Rate of Spread of *Ceratocystis wageneri* in Ponderosa Pine Stands in the Central Sierra Nevada

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ABSTRACT

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Ceratocystis wageneri, cause of black stain root disease, typically spreads locally from disease foci, sometimes producing infection centers of ≥10 ha in ponderosa pine stands. To determine rates of spread and the influence of stand-site variables on spread rate, the enlargement of 52 infection centers was determined from aerial photographs taken during an 11–15 yr period. Average rate of radial spread for all centers was 1.0 m/yr, but it varied from 0 to 7 m/yr. Often, under apparently favorable conditions, annual rates of ≥3 m were sustained for the entire study period. Such rates can lead to substantial losses in pines with rotation ages of 50–80 years. Of the four stand-site variables studied (mortality-center size, ponderosa pine stand density, species composition, and soil moisture drainage class), only ponderosa pine density was strongly associated with spread rate. Rate of generation of new centers in the 2,225-ha study area for a period of 3 yr was only one center per 1,000 ha per year. Besides yielding data useful in developing pest management strategies, the results illustrate the efficacy of sequential aerial photography as a research tool.

Additional key words: root disease, *Verticicladiella wageneri*.

The fungus *Ceratocystis wageneri* Goheen & Cobb (*Verticicladiella wageneri* Kend.) attacks Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and several *Pinus* spp. in California and other parts of western North America (13). Damage to commercial forests has been reported in several localities (15), and we believe future damage could be substantial. The pathogen first infects roots of a live tree, and then spreads through tracheids of the sapwood of the root system, the root crown and finally the lower bole. The most easily identified symptom is the characteristic chocolate-to-black stain in the sapwood (14).

The typical pattern of tree mortality in *C. wageneri* infection centers resembles that associated with other root pathogens such as *Fomes annosus* (Fr.) Cke. or *Armillaria mellea* (Vahl. ex Fr.) Kummer (13). The fungus spreads from tree to tree through root contacts (17) and probably by moving short distances through soil (4,7). Trees that have been dead for several years are often found lying on the ground or standing as snags in the interiors of centers. Recently killed trees, and those infected but still alive, generally occur along the advancing margin.

Although the fungus can be quite virulent and is capable of killing trees within a few years, infected trees are rarely killed outright. Instead, infection induces a general decline in vigor that predisposes the trees to attack by various bark beetles (2), which precedes tree death. Other bark beetles that attack roots may be the vectors responsible for initiation of new infection centers established by *C. wageneri* (5).

To evaluate the potential disease impact in forest stands, information on the pathogen's rate of spread is needed. Therefore, this study was designed to determine the rate of spread of ponderosa pine mortality centers associated with *C. wageneri*; to determine the association of certain aerial-photo-detectable stand/site characteristics with spread rate; and to estimate the frequency of initiation of new infection centers.

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MATERIALS AND METHODS

The study was made on a 2,225-ha area located at 1,300–1,400 m elevation on the Georgetown Divide on the west slope of the central Sierra Nevada. The study area was located within a region normally occupied by the Sierra Nevada Mixed Conifer Type 243 composed of white fir, ponderosa pine, sugar pine, incense-cedar, Douglas-fir and California black oak (16). However, owing to poor logging practices and occurrence of fires in the early 1900s, much of the area was forested by stands of predominantly ponderosa pine (*Pinus ponderosa* Laws.). The stands were relatively even-aged, 60–80 yr old, and most of the trees were 15–50 cm in diameter 1.4 m above ground. Previous studies (1) had indicated that several hundred *C. wageneri* infection centers occurred within the area.

Aerial photography of the entire area was taken periodically (22 flights) from 1963 through 1978. Thus, a unique opportunity existed to study spread rate of *C. wageneri* over an extended period, based on date of tree mortality. Eight sets of good to excellent quality stereo photographs taken at 2-yr intervals were chosen. The 23 × 23 cm positive transparencies varied from large (1:4,000) to medium (1:18,000) scale and were either normal color or color infrared.

A stratified sample of mortality centers was selected from the earlier photography (1963–1967) so that most centers selected were observed for 15 yr and none for fewer than 11 yr. Stratification was based on a matrix of center/site characteristics, ie, mortality center size, pine density, species composition and soil moisture drainage class, which could be observed on the photographs. The three center sizes were designated as small (one to three dead ponderosa pines and/or area <0.1 ha in size), medium (four to 25 dead pines and/or area 0.1–0.4 ha), and large (more than 25 dead pines and/or area >0.4 ha). Ponderosa pine stand density was characterized as light if 120 or fewer pines per hectare ≥15 cm DBH (diameter at

breast height) could be counted on the photos, or heavy (>120 pines per hectare). Species composition was characterized as pine (≥ 75% ponderosa pine) or mixed conifer, and soil moisture as wet (near meadows, creeks, or springs) or dry (rocky sites or ridgetops). To determine size, density, and composition for each center, all fallen or standing dead ponderosa pines and all live pines and trees of other species over approximately 15 cm DBH were counted on the photos for an area that included the center and a surrounding narrow zone of nonsymptom trees about 10 m wide.

A total of 24 combinations of center characteristics was possible. When feasible, enough centers were selected to provide three replicates of each possible combination. Each selected center was examined on the ground to confirm that it was a discrete center containing trees infected by *C. wageneri*. A discrete infection center consisted of one or more diseased trees within 25 m of each other but separated by more than 25 m from other centers. The distance, 25 m, was chosen on the basis of earlier results (4) that indicated the fungus might spread underground a maximum of 20–22 m between adjacent trees of the sizes usually encountered in this study. No infection centers occurred in several of the possible matrix combinations and in some cases, selected centers were excluded because they were less than 25 m apart. Thus, after the ground-check, 52 *C. wageneri* infection centers in 22 of the combinations (one to three replications each) were used.

The perimeter of each center was delineated on the earliest set of photos (usually 1963) on which it appeared. The perimeter was drawn to include all photo-observable fallen trees, standing snags, and recently dead pines. Photos from each subsequent set were carefully inspected for recently killed (dead since last photo date) pines within 25 m of the previous center boundary, and the updated boundary was drawn on the photos. The procedure was repeated for each photo set through 1978. A subsample of centers was ground-checked, and we found that the photo-delineated boundaries accurately reflected the actual extent of the pine mortality associated with the disease centers on the ground.

A basic assumption of this study was that ponderosa pine mortality was always associated with root disease occurrence at centers where *C. wageneri* had been identified, and that the photo detectable spread of pine mortality reflected the spread of *C. wageneri*. This assumption is well supported by the ground checks and data from other studies (2,4), which indicated that approximately 85% of dead pines in a disease center had the characteristic dark stain at the root collar; many of the remaining dead trees were also infected but showed no symptoms above ground.

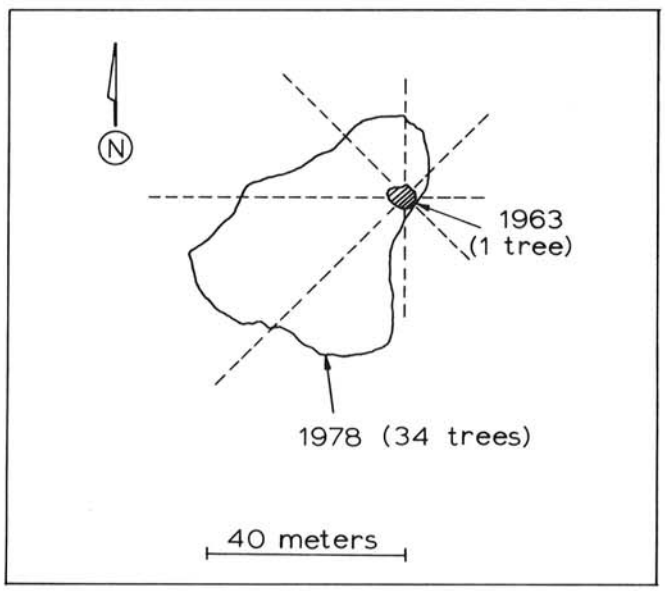

Fig. 1. Diagram of a *Ceratocystis wageneri* infection center in ponderosa pine showing the original perimeter around a single tree in 1963 and the perimeter as it appeared on the aerial photography in 1978. The broken lines radiating from the center represent the octants into which the center was divided for analysis. Spread to the southwest averaged about 2.5 m/yr, whereas it was almost nil eastward because of a change in stand composition to nonsusceptible species.

Since the centers had been delineated on photos of widely varying scales, the boundaries were transformed from all photo sets to a common map scale using a system developed by DeMars (3) which combines a digitizer, minicomputer, and plotter. The earliest and latest boundary for each center were then plotted at a conveniently enlarged scale (Fig. 1); accuracy of these maps is ± 10% of the area.

The boundaries of individual centers varied considerably with respect to stand-site characteristics; as a consequence, the rate of radial spread could be substantially different along the boundary of a given center. To account for the variation, each center boundary was divided into approximately equal octants by extending eight radial lines from the geometric midpoint of the center as it first appeared on the photo (Fig. 1). For each octant the average distance between the earliest and the latest boundary was measured directly on the map and divided by the number of years the center was under study to yield the average radial spread per year.

To obtain data on stand and site factors for analysis with the spread rates, a zone extending about 30 m beyond the initial center boundary was carefully categorized by ponderosa pine density, species composition, and soil moisture. The 30-m zone, rather than a lesser one, was necessary to obtain an accurate characterization of the stand through which the fungus might spread during the 15-yr period of observation. The numbers of stand-site categories were increased beyond those used to make assignments to the selection matrix to insure that more detailed analyses could be made.

Pine density classes were based on the number of live, photodetectable ponderosa pines per hectare (>15 cm DBH). These classes were subsequently checked on the ground to determine the actual number of pines present. There were five classes (D_0–D_4), each with two counts; the first is the photo count range and the second (in parentheses) is the average ground count: D_0 = 0–35 trees (60); D_1 = 36–75 trees (280); D_2 = 76–110 trees (430); D_3 = 111–150 trees (520); and $D_4 \geq 151$ trees (890). Species composition, based on percentage of ponderosa pine in the stand canopy, was divided into four categories: C_0 = 0–25% pine; C_1 = 26–50%; C_2 = 51–75%; and C_3 = 76–100%. There were three soil moisture categories: M_0 = rocky sites and well-drained ridgetops (generally dry in summer); M_1 = moderately well-drained; and M_2 = near meadows, creeks, or springs (relatively moist during the summer).

To estimate the rate of initiation of new centers, three sets (1972, 1973, and 1974) of recent photography were chosen. The entire 2,225 ha study area was examined on each photo set for newly occurring ponderosa pine mortality (usually single trees) farther than 25 m from any previous mortality center. All new mortality was examined on the ground to confirm infection by *C. wageneri* and distance from any previously existing center.

The overall spread rate for each center was calculated as the mean of the octant spread rates along the perimeter. The mean spread rates (MSR) for the 52 centers were tested and found to approximate a normal distribution. A multiple regression was then calculated for MSR as a function of ponderosa pine stand density, stand composition, soil moisture, center size (initial number of dead trees), and years of photo observation. Several mathematical transformations of the data, such as square root and log, were tested for best fit.

As indicated earlier, octants varied widely in their perimeter characteristics and spread rates. Hence, data for octant spread rates (OSR) were treated as an independent set of 416 observations. To produce calculated probabilities closer to their actual values, an approximately normal distribution was obtained with a square root conversion. A two-way analysis of variance was made of the square root of OSR by the five categories of pine density and the four categories of species composition by using Scheffé's (12) procedure to compute exact probabilities of significant differences between individual category means.

RESULTS

The average whole center radial spread rate (MSR) for the complete perimeters of all centers was 1.0 m/yr (Table 1). However, spread rate differed widely among whole centers and among octants (OSR) within centers. Three of 52 centers exhibited no spread during the 11–15 yr covered by the observations, while the perimeters of other centers were expanding at an average of nearly 3 m/yr. MSR was approximately the same for centers in different size categories (Table 1). As expected, OSR exhibited more variation. Eighty-seven of the 416 octants exhibited no spread during the study period, while the OSR of several reached maxima near 7 m/yr.

When analyses of variance were made on ponderosa pine stand density data and species composition data separately, both stand density and composition were significantly related to octant spread rate (Table 2). However, results of the two-way analysis of variance on density and composition together showed that both factors explain the same variation and that only pine stand density was significantly ($P = 0.0001$) related to spread. Interaction between pine density and species composition was insignificant. The analyses showed no significant differences associated with categories of soil moisture.

With the regression analysis of mean spread rate for the 52 centers, only pine density was significant at $P = 0.05$ or higher. The best fit was:

$$\text{MSR} = (0.667 + 0.00183 \text{ pine density})^2$$

The R was equal to 0.337, $R^2_{adj} = 0.096$, and S (residual) = 0.345 (m/yr)½.

Results of the analysis of the relationship between MSR and whole center pine density were compared with those between OSR and octant pine density (Fig. 2). This limit shows significant differences between categories D_0 and D_1, D_2 and D_3, and D_3 and D_4. The whole-center (MSR) regression line, also plotted on the figure, portrays a lower increase in spread rate for a given increase in pine density than that for the octant spread rate. This may be due to a suspected nonlinear relationship between spread rate and pine density and to averaging of low (zero) and high spread rates around the perimeters of many centers.

Initiation of new centers. Based on 3 yr of observation, only eight confirmed, new centers originated in the 2,225-ha study area. Thus, the average rate was one new center per 1,000 ha per year.

DISCUSSION

The average annual spread rate of 1.0 m for the complete perimeters of ponderosa pine infection centers seems substantially slower compared to that reported by Wagener and Mielke (17) in pinyon woodlands. However, the 1.0 m/yr rate is probably an underestimate of the *C. wageneri* potential for spread in many stands. The average value includes three of 52 complete centers (6%) and 87 of 416 octants (29%) that exhibited no spread over the 15-yr period, often because of unfavorable stand or site conditions such as rock outcrops or changes in stand density or composition. The maximum spread for whole centers was 2.3 to 2.9 m/yr and, in stands that appeared to be particularly favorable for the pathogen, the rate for some octants was nearly 7 m/yr. These rates indicate that *C. wageneri* can spread from infection centers at least as fast as other forest tree root pathogens. For example, the spread rate of *Phellinus weirii* in a portion of Oregon was found to be 34 cm/yr (11), and that of *Fomes annosus* in eastern U.S. ranged from 0.6 m/yr to 2.1 m/yr (8).

Initially, a spread rate of 1–3 m/yr may not seem alarming. However, when the crop is a forest stand with a rotation age of 50–100 yr, the long-term effects must be evaluated. For example, if *C. wageneri* is spreading from an initial focus of 0.01 ha at a rate of 3 m/yr, the center will be 0.40 ha in 10 yr. Assuming an average of 400 trees per hectare and a mortality rate of 75%, the number of trees killed will increase from three to 120 in the same 10-yr period.

Of the four stand-site factors (mortality center size, ponderosa pine stand density, species composition, and soil moisture) studied, only ponderosa pine stand density and species composition (when tested separately) were significantly related to spread rate. When analyzed together, composition was nonsignificant also, while pine stand density remained a highly significant factor. Although a mixture of other tree species among the ponderosa pines was

TABLE 1. Rate of spread[a] of *Ceratocystis wageneri* in 52 ponderosa pine infection centers on the west side of the central Sierra Nevada in California as a function of center size

Center size	Initial no. dead trees	No. of centers	Rate of spread (m/yr)[b]			
			Min.	Max.	Mean	S.D.
Small	1–5	21	0.0	2.3	1.0	0.64
Medium	6–25	21	0.0	2.4	0.8	0.60
Large	26–480	10	0.5	2.9	1.3	0.63

[a] Values are averages from aerial photography covering an 11–15 yr period from 1963 to 1978.

[b] None of the differences in spread rate were statistically significant.

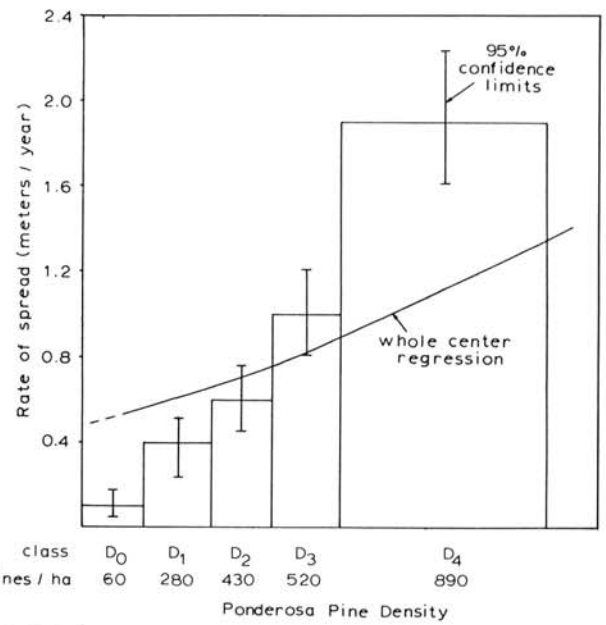

Fig. 2. Relation between estimated average ponderosa pine density, as determined by ground check, and rate of spread of *Ceratocystis wageneri* in disease centers. Height of bars represents mean octant spread rate (OSR); width of bars represents the approximate range in number of stems per hectare in each density category. The regression line represents the mean spread rate (MSR) for whole centers.

TABLE 2. Relationships of ponderosa pine density and stand species composition to *Ceratocystis wageneri* rate of spread (meters per year) on 416 infection octants on the west side of the central Sierra Nevada in California

Species composition[y]		Spread (m/yr) in pine stands of density class with avg. pines/ha[x]					
Class	Pine (%)	D_0 60	D_1 280	D_2 430	D_3 520	D_4 890	Average[z]
C_0	0–25	0.1	0.2	···	···	···	0.1 a
C_1	26–50	0.3	0.4	0.8	···	···	0.4 b
C_2	51–75	···	0.4	0.6	1.1	1.4	0.7 c
C_3	76–100	···	1.5	0.6	0.9	1.9	1.1 d
Average[z]		0.1 a	0.4 b	0.6 b	1.0 c	1.8 d	1.0

[x] Pines per hectare is the average number of ponderosa pines ⩾15 cm in diameter 1.4 m above ground as determined by ground check.

[y] Species composition is the percentage of ponderosa pine in the stand canopy.

[z] Averages in the row or column with different letters are significantly different, $P = 0.05$ (12).

thought to act as a partial barrier to the spread of *C. wageneri* (1), species composition apparently was not important. These results suggest that distance between pines is the overriding factor.

The relationship between spread rate and pine density was much stronger in the octant data than in the whole center data because center data represented averages of octants that often differed substantially. The octant data indicate some spread (0.1 m/yr) when there are less than 60 ponderosa pine trees per hectare, but the rate increases rapidly to 1 m/yr when there are about 500 trees per hectare and to nearly 2 m/yr when there are about 900 trees per hectare. As the ages or sizes of trees change, differences in spread rates may also occur, especially in relation to stand density. However, all stands in the study were approximately the same age (60–80 yr), and were comprised of trees in the same general size range (15–50 cm DBH), thus precluding a comparison of these factors.

The lack of relationship between center size and spread rate appears to indicate that the major difference in size of centers was due to the period of time that a center existed before observations began in 1963, rather than spread rate per se. In several cases, size may also have been influenced by merging centers.

Other studies (4,7) have shown that soil moisture has an effect upon the pathogen and upon incidence of infection. However, our data show no relationship between spread rate and soil drainage class. Very few centers occurred on the "dry," rocky sites; almost all were located on sites with fair to good soil moisture availability for much of the year. Because we could not adequately characterize soil moisture categories with aerial photography under these conditions, no conclusions with respect to soil moisture are possible.

The one center per 1,000 ha per year rate of generation of new centers is somewhat lower than expected. The average rate over the past 60–70 yr had to exceed that to result in the approximately 300 centers now apparent in the study area. Because of the need to be certain that the centers were newly established, we limited the observation period to the 3 yr that we were able to ground check. Obviously, a longer period of observation would improve the estimate.

Traditionally, collection of data to determine rates of spread of forest tree pathogens has involved periodic examination of research plots over many years. The methods are not only time consuming and costly; they also tend to discourage studies, even when data from such studies are essential to sound disease management. Records preserved in the form of aerial photography have proven useful in other studies of incidence (6,9,18) and spread (10,11) of mortality-causing root pathogens in forest stands. The results of this study further show the value of sequential aerial photographs for obtaining spread data, and they expand the usefulness of photos in evaluation of environmental factors affecting spread.

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