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Changes in the composition and structure of the tree and shrub layers in Wytham Woods, Oxfordshire 1974-1991

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CHANGES IN THE COMPOSITION AND STRUCTURE OF THE TREE AND SHRUB LAYERS IN WYTHAM WOODS (OXFORDSHIRE), 1974-1991.

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Summary

1. In 1974-76 164 permanent 10x10m plots were recorded at alternate intersections of a 100x100m grid in Wytham Woods, Oxfordshire. Tree and shrub data were collected from all the plots in 1974-76, from 27 in 1984-85 and from all but one in 1991-92.

2. Changes in the structure and composition of the wood are assessed in terms of canopy cover, mean tree diameter, basal area and species occurrence.

3. The wood has become more open (reduced canopy cover) partly through management, partly natural processes such as windthrow and disease. The shrub cover has also declined greatly, probably because of increased deer browsing.

4. Most stands are predominantly young growth and for the wood as a whole mean tree diameter, basal area and tree height have increased.

5. The overall composition of the wood has changed little, but there has been a significant decline in mean woody species number per plot from 5.8 to 4.1, mainly through declines in understorey species and young oak. Elm cover has been reduced by disease and birch also suffered preferentially from windthrow.

6. Variation in the composition of the plots was grouped into six broad classes using TWINSPAN analysis. These groupings in part reflect the differences in history and management of the woods which are a mixture of ancient and recent, semi-natural and planted stands.

7. The results are used to indicate gains and losses in nature conservation terms for the wood as a whole. The strengths and weaknesses of this system may hold lessons for future woodland monitoring exercises.

Acknowledgements

The original establishment of the plots was funded by a grant form the Natural Environment Research Council (1973-76). We would like to thank those who, over the years, have contributed to the recording and to the maintenance of the grid posts through the wood. Similar thanks go to those who have advised on the analysis or commented on the report. In particular we acknowledge our debt to David Field for the 1974 recording and to Amanda Horsfall for the 1984 work. Finally two of us (KJK & RCT) wish to say how much we owe to the late Colyear Dawkins who inspired us in our re-recording. Without his foresight in setting up the system and his commitment to keeping it going none of the work would have been possible.

Contents

Introduction

Nature conservation is an increasingly important objective of woodland management, particularly in ancient and semi-natural woods (Peterken 1977; Forestry Commission 1985). Recommendations as to how such woods should be treated must allow for the long-term effects that any proposals may have. A decision to fell and restock, or to identify a stand as non-intervention, could determine much of the composition and structure of that patch of woodland and hence its associated wildlife for the next fifty to two hundred years. Studies of change in both managed and unmanaged woodland help us to improve our predictions of the likely impact of different treatments and their interactions with natural processes.

In this paper we describe results from a long-term surveillance system established in Wytham Woods, Oxfordshire, England (National Grid Reference SP4608) by Dawkins and Field (1978) and re-recorded in 1991-92 (Thomas & Kirby 1992). Tree and shrub information was obtained from permanent plots placed systematically through the wood, so that the results are a representative sample of the whole site. The changes in the ground flora in the plots will be reported on separately, while soil changes are described in Farmer (1994).

Site and Methods

Wytham Woods to the west of Oxford are a mosaic of ancient and recent woodland, semi-natural stands and plantations of various ages and species, with small areas of open grassland and scrub (Elton 1966; Gibson 1986; Grayson & Jones 1955). Between 1973 and 1976 (hereafter referred to as the 1974 survey)164 10 x 10m quadrats were established at alternate points on a 100 x 100m grid throughout the wood (Dawkins & Field 1978)(Figure 1).

Each plot was offset to the north-east (all bearings refer to true north) from the grid-intersection marker posts by 14.1m. This reduces the risk of disturbance to the plot by other workers in the woods who use the marker posts as reference points. Two corners of each plot were marked with underground metal markers so that they could be relocated precisely.

In 1984 and 1985 (referred to as the 1984 records) 27 plots in the west of the woods were recorded to test how easy it was to relocate the plots and to see what types of change could be detected (Horsfall & Kirby 1985). The opportunity for a full recording did not present itself until 1991 when 159 plots were re-located with a further 4 completed in 1992(the 1991 data). The one unrelocated plot, on the edge of the wood, has not been included in the analysis.

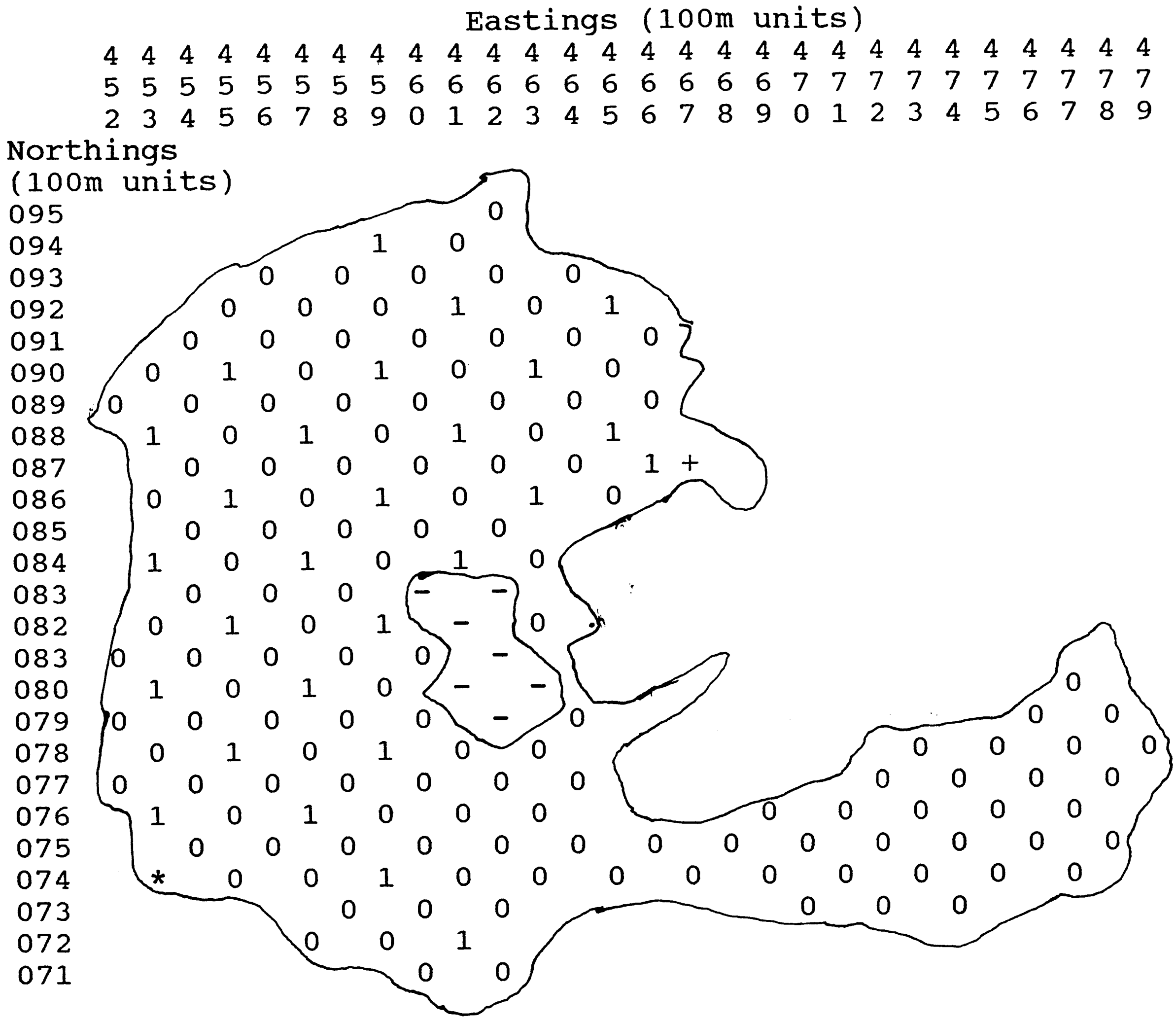

Figure 1. Distribution of plots (0) through the Wytham Woods.
1 plots recorded in 1984 also; + an extra plot included in both the 1974 and 1991 surveys; * plot not found in 1991, - field not included in the survey.

The methods used to collect the data in 1991 follow those described by Dawkins and Field (1978). They are summarised, and any minor differences noted, below.

(a) Vegetation cover was estimated across the south-west to north-east diagonal of the plot in three height bands: top or canopy cover (which was partitioned by species) > 2.5m high; mid or shrub cover 0.5-2.5m high; and ground cover < 0.5m high.

(b) Basal area of trees within the vicinity of the plot was estimated from relascope sweeps taken at south-west and north-east corners in 1974 and at all four corners on the other two occasions.

(c) The four largest diameter trees (or tallest for those less than 2cm diameter at breast height (dbh)) rooted in the plot were identified and their locations noted by coordinates from the south-west corner. The height of the largest of the four was measured using a clinometer or by direct measurement of those less than three metres. The largest tree (referred to as the leading tree) could be a seedling. In 1974 the four largest stems had to come from different stools to be considered if they were of coppice origin; in 1991 the four largest were measured even if two or more came from one stool. The alteration was made because there is ecologically little difference in the impact on the rest of the plot from stems from the same stool compared to two maiden trees growing close together. As comparisons made in this paper only involve the single largest tree in each plot the difference in recording procedure does not affect the results. The leading tree in a plot represents either the present or most likely future canopy dominant in that plot, but this may change through management of the stand or natural events. By comparing the coordinates within the plot of the leading tree at different dates we judged whether the leading tree had survived from one recording time to the next and if not whether the new leader was of the same or a different species.

(d) All trees and shrub species (Table 1) rooted in the plot were listed and were analysed for similarities in composition between plots using TWINSPAN (Hill 1979). Domin cover scores were assigned to the species in 1985 and 1991 to improve future comparison of changes, but are not used in this paper.

(e) Although not classed as a shrub, bramble (*Rubus fruticosus*) and some other tall herbs made a major contribution in some plots to the mid-cover layer (0.5 - 2.5m). Cover of bramble in the plots was estimated on a six-point scale (0, 1 = 1-5% cover, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-100%).

Plots were also classified according to whether they were in ancient or recent woodland using the historical data in (Grayson & Jones 1955) and more recent studies by Gibson (1988). Plantations were recognised using data from the Wytham stock map and ground observations (Figure 2). Some old plantings (more than 150 years old) have been included in the semi-natural category where there structure is now difficult to separate from a self sown stand of similar age.

Results

The change in the woodland between the two complete recordings (1974, 1991) are described for the wood as a whole. The data have also been analysed for differences between ancient and semi-natural stands compared to more recent woodland areas and plantations. The 1985 data provide additional insight into the timing or rates of change.

Changes in species frequency

A biologically significant change in species frequency between 1974 and 1991 was defined as a change greater than 30% of the 1974 value and at least a five plot difference (Table 1). On this basis seven species found mainly in the understorey have declined (field maple, dogwood, hazel, spindle, privet, sallow and wayfaring tree) and four major canopy trees (larch, birch, elm and oak). No large increases were observed. The mean number of trees and shrubs per plot declined significantly from 5.8 (SE 0.2) to 4.1 (SE 0.1).

Northings (100m units)	452	453	454	455	456	457	458	459	460	461	462	463	464	465	466	467	468	469	470	471	472	473	474	475	476	477	478	479
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078		1		4		4		4		4		4										3		1		1		1
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Figure 2. Distribution of ancient and recent stands and plantations and semi-natural areas: 1 ancient semi-natural stands; 2 plantations on ancient sites; 3 recent semi-natural areas and open land; 4 plantations on recent sites. (* = plot not recorded in 1991, - field not included in the survey).

Table 1. Tree and shrub species recorded.
All names follow Clapham *et al.* (1981).

Common name	Scientific name	No of plots in which present 1974	1991
Field maple	*Acer campestre*	**41	25
Sycamore	* *A. pseudoplatanus*	97	82
Horse chestnut	* *Aesculus hippocastanea*	2	0
Silver birch	*Betula pendula*	**37	20
Downy birch	*Betula pubescens*	11	7
Hornbeam	*Carpinus betulus*	2	3
Sweet chestnut	* *Castanea sativa*	7	3
Dogwood	*Cornus sanguineus*	**27	12
Hazel	*Corylus avellana*	**66	42
Hawthorn	*Crataegus monogyna*) *C. oxycanthoides*)	105	105
Spindle	*Euonymus europaeus*	**38	7
Beech	* *Fagus sylvatica*	34	32
Ash	*Fraxinus excelsior*	133	138
Holly	*Ilex aquifolium*	4	3
Larch	* *Larix* spp.	**18	5
Privet	*Ligustrum vulgare*	**27	14
Apple	*Malus sylvestris*	2	1
Spruce	* *Picea* spp.	14	9
Pine	* *Pinus* spp.	4	1
Hybrid poplar	* *Populus* spp.	4	2
Aspen	*Populus tremula*	0	1
Blackthorn	*Prunus spinosa*	29	31
Pedunculate oak	*Quercus robur*	**118	48
Buckthorn	*Rhamnus catharticus*	2	1
Grey willow	*Salix cinerea*	5	3
Goat willow	*Salix caprea*	**30	8
Elder	*Sambucus nigra*	55	42
Lime	* *Tilia europaeus*	3	2
Elm	*Ulmus* spp.	**21	12
Wayfaring tree	*Viburnum lantana*	**7	1
Guelder rose	*V. opulus*	3	0
Other conifers	* *Thuja plicata*) * *Chamaecyparis* spp.) * *Pseudotsuga menziesii*)	5	5

* species that have been introduced to the woods. Most occur largely as planted stands or individuals although there are extensive areas of self-sown and coppice regrowth sycamore. Some of the native species also occur as plantations.
** species showing a decline in occurrence of at least 30% frequency (with a minimum absolute change of five plots).

Changes in canopy cover

The woods contain some areas of permanent grassland which were included in the grid system, but in addition the woods have became more open with a significant decrease in mean canopy cover (>2.5m). In 1991 there were almost double the number of plots where canopy cover was 33% or less (Table 2a).

Table 2 (a)Top (canopy) cover, (b) mid (shrub) cover and (c) bramble cover in 1974 and 1991 for 163 plots.

	1974	1991
(a) Top cover		
Mean % (S.E.)	81 (2.2)	69 (2.5)
No of plots with cover		
0 - 33%	20	39
34 - 66%	34	54
67 - 100%	109	70
(b) Mid cover		
Mean % (S.E.)	44 (2.7)	25 (1.8)
No of plots with cover		
0 - 33%	86	137
34 - 66%	44	22
67 - 100%	33	4
(c) Bramble cover		
No of plots with cover		
0 - 5%	45	129
25 - 50%	66	31
51 - 100%	52	3

The mean mid (shrubby)cover also decreased (Table 2b). This 0.5-2.5m height band included some tall herbs such as bracken (*Pteridium aquilinum*) and bramble in some plots. In 1974 bramble thickets of more than a metre high were not uncommon and it was abundant throughout the wood; by 1991 it had greatly declined (Table 2c). Changes in other tall herbs (such as *Urtica dioica* and *Pteridium aquilinum*) were small or in some cases positive by comparison, so were not a major factor in the shrub layer decline. It is unlikely that changes in the bramble layer alone are the cause of the shrub cover decline and many of the understorey species in Table 1 showed a decline in their frequency of occurrence between 1974 and 1991. Similarly some areas of dense blackthorn thickets showed signs that they had broken up and become more open since the original recording. There is now a very pronounced deer browse line at about 1.5m throughout the wood and increased browsing by fallow *deer Dama dama*, muntjac *Muntiacus reevesi* (with the occasional roe *Capreolus*

capreolus) is believed to be the major cause of change in the shrub layer.

Cover estimates are subjective and the difference in observers between 1974 and 1991 could have introduced a systematic bias in the results. One of the observers was however the same in both 1984 and 1991, and therefore the data were examined just for those plots recorded at all three dates (Table 3). The differences in the timing of the changes suggests that it is not an artifact of sampling. The decline in tree cover between 1984 and 1991, but not earlier, is consistent with increased management of parts of the wood in this period and with gaps created by the 1987 great storm. The earlier reduction in shrub and bramble cover, due to increasing deer populations in the wood after 1974, fits with the observations of A. Gosler (personal communication) who was working in the wood throughout this period.

Table 3. Comparison of tree, shrub and bramble cover for plots recorded in 1984 as well as in 1974 and 1991 (27 plots).

	1974	1984	1991
(a) Top cover			
Mean % (S.E.)	81 (5.4)	81 (5.3)	67 (6.4)
No of plots with cover			
0 - 33%	2	2	6
34 - 66%	8	7	10
67 - 100%	17	18	11
(b) Mid cover			
Mean % (S.E.)	43 (6.7)	29 (5.2)	26 (5.3)
No of plots with cover			
0 - 33%	15	22	23
34 - 66%	7	3	2
67 - 100%	5	2	2
(c) Bramble cover			
No of plots with cover			
0 - 5%	5	12	21
25 - 50%	12	8	5
51 - 100%	10	7	1

Changes in leading (largest diameter) trees

There is a shift in the diameter distribution towards larger trees (representing growth) in 1991 compared to 1974 (Table 4) even though the differences in the overall means for all species are insignificant - 28.2cm (S.E. 1.9cm) in 1974, 31.8cm (S.E. 1.9cm) in 1991. (These mean values exclude plots where the leading tree was less than 2cm dbh).

The leading trees are generally small, reflecting the past treatment of the wood. Most are regrowth of coppice last cut between about 1915 and 1950, natural regeneration on to grassland, or post-war planting of open areas with mixtures of broadleaves and conifers. Leading trees less than 40cm diameter at breast height are mainly ash and sycamore whereas oak contributes more than half the trees in the larger size classes (Table 5). These oaks tend to be former standards in the old coppice compartments and old pollards in former wood pasture areas. Beech is well reasonably well represented in both large and small size classes, being present mainly on the top of the hill as large old pollards in what had been open common and as young planted trees.

Table 4. Size class distribution (dbh) for leading trees (all species)

Size class (dbh, cm)	No of plots 1974	1991
Less than 2cm	25	24
2 - 10	37	21
11 - 20	44	39
21 - 30	23	39
31 - 40	12	17
41 - 50	6	7
51 - 60	3	6
61 - 80	7	4
81 - 100	4	2
101+	2	4

Table 5. Number of plots with leading trees of ash, sycamore, beech and oak in different size classes in 1991.

	Seedling or less than 2cm dbh	2 - 40cm dbh	More than 40cm dbh
Ash	9	42	2
Sycamore	4	23	3
Beech	1	12	3
Oak	1	6	12
All species	24	116	23

There were only 27 plots in 1991 with leading trees in the 2-10cm class compared to 37 in 1974. The cohort of young growth present in 1974 has grown on to the next higher size class but there has not been a corresponding movement of plots up from the <2cm size class because these plots are now mainly permanent open grassland or very dense blackthorn thickets. Unless there are further losses from plots in the upper end of the distribution this cohort effect is likely to intensify. It does not necessarily mean that there are no other saplings and young trees in the plots; only that if they are there they are growing in plots where there is already a larger leading tree. Nevertheless subjectively there seems to be a scarcity of small trees.

About 48% of plots retained the same individual leading tree as in 1974, and for a further 18% there has been no change in the species of the leading tree (Table 6). There was no consistent pattern of one species replacing another (Table 7).

Table 6. Number of plots where there was a change of leading tree and where this caused a change of leading species (1974-1991).

	No of plots (1991)		
Size class (1974) dbh (cm)	Same tree	Different tree, same species	Different species
Less than 2cm	5	7	13
2 - 10	15	12	10
11 - 20	18	31	15
21 - 40	22	4	9
41+	20	1	1

Table 7. Gains and losses for individual leading tree species.

	No of plots retaining the same leading species 1974-1991	Gains from 1974	Losses from 1974
Oak	16	3	7
Sycamore	20	10	8
Ash	38	15	3
Beech	12	0	0
Birch	7	2	5
Field maple	5	2	2
Elm	3	0	5
Spruce	2	1	1
Sallow	2	2	1
Larch	2	0	4
Other conifers	1	1	3
Other broadleaf	3	2	3

High turnover in the smallest size category (<2cm dbh, Table 6) is not unexpected, as in many cases these are seedlings with an ephemeral existence. The five where the same tree was found were saplings. The next two categories include thicket and young pole stage stands where stem density is often high; most of the stems in a plot are fairly similar in size and hence only minor growth changes are needed for a change in leading tree to occur. In managed stands these plots may have been subjected to thinning which could lead to the removal of the erstwhile leader if that tree were damaged or of poor form. In the larger size classes there was a much greater likelihood that the leading tree remained the same until harvesting or natural catastrophe leads to its demise. Therefore the processes leading to change at the plot level were examined in more detail.

Processes leading to change in leading tree

No two plots have changed in exactly the same way between 1974 and 1991, but from the notes for each plot they have been classified according to what appears to have been the major cause of change affecting them (Table 8). This is in some cases a natural process, such as windthrow, and in others deliberate management.

Table 8. The major processes likely to have affected each plot (1974-1991) and the consequences for the leading tree

	No of plots (1991)		
	Same lead tree	Different tree	Different species
(0) No obvious agent of change	76	0	2
(1) Seedling turnover in open plots	1	4	8
(2) Seedling turnover under thickets	0	2	4
(3) Competition/differential growth of young stands.	2	18	11
(4) As (3) but assisted by forest management.	0	4	9
(5) Ride and glade creation.	0	4	5
(6) Wind damage (mainly 1987 and 1990 storms).	1	2	7
(7) Dutch elm disease.	0	1	2

Where change in the leading tree had occurred through differential growth (Table 8, group 3) the new leader was often among the four largest trees in 1974, while the old leader was likewise sometimes still found among the four largest in 1991. This group and that where no change occurred (group 0) showed little change in canopy cover although the mid cover (the shrub layer) was much reduced (Table 9). Where the change had been encouraged by forest management, such as thinning, the stands were also likely to have a reduced canopy cover (group 4). The glade creation and widening of rides (group 5) contributed much to the overall opening up of the wood between 1974 and 1991 (Table 2) and reflected a concern to restore some of the open grassland that had been a major part of the estate prior to 1950. In the three plots (group 7) much affected by Dutch Elm Disease the canopy was not as open as might have been expected, given the reduction in elm cover. Ash and sycamore appear to be the main species filling such gaps. Windthrow (particularly the 1987 and 1990 storms) (group 6) affected birch stands more than the other species. The plots showing a change in the leading tree are spread throughout the wood (Figure 3).

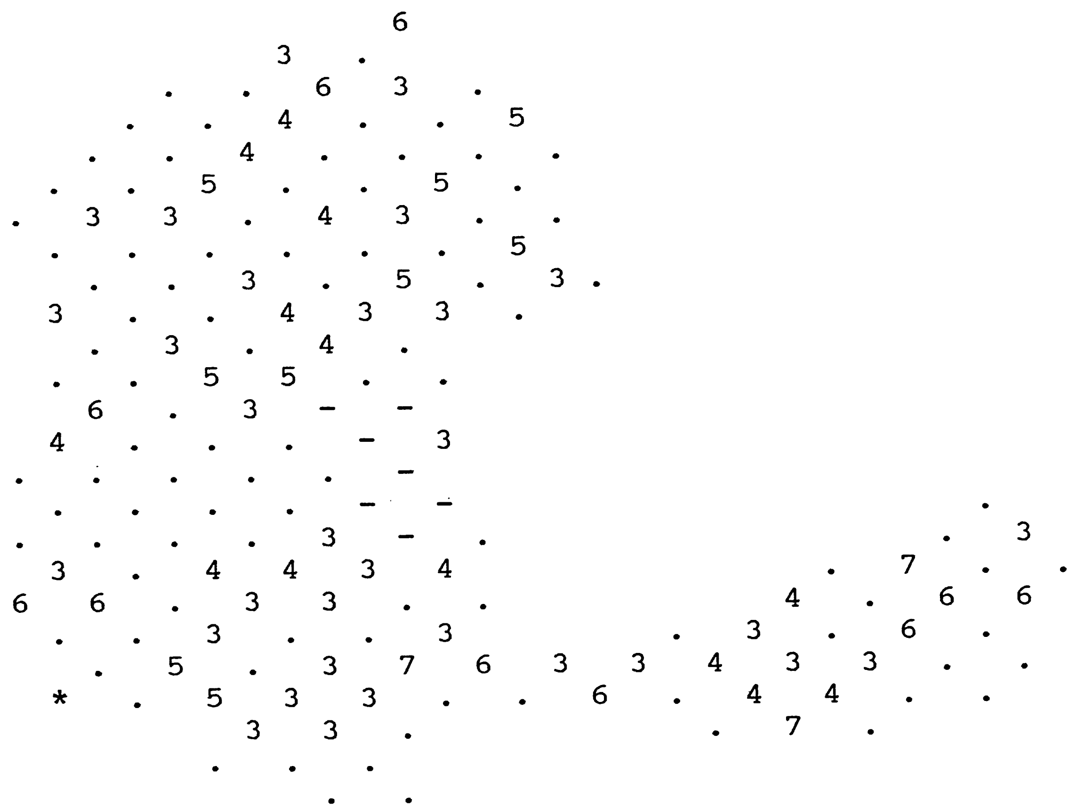

Figure 3. Changes in leading trees (excluding seedling turnover): 3 growth of young stands; 4 forestry management; 5 ride and glade creation; 6 windthrow; 7 elm death. (- field not included in survey).

Table 9. Selected plot characteristics for each of the groups identified in Table 8.

Feature		Group 0	1	2	3	4	5	6	7
Number of plots		78	13	6	31	13	9	10	3
Top cover %	1974	87	40	90	76	81	77	96	100
	1991	83	18	62	80	48	29	44	75
Mid cover %	1974	45	56	54	44	32	21	54	40
	1991	21	41	55	19	21	22	46	15
Birch cover %	1974	3	0	0	3	0	16	34	0
	1991	3	0	0	3	6	0	8	0
Elm cover %	1974	0	0	0	0	1	4	1	80
	1991	1	2	0	0	1	0	0	15

Mean height for leading trees

Heights measured for the leading trees using a clinometer, must be treated with some caution because it was often difficult to see the tops of the trees (Table 10). The overall means, excluding plots where the leading tree was less than 2cm dbh, were 13.6m (S.E. 0.5m) in 1974 and 16.6m (S.E. 0.5m) in 1991, with a more pronounced shift in the size class distribution towards larger trees than for the diameter distribution (Table 4).

Table 10. Height distributions for leading trees (all species) 1974,1991.

Year	Height class (m) <2	2-5	6-10	11-15	16-20	21-25	25+
1974	19	27	47	42	16	5	7
1991	23	13	21	45	38	15	8

Changes in basal area of the main tree species

Total basal area was estimated for 1974 and for 1991 using the relascope readings from south-west and north-east corners only (Table 11). The additional data from 1991 for the south-east and north-west corners provide a test of the reliability of these measures.

Table 11. Mean basal area (m^2/ha) for each plot corner.
(A tally factor of 2 was used, so the relascope scores were half the values given in each case).

(a) All 163 plots recorded in 1974 and 1991.

	1974	1991
Mean score (S.E.)		
South-west corner	14.8 (0.8)	22.0 (1.0)
North-east corner	14.4 (0.6)	21.2 (1.0)
South-east corner	21.8 (1.0)	
North-west corner	21.6 (1.0)	

(b) Only the 27 plots recorded in 1984 as well.

	1974	1984	1991
Mean score (S.E)			
South-west corner	14.2 (1.6)	21.2 (2.2)	26.8 (2.8)
North-east corner	16.2 (1.6)	22.0 (2.2)	25.4 (2.2)
South-east corner		19.8 (2.2)	26.4 (2.4)
North-west corner		19.4 (2.2)	24.2 (2.4)

Table 12. Total relascope scores over the whole of the woods for the main species (1974,1991) for south-west and north-east corners combined for all 163 plots.

	1974	1991
Total (all species)	2372	3498
Oak	500	716
Sycamore	486	728
Ash	458	947
Beech	258	399
Birch	186	137
Field maple	98	117
Larch	97	84
Elm	59	32
Spruce	44	53
Sweet chestnut	43	60
Sallows (*Salix* spp.)	38	48

At the plot scale there were sometimes large differences between the results from different corners where a plot spanned or was close to the boundary with another crop of very different stocking density or tree size, or was next to open space on one side. Over the wood as a whole such irregularities even out.

Basal area of timber in the wood increased by about fifty per cent from $14.6m^2$ in 1974 to $21.6m^2$ in 1991, consistent with the general growth of the trees revealed by increases in leading tree diameters and heights, and with the intermediate recording of 27 plots in 1984. The increases were greatest for ash and sycamore, whereas basal area for elm and birch declined (Table 12).

Changes in the composition of the whole wood (1974-1991)

The composition of the wood can be summarised in four ways using the data described above: from the canopy cover estimates; from the basal area estimates; from the number of times each species was recorded as the leading (largest) tree in a plot; and according to the frequency with which the species occurred in the plots (Table 13).

Little change has occurred in the relative proportions of the main species in the wood as a whole and the three different methods of assessing the composition of the tree layer (excluding species occurrence) are reasonably consistent. This last measure is always larger than the other three because it includes seedlings and young trees that may not contribute to the canopy, are not leading trees and add very little to basal area.

Table 13. Summary of overall changes in Wytham Woods 1974 - 1991 for the main tree species (based on 163 plots).

	Frequency % of plots		% cover on diagonal		Leading tree: % of plots		Basal Area % of total	
	1974	1991	1974	1991	1974	1991	1974	1991
Oak	72	29	12	10	13	12	21	20
Sycamore	59	50	17	15	18	18	20	21
Ash	81	85	18	19	25	32	19	27
Beech	21	20	10	10	7	10	11	11
Birch	23	12	5	3	9	5	8	4
Elm	13	7	3	1	4	2	3	1
Larch	11	3	1	1	4	1	4	2
Spruce	9	5	1	2	3	3	2	1

Oak contributes more to the basal area figures than to leading tree and diagonal cover estimates. It occurs more frequently than other species as very large trees (Table 5) thus adding much to the total basal area. However only rarely do such large trees occur within a plot (so they are not recorded as the leading tree) or are close enough to it to contribute to the canopy cover estimate. That oak has retained its overall contribution to the canopy (however measured) despite a large drop in overall frequency of occurrence suggests a reduction in the number of small trees, saplings and seedlings. This may be related to the general loss of understorey through the wood, or may be something specific to oak. For example if the years preceding 1974 had included a good mast year then the high frequency in 1974 may have been caused by a temporary abundance of seedlings.

Two of the measures indicate a relative increase in ash over the seventeen year period, but this is not reflected in an increase in its contribution to canopy cover or overall frequency. Ash regeneration and understorey growth which either has not yet reached the 2.5m threshold for inclusion in the canopy cover estimate or which has but only adds to existing ash cover in the plot could contribute to the leading tree scores and relascope tallies without affecting the other two measures.

All four measures pick up declines in the amount of birch and elm, believed to be caused by windthrow and Dutch elm disease respectively. The changes in other species at the wood level tend to be too small to show up in this type of comparison, as illustrated by the figures for larch and spruce. While important in determining what happens in individual plots the character of the wood is determined very largely by the changes in the four main tree species.

Species distribution patterns across the wood

The TWINSPAN analysis should bring out any major variations in the composition of the woody species across the wood and between recording times. Seven broad groupings of plots were identified based on the occurrence of species listed in Table 1 (Figure 4). Both sampling dates were included in the analysis and if there was no change in the plot over the period then the two samples from a plot would be expected to appear in the same end group. This was the case for 51% of plots (Table 14) and for groups D and G about 70% of plots from 1974 were still in their respective group in 1991.

Table 14. Distribution of plots between end-groups in 1974 and 1991 (see Figures 4,5).

	No of plots						
End group in 1974	A	B	C	D	E	F	G
End group in 1991							
A	**7**	2					1
B	3	**13**	1	1		1	
C	3	4	**14**	4	6		
D	2	10	5	**16**	2	1	3
E		2	2		**8**	3	1
F				1		**8**	2
G	1	3	1	1	6	8	**17**

Figures in bold represent no change of group.

```
                    |
                    |
              ---------------------
            Elder          Hazel
            Beech          Field maple
              |            Blackthorn
                             |
  ---------------------        ---------------------
  Elder      Sycamore        Sycamore  Blackthorn
  Blackthorn Beech           Birch     Elder
  |          Hawthorn        Oak         |
GROUP A      Birch           Hazel     GROUP G
26 plots       |             Dogwood    61 plots
               |                |
               |                |
        ---------------    ---------------
        Beech      Elm      Sycamore  Blackthorn
          |        Birch      |       Field maple
          |        Spruce     |       Birch
  ---------------  Hazel    GROUP E   Privet
  Sallow  Hazel      |      38 plots    |
  Larch   Beech  GROUP B              GROUP F
  Oak     Hawthorn  53 plots           32 plots
   |       Elder
GROUP C  GROUP D
 54 plots 56 plots
```

Figure 4. Illustration of the TWINSPAN groups with the indicator species at each level.

Table 15. The mean cover of different trees and shrubs for the seven TWINSPAN end groups (see Figure 4).

End group no		A	B	C	D	E	F	G
No of plots in group		26	53	54	62	38	32	61
No of plots from	1974	16	34	23	23	22	21	24
" " " "	1991	10	19	31	39	16	11	37
Mean Cover of:								
Canopy layer	1974	55	81	83	91	83	89	75
" " "	1991	48	68	63	76	84	78	62
Shrub layer	1974	54	42	46	26	39	52	51
" "	1991	35	19	19	20	28	32	32
Ash	1974	6	18	29	6	14	21	30
"	1991	10	19	16	19	30	14	24
Oak	1974	22	15	16	8	14	8	3
"	1991	14	12	11	7	15	6	7
Minor shrubs*	1974	16	3	5	1	0	1	3
" "	1991	7	0	1	0	1	0	1
Elm	1974	7	7	0	0	0	0	0
"	1991	4	7	0	0	0	0	0
Beech	1974	0	8	10	50	0	2	0
"	1991	0	7	9	30	0	4	0
Sycamore	1974	6	19	21	29	43	1	0
" "	1991	7	7	28	19	27	0	5
Hazel	1974	1	7	0	0	5	22	11
"	1991	0	8	0	1	15	21	12
Field maple	1974	0	0	0	0	3	4	12
" "	1991	0	0	0	0	0	11	6
Blackthorn	1974	2	0	0	0	0	3	18
" "	1991	3	0	0	0	1	0	4
Mean species no	1974	3.1	6.6	4.2	6.5	5.7	8.2	5.6
" " "	1991	3.0	5.1	2.9	4.2	4.3	6.2	4.1

* Mainly elder.

```
095                     F
094               G   G
093         G   E   F   F   G
092       E   A   E   F   C   G
091     G   G   D   E   G   G   F
090   G   B   E   E   A   E   E
089 F   E   E   D   B   B   E   A
088   F   C   D   C   C   C   B
087     E   C   C   E   E   C   D  B
086   D   C   B   E   C   E   C
085     C   E   D   A   C
084   F   C   E   D   G   C
083     F   G   D
082   B   E   G   D     D
081 G   E   B   G   D
080   F   B   A   D                                   E
079 F   G   D   D   B       A                       A   F
078   F   C   C   D   A   D                   A   B   B   E
077 F   G   C   B   A   A   D               B   B   B   B
076   G   F   B   B   G   B           D   D   B   F   B
075     G   G   F   F   A   B   B   D    D   B   B   F   A
074   *   G   F   C   C   G   D   B   B   B   B   B   A
073             B   D   C                D   B   B
072           G   C   C
071                 A   A
```

(a) Plot end-groups 1974.

Figure 5a TWINSPAN endgroups 1974

(b) Plot end-groups 1991.

095 **G**

094 G G

093 G **G** **G** **G** G

092 **G** A E F C G

091 G **E** **F** E G G **G**

090 G **E** **C** E **C** E **G**

089 **G** E **D** **C** **G** **C** **D** **C**

088 **D** **E** **C** C C C **C**

087 E C **E** **C** **G** C **G** **D**

086 D C **C** **C** C **C** **D**

085 **D** E **C** **D** **D**

084 **E** C **C** **C** **D** **D**

083 **E** G D

082 B E G D D

081 **F** **B** **C** G D

080 F **D** **G** D **G**

079 F **D** D D B A A F

078 F **D** **B** D A D **D** **G** B **G**

077 F G **G** B **B** A D **D** **D** B B

076 G F B **G** **A** **D** D D **D** F **E**

075 G **F** **F** **E** A B **D** D D B **D** **G** **B**

074 * G **G** C C **D** **B** **D** **D** B B **A** A

073 B **C** C D **A** B

072 G C C

071 **C** **B**

Figure 5. TWINSPAN endgroups (b) 1991. Emboldened figures are those plots which changed end-groups compared to 1974.

Group A was open and scrubby compared to other groups (Table 15) and many of its occurences were around the edge of the wood (Figure 5). Group B included most of the plots where elm occurred in the canopy and was particularly common in south-east section of the woods in 1974. Many of these plots had moved into group D in 1991. Groups B,C and D had most of the beech areas while sycamore was most abundant in C,D and E. In groups E,F and G hazel cover became common with field maple in F and G, and blackthorn mainly in G. Groups F and G were clustered around the sites of the old coppices on the west and north of the woods. All groups showed a decline in species richness, but the two groups that were richest overall in both years (B and F) showed the greatest decline in their representation in 1991 compared with 1974 (from 34% to 18% of the total number of plots). Groups C,D and G showed the greatest increases in the number of plots assigned to them in 1991 compared to 1974; group G particularly in the north and west, the old coppices, while group D gained more in the plantation areas in the south-east.

Differences in ancient versus recent woods and between plantations and semi-natural stands

Differences between the ancient and recent stands within the woods (Figure 2) and between semi-natural stands and plantations are brought out in the distribution of plots between endgroups (Table 16). Ancient semi-natural stands are spread across all groups, but are very poorly represented in both years in group D. They also show some of the biggest changes between years, with much of the overall change in groups C,E and G occurring in this group. Groups A and G which are the more scrubby areas are not surprisingly scarce in both the plantation categories, but common in recent semi-natural stands. Recent plantations ended up mainly in groups C,D and E.

Table 16. Distribution of end-groups amongst different historical and treatment classes.

	Ancient Semi-natural		Ancient Plantation		Recent Semi-natural		Recent Plantation	
No of plots	59		19		50		35	
End-groups	1974	1991	1974	1991	1974	1991	1974	1991
A	7	4	0	0	6	4	3	2
B	9	5	2	2	8	3	15	9
C	7	15	4	3	4	7	8	6
D	2	2	2	3	11	19	8	15
E	14	7	5	8	3	0	0	1
F	10	8	5	1	5	2	1	0
G	10	18	1	2	13	15	0	2

While shrub layer cover declined in all origin/management types the general decline was added to in the young plantations as young thicket stands have grown up, taking the main canopy out of the shrub layer zone. Oak, ash and sycamore, the main species across the wood, showed little difference between types; beech occurred hardly at all in the ancient semi-natural stands, whereas birch and hazel were commonest there (Table 17). Elm had the highest cover in the recent semi-natural areas. Field maple and hawthorn rarely contributed to the canopy in replanted areas, whereas spruce showed the reverse pattern. The leading tree data show a similar breakdown between the four origin/management types (Table 18).

Table 17. Changes in tree and shrub cover (1974-1991) for different historical and treatment classes.

		Ancient Semi-natural	Ancient Plantation	Recent Semi-natural	Recent Plantation
No of plots		59	19	50	35
Mean cover % (S.E.)					
Canopy	1974	84 (3)	72 (7)	80 (4)	83 (4)
	1991	68 (4)	75 (6)	57 (5)	83 (4)
Shrub	1974	41 (4)	56 (8)	42 (5)	46 (6)
	1991	31 (3)	25 (5)	25 (3)	14 (3)
Oak	1974	15 (4)	14 (5)	7 (3)	14 (4)
	1991	11 (3)	11 (3)	6 (2)	13 (4)
Sycamore	1974	20 (4)	12 (6)	12 (6)	10 (4)
	1991	16 (3)	18 (8)	15 (4)	11 (4)
Ash	1974	17 (4)	22 (7)	18 (4)	19 (6)
	1991	17 (3)	21 (8)	20 (4)	22 (5)
Beech	1974	0	15 (8)	12 (4)	24 (5)
	1991	0	17 (8)	9 (3)	24 (6)
Birch	1974	9 (3)	3 (2)	3 (2)	1 (1)
	1991	6 (2)	1 (1)	1 (1)	1 (1)
Hazel	1974	12 (3)	4 (2)	5 (3)	1 (1)
	1991	12 (3)	11 (4)	4 (2)	0
Elm	1974	1 (1)	0	5 (1)	1 (1)
	1991	1 (1)	1 (1)	2 (1)	0
Field maple	1974	5 (2)	0	3 (2)	0
	1991	5 (2)	0	1 (1)	0
Hawthorn	1974	7 (2)	0	7 (2)	1 (1)
	1991	3 (1)	0	4 (1)	2 (1)
Spruce	1974	0	1 (1)	0	3 (2)
	1991	0	3 (3)	0	6 (3)

Table 18. Composition of leading trees by origin/management types.

	Ancient Semi-natural		Ancient Plantation		Recent Semi-natural		Recent Plantation	
No of plots	59		19		50		35	
Species	1974	1991	1974	1991	1974	1991	1974	1991
None	3	3	0	0	5	4	0	0
Oak	11	8	3	5	4	4	4	2
Sycamore	13	12	2	2	11	11	3	5
Ash	9	19	5	6	19	21	8	7
Beech	0	0	2	3	4	4	6	9
Field maple	5	5	0	0	2	2	0	0
Sallow	3	3	0	0	0	1	0	0
Birch	10	5	2	1	1	1	1	2
Elm	3	2	0	0	3	2	0	0
Larch	0	0	2	0	0	0	4	2
Spruce	0	0	1	1	0	0	4	4
Other conifers	1	0	1	0	0	0	2	2
Other broadleaf	1	2	1	1	1	0	3	2

Table 19. Causes of change in leading trees by origin/ management types.

	Ancient Semi-natural	Ancient Plantation	Recent Semi-natural	Recent Plantation
No of plots	59	19	50	35
Nature of change (see also Table 7)				
None	30	12	22	14
Seedling as leading tree	9	0	10	0
Stand growth	8	2	7	14
Stand growth +management	1	4	1	7
New ride/glades	5	0	4	0
Windthrow	5	1	4	0
Elm disease	1	0	2	0

Changes in the leading trees (Table 19) are mainly due to stand growth and management such as thinning in the plantations; in the semi-natural areas the effects of wind, disease and clearance of woodland to create glades have been more significant.

Table 20. Differences in basal area (m^2/ha) in 1974 and subsequent growth in areas of varying origin and treatment.

	Ancient Semi-natural	Ancient Plantation	Recent Semi-natural	Recent Plantation
No of plots	59	19	50	35
Basal area (S.E.) 1974 (m^2/ha)	12.9 (1.2)	18.2 (2.3)	14.0 (1.3)	16.1 (1.5)
Mean growth 1974-1991	7.2 (1.3)	13.0 (2.1)	4.0 (1.3)	7.9 (1.7)

Differences in the forestry potential of the various categories are apparent. Initial basal area of timber in 1974 was not very different across the wood, but growth over the seventeen year period in the plantations is almost double that in the semi-natural areas (Table 20). The lower apparent growth in the recent plantations rather than in those on ancient sites is partly an artifact, as some of the recent plantations have been thinned and felled in recent years.

Discussion

Conclusions on changes in Wytham Woods 1974-1991

The permanent plot system allows us to describe in quantitative terms the changes in the tree and shrub layers over a seventeen year period, and can be summarized as follows.

(a) The woods have become more open and the shrub cover has declined. There has been a reduction in woody species- richness at the plot scale, although no tree or shrub species has been lost from the wood completely.

(b) Much of the woods is in an aggrading phase. The trees are small and most plots and most species show an increases in leading tree diameters and heights, and in basal area over the period.

(c) The composition of the woods has remained broadly stable by all the measures used in terms of the main tree species. However this stability at the wood level is not reflected at the plot level and for minor species. Thus there have been declines in elm and birch through natural causes, some plots have become open because of ride creation, and in others vigorous growth has lead to increases in canopy cover.

(d) Variations in the composition of the woods, in terms of their woody cover, have been identified, in part related to their past history and management. Ride and glade management has been more significant in the semi-natural parts of the wood, whereas growth of young crops has been a more important force for change in the plantations.

The Wytham system

Dawkins and Field (1978) wrote "...we have made no provision for perpetuation,other than attempting to ensure the 'permanence', clarity and accessibility of the observations. If none of the plots are ever re-observed, then they will have shown themselves not worth the effort." They recognised the need to ensure the durability of the plot system (through permanent grid posts and underground markers), of the records and of the knowledge of them (by publication of the methods and placing copies of the data in several places). By recording a variety of parameters including data on soils, ground flora and the woody layer they increased the likelihood that someone would find the system of sufficient interest to be worth repeating, even though they recognised that they could not predict the nature of that interest.

Peterken and Backmeroff (1988) pointed out that many long-term monitoring schemes fail (or are at risk of doing so) because the instigator loses interest or moves on and no-one takes over from them. The Wytham plot system has overcome this hurdle. The Woods are now also part of a national network of sites set up to look at environmental change, so interest in the scheme and the data that it may provide is likely to continue.

The system has fulfilled its originators aims, in that it has survived (both plots and records) and has proved of value in demonstrating effects of factors that were not a concern in 1974, for example deer browsing and soil nutrient enrichment (Farmer 1994).

The one plot in the woods that was not relocated in 1991-92 is exceptional, being on the edge of the wood and not associated with a grid post (which would have been in the adjacent field). It also now lacks large trees as markers (because they had been elms but have now died and been removed). Nor is it traceable easily by reference to the wood boundary because the ditch has been re-aligned at this point and the metal detector merely found large amounts of fence wire (from the reshaped boundry fence). However it is not completely lost as its position could be re-determined from adjacent posts and the underground metal markers are still in place to define it precisely once the approximate location is known.

There are some ambiguities in how particular features should be recorded but these have not affected assessment of change in the main areas of interest. Dawkins and Field (1978) suggested ways of improving the records, for example the recording of the largest tree of each species rather than just the four largest regardless of species. On balance we do not think that this would necessarily add much useful information for most plots in relation to the additional time required. They were also concerned about the accuracy of the diagonal cover estimates and considered whether this should be repeated for the second diagonal. In fact the results from the cover estimates appear to be as consistent as other measures (Table 13) so this concern may be unnecessary. Instead in 1984 and 1991 all species were given Domin cover scores for the whole plot.

The more samples that are taken the more likely it is that a monitoring system such as this will detect relatively rare events such as elm death and the birch windthrow. A large number of samples are also needed if they are then to be split up to look at variation within the woods, for example the differences between ancient and recent sections of the woods. Many fewer are needed to describe the broad trends, with the data from just the 27 plots recorded in 1984 giving a good indication of what was happenning in the total data set, even though they did not cover the whole wood. A possible strategy in future might be therefore to record a quarter of the plots (41) on a rolling programme every three to four years, with a full re-recording every 15 - 20 years.

Extending the data backwards from 1974

The 1959 management plan for the woods drawn up by the Oxford University Forestry Department includes an inventory of the woods (Table 21) (Osmaston 1959).

Table 21. Results from the 1959 management plan inventory.

(a) Treatment classes

	Open areas, coppice and scrub	Regeneration	Poles	Young timber	Mature timber
% area of woods	28	29	17	8	18

(b) Species composition - Size class (no of stems)

	Oak	Ash	Sycamore	Beech	Elm	Larch	Spruce	Other
Small	645	2600	4455	5	1100	740	210	1285
Medium	1765	595	595	5	230	40	35	222
Large	940	230	190	250	85	1	0	55

Small 6-11" quarter-girth; medium 12-17" QG; large 18"+ QG
(Approximate conversions to metric diameter classes: small 19-35cm, medium 36-53cm, large >53cm).

The preponderance of young growth in the woods is emphasised with nearly a third of the wood classed as regeneration and the main timber trees being predominantly small. Oak then as in 1991 dominated in the larger size classes and ash and sycamore in the smaller ones. Beech in 1991 has a more even spread of size classes (through plantation growth) rather than being almost entirely as large trees in 1959. Elm was much more prominent in 1959 than either in 1974 or 1991 suggesting that elm disease had already removed many trees by 1974. The absence of any records for birch probably indicates that in 1959 much of it was too small to be recorded in the survey and its low value to foresters meant that any that was found would be included with "other species".

From this, an earlier plan and the descriptions in Elton (1966) it may be possible to extend the analysis of changes in the woods further back, at least in a qualitative fashion.

Significance of the changes in nature conservation terms

The plots were not set up to assess changes in the nature conservation value of the wood, but they can be used to address such questions. In terms of the tree and shrub layer we can make the following conclusions in nature conservation terms:

(a) the area covered in native trees and shrubs has remained much the same (no change in nature conservation value);
(b) the area of open ground has increased (likely to increase conservation value);
(c) the reduction in the shrub layer is likely to be detrimental because many birds (and invertebrates) make use of low cover (Fuller 1995); breeding nightingales for example have declined over the last 17 years (Gosler 1990)(loss of nature conservation value);
(d) woody species richness has declined (loss of nature conservation value)
(d) the reduction in elm may have had concomitant effects on elm specialist feeders although they are unlikely to have disappeared completely;
(e) the blow down of birch in the neglected coppice areas is a positive feature introducing variety through gap creation and soil disturbance through root plates (Buckley *et al.* 1994).

The Wytham scheme in a wider context

The changes that have taken place in Wytham Woods in the tree and shrub layer are not in themselves exceptional. Some could have been predicted in 1974, in general terms if not in a quantitative way. Other changes such as the reduction in bramble and decline in the shrub layer which we believe is due to the impact of greatly increased deer browsing (Thomas & Kirby 1992)or the 1980's fashion for opening up rides to benefit invertebrates would not have been. In either case there are few woods for which data are available over more than ten years with which to test whether our predictions are correct.

Assessing long-term changes in woodland will become even more important in future if commitments to maintain forest biodiversity are to be achieved; and if we are to learn from exceptional events such as the 1987 great storm (Kirby 1994). Monitoring of woodland will be needed at three scales - of changes to individual stands, of changes within woods and of changes to woodland across landscapes. At present most experience is on the first and the third of these. Changes to stands in a range of woodland types are well-described in, for example, Peterken and Backmeroff (1988) and Peterken and Jones (1987,1989). At the landscape scale forestry censuses and the Nature Conservancy Council's inventories of ancient woodland have been used to chart the change in the extent and broad composition of woodland (Forestry Commission 1984; Peterken & Allison 1989; Spencer & Kirby 1992).

However change at the stand scale is inevitable; many of the species present when it is young are not present later on in the rotation in either natural and unmanaged stands or managed ones (Mitchell & Kirby 1989). Species with restricted requirements (in terms of stand age and condition) must move elsewhere as a particular becomes unsuitable. However in a landscape where woodland exists only as isolated patches movement between woods may be limited for many of the species of highest conservation value (eg Peterken & Game 1984). Therefore continuity of a range of conditions must be maintained at the wood scale - it is impossible at the stand scale and is often ineffective at the landscape scale. The grid system of plots provides a means of testing whether this has been achieved at Wytham. The wood is large enough such that changes in one area may be matched by opposite changes elsewhere. Thus the wood appears stable for some features e.g. canopy cover of oak, ash and sycamore; for other features relatively small changes at any one point repeated over the whole wood can be identified as a significant trend e.g. the decline in woody species richness.

We do not propose that this approach is the best possible, it has weaknesses and is requires considerable resources to set up in this level of detail. Nevertheless it has met its proponents objectives and the lessons that it provides should be considered by those planning other woodland monitoring schemes.

References

BUCKLEY,G.P., BOLAS,M.& KIRBY,K.J. 1994. Some aspects of treefall-induced soil disturbance of understorey vegetation development following the storm of 1987. In *Ecological responses to the 1987 Great Storm in the woods of south-east England* edited by K J Kirby & G P Buckley, pp81-104. Peterborough, English Nature (English Nature Science 23).

CLAPHAM,A.R., TUTIN,T.G. & WARBURG,E.F. 1981. *Excursion flora of the British Isles*. Cambridge, Cambridge University Press.

DAWKINS, H.C.D. & FIELD,D.R.B. 1978. *A long-term surveillance system for British woodland vegetation*. Oxford, Commonwealth Forestry Institute Occasional Paper 1.

ELTON, C.S. 1966. *The pattern of animal communities*. London, Methuen.

FARMER A. 1994. *Changes in the soil chemistry at Wytham Wood (Oxfordshire) 1974-1991*. Peterborough, English Nature (Research report 108).

FORESTRY COMMISSION 1984. *Great Britain: census of woodlands and trees*. Edinburgh, Forestry Commission.

FORESTRY COMMISSION 1985. *The policy for broadleaved woodland*. Edinburgh, Forestry Commission.

FULLER, R J 1995. *Birdlife of woodland and forest*. Cambridge, Cambridge University Press.

GIBSON, C.W.D. 1986. Management history in relation to changes in the flora of different habitats on an Oxfordshire estate, England. *Biological Conservation 38*, 217-232.

GOSLER, A. 1990. The birds of Wytham - an historical survey. *Fritillary 1*, 29-74.

GRAYSON,A.J. & JONES, E.W. 1955. *Notes on the history of the Wytham Estate with special reference to the woodlands.* Oxford, Imperial Forestry Institute.

HILL, M.O. 1979. *TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Ithaca, Cornell University (Ecology & systematics section).

HORSFALL, A.S. & KIRBY, K.J. 1985. *The use of permanent quadrats to record changes in the structure and composition of Wytham Woods, Oxfordshire.* Peterborough, Nature Conservancy Council (Research & survey in nature conservation 1).

KIRBY,K.J. 1994. Storm-related monitoring in a wider context.In *Ecological responses to the 1987 Great Storm in the woods of south-east England* edited by K J Kirby & G P Buckley, pp163-170. Peterborough, English Nature (English Nature Science 23).

MITCHELL, & KIRBY, K.J. 1989. *Ecological effects of forestry practices in long-established woodland and their implications for nature conservation.* Oxford, Oxford Forestry Institute, Occasional Paper 39.

OSMASTON, F.C. 1959. *The revised working plan for the Wytham Woods or the Woods of Hazel for the period 1959/60 to 1968/69.* Oxford, Oxford Forestry Institute (unpublished report).

PETERKEN, G F 1977. Habitat conservation priorities in British and European woodlands. *Biological Conservation 11,* 223-236.

PETERKEN,G.F. & ALLISON, H. 1989. *Woods, trees and hedges: a review of changes in the British countryside.* Peterborough, Nature Conservancy Council (Focus on nature conservation 22).

PETERKEN, G.F. & BACKMEROFF, C. 1988. *Long-term monitoring in unmanaged nature reserves.* Peterborough, Nature Conservancy Council (Research & survey in nature conservation 9).

PETERKEN, G.F. & GAME, M. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology 72*,155-182.

PETERKEN,G.F. & JONES, E.W. 1987. Forty years of change in Lady Park Wood: the old growth stands. *Journal of Ecology 75*, 477-512.

PETERKEN,G.F. & JONES, E.W. 1989. Forty years of change in Lady Park Wood: the young growth stands. *Journal of Ecology 75*, 401-429.

SPENCER,J.W. & KIRBY,K.J. 1992. An inventory of ancient woodland for England and Wales. *Biological Conservation 62*, 77-93.

THOMAS, R.C. & KIRBY, K.J. 1992. Seventeen years of change in the structure and composition of Wytham Woods (Oxfordshire). *Aspects of Applied Biology 29*, 49-55.