ARMILLARIA POPULATIONS IN A *PINUS RADIATA* PLANTATION ON A FORMER INDIGENOUS RAINFOREST SITE

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ABSTRACT

Incidence of Armillaria root disease and populations of the causal fungi *Armillaria novae-zelandiae* (Stevenson) Herink and *A. limonea* (Stevenson) Boesewinkel were monitored in four plots (36 × 28–36 m) in a *Pinus radiata* D. Don plantation on a site converted from an indigenous podocarp-broadleaf forest in the Bay of Plenty district, New Zealand. *Armillaria*-caused mortality in different plots varied between 22% and 35% of all trees 5–6 years after planting, while total infection ranged from 54% to 64%. Among the final-crop trees only, up to 4% were killed by *Armillaria* spp. and between 46% and 51% were chronically infected. In one plot 67% of pine stumps were colonised by *Armillaria* spp. 15 months after a non-commercial thinning, providing potential supplementary inoculum for further infection among remaining trees. *Armillaria* isolates from the four plots belonged to 63 vegetative compatibility groups, of which 27 *A. novae-zelandiae* and 15 *A. limonea* groups were first identified prior to clearing and burning of the indigenous cover, and 21 were found post-burn only. Most pre-burn groups were redetermined in approximately the same positions after burning, but four were collected from new locations within the same plots. Post-burn groups were all *A. novae-zelandiae*, and some appear to represent new colonies introduced by means of basidiospores after burning. Potted seedling experiments were used to confirm the pathogenicity to *P. radiata* of many of the *Armillaria* vegetative compatibility groups.

Keywords: Armillaria root disease; podocarp-broadleaf forest; rainforest; clones; genotypes; vegetative compatibility; pathogenicity; basidiospores; rhizomorphs; *Armillaria novae-zelandiae, Armillaria limonea, Pinus radiata.*

INTRODUCTION

Armillaria root disease is a widespread problem in plantations of *Pinus radiata* in New Zealand (Hood 1989). Although well researched, some aspects of the life history of the pathogens are still incompletely understood. A trial was set up to monitor changes in

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Armillaria populations during conversion from indigenous forest to pine plantation. Vegetative (somatic) compatibility groups of two *Armillaria* species (*A. novae-zelandiae* and *A. limonea*) were previously found to be densely distributed in four plots in a selectively logged podocarp-broadleaf rainforest due to be replaced with pine (Hood & Sandberg 1987). After clearfelling and burning, the incidence of isolation of *Armillaria* spp. decreased significantly, suggesting that heat from the fire had killed a proportion of the soil rhizomorphs in each plot (Hood & Sandberg 1989).

This paper completes a set of three documenting the trial; it describes the subsequent increase in incidence of *Armillaria* populations within the plots and the resultant infection and mortality in the young pine forest. It also reports the results of two seedling inoculation experiments designed to evaluate the relative pathogenicities to *P. radiata* of different *Armillaria* compatibility groups present in the four plots.

METHOD

Field Trials

The four trial plots were located up to 2 km apart in hill country in the Raungaehe Range east of Te Teko in the Bay of Plenty district (Tuararangaia Block, Tasman Forestry Ltd). Plots were 36 m long by 28–36 m wide. The indigenous forest cover was clearfelled and slash was burned between 2 and 13 months later in February 1985 (Plot 2) and February 1986 (Plots 1, 3, 4). *Pinus radiata* was planted within 9 months of burning as part of routine forest operations (Hood & Sandberg 1989). Initial stocking densities ranged between 1100 and 1500 stems/ha in different plots. At age 4–5 years selected trees were low pruned to 2.5–2.8 m height (densities of pruned trees: approx. 300 stems/ha in Plots 1, 3, 4; 450 stems/ha in Plot 2), and unpruned trees were felled in Plot 2 only. Stand mean crop height and dbh at age 5.5–6 years were 8.5–8.8 m and 14.4–15.6 cm, respectively (unpubl. data, Tasman Forestry Limited). Plots 3 and 4 were subject to light cattle grazing at age 3 years without any visible effect on trees or soil quality, and trees in all plots exhibited some infection by the needle fungus *Dothistroma pini* Hulbary at levels typical in *P. radiata* stands in the central North Island.

Mortality due to *Armillaria* infection was monitored several times per year throughout the course of the trial. Dead pines were uprooted and the butt portion was taken to the laboratory for attempted isolation of *Armillaria* spp. At the end of the study (December 1991: tree age 5–5.5 years in Plots 1, 3, 4; 6 years in Plot 2) all residual pine trees were examined for chronic *Armillaria* infection (indicated by resinosis and accompanying rhizomorphs in the root collar region), and the degree of girdling was recorded. Colonisation of thinning stumps in Plot 2 was also noted. Rhizomorph collections from infected trees were sealed in plastic bags and stored at 4°C.

Isolations were attempted from rhizomorphs within 14 days of collection, using methods reported previously (Hood & Sandberg 1987, 1989). Rhizomorphs were surface sterilised for 4 minutes in 10% hydrogen peroxide after a light rinse in tapwater. They were then dipped in sterile distilled water, aseptically cut into short segments, and plated out on 3% malt agar supplemented with 40 ppm ortho-phenylphenol (sodium salt) and 100 ppm streptomycin sulphate. Isolations were reattempted if *Armillaria* was not successfully isolated at the first

try. Isolations from butt samples were made by aseptically placing small pieces of colonised wood on to the same medium. Cultures were maintained on 3% malt agar.

One culture from each field collection was identified to species level as described previously (Hood & Sandberg 1987) using two independent methods: (i) colony morphology on 3% malt agar after 21 days under a 24-hour photoperiod (Benjamin 1983); (ii) compatibility with single-spore tester isolates (Korhonen 1978) of the three known North Island *Armillaria* species—*A. novae-zelandiae*, *A. limonea*, *Armillaria* sp. ex *Nothofagus fusca* (Hook. f.) Oerst. from Whirinaki Forest Park. One only of either method was used for cultures from chronically infected trees at the end of the trial. Cultures were also sorted into vegetative compatibility groups by testing for compatibility with representative cultures (standards) previously isolated from each plot (Hood & Sandberg 1987). Pairings were made on 3% malt agar and evidence of compatibility or incompatibility was recorded by noting the presence or absence of a thin brown antagonism zone. Two identical standard culture banks were separately maintained in order to confirm the stability of standards during the trial period. Standards of the same group from each bank were periodically paired together to test their continued mutual compatibility. Isolates were lodged in the culture banks between 4 months and 3 years after being collected in the field.

Maps showing the distributions of the *Armillaria* compatibility groups were prepared as previously (Hood & Sandberg 1987, 1989), and similar plot maps were constructed of the distribution of infection in *P. radiata*. Statistical comparisons were made of the changes in incidence of compatibility groups before and after clearing and burning of the indigenous forest cover (Fisher's Exact Test).

Pot Trials

Two pathogenicity experiments were carried out by exposing *P. radiata* seedlings to isolates of different compatibility groups of *Armillaria*. Inoculum was prepared by culturing the isolates on freshly collected, bark-encased stem segments of *Beilschmiedia tawa* (A. Cunn.) Kirk 11–14 cm long by 2.5–3 cm in diameter. Segments were buried vertically with ends just protruding from moist sand in 1-*l* jars (3–4 segments/jar). Jars and contents were capped with screw-on metal lids, each pierced by a small hole plugged with cotton wool, and autoclaved for 30 minutes at 103 kPa. The contents of 3% malt agar plate cultures of the *Armillaria* isolates were introduced aseptically to the exposed segment ends, one plate culture to two jars (thus, one isolate per segment). Lids were then replaced, and the jars were sealed in transparent film permeable to air but not water vapour. Segments were assigned randomly to *Armillaria* isolates to ensure that amounts of inoculum were equivalent for each compatibility group. To check this, segment dry weights were estimated by weighing fresh and deducting assumed moisture content, and these were compared by analysis of variance. Moisture content was determined by drying and reweighing one sample segment per *B. tawa* stem, and applying the moisture factor to other inoculum segments cut from the same stem. Stem segment cultures were incubated for 4–4.5 months before being removed from jars. Some segments were discarded from certain jars in which cultures had failed to establish.

Pinus radiata seedlings 20–40 cm tall of one seedlot (per experiment) were potted with inoculum (one *B. tawa* segment and one seedling per 5-*l* pot) in nursery potting mix during September or October (spring). Root systems were trimmed, and segments were buried

vertically or obliquely at a distance of several centimetres from each seeding. Between three and 10 seedlings were treated with each compatibility group, and 20 seedlings were potted without *B. tawa* segments as controls in each experiment. Inoculated and control seedlings were mixed randomly and placed in the open. Seedlings were tended and monitored for mortality over periods of 1 or 2.5 years (Experiments 1 and 2, respectively). Root collars of dead seedlings were examined for infection (indicated by resinosis accompanied by mycelial fans and rhizomorphs). *Armillaria* was reisolated and compatibility groupings were confirmed by pairing with the respective standards. The numbers of seedlings killed by each compatibility group were compared statistically using logistic regression.

RESULTS

Field Trials

Deaths from Armillaria root disease were first observed in the field trial approximately 1 year after planting, and mortality continued throughout the study period. Mortality levels ranged between 22% and 35% in different plots after 5–6 years, while total numbers of trees with root-collar infection (comprising those with green crowns as well as dead trees) varied between 54% and 64% of the original stocking (Table 1). Among pruned (potential final-crop) trees, levels of mortality ranged up to 4% and chronic root-collar infection varied between 46% and 51% in different plots. Infected trees tended to be clustered, and there were pronounced mortality gaps at the end of the trial (Fig. 1–4). In Plot 2, 18 out of 27 pine stumps (67%) were colonised by *Armillaria* spp. 15 months after thinning. Although 15 of these stumps were derived from trees free of root-collar infection, six (40%) had become colonised by *Armillaria* at the conclusion of the trial (Table 1).

TABLE 1–Infection and health status of planted *P. radiata* trees at conclusion of field trial*

Crown condition	Proportion of root collar girdled by *Armillaria* infection†	Plot 1 trees		Plot 2 trees		Plot 3 trees		Plot 4 trees	
		No.	%	No.‡	%	No.	%	No.	%
Healthy§	0.0	68	35	39(15)	34	67	35	51	34
	<0.25	18	9	14 (6)	12	10	5	13	9
	0.25–0.5	12	6	7 (3)	6	11	6	10	7
	>0.5	49	25	13 (3)	11	24	12	19	13
Dead	1.0	43	22	40	35	60	31	52	34
	0.0¶	5	3	2	2	21	11	6	4
Total trees		195	100	115	100	193	100	151	101
Total infected		122	62	74	64	105	54	94	63

* Periods from planting: 5–5.5 years (Plots 1, 3, 4); 6 years (Plot 2)

† Indicated by resinosis accompanied by rhizomorphs

‡ Values include 27 stumps (numbers in brackets) from trees thinned at age 5 years (6 of the 15 stumps without root-collar resinosis were colonised saprophytically by *Armillaria*)

§ Excepting a low incidence of *Dothistroma pini* infection in some trees

¶ Early establishment failure

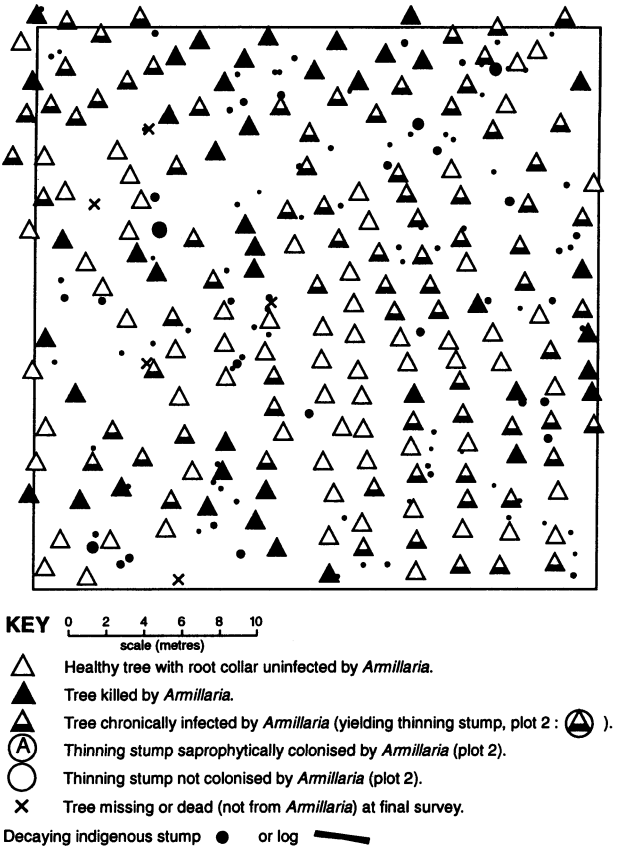

FIG. 1–Distribution of Armillaria root disease in *Pinus radiata* planted on site cleared of indigenous forest, Plot 1.

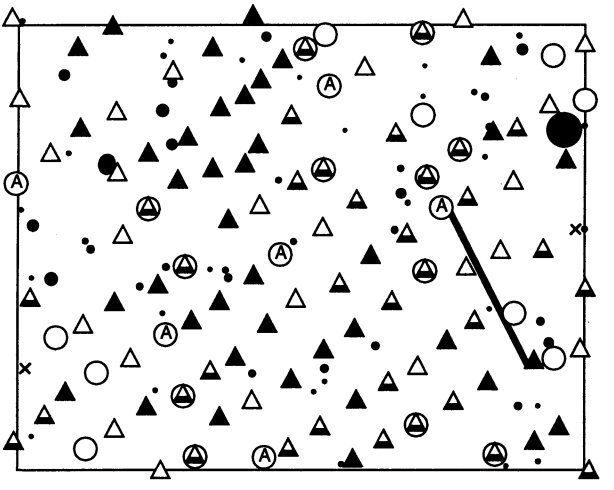

FIG. 2–Distribution of Armillaria root disease in *Pinus radiata* planted on site cleared of indigenous forest, Plot 2 (for Key, *see* Fig. 1).

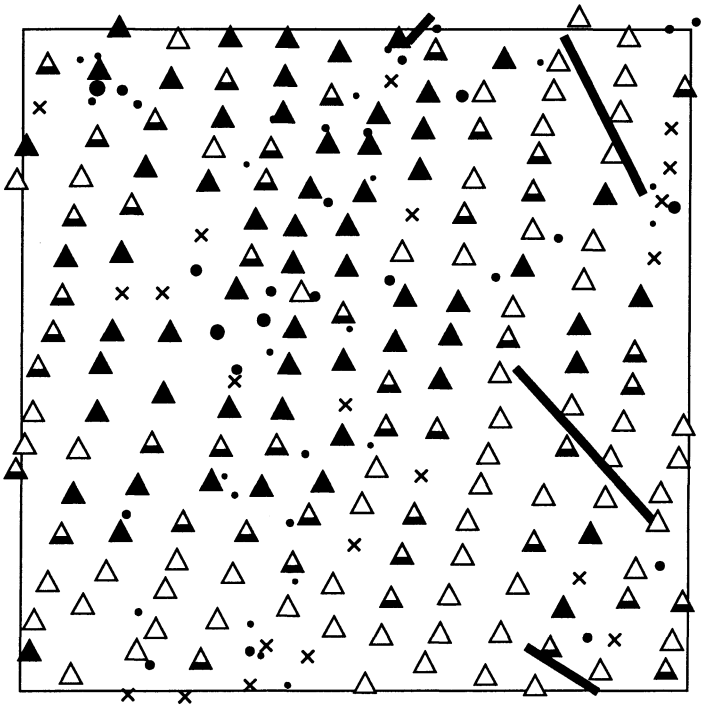

FIG. 3–Distribution of Armillaria root disease in *Pinus radiata* planted on site cleared of indigenous forest, Plot 3 (for Key, *see* Fig. 1).

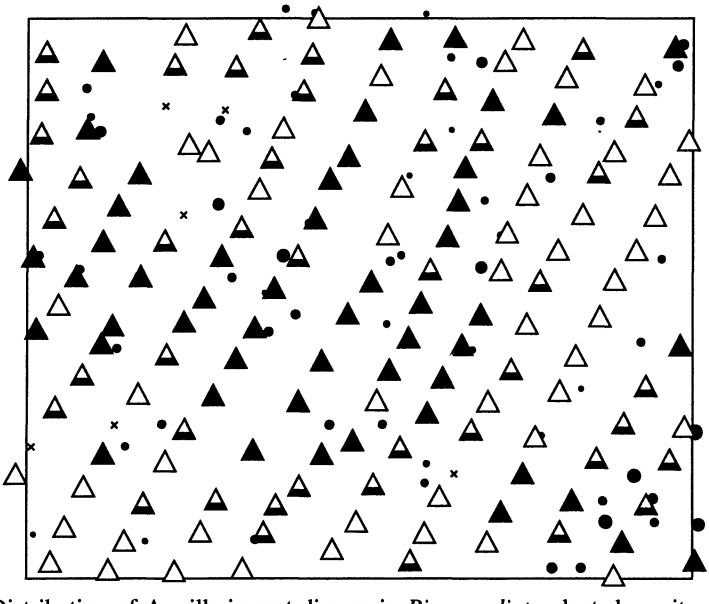

FIG. 4–Distribution of Armillaria root disease in *Pinus radiata* planted on site cleared of indigenous forest, Plot 3 (for Key, *see* Fig. 1).

The distributions of *Armillaria* vegetative compatibility groups identified after burning are shown in Fig. 5–8; those previously reported from post-burn fruitbody and soil rhizomorph isolates (Hood & Sandberg 1989) are included for completeness. Reference to distributions under the original indigenous cover (cf. Fig. 1–4 of Hood & Sandberg 1987) shows that many pre-burn compatibility groups were again detected after burning, the majority approximating to their pre-burn positions. However, four groups were found in different locations in the same plots (29 in Plot 1, 30 in Plot 2, 14 and 35 in Plot 3). Numbers of collections of the different compatibility groups determined before and after burning are given in Fig. 9 and compared in Table 2. There were no significant differences ($p>0.05$) in proportions of groups before and after burning in two of the plots (2, 4) when only the original, pre-burn, compatibility groups were considered in the analyses (Table 2). However, when all groups (including those found post-burn only) were included, patterns differed significantly between surveys in both of these plots (Table 2, Fig. 9). Newly detected post-

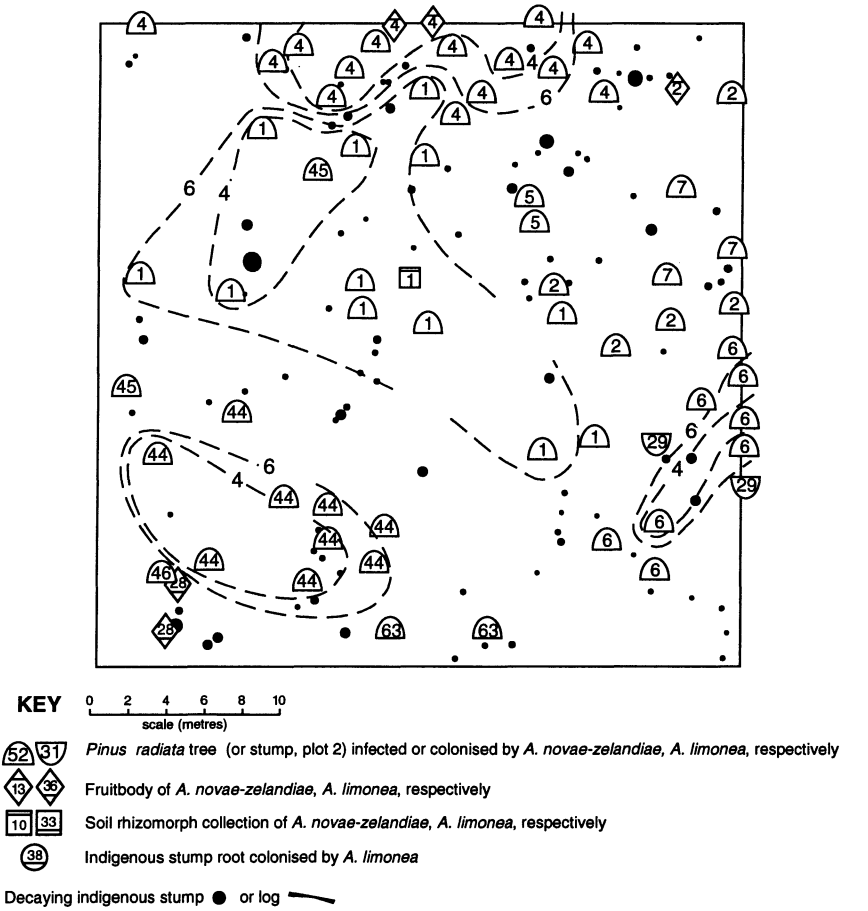

FIG. 5–Post-burn distribution of *Armillaria* vegetative compatibility groups, Plot 1.

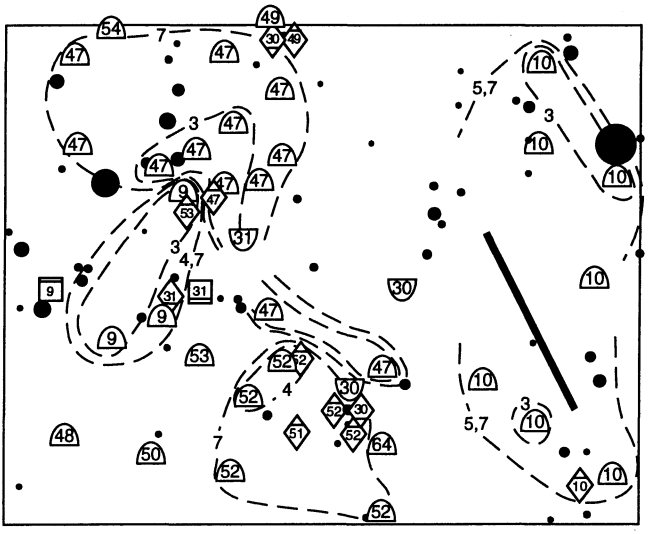

FIG. 6–Post-burn distribution of *Armillaria* vegetative compatibility groups, Plot 2 (for Key, *see* Fig. 5).

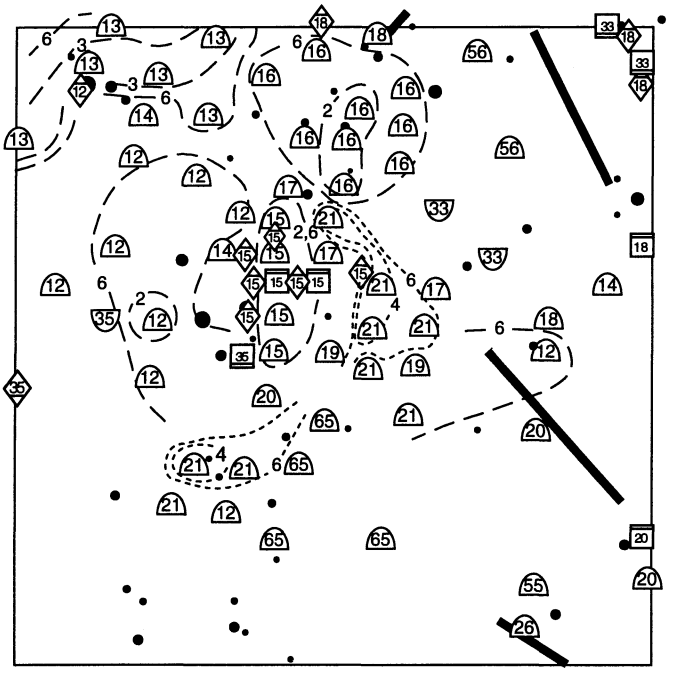

FIG. 7–Post-burn distribution of *Armillaria* vegetative compatibility groups, Plot 3 (for Key, *see* Fig. 5).

burn groups (identified in the text by ¤) all belonged to *A. novae-zelandiae*. Most were represented by single collections or occurred in compact groups occupying areas not exceeding 14 m across (Fig. 5–8), but collections of group 47¤ (Plot 2) spanned 25 m (Fig. 6) and the two collections of group 45¤ (Plot 1) were made 16 m apart (Fig. 5). Pairings

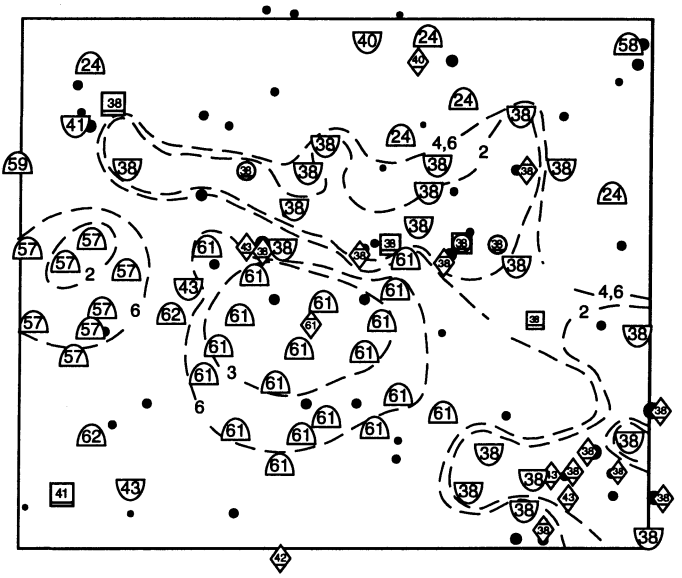

FIG. 8–Post-burn distribution of *Armillaria* vegetative compatibility groups, Plot 4 (for Key, *see* Fig. 5).

TABLE 2–Significance of differences between proportions of vegetative compatibility groups collected before and after burning†

Inclusion of post-burn only groups	Plot			
	1	2	3	4
Not included	0.01*	1.00 NS	0.009**	0.80 NS
Included	0.01*	0.02*	0.05**	0.00***

NS p>0.05
* p<0.05
** p<0.01
*** p<0.001
† Fisher's Exact Test (chi squared test in Plot 3 where scale of data prohibits an exact determination)

between the same vegetative compatibility group standards were all compatible throughout the duration of the trial. These included 28 pairs of standards maintained in separate lines for more than 6 years.

Numbers of planted pine trees killed by different vegetative compatibility groups of *Armillaria* species in each of the four plots are listed in Table 3. Highest field mortalities were generated by groups 1, 4, 44¤ (Plot 1); 10, 47¤ (Plot 2); 12, 13, 16, 21 (Plot 3); 38, 57¤, 61¤ (Plot 4). These groups also showed the greatest spatial distributions (Fig. 5–8). There was a noticeable increase in the ground area occupied by trees killed by each of these groups during the trial (Fig. 5–8), although for some groups extensions ceased 2–3 years before the final survey (groups 9, 10, Fig. 6; 38, Fig. 8). *Armillaria* fruited in season on indigenous stumps and logs, and on the ground after clearfelling but incidence then declined and no fruitbodies were collected after the fourth winter following burning.

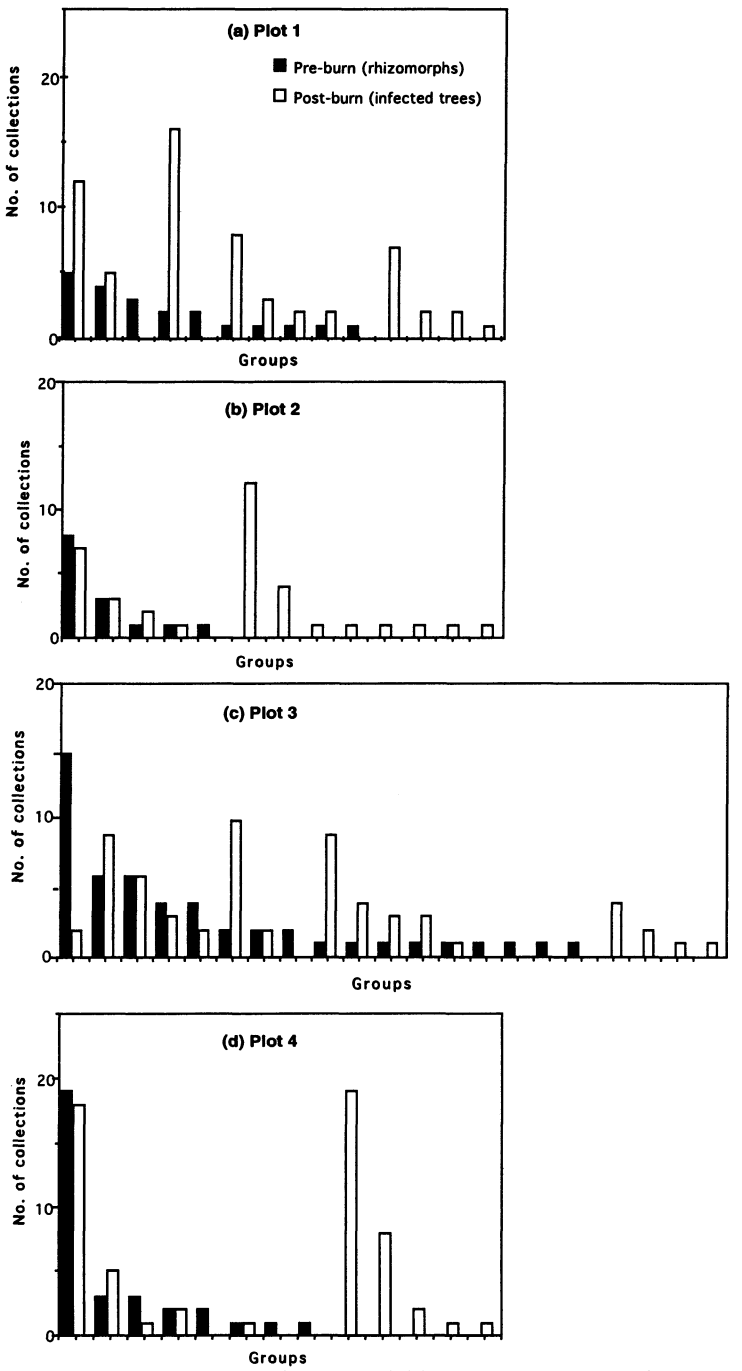

FIG. 9–Incidence of *Armillaria* vegetative compatibility groups before and after clearfelling and burning of the indigenous forest cover (ranked in order of decreasing pre-burn incidence; values for each group in pairs). Post-burn data include living as well as dead trees.

TABLE 3–Numbers of *P. radiata* trees killed by vegetative compatibility groups of *Armillaria** in the field trial

Plot	*A. novae-zelandiae*													*A. limonea*			
1 Group†	4	1	44	6	2	45	46	63						29			
No. trees	10	8	6	4	3	2	1	1						1			
2 Group	47	10	52	9	48	49	50	53	54	64				30	31		
No. trees	12	6	4	3	1	1	1	1	1	1				2	1		
3 Group	16	12	13	21	15	17	18	19	65	14	20	55	56	33	35		
No. trees	9	7	6	6	4	3	2	2	2	1	1	1	1	1	1		
4 Group	61	57	24	62	58	59								38	40	41	43
No. trees	16	7	3	2	1	1								13	1	1	1

* Those isolated and identified

† Group numbers ≥44 indicate genotypes detected post-burn, only

Pot Trials

In the pathogenicity experiments most mortality occurred during the first growth season. Altogether 85% and 65% of all dead seedlings in Experiments 1 and 2 respectively had died within 9 months (Tables 4 and 5). All 41 control plants remained healthy. Significant differences in mortality levels were found between seedlings inoculated with different compatibility groups. For most groups there were no differences between replicates or between experiments ($p > 0.05$; Fisher's Exact Test), but group 48¤ did show a difference between experiments ($p < 0.01$), and replicates of group 18 differed significantly in Experiment 1 ($p < 0.05$). There was a significant difference between *Armillaria* species ($p<0.01$) (Table 4), only three groups of *A. limonea* ranking high in pathogenicity level when compared with *A. novae-zelandiae* (Table 5). There were no significant differences between the estimated dry weights of stem segments assigned to different compatibility groups ($p > 0.05$; mean segment dry weight and standard deviation: 42 ± 6 g, Experiment 1; 44 ± 4 g, Experiment 2).

TABLE 4–Analysis of deviance for proportions of seedlings killed in inoculation experiments

Source	d.f.	Deviance	Significance
Treatment (inoculated plants *vs.* controls)	1	41.9	**
Armillaria species	1	7.2	**
Compatibility group	34	79.9	**
Experiment	1	0.5	NS
Experiment × group	7	27.2	**
Residual	13	25.5	*

NS $p>0.05$

* $p<0.05$

** $p<0.01$

TABLE 5–*Armillaria* vegetative compatibility groups ranked according to the proportions of *P. radiata* seedlings killed in the pathogenicity experiments*

Experiment 1					Experiment 2				
Compatibility group†	Field plot	Species‡	No. seedlings	Proportion killed§	Compatibility group†	Field plot	Species‡	No. seedlings	Proportion killed§
-	-	Control	21	0.00 a	-	-	Control	20	0.00 a
51 PB	2	Anz	10	0.00 ab	38 (r)	4	Alim	6	0.00 ab
33 B(r)	3	Alim	10	0.00 ab	35 B	3	Alim	10	0.10 abc
35 B(r)	3	Alim	10	0.00 ab	41	4	Alim	10	0.20 abcd
33 B(r)	3	Alim	10	0.10 abc	12 B(r)	3	Anz	9	0.22 abcd
35 B(r)	3	Alim	10	0.10 abc	33 B	3	Alim	8	0.25 abcd
10	2	Anz	10	0.20 abcd	60 P	4	Alim	4	0.25 abcde
31 B	2	Alim	10	0.20 abcd	30 B(r)	2	Alim	4	0.25 abcde
48 PB	2	Anz	10	0.20 abcd	51 PB	2	Anz	10	0.30 bcd
47 P(r)	2	Anz	10	0.20 abcd	12 B(r)	3	Anz	9	0.33 bcde
19 (r)	3	Anz	10	0.20 abcd	30 B(r)	2	Alim	10	0.40 bcdef
19 (r)	3	Anz	11	0.27 bcd	31 B	2	Alim	10	0.40 bcdef
53 P	2	Anz	11	0.36 bcde	43 (r)	4	Alim	10	0.40 bcdef
52 P	2	Anz	10	0.40 bcdef	38 (r)	4	Alim	6	0.50 bcdef
9	2	Anz	10	0.40 bcdef	42	4	Alim	6	0.50 bcdef
49 P	2	Anz	10	0.40 bcdef	21	3	Anz	10	0.50 bcdef
20	3	Anz	10	0.40 bcdef	2	1	Anz	10	0.50 bcdef
15 (r)	3	Anz	10	0.40 bcdef	1	1	Anz	7	0.57 bcdef
15 (r)	3	Anz	10	0.40 bcdef	54 P	2	Anz	7	0.57 bcdef
17	3	Anz	9	0.44 cdef	13	3	Anz	7	0.57 bcdef
16	3	Anz	10	0.50 cdef	4	1	Anz	3	0.67 bcdef
30 B(r)	2	Alim	10	0.50 cdef	61 P	4	Anz	9	0.56 cdef
18 (r)	3	Anz	10	0.50 cdef	24	4	Anz	9	0.56 cdef
55 P	3	Anz	11	0.55 cdefg	44 P	1	Anz	9	0.56 cdef
47 P(r)	2	Anz	10	0.60 cdefg	43 (r)	4	Alim	5	0.80 def
15 (r)	3	Anz	9	0.67 defg	40	4	Alim	9	0.89 ef
12 B	3	Anz	10	0.70 defg	48 PB	2	Anz	10	0.90 f
30 B(r)	2	Alim	5	0.80 defg					
30 B(r)	2	Alim	10	0.80 efg					
50 P	2	Anz	10	0.90 fg					
18 (r)	3	Anz	7	1.00 g					

* Some groups are replicated (r); ranking is approximate in Experiment 2 to facilitate statistical presentation.

† 'P' indicates group detected post-burn only; 'B' indicates group tested in both experiments.

‡ Anz, *A. novae-zelandiae;* Alim, *A. limonea.*

§ Values in each experiment with the same letter following are not significantly different ($p > 0.05$, Fisher's Exact Test).

DISCUSSION

Mortality from Armillaria root disease was high in *P. radiata* 5–6 years after planting on a clearfelled and burnt indigenous forest site (Fig. 1–4). Even so, levels were comparable to those previously reported in similar stands (Beveridge 1974; Shaw & Calderon 1977; MacKenzie & Shaw 1977; van der Pas & Hood 1984). Chronic *Armillaria* infection was also considerable in this trial, though less than that reported for a similar but older stand near Rotorua (Shaw & Toes 1977; Mackenzie 1987). Rapid colonisation of thinning stumps (67% of all stumps within 15 months in Plot 2) is likely to assist in maintaining chronic infection during the rotation (MacKenzie 1987) by boosting the inoculum.

It is generally assumed that vegetative compatibility groups mostly (but not exclusively) delineate *Armillaria* mycelia of single genotypes (Korhonen 1978; Kile 1983). In this study economic constraints did not permit a final, direct, systematic survey of the incidence and distribution of compatibility groups as was done previously (Hood & Sandberg 1987, 1989). Instead, groups were in effect detected by using pine trees as pathogen traps planted at intervals broadly comparable to those of the earlier soil rhizomorph samplings. This may explain the changes in the proportions of the original pre-burn compatibility groups detected after burning in Plots 1 and 3 (Table 2, Fig. 9). However, in Plots 2 and 4 the proportions of pre-burn groups did not change significantly after burning. Pre-burn groups that survived the fire were found mainly in the same pre-burn localities, although some may have extended their distributions on the new foodbase provided by the indigenous stumps (e.g., groups 4, 6, Fig. 5; cf. Fig. 1 of Hood & Sandberg 1987). Many pre-burn groups showed elongated, lobed, or disjunct distribution patterns (Fig. 5–8), possibly as a result of concurrent reoccupation of the site from remnants of older, irregular, pre-burn mycelia. Several explanations are possible for the unexpected post-burn positions of four compatibility groups (29, Fig. 5; 30, Fig. 6; 14, 35, Fig. 7). Small, isolated portions of larger, older, fragmented mycelia (all belonging to the same compatibility group) may sometimes have gone undetected in the pre-burn survey. Alternatively, the locations of pieces of some mycelia may have been displaced during clearfelling and burning procedures prior to planting. Another explanation may be the establishment of new basidiospore-derived daughter colonies with sufficient genetic similarity to the original pre-burn parent colonies to be compatible during vegetative pairing (Kile 1983).

Efforts were made to confirm the stability of compatibility group standard cultures, and hence the validity of newly detected post-burn compatibility groups. Unavoidable delays in splitting and separating the cultures of some standards, and also in conducting the compatibility pairings of some isolates later identified as new groups, prevented absolute certainty. However, the complete lack of evidence for a change in the compatibility behaviour of any cultures (including those reisolated from inoculated seedlings) argues for a general genetic stability among the isolates worked with during this study (supported by the continued ability of the standards to identify pre-burn groups at the end of the trial). Smith *et al.* (1992) have commented on the long-term genetic stability of a clone of *A. gallica* Marxmüller & Romagnesi. The high proportion of newly detected groups may be explained in two ways. Some of the groups may have been present before burning but missed because of a limited presence in the soil at the time of the first survey. It cannot be assumed that rhizomorphs are always produced by mycelia in decaying indigenous stumps and logs, although to what extent this is a significant factor remains to be determined. Other post-burn groups may

represent new colonies introduced to the new stump food-bases by means of basidiospores from outside the plots during the fruiting season 3–5 months after burning (Hood & Sandberg 1987). Spore colonisation by *A. novae-zelandiae* has been demonstrated by Horner (1991) in kiwifruit orchards (*Actinidia deliciosa* (A. Chev.) Liange & Ferguson) in the Bay of Plenty district, and in this study all new post-burn compatibility groups were also of this species. Both these explanations for the new groups are consistent with (a) the substantial changes in compatibility group proportions after burning in Plots 2 and 4 when all groups are included in the analyses (in contrast to the close similarity before and after burning when only pre-burn groups are considered—Table 2, Fig. 9); (b) the occurrence of the new groups in compact, regular clusters of limited size (or as single collections). Groups 57¤ and 61¤, for instance, were regular in shape (Fig. 8) and their absence from the pre-burn results suggests they may be genuine new introductions to Plot 4 (Fig. 4 of Hood & Sandberg 1987; *Armillaria* spp. were not found in the area subsequently occupied by these groups although it was fully sampled at 2-m intervals prior to burning). Group 47¤ (Plot 2) is an enigma and it is not easy to explain its comparatively large irregular-shaped distribution. Possibly it was present but not cultured from rhizomorphs collected from this position before burning (refer Fig. 2 of Hood & Sandberg 1987).

Beilschmiedia tawa was used as the inoculum substrate in the pathogenicity experiments since it is commonly colonised by *Armillaria* species in the central North Island, and was the dominant indigenous tree species in the plots prior to burning (Hood & Sandberg 1987). A comparatively small number of seedlings was treated with each compatibility group of *Armillaria* in order to encompass as many groups as possible. All groups tested showed some degree of pathogenicity to *P. radiata,* some more than others. Many groups belonging to *A. limonea* ranked lower in pathogenicity to *P. radiata* than many of *A. novae-zelandiae* (Tables 4 and 5), a result that agrees with previous reports on these species (Shaw *et al.* 1981; Benjamin, 1983). Results of the pathogenicity experiments cannot be compared directly with those from the trial (Table 3) since isolates were not obtained from all *Armillaria*-killed trees, and because field mortality was not dependent only on the relative pathogenicities of the different groups. The number of tree deaths is also influenced by the inoculum potential (which is partly governed by the amount of wood substrate) and by the spatial extent of each group within the plot (which in turn reflects colony age, growth rate, and competitive ability). However, groups which killed most trees in the field trial (Table 3) tended to have medium-to-high pathogenicities in the inoculation experiment (Table 5). The areas of trees killed by the larger compatibility groups increased somewhat in size during the post-burn trial period, seemingly to an outer limit (Fig. 5–8). A similar effect was reported by Roth *et al.* (1979) who argued that although the early distribution of pine mortality is confined to the zone occupied by the stump root system, infection and death occur later nearer the periphery where lengthening pine roots take longer to reach the more dispersed, outer, infective stump roots. It appears that the primary inoculum is not necessarily restricted to a single stump but that colonies of *Armillaria* can extend through several adjoining root systems after clearfelling (Fig. 5–8). This may explain the irregular form of group 47¤ (Fig. 6). Colonisation may be rapid, apparently occurring predominantly in the first 2 years after burning, when fruiting on the new indigenous stumps is already prolific (MacKenzie & Shaw 1977). Fruiting also occurred early in this study on stumps or on the ground (presumably from stump roots), sometimes near the centre of post-burn distribution as revealed by subsequent pine mortality (e.g., group 61¤, Fig. 8).

Less pine is now being planted on indigenous cutover sites than formerly was the case. Nevertheless, Armillaria root disease appears to be widespread in exotic forests in New Zealand including some on sites not previously stocked in indigenous forest (Hood 1989). The results of this trial have provided a clearer picture of the behaviour and population dynamics of the fungi responsible for this serious disease.

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