The Oak-Hornbeam Woods of Hertfordshire Parts III and IV

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THE OAK-HORNBEAM WOODS OF HERTFORDSHIRE
PARTS III AND IV¹

By E. J. SALISBURY

(With two Figures in the Text and XX Tables)

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PART III. THE *QUERCUS SESSILIFLORA*-*CARPINUS* WOODS

(1) General and Introductory

The *Quercus sessiliflora*-*Carpinus* woods, with which the present part deals, comprise some of the largest woodland areas in Hertfordshire and together occupy between two and three thousand acres. For the purposes of this account a few woods have been included in which *Quercus robur* is present in preponderating numbers, but where there is good reason for believing this condition to be the outcome of planting. But, in estimating

¹ Parts I and II appeared in this JOURNAL, 4, pp. 83-117.

the distinctive characteristics of this type, and the frequencies of the constituent species, reliance has been chiefly placed upon observations in the woods at Symond's Hyde (ca. 220 acres) and Sherrard's Park (ca. 250 acres), in which the Oaks are almost exclusively *Quercus sessiliflora*. These two woods have been visited many times at frequent intervals over a period of from three to four years. The necessity for such repeated visits, at all events throughout the vegetative season, cannot be too strongly urged if reliable data as to frequencies are to be obtained. This is all the more important since many of the herbaceous species are common to several types of woodland, but exhibit a prevalence peculiar to each. In addition to the two woods named a further area of considerably over 1000 acres has been carefully examined though at longer intervals.

It is with great pleasure that the author records his indebtedness to the Rt. Hon. the Marquis of Salisbury, Lord Lytton, Sir George Faudel Phillips, the Hon. A. Holland-Hibbert, Lt-Colonel A. D. Ackland, Major Smith-Bosanquet, and other owners for permission to investigate their woods. His thanks are also due to Mr Septimus Beck and to Mr J. C. McCowan for their kindness in affording information with regard to the estates of which they have charge.

For assistance in the determination of Algae, Fungi, and Lichens respectively the author is indebted to the following specialists: Prof. F. E. Fritsch, D.Sc., Mr J. Ramsbottom, M.A., and Mr R. Paulson, F.L.S. The surveys reproduced in Figs. 1 and 2 were kindly prepared by the author's brother Mr A. H. Salisbury, M.S.A.

(2) The Edaphic Conditions

Attention has previously been called to the general distribution in Hertfordshire of the various types of Oak-woods (Salisbury, *loc. cit.*, p. 84). As already stated, the *Quercus sessiliflora*-*Carpinus* woods predominate in the south-west of the county, but they are in addition generally associated with superficial deposits, geologically different from those in which *Quercus robur* is the dominant tree (cf. Table I). The latter woods occur chiefly on the clay-with-flints, whilst the woods here dealt with are found mainly on outliers of the Reading beds, the London Clay, Glacial Gravel, or Boulder Clay. Information regarding the geology of the district has been kindly furnished by the author's friend Mr G. W. Lamplugh, F.R.S., and Dr Sherlock of H.M. Geological Survey, the latter of whom has recently mapped a large part of the area in question.

An interesting case is afforded by the Devil's Dyke, near Marford, reputed to be a pre-Roman earthwork (cf. *Historical Monuments of Hertfordshire*) which occupies an isolated patch of what Dr Sherlock regards as probably Boulder Clay. The dyke is about a quarter of a mile long and some 35 ft deep, with steep wooded sides. At the present day *Quercus sessiliflora* is

entirely absent, but a careful search has revealed two specimens of the hybrid Oak. There are no woods in the immediate vicinity and those which lie nearest contain no *Quercus sessiliflora*. Evidently then *Q. sessiliflora* must formerly have been present, but probably this, like so many of our woods, has been replanted with *Q. robur*, only a few of the original sapling hybrids having survived. The general character of the flora in other respects (e.g. frequent Beech and abundant Holly) suggests a *Q. sessiliflora*, rather than a *Q. robur* wood. This exemplifies the replacement that has probably taken place in several instances (e.g. Balls Wood, Hertford).

It is perhaps nothing more than a coincidence that *Q. sessiliflora* is by far the commoner Oak in Grimm's Dyke, another pre-Roman earthwork, near Wigginton.

It should be noted that both in Hawkshead Wood (North Mimms), and in Oxhey Woods, the local dominance of *Q. sessiliflora* is associated with Reading bed outliers (W. Whitaker, *Mem. Geol. Survey*, vol. 1, pp. 198-203, 1889), and here too human interference may have considerably reduced both the number of individuals and the area occupied by this species. On the other hand *Q. sessiliflora* does occur in small numbers where there is no reason to suppose the present relative frequencies to have been artificially produced. For example, Pryor's Wood, near Ayot, situated on the Clay-with-flints, contains a few Durmast Oaks, but the general character of the flora is entirely that of the *Q. robur-Carpinus* type.

A striking instance of the effect of geological conditions is seen at Symond's Hyde. Here we have a group of contiguous woods, namely Cox's Wood, Titnol's Wood, Great Wood, and Furze-field Wood, which in the order named extend from the higher to the lower ground. The valley is occupied by a loamy boulder clay which gradually thins out as we pass up hill and finally gives place to Clay-with-flints just beyond Cox's Wood. In correspondence with this *Q. robur* and *Q. sessiliflora* occur in nearly equal proportions in Cox's Wood; but the latter becomes more abundant as we pass down hill, so that in Symond's Hyde Great Wood the common Oak is quite rare. In Hitch Wood and Wain Wood, in the north of the county, *Q. sessiliflora* is fairly common, although both according to the old drift maps are situated on the Clay-with-flints.

In connection with the presence of this type upon the Boulder Clay, it should be noted that the latter is often not typical and as it occurs in these woods is frequently a relatively light soil of a loamy character. Possibly washing out of the finer particles from the upper layers has contributed towards this (cf. Whitaker, *loc. cit.*, p. 321), a factor that has also operated in the London Clay areas. In reference to the latter Mr Whitaker mentions that "the upper beds like the basement bed are more sandy than the large mass of the formation" (*loc. cit.* p. 239). Sherrard's and Brock's Woods furnish examples of woods situated mainly upon the Woolwich and Reading

Beds and the same is true of the Ruislip Woods in Middlesex. In all these, the dominant tree is *Quercus sessiliflora* and the undergrowth is chiefly Hornbeam. Still more significant is the occurrence of a similar relation elsewhere. Thus we find the scattered woods near Reigate in Surrey illustrating the same feature. Margery Wood situated on the Clay-with-flints is a typical example of the *Quercus robur-Corylus* type whilst the isolated patches of Reading and Woolwich Beds near Headley are occupied by *Quercus sessiliflora-Corylus* woods with a ground flora that is strikingly similar to that of the *Q. sessiliflora-Carpinus* woods of Hertfordshire.

The enumeration (Table I) shows that this type is then characteristic of Boulder Clay, Glacial Sands and Gravels, and the sandy soil of the Woolwich and Reading Beds. Moreover the composition of the herbaceous flora in areas of scrub bears out the natural relations of the vegetation to these different soil types (cf. Salisbury, "Ecology of Scrub," *Trans. Herts. Nat. Hist. Soc.*, vol. xVII, 1918).

TABLE I. *Geological Character of Soils*

Wood	Type	Geological character of soil
Sherrard's Park	<i>Q. sess.-Carp.</i>	Boulder Clay and Reading Beds
Brock's	" "	" " "
Symond's Hyde Great Wood	" "	Boulder Clay
Titnol's	<i>Q. sess. + Q. robur-Carp.</i>	" "
Blackboy	" " "	" "
Mardley Heath	" " "	Glacial Gravel
Ninning's	" " "	Glacial Gravel and Sand
Harmer Green	" " "	Boulder Clay. Woolwich and Reading Beds
Burnham Green	" " "	Reading Beds, Gravel and Sand
Bramfield	" " "	Boulder Clay
Punchett's	" " "	Glacial Gravel and Boulder Clay
Knebworth (Gt. Wood)	" " "	Glacial Gravel and Clay-with-flints
Wain	(<i>Q. robur d + Q. sess.-Carp.</i>)	Clay-with-flints
Hitch	" " "	" " "
Broxbourne	(<i>Q. sess. + Q. robur</i>)	" " " London Clay with patches of sand and Gravel
Cow Heath	(<i>Q. sess. + Q. robur</i>)	" " " London Clay
Wormley	<i>Q. sess.-Carp.</i>	" " "
Ruislip (Middlesex)	" "	Woolwich and Reading Beds.

A pronounced feature of these woods is the fact that in spite of the coarse texture of the soil they are, compared with the woods of common Oak, extremely wet in winter, a feature well shown by the presence of free water upon the paths and by the character of the path-flora. The not infrequent presence of Beech indicates that the upper layers of soil are relatively dry, since this tree is very intolerant of inundation. One can only conclude therefore that the permanent water-table approaches very close to the surface, so that the slight depression due to the paths, together with the greatly increased water-capacity and capillarity of their soil, resulting from compression and accumulation of finer particles, produces the water-logged condition.

The same general relations as regards types of soil have been found to obtain elsewhere. Thus Wilson ("Plant-distribution in the Woods of North-east Kent," *Ann. of Bot.*, vol. xxv, pp. 857-902, 1911), in the woods of Kent,

found that, whilst *Q. robur* was the dominant tree on the Clay-with-flints, *Q. sessiliflora* was dominant on the London Clay. The latter species was also the more prevalent on the Oldhaven Beds and Thanet Sands. The *Q. sessiliflora-Carpinus* type has been recorded by Tansley as occurring on the more sandy soils near Hampstead (in *Hampstead Heath, its Geology and Natural History*, chap. II, Vegetation, pp. 85-111, London, 1913), derived from the Bagshot Sands and London Clay.

In general it is only on the lighter types of soil that anything approaching purity of *Quercus sessiliflora* is attained, whilst it is on the heavy London Clay that *Quercus robur* is most frequent in woods of this type. However, the dominance of the latter in some of the woods near Broxbourne is probably an outcome of planting.

Usually the soil of these woods is a loam, and mechanical analyses show (cf. Table II) that even in the damper societies the proportion of finer particles

TABLE II. *Mechanical Analyses of Woodland Soils*

Wood	Type	Ground Society	Fine Gravel %	Coarse sand %	Fine sand %	Silt and clay %
Stocking's ...	Q. robur-Carp. ...	Ficaria -	2.4	15.8	21	45.2
Oxhey Grange ...	" "	Mercurialis	0.8	26.48	19.2	50.64
Stocking's ...	" "	Anemone	4.2	8.6	16.2	63.36
Oxhey ...	Q. robur + Q. sess.-Carp.	Pteris ...	8.8	21.0	25.4	35.6
Broxbourne ...	Q. sess.-Carp. ...	Path ...	4.8	19.0	23.4	42.0
Brock's ...	" "	Mercurialis	1.48	11.2	42.52	38.24
Sherrard's ...	" "	Nepeta ...	6.2	32.68	22.4	31.0
Brock's ...	" "	Rubus ...	5.32	46.72	17.76	21.96
Sherrard's ...	" "	Scilla ...	6.8	52.4	15.88	18.72
Wormley ...	" "	Pteris ...	8.2	21.0	31.2	20.0
Brock's ...	" "	Pteris ...	2.2	51.48	21.12	17.76
Average for Q. robur woods ...			2.46	18.29	18.8	53.06
Average for Q. sessiliflora woods ...			5.0	33.49	24.89	27.09

is usually only comparable to that in the drier societies of the *Q. robur* woods. The amount of clay and silt ranges from about 18 % in the lighter soils to 42 % in the wetter parts, namely the paths. That the determining factor for the dominant tree is not here depth of soil (cf. Moss, *Vegetation of Peak District*, pp. 45, 46) is clearly indicated by an examination of the pits which are often present. In these it can be seen that the soil overlying the chalk is at least 16 ft in depth, and at Bricket Wood the Boulder Clay reaches a thickness of about 40 ft (T. E. Lones, "The Gravels, Sands, Clays, and Loams of W. Herts.," *Trans. Herts. Nat. Hist. Soc.*, vol. x, p. 163, 1900). Moreover where the soil thins out, as on some of the lower valley slopes, there is a tendency for *Q. robur* to become more frequent rather than less so, perhaps owing to the increase of moisture and the lower acidity of the soil.

Humus. The amount of humus present is comparatively low (cf. Table III). Where the shrub-layer is dense it ranges from 4.8 % to 9.5 % and though sometimes locally higher this is attributable to cumulative peat-formation by certain members of the ground-flora. The latter feature is especially encountered where the bracken predominates, and here the raw humus of the

surface may attain a depth of over 6 in. The total range is 4·8 %–19·4 %, with an average, for all types of ground-vegetation, of 8·5 %, but in general the amount of humus is considerably lower than in the *Q. robur-Carpinus* woods.

TABLE III. *Average Organic Content of Soil in different Societies*

Wood	Society	Organic matter %	Range %	Average %
Sherrard's	Pteris	7·5–15·76	5·00–15·76	Pteris 9·92
Brock's	"	7·46		
Symond's Hyde	"	11·06		
Broxbourne	"	7·32		
Wormley	"	10·24		
Cow Heath	"	7·8		
Pinner	"	5·0	5·46–12·2	Rubus 8·25
Sherrard's	Rubus	5·46		
Brock's	"	8·24		
Symond's Hyde	"	6·52–6·54		
Wormley	"	12·20		
Broxbourne	"	10·56		
Sherrard's	Nepeta	6·9–7·50	6·32–19·4	Nepeta 7·08
Sherrard's	Scilla	6·0–7·28		Scilla 6·6
Sherrard's	Mercurialis	6·8–11·02		Mercurialis 9·72
Brock's	"	6·56–6·61		
Symond's Hyde	"	11·96–19·4		
Titnol's	"	6·32		
Sherrard's	Ficaria	6·3–11·1	7·44–10·7	Ficaria 8·2
Sherrard's	Path	7·44–8·94		
Symond's Hyde	"	10·1		Path 9·3
Broxbourne	"	10·74		
Wormley	"	9·28		
Sherrard's	Sparse vegetation (dense shrub-layer)	5·36–6·86	4·8–9·5	Sparse veg. 6·8
Brock's	" " "	6·16		
Broxbourne	" " "	8·14		
Wormley	" " "	5·76–8·2		
Symond's Hyde	" " "	4·8–7·0		
Pinner (Middlesex)	" " "	9·5		
Total range	...	...	4·8–19·4	
Average of all estimations	...	...	8·5	

Water-content. The natural water-content shows an average of about 29·5 % on the dry weight. In summer this may fall as low as 19·3 % or in winter rise to over 53 %, but the differences associated with the different ground-societies remain pronounced despite the seasonal changes in any given locality (cf. Table IV).

TABLE IV. *Natural Water-Contents of Composite Soil Samples from the different Societies*

(a) Sherrard's Wood

Ground Society	Range observed %	Average of all estimations %	Acidities %
<i>Pteris aquilina</i> d.	26·5–45·0	29·9	0·51
<i>Rubus fruticosus</i> d.	19·3–27·0	23·0	0·49
<i>Nepeta glechoma</i> d.	18·5–29·5	26·5	0·45
<i>Scilla nutans</i> d.	23·6–30·2	26·1	—
<i>Mercurialis perennis</i> d.	21·4–34·2	28·7	0·31
<i>Ficaria verna</i> d.	27·6–33·6	31·0	0·12
Path Society	28·8–36·4	33·6	—
Dense shrub-layer and sparse ground-flora	25·3–29·6	26·9	—

TABLE IV (continued)

(b) Various Woods

				%
Symond's Hyde	...	6. xi. 15	Dense Shrub-layer	... 23.8
"	...	5. iv. 16	"	... 29.3
"	...	2. iii. 17	<i>Pteris-Rubus</i>	... 27.0
"	...		<i>Pteris</i> d.	... 29.0
"	...	12. x. 16	<i>Rubus fruticosus</i> d.	... 23.4
"	...		Path (<i>Callitriche</i> , etc.)	... 37.4
"	...		Dense Shrub-layer	... 25.5
"	...		<i>Rubus fruticosus</i> d.	... 29.8
"	...	1. i. 17	<i>Mercurialis perennis</i> d.	... 53.4
Titnol's	...		"	... 27.4
"	...	2. iii. 17	"	... 32.3
Brock's	...		<i>Pteris</i> d.	... 21.9
"	...		<i>Rubus fruticosus</i> d.	... 27.0
"	...	19. x. 16	<i>Mercurialis perennis</i> sparse	25.4
"	...		" dense	23.2
Wormley	...	17. iv. 16	Dense Shrub-layer	... 30.2
"	...		"	... 20.5
"	...		<i>Pteris</i> d.	... 29.0
"	...		<i>Rubus fruticosus</i> d.	... 35.2
"	...	26. x. 16	Path Society	... 32.6
Broxbourne	...		<i>Pteris</i> d.	... 30.1
"	...		Path Society	... 42.9
"	...		Dense Shrub-layer	... 30.0
"	...	17. iv. 16	<i>Rubus fruticosus</i> d.	... 38.0
Blackboy	...	6. i. 16	Dense Shrub-layer	... 32.7
Cox's	...	13. xi. 15	"	... 33.2
Sherrard's	...	9. vii. 17	<i>Adoxa-Ficaria</i>	... 26.5
Cow Heath	...	10. v. 17	<i>Pteris aquilina</i> d.	... 25.8
Pinner (Middlesex)	...	28. v. 17	"	... 24.0
"	"	"	Dense Shrub-layer	... 35.2
"	"	"	<i>Pteris</i> Society	... 28.5
"	"	"	<i>Rubus</i> Society	... 28.5
"	"	"	<i>Mercurialis</i> Society	... 31.0
"	"	"	Path Society	... 35.6
"	"	"	Dense Shrub-layer	... 27.8
Average for all estimations	...			
Total range in <i>Q. sessiliflora</i> - <i>Carpinus</i> woods				...18.5-53.4

Acidity. For only five of the woods have acidity-determinations of composite soil-samples been made, and for these the author is again indebted to Dr H. B. Hutchinson. The range (Tables IV, XII) is from 0.12-0.564 % in the uncut wood, with an average of 0.41 %, as compared with 0.44 % in the *Q. robur*-*Carpinus* woods. The ratio of acidity to humus however shows an average of 1 : 19, as compared with 1 : 29.4 (cf. Part I, p. 91) in woods of the latter type. Evidently then the soil-solution in the upper layers is much more acid than in those woods where *Q. robur* predominates.

Before discussing the significance of these facts regarding the soil it may be well to consider briefly what is known as to the occurrence of *Q. sessiliflora* woods elsewhere. In the Peak district Moss (*loc. cit.*, pp. 45, 46) found that the woods of this species were confined to shallow soils overlying the non-calcareous rocks (sandstones and shales), but both species were found growing together on the deep fluvio-glacial sands and gravels. Moss therefore concluded that depth of soil was the chief factor that determined the dominant

species. *Q. sessiliflora* is the characteristic tree of the steep valley-sides on the Cambrian shales of Wales (Salisbury, *Proc. Linn. Soc.*, p. 3, 1916), on the Old Red Sandstone in the combes of Exmoor, and in the Yorkshire valleys on the oolitic sandstones (Smith and Rankin, "Geog. Distribution of Vegetation in Yorkshire," *Geog. Journal*, p. 13, 1903); in North and Central Wales on Ordovician shales and schists; in Herefordshire on May Hill Sandstone; in Devonshire on non-calcareous Upper Greensand, in the same county and in Cornwall on various Palaeozoic rocks; in Co. Wicklow on Ordovician, in Co. Kerry on Old Red Sandstone, and in Co. Galway on metamorphic rocks (*Types of British Vegetation*, p. 137). This species was also perhaps formerly dominant on the Coal Measure shales and sandstones of Gloucestershire (Tansley and Adamson, "Reconnaissance in the Cotswolds and Forest of Dean," *Journ. of Ecol.*, **1**, p. 86, 1913). In all these cases then the woods occupy soil overlying siliceous rocks, and owing to the steep character of the valley-sides this soil is often very shallow. Moreover, since such situations receive the drainage from the surrounding uplands, the water-content is often high. However, as the writer has pointed out, *Q. sessiliflora* woods do occur locally on calcareous soils, as on the Mountain Limestone of Wales (Salisbury, *Proc. Linn. Soc.*, p. 3, 1916), and the same feature is observed near Symond's Yat (cf. Miss E. Armitage, *Journ. of Ecol.*, **2**, p. 103, 1914).

Probably the presence of *Q. sessiliflora* on calcareous rocks is only rendered possible where the soil has a high water-content either owing to high rainfall or drainage water. It should be noted too that the examples quoted are from Mountain Limestone, the soil-water from which is much less hard than that from chalk.

In view of what has been said with regard to the proximity of the water-table in these Hertfordshire woods it is possible that the soil is rendered physiologically shallow owing to water-logging at a comparatively slight depth. It is however probable that there is some underlying feature common to all these habitats, namely dilution of mineral salts especially carbonates, and accompanying acidity. Where as is most commonly the case woods of this type occupy steep valley sides, leaching out of the mineral salts from the surface-layers is bound to result, an effect all the more pronounced if the soil be shallow. Moreover siliceous rocks are notoriously deficient in soluble mineral substances. It is quite in harmony with this view that *Q. sessiliflora* is chiefly found on calcareous rocks in areas of high rainfall.

The presence of both species in association on the deep fluvio-glacial sands and gravels is perhaps an example of a complementary arboreal society. For the shallow-rooted *Q. sessiliflora* will occupy the upper layers of the soil, deficient in mineral salts, whilst the deeper-rooted common Oak will derive its mineral salts from the lower unleached layers that will have been to some extent enriched by the percolation-water from above. It may well be therefore that the distribution as regards depth of soil is but an expression of differ-

ent demands upon the soil-solution. The lower mineral content of the timber of *Q. sessiliflora* as compared with that of *Q. robur* also argues a capacity for growth in poorer soil.

Hall and Russell (*Agriculture and Soils of Kent, Surrey and Sussex*, pp. 180-183, Board of Agric. and Fish., 1911) give analyses from two woodland soils and a permanent pasture on the Clay-with-flints, and from an old pasture and a common on the London Clay. A comparison of these data from uncultivated land shows that a striking feature of contrast is the absence of lime from the London Clay, though it is only present in small amount in the Clay-with-flints. Also the London Clay is characterised by a low proportion of "available" potash. The normal absence of *Q. sessiliflora* from calcareous soils is therefore in harmony with its presence on the London Clay, both in Hertfordshire and Kent, but the deficiency in available potash may well militate also against the occurrence of *Q. robur*.

A comparison of the amounts of mineral salts present in a number of woodland soils was made by shaking up 50 gms. of air-dried soil in 100 c.c. of distilled water and determining the electrical conductivities of the filtered solutions by means of a Kohlrausch Bridge with Telephone. The results show that generally there is a lower resistance and therefore a larger proportion of mineral salts in the soil-solutions from the *Q. robur* woods (cf. Table XV). If the soil previously heated to 100° C. be employed the adsorption effect of the colloidal particles is largely eliminated and a greater difference between the two types is observed. We are however completely in ignorance as to whether the plant is to any extent capable of overcoming this adsorption effect.

In lowland districts we usually find *Q. sessiliflora* on the drier types of soils, and *Q. robur* on the damper, whilst in upland regions it is woods of the former species which occupy the wetter areas. One of the woods in Hertfordshire, namely Wormley Wood, in which *Q. sessiliflora* is dominant, is reputed to be one of the wettest woods in England, on the other hand parts of Sherrard's wood are dry even in winter. Now we have noted that, having regard to the generally low water-capacity of the soils, the acidity where *Q. sessiliflora* is dominant is greater than in the *Q. robur* woods. The low proportion of carbonates in the soil-solution is probably a great contributing factor to this feature, and it may well be that the effect of the impoverished mineral content is as much indirect through its influence on acidity as direct in its effect on nutrition.

Broadly then, both here and elsewhere, *Q. sessiliflora* may be regarded as a tree tolerant of acid conditions and with a capacity for thriving upon soils deficient in mineral salts. Its rare occurrence on calcareous soils however argues that the present distribution may be rather the outcome of competitive pressure than an expression of natural preference. The frequent paucity of saplings of *Q. sessiliflora* suggests that on soils suitable to either species

Q. robur increases at the expense of its congener (cf. also Salisbury, "The Ecology of Scrub," *Trans. Herts. Nat. Hist. Soc.*, vol. xvii, 1918).

(3) Light-conditions

The shrub-layer in these woods is of very variable density, but in general is either moderately well-developed or almost completely absent. As a result there are two types of area presenting very different conditions as regards illumination. Where the shrub-layer is well represented, the intensity of the diffuse light during the Light-Phase (cf. Part II, p. 92) ranges, according to the proximity of the stools, from 25 % to 72 % of the diffuse light-intensity in the open, the average being about 41·5 %. During the Shade-Phase this is reduced from about 1-11 %, with an average of nearly 4 % (cf. Table V).

TABLE V. *Light-intensities in Q. sessiliflora-Carpinus woods*

Wood	Character of Vegetation	Light-Phase %	Average of Light-Phase %	Shade-Phase %
Sherrard's	Dense shrub-layer, sparse ground-flora, chiefly Mosses and Fungi	33-50	40	4-11
Brock's		25-43	34·3	4·1-4·3
Symond's		33-46	38	1·3-4·0
Wormley		30·2		
Broxbourne		38·0		
Cox's	(<i>Q. sess.</i> + <i>Q. robur</i>) „ „			0·9-1·9
Sherrard's	Shrub-layer sparse or ab- sent, <i>Pteris</i> dominant	50-90	70	11-20
Symond's		66-90	70	—
Sherrard's		40-72	59	10-27
Brock's	Shrub-layer sparse or ab- sent, <i>Rubus fruticosus</i> dominant	50-55	50	—
Symond's		50-83	66·4	—
Titnol's		58-66	62	—
Wormley		—	—	16·6
Sherrard's	Shrub-layer sparse, <i>Rubus</i> and <i>Pteris</i> dominant	66-70	66	—
Symond's		73-80	76	—
Sherrard's	Sparse shrub-layer, <i>Nepeta</i> dominant	38-72	50	5-1·1
Sherrard's	Sparse shrub-layer, <i>Scilla</i> dominant	—	48	2·5
Sherrard's	<i>Mercurialis perennis</i> domi- nant	33-72	44·5	4·3-0·5
Symond's		33-43	38·6	4
Sherrard's	<i>Ficaria verna</i> dominant	40-60	54	1-0·1
Sherrard's	Path Society	50 upwards	—	13-20
Symond's		50 upwards	—	5·4-16
Wormley		—	—	8·3-21
Total range	(shrub-layer present)	25-72		0·9-11
Average	„ „ „	39·7		3·9
Total range	(shrub-layer sparse or abs.)	33-90		4·3-27
Average	„ „ „	66·6		13

In regard to these areas the low intensity during the Light-Phase is a noteworthy feature. Compared with the corresponding period in the *Q. robur-Carpinus* woods, the average intensity here, under coppice of similar age, is about 2 % to 10 % less (Salisbury, Part II, p. 93). This feature must be attributed to the fact that although the shrub-layer is scarcely ever as dense as in the *Q. robur* woods, the tree-canopy in these woods is much less open, and the more or less horizontally directed branches of the Oaks have a greater shading effect than the almost vertical branches of the coppice stools.

On the other hand we find that during the Shade-Phase the illumination beneath the shrub-layer is considerably higher than in the *Q. robur-Carpinus* woods. Now even where the shrub-layer in the latter is dense there is usually a considerable ground-flora, whilst in these woods the presence of a considerable shrub-layer is almost invariably associated with an almost complete absence of ground-vegetation. As the writer has already pointed out for the *Q. robur* woods with undergrowth (Part II, p. 97), it is the intensity during the Light-Phase combined with the time-factor which determines the amount of the ground-flora. Here in these woods as we have seen the conditions of illumination where there is a shrub-layer are altogether unfavourable to the ground-flora. For not only is the Light-Phase intensity low, but, since the shading effect is largely due to the tree-layer, there is no frequently recurring periodic impetus (cf. Part II, p. 98).

Whilst however the diminished light probably plays a very large part in bringing about a sparse vegetation, other factors, such as acidity, texture of soil, and water-supply are probably also involved.

The only species apart from Cryptogams which occur in these woods, where the Light-Phase intensity is very low, are extreme vernal forms such as *Adoxa moschatellina* and *Ficaria verna*. *Mercurialis perennis* also occurs in rather less shaded situations where the shrub-layer is fairly well developed.

Turning now to those areas where the Hornbeam is absent, or only represented by sparsely scattered stools, we find that the illumination both during the spring and summer is very much higher. Thus, during the Light-Phase the intensity ranges from 33 % to 90 %, with an average of over 66 %, whilst during the Shade-Phase the intensity does not fall below 4 % and may be as much as 27.2 %, with an average of 13 %.

Such considerable illumination during the Shade-Phase, though low in comparison with that in the open, enables shade-enduring species with aestival foliage to become dominant constituents of the ground-flora. Hence we find that areas where the Hornbeam is absent or scanty are often occupied by dense societies of Bramble or Bracken, whilst Honeysuckle, *Holcus mollis*, *Luzula pilosa*, and Wood Sage are by no means infrequent. All these are species which develop their new foliage relatively late in the year, but can tolerate a considerable degree of shading.

The Ground Ivy is locally abundant in some of these woods, and can survive a lower intensity than most species which retain their foliage throughout the summer. This is perhaps an outcome of the fact that though its new foliage is not produced till March or April yet the old foliage is frequently in large part retained throughout the autumn and winter, so that full advantage is taken of the Light-Phase.

The presence of abundant aestival species necessarily involves a quantitative diminution of those vernal species that might otherwise occupy the

better-lighted regions. Also the increased illumination results in a flora which though poor in quantity is numerically rich in species.

(4) **The Phanerogamic Flora**

If we disregard introductions and the numerous species of *Rubus*, etc., a total of 269 species of vascular plants have been observed in these woods, and of this number 48 represent trees, shrubs, and undershrubs, and the remaining 221 are herbs. From the *Q. sessiliflora* woods of Derbyshire, Moss (*loc. cit.*) has enumerated 231 vascular plants, exclusive of introduced species, but here as there it must be noted that owing to the sparsity of individuals the number of species is no measure of the amount of vegetation. Indeed the herbaceous carpet of the *Q. robur-Carpinus* woods is much more dense, although the Phanerogamic flora comprises only 265 species, of which 31 are confined to woods where *Q. sessiliflora* is also present. Two small woods of the *Q. sessiliflora-Carpinus* type in the neighbourhood of Hampstead, namely Bishop's Wood and Turner's Wood, have been briefly described by Tansley ("Hampstead Heath, its Geology and Nat. Hist.," *Vegetation*, pp. 85-111, London, 1913). Comparison with those here described shows a general agreement in the character of tree- and shrub-layers. But as the list there given is based on "hasty visits during August and September" only, the marked discrepancies, both as to species and frequencies, in the ground-flora are perhaps more apparent than real. According to Mr Tansley, none of the herbaceous species appears to be at all abundant, except the Bracken and *Holcus mollis*, both of which are common in our woods. Mr Whitton however in the same work (p. 169) states that *Scilla nutans* is very abundant in Bishop's Wood, a feature which is of interest in connection with the local occurrence of a society dominated by this species in Sherrard's Wood.

(a) *The Tree-layer.* The dominant tree is *Quercus sessiliflora*, Salisb., but the hybrid Oak and *Q. robur* may be present in considerable amount. The average number of trees to the acre is usually higher than in the *Q. robur* woods (cf. Fig. 1). Seldom much below 30, the number may attain to over 70, and never have we found the trees sparsely scattered over large areas as is so frequently the case in woods where the common Oak predominates. This difference is probably to be attributed in part to better forestry, associated with the larger size of the woods of this type, but it may also be due to the more open texture of the soil and the increased illumination which tend to favour germination (cf. Boerker, R. H., *Ecological investigations upon the germination and early growth of Forest Trees*, Lincoln, Nebraska, 1916). In general it may be said that seedlings of both trees and shrubs are of greater frequency here than in *Q. robur-Carpinus* woods, and this in spite of the greater prevalence of rabbits. In these woods the Hornbeam occurs frequently as a tree and its seedlings are by no means uncommon. The great rarity of Hornbeam seedlings in the *Q. robur* woods is probably largely due to the fact that some years must

elapse before a coppiced stool bears fruit and often this does not take place until it is again cut. Here however the frequent Hornbeam trees supply the requisite seed.

The most important of the associated trees is unquestionably *Betula pubescens*, Ehrh., with which is occasionally associated *B. alba*, L., but never

FIG. 1. Chart of a typical portion of Sherrard's Park Wood, showing the standard oaks (*Q. sessiliflora*) more numerous than the oaks in *Q. robur* woods, the hornbeam stools (C) and the hornbeam saplings (H).

in such quantity. The Birch rapidly colonises areas adjacent to the main woods, but owing to human interference no very advanced stage is usually reached. *Pyrus aucuparia*, Gaertn., though usually rare, is very characteristic as it is also of the *Q. sessiliflora* woods elsewhere, and the same may be said of *Ilex aquifolium*, L., *Alnus glutinosa*, Gaertn., *Pyrus torminalis*, Ehrh., and *P. malus*, L. These are all very rare, but are apparently confined to woods

of this type or *Q. robur* woods in which *Q. sessiliflora* is also present and which are consequently open to suspicion of having been planted. The Aspen is occasional in its distribution, and both the smooth and hairy leaved varieties occur, the latter being sometimes frequent. *Prunus avium*, L., *Ulmus montana*, Sm., and *Fraxinus excelsior*, L., are all trees that occur with considerable frequency in the Oak-Hazel woods, but are generally less common in the *Q. robur-Carpinus* woods. Here these trees are more or less restricted to the hollows and lower slopes of the valleys where the water-content is higher, the soil consists of finer particles, and is richer in mineral salts. In these situations too *Q. robur* may in part replace *Q. sessiliflora*. Both the soil-conditions and the vegetation in these hollows approximate very closely to those in the *Q. robur-Carpinus* woods of the stiffer loams, and it may be significant that the amount of mineral salts, as measured by the electrical conductivities of the soil-solutions, in these situations corresponds with that of the soil-solution from the *Q. robur-Carpinus* woods. There are two woods where the Ash is locally abundant, namely Titnol's Wood and a part of Wormley Wood. They illustrate the two extremes under which the Ash is found (cf. Moss, *Veget. of Peak Distr.*, p. 69). The former locality is relatively dry, and the latter exceptionally wet. As however Titnol's Wood exhibits a lower acidity than any of the other woods of this type we may perhaps here possess a clue to the prevalence of this species (cf. Part II, p. 99).

Several Conifers occur, but none is indigenous. Those most commonly planted are the Spruce, the Larch, and the Douglas Fir, less frequently the Scotch Pine.

(b) *The Shrub-layer.* Here, as in the *Q. robur-Carpinus* woods, the shrub-layer is chiefly composed of *Carpinus betulus*, var. *provincialis*, Grenier et Godson. Both *Rubus fruticosus*, Agg. L., and *Lonicera periclymenum*, L., are very common and the former is locally dominant. The Hazel is frequent, but, like the Dogwood, Elder, Maple, and Blackthorn, is chiefly found where the surface approaches close to the chalk, especially in the damp hollows. Elder is particularly characteristic of the latter situations (cf. Part II, p. 99). Frequent members of the shrub-layer are *Crataegus monogyna*, Jacq., *C. oxycanthoides*, Thuill., and various species of Roses and Willows. Especially characteristic, although very rare, are *Rhamnus frangula*, L., and *Viburnum opulus*, L. The complete list is given in Table VI.

Associated with the more complete arboreal canopy the Hornbeam never attains to the density exhibited in the *Q. robur* woods. But where the shrub-layer proper is present the combined shading effect of trees and coppice is sufficient to restrict the ground-vegetation almost entirely to Mosses and Fungi. As previously stated however there are considerable areas from which the Hornbeam and other shrubs proper are almost completely absent. These areas are often covered by a dense straggling growth of Brambles. Hence we can recognise two distinct societies in the shrub-layer, namely that in which

TABLE VI. *List of trees and shrubs**Trees:*

<i>Quercus sessiliflora</i> , Salisb.	...	...	...	...	dom.
„ <i>robur</i> , L.	...	...	...	...	r-c
<i>Q. robur</i> × <i>Q. sessiliflora</i> , Mocek	...	...	...	...	o-f
<i>Abies excelsa</i> , DC.	...	...	...	...	planted
<i>Acer pseudoplatanus</i> , L.	...	...	...	...	vr
<i>Alnus glutinosa</i> , Gaertn.	...	...	...	...	r-vr
<i>Betula alba</i> , L.	...	...	...	...	o-f
„ <i>pubescens</i> , Ehrh.	...	...	...	...	f-c
<i>Carpinus betulus</i> , var. <i>provincialis</i> , Grenier et Godron	...	...	...	...	f
<i>Castanea sativa</i> , Mill.	...	...	...	...	planted (?), rare
<i>Fagus sylvatica</i> , L.	...	...	...	...	vr-f
<i>Fraxinus excelsior</i> , L.	...	...	...	...	o-lc (damp places, or if dry less acid)
<i>Ilex aquifolium</i> , L.	...	...	...	...	r-lf
<i>Larix decidua</i> , Mill.	...	...	...	...	planted, f
<i>Pinus sylvestris</i> , L.	...	...	...	...	planted, f
<i>Populus alba</i> , L.	...	...	...	...	r
„ <i>tremula</i> , L.	...	...	...	...	o-f
„ „ „ var. <i>glabra</i> , Syme.	...	...	...	...	o-lf
„ „ „ var. <i>sericea</i> , Doll.	...	...	...	...	o-f
<i>Prunus avium</i> , L.	...	...	...	...	r-l
<i>Pseudotsuga douglasii</i> , Carr.	...	...	...	...	planted, f (2)
<i>Pyrus aucuparia</i> , Gaertn.	...	...	...	...	o
„ <i>communis</i> , L.	...	...	...	...	r (2)
„ <i>malus</i> , var. <i>mitis</i> , Wallr.	...	...	...	...	r-vr
„ <i>torminalis</i> , Ehrh.	...	...	...	...	vr
<i>Ulmus montana</i> , Sm.	...	...	...	...	r-lf

Shrubs and undershrubs:

<i>Acer campestres</i> , L.	...	...	...	...	o
<i>Calluna vulgaris</i> , Salisb.	...	...	...	...	lc (3)
<i>Carpinus betulus</i> , var. <i>provincialis</i> , G. and G.	...	...	...	...	sd
<i>Clematis vitalba</i> , L.	...	...	...	...	chalk-pits only
<i>Cornus sanguinea</i> , L.	...	...	...	...	rr-o, near chalk or damp places
<i>Corylus avellana</i> , L.	...	...	...	...	f (lc in damper hollows)
<i>Crataegus monogyna</i> , Jacq.	...	...	...	...	f
„ <i>oxyanthoides</i> , Thuill.	...	...	...	...	f
<i>Hedera helix</i> , L.	...	...	...	...	f
<i>Lonicera periclymenum</i> , L.	...	...	...	...	c-ab
<i>Prunus spinosa</i> , L.	...	...	...	...	f-lc, especially near chalk
„ <i>institia</i> , L.	...	...	...	...	rr (1)
<i>Rhamnus catharticus</i> , L.	...	...	...	...	vr (2), near chalk
„ <i>frangula</i> , L.	...	...	...	...	vr
<i>Rhododendron ponticum</i> , L.	...	...	...	...	r-lf, planted
<i>Ribes rubrum</i> , L.	...	...	...	...	vr (1)
<i>Rosa arvensis</i> , Huds.	...	...	...	...	f (near edge)
„ <i>canina</i> , L.	...	...	...	...	f (near edge)
„ <i>stylosa</i> , Desv.	...	...	...	...	r (1)
„ <i>tomentella</i> , Leman	...	...	...	...	r (1)
„ <i>tomentosa</i> , Sm.	...	...	...	...	r (1)
<i>Rubus fruticosus</i> , L. (agg.)	...	...	...	...	c-ab
(Incl. <i>R. koehleri</i> , Weihe, <i>R. rhamnifolius</i> , Weihe and Nees, <i>R. leucostachys</i> , Schleich, etc.)	...	...	...	...	
<i>Rubus idaeus</i> , L.	...	...	...	...	r-f
<i>Ruscus aculeatus</i> , L.	...	...	...	...	vr (1)
<i>Salix aurita</i> , L.	...	...	...	...	f-r
„ <i>caprea</i> , L.	...	...	...	...	f-r
„ <i>cinerea</i> , L.	...	...	...	...	f-r
<i>Sambucus nigra</i> , L.	...	...	...	...	r-lc (in damp chalky depressions)
<i>Solanum dulcamara</i> , L.	...	...	...	...	f, edge
<i>Viburnum opulus</i> , L.	...	...	...	...	vr

The symbols employed are as follows: d, dominant; sd, sub-dominant; ab, abundant; vc, very common; c, common; fc, fairly common; f, frequent; o, occasional; rr, rather rare; r, rare; vr, very rare; l, local. A number in brackets indicates the number of woods in which the species has been observed when not of general occurrence.

the Hornbeam is present as the dominant and that in which the Bramble is dominant.

The Rubus fruticosus society. A study of the water-content, humus-content, mechanical structure, and light-intensity of the soils of the areas dominated by *Rubus fruticosus* (cf. Tables II, III, IV, and V) indicates a wide range of conditions. Thus whilst the average water-content is about 28.5 % different localities, even during the winter-months, show a variation of between 23 % and 38 %. The organic material too ranges in amount from 5.46 % to 12.2 %. Evidently then the *Rubus* society is not related to any very restricted edaphic conditions and we must seek an explanation for its dominance in other causes. The *Rubus* society often occupies large areas and the dominant species is accompanied by Honeysuckle, sometimes in considerable quantity, and Bracken which is often common. Other frequent species are *Holcus mollis*, *Anemone nemorosa*, and *Oxalis acetosella*. But with these exceptions shrubs and herbs are alike rare. A careful examination of these areas will however often reveal the remains of old stools, in various stages of decay, that bear evidence to the presence here of a shrub-layer at no very distant date. An examination of coppiced or felled areas shows that in the first year after cutting Bramble seedlings appear in large numbers. In the normal course of development these grow for several years, but ultimately die as they become choked out by the shade effect of the sprouting stools. There can be little doubt that the influencing factor to bring about the establishment of the permanent *Rubus* society is the failure of the coppice to develop vigorous shoots, a failure that is brought about mainly by the rabbits which abound on these light soils, and which nibble the young shoots as they develop. Owing no doubt to the armature of prickles, the Bramble seedlings appear to be immune from the depredations of these animals.

Comparison of the light intensities here and in the *Pteris* society (cf. Table V) shows that most of the areas occupied by *Rubus* would in this respect be equally suitable for the Bracken. But whereas the Phanerogam colonises with remarkable rapidity both by seeds and vegetative spread, the Cryptogam but seldom produces prothalli in these woods and its rate of expansion by rhizomes is slower. Both have summer foliage which begins to develop towards the end of May, but can endure a diminution of the light during the Shade-Phase to about 10 %. Owing to the controlling influence of light occupation in a woodland is often a decisive factor, since the late comer has to combat the shade of its competitor as well as that cast by the trees and shrubs. The fact that *Pteris* and *Rubus* do sometimes occur together in the relation of co-dominants bears testimony to the remarkable capacity of the Bracken for waging this unequal warfare. It is however doubtful whether even this species is capable of making headway once the complete dominance of the other has become established. Probably *Pteris* has the advantage in drier situations, whilst *Rubus fruticosus* flourishes best where the soil is

naturally damper. This point is brought out by a comparison of the mechanical analyses (see Table II) from which it will be seen that in the same wood, although the composition of the soil from the two societies is similar, the proportion of fine particles is greater where the Bramble predominates. Finally we may note that although the two societies overlap to a considerable extent, the *Rubus* society extends into deeper shade, both as regards Light and Shade-Phases, than the Bracken society.

(c) *The Ground-flora*. The herbaceous vegetation is strikingly scanty, although embracing a comparatively large number of species. Except locally where the water-content is high (cf. *infra*), the continuous sheets of Wood Anemone, Hyacinth, Dog's Mercury, etc., which are such a feature on the Clay-with-flints, are conspicuously absent. We can however recognise several ground societies, dominated respectively by Bracken, Dog's Mercury, Ground Ivy, Lesser Celandine, and Hyacinth. From the viewpoint of area occupied the first is by far the most important and the three last comparatively insignificant. Here indeed, as in *Q. sessiliflora* woods elsewhere, the continuous sheets of Bracken fronds are the most salient feature. In only one wood, namely Wormley, does the Anemone become locally abundant, whilst typically it is rather rare. A complete list of the shade species is given in Table VII, and it will be seen that comparatively few species attain any degree of frequency, and this is usually of a purely local character. Apart from such species, which become important under special conditions, the more generally distributed are *Anemone nemorosa*, *Epilobium montanum*, *Holcus mollis*, *Luzula pilosa*, *Oxalis acetosella*, *Primula acaulis*, *Teucrium scorodonia*, *Viola sylvestris*, and the ubiquitous Bracken.

The Pteris society. This is the best represented society in the *Q. sessiliflora*-*Carpinus* woods, and often covers extensive areas. It is equivalent to the Mesopteridietum of Woodhead ("Ecology of Woodland Plants in the neighbourhood of Huddersfield," *Journ. Linn. Soc.*, vol. xxxvii, 1906; cf. also Wilson, *loc. cit.*, p. 886). Like the *Pteris* society, so characteristic of the *Q. sessiliflora* woods in Yorkshire, Somerset and Wales, it is poor in species, doubtless due largely to the shading effect of the Bracken. In summer the light beneath its foliage is under 8 % of the diffuse light intensity outside. Even the vernal species do not flourish here, as they are unable to benefit greatly by the Light-Phase owing to the persistence of the dead fronds. The latter are indeed probably as efficient a means of eliminating serious competitions as a rosette habit (cf. Lindman, *New Phytologist*, vol. xii, 1913). The Bracken society typically occurs where the shrub-layer is very sparse, the light intensity during the Light-Phase is from 50-90 %, and during the Shade-Phase is relatively high (cf. Table V). Woodhead (*loc. cit.*, p. 338) noted the same tendency of the Bracken to become abundant where the shrub-layer was sparse in the woods of the Huddersfield district. Here, as there, this condition has probably been brought about through the action of rabbits.

TABLE VII. *List of Species comprising the Shade-Flora*

<i>Adoxa moschatellina</i> , L.	...	...	...	lf (2) (Ficaria-soc.)
<i>Ajuga reptans</i> , L.	...	...	...	lf-lc (Mercurialis-soc.)
<i>Anemone nemorosa</i> , L.	...	...	...	rr-lc
<i>Arctium nemorosum</i> , Lej.	...	...	...	vr
<i>Arenaria trinervia</i> , L.	...	...	...	r
<i>Arum maculatum</i> , L.	...	...	...	o-lc (Mercurialis- and Ficaria-soc.)
<i>Asperula odorata</i> , L.	...	...	...	rr-lf
<i>Athyrium filix-foemina</i> , Roth.	...	...	...	vr
<i>Blechnum spicant</i> , With.	...	...	...	l (2)
<i>Carex pendula</i> , Huds.	...	...	...	vr
„ <i>sylvatica</i> , Huds.	...	...	...	r
<i>Circaea lutetiana</i> , L.	...	...	...	r
<i>Conopodium denudatum</i> , Koch	...	...	...	r-rr
<i>Convallaria majalis</i> , L.	...	...	...	vr (3), probably extinct except in one
<i>Epilobium montanum</i> , L.	...	...	...	o
<i>Epipactis violacea</i> , Bor.	...	...	...	r
<i>Equisetum maximum</i> , Lamk.	...	...	...	l (2)
„ „ var. <i>serotinum</i> , Braun	...	...	...	(1)
<i>Euphorbia amygdaloides</i> , L.	...	...	...	rr (lf, 1)
<i>Ficaria verna</i> , DC.	...	...	...	r-lc
<i>Fragaria vesca</i> , L.	...	...	...	rr
<i>Galeobdolon luteum</i> , Huds.	...	...	...	rr-f
<i>Geum urbanum</i> , L.	...	...	...	vr
<i>Holcus mollis</i> , L.	...	...	...	e-r
<i>Listera ovata</i> , Br.	...	...	...	rr
<i>Luzula maxima</i> , DC.	...	...	...	r-f (3)
„ <i>pilosa</i> , Willd.	...	...	...	o-f
<i>Lycopodium clavatum</i> , L.	...	...	...	(Broxbourne, 1855, now extinct)
<i>Mercurialis perennis</i> , L.	...	...	...	l. ab-rr
<i>Narcissus pseudo-narcissus</i> , L.	...	...	...	lr (1)
<i>Neottia nidus-avis</i> , L.	...	...	...	vr (1)
<i>Nepeta glechoma</i> , Benth.	...	...	...	o-l. ab
<i>Nephrodium dilatatum</i> , Desv.	...	...	...	vr (1)
„ <i>filix-mas</i> , Rich.	...	...	...	rr-vr
„ <i>montanum</i> , Baker	...	...	...	vr (2)
„ <i>spinulosum</i> , Desv.	...	...	...	vr (1)
<i>Orchis mascula</i> , L.	...	...	...	r
<i>Oxalis acetosella</i> , L.	...	...	...	o-f
<i>Paris quadrifolia</i> , L.	...	...	...	r (2)
<i>Primula acaulis</i> , L.	...	...	...	r-f
<i>Pteris aquilina</i> , L.	...	...	...	rc-l. ab
<i>Ranunculus auricomus</i> , L.	...	...	...	lr, damper parts
<i>Rumex condylodes</i> , Biberstein	...	...	...	r-lf
<i>Sanicula europaea</i> , L.	...	...	...	rr-f (Mercurialis- and Ficaria-soc.)
<i>Scilla nutans</i> , Sm.	...	...	...	rr (la, 1)
<i>Scrophularia nodosa</i> , L.	...	...	...	vr
<i>Sedum telephium</i> , L.	...	...	...	r (1)
<i>Teucrium scorodonia</i> , L.	...	...	...	o-f
<i>Veronica montana</i> , L.	...	...	...	rr
<i>Viola riviniana</i> , Reichb.	...	...	...	r-f
„ „ „ <i>f. nemorosa</i> , Neuman	...	...	...	r
„ <i>sylvestris</i> , Kitt.	...	...	...	r-o
„ „ „ var. <i>punctata</i> , Greg.	...	...	...	r-fc

It is probable that the Ferns were formerly more abundant and more generally distributed than at present.

Except where the Bracken only occurs as scattered individuals, the light intensity during the Shade-Phase does not fall below 11 % (cf. Table V), but occasional plants are met with at intensities of as low as 4.1 %. This harmonises with the minimum illumination which Wiesner gives for this plant, namely $L = 1/60$, a value which corresponds to about 5 % of maximum diffuse illumination (Wiesner, J., *Lichtgenuss d. Pflanzen*, p. 165, Leipzig, 1907).

The distribution of the Bracken in these woods corresponds then with that observed by Woodhead and is doubtless correlated with the late development of the assimilatory organs which begin to appear above the ground at about the inception of the Shade-Phase (i.e. middle of May).

The *Pteris* society usually exhibits a natural water-content of about 28.5 % though even in summer this may be as high as 45 % and in winter as low as 25 % (cf. Table IV). But it must be noted that the soil of this society exhibits an unusually high organic content (cf. Table III), ranging from 5.00 % to 15.76 % (average 9.92 %). The accumulation of peat in the upper layers of the soil produced by the Bracken itself may reach a depth of from 5 to 6 in. To this is almost entirely due the large water-content and its extreme variability. That this is the case is shown by the mechanical analyses (cf. Table II) from which it is clear that the *Pteris* society is characteristic of soil with a smaller proportion of silt and clay than in any other society except that dominated by *Scilla nutans*. In the latter, however, *Pteris aquilina* is also common. Here then as in the *Q. robur* woods it may be said that the Bracken occupies areas which, either owing to their configuration or the organic constitution of the soil, are naturally dry and acid. (Acidity .42-.52, Acidity-humus ratio 1:8.8-1:14.1.)

The more characteristic associates of the Bracken are *Rubus fruticosus*, agg. (c), *Lonicera periclymenum* (f-vc), *Teucrium scorodonia* (lf), *Scilla nutans* (lf-r), *Anemone nemorosa* (r-f), and *Holcus mollis* (c), the last-named species in the better-lighted parts.

The Scilla nutans society. This society which is probably to be regarded as a sub-society of that dominated by Bracken occupies one or two very limited areas in Sherrard's Wood, where the soil is derived from the Reading Beds and contains a very high proportion of pebbles. It is particularly rich in coarse particles and deficient in silt and clay (cf. Table II). In addition the humus and water-content are especially low. The *Scilla* society is probably a local variant of the *Pteris* society in which the comparative scarcity of Bracken and abundance of the vernal species are largely the effect of a diminished light-intensity during the Shade-Phase (cf. Table V). The only conspicuous accompanying species, apart from the Bracken, are *Holcus mollis* and *Galeobdolon luteum*. The extremely pebbly character of the soil here is the more surprising in view of Wilson's observations (*loc. cit.*, p. 894) that *Scilla nutans* was absent from very pebbly areas.

The Nepeta glechoma society. Like the preceding this is of local occurrence in Sherrard's Wood and one other. In the former area however several acres are occupied by an unprecedented growth of the Ground Ivy, with which are associated the Dog's Mercury (fc), and the Bugle (f-rr). The soil exhibits a slightly higher humus-content (about 7 %), and a larger proportion of silt and clay than in the *Scilla* society. The low summer water-content is to be attributed to the topographical position of this society. The light-intensity

during the Shade-Phase is probably too low to permit of the growth of Bracken, but nevertheless sufficiently high to admit of an ombrophilous species with persistent foliage becoming dominant.

The Mercurialis society. As in the *Q. robur-Carpinus* woods this society is restricted to situations that are either damp or, when relatively dry, where the soil covering the chalk is shallow. Typically the slopes of the depressions and valleys in these woods are almost always occupied by this society (cf. Fig. 1) which merges below into that dominated by *Ficaria verna*. The light-intensity is low, exhibiting an average of about 42 % during the Light-Phase and of about 4 % during the Shade-Phase. The humus-content of the soil varies between 6.32 % and 19.4 % (cf. Table III), but as a rule is distinctly lower than where the Bracken predominates. The mechanical analysis (see Table II) also indicates that the high water-content here, av. 31 %, is largely an outcome of the physical structure of the soil; thus in Brock's Wood the

FIG. 2. Profile, Brock's Wood. Showing the occurrence of *Rubus* and *Pteris* on the high ground and *Mercurialis* in the valley. Surveyed by A. H. Salisbury, M.S.A.

Mercurialis society has a soil with an average of 38.24 % of silt and clay, whilst the adjoining *Pteris* society has only 17.76 %. In Titnol's Wood the water-content in this society was only 27.4 %, as compared with 53.4 % in Symond's Hyde Wood on the same day. But this low water-content is associated with a low acidity which even after coppicing only amounts to 0.3 %. The facts of distribution here then confirm the view expressed (Part II, p. 104), that the occurrence of *Mercurialis perennis* is mainly conditioned by the low acidity of the soil-solution (31). However, low acidity is often associated with a higher mineral content, a factor that may also play its part in the determination of distribution.

Common associates of the Dog's Mercury are the Bugle and the Ground Ivy. In addition Wood Sorrel, Yellow Deadnettle, Strawberry, Wood Violet, Primrose, Enchanter's Nightshade, Wood Sanicle, and *Veronica montana* are sometimes frequent. *Sanicula europaea* and *Fragaria vesca* are particularly met with in this society when the soil above the chalk is shallow.

The Ficaria verna society. Damp hollows and the floors of the valleys where the shade in the summer is considerable and, owing to the topographical

relations, the soil is always damp in spring, are generally occupied by a society in which the dominant species is *Ficaria verna*. Where the illumination during the Shade-Phase is higher *Mercurialis perennis* becomes frequent and the two societies merge almost imperceptibly the one into the other. As in the *Q. robur* woods, *Arum maculatum* is a frequent associate of *Ficaria*, whilst *Ranunculus auricomus* is confined to this society, though of rare occurrence. The acidity is even lower than in the last society (cf. Table IV).

A sub-society is encountered in two of these woods where there are damp hollows with but a shallow soil in close proximity to the chalk (acidity nil). These are characterised by the frequency or even co-dominance of *Adoxa moschatellina* (cf. Part II, p. 104). Very common constituents of this society are various Hypnaceous Mosses, particularly the unattached form of *Eurhynchium praelongum*, whilst in one wood *Porotrichum alopecurum* is frequent. The light-intensity is about the same as that of the *Mercurialis* society during the Light-Phase, but during the Shade-Phase is somewhat lower.

The Path society. The considerable illumination (cf. Table V) of the paths which even during the Shade-Phase ranges from over 5 % to as much as 21 % (or under exceptional conditions even higher) enables but slightly ombrophilous species to compete here with the more specialised woodland types. Partly as a consequence of this and partly owing to the high water-content and low acidity we find a flora not merely rich in individuals, but comprising more than 80 species. The paths and rides in these woods are very wet in winter and moist even in summer. The humus-content is not particularly high, 7.44—10.7 %, but the percentage of silt and clay is large and comparable to that of the *Q. robur*-*Carpinus* woods (cf. Table III). Usually the path exhibits a higher water-content than any of the other societies, with an average of about 35.6 %. Associated with this fact and the frequent inundation of the paths in autumn we find that the two most characteristic species are the land-form of *Callitriche stagnalis* (vc-f) and *Polygonum hydropiper* (fc-l. ab). The other important species are damp-loving plants, of which may be mentioned *Nepeta glechoma* (fc-vc), *Prunella vulgaris* (c), *Poa annua* (f-l. ab), *Fragaria vesca* (f-c), *Gnaphalium uliginosum* (f-fc), *Galium palustre* (f-c), *Eysimachia nemorum* (c-vc), *Geum urbanum* (c), *Mentha arvensis* (o-c), *Ranunculus repens* (o-c), *Circaea lutetiana* (f-lc), *Juncus bufonius* (lf-fc), *Ajuga reptans* (f-c), *Stellaria uliginosa* (f), *Peplis portula* (lf-c), *Oxalis acetosella* (f-l. vc), and *Mercurialis perennis* (f). In the woods on the London Clay *Cardamine flexuosa* is also a prominent constituent of this society. The presence of both the Enchanter's Nightshade and the Dog's Mercury can be related to the low acidity, and we may remark that many of the more abundant species of the *Q. robur* woods are here almost confined to the path society. It is interesting to note that where these damp paths and rides are deeply shaded there is a carpet of vegetation dominated by Crypto-

gams, especially Mosses. This condition recalls the dominant Cryptogamic flora in the deep shade of many of the wet steep-side valleys of Yorkshire, Somerset, and Wales, occupied by woods of *Q. sessiliflora* (cf. Moss, in *Types of British Vegetation*, p. 138; Salisbury, *Proc. Linn. Soc.*, loc. cit.).

Very locally a dry type of path is located where the soil is gravelly and where the vegetation is comparable to that of a gravel heath. The characteristic species of such situations are *Veronica officinalis*, *Galium saxatile*, *Alchemilla arvensis*, *Hypericum humifusum*, and *Rumex acetosella*. This is such a definite type of vegetation that it may be convenient to designate it by the name of the *Alchemilla arvensis* society, since that species is the most symptomatic of these special conditions. It may here be noted that the particular form of *Alchemilla arvensis* is that found on gravel heaths and is usually an erect and often but little branched plant.

The Anemone society. This society only occurs in the woods of this type on the London Clay and there it is strictly local.

TABLE VIII. *Path and Marginal Species and Coppiced Flora*

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Aegopodium podagraria</i> , L.	... l	—	—
<i>Agrimonia eupatorium</i> , L.	... r	—	r
<i>Agrostis alba</i> , L.	... f-vc	—	f-c
„ <i>canina</i> , L.	... —	—	rr
„ <i>vulgaris</i> , With.	... —	—	r
<i>Aira caespitosa</i> , L.	... lf	vr	—
„ <i>flexuosa</i> , L.	... r	—	—
<i>Ajuga reptans</i> , L.	... f	f-c	f-c
<i>Alchemilla arvensis</i> , Scop.	... —	l (drier parts)	—
„ <i>vulgaris</i> , L.	... —	o	—
<i>Anagallis arvensis</i> , L.	... —	—	o (1)
<i>Anemone nemorosa</i> , L.	... o	—	—
<i>Angelica sylvestris</i> , L.	... r-f (3)	—	—
<i>Anthoxanthum odoratum</i> , L.	... —	o	f-vc
„ „ var. <i>villosum</i> , Lois.	o	o	o-lf
<i>Anthriscus sylvestris</i> , Hoffm.	... f	—	—
<i>Aquilegia vulgaris</i> , L.	... r (2), now apparently extinct	—	—
<i>Arctium nemorosum</i> , Lej.	... f-rr	—	o-f
<i>Arenaria serpyllifolia</i> , L.	... —	—	r (1)
„ <i>trinervia</i> , L.	... o	r	f-c
<i>Arrhenatherum avenaceum</i> , Beauv.	... o	—	—
<i>Arum maculatum</i> , L.	... lf	—	o
<i>Asperula odorata</i> , L.	... c-f	r-rr	r-f
<i>Atropa belladonna</i> , L.	... vr (1)	—	—
<i>Barbarea vulgaris</i> , Br.	... —	—	rr
„ „ var. <i>arcuata</i> , Reichb.	—	—	r (1)
<i>Bellis perennis</i> , L.	... —	r	—
<i>Brachypodium sylvaticum</i> , R. and S.	... lf-f	—	—
<i>Bryonia dioica</i> , Jacq.	... o	—	—
<i>Calamintha clinopodium</i> , Benth.	... f	f	—
<i>Calamagrostis epigeios</i> , Roth.	... rr (3)	—	—
<i>Callitriche stagnalis</i> , Scop.	... —	vc-f	l
<i>Campanula latifolia</i> , L., f. <i>alba</i>	... vr (1)	—	—
<i>Cardamine flexuosa</i> , With.	... f	f (on London Clay)	—
„ <i>pratensis</i> , L.	... —	—	vr (1)
<i>Carex binervis</i> , Sm.	... r (2)	—	—
„ <i>divulsa</i> , Good.	... r (2)	—	—
„ <i>glauca</i> , Scop.	... l (1)	—	—

TABLE VIII (*continued*)

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Carex lepidocarpa</i> , Tausch ...	... l (1)	—	—
„ <i>leporina</i> , L. ...	... lf (1)	—	—
„ <i>pallescent</i> , L. ...	... o-lc	—	r-f
„ <i>pendula</i> , Huds. ...	... lf-f	1 (specially on London Clay	—
„ <i>pilulifera</i> , L. ...	... o	—	o
„ <i>pseudo-cyperus</i> , L. ...	... r (2)	—	—
„ <i>remota</i> , L. ...	... o (1)	—	—
„ <i>strigosa</i> , Huds. ...	... r (on lighter soils)	—	—
„ <i>sylvatica</i> , Huds. ...	... o-rr	—	—
„ <i>vesicaria</i> , L. ...	... r (3)	—	—
„ <i>vulgaris</i> , Fries ...	... vr (1)	—	—
<i>Cerastium glomeratum</i> , Thuill. ...	... —	o (drier parts)	—
„ <i>vulgatum</i> , Fries ...	... —	r-f	r-vr
<i>Chaerophyllum temulum</i> , L. ...	... f	—	—
<i>Chrysosplenium oppositifolium</i> , L. ...	... lf (2) (by stream)	—	—
<i>Cicuta virosa</i> , L. ...	... lr (1)	—	—
<i>Circaea lutetiana</i> , L. ...	... o-lf	r-lc	r-rr (damp spots)
<i>Cnicus lanceolatus</i> , Hoffm. ...	... r-o	—	—
„ <i>palustris</i> , Hoffm. ...	... o-c	—	f-l. ab.
<i>Conium maculatum</i> , L. ...	... —	—	vr (near chalk)
<i>Conopodium denudatum</i> , Koch ...	... r-f	—	rr
<i>Crepis virens</i> , L. ...	... —	—	r
<i>Dactylis glomerata</i> , L. ...	... vr-f	—	—
<i>Digitalis purpurea</i> , L. ...	... r-lf (3)	—	l-c (3)
<i>Dipsacus sylvestris</i> , L. ...	... r	—	o
<i>Epilobium angustifolium</i> , L. ...	... r-f	—	o
„ <i>montanum</i> , L. ...	... f-c	r-f	r-c
„ <i>tetragonum</i> , L. ...	... r	r-o	r
„ <i>obscurum</i> , Schenk ...	... r	—	r
<i>Epipactis latifolia</i> , Sw. ...	... vr	—	—
„ <i>violacea</i> , Bor. ...	... r-vr	—	vr
<i>Erythraea centaureum</i> , Pers. ...	... —	r-f	f-vc
„ „ „ f. <i>alba</i> ...	... —	—	vr (1)
<i>Eupatorium cannabinum</i> , L. ...	... lf (2)	—	—
<i>Euphorbia amygdaloides</i> , L. ...	... rr-l	—	r-lc
<i>Euphrasia officinalis</i> , L. ...	... —	f-lf (2)	—
<i>Festuca gigantea</i> , Vill. ...	... lf (1) (damper spots)	—	—
„ <i>myurus</i> , L. ...	... —	—	o (1)
<i>Ficaria verna</i> , DC. ...	... r	r	—
<i>Fragaria vesca</i> , L. ...	... c-f	f-c	f-c
<i>Galeopsis tetrahit</i> , L. ...	... o (2)	—	o (2)
<i>Galeobdolon luteum</i> , Huds. ...	... f-lc	—	o-l. ab
<i>Galium aparine</i> , L. ...	... f	—	r
„ <i>mollugo</i> , L. ...	... o	—	—
„ <i>palustre</i> , L. ...	... —	f-c	o (damper spots)
„ <i>saxatile</i> , L. ...	... —	l-f (3) (dry parts)	—
<i>Genista tinctoria</i> , L. ...	... r-l (3)	—	—
<i>Geranium columbinum</i> , L. ...	... —	—	o (2)
„ <i>dissectum</i> , L. ...	... rr	—	r
„ <i>robertianum</i> , L. ...	... f	r	r
<i>Geum urbanum</i> , L. ...	... c-f	c	r-f
<i>Gnaphalium sylvaticum</i> , L. ...	... r (2)	—	r-lf (2)
„ <i>uliginosum</i> , L. ...	... f	f-fc	f
<i>Habenaria chlorantha</i> , Bab. ...	... —	—	r (3)
<i>Heracleum spondylium</i> , ...	... o-f	—	r
„ „ „ var. <i>angustifolium</i> , Huds. ...	... r	—	—
<i>Hieraceum boreale</i> , Fries, agg. ...	... o-f	r	—
<i>Holcus lanatus</i> , L. ...	... f	r	f-vc
„ <i>mollis</i> , L. ...	... o-c	—	f-c
<i>Hypericum androsaemum</i> , L. ...	... vr	—	—
„ <i>hirsutum</i> , L. ...	... r (1)	—	—
„ <i>humifusum</i> , L. ...	... —	lf	f-c
„ <i>perforatum</i> , L. ...	... f	—	f-lf
„ <i>pulchrum</i> , L. ...	... —	o (drier parts)	o-r

TABLE VIII (*continued*)

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Hypericum tetrapterum</i> , Fries ... (<i>H. quadrangulum</i> , L. pro parte) —	—	o-f	o-f (damper spots)
<i>Hypochaeris radicata</i> , L. ...	o	—	r
<i>Inula dysenterica</i> , Gaert. ...	l (1) (by stream)	—	—
<i>Juncus acutiflorus</i> , Ehrh. ...	—	l (2)	—
„ <i>bufonius</i> , L. ...	—	lf-fc	o
„ <i>conglomeratus</i> , L. ...	l. vc (1)	o	o-lc
„ <i>effusus</i> , L. ...	—	l	lf
„ <i>supinus</i> , Moench ...	—	(2)	—
<i>Lactuca muralis</i> , Fresen. ...	r (2)	—	—
<i>Lapsana communis</i> , L. ...	rr	—	r
<i>Lathyrus macrorhizus</i> , Wimm. ...	rr (3)	—	—
<i>Listera ovata</i> , Br. ...	—	vr (1)	—
<i>Lolium perenne</i> , L. ...	—	—	r (1)
<i>Lotus major</i> , Sm. ...	o-f	o	r
<i>Luzula maxima</i> , DC. ...	f-rr (3)	rr (3)	r-lf (3)
„ <i>multiflora</i> , Lej. ...	—	o	f-rr
„ „ „ var. <i>congesta</i> , Lej. ...	—	—	o-f
„ <i>pilosa</i> , Willd. ...	o-fc	o	o-fc
<i>Lychnis flos-cuculi</i> , L. ...	—	l	l-f (damp spots)
„ <i>vespertina</i> , Sibth. ...	r (1)	—	r (1)
<i>Lysimachia nemorum</i> , L. ...	—	c-vc	c-ab
„ <i>nummularia</i> , L. ...	—	o (?)	—
<i>Malva moschata</i> , L. ...	r	—	—
<i>Melampyrum pratense</i> , L. ...	o-f (1)	—	f
<i>Melica uniflora</i> , Retz. ...	lf-fc	r	—
<i>Mentha arvensis</i> , L. ...	r	o-c	o (damp spots)
„ <i>pubescens</i> , Willd. ...	f (1, damp places)	—	—
„ <i>sativa</i> , L. ...	r (2)	—	—
<i>Menyanthes trifoliata</i> , L. ...	r-lc (2)	(boggy places)	—
<i>Mercurialis perennis</i> , L. ...	f-lc	—	lc
<i>Milium effusum</i> , L. ...	o	o	—
<i>Molinia coerulea</i> , Moench ...	r (1)	—	—
<i>Montia fontana</i> , L. ...	—	l (2)	—
<i>Myosotis arvensis</i> , L. ...	—	—	rr
„ „ „ var. <i>umbrosa</i> , Bab. ...	vr (1)	—	—
„ <i>versicolor</i> , Sm. ...	—	r (1)	—
<i>Nepeta glechoma</i> , Benth. ...	f-c	f-vc	lc
<i>Nephrodium filix-mas</i> , Rich. ...	—	—	r
<i>Ophrys apifera</i> , Huds. ...	—	—	r (2)
„ <i>muscifera</i> , Huds. ...	r (2)	—	—
<i>Orchis maculata</i> , L. ...	o	o	—
„ <i>mascula</i> , L. ...	—	—	r-lf
<i>Oxalis acetosella</i> , L. ...	f	f-lc	—
<i>Pedicularis palustris</i> , L. ...	—	vr (1, formerly in 2)	—
„ <i>sylvatica</i> , L. ...	o (2)	—	—
<i>Peplis portula</i> , L. ...	—	lf-c	o
<i>Picris echioides</i> , L. ...	—	—	r (1)
<i>Plantago major</i> , L. ...	—	r-rr	r
<i>Poa annua</i> , L. ...	—	f-l. ab	o
„ <i>nemoralis</i> , L. ...	—	—	o
„ <i>pratensis</i> , L. ...	—	r (1)	o (1)
„ <i>trivialis</i> , L. ...	f	o	—
<i>Polygonum convolvulus</i> , var. <i>subulatum</i> , L. and C. ...	—	—	r (1)
<i>Polygonum hydropiper</i> , L. ...	—	fc-ab	lc
„ <i>lappathifolium</i> , L. ...	—	r (1)	—
„ <i>mite</i> , Schrank. ...	—	(1)	—
<i>Potentilla anserina</i> , L. ...	—	o (2)	—
„ „ „ f. <i>concolor</i> ...	—	(1)	—
„ <i>erecta</i> , Hampe ...	—	—	—
„ <i>fragariastrum</i> , Ehrh. ...	o-fc	—	o-f
„ <i>procumbens</i> , Sibth. ...	—	—	—
„ <i>reptans</i> , L. ...	—	r-rr (2)	—
	—	r-o	r

TABLE VIII (*continued*)

Species	Margin of woods and rides	Path	Coppiced Areas
<i>Primula acaulis</i> , L.	—	—	o
<i>Prunella vulgaris</i> , L.	f-r	f-c	r-f
„ „ <i>forma alba</i>	—	—	r (1)
<i>Pteris aquilina</i> , L.	fe	—	r-l. ab
<i>Ranunculus repens</i> , L.	o	o-c	o-vr
„ „ <i>flammula</i> , L.	—	l (1)	—
<i>Roseda lutea</i> , L.	—	—	r (1)
<i>Rubus fruticosus</i> (seedlings)	c	—	c-ab
<i>Rumex acetosa</i> , L.	o	—	o-f
„ „ <i>acetosella</i> , L.	—	lf (2)	l (1)
„ „ <i>condyloides</i> , Biberst.	o-lc	o	o-i
„ „ <i>conglomeratus</i> , Murr.	—	r (1)	—
„ „ <i>obtusifolius</i> , L.	r (1)	—	—
<i>Sagina procumbens</i> , L.	—	lf (2)	o
<i>Sanicula europaea</i> , L.	—	—	rr
<i>Scabiosa succisa</i> , L.	o-fc	r-f	—
<i>Scilla nutans</i> , Sm.	—	—	r-lc
<i>Scirpus setaceus</i> , L.	—	lr (2)	—
„ „ <i>sylvaticus</i> , L.	r (1)	—	—
<i>Scrophularia aquatica</i> , L.	l (1)	—	—
„ „ <i>nodosa</i> , L.	o	r	o
<i>Scutellaria galericulata</i> , L.	—	rr (1)	—
<i>Sedum telephium</i> , L.	r (1)	r (1)	—
„ „ „ <i>var. purpureum</i> , L.	vr (1)	—	—
<i>Senecio aquaticus</i> , Hill	l (1, by stream)	—	—
„ „ <i>jacobaea</i> , L.	r	r	rr
„ „ <i>sylvaticus</i> , L.	—	—	o
„ „ <i>vulgaris</i> , L.	—	—	r
<i>Serratula tinctoria</i> , L.	r (1)	—	—
<i>Silene inflata</i> , L.	—	—	r (1)
<i>Sison, amomum</i> , L.	rr	—	—
<i>Sisymbrium alliaria</i> , L.	o	—	—
<i>Solidago virg-aurea</i> , L.	r-f (3)	—	—
<i>Sonchus asper</i> , Hill	r	—	—
„ „ <i>oleraceus</i> , L.	r	—	—
<i>Spergula arvensis</i> , L.	—	—	r
<i>Stachys betonica</i> , Benth.	f-fc	r	—
„ „ <i>sylvatica</i> , L.	f	—	o
<i>Stellaria graminea</i> , L.	o (1)	—	—
„ „ <i>holostea</i> , L.	o-f	—	o
„ „ <i>media</i> , Vill.	—	—	r
„ „ <i>uliginosa</i> , Murr.	—	f (damper parts)	—
„ „ <i>umbrosa</i> , Opiz.	vr (1)	—	—
<i>Tamus communis</i> , L.	o-f	—	—
<i>Teucrium scorodonia</i> , L.	f-vc	—	rr-f
<i>Torilis anthriscus</i> , L.	f	—	o
<i>Trifolium minus</i> , Sm.	—	l (gravelly places)	—
<i>Triodia decumbens</i> , Beauv.	o (2)	—	—
<i>Urtica dioica</i> , L.	r-f	—	r
<i>Valeriana dioica</i> , L.	—	l (1)	—
„ „ <i>sambucifolia</i> , Mikan.	l (1)	—	—
<i>Verbascum thapsus</i> , L.	r	—	rr-lf
<i>Veronica beccabunga</i> , L.	—	lf (1)	—
„ „ <i>chamaedrys</i> , L.	c	f	f
„ „ <i>montana</i> , L.	—	f	f-fc (damper parts)
„ „ <i>officinalis</i> , L.	—	lf (drier parts)	f-fc
„ „ <i>serpyllifolia</i> , L.	—	o-f	r-rr
<i>Vicia angustifolia</i> , L.	r (1)	—	—
„ „ <i>sepium</i> , L.	f	—	—
<i>Viola hirta</i> , L.	l (1)	—	—
„ „ <i>riviniana</i> , L.	f	—	f
„ „ <i>sylvestris</i> , Kit.	f	—	f
„ „ „ <i>var. punctata</i> , Greg.	f	—	f-fc
Totals 227 spp. vars. and formae ...	146	87	117

The marginal society (cf. Table VIII). Owing to the high illumination in many parts of these woods during the Shade-Phase the distinction between the marginal region and the interior is much less marked than in the woods dealt with in Part II. On the other hand the large areas which many of the *Q. sessiliflora* woods occupy furnish sufficiently extended margins in various directions to enable the full effect of aspect to be clearly presented. The commonest members of the marginal flora are *Agrostis alba*, *Asperula odorata*, *Cnicus palustris*, *Digitalis purpurea*, *Epilobium montanum*, *Fragaria vesca*, *Geum urbanum*, *Heracleum sphondylium*, *Holcus mollis*, *Luzula pilosa*, *Melica uniflora*, *Nepeta glechoma*, *Poa nemoralis*, *Potentilla erecta*, *Pteris aquilina*, *Rumex condylodes*, *Scabiosa succisa*, *Stachys betonica*, and *Teucrium scorodonia*. Of these the most characteristic are the Devil's Bit Scabious, the Betony, Wood Sage, Tormantil, and, though less common, *Carex pallescens*, *C. pilulifera*, the Hawkweeds, and Greater Woodrush. Here too are found several rare species whose occurrence though not general is nevertheless significant. Such embrace *Aira flexuosa*, *Carex strigosa*, *Gnaphalium sylvaticum*, *Hypericum androsaemum*, *Lactuca muralis*, *Lathyrus macrorrhizus*, *Serratula tinctoria*, *Solidago virgaurea*, and *Triodia decumbens*.

(d) *The Flora of the Coppiced Wood*. As might be expected, the effect of coppicing in these woods is not nearly so pronounced as in the *Q. robur-Carpinus* woods. This is due in part to the more complete tree-canopy, and as a consequence areas in which the trees have been felled appear to offer a closer parallel. A comparison of the data given in Table IX with those for areas occupied by a shrub-layer shows that after coppicing there is an increase of the light-intensity during the Light-Phase of over 27 % and during the Shade-Phase of over 17·7 %. The degree of illumination during the latter, which exceeds 21·5 %, is the more important as so many of the constituents of the flora of coppiced areas are aestival species.

TABLE IX. *Light-intensities in Coppiced Areas*

Wood						Light-Phase %	Shade-Phase %
Sherrard's	...	...	...	...	...	80-62	20-10
Brock's	...	...	...	...	...	83-62	40 (av.)
Symond's Hyde	...	...	...	...	...	70-46·6	16·5 (av.)
Average	...	...	...	...	...	67·2	21·6
Approximate increase due to coppicing						+27·5	+17·7

Effects of coppicing. The first and most important effect of coppicing is the great increase of illumination, with consequent increase in the number of species. But in addition there is a marked effect upon the organic content of the surface layer and correlated change in its acidity. Here, as in the *Q. robur-Carpinus* woods, the effect on acidity is in the direction of increase which however would appear to be pronounced for only a short period (cf. Table XI). The observations of Cameron, Baumann and Gully and others have made it appear very probable that the so-called soil acidity is a phenomenon of

adsorption (cf. however E. Truvy, *Journ. Phys. Chem.*, 1916). If this be subsequently established then it must be assumed that the temporary increase of acidity which accompanies the diminution of organic matter is due to an increased adsorptive capacity consequent upon the more rapid decay. It is however easier to explain the results as due to the presence of an actual acid produced during the disintegrating process. The change in humus-content is very pronounced and from the data available (Table X) would seem to depend on a fairly regular diminution of the amount of humus present by approximately 1 % on the dry weight during each period of twelve months. After the first two years the humus-content seems to again increase, owing no doubt to the compensating effect of the developing stools.

TABLE X. *Effect of coppicing on Organic-content*

Wood	Condition	Organic matter %	Decrease %
Sherrard's	Uncoppiced	9.5	} 2
"	Coppiced (2 yrs.)	7.5	
"	Coppiced (3 yrs.)	8.56	} 0.94
"	Uncoppiced	7.34	
"	Coppiced and felled (2 yrs.)	5.8	} 1.54
Brock's	Uncoppiced	7	
"	Coppiced (1 yr.)	6.19	} 0.81
Symond's Hyde	Uncoppiced	6.6	
"	Coppiced (6 months)	6.1	} 0.5
Titnol's	Uncoppiced	6.32	
"	Coppiced (6 months)	5.7	} 0.62
Average uncoppiced		7.35	
Average coppiced		6.25	

TABLE XI. *Effect of coppicing on Acidity*

Wood	Condition	Acidity %	Acidity Humus
Sherrard's	Uncoppiced	0.564	1 : 17
"	Coppiced (2 yrs.)	0.464	1 : 16
"	Coppiced (3 yrs.)	0.58	1 : 14.6
Symond's Hyde	Uncoppiced	0.44	1 : 15
"	Coppiced (6 months)	0.51	1 : 12
Cox's	Uncoppiced	0.25	1 : 22
Titnol's	Coppiced (6 months)	0.30	1 : 19

The flora of coppiced areas. The flora of the coppiced areas comprises some 117 species which, as in the case of the *Q. robur-Carpinus* woods (cf. Part II, p. 112), are derived from three sources, namely (a) the original shade-flora; (b) species of the wood-margins and rides; (c) weeds. In the *Q. robur* woods 61.2 % of the species found in the coppiced areas belonged to the second category and the same preponderance is exhibited here. Out of the total of 117 species no less than 89, or 76 %, are found in the uncoppiced condition situated near the edges of the wood or along the paths and rides. Thirty-three species, or 29.2 %, are members of the shade-flora, though many of these are more especially found in the medium shade near the wood-margins. The weeds are only 13 in number and this low percentage (namely 11.1 %), as compared with 29.4 % in the coppiced areas of the *Q. robur* woods, is

mainly attributable to the smaller area of the latter and the consequent proximity of cultivated ground. In these woods one of the most striking features after coppicing is the abundance of Bramble seedlings which grow and persist for several years, but are finally choked out as the stools develop (cf. however, p. 29). The Honeysuckle too develops vigorously where unchecked by the Hornbeam and Brambles. The commonest constituents of the herbaceous vegetation in these areas are *Agrostis alba* (f-c), *Ajuga reptans* (f-c), *Anthoxanthum odoratum* (f-vc), *Arenaria trinervia* (f-c), *Erythraea centaureum* (f-vc), *Fragaria vesca* (f-c), *Galeobdolon luteum* (o-l. ab), *Holcus lanatus* (f-vc), *H. mollis* (f-c), *Hypericum humifusum* (f-c), *Lysimachia nemorum* (c-ab), *Veronica montana* (f-fc), and *V. officinalis* (f-fc). Of these the Centaury, the Soft Grass (*H. mollis*), the Heath St John's Wort and the Yellow Pimpernel are undoubtedly the most characteristic. Particularly noteworthy is the comparative rarity of the Cowwheat (*Melampyrum pratense*) and the Hemp Nettle (*Galeopsis tetrahit*), whilst the Marsh Thistle only attains abundance in the damper parts. The increased number of species in the interior of the woods which results from coppicing and felling is illustrated by the accompanying table. Felled areas as compared with those only coppiced show an appreciably augmented flora. The influence of the time-factor, though not very pronounced, is nevertheless evident.

TABLE XII. *Effect of felling and coppicing upon the number of species*

Wood	Number of species before coppicing	Number of species after coppicing		
		1st yr.	2nd yr.	3rd yr.
Sherrard's	11	25	31	—
Symond's Hyde	12	31	34	—
Sherrard's	(Felled and coppiced)	—	54	69

Compared with the woods on the Clay-with-flints there is a striking absence of those sheets of bloom furnished by such species as *Ficaria verna*, *Anemone nemorosa* and *Conopodium denudatum*. The paucity of the last named and of *Stellaria holostea* is particularly noteworthy. Here as in other oakwoods (cf. Part II, Table XVII, p. 113) certain members of the shade-flora, especially Brambles, Honeysuckle, Yellow Deadnettle, Bugle and Wild Strawberry, exhibit a pronounced increase correlated with the increased illumination, an augmented frequency which disappears with the growing pressure of competition. Those species therefore which normally occupy the shaded areas probably do so because there alone they can compete successfully with those plants which require greater illumination.

(e) *Colonisation*. Generally artificial restriction gives to the woodland periphery a sharply defined limit so that colonisation and consequent extension of the afforested area is seldom met with. Here and there however, where adjacent "rough" land has been allowed to develop naturally, scrub appears of which saplings of *Betula* are a prominent and often abundant constituent.

Such scrub is seen in an intermediate condition at Bricket Wood Scrubs, in an advanced stage at Hertford Heath, and in an early phase on the south-west border of Wormley Wood. As the two former have already been described by the present writer (*Ecology of Scrub, loc. cit.*) they need not be considered in detail here. It is however important to recognise the fact that the herbaceous flora in these areas of scrub is remarkably similar to that of the wood margin of the *Q. sessiliflora*-*Carpinus* woods, and the same is true with regard to the scrub on Clay-with-flints and the marginal flora of the *Quercus robur* woods. All the three areas quoted above are very wet even in summer and this may perhaps account for the rarity of young trees of *Q. sessiliflora*, for we have noted how in woods of this species the Common Oak tends to become prevalent in the damper hollows. The same edaphic feature is probably responsible for the large proportion of Hazel accompanying the Hornbeam. But even having regard to these departures from the normal it may be said that the scrub-covered areas do tend to emphasise the natural character of the plant aggregates which we have here recognised.

The wet character of the rides in these woods which has often been emphasised above makes it scarcely surprising that *Fraxinus excelsior* is often a conspicuous coloniser where these are allowed to become overgrown.

Areas which have been coppiced sometimes exhibit numerous seedlings of *Populus tremula* and these give rise to the local thickets of this tree found in the uncut wood.

Seedlings of either species of Oak are comparatively scarce, and this is largely a result of the prevalence of rabbits on these light soils. In Wormley Wood where the soil is heavier and too damp to be suitable for these rodents, Oak saplings are frequent. But usually seedlings of the Common Oak are more prevalent than those of the Durmast Oak which is probably to be attributed to the freer fruiting of the former.

(5) **The Cryptogamic Flora**

(a) *Musci*. Most of the Mosses common in these woods are also frequent in those dominated by the Common Oak, though *Polytrichum formosum*, *Dicranum scoparium*, and *Fissidens bryoides* are generally more abundant. Of those species that appear to be especially characteristic may be mentioned *Dicranella heteromella*, *Leucobryum glaucum*, *Mnium punctatum*, *Polytrichum juniperinum*, and in one wood *Tetraphis pellucida*¹ and *Plagiothecium undulatum*. The Moss-flora is as a whole richer both in species and individuals than in the woods of Common Oak. The abundance of *Dicranella heteromella* is a noteworthy feature of the sides of the woodland streamlets. In such situations it grows in great abundance together with the Liverwort *Calypogeia fissa*² and forms a definite cryptogamic society. The damper and more shaded

¹ Kessler (*Beih. z. Bot. Centralbl.* **31**, pp. 358–387, 1914) has shown that the spores of *Tetraphis pellucida* will only germinate in an acid medium.

² This species is characteristic of the *Q. sessiliflora* woods of Somerset.

parts of these woods are frequently occupied by a Moss-society composed of most of the commoner species (cf. Table XIII). This may be regarded as the parallel, under conditions of lower rainfall, to the cryptogamic ground-flora of the *Q. sessiliflora*-woods in the coombs and gills of Somerset and

TABLE XIII. *List of Musci*

Amblystegium serpens, Bruch and Schimper	...	r (1)
Anomodon viticulosus, Hook. and Tayl.	...	o (1)
Aulacomnium androgynum	...	o
Barbula fallax, Hedw.	...	vr (1)
Brachythecium albicans, B. and S.	...	(1)
" purum, Dixon	...	fc-c
" rutabulum, B. and S.	...	f
Bryum pendulum, Schimp.	...	o (1)
Camptothecium sericeum, Kindb.	...	r (1)
†Catharina undulata, W. and M.	...	c-vc
Dicranella heteromella, Schimp.	...	c-ab
" rufescens, Schimp.	...	f-c
§Dicranum scoparium, Hedw.	...	f-fc
Eurhynchium confertum, Milde	...	(1)
" myurum, Dixon	...	o
" piliferum, B. and S.	...	o-f
" praelongum, Hobkirk	...	lc-c
" rusciforme, Milde	...	f
" striatum, B. and S.	...	f-lc
" swartzii, Hobkirk	...	l
Fissidens bryoides, Hedw.	...	o-lc
" taxifolius, Hedw.	...	r-lc
Homalia trichomanoides, B. and S.	...	lf-r
Hylocomium splendens, B. and S.	...	f
Hypnum cordifolium, Hedw.	...	l (1)
† " cuspidatum, L.	...	l
" cupressiforme, L.	...	c
" " var. resupinatum, Schimp.	...	r
† " schreberi, Willd.	...	f
" squarrosus, L.	...	f-c (path)
" triquetrum, L.	...	l-f
†Leucobryum glaucum, Schimp.	...	lf (Pteris society)
Mnium affine, Bland	...	l. vc (1)
† " hornum, L.	...	c
" punctatum, L.	...	l-lf
" undulatum, L.	...	rr
Orthotrichum affine, Schrad.	...	rr
§Plagiothecium denticulatum, B. and S.	...	rr-c
" elegans, Schull	...	f
" sylvaticum, B. and S.	...	o
† " undulatum, B. and S.	...	rr (1)
Pleuridium subulatum, Rabenh.	...	l (1)
†Polytrichum aloides, Hedw.	...	l (1)
§ " formosum, Hedw.	...	c
" juniperinum, Willd.	...	lc
" nanum, Neck	...	rr (1)
Porotrichum alopecurum, Mitt.	...	lf-l. ab (1) (Ficaria-Adoxa society)
Sphagnum cymbifolium, Ehrh.	...	l (2)
†§Tetraphis pellucida, Hedw.	...	rr (1)
Thuidium tamariscinum, B. and S.	...	f-c

The species marked with a dagger (†) are stated by Watson (*New Phytologist*, vol. VIII, p. 92) to be characteristic of the Oakwoods of Somerset (? *Q. sessiliflora*). Those marked § are characteristic of the *Q. sessiliflora* woods of Derbyshire (cf. Moss, *l.c.*).

Yorkshire, which is likewise developed where the light-intensity is low and the water-content high. *Eurhynchium praelongum* is particularly frequent where the chalk is close to the surface and there too the unattached form of *Porotrichum alopecurum* is sometimes abundant.

(b) *Hepaticae*. The often abundant Liverwort-flora is a marked contrast to the meagre occurrence of these plants on the Clay-with-flints. This increase is probably to be attributed to the more open texture of the soil and the proximity of the permanent water-table. The most frequent species are: *Alicularia scalaris*, *Aplozia crenulata*, *Calypogeia fissa*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Lophocolea bidentata*, *L. heterophylla*, *Pellia fabbroniana*, *Plagiochila asplenoides* var. *humilis*, and *Scapania nemorosa*. The last two species are usually most frequent in the *Dicranella-Calypogeia* society mentioned above. In no case has *Metzgeria furcata* or *Radula complanata* been encountered in a wood of this type, although the former is quite common on the tree-trunks of the *Q. robur* woods and the latter is not infrequent. *Madotheca platyphylla* which occurs in the *Q. robur* woods is here confined to the tree trunks where the soil has a low acidity. 33 species of *Hepaticae* have been recorded (cf. Table XIV) in all. This is a small number as compared with the Hepatic flora in the *Q. sessiliflora* woods of the West, but considerably in excess of that in the Derbyshire woods (viz. 21 spp., cf. Moss, *loc. cit.*).

TABLE XIV. *List of Liverworts*

<i>Alicularia scalaris</i> , Corda	...	...	...	lf-c
* <i>Aneura multifida</i> L.	...	...	...	(1)
<i>Aplozia crenulata</i> , Dum.	...	...	...	f-c
" " var. <i>gracillima</i> , Sm.	...	...	...	f
" <i>sphaerocarpa</i> , Dum.	...	...	...	r (1)
<i>Calypogeia fissa</i> , Raddi	...	...	...	vc-lf
" <i>trichomanis</i> , Corda	...	...	...	r (2)
<i>Cephalozia bicuspidata</i> , Dum.	...	...	...	c-f
* " <i>byssacea</i> , Warnst.	...	...	...	(2)
<i>Chiloscyphus pallescens</i> , Dum.	...	...	...	r (1)
" <i>polyanthus</i> , Corda	...	...	...	f-absent
<i>Conocephalum conicum</i> , Dum.	...	...	...	c (1)
<i>Diplophyllum albicans</i> , Dum.	...	...	...	vc-f
<i>Eucalyx hyalinus</i> , Breidel	...	...	...	r-f (3)
<i>Fossombronina pusilla</i> , Dum.	...	...	...	rr-f
<i>Frullania dilatata</i> , Dum.	...	...	...	vr (3)
" <i>tamarisci</i> , Dum.	...	...	...	vr (2)
* <i>Lejeunia cavifolia</i> , Lindb.	...	...	...	(2)
<i>Lepidozia reptans</i> , Dum.	...	...	...	rr (2)
<i>Lophocolea alata</i> , Mitt.	...	...	...	o-r (2)
" <i>bidentata</i> , Dum.	...	...	...	c-f
" <i>heterophylla</i> , Dum.	...	...	...	f-c
* <i>Lophozia incisa</i> , Dum.	...	...	...	(1)
<i>Madotheca platyphylla</i> , Dum.	...	...	...	r (1)
<i>Pellia epiphylla</i> , Corda	...	...	...	r
" <i>fabbroniana</i> , Raddi	...	...	...	lc-f
<i>Plagiochila asplenoides</i> , var. <i>humilis</i> , Lindb.	...	...	...	lf-c
<i>Riccia crystallina</i> , L.	...	...	...	r (1)
" <i>sorocarpa</i> , Bisch.	...	...	...	lr (1)
* <i>Riccocarpus natans</i> , Corda	...	...	...	r (1)
<i>Scapania curta</i> , Dum.	...	...	...	vr (1)
" <i>dentata</i> , Dum.	...	...	...	l (1)
" <i>irrigua</i> , Dum.	...	...	...	f (1)
" <i>nemorosa</i> , Dum.	...	...	...	c-rr
" <i>undulata</i> , Dum.	...	...	...	r (2)
* <i>Trichocolea tomentella</i> , Dum.	...	...	...	r (1)

* These six species were recorded from one or two woods of this type by the late Mr A. E. Gibbs ("List of Hertfordshire Hepatics," *Trans. Herts. Nat. Hist. Soc.*, vol. VII, pp. 233-236, 1893) but have not been observed by the writer. It is therefore probable that they are all of rare or very local occurrence. See also Salisbury, "New records of Hertfordshire Hepatics," *Trans. Herts. Nat. Hist. Soc.*, vol. XVI, pt 4, 1917.

(c) *Algae*. In the *Q. robur-Carpinus* woods the only common terri-colous Alga is *Hormidium flaccidum*, A. Br., which species also occurs in the *Q. sessiliflora* woods. The commonest and most characteristic Alga of the latter however upon the paths and rides is *Zygnema ericetorum*, Hansg. (cf. Fritsch, "Morphology and Ecology of *Zygnema ericetorum*," *Annals of Botany*, vol. xxx, pp. 135-149, 1916), often associated with the liverwort *Alicularia scalaris*. *Mesotaenium violascens*, De Bary, and the *Dactylococcus*-stage of *Scenedesmus obliquus*, Kuetz., are sparsely met with, particularly amongst the leaves of *Bryum*, upon the ground, or amongst Mosses such as *Homalia* and *Hypnum*, upon the tree-trunks. Here too *Gloeocystis vesiculosa*, Naeg., is sometimes encountered. The algal flora may therefore be said to resemble that of heaths (cf. Fritsch and Salisbury, "Further Observations on the Heath Association on Hindhead Common," *New Phytol.*, vol. xiv, p. 134, 1915). One rare Alga, namely *Microcoleus vaginatus*, Gom., is locally frequent upon the paths in a wood of this type situated upon the Boulder Clay.

In view of the high acidity of the soil of these woods it is significant that the algal flora is strikingly similar to that described by Petersen as characteristic of soils with an acid reaction ("Stud. over Danske Aerofile Alger," *Mem. de l'Acad. Roy. d. Sc. et d. Lettr. de Danemark*, t. xii, p. 360, 1915). Moreover, the greater abundance of *Hormidium flaccidum* in the *Q. robur* woods is also in conformity with the characteristic frequency of species of this genus on neutral or alkaline soils. Very few Diatoms have been observed, a sparsity which Petersen noted in the woods and forests of Denmark and which may be an outcome of the prevailing high acidity.

(d) *Lichens*. The members of this group have only been extensively collected in Sherrard's Park and Symond's Hyde Woods. The frequencies apply to the former of these areas only, but with regard to the commoner species a wider application can in most cases be assumed. For the identifications I am entirely indebted to Mr R. Paulson, F.L.S. It may be safely asserted that the Lichen-flora of these woods is much richer than that of the *Q. robur-Carpinus* woods, for not only are there fewer species in the latter, but such as occur are more sparingly distributed.

TABLE XV. *List of Lichens.*

Calcium hyperellum, Ach.	...	...	...	o
Cladonia digitata, var. denticulata, Hoffm.	...	...	...	vr
„ furcata, Hoffm.	...	...	...	lf
„ macilenta, Hoffm.	...	...	...	ab
„ pyxidata, Fr.	...	...	...	lf
„ squamosa, Hoffm.	...	...	...	o
Evernia prunastri, Ach.	...	...	...	c
Graphis elegans, Ach.	...	...	...	c
Lecanora albella, Ach.	...	...	...	vc
„ chlarona, Nyl.	...	...	...	o
„ parella, var. turneri, Nyl.	...	...	...	o
„ rugosa, Nyl.	...	...	...	r
„ varia, Ach.	...	...	...	ab

TABLE XV (*continued*)

<i>Lecidea griffithsii</i> , Masul	...	...	...	...	r
„ <i>quernea</i> , Ach.	...	...	...	...	
„ <i>uliginosa</i> , Ach.	...	...	...	...	
<i>Opegrapha herpetica</i> , Ach.	...	...	...	...	r
<i>Parmelia borrieri</i> , Turn.	...	...	...	...	rr
„ <i>caperata</i> , Ach.	...	...	...	...	c
„ <i>fuliginosa</i> , var. <i>laetevirens</i> , Nyl.	...	...	...	...	c
„ <i>physodes</i> , var. <i>labrosa</i> , Ach.	...	...	...	...	vc
„ <i>saxatilis</i> , Ach.	...	...	...	...	c
„ <i>sulcata</i> , Tayl.	...	...	...	...	f
<i>Peltigera spuria</i> , Leight.	...	...	...	...	lf
„ <i>polydactyla</i>	...	...	...	...	lf
<i>Pertusaria amara</i> , Nyl.	...	...	...	...	c
„ <i>communis</i> , DC	...	...	...	...	f
„ <i>globulifera</i> , Nyl.	...	...	...	...	o
„ <i>wulfenii</i> , DC.	...	...	...	...	rr
<i>Platysma glaucum</i> , Nyl.	...	...	...	...	o
<i>Thelotrema lepadinum</i> , Ach.	...	...	...	...	f
<i>Usnea florida</i> , Ach.	...	...	...	...	c
„ <i>hirta</i> , Hoffm.	...	...	...	...	f
<i>Verrucaria viridula</i>	...	...	...	...	r

(The species referred to in Part I under the name of *Parmelia perlata* as occurring commonly in the *Q. robur* woods is probably *P. sulcata*.)

(e) *Fungi*. It is hoped to give subsequently in conjunction with Mr Ramsbottom a complete account of the Fungus-flora of these woods. The list of species will not therefore be given here. It should however be stated that, inclusive of those previously recorded (vide *Trans. Herts. Nat. Hist. Soc.* excursion lists), over 450 species have been observed in woods of this type. The character of the Fungus-flora is distinctive and far richer than that of the *Q. robur-Carpinus* woods. As indicative of its general facies it may be mentioned that the following species are a few of those generally distributed and appear to be more or less confined to the *Q. sessiliflora-Carpinus* woods, viz. *Boletus parasiticus*, *Craterellus cornucopoides*, *Nyctalis asterophora*, *N. parasitica*, *Scleroderma vulgare*, *Stropharia aeruginosus*, and *Thelephora laciniata*.

(f) *Mycetozoa*. The members of this group have not been studied, and the list of species in Table XVI recorded from the woods dealt with in this paper is extracted from the local lists and two communications by Mr J. Saunders in the *Transactions of the Hertfordshire Natural History Society*, vol. VII, pp. 144, 145, 1893 and vol. VIII, p. 71, 1895.

TABLE XVI. *List of Mycetozoa*

<i>Arcyria cinerea</i>	<i>Stemonitis ferruginea</i>
„ <i>incarnata</i>	<i>Trichia affinis</i>
<i>Fuligo septica</i>	„ <i>fragilis</i>
<i>Hemiarcyria clavata</i>	„ <i>jackii</i>
<i>Leocarpus fragilis</i>	„ <i>scabra</i>
<i>Lycogala epidendrum</i>	„ <i>varia</i>
<i>Physarum leucophaeum</i> .	

(6) **Fauna**

Rabbits are the only common mammals in these woods and they play an important rôle in determining the succession phases (see p. 29). The immunity of Bracken and Brambles from their ravages has been remarked and the same feature with regard to the former species was observed in the Breckland by Farrow (*Journal of Ecology*, vol. v, p. 6). Squirrels are not infrequent and often damage the shoots of young trees. There is no indication that any of the other larger animals directly affect the vegetation, though in a state of nature there can be little doubt that multiplication of the already frequent stoats would greatly diminish the effects of the rabbits.

Amongst the Lepidoptera *Tortrix viridiana* is often exceptionally abundant, and its larvae, which mainly attack the leaves of the Hornbeam, often reduce the assimilatory area of the latter by from 30–50 %.

Perhaps the most interesting aspect of the lower fauna is the poverty both of species and individuals, thus affording a parallel to the sparse flora. This feature is probably to be correlated with the prevalent high acidity. In this connection my friend Dr A. E. Boycott, F.R.S., has kindly made a comparison for me of the Molluscan fauna in two parts of Sherrard's Wood, viz. (1) in the *Q. sessiliflora-Carpinus* wood, and (2) from beneath Beech trees on the edge of the Oak Wood situated at the foot of the Reading Bed escarpment on the chalk outcrop. From the former habitat two species only were noted, viz., *Helix rotundata* and *Arion hortensis*, whilst from the latter no less than 18 species were observed. The number of Beetles, Spiders, etc., also showed a similar relation.

PART IV. COMPARATIVE RESULTS

Comparison of the *Q. robur-Carpinus* and *Q. sessiliflora-Carpinus* woods

(a) *Edaphic conditions.* A study of the data given in Tables IV, XI, Part II and Tables II and III, Part III, shows that the humus-content is lower (average for *Q. s.* = 8.5 %, for *Q. r.* = 10.4 %) and the proportion of silt and clay is smaller in the soil of the *Q. sessiliflora-Carpinus* woods than in that of the *Q. robur-Carpinus* woods. This naturally involves a diminished water-content, and estimations based on soil-samples taken from the two types on the same day (Table XVII) bear out such an assumption. Hence the ground-flora is essentially that of drier types of soil in spite of the close proximity of the water-table.

Moreover if we compare the average of all the estimations of water-content the woods of Common Oak show 33 % on the dry weight as compared with 29.5 % for the Durmast Oak woods.

TABLE XVII. *Water-contents of composite soil-samples, all collected on the same day after heavy rainfall (13/11/15)*

Locality	Type	Water-content %
Symond's Hyde ...	Q. sess.-Carp.	34.1
" " " " " "	" "	36.2
Titnol's " " " "	" "	24.5
Cox's " " " "	Q. sess.-Q. r.-Carp.	26.9
" " " " " "	" "	32.0
Langley " " " "	Q. robur-Carp. "	33.2
" " " " " "	" "	40.12
Cutt's Green " " " "	" "	40.30
" " " " " "	" "	40.20
Puddler's " " " "	" "	40.30
" " " " " "	" "	34.7
" " " " " "	" "	35.4

Av. 31.1

Av. 38.5

The absolute acidity of the two types irrespective of water-content shows 0.41 % for the *Q. sessiliflora* and 0.44 % for the *Q. robur* woods. But we have noted that the acidity-humus ratios indicate a higher acidity for the former, and if we divide the acidity by the average water-content in each case the result shows a very slightly higher acidity for the *Q. sessiliflora* woods. In this connection it is important to recognise the influence of the permanent water-table. It is well known that the present plane of permanent saturation in Hertfordshire is much lower than in times past, a fact sufficiently borne out by the obsolete and obsolescent streams. This implies that formerly the surface soil in the *Q. sessiliflora* woods was water-logged and consequently though the soil-solution would be more dilute this was doubtless more than compensated for by the absence of aeration. In these woods as on several of our commons (cf. Salisbury, *Trans. Herts. Nat. Hist. Soc.* vol. xv, p. 71, 1915) the decrease in amount of *Calluna* and the growing rarity of other peat-lovers is pronounced. At the time then when the present distribution of the two species of Oak was determined one may well suppose that the differences in acidity were more pronounced than now. The electrical resistances (cf. Table XVIII) of solutions obtained with distilled water from air-dried samples (cf. p. 23) indicate that the soluble mineral salts present are more abundant in the soils from *Q. robur* woods. In view of the very considerable dilution the difference in ionisation is most likely negligible. Hence we can probably regard the resistances so obtained as approximately inversely proportional to the percentage of electrolytes present. On this assumption the soluble salts in the soil of the *Q. robur* woods probably amount to over 50 % more than in that of the *Q. sessiliflora* woods.

(b) *Floristic differences. The trees and shrub-layers.* The following are present in the *Q. sessiliflora*-*Carpinus* woods, but absent from the *Q. robur*-*Carpinus* woods: *Populus alba*, *Pyrus communis*, *Rhamnus catharticus*, *R. frangula*, *Ribes rubrum*, *Rosa stylosa*, *R. tomentella*, and *R. tomentosa*. All of these are either very rare or rare, though *Rhamnus frangula* may be regarded as a characteristic species.

TABLE XVIII. *Electrical resistances of soil-solutions*

Locality	Type	Ground-flora	Resistance in ohms
Titnol's ...	Q. sess.-Carp.	Mercurialis dom.	1100
Symond's Hyde ...	" "	Pteris dom.	1100
Brock's ...	" " (coppiced)		1150-1550
Cow Heath ...	" "	Pteris dom.	1200
Sherrard's ...	" "	Nepeta dom.	1400
" ...	" "	Scilla dom.	1450
" ...	" "	Mercurialis dom.	1100
" ...	" "	Ficaria-Adoxa dom.	700
Pinner (Middlesex) ...	" "	Pteris dom.	1400
" " ...	" "	Dense shrub-layer	1550
Ball's ...	Q. robur-Carp.	Sparse	1500
Sauncy ...	" "	Anemone dom.	650-400
Ambrose ...	" "	Scilla-Mercurialis	700
Cutt's Green ...	" "	Anemone dom.	650
Average ...		{ Q. sess.-Carp. 1245	
		{ Q. robur-Carp. 780	

Of much more interest is the fact that several trees and shrubs found in the Oak woods of Hertfordshire are only met with in those of the Common Oak where the Durmast Oak is also present. Such are *Pyrus aucuparia*, *P. torminalis*, *Prunus insititia*, and *Viburnum opulus*, all, except the Bullace, species that occur characteristically in *Q. sessiliflora* woods elsewhere. The Holly, the Red Birch, and the Ling are all much more frequent than in the *Q. robur* woods. On the other hand *Prunus avium* is much less common and the Lime is usually absent. *Clematis vitalba*, which is local on the Clay-with-flints, in these woods is confined to the chalk-pits. The most striking feature is however undoubtedly the abundance of Brambles and Honeysuckle¹ which only attain any considerable frequency in those *Q. robur* woods where *Q. sessiliflora* is also present.

The ground-flora. In the herbaceous flora the distinctions are much more numerous. Some 56 species are met with in the woods of Durmast Oak, which are not present in the Common Oak woods, but the absence of some of these is doubtless purely accidental. Those probably to be regarded as characteristic and which are of frequent or common occurrence are: *Carex pallescens* (o-lc), *C. pendula* (lf-f); *Eupatorium cannabinum* (lf, 2), *Juncus bufonius* (lf-fc), *Lotus major* (o-f), *Luzula maxima* (f-rr), and *Polygonum hydropiper* (fc-ab). Other characteristic but uncommon species also absent from the *Q. robur*-*Carpinus* woods are *Aira flexuosa*, *Carex pilulifera*, *C. pseudo-cyperus*, *C. strigosa*, *Chrysosplenium oppositifolium*, *Menyanthes trifoliata*, *Molinia coerulea*, *Montia fontana*, *Nephrodium montanum*, *N. spinulosum*, *Pedicularis palustris*, *Potentilla procumbens*, *Scirpus setaceus*, *S. sylvaticus*, *Serratula tinctoria* and *Triodia decumbens*. Other species characteristic of the *Q. sessiliflora* woods though absent from the typical *Q. robur* woods are met with in those where *Q. sessiliflora* is also present. They include *Angelica sylvestris*, *Blechnum spicant*, *Callitriche stagnalis*, *Hypericum androsaemum*, *H. tetra-*

¹ This same feature is exhibited in the *Q. sessiliflora*-*Carpinus* woods at Pinner.

pterum, *Lathyrus macrorhizus*, *Luzula multiflora*, *Pedicularis sylvatica*, *Potentilla erecta*, *Scabiosa succisa*, *Scutellaria galericulata*, *Stellaria uliginosa*, and *Nephrodium dilatatum*. Several species show considerable differences in their frequency in the two types of wood (cf. Table XIX).

TABLE XIX. *Comparative Frequencies*(1) *More abundant in Q. robur-Carpinus woods:*

Species	Q. sess.-Carp.	Q. robur-Carp
* <i>Anemone nemorosa</i> ...	rr-lc	vc-ab
<i>Arenaria trinervia</i> (copp.) ...	f-c	c-vc
<i>Arum maculatum</i> ...	lf	f-c
<i>Barbarea vulgaris</i> (copp.) ...	rr	la
<i>Cnicus palustris</i> (copp.) ...	f-l. ab	c-vc
<i>Conopodium denudatum</i> ...	rr-f	f-vc
* <i>Dipsacus sylvestris</i> ...	o	rr-lc
<i>Ficaria verna</i> ...	r-l. ab	c-ab
<i>Galeopsis tetrahit</i> (copp.) ...	r	c-vc
<i>Geranium dissectum</i> ...	rr	f-c
<i>Hypochaeris radicata</i> ...	r-o	r-lc
* <i>Mercurialis perennis</i> ...	l. ab-rr	ab-vc
<i>Primula acaulis</i> ...	r-f	f-rr
<i>Ranunculus auricomus</i> ...	lr	fc-r
* <i>Sanicula europaea</i> ...	rr-f	f-vc
* <i>Scilla nutans</i> ...	rr-l. ab	ab
<i>Scrophularia nodosa</i> ...	o	o-f
<i>Sisymbrium alliaria</i> (edge) ...	o-r	f-c
<i>Stellaria holostea</i> (edge) ...	o-f	f-vc

Species marked * were found by Wilson (*loc. cit.*) to be either occasional or absent in the *Q. sessiliflora* woods of Surrey on the London Clay, but common in the *Q. robur* woods on the Clay-with-flints.

(2) *More abundant in the Q. sessiliflora-Carpinus woods:*

<i>Cardamine flexuosa</i> ...	f (London Clay)	r (1)
<i>Epilobium montanum</i> ...	f-c	o-f
<i>Erythraea centaureum</i> (copp.) ...	f-vc	f-c (light soils)
<i>Fragaria vesca</i> ...	c-f	f-r
<i>Galium palustre</i> ...	fc	o (1)
<i>Holcus mollis</i> (copp.) ...	f-c	r-vc (light soil)
<i>Hypericum humifusum</i> (copp.) ...	f-c	r
† „ <i>pulchrum</i> (copp.) ...	o-r	vr
„ <i>tetrapterum</i> ...	o-f	r
† <i>Luzula pilosa</i> ...	o-fc	o-f
<i>Lysimachia nemorum</i> (path and copp.)	c-ab	r-f
<i>Peplis portula</i> (path) ...	lf-c	o (1)
† <i>Pteris aquilina</i> ...	l. ab-o	r (ab. in 2)
† <i>Stachys betonica</i> (edge) ...	f	r
† <i>Teucrium scorodonia</i> ...	f-c	f
<i>Veronica officinalis</i> (path and copp.)	f-fc	r

Species marked † were found by Wilson to be occasional or absent in the *Q. robur* woods on clay-with-flints and common in the *Q. sessiliflora* woods on the London Clay.

About 50 species are present in the *Q. robur* woods which are absent or very rare in the *Q. sessiliflora* woods, but most of these are not of sufficient importance to particularise. The more characteristic are *Galeopsis ladanum*, *Geranium molle*, *Helleborus viridis*, *Iris foetidissima*, *Lychnis dioica*, *Melilotus officinalis*, *Pimpinella major*, *Plantago lanceolata*, *Polygonum aviculare*, *P. persicaria*, and *Solanum nigrum*.

The differences in the vegetation of the coppiced areas are equally striking, for whilst in the *Q. robur* woods *Cnicus palustris* and *Galeopsis tetrahit* are abundant, in the *Q. sessiliflora* woods these species occur but rarely. Other characteristic species of the former which are infrequent or rare in the coppiced areas of the latter are *Geranium dissectum*, *Barbarea vulgaris*, *Stellaria holostea*, *S. graminea*, *Dipsacus sylvestris*, and *Verbascum thapsus*. *Holcus lanatus* too is usually replaced in *Q. sessiliflora* woods by *Holcus mollis*. On the other hand *Hypericum humifusum*, *Lysimachia nemorum*, *Erythraea centaurium*, and *Veronica officinalis* are common here and infrequent in the *Q. robur* woods.

The foregoing floristic differences emphasise the calcicolous facies of the herbaceous flora in the *Q. robur* woods and its calcifugous character in the *Q. sessiliflora* woods. From this point of view it is interesting to note that R. W. Scully (*Flora of County Kerry*, pp. xlv–xlvi, Dublin, 1916) enumerates the following in his list of calcicole species: *Barbarea vulgaris*, *Sisymbrium alliaria*, *Arenaria trinervia*, *Pimpinella major* and *Verbascum thapsus*, all of which are much more frequent in the *Q. robur* woods. Again the following which are characteristic of the *Q. sessiliflora* woods are stated to be calcifuge: *Stellaria uliginosa*, *Montia fontana*, *Hypericum humifusum*, *H. pulchrum*, *Lathyrus macrorhizus*, *Potentilla erecta*, *Chrysosplenium oppositifolium*, *Peplis portula*, *Galium saxatile*, *Gnaphalium uliginosum*, *Calluna vulgaris*, *Menyanthes trifoliata*, *Digitalis purpurea*, *Pedicularis* spp., *Polygonum hydropiper*, *Luzula maxima*, *L. multiflora*, *Carex binervis*, *Molinia coerulea*, *Pteris aquilina*, *Blechnum spicant*, and *Nephrodium montanum*. The calcifuge tendency of both *Q. sessiliflora* and *Carpinus betulus* has already been dealt with, so that we see this aspect emphasised in trees, shrubs, and herbs alike. Indeed the *Q. robur-Corylus* woods, the *Q. robur-Carpinus* woods, and the *Q. sessiliflora-Carpinus* woods form a series in which the flora becomes more and more calcifuge in character. By the term calcifuge as used here it must however be understood that a distribution normally confined to siliceous soils is implied. It is probably pressure of competition rather than preference that is mainly responsible for the restriction of calcifuge species to siliceous soils.

(2) Comparison with other *Q. sessiliflora* woods

The most detailed account of the vegetation of *Q. sessiliflora* woods in this country is that given by Moss (*loc. cit.*) for those of Derbyshire. Comparison with the Hertfordshire woods shows that of the 231 native species enumerated by that author 73 are not represented in the *Q. sessiliflora* woods of Hertfordshire, whilst the flora of the latter includes 109 species which do not occur in the Derbyshire woods. Of the 153 species, exclusive of varieties, common to both, the most pronounced feature is the close correspondence exhibited by the frequencies in these two such widely separated counties: a fact which not only emphasises the natural character of the ecological

assemblage but also serves to indicate the importance of edaphic and biological as compared with minor climatic differences. The most important discrepancies between the frequencies of species found in the two regions are given in the following table.

TABLE XX. *Frequencies in Q. sessiliflora woods of Hertfordshire and Derbyshire*

Species	Hertfordshire	Peak District
<i>Agrostis vulgaris</i>	r	l. ab
<i>Aira flexuosa</i>	r	l. sd
<i>Ajuga reptans</i>	f-lc	l-o
<i>Anemone nemorosa</i>	rr-lf	l. ab
<i>Asperula odorata</i>	rr-f	l. ab
<i>Cardamine flexuosa</i>	f	o
<i>Carex pallescens</i>	o-lc	vr
<i>Chrysosplenium oppositifolium</i> ...	lf (2)	l. ab
<i>Epilobium montanum</i>	f-c	o
<i>Galeobdolon luteum</i>	f-c	o
<i>Galium aparine</i>	f	l. ab
<i>Hypericum perforatum</i>	f	r
<i>Luzula maxima</i>	rr-f	l. ab
<i>Lysimachia nemorum</i>	c	r-o
<i>Mercurialis perennis</i>	rr-l. ab	o
<i>Molinia coerulea</i>	r (1)	l. ab
<i>Nepeta glechoma</i>	fc	r-o
<i>Poa nemoralis</i>	fc-c	vr
<i>Athyrium filix-foemina</i>	vr	o-la
<i>Nephrodium montanum</i>	vr	l. ab

Of the species absent from the Derbyshire woods but present in those of Hertfordshire the great majority are of rare or uncommon occurrence, but those of greater frequency include *Agrostis alba*, *Brachypodium sylvaticum*, *Callitriche stagnalis*, *Erythraea centaureum*, *Eupatorium cannabinum*, *Euphorbia amygdaloides*, *Galium palustre*, *Gnaphalium uliginosum*, *Hypericum humifusum*, *H. tetrapterum*, *Luzula multiflora*, *Peplis portula*, *Poa annua*, *Polygonum hydropiper*, *Ranunculus repens*, *Scabiosa succisa*, *Stellaria uliginosa*, and *Veronica officinalis*. It will be noted that the most common of these are species characteristic of the paths and rides.

The more important species of the Peak district woods absent from those of Hertfordshire are *Carex laevigata*, *Equisetum sylvaticum*¹, *Geum rivale*, *Lychnis dioica*, *Myrrhis odorata*, *Petasites ovatus*, *Prunus padus*, and *Vaccinium myrtillus*. The remainder are either rare or only of local occurrence.

Finally we may note that many of the species common in the disused quarries, passing into *Q. sessiliflora* wood, described by Mr Margerison (Bradford, 1909), are those characteristic of the woods here dealt with (compare also Rübel, *New Phytol.* vol. XI, p. 55, 1912).

¹ In general species commonly associated with peaty soil are more frequent in the *Q. sessiliflora* woods of Derbyshire, Wales and Somerset, than in those of Hertfordshire. Indeed as might perhaps be expected the *Q. sessiliflora-Carpinus* woods exhibit a vegetation that has something in common with that of the lighter types of clays and so as it were connect the Durmast Oak woods of acid siliceous soils on the one hand with the *Q. robur-Corylus* woods of nearly neutral clays on the other.