Predicting the Incidence of Comandra Blister Rust on Lodgepole Pine: Site, Stand, and Alternate-Host Influences

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ABSTRACT

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Incidence of cankers caused by comandra blister rust (*Cronartium comandrae*) on lodgepole pine (*Pinus contorta*) and distribution of the rust's alternate host, pale comandra (*Comandra umbellata* subsp. *pallida*), were mapped in portions of two Wyoming forests. Rust incidence in 24 stands in the Shoshone National Forest varied from 14 to 64%, and rust incidence in 190 plots in the Medicine Bow National Forest ranged from 0 to 36%. Comandra populations occurred on open, upper slopes surrounded by lodgepole pine stands in the Shoshone study area and on dry ridge tops along the eastern and western slopes of the Medicine Bow study area. Simulations of wind speed and direction during periods favorable for basidiospore dispersal were used to identify comandra populations upwind of surveyed lodgepole pine stands. Rust incidence was highest in stands older than 40 yr along forest edges adjacent to comandra but also was high in some stands 1–10 km downwind of likely inoculum sources. Rust incidence was significantly negatively correlated with distance to comandra and with stand density and was significantly positively correlated with average tree diameter, height, and age. Expected incidence of comandra blister rust across surveyed portions of the two forests can be predicted from average tree height or diameter and distance to comandra.

Additional keywords: hazard rating, risk rating, spatial analysis, wind simulation.

In North America, comandra blister rust (*Cronartium comandrae* Peck) is a widely distributed, heteroecious fungus that alternates between numerous species of hard pines and two species of perennials commonly called "comandra." The rust is found from New Brunswick to the Yukon and from California to Tennessee (19). Significant disease losses from damaging stem cankers occur most frequently in western forests. In California and the Northwest, the important aecial host is ponderosa pine (*Pinus ponderosa* Laws.), and in the central Rocky Mountains and Canada, the major host is lodgepole pine (*Pinus contorta* Dougl. ex Loud. subsp. *latifolia* (Engelm. ex S. Wats.) Critchf.).

Severe top-kill and mortality have been reported in several forests from Wyoming and Utah to Idaho and Montana (21,26). In the Wind River District (Shoshone National Forest, WY), 52% of lodgepole pine trees >12 cm in diameter are cankered, and 39% of the commercial forest area is infested (12). In the central Rocky Mountains, the telial host is pale comandra (*Comandra umbellata* (L.) Nutt. subsp. *pallida* (A. DC.) Piehl), which occurs as a rhizomatous perennial on dry open sites, in association with sagebrush (*Artemisia tridentata* Nutt.) (32). Other subspecies of *Comandra umbellata* found outside the central Rockies are more shade tolerant and grow within small forest openings (23). An additional telial host, northern comandra (*Geocaulon lividum* (Richardson) Fernald), occurs from northern Montana to British Columbia and prefers mesic sites adjacent to or within lodgepole pine stands (23).

As with several other stem rusts (11,15,16,30), severe impacts caused by comandra blister rust occur where aecial and telial hosts are near each other (1,9,17,21). Various site and stand factors also influence stem rust incidence (20,31). Site factors correlated with incidence of various rust diseases include plant association, soil type, site index, topographic position, and slope (2,4,18,29). Stand factors include past rust incidence, average tree size, stand age and density, and silvicultural practices (4,7,25,27). Because temperature, wind, humidity, and solar radiation limit the spread of delicate basidiospores, information on local climate (modified by site and stand conditions) is used to explain and predict spatial distributions of several rusts (6,11,20,31). The epidemiology of these rusts, however, is too complex to permit site-specific predictions of disease incidence on an annual basis (11,20,24,28).

Nonetheless, forest managers in the central Rocky Mountains could benefit from reliable landscape-scale predictions of the distribution, frequency, and severity of comandra blister rust outbreaks (13). Research on frequency of infection and severity of damage are reported elsewhere (5,14). Basidiospore dispersal occurs infrequently in lodgepole pine forests of the central Rocky Mountains: Spore dispersal occurs during periods of 12 or more hours of rain and/or high humidity between July and September and when winds are from the appropriate direction (5,22).

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Large and remote areas need to be sampled to construct landscape-scale models of disease distribution. These temporal and spatial constraints render methods that rely on trapping basidiospores inefficient (3). We surveyed portions of two forest districts, mapped distributions of comandra, and estimated levels of comandra blister rust incidence in stands of lodgepole pine. The two study areas were selected to represent severe rust outbreaks in contrasting landscapes. A wind-simulation model predicting wind speed and direction over complex terrain helped identify comandra populations that were probable inoculum sources for surveyed lodgepole pine stands. Finally, we constructed models that predicted rust incidence, based on variables describing site, stand, and proximity to inoculum.

MATERIALS AND METHODS

Study areas. Studies were conducted from 1983 to 1984 in the Wind River Ranger District, Shoshone National Forest (northwest of Dubois, WY) and from 1987 to 1988 in the Laramie Ranger District, Medicine Bow National Forest (west of Laramie, WY).

The Shoshone study area is dominated by the valleys of the Wind River and DuNoir and Warm Spring creeks, which originate at the Continental Divide and extend to the southeast (Fig. 1). The Wind River and Absaroka mountain ranges form high barriers beyond the northern, western, and southern edges of the 31,500-ha study area. Shrub-steppe communities dominated by sagebrush are found above riparian zones and on south-facing slopes (32). Lodgepole pine stands occur on flat benches and mesic slopes between the upper limits of sagebrush scrub and the lower limits of spruce-fir (*Picea-Abies*) forests. Shrub communities displace forest stands along major streams, and topographic relief is large and complex.

The Medicine Bow study area encompasses a large plateau occupied by forest on the top and by shrub-steppe communities along the eastern and western slopes above the Laramie and Platte rivers (Fig. 2). Within the 115,200-ha study area, shrub communities extend along dry ridges from low, surrounding valleys to forest edges. Lodgepole pine stands occur across the plateau and on mesic, north-facing slopes; spruce and fir trees are common in northern portions of the study area. Sagebrush communities with comandra populations and lodgepole pine stands are adjacent only along eastern and western slopes, and the forest is not broken by any large valleys.

Wind simulation. The influence of landform (topography) on airflow and basidiospore flight was simulated with the WINDS program (10). Airflow maps for each area indicated changes in wind speed and direction due to topography during periods favorable for spore dispersal. Simulated landscapes extended several miles beyond the edges of the Medicine Bow and Shoshone study areas. Wind simulations were calibrated to speeds and directions recorded at weather stations located within inoculum-source areas during potential infection episodes (5). For the Shoshone area, simulations represented winds at 2.5 m/s, from the northeast, east, southeast, and west. For the Medicine Bow area, simulated winds were 2.0 and 5.0 m/s, from the northeast, east, and southeast.

Comandra sampling: Shoshone. Distribution and area occupied by comandra were mapped for all 6,200 ha of shrub-steppe within the Shoshone study area. Sagebrush areas between riparian zones and forest stands were stratified into 152 plots (0.4 × 0.1–1.5 km). These sagebrush areas extended at least 2 km from the forest edge. In each plot, we established transects along contours at four slope positions (lower slope, middle slope, upper slope, and ridge top). The area occupied by comandra was estimated as the product of plot area and proportion of transect-intersecting populations of comandra.

Comandra sampling: Medicine Bow. Distribution and abundance of comandra were mapped for 4,020 ha of sampled shrub-steppe within the Medicine Bow study area. Areas of sagebrush and grass were identified from maps and scouting surveys. Sampling for comandra abundance was conducted on 16 strips (each 1.6 km wide) that were partitioned into 16.2-ha plots. Along the 32-km eastern edge of the study area, 12 strips placed about 2.5 km apart, extended 11.2 km west from the Laramie Valley; the four remaining strips were located along the southern half of the western edge and extended 10 km east from the Platte Valley. Comandra frequency and density were determined for 459 quadrates (each 1 × 1 m) located at 3.5-m intervals along contour transects established for each slope-position class. A general linear model for analysis of variance (SAS, release 6.03, SAS Institute Inc., Cary, NC) tested for differences in comandra density by slope position ($P < 0.0001$).

Pine disease survey: Shoshone. Rust incidence and associated site and stand attributes were determined for 24 lodgepole pine stands in the Wind River District. Stands were selected randomly from more than 100 stands that met six criteria: 1) >50% lodgepole pine, 2) >4 ha, 3) <8 km from a road, 4) not logged since 1940, 5) no severe damage other than rust, and 6) downwind from comandra populations (as determined by WINDS simulations). Stands were surveyed at 1% intensity with 17–45 strip-plots (3.35 × 60.6 m). Site data included elevation, aspect, and percent slope. Live trees were tallied as healthy or rust cankered; and diameter, height, and age were determined for the first 10 cankered trees on each plot. To map disease incidence, we included 10 additional stands surveyed prior to 1983 (B. Geils, *unpublished data*).

Pine-to-comandra distances were measured along simulated wind vectors from sampled stands upwind to the nearest populations of comandra (i.e., center of pine stand to center of comandra plot). Estimates of comandra abundance were determined

Fig. 1. Shoshone National Forest, WY, study area as seen from the Wind River Valley, looking northwest from the middle of the study area. The Wind River and Absaroka ranges are in the background; approximately one quarter of the study area is shown.

Fig. 2. Medicine Bow National Forest, WY, study area as seen from across the Laramie River Valley, looking west at the southern third of the plateau.

as area occupied by comandra in nearest inhabited plots and as cumulative areas occupied by comandra in plots beyond the nearest inhabited plot at 1-, 2-, and 3-km intervals. We disregarded populations between these intervals.

Pine disease survey: Medicine Bow. Rust incidence of lodgepole pine trees on the Medicine Bow study area was determined with 190 plots distributed across the study area on the same 1.6-km-wide strips used to survey comandra. Distance between plots varied with distance from forest edge: Within 6 km, plots were spaced every 0.5 km; and beyond 6 km, plots were spaced every 2 km. Each plot was a 60-m cluster of five subplots with a common radius (2–9 m) sufficient to include about 100 trees per plot. Site data included elevation, aspect, and percent slope. Live trees were tallied by species and disease condition (healthy or cankered) and were measured for height and diameter at 1.3 m; age was determined for one typical lodgepole pine tree on each subplot.

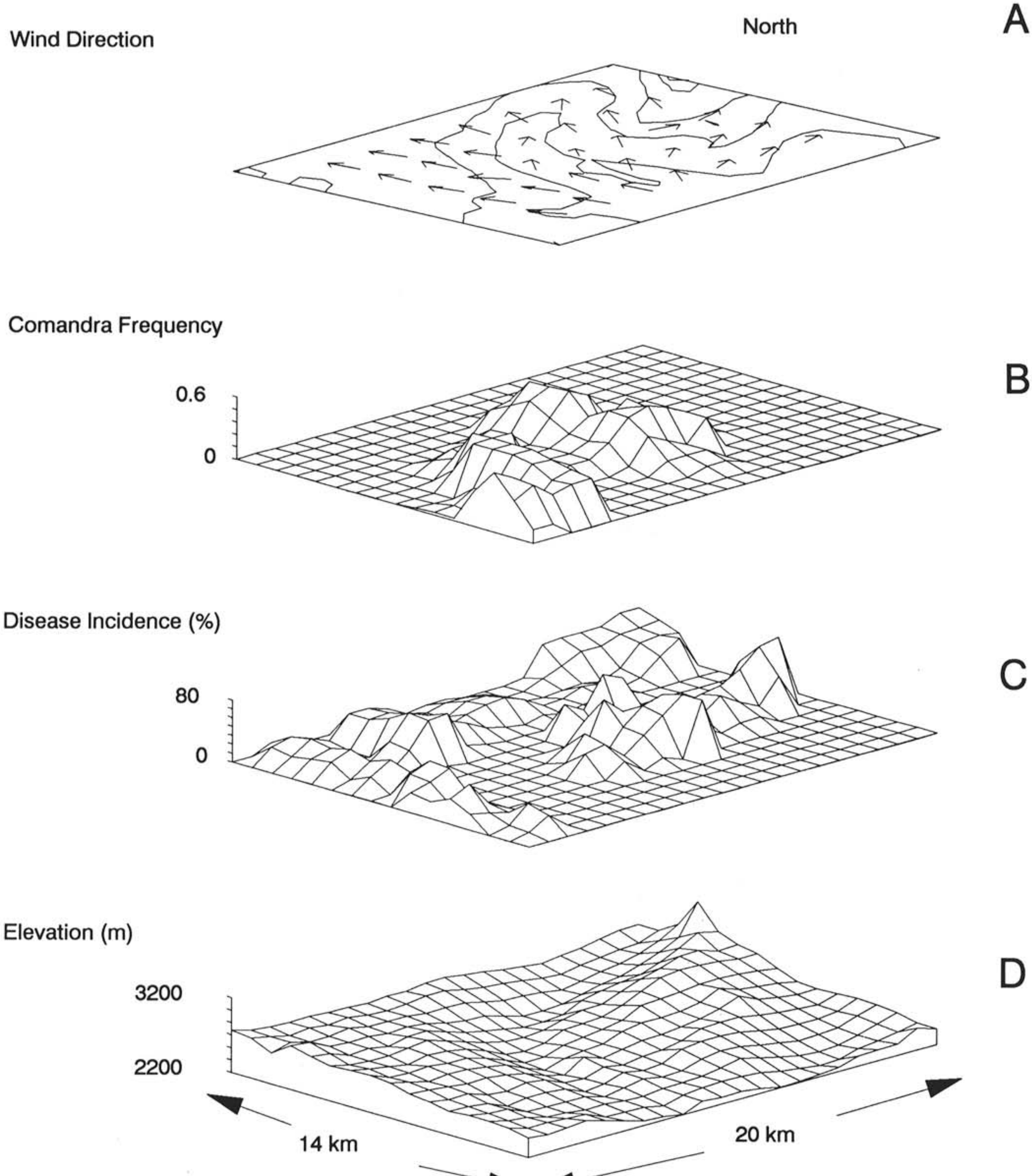

Fig. 3. Shoshone National Forest, WY, study area **A,** simplified vector map of a computer-simulated wind from the east at 2.5 m/s and overlay of elevation contours at 2,250, 2,450, 2,650, 2,850, and 3,050 m; **B,** comandra frequency (percent occurrence on survey transects); **C,** comandra blister rust (*Cronartium comandrae*) incidence (percentage of live trees with stem cankers); and **D,** surface elevation (meters). Southeast corner of map is located at T42N, R108W, S28.

For each sampled lodgepole pine plot, we determined location, extent, and density of comandra populations along east and west slopes of the plateau that were probable sources of rust inoculum (based on simulated-wind maps). Identified source populations included all comandra plants on 16.2-ha plots within 2-km-wide bands, from pine plots to east and west slopes.

Analysis of disease incidence. For each study area, analyses tested whether rust incidence (percentage of lodgepole pine trees cankered by comandra blister rust) was related to site, stand, proximity to comandra, and abundance of comandra variables. Site and stand variables included elevation, aspect, percent slope, stand density, and average tree diameter, height, and age. Comandra-population variables included distance to sampled stand, area occupied, and total number of shoots. Wind direction, comandra density, disease incidence, and elevation were mapped to a 1-km resolution (Surfer version 4, Golden Software, Inc., Golden, CO). Quantitative relationships between rust incidence and factors for site, stand, and alternate-host distribution were examined with graphic, correlation, and regression techniques (SAS, release 6.03). Nonlinear models of rust incidence that utilize variables for pine-to-comandra distance and average tree height or diameter were constructed. Alternative models were evaluated on the basis of adjusted squared regression coefficients and on examination of residuals for normality, heteroscedasticity, bias, and serial correlation. Prediction residual sum of squares (PRESS) was computed with a jackknife procedure and was used to adjust prediction bounds for expected rust incidence (8). Upper and lower bounds of approximate 95% confidence intervals for individual predictions were multiplied by the ratio of PRESS over residual sum of squares (RSS).

RESULTS

Wind simulation. Wind-vector maps (Figs. 3A and 4A) illustrated the effects of topography on airflow and basidiospore flight. Deep, curved valleys in the Shoshone area channelled easterly winds flowing over extensive comandra populations toward northern lodgepole pine stands. Across uniform terrain (southern portion of Shoshone area and plateau of Medicine Bow area), wind directions were unchanged, and presumed spore flights continued east to west. Relief on southeast and southwest slopes of the Medicine Bow plateau, however, altered wind directions and presumed spore flight paths. Wind speeds were unaffected across level terrain, accelerated as air masses passed over steep slopes, and stalled in valley bottoms on the eastern side of the Medicine Bow area.

Comandra survey: Shoshone. Comandra was centrally located in the Shoshone study area (Fig. 3B) and occurred in 83 of 152 plots. Comandra plants were common in sagebrush communities on middle and upper slopes facing southwest and were rare on bottom slopes. Extensive populations of comandra were found in the Wind River Valley and in several low-elevation valleys, but comandra was absent from high-elevation valleys and lodgepole pine stands (32).

Comandra survey: Medicine Bow. Comandra was common along the eastern slope of the Medicine Bow Plateau, infrequent on the southern portion of the western slope, and absent within forested stands (Fig. 4B). Comandra on 3,019 ha of shrub-steppe along eastern slopes was absent on the southernmost transect and was most abundant on a transect 16 km to the north (mean density = 1.9 shoots/m^2, SE = 0.14). Comandra populations on 1,001 ha along the western slopes were restricted to the southwest quadrant (mean density = 0.5 shoots/m^2, SE = 0.1). Comandra was not found in the less-accessible and less-intensively surveyed northwest quadrant. For all comandra populations, shoot densities were significantly greater on ridge tops (186 transects, mean = 2.4 shoots/m^2) than on other topographic positions (739 transects, mean = 1.5 shoots/m^2).

Pine disease survey: Shoshone. The 24 stands (453 ha) were well scattered throughout the lodgepole pine forest and ranged in elevation from 2,400 to 2,600 m on 10–40% slopes; all but south and southeast aspects were well represented. Rust incidence and stand density were determined from a sample of 6,913 trees on 251 strip-plots. Incidence varied from 14 to 64% (mean = 31%, SE = 3), and stand density varied from 190 to 4,200 trees/ha (mean = 1,300, SE = 175). Based on 558 cankered trees, average diameter was 22.7 cm (SE = 1.0); average height was 14.6 m (SE = 0.6); and average age was 118 yr (SE = 10). Stands were 0.4–8.1 km (mean = 2.8, SE = 0.4) downwind from the nearest comandra populations that occupied an average of 14 ha (SE = 2). Cumulative areas occupied by comandra in the nearest populations plus those populations 1 km farther upwind totaled 4–61 ha (mean = 28, SE = 4). Cumulative areas of nearest populations and populations 2 and 3 km farther upwind averaged 41 and 51 ha (SE = 5 and SE = 7), respectively.

Disease incidence was high in lodgepole pine stands on both sides of the Wind River Valley (Fig. 3C). High incidences were found near populations of comandra and on northern and western edges of the study area. These northern and western stands were located at an upper elevation limit for lodgepole pine; beyond these stands were high, steep cliffs and ridges.

Pine disease survey: Medicine Bow. The 190 plots ranged in elevation from 2,470 to 3,110 m on 0–50% slopes (mean = 13, SE = 0.7). Over 40% of the plots were located on nearly level sites; all aspects were well represented on the remaining plots. Approximately 90% of 18,702 sampled trees were lodgepole pine. Rust incidence ranged from 0 to 36% (mean = 8, SE = 0.6) in stands with 580–7,142 trees/ha (mean = 2,842, SE = 92). Average tree diameter was 16.8 cm (SE = 0.3); stands of large-diameter trees occurred more commonly in northern portions of the study area. Average height was 10.0 m (SE = 0.1); stands originated 47–214 yr ago (mean = 96, SE = 2). Sampled pine locations were 0.5–30.6 km (mean = 6.7, SE = 0.4) from the nearest comandra populations along eastern and western slopes and within 2-km-wide source bands. A typical population identified as an inoculum source contained 4.9×10^6 comandra shoots and occupied 257 ha.

Disease incidence in the Medicine Bow area was lower than in the Shoshone area and displayed several large-scale trends (Fig. 4C). Incidence was highest along eastern slopes (15–35%) and along southwestern slopes (8–13%). Disease in southern and central portions of the area decreased to 0–3% at distances of 10 and 6 km from eastern and western forest edges, respectively. Disease incidence in northern portions of the area decreased more gradually from east to west; rust-incidence levels of 5–15% were found 20 km from the eastern edge of the plateau.

Correlation of rust incidence with site, stand, and alternate-host parameters. Incidence of comandra blister rust in stands of lodgepole pine was best correlated with distance to comandra populations that were probable inoculum sources (Table 1). Although there was a strong, negative linear correlation of incidence with distance, scatter-plots indicated a nonlinear trend. Partial correlations controlling for distance identified stand density, average tree diameter, height, and age as additional factors related to disease incidence (Table 1). These stand attributes were correlated with each other and exhibited good correlations with disease incidence. The best partial correlation (controlling for distance) with incidence was average tree height in the Shoshone and average tree diameter in the Medicine Bow studies.

Regression Models. Separate regression models for the Shoshone and Medicine Bow areas related disease incidence to distance from comandra and average tree height or diameter (Table 2) according to INCIDENCE = $b_0 + b_1 \times$ HEIGHT + $b_2 \times \exp(b_3 \times$ DISTANCE) (Shoshone), in which HEIGHT is average tree height in meters, DISTANCE is number of kilometers upwind to nearest comandra population, and to INCIDENCE = $b_0 + b_1 \times$ (DIAMETER)^2 + $b_2 \times \exp(b_3 \times$ EAST + $b_4 \times$ WEST) (Medicine Bow), in which DIAMETER is average tree diameter in centimeters, EAST is distance (kilometers) to comandra population on eastern slope, and WEST is distance (kilometers) to comandra population on western slope. A negative exponential term was used to account for the nonlinear trend of incidence with distance. Distances for both east- and west-slope comandra populations were used in the Medicine Bow model. Average tree height and diameter squared were included as linear terms in the Shoshone and Medicine Bow models, respectively. Because site and stand variables were highly correlated, height and diameter could be considered as surrogates representing stand density, host target size, or years exposed. Residual analyses confirmed selection of model form and included variables; no significant correlations or trends of residuals with other site, stand, or comandra-abundance variables were found. The ratios of PRESS over RSS were 1.55 and 1.05 for the Shoshone and Medicine Bow models, respectively. These low ratios indicate parameter estimates were not affected by highly influential cases.

Both models illustrate how disease incidence increases with tree size (or age) and decreases for stands further from inoculum sources. The Shoshone model projected an additional 20% disease incidence as average tree height increased 10 m and indicated disease incidence would be 20% less for stands 10 km from coman-

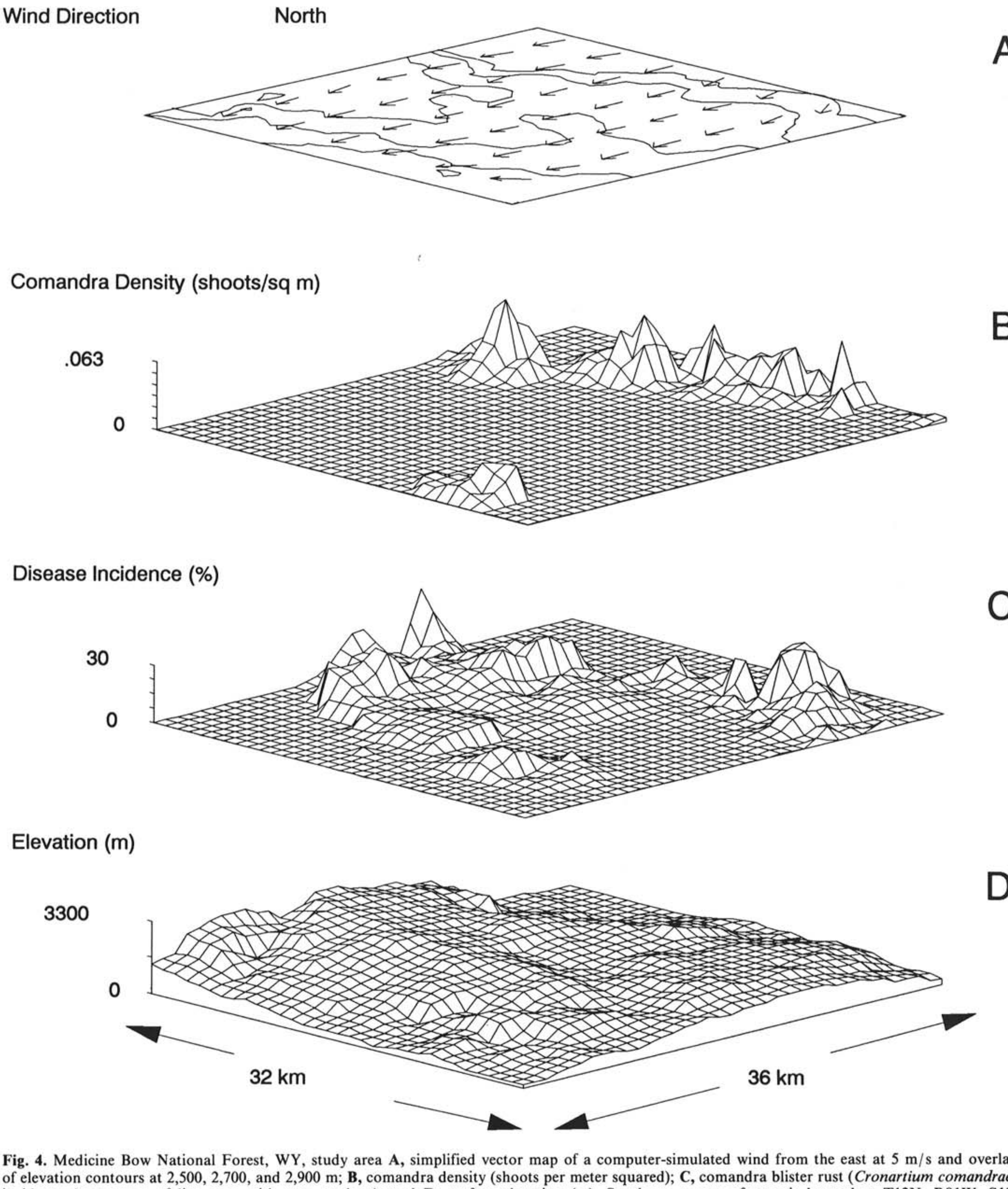

Fig. 4. Medicine Bow National Forest, WY, study area **A,** simplified vector map of a computer-simulated wind from the east at 5 m/s and overlay of elevation contours at 2,500, 2,700, and 2,900 m; **B,** comandra density (shoots per meter squared); **C,** comandra blister rust (*Cronartium comandrae*) incidence (percentage of live trees with stem cankers); and **D,** surface elevation (m). Southeast corner of map is located at T12N, R81W, S18.

dra than for stands only 1 km distant (Fig. 5). The Medicine Bow model projected an additional 12% disease incidence as average tree diameter increased 10 cm and indicated disease incidence would be 20% less for stands 10 km from comandra than for stands only 1 km distant (Fig. 6).

Other similarities and differences between study areas are revealed by comparisons of model parameters (Table 2). Although one cannot compare coefficients for variables measured in different units (meters of height and square centimeters of basal area), an empirical relationship between height and diameter squared (Shoshone data, $r = 0.77$) allowed us to rescale coefficients to common dimensions. The adjusted intercept parameter (b_0) for the Shoshone model was 5.2% disease, and the intercept of the Medicine Bow model was −3.8% disease. Holding other terms equal, the models projected that incidence in the Shoshone study area would be 9% greater than that of equivalent stands in the Medicine Bow study area. Adjusted parameter for size (b_1) was 0.02% disease/cm^2 for the Shoshone model, and the size parameter for the Medicine Bow model was 0.02% disease/cm^2. Increases in disease incidence with respect to tree size were similar for the two areas. Although different criteria were used to identify inoculum sources, pine-to-comandra distances were measured on the same scale (kilometers), and distance-parameter (b_2) values were similar (31.74 and 29.57). Disease-gradient parameters (b_3 and b_4) ranked areas for rate of change in disease incidence relative to distance from comandra. Least rate of change occurred in the Shoshone model (−0.29); and the rate of change was less for the east slope (−0.34) than for the west slope (−0.57) in the Medicine Bow model.

TABLE 1. Pearson correlation coefficients[x] and partial correlation coefficients for the incidence of comandra blister rust (*Cronartium comandrae*) on lodgepole pine with site, stand, and alternate-host parameters for the Shoshone and Medicine Bow study areas

Parameters	Study areas: Shoshone[y]	Medicine Bow[z]
Distance to comandra (km)	−0.41*	−0.54**
Average tree height (m)	0.41*	0.32**
Average tree diameter (cm)	0.19	0.41**
Average tree age (yr)	0.15	0.28**
Stand density (trees/ha)	−0.22	−0.26**
Slope (%)	0.32	0.09
Elevation (m)	0.24	−0.0003
Area occupied by comandra (ha)	0.06	−0.10
Number of comandra shoots	...	−0.04

[x] Correlation coefficients for all parameters except distance to comandra are partial coefficients controlling for distance; * indicates a significant linear relationship at $P < 0.05$ and ** indicates a significant linear relationship at $P < 0.001$.

[y] Twenty-four lodgepole pine stands sampled; no data available on number of shoots in nearest comandra population.

[z] One hundred, ninety lodgepole pine locations sampled.

DISCUSSION

Hazard models. In spite of comandra blister rust, land managers have numerous options for maintaining productive and diverse forests. Commonly used options for rust-infested stands include changing production goals from timber to amenity values, increasing stocking to account for crown loss and mortality, and harvesting cankered trees for sanitation and salvage (19). Less frequently used options in the central Rocky Mountains include converting stands to nonhost species or planting more resistant seedlings. How and when these options should be applied depend on site-specific expectations of disease incidence and damage (hazard) (13). This study illustrates a hazard-rating system that uses information on the distribution of comandra populations and simulations of airflow patterns during basidiospore dispersal to predict disease levels in stands of lodgepole pine.

The importance of an explicit spatial context for hazard-rating stands was demonstrated by our simulations of spore dispersal. The WINDS program provided us with a model for spore dispersal appropriately scaled and readily applied. The simulations indicated that landforms surrounding a stand can have a major influence on airflow patterns and can determine which comandra populations are inoculum sources. Many times comandra populations closest to pine stands were not inoculum sources, as indicated by airflow patterns.

Construction of our disease-hazard models depended not only on a spatial connection between comandra populations and pine stands but also on a temporal constancy of site, stand, and disease conditions. Our observations suggest that significant changes in

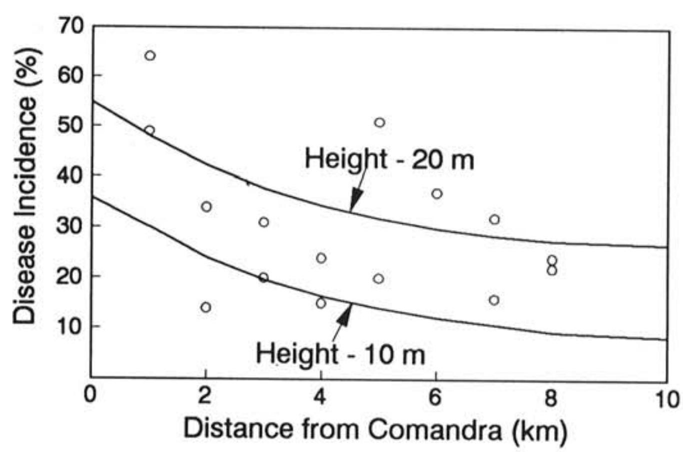

Fig. 5. Incidence of comandra blister rust (*Cronartium comandrae*) on lodgepole pine trees in the Shoshone National Forest, WY, study area by distance to the alternate host: incidence observed (circles) in 24 stands and predicted incidence (solid lines) for stands with an average height of 10 and 20 m.

TABLE 2. Estimated parameters for nonlinear regression models predicting the incidence of comandra blister rust (*Cronartium comandrae*) on lodgepole pine from average tree size and distance to comandra for the Shoshone and Medicine Bow study areas

Model	Parameter estimates[v]: b_0	b_1	b_2	b_3	b_4	SE[w]	r[x]
Shoshone[y]	−11.64 (24.99)	1.80 (0.90)	31.74 (14.90)	−0.23 (0.36)		11.1	0.58
Medicine Bow[z]	−3.87 (1.00)	0.02 (0.002)	29.57 (1.64)	−0.34 (0.04)	−0.57 (0.15)	4.6	0.85

[v] Coefficients (and asymptotic standard errors) for nonlinear models predicting disease incidence (percentage of lodgepole pine trees cankered by comandra blister rust).

[w] Standard error of estimate.

[x] Correlation of observed incidence with predicted incidence.

[y] INCIDENCE = $b_0 + b_1 \times$ HEIGHT + $b_2 \times \exp(b_3 \times$ DISTANCE), in which HEIGHT is average tree height in meters and DISTANCE is number of kilometers upwind to nearest comandra population.

[z] INCIDENCE = $b_0 + b_1 \times (\text{DIAMETER})^2 + b_2 \times \exp(b_3 \times$ EAST + $b_4 \times$ WEST) in which DIAMETER is average tree diameter in centimers, EAST is distance (kilometers) to comandra population on eastern slope, and WEST is distance (kilometers) to comandra population on western slope.

the lodgepole pine and comandra populations have not occurred over the past few decades. The samples of lodgepole pine stands and shrub communities included none with major disturbances due to fire, insect outbreak, timber harvest, or causes other than comandra blister rust. Because older lodgepole pine trees survive cankering and top-kill for many decades (14), observed levels of rust incidence in mature, unmanaged stands, should reflect the cumulative effects of many infection episodes. Because average 10-yr weather patterns favorable for infection have remained constant (5) and comandra populations have been stable, infection rates are unlikely to have exhibited any recent, long-term changes.

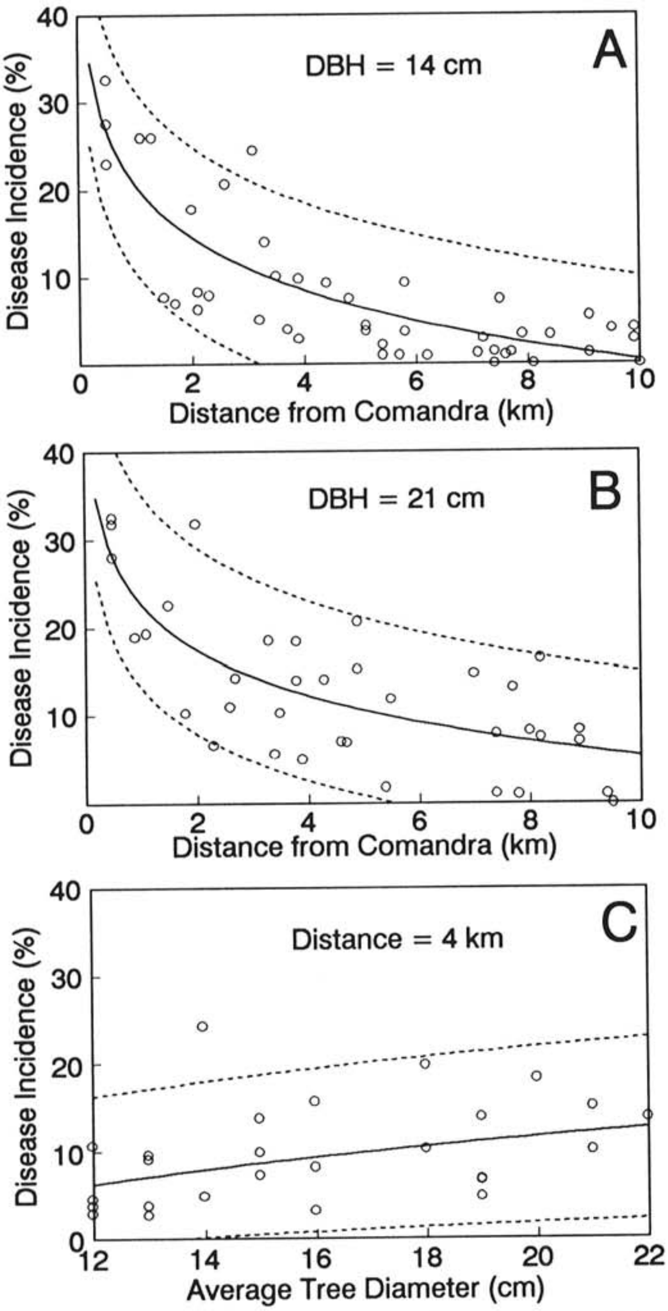

Fig. 6. Incidence of comandra blister rust (*Cronartium comandrae*) on lodgepole pine trees on the east side of the Medicine Bow National Forest, WY, study area by distance to the alternate host and average tree diameter: incidence observed (circles) in selected plots, predicted incidence (solid lines), and 95% prediction bands (dotted lines). **A**, predicted incidence for stands with average diameters of 14 cm and observed incidence for plots with average diameters from 13 to 15 cm; **B**, predicted incidence for stands with average diameters of 21 cm and observed incidence for plots with average diameters from 20 to 22 cm; and **C**, predicted incidence for stands located 4 km west of a comandra population and observed incidence for plots located 3–5 km from comandra.

Therefore, in the absence of major climate and landscape changes, our models should provide useful predictions of rust incidence for mature, unmanaged stands within the study areas. Further research would be needed to develop models that describe the effects of thinning on infection rates and that predict levels of rust incidence where telial populations are widely dispersed and intermixed with aecial hosts.

Patterns of rust distribution. Differences in the incidence of comandra blister rust across the diverse landscapes of the Shoshone and Medicine Bow study areas reveal how site, stand, and alternate-host factors influence rust distribution. These differences are illustrated by our maps and models of rust incidence (Figs. 3–6). Because of the history and complexity of these landscapes, the variability in disease incidence observed from stand to stand is not surprising. Nonetheless, patterns of rust distribution clearly indicate the importance of long-distance dispersal, landform, and arrangement of host populations in the two areas studied.

Just as wind vectors display the probable paths of spore dispersal, disease-distribution maps and incidence models reveal how far and effectively basidiospores are disseminated. The highest levels of rust incidence occurred along forest edges adjacent to comandra populations, and disease incidence decreased exponentially with distance. In general, disease gradients (slopes of incidence-distance curves) were steep (2–4% per kilometer) for the initial 10 km and flat (<0.5%) beyond 10 km. Most cankered trees were located within 10 km of inoculum sources, and only light winds of 2 m/s for 1.5 h would be required to carry basidiospores that distance. In the Shoshone study area, few lodgepole pine stands could be found farther than 10 km from inoculum sources, so greater dispersal distances could not be observed. In the Medicine Bow study area, however, numerous stands up to 20–25 km from inoculum sources were examined, and many in the northern portion of the area exhibited incidence levels of 5–15%. Both distance and gradient coefficients (Table 2, b_2 and b_3—b_4, respectively) were required to describe the shape of disease distribution (effective dispersal). Because distance coefficients were similar for the two areas, contrasts among gradient coefficients were sufficient for comparing rates of incidence decrease with distance from inoculum sources. The steepest gradient was observed on the western slope of the Medicine Bow area; flatter gradients were found on the eastern slope of the Medicine Bow and in the Shoshone areas. This variation in the effective, long-distance dissemination of basidiospores may be the result of differences in local topography and spatial arrangements of host populations between and within study areas.

Landforms in the Shoshone and Medicine Bow areas affect rust distribution by influencing airflow and, therefore, spore dispersal. Valleys and cliffs of the Shoshone area are advantageously situated for rust dispersal. East winds, prevailing during periods favorable for basidiospore dispersal, blow across extensive populations of comandra and are funneled to the north and northwest over a mature lodgepole pine forest. Cliffs and mountains 8 km downwind of the comandra populations disrupt this airflow over the furthest lodgepole pine stands. The result is a generally high level of disease incidence across the study area with a shallow disease gradient that extends to the limit of lodgepole pine distribution. Topography also can partially account for patterns of rust distribution in the Medicine Bow area. For example, winds disperse spores from comandra populations along the eastern slope and deposit them across a broad, uninterrupted lodgepole pine forest. Disease incidence is high at the forest edge and decreases exponentially with distance to the west. Exceptions to this general pattern illustrate the influence of local topography. Although comandra populations are sparse in the southeast corner, nearby pine stands to the west are severely infested. Winds over these stands are affected by landforms to the east and originate not from the east, but from the northeast, where there are large populations of comandra. Along the northern portion of the east slope, comandra populations occur on long, steep ridges perpendicular to strong east winds. In part, the high disease incidence and shallow disease gradient in the northern portion of the area may be explained by older trees and more-efficient spore dispersal off these high ridges in contrast to gentler slopes parallel to the wind in the south (Fig 2.).

Other factors that influence patterns of disease distribution include the extent and relative locations of aecial and telial host populations. The interspersion of extensive comandra populations between lodgepole pine stands in the Shoshone area brings these hosts into close proximity and, thereby, increases overall disease incidence. In contrast, in the Medicine Bow area, less-extensive comandra populations are restricted to the east slope and to a small portion of the west slope. Because comandra populations are small on the west slope and winds favorable for spore dispersal to the east are infrequent (5), the disease incidence is low, and the disease gradient is steep compared to levels observed on the east slope.

The strong associations of site, stand, and alternate-host factors with the incidence of comandra blister rust provide forest managers with a means of determining rust hazard in stands of lodgepole pine. Many of the stands used to quantify these relationships have been harvested since the study for salvage or regeneration, removing visual evidence of rust impact. Because of the persistence of comandra populations and the frequency of long-distance spore dispersal, future stands are expected to become infested. This work has demonstrated that landscape-scale studies of host populations and airflow patterns are useful for predicting the extent and severity of comandra blister rust outbreaks.

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