

Tree Growth and Mortality in a Southern Appalachian Deciduous Forest Following Extended Wet and Dry Periods

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ABSTRACT

We inventoried two 1-ha plots on opposing watersheds (WS2–WS-S, WS18–WS-N) three times (1983, 1989, 1998) over a 16-year period to contrast how differing precipitation (P) regimes affect tree mortality. From 1983 to 1989, annual precipitation averaged 16.5% less than the 64-year mean; from 1989 to 1998, it averaged 12.2% above the mean. In 1989 and 1998, standing crop biomass, aboveground net primary productivity, mortality rates and species composition were determined. In 1989, following the dry period, the highest mortality for canopy tree species was in *Carya* spp. and *Quercus velutina* in both watersheds. Following the wet period in 1998, mortality was highest in *Cornus florida* in both watersheds, presumably due to the *Anthracnose* fungus; however, net change in stem density due to ingrowth was positive for this species in the WS-S watershed (+34%) and negative in the WS-N watershed (–18%). Estimated ANPP for WS-S was 10 and 1,076 kg ha⁻¹ yr⁻¹ for the periods 1983–89 and 1989–98, respectively. In contrast, ANPP on WS-N was 679 and 93 kg ha⁻¹ yr⁻¹ for the same periods. Differences in ANPP are due to higher rates of mortality on WS-N compared with WS-S. In this study, species specific rates of mortality varied by watershed, and were likely due to microclimate-related increased susceptibility at the species level to certain proximal causes.

INTRODUCTION

Forest communities are heterogeneous at both large and small scales—in part due to disturbance (Bazzaz 1983, Halpern et al. 1990, Elliott et al. 1999). Disturbance results from a variety of natural and human-caused events, e.g., drought, windthrow and forest pests (pathogens, insects) and occurs at varying scales. At large spatial scales wind is a primary agent of natural disturbance in many forest ecosystems, although the frequency and magnitude of wind events vary among and within forest types. For example, in a Costa Rican rain forest, Lawton and Putz (1988) found that 80% of forest openings were caused by wind. Similarly, Barden (1981) found that wind contributed to 97% of canopy gap formation in a mature mixed-mesophytic forest (see Braun 1950) in the southeastern United States. Clinton et al. (1993), however, found that in a mature southern Appalachian mixed hardwood forest, wind accounted for only 11% of tree mortality. Therefore, in order to more accurately predict recovery and gain insight into the significance of specific types of disturbance, we found it necessary to investigate stand-level responses to varying disturbance patterns.

Logging, agriculture and the use of fire have been the predominant forms of anthropogenic disturbance in the southern Appalachians (DeVivo 1991, Stephenson et al. 1993). In addition, anecdotal evidence of tornadoes or hurricanes has been documented, although large-scale

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disturbances of that type are extremely rare (Greenberg and McNab 1998). Pollen and charcoal records developed from cored sediments illustrate abrupt shifts in species abundance due to land conversion from forest to agriculture (Delcourt 1979). Fire was an important tool during European settlement, and many catastrophic fires occurred due to the build up of unburned fuels in the form of slash generated from land clearing. More recently (circa 1920), the chestnut blight [*Cryphonectria parasitica* (Murr.) Barr; Anagnostakis and Hillman 1992] introduced an accelerated successional pathway that, in combination with historical land use and the virtual elimination of some common practices (e.g., fire, grazing), helped shape present-day stand composition and structure.

Between 1980 and 1998 there were at least three regionally significant climatic or meteorological events in the southern Appalachians, all of which contributed to tree mortality and/or declines in tree growth rate (Vose and Swank 1994, Clinton et al. 1997). The most recent and dramatic event occurred in October 1995. Hurricane Opal tracked northerly and within 180 km west of the Coweeta basin, bringing heavy rains and high winds. At National Oceanographic and Atmospheric Administration (NOAA) stations in nearby Asheville, North Carolina, wind gusts of up to 26 m sec⁻¹ were recorded at low elevations and up to 37 m sec⁻¹ at high elevations. The result was extensive windthrow throughout the southern Appalachians, particularly near ridge tops (Greenberg and McNab 1998, Clinton and Baker 2000). Estimates of the extent of damage on the Wayah Ranger District of the Nantahala National Forest ranged from 5–15% of the total land area. A second significant event occurred in mid-March 1993, when a severe winter storm brought heavy snow (approx. 75 cm), extreme temperatures (<–15°C) and high winds. The result was substantial structural damage to the forest canopy and in some areas the creation of large forest canopy openings due to the uprooting of trees. To date, no one has made a reliable estimate of tree mortality as a direct result of that winter storm. Finally, a prolonged drought over the period 1984 to 1988 (Figure 1) was the most significant to have occurred in the region for several decades. The return period for a drought of this magnitude was estimated to be about every 200 years (Swift et al. 1989). The result was an increase in tree mortality, particularly of oak (*Quercus*) species, brought on by the combined effect of moisture stress and root pathogens. Over time, as effects of the drought have become manifest, rates of mortality have increased (Starkey et al. 1989, Oak et al. 1991, Clinton et al. 1993, Vose and Swank 1994).

Our objective was to examine tree mortality and growth under contrasting disturbance regimes: an extended drought versus an extended wet period containing two types of catastrophic storms and two growing season droughts (Table 1). To span the range of possible topographic variation with respect to climate and examine the interactions of aspect, climate and species with respect to tree mortality, we established our study plots on watersheds of opposite aspect (N, S).

METHODS

Site Description

This study was conducted within the basin of the Coweeta Hydrologic Laboratory, located in the Blue Ridge Physiographic Province of the southern Appalachian Mountains of western North Carolina approximately 20 km south of Franklin. The Coweeta Basin ranges in elevation from 680–1,600 m over a drainage area of 1,626 ha. Precipitation averages 1,800 mm at the lower elevations with <5% falling as snow or ice. Mean annual temperature is 12.6°C, and ranges from a mean of –4.0°C in January to 24°C in July (Swank and Crossley 1988). In both watersheds woody vegetation is dominated by oak species along with significant components of red maple (*Acer rubrum* L.), yellow poplar (*Liriodendron tulipifera* L.) and hickory species (*Carya* spp.) in the overstory, and black gum (*Nyssa sylvatica* Marsh.), sourwood [*Oxydendrum arboreum* (L.) DC.] and flowering dogwood (*Cornus florida* L.) in the understory. On the most mesic sites and along streams, the understory is dominated by rosebay rhododendron (*Rhododendron maximum* L.), and on the drier sites by mountain laurel (*Kalmia latifolia* L.).

The two watersheds had been cutover prior to purchase around 1920 by the United States government for inclusion in the National Forest System. Salvage of dead and dying American

Coweeta Long-Term Precipitation Record (CS-01)

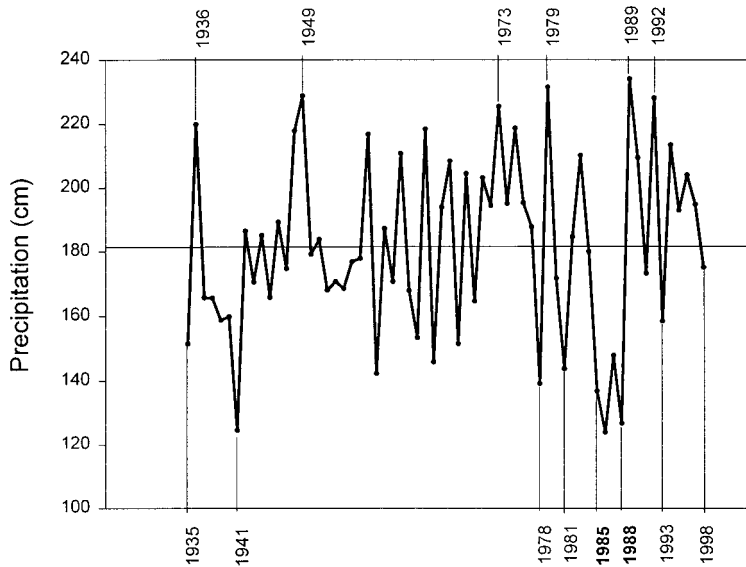


Figure 1. Long-term precipitation record for the main climatic station (CS-01) at the Coweeta Hydrologic Laboratory. The solid horizontal line in the middle of the graph is the long-term mean.

chestnut [*Castanea dentata* (Marsh.) Borkh.], along with heavy overstory removal of other species, continued to take place until around 1930. Although we are not certain when each of these watersheds was logged, no mechanical removal of timber has occurred since logging ceased.

Site Selection and Plot Layout

On the Coweeta site, 1-ha plots were established on north-facing watershed 18 (WS-N) and south-facing watershed 2 (WS-S). Although aspect differs, these watersheds are essentially identical topographically, and the plots are located in the same landscape position. Each plot included 400 contiguous 5- × 5-m subplots. In 1983, all stems ≥10-cm diameter at breast height (dbh) were identified by species, measured for dbh (cm) and tagged. Where possible, snags were identified by species and inventoried. For each plot, the location of all stems and snags on the grid was established to the nearest 0.5 m. In 1989 and 1998, all stems ≥2.5-cm dbh were identified by species and measured for dbh. As in 1983, snags and fallen trees also were measured and identified where possible. The locations of new stems were established to the nearest 0.5 m on the grid for each plot.

Analysis

Estimates of aboveground woody biomass (stem, branch, twig) on each plot were made using locally and regionally developed dbh-based allometric equations of Clark and Schroeder (1986) and Martin et al. (1998) for hardwoods, and equations of Van Lear et al. (1986) for yellow pine species (*Pinus* spp.). Because stems <10-cm dbh were not measured in 1983, comparisons in woody aboveground net primary production (ANPP) between watersheds and across sampling periods were made for stems ≥10-cm dbh, only. A chi-square (χ^2) test of independence was conducted on mortality rates between watersheds by sampling period and species.

Table 1. Comparison of rainfall for the water year May through April between the two sampling periods. Values in parentheses for the number of consecutive growing season droughts represent the range of the deficit relative to the long-term water year mean

Period	May '83–April '89	May '89–April '98
Years	6	9
Mean annual ppt (cm)	152.4	204.7
Relative to long-term mean (%)	–16.5	+12.2
Mean growing season ppt (cm)	66.9	91.2
Relative to long-term mean (%)	–15	+15
# consecutive growing season droughts and deficit range (%)	4 (–14 to –34)	0 (–24 to –27)

RESULTS AND DISCUSSION

Differential responses to the three disturbance events can be seen in differences in standing crop biomass for the two watersheds across sampling periods. For example, for stems ≥ 10 -cm dbh, estimated woody aboveground net primary production (ANPP) on WS-S between 1983 and 1989 was $2.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, compared with $3.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ on WS-N for the same period (Table 2). In contrast, ANPP on WS-S for the period 1989–98 nearly doubled to $4.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, whereas on WS-N, estimated ANPP decreased from the earlier period by 45% to $1.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (Table 2). The loss of production on WS-N was due to higher rates of mortality in that watershed for the period 1989–98, particularly for stems in the larger size classes. Increases on WS-S were presumably due to more abundant and evenly distributed rainfall for the same period. The severe late-winter storm (1993) and hurricane Opal (1995) occurred during the latter sampling period, and their effects on tree mortality were generally confined to the events themselves. On the other hand, the effect of the drought (1984–88), although most apparent in the later portion of the first sampling period (1986–87), was determined to have lasted into the 1990s as a result of individual trees predisposed to mortality by periods of severe moisture stress (Tainter et al. 1983, 1984, 1990).

Relative to the results of other productivity studies in the region, our estimates of ANPP are low. For example, Bolstad et al. (2001) reported a $9.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ average ANPP for the Coweeta Basin. However, to determine productivity without negative effects, they intentionally avoided areas of windthrow and other forms of severe mortality. In addition, their estimates include foliage (approx. 3 to $5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and herbaceous vegetation, neither of which we included. Similarly, Day and Monk (1977) reported an $8.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ANPP for a forest stand on the same landscape position as our study sites. Hence, with the addition of estimates of foliar and herbaceous production, our ANPP values would probably be comparable to those in their studies.

The two watersheds differed in species composition, and there were more stems in the smaller size classes (< 10.0 cm) in the WS-S watershed than in the WS-N watershed. The difference primarily, was due to a more generally open and exposed understory in WS-S, which promoted reproduction. *Acer rubrum*, *C. florida*, and *Oxydendrum arboreum*, which showed increases in density in the WS-S watershed (30%, 33.7%, and 46.1%, respectively, from 1989 to 1998) (Table 3), made up most of the difference in small-size-class stems. Over the same period, notable increases in density occurred in the WS-N watershed for *Nyssa sylvatica* (33.3%) and *A. rubrum* (17.5%); however, *A. rubrum* decreased in total biomass in the WS-N due to the death of large stems (Table 4). A direct comparison in stem density between 1983 and 1989 cannot be made for the small (< 10.0 cm) size classes because those classes were not measured in 1983. Nonetheless, 1989 data for those classes represent a reasonable estimate of the extent of ingrowth for both watersheds since 1983, recognizing that small stems present in 1983 represent a fraction of those values.

Declines in density in the WS-N watershed primarily were due to loss of *Quercus* spp. and *C. florida*; i.e., *Quercus alba* L. (–23.1%), *Q. velutina* Lam. (–20.5%), *Q. rubra* L. (–18.8%),

Table 2. Mortality patterns for the red oaks (*Quercus rubra*, *Q. velutina*, *Q. coccinea*) for the two sampling periods by watershed for stems ≥ 10 cm dbh. Total Live Biomass (kg ha^{-1}) represents total red oak wood standing crop. Total Dead Biomass (kg ha^{-1}) is the sum of standing and fallen red oak stems for a given sampling period, and Biomass Lost (%) is the percent of the total for a given sampling period. No adjustment for loss of wood density was made in the calculation of dead biomass. Aboveground Net Primary Production (ANPP) is for woody biomass

	WS-S (WS2)		WS-N (WS 18)	
	1983–1989	1990–1998	1983–1989	1990–1998
Dead stems (ha^{-1})	8	2	38	16
Live stems (ha^{-1})	24	25	77	70
Mortality (%)	25	7	33	19
Total dead biomass (kg/ha)	5,615	8,597	10,777	14,446
Total live biomass (kg/ha)	45,592	55,273	87,801	88,640
Aboveground net primary production ($\text{kg ha}^{-1} \text{ yr}^{-1}$)	10	1076	679	93
Biomass lost (%)	11	14	11	14

C. florida (–18.0%) and *Q. coccinea* Muench. (–13.3%). Stem density also declined for *Q. prinus* L., but increased by the same amount due to ingrowth, so that net change was zero, although it decreased 3.6% in total biomass (Table 4). In general, the WS-N watershed had higher mortality than the WS-S watershed over the period 1989–98. Of the oaks in the WS-S watershed, *Q. rubra* had the greatest decline in density (–7.7%) and total biomass (–32.0%). *Carya* spp. also decreased in total biomass (–6.2%) (Table 3). Patterns of survivorship, ingrowth and mortality for five important species in the two watersheds are shown in Figure 2.

Climate Related Mortality Rates

Drought severity is defined in terms of intensity and duration, where the magnitude of the precipitation deficit is a measure of its intensity, and duration and intensity together define an event's severity. Although other drought events have occurred in the region—and some of greater intensity since record keeping began at Coweeta (Figure 1), the period 1984–88 was the most severe drought on record (Swift et al. 1989). The resulting mortality was species-specific and related to variation in local microclimate driven by topographic variation across the landscape. On the WS-S watershed in 1989, the highest mortality rates by species ranked *Carya* spp. > *Q. velutina* = *O. arboreum* (L.) DC. = *A. rubrum*; whereas in 1998, mortality rates for that watershed ranked *Cornus florida* > *Acer rubrum* > *Liriodendron tulipifera* = *Carya* spp. = *O. arboreum*. In the WS-N watershed, mortality rates ranked *C. florida* > *Q. prinus* > *A. rubrum* > *Q. velutina* > *Carya* > *O. arboreum*.

During the period 1983–89, annual precipitation—calculated as May through April water year—averaged 16.5% less than the long-term (60+ years) mean, and during the period 1989–98 precipitation averaged 12.2% above the long-term mean (Table 1). Even though the WS-S watershed was subject to the same meteorological variation over the sampling period, mortality rates were less significant. For example, ANPP for the WS-S and WS-N watershed for the period 1983–98 were 3.4 and 2.1 $\text{Mg ha}^{-1} \text{ yr}^{-1}$, respectively. The lower net productivity on WS-N resulted from high rates of mortality following the earlier drought, and to windthrow of large trees.

Species Specific Mortality

Mortality patterns during severe drought have been shown to be species specific, and particularly hard hit were members of the red oak group. For example, Starkey et al. (1989), in a study of oak decline in the southeastern United States, found that over 20% of tree mortality occurred in *Q. coccinea* followed by *Q. velutina* (15%), *Q. alba* (15%), and *Q. prinus* (13%). Similarly, Stringer et al. (1989) found that *Q. coccinea* and *Q. velutina* accounted for 84% of dead

Table 3. Composition and standing biomass dynamics on WS-S from 1989 to 1998. Initial biomass column represents the sum of live and dead stems in 1989. Species are in rank order by initial biomass. Net change is based on change from initial to net. Values in parentheses are stems ha⁻¹

Species	Biomass (Mg ha ⁻¹)				
	Initial	Ingrowth	Mortality	Net	Net Change (%)
<i>Carya</i> spp.	62.8 (77)	<0.1 (3)	3.9 (2)	58.9 (78)	-6.2 (+1.3)
<i>Quercus alba</i>	51.8 (38)	-0-	1.4 (2)	50.4 (36)	-2.7 (-5.3)
<i>Liriodendron tulipifera</i>	31.5 (56)	<0.1 (4)	-0.9 (2)	30.6 (60)	-2.9 (+7.1)
<i>Acer rubrum</i>	31.4 (99)	0.1 (36)	0.2 (6)	31.3 (129)	<0.1 (+30.0)
<i>Quercus rubra</i>	26.9 (13)	<0.1 (1)	8.6 (2)	18.3 (12)	-32.0 (-7.7)
<i>Quercus velutina</i>	24.4 (14)	-0-	-0-	24.4 (14)	-0- (-0-)
<i>Nyssa sylvatica</i>	7.5 (37)	<0.1 (3)	<0.1 (1)	7.6 (39)	<0.1 (+5.4)
<i>Cornus florida</i>	7.0 (309)	1.0 (136)	0.4 (32)	7.6 (413)	+5.7 (+33.7)
<i>Quercus coccinea</i>	5.6 (1)	-0-	-0-	5.6 (1)	-0- (-0-)
<i>Oxydendron arboreum</i>	4.4 (76)	0.1 (39)	0.2 (4)	4.3 (111)	-2.3 (+46.1)
<i>Pinus rigida</i>	4.3 (6)	-0-	-0-	4.3 (6)	-0- (-0-)
<i>Quercus prinus</i>	3.5 (5)	-0-	-0-	3.5 (5)	-0- (-0-)
<i>Robinia pseudoacacia</i>	2.7 (2)	-0-	-0-	2.7 (2)	-0- (-0-)
<i>Betula lenta</i>	1.6 (11)	<0.1 (1)	-0-	1.6 (12)	<0.1 (+9.1)
<i>Tsuga canadensis</i>	0.3 (4)	<0.1 (1)	-0-	0.3 (5)	+2.3 (+25.0)
<i>Ilex opaca</i>	0.2 (2)	<0.1 (1)	-0-	0.2 (3)	+1.0 (+50.0)
<i>Acer pennsylvanicum</i>	0.2 (1)	<0.1 (3)	-0-	0.2 (4)	+7.1 (+300.0)
<i>Castanea denta</i>	<0.1 (4)	<0.1 (2)	-0-	<0.1 (6)	+5.6 (+50.0)

trees across their study sites in eastern Kentucky. Furthermore, Clinton et al. (1993) found that species most susceptible to drought-related mortality were members of the red oak group (particularly *Q. coccinea*) and *Carya* spp. (Figure 3). The same pattern of 'gap-maker' composition is also reflected in the mortality observed in this study. Oak et al. (1986) found oak decline was stand age related. In their study, decline was present in only 3 percent of stands < 40 years old, but was in 29% of stands >80 years old.

The commonly occurring shoestring root rot fungus (*Armillaria mellea* Vahl. Ex Fr.) has been associated with oak mortality (Wargo 1977), and has been implicated as the primary causal agent (D.J. Lodge, pers. comm.) in mortality observed in the southeast during the 1980s. Nonetheless, there is considerable speculation about whether primary or secondary causes of mortality can be assigned to a single vector (Wargo 1977). The effectiveness of the fungus in

Table 4. Composition and standing biomass dynamics no WS-N from 1989 to 1998. Initial biomass column represents the sum of live and dead stems in 1989. Species are in rank order by initial biomass. Net change is based on change from initial to net. Values in parentheses are stems ha⁻¹

Species	Biomass (Mg ha ⁻¹)				
	Initial	Ingrowth	Mortality	Net	Net Change (%)
<i>Quercus prinus</i>	50.4 (102)	<0.1 (18)	1.8 (18)	48.7 (102)	-3.6 (-0-)
<i>Quercus rubra</i>	38.9 (32)	-0-	4.4 (6)	34.5 (26)	-11.3 (-18.8)
<i>Carya</i> spp.	32.8 (66)	<0.1 (3)	0.9 (6)	31.9 (63)	-2.7 (-4.5)
<i>Quercus velutina</i>	31.9 (39)	-0-	5.2 (8)	26.7 (31)	-16.3 (-20.5)
<i>Quercus coccinea</i>	27.7 (15)	-0-	4.8 (2)	23.6 (13)	-17.3 (-13.3)
<i>Acer rubrum</i>	23.1 (166)	0.4 (56)	1.7 (11)	21.8 (195)	-5.6 (+17.5)
<i>Liriodendron tulipifera</i>	13.6 (45)	<0.1 (4)	0.2 (3)	13.4 (46)	-1.5 (+2.2)
<i>Oxydendron arboreum</i>	9.7 (80)	<0.1 (8)	0.5 (6)	9.2 (82)	-5.2 (+2.5)
<i>Robinia pseudoacacia</i>	9.3 (9)	-0-	0.5 (1)	8.8 (8)	-5.4 (-11.1)
<i>Cornus florida</i>	5.4 (206)	<0.1 (28)	0.9 (65)	4.5 (169)	-16.7 (-18.0)
<i>Quercus alba</i>	4.7 (13)	-0-	<0.1 (3)	4.7 (10)	-0- (-23.1)
<i>Nyssa sylvatica</i>	4.0 (30)	<0.1 (11)	<0.1 (1)	4.0 (40)	-0- (+33.3)
<i>Magnolia fraseri</i>	2.4 (8)	<0.1 (11)	-0-	2.4 (19)	-0- (+137.5)
<i>Acer saccharum</i>	1.8 (4)	<0.1 (1)	-0-	1.8 (5)	-0- (+25.0)
<i>Sassafras albidum</i>	0.5 (3)	-0-	<0.1 (1)	0.5 (2)	-0- (-33.3)
<i>Tsuga canadensis</i>	0.3 (16)	<0.1 (8)	-0-	0.3 (24)	-0- (+50.0)
<i>Betula lenta</i>	0.3 (5)	-0-	<0.1 (2)	0.3 (3)	-0- (-40.0)
<i>Hamamelis virginiana</i>	<0.1 (2)	<0.1 (15)	-0-	<0.1 (17)	0 (+750.0)

causing or contributing to mortality is related to an individual tree's condition, its degree of stress due to atmospheric deposition (Swank and Vose 1990/91, Johnson et al. 1993), low moisture availability (Staley 1965), defoliation (Wargo 1977) or the presence of stem borers (*Agrilus bilineatus* Weber; Dunbar and Stephens 1975). To more efficiently support respiration and other metabolic processes during prolonged periods of severe moisture stress, carbohydrates stored in the root systems as starch are converted into simple sugars (Wargo 1972, 1977). The fungus is better able to use simple sugars than complex starches and, therefore, depletes stored energy in roots much more quickly. The added stress on tree physiology often results in mortality or predisposes the individual to mortality brought on by subsequent periods of stress.

By contrast, other species are susceptible to vectors whose optimum influence comes under much different conditions. For example, *Cornus florida* (flowering dogwood) has been

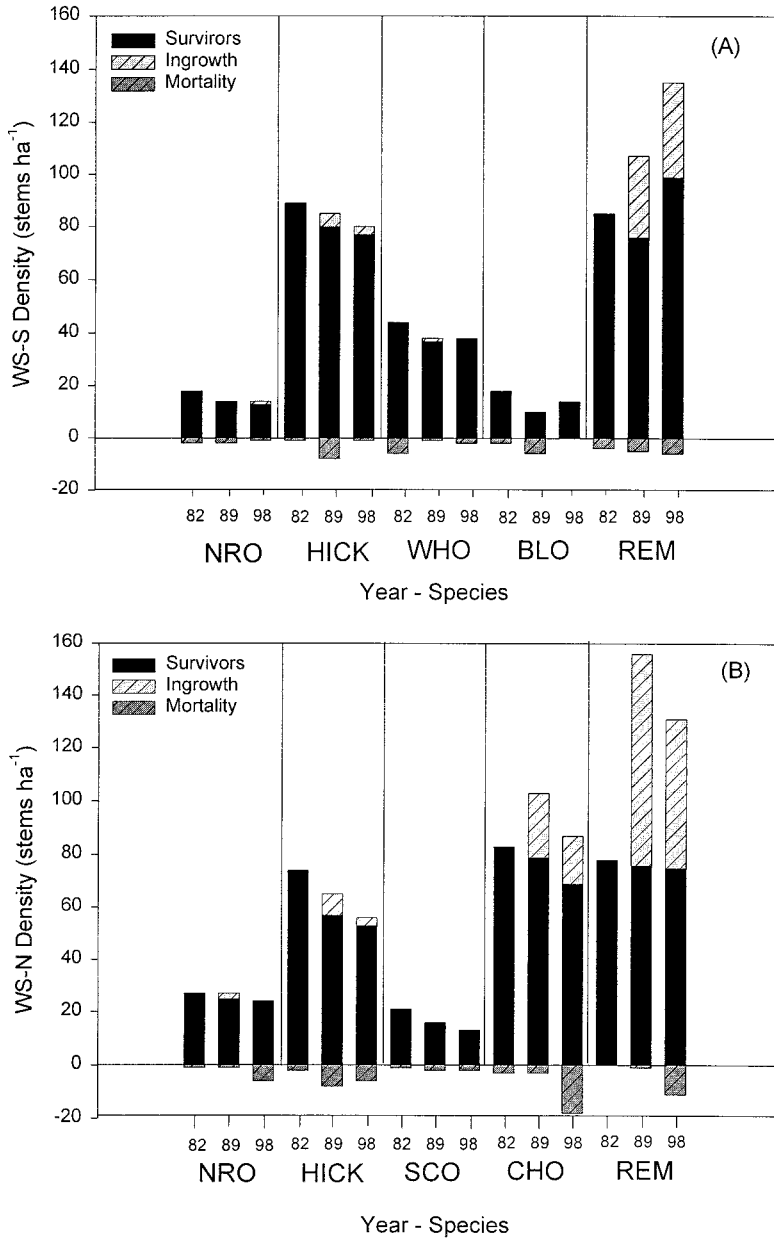


Figure 2. Stem density (stems ha⁻¹) changes over three sampling periods due to ingrowth, mortality and survivorship in WS-S (A) for northern red oak (NRO), hickories (HICK), white oak (WHO), black oak (BLO) and red maple (REM); and in WS-N (B) for northern red oak, hickories, scarlet oak (SCO), chestnut oak (CHO), and red maple. Mortality values for 1983 represent total accumulated mortality for an unknown period, and do not represent background rates of mortality.

under attack by the anthracnose fungus (*Discula destructiva* Redlin.) since it was first observed in the northeastern United States in 1977 (Daughtrey and Hibben 1983), and on some sites the species is in serious decline. In 1992, the fungus was found in 144 southeastern United States counties, particularly in the southern Appalachians and the foothills of the Carolinas and

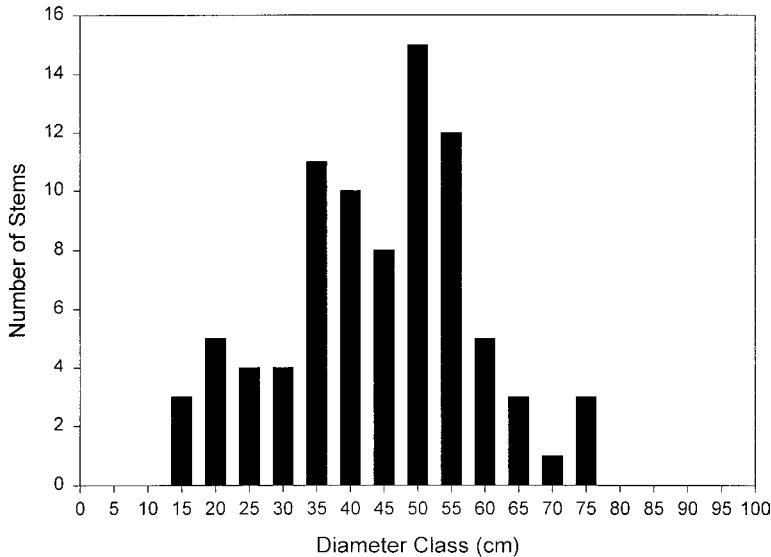


Figure 3. Diameter distribution of major canopy 'gap makers' (scarlet oak > northern red oak > black oak > hickories) as determined from an independent survey of the Coweeta Basin for the period 1983–89 (Clinton et al. 1993).

Georgia. In some areas above 900-m elevation, 100 percent mortality has occurred (Hofacker et al. 1992). The fungus attacks the dogwood's leaves, effectively severing communication between the leaf and the branch and disrupting the exchange of essential metabolites. Mortality results when the fungus moves from the leaves to the shoots and on into the main stem. There, stem cankers coalesce and girdle the tree.

Anthraco­nose is most virulent under cool moist conditions. In a study of the spread of the fungus in the southern Appalachians, Chellemi et al. (1992) found the highest incidence on northeast-facing slopes and the least on southwest-facing slopes. In our study, percent mortality for dogwood was significantly higher during the wetter, second-sampling period (chi-square test, $P < 0.05$) on both watersheds, but it was more pronounced (28% versus 8%) in the cooler north-facing WS-N watershed (chi-square test, $P < 0.05$; Figure 4). By contrast, mortality in the red oak group, measured as loss of stems, was higher during the drier, first sampling period (chi-square test, $P < 0.05$; Table 2). Even though a greater number of stems were lost in the WS-N watershed during both sampling periods, the percent of total biomass lost in the red oak group was similar between sampling periods in both watersheds (Table 2). Further, while growth in the red oak group was much lower in the WS-S watershed during the drier first sampling period (Table 2), growth quickly rebounded during the wetter second sampling period, and mortality was low. By contrast, growth was moderate in the less-exposed WS-N watershed during the drier 1980s, but mortality was higher during the wetter 1990s.

This raises an interesting question: Is an individual tree's susceptibility to drought-related mortality determined, at least in part, by local conditions under which the individual developed? It has been shown that under sufficient selection pressure, even within a localized area some species can develop distinct genotypes that are associated with fine-scale microtopographic variation or with a specific set of resource availabilities (Gram and Sork 2001). For example, Tainter et al. (1990) provided evidence suggesting that periods of prolonged moisture stress can result in differential, within-species responses. In their study of the effects of drought on tree radial increment, two populations emerged following severe drought: (1) relatively healthy, and (2) declining. In some species, gene-switching during fluctuating local climate—to compensate for periods of reduced resource availability (i.e., low moisture availability)—is a common drought-avoidance mechanism. Chang et al. (1996) demonstrated experimentally that genes with a variety

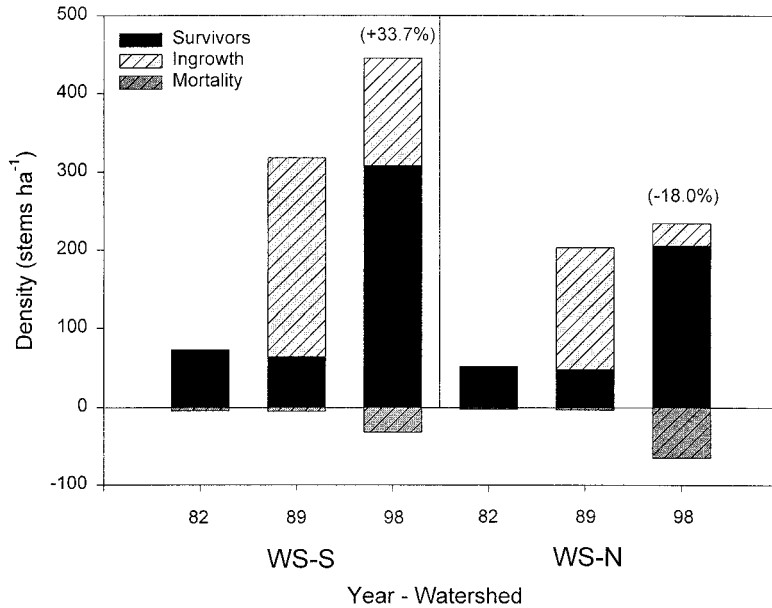


Figure 4. Stem density (stems ha⁻¹) changes in flowering dogwood for the period 1983–98. Values in parentheses represent net change in density from 1989 to 1998. ?1

of drought-avoidance functions are water-deficit-inducible, particularly those that may fulfill a structural role either directly or through participating in the synthesis of cell wall components necessary for turgor maintenance. However, this mechanism may be ineffective where strong within-species genetic selection for specific resource conditions has occurred. That is, under widely fluctuating soil moisture conditions, the capacity for that form of gene expression to aid in the necessary adjustments in water-use efficiency may be exceeded.

Forest communities are heterogeneous at both large and small scales—in part due to disturbance. It is generally accepted that the probability of disturbance changes over time as a result of changes in a stand's physical nature (e.g., stand age, crown architecture, fuels accumulation) (Clark 1991). Physical changes in the understory resulting from canopy mortality drive changes in basic forest processes such as succession. Understanding the level of response to a unit change in a physical resource and the role of topographic variation is essential to understanding forest reorganization following small-scale disturbance.

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