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Armillaria Root Disease in New Zealand Forests - A Review

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Cover: Fruitbodies of *Armillaria limonea* on decaying wood
in podocarp hardwood forest, central North Island

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Commercial in Confidence

Client Report No. **40192**

BioDiscovery

HortResearch

Date: **September 2006**
Client: **New Zealand Forest Biosecurity Research Committee**
Contract No: **FBRC**

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EXECUTIVE SUMMARY

Four species of *Armillaria* are known to occur naturally as decay fungi in indigenous forests in New Zealand, two of which, *Armillaria novae-zelandiae* and *A. limonea* are responsible for Armillaria root disease in a wide variety of exotic tree and shrub hosts in habitats such as pine plantations, kiwifruit orchards, riparian willows, urban parks and home gardens. The disease first became significant in pine forests during the 1920s and substantial mortality occurred during the 1960s and 1970s as extensive areas of pine were planted on sites cleared of native forest (reports of up to 50% of trees killed by age 6 years). An even greater proportion of living trees with green crowns was found to be infected at the root collar. The percentage of mortality is lower in contemporary plantations, including second rotation crops planted on sites not originally stocked in indigenous forest. However, chronic infection is widespread throughout the country in standing trees (means of 12-22% trees infected in many parts of the North and South Islands, with greater values in the more severely infested stands). Populations of *Armillaria* occur in comparatively high colony densities in both natural and planted forests, indirectly implying that new infection centres arise as a result of airborne invasion by basidiospores of *A. novae-zelandiae*, with repercussions for a potentially wider occurrence of the disease in future plantations.

Armillaria root disease became important in kiwifruit orchards during the planting boom in the 1980s, and remains a problem in many orchards today. While a majority of infestations arose from pre-existing inoculum derived from previously growing woody hosts, there was indirect evidence that some infection centres resulted from spores colonizing the poisoned stumps of willow shelterbelts felled to reduce shading and competition. Disease eradication was initially effected by the expensive procedure of mechanically sieving the soil free from all woody debris prior to replanting infected areas, and somewhat less successfully by the use of polyvinyl chloride sheet root barriers buried vertically in strategically placed trenches. Following subsequent research there has been wide use of registered biological control products based on strains of *Trichoderma*, with reports of varying effectiveness. A more recent research programme has achieved substantial control by exposing and washing root collars and surgically excising *Armillaria* lesions. Most of these labour-intensive methods employed in kiwifruit orchards are not applicable to forestry, but some of the biological control technology has been adapted for potential use in forest plantations.

Intensive research has shown that successful disease control in pine forests is achievable by means of stump removal prior to planting the new crop. Because of the high cost and uncertain economic outcome, this method has rarely been used operationally, and current research is investigating cheaper options that could be applied in an integrated fashion to reduce the disease in crops newly planted on risk sites. Methods currently under investigation include the establishment of stands using robust planting material that is physiologically more resistant to infection, the planting of stock showing greater genetic resistance, dipping root systems in a *Trichoderma*-based biological control product prior to planting, and the treatment of stumps with competitive decay fungi to deny *Armillaria* an inoculum substrate and so reduce its ability to attack adjacent pine trees. Most of these approaches are at varying stages of developmental research, but some show distinct promise. Options are limited for remedial treatment of infection in an existing plantation, but silvicultural

research is in progress seeking a suitable thinning regime that would minimize disease impact. Whatever control methods are finally used, a procedure is needed for identifying those stands with higher infestation in which disease management is economically justifiable. Two methods have been researched, one involving root collar inspection of a sample of trees within a stand, the other using visible mortality prior to first thinning as a guide to the distribution and intensity of chronic infection. The latter approach lends itself to a remote sensing procedure which has shown promise in an initial study. There is still a need to verify preliminary conclusions with further testing, and to develop the best method through to an operational protocol.

Other current research is using molecular techniques to resolve the nature of the populations of *Armillaria* species present in New Zealand, partly for biosecurity purposes in the event of incursions of exotic *Armillaria* species, and also to increase our understanding of the nature of their dispersal by means of basidiospores. Outcomes from this research may indicate whether or not thinning or clear felling should be avoided during the *Armillaria* fruiting season on risk sites. It is important to determine the degree to which *Armillaria novae-zelandiae* maybe spreading into new pine plantations in future rotations, and spore trapping is being employed to identify airborne spore dispersal patterns. This research is being complemented by studies to determine the minimum spore concentrations able to colonise pine stumps and partially buried slash, as potential initiators of new infection centres in plantations. Only in this way will it be possible to assess the real downstream significance of Armillaria in future forests, and to be ready with effective management options for severely infested stands as they occur.

Note: in this review, Roman script is used to distinguish the disease, Armillaria, from the causal pathogens whose generic name, *Armillaria*, is inscribed in italics.

Armillaria mortality in young *Pinus radiata.*

Except where stated to the contrary, all photos are the property of Scion.

CLIENT REPORT No: **40192**

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Information for Ensis abstracting:

Contract number	**FBRC**
Client Report No.	40192
Products investigated	Armillaria root disease
Wood species worked on	*Pinus radiata*
Other materials used	*Armillaria novae-zelandiae*, *A. limonea*
Location	New Zealand

1. INTRODUCTION

Fungi in the genus *Armillaria* are responsible for an important root disease in plantations of exotic species throughout New Zealand (Figs. 1,2). They have a wide host range (Gilmour 1966; Dingley 1969; van der Pas *et al.* 1983) and cause an unknown but probably significant number of deaths each year in parks and home gardens. The disease also occurs in fruit trees (Atkinson 1971) and over the last few decades has been important in orchards of kiwifruit (*Actinidia deliciosa* (A. Chev.) Liange & Ferguson), particularly in the Bay of Plenty district (Horner 1985, 1987, 1988a,b). This report reviews past and current work on the disease in plantation forests, and identifies critical areas on which research should be focused in the future. It also considers knowledge gained from research into kiwifruit which might be valuable in helping to manage or control the disease in forest plantations. The disease was thoroughly reviewed by Hood (1989) and published general accounts include those by Gilmour (1966), Forest Research (1976), van der Pas *et al*. (1983), Ridley and Dick (2001), and for kiwifruit orchards, Hill (2000a) and Horner (2005a,b). Armillaria is one of a number of root diseases that occur in forest and related woody habitats around the world. International research on Armillaria root disease in forest plantation and orchard crops worldwide was reviewed by Hood *et al*. (1991).

Figure 1: Armillaria mortality in a young, central North Island, third rotation stand of *Pinus radiata*. Note stumps of previous crop, the source of the *Armillaria* inoculum.

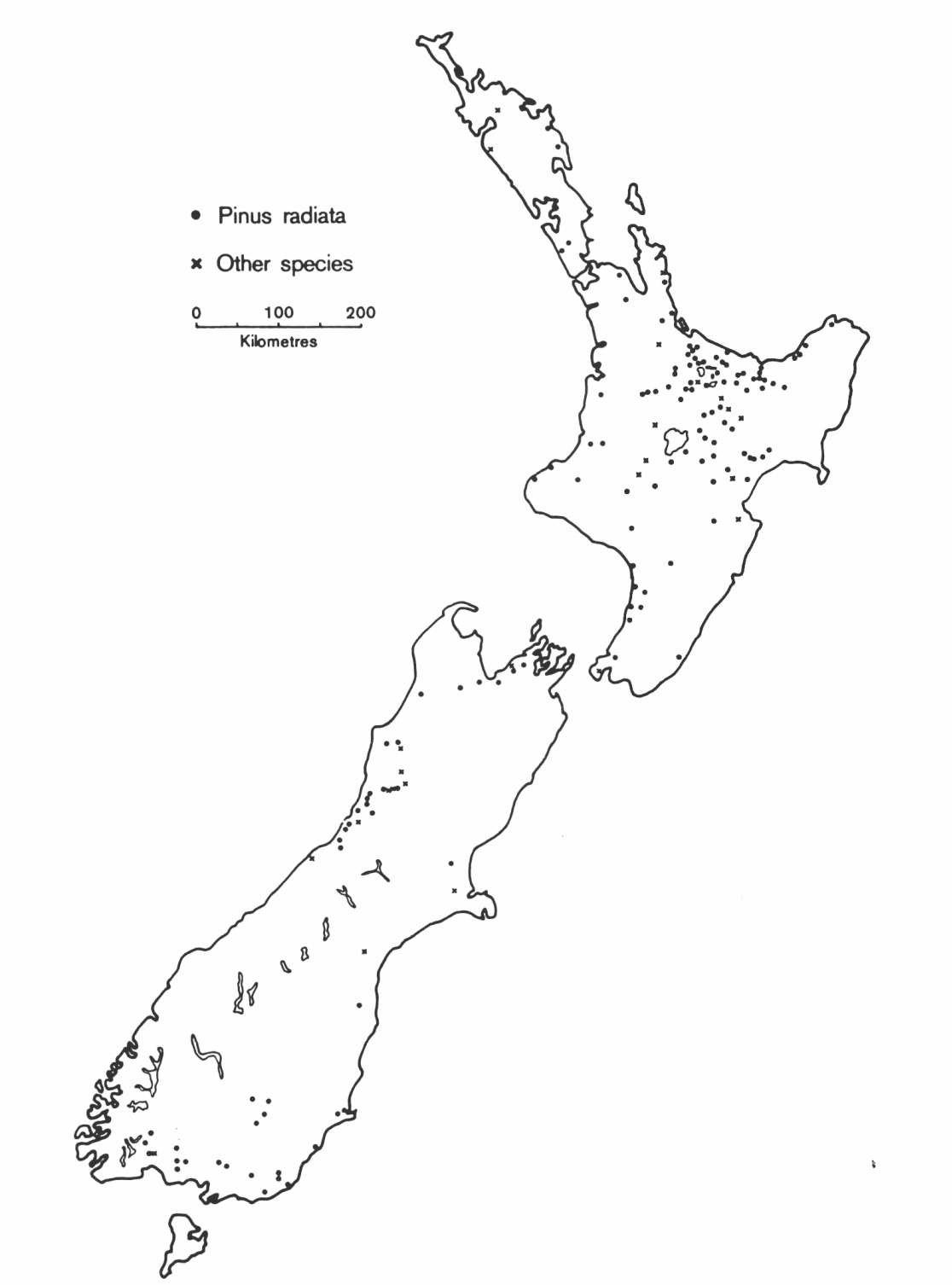


Figure 2: Occurrence of *Armillaria* on introduced host tree species. Symbols indicate locations of one or more infected or colonised seedlings or older trees present mainly in plantations or woodlots (40 years of records from 1950, New Zealand Forest Research Institute; after Hood 1989).

2. CURRENT KNOWLEDGE

2.1 Disease Development

2.1.1 The Pathogens

Although four species of *Armillaria* are recognised in New Zealand, only two, *A. novae-zelandiae* (Stevenson) Herink and *A. limonea* (Stevenson) Boesewinkel are known to be responsible for the disease in forest plantations (Shaw and Calderon 1977). Both species were formally named by Stevenson (1964), but have been collectively recognized in this country since at least 1879 under the incorrectly determined name *A. mellea* (Vahl: Fries) Kummer (Cooke 1879; Colenso 1890; Massee 1898; Farr *et al*. 1919). *Armillaria mellea* has been reported occasionally since 1964 (e.g. Laundon 1973), but there is no basis for assuming that this Northern Hemisphere species has been introduced into New Zealand, and all records of *A. mellea* probably refer to *A. novae-zelandiae* or *A. limonea*. Both species are readily identified during fruiting which occurs over several weeks between May and July on decayed wood in indigenous forests and to a lesser extent in non-indigenous wooded habitats (Hood and Gardner 2004). At other times it is difficult to determine the species unless cultures are isolated. Rhizomorphs of both fungi have dichotomous branching and appear similar (Benjamin 1983; Morrison 1989). Hood and Sandberg (1987) were unable to distinguish rhizomorphs in the field, but according to studies by Benjamin (1983) those of *A. novae-zelandiae* are slightly thicker on average and produced in greater abundance than those of *A. limonea*. Isolates can be identified with comparative ease by pairing in culture and by growing under a 24 hour photoperiod using specified lighting conditions (Fig. 3; Shaw *et al*. 1981; Benjamin 1983; Hood and Sandberg 1987).

Figure 3: Identifying unknown *Armillaria* field isolates to species. Left, diploid-haploid pairing. The dark, circular field culture has been paired with white, fluffy tester isolates of the two common species. The *A. limonea* testers on the left remain white and fluffy, indicating that the unknown is not this species. The testers on the right are darkening and losing their fluffy appearance, demonstrating that they are the same species as the unknown, identifying it as *A. novae-zelandiae*. In the independent 24-hour photoperiod test (right), cultures identified as *A. limonea* (top) produce rhizomorphs under continuous light of a specific intensity and wavelength, whereas the same conditions inhibit rhizomorph production by isolates of *A. novae-zelandiae*.

Figure 4 (top and bottom): *Armillaria limonea* fruiting in podocarp-hardwood forest, May-June.

Figure 5: Fruitbodies of *Armillaria novae-zelandiae* freshly collected from a podocarp-hardwood forest in May.

Figure 6: *Armillaria novae-zelandiae* fruitbodies at the base of a young diseased *Pinus radiata* tree. Fruiting in exotic forests is comparatively uncommon.

Besides *A. novae-zelandiae* and *A. limonea* (Figs. 4,5,6), two other *Armillaria* species occur in New Zealand, both found naturally as decay fungi on woody debris in beech (*Nothofagus* spp.) forests (Hood 1989). *Armillaria hinnulea* Kile & Watling, originally described from eucalypt forest in Tasmania, has also been found on the West Coast of the South Island. Its identity has been confirmed morphologically and culturally (Kile and Watling 1983; Ridley and Ramsfield 2004). The other species, present in central North Island beech forest, is an as yet undescribed indigenous species (Fig. 7; Hood 1989, 1992). It has also been distinguished by morphological means and by cultural pairing tests.

Figure 7: Fruitbodies of the unnamed *Armillaria* species freshly collected from decomposing wood on the forest floor in a central North Island *Nothofagus* forest.

It is now also possible to identify these species using molecular methods (Coetzee *et al*., 2001, 2003, Ridley and Ramsfield 2004). Species-specific primers have been designed from the ITS region of the DNA genome for a diagnostic PCR test which are able to distinguish the four species in field, herbarium and culture collections (Dodd *et al*. 2006b). The specificity of this test is being further confirmed by using the primers to identify an additional series of *Armillaria* isolates (Section 3.3.7).

Inoculation experiments have been used to demonstrate that the two common species, *A. novae-zelandiae* and *A. limonea*, are both pathogenic to seedlings and cuttings of *Pinus radiata* D. Don (Shaw *et al*., 1981; Benjamin, 1983; Benjamin and Newhook, 1984a; Hood and Sandberg, 1993b). In the field, both species have been isolated from *Armillaria*-killed *P. radiata* seedlings, with *A. novae-zelandiae* probably being obtained more frequently than *A. limonea* (Hood and Sandberg, 1993b). MacKenzie and Shaw (1977) found that the incidence of *Armillaria*-caused pine mortality was higher next to stumps with *A. novae-zelandiae* fruitbodies than to those with *A. limonea* fruitbodies, but this result may merely reflect the relative colonizing or fruiting ability of the two species. The pathogenicity of the other two species to *P. radiata* is not known.

2.1.2 Natural occurrence

Armillaria novae-zelandiae is distributed throughout New Zealand from at least the Hokianga Harbour area to Southland and the Chatham Islands (Ridley 1999). *Armillaria limonea* is common in the central North Island, and is also known in the northern South Island. *Armillaria novae-zelandiae* is also reported from Chile, Argentina, and Australia while *A. limonea* is listed from Chile and Argentina (Singer

1969; Horak 1979; Kile and Watling 1983). Recent molecular work has confirmed the presence of *A. novae-zelandiae* in South America, but also indicates that the species identified as *A. limonea* in this region may really be the Australian species, *A. luteobubalina* Watling & Kile (Coetzee *et al*. 2003).

In New Zealand, *A. novae-zelandiae* and *A. limonea* occur naturally in indigenous forests, both podocarp-hardwood and beech, where they are important decay fungi of stumps, logs, and dead trees, and the cause of butt rots in living trees (Birch 1937; Gilmour 1954, 1966; Hood and Sandberg 1987; Hood *et al*. 1989, 2004). One species, possibly *A. novae-zelandiae*, has also been identified as a component in a mycorrhizal system involving the native orchid, *Gastrodia cunninghamii* Hook f., growing in beech forest in Fiordland (Campbell 1962), and *A. novae-zelandiae* has been found colonizing dead plants of the "wood rose" root parasite *Dactylanthus taylori* Hook. f. in podocarp-hardwood forest in the central North Island (Hood 1992). *A. novae-zelandiae* may also form a mycorrhizal association with species of *Gastrodia* in central North Island pine plantations, in effect facilitating indirect parasitism of the pines by the orchid species (Fig. 8; Hood and Gardner 2004b).

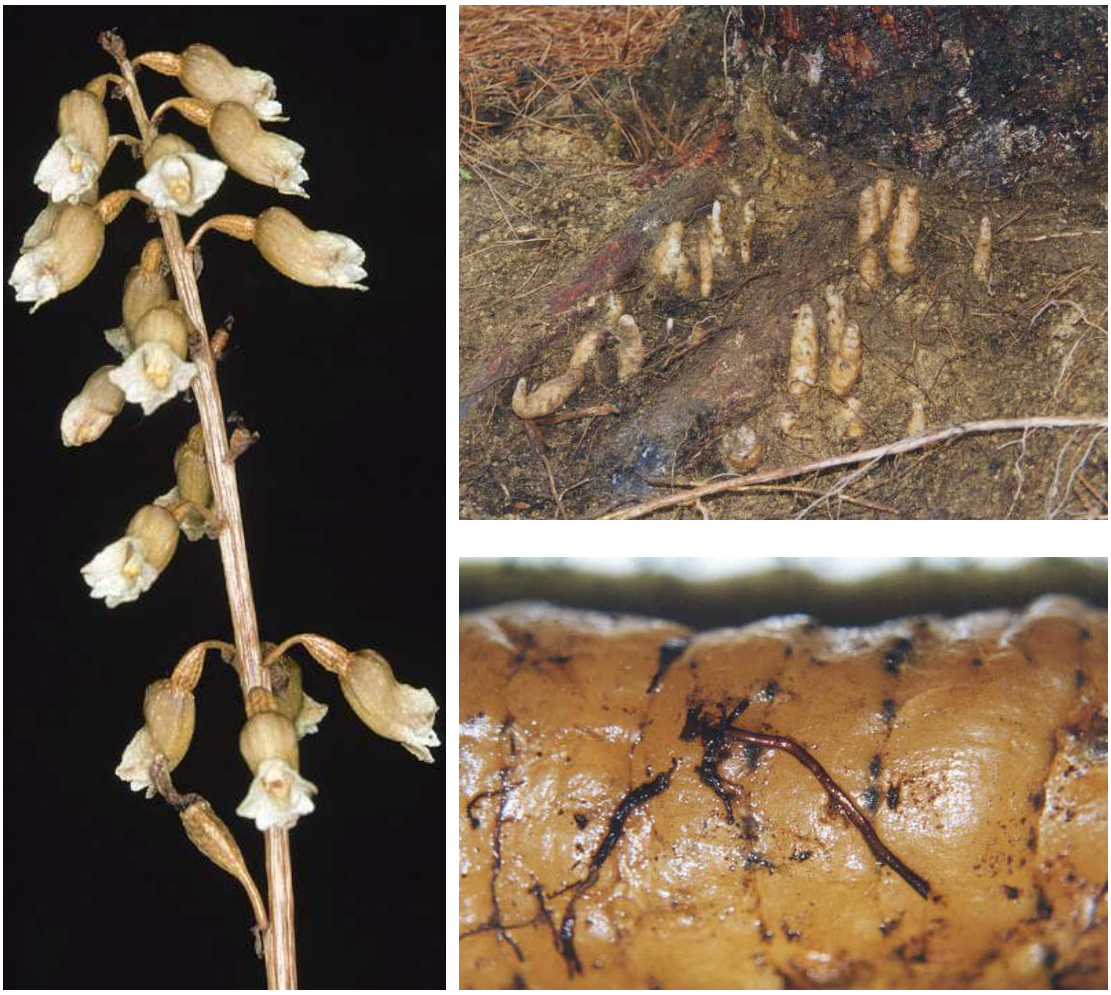


Figure 8: Clockwise from left. Flowers of native *Gastrodia sesamoides* R. Br. Exposed *Gastrodia* tubers in tiers among roots of unhealthy second rotation radiata pine tree on site not previously covered in indigenous forest; patches of resinosis indicate sites of *Armillaria* infection. *Armillaria* rhizomorphs on surface of *Gastrodia* tuber.

Figure 9: Left, *Armillaria* rhizomorphs growing across healthy root of *Beilscmiedia tawa* (A. Cunn.) Kirk excised from tree in podocarp-hardwood forest. Below (left and right), *Armillaria* rhizomorphs sieved from soil from indigenous forest floor.

Figure 10: Planted *Nothofagus menziesii* tree infected with *Armillaria*, entrance to Scion, Rotorua, June 2006.

Rhizomorphs of *A. novae-zelandiae* and *A. limonea* are common in indigenous forest, where they grow freely through the topsoil or adhere to the surfaces of healthy roots (Fig. 9; Hood and Sandberg 1987; Hood *et al*. 1989). They appear unable to parasitise sound roots in podocarp-hardwood forests, and there is no evidence of *Armillaria*-caused mortality among young trees or seedlings in this type of forest (though occasionally planted native trees are killed by *Armillaria* species in urban settings; Figure 10). *Armillaria* species decay the roots of old-growth trees of rimu (*Dacrydium cupressinum* Lamb.) and matai *Prumnopitys taxifolia* (D. Don) Laubenf.) in the central North Island, but it is not clear whether they invade healthy root tissue directly, or merely colonise already dead or weakened roots (Hood *et al*. 1989). Parasitic attack has been reported in disturbed beech forests (Birch 1937; Rawlings 1953; Forest Research 1955 pp. 15-16) and both species have been isolated from specimen trees or saplings of *Nothofagus menziesii* (Hook. f.) Oerst. at Rotorua (Hood 1989). In podocarp-hardwood forests

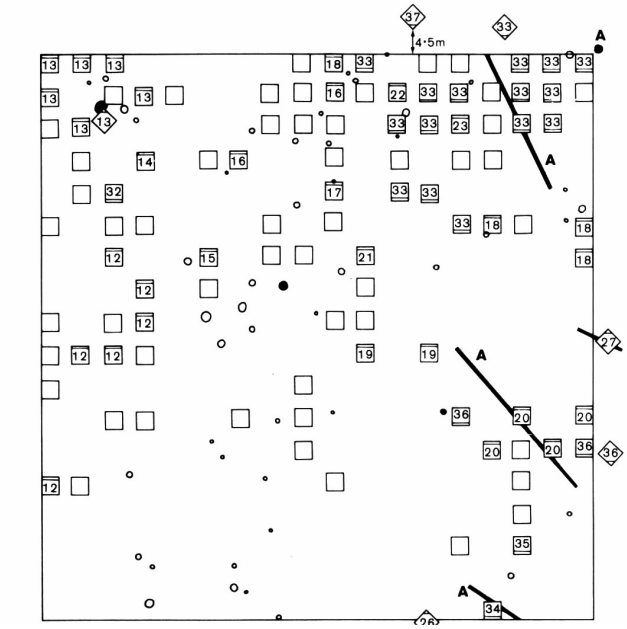
rhizomorph production may be prolific. Hood and Sandberg (1987) reported that the average aggregate rhizomorph length down to a depth of 220 mm beneath such a forest logged of the podocarp element in the Bay of Plenty district ranged from 2 to 9 m/m^2 of soil surface. Cultural pairing studies (Fig. 11) have found that *Armillaria* populations in indigenous forests are composed of high colony densities (Fig. 12; Table 1). Colony numbers of *A*. *novae-zelandiae* ranged 19-93 /ha and of *A*. *limonea*, 15-56 /ha (Hood and Sandberg 1987).

Figure 11: Pairing *Armillaria* field isolates to identify vegetative compatibility groups (interpreted as spore-derived colonies). The two isolates paired at the bottom of the plate belong to the same group, and have merged evenly. Isolates in other pairings belong to different groups or colonies and have produced a barrier zone of mutual incompatibility.

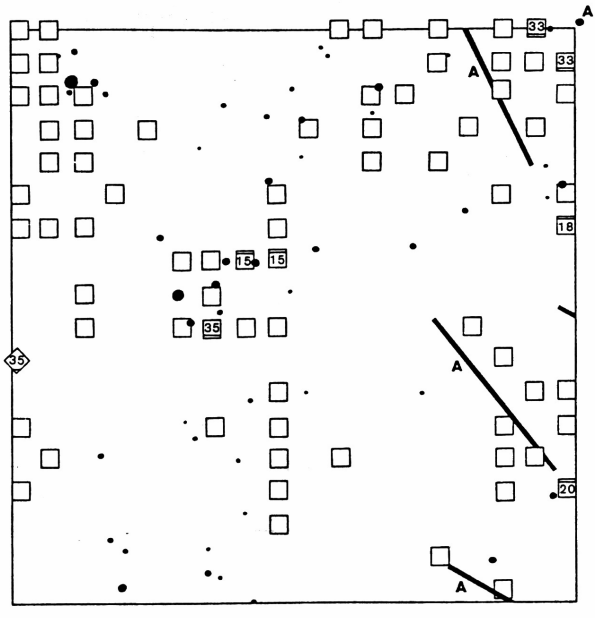
	Species	**Density (groups /ha)**
Beyond New Zealand	*A. gallica* Marxmüller &Romagnesi *A. ostoyae* (Romagnesi) Herink *A. borealis* Marxmüller & Korhonen *A. luteobubalina* (*Eucalyptus*, mainland Australia)	<1 - 8
	A. ostoyae (*Pinus resinosa* Ait., Michigan)	26[1]
	A. hinnulea (*Eucalyptus*, Tasmania)	36-54[1]
New Zealand	Native forest/pine plantation *A. novae-zelandiae* *A. limonea* Both	 13-109 0-56 13-131

[1]attributed, at least in part, to spore dispersal

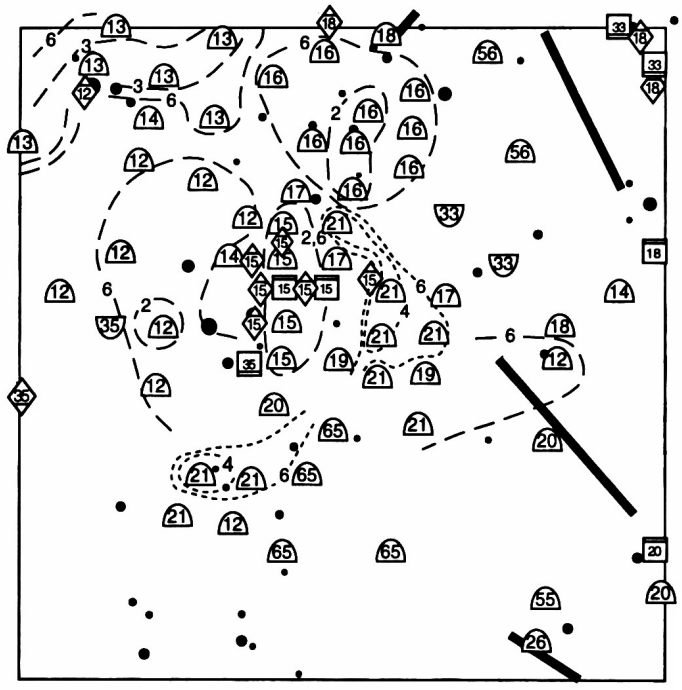
Table 1: Published *Armillaria* population densities (vegetative compatibility groups). Based on information and references provided in Hood and Sandberg 1987, 1993b; Hood *et al*. 2002b; Smith *et al*.1994



(a) Soil rhizomorphs, indigenous forest floor, before felling and burning



(b) Soil rhizomorphs, two months after burning (a small number still viable despite heat from the fire)



(c) In young pine trees, first 5 years after burning.

Figure 12: Monitoring the distribution of *Armillaria* populations on a site converted from indigenous forest to pine plantation. Native forest clear felled, burned, and planted in pine ca. 6 months later (Plot 3, Hood and Sandberg 1987, 1989, 1993).

Scale: plot sides 36m.

o Living tree (to scale) — Fallen tree (not all shown)

● Stump or dead tree A Armillaria decay

□ Armillaria soil rhizomorph sample (not cultured)

10 33 Rhizomorph samples of A. novae-zelandiae, A. limonea respectively

13 36 Basidomata of A. novae-zelandiae, A. limonea respectively

Numbers identify intercompatibility groups

52 31 Pinus radiata tree infected by A. novae-zelandiae, A. limonea, respectively

— — — n — — — **Distribution of trees killed by given group n years after burn (large groups only).**

2.1.3 First rotation pine plantations after indigenous forest

Figure 13: Left (top and bottom), clearing and burning indigenous forest prior to planting radiata pine. Right, *Armillaria limonea* colonising stump and roots of a *Beilschmiedia tawa* tree on site cleared of indigenous forest.

Figure 14: Armillaria mortality in young first rotation pine plantation on site cleared of indigenous forest.

Although little remnant indigenous forest is now converted to exotic pine plantation, it is not so many years since this practice was widespread, and its effects are still with us. Heat from the burning of the clear-felled and dried vegetation in preparation for planting (Fig. 13) led to a temporary reduction of inoculum levels (Fig. 12 (b); Hood and Sandberg 1989). However, site re-colonisation was rapid, and signs of the fungus (mycelial fans and fructifications on stumps) were plentiful within 1-2 years. Mortality of pine seedlings commenced 3 to 6 months after planting on cleared indigenous cutover sites (Forest Research 1973 pp. 32-33; MacKenzie and Shaw 1977) and continued at an increasing rate during the first 3-5 years, thereafter declining (Figs. 14,15; Forest Research 1962 p. 32, 1974 p. 49; Roth *et al*. 1979; van der Pas 1981a).

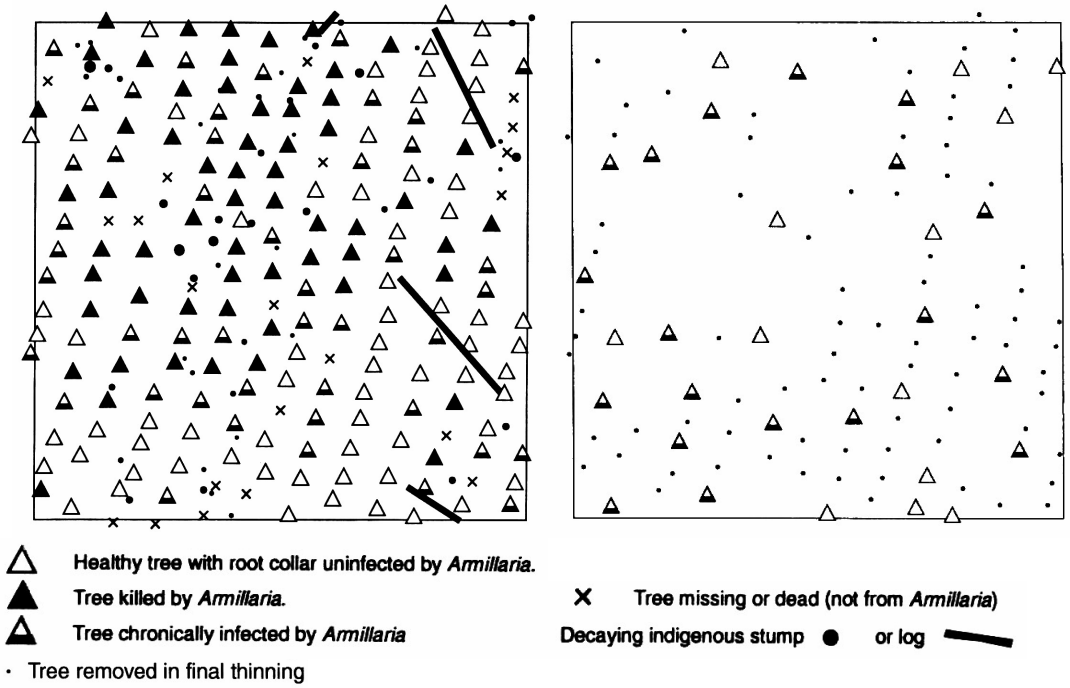


Figure 15: *Armillaria* infection in pine trees planted on the same ex-indigenous forest site as in Figure 12. Left, up to 5 years after felling and burning the previous indigenous cover (unthinned). Right, 12 years after clearing and burning (4 months after the first and final thinning). Scale: plot sides 36m. After Hood and Sandberg 1993; Kimberley *et al*. 2002.

Mortality was associated with the distribution of stumps and led to the formation of stand gaps (mortality centres or disease patches; MacKenzie and Shaw 1977; Roth *et a*l. 1979; van der Pas 1981b). The proliferation of rhizomorphs on stump roots probably increased the likelihood of infection of the young pine trees (van der Pas and Hood 1984; cf. Benjamin 1983; Benjamin and Newhook 1984a). Despite some debate, there has been no evidence of secondary spread of infection through root contact between pines, and it appears that all mortality occurred directly from direct stump root infection (MacKenzie and Shaw 1977; Roth *et al*. 1979; van der Pas 1981b; van der Pas and Hood 1984; Hood and Sandberg 1993b). There was also divergence of opinion as to whether mortality was more likely to occur in association with stumps of *Beilschmiedia tawa*, one of the more common indigenous hardwood species in central North Island forests (MacKenzie and Shaw 1977; Shaw and Calderon 1977; van der Pas 1981b). In inoculation studies Benjamin and Newhook (1984a) found that the wood of a number of indigenous and exotic tree species became colonized and were effective as inoculum substrates for both *Armillaria*

species to infect *P. radiata* seedlings, though rhizomorph production was more prolific on *B. tawa*. The viability of stumps as an inoculum source is also no doubt related to their longevity in the soil (Benjamin 1983).

Mortality tended to decline after age 5 years, but continued at reduced rates for up to 10 years (Forest Research 1962, p.32; Shaw and Calderon 1977). It is assumed that the decline in mortality resulted from increased host tolerance with age (trees being more difficult to kill than seedlings), proportionately fewer target trees remaining as others died, and a reduction in inoculum potential as the stump food base was depleted over time. However, infection still persists in these first rotation stands in a non-lethal cryptic form. In a 10-year-old *P. radiata* stand thinned to its final stocking density, 15% of crop trees were more than 65% girdled at the root collar by *Armillaria* species (Shaw and Toes 1977). Such infected trees may uproot or break off near ground level (Forest Research 1962 p. 32; Gilmour 1966; Shaw and Calderon 1977). MacKenzie (1987) examined the same stand as Shaw and Toes (1977) and found root collar infection still plentiful 9 years later. However the system was dynamic, and although the percentage of living trees with detectable infection present had dropped only slightly (7%) to 53% in the intervening period, root collar infections were no longer visible at age 19 years on approximately one-third of the trees infected at age 10 years. Instead, other trees had become newly infected at the root collar since the earlier evaluation. This evidence of tree recovery confirmed an earlier report (Forest research 1962 p. 32), and was attributed to increased vigour after the final thinning (MacKenzie 1987). MacKenzie (1987) observed that mortality gaps were no longer sharply demarcated in this older stand owing to the growth of surviving trees within disease centres and the thinning of trees elsewhere in the stand.

2.1.4 Second-rotation pine stands

Records of infection in second-rotation stands date back to the 1940s. In Whakarewarewa Forest, Rotorua, up to 3% of 2- to 3-year-old pines were killed after regenerating naturally following the clearfelling of a radiata pine stand (Lysaght 1944). A later report from the same forest stated that more than one-third of 6-year-old pines were attacked by *Armillaria* on a site previously stocked with eucalypts (Forest Research 1954 p. 12). Fenton (1951) found *Armillaria* in naturally regenerated *P. radiata* after a disastrous fire that destroyed 14- to 18-year-old pine plantations north of Taupo.

Figure 16: Armillaria in a third rotation, central North Island radiata pine plantation.

The occurrence of disease in second-rotation stands has not been confined to sites cleared of indigenous forest prior to the first planting. Observations indicated that infection can become established over successive rotations on previously forest-free areas (Figs. 16,17,18; Gilmour 1966). Examples include: *Salix* protection belts near the Ngaruroro River, Napier (Forest Research 1955 p. 16), and in the lower Waimakariri Valley near Christchurch and the lower Waioeka and Otara Rivers near Opotiki (unpublished data); second-rotation pine stands in Waitarere and Santoft Forests established on coastal sand dunes (unpublished data); and stands in Kaingaroa Forest, which will now be discussed.

Figure 17: Root collar resinosis due to *Armillaria* infection in a green-crowned radiata pine tree (second rotation, central North Island stand).

Figure 18: Armillaria mortality in a young second rotation radiata pine plantation.

Armillaria root disease in Kaingaroa Forest was first studied comprehensively by Gilmour (1954), who surveyed over 40,000 ha of 20- to 28-year-old first-crop *P. radiata* stands. He concluded that parasitic attack in trees dying after infestation by the wood wasp, *Sirex noctilio* Fabricius, was virtually non-existent, but he found *Armillaria* to be widespread as a saprobe in stumps and dead trees on better quality sites (sites I and II of Ure 1950). Gilmour assumed that inoculum had been introduced in the form of airborne spores, since the previous cover was mostly either a natural scrub composed of *Leptospermum scoparium* J.R. & G. Forst. and *Pteridium esculentum* (Forst. f.) Cockayne (better sites) or a low, shrub-grassland vegetation dominated by *Dracophyllum subulatum* Hook. f. and *Poa cita* Edgar (poorer sites). Subsequently, *Armillaria* was found colonizing over one-third of 6- to 14-year-old dead or nearly dead stumps from thinning in 50-year-old (approximately)

stands of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) in Kaingaroa Forest (van Boven 1974). In 1962 severe attack by *Armillaria* was found in 80% of the crop trees after the first thinning of a 7-year-old second-rotation stand of *P. radiata* (Forest Research 1963 p.48). Unexpectedly, the first-rotation *P. radiata* stumps were acting as an infection source over a prolonged period. In 1972, *Armillaria* was reported at a site in northern Kaingaroa Forest killing 50-year-old *P. ponderosa* P. & C. Lawson trees debilitated by repeated *Dothistroma pini* Hulbary defoliation (unpublished file data). Attack appeared to develop from colonized stumps from thinnings. Mortality from *Armillaria* in the next rotation (*P. radiata*) was not high on this site (5% at age 4 years; Shaw and Calderon 1977). However, on an adjacent site, also previously stocked with *P. ponderosa*, mortality was ongoing in a 6-year-old replacement stand of *P. radiata* (van der Pas 1981a). Deaths in standing trees then declined, but windthrow associated with infection of the root system was still occurring in the second-rotation stand after age 10 years.

Mortality was also severe in young *P. radiata* stands at Karioi Forest planted on sites previously stocked in *P. ponderosa*, *P. nigra* ssp. *laricio* (Poir.) Maire, or *P. contorta* Douglas ex Louden (van der pas 1981a). This time, although the original inoculum may have been derived from former podocarp-hardwood forest, the disease developed late in the first rotation as *Armillaria* colonised trees in stands stressed by tight stocking and wind damage, or by a poison thinning treatment about 20 years before clearfelling. Roots of living, first-crop trees became infected without showing crown symptoms, and stumps of these trees acted as inoculum sources after clearfelling and replanting. Extensive mortality developed in young second-rotation *P. radiata* stands on these sites, but the death rate in standing trees slowly decreased after the first 3 years, as is typical of stands planted on native cutover sites. However, windthrow of infected trees appeared to be common in old second rotation stands in this forest.

Reports of low-to-moderate mortality from Armillaria have continued periodically in young radiata pine stands in New Zealand plantations. These have been associated with sites previously stocked in *P. ponderosa*, *P. nigra*, or *P. contorta* e.g. in Kaingaroa, Tairua, Erua, and Tarewa Forests in the North Island, although such mortality has not automatically followed these crops (Hood 1989). *Armillaria*-related deaths have also occurred in young *P. radiata* stands following crops of *P. radiata*, *Pseudotsuga menziesii*, and *Larix decidua* Mill. in different parts of the country.

However, of more significance than mortality has been the more recent awareness of the extent of chronic *Armillaria* infection that persists throughout the rotation in the root collar and roots of many green-crowned trees (Figs. 12,17). Such infection was reported in 1955 in Whakarewarewa Forest where 23% of living trees were found to be infected at the root collar (Forest Research 1955 p. 16). More extensive investigation was undertaken in the 1980s by MacKenzie who found variable levels of chronic infection in 27 of 29 5- to 11-year-old *P. radiata* trees on sites previously stocked in *P. radiata*, *P. ponderosa*, *P. contorta*, *P. nigra*, or *Ps. menziesii* (MacKenzie in Hood 1989). In contrast to the earlier work of Gilmour (1954), infested stands were now also present on the lower quality sites (Site III of Ure 1950), and it was conjectured that the incidence would increase in successive rotations (MacKenzie and Self 1988; Essenberg 1988; Self and MacKenzie 1995). An examination of unpublished forest health surveillance reports between the years 1987 and 1998 revealed a low incidence of early mortality from Armillaria in virtually every management unit in both Kaingaroa and Kinleith Forests over this period, implying extensive chronic infestation in both plantations. Essenberg (1988) also studied chronic infection in Kaingaroa Forest and reported that the incidence of windthrow following Cyclone Bola in March, 1988, was greater in more severely

infected stands. She also found that trees near uprooted trees were more likely to be infected than those elsewhere in the stand. Hovell (1992) used some of her data to investigate the effect of *Armillaria* infection on site index.

2.1.5 Armillaria in kiwifruit orchards

Armillaria root disease continues to be a serious problem in kiwifruit orchards in parts of New Zealand and substantial research has been undertaken over the past two decades in an effort to manage and reduce its impact. This work is included as part of this review, in order to consider the disease over a wider front and to see what new insights there might be for forestry from the kiwifruit approach.

Armillaria became a serious problem from 1984 onwards in kiwifruit orchards established extensively during the boom period of the 1970s and 1980s (Fig 19; Hill 1990). Research revealed that in most orchards, *Armillaria* infections were associated with shelterbelts, particularly of *Salix matsudana* Koidz., planted to protect the newly established vines (Figs. 20,21; I.J. Horner, unpublished data). It was standard practice to clear fell every second shelterbelt after four to five years, once the kiwifruit plants were well established, and the stumps and extensive root systems left in the ground provided an entry point and a means of spread for any invading *Armillaria* to spread rapidly throughout the kiwifruit block. Willow, itself, is a very susceptible host for *Armillaria*, and the first sign of *Armillaria* in an orchard was often the decline and death of the willow shelterbelt trees. This occurred especially when shelterbelts were thinned by felling every alternate tree, leaving a stump as a food substrate to start a new infection centre.

Fig 19: Typical Armillaria mortality centre in a Bay of Plenty kiwifruit orchard (I. Horner)

Fig 20: Armillaria mortality in a matsudana willow shelterbelt R. (Hill)

Fig 21: Large gaps in kiwifruit orchards caused by Armillaria mortality following removal of lines of willow shelterbelts, with subsequent soil sieving to remove willow stumps and root material (Section 2.3.5). Lines of newly planted vines are visible in the gap in the left image (R. Hill, left, I. Horner, right).

Where shelterbelts were clear-felled and stumps became colonised by *Armillaria*, it typically took two or three years for the first symptoms to occur on kiwifruit. By this time the infection was likely to have spread a further two rows out, moving rapidly along the dead willow roots at a rate of about one row per year (4-5 m). The initially rapid phase of spread slowed once the willow roots had rotted away. Direct spread between kiwifruit vines was generally slower, roughly one row every two or three years, presumably because of the lower degree of interaction between the smaller root systems.

Excavation of root systems and knowledge of the pre-orchard history revealed that most shelter belt infection originated from residues already present in the ground, such as the roots of previous woody crops, hedges or shelterbelts, or from wood and tree debris buried in hollows during orchard contouring and development (I.J.Horner, unpublished data; Horner 2005b). Occasionally vines became infected directly from this material, and not secondarily from colonized shelterbelt root systems. *Armillaria* invaded some kiwifruit orchards from remnant patches of native forest in adjacent gullies, facilitated by the root systems of willow shelterbelts planted on the boundary, which penetrated both the indigenous forest and the kiwifruit block.

However, disease also developed in some orchards established on farmland with no recent history of woody crops. In these blocks, multiple *Armillaria* infections in kiwifruit vines could be traced to the stumps formed by the clear felling of shelterbelts. In such orchards it seemed that these new infections had arisen as a result of basidiospore colonisation of willow stumps on land previously free of inoculum (see Section 3.1.1).

2.2 Disease impact

2.2.1 First rotation plantations on indigenous forest sites

Interest in Armillaria root disease in pine plantations began during the first planting wave from 1922 to 1937, and intensified when planting again accelerated from about the 1960s. Mortality from Armillaria was first observed in 1930 in 4-year-old stands established on sites cleared of podocarp-hardwood forest (New Zealand State Forest Service 1933; Birch 1937). Occurrence was then only sporadic and Birch suggested that *Armillaria* would probably have minimal effect on the establishment of exotic forests if care was taken with site selection and planting technique. However, subsequent reports revealed that the disease was more significant than first realised (Hocking and Mayfield 1939; Jolliffe 1941; Fenton 1951; Forest Research Institute 1952-57, 1961-63; Newhook 1964). It was estimated that a level of 20% infection was present in *Pinus elliottii* Engelm. planted on indigenous cutover sites in Tairua Forest (Forest Research Institute 1956 p. 18). Significant mortality was reported among young plantings of other exotic species, including *P. radiata*, on similar sites on the South Island West Coast (Forest Research Institute 1957 pp. 15-16) and at Pureora (Forest Research Institute 1961 p. 31). A summary of knowledge up to the mid 1960s was provided by Gilmour (1966).

By the 1970s the extent of the disease in the new planting wave was such that it became necessary to initiate a full-scale research programme at the Forest Research Institute. It was estimated that somewhere between 50,000 and 60,000 ha of land formerly covered in native forest was affected or potentially affected by this disease (Shaw and Calderon 1977; van der Pas 1981a). Evaluation of disease levels on these sites revealed severe mortality losses in the first few years after planting. E.A. Beveridge (Forest Research Institute 1974 p. 52) found mortality levels ranging from 20 to 30% after 5 years in a *P. radiata* plantation established on an indigenous forest

cutover site on the Mamaku Plateau. In another Mamaku study (Shaw and Calderon 1977), *P. radiata* mortality from Armillaria ranged from 11 to 27% after two years on sites previously stocked in residual podocarp-hardwood forest of varying composition. At Pureora, levels of *P. radiata* mortality on several former podocarp-hardwood forest sites were variously recorded as at least 36% after 6 years, 33% after two years (Shaw and Calderon 1977), and over 50% after 6 years (van der Pas 1981a). According to van der Pas (1981a) the overall mortality on former indigenous forest sites was about 5% whereas on former non-wooded sites, where infection was scattered, mortality was considered to be less than 0.1%. All reports quoted observed that mortality was spatially uneven in distribution. It was suggested that stand mortality gaps led to a reduction in stem quality because of excessive branch growth in clearings (Shaw and Calderon 1977). Open areas also became stocked with scrub hardwood weed growth that hindered tending operations. In the South Island, severe mortality was reported in young radiata pine plantations established on sites previously covered in podocarp-hardwood or *Nothofagus* forest in Westland (Forest Research Institute 1957 pp. 15-16) and Southland. On a former *Nothofagus* site in Westland, a mortality rate of 5% after two years was considered unexpectedly low (Shaw and Calderon 1977). The initial period of mortality was prolonged beyond a stand age of 10 years in some Southland plantations such as those at Rowallen Forest, suggesting a possible effect of less favourable climate or soil conditions in this region (Hood 1989).

Besides mortality, significant loss was also found to result from the reduced growth of chronically infected surviving trees. In a 10-year-old, first rotation *P. radiata* stand on an indigenous cutover sites, Shaw and Toes (1977) identified more than 15% of final crop trees with more than 65% of the root collar girdled by *Armillaria* that had increased their dbh by 14-24% less than uninfected trees of equivalent dbh, height and crown depth at the start of the measurement period. Trees in another stand heavily infected by both *Armillaria* and *Dothistroma pini* showed a reduction in growth rate greater than the sum of losses attributed to heavy infection by each fungus alone (Shaw and Toes 1977). Earlier, Etheridge (1967) had found that trees infected by *D. pini* were more susceptible to Armillaria root disease, and this was endorsed by an observation in Sweet (1989).

There have been several attempts to quantify stand growth loss due to *Armillaria* in first-rotation pine stands established on podocarp-hardwood forest cutover forest sites in the central North Island. Equivalent information for infected stands in Southland and Westland has never been determined. Shaw and Calderon (1977) estimated volume losses ranging from 29-32% for 15- to 21-year pulpwood rotations, and a 26-year saw log regime on the Mamaku Plateau. These were calculated assuming an estimated 25-30% loss of land area occupied by mortality patches, and a diameter growth reduction of 14% on 15% of crop trees from age 10 years (based on the study described in the previous paragraph). MacKenzie (1987) considered that this value was overestimated. He found evidence for increased growth rates on trees recovering from chronic infection later in the rotation. In addition, he believed that the losses in productive land early in the rotation were given undue weight by Shaw and Calderon (1977), since he considered that early mortality really amounted to a biological thinning, being compensated for by increased growth on released residual trees. Losses in infected crop trees due to windthrow were considered to be of greater significance, because the residual tree spacing late in the rotation was such that increased increment growth could no longer compensate for loss. He estimated a loss of 6-13% of potential volume for a 28-year saw log regime due to Armillaria-caused windthrow and growth reduction (a total loss of 32-72 m^3/ha from a projected 571 m^3/ha final volume without disease).

More recently, Kimberley *et al*. (2002) used data from a first rotation radiata pine stand on an indigenous cutover site in the eastern Bay of Plenty district to calculate the volume growth loss due to Armillaria as averaging 25% at mid rotation (age 13 years), shortly after their final thinning. This value is only slightly less than that determined by Shaw and Calderon (1977), and as with their analyses was primarily (21%) due to clear gaps in stocking due to Armillaria-caused mortality. Growth increment loss in green-crowned, chronically infected trees was derived using a model developed from measurements of dbh, height, and degree of root collar girdling by *Armillaria*, adjusted by a correction factor to account for competition bias. In this study there was little indication of windthrow attributable to Armillaria among final crop trees at mid-rotation, but it remains to be seen whether this could still become a significant factor.

2.2.2 Contemporary plantations

Increasingly, modern pine plantations consist of second and even third rotation stands, and there is now little direct planting on former indigenous forest sites. As a result, mortality tends to be lower, while chronic infection among green-crowned trees continues to occur at a proportionately greater incidence (Fig. 22). For instance, although overall mortality averaged about 5% in 5- to 6-year-old, second rotation radiata pine stands in Karioi Forest (van der Pas 1981a; levels reached 11% in individual stands), the incidence of chronic infection was found to be around 60-70% (MacKenzie *in* Hood 1989; MacKenzie and Self, 1988). As already noted, chronic infection is also widespread in second rotation *P. radiata* stands at Kaingaroa Forest (MacKenzie and Self, 1988; Essenberg 1988), and this has been confirmed by subsequent study (Hood and Sandberg 1993a; Hood *et al*. 2002b).

Figure 22: Armillaria in a second rotation pine plantation.

Between 1992 and 1996, a survey was undertaken to determine more clearly the extent of chronic *Armillaria* infection in pine plantations in different parts of New

Zealand (Self *et al*. 1998). A total of 74 sites were surveyed in 21 forests during this project. Significant disease was found in pine stands in most parts of the country except in the far north, the southern North Island, and the eastern South Island, where less than 1% of trees were infected, on average. Highest levels (averages 12-22%) occurred in stands in the central North Island, Coromandel, Nelson, South Island West Coast, and Southland. Incidence also varied with previous vegetation cover, but not with topography or soil texture[1], and did not decline with stand age. Highest incidence (mean 38% trees infected) was found on sites previously stocked in indigenous forest, while lowest levels (3%) occurred in stands established on old farmland or on sites previously covered with herbaceous or shrub vegetation. Among second rotation plantations incidence varied between nil and 26%, with highest values on sites where first-crop stands replaced indigenous forest (mean 10%) or scrubland (mean 20%). Despite the extent of this undertaking there was considerable variability about the means, and a further survey may eventually be required to clarify more completely how Armillaria is developing in New Zealand forests as second and third rotation stands increase in age, number, and extent. Even so, it was clear from this project that the disease is present in many second rotation stands.

There has been one study to assess growth loss from Armillaria in a second rotation radiata pine plantation on a site not stocked in indigenous forest prior to the first rotation. Kimberley *et al*. (2002) estimated a volume loss of 2.5% in a second rotation mid rotation stand aged 13 years in which ca. 20% of trees were chronically infected by *Armillaria* prior to thinning. Mortality from Armillaria was not a significant factor in this stand. This information was included with other data in a recent estimate of the national significance of Armillaria root disease (Hood *et al*. 2002c). Two values were calculated, the first being the revenue loss from the national wood harvest for year 2000, and the second the projected reduction in returns for the year 2020 at current log prices. Infection values adjusted from the countrywide Armillaria survey (Self *et al*. 1998) were applied to National Average Yield Tables to derive per hectare values at harvest age 28 years, corrected according to stand type for the effect of infection. Estimates were then made of the proportionate areas of these stand categories that produced or will generate revenue in 2000 and 2020, respectively. This enabled a calculation of total returns after adjustment for Armillaria. Comparison of these values with predicted earnings indicated a deficit in 2000 of $37 million attributable to Armillaria, and a predicted shortfall in 2020 of $20 million. These corresponded to losses of ca. 2% and 0.5%, respectively from the national yield. The decrease in value over two decades, despite an increased plantation area, reflects a reduced area of first rotation stands still being harvested on cutover ex-indigenous forest sites. Although the calculations to derive these values were conducted carefully, it was necessary to make some assumptions. For instance, the 2020 value assumes the spread of *Armillaria* into second rotation stands by means of basidiospores, which at this stage is based on convincing but indirect evidence. Research currently in progress is designed to understand spore dispersal better using direct means (see Section 3.1.1).

[1] Shu *et al*. (1994) using a modelling approach to analyse part of the survey data identified additional weaker trends between incidence of infection and temperature (less infection where mean annual temperature > 13^{o}C, in Northland), mean annual rainfall (more between 1000 and 1600 mm, less beyond either end of this range), soil nature (more in central North Island pumice soils), landform (more in moist valleys, less on drier ridges or slopes, at sites where rainfall was considered limiting); cf. Ridley and Dick (2001). In interpreting these results care is needed in distinguishing between potentially linked primary and secondary causative effects (e.g. is the lower incidence in eastern parts of the South Island primarily due to lower rainfall or because there was formerly less indigenous forest?; is there less infection in far northern pine plantations because of warmer temperatures or is there another reason?). See Ridley *et al*. (1996) for a detailed critique of their results.

2.2.3 Kiwifruit orchards

Prior to about 1983, Armillaria root disease was not considered a major problem in the kiwifruit industry. But from 1984 onwards, infections were encountered with greater frequency as the number of kiwifruit orchards rapidly increased (Table 2; Hill 1990, Cutler and Hill 1994). Hill (1990) confirmed that by 1990 there were 250 kiwifruit orchards infested with Armillaria in New Zealand. The cost to the industry that year was estimated as greater than $2 million, with potential to reach losses of $20 million in the following five years (Hill 1990). More recent figures are not available, but Armillaria remains a major problem, and it is probable that a majority of kiwifruit orchards throughout the country have at least one pocket of disease.

Dec 1984	6?
Apr 1985	16
Mar 1986	35
Jan 1987	64
Apr 1987	77
Aug 1987	88
Nov 1987	108
May 1988	129
Jan 1989	166
Jan 1990	>210

Table 2: Numbers of kiwifruit orchards infested by Armillaria during the 1980s (I.J. Horner, unpublished data predominantly from the Bay of Plenty district, but including records from Northland to Nelson).

2.3 Research into disease management and control

Research into the control of Armillaria root disease in New Zealand forests has been conducted in phases from before the 1970s right up to the present day (Forest Research Institute 1974 p. 49, 1976, 1988 p. 14). Most of this has mirrored methods in overseas research programmes into related root diseases. Good reviews of international research into the control of Armillaria can be found in Hagle and Shaw (1991) and Fox (2000).

2.3.1 Stump removal

The removal of the inoculum food base is probably the most effective method of reducing the impact of root diseases. Extracting previous-crop stumps as a site preparation technique prior to planting is so far the only experimentally proven eradicative control method for Armillaria root disease in New Zealand pine plantations (Fig. 23; Shaw and Kile 1991). In a trial at Pureora Forest, Armillaria-caused mortality of pine seedlings was 33% after two years and 52% after 5 years on a conventionally treated site set aside as the experimental control (Shaw and Calderon 1977; van der Pas 1981a). However, on adjacent sites in which most of the stumps had been pushed out of the ground using a bulldozer blade (some sites also being windrowed or windrowed and ground-cultivated by discing or root ripping) mortality levels were 12-21% after 5 years. Windrowing and ground cultivation appeared to offer no additional disease control over that already achieved by stump removal (van der Pas 1980). In another trial in the eastern Bay of Plenty district, thorough removal of indigenous stumps and clearing of debris into windrows reduced mortality in the first pine rotation to only 2% after 4 years, compared with 23% in

conventionally treated plots (van der Pas and Hood 1984). This treatment also significantly reduced the abundance and frequency of soil rhizomorphs of *Armillaria*.

Stumping, combined with windrowing, was also tested as a control for the disease in two second rotation pine stands following a *P. ponderosa* crop at Karioi Forest (Self 1991; Self and MacKenzie 1995). Mortality was reduced significantly from 10% (untreated) to less than 1% (treated), and from 22% to 5%, respectively, after 5 years. After 8 years the differences in incidence of chronic infection between untreated and treated blocks in the same stands were 85% compared to 10%, and 67% compared to 31%, respectively.

Figure 23: Removing stumps after clearing indigenous forest, to reduce the incidence of Armillaria in the subsequent pine crop.

However, despite its proven effectiveness, stump removal is largely unpracticed as an operational control method for Armillaria in this country, although at one time it was used routinely at Karioi Forest (Self and MacKenzie 1995). It is an expensive procedure which cannot be conducted in forests on steeper slopes. It is also not known how changes in the soil quality (removal of topsoil, ground compaction) influence growth later in the rotation (van der Pas and Hood 1984). Some operators have employed ground cultivation such as "ripping" or "V-blading", which disturbs roots without shifting larger stumps. These operations improve planting efficiency, reduce early frost losses, and probably enhance establishment and growth rates at the start of the rotation period. They *may* also give some measure of Armillaria control but this remains untested.

As a management guide, Shaw and Calderon (1977) attempted to calculate the acceptable cost limits for ground preparation by removal of indigenous forest stumps prior to a first rotation pine planting, up to which the anticipated improved yields due to Armillaria control would still return a net profit at the end of the rotation. As they noted, however, these calculations were hampered because the actual effectiveness of stump removal in increasing yields was unknown for the full rotation period. In part it depended on a precise knowledge of when in the rotation losses from standing mortality or windthrow are no longer compensated for by increased growth of the released residual trees, many of which are growing at reduced rates because of chronic infection (MacKenzie 1987). MacKenzie assumed this cross-over point to occur somewhere between ages 10 and 18 years in a 28-year rotation, whereas Shaw and Calderon (1977) believed it to occur earlier (in which case the anticipated greater returns from control of Armillaria were more likely to justify the treatment cost). From observations of older infected stands, MacKenzie felt justified in assuming that the area of productive ground lost to Armillaria was much less than the 20-30% assumed by Shaw and Calderon, presumably because surviving trees must continue to grow with age and re-occupy the early disease patch areas. On the other hand, as noted earlier, Kimberley *et al*. (2002) found that gaps due to earlier mortality were still significant among crop trees after final thinning on an ex-indigenous forest site, supporting the view of Shaw and Calderon.

Mortality is no longer a significant factor in contemporary second rotation plantations, but Self and MacKenzie (1995) have demonstrated that the benefits of stump removal on chronic infection extend well on in the rotation past the establishment stage. They undertook an economic analysis, applying the estimated volume return from disease control derived from the data of MacKenzie (1987) to the results of their stump removal trial, using current operational stumping costs. This indicated predicted returns at that time of $2,761 to $8,826 (mean $6,249) for a cost of $3,623, at an 8% interest rate. The costs of ground treatment are still significant even after a first rotation pine stand, even though stumps tend to be smaller than after cleared indigenous forest, but clear benefits were demonstrated of using this treatment for economic disease control in the second rotation crop, depending on interest rate and level of disease. The method is effective and reduces the level of inoculum in subsequent rotations, but the significant cost at the start of the rotation provides a strong incentive to find a cheaper control option.

2.3.2 Chemical treatment

Stump removal would not be necessary if colonization of the newly created stumps by *Armillaria* could be prevented. There has been one attempt in New Zealand forests at using chemicals to poison new stumps and so render them toxic to invading mycelia of *Armillaria*. Shortly after clearing and subsequent burning, van der Pas poured a commercial hydrocarbon mixture containing methyl isothiocyanate into holes drilled into indigenous stumps (van der Pas and Hood 1984). Mortality of young pines four years later showed a significant reduction (9% as compared to 23% in untreated plots), although the mechanism of apparent control is not clear since frequencies and quantities of adjacent soil rhizomorphs were not reduced significantly. This method has been used successfully overseas (Hagle and Shaw 1991), and might be worth investigating as part of second rotation site preparation on diseased sites. The procedure may possibly be more effective in the comparatively smaller pine stumps, although potential restrictions on the operational use of toxic chemicals in modern plantation forestry would need to be considered.

Chemicals have also been applied to the soil, but without achieving much effective control. Shaw *et al*. (1980) added sodium pentachlorophenate, pentachlorophenol, or both, to container-grown *P. radiata* seedlings, either by mixing the chemicals with the soil during potting, or by applying them to the soil surface. These chemicals gave no protection against artificially applied inocula of *A. novae-zelandiae* or *A. limonea*. Heavy liming of the soil surface appeared to cause some reduction in natural field mortality of 4-year-old *P. radiata*, but rhizomorph frequencies and amounts were not reduced, and soil pH values were not altered, making it unclear how this treatment was acting (van der Pas and Hood 1984).

2.3.2 Biological treatment

Another technique with potential for controlling Armillaria root disease is to introduce an organism that will compete with or actively attack *Armillaria*, in a form that ensures the survival of the biological control agent in the forest environment. One approach is to use suitable strains and species of fungi in the genus *Trichoderma*, which are known to have competitive, antibiotic or mycoparasitic properties against a number of fungal pathogens, including species of *Armillaria* (Fox 2003; Harman *et al*. 2004; some have also shown an ability to enhance plant resistance). Research was conducted in the 1980s to evaluate the effect of strains of a number of *Trichoderma* species in controlling Armillaria root disease in kiwifruit orchards (Section 2.3.5). A number of these strains were also tested for their ability to control the disease in

plantations of *Pinus radiata* (Hill 1991). In October 1989, root systems of young pine seedlings were immersed in a slurry of an anti-dessicant polyacrylamide gel containing selected *Trichoderma* (Patent 231840) immediately prior to planting out on a Tasman Forestry Limited *Armillaria*-infested trial site on the Mamaku plateau near Rotorua. Four 0.25 ha blocks were divided in half, each half randomly assigned to treatment or to control (plants not treated). Two years after establishment, significantly more plants were healthy in the treatment (94%) than control blocks (78%; $p < 0.05$), and significantly fewer plants were diseased, dying or dead (6%, 22%, respectively; $p < 0.05$; Cutler and Hill 1994). *Trichoderma* strains were found to survive in the polyacrylamide gel, and were not pathogenic to tissue-cultured *Pinus radiata* plantlets in the laboratory. They were antagonistic to species of the mycorrhizal fungal genus *Rhizopogon* in the laboratory but not in the field. Treated plants were taller and with thicker stems and wider crowns than untreated plants, but differences were not significant (Hill 1991). No subsequent work from this trial has been reported, but other trials were established (Cutler and Hill 1994), and similar results were shown when the *Trichoderma* formulation was applied as a single treatment in the forest nursery.

Another approach is to apply a biological control agent to stumps, to hasten decomposition and as a competitor with *Armillaria*, either by depriving it of foodbase or through direct antagonism. Incoculating stumps with a saprobic basidiomycete decay fungus immediately after felling may prevent colonization by *Armillaria* species, in effect shifting the natural fungal population balance to the disadvantage of the pathogen. Use of a chemical such as ammonium sulphamate in conjunction with a biological control agent to maintain a desirable carbon/nitrogen balance may also be beneficial (Rishbeth 1976, 1979). The chosen fungus may act by rapidly depleting food reserves, making them unavailable to the pathogen, by preventing its entry, or else by restricting it to small segments of the stump where it can no longer be active beyond a limited time period (Rishbeth 1976, 1979). Potential contenders might even include isolates of *A. hinnulea* or the unidentified *Armillaria* species present in *Nothofagus* forests, depending on how aggressive they are as colonizers and whether or not they also prove to be pathogenic to *P. radiata*. To achieve success it is necessary to know to what extent stumps are colonized primarily from soil or by means of airborne inoculum.

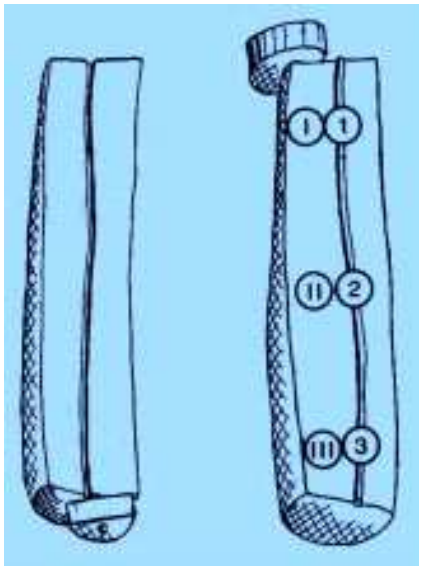


Figure 24: Procedure adopted to test competition between *Armillaria* species and basidiomycete decay fungi.

Yang and Hood (1992) tested the interaction between eight basidiomycete decay fungi known to occur on stumps, slash, or dead trees of *P. radiata* and two isolates each of *A. novae-zelandiae* and *A. limonea* in the laboratory. An isolate of *Trichoderma viride* Pers. aggregate was also assessed for comparison. Seed inoculum, consisting of small wood disc cultures, were attached at opposite ends of small pine branch segments in the laboratory (Fig. 24). After 4-5 months, the degree to which test isolates had prevented colonisation of the cambial, xylem and pith regions of the segments by *Armillaria* was evaluated. The *Trichoderma* isolate was markedly antagonistic to all *Armillaria* isolates. There was also evidence of reduced *Armillaria* colonization in segments treated with *Rigidoporus concrescens* (Montagne) Rajchenberg (previously *R. catervatus* (Berkeley) Corner sensu Cunningham) and *Ganoderma* cf. *applanatum* sensu Wakefield

(previously *G. mastoporum* (Lév.) Pat. sensu Cunningham). It may be relevant that these two fungi are commonly associated with *Armillaria* species in decaying wood in podocarp-hardwood forest (Hood *et a*l. 1989, 2004). The four *Armillaria* isolates varied in their colonizing ability. Despite the effectiveness of the *Trichoderma* isolate, Yang and Hood (1992) suggested that it might be more appropriate to seek a biological control agent among decay fungi in pine plantations able to compete in the longer term with *Armillaria* for lignin and cellulose in stumps and slash. It is not clear how long strains of *Trichoderma* are able to survive and continue to compete with *Armillaria* in such material once sugar reserves are depleted. It may also be necessary to distinguish between colonizing fungi that compete simply by delineating and occupying space in the wood substrate, and those which are positively antagonistic and which may actively replace *Armillaria*.

2.3.3 Stand management

Other options, besides reducing the inoculum substrate or depriving *Armillaria* of its food base, involve managing the stand so that the pathogen, although present, has minimal impact. Beveridge *et al*. (1973) earlier recommended a short first rotation saw log regime combined with grazing on badly infected sites previously covered in podocarp-hardwood forest. Returns from grazing in mortality gaps would help recoup losses from *Armillaria* attack, and at the same time weed growth would be controlled, facilitating stand tending operations. However, Kimberley *et al*. (2002) recorded that grazing tended to encourage unpalatable hardwood shrubs such as wineberry (*Aristotelia serrata* (J.R. & G. Forst.) W.R.B. Oliver), which filled the canopy gaps.

At one time, planting at a greater density was not encouraged as a disease management procedure. It was considered that *Armillaria* would eliminate the majority of trees in the mortality centres, while uninfected areas would carry undesirably high stocking densities. However, MacKenzie and Self (1988) considered that at Karioi Forest high density operational planting (2,400 stems/ha) was an effective management method because inoculum was widespread and uniform in distribution. Enough trees survived to an age where they became more tolerant of infection, giving rise to stands of acceptable stocking intensities over the whole site, even though many surviving trees remained chronically infected. Nevertheless, this argument is unlikely to apply to current second rotation stands where mortality is low but chronic infection well distributed and with significant impact.

Because these cultural methods do not remove *Armillaria* from the site, inoculum may be transferred to the next rotation, perpetuating the problem. However, another suggested control method is to let the land lie in pasture after clearing a forest until stump food reserves are well decayed. Certainly, infection is absent or only scattered and insignificant, in first rotation plantations established on farmland originally in native forest (Self *et al*. 1998). Although not normally seen as a realistic option, it is noteworthy that the current trend to convert some pine plantations to pasture for economic reasons is likely to be beneficial for potential future stands that may be replanted on these sites when the economic tide one day turns (Fig. 25).

Figure 25: Replacing pine forest by pasture.

2.3.4 Use of resistant hosts

Although there are commercial tree species more resistant to Armillaria than *Pinus radiata*, it is hard to envisage any extensive replacement of this host in forest plantations, despite its susceptibility. Nevertheless there is undoubtedly a place for considering resistant hosts as an alternative in some situations, for instance when planting farm or orchard shelterbelts or specimen trees on infested sites. Early references to species variation in resistance to natural *Armillaria* infection were made in reports of the Forest Research Institute (1953 p. 20; 1955 p.16; 1961 p. 31). On sites previously supporting indigenous forest, the species most susceptible to infection and mortality were *P. radiata*, species of *Larix*, and *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Hocking and Mayfield 1939), while the least susceptible were *Cryptomeria japonica* (Linn. f.) D. Don and *Thuja plicata* D. Don. However, there may be other issues to consider, and despite its resistance, *Armillaria* sp. has been found to cause a butt rot in older *C. japonica* trees (G. Steward *in* Hood 1989). In these early field surveys, *Pseudotsuga menziesii* was found to be as susceptible as *P. radiata*, but showed lower mortality rates, and as a result Douglas fir has been planted as a substitute for radiata pine on infested sites in some parts of the country. Although species of *Eucalyptus* proved to be susceptible to infection, losses did not appear to be significant (Newhook 1964). Information on species susceptibilities was summarized by Weston (1957) and Gilmour (1966). More recent observations in plantations have confirmed that *Ps. menziesii* and eucalypts are less prone to mortality from Armillaria than is *P. radiata*. There appear to be differences in susceptibility among *Eucalyptus* species, but field observations are not straightforward.

Using inoculation studies, Benjamin and Newhook (1984a) found significant variation among host species in susceptibility to the two common species of *Armillaria*. More seedlings of *P. radiata* became infected than did those of several *Eucalyptus* species and fewer *Eucalyptus* species died, possibly because *Eucalyptus* seedlings were

Figure 26: Pruned radiata pine tree killed by Armillaria.

more vigorous in growth than were those of *P. radiata*. *Armillaria novae-zelandiae* appeared to be more virulent to eucalypt seedlings than *A. limonea*, but eucalypts demonstrated evidence of species variation when inoculated with either *Armillaria* species. Using a *Beilschmiedia tawa* inoculum substrate, more seedlings of *E. delegatensis* R.T. Baker and, to a lesser extent, of *E. regnans* F. Muell., were killed by *Armillaria* than were those of *E. fastigata* Deane & Maid. and *E. saligna* Smith. In fact, seedlings of *E. saligna* were almost immune.

Within-species variation to the disease is only now being investigated in *P. radiata* (see Section 3.3.5).

Disease susceptibility also appears to increase with stress, and it is important to use healthy planting stock on infested sites (see Section 3.3.2). Mention has already been made of the need to keep stands free of infection by *Dothistroma pini*, by appropriate aerial spraying, and of the need to avoid severe pruning stress on diseased sites (Fig. 26).

2.3.5 Kiwifruit orchards

Research on the control and management of *Armillaria* in kiwifruit was initially undertaken from the mid 1980s to the mid 1990s. Two complementary programmes were conducted simultaneously during this period:

(1) a programme focused primarily on studies of the basic biology and epidemiology of *Armillaria* in orchards, in order to develop physical means of control (Horner 1986, 1987, 1988b, 1990a,b, 1991).
(2) a programme directed particularly towards the detection, screening and testing of potential biological control agents, particularly strains of *Trichoderma* species (Hill 1990).

A subsequent research programme was conducted between 2001 and 2005 investigating a number of physical, biological and chemical control methods (Horner 2005a,b, 2006a,b).

Early control measures involved excavation within disease patches to remove inoculum or their isolation and containment using trenches lined with sheets of poly vinyl chloride (PVC; Horner 1987; Hill 1988). Excavation was the most effective technique, though it was expensive and is no longer economically viable (Fig. 27). Infected wood and roots were removed from the soil, often using heavy machinery and mechanical sieving, and the treated soil was returned to the hole prior to replanting. The key to success was in identifying the full spread of infection on diseased root systems. Follow-up studies over a 4-5 year period showed that in more than 90% of cases such treatment eradicated the infection and no further outbreaks

Figure 27: Removing *Armillaria* from Bay of Plenty kiwifruit orchards by sieving the woody inoculum substrate from the soil and by whole-tree removal of willow shelterbelt trees to avoid leaving stumps (top, I. Horner; bottom; R. Hill)

occurred (Ian Horner, unpublished data). Growers are still encouraged to remove as much of the infected root system as possible. Placement of PVC sheeting in trenches around infected patches was also widely employed in the 1980s, to create a physical barrier between the diseased and healthy areas (Fig. 28). Follow-up studies over 4-5 years showed variable results. In some instances the barriers proved very effective, particularly where a double barrier was employed (one beyond the next healthy vine, with a back-up one further vine out). However, in some orchards the trenching technique failed to stop the spread of infection, largely when the trench was not placed beyond the leading edge of the expanding infection patch. The full underground distribution of infection is difficult to determine, and was often under-estimated by growers.

Trials were carried out in 1986 and 1987 to see if *Armillaria* could be eradicated by soil fumigation (Ian Horner, unpublished data). Willow root and branch segments were artificially infected with *Armillaria* and buried in soil treated with fumigants at rates of 500 kg/ha. Methyl bromide was the most effective, eradicating *Armillaria* from wood pieces 40 mm diameter near the soil surface, and 12 mm diameter at a depth of 1 m. Chloropicrin was ineffective at 1 m depth, and Basamid was ineffective beyond the depth of incorporation (0.3 m). Even methyl bromide was not practical as an operational fumigant, being unable to penetrate and kill *Armillaria* in larger wood fragments (beyond the outer 20 mm, near the soil surface) or deeper than about 1 m soil depth. In the deep, light Bay of Plenty soils where the majority of kiwifruit are grown, *Armillaria* was found growing on the vine tap roots at depths down to about 5 m.

The effectiveness of chemical treatment of kiwifruit vines was also investigated. During the period 1988 to 1991 a trial was carried out in infected kiwifruit vines and willow shelterbelts, to test the efficacy of Foli-R-Fos (phosphorous acid) treatment for

control of *Armillaria* (I.J. Horner, unpublished data). Injecting vines with this agent proved ineffective in controlling *Armillaria* infection after 2 ½ years. In the laboratory, *Armillaria* mycelial and rhizomorph growth rates were unaffected when phosphorous acid was incorporated into an agar media at concentrations up to 200 ppm.

Figure 28: Trenching and placement of polythene-lined barriers to contain *Armillaria* infection centres (R. Hill)

During the same period research was undertaken into the potential for fungi in the genus *Trichoderma* to eradicate *Armillaria* infection biologically from kiwifruit plants and to protect uninfected vines from developing disease. A number of *Trichoderma* isolates were obtained from *Armillaria*-infected Bay of Plenty kiwifruit orchards in areas where there appeared to be disease suppression (Robert Hill, unpublished data). Subsequent collaborative laboratory studies with the University of Auckland (Alison Stewart, Helen Brown, Sarah Dodd) focussed on the antagonism of these cultures to *Armillaria* and their biochemical and molecular characterisation (Dodd-Wilson 1996). In one study, isolates of *Trichoderma viride* and *T. atroviride* P. Karst[2] were more aggressive to *Armillaria novae-zelandiae* than those of *T. harzianum*, and were influenced in their behaviour by both temperature and pH (Taylor 1991). This work identified a number of potentially superior isolates of *Trichoderma*, including several of *T. atroviride*., *T. harzianum* Rifai, and *T. viride* (Hill 1990; Cutler and Hill 1994). Choice was based on both ability to antagonize *Armillaria* isolates in culture and also compatibility with other *Trichoderma* isolates for possible use in blends. Bulk quantities of various formulations incorporating conidia and hyphae of the selected strains were developed and tested in field trials, using solid substrates such as sawdust, wood chips, bark and peat (Hill and Travis 1994). Some products were registered commercially for operational treatment of Armillaria in kiwifruit orchards. Interim results from the field trials were published (Hill 1990). Although readers were urged to treat these findings with caution, it was subsequently concluded that the selected *Trichoderma* isolates gave effective biological control (Cutler and Hill 1994; Hill 2000b). Soil amendments such as mulch and compost incorporating *Trichoderma*

[2] Previously identified as *T. hamatum* (Bonord.) Bainier, but current nomenclature follows recent DNA-based research at the National Centre for Advanced Bio-Protection Technologies, Lincoln University.

as an additive reduced or prevented the spread of disease on treated as compared with untreated sites (Hill 2000b). The majority of infected vines injected or pasted with *Trichoderma* formulations survived and regained vigour, and most plants replanted after dipping in a *Trichoderma* slurry survived whereas many untreated vines died. Complementary trials by Agrimm Technologies Limited also demonstrated positive control of Armillaria after injecting kiwifruit vines with the commercial *Trichoderma*-based product Trichoject® (Hunt 1998). A considerable amount of research work was carried out over 15 years (Robert Hill, unpublished data), but comprehensive results have not been published. As part of the biological control research with *Trichoderma*, it was discovered that the antifungal compound 6-pentyl-α-pyrone (also known as 6-amyl-α-pyrone) produced by *Trichoderma* species appears to be involved in the biological control mechanism (Cutler and Hill 1994; Hill and Travis 1994). This agent was active against *A. novae-zelandiae* in the laboratory and demonstrated control of the disease after injection into infected kiwifruit vines. *Trichoderma* species occur naturally on soil and root material in a variety of habitats, so it is desirable to confirm that any control achieved is in fact due to the introduced culture and not to wild strains already present. Dodd *et al*. (2004a,b) have developed molecular techniques that make it possible to follow the survival and longevity of biological control *Trichoderma* isolates within the complex natural environment into which they are introduced.

Figure 29: Exposing infected kiwifruit root collars for water sluicing and surgery as an Armillaria control (I. Horner)

More recently, a comprehensive trial was conducted between 2001 and 2005 in three Bay of Plenty kiwifruit orchards to evaluate the effectiveness of a range of potential treatments for control of *Armillaria* in a thoroughly objective manner (Horner 2006a,b). The treatments included various biological control applications based on *Trichoderma* (Agrimm Trichoject® and Trichopel®, and Gro-Chem DRH Trichoderma), Enviroblast®, water-blasting to expose root collars combined with surgery to remove diseased tissue, fungicide injection, and compost. One treatment incorporated a combination of water-blasting, surgery and biological control agents. Vines were inspected at intervals, and at the final assessment, root collars were exposed to enable evaluation of below-ground infection. The trial was assessed in a number of ways, but in all cases the water blasting and combination treatments showed significant disease control (e.g. more than twice the percentage of vines so treated showed healing of below-ground lesions due to *Armillaria* infection than did untreated controls, and fewer trees were killed by the pathogen; Fig. 29)). The various *Trichoderma* treatments, Enviroblast®, and compost gave very similar results to those of the untreated control, and there was no evidence in this trial that they had any

positive effect on *Armillaria* control. There was a suggestion of a very slight improvement with the fungicide injection, but this was not statistically significant. There was no evidence that the combination treatment of water-blasting, surgery, and two different *Trichoderma* treatments was any better than the water-blasting and surgery alone. Water-blast sluicing and surgery is therefore currently recommended to aid control of *Armillaria* in kiwifruit orchards.

Since the early 1990s a number of growers employed biological control techniques based on commercial strains of *Trichoderma*. Various formulations have been used, including the products previously listed as well as combinations such as fish fertiliser mixed with *Trichoderma* and various compost formulations. Reports on the effectiveness of these treatments in operational use have been contradictory and largely anecdotal. In many orchards application of these products appears to have made little long term difference whereas in other properties growers claim success (McLaughlin 1996; Hunt 1998). An extensive survey in 1998 of more than 12 thousand vines in 127 Bay of Plenty kiwifruit orchards within four years of treatment with both Trichoject® and Trichodowel® reported survival rates between 87% and 96%, but no untreated control plants were assessed to provide a comparison (Hunt and Clarkin 1998). There is no argument that many *Trichoderma* strains are antagonistic to *Armillaria* species, particularly in laboratory interactions, but consistent effectiveness under practical field conditions appears to be problematic. Following the completion of the recent trial and the accompanying publicity, it is likely that water-blast sluicing and surgery will become much more widely employed, and a large number of growers are already using this system. If applied as a preventative, it is likely that it will provide a highly effective long term control treatment, especially if employed in an integrated system incorporating the removal of dead vines and roots, possibly backed up with PVC-lined barrier trenches. It may even lead to the eventual eradication of *Armillaria* from infected patches.

Current control advice for kiwifruit orchards is based on prevention rather than cure (Horner 2005b; see also Hill 1988). Limiting invasion of orchards by *Armillaria* is far simpler and cheaper than trying to clean up infections once they are established. Recommendations include:

- When planting new blocks, remove stumps and main roots of previous trees.
- Do not bury old stumps, trees, or other wood debris when contouring. These can harbour *Armillaria* and act as a food source for subsequent infestation.
- Avoid the need to remove shelterbelts by planting at the final required spacing.
- Avoid shelter species with widely spreading root systems (e.g. matsudana willows); possible alternatives less susceptible to *Armillaria* include *Bambusa oldhami* Munro, *Cryptomeria japonica* or *Casuarina* sp. (Hill 2000b).
- Prune shelterbelt roots annually to contain spread into kiwifruit blocks.
- If shelterbelts are thinned or clear felled, remove stumps to prevent colonisation by *Armillaria*
- If shelter stumps cannot be removed, do not treat them with herbicides, as this aids *Armillaria* spore colonisation.

3. KNOWLEDGE GAPS AND RESEARCH PRIORITIES

This section reviews our current understanding of the state of the disease as it affects present and future forest plantations, and indicates where more information is needed. Additional research data are provided that give further relevant background

to the setting today. Where some of this work is preliminary and unpublished it is summarized in slightly greater detail.

3.1 Ecology and spread

The nature and behaviour of *Armillaria* in present and future forest plantations are still incompletely understood, although they are clearly influenced by past vegetation history. While seemingly more fundamental and academic, such research is of considerable importance. A full knowledge of the way a pathogen behaves may often bring to light an unexpected control option, and it is often only when this basic research is undertaken are such innovations possible. In addition, only when we fully understand the way the disease is developing and spreading over successive rotations will we be able to judge its future impact with greater reliability.

3.1.1 Basidiospore dispersal

There is now a substantial body of indirect evidence indicating that the dispersal of *Armillaria* basidiospores is more effective in the New Zealand environment than in many other parts of the world (Fig. 30). This possibly reflects a plentiful rainfall throughout much of the year, particularly during winter, providing favourable conditions for spore germination and substrate colonisation.

Figure 30: Fruitbodies of *Armillaria novae-zelandiae* in indigenous forest releasing copious quantities of spores during May.

Gilmour (1954) was the first to propose basidiospore dispersal as an explanation for the occurrence of *Armillaria* as a saprophyte in dead trees in first rotation pine plantations in Kaingaroa Forest, on sites that had not previously supported indigenous forest, and this was endorsed by MacKenzie and Self (1988), and later by Hood and Sandberg (1993a). Prior to the planting of pines, the Kaingaroa plateau was a treeless plain covered in tussock, fern, or scrub (Colenso 1894; Ure 1950; Reischek 1952, p.299; Cowan 1982), a condition induced by pre-European fires rather than volcanic activity (McQueen 1961; Vucetich and Pullar 1963). However,

MacKenzie and Self (1988) found that *Armillaria* was widely parasitic in second rotation plantations in Kaingaroa Forest, being present in stands on all site classes, even those in which it had not been observed by Gilmour, suggesting that infection had spread from inoculum originating from spores invading saprophytically in the first crop.

Figure 31: Trapping to test the ability of airborne *Armillaria* basidiospores to colonise fresh pine stem and branch segments. The plastic shields prevent invasion by soil rhizomorphs. Bottom, mycelial fans beneath the bark confirm successful colonisation (left), and (right) demonstrating hyphal penetration of pine segment wood cells from spores of *A. novae-zelandiae* at the surface.

Hood and Sandberg (1993a) and Hood *et al*. (2002b) provided further support for the importance of basidiospores (Fig. 31) by using the cultural pairing of diploid field isolates from soil rhizomorphs to distinguish somatic compatipility groups (which they interpreted as genotypes, clones or genets, representing separate colonies; see Section 2.1.2) in a young second rotation radiata pine stand following a previous crop

of *P. nigra* ssp. *laricio* in Kaingaroa Forest. They found an average minimum colony density of 44 groups per hectare. This is substantial by world standards, and strongly suggestive of establishment by means of basidiospores in stumps or debris of the first rotation, and perhaps also in heathland material present prior to the planting of this first crop. Furthermore, with one exception, all groups identified culturally belonged to *A. novae-zelandiae*, implying that it is mainly this species that spreads more readily by means of spores, since both *A. novae-zelandiae* and *A. limonea* can be grown saprophytically in pine wood and are common in indigenous forests and in the pine plantations which replace them (Hood and Sandberg 1987, 1989, 1993b). Earlier, Benjamin and Newhook (1984), Hood and Sandberg (1987, 1989, 1993b), and Hood (1989) had demonstrated the presence of both species in indigenous forests and in first rotation replacement pine forests, also in comparatively high group densities (Section 2.1.2), supporting indirectly the wider importance of basidiospore dispersal of *Armillaria* in the natural ecosystem.

In a new approach to understanding the nature of *Armillaria* populations in pine plantations in relation to likely basidiospore infestation, 43 isolates collected from pine forests established after a previous exotic crop were all identified as *A. novae-zelandiae* using a PCR primer specific for this species based on ITS rDNA (Sarah Dodd, Robert Hill, unpublished data; see Section 2.1.1). Molecular methods can also be used to determine within-species differences, and provide independent comparison with the somatic compatibility groupings determined using cultural pairing of diploid field isolates. In a preliminary study, cultures isolated from a first rotation pine stand following indigenous forest, previously typed culturally to species and somatic compatibility groups (Plot 3 in Hood and Sandberg 1987, 1989, 1993b), were assessed for genetic diversity using ITS sequencing and UP-PCR (Dodd *et al*. 2006a). At the species level there was nearly complete agreement between cultural and molecular identification of the two species present, *A. novae-zelandiae* and *A. limonea*. Apart from some discrepancies, there was also good correspondence between the somatic groups determined using cultural pairing nearly 20 years earlier and the molecular approach. However, the molecular technique demonstrated finer distinction below the somatic group level, apparently caused by recombination as haploid basidiospore-derived mycelia fused to form diploid colonies. This high diversity, indicative of a strong level of out-crossing, provides even greater support for dispersal by means of basidiospores. These cultures originated predominantly from within an indigenous forest in which diploid colonies could have arisen from nearby basidiospore sources (ie colonies potentially with one common parent). It will be instructive to examine the within-compatibility group diversity present in plantations such as Kaingaroa Forest which have no long-term history of previous indigenous forest, and where spore sources are situated at some distance.

Armillaria is common, even if frequently unrecognized, as an agent of disease and death in a variety of habitats throughout New Zealand, such as shelterbelts, urban parks (e.g. the Botanic Gardens, Christchurch), home gardens, riparian willows (see earlier), and sand dune forests (Rogan and Ridley 1995). While such infection may be often be traced to soil inoculum in the form of buried wood debris colonized by *Armillaria* from the previous woody vegetation, it seems likely, in view of its widespread occurrence, that in these vegetation types, too, basidiospores may also involved. Additional evidence for the dispersal of *A. novae-zelandiae* by means of basidiospores was provided by research in the 1980s in Bay of Plenty kiwifruit orchards (Horner 1988a, 1991). In many of these orchards disease patches were traced to an earlier woody substrate potentially harbouring *Armillaria* inoculum, derived from debris from old shelter trees, hedges, or previous tree crops, including gullies where logs had been buried and contoured over. However, extensive disease was also found in several orchards established on pasture sites that had been free

from trees for a considerable period. Outbreaks in these orchards occurred only after willow shelterbelts were clear-felled and the stumps immediately poisoned with herbicide to prevent sprouting. In such stumps, *Armillaria* mycelium often appeared to grow downwards from the cut surface.

Laboratory cultural pairing techniques with *Armillaria* isolates obtained from some kiwifruit orchards identified a small number of comparatively large compatibility groups, up to ca. 40m diameter, implying the presence of long-standing inoculum on these sites (Fig. 32; Horner 1991). However, in other orchards numerous small-diameter somatic compatibility groups of *A. novae-zelandiae* were detected, each unique to just one or two poisoned willow shelterbelt stumps. In one instance, seven different *Armillaria* groups were found along a 12 m stretch of willow stumps. Four of these colonies had spread to adjacent kiwifruit vines, demonstrating vegetative spread by means of contact through roots. Only *A. novae-zelandiae* was identified by cultural means in these orchards, and two stumps were found to be colonized by two and three groups of this species, respectively. Similar results were found in a Katikati orchard, where more than 30 groups were identified by somatic pairing among 50 infection sites (Hill 2000b).

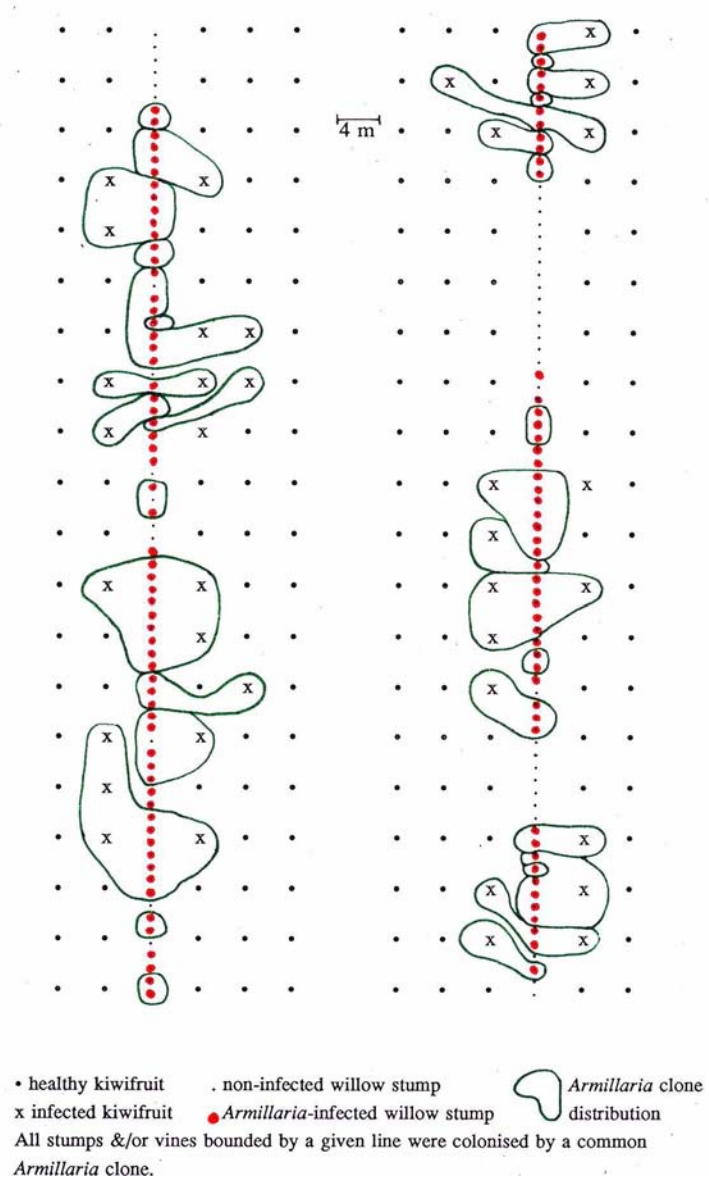


Figure 32: Distribution of *Armillaria* vegetative compatibility groups (colonies) in a Bay of Plenty kiwifruit orchard (after Horner 1991)

In another study, 45 isolates collected from different kiwifruit orchards were identified to species using the molecular technique described above, and as with the pine isolates (see above), all were found to be of *A. novae-zelandiae* (Sarah Dodd, unpublished data). These studies provided strong circumstantial evidence for basidiospore colonisation of cut willow stumps in at least some infected kiwifruit orchards, indicating that infestation of these orchards almost certainly arose in this way (Horner 1991).

Figure 33: Treating pine thinning stumps (top and centre) and partly buried stem segments (bottom) with aqueous suspensions of *Armillaria* basidiospores to resolve minimum spore concentrations necessary for colonisation and establishment of new infection centres. All infested material removed at the conclusion of each study.

However, though compelling, this evidence all remains indirect. There is still a need for direct verification of the role of spores and for information on the extent to which natural spore dispersal may be setting up new colonies in pine plantations. Some initial studies have been conducted by treating pine stumps and bark-encased radiata pine stem or branch segments, kept moist by partial burial, with aqueous suspensions of basidiospores (Fig. 33; Hood and Sandberg 1987; Hood *et al*. 2002; Hood and Gardner 2005). These have demonstrated clearly the ability of high concentrations of spores of *A. novae-zelandiae* (between 10, 000 and 23 million spores per cm^2 segment surface) to colonise freshly cut pine segments, and in one study, fresh pine stumps. Separate colonies of *A. novae-zelandiae* were present in different segments, and in one study (using willow instead of pine), more than one colony was present in the same segment, providing further confirmation that the introduced basidiospores were the source of the different colonies.

Comparable work was undertaken in the 1980s by treating stumps and billets of a range of kiwifruit orchard shelter belt tree species with aqueous basidiospore suspensions of *A. novae-zelandiae* (I.J. Horner, unpublished data). Many freshly cut stumps of *Salix matsudana* treated respectively with glyphosate, 2,4-D, 2,4,5-T or 2,4,5-T and the wound dressing Pruntec in combination, became colonized by *Armillaria* after inoculation at a concentration of 10,000 spores/mL. Stumps not treated with herbicide remained uncolonised. Wood segments of six species (*S. matsudana*, *Acacia* sp., *Alnus* sp., *Casuarina* sp., *Cryptomeria japonica* and *Populus* sp.) were also colonized to varying degrees after treating with a range of basidiospore concentrations and incubating in a humid chamber. Frequency of colonization was greater at higher concentrations, but some segments of willow, alder, casuarina and cryptomeria were colonised at rates down to 10 spores per mL. A similar experiment was undertaken by partially burying segments of *S. matsudana* and spraying the exposed ends with basidiospore suspensions of *A. novae-zelandiae* and *A. limonea* at concentrations of 0, 10, 100, 1000 and 10,000 spores/mL after treating with 2,4,5-T. After nine months, colonisation frequency was greater for both *Armillaria* species at higher spore concentrations, but one segment became colonized by *A. novae-zelandiae* at only 10 spores/mL. Interestingly, freezing spores of *A. novae-zelandiae* did not affect their ability to colonise segments. Segments only become colonized after treatment with herbicide. In a related study, basidiospore germination on willow stump segments was monitored directly by means of a Scanning Electron Microscope (SEM). Spores of *A. novae-zelandiae* germinated 24 hours after being sprayed onto the cut surface under conditions of high humidity, regardless of whether the segment was first killed with herbicide (2,4,5-T), steam, or left untreated. Longitudinal sections showed that in the steamed and 2,4,5-T-treated material, hyphae penetrated into the wood vessels within 48 hours, and after 10 days the mycelium was well established. However, on the untreated wood, growth was restricted to the cut surface. Overall, these spore inoculation studies have provided clear direct evidence that basidiospores of *Armillaria* are able to colonise willow stumps after treatment with herbicide.

In more recent work, partially buried 3-month old segments of *Pinus radiata* became colonized by basidiospores at rates between 50 and 20,000 spores per cm^2 segment surface, and a current study is investigating minimum spore densities able to colonise fresh pine debris (I.A. Hood, unpublished data). This research is being complemented by a spore trap study in which aerially suspended *Armillaria* spores will be determined using molecular means (I.A. Hood, T. Ramsfield). The purpose is to determine the natural patterns and concentrations of spore dispersal from tracts of indigenous forest during the fruiting period in May and June (Hood *et al.* 2002; Hood and Gardner 2005). Initial studies will evaluate airborne spore numbers within indigenous forest, and subsequent studies will then investigate concentrations at distances from the forest edge, and finally in pine plantations. Much remains to be resolved. Do spore concentrations form gradients that decline with distance from the source to a general diffuse background average level extending over greater distances, or do spores disperse in discrete clouds that persist as they drift away down the prevailing wind? How long do spores remain viable (Shaw 1981)? Are there regional differences? Are stumps important, or do spores colonise fresh, partly buried pine slash to a more significant degree? It is usually not difficult to find *Armillaria* fans and rhizomorphs among such material in many pine plantations, and Self and MacKenzie (1995) reported greater mortality within 4m of the slash and debris in windrows than further away, showing that this material is a source of infection, regardless of how it becomes colonised.

3.1.2 Spread within plantations

Figure 34: Excavation studies to investigate the infection process in young second rotation pine plantations.

Our understanding of the behaviour and movement of *Armillaria* mycelium and rhizomorphs within the soil in today's plantations is still quite rudimentary and mostly derived from indirect observation, despite what has already been learnt from painstaking research. The mechanism of spread from the stumps or slash of the previous crop, from and to thinning stumps, between living crop trees (if this takes place), and the degree to which each type of movement occurs, all remain largely undescribed. Some careful preliminary excavation work has been undertaken, but this study is currently in abeyance (Fig. 34; I.A. Hood and J.F. Gardner, unpublished data). However, it has provided some preliminary information, and on several occasions rhizomorph networks were found linking *Armillaria*-colonised roots of first rotation pine stumps with young dying second rotation radiata pine trees (Fig. 35). A more comprehensive picture of the below ground development of *Armillaria* would be potentially useful in devising methods for impeding the spread and impact of this pathogen. It would also help in better predicting the effects of changes in management practices.

Figure 35: Left, close interaction between young pine root system and a previous crop stump root. Right, *Armillaria* rhizomorphs from a decaying stump root (top) infecting a healthy second crop pine root (bottom).

Monitoring of mortality data from first rotation stands has already been discussed above (Section 2.1.3), and has yielded records of the changing spatial and temporal patterns observed early in the rotation. This information was once the subject of some debate, but it was ultimately concluded that only the primary inoculum was significant in these first rotation stands, there being no evidence of secondary spread between young pines in the early part of the rotation, at least. MacKenzie (1987), endorsed later by Hood *et al*. (2002b), demonstrated that infection is not static, but rather "ebbs and flows" on individual trees depending on variation in pathogen aggression and host resistance as influenced by the changing climatic, management, and physiological environment during the rotation. Hood *et al*. (2002b) showed that in one stand the first waste thinning was followed by an increase in the overall incidence of detectable stand infection, but what was actually happening below ground could not be investigated.

We do have useful knowledge of the host-pathogen interaction within the living infected pine tree. Gilmour (1954) carefully explored the development of *Armillaria* within the tree by sectioning at the root collar region to reveal the historical developmental patterns. He demonstrated repeated injury to the growing tissues in successive years, each individual lesion leading either to tissue death or to partial or total recovery. This information was extended by van der Kamp (van der Kamp 1998; van der Kamp and Hood 2002), who also sectioned and studied the internal anatomy of the bole of a number of slightly older (13-year-old) trees in a stand in Kaingaroa Forest, after first carefully excavating their root systems to identify external infections. *A. novae-zelandiae* survived in the bark in the root collar region of the infected tree, causing abnormal bark production, from which it periodically penetrated to the cambium during the dormant season causing small lesions, most of which callused over after several years. Externally, infection was visible mainly at the root collar, but a total of 24 contained root infections were identified on 13 trees. It was concluded

that there is an energy cost to the tree associated with the ongoing struggle to keep the pathogen at bay.

Figure 36: Resin staining in radiata pine. Top left, associated with *Armillaria* infection at the root collar. Top right, unexplained staining associated with flow from compacted roots in heavy clay soil (bottom left). Bottom right, degrade in sawn boards due to the unexplained resin staining.

Resin flow as a host defense response generally accompanies infection by *Armillaria* in living pine trees. For this reason this fungus was a likely suspect when extensive resin soaking was discovered associated with sunken furrows at the base of affected trees during the harvesting of potentially high value pruned radiata pine butt logs in certain forests on clay soils near Auckland and on the Coromandel Peninsula (Fig. 36; Hood and Gardner 2001, 2002). The value is substantially reduced because the affected wood is not amenable to gluing, staining, or mechanical sanding, and is not visually appealing. A survey was undertaken which ruled out *Armillaria* as the cause. In a first rotation stand on a farmland site partly reverted to scrub, *Armillaria* was found infecting the root collar of only one of 34 harvested trees all of which nevertheless had resin impregnation. Part of the problem appeared to result from compaction stress to deformed root systems growing in the clay soils, leading to an upward flow of resin into and along the stem wood. Resin caused by *Armillaria* infection does not normally extend much above soil level (van der Kamp 1998; van der Kamp and Hood 2002).

As noted earlier (Section 2.2.2, footnote) analyses of national survey *Armillaria* data by Shu *et al*. (1994) implied that the distribution and incidence in plantations is affected by climate, landform and the nature of the soil. Although these effects were not detected during the analyses of Self *et al.* 1998, and while a number of the conclusions of Shu *et al*. (1994) are open to debate (Ridley *et al*. 1996), it may be that some environmental aspects should be explored further. Such variables, if significant, could have regional implications and possibly affect distribution within individual forests, and might even be affected by climate change. However, there are no current research plans to address these issues.

3.1.3 Effects of different hosts and management changes

In the past, various operational or other environmental changes have impacted deleteriously on radiata pine stands in association with infection by *Armillaria*. These effects have not always been readily understood or foreseen. Examples include effluent spraying in Tairua Forest which resulted in mortality and heavy *Armillaria* infection among mature pine trees; poison thinning in Karioi Forest, already referred to, which led to the decline of affected stands accompanied by severe *Armillaria* infection (Section 2.1.4); the impact of *Dothisroma pini*, also previously referred to, which enhanced the impact of both fungi (Section 2.2.1); and the stress of excessive pruning which results in the death of young pines if infected by *Armillaria* sp. What is the effect of a regime where trees may be planted at final stocking on infested sites? Loss due to the development of mortality gaps seems a likely outcome.

Sometimes there are unexpected responses related to the use of different forest tree species. Comparatively high early mortality from *Armillaria* has recently occurred in young radiata pine plantations near Tokoroa following first rotation crops of eucalypts. Similarly, Brent Rogan (personal communication) reported a high incidence of *Armillaria* in pines planted among clearfelled eucalypt stumps in Gwavas Forest in Hawkes Bay. How do other hosts behave? In the earlier studies in Kaingaroa Forest, Essenberg (1988) reported a greater incidence of *Armillaria* in *P. radiata* following *P. nigra*, whereas MacKenzie and Self (1988) found that site quality had a greater impact than the nature of the first rotation crop. Not unexpectedly, they did find that incidence was related to the quantity of inoculum, in that there was less disease in an early harvested crop of *P. contorta* which left only small stumps and often displaced root systems. This, of course, is the basis of disease control by means of stump removal.

Douglas fir (*Pseudotsuga menziesii*) generally shows less mortality than *P. radiata* on Armillaria risk sites, and has quite recently been planted as a substitute crop in Southland on sites cleared of *Nothofagus* forest in order to reduce the impact of the disease. Nevertheless, mortality can sometimes be extensive even with Douglas fir, and chronic infection is known to be significant, possibly to a higher degree than is assumed with this species (Fig. 37; Les Renney, personal communication). For instance, *Armillaria* was present at an unexpectedly high incidence in Douglas fir thinning stumps during a study in Kaingaroa Forest (van Boven 1974).

Figure 37: A young, green crowned Douglas fir tree with *Armillaria* root collar infection.

There is therefore a need to understand the relationship between *Armillaria* and a number of the more common forest tree species, such as Douglas fir. A more general knowledge of the factors governing the disease within pine plantations could make it possible to anticipate the effects of changes in management practice, and perhaps provide greater incentive for a practical control in more heavily diseased stands. However, no additional management or alternative host species research is planned in the current programme.

Knowledge gaps: A precise understanding of the way *Armillaria* invades and spreads within modern pine plantations; the role of basidiospores in dispersal; the effect of different management practices within stands; the influence of tree species other than radiata pine. A more definitive understanding of these aspects would be valuable in suggesting novel approaches to reduce the development and impact of Armillaria.

3.2 Stand inventory

The growth loss estimates discussed earlier (Section 2.2.2) are averages, and do not express the levels of infestation in individual stands and compartments, which may be higher. Investigation is underway to devise a realistic method of identifying those stands with greater levels of chronic infection, in order to be able to assign treatment to where it will be most worthwhile. Two potential approaches have been considered (Hood and Kimberley 2002; Hood *et al*., 2006).

The first, direct technique is based on an evaluation procedure applied in several earlier studies, in which the root collar is temporarily exposed with a small, short-handled grubber in order to score the degree of girdling by *Armillaria* (the technique was eventually first described by MacKenzie 1987). The method was employed again by MacKenzie and Self (1988) and Self *et al*. (1998) with a modified design in which a sample of 100 trees were evaluated per stand using 20-tree offset transects. After assessing 20 consecutive trees in an arbitrarily selected planting row, another 20 trees were evaluated by continuing on in the same direction from an equivalent point

in the fifth adjacent parallel row, and the procedure was repeated until all 100 trees had been scored. This approach was investigated further by Hood and Kimberley (2002), who examined the efficiency of the sampling design using pre-thinning spatial data from a 3.1 ha trial in which the level of infection in every tree was determined by exposing the root collar as previously described (Hood *et al*. 2002b). By using a computer to place theoretical transects of different sizes randomly across the site it was determined that single-tree transects were the most efficient, requiring the examination of the least number of root collars for the same level of accuracy. A table was prepared that indicated the number of trees that should be sampled for required levels of precision at different intensities of infection.

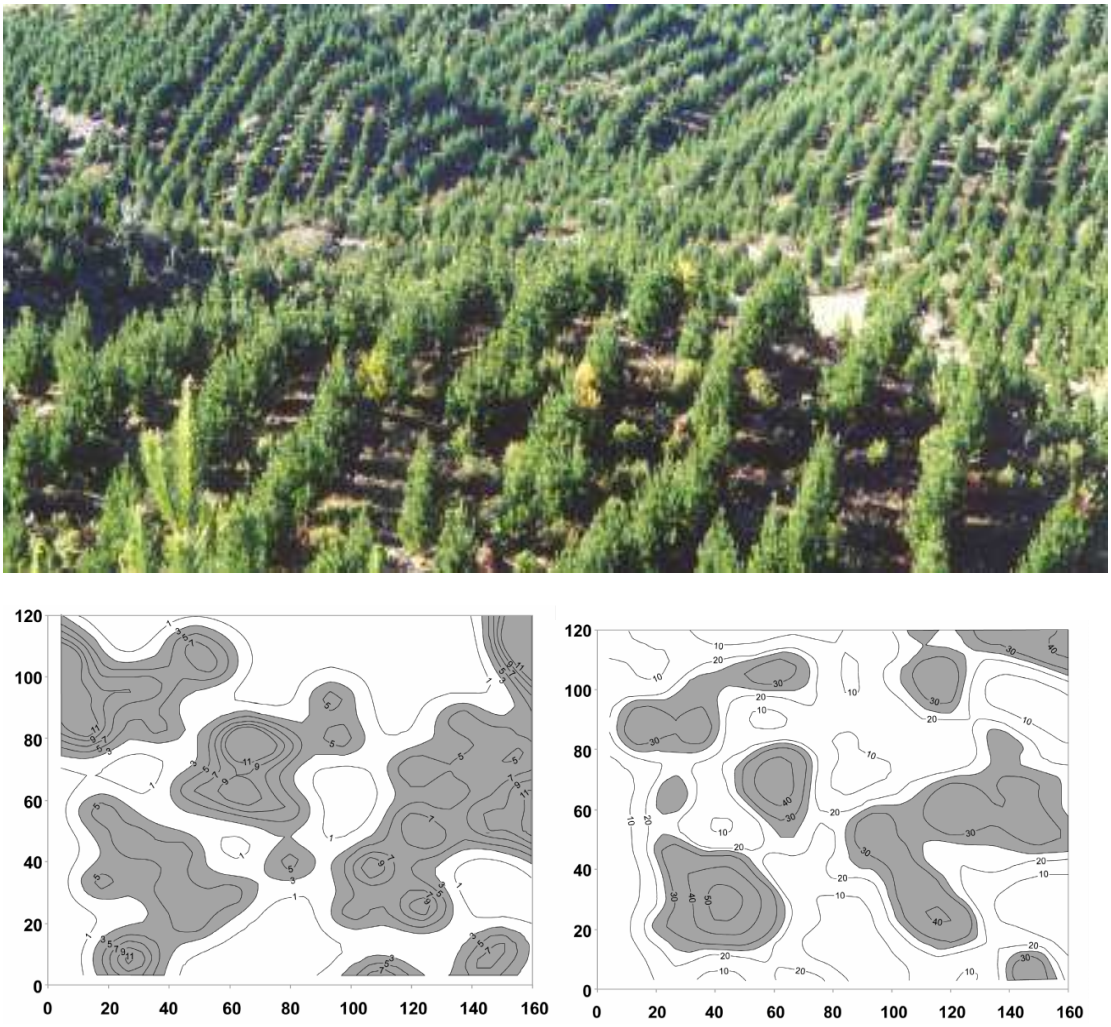


Figure 38: Spatial relationship between visible Armillaria mortality (top) and hidden chronic infection. Left, contour map of percentage trees killed by Armillaria in a young second rotation radiata pine plantation (shaded area, > 3% mortality). Right, map of percentage infection in green crowned trees in same stand (shaded area, > 25% trees infected). Scale: units are in metres (after Hood *et al*. 2006).

The second, indirect method was introduced in an attempt to derive an alternative, possibly more cost-effective approach. Using the data set referred to in the previous paragraph (Hood *et al*. 2002b), Hood and Kimberley (2002) determined that incidence and severity (degree of root collar girdling) of chronic infection in young trees were both greater nearer to trees killed by *Armillaria* early in the rotation.

Contour plots were derived using a computer, which suggested that maps of early mortality prior to first thinning might be used as predictors of the quantitative distribution of chronic infection (Fig. 38). In this way, the distribution of the visible and readily determined early mortality would identify the zones of more heavily chronically infected areas requiring treatment. For instance, the study data suggested that areas with an average pre-thinning mortality greater than 3% would be reasonable indicators of stands with chronic infection exceeding 25%. This relationship is based on detailed work in just one trial, although it has now been endorsed by recent work from another stand (Hood *et al.*, 2006). Nevertheless, further surveys will be needed to ascertain the effectiveness of this approach.

Anticipating the feasibility of the indirect method, Firth and Brownlie (2002) undertook a preliminary investigation of the potential for assessing stand mortality using aerial photography. A sample of trees was assessed on the ground, as described above, and independently using high resolution, colour, stereo aerial photographs, and comparisons were made between the two methods. The majority of trees killed by *Armillaria* greater than 2m tall were detected in the photographs. Trees that had died earlier were too small to be visible and were often hidden by weed growth. Brownlie and Firth concluded that remote sensing was likely to be a practical tool for assessing Armillaria in pine plantations if a relationship between dead and dying trees taller than 2m and total infection can be established. As a further extension to this work, a preliminary glasshouse study is being undertaken to see whether, among plants with green foliage, those that are infected can be distinguished from those that are not, by means of remote sensing in wavelengths other than the visible spectrum (Andrew Dunningham, personal communication). If this proves feasible, it would be a powerful tool for the assessment of stand infection, since it would allow chronically infected trees to be mapped directly from the air.

At this stage the indirect method, in whatever form, appears to have potential, and is likely to be more cost-effective even if mortality is assessed from the ground. Even so, evaluation of further stands is needed before it can be verified as reliable. Use of this method would still require the examination of a sample of trees to verify cause of death, and timing would need to be within a very brief window of peak incidence of mortality, which may vary slightly in different stands (age ca. 4-6 years, before the first thinning). Small plants that die earlier in the rotation would go undetected, even in a ground survey, while others would not have spread their roots sufficiently to encounter inoculum and become infected. On the other hand, once larger dead trees have been removed in the initial thinning operation, there is usually little subsequent mortality. It may not be possible to use the survey information fully until after harvest, when the delineated areas would be treated before the site is replanted with the next crop. However, the short rotation period of *P. radiata*, and the apparent constancy of spatial distribution of infection with time (there being no evidence of secondary spread of infection between pines), makes this a realistic procedure. Practically, a routine survey would probably be conducted at a coarser scale of precision than the resolution appearing in the *Armillaria* distribution contour maps, since it seems unlikely that the extent of any remedial procedure would be less in area than a compartment or sub-compartment unit.

Knowledge gaps: The reduced incidence of mortality in modern plantations and an awareness of the impact of chronic infection impose a need for an effective method of identifying stands with a higher infection incidence (e.g. >25%). Possible methods include direct sampling of stands to evaluate root collar infection, and indirect mapping of chronic infection from the distribution of mortality before initial thinning. The indirect approach is likely to be significantly cheaper, especially if undertaken by remote sensing. However, verification of the method requires a significantly greater

number of stands to be evaluated in order to establish a clear quantitative spatial relationship between mortality and chronic infection.

3.3 Control and management

In present and future pine stands, new cheaper methods of disease control are required that are more cost effective than stumping, and readily targeted to stands with a higher incidence of chronic infection so that there is a clear incentive for their application. In addition, a ready means of identifying such stands is needed, as discussed in the previous section. A number of new control approaches that are currently under investigation show varying degrees of promise. The aim is to develop an integrated procedure which may incorporate several successful, easily applied, cheaper options applicable to targeted sites. It may not be necessary to achieve total effectiveness for the procedure to have a significant economic impact. Among the methods being researched some target the present inoculum, and are therefore eradicative, while others simply modify the effects of infection in order to minimise the impact on the host. Even so, whatever means is used to reduce the disease in the present crop should desirably leave less inoculum available at the commencement of the succeeding rotation.

Research on Armillaria in New Zealand has now proceeded for some years, and it is reasonable to ask why we still lack a good cheap control option and are even now investigating fundamental principles rather than being at a stage where already acquired background knowledge is being used to develop operational control technologies. One reason is that, worldwide, root diseases are very difficult to deal with and require a substantial research investment to make significant progress. Despite considerable input, there are comparatively few international examples of cost-effective operational management of root diseases, although as here, promising new methods are currently under investigation. The second explanation is that resources and input for work on the disease in this country have shown a significant periodic fluctuation, and in some years there has been only minimal research investment into this disease.

In this section new methods of research into control methods are discussed, with emphasis on areas where knowledge is deficient.

3.3.1 Inoculum removal

The extraction and windrowing of stumps and root systems prior to planting is still the one tested method of reducing infection, but it is an expensive procedure. Even so, a contemporary cost analysis of the method based on present day information may be worthwhile. On some soil types whole-tree harvesting may be open to consideration (cutting the log after toppling and uprooting). This aspect was the subject of a recent FBRC bid, but currently no research is planned.

3.3.2 Silvicultural management and other operations

Two currently active long-term trials were established to investigate the influence of silvicultural management on the incidence of *Armillaria* infection in radiata pine plantations. One is exploring the effect of thinning and pruning, and the other the influence of planting stock type (seedlings or cuttings).

The thinning and pruning trial was set up in a second rotation *P. radiata* stand following a crop of *P. nigra* ssp. *laricio* on a site not previously stocked in indigenous forest (Hood and Sandberg 1993a; Hood *et al*. 2002b). Results at mid rotation (age

12.5 years) following a first thinning at age 7 years indicated that those treatments which created thinning stumps appeared to increase the incidence of infection 5.5 years later (to 44% and 46% trees infected, for stocking levels of 500 and 250 stems/ha, respectively), compared with unthinned controls (30% infection, 810 stems/ha; Fig. 39). Not all stumps could be found after 5.5 years, but of the 76% that were, at least 58% were colonized by *Armillaria* (Fig. 40). Incidence and severity of infection appeared unaffected by pruning to 30% of tree height as measured at age 13 years. This is not encouraging when considering thinning as a management treatment for the disease, and it suggests that thinning should be undertaken with care in an infested stand. However, a conclusive outcome will await the results of a subsequent assessment later in the rotation following a second thinning at age 13.5 years.

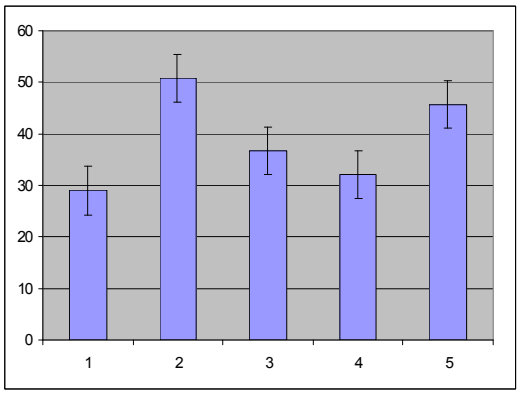


Figure 39: Mean percentage incidence of trees infected by *Armillaria* at age 12.5 years. Treatments:

1. unthinned, unpruned
2. thinned to 250 s/ha at age 7 years, pruned
3. as 2, stumps removed
4. as 1
5. thinned to 500 s/ha at age 7 years, pruned

Figure 40: Stumps colonised by *Armillaria* after thinning in the silviculture trial.

Klomp and Hong (1985) found significantly higher mortality from Armillaria (23%) among rooted cuttings from 7-year-old trees six years after planting on a clearfelled indigenous forest site, than among 6-year-old seedlings (14%), which had better developed root systems. Despite this result, they went on to suggest that better quality juvenile cuttings taken from younger ortets might show greater resistance to infection in future plantings. Following clearfelling of their stand in 1996, a new planting stock trial was established on the same site one year later to compare two seedlot origins of each of seedlings, juvenile rooted cuttings and aged rooted cuttings. Results at age 6.5 years, prior to first thinning confirmed the prediction of Klomp and Hong (1985) by demonstrating that total incidence of infection, mortality, and degree of root collar girdling by *Armillaria* were all significantly lower among trees derived from both juvenile and aged cuttings than among those grown from seedlings (Table 3; Hood *et al*., 2006). It seems that whatever the stock type used, it

is advantageous to establish robust plants on Armillaria infested sites. This trial also remains active for further evaluation later in the rotation.

Stock type	% mortality	% total infection
Seedlings	5.9 a	25.7 a
Stool-bed cuttings	3.3 ab	17.8 b
Field cuttings	1.9 b	18.8 b

Table 3: Incidence and severity of *Armillaria* in different stock types in genetically related seedlings and cuttings at age 6.5 years (2 ha blocked trial, row plots; after Hood *et al*. 2006)

There are other silvicultural aspects that could be explored that might be helpful in the management of pine stands on Armillaria infested sites. A trial to compare different intensities of pruning might assist in developing a suitable pruning prescription. Similarly, the effect of planting at different stocking densities on such a site could resolve whether more intensive planting could be beneficial. However, no research is planned on these aspects, which are currently considered low in priority.

3.3.3 Biological control

3.3.3.1 *Trichoderma*

Research is continuing, to evaluate the effectiveness of *Trichoderma* in reducing the impact of *Armillaria* in pine plantations. In a recent collaboration between one of us (R.A. Hill) and P.F. Olsen and Company, a total of 7000 pine seedlings were planted out on *Armillaria*-infested sites in Kaingaroa and Kinleith Forests (Hill 2005; Dyck 2006). Mortality among stock treated with the product ARBOR-GUARD^{TM}, which contains a mixture of New Zealand *Trichoderma* isolates, was 11% after two years at Kinleith, compared to 14% among untreated controls ($p = 0.978$, 1-year assessment). Equivalent figures for Kaingaroa were 4% (treated) and 7% ($p = 0.010$, 1-year assessment). Nearly all deaths were due to *Armillaria*. Monitoring is continuing, and at four years the trend appears to be holding at both sites. Isolates have been collected from dead and dying trees in this trial for extraction of DNA by Sarah Dodd (Crop and Food), and additional collections will be made and identified in this way to assist in monitoring the trial. In nursery studies, a number of biological or chemical agents in various formulations have increased seed germination, height and diameter growth, and dry matter production by significant amounts. Research now in progress with *Trichoderma* involves determining the minimum effective dose rate; the best delivery system; the optimum application timing and frequency; the development of a cheap, rapid, reliable means of quantifying the agent for quality assurance; and the development of a molecular "fingerprint" for product quality control and identification of Intellectual Property (I.P.).

Research is now underway within the Lincoln CoRE to evaluate the effects of *Trichoderma* bioinoculants on the beneficial ectomycorrhizal infection of pine seedlings. In a field trial the effect of treatment with Arbor-Guard^{TM} on the abundance and diversity of ectomycorrhizas is being assessed by means of mycorrhizal root tip morphology and molecular identification. A related study is being undertaken by means of a potted trial at Lincoln University using a potting mix inoculated with a mixture of the mycorrizal species *Rhizopogon luteolus*, *R. parksii*, *Suillus luteus* and *S. granulatus*. The effect of treatment with Arbor-Guard^{TM} on colonization by specific mycorrhizal species and the resultant effect on seedling growth will be determined.

3.3.3.2 Biological stump treatment

Work currently underway is investigating the interaction between *Armillaria novae-zelandiae* and various basidiomycete decay fungi present in pine thinning stumps (Hood and Gardner, 2005). It is hoped that this will lead to the discovery of naturally occurring, potential biological control agents that could be applied to stumps as competitors of *Armillaria*, in effect shifting the ecological balance to the disadvantage of the pathogen. In one recent study, the decomposition of pine first-thinning stumps was followed for nearly four years after felling by periodically extracting random samples, washing and recording their condition and degree of decomposition. Stumps were then split, and cultures of decay fungi isolated, described and where possible identified, catalogued and lodged in a culture bank. Certain basidiomycetes were isolated regularly whereas many others were cultured only infrequently. In the current programme selected stock cultures are being tested for competitiveness against *Armillaria* isolates initially *in vitro* and later *in vivo* testing is planned. Internationally there has been some work trialing various basidiomycete fungi against *Armillaria* species, following successful work with another root disease pathogen, *Heterobasidion annosum* (Fries) Brefeld complex, for which a commercial product, Rotstop, is now available in some European countries. Rotstop is based on the wood decay basidiomycete *Phlebiosis gigantea* (Fries) Jülich, commonly found in radiata pine stumps in New Zealand (Hood *et al*. 2002a; Hood and Gardner 2005). In Europe it is used to treat stumps normally colonised by basidiospores of *H. annosum*. The northern *Armillaria* stump biological control work has shown some promise (Chapman *et al*. 2004), and seems worth pursuing further in the New Zealand *P. radiata* environment (Fig. 41).

Stump fully colonised by two compatibility groups (colonies) of *Armillaria novae-zelandiae*

Stump partly colonised by *Armillaria novae-zelandiae* (darker zone to left) and an unidentified basidiomycete decay fungus (code HH; paler zone occupying most of stump)

Figure 41: Competition for substrate in radiata pine thinning stumps between *Armillaria novae-zelandiae* and other basidiomycete decay fungi.

3.3.4 Chemical

Refer earlier research (Section 2.3.2). There is no current research work underway, but there could be value in investigating a chemical treatment in modern plantations where stumps are smaller than in cleared indigenous forests, with the possibility of a more complete distribution within the substrate.

3.3.5 Genetic selection

Ensis FBP is currently running a research programme to investigate the potential for variation in resistance to Armillaria within different genetic origins of *Pinus radiata*.

The prospect of being able to plant an "Armillaria-resistant breed" on infested sites is appealing. Even moderate resistance is likely to be economically beneficial. Preliminary results are promising (Table 4; Fig. 42), but research is still at an early stage. Initial experiments were run with seedlings, but now clones are being tested and numbers for each treatment are being increased in order to enhance meaningful statistical precision. It is also necessary to establish whether selected stock is resistant to a representative range of both the common *Armillaria* species, since it is known that different isolates of these fungi vary significantly in pathogenicity (Section 2.1.1).

Host Clone code	***Armillaria* Isolate #1**	**Host Clone code**	***Armillaria* Isolate #2**
E	20 a	E, K	50 a
F	30 a	A, C	60 a
D, H	40 ab	D, H	70 a
C, G, K	50 ab	B, F	80 a
A	60 ab	G, J	90 a
B, J	90 b		

Table 4: Variation in *Pinus radiata* genetic disease resistance (early provisional result: percentage cuttings killed, of 10 plants, by *Armillaria novae-zelandiae*)

Figure 42: *Pinus radiata* plants from different genetic sources showing varying responses to treatment with two strains of *Armillaria novae-zelandiae*.

3.3.6 Alternative species

As discussed above (Section 2.3.4) a greater understanding is needed of the role played by Douglas fir as an apparently resistant substitute for *Pinus radiata* on *Armillaria* sites. No research on this aspect is currently in progress.

3.3.7 Biosecurity

Research is underway to clarify the nature and range of all indigenous *Armillaria* species so that we have a full understanding of the diversity and distribution of the *Armillaria* populations present in New Zealand. In this way we will be in a better position to identify and deal promptly with any potential new incursions or border interceptions of exotic *Armillaria* species that could pose a potential new threat to the forest industry. It has been postulated, for instance, that *Armillaria hinnulea* could be a recent invader as a result of wind dispersal from Australia (Ridley and Ramsfield 2004). Haploid and diploid isolates cultured from collections of *A. hinnulea* and the unnamed *Armillaria* species made at documented locations in *Nothofagus* forests in both Islands are being examined using molecular methods by Tod Ramsfield (Ensis Forest Biosecurity and Protection; Blaza 2006) using species-specific primers provided by Sarah Dodd (Crop and Food). This research will confirm work already undertaken with these species. The species-specific primers are also being tested against a large collection of haploid and diploid *Armillaria* isolates held in the National Forestry Culture Collection (NZFS) in Rotorua. Some of these cultures were isolated from authentically identified fruitbodies and others were identified using cultural pairing techniques, but the identities of the remainder have still to be determined.

To ensure a stable export trade, it is important that pathogenic fungi are not transported in forest produce to other regions where it is liable to be embargoed by quarantine authorities at the border. For instance, mycelial fans of *Armillaria* have been identified beneath the bark at the base of butt logs waiting for export (I.A. Hood, personal observation). Methods of dealing with such material have been explored, and in one preliminary study using small wood blocks, methyl bromide showed effectiveness against *Armillaria* (Hood and Gardner 2000).

Knowledge gaps: There is still no effective cheap proven control for Armillaria root disease in current pine plantations, although a number of aspects are current being investigated. These include silvicultural options (the effect of thinning and pruning, and of planting with different stock types), biological control application (treatment of planting stock root systems with *Trichoderma* and of pine stumps with a basidiomycete decay fungus), and the use of genetically resistant stock. Much research is still at the investigative phase, and for some aspects significant knowledge is still being developed, but steady progress will hasten the start of technological development. There is no planned research into the influence of other hosts such as Douglas fir and eucalypt species on the incidence of Armillaria root disease.

4. CURRENT ARMILLARIA RESEARCH IN NEW ZEALAND

FRST – understanding site, environment and host factors (underway)	**Manipulation to develop downstream control?**
Ecology of stands – host competition and stumps as a pathogen food base (Ensis FBP)	Thinning to influence *Armillaria* incidence? (intensity and timing)
Ecology of stands – influence of stock type (Ensis FBP)	Selection of host planting stock type to reduce incidence?
Biodiversity of pine stumps – competition between populations of stump fungi (Ensis FBP)	Biological control treatments to deny *Armillaria* its stump food source?
Soil, root and whole-plant interactions with *Trichoderma* and *Pinus radiata* (Biodiscovery/Crop and Food/PF Olsen), including effects on ectomycorrhizas (Lincoln University)	Development of an optimized *Trichoderma* biological control treatment for planting stock
Variation in genetic resistance (Ensis FBP)	Deployment of resistant planting stock?

Table 5: Understanding site, environment and host factors in order to develop alternative control options – a strategy

The sub-sections below formally outline the research currently being undertaken on the disease in New Zealand, and include an approximate indication of the present funding levels supporting this work. In brief, research is being conducted under two FRST contracts (with Ensis FBP and with Lincoln University CORE) to resolve the dispersal and development of the pathogens and the extent to which *A. novae-zelandiae* in particular may be invading pine plantations by means of basidiospores (Ensis FBP, Crop and Food). In hand with this dispersal biology research, new potential control methods are being explored with a view to developing the more promising options into a practical integrated control strategy. These potential control aspects are summarized in Table 5. Additional work currently underway includes the refinement of a molecular method for identifying the New Zealand *Armillaria* species both for biosecurity purposes and as a research tool (Crop and Food, Ensis FBP). There is also a small project looking at the potential for remote sensing as a means of delineating risk areas for treatment (Ensis FBP).

4.1 Forest Research/Ensis (Scion)

FRST C04X0302 FOREST PROTECTION years 4-5 (2006-2008) of 5 year contract

$115, 247 per annum on Armillaria.
Supplementary funding: nil.

IO Objective / Milestone Information
Objective Sequence 2: Pest and host interactions in forest environments.
Pests cause significant losses to plantation forests in New Zealand. In addition to the pests that are present in New Zealand, other pathogens and insects in the native

range of our exotic plantation species may seriously impact the forest industry if they were to become established here. This objective will lead to improved management strategies for the pests that are present in New Zealand and will allow a better understanding of the potential impacts of exotic insects and diseases.
Objectived and Final Milestones: By 2008, forest management strategies for reducing the impact of established pests in New Zealand will be relayed to the forest industry through a pest management workshop and industry has adopted a new management strategy for at least one established pathogen. As a result, by 2012 forest managers are utilizing best practice management strategies to reduce pest impacts.
End Date: 30/06/2008
Primary End User: New Zealand Forest Industry, CRIs, Universities

*** Milestone 2.3:** Reducing the impact of root and stem pathogens
Infection of the roots and stems of *P. radiata* results in poor stand establishment and wood quality, respectively. This milestone will increase our understanding of the epidemiology of these pathogens, allowing silvicultural systems to be modified to reduce their impact and thus improve productivity.
Finish Date: 30/06/2008
Achievement Measure: Trials of modified silvicultural systems designed to reduce the impact of Armillaria root disease and *Nectria fuckeliana* have been assessed and information has been communicated to the forest industry. Forest managers have implemented modified silvicultural systems to reduce the impacts of at least one disease.

Outputs and Benefits for End Users
1.6.2 Submit a manuscript to an international scientific journal describing the results of the population genetic study of *Armillaria hinnulea*. (30/06/2008)
2.3.1 Completion of an internal report on the variation in susceptibility of different clones of *P. radiata* to *Armillaria*. (30/06/2007).
2.3.2 Submission of a manuscript on the role of basidiospores in the spread of *Armillaria* in plantation forests. (30/06/2008).

FRST C04X0203. WOOD-FIBRE GROWTH AND QUALITY: TREE TO PRODUCT

$16,000 per annum on Armillaria.
Supplementary funding: nil.

IO Objective / Milestone Information

Objective Statement
This objective aims to develop innovative technologies that integrate remote-sensing information analysis with current inventory using space-based sensors, hyperspectral airborne detectors and analysis, and potentially LIDAR, in order to provide critical, precise and accurate data of key forest parameters (e.g. forest condition and structure) for international, national and regional decision makers and stakeholders. Integration methods for ground and aerial data will be developed and the effects on forest inventory values determined. The results of this research will be used by forest owners for (i) operational inventory for the detection and subsequent mitigation of the effects of diseases and nutrient deficiencies, (ii) tactical and strategic planning, (iii) forest certification. The Government will be able to use these technologies to provide estimates for national planning and international reporting (e.g. Montreal Process, Kyoto Protocol, and The Convention on Biological Diversity). The objective

contributes to Programme Outcomes by providing new technologies for multisource inventory that delivers decision-making information about New Zealand's forest resource. This objective interrelates with the other objectives in the programme by providing efficient and integrated inventory capability in New Zealand's exotic and indigenous forests.

*** Milestone Sequence: 6**
Milestone: Evaluate methods for improving detecting of stress agents, and expand the targeted stressors (e.g. *Armillaria*, Mg, N). The stressors targeted will be determined in conjunction with industry and with the practicality of capturing or using existing data.

4.2 Lincoln University/Centre of Research Excellence (including Biodiscovery, Crop and Food Research, Scion-Ensis FBP)

FRST LINX0304 BIO-PROTECTION OF NEW ZEALAND'S PRODUCTIVE ECOSYSTEMS years 4-5 (2006-2008) of 5 year contract

Approximately $50,000 per annum on Armillaria

Supplementary funding:
FBRC ca. $10,000 per annum (Biodiscovery).
PF Olsen & Co. Ltd: ca. $25,000 per annum "in kind" (Biodiscovery).

Objective 3: Forestry.
Milestone 3 Validate superior performance of nursery enhanced stock in forest plantation sites in New Zealand.

Ongoing monitoring/assessment of tree health (in forest plantation trial sites) and disease (such as *Armillaria, Dothistroma, Cyclaneusma*) incidence, in relation to nursery-applied bio-protection treatments (Kaingaroa & Kinleith forests; new sites to be planted 2005 – 2008; by 30 June 2007, 2008). Biodiscovery.

Validate cause of tree mortality (e.g., *Armillaria*) in forestry plantation trials (Kaingaroa and Kinleith forests; by 30 June 2008). Biodiscovery.

Assess tree vigour/productivity (e.g. height, stem diameter, volume of wood/ha) in collaboration with PF Olsen & Co Ltd. (by 30 June 2008). Biodiscovery.

Molecular techniques that will reveal the level of genetic diversity in isolates of *A. novae-zelandiae* optimised (by 30 June 2007). Crop and Food/Ensis FBP.

Rhizomorph samples collected from pine forest site, DNA extracted and cultures established from the rhizomorphs (by 30 June 2007). Crop and Food/Ensis FBP.

Standardised molecular techniques used to evaluate the genetic diversity of *A. novae-zelandiae* rhizomorph isolates collected (by 30 June 2007). Crop and Food/Ensis FBP.

Data collated and analysed and manuscripts prepared (by 30 June 2008). Crop and Food/Ensis FBP.

Effect of *Trichoderma* bioinoculants on ectomycorrhizal colonization of *Pinus radiata* seedlings determined (by 30 June 2007). Lincoln University.

Assays developed to investigate the population dynamics of *Trichoderma* strains on *Pinus radiata* seedlings *in situ* (by 30 June 2007). Lincoln University.

Conference poster presented on effect of *Trichoderma* inoculants on ectomycorrhizal colonization (by 30 June 2007). Lincoln University.

Research seminar presented on the establishment of *Pinus radiata* seedlings in plantation forest using beneficial micro-organisms (PhD student; by 30 June 2007). Lincoln University.

Article or presentation to end users completed (by 30 June 2007). Lincoln University.

Survival and localization of *Trichoderma* bioinoculants on nursery seedlings determined (by 30 June 2008). Lincoln University.

Journal publication on beneficial microbes in forest nursery systems submitted (by 30 June 2008). Lincoln University.

Conference presentation on *Trichoderma* bioinoculant colonization and survival in forest systems presented (by 30 June 2008). Lincoln University.

5. CONCLUSION

5.1 Lessons from kiwifruit research

It is difficult to make comparisons between forestry and kiwifruit orcharding, given their substantial differences in land history, management practices, scale, and economics. However, the basic principles of *Armillaria* biology remain the same. In kiwifruit orchards, vines are infected from wood borne inoculum in the soil, frequently through contact with roots of adjacent shelterbelts but sometimes directly from debris from previous tree crops. In pine plantations, trees are also infected from Armillaria present in woody debris, either through roots from previous native forest or more commonly today, from stumps and root systems of previous pine crops. The large areas involved in plantation forestry together with the quantities of wood debris in the soil rule out the hygiene practices that have been employed at various times in kiwifruit orcharding. Stump removal is still the only proven control in forestry, but total root removal is not a feasible option. Nor are the placement of physical PVC barriers to prevent spread, nor water-blasting and sluicing around trees, combined with surgery to remove lesions, viable approaches in forestry. Research is being undertaken to adapt the kiwifruit biological control technology to control Armillaria in plantation forestry. Although recent trial work in kiwifruit orchards has not been encouraging, current forestry research is exploring aspects such as application rates, timing, mode, and frequency in greater depth and the early results have shown potential.

Probably the most useful lesson for forestry from the kiwifruit work is the demonstration of basidiospore infection of cut stumps. Research in kiwifruit orchards, as in pine plantations, has confirmed that basidiospores of *A. novae-zelandiae* are able to initiate new infection centres on land initially almost free of *Armillaria*. This has real relevance in second and third rotations where the stumps left after clear-felling provide a large establishment point for potential new infections. *Armillaria* may possibly also invade stands by means of thinning stumps. There is clearly no room for complacency with regard to those plantations that currently appear to carry low levels of *Armillaria*. The “prevention is better than cure” philosophy so relevant in the kiwifruit industry is also pertinent to forestry.

5.2 Armillaria in contemporary and future plantations

Armillaria was once a prominent and unmistakable disease and a serious cause of concern to the forest industry. Though now largely unappreciated, the legacy of that era continues to affect the returns from the current national annual harvest. Since then the nature of plantation forestry in New Zealand has changed, but infection by *Armillaria* remains widespread, though concealed, and indications are that it will continue to be significant in future plantations. It is clearly important to clarify the extent to which spore dispersal is facilitating the establishment of infection centres in new plantations and in succeeding rotations. This will determine the extent to which the disease is likely to impact economically on forestry in the future and allow revision of present disease cost estimates. If invasion by means of spores proves significant, it may also open up new means of management. For instance, timing thinning and harvesting operations to avoid the winter sporulation period may be a realistic option for risk sites. As noted, some research is underway to determine the patterns and extent of airborne spore dispersal and the degree to which stumps and partly buried logging slash may become colonized and hence act as new sources of infection. It is also important to understand the way *Armillaria* develops and spreads,

because as has been shown (Section 3.1.3) the way plantations are managed now can influence the extent of disease downstream.

Regardless of whether or not Armillaria continues to be a major national forestry disease in the future, there will always be stands in which, for one reason or another, a greater level of infection and visible mortality will stimulate forest managers to seek assistance in applying some form of management or control. Despite an extensive history of research, overall funding (predominantly from government sources) has been comparatively limited and somewhat uneven. A great deal is now known, but there are two glaring gaps: identifying the areas that should be treated; and providing an effective treatment procedure. Substantial research has been directed towards the first of these issues (Section 3.2), but this needs to be consolidated and adapted into a practical cost-effective protocol, possibly involving some form of remote sensing. Regarding the second aspect, stump removal has been the one approach that has been demonstrated in trials to provide an effective control. However, this operation has rarely been practiced, even in the days when the disease had such visual impact, largely because of the uncertainty of the return for such an expensive treatment. Despite this, current research suggests there may be potential alternatives that could be developed into some form of integrated management procedure on the worst sites at little or no extra cost (Section 3.3). These include silvicultural measures (e.g. the planting of physiologically and/or genetically resistant stock; possibly an Armillaria-specific thinning regime, though current research seems to indicate that this treatment encourages the disease; a reduction in pruning intensity, which still requires research), chemical (stump poisoning) and biological possibilities (e.g. the use of a *Trichoderma* strain as a bio-protectant or of suitable decay fungi as competitors with *Armillaria* for stump substrate to reduce inoculum potential). Most of these options are still at an early stage of research. It is also worth keeping in mind the possibility of whole-tree harvest on risk sites with sandy or friable soils where trees could feasibly be felled by uprooting rather than cutting prior to log making, in order to leave no residual stumps as a source of inoculum for the subsequent rotation.

Apart from several silvicultural options that still require some developmental research, such as reducing the intensity of pruning and thinning, there is little that can be done to manage an existing severely *Armillaria*-infested stand. Most options listed in the previous paragraph are designed to protect a newly planted stand rather than to give remedial treatment to the disease in a current plantation. As already stressed, this situation requires a consciously proactive approach and a sense of the long term. As with kiwifruit, preventing the disease downstream is the best, if not the only position to be adopted by the forward-looking forest manager.

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