux smooth and rough-barked stems are generally found on good and poor soils respectively. In northern Scotland the smooth-barked type predominates: rough-barked forms are rare.

Differences in the rate of growth are brought out by the data for the total height of mature trees of 120 to 140 years of age. The height of trees in canopy varies from an average of about 60 ft. (18 m.) to an average of 110 feet (33.5 m.). The maximum height recorded is 135 ft. (41 m.) for the Queen Beech, Ashridge (Chiltern plateau), blown down on Nov. 14th 1928. The girths at breast height (4 ft. 3 in.: 1.3 m.) correspond, and vary from 2 ft. 3 in. (68.6 cm.) to 5 ft. 4½ in. (1.6 m.).

The number of trees per unit area of 10,000 square feet (= .23 acre = .093 hectare) and their distribution in crown classes are summarised in the accompanying table (Table 3).

The data from the two areas are not strictly comparable. On the South Downs (Goodwood Estate) and on the Chilterns (columns 1 to 3) interference with the natural development of fully stocked forest is restricted to the elimination of dead, dying and suppressed trees. The crops at maturity are therefore expressions of the potentialities of the habitat and comparison between the plots is legitimate. Nominally the Chiltern woods are managed on the «selection system», but the older age classes predominate, almost to the exclusion of the younger, so that most of the woods are practically even aged or have trees of uniform size. This is true of the carefully managed woods of the Hampden Estate (Chiltern Hills, columns 6—15) from which the above data have been taken, so that the resulting woodlands do not differ so much as to forbid comparison on broad lines.

TABLE 3.

Number of stems etc. per 10,000 sq. ft. (= .23 acre = .093 hectare) in different types of beechwoods.

	I		II												
	(a)	(b)	(a)							(b)			(c)		
Locality:	Chilterns			S. Downs		Chilterns									
Average height in feet of dominant *Fagus* .	79' *)	89' *)	107	100	90	83	81	77	74	70	69	69	62.5	60	59
Average girth of dominant *Fagus* at 4 ft. 3"	3'3"	3'8"	5'4½"	4'10"	4'9"	3'8½"	4'3"	3'8"	3'5"	2'11"	3'0"	3'0"	2'7½"	2'6½"	2'3"
Age	c. 130	—	145	130-150	130-140	130	—	140	130-140	—	125-140	125-140	—	105-140	105-125
Total number of *Fagus*	53	40	20	21	21	43	19	38	41	52	53	62	91	84	95
Total number of *Quercus robur*	0	0	0	0	2	2	0	2	4	0	0	0	0	5	3
Total number of *Fraxinus*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Number of dominant *Fagus*	33	23	15	21	19	18	18	22	27	27	39	40	45	24	51
Number of subdominant *Fagus*	20	10	5	0	2	15	1	8	7	20	10	16	31	27	20
Number of suppressed *Fagus*	0	7	0	0	0	10	0	8	7	5	4	6	15	33	24
Number of dominant *Quercus robur* . . .	0	0	0	0	1	1	0	2	4	0	0	0	0	5	3
Number of dominant *Fraxinus*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

*) These heights are much above the average for the Sanicle (a) and Mercury (b) woods of the Chiltern escarpment, but the data for density of stocking etc. are the only data available. The average heights are 67 ft. (20.4 m.) and 77 ft. (23.5 m) respectively.

The number of stems per unit area decreases with increasing height; conversely, the slower the rate of growth the denser the stocking at the same age. Woods of the same height, as would be expected, contain a larger number of stems on the better soils, e. g. 48 dominants of 70 ft. (21.3 m.) compare with 36 of the same height on a slightly poorer soil. This holds good for the woodlands of the South Downs when comparison is made among themselves, but the comparison may be extended to the Chiltern woods, and shows that where the unit area bears the same or a similar number of dominants (columns 4—8) the height attained is less on the Chiltern plateau than on the South Downs plateau. The different management systems alone may account for this. Height for height the beech under the selection system has a larger girth, but age for age the beech in even-aged high forest is taller and denser.

Age. Schlich gives the duration of life of the beech as something less than 500 years, but data for this country are scarce, partly because a ring count is impossible owing to heartrot, which is prevalent in old trees. Pollarded trees survive at least 350 years, but in high forest the age of the beech in Britain does not greatly exceed 150 years.

6. REGENERATION.

The conspicuous scarcity for long periods of young beech growth conveys the impression of a failure to rejuvenate which would ultimately end in retrogression of the beechwood community. As a matter of fact there is no authenticated case where regeneration is so poor as to fail to ensure the maintenance of natural or semi-natural beech forest: the young growth is adequate to replace the numbers dying. Since deaths frequently follow dry years, in which also seed production is initiated, there is here a time coincidence favourable to the maintenance of beechwood.

From the point of view of forest maintenance and timber production, regeneration in many woods is unsatisfactory. The reasons for this are summarised below, but the practical result is that the crop from partial or intermediate mast years is almost wholly destroyed and what young growth there is survives from full mast years only. Regeneration is most abundant in the beech associes, that is in woodlands of ash or oak, or of the two together, with much successfully established beech in mixture, the young beeches growing up under the shade of ash and oak and forming dense peripheral growth in gaps. This distribution suggests the need of an adequate light intensity for the growth of the beech, the photosynthetic efficiency of whose leaves is reduced by the ubiquitous bug *Typhlocyba douglasii* (Hemiptera). Under a continuous beech canopy the combined effect of reduced light intensity and persistent insect attack on the leaves is to cripple and ultimately to kill the young growth. But the scarcity of young growth in pure beechwoods appears in part to be due to a lack of seed, for while, even during a mast year, trees marginal to woods and to gaps produce seed in abundance, those forming part of a continuous canopy produce relatively few.

The evidence from Britain is inadequate to establish the conclusion that the westward migration of beech has been checked by the Atlantic climate (e. g. by the summers being too cool to ripen seed), though the rate of spread may have been decreased owing to the occurrence of fewer «mast years»: of this, however, there is no positive evidence.

In this country there is little or no endeavour made to utilise the periodic production of seed, either by anticipating a mast year and initiating flower formation by opening up the canopy, or by encouraging the young growth by further timely removal of adults. Woods are often clear felled without reference to seed years, or selectively felled periodically, when a dense undergrowth of brambles (*Rubus fruticosus* agg.) decreases the chances of seedling survival. Singleton Forest on the South Downs is however an instructive exception. This forest was clear felled in blocks during last century and the present dense stand of beech is the result of natural reproduction, the gaps being filled up by larch, most of which were removed during and immediately after the War. For successful regeneration on certain soils the renewal of the forest must be initiated before the development of a field layer of taller growing plants like *Mercurialis perennis* and *Rubus fruticosus* (agg.) puts a check upon seedling establishment and survival.

7. ACCOMPANYING TREES.

In the climax wood beech is dominant. Ash, oak and *Sorbus aria* often occur in small numbers but are relicts from the pre-climax stage. The position of *Prunus avium* on the Chiltern plateau is somewhat different. This tree appears to be a normal constituent of climax beechwood, maintaining itself by vegetative reproduction, but always in small numbers as scattered individuals, and never forming pure groups of adults.

The competitive equipment and soil preferences of the hornbeam *(Carpinus betulus)* and the area of its natural occurrence in England resemble those of the beech, although hornbeam has the greater ability to grow on heavy clay as beech has on shallow chalk soils, while hornbeam extends further north than beech, and beech further west than hornbeam. Yet hornbeam is not a common tree in beechwoods. It is absent from the South Downs (perhaps outside the limit of its natural occurrence), as it is from many of the Chiltern plateau beechwoods, although common in hedgerows; and it is doubtful if its place in the canopy of some beechwoods is permanent, for the hornbeam is excluded from the better grown beechwoods because it is a shorter lived tree and attains a smaller ultimate height than beech. The weak radicle of the seedling probably checks successful establishment in grassland: and the conditions for its natural and fullest expression are apparently found in oakwood *(Quercus robur* and for *Quercus sessiliflora)*, where the woodland communities formed by oak standards with hornbeam coppice are probably the lineal descendants or the little altered modern representatives of natural oakwoods with hornbeam forming a subcanopy to the oak. These woods grow in Essex, Hertfordshire and Middlesex on soils similar to those occupied by beechwoods further west on the Chilterns, and may be considered as an oak-hornbeam associes with beechwood as the potential climax.

The status of the sycamore *(Acer pseudoplatanus)* is still s u b j u d i c e. According to Elwes and Henry, the sycamore was probably introduced by the Romans, but it appears to have remained an uncommon tree until the 17th century. It has since been widely planted, mainly for ornament, less often for a useful purpose, and has proved hardy, wind resistant and an abundant and frequent producer of seed. Despite these advantages the species rarely forms woods of any size and many of the seedlings and young plants perish, perhaps through animal attack combined with the ravages of *Rhytisma aceri-*

num. Its mineral need is, however, similar to that of beech, and its local co-dominance with beech on the South Downs together with its local dominance in a beechwood on the Chiltern plateau suggests the possibility of a beech-maple climax parallel with that in the Eastern United States.

Of trees never attaining the height of the canopy, *Taxus baccata* is occasional in many woods on different soil types, but becomes locally abundant only on chalk, where it may reach subdominance, forming a continuous sub-canopy to beech. It may attain a height of about 20 ft. (6 m.). In contrast with the yew, the holly *(Ilex aquifolium)* has a very wide range, from chalk to very acid soils of the chalk plateaux, where it forms low-growing clumps. On the better soils of the plateau it forms a small tree up to 25 ft. (7.6 m.). In the northern heath beechwoods the rowan or mountain ash *(Sorbus aucuparia)* grows to a height of 10—12 ft. (3—4 m.) in gaps, but remains small under shade.

8. TRANSITIONS TO OTHER TYPES OF FOREST.

The dominance of *Quercus robur* on heavy clays suggests the possibility of beech and oak maintaining themselves in mixture on soils with properties intermediate between the soil types respectively dominated by these trees. No undoubted example of this has been found, although at Bedham (in Sussex) the co-dominance of oak and beech may be interpreted in this way. But we have made no study of the seral development: hence no conclusion has been reached as to the temporary or permanent status of woods in which beech and oak are co-dominant.

Woods intermediate between *Alnetum* and *Fagetum* have not been seen.

Transitional forest representing stages in succession are dealt with in Section 18 (pp. 357—359).

9. INTERNAL CLIMATE.

The canopy of dense beech foliage must produce an internal or local climate different from that in the open or in communities of light-demanding trees. But data are scanty and continuous records covering a year non-existent. We expect a low light intensity (shade phase), a narrower range of temperature variation, a higher relative humidity and a lower evaporation rate at the soil surface; and the few existing data obtained over short periods bear out these expectations.

The penetrability of the beech forest to wind is important and an effect on the ground vegetation is seen to a depth not observed in woods of light-demanding trees where the presence of a layer of taller growing shrubs checks the force and the effect of the wind. The herbaceous vegetation on these exposed margins is scanty: typical mesophytes become scarce or stunted or disappear, siliceous soils become more acid and conditions arise hostile to successful seedling establishment.

10. SHRUB LAYER.

Rubus fruticosus (agg.) and *Vaccinium myrtillus* are the only species able to form a continuous shrub or dwarf shrub layer in any beechwood: *Rubus* does this only in plateau woods (II a and II b) and in woods on the more fertile sands and grayels, *Vaccinium* in woods derived from *Calluna* Heath (type III). The growth form of *Rubus* (evergreen leaves, trailing stems, power to reproduce vegetatively, ability to endure shade) render it able to grow under beech. Inside beechwoods the vigour and high frequency of *Rubus* contrast with scarcity in open pasture or scrub, and the high relative humidity (low evaporation rate), absence of competition, and facilities for rooting in the humus layer of the beechwood appear to be decisive factors. All other shrubs have a low frequency or a high local frequency only *(Ilex, Hedera)* and are often dwarfed with procumbent or prostrate stems.

In the list of species those of I and II (a) are practically the same and this in spite of the soil contrast. As the soil deteriorates the more exacting shrubs are eliminated, leaving only a few in II (b) and II (c). The few shrubs belonging to III (a) and (b) are largely different species, whilst in IV the shrub flora is scanty. *Clematis vitalba* (marginal) and *Rhamnus catharticus* are limited, and *Daphne laureola* is almost limited, to the limestone soils. *Ruscus aculeatus* is the only species peculiar to II (a), *Frangula alnus* to the southern heath beechwoods, whilst in open heath beechwoods of the northern type *Vaccinium myrtillus* forms a continuous dwarf shrub layer and *Sorbus aucuparia* a discontinuous subordinate tree layer. Like *Rubus, Vaccinium* possesses a growth form enabling it to survive and spread under a beech canopy — evergreen shoots, power to endure shade, vegetative reproduction, and ability to compete successfully with beech roots.

About half of the shrubs and dwarf shrubs have evergreen or winter-green leaves or evergreen shoots, and those which attain the higher frequencies belong to this group *(Rubus, Hedera, Ilex, Vaccinium).* The great majority have fleshy fruits, though few produce them under the beech canopy. In most the vigour is subnormal, but at least thirteen can reproduce vegetatively.

11. GROUND FLORA.

A complete list of the observed vascular plants and Bryophytes is given in Table 4. The floristic cortège of beechwoods is by no means uniform and the following 4 major types, with 7 subtypes, corresponding with the soil types described on pp. 303—314, have been investigated in greater or less detail. Other types have been observed but not examined.

I. Beechwood on Chalk. The beechwoods of chalk escarpment (Phot. 1) and correspondingly steep valley side slopes (beech «hangers») are remarkably uniform. They are characterised by floristic wealth, almost entirely herbaceous, and by the absence of «calcifuge» species. On the Chiltern escarpment two sub-types are recognised, dominated respectively by *Sanicula europaea* and *Mercurialis perennis.* The species occurring in both are practically the same, but a few *(Campanula trachelium, Dryopteris filix-mas, Poa trivialis, Ranunculus repens)* are confined to the Mercury wood and several *(Circaea lutetiana, Urtica dioica, Epilobium angustifolium,* etc.) are local only in the Sanicle wood. The species common to both differ mainly in frequency, constancy and vigour, and a clear separation is made on the basis of the biological spectra of the species with high average frequency and for high constancy (see Table 5).

Phot. 1. BEECHWOOD ON CHALK (I). The ground to the right of the photograph slopes steeply downwards, forming the main chalk escarpment. The wood is spreading on to the gentler slope above where occur old «pioneer» beeches with short boles and widespreading crowns, and younger beeches and occasional ash with straighter, cleaner stems. Fringing the wood is a zone of ash scrub, and some dead shrubs are to be seen under the beech. Note the complete absence of a field layer. Near Graffham, South Downs, Sussex.

TABLE 4.
FLORA OF BEECHWOODS.

d = dominant, a = abundant, f = frequent, o = occasional, r = rare, l = local, m = marginal, + = present.

Lifeform	Species	I On Chalk Escarpments		II On non-calcareous Soils of Chalk Plateaux			III Heath Beechwoods			IV „Herbaceous" Beechwoods
		(a)	(b)	(a)	(b)	(c)	(a)	(a 1)	(b)	
	Trees & Shrubs									
M-N	Acer campestre	o-f	o-f	r	—	r	—	—	—	—
MM 2	A. pseudoplatanus . . .	o	o	o-ld	o	—	—	—	r	o
MM 2	Alnus glutinosa	—	—	—	—	—	l	l	—	—
H	Atropa belladonna . . .	—	o	—	—	—	—	—	—	—
MM 2	Betula alba	o	r	—	—	r	o-lf	o-lf	—	—
MM 2	B. pubescens	—	—	—	o	—	o-la	o	o	l
MM 2	B. alba × pubescens . .	—	—	—	—	r	—	+	—	—
H	Bryonia dioica	o	o	—	—	—	—	—	—	—
N	Buxus sempervirens . .	—	o	—	—	—	—	—	—	—
MM 2	Carpinus betulus . . .	o	o	o	l	o	—	—	—	—
MM 2	Castanea vesca	—	—	r	—	—	—	o	—	—
M	Clematis vitalba . . .	m	m	—	—	—	—	—	—	—
N	Cornus sanguinea . . .	o	o	o	—	—	—	—	—	—
N	Corylus avellana . . .	r	o	o	r	—	r	o	—	—
N	Crataegus monogyna . .	o	o	o	o	r	—	r	—	—
N	Daphne laureola . . .	r-lf	r-lf	vr	—	—	—	—	—	—
N	Euonymus europaeus . .	o	o	o	—	—	—	—	—	—
MM 1—2	Fagus silvatica	d	d	d	d	d	d	a-ld	d	d

N	Frangula alnus	—		—	—	—	—	l	—	—	—
MM 2	Fraxinus excelsior . .	o		o	o-f	l	—	—	o	—	o
Ch-MM 2	Hedera helix	f		o-f	o	o	l	—	l	—	o
N-M	Ilex aquifolium	o		o	o-la	o-f	o-ld	o	a-ld	o	r
N	Ligustrum vulgare . .	r-o		r-o	r	—	—	—	—	—	—
Ch-N	Lonicera periclymenum .	r		r	o-la	o-lf	r	o-la	o	l	l
MM 2	Prunus avium	r		o	o-lf	o	r	r	r	r	—
N	P. spinosa	r-o		r-o	—	—	—	—	—	—	—
M	Pyrus malus	r		r	r	—	—	—	—	—	—
MM 2	Quercus robur	r		o	o-f	o-f	o-f	o	f-ld	r-o	+
MM 2	Q. sessiliflora	—		—	—	l	—	o	—	—	o
N	Rhamnus catharticus . .	r		r	—	—	—	—	—	—	—
N	Ribes grossularia . . .	r		r	r	—	—	—	—	—	—
N	R. nigrum	—		r	r	—	—	—	—	—	—
N	R. rubrum	—		—	r	—	—	—	—	—	—
N	Rosa arvensis	o		o-f	o-f	l	—	—	—	—	—
N	R. canina		lf		—	—	—	—	—	—	—
N	R. dumetorum		r		—	—	—	—	—	—	—
N	R. lutetiana		r-o		—	—	—	—	—	—	—
N	R. sarmentacea	r-o		r-o	l	—	—	—	—	—	—
Ch	Rubus caesius	o		o	—	—	—	—	—	—	—
H	R. fruticosus (agg.) . .	o		o	d	d	o	o-ld	lf-ld	o	l
H	R. idaeus	r-o		r-o	o	lf	l	o-lf	—	r	la
N	Salix caprea	r-o		r-o	o	r	l	—	o-lf	r	r
N	S. cinerea	—		—	—	—	—	o	l	—	—
N-M	Sambucus nigra . . .	o		o-f	o	o	—	—	o	—	—
M-MM 2	Sorbus aria	o-f		o	l	r	—	—	—	o	—
N-M	S. aucuparia		r-o		o	r-o	—	—	—	a	r
G	Tamus communis . . .		r-o		r	—	—	—	—	—	—

Lifeform	Species	I (a)	I (b)	II (a)	II (b)	II (c)	III (a)	III (a 1)	III (b)	IV
M	Taxus baccata	o	o-ld	r-o	—	—	—	o-lf	—	—
MM 2	Ulmus glabra (montana)	r-o		—	l	—	—	—	—	—
N	Viburnum lantana . . .	o	o	r	—	—	—	—	—	—
N	V. opulus	r-o		r-o	l	—	—	—	—	—
	Herbs, etc.									
H	Adoxa moschatellina . .	o		—	—	—	—	—	—	lf
H	Agropyrum caninum . .	—	r	l	—	—	—	—	—	—
H	Agrostis alba	r	o	r	o	lf	—	o-f	—	—
H	A. vulgaris	—	o	l	o	o-lf	o-f	f	o-f	o
H	Ajuga reptans	r-o	o	o	—	—	—	la*	—	o-la
G	Allium ursinum . . .	la		—	—	—	—	—	—	l
G	Anemone nemorosa . .	f	o	o-la	—	—	—	—	—	o-d
H	Anthoxanthum odoratum	r-o		—	r-o	o	o-f	o	—	—
H	Aquilegia vulgaris . .	r		—	—	—	—	—	—	—
H	Arabis hirsuta	r-o	r-o	—	—	—	—	—	—	—
H	Arctium minus	o	o	o	—	—	—	o	—	—
T	Arenaria trinervia . . .	r-o		r-o	l	—	—	o	—	o-lf
H	Arrhenatherum elatius .	—	o	o	—	—	—	—	—	—
G	Arum maculatum . . .	o	o	r-o	—	—	—	—	—	—
G	Asperula odorata . . .	f-a	o-f	o-f	—	—	—	—	—	lf
H	Athyrium filix-femina .	—	—	o	o	l	—	o	—	—
H	Blechnum spicant . . .	—	—	—	—	—	—	o-f	o	o-f
H	Brachypodium silvaticum	o-la		o-la	—	—	—	—	—	—
H	Bromus asper	o	o	r-o	—	—	—	—	—	—
Ch-N	Calluna vulgaris . . .	—	—	—	l	l	o-la	la	o	—

H	Campanula rotundifolia .	o	r	—	—	—	—	—	—	—
H	C. trachelium	r	o	—	—	—	—	—	—	—
H	Carduus crispus . . .	r	o	—	—	—	—	—	—	—
G	Carex binervis	—	—	—	—	—	—	—	r	—
G	C. glauca	o	r-o	—	—	—	o	—	—	—
H	C. leporina	—	—	—	l	l	—	—	—	—
H	C. pallescens	—	—	—	—	l	—	—	—	—
H	C. pilulifera	—	—	—	—	lf	o	—	—	—
H	C. remota	—	—	o	o	o-f	—	—	—	—
H	C. silvatica	o-f		o	o	o	l	o	—	—
H	C. strigosa	—	—	l-f	—	—	—	—	—	—
G	Cephalanthera ensifolia .	r		—	—	—	—	—	—	—
G	C. grandiflora.	o-f	o	—	—	—	—	—	—	—
G	C. rubra	r		—	—	—	—	—	—	—
Ch	Cerastium vulgatum . .	r		—	—	—	—	—	—	—
H	Chelidonium majus . .	r		—	—	—	—	—	—	—
H	Chrysosplenium oppositifolium	r		—	—	—	—	la	—	—
G	Circaea lutetiana . . .	l	o-f	o-ld	l	l	—	ld	—	—
H	Cirsium lanceolatum . .	r	o	—	—	—	—	—	—	—
H	C. palustre	o	o	—	—	—	—	—	—	—
G	Conopodium majus . .	o-la		r-o	o	r	—	—	o	o
H	Dactylis glomerata . . .	r	o	o	d	o	—	r-o	—	—
G	Dentaria bulbifera . .	—	—	ld	—	—	—	—	—	—
H	Deschampsia caespitosa .	o-la		o-f-ld	o-la	o	o	—	—	r-o
Ch	D. flexuosa	—	—	—	—	la	la-ld	o-lf	a	o
H	Digitalis purpurea . . .	—	—	o	o-la	—	—	o	—	r o
H	Dryopteris filix-mas . .	—	o	o	o	r	—	o	—	o-la

Lifeform	Species	I (a)	I (b)	II (a)	II (b)	II (c)	III (a)	III (a 1)	III (b)	IV
H-G	Epilobium angustifolium	lf	o-f	o-la	lf-la	l	l	lf	—	—
H	Epilobium hirsutum . .	—	—	—	—	—	—	—	—	—
H	E. montanum	o	o	o	l	l	—	o	—	r
H	E. parviflorum	r	o	—	—	—	—	—	—	—
G	Epipactis latifolia . . .	o	o	o	—	—	—	—	—	—
G	E. purpurata	—	—	r	—	—	—	—	—	—
Ch	Erica cinerea	—	—	—	—	—	o-lf	la	—	—
H	Eupatorium cannabinum	r	—	r	—	—	—	—	—	—
Ch	Euphorbia amygdaloides .	o-f		o	—	—	—	o*	—	—
H	Festuca gigantea . . .	o	o	o	—	—	—	—	—	o
H	F. ovina	r	—	—	l	o-la	—	—	o	—
H	F. rubra	o	l	—	o	o	—	—	—	o
H	Ficaria verna	l		r-la	—	—	—	—	—	la
H	Fragaria vesca	f-a	f	o	—	—	—	o	—	—
T	Galium aparine . . .	l	o	o	—	—	—	—	—	r-f
H	G. palustre	—	—	—	—	—	—	lf*	—	—
Ch	G. saxatile	—	—	—	o	lf	—	lf	o	o
T	Geranium robertianum .	o	o	of	l	—	—	o-lf	—	o-f
H	Geum urbanum . . .	o	o	o	—	—	—	—	—	o-f
G	Habenaria virescens . .	r		—	—	—	—	—	—	—
Ch	Helleborus foetidus . .	r		—	—	—	—	—	—	—
H	H. viridis	r	r	—	—	—	—	—	—	—
H	Heracleum sphondylium .	r-o		—	—	—	—	—	—	lf
H	Hieracium boreale . .	o		—	—	—	—	—	—	—
H	H. murorum	r	—	—	—	l	—	—	—	—

H	H. pilosella	r	—	—	—	—	—	—	—	—
H	H. serratifrons	la		—	—	—	—	—	—	—
H	H. silvaticum	r		—	—	—	—	—	—	—
H	H. vulgatum	—	—	—	—	—	—	—	—	o-lf
H	Holcus lanatus	r	o	o	o-lf	o-lf	o	o	o	lf
G-H-Ch	H. mollis	—	—	o-ld	o-ld	lf	o-ld	o-la	f	o-ld
H	Hordeum silvaticum . .	l	lf-la	o	—	—	—	—	—	—
Ch	Hypericum androsaemum	—	—	r	—	—	—	—	—	—
H	H. hirsutum	r-o	r-o	o	—	—	—	—	—	—
H	H. humifusum	—	—	—	l	—	—	—	—	—
H	H. perforatum	r	o	o	—	—	—	—	—	—
H	H. pulchrum	—	—	—	o	o	—	o	r	—
H	Hypochaeris radicata . .	—	—	—	o	r	o	—	—	—
H	Inula squarrosa	r	r	—	—	—	—	—	—	—
T	Juncus bufonius . . .	—	—	—	—	lf	—	—	—	—
H H	J. conglomeratus . . . } J. effusus . . . . . . }	—	r	l	l	l	o	o	—	—
H	Lactuca muralis	o	o	l	—	—	—	o	—	l
Ch	Lamium galeobdolon . .	o	o-lf	o-f-la	—	—	—	—	—	—
T	Lapsana communis . .	—	r	l	—	—	—	—	—	o
H	Lastrea dilatata	—	—	r	r	—	—	o	o	o-f-la
H	Lathyrus montanus . .	—	—	—	—	—	—	—	r	—
H	Lithospermum officinale .	r		—	—	—	—	—	—	—
G	Listera ovata	r	o	—	—	—	—	—	—	—
H	Luzula erecta	—	—	l	o	o	o	—	o	—
H	L. forsteri	—	—	o	—	—	—	—	—	—
H	L. maxima	—	—	—	—	—	—	—	—	o-d
H	L. pilosa	o-la		o-f	o	o	o-lf	f	o-f	lf
H	Lychnis dioica	r		—	—	—	—	o	—	o-la

Lifeform	Species	I (a)	I (b)	II (a)	II (b)	II (c)	III (a)	III (a 1)	III (b)	IV
Ch	Lysimachia nemorum .	r		o-lf	l	l	—	o-la *	—	o-lf
T	Melampyrum pratense .	r		—	—	—	o-la	o	—	—
G	Melica uniflora	o-la		o-la	l	l	—	lf	—	—
H	Mercurialis perennis . .	o-f	a-d	o-ld	—	—	—	—	—	lf
H	Milium effusum . . .	l	lf	o-lf	o-lf	l	—	—	—	—
H	Molinia caerulea . . .	—	—	—	—	—	o-lf	—	—	—
G	Monotropa hypopitys .	o	o	o	o	o	—	—	—	—
T	Myosotis arvensis . . .	o	o	o	—	—	—	—	—	—
G	Neottia nidus-avis . . .	o	r	r	—	—	—	—	—	vr
Ch	Nepeta glechoma . . .	r	o-la	o	—	—	—	—	—	—
G	Orchis maculata	r	r	—	—	—	—	o	—	—
H	Oxalis acetosella . . .	o	o-f	f-ld	o-ld	o	o	f-ld	—	o-f-ld
T	Poa annua	—	—	o	l	l	—	o	—	—
H	P. nemoralis	o-la	o	r-f	—	—	—	—	—	—
G	P. pratensis	r	o	—	o	o	—	—	o	o
H	P. trivialis	—	o	o	o	l	—	lf	—	r
G	Polygonatum multiflorum	lf		—	—	—	—	—	—	—
G	P. officinale	l		—	—	—	—	—	—	—
H	Polypodium vulgare . .	r	r	r	o	—	o	—	r-o	o
H	Potentilla erecta . . .	—	l	—	—	—	—	o-lf	o	l
H	P. reptans	r	o	—	—	—	—	—	—	—
H	P. sterilis	o	o	o	—	—	—	—	—	o
H	Primula veris	r-o		—	—	—	—	—	—	—
H	P. vulgaris	o-f	r-o	o	—	—	—	f	—	o-la
H	Prunella vulgaris . . .	r	o	o	—	—	—	o	—	r-o

G	Pteridium aquilinum . .	l		l	o	o-la	o	o-lf	lf-ld	o	o
H	Pulmonaria officinalis .		r		—	—	—	—	—	—	—
H	Pyrola minor		l		l	—	—	—	—	—	—
H	Ranunculus acris . . .	r		o	—	—	—	—	—	—	—
H	R. auricomus	r		o	o	—	—	—	—	—	—
H	R. flammula	—		—	—	—	—	—	la*	—	—
H	R. repens	—		o	—	l	l	l	ld*	—	r-ld
H	Rumex acetosa	—		—	—	l	—	o	—	r	lf
Ch	Rumex acetosella . . .	—		—	l	l	la	—	—	—	l
H	R. condylodes		o		o	—	—	—	o-lf	—	—
H	R. nemorosa		r		—	—	—	—	—	—	—
H	Sanicula europaea . . .	a-d		lf-la	o-la	—	—	—	o	—	la-ld
H	Scabiosa succisa . . .	—		—	—	—	—	l	lf	r	o
G	Scilla nonscripta . . .		r-la		o-ld	l	—	l	—	—	o-la
H	Scrophularia nodosa . .	o		o	o	r	—	—	—	—	o
H	Scolopendrium vulgare .		r		—	—	—	—	—	—	—
H	Scutellaria minor . . .	—		—	—	—	—	—	lf	—	—
H	Senecio jacobaea . . .	o		o	o	—	—	—	—	—	o
T	S. silvaticus	—		—	—	r	—	—	—	—	—
H	Sisymbrium alliaria . .		lf		—	—	—	—	—	—	—
H	Solidago virgaurea . .	—		—	—	—	—	—	o	—	l
H	Stachys silvatica . . .	r		r-o	o	—	—	—	l	—	lf
Ch	Stellaria holostea . . .	—		l	o-la	l	—	—	—	—	lf
H	S. nemorum	—		—	—	—	—	—	—	—	ld
H	S. uliginosa	—		—	—	—	—	—	lf	—	—
H	Taraxacum officinale . .	o		l	r	—	—	—	—	—	o
H	Teucrium scorodonia . .		r		—	—	—	o-lf	lf	—	—
G	Trientalis europaea . .	—		—	—	—	—	—	—	o	l
G	Tussilago farfara . . .		r		—	—	—	—	—	—	—

Lifeform	Species	I (a)	I (b)	II (a)	II (b)	II (c)	III (a)	III (a 1)	III (b)	IV
H	Ulmaria palustris . . .	r		—	—	—	—	—	—	—
H	Urtica dioica	lf	la	o-la	—	+	—	la	—	lf
Ch	Vaccinium myrtillus . .	—	—	—	—	—	f	o-la*	d	l
H	Valeriana officinalis . .	o	o	—	—	—	—	—	—	—
H	Verbascum nigrum . .	—	r	—	—	—	—	—	—	—
H	V. thapsus	—	r	—	—	—	—	—	—	—
Ch	Veronica chamaedrys .	o	o-f	o-f	l	—	—	—	l	o-f
Ch	V. montana	o		o	l	—	—	la*	—	d-la
Ch	V. officinalis	o	o	o	o	o	o	o	—	o
H	V. serpyllifolia . . .	r		—	—	—	—	—	—	o
H	Vicia sepium	o-f		o	—	—	—	—	—	o
H	Viola hirta	o-f	o-lf	—	—	—	—	—	—	—
H	V. riviniana	o	o	o-f	o	l	o	o-la	l	o-la
H	V. silvestris	f	f	o	—	—	—	—	—	—
	Mosses and Liverworts.									
	Amblystegium serpens .	o		—	—	—	—	—	—	—
	Anomodon viticulosus .	f		—	—	—	—	—	—	—
	Barbula cylindrica . . .	o		o	—	—	—	—	—	—
	B. fallax	r		—	—	—	—	—	—	—
	B. rubella	o		—	—	—	—	—	—	—
	B. unguiculata	o		r-o	—	—	—	—	—	—
	Brachythecium glareosum	o		—	—	—	—	—	—	—
	B. illecebrum	r		—	—	—	—	—	—	—
	B. purum	o	o	—	—	—	—	—	o	o

B. rutabulum	o-f-a	o-f	o	—	—	—	o	o
B. salebrosum	o-f	—	—	—	—	—	—	—
B. velutinum	f	o	—	—	—	—	—	—
Bryum capillare . . .	r-o	r	—	—	—	—	—	—
Camptothecium lutescens	o-f	—	—	—	—	—	—	—
Camptothecium sericeum	o-f	o	—	—	—	—	—	—
Calypogeia trichomanis .	— —	—	—	—	—	—	o	—
Catharinea undulata . .	r-o	o	o	l	—	—	—	o
Cephalozia bicuspidata .	— —	—	—	+	—	—	+	—
Dicranella heteromalla .	r	r-o	o-la	o-ld	o-la	—	—	—
Dicranum montanum .	o	—	—	—	—	—	—	—
D. scoparium	o-la	o	o-la	lf-ld	o-lf	o	o	o
Diplophyllum albicans .	— —	—	—	o-lf	o	—	+	—
Encalypta streptocarpa .	o	—	—	—	—	—	—	—
Eurhynchium confertum .	o-f	—	—	—	—	—	—	—
E. crassinervium . . .	o	—	—	—	—	—	—	—
E. megapolitanum . .	o	—	—	—	—	—	—	—
E. myosuroides . . . E. myurum . . . . . . }	o	o	o	o-la	—	lf	+	o
E. piliferum	o	—	—	—	—	—	—	o
E. praelongum	o-f	o	o	o	o	o	l	o-la
E. pumilum	r-o	—	—	—	—	—	—	—
E. speciosum	r	—	—	—	—	—	—	—
E. striatum	f	o-f	—	—	—	o	—	o-la
E. swartzii	o	—	—	—	—	—	—	—
E. tenellum	o	—	—	—	—	—	—	—
Fissidens adiantoides .	+	—	—	—	—	—	—	—
F. bryoides	lf	—	—	—	—	—	—	—

Lifeform	Species	I (a)	I (b)	II (a)	II (b)	II (c)	III (a)	III (a 1)	III (b)	IV
	F. taxifolius	o-f		o	—	—	—	—	—	+
	Frullania dilatata . . .	f-a		o	—	—	—	—	—	—
	F. tamarisci	—		—	—	+	—	—	—	—
	Hylocomium loreum . .	o		o	l	o	—	o	o	lf-la
	H. splendens	r		—	—	—	—	ld	o	o-lf
	H. squarrosum	l		—	—	—	—	—	l	l
	H. triquetrum	o		o-f	—	—	—	o	la	o-la
	Hypnum chrysophyllum .	+		—	—	—	—	—	—	—
	H. cupressiforme . . .	o-a		o-f	o	o	o	lf	o	o-ld
	H. cuspidatum	+		—	—	—	—	—	—	—
	H. molluscum	f-a		—	—	—	—	—	—	—
	H. schreberi	l		—	—	o	—	—	o	—
	Lepidozia reptans . . .	l		—	—	o	—	—	—	—
	Leucobryum glaucum .	—	—	—	l	o-lf	o-ld	—	—	—
	Lophocolea bidentata . .	o-f		o	o	+	—	—	o	—
	L. heterophylla	f		+	+	—	—	—	—	—
	Madotheca platyphylla .	o-f		o	—	—	—	—	—	—
	Metzgeria furcata . . .	f		—	—	—	—	—	—	—
	Mnium hornum . . .	o		o-f	o-la	o-ld	o-ld	lf-ld	o	o-d
	M. punctatum	+		—	—	—	—	—	—	—
	M. rostratum	o		+	—	—	—	—	—	—
	M. undulatum	o-la		o	—	—	—	—	—	o-lf
	Neckera complanata . .	f		r	—	—	—	—	—	—
	N. crispa	o		—	—	—	—	—	—	—
	N. pumila	o		—	—	—	—	—	—	—

Orthotrichum affine . .	o	o	—	—	—	—	—	—
O. anomalum	r-o	—	—	—	—	—	—	—
O. pulchellum	r	—	—	—	—	—	—	—
Pellia epiphylla . . .	r	—	—	—	—	—	—	—
Plagiochila asplenioides .	o-f	—	—	—	—	—	—	—
Plagiothecium denticulatum	o	+	+	—	—	—	—	—
P. depressum	o	—	—	—	—	—	—	—
P. silvaticum	—	+	—	—	—	—	—	—
P. undulatum	—	—	—	—	—	o	o	o-la
Polytrichum commune .	—	—	—	—	—	—	l	—
P. formosum	r-o	o-lf	o-f	o-ld	o-f	f	o	o-la
P. gracile	l	—	—	—	—	—	—	—
P. juniperinum	—	+	—	l	—	—	—	—
Porotrichum alopecurum .	o-f	—	—	—	—	—	—	—
Radula complanata . .	o	—	—	—	—	—	—	—
Seligeria calcarea . . .	o-la	—	—	—	—	—	—	—
S. pusilla	o	—	—	—	—	—	—	—
Thuidium tamariscinum .	o-la	o-f	o	o	—	ld	—	la
Ulota crispa	r	—	—	—	—	—	—	—
Webera nutans	—	—	l	—	—	—	—	—
Zygodon viridissimus . .	o	—	—	—	—	—	—	—

*) These species are restricted to «flushes», i. e. tracts of soil which are kept moist by flowing water.

Note. The lists of species in III (a) and III (a. 1.) are compiled from one or two examples only and are therefore not complete. In IV the Hepaticae have not been recorded.

TABLE 5.

BIOLOGICAL SPECTRA OF ALL SPECIES OF THE FIELD LAYER OF DIFFERENT TYPES OF BEECHWOODS.

The data given are percentages: the actual numbers of species are given in brackets.

	Ch.	H. r.	H. s.	H. c.	G. r.	G. b.	G. rad.	G. sap.	T.	Total
I a) „Sanicle“	9.5 (8)	15.5 (13)	**36** (30)	15.5 (13)	13 (11)	3.5 (3)	—	1 (1)	6 (5)	100 (84)
b) „Mercury“	10 (11)	9 (10)	**38** (42)	20 (22)	12 (13)	2.5 (3)	1 (1)	1 (1)	6.5 (7)	100 (110)
II a) Plateau	12 (11)	15 (14)	**27** (25)	23 (21)	11 (10)	3.5 (3)	1 (1)	1 (1)	6.5 (6)	100 (92)
b) „	13 (8)	11.5 (7)	18 (11)	**33** (20)	10 (6)	3.5 (2)	1.5 (1)	1.5 (1)	8 (5)	100 (61)
c) „	13.5 (7)	10 (5)	15.5 (8)	**39** (20)	12 (6)	2 (1)	2 (1)	2 (1)	4 (2)	100 (51)
III a) Heath* (Southern)	**19** (6)	15.5 (5)	12.5 (4)	**34.5** (11)	12.5 (4)	3 (1)	—	—	3 (1)	100 (32)
b) Heath (Northern)	**21.5** (6)	18 (5)	14 (4)	**29** (8)	14.5 (4)	—	3.5 (1)	—	—	100 (28)
a. 1.) Heath* (Southern)	16 (8)	20 (10)	**26** (13)	20 (10)	10 (5)	—	—	—	8 (4)	100 (50)
IV ‚Herbaceous‘ (Scottish)	16 (11)	13 (9)	**37** (25)	15 (10)	9 (6)	4 (3)	—	—	6 (4)	100 (68)
Biological Spectra of species with high (4 and 5) constancy and high average frequency (2.1 and over).										
I a) „Sanicle“	—	**30.4** (7)	17.4 (4)	17.4 (4)	**26** (6)	—	—	4.4 (1)	4.4 (1)	100 (23)
b) „Mercury“	8.5 (3)	17 (6)	**43** (15)	17 (6)	6 (2)	3 (1)	—	—	6 (2)	100.5 (35)
II a) Plateau	14.5 (5)	14 (5)	20 (7)	**26** (9)	17 (6)	3 (1)	—	—	6 (2)	100 (35)
b) „	5.5 (1)	11 (2)	11 (2)	**55.5** (10)	17 (3)	—	—	—	—	100 (18)
c) „	22 (4)	5.5 (1)	5.5 (1)	**50** (9)	11 (2)	—	—	—	5.5 (1)	99.5 (18)
III b) Heath (Northern)	**31** (4)	23 (3)	8 (1)	23 (3)	15 (2)	—	—	—	—	100 (13)
IV ‚Herbaceous‘ (Scottish)	16.5 (4)	**25** (6)	**25** (6)	16.5 (4)	8.5 (2)	—	—	—	8.5 (2)	100 (24)

*) The data are from one or two examples only and are given as an indication and not a definitive expression of the spectra. In III (a. 1.) the species confined to «flushes» have been omitted in working out the spectrum.

Phot. 2. ASH-OAK WOOD showing a dead «pioneer» oak in middle foreground and straighter stems in background. The wood is being invaded by beech (left, background). The rich field layer (not shown in photograph) of *Mercurialis perennis*, *Fragaria versca*, *Sanicula europaea*, etc., is killed out when the ash-oak wood is eventually replaced by beech wood, in which a characteristic vegetation of *Oxalis* and *Rubus* later appears *de novo*. Summit of South Downs, near Graffham, Sussex.

(a) *Sanicle beechwood* is characterised by the dominance of ***hemicryptophyta rosulata*** (with ***Sanicula*** the most frequent species) and by the high percentage of ***geophyta rhizomata***, mainly orchids (*Cephalanthera grandiflora, Epipactis latifolia, Neottia nidus-avis*). The characteristic species also include ***Lactuca muralis*** and ***Bromus asper***.

(b) ***Mercury beechwood*** is dominated by herbs with leafy flowering shoots, mostly ***hemicryptophyta scaposa*** (with ***Mercurialis*** dominant) but including tall rhizome geophytes like ***Epilobium angustifolium*** and ***Circaea lutetiana*** with well marked leaf mosaic. Other characteristic species are: ***Urtica dioica, Scrophularia nodosa, Campanula trachelium, Geum urbanum, Dryopteris filix-mas, Hordeum silvaticum, Poa trivialis, Galium aparine.***

II. Beechwood on the Plateaux. (Phots. 2, 3, 4.) These beechwoods are arranged in three groups.

(a) The woods of the South Downs (Ditcham Park and Goodwood) are classed with the best woods of the Chiltern plateau. In the adult beechwoods there is a shrub layer of ***Rubus fruticosus*** (Phot. 4). They are further characterised by floristic affinity with the Beechwood on Chalk, particularly with the Mercury beechwood. with which most of the characteristic species are shared, although in the majority of plateau woods their frequency is reduced. On the other hand, they are also related to the «Herbaceous» (Scottish) beechwoods. These affinities are brought out by the following list of species common to the Beechwood on Chalk (I), Plateau (a) (II a) and «Herbaceous» (Scottish) beechwoods (IV) but absent from or rarely occurring in Plateau (b) and (c) (II b and c) and the Heath Beechwoods (III a and b).

Ajuga reptans
Anemone nemorosa
Arenaria trinervia
Asperula odorata
Festuca gigantea
Ficaria verna
Galium aparine
Geranium robertianum
Geum urbanum
Lysimachia nemorum
Mercurialis perennis
Primula vulgaris
Sanicula europaea
Scrophularia nodosa
Stachys silvatica
Urtica dioica
Veronica montana.

Phot. 3. PLATEAU BEECHWOOD (IIa). Internal development of the beech associes leading to the formation of a pure even-aged beech consociation. Gaps in the wood are colonised by a peripheral zone of beech and a core of ash. The photograph shows a later stage in this development when most of the ash has been suppressed in competition with beech. Dead stems, mostly ash but some beech, strew the floor. Northside (Goodwood estate), South Downs, Sussex.

Phot. 4. PLATEAU BEECHWOOD (II a). Mature wood showing tall straight stems (100 ft.: 33 m.). Age 140 years. *Rubus fruticosus* (agg.) forms a continuous layer 18 in. (46 cm.) high. Note the clinging stems of *Hedera* and the thick cover of bryophytes on the beech. The rod is 3 ft. (91.5 cm.) long. Goodwood estate, South Downs, Sussex.

Dentaria bulbifera and *Luzula forsteri* are probably restricted to this type (II a).

The acid soils of some examples of this sub-type are shown by the presence of *Scilla non-scripta*, *Pteridium aquilinum*, *Carex remota*, *Stellaria holostea*, *Holcus mollis* and *Oxalis acetosella*.

(b). As in (a) the woods in this group have a shrub layer of *Rubus fruticosus* (agg.) (Phot. 4), but their most striking feature is their floristic poverty. The more exacting herbs which characterise (a) are almost entirely eliminated with the exception of *Viola riviniana* and *Milium effusum*, whilst the residuum of more acid-tolerant species make up the bulk of the vegetation . This sub-type marks a transition between the preceding on well-aerated, and the next sub-type on degenerate, «brown earth».

(c). The process of elimination is practically complete. There is no shrub layer. The more exacting herbs are completely excluded and although much of the ground is devoid of plants, a definite convergence with the heath woods of the next type (III) is indicated by the appearance in open places of *Deschampsia flexuosa*, *Carex pilulifera* and *Calluna vulgaris.*

III. B e e c h w o o d s o n H e a t h. (a) and (b). Two varieties are described (a) from the podsolised sands and gravels of south-eastern England (Phot. 5) and (b) from the heaths of north-eastern Scotland (Phot. 6), where beech forms a post-climax on drained soils. The northern and the southern varieties are floristically similar, with *Deschampsia flexuosa*, *Vaccinium myrtillus*, *Calluna vulgaris*, *Galium saxatile*, etc. among the significant species. But the northern variety has *Trientalis europaea* and in the southern *Vaccinium* is not so common and is less luxuriant. *Melampyrum pratense* is a common member of some southern beechwoods on poor siliceous soils. Allied to the last and forming a definite approach to IV («Herbaceous» beechwoods) there occur in north-eastern Scotland a few examples of beechwoods in which an *Oxalis-Anemone* stage is followed by one of *Vaccinium myrtillus* in the life history of the even-aged wood, recalling the time sequence of *Oxalis* and *Rubus fruticosus* in the life history of type II.

(a. 1.) In southern England a similar approach to type IV is shown by the beechwoods on the sands of well watered but well drained slopes. On the drier areas the prevailing «acidic» flora *(Deschampsia flexuosa*, *Holcus mollis*, *Pteridium*, etc.) is accompanied by species of less acid or basic soils *(Lactuca muralis*, *Melica*, *Sanicula)*, whilst in wet flushes many of the species *(Ranunculus repens*, *Circaea lutetiana*, *Lysimachia nemorum*, *Urtica dioica*, etc.) characteristic of IV and/or II (a) predominate.

Phot. 5. HEATH BEECHWOOD, SOUTHERN TYPE (III a). The short crooked stems with rough bark characterise woods on podsol poor in bases. Note the absence of a field layer and the patches of *Leucobryum glaucum*. On gravel, Reading Beds, near Burnham Beeches, Bucks.

IV. «Herbaceous» Beechwoods (Scottish). On fresh, fertile Old Red Sandstone soils the floristic cortège of the exacting herbs of I (b) and II (a) reappear, but the «freshness» of the habitat is shown by the presence of *Adoxa moschatellina*, *Stellaria nemorum*, *Ficaria verna* and *Ranunculus repens*. There is no shrub layer.

Phot. 6. HEATH BEECHWOOD, NORTHERN TYPE (III b). The mature wood shows an open shrub layer of *Sorbus aucuparia*, well developed in gaps (centre background) and a continuous dwarf-shrub layer of *Vaccinium myrtillus*. Note the white stems and smooth bark of the beech. Age 104 years. Drained heath, Aberdeen, Scotland.

The biological spectra (p. 336) of the field layer emphasise the affinities and differences noted. The major affinities are clear from the spectra of «all species»: I (a), I (b), II (a), III (a. 1.) and IV show a maximum of *hemicryptophyta scaposa*, whilst in II (b), II (c), III (a) and III (b) the *hemicryptophyta caespitosa* predominate. Differences within the larger groupings are brought out in the spectra of the species with high constancy and/or high average frequency. Thus in the first group, I (a) is characterised by a maximum of *hemicryptophyta rosulata* and a high percentage of *geophyta rhizomata:* I (b), by dominant *hemicryptophyta scaposa* and few geophytes; whilst in II (a) there is no clear predominance of any one group, although the maximum of *h. caespitosa* may be regarded as an approach to II (b) and II (c). In IV, dominance is shared by *h. rosulata* and *h. scaposa* — a result indicative of the immaturity of the field layer in some examples of this type. In the second group, the maximum of *h. caespitosa* is outstanding in II (b), is somewhat reduced in II (c), where chamaephytes are prominent, becoming dominant in the northern beechwoods (III b).

The small percentage of therophytes is a well-known feature of beechwoods, both British and continental. The British beechwoods, however, would appear to differ from the continental chiefly in the emphasis on the hemicryptophytes and the general scarcity of geophytes: but it is significant that the nearest approach to southern continental types, such as the Cevennes, is shown by I (a), where the percentage of geophytes in the spectrum of species with high constancy and high average frequency is easily the highest in any British type.

S o c i e t i e s. Local soil changes, especially in moisture content, are responsible for most of the societies observed: *Urtica dioica* on deeper soil in the Sanicle beechwood (I a): *Ficaria verna, Anemone nemorosa* and *Circaea lutetiana* on fresh soil in II (a), and *Juncus communis* in wet depressions in all woods of the Chiltern plateau. *Epilobium angustifolium* appears in gaps in most woods except III (b) and IV.

In the Herbaceous Woods (IV) «seasonally complementary» societies are formed by *Ficaria verna* and *Stellaria nemorum* and in flushed soil by *Ficaria verna, Anemone nemorosa* and *Ranunculus repens.*

On Chalk escarpments and on calcareous soils of the chalk plateau *Hedera helix* forms ground societies, occasionally climbing the trees.

12 a. BRYOPHYTA.

Resemblances and differences established between the various types of beechwoods by the field stratum are emphasised by analysis of the bryophytic flora.

There is a progressive diminution in the total number of species from 74 in type I, through 31 in II (a) to about 20 in the other types. (The full numbers from III (a) and IV are not available).

The change is due largely to the progressive dropping out of species, the more tolerant surviving and making up the bulk of the ground stratum in the woods on podsol, supplemented by a few more commonly associated with acid soils.

The same species are found in the Sanicle (I a) as in the Mercury beechwood (I b), but most of them have a higher frequency in the Sanicle type of wood. In the following select list of bryophytes characteristic of Beechwood on Chalk, those marked S are commoner in the Sanicle type, M in the Mercury type.

Amblystegium serpens
S *Anomodon viticulosus*
S *Brachythecium glareosum*
Encalypta streptocarpa
M *Fissidens taxifolius*
S *Hypnum molluscum*
Madotheca platyphylla
S *Neckera crispa*
S *Plagiochila asplenioides*
M *Porotrichum alopecurum*
Seligeria calcarea.

The near relationship of II (a) to I is shown by the fact that every species found in II (a) occurs in I. All show a similar or a less frequency except *Catharinea undulata*, *Dicranella heteromalla*, *Hylocomium triquetrum*, *Mnium hornum*, *Polytrichum formosum* and *Thuidium tamariscinum*, which have a slightly higher frequency in II (a).

In II (b) only the more acid tolerant are found and *Leucobryum glaucum* comes in. Nearly all these occur in II (c) and the addition of *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Hypnum schreberi* and *Leucobryum* emphasises the affinity of this type with III. Finally, the absence of these species and the presence of *Catharinea undulata*, *Eurhynchium striatum*, *Fissidens taxifolius*, and *Mnium undulatum* confirm the close relationship between the «Herbaceous» Beechwood (IV) and the best type of plateau wood (I a).

12 b. FUNGI.

This section is based on information very kindly supplied by Mr J. Ramsbottom, Keeper of the Department of Botany, British Museum, and ex-President of the British Mycological Society.

There is not sufficient knowledge available of the fungus flora of British beechwood to permit of any close correlation between the fungi and the types of beechwood distinguished in this paper. It is, however, well known to mycologists that beechwoods possess quite a distinctive fungus flora, apart altogether from the fungi actually parasitic on the beech (see Section 17, p. 355). Apart from parasites and mycorrhizal fungi, it is uncertain whether the nature of the soil or the phanerogamic flora is the more important factor in determining the fungal flora. Where the herbaceous vegetation cover is continuous *(Mercurialis, Asperula, Rubus)* fungi are scarce, only such small forms as *Mycena galopoda* and occasionally *Paxillus involutus* occurring, and both are of general occurrence in British woodlands.

The species cited below are more or less characteristic of beechwoods. The list makes no pretence to completeness. The three genera *Amanita*, *Cortinarius* and *Tricholoma* contain many characteristic beechwood species:

Amanita mappa (also in oakwoods)
A. muscaria var. *formosa*
A. pantherina (a special beechwood form of)
A. rubescens (on acid soil)
A. aculeata
A. aspera
A. echinocephala
A. vittadinii
A. strobiliformis (beechwoods and chalk downs)

More or less confined to beechwoods:

Cortinarius alboviolaceus
C. arvenaceus
C. azureus
C. bolaris
C. bulliardi
C. calachrous
C. cinnabarinus
C. crystallinus
C. decoloratus
C. diabolicus
C. multiformis
C. nitidus
C. porphyropus
C. prasinus
C. quadricolor
C. subnotus
C. torvus.

In damp places: *C. paleaceus*, *C. persilis*, *C. phrygianus*.

On very acid soil (also in coniferous woods): *C. caerulescens*, *C. claricolor*, *C. germanus*, *C. illiopodius*, *C. orichalceus*.

Characteristic beechwood species of *Tricholoma* are:

Tricholoma argyraceum
T. coryphaeum
T. oriorubens
T. resplendens.

On more acid soil: *T. albellum*, *T. glaucocanum*, *T. terreum* (the two last also in coniferous woods).

Also the following species:

Lepiota gracilis (beechwood)
L. hispida (beech-pine)
Clitocybe clavipes (beech-pine)
C. phyllophila (among beech leaves)
Omphalia hydrogramma (leaves)
O. polyadelpha (leaves)
O. atropuncta (grass)
Collybia maculata (acid soils)
C. platyphylla (mycelial cords between laminated leaf pads in litter).

Mycena atrovirens, *chelidonia*, *crocata*, *pelianthina*, *sudora* and *tintinnabulum* (all on stumps, twigs or leaves), *M. capillaris*, *setosa* and *fagetorum* (directly on beech leaf litter).

Species of *Inocybe* such as *I. caesariata* are common but not restricted to beechwoods.

Coprinus picaceus (generally in beechwoods), *C. dilectus* (on burned places in the same).

Marasmius fuscopurpureus, *globularis*, *prasiosmus* and *suaveolens*.

Lactarius blennius (leaves), *L. fluens* (grass). *L. flexuosus* and *L. ligniotus* (also in coniferous woods).

Russula fellea (very characteristic), *R. alutacea* (mainly beechwoods), *R. lepida* (woods generally but frequent on beechwood slopes), *R. emetica* and *R. ochroleuca* (acid soil, beech- and pinewoods).

Hygrophorus chrysodon, *H. cossus*, *H. eburneus*, *Craterellus cornucopioides*, *Geaster fimbriatus*, *Lycoperdon echinatum*, *Helvella* ssp. occur on slopes in beechwoods. *Boletus edulis*, *B. felleus* and *B. olivaceus* are commonest in beechwoods: *B. satanas* (also on adjoining chalk pasture).

Clavaria botrytis, *C. flava* and *C. pistillaris* most frequent in, though not confined to, beechwoods.

The conversion of beech leaf litter into humus is mainly the work of fungi and seems to be mainly brought about by the larger fungi. Disintegration does not begin until the leaves are lying damp on the ground. If the dead leaves still remaining on a beech and oak are compared, those of the oak are rarely without a covering of some Hyphomycete such as *Cladosporium*, while those of the beech are usually hardly marked by fungi. But on turning over the layers of beech leaves lying on the ground in damp masses mycelia, many of them belonging to the larger fungi, are to be seen in abundance. Certain Basidiomycetes are generally to be found growing directly on the leaves, for example the small fruit-bodies of *Mycena capillaris*, *M. setosa* and *M. fagetorum* already mentioned, and at almost any time of year, if the leaves are turned over or the laminated pads of leaves pulled apart, the conspicuous mycelia of Basidiomycetes and not infrequently the mycelial cords of Gasteromycetes or of *Collybia platyphylla* are to be seen. The larger fruit-bodies, such as those of *Amanita* or *Collybia* when picked up will often bring away a mass of half-rotted leaves interwoven with mycelium.

12 c. MYCORRHIZA.

No detailed study has been made of the mycorrhiza of English beechwoods, though beech is one of the easiest trees on which to demonstrate it owing to the abundance of surface feeding roots embedded in humus; and a well-grown beech seems always to have mycorrhiza. The mycorrhizal roots may frequently be seen associated with the mycelium permeating the dead leaf mass and occasionally with a fruit-body. Of the list of 13 species given by Peyronnel as showing organic connexion with beech roots only *Russula emetica*, *Lactarius blennius* and possibly *Hydnum repandum* appear likely to be specially concerned in forming mycorrhiza with the beech in our woods. Most of the others are common British species but are not confined to beechwoods. Mr Ramsbottom has however noticed the fruit-bodies of the following species (in addition to *Russula emetica* and *Hydnum repandum)* in rings round the trunks of the trees in beechwoods, suggesting a mycorrhizal connexion:

Amanita mappa
Clitocybe cerussata
Russula cyanoxantha
R. fellea

C. clavipes
C. maxima
C. nebularis
Hebeloma fastibile
Lactarius aurantiacus
Lepiota cristata
R. lepida
R. ochroleuca
Strobilomyces strobilaceus
Stropharia squamosa
Tricholoma argyraceum

Of these only *Russula fellea* may be regarded as restricted to beechwoods.

Stunted beeches may lack normal mycorrhiza, and the inhibition of growth is possibly due to its absence. This is associated with lack of humus, such as occurs on steep slopes where the dead leaves do not settle. Under such conditions dead and blackened rootlets are frequently seen, the fungus having become parasitic. Such roots may also be attacked by moulds, *Penicillium* and other Hyphomycetes being occasionally found.

Practically no work seems to have been done on the microfungi of British woodlands, and we can say no more than that coniferous and deciduous woods respectively appear to possess species which are distinctive, and it is quite probable of course that the nature of the soil and of the humus, which largely determine the species of larger fungi and of the higher plants, are also decisive for the microfungi. The high exclusiveness of the saprophytes *Monotropa* and *Neottia*, and of certain other orchids (Section 13) in beechwoods may depend on the special suitability of beechwood humus for their mycorrhizal fungi on which they are probably absolutely dependent, since it has been shown that orchids cannot germinate without the presence of their fungal partners. In *Neottia* and other British orchids this is a «*Rhizoctonia*».

13. EXCLUSIVE SPECIES.

The floristic poverty of England and the recent entrance of beech combine to make our beechwoods remarkably poor in species with high exclusiveness. The beechwood flora in most cases consists of a selection of those species natural to the related seral woods and able to put up with the new conditions. It is specialised by elimination only. On the whole the floristic relationship of the English beechwoods is with those of the northern part of the European Deciduous-Leaved Forest rather than with the southern European, where the number of exclusives is much higher. Only 6 species are regarded as having the highest value for exclusiveness — *Cephalanthera grandiflora*, *C. rubra*, *Epipactis purpurata*, *Neottia nidus-avis*, *Monotropa hypopitys*, and *Dentaria bulbifera*. All of these reproduce vegetatively, two are saprophytes and five have mycorrhiza. *Dentaria* is not recorded from the examples examined in detail but it has been seen and is probably confined to type II (a): *Epipactis purpurata* (on the authority of Mr H. W. Pugsley) is confined to plateau woods: *Cephalanthera grandiflora* characterises the escarpment woods, where it is quite frequent: *C. rubra* is excessively rare, being confined, so far as is known, to a single locality on the Cotswolds [1]). *Neottia* has a wider range, occurring in I, II (a) and IV, whilst *Monotropa* is found in all except the northern heath woods. To these six species Salisbury adds *Polygonatum officinale*, which is almost confined to ashwoods and beechwoods on limestone: it is absent from or very rare in oakwoods. *Cephalanthera*, *Neottia* and *Monotropa* appear unable to compete with tall herbs like *Mercurialis*, and their prevalence in beechwoods as a whole is perhaps due to the absence of a continuous tall field stratum able to suppress them. Their presence necessarily implies an ability to compete successfully with beech roots. The mycorrhizal relations of these characteristic saprophytic plants have not been worked out.

13 a. MOLLUSCA.

It has been thought well to include the following paragraphs on the Beechwood mollusca, since more is known about this than about any other group of Beechwood animals. For the information given the authors are indebted to the kindness of Prof. A. E. Boycott, F. R. S. and Mr C. Oldham, two of the leading British authorities on the subject. The sentences within inverted commas are in Prof. Boycott's own words. The general conclusion on the relation of mollusca to beechwoods may be set forth at the outset. «The beech has no particular or direct association with any mollusca. The richness, in both species and individuals, of many ancient beechwoods in the

[1]) We are indebted to Mr A. J. Wilmott, of the British Museum, for information on the distribution of some of these species.

south of England, which is well known to conchologists, is due to their geographical situation, their antiquity, and the concurrence of woodland conditions of shelter with a calcareous soil. Ashwoods on calcareous ground have the same mollusca, while beechwoods on acid soils have a much sparser fauna and entirely lack the calcicole species which have been supposed to be characteristic of beechwoods in general.»

The following are the species characteristic of the southern English beechwoods on calcareous soil, i. e. the chalk and oolite «escarpment» beechwoods (I, see p. 322), arranged according to the factors on which they depend.

(1) Confined to the south-east. *Helix obvoluta* occurs along a narrow zone from Winchester to the River Arun: *Ena montana* from Suffolk and Sussex to Somerset and Gloucester. Both live on calcareous soil (though *H. obvoluta* may not be confined to it) and mostly in woods, though also in old hedges and scrubby places.

(2) Confined to woodland. «*Clausilia laminata, Cl. rolphii* and *Ena obscura* are woodland species with marked preference for calcareous soils, to which *Cl. rolphii* (a local southern species) is perhaps restricted.» *Helix lapicida* shows the same preference, but is not restricted to woods, living also in stone walls and fissured rocks: «it is often abundant in beechwoods where it finds the necessary shelter under the butt ends of the boughs and under loose bark».

(3) Confined to calcareous soil. «*Pupa secale*, and especially *Pomatias elegans*, are often found in beechwoods but only because the soil is calcareous: both are absolute calcioles and live in many kinds of habitat other than woodlands.»

The eight species above are all strictly or predominatingly calcicolous and silvicolous also, though not all confined to woodland.

(4) Confined to ancient woodland. «The slugs *Limax cinereoniger* and *L. tenellus* are characteristic of ancient woodlands, but the nature of the soil (calcareous or acid) and the species of dominant tree are immaterial; and both species occur throughout Britain. They are not found in modern beech plantations, which in fact do not as a rule show any mollusca of woodland type, but only such species as live also in unsheltered places.»

(5) «The rest of the common species of slugs and snails which are found in beechwoods have no particular association with this type of habitat, though some of them, e. g. *Helix striolata*, *Clausilia rugosa* and *Carychium minimum*, occur with the special abundance which they commonly show in calcareous surroundings.»

(6) Beechwoods on acid soil. The molluscan fauna is poor and thin. That of Burnham Beeches (III a, p. 341) consists of the woodland *Acme lineata* and about a dozen species which live «anywhere» also *Vitrina major*, known from a few scattered localities in the south and west, *Acanthinula lamellata*, a north-western species here at its southern limit, and *Zonitoides excavatus*, which is absolutely calcifuge. The calcicolous species, and indeed those with a definite preference for lime, are all absent. So too in the plateau beechwoods of the Chilterns slugs, which are indifferent to lime, are abundant, but there are hardly any snails except the ubiquitous *Helix rotundata*, *Hyalinia alliaria* and *Vertigo edentula*.

The mollusca absent from all southern beechwoods are the xerophilous species which avoid woodland and those which live only in the north or in special habitats such as marshes.

14. STATUS AND RANK OF BEECHWOOD COMMUNITIES.

On the view expressed above, beechwood is not a uniform natural unit but is made up of climax stages belonging to very different seres which retain certain differences to the end. At the same time the series II (a), (b), (c), demonstrating progressive elimination of the more exacting herbs, and the appearance of species characteristic of the heath type (III), suggests that continued growth of the beech may bring about convergence with beechwoods on podsol and thus perhaps ultimate destruction of the beech community. Further, it is unknown how far beech, by promoting leaching of chalk on flat soil, may contribute to an increase in depth of the superficial residuum, but here again it is possible that with time a reaction of this kind would result in the development of soil properties inimical to the continued growth of beech. On the other hand, a greater permanence of the Beechwood on Chalk is assured, for the topography of the escarpment prevents the climate from impressing itself on the soil profile, and thus produces and maintains a soil type which has more the character of the soils of a drier and warmer climate.

15. EXPLOITATION.

The selection system of beechwood management is the common one on the Chilterns, although on most estates its practice falls considerably short of the ideal. This system is reputed to have been in use for 700 years, but it is exceedingly doubtful if in its early application it was anything more than a somewhat haphazard utilisation of trees selected for firewood and perhaps for other purposes. The cutting out of the best and fastest growing trees and the leaving, to restock the ground, of those which grow more slowly and whose spreading crowns bear a leaf mosaic and enable them to live under shade where erect forms cannot survive, is held to have led to the dominance of slow growing beeches of poor form. This explanation follows that given by Oppermann on historical and well-attested grounds for the degeneration of some Danish beechwoods. But while the local dominance of racially poor forms may be explained in this way, their limitation to very shallow calcareous soils and degenerate brown earths, and their absence from deeper and more open-textured soils, suggest that this explanation cannot be of general application.

At the present time most of the plateau woods on the Chilterns contain an excessive proportion of the older age classes with a corresponding reduction in the numbers of younger trees. The woods therefore approximate to even-aged high forest, with this difference, that the uneven canopy is denser, casting a heavier shade (which on the brown earths of the plateau is supplemented by the shrub layer of brambles). The effect on the herbaceous vegetation has not been worked out in detail but there is some evidence to show that the maintenance of overstocking leads to an impoverishment of the woodland flora by the elimination of those species more commonly associated with brown earths. The data given in section 4 (p. 302) support the hypothesis that soil degeneration is thus brought about.

On the plateaux of both the Chilterns and the South Downs clear felling is practised, the age at which felling takes place being determined more by economic necessity than by silvicultural considerations. Full exposure to the sun leads to the elimination of true woodland herbs, to a reduction in the vigour of ***Rubus fruticosus*** (agg.) and to the appearance of a nitratophilous flora dominated by

Epilobium angustifolium. Details of the change following clear felling on the South Downs escarpment have been noted by Adamson, who records the disappearance of some and the reduction in vigour of most shade species, the increase of wood edge plants and the appearance of weed species. Clear felling of the plateau beechwood (II a) appears to be normally followed by subseral ash (much of which exists in a suppressed condition in the mature beechwood), but the activities of rabbits may prevent the return to woodland. Failure of this subsere cannot be explained by the soil changes consequent on felling.

Successful restocking of the ground by a mixture of beech, oak and ash has been seen on the edge of the Cotswold plateau. Details of the system followed are not available, but the general appearance suggested partial and progressive felling as regeneration took place.

Coppicing and pollarding of the beech are local but are still to be seen.

16. GRAZING AND FIRE.

The failure of the normal subsere is probably due almost entirely to the activities of animals against seeds, seedlings and young growth: and these also often hinder regeneration within the forest. The free access of the higher grazing animals to the forest (e. g. New Forest) leads to the production of open woodland in which young growth is limited to bushes and clumps of spiny shrubs growing in the spaces between the trees. As a general rule, however, beech forest is not grazed owing to the lack of suitable fodder within the wood, and the ancient practice of feeding swine on beech mast has been discontinued with reputed adverse effects on regeneration. Some people consider that the consumption of large quantities of nuts was satisfactorily offset by the preparation of a suitable seedbed for the survivors. In most beechwoods this is quite unnecessary, as the numbers of established seedlings following a good seed year adequately demonstrate. This is not to deny the beneficial activities of pigs, e. g. by the mixing of the surface humus with the mineral soil, but it has been suggested that their chief claim to usefulness lay in the indirect effect of killing the potential enemies of mast and seedlings (mice, slugs and insect larvae).

The thin-barked beech is ill protected against fire and young plants succumb readily to it. But the moistness of the litter under a beech canopy reduces the liability to fire damage. Hence fires are rare, though not unknown. Wherever and whenever the surface litter is dry (for example along the margins of open woodland, or in late September after a dry summer) it readily burns and the heat generated is sufficiently intense to kill oak and beech saplings.

17. PARASITES.

The study of beech regeneration brought to light the important fact that, apart from certain special habitats where soil factors come into play, failure is due mainly to the activities of animals which feed on the seed, seedlings and young plant. Large quantities of mast are consumed by mice, voles, squirrels, wood pigeons, etc.: slugs and insect larvae attack the fleshy radicle, hypocotyl and cotyledons: rabbits and hares cut off the seedlings and young plants, while leaf-sucking insects like *Typhlocyba douglasii* and *Phyllaphis fagi* combine with leaf-feeding moth larvae and beetles to administer the *coup mortel* to plants crippled by shade. The net result is that, however suitable the edaphic and climatic conditions may be, the depredations of animals (together with the shading effect of parent beeches) effectively check widespread successful regeneration and invasion. The losses due to fungi (e. g. *Phytophthora omnivora)* are small in proportion, and the localities in which the accumulated litter is so deep that the radicle fails to reach and become established in mineral soil are of limited extent in the South but appear to be relatively more important in the North, where the rate of decay of beech litter does not keep pace with the rate of addition.

The pole and adult beech are relatively free from serious enemies. The beetle, *Orchestes fagi*, is common but not serious except in occasional years on isolated trees. *Typhlocyba douglasii*, *Phyllaphis fagi* and *Cryptococcus fagi* — all sucking insects — are widespread. The occurence of the last suggests damage of a secondary nature, since outbreaks may follow very dry years when the susceptibility of the beech may be increased. A bark disease of undetermined nature (fungus?) also follows dry years. The many species of fungi recorded from beech are of quite minor importance in high forest: but old and pollarded trees (e. g. at Burnham Beeches) harbour a number of wound parasites mostly belonging to the Polyporaceae and Agaricaceae.

«Wherever there are old trees *Armillaria mucida* may be seen, usually on dead branches though not infrequently on the bole, causing debility and finally downfall. Another very common parasite occurring on the trunks about ground level is *Fomes (Ganoderma) applanatus*, which causes a «heart-rot» and is partly responsible for the fall of trees: this has an effect in opening up «light chimneys» in a dense canopy. *Polyporus giganteus* is common about the bases of beech trees. Another destructive parasite is *Stereum purpureum*, though not so common as on fruit trees. Less frequently *Panus torulosus* is to be found at various heights on the bole, and more rarely still *Hydnum erinaceum*. *Pleurotus lignatilis* has its characteristic habitat in hollow trunks. Beech stumps have their characteristic species such as *Lenzites flaccida* and *Trametes gibbosa*, together with more widely distributed species such as *Hypholoma fasciculare*, *Armillaria mellea*, *Polystictus versicolor:* the reduction of stumps to a pulp-like mass is astonishingly rapid. The hard carbonised surface often seen on stumps is the so-called «black line» which is well developed by *Armillaria mellea* (the common cause of luminescence in England) and by *Ustulina vulgaris*, a common parasite of beech. When a tree has fallen it is soon covered with various species of fungi: *Bulgaria inquinans (polymorpha)* and *Hypoxylon* spp. are general, while *Hydnum coralloides* is very characteristic but rare.» [1]) Here we have passed into the realm of saprophytic rather than parasitic fungi (see Section 12b, p. 346). An exact appreciation of the part played by the parasites of adult beeches and their degree of importance in the economy of beechwoods must wait upon a detailed knowledge of fungal ecology, which in England is still very backward.

18. SUCCESSION.

The competitive ability of the beech and its adaptability to a wide range of soils make it the potential climax wood former over considerable areas. Owing to biotic disturbance the full succession is not easily traced in its entirety, but on the South Downs and Chilterns,

[1]) Kindly communicated by Mr J. Ramsbottom.

both on the escarpments and on the plateaux, adequate material exists to establish the fact of its existence.

I. [2]) On the chalk soils of the escarpment the generalised succession is:

Grassland — Chalk Scrub — ± Ashwood — Beechwood.

On the Chilterns, and on the South Downs, as far as they have been worked out, two well-marked seres may be recognised: (a) on shallow soils (31 cm.), (b) on deeper soils (51 cm.).

(a) Grassland — Juniper Scrub — Beechwood (*Sanicula* dominant);

(b) Grassland — Hawthorn Scrub — ± Ashwood — Beechwood (*Mercurialis* dominant).

The grasslands have not been investigated in this connexion, but it is believed that different types exist corresponding with these two seres.

Juniper scrub with *Juniperus communis* dominant contrasts sharply with the Hawthorn (*Crataegus*) scrub, but the accompanying species in both are the same. The ash consocies is limited to the Hawthorn sere. The beechwoods differ mainly in height and form of the trees: those in the Hawthorn sere are taller and straighter than those in the Juniper sere. In the ground vegetation *hemicryptophyta scaposa*, with *Mercurialis perennis* dominant in the climax of the Hawthorn sere, contrast with a vegetation in which *hemicryptophyta rosulata* (with *Sanicula europaea* dominant) and *geophyta rhizomata* (half of them orchids — *Cephalanthera grandiflora, Helleborine latifolia, Neottia nidus-avis*) play the chief part. It is of interest to note that the *hemicryptophyta scaposa* are excluded from the Sanicle beechwood by edaphic factors, whilst the species characteristic of the Sanicle beechwoods are, or tend to be, excluded from the Mercury beechwoods by competition with the taller growing forms.

II. On the brown earths of the plateaux the generalised succession is:

Grassland — Scrub — Ash-oakwood or Oakwood (Phot. 2) — Beechwood.

Many variations are found corresponding with the differences in the character of the plateau soils, but the communities so far as

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[2]) The numbers correspond with those of sections 4 and 11 and Tables 3, 4 and 5.

studied are grouped into three seres: two of these show the following generalised sequence in which initial communities may be much modified by grazing and interference.

(a) Chalk Grassland ranging to Neutral Grassland *(Pteridium* 6 feet: 1.8 m.), Scrub *(Crataegus, Prunus spinosa; Ulex europaeus),* Ash-oakwood, Beechwood.

(b) Grass Heath *(Calluna,* 18 in., 46 cm.: *Pteridium,* 4—6 feet, 1.2—1.8 m.), *Ulex,* Oakwood, Beechwood.

The chief differences between the initial communities of these two seres are the absence of typical chalk grassland species from (b) and the heights attained by the locally dominant *Pteridium.* In (b) scrub is mainly represented by *Ulex europaeus,* which is locally dominant, but oak may colonise the grassland direct. The ash-oakwoods (a) vary much in the relative proportions of ash and oak, with ash the more frequent on the shallower and less acid soils. In (b) ash is absent and an oak *(Quercus robur)* consocies is preclimax to beech. In (a) the beech varies in height from about 80 feet (24 m.) to 110 feet (33.5 m.), whilst in (b) it is only 70 feet (21 m.). In both seres a shrub layer of *Rubus fruticosus* (agg.) is found in all woods, though it differs in density and vigour; but in (a) *Rubus* is accompanied by a scanty field layer of several of the more exacting herbs *(Asperula odorata, Fragaria vesca, Lamium galeobdolon,* etc.) which are absent from (b). In even-aged high forest the *Rubus* stage is preceded by a stage in which *Oxalis acetosella* is dominant.

The third sere (II c) is found on the Chiltern plateau where degenerate brown earth bears a succession the full details of which are not available, but which appears to resemble the succession on the podsolised sands and gravels of south-east England. This is as follows:

Heath *(Calluna,* 4—5 in., 10—12.5 cm.: *Pteridium,* 18 in., 46 cm.) — Oakwood — Beechwood.

Oakwood *(Quercus robur)* succeeds *Calluna,* heathy pasture or *Pteridium,* and is in turn succeeded by beechwood of poor growth. Locally birchwood succeeds *Calluna,* but how far birchwood enters into the general succession on these soils on the Chiltern plateau is not decided.

III (a) On typical podsol of south-eastern England the succession is:

Calluna Heath — Birchwood(*Betula* spp.) — Oakwood (*Quercus robur* and *sessiliflora)* — Beechwood.

(b) A northern form of the Heath sere is found in north-east Scotland, where planted conifer wood when progressively felled is replaced by a rowan-birch (*Sorbus aucuparia-Betula* spp.) associes, which in turn is succeeded by beechwood arising from seed derived from planted trees.

IV. No succession studies have been made as material is lacking.

Floristically and edaphically the beechwoods on the degenerate brown earth of the Chiltern plateau show a definite convergence with the Heath Beechwoods; and whatever may be the immediate cause beech regeneration is precarious, growth is poor, and it is improbable that beech can maintain itself for long as the climax. The accumulation of acid humus, the leaching of bases and the depression of animal activity will be accentuated by the maintenance both in space and time (selection system) of a beech canopy. It seems impossible to avoid the conclusion that, as has happened in other countries on the North Atlantic frontier of beech distribution, beechwood will give way to heath. But we have no record that this has actually happened.

One expects this retrogression to be more evident in the cooler climate of northern Scotland, but the fact that the beechwoods examined grow on soils containing large reserves of bases, and have only existed for a short time, accounts for the lack of confirmatory evidence. The existence of these woods and their maintenance depend on the adequate removal of the drainage water by continued human control. They are therefore to be considered as post-climax woods. Whether or not there exist beechwoods in the north which could maintain themselves indefinitely is not known, but in some examples on brown earth the humus does not at present accumulate.

19. HISTORICAL RECORDS.

Available historical records are unfortunately too scanty to be of much value. The records of fossil beech from Neolithic deposits might seem to establish the nativity of beech, but, as already stated on

p. 295, none of these records is beyond doubt. Records also exist of the discovery of beech charcoal along with Romano-British pottery in the New Forest and of beech piles at Hedsor dating from the period of the Roman occupation. But these Roman records are not, by themselves, conclusive evidence, since the Romans occupied Southern England for a period long enough (about 400 years) for introduced beech to attain maturity and for self-sown descendants to become widely established.

On the other hand, Caesar writes *(De Bello Gallico*, V. 12, § 5) that all the Gallic trees occurred (in south-east England) except the beech and fir (see p. 295). Crawford has shown that the Chalk uplands of the South were cultivated by the «Celts» from about 450 B. C. to 450 A. D.; and terraces, upon the existence of which he bases his conclusions, are common throughout the beechwoods of the Goodwood area. The occurrence of beech pollen in post-glacial peat is too scanty to yield satisfactory data confirming pre-Roman colonisation of the tree, though a few beech pollen grains have been found in late sub-boreal and in sub-atlantic peats.

In later times we have the records in the Domesday Book (eleventh century) of the value of forests in terms of the head of swine the mast can feed, but the absence of specific reference to beech admits of the interpretation that oak supplied the bulk or the whole of the mast.

Subsequently, from the 12th century onwards, beech is mentioned from several Royal forests — Windsor, Bere, Clarendon (Wiltshire), Northampton (Midlands) and Pickering (north).

The conclusion reached from the available evidence and from the behaviour of beech and the present structure of beech forest is that although beech now behaves in all respects as a native tree, the evidence on which the belief in its spontaneous migration into this country is based is doubtful, though there is nothing to contradict the possibility of its immigration in late sub-boreal or sub-atlantic times. It is, however, improbable that beech forest as extensive even as that now existing was present in the south-east at the time of the Roman invasion, and in the Goodwood area it may be considered certain that such was not the case.

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