Influence of Site Factors on Dogwood Anthracnose in the Nantahala Mountain Range of Western North Carolina

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ABSTRACT

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Sixty-five 0.08-ha plots located within the Nantahala Mountain range of western North Carolina were surveyed for dogwood anthracnose, caused by *Discula destructiva*. The incidence of disease and disease severity (extent of foliar symptoms and limb dieback) within canopies of *Cornus florida* was determined for all trees with a diameter of 1.0 cm or greater at 1.37 m aboveground. The incidence of dogwood anthracnose ranged from 53 to 100%; the severity of foliar symptoms, from 3 to 65%; and limb dieback, from 8 to 65%. Plots were inventoried, and the relationship between dogwood anthracnose and 14 variables representing indices of host density, stand composition, and topography was examined. Host density or relative host density, expressed in stems per hectare or importance value, respectively, and azimuth accounted for a significant portion of explainable variation in dogwood anthracnose. Anthracnose was inversely related to absolute or relative measurements of host density. Disease was greatest in northeast-facing plots and lowest in southwest-facing plots. Elevation had a minor influence on disease incidence and limb dieback. Geographic features, as described by the landform index, had a minor influence on disease incidence.

Dogwood anthracnose, caused by *Discula destructiva* Redlin., is a serious threat to native flowering dogwood (*Cornus florida* L.) in the eastern United States (13,17). The disease is capable of destroying large numbers of trees over a short period of time in naturally forested areas (15,19). Since it was first observed in three northeastern states in 1977 (10), dogwood anthracnose has been found to extend throughout the northeastern United States (13) and down the Appalachian mountain range into northern Alabama and Georgia (1). In the southeastern United States, an estimated 5.7 million acres of forest were affected by December 1990 (1).

C. florida is an important understory component in forested areas of the eastern United States. The high calcium content and rapid decomposition of leaf tissue enhance fertility in the upper layers of forest soil (9,23). The berrylike fruit are consumed in quantity by wildlife in the fall and early winter. *C. florida* is one of the first woody species to colonize regenerating areas of disturbed forests (3). Dogwood also has economic and social value as an ornamental tree whose springtime blossoms are celebrated in festivals across the southeastern United States. Because of its importance, there is much concern over the fate of *C. florida* in both affected and unaffected areas of the eastern United States.

The ecological range of dogwood anthracnose is not known. Disease intensity is often quite variable in infested areas. The heaviest infestations are known to occur in forested areas in the northeast (13), but along the eastern shore of Maryland more severe infestations were observed in urban and roadside settings (W. A. Jackson, *personal communication*). Disease levels have been reported to vary significantly across the landscapes of three separate areas within the Great Smoky Mountains National Park (1). Additional observations have indicated that disease is most common at high elevations and in cool, wet coves (1). In the southeastern United States, the disease is found primarily in the mountains, foothills, and upper Piedmont physiogeographic provinces (1).

This study was undertaken to gain a better understanding of the factors that influence the range of dogwood anthracnose. Our specific objective was to examine the relationship of various site factors, including topographic features and stand composition, to incidence and severity of disease. A rugged, undisturbed area of the southern Appalachian Mountains where the disease is known to occur was used as the study site.

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MATERIALS AND METHODS

Study area. A survey was conducted at the USDA Forest Service, Coweeta Hydrologic Laboratory. Located in the Nantahala Mountain Range of western North Carolina, the laboratory is a biosphere preserve consisting of adjacent east-facing, bowl-shaped basins with elevations ranging from 675 to 1,592 m (21). Sixty-five rectangular 0.08-ha plots were selected from a group of 400 permanent plots established in 1934. Plots were distributed over nine northeast-southwest transects across the entire Coweeta Basin (1,626 ha) and encompassed a variety of terrains and vegetation types. All plots were located in areas undisturbed since 1923 and included a minimum of five *C. florida* trees.

Disease ratings. Disease surveys were made during a 2-wk period in August 1990. Measurements of trunk diameter, disease incidence, severity of foliar symptoms, and limb dieback were taken on all *C. florida* with a diameter of 1.0 cm or greater at 1.37 m aboveground. Severity of foliar symptoms was recorded as the percentage of canopy with symptoms of dogwood anthracnose, using a scale of 0–10, with 0 indicating no disease present, 1 = 1–10% disease, 2 = 11–20% disease, and so on, to 10 = 91–100% disease. Limb dieback was recorded as the percentage of dead limbs on each tree, using the same 0–10 scale. Dead trees were rated as 10 for both disease severity and limb dieback. The mean ratings for severity of foliar symptoms and limb dieback in each plot were expressed as percentages. Disease incidence was expressed as the ratio of infected to healthy trees per plot.

Stand level variables. The plots were inventoried for stand composition in the fall of 1990. Trunk diameter at 1.37 m aboveground was measured to the nearest 1.0 cm on the living stems of all woody species. Diameters were grouped into 2.5-cm classes following the procedures of Avery and Burkhart (2). Basal area was calculated for all species using measurements of trunk diameter and expressed in m^2/ha.

The inventory data from each plot were used to compute seven stand level variables for each plot. Average size of *C. florida* was determined from measurements of mean trunk diameter. Abundance of *C. florida* was determined from the total number of stems and the sum total of basal area and expressed in stems per hectare and basal area per hectare, respectively. Total basal area of all vegetation with a trunk diameter of

1.0 cm or greater was also determined. The relative density of *C. florida* was determined by calculating the importance value (IV), where IV = (relative basal area + relative abundance)/2 (20). Relative basal area and relative abundance for *C. florida* were calculated as the proportion of total basal area and the proportion of total number of stems, respectively.

Plant diversity and stand composition in each plot were evaluated through the Margalef index and Shannon index, respectively (20). The Margalef index (Rl) provides an indication of the richness of species and is denoted by $\mathrm{Rl} = (S - 1)/\ln(N)$, where S = total number of species and N = total number of individuals. The Shannon index provides an indication of both richness and evenness of plant species in an area and is denoted by $H' = -\Sigma_{i=1}^{S} [p_i \ln(p_i)]$, where S = total number of species, $p_i = n_i/N$, n_i = basal areas for species i, and N = total basal area. $H' = 0$ if only one species is present in the plot, and H' = maximum if all species are represented by an equivalent basal area. H' was expressed as the ratio of calculated H' to maximum H' for each plot.

Site characteristics. The following seven site characteristics were computed for each plot: elevation, surface inclination (% slope), surface orientation (azimuth), landform index, terrain shape index, topographic relative moisture index, and radiation index. The landform index (LI) provides an indication of the influence of prominent geographic features and is computed as $\mathrm{LI} = \Sigma(\text{gradient})/(N100)$, where gradient is the percent change in inclination between the plot center and the horizon and N = number of directions in which the gradient was computed (W. H. McNab, *personal communication*). In this study, gradients were measured in eight directions (north, northeast, east, southeast, west, southwest, south, and northwest). Terrain shape index (TSI) expresses the geometric shape of the plot (convex or concave) and is computed as $\mathrm{TSI} = \Sigma(\text{slope gradient})/N$, where slope gradient is the change in inclination between the plot center and a point 10 m away, and N = number of directions in which the slope gradient was determined (14). Slope gradients were measured in four directions (north, east, south, and west). Topographic relative moisture index indicates the relative soil moisture availability among sites in mountain terrain (16). The topographic relative moisture index is a summed scaler index of four slope parameters: topographic position, azimuth, slope, and geometric shape of the plot. Radiation index allows the quantitative differentiation of potential solar beam irradiation between plots and is expressed as the ratio of the total annual potential solar beam insolation received at a site to the total annual maximum potential solar beam insolation (11). Maximum potential solar beam insolation is the quantity of energy received by a horizontal surface, whereas the potential solar beam irradiation received at a site is dependent upon terrestrial latitude, surface inclination, and surface orientation.

Data analyses. A total of three dependent variables and 14 independent variables were calculated for each plot. Direct gradient analysis was performed by plotting disease ratings along each individual independent variable (12). Azimuth values greater than 270° were modified by the equation $\mathrm{MAZ} = 270 - (\mathrm{AZ} - 270)$, where MAZ = modified azimuth and AZ = azimuth values between 270 and 360°, to account for an observed negative relationship between disease ratings and azimuth values between 0 and 270° and a positive relationship between 271 and 360°

Data were checked for normality and, when appropriate, were transformed to satisfy assumptions of normality. Stepwise forward multiple regression analysis was used to regress disease incidence, foliar symptoms, and limb dieback on the independent variables (18). Alphas for independent variables to enter and exit the analyses were both 0.15. To further safeguard against inclusion of nonsignificant variables, adjusted R^2 values were calculated for all models following the procedures of Campbell and Madden (6).

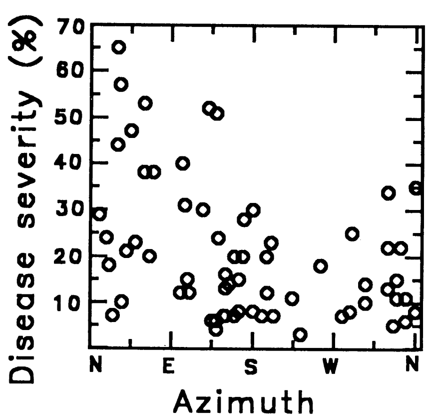

Fig. 1. Relationship between azimuth and average disease severity in 65 0.08-ha plots, with disease severity expressed as the percentage of *Cornus florida* canopy with foliar symptoms of dogwood anthracnose.

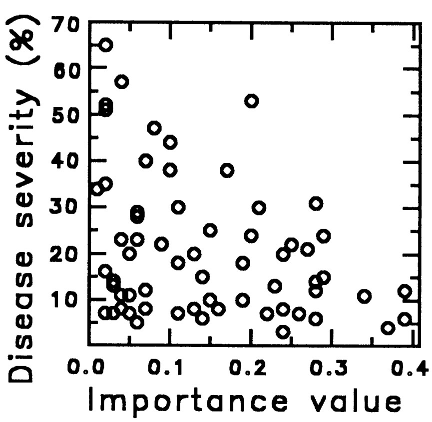

Fig. 2. Relationship between importance value and average disease severity in 65 0.08-ha plots. Disease severity is expressed as the percentage of *Cornus florida* canopy with foliar symptoms of dogwood anthracnose. Importance value = (relative basal area + relative density)/2.

RESULTS

Disease incidence ranged from 0.53 to 1.00 and averaged 0.87 per plot. The extent of foliar symptoms ranged from 3 to 65%, with an average of 20% per plot. Limb dieback ranged from 8 to 65%, with an average of 29% per plot.

Slope and elevation of plots ranged from 12% and 717 m to 75% and 1,062 m, respectively. Density of *C. florida* stems ranged from 86 to 1,520 stems per hectare, and basal area ranged from 0.51 to 7.01 m^2/ha. Importance values for *C. florida* were between 0.01 and 0.39 and averaged 0.15. The terrain shape index revealed many concave and convex plots in addition to planer plots. The ratio of calculated to maximum values for the Shannon index varied from 0.48 to 0.83, which indicated the presence of both uniform and nonuniform stands.

Scatter plots revealed a curvilinear relationship between azimuth and severity of foliar symptoms (Fig. 1). Severity was greatest in plots that faced northeast and lowest in plots that faced southwest. Similar relationships were observed between azimuth and disease incidence and between azimuth and limb dieback. Severity of foliar symptoms was inversely related to relative host density as expressed by importance value (Fig. 2). As the importance value increased, the extent of foliar symptoms decreased. Similar negative relationships were observed between host density (stems per hectare) and disease incidence and between host density (stems per hectare) and limb dieback. No other discernable relationships were revealed in scatter plots of disease measurements versus topographic or plant diversity indices.

Results from stepwise regression analysis on disease incidence indicated that 49% of the total variation in disease incidence was explained by four variables (Table 1). Stems per hectare had the greatest effect on disease incidence, followed by azimuth, elevation, and landform index. Adjusted R^2 values did not decrease significantly upon inclusion of each additional variable.

Results from stepwise regression analysis on the extent of foliar symptoms indicated that 37% of the total variation in foliar symptoms was explained by just two variables (Table 2). Azimuth had the greatest effect on the extent of foliar symptoms. Adjusted R^2 values did not decrease significantly upon inclusion of the second variable.

Results from stepwise regression analysis on limb dieback indicated that 39% of the total variation in limb dieback was explained by three variables (Table 3). Stems per hectare had the greatest effect on limb dieback, followed by azimuth and elevation. Adjusted R^2 values did not decrease significantly upon inclusion of each additional variable.

DISCUSSION

The Coweeta Basin is an area of unusually high rainfall, receiving an average of 152 cm/yr at the base and 228 cm/yr at the peak of Albert Mountain. This high rainfall, coupled with the cool temperatures prevalent at elevations within the study area (717–1,062 m), provides a climate extremely conducive to disease development. Incidence and severity of anthracnose averaged 87 and 20%, respectively, in this survey. In a recent impact survey of dogwood anthracnose in the southeastern United States, incidence averaged 50% and severity averaged 31% in plots where anthracnose was present, based on weighted average of six severity classes, and assuming the maximum severity in each range (1).

Azimuth significantly impacted all disease measurements. This impact may be due to the effect of azimuth upon microclimates within plots. Northeast- and southwest-facing plots differ in the total amount of maximum potential solar beam irradiation they receive, with higher levels received in the southwest-facing plots (10). They also differ in the time of day at which maximum potential solar beam irradiation is received. The maximum occurs in the morning in northeast-facing plots and in the afternoon in southwest-facing plots. However, dense morning fogs common to this region of the southern Appalachian mountains limit the potential incoming solar beam irradiation in northeast-facing plots.

Although the prevailing wind direction during precipitation events in the Coweeta Basin is southwest to southeast, the highest precipitation points in the basin occur in northeast facing sites (22). Swift et al (22) hypothesized that high precipitation points are the result of dump zones for rain transported away from ridges by accelerated air movement through gaps and across ridges. Thus, in addition to lower levels of incoming solar radiation, northeast-facing sites also receive higher levels of total precipitation. Similar conditions have been observed to favor disease development in other regions (5,13). The combination of reduced solar radiation and high rainfall will limit the evaporative potential within sites. Previous studies have shown an inverse relationship between evaporative potential and dogwood anthracnose (8).

Elevation and geographic features had a small impact on disease. However, these variables can also impact microclimate. Lower temperatures are found in the higher elevations. By quantifying the degree of inclination between the plot and the horizon, the landform index can differentiate the duration of direct sunlight reaching plots.

Observations suggest that, even under heavy inoculum pressure, at least 3–5 yr are required from initial infection to death of mature trees. The high incidence of disease at Coweeta further indicates that the disease has probably been present for at least 5 yr. As numerous secondary cycles occur from April to October in wet years (K. O. Britton, *unpublished*), it seems likely that considerable spread within plots has also occurred. Thus, the inverse relationship between host density and disease was surprising in light of the ability of *D. destructiva* to produce abundant amounts of conidia on infected leaves and twigs and the high density of *C. florida* observed in many plots.

To ensure that the inverse relationship between host density and disease was not influenced by the location of *C. florida* stands within the Coweeta basin, the relationship between azimuth and importance value was examined. No clear relationship was observed in a scatter plot, and an R^2 of 0.003 was obtained when azimuth was regressed against the importance value. Thus, the density of *C. florida* was not related to azimuth in the Coweeta basin.

Several hypotheses are plausible to explain the observed relationship between host density and disease. One is based upon the reproductive habits of *C. florida.* In a summary of 64 studies on the effect of host density on disease in mostly agricultural situations, 89% showed a positive correlation between host density and disease when only the pathogen reproduced during the epidemic (4). Of six studies under situations where both the host and pathogen reproduce, only two showed a positive correlation. In another study using natural systems where both the pathogen and host reproduce, no relationship was observed between host density and disease in two of three host-pathogen systems studied (7). To date it appears that in the majority of natural systems studied where reproduction of the host is considered, increased host density does not necessarily correlate to increased levels of disease. In this study, age of *C. florida*, expressed as the average basal area per stem, was not related to disease, indicating that regeneration of *C. florida* was no more adversely affected than other stages in the life cycle. Reproduction of *C. florida* may compensate

Table 1. Stepwise regression analysis of disease incidence of dogwood anthracnose within canopies of *Cornus florida* on 13 independent variables

Variable	Parameter estimate	Standard error	Partial R^2	Model R^2	Adjusted R^2
Intercept	0.35	0.43	...	...	...
Stems/ha	-4.9×10^{-4}	9.0×10^{-5}	0.28	0.28	0.27
Azimuth	−0.0016	4.3×10^{-4}	0.13	0.41	0.39
Elevation	-9.8×10^{-4}	3.5×10^{-4}	0.05	0.46	0.43
LI[a]	0.74	0.36	0.03	0.49	0.46

[a] Landform index, which provides an indication of the influence of prominent geographic features and is computed as LI = Σ(gradient)/(N100), where gradient is the percent change in inclination between the plot center and the horizon, and N = number of directions in which the gradient was computed (W. H. McNab, *personal communication*).

Table 2. Stepwise regression analysis of severity of foliar symptoms of dogwood anthracnose within canopies of *Cornus florida* on 13 independent variables

Variable	Parameter estimate	Standard error	Partial R^2	Model R^2	Adjusted R^2
Intercept	49.37	5.16	...	...	...
Azimuth	−0.11	0.02	0.23	0.23	0.21
IV[a]	37.96	10.21	0.14	0.37	0.35

[a] Importance value, where IV = (relative basal area + relative abundance)/2 (20).

Table 3. Stepwise regression analysis of limb dieback of *Cornus florida* caused by dogwood anthracnose on 13 independent variables

Variable	Parameter estimate	Standard error	Partial R^2	Model R^2	Adjusted R^2
Intercept	−1.67	0.55	...	...	...
Stems/ha	-6.8×10^{-4}	1.5×10^{-4}	0.20	0.20	0.19
Azimuth	−0.0027	7.3×10^{-4}	0.15	0.35	0.33
Elevation	0.0011	5.7×10^{-4}	0.04	0.39	0.36

for increased levels of disease in areas where the microclimate is only marginally favorable for disease.

Another hypothesis relates to the health of *C. florida* in dense stands. It seems reasonable that dogwoods are numerous on sites most conducive to their vigorous growth and reproduction. More vigorous trees possess more carbohydrate reserves, permitting new growth flushes to replace defoliated infected leaves and providing greater cold-hardiness. Trees on good sites would therefore be more numerous and could be better able to withstand disease pressure from this necrotrophic parasite.

It should be noted that disease levels within the communities included in this study may also depend on the composition of local mycoflora, genetic makeup of the host population, and other factors unique to the southern Appalachian region that were not included in the study. The results obtained in this study may not apply to the pathosystem of *D. destructiva* and *C. florida* in other ecological communities. However, the study does reveal several important points. In regard to the ecological range of dogwood anthracnose, it lends further support to the importance of microclimate. The inverse relationship between host density and disease illustrates the point that the dynamics of host-pathogen systems in undisturbed plant communities are complex and should be evaluated on an individual basis.

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