Effect of Stand Conditions on Advance of *Phellinus weirii* in Douglas-fir Plantations

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The assistance of A. A. Hall and A. L. S. Johnson is greatly appreciated.
Accepted for publication 18 December 1989 (submitted for electronic processing).

ABSTRACT

Bloomberg, W. J. 1990. Effect of stand conditions on advance of *Phellinus weirii* in Douglas-fir plantations. Phytopathology 80: 553-559.

Advance of *Phellinus weirii* in 62 infection centers over five intervals of 5–6 yr from 1958 to 1985 was studied in relation to stand conditions in three Douglas-fir plantations. Stocking level (number of trees per hectare) and average tree diameter were higher in sectors where the fungus advanced than in those where no advance occurred. Advances were more strongly related to tree diameter, whereas failures to advance were more strongly related to stocking level. Species composition or unrelated tree mortality also were associated with failure to advance. The fungus advanced unevenly among octants of centers. Only 1–3% of advances in an octant followed an advance during the previous period, and 76–96% of nonadvances followed nonadvances in the previous period. There were significant differences in advances among plantations, centers, and stand ages. Incidence of *P. weirii* in plantations was related to both stocking level and degree of tree aggregation.

Additional keywords: disease spread, root rot.

Few studies have been published on factors affecting advance of the root-rot fungus *Phellinus weirii* (Murr.) Gilbertson in forests of the Pacific Northwest. Nelson and Hartman (7) measured spread along selected diameters of infection centers from aerial photographs taken at 26-yr intervals. McCauley and Cook (6) derived radial spread in cardinal directions by relating the ages of the oldest successional ingrowth trees in infection centers with their positions on the radii. Bloomberg (1) derived spread rate from the mean radii of polygons circumscribing infection centers during 5- to 10-yr periods up to 35 yr. All three studies produced almost exactly the same estimates of mean annual advance of the fungus, viz 34–35 cm/yr. Because the studies were conducted in different forest compositions and geographic locations, their results create an impression of general uniformity and regularity of the advance of *P. weirii* independently of forest conditions. Yet observational evidence has shown the opposite situation to be truer: for example, varied sizes, shapes, and fungal activity of infection centers within small distances of one another.

Variation in advance of *P. weirii* in forest stands could be due to one or more of the following influences: genotype and physiological state of the fungus, ecological and site factors, and stand conditions; these influences probably interact. Stand conditions could be especially important with respect to infection of different tree species (11), ages, and condition. Spatial distribution could affect the frequency of root contacts among trees, the means by which the disease can spread (11). Herein, I describe a study of stand conditions as they relate to advance of *P. weirii*.

MATERIALS AND METHODS

The advance of *P. weirii* in relation to stand conditions was studied in three Douglas-fir plantations on east Vancouver Island in British Columbia, Canada (Fig. 1). The plantations were representative of many that were established in the 1940s (4). At intervals of 5–6 yr from 1958 to 1985, the coordinates, growth, condition, and disease status of each tree were recorded (3). The plantations varied widely in their stocking levels (trees per hectare), composition of tree species, and origins of trees (Table 1). Logging had preceded the first recording by approximately 28 yr in plantations 1 and 2, and by 18 yr in plantation 3. The remaining Douglas-fir stumps averaged 70 cm and were well decomposed with few traces of viable mycelium of *P. weirii* (A. L. S. Johnson, *personal communication*). Three aspects of fungal advance were studied in relation to stand variables: advance over time, pattern of advance, and incidence of infection.

Fungal advance over time. At each interval, coordinates of *P. weirii* were mapped based on disease symptoms in tree crowns and ectotrophic mycelium on root collars and/or decay in roots (11). The origin of an infection center was taken as the coordinates of the earliest tree showing infection by *P. weirii*. Where occa-

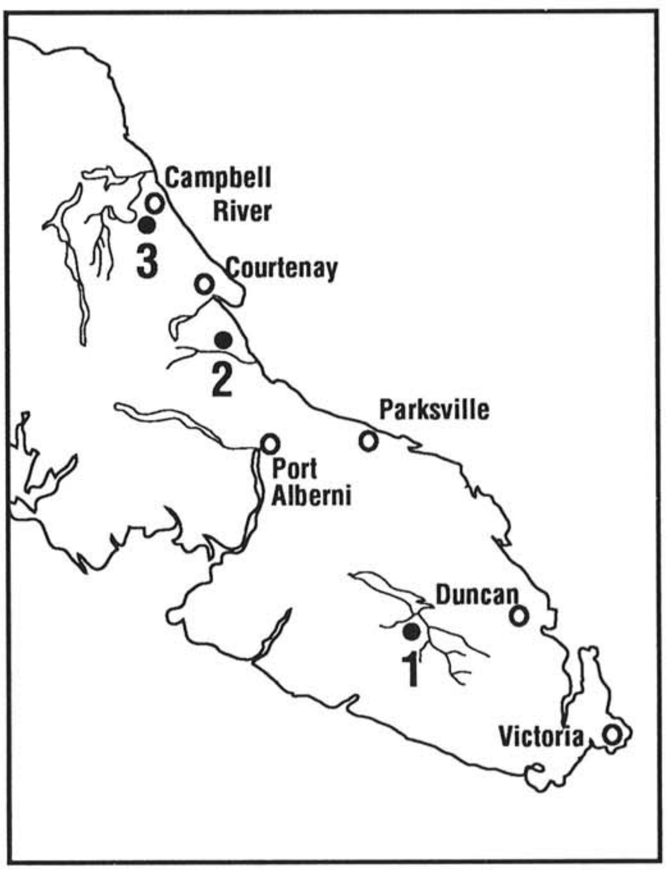

Fig. 1. Location of plantations on Vancouver Island, British Columbia, Canada, studied for advance of *Phellinus weirii* in Douglas-fir. Detailed descriptions of the plantations are given in Table 1.

TABLE 1. Description of plantations studied for advance of *Phellinus weirii*

Plantation	Location	Area (ha)	Year planted	No. trees/ha		Species (%)		Origin (%)	
				Original	Current	Douglas-fir	Other[a]	Planted	Ingrowth
1	Robertson R.	3.64	1944	1,446	1,987	84	16	67	33
2	Campbell R.	2.86	1943	2,335	2,374	93	7	93	7
3	Tsable R.	1.96	1946	2,966	3,273	92	8	64	36

[a]Includes western hemlock, western red cedar, and white pine.

sionally two or, rarely, three immediately adjacent trees constituted the earliest infections, a central point between them was used as the origin. A center was defined as an aggregation of infected trees with a common origin. Centers with ambiguous origins, for example, possibly more than one, were excluded. Uninfected trees within centers were not used to define the centers. A total of 62 centers was identified.

Eight equi-angled sectors (octants) subtended from the origin were superimposed on the maps of each center. The initial advance by the fungus in each sector was measured along the radius from the origin to an arc drawn through the most distal symptomatic tree in the sector at the next examination. Subsequent advances were measured along the radial distances between arcs of successive examinations. The areas of advance were measured as the portions of stands contained by the boundaries of a sector and adjacent arcs, with a 2-m buffer zone added distally to the outer arc (Fig. 2). The purpose of the buffer was to include potentially infected trees beyond the visible limits. The 2-m width was based on the average planting distance between trees. If no advance occurred, the area of advance was that of the buffer zone only. A total of 253 advances and 2,227 failures to advance were recorded for all infection centers, sectors, and examinations combined. Ten advances were judged to have crossed sector boundaries and were excluded.

The following stand variables were computed within each area of advance: number of trees infected by *P. weirii*, healthy trees, and all trees; number of trees infected by Armillaria root rot (*A. ostoyae* (Romagn.) Herink), as determined from presence of tree crown symptoms and mycelial fans below the bark of the lower stem (5); and number of trees that had died from causes other than root disease. Numbers were converted to a per hectare basis. Average tree diameters at 1.35 m above ground were computed for the above classes of tree. Stand ages were derived from the planting years of each plantation. Student's *t* tests were performed for each stand age and for all ages on differences between means of variables in sector areas in which *P. weirii* had advanced and in those in which it had not. Discriminant analysis was performed to determine those variables that had the greatest influence on fungal advance at each stand age and for all stand ages.

Pattern of advances. Analysis of variance was performed to examine differences among plantations, stand ages, centers, and sectors with respect to length of advance. Regression analysis was performed to examine the relationship between the variables and length of advance. Frequencies of advances within sectors and stand ages were compared.

Stand conditions associated with the arrest of *P. weirii*, that is, its failure to make further advances, were studied in 3-m-radius, semicircular plots distal to the arrested margins of centers, that is, the outermost infected trees in each sector. The following variables were recorded from stem maps: tree species and condition (healthy, symptoms of Armillaria root rot, or death from other causes); source of trees (planted or ingrowth); suppressed trees; or absence of any trees. Mean numbers of each variable were calculated for each stand age at which advance by *P. weirii* had been arrested.

Incidence of disease. Numbers of trees infected by *P. weirii* were compared among infection centers, plantations, and stand ages. Coordinates of trees in 0.50- to 0.75-ha blocks with different stocking levels in each plantation were classified by spatial distribution by Pielou's test of irregularity (8), with 100 samples per block.

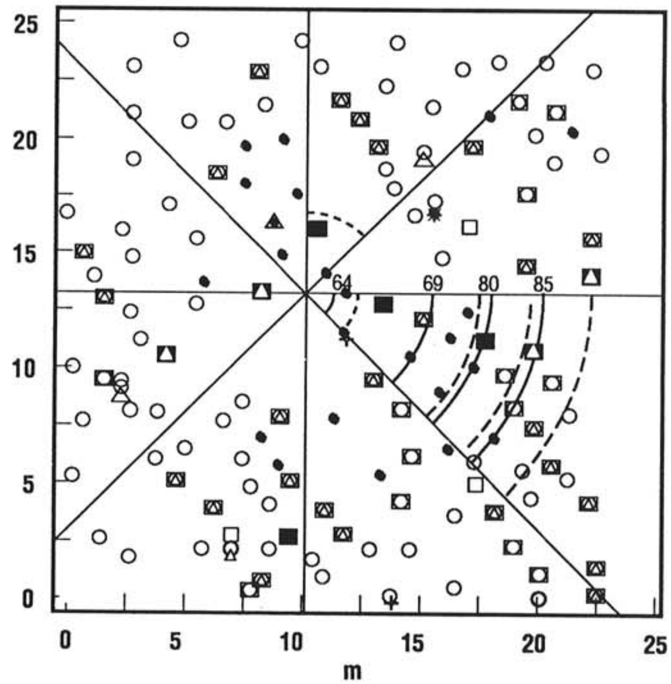

Fig. 2. Method of measuring advance of *Phellinus weirii* in infection centers in Douglas-fir plantations. In each octant, solid-line arcs represent farthest advance of the fungus at each year of examination (1964, 1969, 1980, 1985). Broken-line arcs represent 2-m buffers beyond farthest advance. Trees are: uninfected (○); infected by *P. weirii* (●); infected by *Armillaria* (■); ingrowth (+); species other than Douglas-fir (X); suppressed (△); dead (□). Tree condition may be shown by combinations of symbols.

RESULTS

Fungal advance over time. In all plantations and at all stand ages except one in each of plantations 1 and 3, the mean stocking level and tree diameter were significantly higher in areas of sectors in which *P. weirii* advanced than in those in which it did not (Tables 2 and 3). Except at two ages in plantation 2, the number of trees infected by *Armillaria* was lower in areas in which *P. weirii* advanced than in those in which it did not (Table 4). There were no significant differences between mean numbers of trees killed by other causes in areas where *P. weirii* had advanced compared with those in which it had not advanced.

Both tree diameter and stocking level were significant variables for discriminating advancement status, that is, advance or no advance. Accuracy of classification varied among plantations and stand ages. In plantation 2, tree diameter correctly classified more advances than failures to advance (Table 5), whereas stocking level correctly classified more failures to advance (Table 6). Number of trees affected by Armillaria root rot and/or killed by other causes was not significant as a discriminant variable.

Pattern of advances. The distance advanced by *P. weirii* differed significantly among plantations, stand ages (Table 7), and centers. There was no significant difference among sectors. There was no significant regression of length of advance on any of the stand variables.

Number of sectors in which *P. weirii* advanced within a center varied among plantations and stand ages (Fig. 3A and B). In general, centers that did not have any advances were the most frequent. No centers had advances in more than five sectors at any one age. There appeared to be no trend in the frequency of advances over time.

Failures of the fungus to advance were much more frequent than advances and almost always followed a failure to advance at the preceding stand age (Table 8). Advances were least frequent

TABLE 2. Relationship of stocking level (number of trees per hectare) to stand age and advancement status[a] of *Phellinus weirii* in Douglas-fir plantations

Plantation	n[b]	Status	Stand age (yr) 17–22	23–27	28–32	33–37	38–42	Mean[c]
1	24	Advance	...	...	3,570	1,770 A[d]	3,680	3,006
		No advance	1,062	1,062	1,385	1,540 A	1,617	1,326
2	264	Advance	5,082	3,890	3,948	3,997	4,215	4,235
		No advance	1,928	2,088	2,585	2,409	2,580	2,331
3	218	Advance	7,444	5,486	...	4,676	4,087 B	5,541
		No advance	1,997	2,082	3,516	3,464	3,908 B	3,010

[a] An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.
[b] Total number of advancements recorded in all octants of all centers.
[c] Weighted mean of all stand ages. Ages with no advances were excluded in calculating mean advance.
[d] All differences between advance and no advance within ages are significant ($P = 0.05$) except for those followed by the same uppercase letter.

TABLE 3. Relationship of mean tree diameter (cm) to stand age and advancement status[a] of *Phellinus weirii* in Douglas-fir plantations

Plantation	n[b]	Status	Stand age (yr) 17–22	23–27	28–32	33–37	38–42	Mean[c]
1	24	Advance	...	...	10.5	11.8	7.8 A[d]	8.6
		No advance	5.5	6.2	6.8	7.7	7.7 A	7.4
2	264	Advance	10.1	11.9	11.4 B	14.2	16.3	12.7
		No advance	8.5	9.9	11.2 B	11.6	13.0	11.3
3	218	Advance	9.1	8.7	...	11.3	12.1	10.9
		No advance	7.5	7.5 c	8.4	8.8	8.8	7.6

[a] An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.
[b] Total number of advancements recorded in all octants of all centers.
[c] Weighted mean of all stand ages. Ages with no advances were excluded in calculating mean advance.
[d] All differences between advance and no advance within ages are significant ($P = 0.05$) except for those followed by the same uppercase letter.

TABLE 4. Relationship of incidence of Armillaria root rot (number of symptomatic trees per hectare) to stand age and advancement status[a] of *Phellinus weirii* in Douglas-fir plantations

Plantation	n[b]	Status	Stand age (yr) 17–22	23–27	28–32	33–37	38–42	Mean[c]
1	24	Advance	...	...	0	0	0	0
		No advance	265	265	277	277	277	272
2	264	Advance	420 A[d]	314	550 B	170	96	276
		No advance	378 A	510	487 B	338	323	408
3	218	Advance	0	320	...	333	0	224
		No advance	667	565	517	589	399	525

[a] An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.
[b] Total number of advancements recorded in all octants of all centers.
[c] Weighted mean of all stand ages. Ages with no advances were excluded in calculating mean advance.
[d] All differences between advance and no advance within ages are significant ($P = 0.05$) except for those followed by the same uppercase letter.

TABLE 5. Reliability (percent correct classification) of mean tree diameter as an indicator of advancement status[a] of *Phellinus weirii* in Douglas-fir plantations at different ages

Plantation	n[b]	Indicated status	Stand age (yr) 17–22	23–27	28–32	33–37	38–42	All
2	264	Advance	67	72	89	75	67	79
		No advance	58	47	44	54	66	57
3	208	Advance	85	43	...[c]	78	50	80
		No advance	56	63	...	55	66	63

[a] An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.
[b] Total number of advancements recorded in all octants of all centers.
[c] No advances occurred.

TABLE 6. Reliability (percent correct classifications) of stocking level as an indicator of advancement status[a] of *Phellinus weirii* in Douglas-fir plantations at different ages

Plantation	n[b]	Indicated status	Stand age (yr) 17–22	23–27	28–32	33–37	38–42	All
2	264	Advance	55	73	89	13	61	58
		No advance	74	74	66	93	69	76
3	208	Advance	46	13	...[c]	91	87	72
		No advance	73	95	...	68	65	65

[a]An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.
[b]Total number of advancements recorded in all octants of all centers.
[c]No advances occurred.

TABLE 7. Relationship of advance[a] (cm/yr) of *Phellinus weirii* in Douglas-fir plantations to stand age (based on all sectors or those with advances)

Plantation	Sectors	Stand age (yr)[b] 17–22	23–27	28–32	33–37	38–42	All
1	All	0 x	0 x	1 x	5 x	2 x	1
	Advances only	...[c]	...	32	116	40	63
2	All	7 yz	12 y	1 z	19 x	3 z	8
	Advances only	43	61	43	81	50	58
3	All	2 x	5 xy	0 x	7 y	2 x	3
	Advances only	29	50	...	64	61	54

[a]An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.
[b]Means within plantations followed by the same letter are not significantly different ($P = 0.05$). No statistical analysis possible for sectors with advances only becasue of missing values.
[c]No advances occurred.

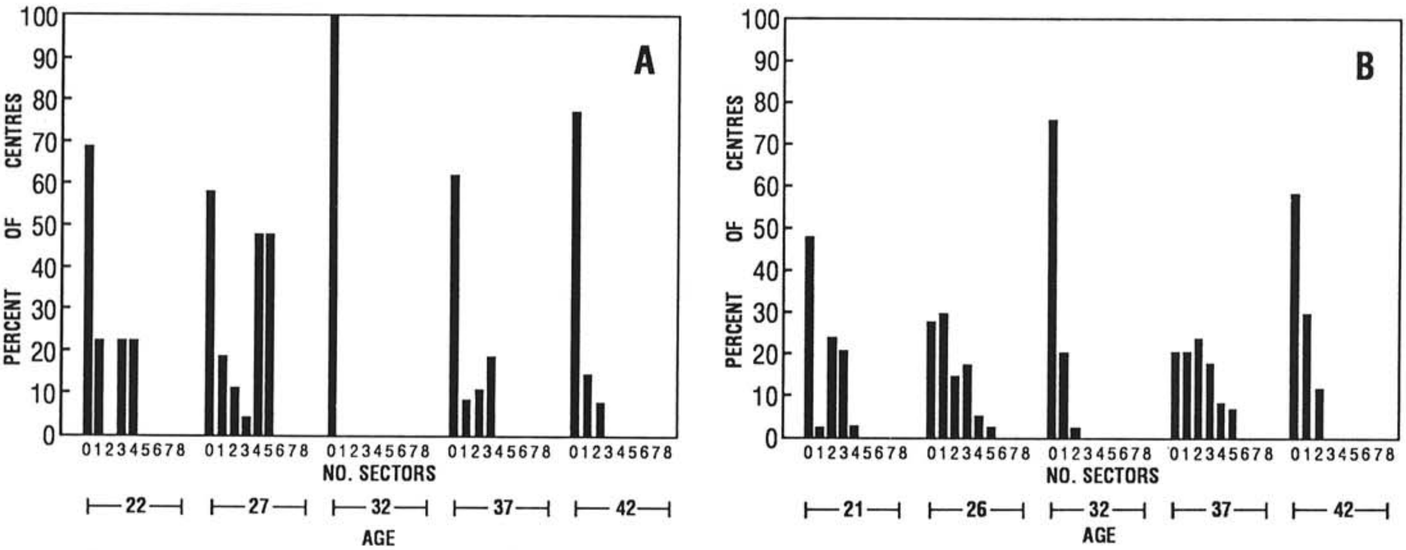

Fig. 3. Distribution of infection centers in Douglas-fir plantations by number of sectors (octants) with advances of *Phellinus weirii* at different stand ages. **A,** Plantation 2. **B,** Plantation 3. Plantation 1 had insufficient advances to determine their frequency. An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.

following an advance at the previous stand age.

At the youngest stand ages (15–19 yr), the percentage of 3-m-radius plots distal to the arrested margins of centers, that is, the outermost infected trees of sectors, was highest for those devoid of trees, lower for those containing healthy Douglas-fir, and lowest for those with dead trees or species other than Douglas-fir (Table 9). As stand ages increased, the percentage of plots devoid of trees generally declined and that of the other categories increased. There was insufficient data for the analysis of plots in stand 1.

Disease incidence. Incidence of infection by *P. weirii* differed significantly among plantations (2, 117, and 59 infected trees per hectare, or 0.2, 2.2, and 12.2% of trees in plantations 1, 2, and 3, respectively). Less than 5% of infections occurred on ingrowth trees and species other than Douglas-fir. Numbers of infected trees per center differed widely among and within plantations

TABLE 8. Frequency (%) of advancement status of *Phellinus weirii* in Douglas-fir plantations in relation to previous status[a]

Plantation	n[b]	Status	Previous status: Advance	No advance
1	120	Advance	1	2
		No advance	2	95
2	1,320	Advance	3	11
		No advance	10	76
3	1,040	Advance	1	6
		No advance	5	88

[a]An advance was recorded in each octant of an infection center if the outermost symptomatic tree was beyond the outermost symptomatic tree at the previous stand age; otherwise, no advance was recorded.
[b]Total of all advancements in all octants of all centers at all stand ages.

(Fig. 4). In general, frequency of centers decreased as their size increased.

In plantations 2 and 3, rankings of blocks by number of infected trees corresponded only partly with rankings by stocking level or Pielou's (8) index of irregularity but corresponded fully with ranking by composite index (irregularity index × stocking level, Table 10). There was an insufficient number of infected trees in plantation 1 to rank the blocks.

Small- and medium-diameter trees were infected more frequently by *Armillaria*, whereas medium- and large-diameter trees were infected more frequently by *P. weirii* (Fig. 5).

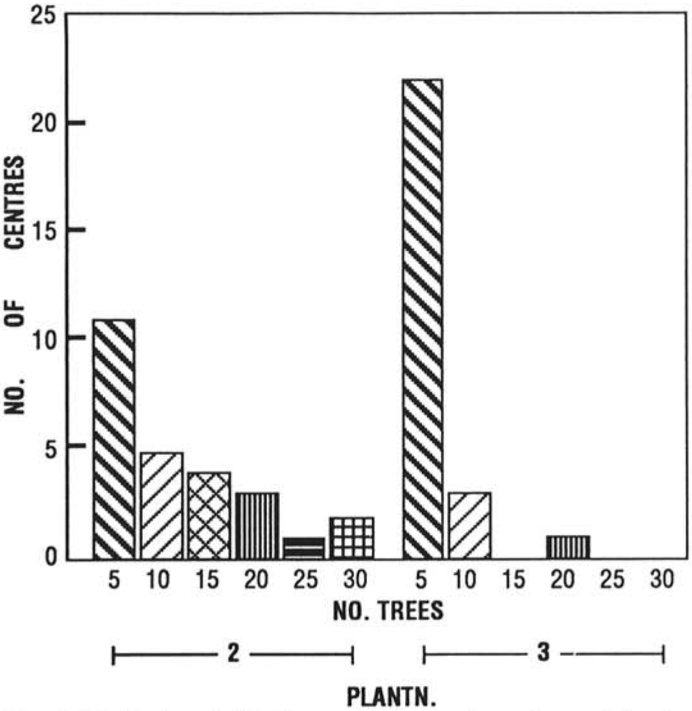

Fig. 4. Distribution of infection centers by numbers of trees infected by *Phellinus weirii* in Douglas-fir plantations.

DISCUSSION

The virtual absence of viable mycelium of *P. weirii* in stumps of the preceding stands at the first recording of symptoms suggests that they had little importance in subsequent advances by the fungus. The spatial distribution of symptoms over time strongly indicated advance among trees. The significant relationships between advances of *P. weirii* in Douglas-fir plantations and stocking level and average tree diameter emphasize the importance of con-

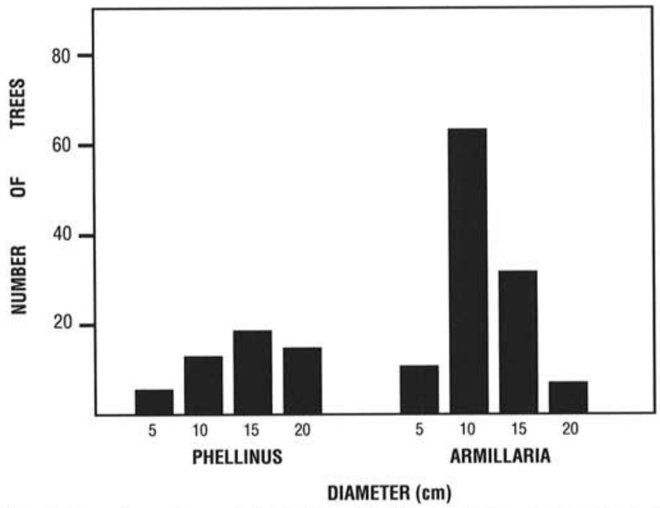

Fig. 5. Number of trees infected by *Phellinus weirii* and *Armillaria* in different diameter classes in Douglas-fir plantations.

TABLE 9. Relationship of stand age to percent plots with different tree components distal to outermost trees in each octant[a] infected by *Phellinus weirii* in Douglas-fir plantations

			Tree component				
Plantation	Stand age (yr)	No. plots	None	Healthy (Douglas-fir)	Dead (nondisease)	Dead (*Armillaria*)	Other species
2	15	144	45	30	14	12	6
	21	17	41	24	18	12	6
	26	31	19	52	26	19	10
	32	3	0	33	67	33	0
	37	51	25	55	33	12	16
3	19	148	36	28	4	15	33
	24	13	0	46	23	0	46
	29	14	21	36	7	14	57
	34	17	6	65	18	18	82

[a]See text for definition of octant.

TABLE 10. Relationship of infection by *Phellinus weirii* to stocking level and spatial pattern in Douglas-fir plantations

Plantation	Block	Area (ha)	Stocking (trees/ha)	Irregularity index[a]	Composite index[b]	No. infected (trees/ha)
1	1	0.57	2,104	1.057	2,223	0
	2	0.57	1,988	0.929	1,846	2
2	2	0.71	2,625	0.715	1,876	0
	4	0.75	2,179	0.899	1,958	31
	1	0.51	3,027	0.724	2,191	169
	3	0.81	2,113	1.001	2,241	220
3	2	0.57	3,381	0.811	2,741	9
	1	0.57	2,906	1.077	3,129	18
	3	0.57	3,493	1.017	3,552	101

[a]Based on Pielou's (8) point-to-plant test.
[b]Irregularity index multiplied by trees per hectare.

tacts between tree roots as the means by which the fungus passes from tree to tree. High stocking levels increase the probability of contacts because of close proximity of trees, and large diameters do so because of the associated large root systems (2,9). If trees were planted sufficiently far apart to preclude contact among roots, the fungus could advance only from infected stumps to trees fortuitously planted near them. However, irregularities in planting distance are unavoidable in practice, and aggregations of trees do occur. Also, microsite variation within plantations could affect localized stocking levels and tree diameters because planting survival and growth likely would be higher in better microsites. If aggregations of trees coincide with the location of an infection source, then limited advance of the fungus can occur, as exemplified in plantation 1, which had the lowest stocking level of all three plantations but, in parts, had the highest index of irregularity.

Conversely, aggregation is less important to fungal advance if stocking levels are high enough to result in many root contacts, as exemplified by plantations 2 and 3. Even within plantations, stocking levels and patterns vary sufficiently to cause variation in disease incidence. The importance of the combined effect of both factors was demonstrated by the superior correlation of disease incidence with their product (composite index) than with either alone (Table 10).

Stocking level was a more reliable indicator of failure rather than success of the fungus to advance, whereas average diameter was more reliable in indicating successful advance than failure to advance. Apparently, low stocking levels were most important in preventing advance, whereas, because of additional factors, for example, absence of infected neighboring trees, high stocking levels alone were only partly responsible in permitting the fungus to advance. Large average diameter apparently was the most important factor in permitting the fungus to advance because of the increased probabilities of root contacts and of neighboring trees having been infected. Small average diameter alone was less important in preventing advance by the fungus because other factors, for example, high stocking levels, could negate its effect. Thus, stocking level and tree diameter had largely independent effects on advance.

The reliability of stocking level and diameter as indicators of fungal advance varied among plantations and stand ages. There were no obvious trends, and the variation could be attributed only to the random distribution of stocking and tree diameters. The low reliability of the factors at some stand ages was attributable to the small number of advances that occurred.

The importance of stand composition to advance of *P. weirii* was shown by the significant differences in incidence of trees with Armillaria root rot or dead from other causes between areas with different advancement status. Apparently, such trees served as barriers to the fungus because their roots were unsuitable substrates, probably through competition from other fungi that were already established. However, neither variable was reliable as a predictor of fungal advance due to the large variation among sectors.

The arrest of *P. weirii*, that is, failure to make any further advances, most frequently was associated at the youngest stand age with adjacent areas devoid of trees, but, as stands aged, trees killed by Armillaria root rot or other causes and other tree species became more frequent because of their increase in the stand as a whole. Because areas devoid of trees were associated with the longest period of fungal arrest (up to 29 yr), they were probably more enduring barriers to the fungus than other variables associated with shorter periods of arrest. A reasonable conclusion is that low stocking levels are paramount but stand composition factors can play an accessory role in slowing or arresting the advance of *P. weirii*.

The irregular pattern of advances by *P. weirii* spatially and over time could be attributed largely to the stand conditions encountered by the fungus. However, other factors probably play some role in view of the low number of advances in all plantations from 1969 to 1975. Also, the low probability of two successive advances in a sector suggested that a period of colonization of root systems may precede each advance.

The absence of relationships between the length of fungal advance and any stand variables can be explained in terms of root contacts; that is, trees whose roots overlapped those of an infected tree or stump could become infected regardless of their distance from it, whereas those beyond the overlap distance could not. The root overlap distance probably varies with stand conditions, but no trends were apparent in average lengths of advances.

Mean length of advance including all sectors (Table 7) was less than the previously measured 34–35 cm/yr (1,6,7). Those measurements, based on selected diameters or radii along which the fungus had already advanced, contrasted with measurements in sectors in which the fungus often failed to advance. Applying the 34–35 cm/yr rate to all sectors would produce a gross overestimate of disease incidence in the three plantations. Conversely, applying the mean rate and excluding sectors with no advances most likely would overestimate radially measured advances. Probably, advance measured along selected radii is appropriate only in centers where stand conditions are relatively uniform in all sectors and stocking levels resemble the stand average. Although such centers may have been selected as examples of typical radial advance of *P. weirii*, they were a very small minority of those in the three plantations.

Differences among plantations in the incidence of Phellinus root rot largely can be explained by factors that affect fungal advance. Plantation 1, which had the lowest incidence, had a much lower stocking level, a higher percentage of species other than Douglas-fir, and a high percentage of ingrowth trees. Plantation 2, which had the highest incidence, had low percentages of other species and ingrowth trees and a higher stocking level than plantation 1. Plantation 3 had an intermediate incidence; it had the highest stocking level, the highest percentage of ingrowth, and the highest incidence of Armillaria root rot.

Variation in incidence within plantations could be explained partly by local variations in stocking level and aggregation of trees. However, some parts of plantations 2 and 3 almost were devoid of any infected trees, suggesting an almost total absence of inoculum. In view of the dependence of infection on the distribution of the disease in the previous rotation (10), it must be assumed that these areas previously lacked infected trees.

Possibilities for control of root rot caused by *P. weirii* exist through silvicultural practices that balance stocking levels with tree diameter growth to restrict advance of the fungus. Choice of planting density and regularity, selective thinning, and mixtures of tree species are some examples. Specific prescriptions will be required for each situation. The use of modeling to evaluate these possibilities will be described later.

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