SPATIAL RELATIONSHIPS BETWEEN *ARMILLARIA* ROOT-ROT OF *PINUS RADIATA* SEEDLINGS AND THE STUMPS OF INDIGENOUS TREES

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ABSTRACT

Within 27 months, infection by species of **Armillaria** killed 16% of the **Pinus radiata** seedlings that were planted at 1 × 1 m spacing on a site freshly cleared of indigenous mixed hardwood forest. Mortality was grouped around stumps of **Beilschmiedia tawa**, suggesting that these were the major inoculum source. Stumps of **B. tawa** that had borne either sporophores of **A. novae zelandiae** only or those of both **Armillaria** species had significantly greater seedling mortality near them than stumps bearing only **A. limonea** sporophores or with no sporophores, and mortality was significantly greater around stumps with only **A. limonea** sporophores than around stumps with no sporophores. This difference suggests that **A. novae zelandiae** may be more pathogenic to **P. radiata** seedlings than **A. limonea**, and that sporophore presence is an indicator of stump infection. The few stumps of hardwood species other than tawa which bear **Armillaria** sporophores may also be important sources of **Armillaria** inoculum. After 27 months, 28% of the living trees were infected with **Armillaria** and these were grouped around trees previously killed by **Armillaria**.

INTRODUCTION

In the central North Island of New Zealand *Armillaria* root rot (caused by *Armillariella novae-zelandiae* Stevenson or *Armillariella limonea* Stevenson†) is the main cause of mortality in *Pinus radiata* D. Don established on sites freshly cleared of indigenous forest (Anon, 1976). On a former podocarp/tawa site in the Mamaku Plateau, mortality of *Pinus radiata* reached 40-50% in 5 years; of this 78-96% was attributable to pathogenic *Armillaria* attack (Beveridge, 1973). On other central North Island sites, once dominated by *Beilschmiedia tawa* (A. Cunn.) Benth et Hook f. ex Kirk (tawa) levels of mortality attributed to *Armillaria* have reached 33% within 2 years (Shaw and Calderon, 1977). With this disease causing such substantial mortality and large areas of logged indigenous forest under consideration for conversion to exotics (Chavasse, 1969), more information concerning the field dynamics of the disease was needed.

The objectives of this study were three-fold: (1) to follow the level of early mortality caused by *Armillaria* root rot in *P. radiata* seedlings planted on a site freshly

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† Although Stevenson (1964) described the genus as **Armillariella**, the convention of Shaw **et al.** (1976) will be followed here: the genus name **Armillaria** being used throughout. See Shaw and Calderon (1977) for further details on these fungi.

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cleared of native forest; (2) to determine whether there was any relationship between pine seedling deaths and their proximity to stumps of indigenous trees; and (3) to determine if there was a relationship between trees killed by *Armillaria* root rot and living but infected trees.

METHODS

Site Description and Plot Establishment

The study area was on the Mamaku Plateau, 470 m in elevation, on a site once covered by Forest Vegetation Type N7 (Nicholls, 1964); a rata/tawa-rewarewa-mangeao-kamahi type. (*Meterosideros robusta* / tawa-*Knightia excelsa*-*Litsea calicaris*-*Weinmannia racemosa*). The rainfall, temperature and soil properties are all conducive to rapid growth of *P. radiata.* The area was logged for merchantable tawa late in 1973. The remaining stems were clearfelled and broadcast burnt in mid-1974. On a flat area of 72 × 50 m (0.36 ha), 3597 *P. radiata* seedlings (1½/0 ex FRI nursery) were planted at a nominal spacing of 1 × 1 m. Prior to planting, slash and logging debris were removed where possible. This removal aided planting and ensured that the residual stumps of indigenous trees represented the major source of *Armillaria* inoculum. The plot was divided into 15 blocks each containing 24 ten-tree rows. Five randomly selected blocks were planted on each of the following dates: 7.6.74, 25.7.74, and 19.9.74 (for data analysis 25.7.74 was used as the overall planting date).

Assessment of Seedling Mortality

Seedling mortality was assessed at approximately three-monthly intervals. Dead trees were categorised into those killed through attack by *Armillaria* and those killed by other causes. Only trees showing *Armillaria* signs and a symptomatic host response (basal resinosis) were recorded as having been killed by *Armillaria*. *Armillaria* was identified by the presence of attached rhizomorphs and/or mycelial fans in the cambial zone. The "killed by other causes" category included a small percentage of seedlings that showed signs of *Armillaria* infection, but no host resinosis. To minimise the possibility of pine-to-pine disease spread, all dead trees were dug up and as much as possible of the root system removed at assessment.

Location of Pine Seedlings and Stumps of Indigenous Trees

The location of every pine seedling and stump of an indigenous tree was mapped (scale = 1 : 78) to within 300 mm. Six parallel rows of 25 × 25 mm pegs formed the reference grid from which map co-ordinates were taken. The rows were 10 m apart and contained 72 pegs at 1 m intervals.

On the map a series of equidistance contours were drawn about the centre of each stump, seven distance classes (0-6) being recognised. All except the extreme classes ranged 0.5 m either side of the integer metre distances from stump centres. Class "0" (0.0-0.5 m) rarely contained seedlings and the few therein were ultimately grouped in class "1" (nominally 0.5-1.5 m). Class "6" contained all ground further than 5.5 m from a stump and was used only in calculating the overall plot level of mortality.

Where necessary the tree species to which individual stumps belonged was identified by comparing microscope slides of wood samples with the Forest Research Institute reference collection. Stumps were initially divided into two groups; those of tawa, and other non-tawa species. These groups were further categorised by the species of

Armillaria sporulating on them in either 1975 or 1976 (Table 1). Bi-weekly checks were made for sporophores in May-June of both years.

Tawa stumps were placed in three categories based on the species of *Armillaria* sporophores present. Those that had borne sporophores of both *A. limonea* and *A. novae-zelandiae* were placed in the first, those with only *A. limonea* or *A. novae-zelandiae* in the second, and those with no sporophores in the third. Superimposed on the distance contour map a single circle of 3.5 m radius was drawn about each tawa stump. These circles were taken to delineate the stump's "circle of influence". An arbitrary circle of 3.5 m was taken as it encompassed the majority of the mortality (all that was greater than the plot average) and had the least influence from other stumps (i.e. overlapping distance classes). Where circles from different classes overlapped the common area was placed in the higher class. Where the circle from a stump that had borne only sporophores

TABLE 1—Characterisation of indigenous tree stumps by species, prevalence, and the presence/absence of **Armillaria** sporophores

	Stump characters			Species of **Armillaria** sporophores present in either 1975 or 1976			
Species[a]	No. of stumps	Mean dia. (mm)	Total basal area (m^2)	**A. novae-zelandiae** (only)	**A. limonea** (only)	Both species	No sporophores
Beilschmiedia tawa (tawa)	69	460	13.30	18	20	13	18
Knightia excelsa (rewarewa)	7	330	0.62	2	2	2	1
Litsea calicaris (mangeao)	5	480	1.05	2	0	0	3
Weinmannia racemosa (kamahi)	2	430	0.29	0	0	0	2
Metrosideros robusta (rata)	4[b]	620	2.57	0	1	0	3
Griselinia littoralis (kapuka)	1	140	0.01	1	0	0	0
Melicytus ramiflorus (mahoe)	3	290	0.20	0	0	0	3
Dicksonia spp. and **Cyathea** spp. (tree ferns)	15	270	1.01	0	0	0	15
Laurelia novae-zelandiae (pukatea)	3	490	0.66	1	0	0	2
Elaeocarpus dentatus (hinau)	1	390	0.12	0	0	0	1
Hedycarya arborea (pigeonwood)	37	190	1.16	0	0	1	36
Other species	11	220	0.46	0	0	0	11
Total	158	—	21.45	24	23	16	95

a. Nomenclature according to Allan (1961).

b. Includes one stump (1.75 m diam.) which died long before the plot was established.

of *A. novae-zelandiae* overlapped with the circle from a stump that had borne only *A. limonea* sporophores, the common area was considered to be occupied by both species and placed in category one. Pine mortality could thus be related to the distance from a species of stump, and the presence or absence of a particular species of *Armillaria* sporophore on it.

Inspection of Living Trees

To avoid inter-tree competition and further reduce the possibility of pine-to-pine disease spread, thinning, through tree excavation, was conducted 26 months after planting. Every second tree of the original planting was scheduled for thinning and those still living were removed. An attempt was made to ensure that every major lateral root of the thinnings was removed.

The root systems of the thinnings were examined for infection by *Armillaria.* Infection was defined by the same criteria used to decide if the trees had been killed by *Armillaria.* Using their mapped positions living trees infected with *Armillaria* were related to trees which had previously been killed by *Armillaria.*

RESULTS

Seedling Mortality

The first seedlings died within six months of planting. After one and two years respectively 7.0 and 15.8% of the seedlings had been killed by *Armillaria.* In contrast, only 1.8% of the seedlings were killed by causes other than *Armillaria* after two years. In the first 18 months the seedlings were hand released from weed competition three times. This releasing must explain in part the level of mortality from agencies other than *Armillaria,* lower than that which the authors have observed in normal plantations on such sites.

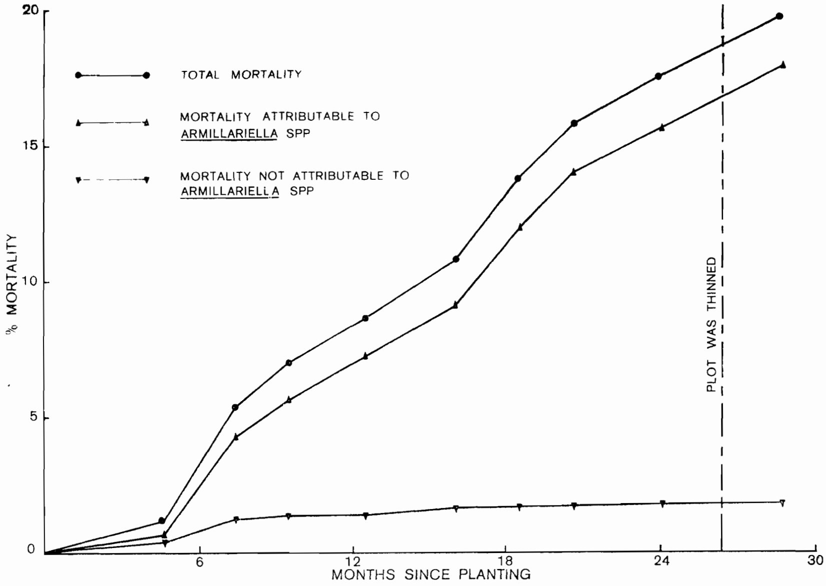

FIG. 1—Cumulative mortality of **P. radiata** seedlings planted on a mixed hardwood, indigenous cut-over site at 1 × 1 m spacing.

Distribution of Stumps and Sporophores

Tawa was the dominant species in the trial area. It represented 44% of the stumps by number and accounted for 62% of the stump basal area and 81% of the stumps bearing *Armillaria* sporophores (Table 1).

There was abundant sporulation of both species of *Armillaria* in May-June of 1975 and 1976. Stumps of seven different indigenous species bore sporophores, however, almost all sporulation occurred on tawa. Each *Armillaria* species appeared on almost an equal number of stumps; although it was noticeable that *A. limonea* sporulated more profusely, but over a shorter period. A total of 16 stumps (3 tree species) bore sporophores of both species.

In only one case did a stump that had borne sporophores in 1975 not bear them again in 1976. On three stumps *A. limonea* fructifications were replaced by those of *A. novae-zelandiae* in the second year. A further stump which had fructifications of both species in 1975 had borne only those of *A. limonea* in 1976. The assumption was made that if a stump bore a species of *Armillaria* fructification in 1975 then it was still colonised by at least that species in 1976.

Association of Mortality with Stumps and Sporophores

Mortality caused by *Armillaria* spp. was clustered around tawa stumps (Fig. 2). The mortality rates within distance classes around all stumps of tawa differed significantly from their mean ($\chi^2 = 79.4$; d.f. $= 4$; $P < 0.01$). The mortality rates within distance

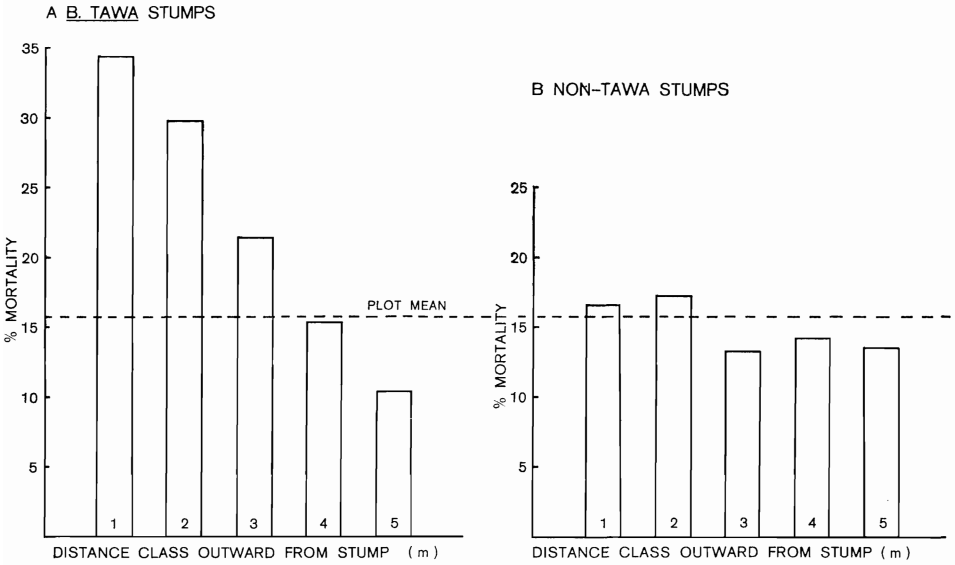

FIG. 2—Distribution of **P. radiata** seedling mortality caused by **Armillaria** in relation to (a) the proximity of tawa stumps, irrespective of the presence of non-tawa stumps, and (b) in relation to proximity of non-tawa stumps, irrespective of the presence of tawa stumps. Results for distance classes are pooled over all individual stumps involved, and irrespective of **Armillaria** sporulation (Numbers of seedlings involved for each distance class: (a) 1, 123; 2, 133; 3, 116; 4, 84; 5, 48
(b) 1, 96; 2, 117; 3, 88; 4, 79; 5, 57.

classes around all non-tawa stumps did not differ significantly from their mean ($\chi^2 = 5.5$; d.f. = 4; $P > 0.05$). The level of seedling mortality decreased consistently with increasing distance from stumps of tawa and remained relatively constant with increasing distance from the remaining (non-tawa) stumps (Fig. 2).

An examination of mortality by distance class, up to 3.5 m, from stumps of tawa in the four sporophore categories, showed that mortality levels significantly decreased with distance from stumps that had borne only sporophores of *A. novae-zelandiae* ($\chi^2 = 8.6$; d.f. = 2; $P < 0.05$). There were no significant differences ($P > 0.05$) in seedling mortality rates by distance classes from stumps that had borne: only *A. limonea* sporophores, sporophores of both species, or no *Armillaria* sporophores (Fig. 3). Thus, the pattern of mortality depicted in Fig. 2a is primarily attributable to stumps that had borne only sporophores of *A. novae-zelandiae.*

Seedling mortality within 3.5 m of tawa stumps (distance classes "1 "2" and "3" of Figs. 2a and 3) was related to the type of sporophores the stumps bore (Fig. 4). The level of *Armillaria*-caused mortality of seedlings could be ranked as follows: stumps bearing sporophores of both species (A) *equal to* stumps bearing sporophores of *A. novae-zelandiae* only (B) *greater than* stumps bearing sporophores of *A. limonea* only (C) *greater than* stumps bearing no *Armillaria* sporophores (D). A and B did not differ significantly ($P > .05$) while all other combinations (A and C; A and D; B and C; B and D; C and D) did differ significantly ($P < .01$).

Considering all stumps (irrespective of tree species) the results were similar. The magnitude of difference between sporophore categories was larger even if not more significant. In this case there was marginally higher seedling mortality ($\chi^2 = 5.8$; d.f. 1; $0.01 < P < 0.05$) within 3.5 m of stumps bearing sporophores of *A. novae-zelandiae* than within 3.5 m of those with both species.

Distribution of Living Trees Infected by Armillaria *spp.*

Of the 2971 living trees, 1468 were thinned, by excavation, and examined. Of these trees 28% (413) were infected with *Armillaria.* The distribution of these infected trees was very strongly related to their proximity to trees previously killed by *Armillaria.* The infected but still living trees were grouped around trees previously killed by *Armillaria* (Fig. 5).

DISCUSSION

Tawa was once the dominant species in the study area. Much of the Mamaku Plateau as well as other central North Island areas, are still or were once dominated by this species. Thus, many of the relationships between *Armillaria* root rot and indigenous stumps reported here are likely to be applicable over a much larger area.

The failure of an *Armillaria* species to sporulate on a particular stump does not show that the stump is uncolonised by that species. However, the level of mortality associated with non-sporophore bearing tawa stumps is consistently lower than that associated with the other three categories (Fig. 4), suggesting that most of the colonised stumps bore fructifications within the first two years. If sporophores are a reliable indicator of stump infection, they may be useful in predicting where localised high mortality could be expected. Yet in the Mamaku Plateau at least, *Armillaria* fructifications do not become plentiful on stumps until the second season after burning, by which time the land has usually been planted.

The significant difference in the level of mortality around tawa stumps that bore only sporophores of *A. novae-zelandiae* from those with only *A. limonea* suggests that under field conditions *A. novae-zelandiae* is more pathogenic to *P. radiata* seedlings. FRI records (unpublished) show that of the two, *A. novae-zelandiae* has been observed fruiting on a larger number and range of host substrates. Perhaps the significant difference in mortality levels under field conditions result from the relative rates of substrate colonisation and/or rhizomorph production by the two species. Preliminary results from inoculation studies with root segments of indigenous trees suggest that *A. novae-zelandiae* is a more prolific rhizomorph producer than *A. limonea* (Shaw,

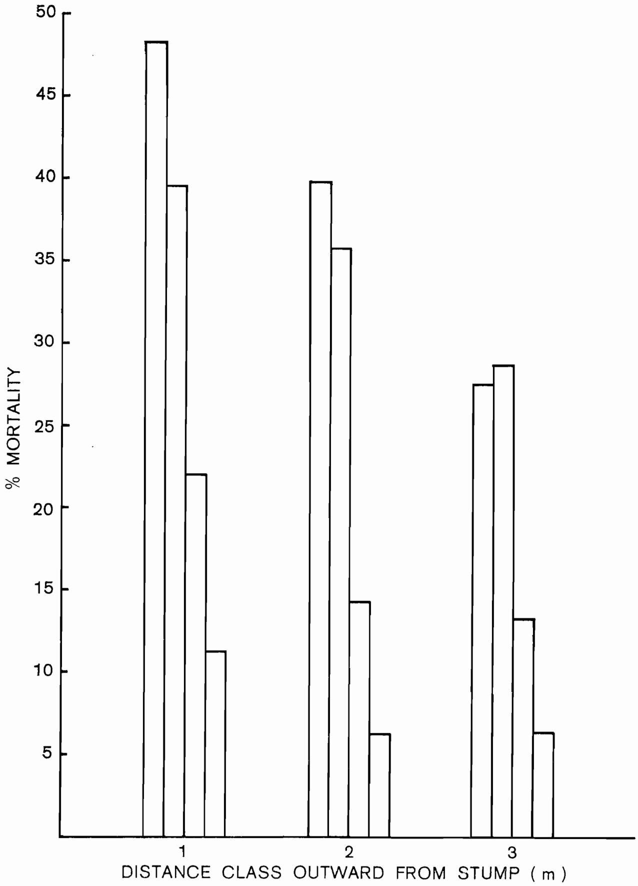

FIG. 3—Distribution of **P. radiata** seedling mortality caused by **Armillaria** spp. in relation to the proximity of tawa stumps and the species of **Armillaria** sporophore (as given in Fig. 4) seen thereon.

unpubl.). If the two *Armillaria* species differ in their field pathogenicity on *P. radiata,* then the lack of a significant difference in seedling mortality in the areas surrounding tawa stumps supporting sporophores of either *A. novae-zelandiae* or those of both species (Fig. 4) requires explanation.

The results with all stumps suggest that mortality is strongly associated with sporophore bearing stumps rather than with *B. tawa* stumps *per se.* However, tawa stumps are so numerous that they must be considered the prime source of inoculum in this disease situation.

The earliest seedling mortality was adjacent to old forest debris which had either been partially buried or was too large to remove in site preparation. This debris consisted of spars and limbs which had accumulated on the forest floor during the life time of the previous indigenous forest. It was colonised by *Armillaria* spp. and in one case bore fructifications of *A. novae-zelandiae.* These initial deaths did not lead to the development of debris-based centres of infection.

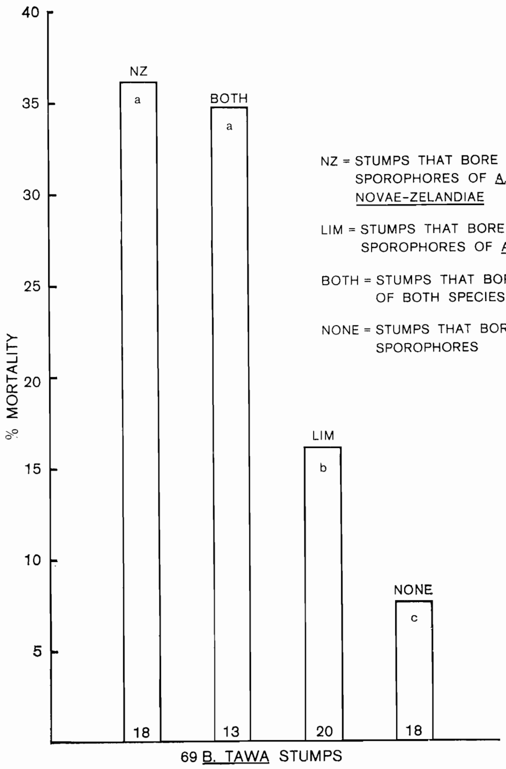

FIG. 4—Mortality attributed to **Armillaria** in **P. radiata** seedlings planted within 3.5 m of tawa stumps, stratified by the species of **Armillaria** sporophores seen thereon. Numbers within bars are the number of stumps within each category. Bars annotated with different letters differ significantly ($P < .01$).

Our data suggest that mortality will continue in radially expanding infection centres (cf. Redfern, 1973), putting more ground out of production. Beveridge (1972) reported that in a similar stand the incidence of *Armillaria*-caused mortality reached a maximum in the second and third year and declined after the fifth year, from planting. By this time mortality had reached 40-50%. Assuming that all the infected trees in our plot die, a level of 38% mortality, markedly grouped, would be reached. But the level of infection will not remain static; more trees will undoubtedly become infected.

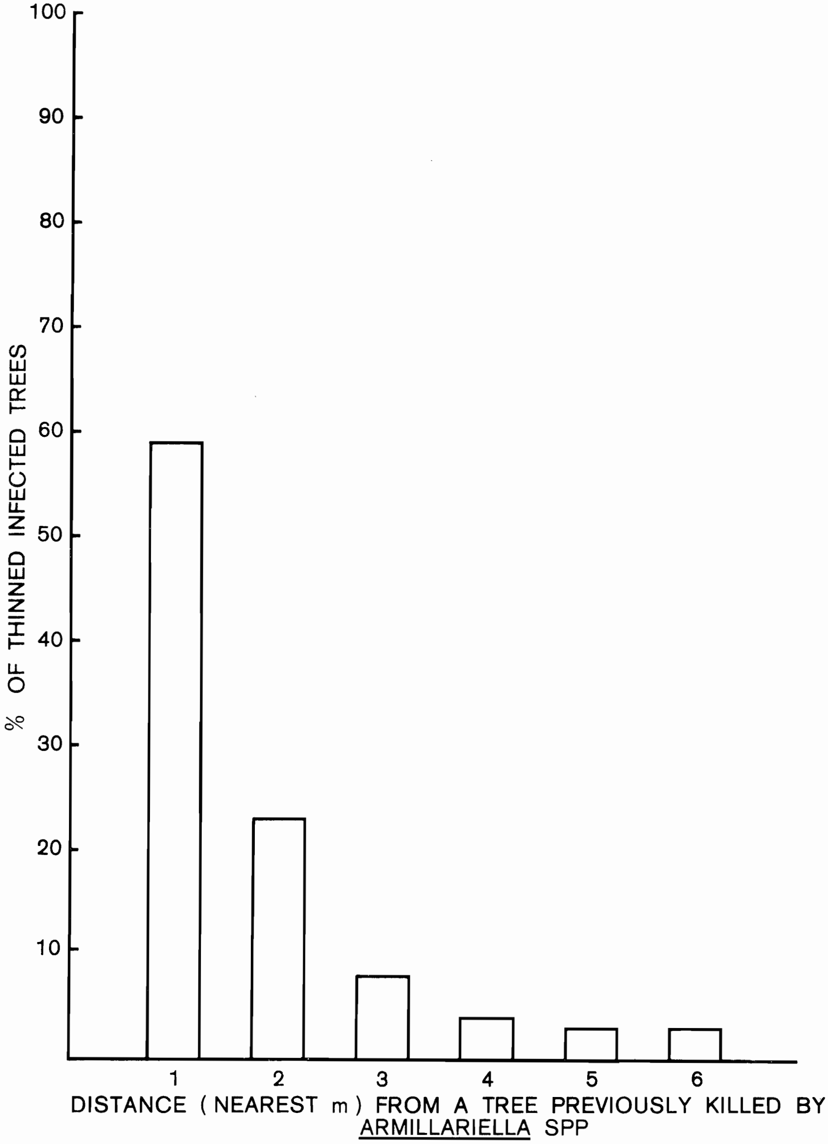

FIG. 5—Spatial relationship between living trees (thinned from the stand) that were infected with **Armillaria** spp. and those previously killed by **Armillaria** spp.

Although the root collar resinosis of young trees does not provide adequate protection from *Armillaria* attack, the trees may become more tolerant of infection with age. Ten year old *P. radiata* with 65-80% basal girdling due to *Armillaria* infection can continue to grow, although significantly slower than uninfected trees, for at least 1 year (Shaw and Toes, 1977). Only when the basal girdling reached 100% did these authors record any mortality during their study period. It would appear that in older trees the effect that *Armillaria* infections have in cutting off part of the root system, is reflected in a reduced growth rate and lessened wind stability. The decline in mortality rates after 5 years (Beveridge, 1972) may be more a result of the longer time it takes older trees to succumb than of any decline in *Armillaria* activity. Thus, what is the economic future of a stand that after 27 months has already suffered 16% grouped mortality through *Armillaria* root rot and has 28% of the remaining living stems affected by the disease?

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