Disease Detection and Losses

Relationship of Growth Reduction in Douglas-fir to Infection by Armillaria Root Disease in Southeastern British Columbia

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ABSTRACT

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Stem volume growth during consecutive 5-yr periods was measured in four Douglas-fir (*Pseudotsuga menziesii*) stands infected by *Armillaria ostoyae* in the interior cedar-hemlock and montane spruce biogeoclimatic zones of southeastern British Columbia. Growth, expressed as percent of stem volume at the start of each period, decreased significantly as resinosis increased due to mycelial colonization of the tree base. It was highest in resinosis severity class 0 (healthy), lowest in classes 3 ($>$ 50–100% of basal circumference showing resinosis) and 4 (recently killed, 100% resinosis), and intermediate in classes 1 (no basal resinosis but root[s] infected within 1 m of root collar) and 2 ($\leq$ 50% basal resinosis). Differences among classes were greatest for the past 5-yr period and least, though still significant, for the past 15-yr period. Trends during the past 30 yr showed greater declines in severity classes 3 and 4 relative to class 0 than in classes 1 and 2. The period in which decline was initiated also occurred earlier (up to 25 yr ago) in classes 3 and 4 than in other classes. The percentage of basal circumference that was affected by lesion was strongly related to percent roots infected but only weakly to percent volume growth. The relation of percent basal circumference affected by lesion to percent volume growth was greatly strengthened by including the period in which decline was initiated in the regression equation.

Additional keywords: root rot.

Armillaria ostoyae (Romagn.) Herink causes a root disease of conifers in southern British Columbia and the northwestern United States (6,7,10,15), attacking trees of all commercial species. In coastal forests, mortality usually has ceased by age 25, whereas in interior forests mortality occurs throughout the rotation (9). In the southern one-third of British Columbia, east of the Coast Mountains, *A. ostoyae* occurs in the interior Douglas-fir, interior cedar-hemlock, montane spruce, and Engelmann spruce-subalpine fir zones (9), of which interior cedar-hemlock covers the largest area (14). All age classes and sites are considered susceptible to losses from Armillaria root disease. Within the interior cedar-hemlock and the adjacent interior Douglas-fir (drier) and montane spruce (wetter) zones, Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in mixture with other conifers, is the leading commercial species.

The interior Douglas-fir zone occurs at low elevation; many of the readily accessible Douglas-fir stands have been cut selectively on one or more occasions. Hence, few undisturbed stands remain. Selective logging in Armillaria-diseased stands has exacerbated the disease by creating new food bases and by allowing more rapid spread of the fungus in roots of harvested trees (9). In severely affected stands, few trees reach merchantable size.

In the interior cedar-hemlock and montane spruce zones, undisturbed stands of Douglas-fir, alone or with other conifers, that are affected by Armillaria root disease usually have discernible disease centers, occupying up to 30% of stand area (9). Within centers, up to 95% of the original stand has been killed or is infected. Annual losses of timber in the interior cedar-hemlock zone due to Armillaria root disease are estimated to be 105,000 cubic meters (13).

In the interior cedar-hemlock zone of the Kamloops and Nelson Forest regions, more than 20 and 40% of the productive forest area, respectively, comprises Douglas-fir in age classes 4 and 5 (60–100 years old, that is, from near to full rotation age (2). Estimates of growth loss currently are based only on a reduction factor applied to the total susceptible forest area, and there is an urgent need for growth losses to be quantified by each disease and severity level.

The objectives of this investigation were to measure the growth loss caused by *A. ostoyae* in 80–100-yr-old Douglas-fir and to relate loss to disease severity.

MATERIALS AND METHODS

Basis for methods. Given the wide range in site, stand composition, age class structure, and harvesting practices in the regions, we first studied the effects of the disease on trees in the dominant or codominant crown classes in relatively uniform microsites within undisturbed stands. In studies on other root diseases of forest trees, tree stem growth appeared to be more sensitive to the effects of disease than total tree size (3,4). Also, because of the manner of disease spread from tree to tree, differences in age at infection confound growth reduction with tree size. Therefore, we used a measure of relative tree growth rate during short periods (growth during a period expressed as a percentage of total size at the beginning of the period).

Classification of Armillaria root disease severity by tree-crown symptoms generally is unreliable (8) and is difficult to apply to mature trees. However, Douglas-fir trees infected by *A. ostoyae* produce a visible resinous flow at the base of the stem above diseased roots (basal resinosis) (9), usually long before crown symptoms are visible. The extent of basal resinosis on a stem probably is proportional to root system invasion by the fungus. Shaw and Toes (11) recorded highly significant differences in diameter growth between healthy 9-yr-old trees of *Pinus radiata* D. Don and those with more than 60% of the root collar circumference expressing symptoms of Armillaria root disease.

We used basal resinosis to assign trees to one of the following disease severity classes: 0 = no basal resinosis, no crown or root symptoms, that is, no mycelium or decay in roots within 1 m from the root collar; 1 = no basal resinosis, mycelial fans in bark or cambial layer or decay in roots within 1 m of the root collar; 2 = basal resinosis $\leq$ 50% of basal circumference, mycelial fans in bark or cambial layer beneath resinosis; 3 = basal resinosis $>$ 50 to $<$ 100% of basal circumference, mycelial fans in bark or cambial layer beneath resinosis; and 4 = basal resinosis 100%, tree dead, mycelial fans in bark or cambial layer beneath resinosis.

Procedures. Candidate stands in the interior cedar-hemlock and adjacent biogeoclimatic zones of the Kamloops and Nelson Forest regions were identified from field reports (D. Norris, B. C. Ministry of Forests, *personal communication*) and previous surveys (10). Stands for sampling were selected by field examination with the criteria of no previous logging, age 80–100 yr, more than 70% Douglas-fir stems, and infection by *A. ostoyae* present. The four stands selected were in the eastern, southern, and western parts of the regions (Fig. 1); one stand was in the montane spruce zone and three were in the interior cedar-hemlock zone (Table 1). The stands had regenerated naturally following wildfire. Portions of each stand, 0.5–1 ha, with apparently uniform microsite (slope, indicator vegetation, etc.) were searched for candidate sample trees. Sample trees were Douglas-fir with a diameter at 1.4-m height within 5 cm of the diameter of the mean tree of each site in the dominant or codominant crown classes and were free from stem deformities but with disease symptoms in one of the severity classes. Openings caused by root disease were not searched to avoid selecting trees whose growth could have been affected by the opening. Class 4 trees had been killed within the last 2 yr as evidenced by the presence of dry foliage and fine twigs. Broad severity classes were necessary because irregular bark surfaces obscured precise determination of the percent basal circumference showing resinosis. Candidates for classes 0 (healthy) and 1 (infected without basal resinosis) were verified by excavating lateral roots for 1–1.5 m from the root collar. Six sample trees in each severity class were selected randomly from the candidates.

Diameter over bark at 1.4 m (breast height) of sample trees was measured; then the trees were felled. Total tree height (length) was measured. Cross-sectional disks were cut at breast height and at every 2 m above breast height in stand 1. Tree volume calculated from disks measured at 4-m intervals was 98.5 ± 1.5% of that measured from disks measured at 2-m intervals; therefore, measurements in the remaining three stands were taken at 4-m intervals. Disks were not cut beyond a top stem diameter of 10 cm. A basal disk was cut from the stump as close to the ground (< 30 cm) as possible.

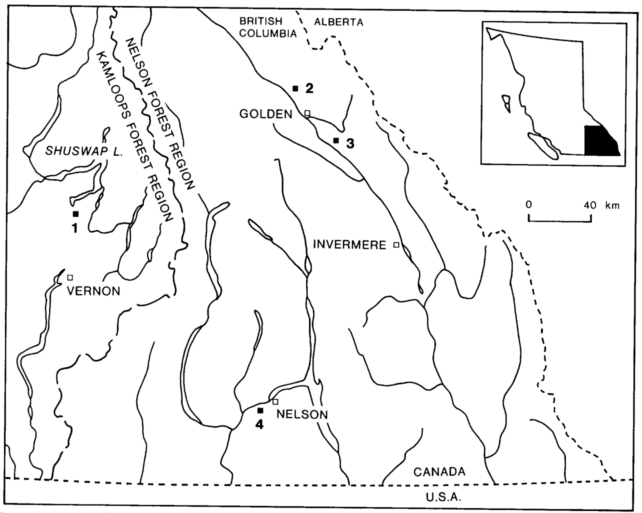

Fig. 1. Location of stands sampled for effects of infection by *Armillaria ostoyae* on growth of Douglas-fir.

TABLE 1. Douglas-fir stands sampled for effects of *Armillaria ostoyae* on tree growth

Stand	Location[a]	Biogeoclimatic subzone[b]	Age[c] (average)	DBH[d] (cm)	Height[e] (m)
1	Salmon Arm	ICHa1	83	26.0 (0.39)	26.1 (0.45)
2	Golden	ICHa2	106	33.4 (0.53)	29.3 (0.46)
3	Invermere	MSa	108	34.2 (0.71)	32.0 (0.35)
4	Kootenay	ICHa1	100	38.6 (0.57)	31.1 (0.31)

[a] British Columbia Ministry of Forests district.

[b] ICH = interior cedar-hemlock; MS = montane spruce; a, 1, 2 denote variants of subzones.

[c] Range ± 5 yr.

[d] Diameter at breast height (1.4 m). Means of sample trees; standard error of means in parentheses.

[e] Means of sample trees; standard error of means in parentheses.

Roots of each sample tree were excavated to a distance of 1–1.5 m from the root collar. The diameter of each primary lateral root was measured at its junction with the root collar and classified as healthy or infected based on the presence of resinosis and mycelial fans. For each tree, the cross-sectional area of primary roots was used to calculate the percentage of root system that was infected.

In the laboratory, bark was removed from each basal disk, and the length of lesion was measured between the margins of resin-impregnated wood on the disk circumference immediately beneath the bark resinosis. Lesion length was expressed as a percentage of the total circumference. Age of each tree was estimated from the number of rings on its basal disk.

Two radii were marked on the cross-sectional disks of each stem, excluding the basal disk. The sum of the largest diameter inside bark and the diameter at right angles to it was divided by four; then two radii equal to this length were selected (5). Five-year-diameter increments were measured from the annual rings along each radius, beginning with the outermost ring. The procedures of Alfaro et al (1) were used and measurements were made with a Digimic tree-ring measurer (Holman Electronic Controls Ltd., Fredericton, NB, Canada).

Stem volume of each tree at the end of each 5-yr period, from the most recent to the earliest, was calculated from the sum of 4-m bolt volumes; the mean of diameters at both ends of bolts and their lengths were used for the calculations. The volume of the basal bolt (ground to breast height) was calculated as a cylinder of diameter at breast height to exclude butt flare. The length of the topmost bolt to a top diameter of 10 cm was calculated from the taper of the preceding bolt. Volume growth was calculated for each 5-yr period as a percentage of the tree volume at the beginning of the period. It also was calculated for the most recent 5-, 10-, and 15-yr periods.

Analysis of variance was applied to test significance of differences in percent volume growth among stands, severity classes, and period lengths of 5, 10, and 15 yr. Stands were treated as blocks in the undisturbed 80–100-yr-old Douglas-fir type. Periods were analyzed for repeated measures to exclude correlation between measurements on the same tree (12). Duncan's multiple range test was applied to separate means of stands and severity classes. Orthogonal polynomial contrasts were made between periods for stands and severity classes. Multiple regression analyses were applied to relationships between percent volume growth, percent lesion, and percent root system infected. Percentages were transformed to arcsins for analysis.

RESULTS

Analysis of variance of percent volume growth showed highly significant differences ($P = 0.0001$) among stands. Stand 2 had the greatest volume growth (2.2%); 1 and 4 were not significantly different (1.7 and 1.8%, respectively); and 3 had the smallest volume growth (1.4%). Differences among severity classes and among the 5-, 10-, and 15-yr periods were significant ($P = 0.0001$). Percent volume growth decreased with increasing severity class. It also decreased as the period length decreased. However, there was a significant ($P = 0.0001$) interaction between severity class and period length because greater differentiation occurred among classes 2–4 at the 5-yr period than at the longer periods (Fig. 2). There also was a significant ($P = 0.01$) interaction between stands and period length because, in stand 1, percent volume growth in severity class 1 was significantly ($P = 0.001$) less than in class 0, whereas it did not differ in the other stands.

Reduction in percent volume growth in classes 1 to 4 relative to class 0 ranged from slight but nonsignificant ($P = 0.05$) increases in class 1, stands 2 and 3, to nearly 60% in class 4, stand 3 (Table 2).

Trends of percent volume growth for consecutive 5-yr periods showed severity classes 3 and 4 continuously declining relative to class 0 within the last 30 yr (Fig. 3). The period in which decline was

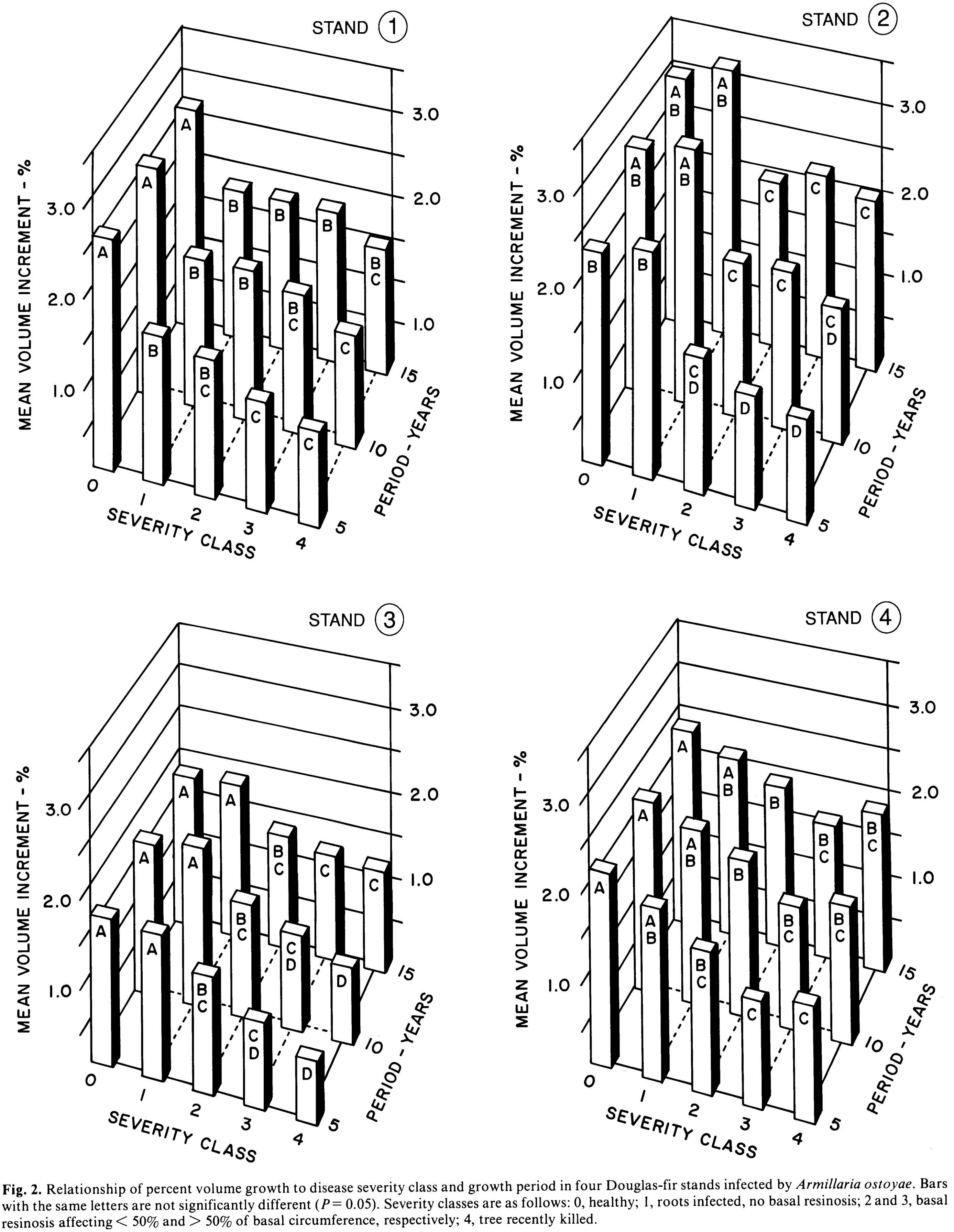

Fig. 2. Relationship of percent volume growth to disease severity class and growth period in four Douglas-fir stands infected by *Armillaria ostoyae*. Bars with the same letters are not significantly different ($P = 0.05$). Severity classes are as follows: 0, healthy; 1, roots infected, no basal resinosis; 2 and 3, basal resinosis affecting < 50% and > 50% of basal circumference, respectively; 4, tree recently killed.

TABLE 2. Difference in percent volume growth in Douglas-fir infected by *Armillaria ostoyae* relative to healthy trees during three measurement periods[a]

Stand	Period (yr)	Percent difference[a] in each severity class[b]: 1	2	3	4
1	5	35.3	38.5	57.0	55.5
	10	32.9	29.6	44.5	46.5
	15	30.3	25.8	32.8	37.8
2	5	+6.1	37.5	48.2	52.8
	10	+4.6	37.2	36.0	45.9
	15	+7.5	33.5	26.4	32.3
3	5	2.5	23.0	37.0	59.3
	10	+4.7	23.5	37.0	49.3
	15	+2.7	24.7	30.5	33.1
4	5	11.7	26.7	45.5	41.0
	10	9.8	19.7	36.1	31.8
	15	9.5	17.6	31.8	20.3
Mean	5	10.8	31.4	46.9	52.1
	10	8.3	27.5	38.4	43.3
	15	7.9	25.4	30.4	30.9

[a] All differences are negative unless shown as positive.

[b] 0 = healthy; 1 = roots infected, no basal resinosis; 2 = basal resinosis affecting <50% of basal circumference; 3 = basal resinosis affecting >50% of basal circumference; 4 = tree recently killed.

initiated in class 4 trees ranged from 10 yr ago in stand 3 to 25 yr ago in stand 1. The period in which decline was initiated in class 1 was more recent and the declines were more gradual than in classes 3 and 4. The period in which declines were initiated in class 2 varied from 25 yr ago in stand 1 to being nonexistent in stand 2. Before the period in which decline was initiated, percent volume growth in class 4 trees exceeded that of class 0 trees in all stands except stand 2. Percent volume growth in classes 1 or 2 or both was consistently below that of healthy trees. Fluctuation was greater in class 4 trees than in the other classes.

Regressions of percent of basal circumference affected by lesion on percent root system infected were significant for individual stands and for all stands combined (Table 3, Fig. 4). The relationship ranged from moderate to strong ($r^2 = 0.45$ to 0.72). Regressions of percent volume growth on either percent basal circumference affected by lesion or percent root system infected were not all significant and the relationship was weak ($r^2 < 0.25$). Regressions of percent volume growth on the period in which decline was initiated were significant for individual stands and all stands combined (Fig. 5). The relationship was moderate to strong ($r^2 = 0.49$–0.70). Regression coefficients for stands 1 and 2 (−0.048 and −0.052, respectively) were significantly different from those of stands 3 and 4 (−0.027 and −0.028, respectively). Regression coefficients were significant for 5-, 10- and 15-yr periods; the strength of the relationship decreased with increasing period ($r^2 = 0.61$, 0.56, and 0.50, respectively). Multiple regression

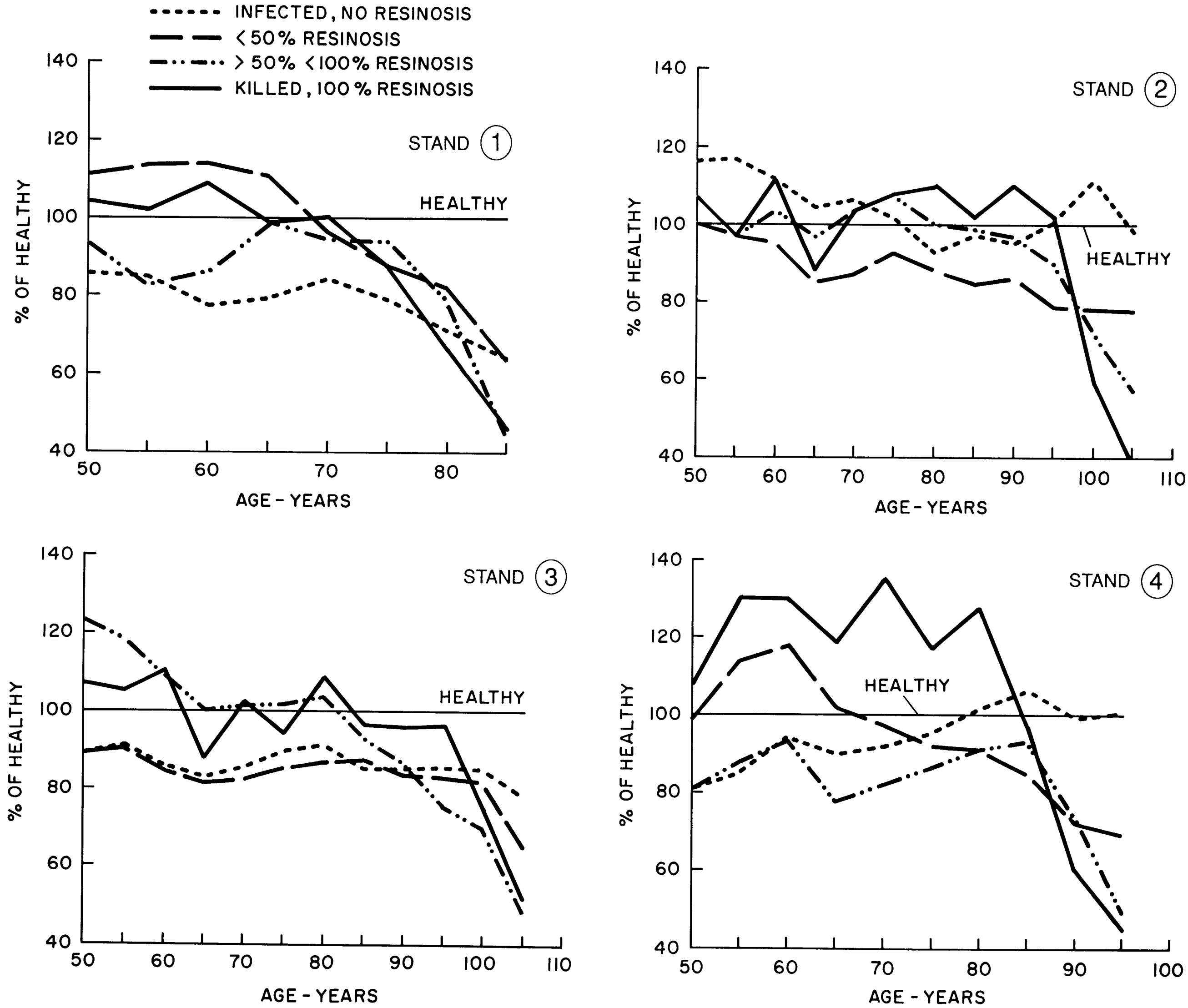

Fig. 3. Trends of percent volume growth in four Douglas-fir stands infected with *Armillaria ostoyae* relative to that of healthy trees (horizontal line).

coefficients of percent volume growth on both the period in which decline was initiated and percent basal circumference affected by lesion were significant for individual stands and for all stands combined. The relationship was stronger ($R^2 = 0.52$ to 0.71) than the relationships with the individual variables (Table 4).

DISCUSSION

Disease severity classification by basal resinosis due to infection with *A. ostoyae* successfully separated Douglas-fir trees into broad growth-reduction classes according to a convenient symptom rating. Estimates of stand growth losses can be derived from surveys of the numbers of trees in each class. The classification also differentiated among severity classes in the duration of growth reduction and could aid decisions about the timing of final or salvage harvest.

Growth reduction varied among stands, as did the rate of growth reduction over time as evidenced by the regressions of percent volume growth on the period in which decline was initiated. Differences in growth reduction, therefore, probably reflected differences among stands in factors affecting initial disease levels (for example, original inoculum loads), as well as those that modified subsequent rate of disease spread or tree responses (that is, other site or stand conditions). The greater growth reduction in severity class 1 in stand 1 compared with the other stands suggests that the root systems were less resilient to attack by the fungus, possibly because of the smaller tree sizes in this stand compared with the others.

Growth reductions were greatest in the most recent 5-yr period and diminished with increasing period length. This pattern is consistent with that of a progressive disease, with growth reductions cumulative over time caused by a rather slowly spreading mycelium. It suggests that infection by *A. ostoyae* occurred in class 3 and 4 trees at approximately mid-rotation, probably in distal parts of root systems, then spread proximally along roots. Basal lesions probably did not develop until the fungus approached the root collar, as evidenced by the significant correlation of percent basal circumference affected by lesion and percent roots infected within 1 m of the root collar. These conclusions are confirmed by observations on root systems of infected Douglas-firs over a 10-yr period. The fungus moved along roots toward the root collar at up to 10 cm/yr, and resinosis appeared above roots when mycelial fans were 10–15 cm from the root collar (D. J. Morrison, *unpublished*).

TABLE 3. Statistics for regressions of percent basal circumference affected by lesion on percent roots infected by *Armillaria ostoyae* in Douglas-fir[a] (data transformed to arcsins)

Stand	Regression statistic		Coefficient of determination
	Intercept	Slope[b]	
1	−0.149	0.715	0.45
2	−0.159	0.811	0.65
3	−0.139	0.900	0.68
4	−0.238	0.962	0.72
All	−0.157	0.814	0.60

[a] Percent circumference of tree base exuding resin due to fungal invasion.

[b] All slope coefficients were significant ($P = 0.0001$).

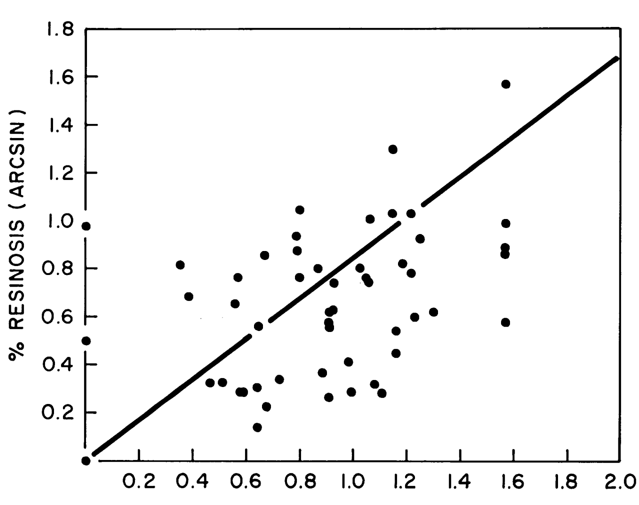

Fig. 4. Relationship of percent basal circumference affected by lesion to percent roots infected in Douglas-fir infected by *Armillaria ostoyae*. Data from four stands.

Infection of Douglas-fir in young plantations usually leads to rapid death of trees, leaving few traces of early mortality in 40- and 50-yr-old stands. At about stand age 20 yr, inoculum in residues from the previous stand ceases to be infective and, as root contacts develop between trees, the fungus spreads from diseased to healthy trees. Over the next several decades, the size of disease centers and the number of diseased trees gradually increase (D. J. Morrison, *unpublished*). Healthy trees become infected continually, resulting in a range of severity classes and growth reductions.

Although disease severity classification was satisfactory for assigning growth reduction categories, it did not fully account for

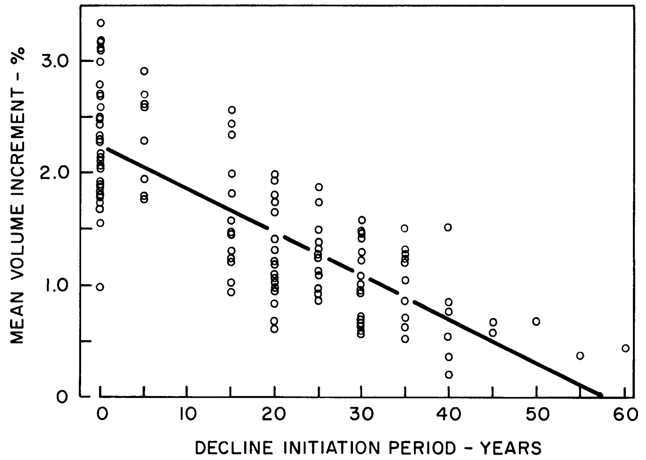

Fig. 5. Relationship of percent volume growth in Douglas-fir infected with *Armillaria ostoyae* to the period in which decline in growth was initiated. Data from four stands.

TABLE 4. Statistics for multiple regressions of percent volume growth on the period in which decline was initiated (PDI) and percent basal circumference affected by lesions (BCAL) in Douglas-fir infected by *Armillaria ostoyae*[a]

Stand	Years	Regression statistic			Coefficient of determination
			Coefficient		
		Intercept	PDI[b]	BCAL[b]	
1	5	2.51	−0.045	−0.132	0.71
	10	2.58	−0.044	0.077	0.64
	15	2.56	−0.044	0.280	0.62
2	5	1.85	−0.020	−0.411	0.71
	10	1.97	−0.217	−0.355	0.69
	15	1.20	−0.022	−0.177	0.65
3	5	2.23	−0.027	−0.169	0.69
	10	2.35	−0.026	−0.067	0.63
	15	2.44	−0.027	0.064	0.59
4	5	2.67	−0.051	−0.162	0.70
	10	3.15	−0.055	−0.083	0.62
	15	3.30	−0.050	−0.001	0.52
All	5	2.29	−0.034	−0.230	0.65
	10	2.50	−0.037	−0.097	0.57
	15	2.57	−0.037	0.071	0.51

[a] Continuous downward trend relative to healthy trees.

[b] All regression coefficients were significant ($P = 0.0001$). BCAL was transformed to arcsin.

the relationship, as evidenced by the weak relationship between percent volume growth and percent basal circumference affected by lesion. Basal lesion development occurs only in the later stages of the disease and depends on the fungus's invading the cambial zone of the lower stem. Further, growth reductions of a progressive disease certainly must depend in part on how long ago infection occurred. The period in which decline was initiated serves as an approximate measure of this period but may be conservative in that initial low levels of root infection may not cause detectable stem-growth reduction. The earlier period in which decline was initiated in the trend of class 1 severity trees in stand 1 appears to have been responsible for the greater growth reduction that occurred in that class compared with the same class in the other stands. Growth reduction also will vary due to adventitious root production by the host and changes in the inoculum potential of the fungus. The substantial contribution of the period in which decline was initiated to the percent volume growth regression and a lesser contribution by percent basal circumference affected by lesion is good evidence for the epidemiological scenario proposed.

The phenomenon that class 4 trees often had higher percent volume growth than class 0 trees before the period in which decline was initiated is consistent with observations in stands infected by *Phellinus weiri* that vigorous trees are likely to become infected sooner and at more loci than slower-growing trees due to their larger root systems (4). Conversely, percent volume growth of classes 1 and 2 trees often was less than that of class 0, suggesting that the root systems of less vigorous trees had lower probabilities of infection. The pronounced fluctuation of percent volume growth in class 4 before the period in which decline was initiated may reflect compensatory host defense responses, such as callus and adventitious root production, of vigorous trees in the early stages of infection.

We conclude that the classification based on severity of basal resinosis has good potential for estimating growth losses due to Armillaria root disease in Douglas-fir stands in the interior cedar-hemlock zone of British Columbia, that individual losses in tree growth are substantial and cumulative over a prolonged period, and that reductions in growth are due to a slow movement of the fungus through the root system toward the root collar. Lesion development at the base of trees appears late in disease development.

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