The Ecology and Biodiversity Value of Sycamore (Acer pseudoplatanus L) with particular reference to Great Britain

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Abstract

Sycamore (*Acer pseudoplatanus* L.) offers considerable promise for multiple-objective forestry being fast-growing, yielding a valuable timber, being a deciduous broadleaved species and tolerant of a wide range of climatic and soil conditions. Sycamore is naturalised in Great Britain, with a poor reputation amongst conservationists due to the perception that it supports only low levels of biodiversity, that it is not native and that it is invasive in ancient semi-natural woodlands. Yet evidence shows that sycamore can support a high diversity of certain taxa, such as lichens. Furthermore the aphids that feed on sycamore provide a resource for many animals, directly as prey and indirectly through their honeydew. In certain cases sycamore invades semi-natural woodland, with disturbance favouring its colonisation. However, there is evidence in some cases that its dominance in the canopy will alternate with other species or that some sort of equilibrium will develop between it and other tree species.

Introduction

A study in 1987 of the financial returns from silvicultural practices in Britain showed that sycamore (*Acer pseudoplatanus* L.) in a shelterwood can provide one of the best financial returns of any hardwood tree (Crockford *et al.*, 1987) due to its rapid growth and high value timber. A recent analysis (Pryor and Jackson, 2002) using ash (*Fraxinus excelsior* L.), a species with similar growth rates but lower timber value, predicted high returns with a Net Present Value of £2032/ha at a 2% discount rate, using their basic crop model for a rotation of 70 years under the clear fell system. This was the highest return for all broadleaves in their analysis and better than all conifers, except Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco).

Despite this high financial return, sycamore has acquired a negative image with the public, due to its invasive regeneration in urban and rural areas, the honeydew that it sheds, and the low level of biodiversity that it supports (Taylor, 1985). This poor image has been associated with sycamore for over three hundred years; Evelyn in his seminal seventeenth century publication *Sylva* described sycamore with disdain due to the copious honeydew it produced and the mess made from its decomposing leaves and noted *"[sycamore] are therefore to be banish'd from all curious gardens and avenues*" (Evelyn, 1662, p.121). According to Bingelli (1994) the poor image of the tree with the public has been reversed in recent years.

More recently sycamore has been an unpopular species with conservationists; a survey published in 1985 (Taylor, 1985) of the opinions of staff working in conservation organisations highlighted their antagonism to sycamore with half of the organisations having a policy of eradicating sycamore in all habitats and the other half removing sycamore in specific habitats. The main conservation issues relating to sycamore in the forest sector in recent years are concerns regarding its invasiveness in certain semi-natural woodland types and the perception that it supports relatively low levels of biodiversity (Taylor, 1985). One further factor is the status of sycamore as a naturalised exotic (Peterken 2001).

The *Acer* genus is widely distributed in the Northern Hemisphere, being found in temperate North America and Eurasia but also in tropical Southeast Asia (Oterdoom, 1994). Sycamore is the largest species of the genus in Europe and is native to the mountain areas of central Europe but has become naturalised over an extensive area, including Britain, preferring areas of disturbance (Rusanen, 2003). It has been planted, and has also naturally regenerated extensively, in Britain, being the dominant species in 67,000 ha of woodland (Forestry Commission, 2003). There have been no surveys of genetic variation in Britain, but it is known that populations of sycamore can thrive despite having a narrow genetic base. In Denmark, plantations raised from seed from a single tree have not exhibited depression of vigour. This may be because sycamore has existed in the past in certain areas as small, isolated populations and damaging recessive genes may have been bred out of such populations (Roulund, 2003).

This article describes the ecology of sycamore, focussing on Britain, but also using relevant information from other countries and examines some of those areas that have been raised as concerns by conservationists. The first part describes the soil and climatic tolerances of sycamore to provide background for later discussion on the colonisation of woodland types, and presents recent predictions of the future suitability of different parts of Great Britain for sycamore due to the effects global warming. The remainder of the article is a review of three areas of concern for conservationists; its non-native status (Peterken, 2001), the biodiversity value of sycamore and its colonisation of woodland (Taylor, 1985).

Soil and Climatic Tolerances of Sycamore

To understand the threat sycamore may pose as an invasive species it is useful to describe its soil requirements and compare them with native tree species that occupy similar ecological niches, particularly ash. It is also worthwhile examining the climatic tolerances of sycamore and relating them to predicted changes in the climate of Great Britain, to assess whether it will become more or less of a threat to native woodland.

The Effect of Soils

In terms of soil quality, sycamore is less demanding than ash (*Fraxinus excelsior* L.) (Savill, 1991) and this is reflected in a comparison of their soil nutrient and soil moisture requirements (Figure 1 and Figure 2) as described in the Ecological Site Classification (ESC) (Pyatt *et al.*, 2001). Although sycamore can tolerate a wide range of soils it is known to be nitrophilous (Jones, 1945) and grows best on fertile, moist soils. Although not ideal, sycamore can also grow on highly acidic soils where there are levels of aluminium, which would be toxic to most other plants (Weber-Blashke *et al.*, 2002). This characteristic, and its ability to improve soil chemistry, like many other broadleaves (Ulrich, 1987 cited Gloser and Gloser, 2000 p76), may make it a candidate for improvement of degraded sites. However pot experiments have shown that on highly acidic sites nutrient uptake is relatively poor compared with some other plant species such as the grass *Calamagrostis villosa* (Chaix) J.F. Gmel. (Gloser and Gloser, 2000).

The Influence of climate

The climatic tolerances of sycamore are wide, and it can survive in areas of considerable exposure. In Britain, Jones (1945) notes that it can be found to an altitude of at least 460m in areas, including the Pennines, the Lake District and Shropshire. It is also likely that it would tolerate higher altitude if suitable soils and opportunities for regeneration were present. Of the broadleaves only birch (*Betula spp.*) and rowan (*Sorbus aucuparia* L.) are known to have higher altitudinal limits (Jones, 1945). It is also a species that can cope with the extreme conditions of northern Scotland; the most northerly woodland in Britain on the exposed Mey Estate in Caithness is composed of sycamore (Harris, 1987).

Figure 1: Sycamore soil nutrient status

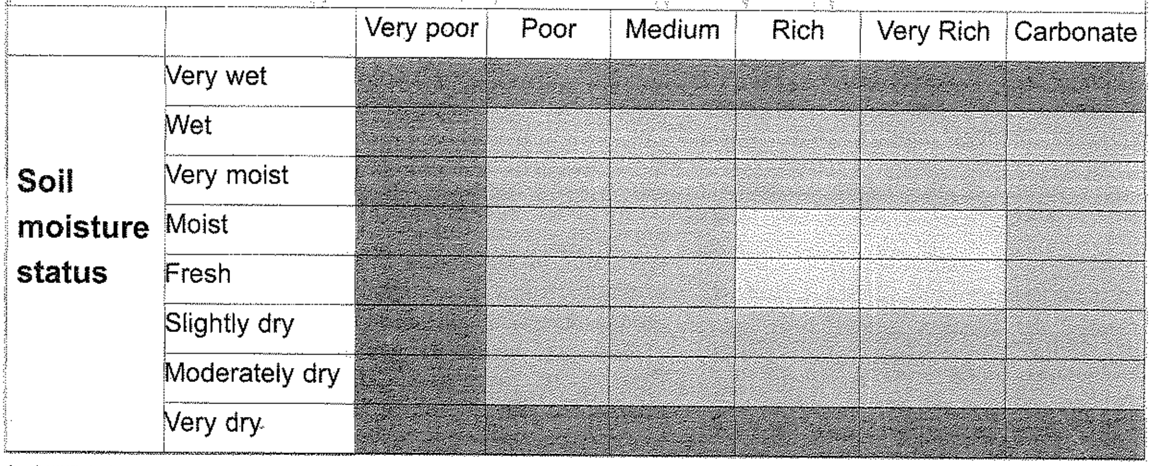
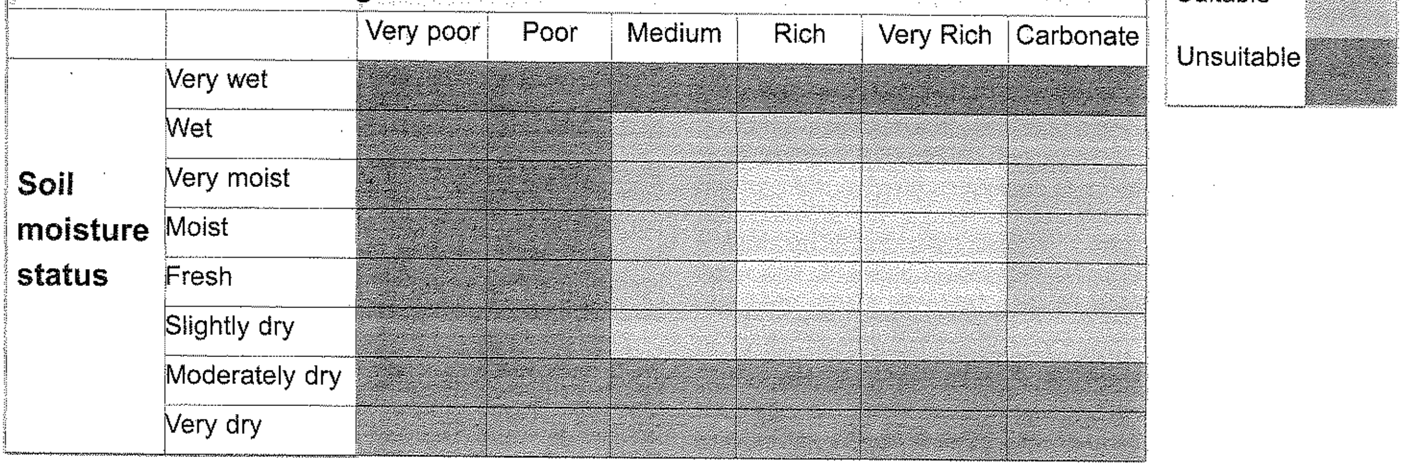


Figure 2: Ash soil nutrient status



Continental authors note that sycamore is favoured by cold, moist conditions (Jones, 1945). Sycamore has evolved certain adaptations to exposed conditions and can produce a vigorous, luxuriant canopy even in areas of high wind and salt spray. However on particularly exposed sites there is considerable bud and shoot death, although new shoots are readily produced from dormant buds (Bingelli and Blackstock, 1997). This is a successful survival strategy but precludes such sites for the growing of sycamore as a timber tree (Bingelli and Blackstock, 1997).

The climate in Great Britain is changing and this is a factor that will affect the success of sycamore in the future. It will affect trees directly through changes in factors such as potential evapotranspiration but also indirectly by altering the competitiveness of other organisms within the trees' ecosystem. Predictions by Forest Research (Ray and Broadmeadow, 2004) of the effect of climate change on the productivity of sycamore, have been generated using the UKCIP02 climatic model and the ESC computer programme.

The maps indicate that areas of south-east England and the Midlands will be less suited to growing sycamore than at present, while areas in south east Scotland will become more favourable. In those areas where trees are under environmental stress through the earlier advent of spring and extended, hot, dry summers secondary pathogens may be favoured. For sycamore there is concern that climate change will favour certain pathogens, particularly sooty bark disease caused by the fungus *Cryptostoma corticale* Ell. & Ev. (Reynolds, 2004). This is based on the observation that the spread of the fungus through the wood of live trees seems to increase with summer temperature (Young, 1978). The fungus causes lesions in the bark, which if severe can extend completely around the stem, killing the tree (Gibbs 1997). Given the complexity of the direct and indirect effects of global warming on sycamore it is difficult to predict whether it will improve or undermine the success of sycamore as a woodland species in Great Britain.

The Main Concerns about Sycamore

In nature reserves management has often been directed at usually unsuccessful efforts to eliminate or reduce sycamore as a component of woodland (Green, 2005). This intervention is because it is considered an exotic tree species; it is thought to support limited biodiversity and the perception that it is an invasive species.

An Exotic Species

Sycamore is not considered part of the native flora of Britain and this in itself is a major source of prejudice against the species by conservationists (Green, 2005). There are some, however, who believe that sycamore may be a native species because its date of introduction into Britain is not recorded and maple pollen does not preserve well in peat and sediments (Harris, 1987, Green 2005). In addition, where pollen does survive, the pollen of sycamore is identical to that of its native relative, the field maple (*Acer campestre* L.) (Morton Boyd, 1992,), making it impossible to ascertain whether one or both species are native to Britain (Green 2005).

However the general view is that it is a naturalised species, possibly introduced in Roman times (Mitchell, 1974) but probably in the Middle Ages (Stern, 1982) and initially to Scotland (Jones, 1944). It has since become naturalised over much of Britain. Even if it is accepted as an exotic tree, Brown (1997) cautions against dismissing the biodiversity value of introduced tree species, simply because they are not native.. He argues that there is a continuum, from original prehistoric tree colonists of the wildwood to those tree species that have been introduced in recent times, and that a sophisticated approach is needed when assessing a tree species' contribution to society. Factors that contribute to a tree species' value include the habitat value it provides, whether it has populations that are genetically distinct and its aesthetic value. Sycamore, despite being an exotic makes a considerable contribution to biodiversity conservation (Morton Boyd, 1992), is likely to have evolved ecotypes in Britain, provides important structural diversity in the uplands and can provide important features in the landscape. In addition sycamore, being a shade bearing tree, at least when young, is a useful addition to the native tree flora of Britain, which is dominated by light demanding tree species and may fill an ecological niche formerly occupied by species such as wych elm (*Ulmus glabra* Huds.) in northern and western Britain (Peterken 2001).

Supporting biodiversity

One factor contributing to the perception that sycamore has a poor biodiversity value is the relatively small number of species of phytophagous insects that it supports (Kennedy and Southwood, 1984) (Table 1). The diversity of such insects on a tree species is largely explained by the availability of that tree, or the area where the tree is found and the time it has been present in Britain (Kelly and Southwood, 1999). However, other variables such as the structural complexity and taxonomic isolation can have an influence (Kennedy and Southwood, 1984). Although sycamore is widespread in Britain, it only became common in the seventeenth and eighteenth centuries (Stern, 1982) and there may not have been sufficient time for a diverse insect community to develop to feed on its foliage. However, using the number of phytophagous insect species as a measure of a tree's importance to an ecosystem has been questioned (Taylor 1985), as it focuses on such a narrow subset of the biodiversity a tree supports.

If lichens are chosen as an indicator of the tree's importance to biodiversity, sycamore supports a relatively large number of species, some 170 lichen taxa. This is because the bark has a high pH, often likened to that of elm (Rose, 1974). This is a higher diversity than is supported by the native limes (*Tilia* spp.) (Morton Boyd, 1992) and field maple (Rose, 1974), as shown in Table 1. Furthermore in addition to supporting a wide diversity of lichens, sycamore also supports some rare lichen species. Of twelve core sites that have been identified for the now rare lichen *Teloschistes flavicans* (Schwarz), two were rows of sycamore trees near the coast and when found on trees, sycamore and ash trees are the most common hosts (Gilbert and Purvis, 1996).

If the contribution to ecosystem function is viewed more broadly than the species richness a tree supports, sycamore plays a number of important roles in forest ecosystems. Aphids, particularly *Drepanosiphum platanoidis* Schrank and *Periphyllus testudinaceus* Fernie, are abundant on sycamore (Elton, 1979), with an estimated 2.25 million individuals on a 20m tall mature tree (Dixon, 1971). Their feeding has a profound effect on the productivity of the tree, with wood production increasing an estimated 2.8 times with their

Table 1
The lichens and insect species (phytophagous insects and mites) associated with British trees.

Tree species	Lichen taxa[1]	Insect species[2]
Field Maple, (*Acer campestre*)	88	51
Sycamore (*Acer pseudoplatanus*).	170	43
Alder (*Alnus glutinosa*)	72	141
Birches (*Betula pubescens, B. pendula*)	93	334
Hornbeam (*Carpinus betulus*)	42	51
Hazel (*Corylus avellana*)	124	106
Beech (*Fagus sylvatica*)	194	98
Ash (*Fraxinus excelsior*)	230	68
Holly (*Ilex aquifolium*)	68	10
Oaks (*Quercus petraea, Q. robur*)	303	423
Willows* (*Salix* spp)	128	450
Limes (*Tilia* spp.)	66	57
Elms (*Ulmus* spp.)	171	124

1 (Rose 1974),
2 (Kennedy and Southwood 1984). * two species (*Salix capraea, S. cinerea*) for lichens, five species for insects

removal (Dixon, 1971). The honeydew that is produced by the aphids may however have some benefit to the tree. It was found for lime, another genus where resident aphids produce copious honeydew, that the enrichment of sugars in the soil under the tree increased the numbers of nitrogen fixing bacteria in the soil, potentially benefiting the tree (Anon. 1984 cited in Mabberley, 1997 p715).

The numerous aphids provide other woodland organisms with a ready source of food including other insects such as ladybirds, hoverfly larvae and lacewings (Speight, 1980) and where the sycamore's canopy overhangs water the aphids provide a source of food for trout and salmon (Gray, 1993). The rare ant, *Lasius fuliginosus* Latreille was observed tending sycamore aphids for honeydew at Gait Barrows National Nature Reserve in Silverdale, North Lancashire (Petley-Jones, R.. 2004, pers. comm.). The importance of aphids may be of further importance in the food chain as Green (2005) notes that aphid numbers peak late in summer, when populations of invertebrates on oak, for example have largely disappeared.

In addition to aphids being an important source of food, the sycamore supports other organisms in other ways. A survey of dead sycamore in Nunhead Cemetery on the outskirts of London identified a number of arthropods, mainly insects associated with these trees, including ten beetle species that appear to be associated with sooty bark disease of sycamore (Jones, 1993). Two of these mycophagous species were described as being rare or endangered, *Synchita separanda* Reit and *Cicones undatus* Guerin-Ménevill, although *Cicones undatus* may be a recent colonist to England, perhaps due to climate change (Jones R.A. pers. comm., 2004). It has been found now in many localities in London (Jones, 1996). Dead sycamore have provided a site for nests of the nationally scarce ant *Lasius brunneus* Latreille, noted on the ornamental islands in Battersea Park, London, while stag beetles (*Lucanus cervus* L.) also exploit dead sycamore (Jones, R.A. 2004, pers. comm.), although these two insect species are not specific to sycamore.

A study in a mixed woodland in Hamsterley Forest, County Durham, of the foraging habits of six arboreal, passerine bird species showed that sycamore was markedly preferred by all the bird species (Peck, 1989). This was thought to be due to the vast numbers of aphids the sycamore supports; an important food source particularly when other food is lacking. The study also showed that tree species had a greater influence on the birds' preferences for feeding and thus niche separation than other attributes such as tree height or location. Elton (1979) in a study in Wytham Woods, Oxfordshire, described sycamore as being more important in providing a food source for birds than beech (*Fagus sylvatica* L.), ash and hazel (*Corylus avellana* L.). In this woodland only oak (*Quercus* spp.) was considered to supply a more important source of food with a combination of aphids and caterpillars.

Insects living under the flaky bark of older trees are an important source of food for migrating birds on the eastern coast of England (Bingelli, 1994 p15).

A study of sand dune colonisation by sycamore and sea buckthorn (*Hippophae rhamnoides* L.) at the Murlough dune system, Co Down in Ireland, yielded information on the development of sycamore woodland and its effect on bird numbers and diversity. A comparison of an area with sea buckthorn alone with that of sea buckthorn and sycamore showed that the latter had three times the density of breeding pairs of birds, and there were differences in the types of birds present if not the overall number of bird species (Nairn and Whatmough, 1978 cited Bingelli, 1992 p132). As the sycamore matured and formed a closed-canopy woodland, the number of species and density of pairs of birds declined.

Due to its innate tolerance of harsh climates, sycamore is often the only large broadleaf tree in some upland areas and enhances vertical and horizontal structural heterogeneity. The more complex the field, shrub and tree layer in a habitat the more diverse the community of breeding birds (Fuller, 1982). Therefore, it is likely that sycamore has a beneficial influence on bird diversity in otherwise tree-less areas of the uplands.

Natural regeneration and colonisation of woodland

Although seed is produced by sycamore each year, not all individuals produce viable seed. Furthermore, the sex of sycamore trees is complicated, with most inflorescences supporting male and female flowers. The normal pattern involves flowering on an inflorescence starting with either male or female flowers then switching to the opposite sex as flowering continues. There can be up to five changes in the expression of sex on any inflorescence (Bingelli, 1992). Individual trees can be divided into those that start by producing male flowers (protandrous) and those that begin by producing female flowers (protogynous). Those individual trees that are protandrous tend to be predominantly male, while those that are protogynous tend to be predominantly female. The setting of seed was generally lower for protandrous than protogynous trees (Bingelli, 1992).

The seed is wind dispersed and recalcitrant (Harmer, 1999), although a study by Greggains *et al.* (2000) showed that the seeds were relatively tolerant of desiccation in comparison with other recalcitrant seeds. Seed production of sycamore often varies in quantity from year to year and seeds remain viable for less than one year. To ensure exploitation of any opportunities for growth, seedling banks are employed. As such, fluctuations in seed production may be less important for shade tolerant trees, as their seedlings can persist in these seedling banks under the canopy (Deiller *et al.*, 2003), although the relatively slow colonisation of woodlands by sycamore has been attributed to variable seed production (Bingelli, 1994).

Despite being considered a shade tolerant species (Mason *et al.*, 1999), at least when young, colonisation of woodlands in Britain is facilitated by disturbance and sycamore can have difficulties colonising, for example oak or beech forest with a closed canopy (Waters, 1992b). Bingelli (1994) describes sycamore as being a gap species, which takes advantage of tree fall gaps, disturbed areas or establishes under light canopies such as those produced by alder (*Alnus glutinosa* L.) and birch (*Betula* spp.). Hill *et al.* 1999 (cited in Pyatt *et al.*, 2001 p36) describes sycamore as tolerating shade but only early in life.

Natural regeneration of sycamore in Norway spruce (*Picea abies* L. Karst.) plantations in what would naturally be silver fir – beech forest in the Slovenian alps was examined in response to different light conditions and protection by fencing (Diaci, 2002). There were no significant differences in sycamore seedling density in four different regimes of diffuse and direct solar radiation, although the gaps with the highest levels of both types of radiation supported the highest number of sycamore saplings in the final enumeration (Diaci, 2002). These were also the gaps where the most aggressive growth of ground vegetation was found. When only old gaps, where the ground vegetation was well established, were sampled sycamore saplings were only found in the larger gaps, suggesting that light is more important to survival than the competition from the ground flora (Diaci, 2002). Taylor (1985) notes that the disturbance to the canopy through policies of reduction or elimination of sycamore in nature reserves may therefore be counter-productive, given the favourable conditions to natural regeneration provided by canopy gaps.

Sycamore regeneration is highly palatable to certain deer. A study in the Czech Republic of natural regeneration of nine broadleaved species showed that sycamore was one of the most heavily browsed, along with hornbeam (*Carpinus betulus* L.), ash and smooth leaved elm (*Ulmus carpinifolia* Gleditsch), with 90% or more of seedlings being damaged (Modny *et al.*,2004). In contrast only 15% or less of beech, and 24% or less of small leaved lime (*Tilia cordata* Mill.), were browsed. This negative impact on sycamore regeneration from browsing is described in other studies. In Slovenia fenced gaps provided better opportunities for sycamore to regenerate, but once seedlings were established the competing vegetation in fenced areas meant that there were fewer saplings in such areas than those that were not protected from roe deer (*Capreolus capreolus* L.) (Diaci, 2002). Harmer (1999) in a clipping experiment showed that lack of light reduced sycamore's ability to withstand browsing. Although there was no mortality, growth of clipped sycamore seedlings under 80% shade were producing progressively less shoot growth, and it is conceivable that if the experiment had continued they would have died. Another explanation for the seedlings' survival may be that the level of shade was insufficient, but it was chosen to mimic the light levels found under the open canopies of most British woodlands.

Another mammal that has an important impact on sycamore is the grey squirrel (*Sciurus carolinensis* L.), which strips and gnaws away bark of trees to eat the phloem tissue beneath. Sycamore, along with beech, ash, oak, sweet chestnut (*Castanea sativa* Mill.), larch (*Larix* spp) and Norway spruce are the preferred species (Mayle *et al*, 2003). Most damage is concentrated on trees between 10 and 40 years old as the bark on the stem of older trees becomes too thick to strip (Mayle *et al*, 2003). Severe attack can lead to death of the tree, while in extreme cases whole groups of trees are killed. Where trees survive, their yield is reduced and their potential as timber trees is often compromised through broken tops, stem deformation and decay, and discolouration of the wood at the site of the wound. It is probable that the damage caused by squirrels will have an influence on the composition of mixed stands, disfavouring the dominance of tree species that are most vulnerable to damage, such as sycamore.

A change in the tree species composition in woodland has been predicted in a study of the influence of grey squirrel over ten years on beech in Lady Park Wood in the Lower Wye Valley (Mountford 1997). The preference for stripping the bark of beech was likely to lead to a decline in the abundance of beech (Mountford, 1997). The grey squirrel is likely to have a similar impact on the abundance of sycamore in woodlands and, furthermore, the amount of sycamore planted is likely to be less in the future, given the risk of attack by grey squirrel.

In semi-natural woodland, sycamore rarely exists in pure stands (Taylor 1985). It is known to colonise a wide range of woodland communities in Britain including ash, alder, oak and birch woods (Bingelli, 1994), yet there is little evidence that it reduces biodiversity in woodlands (Peterken, 2001). An overlay of the soil requirements of sycamore with the suitability of soils to different National Vegetation Classification (NVC) woodland types derived from the ESCis shown in Figure 3, and indicates those most at risk from colonisation by sycamore. This overlay is a similar approach to that used by Taylor (1985) but using the NVC woodland classification. Those woodland types most at risk, i.e. where soil conditions for sycamore are very suitable, coincide with woodland types W6, W8, W9, W10, W12, W13 and W14.These are described in Table 2. Woodlands where conditions mirror the optimum conditions for sycamore are predominantly ash and beech woodlands. Peterken (1981) notes that ash woodlands were those most likely to becolonised by sycamore, particularly within the *Tilio-Acerion* association (NVC W8 and W9), an association where sycamore occurs naturally in parts of continental Europe.

A survey of mature trees in ash woodlands in Derbyshire by Okali (1966b) identified characteristics of ash and sycamore that explained their distribution in the woodlands. Ash was found to develop familial clumps of individuals whereas individuals of sycamore were more scattered (Okali, 1966b). The concern about sycamore dominating ash would

Figure 3

		Very poor	Poor	Medium	Rich	Very Rich	Carbonate
Soil moisture status	Very wet		4	1, 2, 3, 4	1, 2, 3, 5	2, 5	
	Wet		4	1, 2, 3, 4	1, 2, 3, 5	2, 5	
	Very moist		4, 20	4, 7, 20	7	6, 7, 9	
	Moist		19, 20	11, 19, 20	10	6, 9	
	Fresh	18	16, 17,19	11, 15, 19	10, 14	8, 9, 12, 13	
	Slightly dry		16, 17	11, 15	10, 14	8, 12, 13	
	Moderately dry		16	15	10, 14	8, 12, 13	
	Very dry						

appear to be based on differences in shade tolerance of seedlings of the two species (Okali, 1966a). Shirley (1935 cited Okali, 1966a p140) determined that if persistence in shade is a measure of shade tolerance then ash is less tolerant than sycamore. However, ash is more competitive in open conditions, having a higher growth rate in full light. This is supported by observations by Brotherton (1973) who described a canopy gap where ash had overtopped a dense clump of sycamore. Thus the situation is complex, and Okali (1966a) notes in his survey that the relative abundance of sycamore and ash varies between sites. In the woodlands surveyed by Okali (1966a) there were more ash seedlings, which would give this species a distinct advantage over sycamore when exploiting tree-fall gaps. However this may have been due to the relatively recent arrival of sycamore. Given the complexities of the competition between these species and their different site requirements, the final equilibrium between abundance of the two species would be difficult to predict on a given site.

The phenomenon of alternation of sycamore with ash has been described in several studies (Brotherton, 1973; Waters and Savill, 1991; Waters, 1992a. Waters 1992b and Owen,

Table 2

NVC woodland types predicted to be most at risk from colonisation by sycamore and their equivalent BAP Priority Habitats and Habitat Directive Annex 1 woodland types

(from Hall, Kirby and Whitbread 2001)

NVC Code	NVC title	BAP Priority Habitat	Habitats Directive Annex 1 Type
W6	*Alnus glutinosa - Urtica dioica* woodland	Wet woodland	Residual alluvial forests
W8	*Fraxinus excelsior - Acer campestre - Mercurialis perrenis* woodland	Lowland mixed deciduous woodland, upland mixed ashwood	*Tilio - Acerion* ravine forests
W9	*Fraxinus excelsior - Sorbus aucuparia - Mercurialis perrenis* woodland	Upland mixed ashwood	*Tilio - Acerion* ravine forests
W10	*Quercus robur – Pteridium aquilinum - Rubus fruticosus* woodland	Lowland mixed deciduous woodland, upland oakwood, upland birchwood	*Stellario - Carpinetum* oak - hornbeam forests, Old oakwoods with *Ilex* and *Blechnum*, old acidophilous oakwoods with *Quercus robur* on sandy plains
W12	*Fagus sylvatica - Mercurialis perrenis* woodland	Lowland beech and yew woodland	*Asperulo - Fagetum* beech forests
W13	*Taxus baccata* woodland	Lowland beech and yew woodland	*Taxus baccata* woodland
W14	*Fagus sylvatica - Rubus fruticosus* woodland	Lowland wood pastures	Beech forest with *Ilex* and *Taxus*, rich in epiphytes

1993). This is based on the premise that each tree species provides conditions under the canopy that promotes natural regeneration of the other. It has been proposed that ash produces a lighter canopy than sycamore, under which develops a denser and more closed ground vegetation, which then favours sycamore regeneration (Brotherton, 1973). Also, sycamore seedlings require higher levels of light than ash in spring to expand their leaves, and so their survival and growth is promoted under the sparser canopy of ash (Waters 1992a). In contrast sycamore provides a canopy that is denser and a sparser ground cover, which favours ash regeneration (Brotherton, 1973) and also inhibits leaf expansion of sycamore seedlings (Waters, 2002a). Furthermore, greater damage of the seedlings by insects under a sycamore canopy was found to be another factor favouring alternation (Waters, 1992a). By mature trees of one species creating favourable conditions of regeneration of the other, there is a mechanism for these species to alternate in woodland.

This alternation of ash and sycamore was found in six woodlands surveyed by Waters and Savill (1991) in Oxfordshire and Gwent. Natural regeneration under each canopy was composed predominantly, i.e. more than 80%, by that of the other species. A study of ash woodlands in Derbyshire confirmed that sycamore regenerated better under an ash canopy and vice versa, supporting the process of alternation (Owen, 1993). Overall, however, the same study showed that sycamore was most successful where there was some form of disturbance or on woodland edges. Gaps caused by natural tree fall did not promote sycamore colonisation, and it was only on woodland edges close to where large numbers of sycamore had been planted that encroachment was successful. Where alternation takes place, Green (2005) suggests that it may provide evidence for sycamore being a native species, arguing that if sycamore were a recent introduction, insufficient time has passed for such a co-evolutionary strategy to develop.

The alternation of sycamore and oak in W10 *Quercus robur – Pteridium aquilinum – Rubus fruticosus* woodland has also been studied. There was no evidence for alternation, at least on a generation by generation basis below either oak or sycamore canopies, as regeneration under both was dominated by sycamore (Hunt 1995). Sycamore is known to be a strong competitor, and breaks bud up to two months earlier than penduculate oak (*Quercus robur* L.) (*Nature's Calendar* 2004). However another explanation is that sycamore regeneration was filling in gaps where oak had failed and has had no competitive effect. Failure of oak to regenerate elsewhere has been widely reported (Anon., 1994; Worrell and Nixon, 1991; Newbold and Goldstein, 1981) yet competition from sycamore is not mentioned as a major cause. Examination of sycamore invasion in acid oak woods in the Derbyshire Peak District showed that sycamore (and ash) colonisation was largely unsuccessful due to the habitat being less suited to these species than to oak (Owen, 1993). In this case sycamore was not considered a threat to this woodland type being dominant only on woodland fringes.

Conclusion

In a country like Great Britain, where the influence of people on the natural environment has been considerable and has been present for thousands of years, it is impossible to disentangle human influences from natural processes. The basis for defining native species in such a situation and its relevance in Britain has been questioned (Brown 1997). Brown instead supports a view that a tree species' worth should be measured by more objective criteria. Despite being an exotic species, sycamore provides many benefits, being a deciduous broadleaved tree with considerable ecological tolerances. Sycamore makes a considerable contribution to conserving biodiversity, especially taxa such as lichens, more so than many native tree species. Whilst sycamore is sometimes invasive, evidence suggests that the opportunities for it to become dominant in ancient semi-natural woodlands are limited. Where sycamore is present it is likely that, through time, some balance will develop between the proportion of sycamore and other tree species in woodlands (Elton, 1979; Peterken, 2001). As such an indiscriminate policy of eradication, which has been practised in some nature reserves for example, would seem excessive and by opening up the woodland canopy, may in the long-term promote sycamore regeneration. Instead, perhaps it is time to recognise the cultural, financial and biodiversity value of one of our most adaptable broadleaved trees.

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