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Forty-year changes in the canopy and the understorey in Wytham Woods

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Summary

This study investigates changes in the composition of part of Wytham Woods (southern England), between the 1960s and 2007. The study focussed on an area of ~4 ha shown on a 1961 aerial photograph, part former open common, part ancient woodland. Changes in the canopy appearance were considered using a recent (1999) aerial photograph. Trees and shrubs were recorded in a 200 × 10 m transect to illustrate current stand structure across the historic management division. In the north-east corner of the area, tree diameters and understorey abundance from 1968 were compared with the current stand structure.

Since the 1950s, *Fraxinus excelsior* has colonized the open areas. Tree growth was estimated from comparison of diameter/girth measurements from 1968 and 2007. *F. excelsior* diameter increment was greater than that of *Acer pseudoplatanus* and both showed faster growth than *Quercus robur*. Some canopy trees died, but no large gaps formed in the closed woodland. The abundance of understorey stems declined. The current stand structure reflects effects of past management, browsing pressure and climatic stresses over the last four decades. Multiple causes of change are probably commoner than single factors in explaining woodland structure.

Introduction

Data on long-term change in forest structure and function are necessary for the establishment and development of sustainable forest management practices that mimic natural processes (Lindenmayer *et al.*, 2000; Kirby *et al.*, 2005). In Britain, long-term monitoring and survey data vary in their spatial scale and focus, from broad-scale surveys such as the Countryside Survey (Haines-Young *et al.*, 2000) or the National Inventory of Woodland and Trees (Forestry Commission, 2003), to detailed surveys of particular stands, such as at Lady Park Wood (Gloucestershire) (Peterken and Jones, 1987, 1989; Peterken and Mountford, 1995).

Hopkins and Kirby (2007) summarized the ecological changes in British broadleaved woodland since 1947. Woodland habitats in Britain have become more ecologically isolated (although the total forest area has increased) because of the loss of other semi-natural habitats such as hedges and field trees in the surrounding landscape. Within woods, the main causes of woodland changes over this period include climate change, eutrophication and acidification, adjacent agricultural intensification, increased shade and changes in grazing regimes. Some of the variations over time can be ascribed to specific events, an exceptional storm for example; others are the result of impacts operating over many years such as the effects of atmospheric nitrogen deposition. Some are deliberate and within the control of forest managers, for example, the shift from traditional coppice to high forest management radically changes the woodland structure; others are not. At any one site, the significance of different impacts varies; forest managers therefore need to be able to identify how the decisions they make will interact with those factors over which they have little or no control.

In this paper, we investigate the long-term changes in species composition and structure, in the canopy and in the understorey layer in just one part of Wytham Woods namely Holly Hill Copse. The inspiration was an aerial photograph, taken in 1961 (Elton, 1966), which covers an area of ~4 ha of mixed woodland. A historic boundary bank (Figure 3) marks the division between what had once been open common (indicated by large trees and extended glades) and ancient woodland with more continuous canopy.

Our aims were to explore (1) changes that had taken place in the composition and structure of this patch of mixed woodland between the 1960s and 2007 and (2) what biotic and abiotic factors might best explain the changes. Our expectations were that infilling of the open ground by young trees would be the predominant change in the recent woodland: F.C. Osmaston (unpublished data) in the management plan for the Woods comments on the abundance of young stems that were developing in many places following the virtual elimination of rabbits from myxomatosis (Southern, 1955). In the ancient woodland, the overall change would be more variable, depending on the balance between tree deaths and gap creation and subsequent regeneration and growth of young trees within the gaps. Shade-bearing trees were expected to increase in cover.

Site

Wytham Woods in Oxfordshire, southern England, is a 410-ha area of mixed woodlands and grassland, on a hill 6 km north-west of Oxford city (centred on 1° 20′W, 51° 47′N; UK National grid reference SP462082) (Figure 1). The hill consists of corallian limestone on top of sand, with Oxford clay on the lower slopes. The mean monthly precipitation is between 31 and 77 mm (calculated for the period 1993–1997), the mean monthly temperature is between 4 and 17.1°C (calculated for the period 1993–1997, source: Environmental Change Network (ECN) database).

The Woods, owned since 1943 by the University of Oxford, have been the subject of ecological research carried out over many decades (Kirby *et al*., 1996; Buse *et al*., 1999; Morecroft *et al*., 2001; Kirby, 2004; McCleery *et al*., 2004). Since 1992, the Woods have been part of the UK ECN, under which environmental (climate, air pollution and soils) and species population parameters have been monitored (Sykes and Lane, 1996). The management history of the site is also well documented (Gibson, 1986).

Approximately, one-third of the woodland is comprised of ancient woodland, traditionally managed by coppicing, although this practice has now been abandoned. Hazel (*Corylus avellana* L.) was the main coppice species but locally sycamore is abundant (*Acer pseudoplatanus* L.), both as former coppice and maiden stems. Pedunculate oak (*Quercus robur* L.) is present as standard trees in the former coppice areas. A second third of the Woods is naturally regenerated secondary woodland in which ash (*Fraxinus excelsior* L.) and sycamore are dominant tree species. There are some scattered large trees, among the younger growth, that had previously been growing as scattered individuals on the open common grazing (Gibson, 1986). The remaining areas are plantations, some from the nineteenth century, but most younger than 60 years old, or open grassland.

The part of Holly Hill Copse covered by the 1961 aerial photograph (Figure 2a), centred on SP 46230863, includes both ancient woodland and former open common. The photograph (taken by Dr J. K. S. St Joseph, 9 June 1961) is black and white and ~1 : 1500 scale.

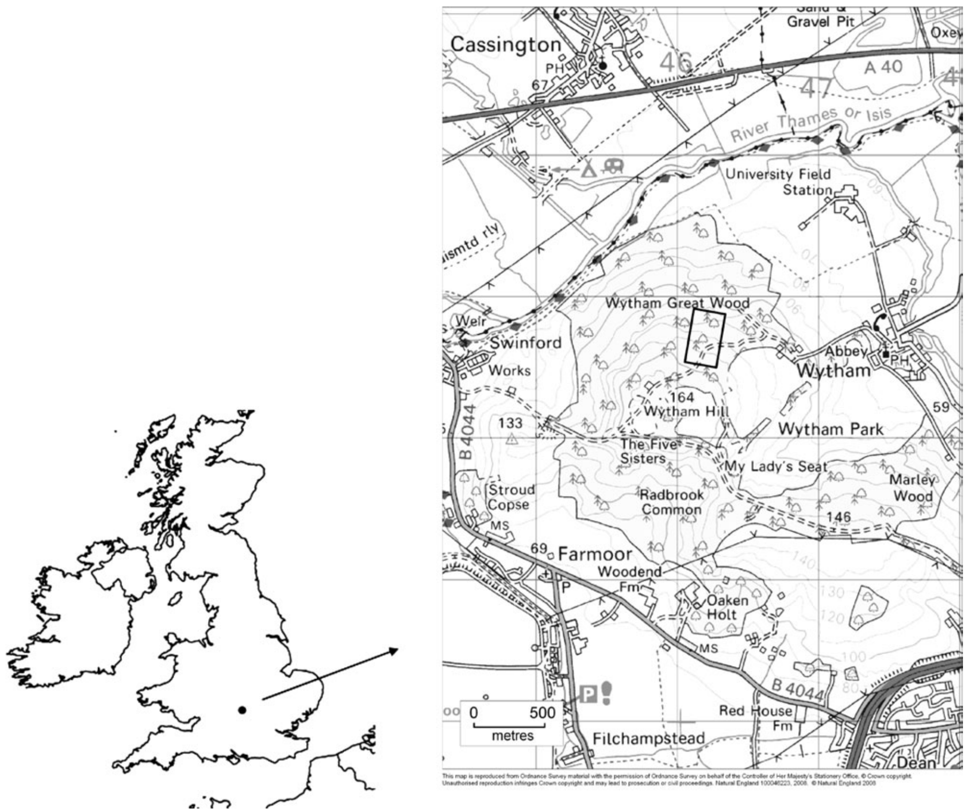

Figure 1. The location of the sampling site in Wytham Woods, Oxfordshire, UK (Reproduced by permission of the Ordnance Survey, @ Crown copyright).

Methods

Initially, we used two recent aerial orthophotographs: one from 1999 (origin: Natural England, Figure 2b), referenced to the British National Grid, and another from the Google Earth (dated 2007) to compare the overall change in the canopy of the study area since the 1961 photograph (Figure 2a). The aerial photograph from 1961 and accompanying tree map (Elton, 1966) were adjusted to the 1999 photo and the Google Earth photo using the rubber sheet technique (ArcGIS 9.2). This technique refers to the process by which a layer is distorted to allow it to be joined seamlessly to an adjacent geographic layer of matching imagery, e.g. satellite imagery by using a set of common points (e.g. Petry and Somodevilla, 2000). The tree map was then transformed into a vector layer.

Two field surveys were carried out in May to June 2007. Firstly, a 10 × 200 m transect was established running south-north through the area covered by the photograph. This was mainly in the former common, but a quarter was in ancient woodland, with the centre point located at the National Grid Reference grid point SP461086 (Figure 3). From this point, ten 10 × 10 m^2 adjacent sections were recorded in a northerly direction and ten 10 × 10 m sections to the south – the plots were then renumbered 1–20, starting at the southern end of the transect. The location of each tree with a diameter larger than 2.5 cm was recorded and its diameter measured at breast height (d.b.h.) (1.3 m). For stems with d.b.h. less than 2.5 cm, their species and diameter were recorded, but not their locations. Basal area of trees in the vicinity was estimated by taking a relascope sweep at 10 m intervals along the transect.

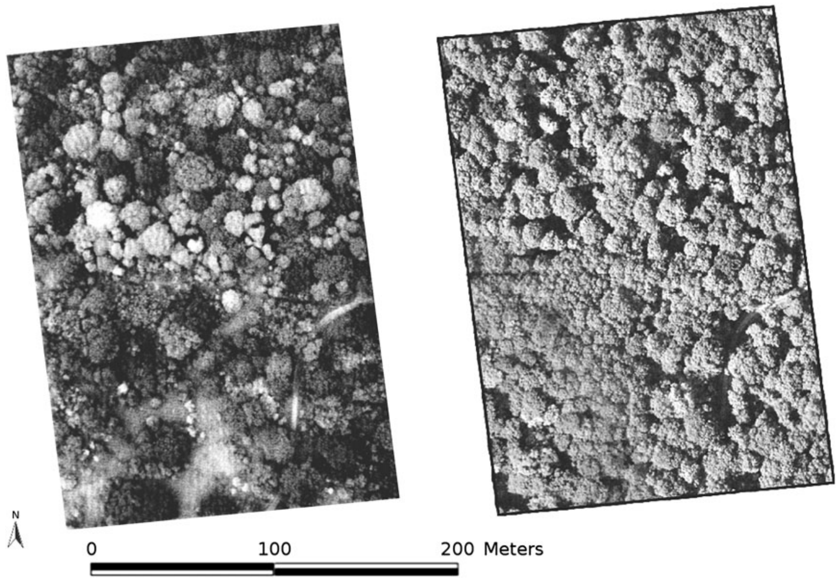

Figure 2. The aerial photograph of the sampling site (grid reference SP 461086) from 1961 (left) (Elton, 1966) and 1999 (right). The photographs have been re-orientated to run south-north compared with the version in Elton (1966). Note the increased canopy closure and abundance of small-canopied trees in the south of the area by 2007.

The second set of measurements was made in the north-east quarter of the area shown in the 1961 photograph (Figure 3), mainly in the ancient woodland. This had been studied in 1968 by Paviour-Smith and Elbourn (1993) to assess the amount of dead and dying wood still attached to trees, as part of a study of the fauna of this habitat. All canopy trees (>4.6 m high) in a 1.2-ha area were mapped and their girth and canopy area measured. The number, size and state of health of understorey stems (tree and shrub species > 1 cm) were assessed in a systematic grid of one hundred and twenty-five 10 × 10 m^2squares. Both live and dead stems were included; the majority of stems were alive, although in the most crowded squares many showed some signs of dieback. The understorey was classified according to stem diameter: Class 0 (d.b.h. 1–2 cm), Class 1 (d.b.h. 2.1–5 cm), Class 2 (d.b.h. 5.1–10 cm), Class 3 (d.b.h. 10.1–15 cm) and Class 4 (d.b.h. > 15 cm).

In 2007, the d.b.h. of the canopy trees across the whole of the 1968 grid was remeasured (excluding a few shrubs such as hawthorn (*Crataegus monogyna* Jacq. and elder (*Sambucus nigra* L.) included in the 1968 records). The layout of the 1968 grid was reconstructed from the known positions of surviving canopy trees in relation to the grid. The understorey was resampled in 20 of the 10 × 10 m plots spread across six lines over the whole 1.2-ha area (Figure 3). Within each plot, the understorey trees and shrubs (both live and dead) were counted, as in 1968 study, according to size class (see above), except that if their d.b.h. was above 15 cm (Class 4), then their actual d.b.h. was measured. Basal area of trees in the vicinity of each plot was estimated from a relascope sweep at the plot corner.

Data analysis

The area of open ground, i.e no canopy, was estimated using Geographic Information Systems (GIS) from the 1961 and the Google Earth photograph which proved to be more visible and reliable than the 1999 photograph shown in Figure 2b. The proportions of the open areas were calculated separately for the ancient woodland and the open common area.

The canopy composition for the area shown in the 1961 photograph was also estimated using a

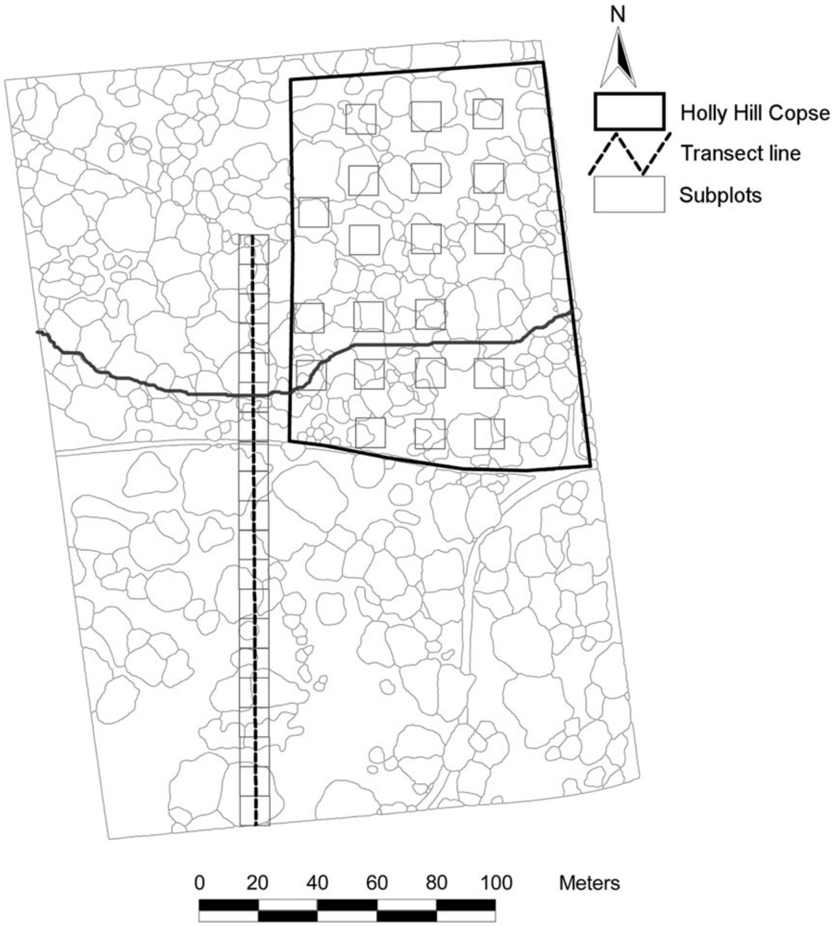

Figure 3. The location of the south-north transect established in 2007 and the subset of 21 plots from the 1968 grid, both overlain on the stand map drawn by C.A. Elbourn after the 1961 aerial photograph (published in Elton, 1966). The former common lies to the south of the boundary bank shown by the thick black line, the former ancient woodland to the north.

systematic dot pattern superimposed on the canopy map, with one dot (425 in total) for approximately each 100 m^2. Each point was classified according to whether it fell in the former common or ancient woodland areas, in the north-east corner used in the Paviour-Smith and Elbourn (1993) study, or in an ~30-m strip along the transect line; because of possible photographic distortions, it is difficult to place the transect line precisely in relation to the photograph, so a wider strip was used. The significance of differences in the occurrence of the main species was tested using chi-squared analysis on the numbers of points.

Canopy area estimates for individual species were not made for the 2007 photograph; we did not have time to identify and map every individual canopy because of the many smaller trees that have grown up into the canopy since 1961. However, there is a strong relationship for common broadleaved trees between stem diameter and canopy diameter (Savill, 1991); similarly for the 105 trees measured in the north-east grid in 1968 by Paviour-Smith and Elbourn, the relationship between canopy area and basal area was highly significant ($P < 0.001$) with an R-squared of 73 per cent (canopy area = 15.5 + 362 × basal area). Hence, basal area data have been used as a surrogate for canopy area in 2007. For the transect and the north-east corner (the grid), the species composition was compared in terms of the relative basal area calculated from the stem diameter measurements and relascope sweeps taken in the 10 × 10 sections of the transect and the grid samples.

For the 1.2-ha grid, the species and d.b.h. distribution of the canopy trees (converted from the original girth measurements) recorded in 1968 were compared with those measured in 2007. The differences between the d.b.hs measured in 1968 and 2007 were calculated in different d.b.h. ranges, based on their 1968 d.b.h. (0–20, 20–40, 40–60, 60–80 and 80–100 cm) for each species. Some trees recorded in 1968 were not present in 2007; to test whether this might introduce a bias in the results, the trees were re-recorded and those 'missing' in 2007 were compared in terms of their 1968 d.b.h.. The non-parametric Mann–Whitney *U*-test was used because of the small sample size and the non-normal distribution.

For the understorey records from the grid, the 1968 data from the 20 plots resurveyed in 2007 were compared with the 1968 data from all the plots in terms of numbers of individuals in different size classes. This provided a test of how well the 20 plots might represent the whole area. For just the 20 resurveyed plots, the number of individuals by size classes and by species were then compared for 1968 and 2007. In this comparison, canopy trees were added to Class 4 (>15 cm d.b.h.) for both datasets because by 2007, there was no clear distinction between the original canopy trees and those in the Class 4 category in terms of their canopy contribution.

We used Statistica 6 software (StatSoft, 2001) for the statistical analyses.

Results

Evaluation of the aerial photographs

In the 1961 photograph oak and ash contribute similarly to the canopies of the former common and ancient woodland but the common had much more open space, whereas sycamore was most abundant in the ancient woodland (Figure 4).

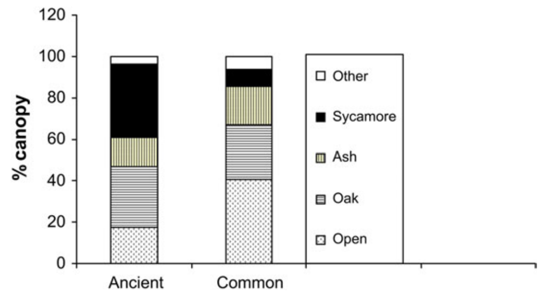

Figure 4. Percentage contribution to canopy layer (1961) based on a superimposed pattern of 425 points across the photograph of which 184 fell in the ancient woodland and 241 in the former common land.

The GIS analysis confirmed that in 1961, the common was ~40 per cent open canopy and the ancient woodland ~20 per cent open canopy. By 1999 (Figure 2a,b), the southern half of the sampling site (the formerly open area) had closed over, as had the smaller gaps in the north-east corner. The ride visible in the middle of the 1961 photo is no longer apparent although it is still just traceable on the ground. The crowns of the large trees appear to have increased with little evidence for the formation of new canopy gaps. The GIS analysis of the 2007 Google Earth photograph found less than 3 per cent open space in both areas.

South-north transect

From the point counts on the 1961 photograph, most of the open space along the line of the transect was in the south, in the former common, whereas the sycamore records were concentrated in the north in the ancient woodland. By 2007, the open canopy areas had almost all closed over and 95 trees and 30 shrub stems were recorded with d.b.h. >2.5 cm actually in the 200 × 10 m transect (Figure 5).

Numerically, ash dominates in the canopy, while hawthorn was the most common shrub. The largest diameter trees were, however, oak and sycamore. Sycamore remained present in greater numbers and with bigger individuals in the northern half of the transect; ash was more evenly spread throughout. The dense ash patches

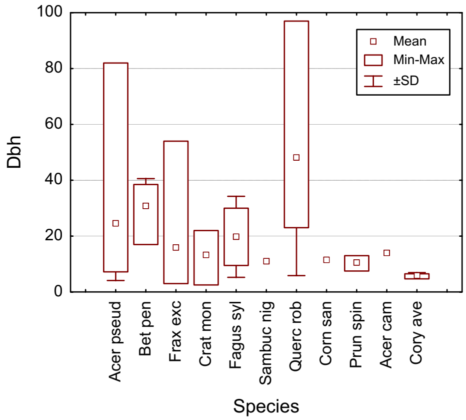

Figure 5. Mean, minimum, maximum and standard deviation of d.b.h. of the different species (d.b.h. > 2.5 cm) recorded in the transect (n_{all} = 125, $n_{Acer\ pseudoplatanus}$ = 16, $n_{Betula\ pendula}$ = 5, $n_{Fraxinus\ excelsior}$ = 68, $n_{Crataegus\ monogyna}$ = 21, $n_{Fagus\ sylvatica}$ = 2, $n_{Sambucus\ nigra}$ = 1, $n_{Quercus\ robur}$ = 3, $n_{Cornus\ sanguinea}$ = 1, $n_{Prunus\ spinosa}$ = 4, $n_{Acer\ campestre}$ = 1 and $n_{Corylus\ avellana}$ = 3).

in the middle plots (sections 8–13) correspond to the most open canopy area on the 1961 photograph. Birch (*Betula pendula*) and shrubs, particularly hawthorn, occurred mainly in the southern half of the transect (Table 1).

The basal area estimates by species show that in 2007, ash's contribution was much more than its canopy contribution along the transect in 1968 (Table 2).

Holly Hill Copse grid: canopy tree mortality and growth

In 1968, 105 trees were recorded as canopy trees in the grid (Table 3): 29 oak, 65 sycamore, seven ash, 2 field maple (*Acer campestre* L.), 1 beech (*Fagus sylvatica* L.) and 1 (*Pinus sylvestris* L.). The largest three trees with a diameter above 1 m were all ash trees and still alive in 2007. Sycamores were on average smaller than the oak and ash.

By 2007, 34 trees were no longer present: 4 ash, 3 oak, 1 field maple and 26 sycamore. Nine were still present as large fallen trunks (mean d.b.h. in 1968 was 59 cm (SE 7 cm) including three each of the missing ash and oak); 13 smaller stems appear to have died (all sycamore, mean d.b.h. in 1968 35 cm (SE 2 cm)) leaving little trace other than occasional remnant stumps. The other 11 sycamore and 1 ash had probably been cleared as part of the ride widening on the eastern edge of the grid, although it is possible that some had died previously.

The mean diameter in 1968 of all the trees not re-recorded in 2007 was 42 cm, with the minimum of 24 cm and the maximum of 100 cm. Mann–Whitney *U* testing showed no significant differences between the diameter in 1968 of these missing trees and the surviving trees. However, the effect of differential loss of smaller trees on the statistics for small populations can be seen in the sharply increased mean and minimum d.b.h. figures for ash. When the results for individual trees were compared, however, most showed some growth in diameter but with differences between size classes and species. Sycamore for example grew faster than oak, especially in the d.b.h. class 40–60 cm category (Figure 6). (There were too few ash surviving to make a valid comparison across size classes.)

In 1968, only eight trees were considered to be contributing to the canopy within the twenty 10 × 10 m plots resurveyed in 2007, with a further nine sub-canopy trees of diameter greater than 15 cm. By 2007, there were the eight original canopy trees plus 42 others (22 ash, 18 sycamore and 2 beech) with a diameter greater than 15 cm. At least 33 of the 'new' canopy trees must have been less than 15 cm in 1968 and 8 less than 10 cm, even if all the trees in Classes 3 and 4 in 1968 in these plots had grown up into the canopy by 2007.

To estimate the growth of these 42 new canopy trees, we assumed a nominal d.b.h. for them in 1968 of 15 cm (the upper bound of class 3 in 1968 from which most were probably derived). The difference between the measured (2007) d.b.h. and the assumed 15 cm d.b.h. in 1968 gives an estimated mean diameter growth of 10.2 cm for ash and 9 cm for sycamore.

As in the transect area, the contribution of ash to the overall basal area in 2007 was much greater than its canopy contribution in 1968 (Table 2).

Holly Hill Copse grid: changes in the understorey

In 1968, in the whole grid, 5509 individuals of 15 trees and shrub species were recorded in the

Table 1: Distribution of tree and shrub stems by transect section from south to north

Transect section	No. of stems	*Acer pseudoplatanus*	*Fraxinus excelsior*	*Betula pendula*	Other trees	Shrubs
Old common						
1	4	2	1	1	0	0
2	6	3	0	1	1	1
3	3	0	0	1	1	1
4	10	0	1	2	2	5
5	5	0	0	0	0	5
6	5	0	0	0	0	5
7	0	0	0	0	0	0
8	19	0	15	0	0	4
9	7	0	6	0	0	1
10	1	0	1	0	0	0
11	13	2	6	0	1	4
12	6	3	3	0	0	0
13	25	1	24	0	0	0
14	8	2	6	0	0	0
15	0	0	0	0	0	0
Ancient woodland						
16	2	2	0	0	0	0
17	3	0	3	0	0	0
18	1	0	1	0	0	0
19	1	1	0	0	0	0
20	6	0	1	0	1	4

Table 2: The percentage contribution of different species in the transect and grid areas based on canopy cover in 1968 and two independent measures of basal area in 2007

Tree species	*Quercus robur*	*Acer pseudoplatanus*	*Fraxinus excelsior*	Other	Ride*	Open sky†
Transect area						
Canopy cover 1961‡	24	15	26	4		31
Basal area 2007						
From d.b.h.§	18	43	28	11		
From relascope sweep¶	19	55	23	5		
North-east grid area						
Canopy cover 1961‡	29	12	26	6	6	21
Basal area 1968#	39	15	33	6	6	
Basal area 2007						
From d.b.h.§	36	28	28	8		
From relascope sweep¶	25	30	39	6		

Tree species: *Q. robur*, *Acer pseudoplatanus*, *Fraxinus excelsior*.

* Trees present in 1968 but lost to ride widening.

† The comparison was also done excluding the 'open' contribution in 1968. It did not affect the general pattern of the results.

‡ Based on count of 46 dots falling within the transect area and 107 dots in the grid area on the 1961 photograph.

§ Calculated from diameter measurements, assuming circular stems within the transect, so does not include contribution of large trees adjacent to the transect.

¶ Based on relascope sweeps and hence estimates basal area over a wider areas than just the transect.

Based on trees measured by Paviour-Smith and Elbourn (1993).

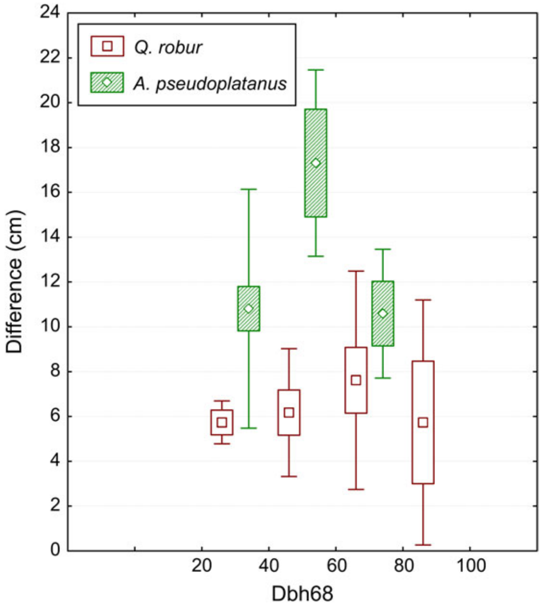

Figure 6. Differences between d.b.h.s measured in 1968 and 2007 in various size classes based on 1968 d.b.h. data ($n_{Quercus\ robur}$ = 26, $n_{Acer\ pseudoplatanus}$ = 36; mean; box: mean ± SE; Whisker: mean ± SD).

understorey (Paviour-Smith and Elbourn, 1993). Sycamore and ash saplings were very abundant and several shrub species, such as spindle (*Euonymus europaeus* L.), and elder were present in great numbers.

The 20 plots resurveyed in 2007 were representative of the grid as a whole: they covered ~16 per cent of the whole area and contained ~16 per cent (910) of the tree and shrub individuals in 1968. Only a few species rare in the grid, such as horse-chestnut (*Aesculus hippocastaneum* L.) and pine, were not present.

By 2007, birch, willow (*Salix* spp.), spindle, elder and dogwood (*Cornus sanquinea* L.), which had been present, were not found in the re-recorded plots although they still occurred at low density elsewhere on the grid. Ash, sycamore and hawthorn remained relatively common (Table 4), but the overall number of stems had decreased dramatically (Figure 7). There were no individuals found in the 1–2 cm class, and only six with d.b.h.: 2.1–5 cm. There was less of a decline in the larger size classes, and by 2007, there were more trees above 15 cm d.b.h. (including the canopy trees) than in 1968.

Discussion

The effect of management history

The open common on Wytham Hill had formerly been used for grazing by sheep and cattle (C. Gibson, personal communication; Gibson, 1986). Stock grazing gradually declined but was replaced by wild rabbit grazing. After the myxomatosis epidemic in the 1950s, the last main grazing agent, the rabbit, was temporarily eliminated. An intense wave of regeneration began in the formerly open areas (Southern, 1955; F.C. Osmaston, unpublished data).

In our study area, the 1961 aerial photograph clearly identifies the open nature of the former common land, although by 1968 this had filled with bracken and bramble as well (Elton, 1966). The regeneration pulse is also reflected in the dense understorey in 1968 in grid plots. By the 1999 photograph, enough of this regeneration had grown up to fill the gaps shown in 1961, reflected for example in the groups of young ash poles found in the south-north transect.

The northern area had been managed as a coppice stand and then as a high forest before it was abandoned. Very little management took place in this area after the 1960s apart from the recent clearance of trees and shrubs along the eastern edge of the grid to widen the ride (N. Fisher, personal communication).

The loss of open space seen in the former common section is similar to that described by Hopkins and Kirby (2007) for British broadleaved woodland generally. However in Wytham Woods as a whole, the closing over of areas such as Holly Hill Copse has been at least partially offset by opening up of other stands by management or natural disturbance (Kirby *et al.*, 1996).

The characteristic large trees of open grown trees (ash and oak) in the former common in the south of the study area can still be identified in the aerial photographs. In the northern part of the study area, large oaks are also common but are more likely to be the surviving standards from the former coppice with standards management. The lack of smaller size classes of oak (under 30 cm in diameter), in comparison to the abundant regeneration over the last 50 years of ash and sycamore, has been found in other studies and reflects in part changing management practice

Table 3: Survival and d.b.h. for the 105 canopy trees recorded in 1968 on the Holly Hill Copse grid

	No. of trees	Mean d.b.h.	Minimum d.b.h.	Maximum d.b.h.	SD
All species					
1968	105	48.6	24.2	120.7	21.8
2007	71	61.3	22.6*	149.3	24.1
Main individual species					
Acer pseudoplatanus					
1968	65	36.7	24.2	75.4	11.6
2007	40	48.7	22.6*	87.9	15.7
Q. robur					
1968	29	65.0	35.3	100.3	15.6
2007	26	70.6	40.1	98.4	15.5
F. excelsior					
1968	7	84.0	48.1	120.6	31.7
2007	3	130.7†	118.4†	149.4	16.4

* Small reductions in the minimum d.b.h. for 'all species' and *A. pseudoplatanus* may be due to differences in how the stems were measured, rather than actual loss of d.b.h.

† The large increase in mean and minimum d.b.h. for ash reflects the loss of four of the smaller ash present in 1968.

Table 4: Number of individuals of the different understorey and canopy species recorded in the 20 subplots in 1968 and in 2007

Understorey species in 1968 and 2007	<15 cm d.b.h. (classes 1–3)		>15 cm d.b.h. (class 4 plus canopy trees)	
	1968	2007	1968	2007
Acer campestre	9	2	1	1
Acer pseudoplatanus	260	45	9	19
Corylus avellana	10	1	0	0
Crataegus monogyna	13	14	0	1
Euonymus europeaeus	14	0	0	0
Fagus sylvatica	2	1	0	2
Fraxinus excelsior	585	11	2	23
Quercus robur	1	0	5	5
Salix spp.	4	0	0	0
Sambucus nigra	3	0	0	0

and oak's need for large open areas for regeneration (Vera, 2000; Kirby *et al.*, 2005). By contrast, Marigo *et al.* (2000) considered the reproductive traits of ash (e.g. compromise between seed number and weight) and vegetative (e.g. sprouting) made it very successful in colonizing open areas next to forest patches – the situation observed at Wytham.

Sycamore was introduced in this part of the wood in the nineteenth century and is mainly in the north of the Woods; the northern half of the transect and the grid both included areas of sycamore abundance. It has been considered a highly invasive species (Peterken, 1996) and in Wytham Woods is often more abundant in areas where the canopy was relatively open at the time of tree establishment (Morecroft *et al.*, 2008). Nevertheless, on the whole, ash appears to have been more successful in establishing in the open southern part of the transect. Ash parent trees were more frequent in the former common than sycamore, but no area of the transect is more than ~100 m from a sycamore, so should be within dispersal range. Possibly, the sycamore seeds were less effective than ash at establishing in the dense rabbit-grazed turf prior to myxomatosis – consistent with its regeneration being more abundant in disturbed areas.

The greater frequency of the less common, tree and shrub species in the southern part of the transect, on the more open former common, was expected, given their light-demanding requirements. The decrease in their frequency and abundance over the last 40 years is consistent with the expected successional trend but also mirrors a decline of shrubs in Wytham (Kirby *et al.*, 1996), and in other woods throughout Britain (Crampton *et al.*, 1998; Kirby *et al.*, 2005) that is linked with the increased browsing pressure from large herbivores.

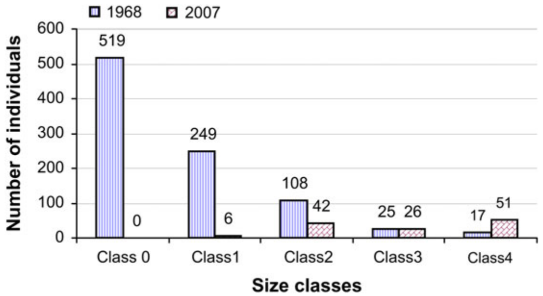

Figure 7. Number of understorey individuals in the different size classes in 1968 and 2007 recorded in the 20 subplots. Numbers on columns indicate the data. Diameter class: Class 0 (1–2 cm); Class 1 (2.1–5 cm); Class 2 (5.1–10 cm); Class 3 (10.1–15 cm); Class 4 (>15 cm) which includes canopy trees as well.

The impact of increasing deer numbers

The population density of various deer species has increased substantially in the last 75–150 years both in Europe and in North-America (Cote *et al.*, 2004) and has become a major ecological force in British woodland in the last decade (Fuller and Gill, 2001). Increased deer numbers have a significant effect on the composition and abundance of trees and shrubs (Gill and Beardall, 2001) and can limit height growth and regeneration (Hester *et al.*, 2000).

In Wytham, deer populations substantially increased after 1968. Fallow deer (*Dama dama* L.) were present in very low numbers (ca. 20) until the 1970s; however, their numbers began to increase to hundreds in the 1980s and 1990s (Perrins and Overall, 2001). Roe deer (*Capreolus capreolus* L.) remained in low densities in Wytham, but muntjac (*Muntiacus reevsii* Ogilby) showed a similar increase in density to that of fallow, since their arrival in Oxfordshire in the mid-1970s (Perrins and Overall, 2001).

Much of the current population of young trees thus derives from a window of low grazing pressure that occurred after the decline of rabbits in the 1950s and before the increase of the deer population (1970s onward). After the 1970s, recruitment became increasingly difficult. The wood has, however, now been fenced since 1989 and there are systematic approaches to reduce the deer population within the wood. Casual observations, by the authors, suggest that a new cohort of saplings is gradually starting to develop as a consequence of the reduced browsing pressure, though these are still generally less than 30 cm high and 1 cm d.b.h.

Climatic stresses and the effects of climate change

Global temperatures are gradually rising, and seven of the 10 hottest years on record have occurred during the 1990s (IPCC, 1996; Broadmeadow, 2000; Perrins and Overall, 2001). In the last four decades, these climatic events and stresses may have played an important role in the establishment and growth of trees and shrubs. There were for example serious droughts in 1976, 1995–1997 and 2003. Although both ash and sycamore are often associated with fresh or moist soils (Savill, 1991), ash appears to tolerate drought somewhat better. Morecroft *et al.* (2008) found that sycamore in Wytham showed slower d.b.h. increase in the period 1993–2005 than ash did in every size class, and the d.b.h. increment of oak was similar to the d.b.h. increment of sycamore. Sycamore also showed a significantly higher growth rate during the relatively wet period 1999–2002. Sycamore came into leaf earlier than oak and ash in almost every year of the study period, but the longer growing season may not outweigh its reduced growth due to drought sensitivity. The higher d.b.h. increment of ash that we found in the Holly Hill Copse grid trees could be in part the result of the droughts.

An increase in extreme events such as storms may also be a consequence of climate change. In Wytham, this could have a particularly serious effect on the population of veteran trees – the open grown ashes of the old common and the oak standards in the former coppice with standards stands (Cleveland, 1997). Some of the missing trees in the grid plots had blown over, possibly in the severe storms of 1987 and 1990 and elsewhere in the Woods there has been a continuing gradual loss of old trees in most winters to windthrow.

The effects of climate change on woodland in the UK (e.g. Broadmeadow, 2000; Broadmeadow *et al.*, 2005) may also be indirect. In Wytham, populations of the grey squirrel, which can damage sycamore trees seriously, are favoured by mild winters. The same is true for deer. Milder winters may therefore facilitate the population increase of herbivores and other damaging factors or diseases (Broadmeadow, 2000; Broadmeadow *et al.*, 2005; Kirby *et al.*, 2005).

Conclusions

To prepare for future changes in tree growth and distribution, we need to understand past change. This study has illustrated how in even a very small area the current composition and stand structure reflect a complex interaction of human interventions including former land use and variations in active management and more 'natural' factors such as the changing grazing pressures and climate change.

The Woods are not in a stable state (if they ever have been over the last few hundred years) but are changing as a result of the 1950s cohort of ash and sycamore regeneration. Sycamore is more shade bearing, but both in regeneration capacity and growth ash seems likely to at least hold its own. The other major shade-bearing broadleaved tree in the Woods is beech. There was a single mature beech in the middle of the 1961 photograph area – and it has survived through to 2007. However, little successful regeneration has occurred. Concern about the expected spread of heavy shade-casters and impacts on the character of the wood do not in this stand seem to be justified.

Oak would not be expected to regenerate in the closed canopy ancient woodland, but, and contrary to some expectations (Vera, 2000), neither does it feature particularly in the regeneration on the former common, despite mature oak being spread through both the former common and ancient woodland. Indeed, this is one of the densest areas for oak in Wytham (24–29 per cent canopy cover in 1961) since in the Woods as a whole it tends to form only ~10–20 per cent of the canopy. Creating large gaps in the canopy may not necessarily therefore increase the amounts of young oak under current conditions. The emphasis in oak management should therefore be on maintaining the old trees (recognizing that these are a diminishing resource) and perhaps more active intervention through planting.

The key lesson therefore would seem to be to recognize the windows of opportunities, such as the regeneration phase of the late 1950s that are likely to shape significantly the future of the wood and to intervene strongly at these points; at other times, management, without major effort, may be unlikely to make major shifts in the wood.

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Conflict of Interest Statement

None declared.

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