The root systems of Fraxinus excelsior and Fagus sylvatica and their competitive relationships

S. RUST¹ AND P.S. SAVILL²

¹ Institut für Forsbotanik der Georg-August-Universität, Göttingen, Germany
² Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, England

* Present address: Institut für Forstbotanik und Forstzooologie der TU Dresden, Tharandt, Germany

Summary

Following reports from field foresters on so-called ‘beech regeneration dieback’, the root systems and competitive relationships of sapling-stage mixtures of beech (Fagus sylvatica L.) and ash (Fraxinus excelsior L.) were investigated in vivo and in vitro. Ash has a plate-root system from an early age, and beech a heart-root system. The distribution of ash roots is determined by competition for light under a closed overstorey of beech while the distribution of beech roots changes if there is competition with ash roots. In a replacement series experiment in a greenhouse, interspecific competition for water strongly reduced growth and survival of beech saplings. It is concluded that this competition for water could be the reason for beech regeneration dieback on sites where it occurs.

Introduction

In some parts of Germany foresters have observed that on certain sites in naturally regenerated mixed stands of beech and ash, the beech disappears before about age 20 years. This phenomenon is known as ‘Vereschung’ or beech regeneration dieback. In pure ash stands grass cover is dense and tree dry matter increment slow (Dengler, 1980; Roloff and Peik, 1990). A proportion of beech is desirable to shade out the grass and to keep the boles of the ash free from epicormic shoots.

Many factors could cause the dieback of beech. They include moisture deficits on shallow soils (Mayer, 1977; von Lüpke, 1989) and consequent poor establishment, competition for water and light, rodent damage and deer browsing (Wagner, 1990). Too extensive an opening of the canopy above natural regeneration with too low a proportion of beech seedlings may also be a cause (Faust, 1963; Conrad, 1966; Wagenhoff, 1975).

Until now, there has been no scientific investigation into dieback, nor any survey of affected sites or stands. The reported growth check of beech in pure ash stands has not been supported by any data, nor have there been any attempts to explain the death of beech seedlings after heavy or sudden openings of the canopy.

This paper sets out to describe the root systems
of beech and ash saplings in two naturally regenerated stands quantitatively, and to evaluate possible reasons for differences between them. The ecological relevance of differences is examined with special reference to beech regeneration dieback. Interactions between the root systems of the two species, especially in terms of competition for water, are investigated. More detailed qualitative descriptions of the excavated root systems can be found in Wedler (1991).

**Sites and methods**

Most of the excavations and all the soil core sampling described below were carried out in two adjacent compartments (143 and 145) of BoWedden forest near Göttingen in Lower Saxony, Germany. The compartments are situated on a limestone plateau at 370 m above sea level. The soils are rendzinas and pseudogley–brown earths of variable depths (5–60 cm). The nutrient status is good, but some soils, especially the rendzinas are liable to drought. The climate is subatlantic.

The vegetation is as variable as the soils. On sites with loess, the plant community is a species-rich Melico–Fagetum. Where the loess layer is shallow or absent it changes to a Lathyro–Fagetum. The presence of Dechampsia caespitosa (L.) Beauv. indicates waterlogging on loess soils. Dactylis glomerata L. and Stellaria holostea L. indicate a liability to summer drought.

In one compartment, 123-year-old beech made up 95 per cent of the growing stock and ash the remaining 5 per cent. The stand was fully stocked, having 100 per cent of the yield table basal area for that age. Natural regeneration of ash and beech occurred only in small gaps. This is the ‘shade’ variant.

In the other compartment the beech was 131 years old. The stocking was low, at 20 per cent of the yield table basal area, and the canopy consequently open. This allowed an understorey of naturally regenerated ash (70 per cent) and beech (30 per cent) to grow. The average age of the regeneration was 22 years but, as with height and composition, it was very variable. Because of the very low overstorey stocking, this is termed the ‘full light’ variant. The ground flora in this compartment was relatively dense compared with that in the shade variant.

**Excavations of roots**

In order to investigate their structure and distributions, whole root systems of saplings as well as parts of them were excavated. Ten pairs consisting of one beech and one ash in close proximity (20–30 cm apart) and of equal height (2–2.5 m) were chosen to ensure as comparable conditions as possible for the two individuals. The methods employed for the excavations of entire root systems and for the profile trenches are similar to those described in Böhm (1979).

**Core sampling**

Ten sample plots were established in each compartment. Each plot was located at random but was at least one crown diameter in distance from the closest mature beech, since most roots of beech do not extend further (Hilf, 1927). Plots were selected that contained different proportions of beech to ash saplings, ranging from 10 per cent beech and 90 per cent ash, 30 per cent beech and 70 per cent ash, up to 90 per cent beech and 10 per cent ash. Each plot was then sampled as follows.

A beech tree 2–2.5 m tall was chosen as the centre of the plot. At 10 cm from it and on opposing sides (north and south), two soil cores were taken with an 8 cm diameter soil corer to 50 cm depth, just below the root zone. They were cut into 5 cm slices. The roots were extracted with a semi-automatic soil washing system, and then the living ash and beech roots were separated, by species, dried at 80ºC and weighed. It is easy to distinguish between the white ash roots and the reddish beech roots. Because of the constraints of time, dry weights were used rather than measuring root length density in the samples. The latter is often considered to be a better measure of root activity, and in this case could have been quite significant because beech has finer roots than ash.

**Greenhouse replacement series experiment**

In March 1991 a factorial experiment was laid out in Oxford to study the competitive interactions of beech and ash grown in mixture. 300 beech (2 years old, 40–80 cm tall) and 300 ash trees (1 year old, 49–65 cm tall) were arranged in 100, 20 cm diameter pots to give replacement
series with 0, 25, 50, 75 and 100 per cent beech. In 50 pots the density was four plants per pot, in the other 50 it was eight. The densities, equivalent to 0.96 million and 1.92 million trees ha⁻¹, were well within the range reported for natural regeneration. Half of the pots were well watered, and the others were watered (all with the same amount of water) as soon as the beech showed indications of wilting to give a ‘drought’ treatment. The pots were arranged in 10 blocks, the blocking criteria being heights of the plants and location in the greenhouse. At the end of July 1991 the trees were harvested and the dry weights of the roots and leaves were recorded as well as the current and previous years’ shoots.

Results

Root systems in the field

Beech The roots of beech are much finer than those of ash and whereas the main direction of growth is horizontal in ash, it is downwards, at an angle of roughly 45° in beech. The beech roots divide early into increasingly fine rootlets and end in fine tips. By contrast, the fine roots of ash usually end suddenly and bluntly. A hemispherical volume under the base of each tree is extremely intensively rooted. Beech roots do not extend very far and the rooting, especially in the top 5–10 cm is very intensive, although where there is a high proportion of ash and sufficient light, the soil is dominated by tough ash rootlets.

Ash The ash root systems are superficial but far-reaching, with tough horizontal roots that send laterals vertically downwards. The main horizontal roots decrease rapidly in diameter to 2–4 cm and then extend rope-like through the upper soil horizons. The fine lateral roots are concentrated in clumps and between them are root-free zones. The clumps often originate directly from much thicker ‘ropes’ and are concentrated in the upper horizon. The superficial rooting is very intensive and dominates the upper 0–5 cm of the soil profile (0–5 cm). Single roots of trees as small as 2–2.5 m tall extend for several metres and end in a tuft in the litter layer after travelling at a depth of down to 20 cm, only rarely branching and with an almost constant diameter. The primary root is a taproot, which often turns to horizontal growth. No reason for this behaviour was apparent from the soil profiles. The extensiveness of the root system is in stark contrast to beech.

Core sampling

Core sampling gave a much more comprehensive, quantitative picture of the rooting of the two species. The analysis concentrated on the distribution of roots of less than 2 mm in diameter. The saplings only rarely developed roots thicker than this because of their youth. There was a very high variability in the data; coefficients of variation were in the order of 100–300 per cent. Table 1 compares the distribution of fine roots of beech and ash in light and shade.

In terms of dry weights, the root biomass of beech decreases relatively slowly with depth, whereas that of ash in full light drops very quickly. These are the typical features of ‘heart-root’ and ‘plate-root’ systems, respectively. The root biomass of beech is always much greater than that of ash, and only in the top 5 cm are they of similar magnitude, contrasting the very extensive surface rooting of ash and the intensive rooting of beech. The data showing relative root distributions in Table 1 illustrate the different strategies. In the ‘light’ variant almost 60 per cent of ash roots are close to the surface. The beech, however, roots much more uniformly with depth and has only 30 per cent in the top 5 cm.

The distribution of beech roots in the different soil levels, and the relative distributions of the roots are the same in both the ‘shade’ and ‘light’ variants (Table 1). The ash, however, is strongly affected by light. In shade its root mass in the top 5 cm is only a quarter of that in full light. Biomass at lower levels in shade does not differ significantly to that at similar depths in the light. In addition, the relative distribution of ash roots in shade is very similar to that of the beech.

Further analysis of the data (see Table 1) reveals that the rooting patterns are not only affected by physical factors like light and those which are integrated by the effect of ‘depth’, but also by the presence or absence of competing trees and their vigour.

Under ‘full light’ conditions ash, a pioneer species, is much more vigorous than in the
compartment fully stocked with beech, and consequently has a larger root biomass.

There were significant correlations between the percentage of beech saplings in the ‘full light’ compartment (i.e. low mature beech overstorey) and the ratio of its root biomass in any one horizon to the total beech root biomass found in the whole soil profile sampled (i.e. between 0–30 cm depth). In the 5–10 cm horizon this relationship is shown in Figure 1.

In the 5–10 cm horizon the proportion of beech roots diminished as numbers of ash trees in the sample plot increased, but in the 10–15 cm horizon (not shown) the proportion of beech roots increased as the proportion of ash above-ground decreased. No such patterns were found

Table 1: Absolute (g per 250 cm³ soil) and relative (percentage of total root dry weight) distributions of fine root biomass by soil depth

<table>
<thead>
<tr>
<th>Soil depth (cm)</th>
<th>Ash Shade</th>
<th>Ash Light</th>
<th>Beech Shade</th>
<th>Beech Light</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g</td>
<td>%</td>
<td>G</td>
<td>%</td>
</tr>
<tr>
<td>0–5</td>
<td>86</td>
<td>22</td>
<td>392</td>
<td>59</td>
</tr>
<tr>
<td>5–10</td>
<td>81</td>
<td>21</td>
<td>107</td>
<td>16</td>
</tr>
<tr>
<td>10–15</td>
<td>34</td>
<td>9</td>
<td>45</td>
<td>7</td>
</tr>
<tr>
<td>15–20</td>
<td>111</td>
<td>28</td>
<td>63</td>
<td>10</td>
</tr>
<tr>
<td>20–25</td>
<td>65</td>
<td>17</td>
<td>20</td>
<td>3</td>
</tr>
<tr>
<td>25–30</td>
<td>13</td>
<td>3</td>
<td>34</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>390</td>
<td>100</td>
<td>661</td>
<td>100</td>
</tr>
</tbody>
</table>

Each figure is a mean of 20 core samples over the whole range of beech and ash saplings selected.

Figure 1. Light variant compartment. Ratio of beech root biomass at 5–10 cm depth to the total biomass between 0 and 30 cm soil depth plotted against the proportion of beech saplings in the sample plot. The \( r^2 \) value is 0.90. Each point represents the results from 10 sample trees.
in the top 0–5 cm. No similar correlation was found for ash root growth in the ‘full light’ compartment.

In the fully stocked ‘shade’ compartment no correlations of the kind shown in Figure 1 existed for beech, but the proportion of fine root biomass of ash in the 0–5 cm layer diminished as the proportion of beech saplings increased ($r^2 = 0.52$, $P > 99$ per cent).

Greenhouse replacement series experiment

Establishment and survival The ash flushed early in April and all trees survived to the end of the experiment, but this was not so for beech. In May 80 per cent of the beech had flushed but some of the remainder produced only small shoots and their growth was minimal (hereafter referred to as ‘dead’). During late July 20 per cent of the surviving beech became desiccated during a particularly hot period that occurred immediately before the harvest (the maximum temperature in the greenhouse was 35ºC). The leaves of entire trees wilted and dried out rapidly, often within a matter of hours. Both treatments had been watered well in an attempt to prevent the trees from becoming dehydrated.

Increasing proportions of ash in the pots significantly reduced survival of the beech ($P > 99.9$ per cent using arcsine-transformed data). Mortality was 10 per cent in the pure beech pots and 82 per cent where beech was only 25 per cent of the ash/beech mixture. There were no other significant effects or interactions.

The proportion of beech that became desiccated in late July was mainly affected by the proportion of ash in the pots: the more ash the higher the risk of wilting, the rate significantly increasing from 0 per cent desiccation in pots with 100 per cent beech to 43 per cent in those with 75 per cent ash.

Biomass growth per tree The effects of the treatments on individual trees are summarized in Table 2 for the 5-month period of the experiment. Statistical analyses were carried out with the MINITAB General Linear Model, using the dry weights of old shoots (i.e. the shoots that existed at the time of planting) as covariates where they improved the significance of results. In general, the percentage of beech in each pot and the planting density affected the production of new shoots, leaves and roots of both species though the effects were particularly strong with ash. The watering treatment had less well-marked effects.

The percentage of beech present in each pot had significant effects on the production of roots per tree of both ash and beech – the greater the percentage of beech present the more were produced. The percentage of beech also significantly affected new shoot and leaf production in ash, but not in beech. With beech, dry weights of leaves, shoots and roots per tree were respectively 42 per cent, 39 per cent and 31 per cent greater when comparing pots with 100 per cent beech with those with 25 per cent beech. In ash, the contrasts were much bigger, all being around 200 per cent.

Planting density (four or eight plants per pot) also had significant but contrasting effects on the weights of new shoots, leaves and roots. In ash, the effect of increasing the density was to reduce production per tree, whereas in beech it increased. For example, mean leaf weight of ash per tree decreased by 30 per cent at the higher density (5.72 g per tree to 3.96 g), while in beech it increased by 49 per cent (0.74 g to 1.10 g).

Replacement series Replacement diagrams such as those shown in Figure 2 provide a method for analysing and displaying competitive relationships of two species grown in replacement series. They are constructed by dividing the biomass attained by a species in one treatment by the biomass attained in the pots with 100 per cent of that species. Adding the relative yields of the two species gives the relative yield total (RYT). A RYT of near unity indicates competition for the same resource whereas a RYT below it points to mutually damaging effects and a RYT greater than unity shows that competition is less severe between species than within species. A concave response such as that for beech in both parts of Figure 2 indicates that the species is suffering interspecific competition, since the yield-density response in monoculture can only be linear or convex. The convex response found for ash in this experiment indicates that ash suffers more from intraspecific than from interspecific competition. This is also confirmed by the figures shown in Table 2 when calculating the effect of substituting one beech for one ash.
Discussion

Ash root systems

All results from this study indicate that the plate root system of ash is developed from an early age, when it grows in open conditions. Saplings exhibit most of the features reported for the few mature specimens that have been excavated so far, though in comparison with mature trees the rooting is very shallow.

The character of ash root systems changes dramatically in the shade of tree canopies where rooting patterns cannot be distinguished from those of beech. In the surface horizon (0–5 cm) rooting is reduced by 78 per cent compared to ash trees growing in the open. A likely cause of the

Figure 2. Replacement diagrams for leaf dry weight. For explanation see text.
difference is the comparatively low level of light. In shade, mortality of ash is high and young trees often have an etiolated appearance. Apparently the root:shoot ratio changes in favour of the shoot. Helliwell and Harrison (1979) found that root:shoot ratios in 2-year-old ash seedlings fell from 2.21 at 82 per cent full light to just 0.76 at 7 per cent.

A further reason for the change is indicated from the core sampling data, which showed that the proportion of ash roots in the top 5 cm is reduced where there is more beech (Table 1). This could either be caused by shade from the beech saplings, or, more likely, from competition with the beech roots.

Although the shade tolerance of ash seedlings (e.g. Gia, 1927; Dengler, 1944; Miegroet, 1956) and the inflexibility of the ash root system (Köstler et al., 1968) have been much emphasized, the changes in root, and certainly shoot morphology are great. The root systems of ash saplings growing in shade lose their plate-root structure with the typical concentration of roots in the surface layer and become more of a heart-root system.

### Table 2: Mean weights (g per tree) of new shoots, leaves and roots

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ash</th>
<th>Beech</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>New shoots</td>
<td>Leaves</td>
</tr>
<tr>
<td>Species proportion (% beech)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>1.59</td>
<td>3.56</td>
</tr>
<tr>
<td>25</td>
<td>1.90</td>
<td>4.20</td>
</tr>
<tr>
<td>50</td>
<td>2.52</td>
<td>5.19</td>
</tr>
<tr>
<td>75</td>
<td>3.29</td>
<td>6.42</td>
</tr>
<tr>
<td>100</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SE&lt;sub&gt;d&lt;/sub&gt;</td>
<td>0.88</td>
<td>1.40</td>
</tr>
<tr>
<td>P*</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Planting density (plants per pot)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2.96</td>
<td>5.72</td>
</tr>
<tr>
<td>8</td>
<td>1.69</td>
<td>3.96</td>
</tr>
<tr>
<td>SE&lt;sub&gt;d&lt;/sub&gt;</td>
<td>1.08</td>
<td>1.50</td>
</tr>
<tr>
<td>P*</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Watering</td>
<td></td>
<td></td>
</tr>
<tr>
<td>‘Drought’</td>
<td>2.11</td>
<td>4.47</td>
</tr>
<tr>
<td>Well watered</td>
<td>2.54</td>
<td>5.22</td>
</tr>
<tr>
<td>SE&lt;sub&gt;d&lt;/sub&gt;</td>
<td>0.37</td>
<td>0.63</td>
</tr>
<tr>
<td>P*</td>
<td>0.063</td>
<td>0.052</td>
</tr>
<tr>
<td>Overall mean</td>
<td>2.32</td>
<td>4.84</td>
</tr>
</tbody>
</table>

* P = probability of a significant difference between means.

---

**Beech root systems**

The root system of beech in the naturally regenerated stands that were studied is a typical heart-root system. The root distribution and biomass are independent of the light conditions within the range observed. This is surprising, because it is in contrast to the findings of Burschel and Huss (1964) and Burschel and Schmaltz (1965a, b). They found that beech root biomass reacts to only small reductions in light and that the reduction in root growth is more pronounced than that of the shoot. Since sapling densities in this study were similar in both light and shade, the findings presented here seem to provide a clear indication of the shade tolerance of beech saplings, which retain their root biomass in shade.

The shift downward in the root distribution of beech, which is correlated with an increasing proportion of ash above ground (see Figure 1) could...
be an indication of root competition with ash and/or with grasses that develop where ash is common. If ash is a more successful competitor for water and can deplete the soil moisture to levels below those accessible to beech roots, ash could reduce soil water potential to an extent that causes death of fine roots of beech and reduced root extension growth. Göttscbe (1972) has shown that in dry soils the root biomass of beech can decline sharply. That interspecific competition can reduce root biomass and change its distribution has been reported by Richardson (1953), quoted in Messenger (1976) for Acer pseudoplatanus L., by Farré (1979) quoted in Atkinson (1983) for fruit trees, by Nielsen and Mackenthun (1991) for Fagus sylvatica L. and Picea abies (L.) Karsten and by Noordwijk et al. (1996) for many other trees and crops. They emphasize the importance of the top 5 cm of soil for nutrient procurement and obtaining moisture from light showers in summer.

Greenhouse replacement series experiment

The greenhouse experiment supports the contention that ash is more drought tolerant than beech (Faust, 1963; Röhrig, 1966a, b), and that it has the potential to reduce severely the chances of survival of beech seedlings. It has been clearly demonstrated that the likelihood of mortality of beech is strongly correlated with the proportion of ash in the mixture. A. Roloff and M. Wedler (personal communication) found substantial numbers of recently dead beech in mixture with ash after prolonged periods of low rainfall in the late summers of 1989 and 1990.

It seems possible that beech seedlings can tolerate strong competition for water without reduction in growth rate up to the point where it is lethal. Ash is adapted to regeneration in larger gaps and therefore copes with competition with plants of similar size where resource pre-emption is possible and of adaptive value. It might therefore be able to deplete soil resources rapidly.

Ecological implications of root distributions

In temperate regions, the availability of water in periods of drought increases with depth and the proportion of water drawn from deep horizons increases with the duration of a drought (Eastham et al., 1990). Situations are rare where deep reserves dry up and only small precipitation events occur, thus making a shallow and extensive root system of greater adaptive value than a deeply penetrating one (Schlichter et al., 1983). The fact that ash saplings survive droughts better than beech (Faust, 1963; Röhrig, 1966a, b), despite their shallow rooting, combined with the results of the greenhouse experiment, indicate that ash is relatively drought resistant, because it is more likely to experience dry soil throughout the soil volume exploited by its roots.

On the sites investigated, roots had no access to groundwater. On the sites threatened by beech regeneration dieback, shallow soils on limestone predominate. The water storage capacity in the rooting space is low at 80-120 mm though the water storage capacity per unit volume of soil is high, about 25 mm per 10 cm. The roots of beech and ash are largely confined to the same space because of the shallow soils (rendzinas). Competition for soil resources, especially water, is necessarily intense. The low water storage capacity is a threat to the beech. Beech roots are turned over rapidly and in dry horizons their biomass declines quickly (Göttscbe, 1972). The greenhouse experiment has shown the strong potential of ash to reduce the viability of beech seedlings, where their roots are confined to the same space. The possible trend towards hotter and drier summers could make the situation worse. A drought year occurs about once every 10 years in much of Europe.

It is postulated that the greater drought resistance of ash and weaker competition by beech for water with vigorous ash saplings are likely to be important causes of beech regeneration dieback. The latter is supported by observations by Conrad (1966), Wagenhoff (1975) and Beck and Göttscbe (1976), who found pure groups of ash mostly where the canopy had been opened too fast and too early. This allows ash to develop a dense and superficial root system that is not only better adapted to water procurement in drought periods but also outcompetes the beech saplings.

Silvicultural implications

Over a whole rotation, beech and ash compete on unequal terms. During the first 60 years or so, ash dominates the upper storey of the regeneration
because of its more rapid growth. On dry sites it can outcompete the beech and reduce the proportion of beech to lower than desirable levels. Ash must have a head start; however, to make coexistence possible in the second half of the rotation when beech can shade it. There is therefore a trade-off between a reduction in the vigour of ash sufficient to ensure survival of the beech on the one hand, and a large enough growth advantage of the ash on the other.

When the main reason for the failure of beech in mixture with ash is competition for water, there are two conceivable ways of safeguarding the survival of beech. Either the two species are grown in intimate mixture, in which case the vigour of the ash has to be reduced by removing the overstorey very slowly, or they can be grown in separate groups, achieved in the early cleaning operations.

Reducing the vigour of ash in the regeneration phase entails risks because ash is very likely to lack the necessary growth advantage to survive later in the rotation without a high management input. A rather dense beech overstorey has the additional advantage of suppressing the growth of grass that can not only compete with the seedlings for water and light but also provide a habitat for rodents that can severely damage beech seedlings.

A mixture by groups reduces the interface between the two species. It is therefore possible to maintain the growth advantage of ash, without risking the failure of beech. Thus, it is necessary to direct the regeneration towards a sufficient density of beech saplings by opening the canopy after a good mast year. Obtaining sufficient number of ash saplings is usually no problem, since ash reproduces regularly and abundantly and the saplings grow rapidly as soon as the canopy is opened. Then groups of pure beech and pure ash of the size of at least one crown diameter width of a mature tree of the species can be created.

Acknowledgements

We wish to record our thanks to Frank Thompson, Jacqueline Birks and Alan Grafen of the University of Oxford, and to Andreas Roloff and Michael Wedler off University of Göttingen for their invaluable support during various parts of this project.

References


Received 30 April 2000