Fomes root rot in Thetford Forest, East Anglia: past, present and future

J.N. GIBBS¹, B.J.W. GREIG¹ AND J.E. PRATT²

¹ Forestry Commission Research Agency, Alice Holt Lodge, Wrecclesham, Farnham, Surrey GU10 4LH, England
² Forestry Commission Research Agency, Northern Research Station, Bush Estate, Roslin, Midlothian EH25 9SY, Scotland

Summary

Fomes root rot caused by the pathogenic wood-rotting basidiomycete, *Heterobasidion annosum*, has caused much mortality in the pine plantations of Thetford Forest, East Anglia, which were first established in the period between the two World Wars. This paper presents an evaluation of over 50 years of research into the disease, and includes much previously unpublished data. Special emphasis is given to the position of Corsican pine, *Pinus nigra* ssp. *laricio*, as this is now the principal tree used in the plantations. Freshly cut stumps of both Corsican and Scots pine (*P. sylvestris*) are equally susceptible to colonization by air-borne basidiospores of *H. annosum* and, in both species, this colonization can be effectively prevented by treatment with spores of *Phlebiopsis gigantea*. It is well known that on first-rotation sites, a high soil pH favours the development of disease from thinning stumps. Data from one experiment show that on a site with a pH of 7.5–8.0, 1095 trees per hectare had been killed by the time the crop of Scots pine was 36 years old; representing 25 per cent of the original planting. Losses tend to fall as the crop reaches the end of the rotation. There are some data to show that pure Corsican pine is less vulnerable than Scots pine to disease developing after thinning. When a new crop of pine is planted on a site carrying *H. annosum*-colonized stumps, losses averaging 30 per cent can occur during the first 10 years on soils with a pH >6.0. Even on soils with a pH <6.0, losses average nearly 20 per cent. At this early age, Corsican pine is as susceptible to the disease as Scots pine. A series of experiments has shown that it is only through stump removal that adequate control can be achieved, and for 30 years, this process has been standard practice as the first-rotation crops have been progressively felled. Experiments with a wide range of trees on different soil types have shown that very few species are resistant both to killing and to buttrot caused by *H. annosum*. Those that have performed best – most notably *Picea omorika*, *Abies grandis* and *Fagus sylvatica* – have major limitations for use in the forest. Nevertheless it is concluded that, while the justification for using Corsican pine as the principal species is well founded, there are reasons for making some continued use of other species, most notably Scots pine, on certain sites. A continued commitment to good quality stump treatment is required in order to minimize *H. annosum* problems in future rotations.

Introduction

Few tree plantations are so tightly linked with a particular disease as are the pine plantations of Thetford Forest with Fomes root rot, caused by the pathogenic wood-rotting basidiomycete, *Heterobasidion annosum* (Fr) Bref. It was serious losses through this disease in the late 1930s and
the 1940s that led to the research involvement of the late John Rishbeth FRS, during the course of which he showed that infection of freshly cut stumps by airborne basidiospores of *H. annosum* allowed the pathogen to enter previously healthy plantations (Rishbeth, 1951a). Also, it was here that he demonstrated the biological control that could be exercised at the stump surface by the non-pathogenic wood-rotting basidiomycete *Phlebiopsis* (*Peniophora*) *gigantea* (Fr) Jul. (Rishbeth, 1963). This discovery led to the development of various formulations of *P. gigantea* for the treatment of conifer stumps, both in the UK and elsewhere (Holdenrieder and Greig, 1998; Pratt et al., 2000).

The first crops planted in Thetford in the 1920s were principally of Scots pine (*Pinus sylvestris* L.). Now, Corsican pine (*Pinus nigra* J.F. Arnold ssp. *laricio* (Poir.) Maire) is predominant (Dannatt, 1996). This paper evaluates data obtained by scientists working at the Botany School, Cambridge University and in the Forestry Commission’s Pathology Branch over a 50-year period to analyse the behaviour of the disease in the past and, perhaps more importantly, to try to determine what will happen in the future. Does *H. annosum* pose as much of a threat to the currently developing second rotation of Corsican pine as it posed to the first-rotation crops of Scots pine, and the same seems to have been true of his research associates, Meredith (1959) and Punter (1964), both of whom studied the processes of stump colonization by *H. annosum* and other microorganisms in some detail. However, in the early 1960s, when Rishbeth was studying the relationship between *H. annosum* and *P. gigantea* in more detail, he did make some limited comparisons between the two pine species and did not conclude that they behaved differently (Rishbeth, 1963). A much more substantial body of data comes from a Forestry Commission experiment established in November 1963 in adjacent 20-year-old Scots and Corsican pine plantations. Trees were felled at monthly intervals until November 1964 and the stumps sampled for the decay fungi after 4 months (B.J.W. Greig, unpublished report). The data in Table 1 show that, for the stumps exposed to natural infection, the mean percentage of stumps colonized by *H. annosum* was almost identical in the two pine species, as was the percentage of the stump surface in which the fungus was established. The data for natural colonization by *P. gigantea* are also extremely similar in the two species.

**Prevention of stump infection**

Once Rishbeth had realized that stump infection was critical to the establishment of *H. annosum* in first-rotation plantations, he proceeded to examine various approaches to prevent it from happening (Rishbeth, 1951a, 1959a, b). The story of this work and that of others in the same field is well told by Pratt et al. (1998). Creosote was the first stump treatment material to achieve success and this was introduced throughout Thetford Forest in 1954. However, Rishbeth’s interest in *P. gigantea* as a possible biological control agent was continuing and he showed that treatment with *P. gigantea* oidia (asexual spores) at the
rate of $5 \times 10^3$ per 100 cm$^2$ of stump surface would be sufficient to prevent the development of any natural inoculum of *H. annosum* (Rishbeth, 1963). In 1962, treatment with the fungus was introduced on a trial basis in parts of the forest. Various formulations of *P. gigantea* were tried in a series of Forestry Commission experiments (B.J.W. Greig, unpublished report) and Table 1 shows typical data for one particular formulation in relation to the data for naturally infected stumps already discussed. It can be seen that application of *P. gigantea* oidia reduced the amount of *H. annosum* colonization of both Scots and Corsican pine stumps to an almost identical degree. In 1966 a small company, Ecological Laboratories Ltd, undertook the production of *P. gigantea* spores and a formulation was developed in which oidia were suspended in a sugar solution. An analysis of worldwide developments in the use of *P. gigantea* can be found in Holdenrieder and Greig (1998) and of the issues surrounding its registration for approval under the UK Control of Pesticides Regulations by Pratt et al. (1999). Current work is aimed at ensuring that applications via tree harvester are working satisfactorily.

**Transmission of disease in first rotation crops**

**Effect of soil type and crop age**

*Heterobasidion annosum* cannot grow freely through the soil, and it is only at points of contact between roots that the pathogen can spread from a stump to a healthy tree; this process occurring very much more readily on calcareous soils than on acid soils (Rishbeth, 1950). The newly diseased trees then act as sources of infection for others and so on. Rishbeth (1950, 1951b) reported that large groups of dead trees centred on one or more thinning stumps could be found, and that, on calcareous soils, gaps of up to 25 m across might eventually be created. Around one stump, up to 20 trees might die as a result of tree-to-tree infection (Rishbeth, 1951b). Rishbeth’s work was taken further by his research associate, Wallis (1961), who showed, through inoculation studies, that growth of *H. annosum* was very much more rapid on the roots of trees growing on calcareous soils than in those on acid soils. Wallis also collated a great deal of data from Forestry Commission thinning records in which the volume of trees killed by *H. annosum* was recorded. He then visited the relevant compartments to assess soil characteristics. From this he was able to substantiate the view that soil pH was of critical importance to losses caused by *H. annosum*. Thus at third thinning, the volume of trees killed by *H. annosum* decreased from 12.1 per cent of the thinning volume on soils with a pH >7 to 0.6 per cent on soils with a pH <5. Wallis also conducted some more detailed studies. In five compartments which contained soils of varying pH, he showed that the mean percentage of trees killed annually by the disease was between 4.5 and 11.0 per cent in sectors with a pH of >6.0, as compared with only 0–0.9 per cent.

**Table 1:** Scots and Corsican pine: colonization by *Heterobasidion annosum* and *Phlebiopsis gigantea* of stumps exposed to natural infection or inoculated with *P. gigantea* spores

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Percentage of stumps infected with:</th>
<th>Percentage stump surface colonized by:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>H. annosum</em></td>
<td><em>P. gigantea</em></td>
</tr>
<tr>
<td></td>
<td>SP*</td>
<td>CP</td>
</tr>
<tr>
<td>Stumps exposed to natural infection</td>
<td>49†</td>
<td>49</td>
</tr>
<tr>
<td>Stumps inoculated with <em>P. gigantea</em> spores</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

* SP = Scots pine; CP = Corsican pine.
† Each figure is based on 208 stumps.
in sectors with a pH of <5.0 (Wallis, 1960). It may be noted that there is some evidence that this difference is a consequence of the relative activity of antagonistic microorganisms at or near the root contacts where transfer of disease takes place (Rishbeth, 1951b; Gibbs, 1967).

Some information on the development of *H. annosum* from thinning stumps through pole-stage Scots pine on a calcareous soil is available from a randomized block experiment with four replicates, established by the Forestry Commission in 1961 on 21-year-old Scots pine planted at 1.4 × 1.4 m spacing (B.J.W. Greig, unpublished report). A comparison was made here between three treatments: thinning with and without stump treatment, and 'no thinning'. The site had previously been used for agriculture and the pH ranged from 7.5 to 8.0. In the first two treatments, all trees killed by the pathogen were recorded at thinning. In the no-thinning treatment, losses through disease were assessed every time that plots receiving the other treatments were thinned. Unfortunately some unthrifty trees had already been removed during a brashing operation to enable the crop to be inspected, and this resulted in the development of large disease foci that had to be mapped and eliminated from the areas under assessment.

The data (Table 2) show that, where there was no stump treatment, only a few trees died of disease between 1961 and 1965, but that over the next 8 years mortality increased rapidly. By 1976, 1095 trees ha⁻¹ had died: around 25 per cent of the original crop. In the plots in which the stumps were treated, disease losses were initially lower, but here also they increased rapidly and by 1976 were almost as large as in the control treatment. The reasons for this are not clear. Stump protection was with creosote and may not have been very effective – although 4 years after first thinning, samples indicated that *H. annosum* was present in only 4 per cent of the treated stumps compared with 40 per cent of those that had not been treated. Also full account may not have been taken of disease arising from the pre-experiment tree removal. In the no-thinning treatment there was very little mortality due to *H. annosum* (Table 2) but, as would be expected, the incremental growth of the trees was too poor for this approach to offer a means of disease management.

Rishbeth considered crop age as a factor in the rate of disease spread in first-rotation crops and expressed the view that the most dangerous situation was created when stumps were created in stands of trees that were about 15 years old. He particularly identified the dangers of 'pre-thinning' in which coarsely grown trees were removed at an early age (Rishbeth, 1957). This is consistent with the FCRA experience noted above on the effect of cutting out trees before first thinning.

The dynamics of the disease in a first-rotation crop are necessarily complex. As young trees grow, root contacts between them become established and then increase in frequency. After each thinning there will be a reduction in the number of root contacts that exist between living trees, but this situation will change as root systems expand to exploit the available soil. Concurrent with these developments will be changes in the resistance of individual trees: there is some evidence that this increases both after thinning and with age (Gibbs, 1968). Even on calcareous soils, killing by *H. annosum* decreases as the stand approaches the normal rotation age of 50–60 years – although butt-rot can become a problem on some sites (Greig, 1995). This condition is uncommon in pines and seems to have

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Table 2: Mortality due to *Heterobasidion annosum* in first-rotation Scots pine following first thinning on a calcareous soil

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cumulative number of trees/ha killed by <em>H. annosum</em> at intervals after the first stumps were created in the thinned treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4 years</td>
</tr>
<tr>
<td>Thinned, stumps not protected</td>
<td>20</td>
</tr>
<tr>
<td>Thinned, stumps protected</td>
<td>6</td>
</tr>
<tr>
<td>Unthinned</td>
<td>0</td>
</tr>
</tbody>
</table>
been linked to a high level of root disease in the affected trees.

**Effect of species: Scots versus Corsican pine**

Scrutiny of Rishbeth’s papers (1950, 1951a, b, 1957) reveals little to indicate that he thought any significant difference might exist between the resistance of Scots and Corsican pine. However, some interesting and, indeed, encouraging data are available from the study by Wallis of the Forestry Commission data on *H. annosum* losses recorded at thinning (Wallis, 1960). The data showed that on soils with a pH of $>6.0$, losses due to disease in Corsican pine were very much less than in Scots pine: 1.1 per cent of thinning volume at third thinning compared with 11.2 per cent. Moreover while losses in Scots pine increased from thinning to thinning, in Corsican pine the reverse was true. Data for mixtures of Scots and Corsican pine suggested that they behaved very much like pure Scots pine.

Gibbs (1967), another of Rishbeth’s research associates, attempted to examine the position in Scots and Corsican pine further through inoculation experiments. No differences between the species were found using the technique employed, but Gibbs did draw attention to large differences in the capacity of the two species to produce oleoresin and suggested that this might be a factor in the differential resistance reported by Wallis (1960). Prior (1976) studied the situation further and from a range of studies on Corsican pine concluded that the resistance of the latter species lay principally in its ability to produce toxic phenolic compounds (pinosylvins) to halt an infection and then to mobilize resins to contain further development of the pathogen.

An intriguing situation occurred in a Forestry Commission experiment established in 1971 and designed to provide information on the effect of using *P. gigantea* for stump treatment on disease development over a whole rotation (B.J.W. Greig, unpublished report). A block of 20-year-old trees growing on an alkaline soil in a former nursery was used. Despite the fact that *H. annosum* became well established in the stumps not receiving *P. gigantea*, no disease developed in the adjacent trees. Was this due, at least in part, to the intrinsic resistance of Corsican pine?

Not all the data point in the same direction, however, and significant losses can undoubtedly occur in pure Corsican pine under some circumstances. An example was recently provided by a crop that was planted in 1955 and thinned in ~1977. Despite routine stump treatment the stand was very understocked by 2000 and, although there was no evidence of recent deaths, it was clear that a killing attack had been progressing until at least 1995. It may be that disease entered this stand before first thinning, as anecdotal evidence indicates that some small poles may have been removed at a very early stage.

**Experiments aimed at reducing disease losses in the second rotation**

**The 1955 experiment**

By the time stump treatment was introduced in Thetford in 1954, *H. annosum* was already established in most of the plantations of Thetford Forest, and it was evident that there would be a significant problem when the time came to fell the first-rotation crops and replant. As early as 1955, an experiment was established by Forest Research staff to examine the possibilities for disease management in the second rotation (Greig and Low, 1975). The crop used for the experiment was a 25-year-old plantation of Scots pine on former agricultural land with a somewhat variable pH (from 4.3 to 8.4). *H. annosum* had entered the stand at first thinning in 1948, and by 1955 was well established; dead and dying trees being frequent. A variety of treatments were applied to the crop at or before felling, but only stump removal (albeit crudely conducted) reduced disease incidence in the next rotation. Scots pine was the principal species employed in the replanting but Corsican pine was also used, albeit with fewer replicates. In both Scots and Corsican pine, losses rose sharply in the control plots (Figure 1) and by age 10 half the young trees had died (Table 3). Thereafter, the rate of loss decreased: by age 18, cumulative losses had reached 59 per cent and there was no appreciable increase over the next 12 years until assessments ceased at age 30. In the destumping treatments (removal of all stumps, removal of ‘clear-fell’ stumps only), losses reached about 20 per cent at age 10 but increased little thereafter (Table 3).
Because all the trees were mapped and the experiment was assessed annually, it was possible to determine there was virtually none of the tree-to-tree spread that was such a feature of disease development in the first rotation. Treatments involving various delays in replanting were also incorporated into the experiment. A delay in replanting resulted in some reduction in losses, but high levels of mortality still occurred. Thus, in Scots pine, even after a 10-year delay, losses had reached 35 per cent by the time the young crop was 8 years old. This reflects the ability of *H. annosum* to survive for long periods in old stumps. Such survival was clearly demonstrated when 40 19-year-old Scots pine stumps from the experiment were removed from the ground and *H. annosum* was found still to be viable in 22 of them (Greig and Pratt, 1976). As described by Greig and Low (1975), data on the composition and condition of the first-rotation Scots pine crop were used to identify factors which accounted for most of the variation in mortality in the second-rotation crop. From this analysis, an equation was developed for estimating mortality at year 18 which has been used as the basis for forecasting losses in the second rotation and hence for identifying areas requiring destumping (see later).

**The 1961 experiments**

In 1960, a management decision was made to use Corsican rather than Scots pine for the second rotation in Thetford Forest. Thus, when two further experiments on disease control in the second rotation were established in 1961, the main emphasis was on Corsican pine, although both species were used in control plots. The experiments were both on calcareous soils and were established after felling Scots pine stands that were 32–35 years of age. *H. annosum* was well established in thinning stumps and in the roots of standing trees on both site. The design was a randomized block with six replicates. Stumps were removed by a crawler tractor fitted with a grubber blade and there were various other treatments in which chemicals or *P. gigantea* were applied.

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**Figure 1.** Heavy mortality due to *Heterobasidion annosum* in second-rotation pine; picture taken in a control plot in the 1955 experiment.

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**Table 3: Effect of stump removal on the killing of young pine by *Heterobasidion annosum***

<table>
<thead>
<tr>
<th>Species</th>
<th>Percentage mortality following:</th>
<th>Percentage mortality following:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No treatment</td>
<td>Removal of all stumps</td>
</tr>
<tr>
<td></td>
<td>At age 10</td>
<td>At age 18</td>
</tr>
<tr>
<td>Scots pine</td>
<td>50</td>
<td>59*</td>
</tr>
<tr>
<td>Corsican pine</td>
<td>51</td>
<td>65*</td>
</tr>
</tbody>
</table>

* Differences between the control and the stump removal treatment significant at 0.01%.
applied to the stumps (B.J.W. Greig, unpublished report). Losses in the control plots were very similar to those in the 1955 experiment (Table 4). Mortality in the stump removal treatment was lower than before, almost certainly the result of using a more efficient machine. Mortality following Peniophora or chemical treatments was not significantly different from that in the control, and only those for Peniophora are shown in the table. Again, the assessments showed that there was very little tree-to-tree spread of infection.

The 1969 experiment
In 1969, an experiment on a larger scale was established. The site was ex-agricultural, with a pH of ~8.0 following the application of marl many years earlier. It was carrying a 43-year-old Scots pine crop in which disease was well established. In addition to the control, there were two destumping treatments, one involving the removal of all stumps and the other involving the removal of clearfelling stumps only. Destumping was done with a crawler tractor fitted with a five-tooth bulldozer blade and the excavated stumps were then pushed into rows at the edge of the plots. P. gigantea treatments were also included but they were not very effective and will not be described further here (for full details, see J.E. Pratt, in preparation).

The treatments were applied in randomized blocks with five replicates. Each treatment plot was 0.4 ha in size and the plots were split equally, giving subplots of 64 × 32 m. Replanting of subplots was with Corsican pine, either immediately or after a delay of 6 years. Assessments for mortality were conducted in a central assessment plot of 16 rows × 18 trees. These commenced in 1972 and continued until 1988. Mortality in the control plots was less in this experiment than in the previous ones. However, it had reached nearly 25 per cent by 1988 (Figure 2). The two destumping treatments did not differ significantly from each other and losses did not exceed 10 per cent by year 18. Where there was a delay of 6 years before replanting, losses were somewhat lower, although they followed a similar trend (Figure 2). Thus with delayed replanting the mortality in the control plots at age 10 was 12 per cent, whereas with immediate replanting it had been 17 per cent.

Disease losses in areas subject to FC restocking and management
By the early 1970s it was evident that significant mortality was occurring in restocked Forestry Commission plantations. In order to obtain more information, a series of observation plots was set up over the period 1973–1980 on a variety of sites (B.J.W. Greig, unpublished report). In each selected compartment, four points were chosen at random and a sub-plot of 10 rows each containing 10 trees was established. Starting at age 5, the numbers of trees killed by H. annosum or other damaging agents were recorded for each plot at 1–2 year intervals. These data and additional information on the previous history of these plots are shown in Table 5. It should be noted that Scots pine had formed the previous crop in most cases. Not only was the amount of first rotation Corsican pine small, but it tended to have been planted somewhat later than the Scots pine. As a result, by the time most of it came to be felled, destumping had been introduced as the standard treatment on high-risk sites. The data show that significant killing by H. annosum occurred in almost all the areas in which stumps were

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**Table 4:** Two experiments to determine percentage mortality in second rotation pine established on Heterobasidion annosum-infested calcareous sites: (data at 30 years of age)

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Scots pine control</th>
<th>Corsican pine control after destumping</th>
<th>Corsican pine after P. gigantea stump treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redneck</td>
<td>51</td>
<td>10</td>
<td>40</td>
</tr>
<tr>
<td>High Lodge</td>
<td>50</td>
<td>37</td>
<td>33</td>
</tr>
</tbody>
</table>
However, losses were appreciably higher in the plots with a soil pH >6 than in the others. Thus after 20 years, current average mortality in these high-pH plots was 30 per cent, compared with 19 per cent on the more acidic soils. The four plots from which the stumps had been removed showed negligible losses.

It should be noted that *H. annosum* was by no means the only cause of mortality in these plots. The early years of the restocking programme...

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**Figure 2.** Cumulative mortality due to *Heterobasidion annosum* in Corsican pine planted after various treatments of the previous Scots pine crop. Data are shown separately for immediate replanting and replanting after a delay of 6 years. Control, continuous lines; stumps of standing trees removed, dot-dash lines; all stumps removed, dotted lines.

**Table 5:** Cumulative mortality in 20-year-old second-rotation Corsican pine on sites with different histories and soil characteristics

<table>
<thead>
<tr>
<th>Treatment of first rotation stumps</th>
<th>Soil pH</th>
<th>No. of sites</th>
<th>Mean percentage trees killed by:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>H. annosum</em></td>
</tr>
<tr>
<td>Retained</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scots pine as previous crop*</td>
<td>&gt;7</td>
<td>10</td>
<td>30 (23–39)†</td>
</tr>
<tr>
<td></td>
<td>6–7</td>
<td>5</td>
<td>31 (19–52)</td>
</tr>
<tr>
<td></td>
<td>5–6</td>
<td>4</td>
<td>18 (11–25)</td>
</tr>
<tr>
<td></td>
<td>&lt;5</td>
<td>4</td>
<td>19 (11–24)</td>
</tr>
<tr>
<td>Corsican pine as previous crop</td>
<td>&gt;7</td>
<td>2</td>
<td>35 (18–53)</td>
</tr>
<tr>
<td></td>
<td>5–6</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Removed</td>
<td>&gt;7</td>
<td>4</td>
<td>3 (2–7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Two sites comprised Scots and Corsican pine in mixture.
† Range of percentages shown in parentheses.
were bedevilled with problems such as poor plant quality and handling, spring frost, etc. (Low and Greig, 1973). Table 5 shows that these losses averaged 18 per cent on sites with retained stumps and 13 per cent on destumped sites.

**Stump removal on a forest-wide basis**

The decision to adopt the practice of stump removal on the calcareous soils most vulnerable to disease was taken in 1970. In the early 1980s, Greig reviewed the situation and described how information on disease levels obtained from aerial photographs and data on soil pH were used to identify sites requiring ground survey. In the survey additional information on disease level and soil conditions was gathered and used to designate areas requiring stump removal. After felling, stumps were individually removed with a hydraulic excavator fitted with a single tine and pushed into rows 80 m apart; ~1 ha being destumped each day (Greig, 1984). At 1983 prices, destumping cost £110 ha⁻¹ and raking £90 ha⁻¹. Since it was estimated that after stump removal the crops would have a discounted revenue (DR) value of £1400 ha⁻¹, while without destumping the DR would only be £700 ha⁻¹, the costs could easily be justified. At that time about 200 ha were destumped annually. Over the years, costs have risen in line with inflation and the overall price is now around £450 ha⁻¹.

The procedure has remained much the same over subsequent years. Currently, a site visit is made to each compartment due for felling and soil pits are dug to confirm the information from the soil maps. Top candidates for destumping are compartments with a pH >7.0, poor stocking due to past disease and the evident presence of *H. annosum* fruitbodies on existing stumps. If the soil pH is high but stocking is good, destumping may not be recommended but a note will be made that great care should be taken over stump treatment at the time of clear-felling. As of 2000, there were ~2400 ha of remaining first-rotation crops in the forest, of which 800 ha are likely to need destumping. The main recent development has been in respect of whole-tree harvesting, with the possibility that a market could be found for the stumps in a local power station. The advantage of this is that it would eliminate the loss of plantable ground to the stump rows which currently amounts to ~10 per cent.

**The behaviour of various tree species in the second rotation**

When the decision was made to use Corsican pine for the second rotation in Thetford, it was also recognized that more information was required on the growth and resistance to *H. annosum* of a greater variety of tree species. As a consequence a series of experiments was established, of which the most important were those set up in 1964 on the three main soil types found in the forest: a deep acid sandy soil (pH ~4.3); a brown calcareous soil of variable depth (pH generally >6.0) and a shallow soil over chalk (pH ~8.0). Experimental details are to be found in Greig (1974). In brief, the existing crops of Scots pine (30–40 years old) were thinned to leave ~500 stems ha⁻¹. Stumps were not treated, and indeed on the acid site, some stumps were inoculated with *H. annosum* basidiospores to increase the potential for disease. The areas were underplanted in 1964 with 18 species each in 0.04 ha plots. A randomized plot design was used to give three replications of each species on each soil type. Each year from 1967 onwards, all dead trees were removed from the plots and the cause of death established. The results in terms of cumulative mortality after 13 years are shown in Table 6 (data at 8 years can be found in Greig (1974)). As would be expected, mortality on the acid sand was much less than on the other two sites. The rather lower mortality on the shallow calcareous soil than on the deep calcareous soil was due, in large part, to poorer growth of the trees, leading to fewer root contacts with the Scots pine stumps (Greig, 1974). Differences in growth between the species on the same site probably had a similar effect: the low level of disease in the very slow-growing common silver fir, *A. alba* Mill., is an example of this.

The losses on the deep calcareous soil were very high. Thus the mortality figures for Leyland cypress (*× Cupressocypris leylandii* Dallim et A. B. Jacks) at 58 per cent and Douglas fir (*Pseudotsuga menziesii* France) at 65 per cent were the heaviest recorded anywhere in Britain. The high mortality in the red oak (*Quercus rubra* du Roi) and the Roble beech (*Nothofagus obliqua*...
(Mirb.) Bl.) was also noteworthy. A relatively low level of killing was found in western red cedar, (Thuja plicata D. Don), Serbian spruce (Picea omorika, Panchic Purkyne), grand fir (Abies grandis Lindl.,) and Colorado white fir (A. concolor (Gord.) Hildebrand). Several of these species had grown very poorly, however. Beech (Fagus sylvatica L.) also showed very little disease.

Such was the mortality on the two calcareous soils that normal thinning regimes could not be adopted. However, on the acid sand, thinnings were carried out and data on butt-rot susceptibility, in terms of the incidence of infection in the stems removed in the thinnings of 1981/83 and 1994/95 are shown in Table 6. High figures were recorded for western hemlock (Tsuga heterophylla Sarg.), hybrid larch, (Larix × eurolepis Henry), Leyland cypress and Douglas fir; results that are broadly in line with those obtained for decay susceptibility in other experiments (Greig et al., 2001). As expected, the two pines performed well in this respect, as did the species mentioned above that had been characterized by low mortality. Among possible candidate species for planting at Thetford, high infection levels were found in western hemlock, hybrid larch and Douglas fir. Serbian spruce was notably resistant and the results from this experiment inspired some local forest trials in which several compartments were planted up with this species. Unfortunately they all failed; this apparently being due to a combination of frost susceptibility and vulnerability to deer browsing.

Conclusions

Disease development in the second rotation

There are a number of reasons for thinking that the tree population that comprises the second rotation in Thetford Forest should be less vulnerable to killing by H. annosum than was the first rotation. First, there is some evidence that Corsican pine is more resistant than Scots pine to disease developing from thinning stumps. Secondly, second-rotation crops are more widely spaced than were first-rotation crops. Thus on the destumped alkaline soils they are around 2.5 ×
1.7 m compared with 1.4 × 1.4 m in the first rotation. *Inter alia*, this means that first thinning will come later in the life of the crop than was formerly the case, and hence at a time when the resistance of the trees that are retained may well be higher.

**The role of species other than Corsican pine**

Corsican pine has many qualities that make it suitable for use as the principal species in the second rotation. It provides a desirable timber that sells well. In addition it is resistant to stem rust caused by *Peridermium pini* (Pers) Lév., which has had a significant impact on the older Scots pine in the forest (Gibbs *et al.*, 1987). However, on the negative side, there is the well-recognized vulnerability of young Corsican pine to spring frosts (Low and Greig, 1973) and to damage caused by Brunchorstia shoot dieback. This disease, caused by *Gremeniella abietina* (Lagerb.) Morelet, has occasionally caused significant damage to poorly ventilated pole-stage plantations in the forest (Gibbs, 1984). The impact of red band needle blight, caused by *Scirrhia pini* (Funk & Parker), which was common in parts of Thetford Forest in 2000 has yet to be determined. In France, where heavy successive attacks of this disease have occurred in the 1990s (de Villebonne and Maugard, 1999), there are no reports of mortality, although it seems likely that some growth reduction has occurred.

There would thus be good reasons for making some use of other species even if it were not part of the certification standard of the UK Woodland Assurance Scheme (UKWAS) that, where several species are suited to the site and matched to the objectives, no one species should comprise more than 65 per cent of the planting (Anon., 2000). In the case of Thetford, the principal alternative remains Scots pine, particularly if genotypes can be found that are better for timber production than the present provenances without showing a greater susceptibility to diseases and pests. Douglas fir is not suitable for any site (acid or alkaline) where the *H. annosum* is well established in pine stumps of a previous crop, but it may be a candidate for use on some de-stumped sites. However due consideration will have to be given to its susceptibility both to frost and to browsing by deer. Serbian spruce clearly has an appreciable level of disease resistance, but is subject to similar constraints over its establishment. Among the *Abies* species, grand fir undoubtedly possesses significant resistance (see also Greig *et al.*, 2001; Redfern, 2002) but the wood is not well-regarded. Beech also shows disease resistance, and already has an accepted place in the amenity woodland of the forest. However, there is little scope for increased use, given its slow growth rate. Finally, in a recent review of the various species trials conducted in Thetford, R. Jinks (unpublished report) has suggested that western yellow pine (*Pinus ponderosa* Dougl.) might have a contribution to make. Even if no more resistant to the disease than Scots pine, it could offer a useful addition to the options for planting on the acid soils.

**The importance of effective stump treatment**

A continuing commitment to stump treatment remains a vital part of the management strategy for the forest. It seems possible that current and future crops will not be as vulnerable to the epidemic development of Fomes root rot as were the closely spaced first-rotation Scots pine plantations in which stumps were created when the trees were only 15 years of age. However, without effective treatment, some mortality will undoubtedly occur after thinning on calcareous soils, and serious losses will be experienced each time a crop is felled and a new one is planted. Stump removal is an expensive operation and it must be the forest manager’s aim to ensure that it does not need to be repeated after the remaining areas of the first rotation have been cleared.

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