Survival and growth of tree seedlings in relation to changes in the ground flora during natural regeneration of an oak shelterwood

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Summary
The development of the ground flora, and survival and height growth of tree seedlings, were observed annually over the 5-year period following a mast year in an oak woodland in southern England. After removal of the coppice understorey and thinning of the tree-canopy to leave 60–70 per cent cover there was a rapid development of the ground flora which was dominated throughout by *Rubus fruticosus* (bramble), although the frequency and amount of *Pteridium aquilinum* (bracken) increased with time. More than 10 woody species regenerated but only three, *Quercus robur* (oak), *Fraxinus excelsior* (ash) and *Betula pendula* (birch), were found in substantial amounts. Many birch and *Corylus avellana* (hazel) seedlings grew sufficiently well to emerge above the bramble and bracken; in contrast, after 2 years few oak and ash were taller than the bramble and none were taller than the bracken. The number of oak and ash seedlings was positively related to the number and proximity of parent trees. There were no consistent relationships between decreases in the sizes of the seedling populations and the type, amount and height of vegetation. The size of seedling populations generally declined with time with annual reductions varying from 0 to 90 per cent depending on species and year; for most of the study, oak and ash populations fell by 40–50 per cent each year. There were some significant relationships between seedling height and site characteristics but these were inconsistent, varying between tree species and year. Results are discussed in relation to the natural regeneration of oak.

Introduction
During the last few centuries almost all restocking and afforestation in Great Britain has relied on the use of seedlings grown in nurseries. At the start of the twentieth century methods of natural regeneration were described in important silvicul-
(Matthews, 1989). Whilst such systems have been used with some success in Great Britain (e.g. Everard, 1987; Everard et al., 1994; Pakenham, 1995) many woodland managers and ecologists currently favour a more natural process of restocking with less intensive management. This approach can be successful, particularly on well-drained, infertile, mineral soils where woodlands mainly comprise Quercus and Betula spp. mixed with others such as Sorbus aucuparia (nomenclature follows Stace, 1991). However, many broad-leaved woodlands in the lowlands occur on relatively fertile, moisture-retaining, clay soils where successful restocking by natural regeneration is less easy to predict.

The conditions in many broad-leaved woodlands in lowland England are unfavourable for successful natural regeneration, with few good parent trees, well-developed ground floras and high numbers of browsing animals (Harmer et al., 1997; Fuller and Gill, 2001). Although it is usually possible to find some naturally occurring seedlings of the most common species within a woodland, a survey of 78 sites found that about 50 per cent of woodlands had <20 000 seedlings ha\(^{-1}\), and most seedlings were <20 cm tall (Harmer et al., 1994, 1997). From an ecological viewpoint a small number of well-established seedlings may be acceptable for the long-term maintenance of woodland cover, but they may be insufficient for a forester who wishes to establish a dense stand of a preferred timber species. In general, in many British woodlands, the number and sizes of seedlings present as advance regeneration are low relative to the number required for successful regeneration in hardwood forests in North America (Marquis et al., 1992).

It is well known that the ground flora can inhibit the growth of small trees, and mechanical or chemical methods to control weeds are commonplace on sites where the crop is established by planting (e.g. Davies, 1987). Competition from the ground flora is also a problem when using natural regeneration. It can cause failure despite very large numbers of seedlings (Pakenham, 1995), and the successful regeneration of oak is related to the competition that the young plants experience (Johnson et al., 2002). The ground flora can affect seedlings in a variety of ways such as competing for moisture and soil nutrients, creating shade, physical smothering, and providing suitable habitats for small mammals and other animals that can damage seedlings. Although the growth and survival of seedlings is affected by the ground flora, the magnitude of the effect varies with species and site. Some ground floras are relatively non-competitive for natural regeneration, e.g. the mixed ericaceous communities on dry heathland. In contrast, other sites that can support luxuriant growth of bramble and bracken are likely to have a very competitive ground flora and are generally difficult to regenerate: in Britain, many lowland oak woods fall into this category (Rodwell, 1991).

Oak is typically regenerated using shelterwood systems, but despite efforts to introduce such methods into Britain, notably in the Forest of Dean (Everard, 1987; Everard et al., 1994), the results have been disappointing for reasons which are unclear. In the spring following a mast year, large numbers of seedlings can germinate, but in subsequent years these often fail to establish. Whilst there have been some detailed studies describing the growth and survival of oak seedlings (Watt, 1919; Shaw, 1968, 1974; Crow, 1992; Kelly, 2002), none have been made in Britain during the early regeneration phase of a typical lowland oakwood following a shelterwood thinning. The following study was made within a mixed oakwood in lowland England that had received a shelterwood thinning following the 1995 mast. Annual observations of tree seedlings and competing vegetation were made in order to investigate the relationship between the development of the ground flora and the growth and survival of tree seedlings. The information gained will provide a greater understanding of the process of tree regeneration in lowland oakwoods in Britain, help give reasons for the failure of natural regeneration, and aid the development of silvicultural practice.

**Methods**

This study was conducted at Stansted Park, West Sussex, southern England (0° 56' W, 50° 53' N). The site is 35 m a.s.l. and the soil is a seasonally waterlogged fine loam (pH 4.4) overlaying glacial drift. A small central depression, that dries out in summer, runs along the length of the site.
The woodland was a neglected coppice with standards, best classified as National Vegetation Classification W10 Quercus robur–Pteridium aquilinum–Rubus fruticosus woodland (Rodwell, 1991); it is dominated by broadleaved trees, although there are occasional planted conifers throughout. The experimental site was part of larger woodland located in an area of mixed countryside including farmland and parkland. During autumn 1995 the hazel (Corylus avellana) coppice understorey was removed and understorey trees thinned to leave a shelterwood dominated by oak (Q. robur) with 60–70 per cent canopy cover. Prior to felling there were small numbers of birch and ash seedlings in isolated clusters and scattered individuals of other species including oak, hawthorn and holly. No seedlings >10 cm tall were seen. The ground flora was generally sparse comprising species typical of NVC W10 oak woodlands.

In 1996, 50 2 × 2 m permanent quadrats were established with ~10 m intervals between centres (avoiding trees, coppice stools and stumps) in a grid of 10 rows × 5, the total area with quadrats being 0.37 ha. Forest operations damaged three quadrats that were not assessed in 1999 and 2000. The positions of the quadrats, the ditch and any seed-bearing trees within 50 m of the quadrats were mapped. The species, diameter at breast height (d.b.h.) and maximum and minimum crown diameters were recorded for each tree. For each quadrat a visual estimate of canopy cover was made, and the quadrat’s position either beneath or away from the crown of an overstorey tree was recorded. There were nine quadrats with poor drainage, where bare ground with standing water was present in spring 1996. The experimental site was not fenced.

Assessments were made every September from 1996 until 2000. In the first year the information was gathered over the whole 2 × 2 m quadrat, but in subsequent years the quadrats were divided into four 1 m × 1 m sub-quadrats. Cover (percentage) and average height (in 10-cm classes) of the following seven categories of vegetation were assessed:

- **Bramble** (*Rubus fruticosus*)
- **Bracken** (*Pteridium aquilinum*)
- **Tall herbs**: *Chamerion angustifolium*, *Circaea lutetiana*, *Cirsium palustre*, *Digitalis purpurea*, *Epilobium sp.*, *Hypericum pulchrum*, *Mycelis muralis*, *Rumex sanguineus*, *Senecio jacobaea*, *Senecio sylvaticus*, *Teucrium scorodonia* and *Lonicera periclymenum*
- **Small herbs**: *Ajuga reptans*, *Galium aparine*, *Lysimachia nemorum*, *Polygonum aviculare*, *Stellaria media* and *Viola reichenbachiana*
- **Ivy** (*Hedera helix*)
- ** Shrubs**: *Corylus avellana* coppice shoots, *Rosa* sp., *Rubus idaeus*, *Ruscus aculeatus* and *Sambucus nigra*
- **Grasses (including sedges and rushes)**: *Agrostis stolonifera*, *Deschampsia cespitosa*, *Poa annua*, *P. trivialis*, *Carex pilulifera*, *C. sylvatica*, *C. remota*, *C. vulgaris*, *Juncus conglomeratus* and *J. effusus*

In 1996 no assessment of cover or height was made for shrubs. Within each quadrat the vegetation’s cover and height were assessed before the vegetation was disturbed to find seedlings.

The number of each species of tree seedling present was recorded. In 1996 the height of the five tallest tree seedlings, irrespective of species, was measured in each quadrat, but between 1997 and 2000 the height of the tallest seedling of each species present in each sub-quadrat was recorded. New seedlings of *Corylus avellana* and *Sambucus nigra* were included in these assessments and the data were kept separate from that collected for established shrubs.

General descriptions of vegetation cover and height, seedling numbers and heights, and changes in population sizes are based on whole (2 × 2 m) quadrat data. For each 2 × 2 m quadrat the seedling numbers are the sums of those found in sub-quadrats; seedling heights are the means of the tallest seedlings in the sub-quadrats; vegetation covers and heights are the mean values for quadrats where the vegetation type was present. The distributions of data for seedling numbers were skewed and median values are presented. Relationships between seedling numbers and heights, and site characteristics, were investigated for sub-quadrats between 1997 and 2000 by multiple regression using generalized linear models with a Poisson error distribution and a log-link function; the dispersion parameter was estimated within the model (Payne et al., 1993). Similar analyses were carried out on the 2 × 2 m quadrat data collected in 1996. The model used to investigate the relationships...
between changes in the size of the seedling populations and the vegetation present was conditional on the number of seedlings present in the previous year. Seedling height data were transformed to logarithms. The relationships between numbers of seedlings, and the number of parent trees within specified distances from each quadrat (e.g. number of trees within 5 m, 10 m, 15 m ... 50 m of the quadrat) were investigated for data collected in 1996, the best distance–number of trees relationship was then used in the models investigating the initial site and seedling relationships in 1996.

Results

On the experimental area there were 34 trees of six species with a basal area of 10.4 m² (= 91 stems and 28 m² ha⁻¹); the majority of the trees were Quercus robur (Table 1). Mean tree d.b.h. varied between 74 cm for Q. robur and 18 cm for Acer campestre and A. pseudoplatanus; crown diameters were also greatest for Q. robur, but Betula pendula had the smallest crowns. All six of these were found as seedlings on the quadrats. There were an additional 12 species of tree within 100 m of the site, many were present as seedlings within the experimental quadrats (Tables 1 and 2), but others such as Fagus sylvatica, Prunus avium and Malus sp. were never seen as seedlings anywhere on the site.

Development of the ground flora

Cover developed quickly after felling and more than 30 species were recorded on the site. However, most were present at low frequencies, had low cover scores, and restricted height growth. At the end of the first season, bramble was found on every 2 × 2 m quadrat and was the most frequent category of vegetation throughout the experiment (Figure 1a). Bracken spread slowly and was eventually found on 80 per cent of quadrats (Figure 1a). The frequency of quadrats with tall herbs increased initially, whereas small herbs declined, while ivy and grasses changed little. The increasing frequency of quadrats with shrub cover was largely caused by regrowth of hazel coppice stools, whose shoots overhung the quadrats.

The mean percentage cover present on quadrats varied with type and year; the data presented in Figure 1b are for those types where cover exceeded 20 per cent in any year. Bramble and bracken were the most abundant species throughout and final mean covers were about 50 per cent, but the maximum values that were recorded for each on a single quadrat exceeded 90 per cent. Shrub cover changed little between 1997 and 2000. The cover of herbs, grass and ivy remained below 10 per cent and small herbs had almost disappeared by 1998.

The mean heights of the predominant types of vegetation (bramble, bracken and shrubs) more or less doubled in height between 1996 and 2000 (Figure 1c). By 1999, bracken was ~120 cm tall, about twice the height of bramble. By 2000 the height of shrub cover from hazel coppice shoots exceeded all other categories of vegetation.

Development of seedlings

A total of 1628 tree seedlings was recorded at the first assessment in 1996, 54 per cent of these

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Common name</th>
<th>Stems</th>
<th>Diameter (cm)</th>
<th>Crown (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Max</td>
</tr>
<tr>
<td>Acer campestre</td>
<td>Field maple</td>
<td>1</td>
<td>18</td>
<td>4</td>
</tr>
<tr>
<td>Acer pseudoplatanus</td>
<td>Sycamore</td>
<td>3</td>
<td>18</td>
<td>5</td>
</tr>
<tr>
<td>Betula pendula</td>
<td>Silver birch</td>
<td>3</td>
<td>21</td>
<td>4</td>
</tr>
<tr>
<td>Castanea sativa</td>
<td>Sweet chestnut</td>
<td>2</td>
<td>53</td>
<td>7</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>Ash</td>
<td>5</td>
<td>44</td>
<td>7</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>Pedunculate oak</td>
<td>20</td>
<td>74</td>
<td>9</td>
</tr>
</tbody>
</table>

Stems = number of trees within the experimental area; Diameter = mean d.b.h.; Crown = mean maximum and minimum crown diameters.
were oak, and 27 per cent and 14 per cent were birch and ash, respectively. The dominance of these major species reflects the abundant acorn production in 1995 and the composition of the overstorey canopy. By 2000 the number of seedlings had declined to 386, the three major species comprising 85 per cent of the total. Eight other species were represented by small numbers of seedlings in 1996 (Table 2), the number of these minor species rose to 10 by 2000. A single seedling of willow (*Salix* sp.) grew in 1997 but disappeared before 2000.

Oak was the most frequent species with seedlings growing on about 80 per cent of quadrats in 1996 and 60 per cent in 2000 (Figure 2a). There were similar declines for the percentages of quadrats with ash and birch. The minor species were much less frequent and most occurred on <10 per cent of the quadrats, and there was generally only one seedling of each on quadrats where they were present (Table 2). For quadrats with seedlings of the major species the initial number of seedlings present varied greatly: for oak the number ranged between 1 and 128, for birch 1 and 246, and ash 1 and 37. Median values for the number of seedlings on each quadrat are shown in Figure 2b, initially these were greater for oak, but by 2000 numbers were generally similar for all three major species, suggesting differences in rates of mortality.

Initially the mean height of the tallest seedlings for all major species was ~20 cm (Figure 2c). Subsequently oak and ash grew very little with mean height increments between 1996 and 2000 of 12 and 4 cm, respectively. In contrast, the mean maximum heights of birch seedlings increased six-fold to ~150 cm in 2000 (Figure 2c). The heights of most minor species increased, most notably for hazel (Table 2). Sycamore declined in height; the reason for this is unknown.

### Relationships between seedlings, ground flora and site characteristics

In 1996, for both oak and ash, there were significant positive relationships between seedling number and parent trees. For ash, the number of parent trees within 35 m was the most important variable related to seedling number (*P* ≤ 0.001) and for oak the number of parent trees within 25 m was the only significant variable (*P* ≤ 0.001). In contrast the number and proximity of parent trees had no significant effect on the number of birch seedlings. The only significant effects of vegetation on the number of seedlings present in 1996 were for ash, which was positively related to the height of grass but negatively to height of bracken (both *P* ≤ 0.01).

The average size of the seedling population of major species present on main quadrats declined

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**Table 2: Minor tree and shrub species present as seedlings on 2 × 2 m quadrats in 1996 and 2000**

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>1996</th>
<th>2000</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sambucus nigra</em></td>
<td>Elder</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><em>Acer campestre</em></td>
<td>Field maple</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td><em>Crataegus monogyna</em></td>
<td>Hawthorn</td>
<td>24</td>
<td>6</td>
</tr>
<tr>
<td><em>Corylus avellana</em></td>
<td>Hazel</td>
<td>6</td>
<td>19</td>
</tr>
<tr>
<td><em>Ilex aquifolium</em></td>
<td>Holly</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td><em>Carpinus betulus</em></td>
<td>Hornbeam</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td><em>Castanea sativa</em></td>
<td>Sweet chestnut</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td><em>Acer pseudoplatanus</em></td>
<td>Sycamore</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>-</td>
<td>Unknown conifer</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td><em>Taxus baccata</em></td>
<td>Yew</td>
<td>14</td>
<td>9</td>
</tr>
</tbody>
</table>

% = percentage of 2 × 2 m quadrats with at least one seedling; No. = median number of seedlings on each quadrat where the species was present; Ht = mean height of seedlings (cm) ± standard error, where possible to calculate; – = data unavailable.
annually, except for ash where there was no change between 1996 and 1997 (Table 3). Initially the change in population size was greatest for birch, but it was the least between 1999 and 2000, reducing by ~10 per cent. The type of vegetation present had few significant effects on the proportion of the population remaining each year and there were no consistent trends either between or within species. The significance of relationships was weak, except for the proportion of ash and oak remaining in 1998 where the negative relationships with bramble height were significant at 1 per cent probability or better.

Analyses showed that in some years the mean heights of the tallest seedlings were significantly related to the site characteristics observed. However, with the exception of parent trees and canopy cover, which were never important variables, the relationships were difficult to interpret. There were no clear trends with differences in the significant variables occurring not only between species but also between years. The most consistent results were found for birch, where seedling height was positively related to bramble height between 1998 and 2000 (all $P \leq 0.001$). For oak and ash the relationships were so inconsistent that little can be concluded.

In all years, for each species present as seedlings, the height of the dominant ground vegetation exceeded that of many seedlings. The percentage of sub-quadrats on which the tallest seedling exceeded the height of bramble or bracken is shown in Figure 3. In 1997, seedlings of eight species exceeded the height of bramble on the sub-quadrat on which they were present; the percentage varied between 8 and 100 for ash and hornbeam, respectively (Figure 3a and b). For oak, the most frequent species, only 5 per cent of sub-quadrats had seedlings taller than bramble in 2000. In contrast, >60 per cent of sub-quadrats with birch and hazel had seedlings taller than bramble. The height of bracken cover was greater than bramble and relatively fewer sub-quadrats had seedlings that exceeded the height of bracken. In 1999 and 2000 there were no oak and ash seedlings taller than bracken (Figure 3c). In contrast, some sub-quadrats always had hazel seedlings that were taller than bracken, and there was a general increase in the percentage of sub-quadrats with birch taller than bracken.

Figure 1. Changes in the vegetation on 2 × 2 m quadrats between 1996 and 2000. For (b) and (c) data are mean values for quadrats on which the vegetation was present; where no error bars are shown they were smaller than the size of the symbol. (a) Frequency of quadrats with each type of vegetation is expressed as a percentage; (b) Percentage cover of predominant vegetation types; (c) mean height (cm) of predominant vegetation types.
The broad changes that occur in the type and amount of ground vegetation following thinning and clearfelling are common knowledge amongst practising foresters, and they have been the subject of many studies internationally (e.g. Dyrness, 1973; Brunet et al., 1996; Bailey et al., 1998; Thomas et al., 1999; Bauhus et al., 2001). However, the dynamics of the changes in the ground flora following reduction in the tree canopy are poorly understood as there have been few sequential observations made in the years immediately following operations (e.g. Collins and Pickett, 1988). Although the precise changes and their duration vary, the results generally show initial increases in species richness and abundance that decline as the tree canopy is restored. Similar observations within British forests are relatively scarce (Mitchell and Kirby, 1989), but most have inferred time-related changes from studies of similar woodland at different ages (Ash and Barkham, 1976; Ford and Newbould, 1977; Harris and Kent, 1987; Hill, 1979). The sequential data collected during the 5 years following thinning in the experiment described are similar to those reported elsewhere (Kirby, 1990; Mason and MacDonald, 2002) with a reduction in herbaceous species (annual, biennial and small species) as the site becomes dominated by bramble and bracken, which are perennial and grow vigorously under partial shade. Although >30 species were initially recorded in this experiment, there was very little differentiation in the vegetation that eventually developed across the site, which was a continuous cover mixture of bramble and bracken. This probably explains why it was not possible to identify clear relationships between the changes in the number of tree seedlings between years and the type, amount and height of vegetation present in the ground flora. In general, tree seedlings performed poorly amongst the dominant vegetation of bramble and bracken, which is consistent with the known adverse effects that they can have on natural regeneration (Leibundgut, 1945; Humphreys and Swaine, 1997; Ouden, 2000; Schreiner et al., 2000).

Although there were 15 species of tree seedlings found within the woodland, only ash, birch and oak were present in significant numbers. Precise reasons for this are unclear. Whilst the numbers probably reflect seed production, dispersal and germination, the frequency and dominance of species in the overstorey will also be more important. For oak, the presence of any seedlings in the quadrats was due to the occurrence of a mast year in 1995. The distribution of

Table 3: Annual changes in the size of seedling populations of oak, ash and birch and their relationships with site factors

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Prop</th>
<th>Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1997</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>0.53</td>
<td>Bramble ht $P \leq 0.01$</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>Oak</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.0</td>
<td>Small herb, $P \leq 0.05$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bramble ht $P \leq 0.001$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.57</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td>Ash</td>
<td></td>
<td>0.32</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.91</td>
<td>Grass $% P \leq 0.05$</td>
</tr>
</tbody>
</table>

Prop = number of seedlings in year $N$ divided by number of seedlings in year $N-1$; values are median (lower – upper quartiles); values >1 indicate that the size of the seedling population has increased whereas values <1 indicate a decrease in the number of seedlings.

Variable = variables which have a significant effect on Prop; variables in bold were positively related to Prop, those in normal font were negatively related.

ht = height; $\%$ = percentage cover; – = no significant effects.
quadrats with seedlings, and the relationship between seedling number and proximity of parents suggest that the distribution of seedlings was heterogeneous. As seed rain and number of germinating seedlings were not assessed it is not known whether the heterogeneity was due to lack of seed input, poor germination or mortality during the first season’s growth which is often high (Streng et al., 1989; Houle, 1992; Jones et al., 1994; Küßner, 2003).

The growth of tree seedlings within a woodland is often constrained by the availability of light and water (Toumey and Korstian, 1947; Coomes and Grubb, 2000). The ~70 per cent canopy cover retained at the experimental site was within the range typical for oak shelterwoods (Everard, 1987; Matthews, 1989), but the conditions produced did not favour the growth and establishment of tree seedlings. The failure of many tree seedlings of most species to emerge above the ground flora is probably due to a combination of several factors. Intrinsic differences in growth rate may be important, e.g. birch and hazel grow faster than oak. Ash can grow quickly in partially shaded conditions but the soil acidity at this site is well below the optimum of pH 7–8 for this species (Savill, 1991). In addition to the extra shade cast by the dense bramble and bracken, seedling growth may be adversely affected by physical smothering as bramble canes grow, or by the litter produced when bracken fronds die (Humphrey and Swaine, 1997).

A seedling bank (Grime, 1979) of advance regeneration has often been shown to be an important feature of successful forest regeneration following felling or natural disturbance (for references see Streng et al., 1989). The development of advance regeneration requires the establishment of seedlings that can persist within the ground flora beneath a forest canopy. Studies investigating the survival of such seedlings have shown that the annual mortality rate is often greatest during the first season’s growth and that it subsequently declines with age (Good and Good, 1972; Streng et al., 1989; Jones et al., 1994). Studies in North America have shown that the mortality of oak seedlings after germination is affected by the conditions in which they develop (Crow, 1992; Lorimer et al., 1994; Buckley et al., 1998). Survival of naturally regenerating European oaks shows broadly similar trends with estimates of

Figure 2. Oak, ash and birch seedlings on 2 × 2 m quadrats between 1996 and 2000. Values for (b) and (c) only include those quadrats with seedlings of each species. (a) Percentage of quadrats with seedlings; median number of seedlings. Data are for quadrats on which seedlings of each species were present. The vertical bars shown indicate the upper and lower quartiles for each species for 1996 and 2000, other years are omitted for clarity. (c) Mean maximum height of the tallest seedlings. Standard errors are shown where they exceed the size of the symbol.
is not possible to determine rates of mortality. However, newly germinated seedlings were not seen and it may be reasonable to assume that the changes in seedling numbers observed were caused by losses from the original population. The annual decline in population size of about 40–50 per cent is similar to those for annual mortality described above.

The longevity of the oak seedlings observed is unknown, but previous studies have shown that under woodland conditions few oak seedlings live longer than 5 years (Watt, 1919; Shaw, 1968; Kelly, 2002). Although oak seedlings survived and grew for at least 8 years under woodland conditions where light levels were 15 per cent of natural daylight (Shaw, 1974), their height was only 15 per cent of those growing in 85 per cent of daylight. Few of the oak seedlings observed in this study were taller than the bramble and bracken that dominated the ground flora, and annual height increments were much lower than the 20 cm cut-off which indicates that light may be insufficient (Bruciamacchie et al., 1994). Between 1997/98 and 1998/99 mean annual height increments were less than that of the previous years suggesting that the oak natural regeneration was not viable (Szappanos, 1969). Despite the initially large number of oak seedlings present on some quadrats, the adverse competitive conditions within the ground flora of the oak shelterwood studied suggest that very few will survive to the sapling stage.

There are well-defined procedures that may be used for the natural regeneration of oak (Teissier du Cros, 1987), but it is a species that is generally regarded as difficult to regenerate (Crow, 1988; Savill, 1991; Lorimer et al., 1994). Ground preparation is often recommended to improve natural regeneration of oak by burying seed and controlling vegetation (Nilsson et al., 1996; Löf et al., 1998), but on richer sites soil disturbance may stimulate germination of seeds in the soil and enhance development of the ground flora, especially if canopy cover is reduced by a shelterwood thinning. There was no soil disturbance at the study site other than that associated with thinning operations, but it was sufficient to stimulate the germination of bramble seed (Collins and Pickett, 1988). It has been suggested that oak can grow up through bramble cover (Evans, 1988) which may also protect seedlings from browsing.

**Figure 3.** The percentage of 1 × 1 m sub-quadrats in each year with at least one tree seedling taller than the bramble (a and b) or bracken (c) on the same sub-quadrat.
damage (Kelly, 2002). Whilst this study found that the initial heights of the tallest oak seedlings were positively related to bramble height and cover, the generally poor performance of oak amongst the ground flora at the site, and the disappointing amounts or absence of regeneration from areas of bramble reported elsewhere (Linhart and Whelan, 1980; Everard, 1987), suggest that the effects of bramble may often be negative. Further experiments on the regeneration of oak and other tree species have been carried out elsewhere in southern England, and initial observation of the results also indicates that the effects of bramble on survival and growth are adverse. Unless repeated interventions are made to control the growth of bramble it is unlikely that natural regeneration of oak will be very successful on sites where bramble overwhelms the site before oak seedlings have grown into saplings.

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