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Effects of climate and management history on the distribution and growth of sycamore (*Acer pseudoplatanus* L.) in a southern British woodland in comparison to native competitors

Morecroft M.D.*[1], Stokes, V.J[2], Taylor, M.E.[3], Morison J.I.L.[4]

[1]Centre for Ecology & Hydrology, Maclean Building, Crowmarsh Gifford,
Wallingford. OX10 8BB. 01491 692461. mdm@ceh.ac.uk
* Corresponding author

[2]Forest Research, Alice Holt Lodge, Wrecclesham, Farnham, Surrey, GU10 4LH.

[3]Centre for Ecology & Hydrology, Oxford University Field Station, Wytham, Oxford.
OX2 8QJ.

[4] Department of Biological Sciences, University of Essex, Wivenhoe Park,
Colchester, CO4 3SQ.

Summary

Sycamore (*Acer pseudoplatanus* L.) is an invasive, non-native species in Great Britain and its management in conservation areas is controversial. Climate change adds further uncertainty to decision-making. We investigated the role of management history in determining present-day abundance and the effects of climatic variability on growth, photosynthesis and phenology at Wytham Woods, a UK Environmental Change Network (ECN) monitoring site. Relatively few sycamore trees were found in undisturbed ancient, semi-natural woodland and recent plantations, despite being common in other areas of the site. Sycamore grew more slowly than ash (*Fraxinus excelsior* L.), its principal competitor, but at a similar rate to pedunculate oak (*Quercus robur* L.) in the period 1993-2005. There were fewer sycamore than ash seedlings, regardless of which species dominated the canopy. Growth of sycamore was slower in dry periods than wet ones and lower photosynthetic rates were measured in canopy leaves under dry compared to wet soil conditions. This study therefore suggests that sycamore does not present a serious threat to undisturbed ancient woodland on the site and that it may eventually decline in areas of the site where it competes with ash, in the absence of disturbance. It may also decline under climate change if summer droughts become more frequent.

Introduction

Sycamore has expanded its range in north west Europe in recent centuries. It is non-native in Great Britain and has colonised widely since it was introduced, probably in medieval times (Jones, 1945). It grows quickly compared to most broadleaved species and can produce a good timber crop (Savill, 1997; Binggeli & Rushton, 1999). Its invasive nature has however led to sycamore being regarded as a threat to the conservation of native woodlands, particularly where ash has historically been the dominant tree species (Scurfield, 1959; Binggeli, 1992, 1993; Peterken, 1996). Attempts are often made to remove the species in conservation areas, although this is usually only practical for the most sensitive sites (Morton Boyd, 1992). The view of sycamore as a threat to biodiversity has moderated in recent years as studies have shown that it supports a range of epiphytes, herbivores and ground flora, comparable to those of many native species (Binggeli, 1993; Peterken, 2001). There is also evidence that sycamore and ash each tend to regenerate better under the canopy of the other species and may establish a cyclical pattern with dominance alternating between the two species (Waters and Savill, 1992; Savill *et al.*, 1995). Sycamore may therefore potentially offer good opportunities for combining wood production with the support of biodiversity in some circumstances, such as the creation of new farm woodlands, where preserving existing tree species composition is not a priority. However, sycamore remains a controversial species and the necessity for control to protect conservation sites is still a matter for debate. Much information on the species is essentially anecdotal and there is a need for more detailed scientific study.

Climate change adds to the complexity of the issues surrounding sycamore. Current projections (Hulme *et al.*, 2002) indicate that Great Britain is likely to become warmer, with proportionally less precipitation falling in summer, leading to an increased incidence of summer droughts in southern and eastern areas, including most of England. Modelling by Broadmeadow *et al.* (2005) indicates that the productivity of sycamore will decline in much of central, southern and eastern England because of its sensitivity to drought. The same projections indicated that most of its competitors, such as ash and pedunculate oak, would be less adversely affected. Drought sensitivity is consistent with sycamore's natural distribution, which is centred on cool, damp, mountainous regions in central Europe (Jones, 1945; Rusanen & Myking, 2003). It is also consistent with the observation that within semi-natural British woodlands, sycamore is most dominant in the relatively cool, wet areas of the north and west (Pigott, 1984; Rodwell *et al.*, 1991; Forestry Commission, 1997). These conjectures are however based on the extrapolation of correlations with geographical variations in present-day climate. Geographical patterns are not an infallible guide to the climatic sensitivities of species as distributions and productivity can also be influenced by, for example, soil type and management history. It is therefore important to understand the underlying processes which control species responses to climate change and to look for direct evidence of climatic impacts.

There is some evidence of sycamore's drought sensitivity, although examples are not extensive. Lemoine *et al.* (2001) and Tissier *et al.* (2004) present evidence from within the natural range of sycamore in France, that its xylem vessels are relatively susceptible to cavitation under dry conditions. During drought in the UK in 1976, Coultherd (1978) reported some death of sycamore, but only in association with sooty bark disease (*Cryptostroma corticale*).

Rising temperatures may have an effect on the competitive balance between sycamore and other species, distinct from any effects of an increased frequency of droughts. In particular, the sensitivity of phenology to temperature is well known and earlier leafing of trees in recent decades has been documented at the European scale (Menzel *et al.* 2006) and within the UK (Sparks & Carey, 1995; Fitter & Fitter 2002). There is some evidence (Fenn, 2005; T. Sparks, unpublished data) that the timing of sycamore leafing is more sensitive to temperature than that of ash and that its growing season is therefore lengthening to a greater extent. In these circumstances, warming may have the opposite effect to that of drought by giving sycamore a competitive advantage.

Further understanding of sycamore's ecology and ecophysiology is therefore necessary to develop a better understanding of its likely responses to climate change. Recent decades have seen a wide range of different weather conditions in Britain (Fig. 1). The summer of 1995 was very dry (Marsh, 1996) and was followed by two years of unusually low rainfall; the period 1998 to 2002 was, however, marked by very high precipitation. The summer of 2003 was extremely hot and dry. This range of weather conditions provided an opportunity to investigate the effects on sycamore. We have done this by bringing together a range of physical and biological monitoring data collected at Wytham Woods, in southern England, under the UK Environmental Change Network programme. This is a well-studied and instrumented site where it is also possible to take account of management history and to gain access to the tree canopy, by means of a walkway. This range of research and monitoring allows us to address the following questions:

1) Is there any difference in the extent to which sycamore has colonised different areas of Wytham Woods? Do different management histories make the stand more or less susceptible to invasion?

2) Is there any evidence that sycamore is out-competing ash or growing faster?

3) Has tree growth decreased or mortality increased in sycamore trees during dry compared to wet periods?

4) Does tree growth reflect changes in photosynthesis in the canopy during wet and dry periods?

5) Is there any interspecific difference in phenological responses to temperature which might affect the outcome of competition in the long-term?

Throughout the paper we compare sycamore with ash because of the interest in their relative competitive advantages and pedunculate oak, which is also found widely in British woods. Oak and sycamore are both accessible from a canopy walkway at Wytham. Earlier work in the canopy showed that photosynthesis of sycamore was lower than that of oak (Morecroft & Roberts, 1999). This work was carried out in the summer of 1996, which was a relatively dry year, following an extremely dry summer in 1995, leading to reduced soil moisture levels. One possible explanation for the difference in photosynthetic rates was a greater sensitivity of sycamore than oak to these dry conditions. A PhD study (Stokes, 2002), made similar measurements on the same trees in wetter conditions in 1999 and 2000 and gave us the opportunity to test this hypothesis.

Materials and Methods

Study site

Wytham Woods (51° 46’ N 1° 20’ W; UK National Grid: SP 46 08) covers approximately 400 ha and includes a wide range of different soil and vegetation types. It has been a research site, owned and managed by Oxford University, since the 1940s. Present and historical management of the site are well-documented (Gibson, 1986, Grayson & Jones, 1955) and tree, shrub and ground layer have been monitored since the mid 1970s (Dawkins & Field, 1978, Kirby *et al.*, 1996; Kirby & Thomas, 2000). Since 1992 the site has been part of the ECN, under which climate, air pollution, soils and selected animal populations have been monitored in addition to further recording of vegetation and tree growth (www.ecn.ac.uk; Sykes & Lane, 1996).

For the purposes of this paper five broad types of management histories can be recognised (Fig. 2), based on the work of Gibson (1986) and Grayson & Jones (1955): *1) Undisturbed ancient semi-natural woodland.* Ancient woodland is woodland which has had a continuity of forest cover since approximately 1600; the period for which historical records are usually available in England (Peterken, 1981). At Wytham, this woodland was managed as a ‘coppice with standards’ system (mixture of coppice stools interspersed with full height trees). However coppicing was discontinued over the course of the twentieth century and these areas have been largely unmanaged for between 40 and 100 years (differing locations were abandoned at different times). Hazel (*Corylus avellana* L.) is the most frequent coppice species and pedunculate oak the most frequent standard.

2) Disturbed ancient woodland. Ancient woodland areas which were formally managed as coppice with standards, but converted to high forest during the twentieth century. Timber has been extracted at various times but they have not been clear-felled. Extensive natural regeneration has occurred, along with some localised planting.

3) *Secondary woodland.* Areas which have naturally reverted to closed canopy woodland over the last 200 years, having previously been grassland or wood pasture, (with scattered trees but no continuous canopy). A small amount of localised planting has taken place and there has been some timber extraction.

4) *19th century plantations.* Formerly open areas which were planted in the 19th century. This planting was largely ornamental with widely spaced trees, particularly of beech (*Fagus sylvatica* L.). Management has been minimal in recent decades.

5) *20th century plantations.* Plantations, mostly of beech and pedunculate oak, mixed with exotic conifers in some places, planted between 1950 and 1970. Some were planted on grassland others on cleared ancient woodland areas. Most have been managed by thinning, following standard forestry practice.

For the last 30 years, only the twentieth century plantations have been subject to silvicultural management, entailing occasional thinning.

Long-term Monitoring

A survey of tree species in 294 sample plots of 10 x 10 m (0.01 ha), systematically located on a 100m grid, was carried out in the summer of 1993 and in a few cases 1994 (subsequently we refer to 1993 to include plots surveyed in either year), following the ECN ‘baseline’ survey methodology (Sykes & Lane, 1996). 41 of these plots were randomly selected for on-going monitoring, with tree diameter at breast height (DBH – diameter at 1.3m) measured every 3 years and tree height every 9 years. Up to 10 trees over 5cm DBH were selected on the basis of proximity to random coordinates in each plot and the DBH measured with a diameter tape. Tree height was measured with a hypsometer (Blume-Leiss altimeter, Berlin-Steglitz, Germany) at a known distance (measured with a tape measure) from each tree. Trees were classified according to their crown classes (Sykes & Lane, 1996):

1. Dominant - trees with crowns extending above the general level of the crown cover and receiving full light from above and partly from the side.
2. Subdominant - trees with crowns forming the general level of the crown cover and receiving full light from above but comparatively little from the sides.
3. Intermediate - trees shorter than those in the two preceding classes but with crowns extending into the crown cover formed by dominant and co-dominant trees; receiving a little direct light from above but virtually none from the sides.
4. Suppressed - trees with crowns entirely below the general level of the crown cover, receiving little light either from above or from the side.

We report data for the period 1993 to 2006, comprising 4 measurement periods of three years each. Tree seedlings (young trees or shrubs, grown from seed, with a DBH less than 0.5 cm) were counted by species in each plot in 10 400 x 400mm quadrats (selected with a random number table), within the plots.

The date of first leafing in all three species across the site as a whole was recorded from 1994 onwards. This was defined as the first observation of a leaf having fully emerged from the bud (but not expanded). Observations were made by professional scientists working on the ECN programme and visiting the same areas of the site regularly (several times per week).

Meteorological variables, including temperature and precipitation were monitored with an Automatic Weather Station (Didcot Instruments, Didcot, UK) at a grassland area in the middle of the site as part of the ECN programme (Morecroft *et al.* 1998).

Photosynthesis measurements

A scaffolding walkway, approximately 12 m above the ground, gave access to the canopies of 5 sycamore and 5 oak trees. The sycamore trees were approximately 50 – 100 years old (27 cm mean DBH), the oak 150-200 years old (66cm mean DBH). The location is described in more detail by Morecroft & Roberts (1999) and Roberts *et al.* (1999).

In this paper we compare rates of photosynthesis in 1996, when soil conditions were dry with those made in 1999 and 2000 when they were wet. Measurements were taken throughout the growing season when conditions were suitable (particularly that the leaves were dry). In 1996 an ADC LCA 2 infrared gas analyser (IRGA) with PLC(B) leaf chamber (ADC Ltd., Hoddesdon, Herts, UK) was used. In 1999 and 2000 this was replaced by a PP Systems CIRAS 1, with PLC(B) leaf chamber (PP Systems, Hitchin, Herts, UK). For each species 5 leaves exposed to full sunlight in the upper canopy were measured on each of the 5 trees (intermediate and shade leaves were also sampled; data not presented). In 1996 a single measurement was taken for each leaf, in the later years a mean of 5 measurements over one minute was used for each leaf. Measurements were taken in the middle part of the day (09.00-14.00 GMT) when gas exchange rates were maximal (Stokes, 2002). In order to estimate maximum net photosynthetic rates (A_{max}), only those measurements made when the light was saturating for photosynthesis are included here. This was defined as a Photosynthetic Photon Flux Density of greater than 1000 μmol m^{-2} s^{-1}, as measured by the leaf chamber sensors. Further details can be found in Morecroft & Roberts (1999) and Stokes (2002).

Data analysis

Data were analysed using Systat 11 (Systat Software Inc, 2004). Differences in distribution of species between contrasting areas were tested using chi-squared tests. DBH increments were analysed using Analysis of Variance (ANOVA) and Repeat Measures Analysis of Variance (RMANOVA). Initial investigations indicated that diameter increment in all species was related to starting DBH, so DBH in 1993 was included as a co-variate in ANOVA and RMANOVA models. Gas exchange measurements were compared visually with means and standard errors. Trees which died during the period and those for which measurements started after 1993 were not included in the analysis of growth. Phenological data were tested for correlations with temperature in preceding periods.

Results

Distribution of Sycamore

Sycamore was the second most frequently occurring tree species in the baseline survey plots (Table 1), with ash the most frequent species. Sycamore was not randomly distributed (chi squared test: χ^2=67.09; d.f. = 4; *P* <0.0001) but was found more frequently in plots located in secondary woodland, disturbed ancient woodland and 19th century plantations (Fig. 3a). Proportionally fewer plots in undisturbed ancient woodlands and twentieth century plantations had sycamore trees. There were significant differences in the frequencies with which sycamore occurred with other species (χ^2=20.09; d.f. = 9; *P* = 0.017). The species with which it was most frequently associated was ash (Fig. 3b); they were found together in 56 of the 143 plots in which sycamore occurred. Other species with which sycamore frequently occurred included elder (*Sambucus nigra* L.) and hawthorn (*Crataegus monogyna* Jacq.). Ash is also non-randomly distributed (χ^2=14.24; d.f. = 4; *P* = 0.007) being most common in secondary woodland (60% of plots) and least common in ancient woodland (28% of plots). It therefore shows similar patterns to sycamore, although the differences are less pronounced.

Growth and Mortality

Between 1993 and 2005 mean diameter growth was lower in sycamore (1.5 ± 0.3 cm) than either ash (4.5 ± 0.5 cm) or oak (2.2 ± 0.5 cm). ANOVA showed a significant effect of species (F=17.049, d.f. = 2; *P* < 0.001) and starting DBH (F=15.239, d.f. = 1; *P* < 0.001). Because of the effect of starting DBH, size and growth were investigated separately in canopy dominant, sub-dominant and intermediate trees (there were too few suppressed ash and oak trees to compare). In each of these three categories the increment in DBH was larger in ash than sycamore or oak (Fig. 4a). The starting DBH of sycamore and ash were very similar in canopy dominant and intermediate trees (Fig. 4b); amongst sub-dominant trees, it was higher in sycamore than ash (Kolmogorov Smirnov test, p=0.041) (Fig. 4b). Sycamore and ash increments were also compared in the 12 plots where the two species occurred together; in all plots mean diameter growth of ash was higher than that of sycamore. The difference in growth rates between sycamore and ash is therefore not likely to be an artefact of size or canopy position. The mean starting diameter of canopy dominant oak trees was, however, substantially larger than those of ash and sycamore and the greater growth increment in oak than sycamore presumably reflects this; sub-dominant and intermediate oaks were similar in size to sycamore and similar increments were found (Fig. 4b).

Measurements in 1993 and 2002 indicated that height had increased most in ash trees (1.7±0.4 m), with little or no height growth in sycamore (0.2±0.3 m) and oak (0.3±0.7 m).

DBH growth in each of the 3-year intervals was examined separately (Fig. 5a) for each of the three species by RMANOVA. To facilitate comparison between species in different periods on a like-for-like basis, trees over 50 cm DBH (6 oak, 1 sycamore, 1 ash) were excluded. Sycamore was the only species in which there was a significant difference with time (Table 2), with growth highest during the period 1999-2002 (Fig. 5a), which climate records show was 24% wetter than the other periods (Fig. 5b). There was no significant difference between periods in oak (Table 2), although it showed a similar pattern to sycamore (Fig. 5a).. Ash grew more than the other two species in all periods (Fig. 5a) with no significant difference between time periods (Table 2).

Mortality of the three species was low and there was no significant difference between species. Of the 290 trees and shrubs which were originally monitored in the plots, 31 died between 1993 and 2005 including 3 of the original 54 sycamores, 2 out of 21 oaks and 1 out of 54 ash.

Seedlings

There was no evidence that sycamore seedlings were more abundant under ash canopies, or vice-versa, in the monitoring plots in either 1993 or 2002 (Fig. 6). The larger baseline survey also failed to show any effect (data not presented). However numbers of seedlings of all species were very low, particularly in 1993 and very few were older than one or two years old; saplings were almost absent from the wood.

Photosynthesis

Of the 3 years in which photosynthesis was measured in the canopy, A_{max} values in sycamore were lowest in the dry year, 1996 (Fig. 7); The highest mean A_{max} on any particular day in 1996 was only 6.1 μmol m^{-2} s^{-1}, compared to 12.1 μmol m^{-2} s^{-1} in 1999 and 10.4 μmol m^{-2} s^{-1} in 2000. Values of A_{max} in oak were also lower in 1996 (Morecroft *et al.* 2003) but the difference between years was smaller. Comparing the two species in different years, it can be seen that oak consistently had higher A_{max} than sycamore, but the difference between the two species was greatest in the 1996. This difference in A_{max} was associated with differences in stomatal conductance (the capacity for CO_2 to diffuse into the leaves, which is largely regulated by the number and degree of opening of the stomata) of the two species.

Phenology

Sycamore came into leaf earlier than the other species in 12 of the 13 years (Fig. 8a). The date of leafing was significantly correlated with March temperature in all three species (Table 3; Fig. 8b). This correlation was less strong in ash than the other two species and its leafing was more strongly correlated with mean March-April temperature than that for March alone (Table 3).

Discussion

Is there any difference in the extent to which sycamore has colonised different areas?

It is striking how little sycamore has colonised the undisturbed ancient woodland areas of Wytham, despite its abundance in other parts of the site. This may reflect poor establishment and growth in shade as these areas have been largely unmanaged for much of the twentieth century. This is consistent with the observations of Savill (1997) and Morton Boyd (1992) that sycamore tends not to become dominant in woodlands with a dense canopy. There was also relatively little colonisation of recent plantations which were managed for timber production; in this case establishment of sycamore may have been prevented by weed control and thinning as well as low light levels following canopy closure. It is also possible that more colonisation of recent plantations would take place with time.

Is there any evidence that sycamore is out-competing ash or growing faster?

We found no evidence of sycamore out-performing ash, its main competitor, either as amongst mature trees or seedlings.

DBH increment was consistently higher in ash than sycamore throughout the period and ash also showed greater height growth. Drought sensitivity (discussed further below) appears to have contributed to sycamore's overall lower growth rate, but it still grew less than ash during the relatively wet period, 1999-2002. Data from the Radcliffe Meteorological Station, 5km away from the site in Oxford, showed that this was the eighth wettest such period since 1767. It is therefore unlikely that the growth of sycamore would have exceeded that of ash under any climatic conditions over the last two centuries at this site. One possible factor contributing to the lower overall growth rates of sycamore is damage by grey squirrel (*Sciurus carolinensis*), which sycamore is vulnerable to (Mayle *et al.*, 2007). In writing about Wytham, Elton (1966, p.227) commented that squirrels 'cause tremendous damage to sycamores by stripping the bark, frequently killing parts or all of the younger trees'. Squirrel damage has continued at the site, despite regular control by shooting and poisoning; we did not however identify it as a cause of mortality in our study.

Ash seedlings were more abundant than those of sycamore in both 1993 and 2002. During the period of our study, the site has been subject to grazing pressure from large deer populations (fallow, *Dama dama*, muntjac, *Muntiacus reevsii* and roe, *Capreolus capreolus*) (Kirby & Thomas 2000; Morecroft *et al.* 2001; Perrins & Overall, 2001). Linhart & Whelan (1987) reported that sycamore seedlings were more adversely affected by sheep grazing than those of ash and they may also be more sensitive to deer herbivory. There was no evidence of sycamore seedlings performing better under ash canopies and ash growing better under sycamore canopies, contrasting with the results of Waters & Savill, (1992) and Savill *et al.* (1997), despite the study being carried out on the same site. This may however, be obscured by the high levels of deer herbivory.

Has tree growth decreased or mortality increased in sycamore trees during dry compared to wet periods?

The proposition that sycamore is drought-sensitive is supported by the fact that it grew more during the 1999-2002 wet period than the dry ones. On this basis, it is also clear that ash is less drought-sensitive than sycamore; the evidence for oak is more ambiguous. There was, however, no evidence of increased mortality in dry periods. The relatively dry 3 year intervals (1993-6, 1996-9, 2002-5) were in fact slightly wetter than average in the Radcliffe meteorological record. The dry weather that they included, particularly the summers of 1995 and 2003 (Fig. 1), may, to some extent, have been offset by the wetter weather in the three year periods (by, for example, ensuring high soil water contents at the start of the summer). In the context of climate change further work is required on the interactive effects of precipitation at different times of year.

Does tree growth reflect changes in photosynthesis in the canopy during wet and dry periods?

The reduction in sycamore growth during dry conditions is most easily interpreted as a result of reduced photosynthesis resulting from stomatal closure. The gas exchange measurements support this interpretation, demonstrating that sycamore photosynthesis was lower in the drier conditions of 1996 than in 1999 and 2000. Photosynthesis of oak was slightly lower in 1996 than 1999 and 2000 but to a lesser extent than sycamore. The difference between the two species observed by Morecroft & Roberts (1999) in 1996 is therefore likely to be an effect of differing responses to the dry conditions. Sooty bark disease is promoted by hot, dry conditions (Coultherd, 1978; Desprez-Loustau *et al.*, 2006) and was associated with sycamore mortality in the 1976 drought, but no outbreaks were noted in this case.

Is there any interspecific difference in phenological responses to temperature which might affect the outcome of competition in the long-term?

The sensitivity of phenology to temperature has been demonstrated for all three species, with similar relationships to temperature. The time series is relatively short and the different species' sensitivities to different periods in the spring (which may differ in their relative warmth in different years) complicates the interpretation of results. It is, however, unlikely that a lengthening of the growing season would give sycamore a competitive advantage over ash. Not only is there little difference in responsiveness to temperature, but also solar radiation increases substantially over the course of the spring. An extension of ash's growing season in late April or early May would have a proportionally bigger impact on total carbon uptake than a similar extension of sycamore's growing season, earlier in the year. The predicted increase in drought frequency would also tend to outweigh the effects of an earlier start to the growing season.

Conclusions and application

These results suggest that sycamore does not currently pose a serious threat to the undisturbed ancient woodland at Wytham and that it is not outcompeting ash in the rest of the woods. The evidence is that ash is growing faster and producing more seedlings than sycamore. Sycamore is likely to have been planted at Wytham from the early 19th century onwards (Elton, 1966), but many of the present trees have naturally regenerated and this appears to have been favoured by the conditions in the secondary and disturbed woodlands. In contrast the minimum intervention regime in the undisturbed ancient woodland has presented few opportunities for sycamore to gain a foothold. It is possible that sycamore would eventually decline in those areas where it currently coexists with ash, in the absence of active management.

The resistance of ancient woodlands to sycamore invasion under a minimum intervention regime, may not be so clear cut in other situations; in particularly sycamore is likely to be more of a threat in wetter areas. However, Climate change will tend to decrease sycamore growth over much of England, if, as projections suggest, summer droughts increase in frequency. Our results provide empirical support for the projections of Broadmeadow *et al.* (2005), indicating a decline in the productivity of sycamore with climate change over much of England. Sycamore is therefore likely to be a reduced threat to conservation in future, however, as a timber crop, foresters may find it a less productive species.

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Tables

Table 1 Number of ECN baseline plots in which different tree species were recorded in canopy and shrub layer (seedlings excluded).

Species	**Number of plots**
Fraxinus excelsior	143
Acer pseudoplatanus	114
Corylus avellana	109
Crategus monogyna	105
Quercus robur	82
Sambucus nigra	53
Fagus sylvatica	43
Acer campestre	40
Prunus spinosa	32
Betula pendula	29
Salix caprea	12

Table 2 RMANOVA results for growth increments in 3 year periods between 1993 and 2005. Time with starting DBH (1993) as a covariate.

	Time			DBH in 1993			Time x DBH		
	F	d.f.	*P*	F	d.f.	*P*	F	d.f.	*P*
Sycamore	4.761	3	0.003	4.831	1	0.033	3.5	3	0.017
Ash	1.415	3	0.241	6.429	1	0.014	2.052	3	0.109
Oak	1.702	3	0.186	0.675	1	0.429	1.597	3	0.209

Table 3 Correlation coefficients (r^2) between date of leafing and mean temperature of different months or combination of months for three species between 1994 and 2006 at Wytham Woods. Bold text indicates significant differences: *p<0.05; **p<0.01.

	Species		
Period	**Sycamore**	**Ash**	**Oak**
January	0.00	0.06	0.07
February	0.09	0.16	0.03
March	**0.44***	**0.36***	**0.43***
April	0.11	0.33	0.04
January-April	0.15	0.26	0.06
January-March	0.23	0.17	0.09
February-April	0.18	**0.45***	0.15
January-February	0.05	0.02	0.00
February-March	0.29	**0.33***	0.21
March-April	0.17	**0.53****	0.22

Figure Legends

Fig. 1 Temperature and precipitation at Wytham, 1993-2005. Data are presented as mean temperature and total precipitation for each season: spring (March-May), summer (June-August), Autumn (September-November), winter (December – February).

Fig. 2 Map of Wytham Woods showing location of ECN baseline plots in relation to management history, categories defined in Methods section. Plots in which sycamore was recorded are solid black, those in which it was not recorded are filled white.

Fig. 3 (a) Frequency of occurrence (percentage) of sycamore in plots in areas with contrasting management histories. (b) Frequency (percentage) of occurrence of sycamore in the same plot as other species.

Fig. 4 (a) Diameter (DBH) growth of the three species over the whole period, 1993-2005 broken down according to crown class. (b) Starting DBH (1993) of different species according to crown class

Fig. 5 (a) Growth (DBH) of sycamore, ash and oak in four contrasting 3-year periods from 1993 to 2006. (b) Climate (total precipitation and mean temperature) during the same four periods.

Fig. 6 Number of seedlings of sycamore and ash recorded in plots under sycamore and ash canopies in (a) 1993 and (b) 2002.

Fig. 7 Maximum photosynthetic rate (A_{max}) of sycamore throughout the growing season in (a) 3 contrasting years and then in comparison to oak for (b) a dry year, 1996, and for two wet years: (c) 1999 and (d) 2000. Where data were collected on more than one day within the same week they have been combined for clarity. (The data in (b) have been previously presented in Morecroft & Roberts (1999) and are included here for comparative purposes).

Fig. 8 (a) Leafing date (day of year) of sycamore, ash and oak from 1994 to 2006, with mean March temperature. (b) Relationship between leafing date of sycamore, ash and oak and March temperature. Correlation coefficients are given in Table 2. Linear trend lines are fitted to the data series. Equations: sycamore $y = -6.2x + 133$; ash $y = -5.1x + 139$; oak $y = -4.1x + 139$.