Receptivity of *Picea sitchensis* stumps to infection by *Heterobasidion annosum* basidiospores

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Summary

Picea sitchensis stumps were inoculated with *Heterobasidion annosum* basidiospores either immediately or 24 h, 7 days or 28 days after cutting, in order to determine the length of time they remained susceptible to infection. Control stumps were inoculated with sterile water; those that became colonized were presumed to have been infected by natural inoculum. The degree of colonization of inoculated stumps declined when spores were applied more than 24 h after cutting but was still greater than in the control stumps at 7 days. Spores applied at 28 days did not result in stump infection. These data indicate that stump protection measures applied after felling must remain effective for at least 7 days, and that if stump treatment is not applied immediately after cutting, it could still have some protective value up to 7 days later.

Introduction

Heterobasidion annosum (Fr.) Bref. (*Fomes annosus* (Fr.) Cke) causes a serious root and butt rot of conifers in the North Temperate region (Hodges, 1969). It becomes established in first rotation plantations principally by basidiospore-infection of fresh stump surfaces (Rishbeth, 1951a, b). Following spore germination, *H. annosum* grows from the stump surface into the body of the stump and roots and infects neighbouring trees through root contacts. The success of stump colonization is affected by factors such as temperature (Yde-Andersen, 1962; Driver and Ginns, 1964, 1969; Ross, 1973; Kallio and Hallaksela, 1979; Brandtberg *et al.*, 1996) and the number of spores available at the stump surface (Redfern *et al.*, 1997). In Sitka spruce (*Picea sitchensis* (Bong.) Carr), stump moisture content is an important factor influencing the success of infection (Redfern, 1993). In addition, Redfern (1993) found a positive correlation between infection in the heartwood and sapwood, which suggests there are also intrinsic differences in stump susceptibility.

Research on control measures has led to stump treatment with chemicals such as creosote, sodium nitrite and currently urea (Rishbeth, 1959a, b; Phillips and Greig, 1970) and to biological control on pine (*Pinus* spp.) using the

fungus *Phlebiopsis gigantea* (Fr.) Jülich [*Peniophora gigantea* (Fr.) Massee] (Rishbeth, 1963). Recently, in Scandinavia, a commercial formulation of *P. gigantea*, 'Rotstop', has also been used successfully on Norway spruce (*Picea abies* (L.) Karst.) (Korhonen *et al*., 1994).

Chemical or biological control agents are applied to stumps immediately after cutting and must remain effective for at least the time during which stumps are susceptible to infection (Pratt and Redfern, 1989). This period can vary with tree species. In North America, Ross (1968) reported that Loblolly pine (*Pinus taeda* L.) stumps were susceptible to *H. annosum* for up to 12 days after cutting, after which time a rapid increase in *P. gigantea* appeared to limit colonization. Cobb and Schmidt (1964) found that stumps of white pine (*Pinus strobus* L.) inoculated with conidia were highly susceptible to *H. annosum* infection for only 3 days, whereas Cobb and Barber (1968) found that Redwood (*Sequoia sempervirens* (D. Don.) Endl.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Ponderosa pine (*Pinus ponderosa* Laws.) were susceptible for at least 4 weeks. In Europe, Yde-Andersen (1962) suggested that Norway spruce stumps were susceptible to natural infection for no more than 1 month and Schönhar (1979) found that they were only receptive to conidial infection for 28 days, with most infection occurring the day after felling. Rishbeth (1951a) suggested that competition from fungi, such as *P. gigantea*, limited to only 2–3 weeks the period during which Scots pine (*Pinus sylvestris* L.) stumps were susceptible. No equivalent data are available for Sitka spruce and this paper reports the results of an experiment to determine the receptivity of stumps of this species within 28 days of cutting.

Materials and methods

Basidiospore inoculum

Heterobasidion annosum basidiospores were collected on glass slides placed horizontally in the bottom of 10 × 10 cm glass staining dishes beneath basidiocarps growing on Douglas fir stumps and fallen trees in Kirkhill Forest, Aberdeenshire. The spore deposits were collected after 24 h, air-dried for 1 h at room temperature, and stored at 2°C for up to 7 days. Basidiospore suspensions were made up 5 min before inoculation by immersing the slides in a flask containing 1 l of sterile distilled water and gently agitating the dry spores with a small paintbrush. Sufficient basidiospores were used to form a cloudy suspension.

Experimental procedure

The experiment was set up in an unthinned first rotation stand of 24-year-old Sitka spruce in Bunzeach Forest, Aberdeenshire, Scotland (57°11′ N, 3°01′ W). On 12 August 1994, 120 trees were felled leaving stumps 40–45 cm tall. Stumps were in four rows with four rows of trees between each treatment row. Two days later, at the start of the experiment, stumps were all re-cut to a height of 20 cm above the level of the buttress roots. Stumps were inoculated with either a basidiospore suspension of *H. annosum* or with sterile distilled water, applied immediately, 1 day, 7 days or 28 days after re-cutting. The eight treatments were allocated at random in 15 replicate blocks, with each block consisting of eight consecutive stumps along a row. For each time treatment, control stumps were treated first, followed by the stumps to be inoculated with the basidiospore suspension.

A new pair of latex medical gloves was worn for each treatment and swabbed down with 75 per cent ethanol before use. Spore suspensions were shaken vigorously prior to inoculation and agitated at regular intervals. Stumps were inoculated by applying water or a freshly made basidiospore suspension dropwise using different sterile pipettes. The volume of suspension required to wet the stump surface was recorded, together with the under-bark diameter of the stump.

Each stump was covered with a polythene sheet for 24 h after inoculation to prevent spores being washed off by rain. Contact between the polythene and the stump surface was prevented by placing a piece of 15 mm diameter plastic tubing across the stump surface and stapling the polythene to the stump sides.

Immediately after inoculation, the viability of

the spore suspension was assessed by plating aliquots (1 ml) of each of six successive 10-fold dilutions of each suspension onto a selective medium (Kuhlman and Hendrix, 1962). There were three replicate dishes per dilution. Cultures were incubated at 22°C in the dark and examined daily from 3 until 7 days after inoculation for *H. annosum* colonies. The concentration of viable spores was calculated from the dilution that yielded no more than 25 colonies per Petri dish, and a haemocytometer count of the total number of spores. Spore concentration data were combined with data on the volume of spore suspension applied to produce a figure for the number of basidiospores applied to each stump.

Sampling and assessment of colonization by H. annosum

Stumps were sampled 7–9 months after inoculation by cutting two 3 cm-thick discs from the top with a chain saw. Discs were placed in individual plastic bags after cutting and transported to the laboratory. Within 24 h of sampling, the bark was removed and discs were washed with running tap water in order to remove any sawdust that might impede the subsequent observation of fungal colonies and be a possible source of contamination (Morrison and Redfern, 1994). After drying for 2 h in a vertical position, discs were wrapped individually in newspaper (Rishbeth, 1957) and placed vertically in clean plastic dustbins that had been swabbed out with 70 per cent ethanol prior to use. Each bin was covered by a lid and aeration was provided by seven evenly spaced 1 cm diameter holes drilled 7 cm below the rim. The bins were incubated for 7–10 days outdoors, where the ambient temperature did not exceed 10°C. If the temperature remained around 0°C for several days, the bins were transferred to room temperature 3 days prior to observing the discs under a dissecting microscope for conidiophores of *H. annosum*. Colonies were outlined with an indelible felt tip pen.

The cross-sectional area of heartwood and sapwood occupied by *H. annosum* on the upper surface of the lower disc (i.e. at a depth of *c.* 38 mm) from each stump was measured in the following manner. The outline of the stump disc, heartwood and sapwood areas and *H. annosum* colonies were transferred to tracing paper and photocopied. The boundary between heartwood and sapwood was identified on the basis of wood colour and moisture content. For the purposes of this study the heartwood was considered to be the dry inner area of the stump including the lighter coloured transition zone that surrounds it, and the sapwood was the wetter outer area. The difference between these tissues is clearly defined in freshly cut stump discs. The stump outline was cut out and weighed, followed by the heartwood and sapwood areas and finally the *H. annosum* colonies in the heartwood and sapwood separately. From these data the percentage of the cross-sectional area of heartwood and sapwood occupied by *H. annosum* was calculated.

Ancillary observations

In *P. sitchensis*, some stumps remain alive due to the formation of root grafts with neighbouring trees, and previous observations (Redfern, 1982, 1993) have suggested that these stumps may be more susceptible to *H. annosum* than those that die quickly. The incidence of living stumps was therefore determined at the end of the experiment by examining the condition of the phloem and vascular cambium tissues on the lowest sample disc. When the stump dies, these tissues deteriorate, causing the bark to loosen.

The incidence of other stump fungi was also noted, particularly *Melanotus proteus* (Kalchbr.) Singer, a small crepitoid hymenomycete common on Sitka spruce stumps, with a distinctive white mycelium (Redfern, 1991, 1993; Woods, 1996). The area occupied by this fungus on incubated discs was outlined and measured in the same way as for *H. annosum*.

Statistical analysis

The figures for the percentage of cross-sectional area colonized by the fungi were transformed to the arcsine scale prior to conducting an analysis of variance (ANOVA) to determine whether treatment differences were significant at the 95 per cent level. Tukey's test was used to determine which treatment differences were significant at the 95 per cent level.

Results

Period of stump susceptibility

The incidence of infection for each treatment is given in Table 1. Up to 7 days after cutting, the proportion of stumps infected by *H. annosum* was much greater among those that were inoculated than among the controls, whereas at 28 days the proportions were little different.

The area occupied by *H. annosum* in the stumps is shown in Table 2. It was significantly greater in stumps inoculated with basidiospores than in the controls for up to 7 days after cutting. However, in stumps inoculated at day 7, the area was smaller than in those inoculated at earlier times. Colonization was much greater in the heartwood than in the sapwood, in which colonization was negligible by day 7.

The mean number of viable spores applied to the stumps is shown in Table 1. No viable spores were detected in the water used to inoculate control stumps.

Pattern of stump colonization

In stumps inoculated both immediately and 1 day after cutting, *H. annosum* either occupied large irregular areas within the heartwood and sapwood (Figure 1a) or occupied a single extensive area within the heartwood (Figure 1b). In stumps inoculated after 7 days, heartwood colonization was less extensive and occurred in

Table 1: Infection of Sitka spruce stumps by *H. annosum* following inoculation with basidiospores at various times after cutting

	Inoculation with *H. annosum*		Inoculated with sterile water
Delay after cutting (days)	Mean no. of viable *H. annosum* spores cm^{-2} stump surface	No. of stumps infected*	No. of stumps infected*
0	6.6×10^3	15	2
1	92.7×10^3	15	1
7	87.1×10^3	13	1
28	350.4×10^3	3	0

*Out of 15.

Table 2: Colonization of Sitka spruce stumps by *H. annosum* following inoculation with basidiospores or sterile water at various times after cutting

	Mean percentage cross-sectional area occupied					
	Heartwood		Sapwood		Total	
Delay after cutting (days)	*H. annosum*	Sterile water	*H. annosum*	Sterile water	*H. annosum*	Sterile water
0	37.2[a]	0.0*	4.4[a]	0.0	15.8[a]	0.0*
1	50.4[a]	0.0*	2.3[ab]	0.0	15.6[a]	0.0*
7	15.6[b]	0.0*	0.5[ab]	0.0	4.3[b]	0.0*
28	0.0*[c]	0.0	0.0*[b]	0.0	0.0*[c]	0.0

Mean values for the heartwood, sapwood and total areas inoculated with *H. annosum* or sterile water followed by dissimilar letters differ significantly ($P < 0.05$). Comparisons should not be made between columns.
*Trace = not measurable.

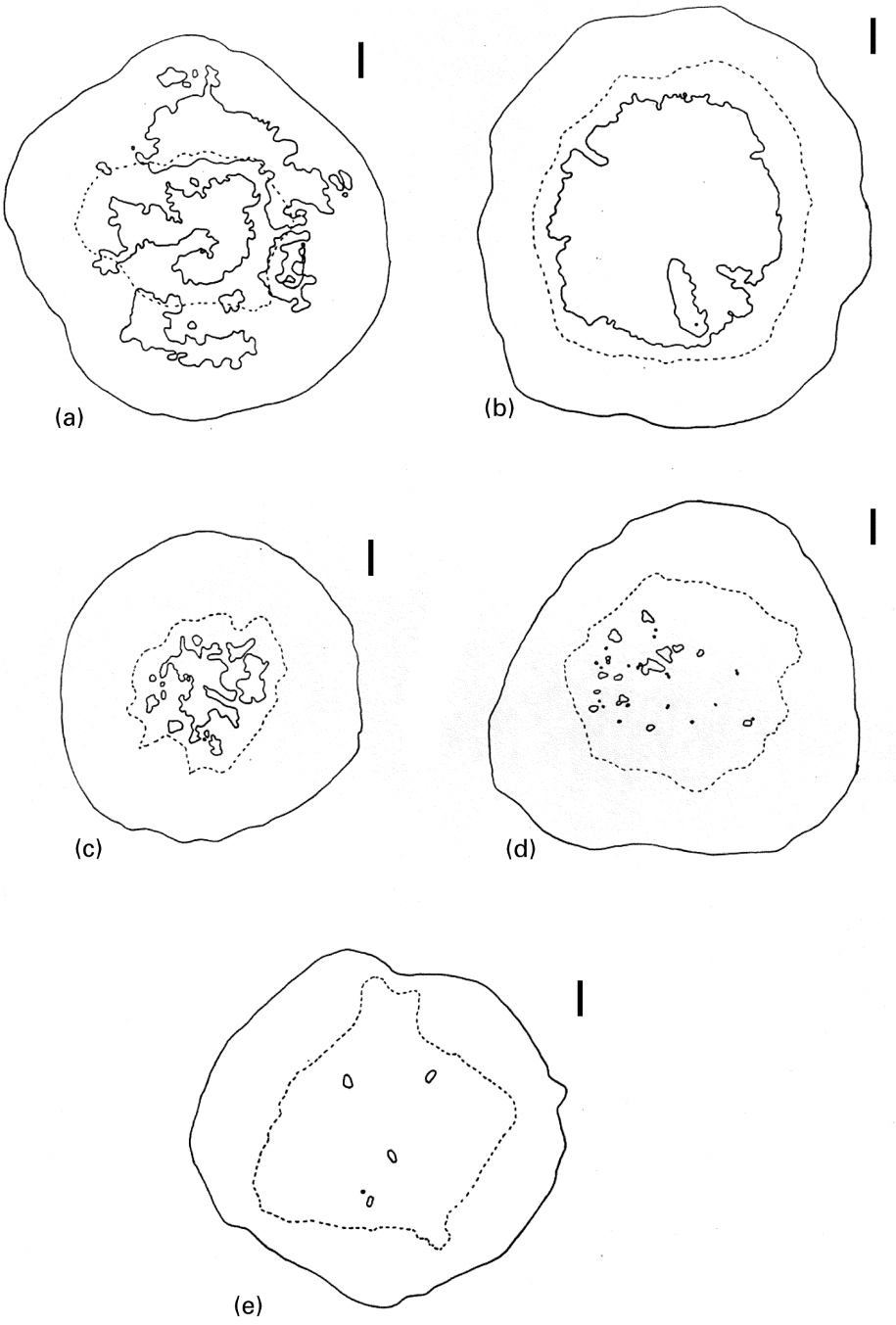

Figure 1. Distribution of *H. annosum* in representative *P. sitchensis* stumps 7 months after inoculating the stump surface with *H. annosum* basidiospores applied (a) immediately, (b) 1 day after cutting, (c, d) 7 days after cutting and (e) 28 days after cutting. Areas occupied by *H. annosum* are outlined. The dotted line indicates the boundary between heartwood and sapwood. Bar represents 25 mm.

discrete areas (Figure 1c, d). In some stumps it was absent entirely. Colonization of the sapwood was rare in stumps inoculated 28 days after cutting, and most colonies occupied small areas within the heartwood (Figure 1e).

Colonization by other fungi

M. proteus was found on 68.3 per cent of inoculated stumps and on only 46.7 per cent of stumps treated with sterile distilled water. Colonization was most extensive in stumps inoculated with *H. annosum* 1 day after cutting (Table 3), and was greater than in stumps inoculated with sterile water for three out of the four inoculation times, but the differences were not significant. No other Basidiomycotina were observed on the discs.

Stump condition

At the time of sampling 29 out of 120 stumps were alive. *H. annosum* was present in 28 per cent of these stumps whereas *M. proteus* was observed in only 10 per cent. By contrast the respective figures for dead stumps were 53 per cent and 72 per cent.

Discussion

Sitka spruce stumps were highly susceptible to colonization by *H. annosum* basidiospores up to 7 days after cutting but susceptibility declined to almost zero between 7 and 28 days. These results indicate that stump treatment must remain effective for at least 7 days after felling and that if treatment is delayed it could still have some protective value if applied up to 7 days later.

Broadly similar results have been obtained for other conifers, but the reported rate of decline in receptivity has varied (Rishbeth, 1951a; Cobb and Schmidt, 1964; Yde-Anderson, 1962; Cobb and Barber, 1968; Ross, 1968; Schönhar, 1979). Apart from the effects of environmental factors (Yde-Anderson, 1962; Driver and Ginns, 1964, 1969; Ross, 1973; Kallio and Hallaksela, 1979; Brandtberg *et al.*, 1996; Redfern, 1993; Redfern *et al.*, 1997), some variation may result from the degree of host specificity shown by the different species of *Heterobasidion* (previously referred to as intersterility groups; see Niemelä and Korhonen, 1998) present in Europe, and the relative abundance of inoculum of these species in different forest types. Some degree of host specificity in living trees has been suggested (Stenlid and Swedjemark, 1988; Capretti *et al.*, 1994), but there is conflicting evidence on the importance of this factor in stump infection (Harrington *et al.*, 1989; Otrosina *et al.*, 1992; Korhonen and Piri, 1994; Hanso *et al.*, 1994). The basidiospore inoculum used in this study originated from *H. annosum sensu stricto* (Niemelä and Korhonen, 1998), as confirmed in molecular studies (Kasuga *et al.*, 1993).

It has been suggested that pine stumps become less receptive to *H. annosum* with increasing age because they are colonized by competing fungi (Rishbeth 1951a; Ross, 1968). However, in this study, in which *M. proteus* was the only other fungal colonist recorded, there was no evidence from the frequency of colonization by the two fungi in live and dead stumps that *M. proteus* restricted infection by *H. annosum*. Both fungi were more common in dead stumps than live ones and *M. proteus* was no more common in stumps in which inoculation was delayed than in those inoculated earlier.

Table 3: Colonization of Sitka spruce stumps by *M. proteus* following inoculation with *H. annosum* basidiospores at various times after cutting

Delay after cutting (days)	Mean percentage cross-sectional area occupied by *M. proteus*	
	Inoculation with *H. annosum*	Inoculation with sterile water
0	3.6	4.7
1	5.6	1.6
7	3.4	1.1
28	2.7	2.4

Although the frequency of stump infection is a major determinant in the development of the disease within a stand, the ability of *H. annosum* to survive within colonized stumps is also important. Several authors have reported a rapid decline in the survival of *H. annosum* in stumps, whether inoculated or infected naturally (Dimitri *et al.*, 1971; Morrison and Johnson, 1978; Shaw, 1989; Morrison and Redfern, 1994). The last authors observed that *H. annosum* was absent from stumps that 6 years previously had been infected only in the heartwood, whereas it was still present in those infected in the sapwood. In these latter stumps the fungus had entered the roots and infected neighbouring trees (Morrison and Redfern, 1994). In the experiment reported here, although there was little difference in the number of stumps infected up to 7 days, the proportion in which the sapwood was colonized declined from 53 per cent and 73 per cent in the immediate and day 1 inoculations, respectively, to 20 per cent at 7 days. A consequence of this could be that stumps colonized within 1 day of felling are more likely to cause infections in surrounding trees than those colonized later.

Unfortunately the number of viable spores applied to stumps varied (more than 10-fold) between inoculation times. The greatest number was used on the oldest stumps (28 days) and it is arguable that the reduced colonization resulting from inoculation at this time was due to intraspecific competition between genets rather than to a decline in stump receptivity. However, this seems unlikely as, although Redfern *et al.* (1997) detected such an effect of competition, it was relatively small. Furthermore the greater number of spores applied at day 1 compared with the immediate treatment was associated with increased heartwood colonization.

Although the effect was not significant, *M. proteus* was generally more common on stumps inoculated with basidiospores than on those that received only sterile water. Redfern *et al.* (1997) observed that stumps inoculated with higher concentrations of *H. annosum* basidiospores were colonized by a greater abundance of fungi such as *R. bicolor*, *H. fasciculare* and *M. proteus* than those inoculated with lower numbers of spores. They suggested that colonization by these fungi might have been favoured by the effect of mutual inhibition between *H. annosum* genets or simply by the huge numbers of *H. annosum* spores applied.

The low level of infection (8.3 per cent) in the control stumps suggests that the risk of natural infection in *P. sitchensis* was extremely low in this forest at the time the work was done. Similarly low levels (4.2 and 13.3 per cent) have been found elsewhere in Scotland by Redfern (1993) and Redfern *et al.* (1997). Nevertheless, the response to inoculation suggests that if spore loads increase, levels of infection could become much higher.

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