OCCURRENCE OF ARMILLARIA RHIZOMORPH POPULATIONS IN THE SOIL BENEATH INDIGENOUS FORESTS IN THE BAY OF PLENTY, NEW ZEALAND

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ABSTRACT

The distribution of rhizomorphs of species of **Armillaria** was determined in indigenous forests at three sites up to 80 km apart in the Rotorua-Bay of Plenty district, New Zealand, by systematically taking cylindrical soil core samples 16 cm diameter by 22 cm deep. There was significant between-site variation in the frequency of occurrence of rhizomorphs (4–19%; $p < 0.05$). At one site with four plots (36 × 28–36 m; up to 1.4 km apart), there was between-plot variation in rhizomorph frequency (13–31%; $p < 0.01$), mean rhizomorph length per unit area of soil surface (2–9 m/m^2; $p < 0.01$), and yield of isolates from samples containing rhizomorphs (41–89%; $p < 0.01$). Distribution of viable rhizomorphs was clustered in two plots ($p < 0.05$). Cultural techniques were used to identify species and intercompatibility groups among isolates made from rhizomorphs and basidiomata. Plots contained 19–93 groups of **A. novae-zelandiae** (Stevenson) Herink per hectare and 15–56 groups of **A. limonea** (Stevenson) Boesewinkel per hectare. Dimensions of intercompatibility group clusters varied from less than 4 m to at least 30 m across. Five out of eight billets of **Beilschmiedia tawa** (A. Cunn.) Kirk and **Pinus radiata** D. Don, protected from soil rhizomorphs by plastic shields, were each colonised by **Armillaria** species 20–22 months after being partially buried 1–5 m from a dense cluster of sporulating basidiomata of **A. novae-zelandiae**. This result, together with the high numbers of intercompatibility group density, suggests that basidiospores may play an important role in the establishment of infection centres in New Zealand forests.

Keywords: rhizomorphs; basidiospores; podocarp/hardwood forest; **Nothofagus** forest; **Armillaria novae-zelandiae**; **Armillaria limonea**; **Armillaria hinnulea**.

INTRODUCTION

It is almost 60 years since species of *Armillaria* were shown to be the cause of a lethal root disease of *Pinus radiata* planted on sites previously stocked in indigenous forest (Birch 1937). Although then attributed to *A. mellea* (Vahl ex Fries) Kummer, the disease is now known to be caused by two indigenous species, *A. limonea* and *A. novae-zelandiae* (Shaw & Calderon 1977). A third species, *A. hinnulea* Kile & Watling, has recently been recognised in stands of *Nothofagus* (Kile & Watling 1983; Kile 1983b), but the role of this fungus in the disease is unknown. Intensive research has been conducted over the past decade, and the currently recommended control is to

remove stumps mechanically prior to planting (Shaw & Calderon 1977; van der Pas 1981b; van der Pas & Hood 1984). Though this method is effective, forest managers rarely use it because it is expensive, and it is impracticable for use on steeper slopes.

In order to devise a soundly based alternative control option, it is necessary to understand the disposition of *Armillaria* at the time of infection. Although the occurrence of basidiomata and the spatial pattern of stand mortality provide an indirect guide to inoculum distribution during the first years after planting (MacKenzie & Shaw 1977; Roth *et al.* 1979; van der Pas 1981a), there is no direct knowledge of the behaviour and spread of the fungus during the transition from natural to planted forest. A trial was therefore established on a site due for conversion to plantation forest, in order to monitor the changes in *Armillaria* rhizomorph populations within the soil during and after the conversion phase. During the first stage of the trial the distribution of *Armillaria* was determined under an indigenous forest prior to felling and burning. To augment these results, the incidence of *Armillaria* was also evaluated at two other sites in the district, in order to compare values from different forest types and locations. Part of the study included a small spore-trapping experiment designed to investigate the role of basidiospores in establishing new infection centres.

METHODS

Sites

Plots were established at three sites in indigenous forests disturbed by early logging operations. One temporary plot was set up at each of the first two sites, while at the third site four permanent plots forming the main trial were marked out using fireproof steel pegs. Plots were square or rectangular. Temporary plots were sited in Rotoiti Forest (Haroharo Road, Tasman Forestry Ltd; Long. 176° 29′ 20″ E, Lat. 38° 05′ 50″ S) and in Kaimai-Mamaku Forest Park (Capricorn road; Long. 175° 58′ 20″ E, Lat. 38° 02′ 10″ S). Vegetation at the Rotoiti Forest site consisted of residual broadleaf forest (*Beilschmiedia tawa, Laurelia novae-zelandiae* A. Cunn., *Litsea calicaris* (A. Cunn.) Kirk, *Knightia excelsa* R. Br., *Hedycarea arborea* J.R. et G. Forst., *Melicytus ramiflorus* J.R. et G. Forst.), with the podocarp element removed by logging. That at the Kaimai-Mamaku site was composed of residual *Nothofagus truncata* (Col.) Ckn., with regrowth or remnant *N. truncata, Weinmannia racemosa* Linn. f., and *Ixerba brexoides* A. Cunn. (Hosking & Hutcheson 1986).

Permanent trial plots were established in the Raungaehe Range, east of Te Teko (Tuararangaia Block, Tasman Forestry Ltd, Tuhoe lease; Long. 176° 50′ 30″ E, Lat. 38° 10′ 10″ S). Plots measured 36 m long by 36 m (Plot 1), 28 m (Plot 2), 36 m (Plot 3), and 30 m wide (Plot 4) respectively, and were situated up to 1.4 km apart. Two (1, 2) were situated near the tops of ridges, and two (3, 4) were in a valley floor, 25 m apart on either side of an old logging track. Vegetation at the permanent trial site consisted of residual broadleaf forest, with the canopy intact beneath scattered, emergent, dead trees of *Metrosideros robusta* A. Cunn. Logging of lightly stocked podocarps (mainly *Dacrydium cupressinum* Lamb.) was carried out, apparently for the first time, during 1954–56 (V. J. N. Tunnicliffe, pers. comm.). All plant species in Plots 1–4 of 10 cm dbh or greater (excepting tree ferns) were mapped and measured (dbh) immediately prior to sampling. A breakdown of stand composition in each of the main trial plots

is given in Table 1. Basal area varied between 28 and 50 m^2/ha, and was made up largely of *B. tawa, Melicytus ramiflorus,* and (in Plot 1) *Elaeocarpus dentatus* (J.R. et G. Forst.) Vahl and *L. calicaris.* Stocking levels varied between 383 and 809 stems/ha. Plots also varied in the proportions of minor broadleaf species present. The basal area of non-living material was comparatively large in Plot 2 (47 m^2/ha) due to the presence of a dead tree of *Metrosideros robusta* (dbh 205 cm) and a sawn podocarp stump *(D. cupressinum;* diameter 105 cm) with remnant *Armillaria* butt rot. No living podocarps were present in any plot.

Soil at all sites was friable and well drained, being derived from volcanic ash showers.

Sampling

Cylindrical soil core samples, 16 cm diameter by 22 cm deep, were taken at intervals of 1 m (temporary plots; 1.0% sample of soil surface) or 2 m (permanent plots; 0.5% sample) at the intersections of two mutually perpendicular sets of parallel, straight, grid lines laid out across each plot. Seventy and 100 samples, respectively, were taken in each of the temporary plot sites, while at the main trial site between 249 and 322 samples (1161 total) were taken in each permanent plot, nine sample points being rendered inaccessible by obstructing trees. Permanent plots were sampled between December 1984 and May 1985 prior to clearfelling. Samples were collected using a mechanically rotated drum with saw-teeth around the lower rim for root cutting. Soil samples were sieved through an 8-mm-square mesh and residues were carefully searched in the laboratory for rhizomorphs of *Armillaria,* which were washed in tap water. Identity was confirmed using a stereomicroscope where necessary. Brittle, disintegrating, hollow shells seen occasionally in several sample residues were discarded. Each rhizomorph collection (all those in one sample) from the temporary plots was oven-dried and weighed. Permanent plot collections were each measured for total length. Larger collections in Plots 3 (62% of rhizomorph collections) and 4 (19%) were determined using a Comair root length scanner (Commonwealth Aircraft Corporation Ltd, Melbourne; 38 additional machine-measured collections were also measured by hand as a check on this method). Rhizomorph collections from permanent plots were held at 4°C in plastic bags, as were soil sample residues prior to searching.

The spatial distribution of rhizomorphs in each main trial plot was analysed using a computer-based procedure. The actual numbers of rhizomorph-containing samples in three nearest-neighbour distance classes of association (2 m, $2\sqrt{2}$ m, and more than $2\sqrt{2\,m}$ apart; total number = n) were compared (χ^2 test; df = 2) with the expected values in the same distance classes for a random distribution of n points. The expected values were derived from the means of 100 or more random assignments of n points to the co-ordinates of a grid of the same dimensions as the plot. Where expected values in the first two distance classes were less than 5, due to a small value of n, they were combined prior to analysis (df = 1).

Cultural Identification

Isolations were attempted from collections of rhizomorphs and basidiomata from main trial plots, and those obtained were identified using three cultural techniques. Rhizomorphs were surface sterilised in 10% hydrogen peroxide, usually after first

TABLE 1—Stand composition, main trial

Species	Plot							
	1		2		3		4	
	Stocking*	BA†	Stocking	BA	Stocking	BA	Stocking	BA
Beilschmiedia tawa	60	2.63	32	3.02	29	2.50	34	3.62
Melicytus ramiflorus	2	0.15	16	0.76	6	0.21	11	0.24
Elaeocarpus dentatus	2	1.55	-	-	2	0.03	-	-
Litsea calicaris	7	0.49	-	-	-	-	-	-
Hedycarea arborea	6	0.10	1	0.01	-	-	-	-
Knightia excelsa	2	0.06	-	-	1	0.30	-	-
Paratrophis microphylla (Raoul) Ckn.	1	0.01	-	-	-	-	-	-
Coprosma robusta Raoul	1	0.01	1	0.01	-	-	-	-
Schefflera digitata J.R. et G. Forst.	-	-	3	0.04	-	-	-	-
Geniostoma ligustrifolium A. Cunn.	-	-	1	0.01	-	-	-	-
Myrsine australis (A. Rich.) Allan	-	-	-	-	-	-	2	0.02
Alectryon excelsus Gaertn.	-	-	-	-	-	-	1	0.01
Total	81	5.00	54	3.85	38	2.77	48	3.89
Dead‡	1	0.09	5	4.68	3	0.62	1	0.03

* No. trees/0.1 ha

† Basal area, m^2/0.1 ha (breast height)

‡ Stumps (below breast height) and standing dead trees; excludes occasional smaller stumps and all fallen trees.

dipping in 95% ethanol, and were then normally washed in sterile distilled water. Approximately 5–15 short segments per collection were cut from one or more rhizomorph pieces and plated out, with or without the outer cortex retained, on to 3% malt agar supplemented with 40 ppm *o*-phenylphenol (sodium salt) and 100 ppm streptomycin sulphate (medium modified from Rishbeth 1972; cf. Russell 1956). Isolations were carried out within 4 weeks of field sampling. Cultures were also isolated from the tissues of basidiomata collected from dead wood within the still-standing forest in or near Plots 3 and 4 during early May 1985.

The species identity of cultures was determined using two independent methods based on: (a) colony morphology on 3% malt agar after 21 days at 18–25°C under a 24-h 5-watts/m^2 photoperiod provided by cool white fluorescent tubing (all isolates; Benjamin 1983); (b) compatibility with standard single basidiospore tester isolates obtained from basidiomata of three *Armillaria* species: *A. limonea, A. novae-zelandiae,* and a third *Armillaria* sp. ex *Nothofagus fusca* (Hook. f.) Oerst. (one isolate from each rhizomorph collection; Korhonen 1978). Tester isolates from the first two species were used with isolates from all plots, and from the third species with Plot 4 isolates, only. The reliability of these two techniques was examined by culturally confirming the identity of isolates taken from the tissues of basidiomata of *A. limonea, A. novae-zelandiae,* and *Armillaria* sp. In addition to determining the species of main trial isolates, those belonging to common intercompatibility groups were identified by pairing them on 3% malt agar in various combinations and noting the presence or absence of a demarcation line, accompanied by a thin brown pigment zone, between members of each pair (Adams 1974; Korhonen 1978).

Spore Trapping

A spore-trapping experiment was established under shade conditions within the edge of an unlogged podocarp-broadleaf forest in the Mokaihaha Ecological Area, Mamaku Plateau, near Rotorua. Billets of freshly cut wood, with bark retained, were partially buried in a vertical position in June 1983, 1–5 m from a thick profusion of basidiomata of *A. novae-zelandiae* along an 8-m length on a large log. Five billets consisted of *P. radiata* (14–22 cm diameter by 58–61 cm long) and four of *B. tawa* (13–17 cm by 59 cm). Each billet extended 12–16 cm above soil level. *Pinus radiata* billets were buried within 15 days of felling several source trees (stand thinnings, with foliage fully retained and still green), and *B. tawa* billets 1 day after. In order to prevent colonisation by soil rhizomorphs, each billet was enclosed in an open-ended, rigid, plastic, cylindrical sheath 30 cm diameter by 66 cm long. The space within each sheath not occupied by the billet was filled with soil sieved through an 8-mm-square mesh. The base of the sheath extended 18–22 cm below the bottom of each billet, and the top was approximately 2–3 cm above ground-level. During a period of 5 weeks from the start of the trial, pilei were periodically detached from basidiomata on the log and suspended in a wire cage with the lamellae directly above the cambial region of two billets only (*B. tawa* and *P. radiata*). All billets were exhumed 20–22 months after burial. Soil beneath the base of each billet (within the sheath) was searched by re-sieving through an 8-mm-mesh screen. Bark was removed from each billet and the presence and appearance of mycelial fans and rhizomorphs of *Armillaria* were recorded.

RESULTS

Rhizomorph Distribution

Rhizomorphs of *Armillaria* species were present in the soil at all sites (Tables 2 and 3). Those sampled were free, closely attached to segments of living roots, or occasionally penetrating extensively decayed roots. Rhizomorphs occurred more frequently in main trial Plot 3 (31%) than in other plots of the study (4–15%; $p < 0.001$; Fisher's exact test; Tables 2, 3). Other plots in podocarp-hardwood forest did not vary significantly in frequency of occurrence of rhizomorphs (9–15%; $p > 0.05$). Rhizomorphs occurred less frequently in the Kaimai-Mamaku *N. truncata* plot (4%) than in the main trial (13–31%; $p < 0.05$) but not the Rotoiti (9%; $p > 0.05$) plots in podocarp-hardwood forests. Rhizomorph lengths determined using the Comair root length scanner (y) were related to hand-measured lengths (x) by the regression $y = 1.396x - 3.624$ ($n = 38$; $r^2 = 0.82$; $p < 0.001$). Values of rhizomorph length ranged up to an extreme of 558 cm/sample (hand-measured). On average, Plot 3 contained a greater length of rhizomorphs per unit surface ground area (9 m/m^2) than did the other plots in the main trial (2–4 m/m^2; $p < 0.01$, Table 3). The distributions of main plot samples containing rhizomorphs are shown in Fig. 1–4. Samples with rhizomorphs were clustered (more than expected were 2 m apart) in Plot 3 (all samples and those viable, only) and Plot 4 (viable samples, only; Table 4). Clustering of rhizomorphs was not demonstrated statistically in other plots.

TABLE 2—Quantities and frequencies of rhizomorphs in temporary plots

Site	Plot size (m)*	No. samples	Mean rhizomorph dry weight (g/m^2 soil surface)†	Percentage of samples with rhizomorphs
Kaimai-Mamaku Forest Park	11 × 8	70	0.05	4
Rotoiti Forest	11 × 11	100	0.66	9

* Rectangular, samples 1 m apart.
† Means of all samples, including zero values.

Cultural Identification

Reliability of the two techniques used to determine cultures to species level was examined by checking the identity of isolates from tissues of *Armillaria* basidiomata (Table 5). The 24-h photoperiod technique was used to identify successfully 59 out of 60 of the isolates. After 21 days under a 24-h photoperiod, cultures of *A. novae-zelandiae* produced dark-coloured circular colonies with a fine light-coloured tomentum and little or no rhizomorph growth, while colonies of *A. limonea* invariably formed dark, nearly glabrous crusts with extensive rhizomorph development (Benjamin 1983). Tissue and polysporous isolates, respectively, from basidiomata in two central North Island collections of a third *Armillaria* species (ex *Nothofagus* spp., Whirinaki Forest Park and Tongariro National Park, respectively) formed colonies similar to, but smaller

TABLE 3—Quantities and frequencies of rhizomorphs, main trial site*

Plot No.	No. samples†	Mean rhizomorph length (m/m² soil surface)	Percentage samples with rhizomorphs			Percentage rhizomorph samples yielding isolates		
			Viable		All	*A. n-z.*	*A. lim.*	Total
			A. n-z.	*A. lim.*				
1	321	2.6 a	6 a	1 a	15 a	38 a	7 a	45 a
2	247	3.6 a	5 ab	1 a	15 a	35 ab	6 a	41 a
3	318	9.2 b	9 a	6 b	31 b	31 ab	21 a	52 a
4	268	2.2 a	2 b	11 b	13 a	11 b	78 b	89 b

* Values in each column linked by a common letter are not significantly different ($p<0.01$; percentages: Fisher's exact test on sample numbers; rhizomorph lengths: Mann-Whitney non-parametric test on all data, including zero values).

† Numbers do not include 3,3,2, and 1 samples in Plots 1,2,3,4 respectively, which coincided with obstructing trees, and 2,4 and 1 rhizomorph collections in Plots 2,3,4 respectively, which were not measured and from which isolations were not attempted.

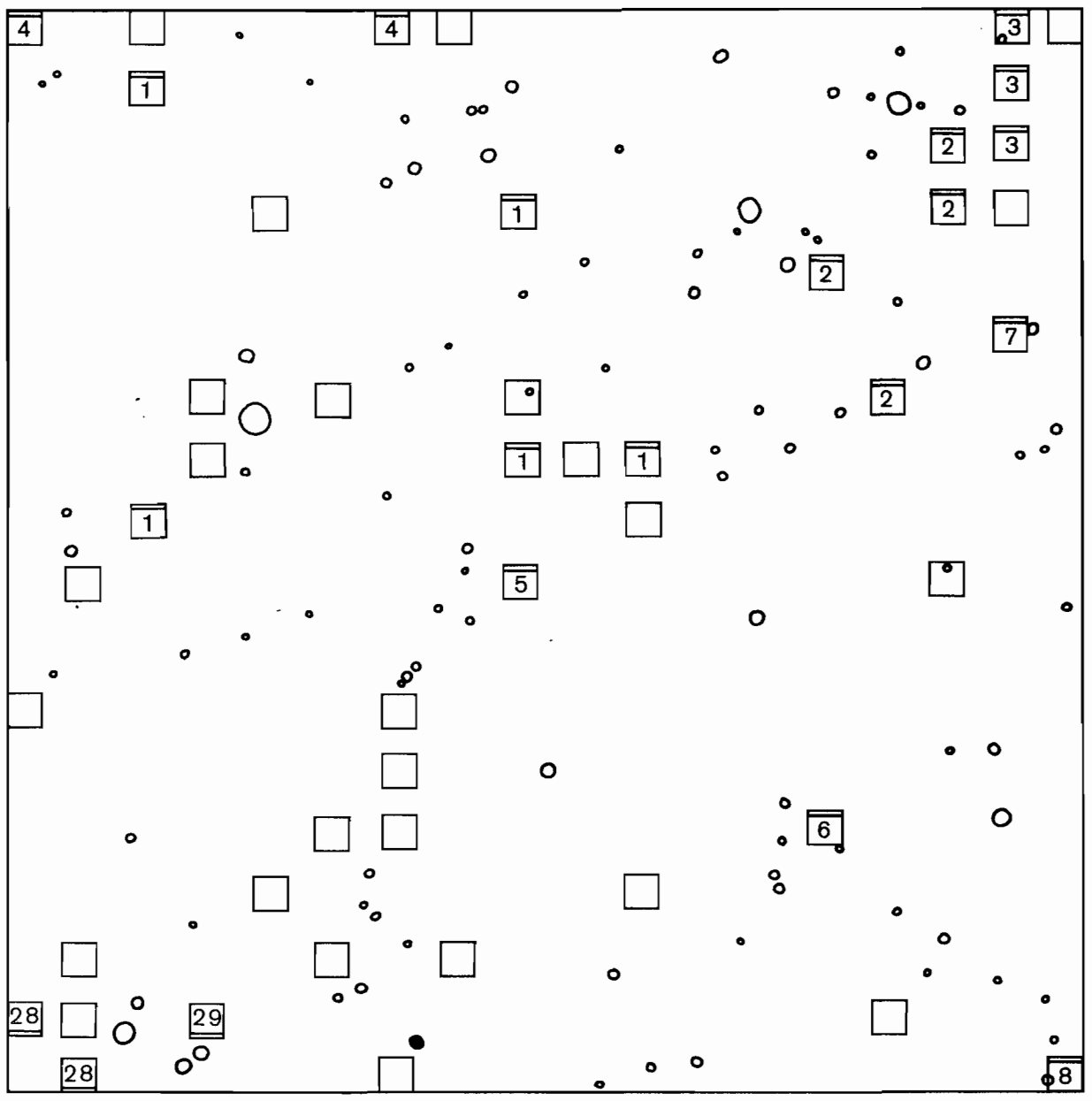

FIG. 1—Distribution of rhizomorph samples, Plot 1, main trial (for Key, see Fig. 2).

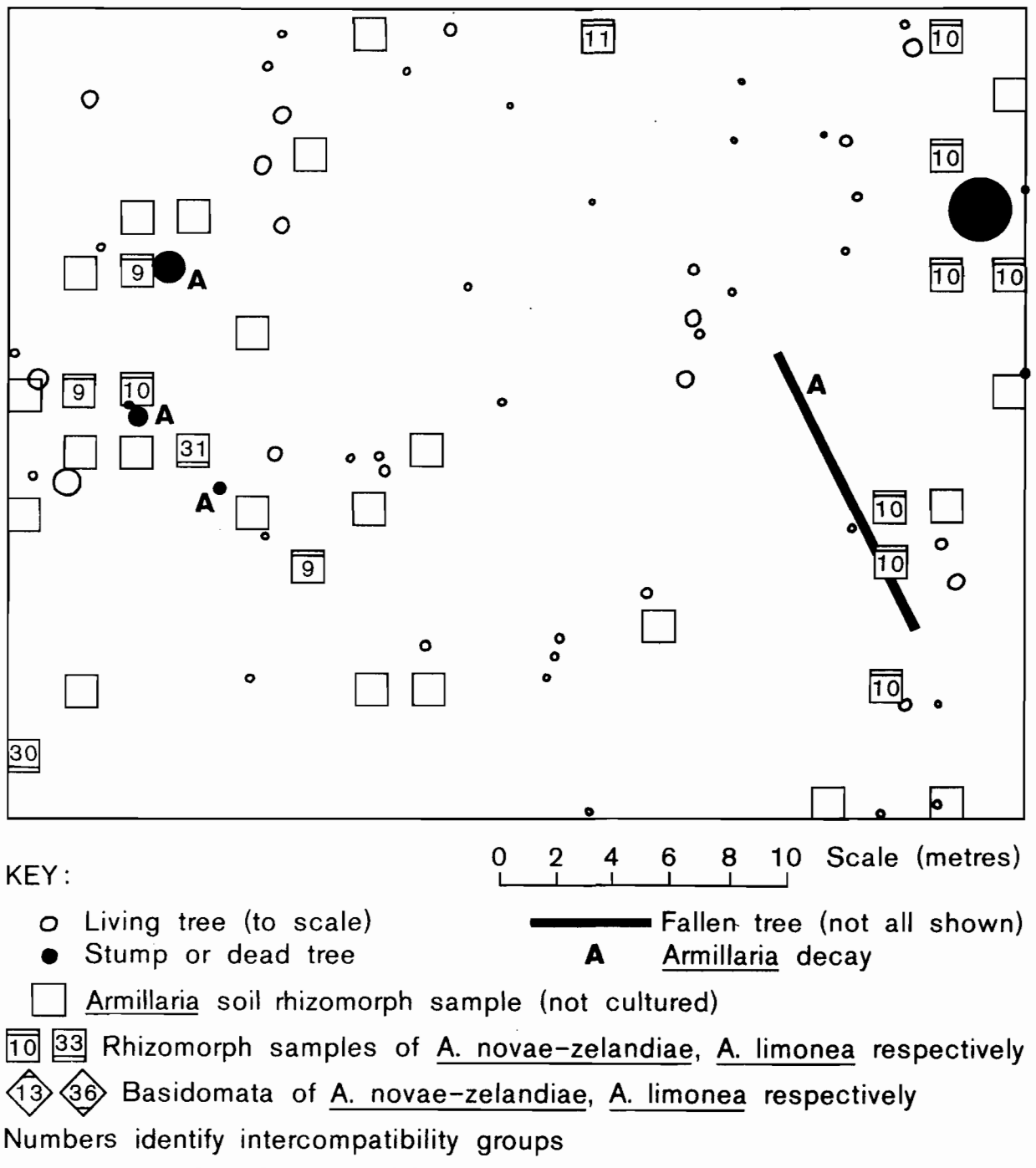

FIG. 2—Distribution of rhizomorph samples, Plot 2, main trial.

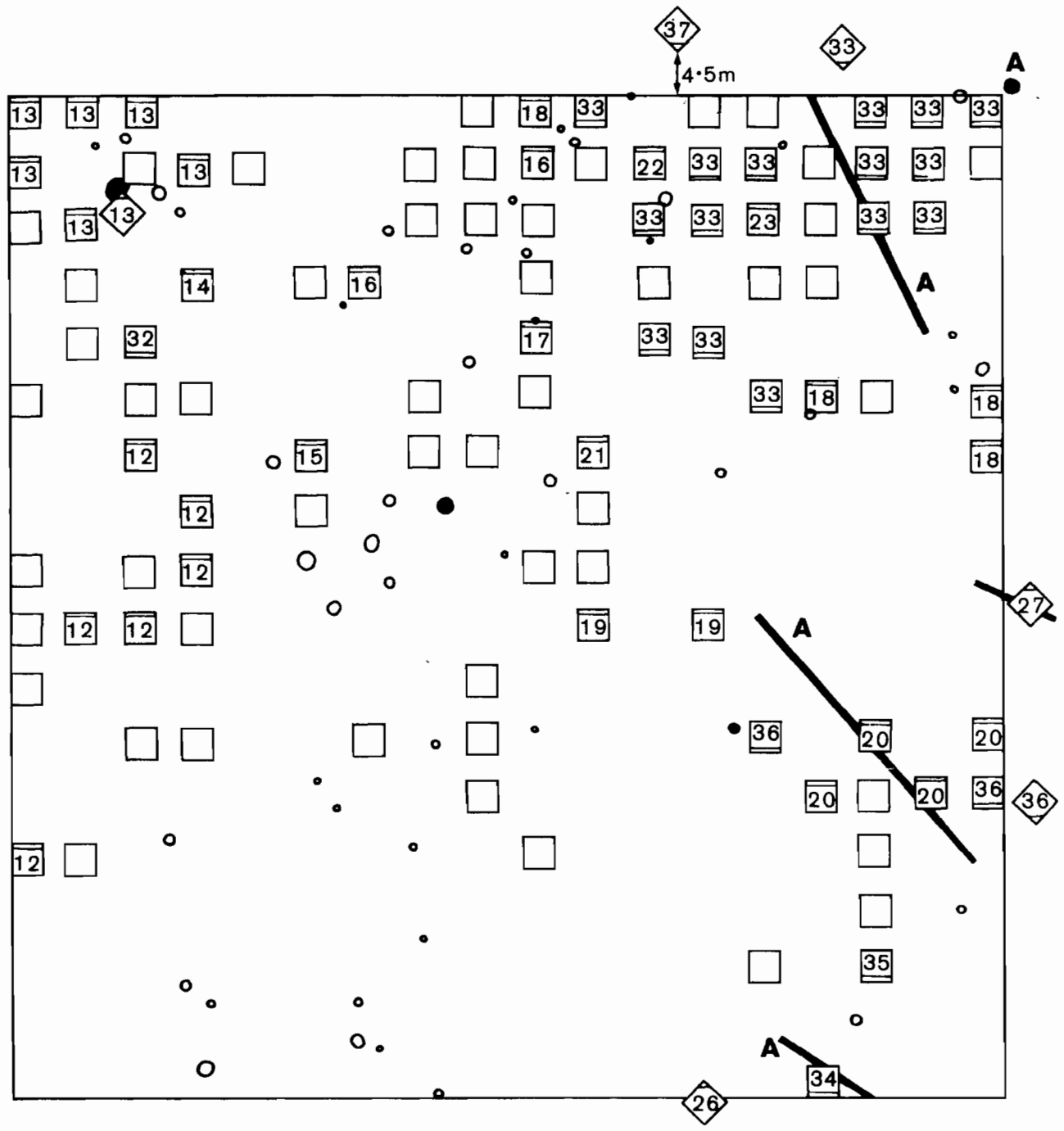

FIG. 3—Distribution of rhizomorph samples, Plot 3, main trial (for Key, see Fig. 2).

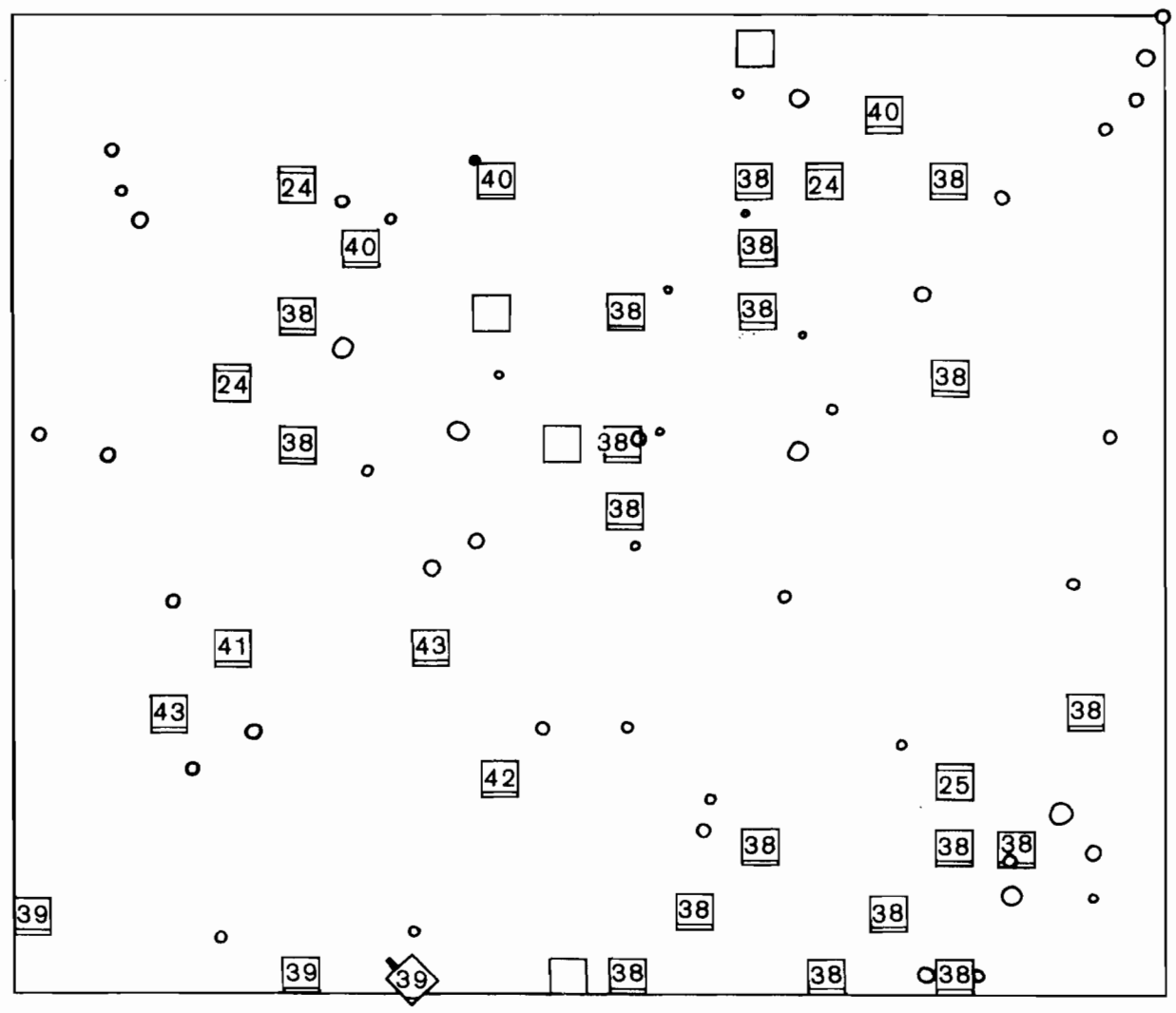

FIG. 4—Distribution of rhizomorph samples, Plot 4, main trial (for Key, see Fig. 2).

TABLE 4—Randomness of distribution of rhizomorph samples in main trial plots

Plot No.	All rhizomorph samples				Those yielding isolates			
	n	χ^2	df	Significance†	n	χ^2	df	Significance
1	47	5.8	2	NS	21	0.2	1	NS
2	36	1.2	2	NS	14‡	-	-	-
3	101	16.3	2	**	50	8.9	2	*
4	36	5.5	2	NS	32	11.2	2	**

† NS, $p>0.05$; *$p<0.05$, **$p<0.01$
‡ Insufficient numbers for valid test

TABLE 5—Numbers of test isolates* identified to species using two cultural techniques

Species	Technique			
	24-h photoperiod		Compatibility with basidiospore tester isolates	
	Confirmed	Total	Confirmed	Total
A. limonea	13	14	16	20
A. novae-zelandiae	46	46	30	33
Total	59	60	46	53

* Isolated from tissues of morphologically identified basidiomata.

than those of *A. novae-zelandiae,* and produced intensive dark staining in the surrounding agar (cf. Forest Research Institute 1976) during the 24-h photoperiod test. These isolates were compatible with a single spore tester isolate from one of the collections (ex Whirinaki Forest Park), but were incompatible with similar tester isolates of *A. limonea* and *A. novae-zelandiae,* which remained white and fluffy, showing no tendency to darken or become appressed (Korhonen 1978). The *A. limonea* and *A. novae-zelandiae* tester isolates successfully identified 46 out of 53 cultures made from basidioma tissues of these two species (Table 5). Identities of tissue isolates from seven basidiomata in or near main trial plots (Fig. 3, 4) determined using both cultural techniques all matched the morphologically derived identifications.

Up to 11 isolates of *Armillaria* were obtained from each rhizomorph collection from the main trial plots. Yield appeared unaffected by the presence or absence of the outer cortex. Plot 4 rhizomorph collections yielded more isolates (89%) than did those from the other plots (41–52%; $p<0.01$, Table 3). All isolates from each plot were identified as either *A. limonea* or *A. novae-zelandiae,* only, using the 24-h photoperiod technique (Fig. 1–4). These identifications were confirmed for 99% of tests with the compatibility technique. Results were unclear, but not contradictory, for the remaining 1% of tests. Isolates were further subdivided into 5–17 intercompatibility groups per plot (40,

total; Table 6), by noting antagonisms during multiple pairings. Isolates from the same rhizomorph collections were all mutually compatible. Representative isolates from each intercompatibility group in Plot 3 were incompatible with similar isolates from all groups in the adjacent Plot 4. Inter-plot pairing was not carried out between more distant plots. Tissue isolates from two basidiomata in Plots 3 and 4 were compatible with nearby soil rhizomorph isolates (Fig. 3 and 4). Those from five basidiomata immediately outside Plot 3 varied in their compatibility with plot rhizomorph isolates. Samples belonging to a common intercompatibility group tended to occur in clusters, each cluster varying in size from at least 30 m diameter (Group 10, Fig. 2) down to just single sample points (Fig. 1–4).

TABLE 6—Numbers of intercompatibility groups among main trial plot rhizomorphs*

Plot	*A. novae-zelandiae*	*A. limonea*	Total
1	8	2	10
2	3	2	5
3	12	5	17
4	2	6	8
Total	25	15	40

* Ratios of numbers for each species not significantly different between plots ($p > 0.05$; Fisher's exact test)

Spore Trapping

Prolific fruiting continued for 3 weeks after the start of the spore trapping experiment, and basidiomata were still present 4–5 weeks after. With one exception, no rhizomorphs were found in the soil beneath the bottom of each billet. One billet of *B. tawa* was surrounded by extensive rhizomorph growth which extended below the base. Rhizomorphs were also found attached to the bark of a second *B. tawa* billet and two *P. radiata* billets, within the plastic sheaths, but these did not extend downwards. Rhizomorphs were present in the soil outside the plastic sheaths surrounding one *B. tawa* billet and two of *P. radiata.* These extended to depths of 30, 30, and 54 cm, respectively, below the soil surface. Mycelial fans of *Armillaria* were found in the cambial region beneath the bark of one *B. tawa* and four *P. radiata* billets. Fans varied in width and appeared strap-like, with tiny side branches at right angles (cf. Fig. 2, Rishbeth 1970). Species was not determined. On the other three *B. tawa* billets (including the one with rhizomorphs beneath the base) a distinctive colonisation pattern of narrow, branched, radiating, mycelial fans enclosed within a network of intense, black, double zone lines was present under the bark. This closely resembled the pattern produced in 2-cm-diameter *B. tawa* stem segments after the ends were each inoculated with a single-spore isolate of one of the three *Armillaria* species and incubated for 4 months in moist sand (unpublished results).

DISCUSSION

Armillaria spp. have been recognised as a component of the mycoflora of indigenous forests in New Zealand since 1879 (Cooke 1879; Colenso 1890; Birch 1937). *Armillaria limonea* and *A. novae-zelandiae* fruit prolifically for several weeks each year between April and July, and infrequently at other times, in both podocarp-broadleaf and *Nothofagus* forests in the central North Island. *Armillaria novae-zelandiae,* at least, is also present in South Island stands. Both species have been isolated from a distinctive wood decay described by Gilmour (1954), which is commonly seen in logs and dead trees in indigenous forests. A third species, *A. hinnulea,* has been collected only from the South Island west coast, but may also be present in central North Island *Nothofagus* forests (Kile & Watling 1983). Isolates from *Nothofagus* basidiomata collections used in this study may also be *A. hinnulea,* but this requires confirmation. Although *Armillaria* species are responsible for butt heartwood rots in old growth podocarp and *Nothofagus* trees (Gilmour 1966), younger trees in podocarp-hardwood forests do not appear to be susceptible. However, root disease and decay have been reported in overstocked sapling and pole stands of *Nothofagus menziesii* (Hook.f.) Oerst. in the South Island (Birch 1937).

In this study all plots were systematically sampled at intervals of 2 m or less. Kile (1986) has demonstrated the need for such intensive sampling in population studies with *A. hinnulea.* Results confirmed the ubiquitous presence of *Armillaria* species in native forests. Rhizomorphs were present in the soil at all sites sampled, either free or attached to roots. Free rhizomorphs may have become detached or severed during sampling. Sampling was confined to the top 22 cm, because rhizomorphs appear to concentrate in the upper humified soil layers (Redfern 1973; Morrison 1976; Pronos & Patton 1978; Singh 1981; Wargo *et al.* 1987). Naturally occurring rhizomorphs were not found below 54 cm in the spore-trapping experiment, and appeared infrequent at this depth. Horizontally, rhizomorphs varied in occurrence between sites, between plots in the main trial site, and within two plots. The generally widespread occurrence of rhizomorphs under indigenous forest at the main trial site was somewhat unexpected, in view of previous notions of an inoculum build-up on freshly killed root systems after clearfelling (Roth *et al.* 1979; van der Pas 1981a). Even so, frequency of occurrence (13–31%) was less than that in a *P. radiata* stand (32–41%) on land cleared of logged podocarp-broadleaf forest 4 years previously (van der Pas & Hood 1984), suggesting that rhizomorphs may become more abundant after clearfelling. Kile (1980) has demonstrated extensive colonisation of *Eucalyptus obliqua* L'Herit stumps by *A. hinnulea* in Tasmania within 3 years of felling, although with this species rhizomorphs were restricted to the host root and root collar surfaces, and not found further out in the soil. Even though parasitism of living roots was not seen in this study, variation between plots in rhizomorph occurrence could reflect variations in species composition (Table 1). The absence of certain other major tree species known to be in the area (e.g., *Laurelia novae-zelandiae*) also indicates that plot sub-units were too small to uniformly represent the vegetation present at the main trial site. Between-plot rhizomorph variation did not correspond with the occurrence of stumps and dead trees since Plot 2, with the largest basal area of dead wood (Table 1), did not have the highest rhizomorph frequencies or quantities (Table 3). However, these figures do not include decaying

logs or buried wood. The higher proportion (31%) of rhizomorph samples concentrated in the upper corner of Plot 3 (Fig. 3) could reflect the presence of windthrown trees just beyond the upper edge. Rhizomorphs were distributed in a mosaic pattern across main trial plots (Fig. 1–4). Significant clustering was demonstrated for two plots (Table 4), while distribution in other plots may also have been clustered (detectable with more intense sampling) or truly random. Clustering may reflect localised concentrations of rhizomorphs in the vicinity of undefined food bases.

Isolates of *Armillaria* were made from many rhizomorphs in all plots, confirming their identity and viability. It is not clear why yields varied between plots, nor whether failure to yield isolates was a true indicator of nonviability. Cultures were not obtained from several rhizomorph collections in which the inner cores were weak and easily broken. Isolates were readily identified to species using the 24-h photoperiod technique devised by Benjamin (1983), which gave greater cultural contrast between species than did the 24-h dark-period method of Shaw *et al.* (1981). The single-basidiospore isolate compatibility test (Korhonen 1978) occasionally (1% of tests) gave unclear but never contradictory results, and was a useful independent means of confirming species identity. In this study (in contrast to earlier attempts: Hood & Morrison 1984) pairing on agar ("intraspecific antagonism", Rayner & Todd 1977; "somatic incompatibility", Stenlid 1985) reliably distinguished members of different intercompatibility groups, results being mutually consistent among multiple pairings of all isolates. Occasional uncertainty in interpretation of results was clarified by repetition. In these tests a thin, brown, pigment line of varying intensity commonly formed between isolates of different species and of different intercompatibility groups within the same species. The latter observation differs from that of other workers who dealt with different species (Korhonen 1978; Anderson *et al.* 1979; Rishbeth 1982; Kile 1983a).

All isolates from rhizomorphs and basidiomata in the main trial were identified culturally as either *A. limonea* or *A. novae-zelandiae*. The third *Armillaria* species may therefore be rare or absent in podocarp-broadleaf forests in the Bay of Plenty district. Rhizomorphs of the two species identified could not be distinguished morphologically. Populations of these species were composed of numerous intercompatibility groups which were distributed in clusters with diameters ranging from less than 4 m up to at least 30 m across. The maximum dimensions of these group clusters are not known because of their possible existence beyond the area surveyed, and because they may not have been detected in some samples, including those with rhizomorphs belonging to other groups; isolates were not obtained from all rhizomorph pieces in every collection. Korhonen (1978) and Kile (1983a), using other *Armillaria* species, have shown that isolates belonging to each intercompatibility group usually have identical mating factors, and are therefore probably of identical genotype and members of a common clone. Others (e.g., Rayner & Todd 1977, 1979; Stenlid 1985) have demonstrated similar behaviour with different basidiomycete fungi, and drawn the same conclusions. Maximum dimensions of intercompatibility groups certainly indicate the upper limits of clone size, since isolates known to be identical always merge evenly, without displaying antagonism. Unless they arise from mutations of the vegetative mycelium (Korhonen 1978), intercompatibility groups probably represent basidiospore-derived colonies (Rishbeth 1978; Korhonen 1978; Ullrich & Anderson 1978; Anderson *et al.* 1979; Kile 1983a).

The numbers of intercompatibility groups per unit area in the main trial (51 groups/ha, *A. novae-zelandiae;* 32 groups/ha, *A. limonea;* plot means) can be compared with the values determined in three, square, 0.25-ha plots in a 4- to 6-year-old *P. radiata* stand planted on a site cleared of indigenous forest near Rotorua (32 groups/ha, *A. novae-zelandiae;* 3 groups/ha, *A. limonea;* Benjamin 1983; Benjamin & Newhook 1984). These values are generally high when contrasted with those in many other parts of the world (e.g., 1.5 groups/ha, *A. luteobubalina* Watling & Kile, eastern Australia, Kile 1983a; less than 4.5 groups/ha, Northern Hemisphere *Armillaria* species, data in or estimated from Figures in papers by Korhonen 1978; Ullrich & Anderson 1978; Anderson *et al.* 1979; Rishbeth 1985; Siepmann 1985; but *see* Thompson & Boddy 1983). However, the numbers in this study are of similar order to those found for *A. hinnulea* (c. 36–54 groups/ha) in *Eucalyptus* forests in Tasmania by Kile (1986), who suggested that these larger population densities might be due to a greater frequency of colonisation by basidiospores. Basidiospore colonisation may also, therefore, be particularly significant in New Zealand forests. This applies, even if logging disturbance during the 1950s may have led subsequently to higher numbers of new colonies. Indirect supporting evidence is the occurrence of *Armillaria* in certain pine plantations (Kaingaroa, Santoft, and Waitarere Forests) on sites not previously stocked in indigenous forest cover (Gilmour 1954; M. A. Stoodley, pers. comm.). Direct evidence for the role of basidiospores is provided by the relatively high incidence of colonisation of billets in the spore-trapping experiment under what was probably a high inoculum pressure. Five of the eight billets (63%) screened from soil inoculum became colonised by *Armillaria* spp. and bore mycelial fans beneath the bark. Three of these billets also produced rhizomorphs. Other billets may also have been colonised by *Armillaria* spp., but this was not confirmed. In most overseas studies (Rishbeth 1964, 1970, 1985; Kile 1983a) basidiospore stump inoculations have achieved only low or zero rates of infection, but this was possibly due to residual resistance in still-living stumps immediately after cutting (Rishbeth 1964, 1970). Rishbeth (1978) has provided circumstantial evidence for the initiation of new disease centres by basidiospores in forests in England. Fedorov *et al.* (1985) considered that new infection centres in conifer plantations outside natural forest in Belorussia are due to spore dispersal.

The results of this work imply that infection centres in young stands of *P. radiata* may not originate solely from the vegetative growth of existing inoculum into the food base derived from new stumps and logs after clearing the indigenous cover. Subsequent surveys are planned in order to evaluate the effect of hot fires on the present soil populations of *Armillaria* species and to determine if a significant number of new centres become initiated by basidiospores. If this proves to be so, attempts at controlling this disease by preventing spore colonisation may be worth considering.

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