Field Studies 5 (1980) 289-306

STAND STRUCTURE, SPECIES COMPOSITION AND SUCCESSION IN SOME SHROPSHIRE WOODS

By R. A. D. CAMERON
Department of Extramural Studies, University of Birmingham, PO Box 363, Birmingham 15

INTRODUCTION

THE sequence of events leading to the establishment of woodland on previously open ground, and the processes of regeneration inside established woods have long been subjects of study (Tansley 1949, and 1968, Grubb 1977). This paper reports on studies made in five Shropshire woodlands by adult students and volunteers attending courses at Preston Montford Field Centre and at Ludlow. Data on stand structure and species composition are used to examine the course of succession and regeneration in these woods. Four are ash or ash-elm woods characteristic of rich soils in northern and western England, the status and development of which have been the subject of much study (Tansley 1949, 1968, Scurfield 1959, Pigott 1969, Merton 1970). The other is a once-managed oakwood on dry acid soil, fitting midway between the dry soil variants of the two most acid oakwood types described by Steele (1974).

METHODS

The tree populations of the study areas were sampled using the point-centred quarter method of Cottam and Curtis (1956). This is one of a number of distance-measure methods discussed by Cottam and Curtis and was chosen because of the large amount of information gathered per sample point. Distance measures in general are much more economical in time and effort than quadrat sampling, but are subject to systematic errors in estimating density if the trees are not randomly distributed.

The area to be sampled is traversed in parallel lines (determined by compass) a set distance apart, and sample points are established at set distances along each line, usually with the interpoint and interline distances equal, so that the area is covered with a grid of sample points, (Figure 1a). At each sample point the wood around it is divided into quarters, using the line of traverse as the reference, and for the nearest tree to the sample point *in each quarter considered separately* (Figure 1b) distance to the sample point, species, and girth at chest height (1.5m) are recorded. In this study each traverse line was followed by a team of 3-4 students, and the results entered on a standard form. A systematic sampling technique of this sort may be more useful than a randomised one in forestry surveys (Finney 1948).

Steep slopes (occasionally precipitous) and dense understory made pinpoint accuracy impossible. Such errors are not serious unless they allow bias in selection of sampling points in relation to neighbouring trees.

The information obtained from this method has been used to study species and size distribution within each area, to estimate density thus:

$$\text{trees/hectare} = \frac{10{,}000}{\text{mean distance}^2\text{(m)}}$$

(Cottam and Curtis 1956) and also the per cent frequency and per cent total basal area for each species. Girth measurements have been used to study age and stand structure.

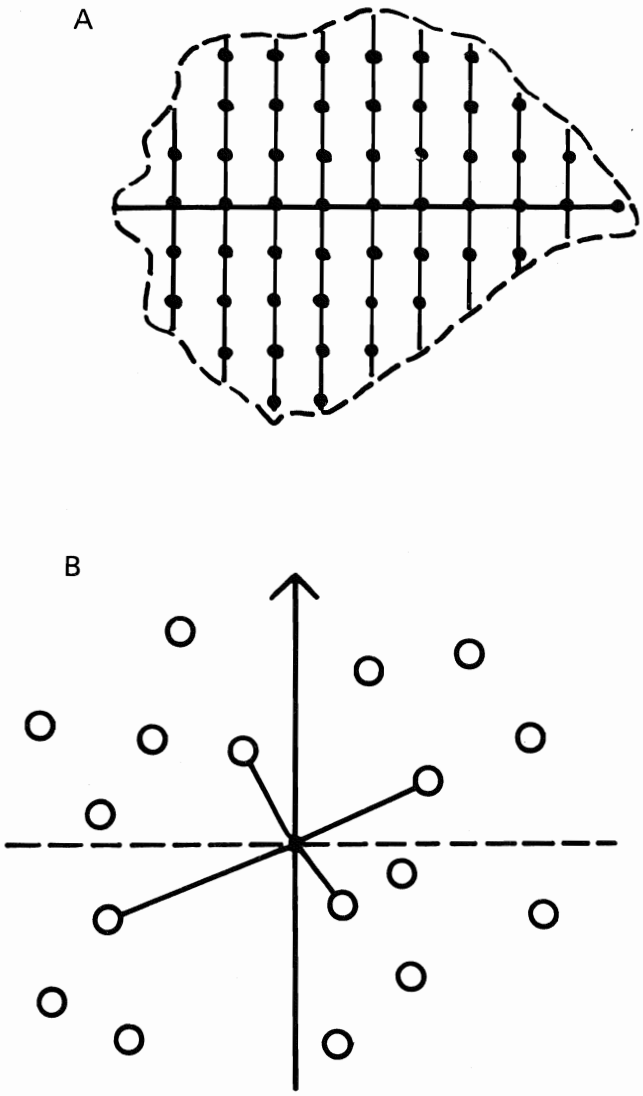

FIG. 1.
Survey methods. A: a grid of traverse-lines and sampling points based on a central base-line. B: tree recording; four quadrants defined by line of traverse (arrow) and distances to nearest tree in each quadrant.

Two conventions in recording caused problems in the study.

(i) Dead trees are usually ignored. In the ashwood at Earl's Hill in 1978 many wych elms were dying of Dutch elm disease. Only trees completely devoid of green leaves were ignored—we were concerned to describe the wood prior to the effects of the disease.

(ii) Minimum recordable girth is normally 15 cm, trunks below this size being ignored. Distance methods were devised for use in virgin forest or forestry plantations, and Cottam and Curtis do not mention procedures or conventions to be followed for multi-trunked specimens. In these study areas many trees and

shrubs have more than one trunk at chest height, as a consequence of coppicing, grazing damage or the natural growth form of the species. In such cases all trunks of greater than 10 cm girth are recorded for each tree and used in the calculation of basal area. A few hazel bushes had twenty or more densely packed stems; these were counted, and the girth of an "average" stem recorded for multiplication to obtain basal area. Errors involved in this simplification are small relative to the total basal area of each study area.

Other woody species noticed in passing were also recorded, and a list of species is given in the appendix with scientific nomenclature following Clapham, Tutin and Warburg (1968).

For some of the analysis, canopy trees are distinguished from shrubs by species, regardless of present size i.e.: those species which have the potential of forming part of the canopy of a mature wood. Inevitably, there are difficulties with some species and those included are indicated by asterisks in the tables. Inclusion of others (e.g. rowan, maple) has little effect on the results.

Full details of grid layouts etc, are available from the author, and are not published here.

The Study Sites and their History

Five study sites have been surveyed, all in south Shropshire (Figure 2). One is in and one adjacent to the Earl's Hill Nature Reserve near Pontesbury, and two more are on the southern slopes of Clee Hill near Knowle. One of the latter (Knowle Wood) is also a nature reserve, while the other (The Novers) is privately owned, as is the fifth site at Caynham Camp Wood near Ludlow.

1. *Earl's Hill ashwood*

The eastern slopes of Earl's Hill descend to the Habberley Brook. The upper slopes consist of scree, cliffs and grassland, descending through open scrub to woodland in various stages of development on the lower slopes. The area sampled is the most southerly portion of this woodland, bounded by a fence; it runs along the streamside for c.400m, and c.150m up the hill. This area contains most of the mature woodland on the slope, areas above and to the north of this being scrub. Except near the stream, slopes are steep (25°+). The soils are brown earths, becoming gleyed near the stream, and there is a marked catena, soil pH varying from c.5.0-5.5 at the top of the area to 7.0-7.5 at the base, a change mirrored in the ground flora, bracken *Pteridium aquilinum* and brambles *Rubus* spp. dominating at the top, and dog's mercury *Mercurialis perennis* and, locally, ramsons *Allium ursinum* at the base.

The area is not well documented, but the first edition of the Ordnance Survey (1832-3) shows these slopes unwooded, and with small-holdings (since vanished) c.1km to the north. Maps made in the early years of this century show the area as a mixture of trees and underwood. It is clear that in the late eighteenth century at least, the area was not wooded. Our sampling was done in June of 1976 and 1978.

2. *Oaks Wood*

The sample area lies on the eastern side of the Habberley Brook, opposite, but slightly north of, the Earl's Hill ashwood. These slopes lie on older and more acidic

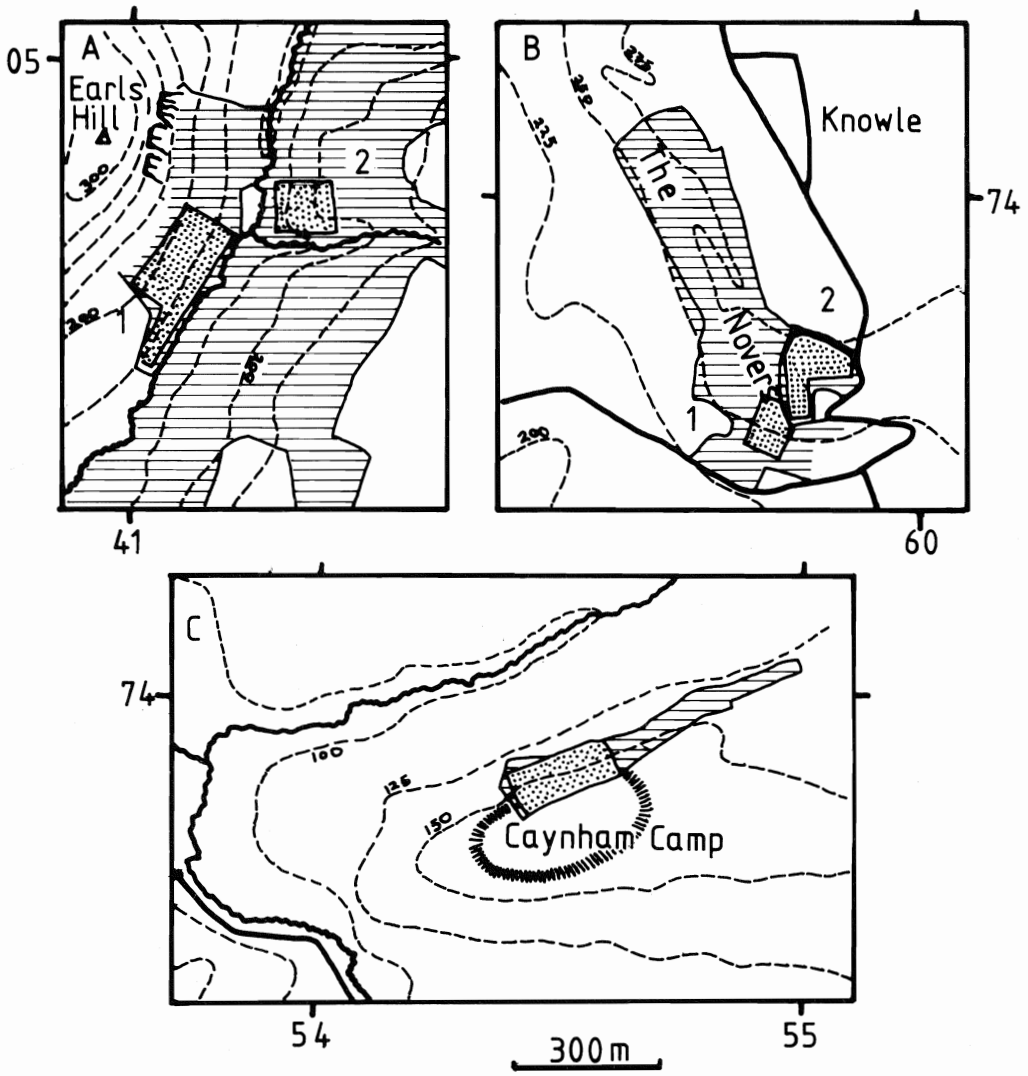

FIG. 2.
Maps showing location and extent of study sites. Ordnance Survey grid shown on margins, contours at 25m intervals, woodland and scrub hatched, study sites stippled. A: 1 Earl's Hill Ashwood, 2. Oaks Wood B: 1 The Novers, 2. Knowle Wood. C: Caynham Camp Wood.

rocks, and evidence from early maps indicates that the area has been wooded for many centuries.

Most of these slopes now carry conifer plantations, but a small area of once-managed oakwood remains, in which a sample area of about 250×200 m was studied.

Oaks Wood is distinct from all the others. It is the only one on a site known to have been wooded for many centuries, and yet its structure and species composition are more like that of a plantation than any of the others. The poor soil and absence of understory also distinguish it. The presence of old oak stumps, a diverse ground flora and the nearby large-leaved limes *Tilia platyphyllos* all suggest that plantation, if

it occurred, took place immediately after felling, and at unusually low density. Regeneration from coppice stools by allowing only one pole per stool to grow is likely (Rackham 1976), as there are many trees with decayed stumps much larger than the surviving boles. The oaks show hybrid characters; although a quantitative study has not been made, the proportion of *Quercus petraea* characters is high. All the oaks in the ashwood opposite are *Q. robur*.

The area can be divided into upper and lower parts. In the upper part, the soil is very thin (there are rock outcrops and crags) and the field layer has only sparse *Calluna vulgaris* and *Vaccinium myrtillus;* lower down the soils are deeper, with *Pteridium aquilinum* and, lower still, *Rubus spp*. The streamside vegetation (outside the survey area) includes *Mercurialis perennis* and *Allium ursinum,* and the trees and shrubs are similar to those in the ashwood on the opposite bank; the two wych elms in the survey area represent the upper limit of this richer community. Sampling was done in June of 1976 and 1978.

3. *The Novers and Knowle Wood*

These two areas are adjacent, and lie on an outcrop of Carboniferous limestone to the south of Clee Hill. The whole area was once extensively quarried and mined for lime, and remains of these workings are still visible all over the site. Lime works are marked on the 1832 Ordnance survey maps, and are still shown in maps made in the early years of this century.

The subsequent history of the two areas appears to be different. Parts of the Novers (especially in the north) and Knowle Wood were planted with conifers, but in many areas these failed, or were prematurely felled. In Knowle Wood, little or no grazing seems to have occurred, and extensive recent regeneration has produced a dense canopy cover. In the extreme south of the Novers (the area sampled), there has been some grazing pressure by sheep, which is still maintained, and there are some areas of pasture and open scrub.

A small area of the Novers, about 200×150m was sampled in May 1975, while all of Knowle Wood (total area c.4 ha) except a large central clearing was sampled in July 1977.

4. *Caynham Camp Wood*

This long strip of woodland lies on a north-facing slope immediately below the earthworks of Caynham Camp. The eastern end of the wood, with extensive plantings of beech, was not studied. The western end contains many limestone quarries; the lime works are shown on the Ordnance Survey first edition map. Trees are shown inside the earthworks on this map (the area is pasture now), but not on the site of the present wood. Maps from the earlier part of this century show the old workings with underwood, but larger trees are shown round the perimeter, and this situation prevails to the present day, with a ring of older (and more varied) trees surrounding a simpler and younger wood. An area of c.250×150m was sampled in June 1975, entirely in the interior of the wood.

Results

1. *Earl's Hill Ashwood*

Table 1 gives details of the survey results, and the Appendix the total woody plant flora observed. Although the number of species recorded is large, the wood can be

Table 1. *Survey results for the Earl's Hill ashwood * = canopy species (see text).*

Earl's Hill: Ashwood				
Species	nos.	%	Basal Area (m^2)	%
*Ash	38	19.0	6.66	26.3
*Wych Elm	39	19.5	9.96	39.3
*Alder	7	3.5	0.33	1.3
*Oak	5	2.5	2.41	9.5
*Larch	1	0.5	0.27	1.1
*Sycamore	1	0.5	0.003	—
Hawthorn	82	41.0	4.53	17.9
Hazel	3	1.5	0.30	1.2
Elder	19	9.5	0.23	0.9
Sallow	1	0.5	0.002	—
Crab Apple	1	0.5	0.36	1.4
Field Maple	1	0.5	0.23	0.9
Holly	1	0.5	0.02	—
Damson	1	0.5	0.02	—

Mean distance = 5.00±0.184m
Density = 400 trees/hectare (Confidence limits 347-466)
Basal area/hectare = 50.64m^2

described in terms of species composition as an ash-elm wood with a dense understory of hawthorn. Alder and oak are subsidiary species of the canopy, and elder of the understory. All other species make up only 5 per cent of the total. In terms of basal area a similar result is obtained, but the importance of the canopy species is emphasised: only 45.5 per cent of individuals, but 77.4 per cent of basal area are attributable to them. Wych elm is considerably more important than ash, and the few large oaks make a substantial contribution.

The only important spatial heterogeneity is between the lowest (streamside) traverse and the rest. The lowest traverse, on flat ground and often on gleyed soils has nearly all the alders (the others are associated with gleyed soil slightly higher up at a spring) and has a marked deficiency of large trees—there being only one tree over 2m girth compared with 21 in the other four traverses combined.

Figure 3 shows the girth size distributions of the major canopy species. For multi-trunked specimens only the largest trunk of each is entered—omitting these altogether does not affect the results substantially. Ash and wych elm have different distributions—ash showing a marked peak between 0.8 and 2.0m, while amongst the elms very small and larger trees are more frequent. There are no small oaks. If we assume a general relationship between age and girth (see below, discussion), then wych elm has had better regeneration in the recent past than ash, while oak appears to have failed completely.

Most of the hawthorns have girths between 0.4 and 0.8m, but a few are more than 1.0m and one exceptional tree has a girth of 2.1m.

2. *Oaks Wood*

The survey results are given in Table 2, and the Appendix lists all woody plants observed. The number of species recorded is small, and understory species are

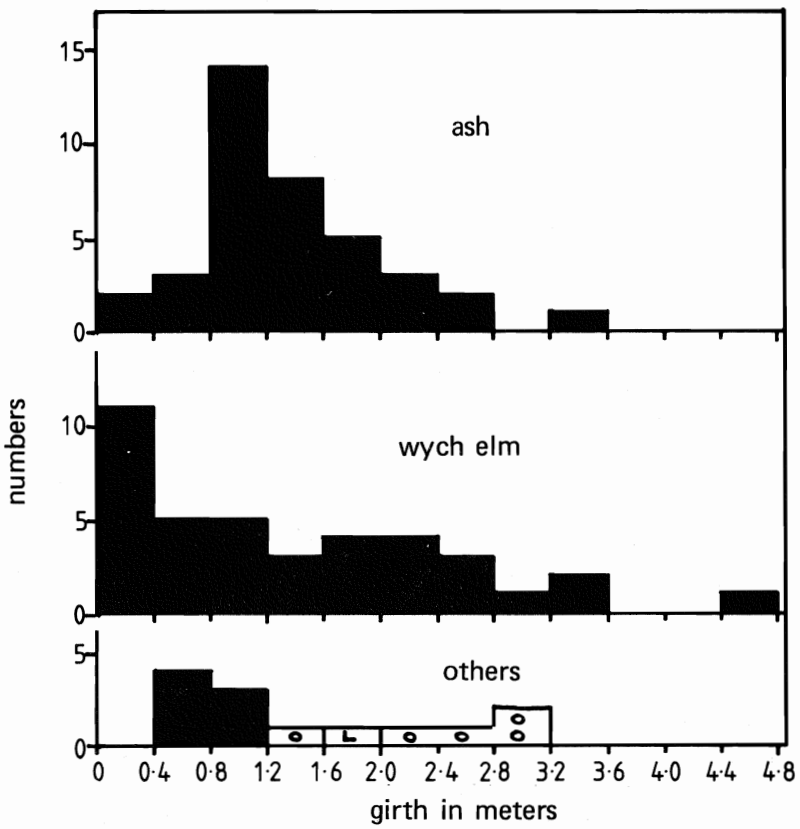

FIG. 3.
Earl's Hill ashwood. Distribution of girth-sizes of canopy trees. For others, black=alder, o=oak, 1=larch.

absent. Nearly 90 per cent of total basal area is oak, and silver birch is the only other species of any importance.

The upper and lower parts of the area surveyed differ in species composition and tree size distribution (Table 3). The oaks in the upper area are more frequent, and smaller in the upper area than in the lower, while the reverse is true for birch. Multi-boled oaks are also most frequent in the upper area.

Table 2. *Survey results for the Oaks Wood * = canopy species*

Oaks Wood				
Species	nos.	%	Basal Area (m^2)	%
*Oak	110	70.5	14.43	89.6
*Silver Birch	37	23.7	1.61	10.0
*Wych Elm	2	1.7	0.06	0.4
*Sycamore	1	0.8	0.002	
*Scots Pine	1	0.8	0.002	
Rowan	5	3.2	0.03	

Mean distance = 4.873m±0.201m
Density = 421 trees/hectare (Confidence limits 359-458)
Basal area/hectare = 43.45m^2

Table 3. *Oaks Wood. Differences between the upper and lower area in species composition and mean basal areas.*

	upper area			lower area		
Species	nos.	%	Mean basal area/tree (m^2)	nos.	%	Mean basal area/tree (m^2)
Oak	75	85	0.100	35	51.5	0.198
Silver Birch	10	11	0.063	27	40.0	0.036

Figure 4 shows the girth-size distributions of oak and birch separately for each area. There is little sign of oak regeneration in either area, and there is a marked peak of girth-size in each, that in the lower area being at a slightly greater girth. The lower area also has a few much larger oaks. With the exception of the latter, the size distribution of the oaks is consistent with their being an even-aged stand (see below, discussion). Birch has clearly been regenerating successfully in the lower area, but most birches in the upper area are older trees. Seedlings of other species, especially Scots pine, can be found especially along the southern boundary of the survey area, where the canopy is more open.

3. *The Novers*

Table 4 gives the survey results, and the Appendix the full list of woody species. Canopy species are less than a fifth of all individuals, and only comprise just over half the total basal area. There is considerable spatial heterogeneity in species distribution, with patches of pure hawthorn scrub and clearings intermixed with areas of canopy trees and a more diverse understory, the biggest of which in the north-east corner of the survey area, shows signs of being protected from grazing for much longer, and should properly be regarded as a part of Knowle Wood (see below).

Table 4. *Survey results for the Novers* * = *canopy species*

The Novers				
Species	nos.	%	Basal Area (m^2)	%
*Ash	4	3.7	0.82	13.0
*Wych Elm	13	12.1	2.44	40.0
*Silver Birch	1	0.9	0.02	0.3
*Norway Maple	1	0.9	0.003	—
Hawthorn	55	51.4	1.72	28.0
Hazel	19	17.8	0.53	9.0
Field Maple	7	6.5	0.39	6.0
Blackthorn	4	3.7	0.06	1.0
Sallow	1	0.9	0.02	0.3
Spindle	1	0.9	0.003	—
Holly	1	0.9	0.08	1.3

Mean distance = 4.073±0.253m
Density = 603 trees/hectare (Confidence limits 477-786)
Basal area/hectare = 34.5m^2

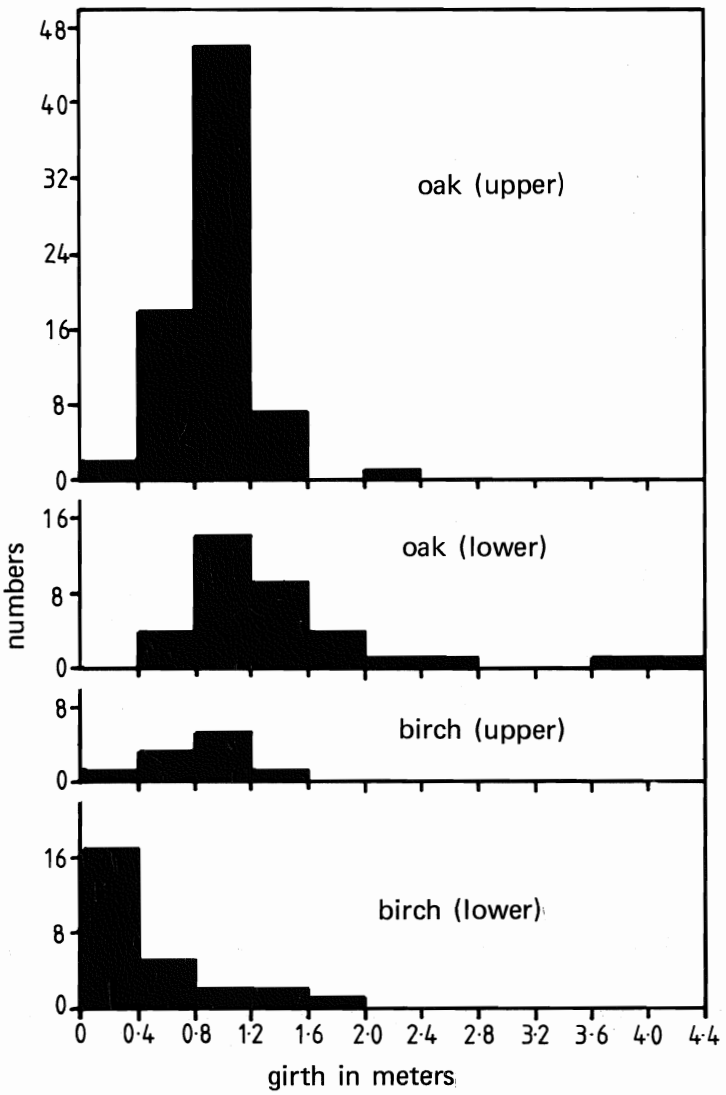

FIG. 4.
Oaks Wood. Distribution of girth-sizes of canopy trees in upper and lower parts of the wood (see text).

The girth-sizes of the few canopy trees are evenly distributed over the range 0.2-2.4m, suggesting a slow but continuous process of regeneration (see Figure 7 p. 302).

The areas of dense hawthorn scrub and grazed glades emphasise the importance of grazing pressure in the area. However the list of woody species is exceptionally rich, and even a very cursory survey of the ground-flora reveals 11 species which might be considered as indicators of ancient woodland (Peterken 1974).

4. *Knowle Wood*

Table 5 gives the survey results, and the Appendix the list of woody species. The sallows were not specifically identified. The wood has a great diversity of trees and shrubs with ash, Norway maple, wych elm and oak all abundant in the canopy (which also has many other species at lower frequencies), while the understory is dominated by hawthorn, hazel and sallows. The density of trees and bushes is very high. All parts of the wood have a high species diversity, but oaks are concentrated in the north-west quarter, and Norway maple in the southern and eastern areas.

Figure 5 shows the girth-size distributions of the principal species. There is a massive preponderance of young trees, especially amongst ash and Norway maples, implying simultaneous regeneration. There is a higher proportion of large trees amongst the oaks, and the subsidiary species (birch, yew, sallow) show a distinct deficiency of very small individuals. In all species, the numbers with girths less than 0.2m is very small, suggesting that regeneration is now on a very small scale.

5. *Caynham Camp Wood*

Table 6 gives the survey results, and the Appendix the list of woody species. Wych elm and ash dominate the canopy, and between them account for 96 per cent of the basal area, the few large wych elms increasing the dominance of that species. The understory in the centre of the wood is made up of small specimens of hazel, elder and hawthorn, but the woodland edge (not quantitatively surveyed) is much more diverse. Wych elm tends to predominate at the top of the hill, and ash (and alder) at the bottom.

Figure 6 shows the girth-size distributions for ash and wych elm. All the large trees are wych elm, and the peak girth sizes for younger trees are also higher than for ash. In both, trees of less than 0.4m girth are rare. Many trees of both species have multiple boles, often of a form which suggests cutting rather than grazing damage.

Table 5. *Survey results for Knowle Wood.* * = *canopy species*

Knowle Wood				
Species	nos.	%	Basal Area (m^2)	%
*Ash	26	18.7	0.68	13.6
*Wych Elm	12	8.6	0.47	9.4
*Norway Maple	20	14.4	0.83	16.6
*Oak	10	7.2	0.80	16.0
*Scots Pine	1	0.7	0.03	0.7
*Larch	3	2.2	0.30	6.1
*Yew	6	4.3	0.29	5.8
*Birch	6	4.3	0.20	4.0
Field Maple	2	1.4	0.03	0.6
Hazel	11	7.9	0.26	5.2
Hawthorn	16	11.5	0.36	7.2
Holly	6	4.3	0.17	3.4
Sallow	13	9.3	0.50	10.0
Blackthorn	3	2.2	0.01	0.2
Elder	3	2.2	0.07	1.3
Spindle	1	0.7	0.002	—

Mean distance = 3.197±0.183m
Density = 978 trees/hectare (Confidence limits 788-1248)
Basal area/hectare = 35.6m^2

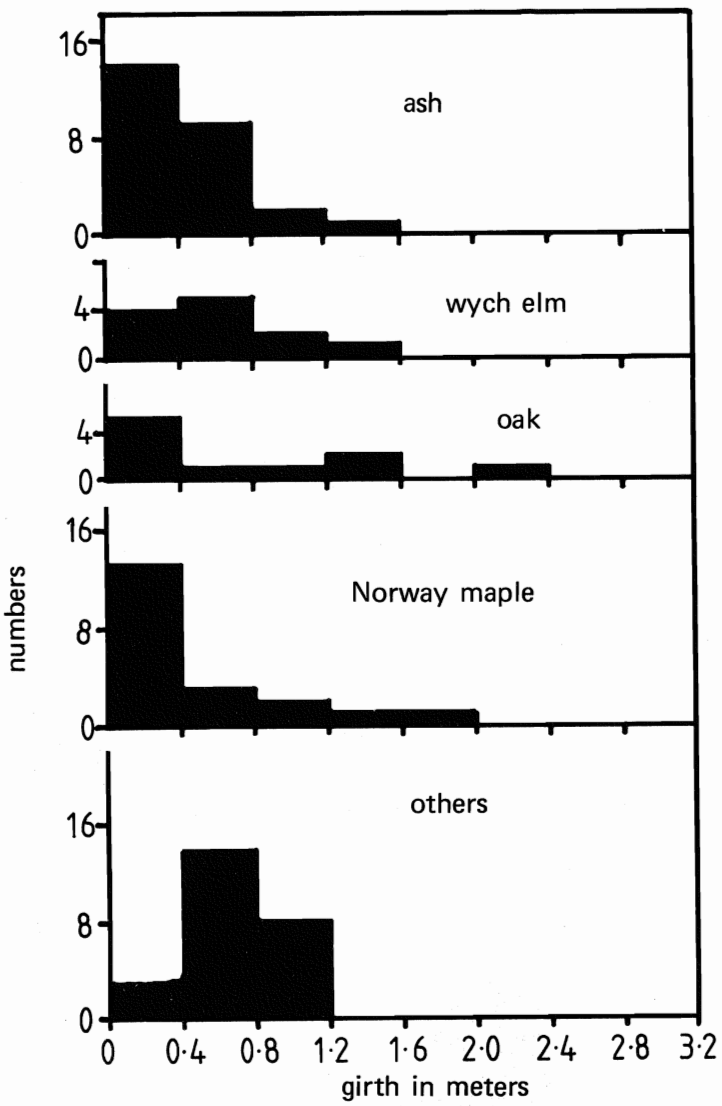

FIG. 5.
Knowle Wood. Distribution of girth-sizes of canopy trees. Others include silver birch, sallows and yew.

DISCUSSION

Oaks Wood is clearly distinct from the others. Although ancient, its appearance is that of a plantation, or, more probably a flush regeneration (Merton 1970) from coppice stools which have been singled, with a few larger survivors of an earlier clearance. The larger size of oaks in the lower area is probably a consequence of better soils and lower density rather than greater age. Ford and Newbould (1970) and Ford (1975) have shown that even aged stands tend to develop a size distribution which is both bimodal and positively skewed (with a larger tail towards larger values); this distribution is related to intraspecific competition. This population of oaks shows no sign of bimodality, and has a slight negative skew, suggesting some

Table 6. *Survey results for Caynham Camp Wood* * = *canopy species*

Caynham Camp Wood				
Species	nos.	%	Basal Area (m^2)	%
*Wych Elm	28	37	6.69	72
*Ash	23	30	2.29	24
*Alder	3	4	0.14	1.5
Hazel	7	9	0.06	0.5
Elder	9	12	0.06	0.5
Hawthorn	6	8	0.15	1.5

Mean distance = 3.752±0.231m
Density = 710 trees/hectare (Confidence limits 563-924)
Basal area/hectare = 89.5m^2

regeneration later than the main flush. This, and the free regeneration of birch under the oaks suggest that intraspecific competition has not been intense. Regeneration must have been from widely spaced stools, or from a plantation subject to heavy early mortality causing an unusually low stocking density.

The modal class of the flush regeneration has girths of 1.0 to 1.2m. Under optimum growth conditions this would suggest an age of 70-80 years for the present trunks but on this soil this is certainly a minimum, and 100 years is a more likely figure (Rackham 1976), while most of the birches would be between 20 and 50 years old.

In the lower part of the area, at least, birch appears to be increasing, while the population of oaks remains static. The soil is very suitable for birch (and for Scots pine, seedlings of which are developing fast) and this area may become an example of what Rackham (1976) calls reverse succession, from a presumed climax to a pioneer species.

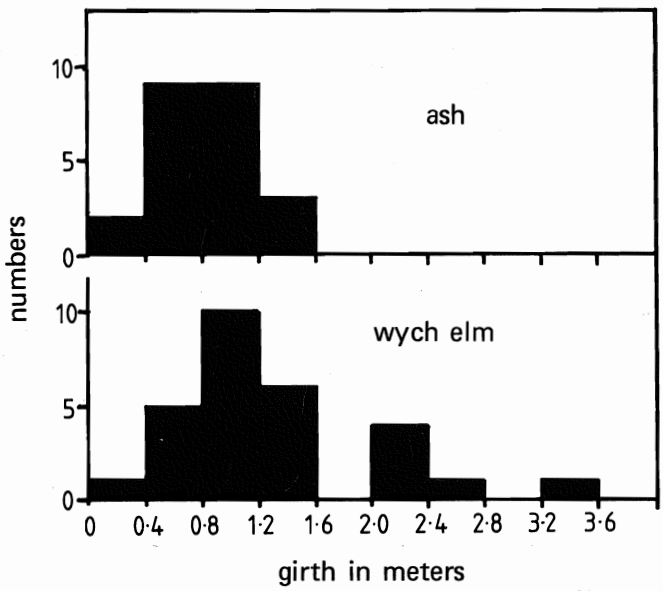

FIG. 6.
Caynham Camp Wood. Distribution of girth-sizes of canopy trees.

The other four woods share many features. All have ash and wych elm dominant in the canopy, and have several understory species in common. Three of the four are on limestone, on the sites of disused quarry workings, while Earl's Hill ashwood has more acid soils, and no evidence of quarrying. All four fit into the general class of ash-elm woods on base-rich soils (Tansley 1968, Merton 1970), which, in spite of earlier claims that they represent an edaphic climax (Tansley 1949) are now thought to be the result of a secondary succession from open grassland or limestone scree (Pigott 1969, Merton 1970). The latter view is confirmed by historical evidence in this case; none of the sites are marked as woodland on the first edition of the Ordnance Survey (1832 and 33), and physical evidence of quarrying remains in the three limestone sites. Knowle wood has been partially felled once since succession started, but it is clear that we are dealing with woods developing from one-time open ground.

In no case, however, is the succession straightforward. As is the case in some similar woods in the Peak District (Merton 1970) there are a few trees present which are clearly much older than the wood, some being at least 200 years old. Most of the oaks found at Knowle and Earl's Hill belong to this category. Such trees usually have a "pioneer' growth form, with branches spreading out from low down the trunk, indicating that they are not survivors of a once dense forest—a conclusion supported by the historical evidence. At Caynham Camp, such trees are mostly on the perimeter of the wood, but at Knowle and Earl's Hill they are widely distributed. Such trees indicate that grazing pressure or lime-working cannot always have prevented some succession or tree survival, and these survivors (and any understory shrubs associated with them) will have been important seed sources at the beginning of the present succession to full woodland cover.

Further botanical evidence supporting the idea that there was some woodland survival throughout the open phase includes the comparatively high frequency of hazel in the three limestone woods (Table 7) (Pollard 1973, Peterken 1974), while its comparative rarity in Earl's Hill ashwood suggests greater and more sustained grazing pressure there. Evidence from the herb layer points to the same conclusion—Earl's Hill ashwood is floristically poor, except near the stream (C. A. Sinker, *personal communication*) while at the Novers a single afternoon's recording revealed 11 species regarded as indicators of ancient woodland by Peterken (1974), although some of these may be less sensitive in the damper climate of the Marches than they are in the East Midlands. I do not have detailed floristic information for the other two woods, which in any case may have been impoverished at ground level by the very dense canopy resulting from flush regeneration.

Table 7. *Some features of the four ash-elm woods.*

	Earl's Hill Ashwood	Novers	Knowle	Caynham
Trees/hectare	400	603	978	710
Basal Area/hectare (m^2)	50.6	34.5	35.6	89.5
%canopy species—numbers	45	18	60	71
% canopy species—basal area	77	53	72	97
% of shrubs which are hawthorn	75	62	29	27
% of shrubs which are hazel	3	22	20	32

The process of succession can be followed in more detail by considering the species composition, size distribution and other details of the trees and shrubs in each wood (Table 7 and Figure 7). Considerable differences between the four are apparent. Knowle and Caynham are currently free of grazing, and have probably been so for some time—both have areas of old quarry working dangerous to stock. In both there are very high densities of trees, a clear single peak in the size classes of canopy trees, a very high proportion of canopy forming species, and a low frequency of hawthorn amongst the shrubs. Both seem to be the result of abandonment of open ground (with some wooded patches) and its immediate enclosure to exclude stock, with consequent successful regeneration of grazing-intolerant canopy species without the protection of spiny shrubs (Tansley 1968).

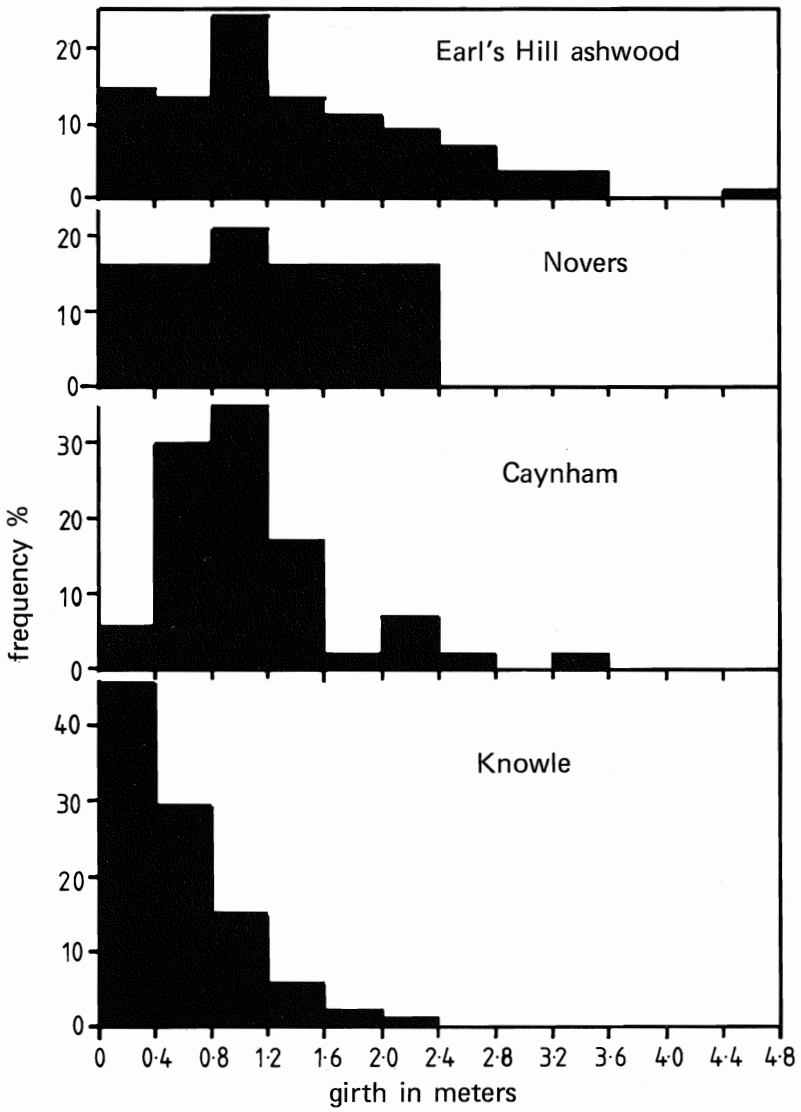

FIG. 7.
Frequency-distribution (%) of girth-sizes of all canopy trees in the four ash-elm woods.

By contrast, the pattern of events at the Novers and Earl's Hill seems to have been different, with a gradual decline in grazing pressure allowing a succession to woodland through thorny scrub. Earl's Hill is now fenced against stock—but the Novers is still lightly grazed by sheep, and retains patches of rich grassland vegetation. The proportion of canopy species is lower, and the proportion of hawthorn in the understory greater. At Earl's Hill a few of the hawthorns are extremely large and may pre-date most of the canopy trees. In the relatively mature Earl's Hill ashwood the density of trees has also fallen.

The most frequent girth class at Caynham is 0.8-1.2m, whereas in Knowle it is <0.4m. Current regeneration at Caynham is only on a very small scale, whereas it has been extensive at Knowle until very recently, no doubt as a result of recent clearance. The regeneration flush at Caynham might thus be 50-90 years old or even older (Merton 1970); maps made in the first 20 years of this century show deciduous woodland with much "underwood". No real peak exists at the Novers (where the sample of canopy trees is very small), while at Earl's Hill there is no distinct flush, but a peak of similar age to that at Caynham; the same maps again show a wood with much "underwood".

There is also evidence of successional change in canopy species. Oaks seem uniformly bad at regeneration in these circumstances, as indeed elsewhere, and may need gaps in the canopy caused by the falling of other trees (Tansley 1968, Shaw 1974), or more open conditions generally; there has been considerable regeneration higher up the slopes of Earl's Hill in what is now open scrub. Apart from the occasional planted or adventitious exotic, such as larch, the other canopy trees present all seem to have participated in the succession to woodland, but to differing degrees. Ash and wych elm are very successful, and apparently similar in their patterns, except at Earl's Hill, where ash regeneration now is less vigorous, (Figure 3). If it were not for the intervention of Dutch elm disease in recent years, the pattern would suggest a gradual successional replacement of ash by wych elm. Wych elm seedlings are generally more shade tolerant than those of ash, which may, in addition, be inhibited by dense ground cover of *Mercurialis perennis,* which is very abundant in the lower parts of the wood (Wardle 1959), Rackham (1976) suggests that wych elm does not form secondary woodland—here, however, the presence of relict seed parents may enable it to grow through a developing secondary ashwood to achieve dominance. The ash trees in the ashwood appear to be very susceptible to canker, which may account for the rarity of old trees. (C. A. Sinker, *personal communication*).

Other species seem generally to be of little importance. Alder is strongly associated with areas of waterlogging, while other pioneer species seem doomed to extinction or to a minor role as suppressed canopy trees or high understory; this is particularly clear at Knowle, where birch, yew and sallows are still comparatively common. Norway maple there, however, is a conspicuous exception; this exotic is an important component of the existing canopy, and appears to have been more successful at regeneration than other species. In this respect, it resembles its close relative sycamore, which is frequently abundant in Peak District ashwoods (Merton 1970). In these circumstances, sycamore seedlings are often more numerous than those of ash (Okali 1966) but whether this is compensated for by heavier mortality, or is leading to successional change is not clear. Sycamore certainly invades other ash-elm woods in Shropshire (e.g. the eastern end of Benthall Edge Wood,

Ironbridge, Cameron *unpublished*) and may be the only effectively regenerating species. Its absence from these woods may be due to lack of nearby seed parents.

The future development of these woods must be uncertain. At Caynham and Knowle there is already a closed canopy of young trees, and in the absence of management the proportions of understory species can be expected to decline still further, and the ground flora will also become impoverished. Since there are few old trees, only windblow or management will create new gaps in the canopy for the regeneration cycle to continue (Grubb 1977). At the Novers, by contrast, the continuation of light sheep grazing is likely to slow down the development of the full canopy, and understory species, especially hawthorn, are likely to remain abundant for some time.

The ashwood at Earl's Hill, which seems to retain the least traces of continuous woodland cover in terms of species composition, is, ironically, the most like natural forest in structure, with a wide range of ages in the canopy trees, and evidence of present (or very recent) regeneration (Jones 1945). It has reached a stage of development suitable for some of the complex regeneration cycles described by Pigott (1975) for the near-primaeval forests of eastern Poland. Unfortunately, nearly all the larger wych elms, the dominant canopy species, are now dead or dying from Dutch Elm Disease, thus altering the timing and nature of future succession. It will be interesting to see which species utilize the gaps thus created.

SUMMARY

1. Estimates of species composition, density and girth size and basal area distributions have been made for the trees and understory in five Shropshire woods.

2. In one oakwood, on ground showing evidence of continuous forest cover, most of the existing canopy trees are the product of a single planting episode, or have regenerated simultaneously from previous coppice. Oaks are not currently regenerating, understory is absent, and there are signs of a "reverse" succession to birchwood.

3. In four ash-wych elm woods which have developed from at least partly open ground, differences in stand structure and composition can be related to earlier history. Woods on land from which grazing animals have been completely excluded have developed dense canopies and high densities; the understory is reduced. Where grazing pressure has declined gradually, a more varied structure has resulted. Evidence suggests that some relics of woodland survived the open phase, and that successional changes in canopy species are still occurring, although in one site the replacement of ash by wych elm has been halted by elm disease.

ACKNOWLEDGEMENTS

My thanks are due to the owners of the woods for permission to work on their land, to my students and to volunteers from the Shropshire Conservation Trust who carried out the surveys, and to C. A. Sinker for unpublished information, and for reading a draft of this paper.

References

Clapham, A. R., Tutin, T. G. and Warburg, E. F. (1968). *Excursion flora of the British Isles.* C.U.P.

Cottam, G. and Curtis, J. T. (1956). The use of distance measures in phytosociological sampling. *Ecology,* **37,** 451-460.

Finney, D. J. (1948). Random and systematic sampling timber surveys. *Forestry,* **22,** 64-69.

Ford, E. D. (1975). Competition and stand structure in some even-aged plant monocultures. *Journal of Ecology,* **63,** 311-333.

Ford, E. D. and Newbould, P. J. (1970). Stand structure and dry weight production through the sweet chestnut (*Castanea sativa* Müll) coppice cycle. *Journal of Ecology,* **58,** 275-296.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews,* **52,** 107-145.

Jones, E. W. (1945). The structure and reproduction of the virgin forest of the north temperate zone. *New Phytologist,* **44,** 130-148.

Merton, L. F. H. (1970). The history and status of the woodlands of the Derbyshire limestone. *Journal of Ecology,* **58,** 723-744.

Okali, D. U. U. (1966). A comparative study of the ecologically related tree species *Acer pseudoplatanus* and *Fraxinus excelsior.* II. The analysis of adult tree distribution. *Journal of Ecology,* **54,** 419-425.

Peterken, G. F. (1974). A method for assessing woodland flora for conservation using indicator species. *Biological Conservation,* **6,** 239-245.

Pigott, C. D. (1969). The status of *Tilia cordata* and *T. platyphyllos* on the Derbyshire limestone. *Journal of Ecology,* **57,** 491-504.

Pigott, C. D. (1975). Natural regeneration of *Tilia cordata* in relation to forest-structure in the forest of Bialowieza, Poland. *Philosophical transactions of the Royal Society B,* **270,** 151-179.

Pollard, E. (1973). Hedges VII. Woodland relic hedges in Huntingdon and Peterborough. *Journal of Ecology,* **61,** 343-352.

Rackham, O. (1976). *Trees and Woodland in the British Landscape.* Dent, London.

Scurfield, G. (1959). The ashwoods of the Derbyshire Carboniferous limestone: Monk's Dale. *Journal of Ecology,* **47,** 357-369.

Shaw, M. W. (1974). The reproductive characteristics of oak. In: *The British Oak* (eds. M. G. Morris and F. H. Perring) 162-181 Classey, Faringdon.

Steele, R. C. (1974). Variation in oakwoods in Britain. In: *The British Oak* (eds. M. G. Morris and F. H. Perring) 130-140. Classey, Faringdon.

Tansley, A. G. (1949). *The British Islands and their Vegetation* 2nd edition, Cambridge.

Tansley, A. G. (1968). *Britain's Green Mantle* 2nd edition. Allen and Unwin, London.

Wardle, P. (1959). The regeneration of *Fraxinus excelsior* in woods with a field layer of *Mercurialis perennis. Journal of Ecology,* **47,** 483-497.

Appendix

A list of all woody plants found in the study areas and their immediate vicinity, with scientific names following Clapham, Tutin and Warburg (1968). A=Ashwood, Earl's Hill, C=Caynham, K=Knowle, N=Novers, O=Oaks Wood. Knowle and the Novers have many planted exotics, but also a very rich mixture of native species; the other sites are poorer. Brambles, ivy and woody plants of the field layer (e.g. heather) are excluded.

Alder	*Alnus glutinosa*	AC
Ash	*Fraxinus excelsior*	ACKN
Aspen	*Populus tremula*	N
Beech	*Fagus sylvatica*	C O
Blackthorn	*Prunus spinosa*	ACKN
Crab Apple	*Malus sylvestris*	A
Damson	*Prunus domestica*	A
Dogwood	*Cornus sanguinea*	CKN
Downy Birch	*Betula pubescens*	K
Elder	*Sambucus nigra*	ACKN
Field Maple	*Acer campestre*	ACKN
Gooseberry	*Ribes uva-crispa*	KN

APPENDIX—*cont.*

Guelder Rose	*Viburnum opulus*	AC
Hawthorn	*Crataegus monogyna*	ACKN
Hazel	*Corylus avellana*	ACKN
Holly	*Ilex aquifolium*	ACKN
Honeysuckle	*Lonicera periclymenum*	K O
Larch	*Larix decidua*	A KN
Large Leaved Lime	*Tilia platyphyllos*	O
Norway Maple	*Acer platanoides*	KN
Norway Spruce	*Picea abies*	KN
*Oak	*Quercus robur*	ACKNO
Red Currant	*Ribes rubrum*	N
Rowan	*Sorbus aucuparia*	KN
Sallows	*Salix spp.*	A KN
Scots Pine	*Pinus sylvestris*	K O
Silver Birch	*Betula pendula*	KNO
Spindle	*Euonymus europaeus*	KN
Sweet Chestnut	*Castanea sativa*	K
Sycamore	*Acer pseudoplatanus*	AC O
Wild Cherry	*Prunus avium*	KN
Wych Elm	*Ulmus glabra*	ACKNO
Yew	*Taxus baccata*	KN

*Oaks in Oaks Wood are hybrid, tending to sessile