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Michael A. Jenkins; Peter S. White

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Cornus florida L. mortality and understory composition changes in western Great Smoky Mountains National Park¹

Michael A. Jenkins²

National Park Service, Twin Creeks Natural Resources Center, 1314 Cherokee Orchard Road, Great Smoky Mountains National Park, Gatlinburg, TN 37738

Peter S. White

Department of Biology—Campus Box 3280, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599-3280

JENKINS, M. A. (Twin Creeks Natural Resources Center, Great Smoky Mountains National Park, Gatlinburg, TN 37738) AND P. S. WHITE (Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599). *Cornus florida* mortality and understory composition changes in western Great Smoky Mountains National Park. J. Torrey Bot. Soc. 129: 194–206. 2002.—Remeasurement of woody vegetation on permanent plots in western Great Smoky Mountains National Park indicated that understory composition and dominance have changed over the past two decades (between 1977–1979 and 1995–2000). We observed heavy mortality of *Cornus florida* L., likely as a result of infection by *Discula destructiva* Redlin, a destructive fungus that causes dogwood anthracnose. Mortality was highest in smaller size classes and seedling density generally decreased. Cove and alluvial forests, where heavy shading favors dogwood anthracnose, had the highest mortality. While still high, mortality in oak-hickory and oak-pine forests was lower than that of cove and alluvial forests. *Cornus florida* density more than doubled on three plots located within an area that burned in 1976, likely as a result of sprouting and reduced shading in these fire-thinned stands. Over the same two decades, the importance of *Tsuga canadensis* (L.) Carr. greatly increased in cove, alluvial, oak-hickory, and oak-pine stands. Changes in understory composition in conjunction with the widespread loss of *C. florida* may greatly impact numerous ecological relationships in these forests, including calcium availability, nutrient cycling, and food source availability for wildlife.

Key words: *Cornus florida* L., *Discula destructiva* Redlin, dogwood anthracnose, southern Appalachians, mortality, understory composition change.

Cornus florida L. (flowering dogwood), one of the most common understory tree species in eastern North America, is currently threatened across much of its range by *Discula destructiva* Redlin, a destructive fungus that causes dogwood anthracnose (Hibben and Daughtrey 1988; Daughtrey and Hibben 1994). Although the origin of this fungus is not certain, genetic testing suggests that it has been introduced recently, possibly from Asia (Britton 1994). In infected trees, purple-rimmed lesions first appear on leaf margins and expand up the veins into the petiole. As the infection progresses, trees undergo

twig and branch dieback and develop stem cankers, which results in tree-death.

Cornus florida typically is not found on hydric or very xeric sites (McLemore 1990), but is prominent on mesic and dry-mesic sites throughout the eastern United States (Muller 1982; Gilliam et al. 1993; Jenkins and Parker 1998). Although its importance is greatest in second-growth stands that have reinitiated after logging and agricultural use (Leopold et al. 1985; Orwig and Abrams 1994; Jenkins and Parker 1998), *C. florida* is also a common understory component of old-growth forests (Muller 1982; McCune et al. 1988; Goebel and Hix 1996). In western North Carolina, *C. florida* was the dominant species in a mixed-oak hardwood stand 10 years after clearcutting (Elliot et al. 1997). In mixed hardwood stands of southeastern Kentucky (Muller 1982), *C. florida* had the second highest density of any tree species less than 10 cm dbh in a 37 year-old stand (250 stems/ha; *Acer rubrum* L. density was 328 stems/ha), and the fourth highest density in an old-growth stand (95 stems/ha).

Mortality of *C. florida* has been severe over

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² Author for correspondence. E-mail: mike.jenkins@nps.gov

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the past two decades. At Catoctin Mountain Park in Maryland, Sherald et al. (1996) observed a 77% reduction in *C. florida* density between 1976 and 1992. In Franklin County, Tennessee, Hiers and Evans (1997) observed a 98% reduction in density within a cove forest between 1983 and 1995. The loss of such an important species from stands throughout the region may have serious ecological effects. Because of the high calcium content and quick decomposition of *C. florida* leaves (Thomas 1969; Hepting 1971), its litter is an important source of calcium in the surface horizon of forest soils. In addition, its fruit provides a high-protein fall food source for neo-tropical migrant birds (Stiles 1980).

Although mortality from anthracnose has been high, the severity and rate of anthracnose infection varies with several environmental factors. Within the southern Appalachians, the severity of infection is greatest on more mesic, northwest facing slopes with more closed canopies and lowest on drier, southwest facing slopes with more open canopies (Chellemi and Britton 1992). Within individual stands, disease severity increases with decreased light availability, increased moisture, and decreased evaporative potential of the leaf surface (Hibben and Daughtrey 1988; Chellemi et al. 1992). More information is needed to determine how dogwood anthracnose has impacted forests of the southern Appalachians over the past decade.

Great Smoky Mountains National Park (GSMNP) is internationally renowned as a center of biological diversity within North America and was designated as an International Biosphere Reserve in 1976. Due to its biotic diversity, large size (>200,000 ha), and protected status, GSMNP serves a vital role in biological conservation within the southeastern United States. Changes that occur within the biological communities of GSMNP often serve as baselines for comparison to other state and federal lands within the region. Dogwood anthracnose was first identified in GSMNP in the late 1980s and has spread across a wide range of forest types in which *C. florida* is found. In the western half of GSMNP, Wilds (1997) observed anthracnose infection in 98% of plots established to assess the distribution and severity of the disease. As part of the long-term monitoring program of GSMNP, permanent vegetation plots established in the 1970s have been resampled to monitor changes in the Park's vegetation communities. In this paper, we use data from these plots to answer two questions. First, how has the severity

of dogwood mortality varied with *C. florida* size class, forest type, and stand structure? Second, within a given forest type, how has understory species composition shifted in conjunction with *C. florida* mortality?

Methods. Between 1977 and 1985 over 400 permanent 0.1 ha (20 m x 50 m) plots were established and sampled in GSMNP by National Park Service Upland Field Research Laboratory staff (White and Busing 1993). Of these, 287 were established in the western end of the Park between 1977 and 1979, almost exclusively on the Tennessee side of the state line (Fig. 1). For sampling, watersheds were divided into sample sites based upon elevation, slope position and aspect, and plots were randomly located within each sample site. These plots cover a broad-range of site conditions and disturbance histories and include areas of mature forest, abandoned agricultural land, limestone windows (discrete areas of limestone substrate exposed by erosion) and past burning. Of these 287 plots, 154 contained *Cornus florida* trees in 1977–1979. For this study, we use data from 86 of these plots that were resampled as part of GSMNP's ongoing long-term monitoring program and other research projects. Plot data were used to classify plots into 6 broad forest types: acid cove, typic cove, alluvial, oak-hickory, oak-pine, and a 36 ha area called Revenue Hill that burned in early November of 1976. Recent evaluation of data from plots that did not contain dogwood in 1977–1979 revealed that there has been little or no invasion of *C. florida* into new areas.

Acid cove forests were on gentle to moderately steep slopes and flats between 430 and 860 m occurring on acid soils. They were often located near streams within concave and v-shaped drainages. Typic cove forests were in more-protected topographic positions on gentle to moderate slopes with northerly aspects and elevations of 410 to 890 m. Alluvial forests were found on flats along medium-sized perennial streams between 330 and 640 m elevation. Soils underlying this forest type were relatively deep and loamy with large rocks. Most alluvial forest stands were formerly cleared for farming and settlement.

Oak-hickory forests were generally on moderately steep northwest to south facing slopes ranging from 310 to 1020 m elevation and oak-pine forests were typically found on narrow ridges and knobs, mid and upper slopes, and other exposed sites. Aspects were generally south-

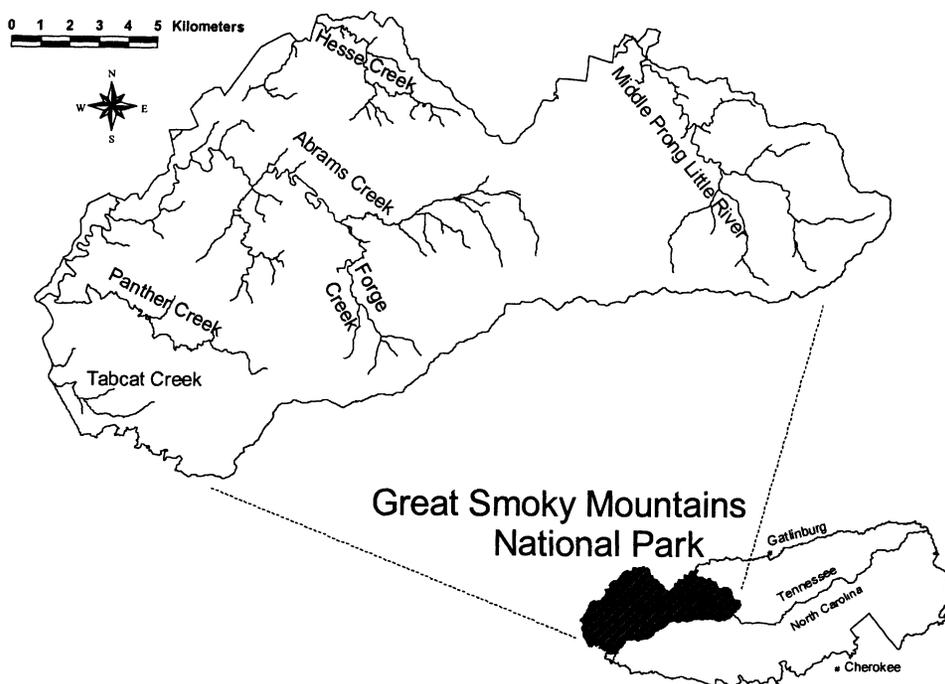


Fig. 1. Location of study area within western Great Smoky Mountains National Park.

east-northwest and slopes were gentle to moderately steep. Three plots were located within the area that burned in 1976. Two of these three plots were located in oak-hickory stands and the third in oak-pine.

FIELD METHODS. Data were collected from 86 permanent plots during two sampling intervals: 1977–1979 and 1995–2000. Within each 20 m × 50 m plot, the dbh of all living stems ≥ 1 cm dbh was measured to the nearest tenth-cm and recorded by species during the 1977–79 survey and for 75 of 86 plots remeasured during the 1995–2000 survey. For 11 plots remeasured between 1995 and 2000, the dbh of all trees < 10 cm dbh were tallied by species into 2 dbh classes: 1–4.9 cm and 5.0–9.9 cm. On these 11 plots, the dbh of all trees > 9.9 cm was measured and recorded by species. On the three plots within the 1976 burn area, trees that appeared to have died prior to the fire were distinguished from those that appeared to have been killed by the fire. This allowed an approximate reconstruction of the pre-fire stand (Harmon 1984).

For the 1977–1979 survey, seedling (stems < 1 cm diameter at 1.4 m) presence by species was recorded in twenty-five 4 m² quadrats distributed along 5 systematically placed transects within each plot. This method was also used to sample

76 of the plots remeasured between 1995 and 2000. In the remaining 11 plots sampled from 1995–2000, seedling presence by species was recorded in four 3.16 m X 3.16 m subplots distributed across the 0.1 ha plot. Seedlings originating from sprouts were not distinguished from those originating from seeds.

Before statistical comparison, all data were tested for normality using the Kolmogorov-Smirnov test for goodness of fit ($\alpha = 0.05$). The null hypothesis of normality was rejected for *C. florida* density data. These data were natural log transformed to improve normality and equalize variances. After transformation, data were retested to verify that the goodness of fit was improved and variances were equalized. Summary statistics presented in this paper for *C. florida* density were compiled from back-transformed data. Consequently, means presented are geometric means and not arithmetic means (Sokal and Rohlf 1981). Forest structure, understory importance, and seedling frequency data all complied with assumptions of normality and equal variance and were not transformed.

CORNUS FLORIDA DENSITY. Diameter data for *C. florida* trees were combined into 3 size classes for comparison: 1–4.9 cm, 5–9.9 cm, and > 9.9 cm dbh. We used two-way repeated mea-

Table 1. Repeated measures two-way analysis of variance for forest type differences in *Cornus florida* stem density between the two sampling intervals (1977–1979 and 1995–2000). Mean squares were calculated from ln-transformed data.

Source of Variation	df	Total density		Stems 1–4.9 cm		Stems 5–9.9 cm		Stems > 9.9 cm	
		MS	<i>P</i> > <i>F</i>	MS	<i>P</i> > <i>F</i>	MS	<i>P</i> > <i>F</i>	MS	<i>P</i> > <i>F</i>
Forest type	5	15.03	0.009	26.98	<0.001	10.13	0.036	15.39	0.092
Error (forest type)	80	4.51		5.67		4.02		7.81	
Interval	1	66.35	<0.001	93.14	<0.001	22.15	<0.001	11.79	0.108
Forest type × interval	5	5.77	<0.001	8.83	<0.001	1.62	0.425	2.42	0.743
Error	80	1.19		1.14		1.63		4.46	

MS = Mean squares.

ures analysis of variance (ANOVA) with sampling interval as the repeated factor to compare data between sampling intervals and among forest types. When ANOVA revealed significant main effects or a significant interaction, we used the Tukey multiple comparison test for post-hoc comparisons.

STAND STRUCTURE. To examine changes in stand structure, diameter data from the two sampling intervals were separated into two groups, understory (dbh < 20 cm) and overstory trees (dbh ≥ 20 cm). We calculated the total basal area and density of understory and overstory trees for each of the two sampling intervals. Paired t-tests were used to compare data from the two sampling intervals for each forest type.

CHANGES IN COMPOSITION. To compare changes in understory composition, we calculated species importance value [IV = (relative density + relative basal area)/2] of all stems < 20 cm dbh. Paired t-tests were used to compare changes in IV between sampling intervals for each forest type. To examine changes in seedling composition, we calculated species frequency [(# of quadrats in which a species occurs/total # of quadrats)*100].

Results. *CORNUS FLORIDA* DENSITY. Total stem density and density of stems ≤ 9.9 cm differed significantly among forest types and between sampling intervals (Table 1). Differences were most pronounced in the smallest stem size class (1–4.9 cm; *P* < 0.001). For total density and stems 1–4.9 cm, we observed a highly significant interaction between forest type and sampling interval (*P* < 0.001), indicating differences in the decline of *C. florida* density among forest types. According to Tukey pairwise multiple comparison tests, there were no significant differences in the densities of any stem size class among forest types for the first interval (1977–

1979; *P* > 0.40 for all types). However, for the 1995–2000 interval, burned plots contained a greater total density of stems than either acid or typic coves (*P* < 0.001 and *P* = 0.007, respectively). In 1995–2000, the mean density of small trees (stems 1–4.9 cm) on burned plots was significantly greater than that in acid or typic coves (*P* < 0.001 for both forest types). Oak-hickory stands contained significantly more small *C. florida* trees than acid and typic coves (*P* < 0.001 and *P* = 0.002, respectively). Oak-pine and alluvial stands also contained significantly more small trees in 1995–2000 than acid coves (*P* = 0.021 and *P* = 0.037, respectively).

According to Tukey pairwise multiple comparison tests, *C. florida* density within typic cove, acid cove, alluvial, oak-hickory, and oak-pine stands decreased between the two sampling intervals (1977–1979 and 1995–2000). Overall decline was greatest in acid cove forests, where mean *C. florida* density decreased by 94% (from 101 stems/ha in 1977–1979 to 6 stems/ha in 1995–2000; *P* < 0.001). Typic cove and alluvial forests experienced the next greatest decreases in *C. florida* density (92% for both forest types). Mean density decreased from 180 stems/ha to 14 stems/ha in typic cove forests (*P* < 0.001) and from 364 stems/ha to 28 stems/ha in alluvial forests (*P* < 0.001). The two driest forest types, oak-hickory and oak-pine, experienced less of a decline than cove and alluvial forests. Prior to anthracnose, *C. florida* mean density in oak-hickory forests was the second highest of any forest type (298 stems/ha); mean density decreased 80% to 61 stems/ha in 1995–2000 (*P* < 0.001). Mean *C. florida* density decreased 69%, from 132 stems/ha to 41 stems/ha, in oak-pine forests (*P* = 0.018). On the three plots that were part of the 1976 burn, *Cornus florida* density increased 200% from 205 stems/ha to 614 stems/ha (*P* = 0.222).

Cornus florida stem density decreased the

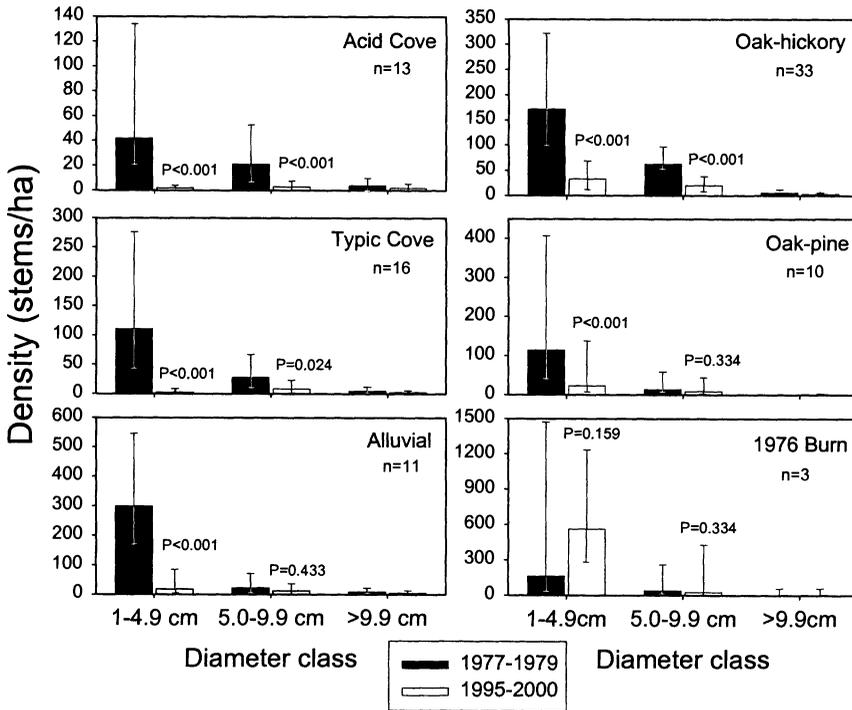


Fig. 2. Density (mean \pm 95% confidence interval) of *Cornus florida* in acid cove, typic cove, alluvial, oak-hickory, oak-pine, and burned stands by size class for the two sampling intervals (1977–1979 and 1995–2000). Means and confidence intervals were back-transformed from ln-transformed data. Geometric, not arithmetic, means are presented.

most among smaller trees (Fig. 2). With the exception of the 1976 burn area plots, the density of trees 1–4.9 cm dbh decreased greatly across all forest types. Decreases in small trees were particularly heavy in acid cove forests, which experienced a 95% decrease in density (42 stems/ha in 1977–1979 to 2 stems/ha in 1995–2000; $P < 0.001$), and typic cove forests, which experienced a 97% decrease (from 111 stems/ha to 3 stems/ha; $P < 0.001$). Density of small *C. florida* trees in alluvial forests also decreased greatly from 299 stems/ha to 18 stems/ha (94%; $P < 0.001$). Although less than cove and alluvial forests, the drier forest types also experienced large decreases in the density of small trees (1–4.9 cm dbh). In oak-hickory stands, density decreased 81% from 172 stems/ha in 1977–1979 to 33 stems/ha in 1995–2000 ($P < 0.001$). Oak-pine stands experienced a similar 80% decrease from 114 stems/ha to 23 stems/ha ($P = 0.001$). Within the 1976 burn area, density increased from 163 stems/ha to 562 stems/ha (245% increase; $P = 0.159$).

Compared to smaller trees, there were fewer changes in the density of larger *C. florida* trees

(Fig. 2). The density of trees 5.0–9.9 cm dbh decreased in acid cove forests (84%; $P < 0.001$), typic cove forests (70%; $P = 0.024$) and oak-hickory forests (68%; $P < 0.001$). The density of trees 5.0–9.9 cm dbh changed little in alluvial, oak-pine and burned stands. There was little change in the density of *C. florida* trees >9.9 cm dbh across the 6 forest types (two-way RM ANOVA, $P = 0.092$).

STAND STRUCTURE. Decreases in *C. florida* density varied with stand structure across the 6 forest types (Table 2). The four forest types with the greatest decrease in *C. florida* density (acid cove, typic cove, alluvial, and oak-hickory) also had the greatest overstory basal area in 1995–2000. Generally, overstory density and basal area of all forest types have remained relatively stable. Alluvial stands experienced the greatest increase in both overstory density and basal area between the two sampling intervals. Understory basal area and density decreased across all forest types, except the burned area, between the two sampling intervals (Table 2). On the burned plots, overstory basal area and density changed

Table 2. Total understory and overstory basal area and density (mean \pm 1 SE) of all forest types for the two sampling intervals (1977–1979 and 1995–2000).

	Understory			Overstory		
	1977–1979	1995–2000	P	1977–1979	1995–2000	P
Basal Area (m²/ha)						
Acid Cove	12.0 \pm 1.7	7.0 \pm 0.8	0.002	33.8 \pm 5.2	29.8 \pm 3.1	0.437
Typic Cove	6.2 \pm 0.8	4.0 \pm 0.5	0.001	36.4 \pm 4.1	37.1 \pm 3.6	0.890
Alluvial	12.2 \pm 1.2	8.8 \pm 0.8	0.012	18.0 \pm 2.0	24.9 \pm 2.3	0.002
Oak-hickory	10.3 \pm 0.9	7.9 \pm 0.6	0.002	20.2 \pm 1.6	21.8 \pm 1.2	0.178
Oak-pine	10.4 \pm 0.9	9.1 \pm 0.8	0.105	16.3 \pm 1.9	18.7 \pm 2.0	0.261
1976 Burn	8.2 \pm 0.9	9.2 \pm 4.9	0.845	17.0 \pm 2.8	17.0 \pm 7.0	0.941
Density (stems/ha)						
Acid Cove	5305 \pm 894	2040 \pm 260	0.002	240 \pm 29	215 \pm 23	0.473
Typic Cove	2183 \pm 233	1400 \pm 352	0.059	226 \pm 23	205 \pm 21	0.334
Alluvial	3798 \pm 424	2089 \pm 299	0.017	261 \pm 35	315 \pm 30	0.123
Oak-hickory	3619 \pm 370	2247 \pm 226	<0.001	186 \pm 11	208 \pm 10	0.031
Oak-pine	2877 \pm 284	1878 \pm 197	0.004	192 \pm 17	245 \pm 21	0.014
1976 Burn	2247 \pm 260	3890 \pm 1761	0.491	153 \pm 3	137 \pm 49	0.757

little. However, immediately following the 1976 fire, overstory basal area was reduced to 13.6 m²/ha and density was reduced to 113 stems/ha. Understory basal area and density on the burn plots were also much lower immediately following the fire (4.5 m²/ha and 1177 stems/ha, respectively) than in 1995–2000.

CHANGES IN COMPOSITION. Most of the forest types we sampled experienced large decreases in the understory importance of *C. florida* (Tables 3 and 4). In acid coves, *C. florida* IV (importance value) decreased 80% between the sampling intervals. Typic cove, alluvial, and oak-hickory forests also experienced decreases in the IV of *C. florida* (53%, 48%, and 29%, respectively). *Cornus florida* IV did not decrease in oak-pine stands, perhaps because there was an overall decrease in understory density on these plots. Although not statistically significant ($P = 0.152$) due to small sample size, *C. florida* importance more than doubled in the 1976 burn area.

Between the two sampling intervals, the relative importance of other species has shifted. *Tsuga canadensis* (L.) Carr. importance has increased greatly in the understories of acid cove ($P = 0.003$), typic cove ($P = 0.021$), and alluvial forests ($P = 0.001$). The understory IV of *T. canadensis* also greatly increased within the drier forest types. Oak-hickory stands have experienced a 113% increase in the IV of this species (12.5 ± 3.0 to 26.6 ± 4.3 ; $P < 0.001$) and oak-pine stands a 272% increase (2.9 ± 1.1 to 10.8 ± 3.6 ; $P = 0.016$). Unlike the other forest types, *T. canadensis* importance did not increase on

burned plots ($P = 0.423$). Overall, the importance of this species within the burn area was very low (0.5 ± 0.5 in 1995–2000). Oak-hickory and oak-pine stand understories have experienced sizeable decreases in the IV of three shade intolerant species since 1977: *Carya alba*, *Quercus prinus*, and *Quercus velutina*. Although *Rhododendron maximum* dominates the understory of acid cove forests, its IV has remained relatively constant across all forest types since the late 1970s.

Changes in the frequency of *C. florida* seedlings varied with forest type, but generally declined (Fig. 3). Typic coves and oak-hickory stands experienced large decreases in *C. florida* seedling frequency. In typic coves, frequency declined from 11% to less than 1% ($P < 0.024$), while in oak-hickory stands frequency declined from 33% to 11% ($P < 0.001$). *Cornus florida* seedling frequency also declined in oak-pine stands ($P = 0.022$), but remained relatively constant in alluvial, acid cove and burned stands.

Changes in the seedling frequencies of other species also varied with forest type. Seedlings of *Acer rubrum*, the most common seedling species across the 6 forest types, increased greatly in frequency in all forest types except the 1976 burn area. The seedling frequency of *T. canadensis* increased in acid cove, typic cove, alluvial, and oak-pine stands, but did not change in oak-hickory and burned stands. While the understory tree importance of *Q. prinus* and *Q. velutina* decreased drastically in oak-pine and oak-hickory stands, the seedling frequency of these two species increased in both forest types. In

Table 3. Importance values (mean \pm 1 SE) of selected species in acid cove, typic cove, and alluvial plots for the two sampling intervals (1977–1979 and 1995–2000).

Species	Acid Cove (n = 13)		Typic Cove (n = 16)		Alluvial (n = 11)	
	1977–1979	1995–2000	1977–1979	1995–2000	1977–1979	1995–2000
<i>Acer pensylvanicum</i>	1.0 \pm 0.4	0.6 \pm 0.4	2.3 \pm 0.6	2.4 \pm 0.6	0.1 \pm 0.1	<0.1
<i>Acer rubrum</i>	7.4 \pm 2.8	5.5 \pm 2.1	6.9 \pm 1.7	6.3 \pm 1.7	15.6 \pm 3.9	16.6 \pm 3.8
<i>Acer saccharum</i>	1.1 \pm 0.6	0.6 \pm 0.5	6.3 \pm 2.4	8.2 \pm 4.0	0.1 \pm 0.1	<0.1
<i>Betula lenta</i>	4.0 \pm 1.3	4.4 \pm 0.8	2.0 \pm 0.6	2.1 \pm 0.7	1.2 \pm 0.6	1.6 \pm 0.9
<i>Carpinus caroliniana</i>	<0.1	0.1 \pm 0.1	<0.1	A	3.9 \pm 2.1	5.8 \pm 3.3
<i>Cornus florida</i>	5.0 \pm 1.9	1.0 \pm 0.3**	12.0 \pm 2.7	5.7 \pm 2.5**	9.4 \pm 2.4	4.9 \pm 1.8***
<i>Fraxinus americana</i>	0.3 \pm 0.1	0.1 \pm 0.1	4.2 \pm 1.6	0.6 \pm 0.3**	0.3 \pm 0.1	0.4 \pm 0.2
<i>Halesia tetraptera</i>	1.8 \pm 1.6	2.1 \pm 1.8	16.8 \pm 4.5	18.5 \pm 5.5	0.4 \pm 0.3	0.5 \pm 0.4
<i>Liquidambar styraciflua</i>	0.5 \pm 0.4	0.4 \pm 0.3	<0.1	A	4.3 \pm 1.4	3.4 \pm 1.2
<i>Liriodendron tulipifera</i>	1.1 \pm 0.4	1.4 \pm 0.7	3.5 \pm 1.2	1.5 \pm 0.7*	7.6 \pm 3.9	6.0 \pm 2.0
<i>Oxydendrum arboreum</i>	2.3 \pm 0.6	1.1 \pm 0.5**	0.7 \pm 0.3	0.5 \pm 0.4	5.1 \pm 1.3	5.2 \pm 1.6
<i>Pinus strobus</i>	1.3 \pm 0.5	0.8 \pm 0.2	0.1 \pm 0.1	1.1 \pm 1.1	7.6 \pm 2.2	11.3 \pm 4.9
<i>Pinus virginiana</i>	0.1 \pm 0.1	A	A	A	10.9 \pm 4.1	2.1 \pm 0.9
<i>Quercus alba</i>	1.1 \pm 0.8	0.3 \pm 0.3	A	A	1.7 \pm 1.3	3.2 \pm 2.8
<i>Rhododendron maximum</i>	39.4 \pm 9.3	39.2 \pm 9.6	7.5 \pm 4.4	7.9 \pm 4.5	0.3 \pm 0.2	0.3 \pm 0.3
<i>Tsuga canadensis</i>	21.0 \pm 5.3	34.5 \pm 8.4***	15.9 \pm 4.7	23.5 \pm 6.1**	13.0 \pm 5.6	26.7 \pm 7.7***
<i>Vitis</i> spp.	0.4 \pm 0.2	0.2 \pm 0.2	5.8 \pm 1.9	6.3 \pm 2.6	0.8 \pm 0.2	0.1 \pm 0.1

* P < 0.1, ** P < 0.05, *** P < 0.01, **** P < 0.001.

A = absent from forest type.

Table 4. Importance values (mean \pm 1 SE) of selected species in oak-hickory, oak-pine, and 1976 burn area plots for the two sampling intervals (1977–1979 and 1995–2000).

Species	Oak-Hickory (n = 33)		Oak-Pine (n = 10)		1976 Burn (n = 3)	
	1977–1979	1995–2000	1977–1979	1995–2000	1977–1979	1995–2000
<i>Acer pensylvanicum</i>	2.5 \pm 1.0	3.5 \pm 1.0	0.3 \pm 0.3	0.4 \pm 0.4	0.1 \pm 0.1	0.2 \pm 0.2
<i>Acer rubrum</i>	16.0 \pm 2.4	13.9 \pm 1.7	18.0 \pm 4.7	17.2 \pm 4.0	11.7 \pm 6.2	18.6 \pm 8.7
<i>Carya glabra</i>	3.7 \pm 0.7	2.7 \pm 0.6*	0.8 \pm 0.3	0.8 \pm 0.3	7.9 \pm 0.8	3.8 \pm 1.5
<i>Carya alba</i>	3.7 \pm 0.9	0.4 \pm 0.4****	3.0 \pm 1.3	A***	3.5 \pm 1.9	A
<i>Cornus florida</i>	16.3 \pm 2.7	11.5 \pm 2.6**	8.5 \pm 3.0	8.2 \pm 3.8	7.7 \pm 3.2	16.2 \pm 5.7
<i>Halesia tetraptera</i>	3.9 \pm 1.4	6.9 \pm 2.0***	<0.1	0.5 \pm 0.5	A	A
<i>Kalmia latifolia</i>	3.6 \pm 1.6	3.0 \pm 1.4*	1.0 \pm 0.9	2.0 \pm 1.9	A	A
<i>Liriodendron tulipifera</i>	2.0 \pm 0.7	2.1 \pm 0.8	0.1 \pm 0.1	0.1 \pm 0.1	0.4 \pm 0.1	15.0 \pm 12.9
<i>Magnolia fraseri</i>	2.2 \pm 0.5	2.3 \pm 0.5	A	<0.1	A	A
<i>Nyssa sylvatica</i>	2.2 \pm 0.5	2.3 \pm 0.5	9.4 \pm 2.9	12.3 \pm 5.0	4.8 \pm 2.9	6.3 \pm 3.1
<i>Oxydendrum arboreum</i>	4.3 \pm 0.6	2.4 \pm 0.5***	5.6 \pm 1.4	2.7 \pm 0.5**	9.3 \pm 4.2	7.3 \pm 2.4
<i>Pinus rigida</i>	0.5 \pm 0.5	A	2.7 \pm 1.6	1.3 \pm 0.8	1.0 \pm 0.7	A
<i>Pinus strobus</i>	2.4 \pm 0.6	2.7 \pm 0.5	12.5 \pm 3.5	19.4 \pm 4.7**	0.7 \pm 0.1	0.5 \pm 0.5
<i>Pinus virginiana</i>	0.1 \pm 0.1	0.1 \pm 0.1	10.8 \pm 5.0	8.0 \pm 4.8	6.5 \pm 2.2	1.7 \pm 0.9
<i>Quercus alba</i>	1.5 \pm 0.5	0.7 \pm 0.3***	4.7 \pm 3.4	2.6 \pm 2.1	13.5 \pm 9.6	5.4 \pm 3.8
<i>Quercus coccinea</i>	0.3 \pm 0.1	<0.1	2.8 \pm 1.1	1.3 \pm 0.5	13.5 \pm 9.6	5.4 \pm 3.8
<i>Quercus prinus</i>	4.8 \pm 0.8	A****	7.1 \pm 1.7	A****	16.9 \pm 8.6	A
<i>Quercus rubra</i>	2.1 \pm 0.5	0.8 \pm 0.3***	0.2 \pm 0.1	<0.1	1.1 \pm 1.1	0.4 \pm 0.4
<i>Quercus velutina</i>	0.7 \pm 0.2	0.1 \pm 0.1****	3.3 \pm 0.9	0.3 \pm 0.2***	4.5 \pm 1.8	4.9 \pm 2.8
<i>Rhododendron maximum</i>	5.3 \pm 2.2	5.9 \pm 2.5	A	A	A	A
<i>Tsuga canadensis</i>	12.5 \pm 3.0	26.6 \pm 4.3****	2.9 \pm 1.1	10.8 \pm 3.6**	0.3 \pm 0.3	0.5 \pm 0.5

* P < 0.1, ** P < 0.05, *** P < 0.01, **** P < 0.001.

A = absent from forest type.

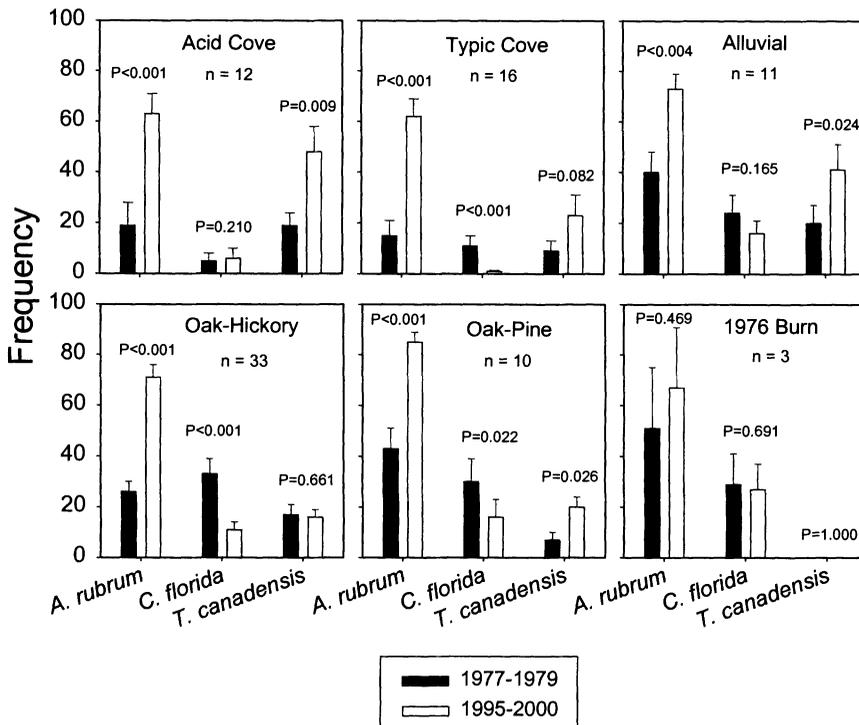


Fig. 3. Seedling frequency (mean \pm 1 SE) of *Acer rubrum*, *Cornus florida*, and *Tsuga canadensis* in all forest types for the two sampling intervals (1977–1979 and 1995–2000). Seedling data were unavailable for one acid cove plot.

oak-pine stands, the frequency of *Q. prinus* seedlings increased from 26% in 1977–1979 to 52% in 1995–2000 ($P = 0.005$), while frequency of *Q. velutina* seedlings increased from 18% to 32% ($P=0.030$). In oak-hickory stands, *Q. prinus* frequency increased from 12% to 33% ($P < 0.001$) and *Q. velutina* frequency increased from 6% to 17% ($P = 0.002$).

Discussion. *CORNUS FLORIDA* MORTALITY. Heavy rates of infection and mortality of *Cornus florida* resulting from dogwood anthracnose have been observed throughout the species range, including Pennsylvania (Williams and Moriarity 1999), Illinois (Schwegman et al. 1998), Virginia (Carr and Banas 2000), Maryland (Sherald et al. 1996), Kentucky (McEwan et al. 2000), and Tennessee (Hiers and Evans 1997). Between 1983 and 1995, Hiers and Evans (1997) observed a 91% decline in the density of *C. florida* trees greater than 1.5 m tall, which was comparable to the density decline we observed in typic and acid coves (92% and 94%, respectively). In an oak-hickory forest, Hiers and Evans (1997) also observed an 87% decrease in *C. florida* stems, which was high-

er than the 80% decrease we observed in oak-hickory stands.

The three most mesic forest types (acid coves, typic coves, and alluvial stands) had the greatest declines in *C. florida* density. The two cove types were mostly in topographically protected areas with generally northerly aspects, and the alluvial stands were in sheltered bottoms adjacent to streams. Local topographic features and stand conditions that increase understory moisture, decrease light availability, and reduce the evaporative potential of leaf surfaces are associated with higher rates of dogwood anthracnose infection (Hibben and Daughtrey 1988; Chellemi and Britton 1992; Erbaugh et al. 1995; Wilds 1997). In our study, the three forest types with the greatest overstory basal area in 1995–2000 (acid coves, typic coves, and alluvial areas) experienced the greatest mortality, likely as a result of increased shading and reduced evapotranspiration.

The effects of anthracnose have been well documented, but other factors may cause or contribute to mortality of *C. florida* trees. In eastern Kentucky, McEwan et al. (2000) observed a

36% percent decline in *C. florida* density in an old-growth forest prior to documented anthracnose infection. The authors suggested that canopy closure, environmental stress such as drought, and gap-dynamics might contribute to long-term mortality trends. In northern Indiana, an observed 43% decline in *C. florida* density since 1980 in an uninfected forest was attributed to increased competition from *Acer saccharum* in fire-suppressed stands (Pierce 2001). In our study, the lack of data between 1977–1979 and anthracnose infection during the late 1980's prevented us from distinguishing mortality that occurred prior to anthracnose infection. However, widespread infection and relatively sudden and heavy die-off of *C. florida* trees observed throughout GSMNP during the late 1980s and early 1990s (Windham et al. 1993) likely accounted for much of the mortality we observed. Other factors, including past drought, may have contributed to *C. florida* mortality. *Cornus florida* has been shown to have low dehydration tolerance (Tschaplinski et al. 1998) and drought stress may predispose trees to anthracnose infection (Erbaugh et al. 1995).

As in other studies (Hiers and Evans 1997; Schwegman et al. 1998; McEwan et al. 2000), we observed greater loss of *C. florida* stems in the smaller size classes. In smaller trees, increased shading combines with limited crown area to accelerate infection and mortality. The larger trees we observed had larger, more widely-spread crowns. As the disease kills the lower branches of larger trees, their crowns become very thin and umbrella shaped. The large surface area of these thin and widely spread crowns increases evapotranspiration and exposure to light, thus slowing the progress of the disease. Because they are near the forest floor, smaller stems also are susceptible to infection by airborne conidia falling from larger infected stems (McEwan et al. 2000).

CHANGES IN UNDERSTORY COMPOSITION. Dogwood mortality, combined with fire suppression, has caused shifts in understory composition in western GSMNP. The understory IV (stems < 20 cm dbh) of *C. florida* has decreased in acid coves, typic coves, alluvial forests, and oak-hickory forests. Across all forest types except the 1976 burn area, *Tsuga canadensis* IV has generally increased. This increase was greatest in oak-hickory forests, where *T. canadensis* IV in the understory has more than doubled since 1977–1979, a trend that has also been noted on

xeric sites within GSMNP (Harrod et al. 1998). The increased understory dominance of *T. canadensis* could amplify anthracnose infection rates. *Tsuga canadensis* often creates a fairly continuous layer within forest understories, which could increase shading and surface moisture retention, further hindering the survival of small *C. florida* trees. However, with the recent onset of the exotic hemlock adelgid (*Adelges tsugae*) within GSMNP, *T. canadensis* will likely experience heavy mortality, further altering understory conditions (Johnson et al. 1999). Although *Acer rubrum* was a dominant understory component across all forest types, its importance remained fairly constant between 1977–1979 and 1995–2000. This species has shown a dramatic increase in dominance over the past century throughout forests of eastern North America (Abrams 1998). According to Harrod et al. (1998), the overstory importance of this species within western GSMNP has greatly increased in fire suppressed stands since the 1970s. However, the understory importance of this species remained stable in the stands we sampled. Although *A. rubrum* seedling frequency has increased since 1977–1979 and was the highest of any species, it appears that most of these seedlings are not advancing into larger size classes.

Several studies have shown that *Rhododendron maximum* has increased in abundance in forests of the southern Appalachians (Monk et al. 1985; Phillips and Murdy 1985; Baker and Van Lear 1998), largely as a result of various types of overstory disturbance (Woods and Shanks 1959; McGee and Smith 1967; Phillips and Murdy 1985). In 1995–2000, *Rhododendron maximum* dominated acid coves and was a common species in typic cove understories, but its importance has not increased since 1977–1979. This suggests that low light levels in these closed-canopy stands have prevented *R. maximum* from increasing in importance.

EFFECTS OF FIRE ON *CORNUS FLORIDA*. Although the small sample size of plots within the 1976 burn area resulted in reduced statistical power, we did observe several promising trends that need further investigation. After the fire, *C. florida* density greatly increased (200%) as a result of prolific sprouting, which is typical of the species (McLemore 1990). With time, these stems may self-thin and density of *C. florida* may return to a level more typical of pre-anthracnose stands. Although the fire occurred over two decades ago, the structure within these

stands still appears sufficiently open to allow high light levels to reach the understory, which reduces the virulence of *Discula destructiva* (Hibben and Daughtrey 1988; Chellemi and Britton 1992; Erbaugh et al. 1995). Post-fire conditions in these stands suggest that prescribed burning may be used to maintain *C. florida* as a component of oak-hickory and oak-pine forests. However, more work is needed to determine whether *C. florida* density has increased in other areas that have burned. In addition, fire could be detrimental to the long-term maintenance of *C. florida* if diseased individuals do not have sufficient energy reserves to resprout after fire.

ECOLOGICAL IMPACTS OF *CORNUS FLORIDA* MORTALITY. Since mortality was highest in the smaller size classes, *C. florida* density will continue to decrease as larger trees senesce and are not replaced by new individuals. Unless management practices can be developed to stop or slow the effects of dogwood anthracnose, negative ecological impacts may occur. The fruit of *C. florida* are rich in crude fat and are considered to be an excellent food for wildlife, including over 36 species of birds (Stiles 1980; McLemore 1990). Hiers and Evans (1997) observed an increase in the density of two other soft-mast producing species, *Nyssa sylvatica* and *Lindera benzoin*, in forest understories following *C. florida* mortality. In our study, *T. canadensis*, which does not produce soft mast, has largely filled the compositional void created by the loss of *C. florida*, contributing further to the loss of this important food source.

Because of its high calcium content (2.0–3.5% dry weight) and rapid decomposition rate (64% reduction in litter mass after 2 years), *C. florida* foliage plays an important role in building and retaining calcium within the surface horizon of forest soils (Thomas 1969; Blair 1988). The soils of western GSMNP are typically sandstone-derived with relatively low pH and poor buffering capacity and calcium is rapidly leached from the system. The widespread loss of *C. florida* from lower elevation forests may have serious impacts on soil pH and nutrient availability. Soils under *T. canadensis* trees are typically more acidic and have higher quantities of exchangeable aluminum and iron (Messenger 1975; Boettcher and Kalisz 1990; Finzi et al. 1998), thus replacement of hardwood species by *T. canadensis* may further alter soil conditions

due to changes in foliar quality (Messenger 1975).

As larger *C. florida* stems are killed within GSMNP and are not replaced by new cohorts of regeneration, this species will largely disappear from the landscape. Infected individuals exhibit poor fruit production and thus reduced fecundity (Windham et al. 1993). Mortality and reduced fecundity of infected trees may inevitably result in a loss of genetic and phenotypic variability within surviving population remnants (Wilds 1997). Management techniques to control dogwood anthracnose have received little attention, although methods that reduce shading offer some promise (Britton et al. 1994). Our study suggests that fire may reduce shading and allow *C. florida* stems to persist. More work is needed to determine how infected forest stands should be managed to prevent or slow the loss of this species from eastern temperate forests.

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