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Drought Impacts on Tree Growth and Mortality of Southern Appalachian Forests

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The Coweeta LTER Program represents the eastern deciduous forests of the southern Appalachian Mountains in the United States. Coweeta Hydrologic Laboratory was established in 1934 and hence has a long record of climate measurement and vegetation response to both natural and human disturbance (Swank and Crossley 1988). The general climate of the area is classified as marine humid temperate because of high moisture and mild temperatures (Critchfield 1966; Swift et al. 1988). These conditions have favored the evolution of high species diversity in organisms in the southern Appalachians at many levels.

In recent years, however, Coweeta has experienced several droughts that have caused significant tree growth reduction and increased mortality rates (Swift et al. 1990; Clinton et al. 1993; Vose and Swank 1994; McNulty and Swank 1995). In this chapter, we describe the general climate and features of Coweeta as well as the impact of droughts on tree growth and mortality. The timescale of this climate variability is annual, with the potential for preexisting soil moisture conditions either providing a buffer or further exacerbating the drought conditions.

Coweeta Hydrologic Laboratory

Climate

Mean annual precipitation at Coweeta Hydrologic Laboratory (latitude 35°14' N, longitude 83°26' W) varies from 1798 mm at the base climate station (686 m) to 2373 mm at the high-elevation Mooney Gap climate station (1364 m). Mean annual growing season precipitation, defined as May to October, is 782 mm at the

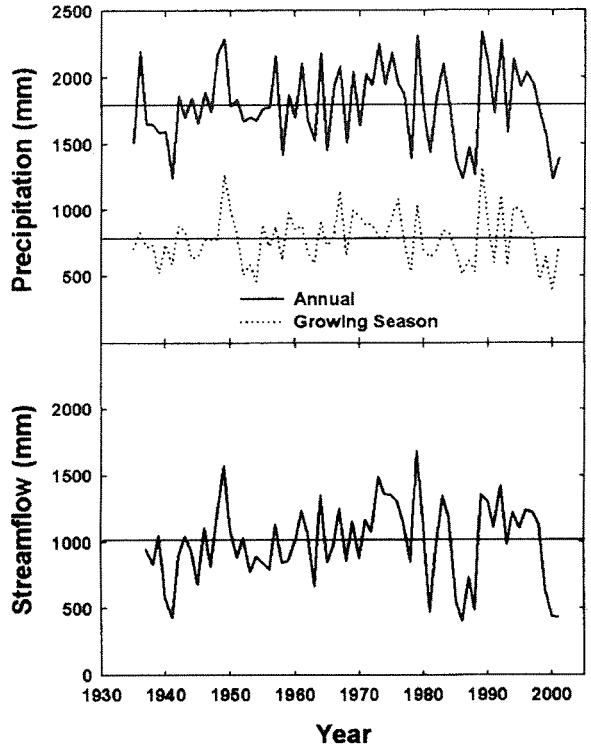

Figure 3.1 Precipitation from 1935 to 2001 (standard gauge 19) and streamflow from 1937 to 2001 (reference watershed 18) at Coweeta Hydrologic Laboratory near Otto, North Carolina, United States. The mean total annual precipitation (1798 mm), mean May–October growing season precipitation (782 mm), and mean streamflow (1011 mm) are shown by straight solid lines.

base climate station (figure 3.1). Mean annual streamflow from watershed 18, a low-elevation reference watershed, is 1011 mm or 56% of precipitation (figure 3.1).

Short-duration thundershowers at Coweeta are typical for midsummer and fall with occurrences of large rainfalls stimulated by tropical disturbances near the Atlantic or Gulf coasts. Forty-nine percent of the 133 storms each year have a total precipitation amount less than 5 mm, and 69% of the annual precipitation falls with an intensity less than 10 mm per hour. Snow is a minor part of the annual precipitation, averaging 2–5% depending on elevation. Snow cover rarely lasts for more than 3 or 4 days, even on the upper slopes. Compared with other mountain sites, wind speeds at Coweeta appear to be low and even imperceptible in the valley bottoms.

Periodic droughts occur in the southern Appalachians. The summer drought of 1925 in Asheville, North Carolina (May to August), generated only 32% of mean

precipitation (Hursh and Haasis 1931). At Coweeta during the period 1985–1988, a severe drought occurred, totaling 1837 mm of precipitation deficit (mean minus annual precipitation), a 26% reduction, and 1849 mm of streamflow deficit (mean minus annual streamflow), a 46% reduction. A recent drought totals 1246 mm of precipitation deficit from 1998 to 2001, a 17% reduction, and 1349 mm of streamflow deficit from 1998 to 2001, a 34% reduction.

Physical Features

Coweeta Hydrologic Laboratory is located in the Nantahala Range of the southern Appalachian Mountains approximately 200 km north of Atlanta, Georgia, and 119 km southwest of Asheville, North Carolina. The laboratory comprises two adjacent, east-facing, bowl-shaped basins. The Coweeta Basin encompasses 1626 ha and has been the primary site for watershed experimentation, whereas the 559-ha Dryman Fork Basin has been largely held in reserve for future studies. More than 50 km of streams drain the area, including first- through fifth-order drainages. Ball Creek and Shope Fork are fourth-order streams draining the Coweeta Basin; they join within the laboratory boundary to form Coweeta Creek, a fifth-order tributary that flows 9 km east to the Little Tennessee River. Elevations range from 675 m in the administrative area to 1592 m at Albert Mountain. The diverse topography, including various aspects and slope positions distributed across the elevational gradient within the Coweeta Basin, creates a complex mosaic of environmental conditions that influence hydrologic, climatic, and biological characteristics of forest and stream ecosystems.

Since Coweeta Hydrologic Laboratory was established, numerous weirs have been installed on streams within the laboratory; currently 18 are operational. Stream gaging was initiated on most watersheds between 1934 and 1938. Relief in the watershed (weir to ridge top) averages 300 m on smaller catchments and 550 m on larger watersheds. Side slopes average about 50% and a variety of aspects are present within the basin. Eight Coweeta watersheds have remained relatively undisturbed since the establishment of the laboratory and serve as reference watersheds in paired watershed experiments. Over the 68-year history of Coweeta, a variety of watershed experiments have produced a diverse array of forest and stream ecosystems with respect to composition, structure, productivity, and successional state.

Eight long-term (60+ years) climatic stations are distributed across the basin, and bulk precipitation chemistry has been measured weekly at each station since 1971. In addition, stream water inorganic chemistry has been measured weekly for many of the watersheds since 1971. Over 400 permanent plots, established in 1934, remain undisturbed and provide a basis for assessing forest successional trends. This network of forested plots has been periodically resampled in 5- to 15-year increments to document changes in species composition, tree density, and tree basal area. Other long-term research on processes is facilitated by a five-site environmental gradient, canopy gap sites, riparian focused studies, and stream litter exclusion studies, to name a few.

Biological Features

Forests at Coweeta were traditionally classified as belonging to the oak–chestnut association. However, with the loss of chestnut (*Castanea dentata*) as the dominant canopy species, the area is more appropriately included in the oak–hickory or Appalachian oak association. The plant communities in the Coweeta Basin are distributed in a reasonably predictable mosaic over the highly varied topography in relation to complex moisture and elevational gradients (Bolstad et al. 1998). Generally, deciduous oak species are the dominant canopy species with an abundant evergreen understory component composed primarily of *Rhododendron maximum* and *Kalmia latifolia*. Four major forest types are recognized: (1) northern hardwoods, (2) cove hardwoods, (3) oak (–chestnut), and (4) oak–pine. These forest types exhibit successional change in response to historical disturbances (logging, fire, windstorm, drought, and chestnut blight). Generally, species that were codominants with chestnut at the time of the blight have increased in basal area. More opportunistic species, such as yellow birch, yellow poplar, and red maple, have also increased in relative basal area since the blight. The evergreen understory species, *Rhododendron* and *Kalmia*, have also increased in importance since the 1930s.

In addition to the variety of watershed experiments previously discussed are forest stands in a range of successional status and vegetation types within the Coweeta Basin. Two watersheds (WS 1 and WS 17) have 46-year-old eastern white pine (*Pinus strobus*) plantations (dating from 1957). Past treatments in other experimental watersheds in the basin have included light selection cutting, clearcutting without roads or products removed, commercial clearcutting with and without cable yarding, whole tree harvesting, a combination of thinning and clearcutting, and clearcutting followed by grass planting and then applying herbicide. These treatments have produced naturally regenerating forests ranging in age from 6 to 100 years, thus providing a unique opportunity to assess both the extent of ecosystem alteration following treatment and the patterns, rates, and mechanisms of post-treatment recovery. Superimposed on the environmental gradient in the Coweeta Basin are disturbed ecosystems that contain a wide range of biotic diversity.

Paralleling the diversity of forest ecosystems within the Coweeta Basin is a comparable diversity of stream ecosystems with a variety of bottom substrate types. These diverse headwater streams are characterized both by distinct biotic assemblages, particularly with reference to benthic invertebrates, and by distinct functional processes (e.g., organic matter processing).

Effects of Drought on Overstory Tree Species

Growth Rates

Observed values of species-specific basal area growth rates vary considerably at Coweeta Hydrologic Laboratory (figure 3.2). Because of the wide range in tree diameters, data are expressed on a relativized basis, annual basal area growth (cm^2)

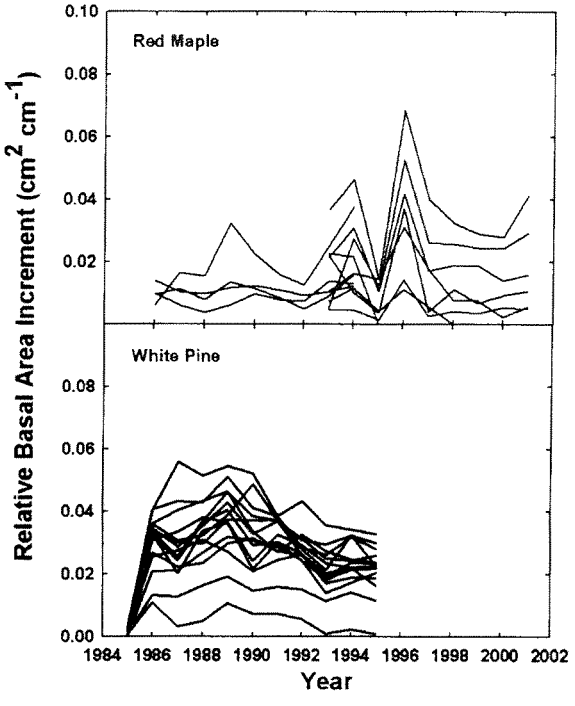

Figure 3.2 The relative basal area increment (cm^2 tree growth per cm tree diameter) of two selected species at Coweeta Hydrologic Laboratory near Otto, North Carolina. Each connected line represents a single tree over the measurement period. The deciduous red maple (*Acer rubrum*) and the evergreen white pine (*Pinus strobus*) exhibit wide variation of relative basal area increment between trees.

per diameter of the tree (cm). The species measured at Coweeta range from the greatest relative growth rate in *Acer rubrum* (see figure 3.2) to the lowest rate in *Quercus prinus* (data not shown). *Quercus rubra*, *Q. coccinea*, and the subcanopy species *Oxydendrum arboreum* are intermediate along with the combined "other" species. The understory *Rhododendron maximum* has widely varying growth rates, which likely depends on light availability, whereas the evergreen *Pinus strobus* (see figure 3.2) in watersheds 1 and 17 exhibits some of the greatest growth rates at Coweeta. *Acer rubrum* exists on a variety of sites with a wide range in moisture availability, whereas the *Quercus* species predominate on dry sites except for *Quercus rubra*.

A condensed summarization of the relativised growth rate data indicates that oaks maintained more consistent growth rates during dry and wet conditions, whereas white pine was more sensitive to moisture availability and hence exhibited a growth decline (figure 3.3; McNulty and Swank 1995). This observed difference between oaks and pines suggests that the oaks may be more deeply rooted than the white pines. Hence, the oaks were drawing from a deeper soil water resource that was more available during periods of precipitation decline.

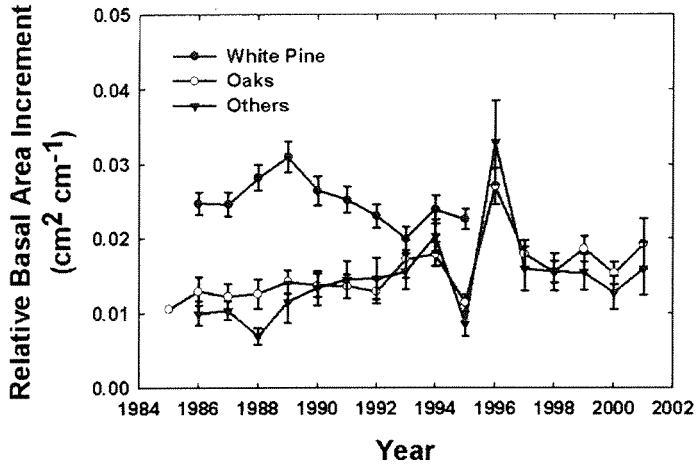

Figure 3.3 Mean (± standard error) relative basal area increment (cm^2 tree growth per cm tree diameter) for oaks, white pine (*Pinus strobus*), and other species at Coweeta Hydrologic Laboratory near Otto, North Carolina. "Oaks" include white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), and black oak (*Q. velutina*). "Others" include sweet birch (*Betula lenta*), hickory species (*Carya* spp.), yellow poplar (*Liriodendron tulipifera*), blackgum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), and black locust (*Robinia pseudoacacia*).

Mortality Caused by Southern Pine Beetle

In the southern Appalachians, most pine species can be considered hosts for the southern pine beetle (SPB; *Dendroctonus frontalis*), although historically the SPB has been associated primarily with yellow pine species (subgenus *Diploxylon*). Yellow pine species native to the southern Appalachians include pitch pine (*Pinus rigida*), shortleaf pine (*P. echinata*), Virginia pine (*P. virginiana*), and table mountain pine (*P. pungens*), as well as small populations of planted and naturalized loblolly pine (*P. taeda*). More recently, eastern white pine (*P. strobus*), which occurs throughout the southern Appalachians, has also been under attack by the SPB, resulting in widespread mortality. There have also been reports of isolated SPB attacks on eastern hemlock (*Tsuga canadensis*).

SPB populations, as with most insect species, are cyclic. The coincidence of SPB outbreaks at epidemic levels with severe and sustained drought can result in significant impacts on pine populations, particularly the yellow pines. The primary mechanism used to combat bark beetle attack is the production of large quantities of oleoresins at the point of attack. Drought stress reduces oleoresin flow and pressure, disabling the trees' primary defense system (Lorio and Hodges 1977). During the period 1971–1988, the land area occupied by yellow pine species in the Coweeta Basin was reduced by 97% as a result of SPB attack (Smith 1991). More recently, watersheds planted in eastern white pine within the Coweeta Basin sustained heavy mortality caused by SPB attack. There are two monocultures of eastern white pine at Coweeta: one in the north-facing watershed 17 and another in the

Table 3.1 Eastern white pine density (stems ha-1) and basal area (m^2 ha^{-1}) (mean + SE) characteristics for the south-facing watershed 1 and north-facing watershed 17 at Coweeta Hydrologic Laboratory near Otto, North Carolina, USA.

Watershed	Variable	Total	Living	Dead	Beetle-Killed Dead[a]
1	Density	1064 ± 56	695 ± 36	369 ± 39	33 ± 22 (4.7)
	Basal area	66.2 ± 1.9	55.0 ± 2.4	11.2 ± 1.9	2.1 ± 1.4 (3.8)
17	Density	899 ± 34	600 ± 23	299 ± 19	7 ± 6 (1.2)
	Basal area	68.3 ± 2.0	59.3 ± 1.7	9.0 ± 0.8	0.6 ± 0.5 (1.0)

[a]Values in parentheses are the percentage of mortality caused by southern-pine beetle attack.

south-facing watershed 1. On the more exposed watershed 1, mortality from the SPB was estimated to be 5% of the density and 4% of basal area (table 3.1). By contrast, in north-facing watershed 17, only 1% of the density and 1% of the basal area was lost (table 3.1). The apparent difference in susceptibility to SPB attack between the two watersheds suggests the linkage between moisture availability (higher on the north-facing watershed) and susceptibility to attack.

Mortality Caused by Pathogens

The commonly occurring shoestring root rot fungus (*Armillaria mellea*) has been associated with oak mortality species (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 causing or contributing to mortality is related to an individual tree's condition, its degree of stress because of 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 1977 and 1996). 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 during subsequent periods of stress.

By contrast, other species are susceptible to vectors whose optimum influence comes under much different conditions. Fungal pathogens tend to be more virulent under the cool, moist conditions characteristic of periods of abundant rainfall. For example, *Cornus florida* (flowering dogwood) has been under attack by the anthracnose fungus (*Discula destructiva*) since it was first observed in the northeastern United States in 1977 (Daughtrey and Hibben 1983), and at some sites the species is in serious decline. In 1992, the fungus was found in 144 southeastern U.S. counties, particularly in the southern Appalachians and the foothills of the Carolinas and Georgia. Some areas above 900 m in elevation have 100% mortality (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 into the main stem, where stem cankers coalesce and girdle the tree. Chellemi et al. (1992) found that the disease was more prevalent and active on cooler, moister northeast-facing slopes than on drier southwest-facing slopes. Similarly, B. D. Clinton et al. (unpub. data, 1999) found that dogwood mortality rates were highest on north-facing slopes but were also higher during a wet period (1989–1998) than during a dry period (1983–1988), whereas oak mortality was higher during the dry period. Hence, in the dogwood example, drought has the effect of mitigating against mortality.

Interactions with Insects and Disease

The dogwood example raises an interesting question: Is an individual tree's susceptibility to drought-related mortality determined, at least in part, by the local conditions under which the individual developed (Waring 1987)? Gram and Sork (2001) have 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. 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 radial increments of trees, two populations emerged after a severe drought: a relatively healthy population and a declining population. In some species, gene switching during a 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 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 maintaining turgor. 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.

Another mechanism responsible for variation in within-species responses to drought occurs when plants undergoing moisture stress incur increased levels of abscisic acid (ABA), which elicits a myriad of physiological responses, such as increased root/shoot ratios and regulation of stomatal function (Nilsen and Orcutt 1996). Long-term exposure to moisture stress, particularly during development, may result in greater sensitivity to ABA, as well as a more "hardened" physiological state, which would allow quicker responses to moisture stress and the maintenance of a higher level of drought resistance (Nilsen and Orcutt 1996). More research is needed to better explain spatial patterns of within- and among-species responses to stress.

A growing body of evidence in the literature supports the notion that the risk of tree death increases with a decreasing growth rate (Pedersen 1998). The rationale behind this assertion is that recovery from periods of stress becomes increasingly

difficult and that the effects of repeated periods of stress compound problems of recovery (Pedersen 1999). Wyckoff (1999), through the use of various growth-mortality functions, showed that the probability of mortality increases with a decreasing growth rate. Specifically, dead trees of the two species he examined (*Cornus florida* and *Acer rubrum*) tend to have lower growth rates in the 5 years prior to mortality than their living cohorts. Conversely, fitted mortality functions show that the risk of death decreases with increasing growth for both species. Furthermore, he examined the effect of tree size on growth-mortality functions and found that when small trees and large trees are examined independent of one another, their respective mortality functions diverge, implying that their rates of mortality are driven by tree size.

Species-Specific Mortality

Mortality patterns during severe drought are often species specific (Tainter et al. 1984; Starkey et al. 1989; Clinton et al. 1993; Elliott and Swank 1994). For example, Clinton et al. (1993) found that the species most susceptible to drought-related mortality were members of the red oak group (particularly *Quercus coccinea*) and *Carya* spp. This pattern of mortality was observed across the southeastern region during the mid- to late 1980s (Starkey et al. 1989; Stringer et al. 1989; Oak et al. 1991). The same pattern of mortality was observed in other studies at Coweeta. B. D. Clinton et al. (unpubl. data, 1999) examined tree mortality on two opposing (north- and south-facing) mixed hardwood watersheds in the Coweeta Basin. The period of study covered 18 years and was generally split between an extremely dry period (1984–1988) and a period of above-average precipitation (1989–1997; table 3.2). During the dry period, annual precipitation averaged 20% less than the long-term (60+ years) mean, and, during the wetter period, precipitation averaged 12% above the long-term mean (table 3.2). In the study of Clinton et al., mortality varied considerably between watersheds and within species. On south-facing watershed 2 for the period 1983–1989, the highest mortality rates by species ranked *Carya* spp. > *Q. velutina* = *Oxydendrum arboreum* = *Acer rubrum*; in 1998, mortality rates for that watershed ranked *Cornus florida* > *A. rubrum* > *Liriodendron tulipifera* = *Carya* spp. = *O. arboreum*. On north-facing watershed 18, mortality rates ranked *C. florida* > *Q. prinus* > *A. rubrum* > *Q. velutina* > *Carya* spp. > *O. arboreum*. Even though watershed 2 was subject to the same meteorological variation over the sampling period, mortality rates were less significant for watershed 2 than for watershed 18. For example, aboveground woody net primary productivity (ANPP) for watersheds 2 and 18 for the period 1983–1998 were 3.4 and 2.1 Mg ha^{-1} yr^{-1}, respectively. The lower productivity for watershed 18 resulted from high rates of mortality following the earlier drought. For the oak species, variation in rates of mortality were considerable (table 3.3).

Drought as a Disturbance Regime

Severe drought has been implicated as a contributing factor to recent accelerated rates of tree mortality in the southeastern United States (Tainter et al. 1984; Starkey

Table 3.2 Comparison of rainfall between two sampling periods at Coweeta Hydrologic Laboratory near Otto, North Carolina, USA

Period	1984–1988	1989–1997
Years	5	9
Mean annual precipitation (mm)	1431	2010
Relative to long-term mean (%)	−20	+12
Mean growing season precipitation (mm)	634	913
Relative to long-term mean (%)	−14	+17
Number of consecutive growing season droughts and deficit range (%)	4 (−13 to −34)[a]	0 (−23 and −26)

[a]Values in parentheses for the number of consecutive growing season droughts represent the range of the deficit relative to the long-term mean.

Adapted from Clinton et al., unpubl. data, 1999.

Table 3.3 Mortality patterns of the red oaks (*Quercus rubra, Q. velutina, Q. coccinea*) for the two sampling periods by watershed for stems > 10 cm dbh at Coweeta Hydrologic Laboratory near Otto, North Carolina, USA

	South-Facing Watershed 2		North-Facing Watershed 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 wood biomass (kg ha^{-1})[a]	5615	8597	10777	14446
Total live wood biomass (kg ha^{-1})[b]	45592	55273	87801	88640
Biomass lost (%)[c]	11	14	11	14
Aboveground woody net primary production (kg ha^{-1} yr^{-1})	10	1076	679	93

[a]This is the sum of standing and fallen dead red oak stems for a given sampling period.

[b]This represents total red oak wood standing crop.

[c]This is the percentage of the total for a given sampling period.

No adjustment for loss of wood density was made in the calculation of dead biomass.

Adapted from Clinton et al., unpubl. data, 1999.

et al. 1989; Stringer et al. 1989; Clinton et al. 1993). This pulse of mortality may have a long-term impact on stand structure and function (Clark et al. 2002). The structural pattern associated with drought-induced mortality (i.e., standing-dead snags) implies that important types of microhabitats are not produced. For example, species such as pitch pine that require large openings (Barden and Woods 1976) commonly associated with large-scale, wind-induced mortality or wildfire are at a distinct disadvantage. In addition, the lack of a pulse addition of coarse woody debris, typical of wind-induced gap formation, may reduce regeneration opportunities

for species such as sweet birch (*Betula lenta*) and eastern hemlock (*Tsuga canadensis*), whose regeneration strategies include "nurse logs" as fresh substrate for seed germination (Burns and Honkala 1990). This is not to say that other important classes of microhabitat are not produced. The standing-dead tree and the shade it casts are an important microhabitat for many organisms and processes (Franklin et al. 1987). Thus, effects of drought-induced mortality may have important influences on micro- as well as macro-level processes (Mueller-Dombois 1987).

We must also begin to assess ecosystem-level impacts of such climatic alteration of the forest structure. Canopy openings and shifts in species composition alter microclimatic factors such as light, temperature, and moisture (B. D. Clinton, unpubl. data, 1999) that regulate nutrient cycling processes. For example, the response of the nitrogen-fixing black locust (*Robinia pseudoacacia*) in large gaps and shifts in litter quality or decomposition rates of leaves of different species are two potential manifestations. The long-term importance of increasing our understanding of drought impacts on forest structure and function is central to anticipating the full impacts of predicted long-term climate change.

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