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A review of site factors affecting the early growth of ash (*Fraxinus excelsior* L.)

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Abstract

This paper reviews site factors that influence early growth of ash (*Fraxinus excelsior* L.). Sites where ash will grow well can now be described in terms of the ecological site classification of Pyatt et al. (2001) [An ecological site classification for forestry in Great Britain. Forestry Commission Bulletin 124. Forestry Commission, Edinburgh]. Good sites are where the climate is ‘warm’ (>1376 day-degrees $> 5.6\,^{\circ}$C), soil moisture is ‘fresh’ to ‘very moist’ (generally meaning that depth to the winter water table is between 40 and 100 cm) and soil nutrient status is ‘rich’ and ‘very rich’ (generally soil pH in the range of 5.0–7.5). These preferences are explored with reference to more detailed information concerning the influence of water, nutrients, light and patterns of shoot and root growth.

Keywords: *Fraxinus excelsior*; Site factors; Early growth; Silviculture; Ecophysiology

1. Introduction

Ash (*Fraxinus excelsior* L.[2]) is an important tree species throughout Europe (Thill, 1979; Asche, 1995; Duflot, 1995; Helliwell, 1982; Joyce et al., 1998; Pilard-Landeau and Le Goff, 1996), and is present in parts of western Asia and north Africa. The attraction of ash is that it offers the prospect of the production of valuable timber on relatively short rotations (Kerr and Evans, 1993) and is a very versatile hardwood (Oliver-Villanueva and Becker, 1993). It also has the advantage, compared with many other broadleaves, of being relatively free from attack by grey squirrels (*Sciurus carolinensis* Gmelin.) (Evans, 1984). These attributes have led to much interest in ash and it is now the second most widely planted broadleaved tree in Britain (Harmer and Forrester, 1994).

This paper is an attempt to present more detailed information on site factors that influence early growth of ash. One of the most important decisions a silviculturist will make is to select the correct species and provenance for a site. This is best done by a combination of objective information of the site, understanding the requirements of the species and experience. Without this understanding ash may be planted on sub-optimal sites and hence the species’ productive capacity will not be fully utilized.

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[2] Authorities throughout are according to Stace (1991) or Mitchell (1974) for non-native trees.

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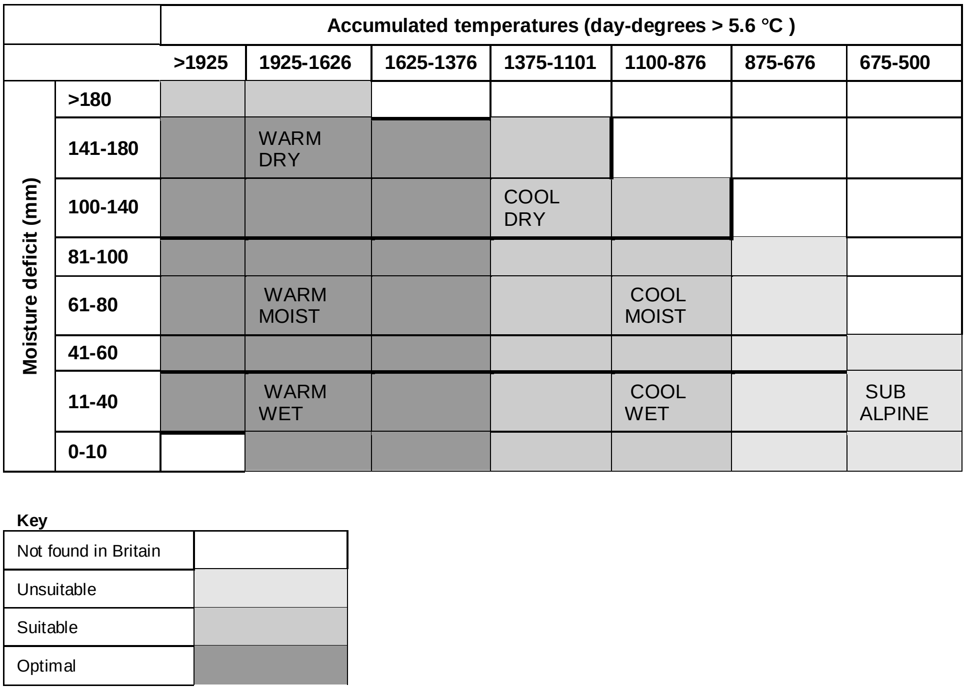
2. Site requirements

Kerr (1995) attempted to describe the range of sites on which ash will grow, however, since then an ecological site classification (ESC) for Britain allows a more objective approach to define the most suitable sites for ash (Pyatt et al., 2001). ESC assumes that three principal factors can describe a site: climate, soil moisture and soil nutrient regime. Each of these factors is divided into zones; there are seven climate zones, eight soil moisture zones and six soil nutrient zones. The three factors can be thought of as forming the axes of a cube which, if divided into the zones described above, would represent $7 \times 8 \times 6 = 336$ 'mini-cubes', or site types, for the whole of Britain. Tree species suitability for each zone has been determined as 'optimal', 'suitable' or 'unsuitable' according to expected productivity. Under 'optimal' conditions the species is expected to grow at a rate equivalent to the upper third of the yield models of Edwards and Christie (1981); for ash this would be general yield class 10 or 12 (a top height of 21.5 m at age 50). At the other end of the range, 'unsuitable' is when the risks of the species being incapable of producing sawlogs are high (Pyatt et al., 2001). To define an overall site suitability, the most limiting factor sets the limit for all factors, e.g. 'optimal' for climate and 'suitable' for soil moisture and soil nutrient regime would be an overall 'suitable'. This section describes the site requirements of ash in Britain using mainly ESC criteria; more detailed accounts of the influence of water, nutrients and light on growth are discussed in the following section.

2.1. Climate

The main climatic parameters used in ESC are accumulated temperature (day-degrees above 5.6 °C) and moisture deficit (precipitation minus potential evapotranspiration for grass from Thompson et al. (1981)). Using standard ESC information, Fig. 1 shows that ash is 'optimal' on sites in the 'warm' parts of Britain, except the most dry, and is 'suitable' on a high proportion of 'cool' sites. However, in some areas in the more northerly and westerly parts of Britain wind may become an important constraint to productive growth. In ESC climate is principally defined by warmth and wetness; however, winter cold,



		Accumulated temperatures (day-degrees > 5.6 °C)						
		>1925	1925-1626	1625-1376	1375-1101	1100-876	875-676	675-500
Moisture deficit (mm)	>180	▒	▒	□	□	□	□	□
	141-180	▓	▓ WARM DRY	▓	▒	□	□	□
	100-140	▓	▓	▓	▒ COOL DRY	▒	□	□
	81-100	▓	▓	▓	▒	▒	░	□
	61-80	▓	▓ WARM MOIST	▓	▒	▒ COOL MOIST	░	□
	41-60	▓	▓	▓	▒	▒	░	░
	11-40	▓	▓ WARM WET	▓	▒	▒ COOL WET	░	░ SUB ALPINE
	0-10	□	▓	▓	▒	▒	░	░

Key

Not found in Britain	□
Unsuitable	░
Suitable	▒
Optimal	▓

Fig. 1. ESC climatic zones for ash.

continentality, windiness and aspect can also be used as refinements. The latter two indicate that for sites with a DAMS (detailed aspect method of scoring; see Quine and White (1992)) score of more than 19 ash is 'unsuitable'. A typical site with a DAMS score of 19 would be on the western coast of Scotland at and elevation of 300 m above sea level.

An aspect of climate that is not fully taken into account by ESC but is important for ash is unseasonal frost, in the early autumn and late spring. For example, ash has been shown to be very sensitive to late spring frosts with opening buds of seedlings being killed after 18 h exposure at −3 °C (Wardle, 1961). This may affect the form of a tree because the terminal bud is flanked by a pair of lateral buds in the axils of the uppermost leaves of the shoot. If the terminal bud is lost or damaged and fails to elongate in the spring, there are two possible successors which, if both develop, will form a fork.

2.2. *Soil moisture and soil nutrient regime*

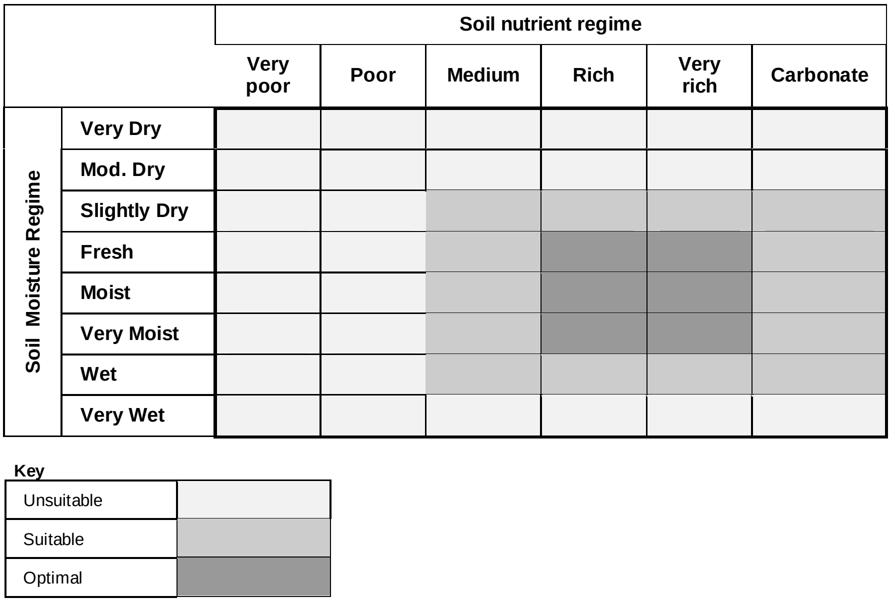
In terms of the ESC soil moisture zones, ash will grow optimally on sites that are 'very moist', 'moist' and 'fresh', and will be suitable on 'wet' and 'slightly dry' sites. Ash will also grow optimally on sites in soil nutrient zones 'rich' and 'very rich', and will be suitable on 'medium' and 'carbonate' sites. This information has been combined for ash on the ESC soil quality grid in Fig. 2. This shows that ash will grow best on base rich soils which have high levels of soil moisture, these are generally typical of the national vegetation classification (NVC) woodland types W8 (*F. excelsior–Acer campestre–Mercurialis perennis*) and W9 (*F. excelsior–Sorbus aucuparia–M. perennis*) (Rodwell, 1991).

Recent work in Belgium has generated site index curves for ash. The parameters in the model were related to topography, soil depth, soil moisture and geological strata (Claessens et al., 1999). The favorable and unfavorable influences on the growth of ash in their study are shown in Table 1, and broadly support the conclusion that ash grows well on nutrient rich sites with a good water supply.

3. Influence of water, nutrients and light on growth

3.1. *Water*

Compared with other broadleaved trees, ash has the ability to transpire large volumes of water (Ladefoged,



		Soil nutrient regime					
		Very poor	Poor	Medium	Rich	Very rich	Carbonate
Soil Moisture Regime	Very Dry	░	░	░	░	░	░
	Mod. Dry	░	░	░	░	░	░
	Slightly Dry	░	░	▒	▒	▒	▒
	Fresh	░	░	▒	▓	▓	▒
	Moist	░	░	▒	▓	▓	▒
	Very Moist	░	░	▒	▓	▓	▒
	Wet	░	░	▒	▒	▒	▒
	Very Wet	░	░	░	░	░	░

Key

Unsuitable	░
Suitable	▒
Optimal	▓

Fig. 2. ESC soil quality grid for ash.

Table 1
Factors affecting the productivity of ash in Wallonia, Belgium[a]

Factor	Favorable	Unfavorable
Topography	Valleys and hollows, H50 = 27.5 m	Plateaux and slope > 10°, H50 = 24.2 m
Soil depth	>100 cm, H50 = 26 m	<40 cm, H50 = 22.6 m
Soil moisture	Permanent water-table, H50 = 27.5 m	Without water-table, H50 = 24.5 m
Geological strata	Alluvium, H50 = 28.1 m	Famenne, Dinant, Loess, H50 = 24.8 m

[a] H50 = height at age 50 years. Source: Claessens et al., 1999.

1963; Braun, 1977). This was investigated by Kozlowski et al. (1974) for white ash (*Fraxinus americana* L.) and compared with sugar maple (*Acer saccharum* Marsh.). Their study found that white ash had fewer but larger stomata (length 26.7 μm, density 118 mm^{-2} compared with 15.3 μm and 504 mm^{-2} for sugar maple), less efficient stomatal closure and higher water loss through the cuticle due to lower cuticular resistance. On a site with good water supply, Besnard and Carlier (1990) recorded a maximum stomatal conductance of 16×10^{-3} m s^{-1} for ash. This compares with values in the range of $(2\text{–}5) \times 10^{-3}$ m s^{-1} reported for a wide range of north temperate broadleaved tree species in reviews by Hinckley et al. (1978) and Körner et al. (1979). Similar values have been recorded for fast growing broadleaved trees, for example, 20×10^{-3} m s^{-1} for grey alder (*Alnus incana* (L.) Moesch) and 16×10^{-3} m s^{-1} for grey willow (*Salix cinerea* L.) (Besnard, 1987, cited in Besnard and Carlier, 1990) and 14×10^{-3} m s^{-1} for some poplars (Pallardy and Kozlowski, 1981). The importance of site water status for the productive growth of ash has been demonstrated by Kassas (1950), Frochot et al. (1992) and Levy et al. (1992), but, of course, many sites where ash grows do not have ideal water conditions. In fact the range of sites, in terms of water status, where ash grows is quite surprising. Iremonger and Kelly (1988) showed that ash seedlings can tolerate flooding to ground level for two growing seasons and Wardle (1961) observed that when water is severely limited ash remains a shrub.

The site studied by Besnard and Carlier (1990) was an alluvial forest in the upper Rhône valley in France. The maximum stomatal conductance (16×10^{-3} m s^{-1}) was recorded for that part of the day when the amount of light exceeded 700 μmol m^{-2} s^{-1}. During the study the minimum leaf water potential never fell below −2 MPa, a figure in the range which would trigger stomatal closure of several other broadleaved species (Hinckley et al., 1978). Besnard and Carlier (1990) suggested that light was the main factor controlling the aperture of stomata and that, in this environment of good water supply, other microclimatic factors than light only limit stomatal opening in dry and very warm weather.

Further information on water relations is provided by a study of ash growing in the foothills of the Alps where summer droughts are common (Carlier et al., 1992); this is a contrast to the alluvial site studied by Besnard and Carlier (1990). In the foothills of the Alps, the water requirements of ash were moderate compared with those on the alluvial site, mainly due to a much lower maximum stomatal conductance and better control of stomata. Partial closure of stomata occurred at mid-day or earlier, but this did not prevent the leaf water potential falling to −5.5 MPa. This level is usually associated with trees of dry or desert regions, and yet no damage was observed on the ash trees, although drought symptoms were noted on other tree species.

Three strategies for responding to water stress have been described by Ludlow (1989): escape, avoidance and tolerance. Plants with an escape strategy have a life cycle during which they rarely experience water shortage (e.g. desert annuals); those with the avoidance strategy have tissue which is very sensitive to water loss and prevent large decreases in leaf water potential by minimizing water loss or increasing water uptake (e.g. desert succulents). Plants with the tolerance strategy, which best describes the response of ash to water stress, have tissues that can tolerate dehydration. Work by Carlier et al. (1992) and Peltier and Marigo (1996) have indicated that osmotic changes and elastic adjustment of the cell walls both contribute to the drought adaptation mechanisms of ash.

Another element in the tolerance strategy in response to moisture stress is altered growth; it is frequently reported that ash is very sensitive to moisture stress (Helliwell and Harrison, 1979; Kolb et al., 1990). The link between moisture stress and growth was investigated by Aussenac and Levy (1983) in a study of potted trees of 5-year-old English oak (*Quercus robur* L.) and 4-year-old ash. In controlled conditions, water supply was withheld until predawn water (base) potential reached -1.9 MPa. As the soil dried the stomatal conductance of oak decreased much more quickly than that of ash with low values (i.e. 1×10^{-3} m s^{-1}) occurring at xylem water potential of twigs of -1.5 MPa for oak and -4 MPa for ash. In response to soil drying both species stopped growing when predawn water (base) potential reached -1.1 MPa, although this occurred earlier in ash due to its higher rate of transpiration. This study requires careful interpretation as the trees were different ages and the two species have different patterns of growth, with ash having predetermined growth extending generally in one flush and oak growing intermittently in a series of flushes. However, the study is a good example of altered growth of ash as part of its strategy of tolerance in response to water stress.

It is clear from the above information that the growth of ash is very sensitive to moisture stress. This fact probably explains the recommendation that ash should not be planted pure on exposed ground (Maurer, 1963; Evans, 1984). Planting ash pure on exposed ground would create conditions which would maximize water loss from transpiration and lead to restricted growth, particularly if weed control around the trees was also poor (Davies, 1987). On such areas suitable shelter can be provided by planting in mixture with compatible species such as Norway spruce (*Picea abies* (L.) Karst.), European larch (*Larix decidua* Mill.) or other broadleaved species (Kerr and Evans, 1993). Shelter has also recently been put forward as one of the possible explanations of improved height and stem diameter growth of ash at close spacings (1 m × 1 m) in the first 4 years after planting (Kerr, 2002). This is an interesting result from the first objective study of the relationship between initial spacing, growth and form for ash. The finding may well lead to different recommendations for the initial spacing of ash than given in Kerr and Evans (1993) and Kerr (1995) which are in the region of 2 m × 2 m.

3.2. *Nutrients*

Ash is generally considered to be a demanding species in terms of nutrient requirements, reflected in the ESC soil nutrient preferences for ‘rich’ and ‘very rich’ sites. On these soils, ash should have minimum foliar nutrient concentrations of 2.3% nitrogen, 0.22% phosphorus and 0.9% potassium, which Taylor (1991) recommends for optimal growth. Figures for other nutrients are given by Bergmann (1983) (quoted in Tobolski et al., 1995). The importance of foliar nitrogen concentrations for good height growth has been demonstrated by Gordon (1964) for ash growing in the Lake District. Using data from 31 stands, height/age relationships were developed and these were used to estimate height at a standard age of 50. This height was then related to foliar nitrogen concentration. The equation:

$$y = 58.31x - 83.7$$

where y is the estimated tree height at 50 years in feet (meters = feet × 0.305) and x the foliar nitrogen as % dry weight, was found to explain 77.7% of the variation in height within the range of foliar nitrogen (1.8–2.6%).

Miller (1984) suggested that broadleaved species were generally ‘site demanding’ rather than ‘nutrient demanding’ because site requirements relate more to their relative inability to obtain nutrients from the soil compared with conifers, rather than actual high nutrient requirements for growth. The possible exception to this is cited by Miller (1984) is in the early stages of growth when the tree is building a crown. However, no evidence for this was found by Culleton et al. (1996), who found no response of ash to a range of fertilizers applied during establishment. However, the site was a fertile mineral soil and probably adequately provided the nutrient requirements of ash.

The most common symptom of nutrient related problems reported for ash is chlorosis, which is a consequence of excessive supply of calcium and a deficiency of iron and manganese (Marschner, 1986), usually associated with calcareous soils. This is one reason why it is generally recommended on soils over chalk or limestone to have a minimum depth of soil of 30 cm (Kerr and Evans, 1993); these sites are described as ‘carbonate’ in ESC. Hutchinson (1970) described the general consequences of chlorosis for plants and showed that ash was much more prone to desiccation when its foliage was chlorotic.

3.3. Light

The effects of light on the growth of trees is complex. A wide range of approaches have been taken to detect, measure and quantify competition for light (Hart, 1988; Cannell and Grace, 1993). Studies within the genus *Fraxinus* have ranged from the effects of light on the development of mycorrhiza (Borges and Chaney, 1993), to the effects on dry matter partitioning (Jones and McLeod, 1990) and tree form (Harris and Bassuk, 1993). An early study of the effects of light on the growth of ash by Van Miegroet (1970) investigated changes in leaf characteristics in response to changes in light intensity, light quality and photoperiod. The aim was to improve understanding of the empirical classifications of *light demanding* and *shade tolerance* frequently used by silviculturists. The work demonstrated that such terms are an over-simplification and that the light requirements of a tree can change under the influence of a range of factors, particularly water supply and tree age.

The light requirements of ash change over different stages of development (Savill, 1991). The canopy leaves of trees and older saplings are distinguishable from juvenile leaves of seedlings, young saplings and young coppice shoots even when all are grown in full light. In adult foliage, only sun leaves are developed whereas in juvenile foliage both sun and shade leaves are present (Wardle, 1961). The main difference between sun and shade leaves is that shade leaves are thinner because they generally have no or only a single layer of palisade cells, whereas sun leaves have two distinct layers. The ability of young seedlings to produce shade leaves enables new regeneration to survive under canopies for many years (Okali, 1966; Tapper, 1992; Tabari et al., 1998). A study by Wardle (1959) found that the compensation point of young ash regeneration was reached at 7–9% of full daylight. However, in many NVC W8 type woodlands there is a dense carpet of dog's mercury (*M. perennis* L.) in the field layer and light levels can be lower than 7–9% of full daylight. In such situations Gardner (1976) estimated that the half-life of ash seedlings is 7–8 months. These characteristics are all part of the regeneration pattern of ash, which depends on the existence of persistent juveniles that can develop rapidly in response to canopy opening (Tapper, 1992, 1993).

Like most other tree species, adult ash trees respond to an increase in resources by accelerating their rate of growth; silviculturists encourage this by thinning. However, knowledge of the dynamics of even-aged stands of ash is poor; for example, there is not yet any explanation for the belief that the window for a response to thinning is smaller for ash than for some other broadleaved species (Kerr, 1995). Ongoing work by Le Goff et al. (1995), Ottorini et al. (1996) and Le Goff and Ottorini (1996) is investigating relationships between crown development and stem volume increment and should ultimately lead to a better understanding of the stand dynamics of ash.

4. Patterns of shoot and root growth

4.1. Shoot growth

The pattern of shoot growth in ash conforms to the model described by Rauh (1939). Tree architecture is determined by a monopodial trunk which grows rhythmically and so develops tiers of branches which are morphogenetically identical with the trunk. Many temperate deciduous tree species exhibit this rhythmic growth, which has been defined by Hallé and Martin (1968) as one in which shoots have a marked endogenous periodicity of extension (the alternative is continuous growth where there is no periodicity of extension). In ash the period of extension growth begins with bud-break in early May (although understorey trees can flush much earlier) and ceases at the formation of the new terminal bud, generally in July. Detailed accounts of rhythmical growth in *Fraxinus* have been given by Gill (1971) for white ash, by Merrill (1990) for green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl.) Fern.), and under controlled conditions by Collin et al. (1995) for ash.

In general, ash leaves are preformed and the buds are determinate (Hallé et al., 1978). Hence the vegetative shoot is fully developed in the dormant bud and the number of foliage leaf primordia will be essentially the same as the number of foliage leaves on the following year's shoot. Gill (1971) reported one of the first studies on white ash, although it was limited to comparing only 15 terminal buds of opposite branches. More detailed work by Remphrey and Davidson (1994) and Davidson and Remphrey (1994) has shown that green ash has the capacity for both preformation and neoformation; the latter is where shoots are not entirely preformed in the resting bud and a proportion of the leaves is formed during the growth season. This was the first report of neoformation in *Fraxinus* and was shown to be an important part of the plant's recovery strategy after pruning or the loss of terminal buds in late spring frosts. Observational evidence for the existence of neoformation in ash has also been presented by Kerr (2002).

In ash, there have been detailed studies of the physiology of the terminal bud and its entry and exit from dormancy (Barnola et al., 1986a,b; Lavarenne et al., 1986; Cottignies, 1990). However, a review by Collin and Badot (1997) concluded that the research was too fragmentary to propose a reliable model explaining the growth and development of ash. One interesting result was the response of ash to defoliation after the cessation of shoot elongation under controlled conditions (14 h light/10 h dark; 27 ± 1 and 19 ± 1 °C) (Collin et al., 1994). Up to 40 days after the end of shoot elongation, defoliation caused immediate flushing of the terminal bud and a resumption of shoot elongation. Under the conditions described, the ash trees produced in 5 months the same stem growth as planted ash trees after 2 years. The use of defoliation as a method of enhancing growth of ash during establishment may be worthy of further examination, although, even if similar results were obtained under field conditions, there may be enhanced risk of damage from unseasonal frosts.

4.2. Root growth

Difficulties of studying roots means that there is much less information on root growth of ash than on other aspects of its biology. The morphology of ash roots has been described by Majid (1954), Köstler et al. (1968) and Wardle (1961). Generally the root system is of a typical 'plateroot' type with long, shallow horizontal roots from which laterals grow vertically downwards. This type of root system mainly exploits the upper horizons of the soil (Rust and Savill, 2000). For example, Wardle (1961) observed a much greater concentration of roots in the top 5 cm than at lower horizons of soil with greater densities in fen peat or sandy soils (1500 cm of root per 85 cm^3) than in heavier loams (230–400 cm of root per 85 cm^3). The lower limit of rooting depth is usually set by the permanent water table. The roots are generally of two types. 'Coarse' roots (>2.0 mm diameter at the tip) are persistent and can withstand long periods of poor aeration. 'Fine' roots are more numerous, mostly abscised after 1 year, and are killed if the water table rises temporarily. The root mass of ash, for equivalent stem diameters, is greater than that of beech (*Fagus sylvatica* L.), sycamore (*Acer pseudoplatanus* L.) or English oak (Köstler et al., 1968). Asthalter (1984) (cited in Rust, 1991) claims that ash is the most aggressive root competitor of all economically important tree species in Germany.

Root growth is related to soil temperature, the lower limit being 4–6 °C and the upper limit 30 °C. Collin et al. (1995) recorded continuous root growth under controlled conditions (14 h light/10 h dark; 27 ± 1 and 19 ± 1 °C). The change in the permeability of ash roots in response to drought has been studied by Wiersum and Harmanny (1983). They compared ash with five other tree species representative of urban tree planting (*Ulmus* × *hollandica* Mill. 'Groeneveld', *A. pseudoplatanus* 'Negeria', *Q. robur* L., *Populus* × *canadensis* Moench 'Robusta' and *Salix alba* L. 'Belders'). The results showed that ash was relatively slow to adjust the permeability of its roots in response to drought, but that on rewatering recovery was similar to that of the other species. These results are further evidence for ash being classified as having a strategy of tolerance in relation to water stress, as previously discussed.

Harmer (1996) studied seedlings of ash, sycamore and oak grown in swards of *Deschampsia flexuosa* (L.) Trin. and *Poa trivialis* L.cv. Ino Daehnfeldt, and in weed free conditions. The results showed the tolerance of weed competition declined oak > ash > sycamore; it was also shown that in response to competition oak produced more fine roots (<2 mm in diameter at the tip) although, interestingly, there was no difference between ash and sycamore in this respect.

Tobolski et al. (1995) reports that roots of ash trees are generally heavily mycorrhizal, and that the association is generally with endomycorrhizae and belongs to an arbuscular type of symbiosis. He quotes several examples of arbuscular mycorrhizae increasing the growth of *Fraxinus* species and proposes a strategy of inoculation to improve the performance of seedlings when they are out-planted. However, the subject of mycorrhizal associations in ash has received little attention in forest research in Britain.

General silvicultural experience is that ash is relatively easy to establish compared with oak or beech (Kerr, 1995). Contributory factors to ease of establishment may include the ability of dormant ash to survive and grow after desiccation and rough handing. This has been examined by McKay et al. (1999) who reported greater than 95% survival of 1-year-old ash trees after 36 h of desiccation and 10 drops from 1 m above the ground, although treatments did have effects on growth. In the same paper, data were also presented which show that the ash trees that were not undercut had a root:shoot ratio (dry weight basis) of 3.35, compared with 2.49 for beech and 0.48 for silver birch (*Betula pendula* Roth). These data suggest that in early growth after germination, ash invests heavily in developing a root system to supply water and nutrients, which are essential during establishment.

5. Conclusions

1. Ash grows best on sites where the climate is ‘warm’ (>1376 day-degrees $> 5.6\,^{\circ}\mathrm{C}$), soil moisture is ‘fresh’ to ‘very moist’ and soil nutrient status is ‘rich’ and ‘very rich’ as described in the ESC of Pyatt et al. (2001).
2. Ash has a tolerance strategy in response to moisture stress and growth is affected on sites where water is limiting.
3. In common with many other broadleaved species ash is ‘site demanding’ rather than ‘nutrient demanding’ because of its relative inability to obtain nutrients from the soil, compared with conifers. Growth has been shown to be closely linked with levels of foliar nitrogen.
4. Ash has the ability to produce ‘sun’ leaves (the usual adult foliage) and ‘shade’ leaves (the usual juvenile foliage) and the light requirements of the tree change with age.
5. Ash leaves are preformed and the buds are determinate although some evidence for neoformation exists in other members of the genera and this could be further investigated for *F. excelsior*.
6. The general observation that ash is relatively easy to establish compared with some other broadleaved species is most likely to be explained by its ability to develop a robust and extensive root system soon after establishment.

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