INFECTION CHANGES AND VOLUME LOSS IN A 19-YEAR-OLD PINUS RADIATA STAND AFFECTED BY ARMILLARIA ROOT ROT

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ABSTRACT

The level of infection by **Armillaria** spp. in a 19-year-old, wide-spaced **Pinus radiata** D. Don stand was re-assessed after 9 years. Although the over-all infection level had changed little, the individual trees infected at the end of the period were not necessarily the same ones which had been infected at the start. Thirty-one percent of the trees infected at the start were uninfected at the end of the 9-year period. Sectional measurements showed that growth trends reflected changes in infection by **Armillaria** spp. Volume loss due to lethal infections was predicted to be between 26 and 61 m^3/ha on a 28-year rotation. Over the same period of time the loss of potential volume attributable to sub-lethal infections was estimated at 5.5 to 11 m^3/ha.

Keywords: infection level; volume loss; Armillaria root rot; mortality; **Pinus radiata**.

INTRODUCTION AND STAND HISTORY

Armillaria-caused infection of forest trees in New Zealand has been most extensively documented in stands of *Pinus radiata* established on sites recently cleared of their indigenous forest cover (MacKenzie & Shaw 1977; Shaw & Calderon 1977; Shaw & Toes 1977; Roth *et al.* 1979; van der Pas 1981a; van der Pas & Hood 1984). This documentation of impact has dealt with mortality in the first 5 years. Dendrometer bands were used by Shaw & Toes (1977) to measure the loss of potential diameter increment of infected trees in their tenth year of growth. Based upon this information Shaw & Calderon (1977) predicted the amount of money which could be spent upon site preparation if this would reduce volume losses by 60%.

This study was conducted in the same stand as the earlier study (Site 2 of Shaw & Toes 1977). The objectives were to document the changes in the pattern of *Armillaria* spp. infection 9 years after the final prescribed thinning and to reassess the predictions of Shaw & Calderon (1977). The studied stand was established as part of a site preparation trial in reverted cut-over native forest (Block E of Beveridge 1966). As stand openings caused by *Armillaria* spp. filled in with weeds, notably toetoe (*Cortaderia fulvida* (Buch. Zotov), a silvicultural solution was sought in a wide spacing and grazing regime. The relationship between this weed and *Armillaria* spp. infections of pines was investigated by Shaw *et al.* (1976) and an account of the early grazing has been provided by

Beveridge *et al.* (1973). The stand was sprayed with copper to control foliar infections by *Dothistroma pini* Hulbary in its fourth, fifth, and sixth years and was probably sprayed in every year that *D. pini* infection of the tree crowns reached the 25% level described by Kershaw *et al.* (1982)..

METHODS

Unpublished data collected for the earlier study (Shaw *et al.* 1976) formed the base for both the dendrometer band study (Site 2 of Shaw & Toes 1977) and this study. In the earlier studies, the soil was carefully removed from around the root collar of each tree (and later replaced) so that symptoms of infection by *Armillaria* spp. could be detected. The author examined each tree in 1976 and in 1985.

In the 1976 study each tree was examined and classified independently by the author and one or (frequently) two other people. Any discrepancies in classification were resolved at a final joint examination. Using further unpublished data gathered by Shaw & Toes (1977), the *Armillaria* spp. infection data for all trees living on the site in 1976 were reclassified into one of four classes, depending on the extent of the root collar circumference which had been girdled by resinosis (see below). After examination of all trees in 1985 the changes in infection in 9 years were assessed. A fifth class was established to accommodate the trees which had died and or been windthrown since 1976.

A tree was considered to be infected if it had resinosis at the root collar, and rhizomorphs were found attached to the region of resinosis. Frequently, in very heavily infected trees, mycelial fans could be found under the bark in the region of resinosis. Although rare, cases of resinosis alone were considered to be caused by mechanical damage and such trees were not counted as infected. Trees were placed into one of the following five classes:

I — root collar circumference free from infection by *Armillaria* spp.
II — infected, but basal resinosis extending <5 cm around root collar
III — infected, with basal resinosis extending >5 cm but <50% around root collar
IV — infected, with basal resinosis extending over >50% of basal circumference
V — tree dead or windthrown.

Since a living tree could have started in any one of four classes and ended up in any one of five a total of 20 sets of classification were possible. To have adequately sampled all 20 sets would have resulted in an unscheduled, non-productive, thinning of the stand. For this reason, annual volume increments were computed for only four of these sets. The first pair of sets was composed of trees which had started out uninfected (i.e., Class I in 1976) and by 1985 were either heavily infected (Class IV) or had remained uninfected (Class I). These were known as the I-to-IV and I-to-I sets respectively. The second pair of sets had started out heavily infected (i.e., Class IV in 1976) and by 1985 were either still heavily infected (Class IV) or had apparently recovered from the infection (now Class I). They were known as the IV-to-IV and IV-to-I sets respectively.

Using the method of van der Pas *et al.* (1984) annual volumes were computed for each tree for the years 1973 to 1985. These data were used to produce volume lines for each of the sampled sets. All 12 available unsuppressed trees in the I-to-IV set were sampled, and a similar-sized sample was taken of the I-to-I set. Samples from the IV-to-I and IV-to-IV sets contained 15 trees each. The diameter over bark at breast height was recorded for each tree in the four sets and the sample trees were selected so that their mean and diameter distribution were similar to that of the set they represented. As the outermost ring did not represent a full growing season, volume computations were based upon the penultimate ring (i.e., yielding volumes for 1984). As a living tree could start in any one of four classes and (if still living) end up in any one of four classes, there is a 4 × 4 matrix of infection classes (see Table 1). The four sets sampled (I-to-IV, I-to-I, IV-to-I, and IV-to-IV) form the corners of this matrix. The assumption was made that the corner set in each quarter of the matrix could be taken to represent that quarter. Thus, by weighting the volume lines for the four sampled sets by the number of trees in their quarter of the matrix and summing them, a stand volume line was obtained. The Kaingaroa Growth model (Elliott & Goulding 1976) was used to extrapolate this line to 1994 (a harvest at 28 years). The site index was chosen so that the predicted line was the best fit for the existing data (up to 1984).

TABLE 1—Redistribution of the health classes for the 451 trees from 1976 to 1985

		1985 Classification* [TO]				
		I	II	III	IV	V (dead)
1976 Classification [FROM]	I (181)[†]	115[‡]	13	31	14	8
	II (73)	35	12	17	5	4
	III (64)	26	13	15	8	2
	IV (133)	23	32	37	27	14

* Health classes as defined in Methods

[†] 1976 class totals

[‡] The four sets which were sampled are circled and the quarters of the matrix they were assumed to represent are separated by a broken line.

The size of the health classes in 1994 was predicted. To do this, the assumption was made that the trends of the redistribution of infection class redistribution in the 9 years from 1976 to 1985 would continue in the next 9 years (i.e., from 1985 to 1994). A transition matrix, which showed the proportion of trees in one class moving into another between 1976 and 1985, was produced. The 1994 class sizes were obtained by post-multiplying the vector of numbers for 1985 by this matrix.

RESULTS

In 1976, 60% of the trees in the stand were infected by *Armillaria* spp. By 1985, 6% of the trees had died or been blown over, and 53% of the remaining stems were infected.

The redistribution of the trees within health classes from 1976 to 1985 is shown in Table 1 and the observed class totals for 1976 and 1985 along with the predicted totals for 1994 are presented in Table 2. Volume lines for the sectionally measured sets of trees are provided in Fig. 1.

TABLE 2—Health class size in 1976, 1985, and 1994

Year	Living trees infected (%)	Health class* I	II	III	IV	V	
1976	60	181	73	64	133	0	Observed
1985	53	199	70	100	54	28	Observed
1994	48	210	59	89	44	49	Predicted

* Health class as defined in Methods

DISCUSSION

A simplistic view of the data (Tables 1 and 2) indicates that a 6% loss of potential crop trees was accompanied by a 7% reduction in the number of living stems infected by *Armillaria* spp. The pathosystem has not been as close to equilibrium as this would suggest; it has, in fact, been quite dynamic. Despite little change in the over-all infection level, the individual trees that were infected in 1976 were not necessarily the same trees that were infected in 1985. In fact, about one in three of the trees infected in 1976 was not infected in 1985. If it had not been for recruitment from the uninfected class of 1976 into all other classes the level of stand infection would have declined by not 7% but 21% in 9 years! Thus, when the vectors of population movements between classes are summed they largely cancel each other out. This not withstanding, the over-all trend has been towards an increase in the size of the uninfected class and an associated decline in the number of heavily infected Class IV trees (Table 2).

The observation that most of the recruits from the uninfected class moved by more than one health class (Table 1) highlights one of the limitations of this study. The 1976 and 1985 classifications are but two "frozen frames" from an otherwise unobserved "motion picture". The author could not tell if a lesion was healing over or actively expanding. Some lesions grew from nothing to occupy over half the root collar circumference in 9 years; 23 other lesions changed in the opposite direction (i.e., from Class IV to I). There is no way of knowing when these changes began or how long they took. Further, how many lesions appeared and subsequently healed over in the 9-year span is also unknown.

The volume lines (Fig. 1) must be interpreted with care as they were derived from probably heterogeneous sets. The sets with the least heterogeneity are likely to have

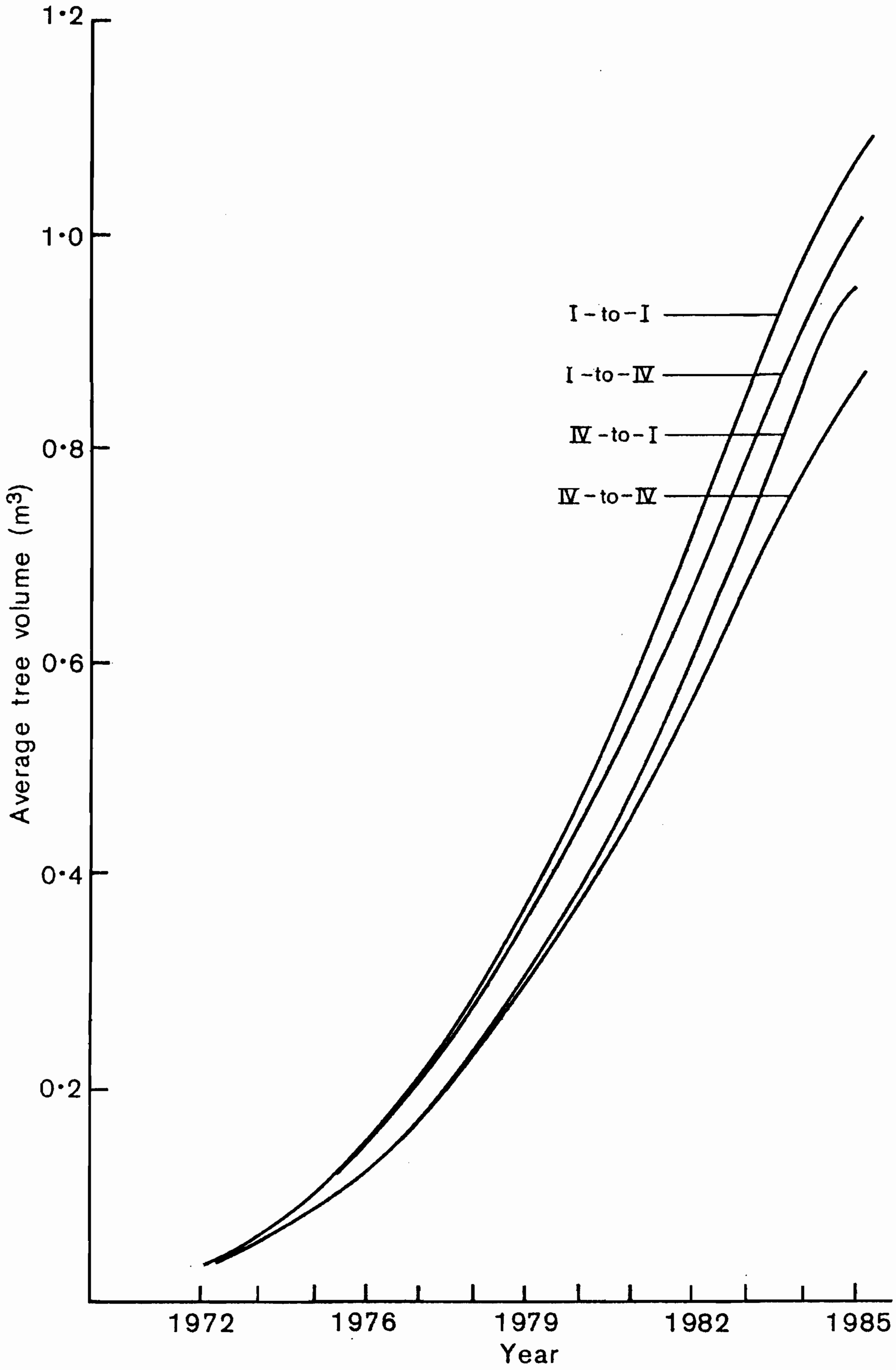

FIG. 1—Average tree volumes in four health classes. Class I-to-I: not infected in 1976 or 1985; Class I-to-IV: infected after 1976; Class IV-to-I: infected prior to 1976 but not after 1985; Class IV-to-IV: infected in 1976 and 1985.

been the I-to-I and IV-to-IV sets. Given the problems of interpreting the sets, it is wisest to do no more than note the trends in the volume lines derived from them. The volume lines for the I-to-I and I-to-IV sets are similar before and for several years after the 1976 assessment. This similarity would be expected as they had been derived from a common class (i.e., uninfected) and had diverged only as infection had an impact on one of the sets. Similar statements can be made about the volume lines for the IV-to-IV and IV-to-I sets. Here the divergence can be attributed to infection having a decreased impact upon the IV-to-I sets. The I-to-I and IV-to-IV volume lines started out at different points in 1976 and have continued to diverge since.

However, the dilemma still remains: are the trees in the IV-to-IV set slow-growing because they became infected, or did their slow growth lead to infection? Many of the uncertainties of this study could have been eliminated if the period between repeated observations had been shortened to a time span in which trees were observed to change by no more than one class. Sectional measurements could then be carried out, at the end of the rotation, on samples with a better-documented history.

Volume Losses Attributable to Armillaria **spp.**

If a tree is killed by infection with *Armillaria* spp. early in the rotation the increased growth of the adjacent living trees may compensate for the volume loss of the dead tree so that there is a negligible net loss in volume. When death occurs late in the rotation it must be considered a direct volume loss, for the adjacent living trees will not have sufficient growing time to fully exploit their increased growing space. A second form of loss comes from the sub-lethal infections. As the parasite diverts tree resources for its own use the tree fails to achieve its full potential size. Consequently, infections caused by *Armillaria* spp. can be divided into two classes:

(1) Lethal infections, which kill the tree;

(2) Sub-lethal infections, which the tree either tolerates or recovers from.

Volume losses attributable to lethal infections

Mortality caused by *Armillaria* spp. on sites similar to the one studied here can reach 40–50% in 5 years (van der Pas 1981b). The mortality rate reaches a peak in the third and fourth years, and rapidly declines from the fifth year (Beveridge 1974). In the studied stand, 4% of the potential crop trees died in the 2 years after the first thinning at age 5 (Beveridge 1974). The final thinning took place in 1976, and in the first year after it 2.7% of the potential crop trees died (Shaw & Calderon 1977). The author examined the dead trees in 1977 and attributed their deaths to *Armillaria* spp. In the course of the dendrometer band study, Shaw & Toes (1977) lost 10 of the 29 sample trees that had over 90% of their root collar circumference girdled by infection with *Armillaria* spp. Seven died standing and three were windthrown.

A windthrown Class IV tree from the studied stand was illustrated by Shaw & Calderon (1977, Fig. 3). In a study of the anchorage and root morphology of *P. radiata,* Somerville (1979) presented photographs and descriptions of three types of failure of trees winched over. His classes were:

(1) Uprooting

(2) Root failures

(3) Stem failures.

None of the windthrown trees in this study fitted Somerville's (1979) description of uprooting or stem failure. All were root failures and most looked like either Fig. 3 of Shaw & Calderon (1977) or Fig. 2b of Somerville (1979). On all the examined trees that were windthrown between 1976 and 1985, evidence of pathogenic attack by *Armillaria* spp. was found. Although it was windthrow that ultimately killed these trees, their deaths have been attributed to *Armillaria* spp. The author does not think that this bias will lead to a significant over-estimation of losses caused by *Armillaria* spp. in this stand.

MacKenzie & Shaw (1977) described the early development of centres of *Armillaria* spp. infection in a young pine stand. Roth *et al.* (1979) cautioned that this development may be more apparent than real. When the stands were older still, van der Pas (1981a) re-examined them and demonstrated that the interpretation of Roth *et al.* (1979) was correct: initial mortality may be clustered about indigenous stumps as reported by MacKenzie & Shaw (1977), but subsequent mortality is apparently randomly distributed. In New Zealand the classical concept of circular ever-expanding centres of infection caused by *Armillaria* spp. is not applicable to *P. radiata* stands over 10 years old since many trees older than 10 years apparently recover from even very heavy infections (Table 1). Despite having been affected by *Armillaria* spp. for 19 years the stand has no unacceptably large gaps in it. Much of the mortality in the first half of the rotation has, in part, been a "biological thinning". Living trees adjacent to "*Armillaria*-kills", released from competition, may respond by increasing their rate of growth. In addition to this ongoing "biological thinning", the stand has received three prescribed thinnings and four pruning lifts resulting in widely spaced trees pruned to 6 m. Some of the apparent recovery of infected trees between 1976 and 1985 may have been caused by the third prescribed thinning in 1976. As the trees were so widely spaced by 1985 it is unlikely that future deaths will have a significant releasing effect upon the growth rate of the remaining stems. For this reason all of the mortality occurring after 1985, and some of it occurring before, must be considered as a volume loss and not as a thinning. Mortality occurring before the final thinning constitutes a loss or reduction in the number of trees available from which to select the final crop, and not a volume loss.

The question is, at what time after final thinning does mortality caused by *Armillaria* spp. cease to be a "biological thinning" and become a volume loss? To provide estimates of this volume loss two dates were selected as the point at which this loss was assumed to become significant. Volume loss calculations were made assuming there would be no compensation over either the last 9 or 18 years of the rotation. When the four volume lines (Fig. 1) were weighted by the numbers of trees in the four quarters of the matrix (Table 1) and summed, their projected on-site volume at age 28 was 525 m^3/ha. Should the mortality trends of the first 9 years after final thinning (1976–85) continue in the last 9 years of the rotation (1985–94), then 21 more trees will die (see Table 2). If there is no compensating increase in the growth rate of the remaining "biologically released" trees then these deaths will amount to a volume loss of 26 m^3/ha at a rotation age of 28 years. Assuming that there had been no increase in growth rate to compensate for deaths since the final thinning (i.e., in the 18 years 1976 to 1994) the volume loss attributable to the 49 dead trees would be 61 m^3/ha. These two estimates, 26 and 61 m^3/ha, can be taken as probable lower and upper limits for volume losses which can be attributed to mortality caused by *Armillaria* spp.

The average rate of mortality of potential crop trees in the 9 years after the final thinning was 0.7% of the trees/year. It is predicted that the average rate of mortality for the next 9 years will be 0.6% of the trees/year. Although these rates are below 1% per annum and appear insignificant, they are more important than the loss of 40–50% of all trees in the first 5 years.

Volume loss attributable to sub-lethal infections

Shaw & Toes (1977) used dendrometer bands to show that the diameter increment of trees heavily infected by *Armillaria* spp. was 14–24% less than that of similar-sized uninfected trees. In modelling the potential volume loss caused by sub-lethal infections Shaw & Calderon (1977) assumed that the annual volume increment of heavily infected trees would be reduced by 14% over the last 10 years of the rotation. As stem volumes vary as a function of diameter squared, a volume reduction of 26% might have been more applicable. The infected trees studied by Shaw & Toes (1977) had resinosis girdling over 65% of the root collar circumference. As the study of Shaw & Toes (1977) and the one reported here were conducted in the same stand, their infected trees were drawn from the Class IV of 1976. In the study described here it was assumed that the annual volume increment of the trees predicted to be in the Class IV of 1994 (Table 2) will have been reduced by 26% over the last 9 years of the rotation. As it is unlikely that all of the Class IV trees of 1994 will have been in that class for the full 9 years, this estimate is likely to be an over-estimate of the volume loss attributable to sub-lethal infections caused by *Armillaria* spp. Nonetheless, this calculation predicts a maximum potential volume loss of 11 m^3/ha at 28 years. If 11 and 5.5 m^3/ha are taken as the upper and lower limits for potential volume loss attributable to sub-lethal infections, the total impact of infection by *Armillaria* spp. on this stand is estimated at 31.5–72 m^3/ha at 28 years. This is 6–13% of the projected 571 m^3/ha final volume without disease. In modelling disease loss Shaw & Calderon (1977) estimated that loss caused by *Armillaria* spp. would amount to 144 m^3/ha (or 29% of potential yield) on a 26-year sawlog rotation. The major difference between the two studies is that in the Shaw & Calderon (1977) model it was assumed that radially expanding mortality centres would develop and remove significant areas from production. It was assumed that in a sawlog regime 25% of the area would be unproductive; for pulpwood rotations the unproductive area was increased to 30%. The author has seen stands heavily infected by *Armillaria* spp. in which, after the final thinning, the crop trees were unevenly distributed. However, such stands are not as common as heavily infected stands in which large areas have not been taken out of production by this disease. Thus, the author suggests that a loss of 6–13% of potential volume is a realistic estimate of the impact that infection by *Armillaria* spp. is likely to have upon a 28-year wide-spacing and grazing sawlog regime on a native cutover site.

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