Stock-Type Susceptibility and Delineation of Treatment Areas for a Cryptic *Pinus radiata* Root Disease

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ABSTRACT

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Planting material with superior resistance to Armillaria root disease was identified in a field trial established to investigate variation in *Armillaria* infection among different *Pinus radiata* nursery stock types. At stand age 6.4 years, total infection incidence, mortality, and degree of root collar girdling by *Armillaria* spp. were all significantly lower among trees derived from both rooted stool bed cuttings (physiological age 1 to 3 years) and rooted field cuttings (physiological age 3 to 6 years) than among those grown from seedlings. Cutting types did not differ significantly from one another. No significant differences were found between stock types in stem diameter, but trees from stool bed cuttings were significantly taller than seedling trees. Whether these differences remain detectable later in the rotation, initial results suggest that it may be advantageous to plant robust stock, of either cuttings or seedlings, on *Armillaria*-infested sites. The incidence of infection in living, green-crowned trees was unevenly distributed across the trial site, and was greater nearer to trees killed by *Armillaria* spp. than further away (significant within a radius of 10 m). By mapping visible *Armillaria*-caused mortality prior to thinning, it may be possible to delineate areas with a higher incidence of concealed chronic infection, thus defining infested sites for postharvest treatment.

Armillaria root disease, caused by species of *Armillaria*, continues to have a significant impact on plantation forestry worldwide (6,13,25). Although effective (16,17,21,23,24,34), the removal of infested stumps or root systems of the previous or current crop is rarely practiced as an operational control because the method is costly and impracticable on difficult terrain. Alternative options being explored include the potential influence of thinning and the reduction of inoculum by applying chemical or biological control agents or by controlled burning (1–4,7,9,18, 26,34,37).

Another possibility may be to plant genetically or physiologically resistant stock on infested sites. In New Zealand, Klomp and Hong (14) found a significantly lower incidence of mortality from *Armillaria novae-zelandiae* (Stevenson) Herink and *A. limonea* (Stevenson) Boesewinkel among seedlings than cuttings of *Pinus radiata* D. Don in a first-rotation stand established on an indigenous forest site. 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. A trial was therefore established to compare the relative susceptibilities of seedlings, young stool bed cuttings, and physiologically older field cuttings planted on an *Armillaria*-infested field site. Care was taken to ensure some degree of genetic relatedness between all three types of planting stock in order to minimize the confounding effect of any potential variation in inherent resistance. Cuttings have some advantages over seedlings (e.g., longer internodes, narrower branches, less taper, and a straighter butt log), and both types are readily available, being currently in wide use in the establishment of new radiata pine plantations.

To be economically beneficial, control methods such as the planting of potentially resistant stock must be applied to sites sufficiently infested by *Armillaria* spp. to justify the expense of treatment (6,25). A comprehensive management plan should therefore include a procedure for defining the more heavily diseased stands, particularly when the full extent of infection is not obvious (38), e.g., through predictive modeling using data from surveys of readily visible symptoms (11,15,27). In New Zealand, the incidence of mortality from *Armillaria* spp. is generally low in second-rotation pine stands, and loss is mainly due to reduced growth on living, green-crowned trees resulting from hidden chronic infection (13). A possible method for mapping the incidence and distribution of chronically infected trees has been suggested, which relies on an association with visible mortality before dead trees are removed during the first thinning early in the rotation (5,10). This trial provided an opportunity to check this relationship and examine the feasibility of the method.

The aims of the study were therefore twofold (i) to compare the relative susceptibilities of seedlings and cuttings to Armillaria root disease in order to identify a stock type more suitable for planting on infested sites, and (ii) to consider whether plotting the distribution of early mortality prior to first thinning might be used as a tool to map total infection quantitatively, in order to identify stands requiring treatment in the next rotation. This paper reports the results of the trial, covering the period from planting to 6.5 years, and discusses the implications in the light of these objectives.

MATERIALS AND METHODS

The trial is located on a gently rolling site on the Mamaku Plateau near Rotorua originally covered in podocarp broadleaf forest (latitude 38° 1.95′S; longitude 176° 2.00′E; altitude 570 m above sea level). Soil is derived from volcanic tephra overlying an ignimbrite base (Mamaku loamy sand) (19). Following earlier logging of the podocarp element, the remnant indigenous hardwood vegetation was clearfelled in 1969, burnt, and planted 1 year later in alternate rows of *P. radiata* seedlings and cuttings, as described by Klomp and Hong (14) who conducted their study on the same site. The pine stand was clearfelled in 1996 at 26 years

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of age, and the logging debris was left unburnt and the site uncultivated. At the time of trial establishment, residual, largely undecayed slash and an even distribution of stumps from the first pine crop extended across the site.

The trial incorporates a total of 18 blocks, each of dimensions 60 × 20 m (2.2 ha total), distributed contiguously within two rectangular areas located ca. 100 m apart, on either side of a lower-elevation portion of frost-prone ground lying between (Fig. 1). The larger area (120 × 160 m) contains 16 blocks and the smaller area (60 × 40 m) holds two blocks. The site was planted on 18 to 20 August 1997, at a density of 3.3 × 3.3 m (900 stems per ha). Each block contains six rows of 18 trees, each row of plants being arbitrarily assigned to one of six treatments (due to a shortage of plant numbers, two rows received the same treatment in one block). The treatments consist of two seed sources of each of three stock types: seedlings, rooted stool bed cuttings (physiological age at cutting and setting between 1 and 3 years), and rooted field cuttings (physiological age 3 to 6 years) (Table 1). The same seed source (93/326) was used for one treatment of each type of cutting. All plants spent 1 year in the nursery after sowing or setting prior to planting out in the trial. The design is therefore as follows: 18 blocks × 6 row plots (2 seed sources × 3 stock types) × 18 plants = 1,944 plants (Fig. 1).

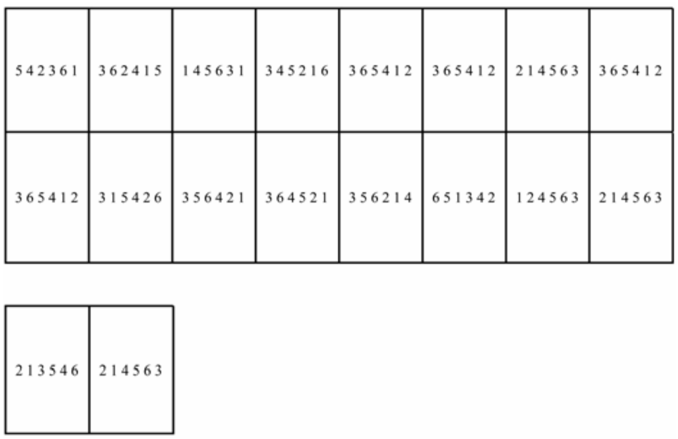

Fig. 1. Trial design, displayed diagrammatically for the 16-block and 2-block areas. Each seed lot number represents a vertically orientated row plot of 18 trees (seed lot codes: 1 and 2, seedlings; 3 and 4, stool bed cuttings; and 5 and 6, field cuttings).

All plants were inspected at 5- to 7-month intervals between planting and 2.9 years of age in order to record those killed by *Armillaria* spp., as indicated by attached rhizomorphs, mycelial fans beneath the bark, or both, accompanied by resinosis. Additional records of mortality were made at 3.5 and 4.5 years. At ca. 6.4 years of age (between November 2003 and January 2004), all trees were assessed for infection by *Armillaria* spp. A light, short-handled grubber was used to expose each root collar in order to make a record of the percent girdled by infection, as indicated by resinosis accompanied by rhizomorphs. The direction (aspect or azimuth) of the midpoint of the girdling zone was also noted. Soil was replaced immediately after completing each assessment. Tree growth was recorded over a 2-week period in February 2004 (6.5 years). All living trees were measured for diameter breast height (dbh) with a diameter tape and for height with a Forester Vertex hypsometer (or with a graduated height pole for trees less than 3 m tall). At the time of measurement, the stand had not been thinned nor the trees pruned, and there had been no aerial spraying of fungicide to control *Dothistroma pini* Hulbary, which was common on the lower foliage of many trees from 5.5 years of age. Trial access was facilitated by hand application of herbicides (grazon and glyphosate, or tordon) to control blackberry (*Rubus fruticosus* L. agg.) in April 1998, February 1999, and January 2000.

Data were examined using analyses of variance (ANOVAs) to test the effects of stock type, and seed lot origin within stock type, for the following variables: percentage of trees killed by *Armillaria* spp., percentage of trees infected (both living with green crowns and dead), percentage of root collar girdling, dbh, and height. These ANOVAs were performed on plot means using the SAS/STAT procedure GLM (version 9, SAS Institute, Cary, NC). Trees that died from causes other than infection by *Armillaria* spp. were excluded from the analyses, but were examined separately. The orientation of infection around the root collar was investigated by sorting the recorded directions into each of four quadrants and testing the observed counts with those expected assuming a random distribution (chi-square test). To assess the spatial relationship between trees killed and chronically infected by *Armillaria* spp., mean infection incidence and mean

TABLE 1. Details of seed lot origins and planting stock type

Seed lot code	Stock type	Seed collection no.[x]	Growth and form rating[y]	Seed orchard (orchard, block numbers, and year established)	Clonal series[z]	No. of clones from which collected	No. of parents involved in mix of controlled pollinated crosses
1	Seedlings	96/031	GF 27	Amberley 3A-15F Waikuku 2F-12E (1986–93)	850, 268, 875, 880	48	58
2	Seedlings	96/030	GF 30	Amberley 4B-15G Waikuku 4E-10A (1986–93)	850, 268, 875, 880	9	15
3	Stool bed cuttings	95/290	GF 30	Amberley 3C; 4C; 8E-G, I; 9F-G, I; 11F; 12G, I; 14F-G; 15E, G Waikuku 3A-B, E; 4F, 5, 6 (1986–92)	850, 268, 875, 880	9	17
4	Stool bed cuttings	93/326	GF 28	Amberley 1B, D; 2C-D; 3A, C-D; 9E; 10I; 12G; 13G; 14H Waikuku 3A (1980–89)	850, 268, 875	19	21
5	Field cuttings	93/326	GF 28	Amberley 1B, D; 2C-D; 3A, C-D; 9E; 10I; 12G; 13G; 14H Waikuku 3A (1980–89)	850, 268, 875	19	21
6	Field cuttings	91/298	GF 28	Amberley (1980–86)	850, 268, 875	14	15

[x] First number indicates year of collection.
[y] Genetics and Tree Improvement (8).
[z] First digit indicates a stand location; remainders are collection year; later series are derived as narrower selections from earlier, broader series of clones.

girdling score were calculated for trees within circles of varying radii centered on each dead tree killed either by *Armillaria* spp. or from some other cause. These values were determined from the means of averages computed separately for seedlings and stool bed and field cuttings, in order to adjust for potential variation in susceptibility between different stock types. Differences from the general trial means were analyzed using *t* tests for different radii. Contour maps of the local incidence of trees killed and infected by *Armillaria* spp. were produced from smoothing splines fitted using the SAS/GRAPH procedure G3GRID (SAS Institute).

RESULTS

Infection by *Armillaria* spp. was greater for planted seedlings than for cuttings of both types, whether expressed as percent mortality, percentage of trees infected, or percentage of root collar girdling (Tables 2 and 3). Infection was not significantly different between stool bed and field cuttings. Among seedling stock, 26% of trees were infected and nearly 6% killed by *Armillaria* spp. (Table 3). Among cuttings, 18 to 19% of trees were infected and 2 to 3% killed. Infection did not vary significantly between blocks or between seed lot origins within stock type (Table 2). Seedling trees averaged 14% root collar girdling, whereas cuttings were only 9 or 10% girdled (Table 3). Orientation of infection incidence around the root collar was not significantly different from that expected for a random distribution ($\chi^2 = 2.26$, $P = 0.52$; numbers of trees in each direction: north, 45; east, 58; south, 59; and west, 55).

The incidence of dead trees not killed by *Armillaria* was also significantly greater for seedlings (30% of those planted) than for both stool bed cuttings (15%) and field cuttings (19%), which did not differ significantly (Tables 2 and 3). Non-*Armillaria*-related mortality did differ significantly between blocks across the trial site (Table 2). Causes of death were mainly initial establishment failure, suppression by excessive weed growth (dense grass in the first 1 to 2 years, then thickets of blackberry and bracken, *Pteridium aquilinum* var. *esculentum* (Forst. f.) Kuhn). Several trees also died at 5 years of age following debarking by deer. Many plants that died in the first 2 years were attacked by the black pine bark beetle, *Hylastes ater* (Paykull).

At 6.5 years of age, there were no significant differences between stock types in stem diameter (Table 2). Trees averaged between 10.9 and 11.2 cm dbh (Table 3). Heights of trees derived from seedlings (6.2 m) were slightly shorter than those from field cuttings (6.5 m), but stool bed-derived trees were not significantly different from either (6.4 m) (Table 3). Diameter and height both differed among blocks across the site, and for field cuttings, only, between seed lot origins. Trees from field cuttings of seed lot 6 were significantly taller (6.6 m) and with greater stem diameter (11.3 cm dbh) than were those of seed lot 5 (6.4 m, 10.9 cm, respectively; $P < 0.01$).

The development of mortality from *Armillaria* spp. over time is shown for the whole trial in Figure 2. Mortality rate was greatest

TABLE 3. Means for planting stock type

Variable	Type	Mean[v]
% Trees killed by *Armillaria* spp.[w]	Seedling	5.9 a
	Stool bed cutting	3.3 ab
	Field cutting	1.9 b
% Trees infected[w,x]	Seedling	25.7 a
	Stool bed cutting	17.8 b
	Field cutting	18.8 b
% Root collar girdling[w,y]	Seedling	14.0 a
	Stool bed cutting	9.5 b
	Field cutting	9.0 b
% Trees missing or dead, not from *Armillaria* spp.	Seedling	29.6 a
	Stool bed cutting	15.1 b
	Field cutting	18.7 b
Diameter breast height (cm)[z]	Seedling	10.9 a
	Stool bed cutting	11.2 a
	Field cutting	11.0 a
height(m)[z]	Seedling	6.2 a
	Stool bed cutting	6.4 ab
	Field cutting	6.5 b

[v] For each variable, means sharing the same letter subscript are not significantly different (least significant difference test, $P \geq 0.05$).
[w] Excluding dead trees not killed by *Armillaria* spp.
[x] Including those killed by *Armillaria* spp.
[y] Including trees uninfected (0% girdling) and killed by *Armillaria* spp. (100% girdling).
[z] All living trees, only.

TABLE 2. Analyses of variance for infection and tree size

Variable	Source of variation[u]	df	Sum of squares (type 1)	Mean square	*F* value	$P > F$[v]
% Trees killed by *Armillaria* spp.[w]	Block	17	326.588	19.211	0.64	0.8534 NS
	Stock type	2	323.312	161.656	5.36	0.0065**
	Seed lot (type)	3	123 298	41.099	1.36	0.2602 NS
% Trees infected[w,x]	Block	17	3,712.525	218.384	1.43	0.1411 NS
	Stock type	2	1,167.197	583.599	3.83	0.0255*
	Seed lot (type)	3	122.278	40.760	0.27	0.8484 NS
% Root collar girdling[w,y]	Block	17	985.474	57.969	0.98	0.4834 NS
	Stock type	2	467.576	233.788	3.97	0.0225*
	Seed lot (type)	3	156.207	52.069	0.88	0.4529 NS
% Trees missing or dead, not from *Armillaria* spp.	Block	17	4,571.295	268.900	2.92	0.0005***
	Stock type	2	4,166.867	2,083.434	22.66	<0.0001***
	Seed lot (type)	3	743.062	247.687	2.69	0.0512 NS
Diameter breast height[z]	Block	17	8,895.474	523.263	2.55	0.0025**
	Stock type	2	56.263	28.131	0.14	0.8719 NS
	Seed lot (type)	3	3,222.328	1,074.109	5.24	0.0023**
Height[z]	Block	17	16.6834	0.98138	2.60	0.0021**
	Stock type	2	1.7418	0.87089	2.31	0.1055 NS
	Seed lot (type)	3	3.1756	1.05855	2.81	0.0445*

[u] Three stock types, 18 blocks, two seed lots within each stock type.
[v] NS = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; and *** = $P < 0.001$.
[w] Excluding dead trees not killed by *Armillaria* spp.
[x] Including those killed by *Armillaria* spp.
[y] Including trees uninfected (0% girdling) and killed by *Armillaria* spp. (100% girdling).
[z] All living trees, only.

in the first half of the second year, but *Armillaria* spp. continued to kill trees throughout the 6.5-year monitoring period.

The spatial distribution of infection in the larger trial area, containing 16 of the 18 blocks, is presented in Figure 3, showing the locations of healthy trees and those chronically infected and killed by *Armillaria* spp. Trees killed by *Armillaria* spp. appeared to group with those that were chronically infected, and this was supported by analyses of infection incidence and girdling score with distance from *Armillaria*-killed trees (Figs. 4 and 5). There was a trend for a higher incidence of infected trees and a greater degree of root collar girdling for trees within a short radius of trees killed by *Armillaria* spp., reducing and stabilizing to the background mean as the radius increased (statistically significant for radii less than 10 m, $\alpha = 0.05$; note that the background means in these graphs are lower than those given in Table 3 because they exclude killed trees). By contrast, there was no increase in the incidence of infected trees and of root collar girdling nearer to trees not killed by *Armillaria* spp. (Figs. 4 and 5). Contour maps of the local incidence of trees killed and infected by *Armillaria* spp. are presented in Figures 6 and 7, respectively. Areas where incidence of dead trees exceeded 3% approximate to those where infection incidence in living trees exceeded 25%.

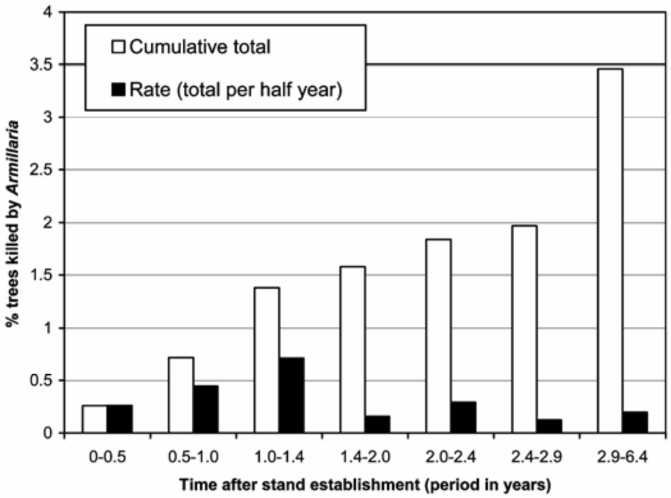

Fig. 2. Mortality due to *Armillaria* infection during the monitoring period (full trial area; rate is defined as the percentage of planted trees newly killed by *Armillaria* spp. within the specified period, after excluding all trees killed from other causes up to the end of that period, transformed to a half-year equivalent interval; cumulative percentages also exclude all non-*Armillaria* killed trees up to the end of each period).

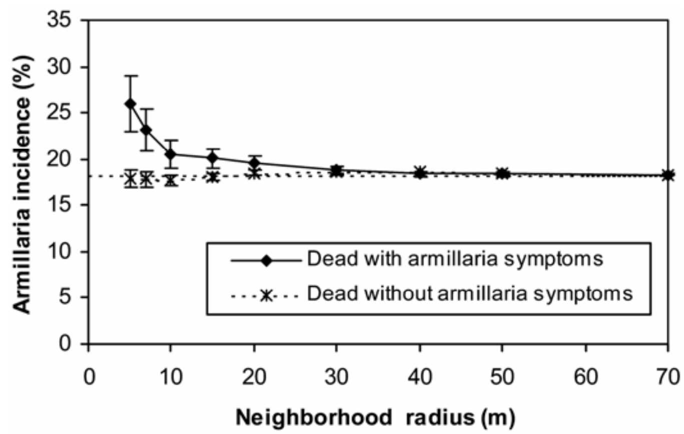

Fig. 4. Mean percentage incidence of *Armillaria*-infected living trees in the larger trial area at 6.4 years of age within a given radius of trees killed by *Armillaria* spp. (◆) or from some other cause (×). Error bars indicate standard errors. The horizontal broken line indicates the average stand incidence, independent of distance from dead trees.

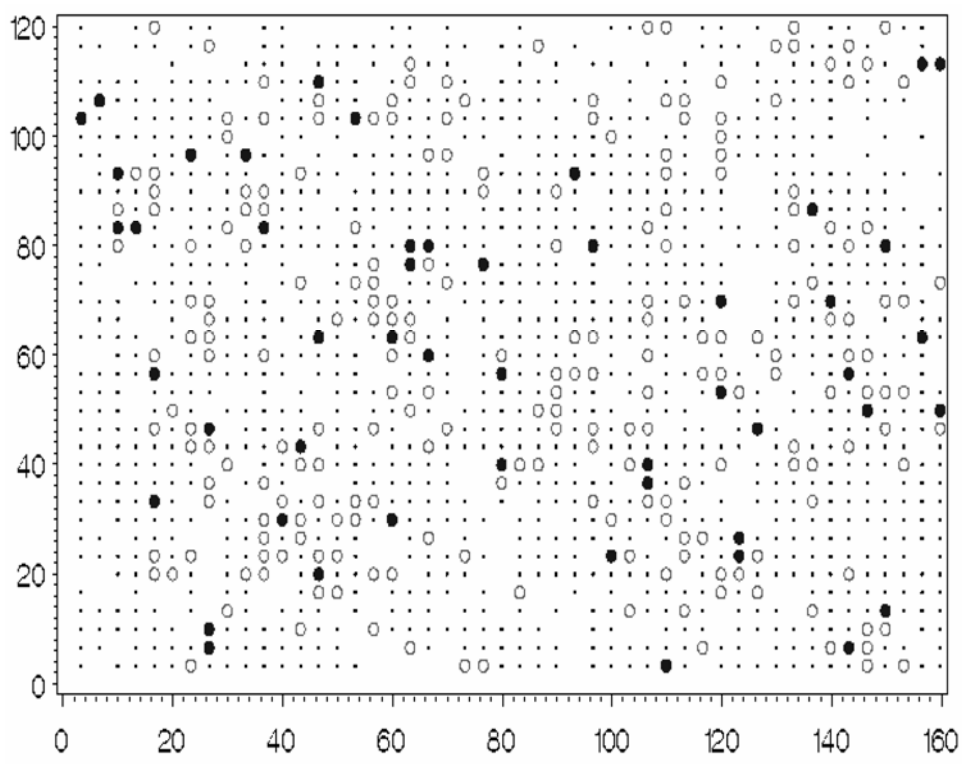

Fig. 3. Distribution of *Armillaria* infestation at 6.4 years of age in the larger trial area. Living, healthy trees are shown as dots (·), infected living trees (crowns green) as open circles (○), and all trees killed by *Armillaria* as solid circles (●). Gaps indicate trees dead or missing from causes other than *Armillaria* spp. The 16 blocks, not shown, are arranged with their long axes aligned vertically, eight blocks across the bottom and eight across the top. Scale units are in meters.

DISCUSSION

Although recommendations for the management of Armillaria root disease sometimes advise the planting of healthy, vigorous stock combined with good establishment practice (6,25), there has been comparatively little research into the relative susceptibilities of different types of planting material. Greater mortality has occasionally been reported among bare-root plants than container-grown plants and in planted stock than in natural regeneration (12,28,36). In a trial comparing bare-root *P. radiata* plants, Klomp and Hong (14) found rooted cuttings to be more susceptible than seedlings to mortality from *Armillaria* infection. Their cuttings were taken from 7-year-old trees, and with less than adequate root systems and poor vigor more typical of that era (29, 30), survival was generally lower than with seedlings even when mortality was not caused by *Armillaria* spp. Klomp and Hong (14) suggested that the rooted cuttings being produced from younger ortets for newer plantations might be more resistant to *Armillaria* spp. than those taken from older stock.

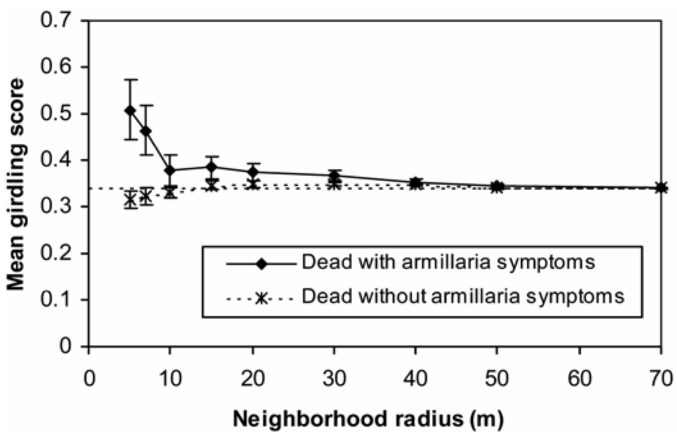

Fig. 5. Mean percentage girdling severity score of *Armillaria*-infected living trees in the larger trial area infected by *Armillaria* spp. at 6.4 years of age within a given radius of trees killed by *Armillaria* spp. (◆) or from some other cause (×). Error bars indicate standard errors. The horizontal broken line indicates the average stand score, independent of distance from dead trees. Score categories: 0 = 0% girdled, 1 = 1 to 25%, 2 = 26 to 50%, 3 = 51 to 99%, and 4 = 100%.

This possibility was confirmed in the current study, which compared seedlings and two types of cutting material physiologically 5 years old and younger. Infection was less for both types of cutting than with seedlings, and non-*Armillaria*-related mortality followed the same trend, which may indicate that it was the seedlings that were now less robust. Although measurements were not taken, root collars of cuttings are likely to have been around 9 to 12 mm diameter when planted (cuttings do not leave the nursery with a diameter less than 8 to 9 mm), whereas those of seedlings would have been closer to 4 to 6 mm, and root systems of bare-root juvenile cuttings are larger and stiffer than those of seedlings (M. Menzies, *personal communication*). A greater predisposition to infection by less vigorous plants is the most likely explanation, even if the reason for this is not immediately apparent (35). The difference cannot be attributed to variation in planting technique, since cuttings and seedlings were planted arbitrarily by the same personnel. The results of this trial, together with those of Klomp and Hong (14), therefore appear to endorse the planting of vigorous, well-rooted nursery stock, whether of cuttings or seedlings, on sites infested by *Armillaria* spp. This should be included as one component of a potential integrated disease management procedure, along with other elements such as conceivably a biological control technique or possibly the planting of genetic lines selected for inherent resistance to *Armillaria* spp. In this study, pains were taken to minimize any potential genetic variation to ensure that results reflected a genuine effect for stock type. Even small reductions in infection levels by these means may lead to useful gains in stand growth (13), but it will be necessary to determine the longer-term effect of stock type on disease impact. Size variation between seedlings and cuttings was less apparent at stand age 6.5 years, and a later survey of the trial will indicate whether the early differences in vulnerability to *Armillaria* spp. continue to remain detectable.

Trees infected by *Armillaria* spp. in this study appeared to form a clustered distribution pattern (Figs. 6 and 7) typical of most root diseases in which infection incidence and severity are influenced by the uneven disposition of inoculum from the previous crop (26,31). A similar pattern was observed in an equivalent-aged, unthinned, second-rotation stand established operationally from seedlings in Kaingaroa Forest 75 km to the southeast on a site of comparable soil type, but not covered in indigenous forest prior to the first pine crop (10). A relationship was demonstrated at Kaingaroa between *Armillaria*-caused mortality and chronic in-

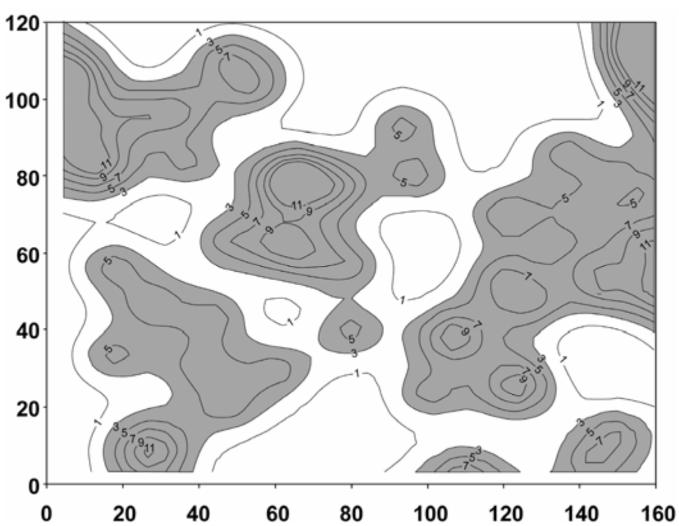

Fig. 6. Contour plot of larger trial area showing percentages of all trees killed by *Armillaria* spp. by 6.4 years of age (shaded area with >3% of trees killed). Calculations exclude non-*Armillaria* related mortality. Scale units are in meters.

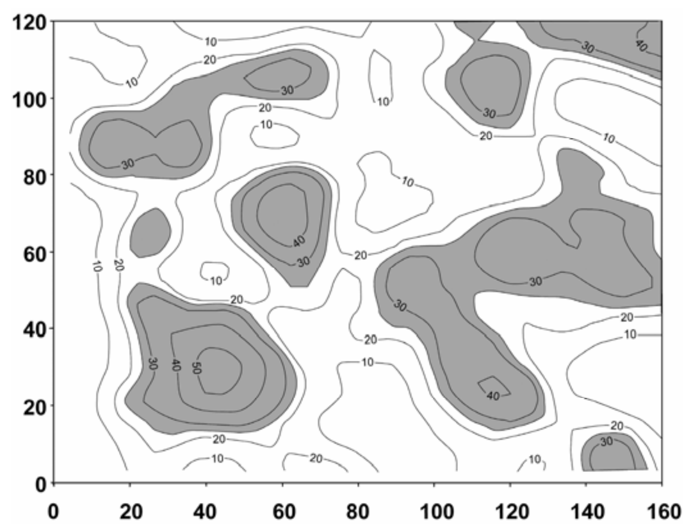

Fig. 7. Contour plot of larger trial area showing percentages of infected living trees at 6.4 years of age (shaded area with >25% of trees infected). Calculations exclude all dead trees, whether or not due to *Armillaria* spp. Scale units are in meters.

fection, significant for radial distances up to 50 m. This suggested that a survey of the incidence and distribution of visible mortality before thinning may be used to map stands with heavier chronic infestation, thus delineating zones for treatment in the subsequent rotation (5,10).

Although there was a similar trend at Mamaku, the association was significant only at the local scale (for radii less than 10 m), reflecting a general mosaic distribution of infection across the whole trial area, without larger zones free of infestation as occurred at Kaingaroa. Both trial areas are possibly too small to reveal the complete extent of larger-scale variation, and in order to verify the feasibility of the method, it is therefore necessary to sample a number of additional stands covering a wide range of infection intensities, soil types, and site histories (22). It is noteworthy that the proportions of chronic infection and mortality from *Armillaria* spp. were comparable at both Mamaku and Kaingaroa. In both stands, the zones with higher chronic infection appear too small and irregular to be of practical use as a basis for operational control. On the other hand, it would be realistic to treat in entirety a larger management unit, such as a forest compartment or subcompartment, when the proportion of the severely infested areas within the unit is greater than a specified threshold. This would also reduce the risk of neglecting smaller zones of chronic infection not captured when mapping *Armillaria*-caused mortality.

The suggested procedure of surveying young stands for mortality prior to thinning assumes that the zones of infection mapped in this way are unlikely to alter significantly during the course of the rotation in central North Island *P. radiata* plantations. In these stands, infection occurs mainly at the root collar, and there is no evidence for the expansion of disease foci through secondary root contact between adjacent trees (20,32,33). Although the incidence of chronic infection may intensify locally in response to thinning, due to the creation of potential new inoculum substrate in the form of thinning stumps (9), it appears that the short rotation period does not give opportunity for significant spatial expansion. The method also assumes that the majority of mapped dead trees have been killed by *Armillaria* spp. In this study, most of the non-*Armillaria*-related mortality (nearly 80% of such deaths) occurred in the first 2.5 years when plants were still small. Because of this, and their eventual breakdown and loss of foliage, they would be excluded during a prescribed operational survey for *Armillaria*-caused mortality closer to the time normal for a first thinning, which would detect mainly *Armillaria*-killed trees (5). Nevertheless, sampling to verify the cause of death will be an essential element of the procedure.

In conclusion, the results of this work support the use of healthy, vigorously growing, well-rooted plants for establishing new plantations on disease-prone sites. In the second-rotation stand of *P. radiata* investigated in this study, for instance, healthy rooted cutting stock was notably less infected than seedling trees after 6 years. The study also lends support to the principle that areas with a higher incidence of infection may be delineated for treatment in the subsequent rotation by mapping the distribution of trees with visible crown symptoms prior to first thinning. However, additional testing is needed to validate the method at other infection intensities, on various soil types, and with different site histories.

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