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Colonisation of woody material in *Pinus radiata* plantations by *Armillaria novae-zelandiae* basidiospores

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Abstract. Partly buried stem segments and stumps of thinned trees were treated with basidiospores at varying densities to test the likelihood that spread of *Armillaria novae-zelandiae* into *Pinus radiata* plantations in New Zealand is occurring through the colonisation of woody material by airborne spores. Colonisation of stem segments was confirmed at densities ranging between 20 million and 5 spores/cm^2 of exposed cut surface. Degree of colonisation was not influenced by the presence or absence of a protecting wood disc placed over the surface after treatment. In one study, the incidence of colonisation was significantly greater in segments taken from trees felled 3 weeks rather than 3 months earlier, but colonisation was still effective in the older material. The colonisation of freshly cut pine stumps was also demonstrated at densities exceeding 13 million spores/cm^2 surface, but stumps may be less receptive to spore colonisation than stem segments. Tiny mycelial ribbons present beneath the bark of stem segments but not stumps in all studies were found to belong to *Rosellinia thelena*, a species newly recorded in New Zealand.

Additional keywords: *Armillaria novae-zelandiae*, dispersal, infection centres, *Rosellinia thelena*.

Introduction

Species of *Armillaria*, particularly *A. novae-zelandiae* (Stevenson) Herink cause a significant root disease of *Pinus radiata* D. Don in New Zealand. Indirect evidence implies that *A. novae-zelandiae* spreads into pine plantations by means of basidiospores dispersed from nearby indigenous forests during May and June. The pathogen is widespread in some second rotation stands on sites not originally covered in indigenous forest, suggesting that infection has arisen from an external source (Gilmour 1954; Hood *et al*. 2002*b*). Populations of *Armillaria* species are composed of comparatively high densities of small colonies, implying that infection centres have established through the ingress of spores (Hood and Sandberg 1987, 1993; Hood *et al*. 2002*a*, 2002*b*; Dodd *et al*. 2006). However, because of the implications for commercial forestry in the future, it is important to determine the distribution pattern directly and to clarify the extent to which infection may be invading plantations through spore dissemination. Research is currently underway using spore trapping combined with a molecular identification technique to monitor the dispersal of basidiospores of *A. novae-zelandiae* (Power *et al*. 2007). The present paper reports the results of four studies undertaken to determine the threshold spore densities necessary to achieve successful colonisation of woody substrate in pine forests. A fifth complementary experiment was conducted to examine the ability of basidiospores of *A. novae-zelandiae* to colonise two common types of substrate created during forest operations, freshly cut thinning stumps and partially buried stem fragments. This was performed to determine the predominant source of new infection centres.

During the course of the work, several other fungi were frequently encountered as natural colonisers of the stumps and segments (Hood and Gardner 2005). These were investigated and identified, and are also reported in the present paper. In particular, research was undertaken to determine the nature and identity of tiny mycelial ribbons, which superficially resembled those produced by species of *Armillaria*.

Methods

The four spore density studies were carried out during successive winters on separate portions of a well drained, level Rotorua lawn site (Table 1). Small pine stem segments of dimensions 6–7 cm diameter × 35 cm long with bark retained were partly buried vertically 1 m apart with 5 cm length exposed, in two lines. Segments were cut within 2 days before treatment from trees previously felled during routine first thinning operations in young (8- to 12-year-old) pine stands.

Basidiospores to be used for treatments were dropped onto plastic sheets in the laboratory from basidiocarps of *A. novae-zelandiae* freshly collected from neighbouring indigenous podocarp-hardwood forest. Spore powders were stored in clean, dry stoppered vials at 4°C, until suspended in distilled water and diluted quantitatively on the day of application within 25 days of collection. Dosages were estimated from haemocytometer counts using samples of the

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Table 1. Numbers of *Pinus radiata* stem segments colonised by *Armillaria* after treatment of the freshly cut surface with different concentrations of *A. novae-zelandiae* basidiospores and replacing or not replacing the detached segment cap

Study	Date treated	Segment age (approx. no. weeks since felling)	Application rate (spores/cm^2 cut surface)[A]	No. segments colonised by *Armillaria*/ no. segments treated	
				Cap replaced	Cap not replaced
1	4 June 2003	2–3	20 000 000	2/4	2/4
			200 000[B]	0/4	2/4
			5000	0/4	0/4
			100	0/4	0/4
2	19 May 2004	<4	10 000 000	4/4	2/4
			1 000 000	4/4	4/4
			100 000	4/4	4/4
			10 000	4/4	3/4
3	14 June 2005	11–12	20 000	2/4	4/4
			2000	3/4	4/4
			200	2/4	4/4
			50	3/4	2/4
4	2 June 2006	3	2000	–/0	2/3
			200	–/0	3/3
			50	–/0	2/3
			5	–/0	3/3
		12	2000	–/0	1/3
			200	–/0	0/3
			50	–/0	1/3
			5	–/0	2/3

[A]Means and standard deviations from counts of undiluted suspensions (highest rate in each study): 22.5 ($\pm$3.2) $\times$ 10^6 (study 1); 8.6 ($\pm$1.9) $\times$ 10^6 (study 2); 20.3 ($\pm$5.1) $\times$ 10^3 (study 3); 2.0 ($\pm$0.3) $\times$ 10^3 (study 4).
[B]Corrected value (Hood and Gardner 2005).

undiluted suspension. Immediately before treatment, an end disc was cut from the top of each segment. After mixing the spore suspension, a measured quantity was pipetted either entire or in portions across the newly exposed surface, allowing time for absorption of the fluid between applications. Treatments were assigned to segments at random. However, in study 4, which also compared the effect of segment age (the period since felling of source trees), treatments were randomised within six alternating blocks of four segments, those in each block originating from a stand thinned on the same date. Besides spore density, and segment age, experimental variables included the retention or non-retention of the disc as a protective cap replaced after treatment. Weather remained dry for at least 24 h after treatment in studies 2–4, but a tarpaulin was used to shield segments from light rain during this initial period in study 1. A shade cloth (50% light reduction) was extended as a cover over the segments during the full period in all studies to simulate the lighting within young plantations.

The fifth study was conducted in a young, first rotation rural stand on a pasture site near Rotorua. Ten scattered smaller trees were felled and one bark-encased segment 70 cm long $\times$ ~14 cm in diameter was cut from each stem. Stem segments were partially buried vertically 2–3 m distant from their parent stumps, protected from possible *Armillaria* soil rhizomorphs by a 30-cm-diameter, open-ended, cylindrical, earth-filled plastic sheath extending 8–10 cm below the segment base (Hood and Sandberg 1987; Hood *et al*. 2002*a*). A narrow disc was cut from the top of each stump or segment, and a precise quantity of basidiospore suspension was sprayed onto the freshly exposed surface within 4 h of felling. The lower surface of the disc cap was also treated before replacing it on the segment or stump surface.

Segments were uplifted between 31 and 35 weeks after inoculation in lawn site studies 1–4. On the pasture site (study 5), segments and stumps were removed randomly at intervals between 28 and 40 weeks after treatment, complementary pairs being uplifted together on the same day. Stumps and segments were cleaned and examined for signs of *Armillaria* (attached rhizomorphs and characteristic mycelial ribbons and fans beneath the bark; Fig. 1*a*). Where applicable, and where numbers allowed, comparisons were made between different treatments: spore application density, cap retention, segment age, and substrate type (stump or segment). In study 5, isolations were attempted from decayed stump wood and from mycelial ribbons of *Armillaria* by plating aseptically onto 3% malt agar supplemented with 100 ppm streptomycin sulfate and 10 ppm benomyl. *Armillaria* cultures obtained were identified to species using cultural methods outlined in Hood and Sandberg (1987).

The identity of tiny, mycelial ribbon-like colonies observed beneath pine bark during the project was investigated by isolating onto 3% malt agar with and without the supplements previously listed. To confirm isolation and investigate growth behaviour, cultures obtained from such ribbons on four stem segments in study 5 were grown on freshly cut *P. radiata* branch segments (2–3 cm in diameter $\times$ 12 cm long) partially buried in jars of moist sand. Jars and contents were autoclaved for 50 min to sterilise, allowed to cool, seeded with part of a 3% malt agar culture of one isolate per jar, sealed with Gladwrap (Clorox New Zealand Limited, Auckland,

Fig. 1. Results from *Armillaria novae-zelandiae* basidiospore application studies using *Pinus radiata* stem segments or stumps. (*a*) *Armillaria* mycelial ribbons on treated segment in study 2 (lawn site). (*b*) Extracted treatment stump from study 5 (pasture site) showing mycelial fans and ribbons of *A. novae-zelandia*e. (*c*) Radiating mycelial ribbons of *Rosellinia thelena* on stem segment in study 2. (*d*) Mycelial colonies produced after inoculating pine branch segment with culture of *R. thelena* in jar. (*e*) Fruitbodies of *R. thelena* on the surface of bark near soil level on segment in study 4 (lawn site). (*f*) Ascospore (right), with hyaline appendages, and part of ascus, apical ring stained positive in iodine (bottom), of *R. thelena* from fruitbody in (*e*). Bark removed in (*a*–*d*). Scale: bar length = 10 cm (*b*), 1 cm (*a*, *c*, *d*), 1 mm (*e*), 25 µm (*f*).

New Zealand) film to retain moisture and then examined after incubation for 18 weeks. Cultures were described and coded using the method of Nobles (1965), Stalpers (1978) and Nakasone (1990) as adapted previously (Hood *et al*. 1989).

Results

Colonisation by Armillaria *basidiospores*

Stem segments became colonised by *Armillaria* following treatment with basidiospores of *A. novae-zelandiae* in all studies. Mycelial ribbons of *Armillaria* were readily recognisable (Fig. 1*a*), and characteristic rhizomorphs were often present on the bark surface or at cut ends. When data from studies 1–4 were examined together (Table 1), there was a slight but significant indication of greater colonisation at higher spore treatment densities. Mean percentage of segments with *Armillaria* after treatment with up to 5000 basidiospores/cm^2 surface was 51% compared with 73% after treatment with between 10 000 and 20 000 000 spores per cm^2 ($P = 0.014$, $n = 16$, Fisher's exact test). However, spore treatments as low as 5 spores/cm^2 gave rise to effective colonisation (Table 1). There was no significant difference in colonisation by *Armillaria* whether cap discs were replaced (mean 58% of segments colonised) or were not replaced (63%; $P = 0.705$, $n = 28$). Segments of both ages were colonised by *Armillaria* in study 4, but younger segments (3-week-old; mean 83% colonised) were significantly more colonised than older segments (12-week-old, 33%; $P = 0.036$, $n = 8$; Table 1). Segments in the older set were noticeably drier at the time of treatment.

At the first rotation pasture site (study 5), 5 of 7 stem segments (71%) and 2 of 7 stumps (29%) treated with spores of *A. novae-zelandiae* were colonised by *Armillaria* when harvested (Table 2). Cultural testing confirmed that isolates obtained from all segments and stumps were of *A. novae-zelandiae*. Mycelial fans of *Armillaria* were extensive beneath the bark and clearly descending from the cut surface in some segments and both stumps (Fig. 1*b*). *Armillaria* was not present in any of the untreated stump or stem segment controls. Soil beneath all segments within the plastic shields was free of woody material with no evidence of invasion by potential external rhizomorphs.

Rosellinia thelena *and other fungi*

Wood colonising fungi besides *Armillaria* were identified on pine stem segments and stumps during the project. Of several basidiomycete species cultured from decayed stump wood in the pasture site study (study 5), the most frequently obtained was *Phlebiopsis gigantea* (Fries) Jülich, which was isolated from two stumps and the disc cap belonging to a third stump, in some cases associated with characteristic white cords. *P. gigantea* was also cultured from a non-study stump on the pasture site, which additionally bore cords of *Resinicium bicolor* (Albertini & on Schweinitz: Fries) Parmasto. The ascomycete, *Neonectria discophora* (Mont.) Mantiri & Samuels, was observed fruiting near ground level on 23 segments in study 2 on the lawn site.

In study 5, circular colonies 1–5 cm in diameter were scattered beneath the bark in areas of otherwise clean, white cambial surface in 9 of the 10 segments, but in no stumps. Identical colonies were also present in many of the segments in the other four studies (Fig. 1*c*). Colonies consisted of tiny, dichotomously branched, mycelial ribbons radiating out spoke-like from a central point. Ribbons were a few millimetres wide, composed of septate and clampless hyphae, and yielded isolates on 3% malt agar only when devoid of benomyl and streptomycin sulfate. Radiating ribbon colonies were reproduced after 18 weeks beneath the bark of the *P. radiata* branch segments in the jar experiment (Fig. 1*d*), which yielded the same cultures on reisolation. Ascocarps present in one culture after 22 weeks matched others observed on the bark surface near soil level directly above typical radiating ribbon colonies in five segments in study 1, three segments in study 2, one segment in study 3 and one segment in study 4 (Fig. 1*e*). Polyspore cultures isolated from a black spore mass capping the ostioles of ascocarps from a field segment collection were indistinguishable from those isolated from the mycelial ribbon colonies. These results identified the species forming the ribbon colonies as *Rosellinia thelena* (Fr.:Fr.) Rabenh. (Petrini 1993). This is the first confirmed record of this species in New Zealand.

R. thelena was characterised by a dark-brown, felty, persistent subiculum, and subglobose, black, (deep red-brown when immature) stromata with a wrinkled surface at the base, and up to 150 µm long pointed ostioles. Stromata were ~1 mm in diameter, mostly separate in dense clusters, but some confluent (Fig. 1*d*). In cross section, the ectostroma measured <25 µm. The entostroma was white, turning brown in old material. The apical ascus ring blued in iodine (Fig. 1*f*), and measured 8–10 µm in length by 5–7 µm in width. Ascospores were dark-brown with a straight germ slit nearly the full spore length, with both extremities capped by a narrow, pointed, hyaline appendage up to 7 µm long (Fig. 1*f*). They measured 21–29(–38) µm × 7–8(–10.5) µm excluding the hyaline appendage, and were variable in shape and size within and between collections from four pine segments.

Table 2. Numbers of *Pinus radiata* stumps and stem segments colonised by *Armillaria* after treatment of the freshly cut surface with basidiospores of *A. novae-zelandiae* and replacing the detached segment cap (study 5)

Date treated	Substrate age (period since felling)	Application rate (spores/cm^2 cut surface)	Substrate and treatment (controls not treated)	No. stumps or segments colonised by *A. novae-zelandiae*/no. treated
15 May 2002	4 h	13 000 000[A]	Stumps	2/7
			Control stumps	0/3
			Segments	5/7
			Control segments	0/3

[A]Plus 5 000 000/cm^2 to lower disc cap surface [means and s.d.: 13.1 (±1.4) × 10^6 and 4.9 (±0.5) × 10^6].

Ascospore apices were blunt or with a tapering pointed 'beak' at each end.

Cultures at 6 weeks on plates of 3% malt agar produced low, white, silky, prostrate aerial mycelia in a pattern of radial dichotomously branching, diffuse arms. Older cultures developed as a low, white mat, sometimes forming a blackish central zone of brown hyphae, or spherical black nodes 50–120 µm in diameter with a dark narrow wall of brown interlocking plectenchyma at the colony margin. Fertile stromata were present at the edge of one culture after 22 weeks. Culture code (refer to Methods): 2/(1), 6, 7, 32, 36, 38/(39, 40), 42/43/44/(45), 55.

Specimens examined (Forest Research Mycology Herbarium and Culture Collection): NZ: Rotorua, Forest Research Nursery, on *P. radiata* wood: 5 Jan. 2004, NZFRI (M) 5139; 18 Jan. 2005, NZFRI (M) 5432; 26 Jan. 2006, NZFRI (M) 5433; 30 Jan. 2007, NZFRI (M) 5434. Cultures: NZFS 1548, NZFS 1549, NZFS 1550, NZFS 1551. Collections and cultures, I. A. Hood.

Discussion

This work has confirmed that basidiospores of *A. novae-zelandiae*, the main cause of Armillaria root disease in contemporary *P. radiata* plantations, readily colonise moist pine stem segments. Partly buried pine wood debris is a normal feature following harvest operations and is, therefore, a suitable substrate for basidiospores to invade, potentially leading to the establishment of new infection centres in the succeeding crop. Preliminary work appeared to indicate that high spore densities are required (Hood and Gardner 2005), but the subsequent studies reported here have shown that colonisation can occur at densities down to at least 5 spores/cm^2 of wood surface. Rishbeth (1970) also reported colonisation of segments of Norway spruce [*Picea abies* (L.) H. Karst.] at comparably low spore densities in the laboratory. It remains to be demonstrated whether natural air spore numbers will accommodate densities of this order within pine stands, taking into consideration the possibility of a gradual increase by deposition in viable form over time (Shaw 1981). The results of study 4 indicate that *A. novae-zelandiae* basidiospores prefer fresh pine debris, but even material from 3-month-old pine thinnings is still receptive. Study 5 confirmed that newly cut pine stumps can also be colonised by basidiospores of *A. novae-zelandiae*, at least when subjected to high spore densities, and when protected by a disc cap covering the treated surface. Stem segments appear to be a more satisfactory substrate than stumps, though numbers were insufficient to test this statistically. However, it has not been possible to find a suitable stand in which to explore further the effect of reduced spore density or stump age on the susceptibility of stumps to colonisation. Care was taken to remove all treated stumps and buried stem segments to ensure no introduced *Armillaria* inoculum remained at the end of the experiments.

It was found during earlier work that results from second rotation pine stands were confounded by viable *Armillaria* naturally present in the residue of the previous crop (Hood and Gardner 2005). This was not an issue for the studies reported here, which were conducted on sites that had been in lawn or pasture for many years in order to ensure the absence of any pre-existing woody material, and as anticipated, there were no signs of invading rhizomorphs beneath the open-ended shields in study 5. Nevertheless, there are obvious discrepancies in the results from some of these studies. In study 1, spore densities of up to 5000/cm^2 failed to colonise segments, while in study 3, colonisation was successful at all densities on segments 11–12 weeks old, both results contrasting with those in study 4 (lower spore densities and older segments were not considered as variables in study 2). Such differences may be due to disparities in conditions not subject to experimental control between years, such as uneven exposure to sunlight, wind or rain (Rishbeth 1970). For instance, segments in study 3 did not appear as dry as the 12-week-old material in study 4. Even so, direct exposure of treated segments, without the protection of a cap disc, was not inhibitory to colonisation in a shaded environment under central North Island conditions. Segments in study 1, only, were cut from trees previously subjected to operational spraying with treated waste water, possibly influencing their receptivity to germinating spores. Unevenness in basidospore viability might also account for some of the differences observed, even though spores were of comparable age when applied soon after collection from fresh fruitbodies in the same locality in all studies. Spore germination rates were not determined *in vitro*, partly because these do not necessarily represent true viability or indicate actual germination on stem or stump surfaces (Merrill 1970). Total spore concentration data are probably more useful when comparing with results from spore trapping. During treatment, care was taken to agitate the mixture to ensure an even application of the correctly determined quantity of spores to the freshly cut surfaces. Spore counts were made from the original mix to improve the reliability of lower density values at greater dilutions.

Other fungi besides the applied *A. novae-zelandiae* colonised the segments and stumps naturally during the study periods, notably *P. gigantea* and *R. bicolor*, which are among several basidiomycete species commonly found on woody residue in pine plantations in New Zealand (Butcher 1967, 1968; Hood *et al*. 2002*a*; Hood and Gardner 2005). It was initially conjectured that the tiny, radiating ribbons commonly observed beneath the bark of partially buried *P. radiata* segments might simply be smaller mycelia of *Armillaria* (Hood *et al*. 2002*a*). However, they are recognisably distinct in appearance (Fig. 1*a*, *c*), and it is now confirmed from these studies that the tiny, radiating ribbons belong to *R. thelena*. Hood *et al*. (2002*a*) excluded them from the *Armillaria* data in their earlier study. *R. thelena* occurred only on stem segments, suggesting that fresh pine stumps may still retain some of the resistance of the living tree.

R. thelena is found on coniferous hosts in Europe and North America, and is reported here for the first time from New Zealand (Petrini 1993, 2003). Collections were readily identified from the ascocarps frequently produced on the colonised segments, and occasionally, also in culture. *R. thelena*, as observed in these studies is, therefore, not conspecific with another species of *Rosellinia*, assigned by some (Dingley 1969; Boesewinkel 1977; Pennycook 1989) to *R. necatrix* Berl. ex Pril., which causes a root disease of introduced hosts in New Zealand, including young

P. radiata (Gilmour 1966; Gadgil 2005). This *Rosellinia* sp. also forms tiny, radiating ribbon-like colonies beneath the bark, but does not produce sexual fruitbodies. It does produce a *Dematophora* anamorph (Petrini 2003), whereas a *Nodulisporium* anamorph is reported for *R. thelena* in Europe (Petrini 1993). *R. thelena* is known to be endophytic in Europe, but its pathogenicity on conifers is so far not ascertained (Petrini 1993). However, it is reported to be pathogenic to oak seedlings (Kluge 1967).

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