

A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall[†]

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Summary Global climatic change may cause changes in regional precipitation that have important implications for forest growth in the southern United States. In 1993, a stand-level experiment was initiated on Walker Branch Watershed, Tennessee, to study the sensitivity of forest saplings and large trees to changes in soil water content. Soil water content was manipulated by gravity-driven transfer of precipitation throughfall from a dry treatment plot (–33%) to a wet treatment plot (+33%). A control plot was included. Each plot was 6400 m². Measurements of stem diameter and observations of mortality were made on large trees and saplings of *Acer rubrum* L., *Cornus florida* L., *Liriodendron tulipifera* L., *Nyssa sylvatica* Marsh, *Quercus alba* L. and *Quercus prinus* L. every 2 weeks during six growing seasons. Saplings of *C. florida* and *A. rubrum* grew faster and mortality was less on the wet plot compared with the dry and control plots, through 6 years of soil water manipulation. Conversely, diameter growth of large trees was unaffected by the treatments. However, tree diameter growth averaged across treatments was affected by year-to-year changes in soil water status. Growth in wet years was as much as 2–3 times greater than in dry years. Relationships between tree growth, phenology and soil water potential were consistent among species and quantitative expressions were developed for application in models. These field growth data indicate that differences in seasonal patterns of rainfall within and between years have greater impacts on growth than percentage changes in rainfall applied to all rainfall events.

Keywords: *Acer rubrum*, *Cornus florida*, climate change, drought, *Liriodendron tulipifera*, *Nyssa sylvatica*, phenology, *Quercus alba*, *Quercus prinus*, soil water.

Introduction

Continuing increases in greenhouse gas concentrations are expected to induce a 1 to 3.5 °C increase in mean global land surface temperature by the year 2100 (Kattenberg et al. 1996). This warming is expected to modify the hydrologic cycle, leading to increased winter precipitation at high latitudes, more hot days and fewer cold days, and changes in the numbers of droughts or floods depending on location (Rind et al.

1990, Kattenberg et al. 1996). Changes in climate have also raised concerns about potential impacts of temperature and precipitation on terrestrial ecosystem productivity, biogeochemical cycling, and the availability of water resources (Melillo et al. 1990, 1996, Kirschbaum and Fischlin 1996). Forest responses to decreased soil water availability or increased drought frequency or intensity, or both, are key issues associated with climatic change (Wigley et al. 1984, Gregory et al. 1997), and Neilson et al. (1989) concluded that forests throughout the USA could be severely impacted by climate warming. This might be especially so in the southeastern states, where potential evapotranspiration is predicted to increase and exceed future summer precipitation (Smith and Tirpak 1990, Melillo et al. 1995 and <http://goldhill.cgd.ucar.edu/vemap/>). Both the direction and magnitude of future precipitation changes are uncertain, however, and scenarios for regional climatic change are only preliminary (Schneider 1989, Mohnen and Wang 1992, Rind et al. 1992, Cooter et al. 1993). Nonetheless, climatic change during the next several decades may exceed the ability of forests to adapt through changes in species composition (Pastor and Post 1988, Davis 1989, Overpeck et al. 1991). This possibility is supported by model predictions indicating that future climatic change will lead to extensive forest dieback and species migration (Solomon 1986, Leverenz and Lev 1987, Pastor and Post 1988). However, these predictions have been questioned (Fischlin et al. 1995, Loehle and LeBlanc 1996). The evaluation of model predictions with long-term and large-scale manipulative studies is needed to reduce uncertainty about impacts of climatic change (Mooney 1991, Woodward 1992).

To study impacts of precipitation changes on forest productivity and ecosystem processes, Hanson et al. (1995, 1998) implemented the Walker Branch Throughfall Displacement Experiment (TDE) to modify soil water availability in an upland oak forest over several years. This paper describes daily growth, annual growth and mortality of saplings and large trees during 6 years (1994–1999) of throughfall manipulation. Growth and mortality integrate physiological responses to water stress, and represent key end points for the investigation of forest response. We hypothesized that small-stature vegetation (saplings) are more sensitive to altered soil water content

[†] Equation 1 has been revised in accordance with a correction to be published in a forthcoming issue of Volume 21.

than canopy trees, because they have limited rooting depth and smaller carbohydrate reserves. Intra-annual growth data for non-stress versus drought periods were also combined with soil water potential data to yield quantitative relationships between soil water potential and tree basal area growth rate. Such relationships may provide modelers with better methods for predicting growth responses to soil water deficits in eastern hardwood forests.

Materials and methods

Experimental system

The experimental system and its performance have been described in detail by Hanson et al. (1995, 1998). Manipulations of throughfall amounts reaching the forest floor were made by passively transferring a fraction of the throughfall from one experimental plot to another. There were three (80 × 80 m) experimental plots: one wet, one dry and one control. Each plot was divided into 100, 8 × 8 m subplots that served as locations for repetitive, nondestructive measurements of soil and plant characteristics. An 8-m buffer zone around the edge of all plots (16 m between plots) was treated but not used for the observations of tree and sapling growth. On the dry plot, throughfall precipitation was intercepted in about 1900 below-canopy troughs (0.3 × 5 m) made of greenhouse-grade polyethylene that were suspended at an angle above the forest floor (~33% of the ground area was covered). The intercepted throughfall was transferred by gravity flow across the control plot and distributed onto the wet treatment plot through paired drip holes spaced about 1 m apart. The troughs were arranged in 21 rows of about 80 to 90 troughs each. Subplots of troughs containing holes were included on the wet and control plots until 1996. The subplots were removed after impacts of trough infrastructure on understory microclimate were found to be small (Hanson et al. 1995).

The experimental area was located at the upper divide of the watershed, so that lateral flow of water into the plots from up-slope did not occur. The site had a southern aspect. Reductions in soil water content anticipated from the experimental removal of 33% of the throughfall were designed to be comparable to that of the growing season having the lowest recorded rainfall during the dry 1980s (Cook et al. 1988), which resulted in sapling mortality and reduced growth of some vegetation (Jones et al. 1993).

Site description

The experiment was located on the Walker Branch Watershed (35°58' N and 84°17' W), part of the U.S. Department of Energy's (DOE's) National Environmental Research Park near Oak Ridge, Tennessee (Johnson and Van Hook 1989). Long-term (50-year) mean annual precipitation is 1352 mm and mean annual temperature is 14.2 °C. The acidic forest soils (pH 3.5 to 4.6) are primarily typic Paleudults. Plant extractable water (water held between 0 and -2.5 MPa) for the upper 1 m of soil is approximately 183 mm. A large fraction of

this water (44%) is held in the upper 0.35 m of the soil profile, which contains 60% of all fine roots in the 0–0.90-m soil profile (Joslin and Wolfe 1998). Depth to bedrock at this location is approximately 30 m, so deep rooting may be a source of some water. The site was chosen because of its uniform slope, consistent soils and a reasonably uniform distribution of vegetation. Early aerial photographs show that the TDE study area was forested in the late 1930s, but several large dominant trees show open growth characteristics, an indication of some harvesting before that time.

Before the experiment, all trees greater than 0.1 m in diameter at 1.3 m height (diameter at breast height, DBH) were identified to species (729 individual trees), and heights and crown widths were measured directly or derived from allometric relationships from a subset of the measured data. *Quercus* spp. and *Acer* spp. were the major canopy dominants, *Liriodendron tulipifera* L. was a canopy dominant on the lower slope positions, and *Nyssa sylvatica* Marsh. and *Oxydendrum arboreum* (L.) D.C. were the predominant species occupying mid-canopy locations. In March 1994, stand basal area averaged 21 m² ha⁻¹, with nearly identical basal area on each plot. By December 1999, mean basal area across all plots had increased to 22.8 m² ha⁻¹ (Table 1). The number of saplings (trees < 0.1 m DBH) across the TDE area averaged 3073 ha⁻¹ in 1994 and 2112 ha⁻¹ in 1999. Saplings contributed an additional 3 and 2.6 m² ha⁻¹ to total stand basal area in 1994 and 1999, respectively (Table 1). *Acer rubrum* L. and *Cornus florida* L. together made up 59% of all saplings and 53% of the sapling basal area.

Soil water content, water potential and weather

Soil water content (% v/v) was measured with a time domain reflectometer (TDR) (Soil Moisture Equipment Corp., Santa Barbara, CA) following the procedure of Topp and Davis (1985) as documented for soils with high coarse fraction content (Drungil et al. 1987). Three hundred and ten sampling locations were installed at an 8 × 8 m spacing across the site, giving more than 100 soil water monitoring locations per plot. At each location, two pairs of TDR wave-guides were installed in a vertical orientation (0–0.35- and 0–0.7-m soil depths). The surface (0–0.35-m soil depth) TDR measurements coincide with the zone of maximum root density in these soils. The TDR measurements were obtained every 2 weeks during the growing season and approximately monthly during the dormant season.

The TDR soil water content measurements were adjusted for the coarse fraction of these soils (mean coarse fraction of 14%) and converted to soil water potentials based on laboratory-derived soil water retention curves for the A, A/E and E/B horizons (Hanson et al. 1998, <http://www.esd.ornl.gov/programs/WBW/TDEPERFA.HTM>).

To facilitate comparisons of the severity of soil water deficits between years, we report the minimum soil water potential (MPa) and calculate a water stress integral (units of MPa day, Myers 1988) for all years and treatments. Although Myers (1988) used integrated leaf water potentials, we summed daily

Table 1. Cumulative basal area of (A) individual tree species > 0.1 m DBH and (B) saplings across the Throughfall Displacement Experiment in March 1994 and December 1999. The direction of change is also indicated. Abbreviation: nc = no change.

Species ¹	Cumulative basal area (m ² ha ⁻¹)		Change
	March 1994	December 1999	
A. Trees > 0.1 m DBH¹			
<i>Acer rubrum</i>	2.40	2.92	+
<i>Acer saccharum</i> Marsh.	0.56	0.66	+
<i>Carya</i> sp.	0.44	0.42	nc
<i>Cornus florida</i>	0.18	0.13	-
<i>Liriodendron tulipifera</i>	1.64	1.62	nc
<i>Nyssa sylvatica</i>	2.95	3.07	+
<i>Oxydendrum arboreum</i>	0.77	0.83	+
<i>Prunus serotina</i> Ehrh.	0.11	0.16	+
<i>Quercus alba</i> L.	4.56	4.95	+
<i>Quercus prinus</i> L.	5.54	6.02	+
<i>Quercus</i> sp.	1.66	1.83	+
Miscellaneous conifers	0.15	0.15	nc
Miscellaneous hardwoods	0.00	0.04	nc
Total trees	20.96	22.80	+
B. Saplings > 1 m in height and < 0.1 m DBH²			
<i>Acer rubrum</i>	0.97	0.96	nc
<i>Acer saccharum</i>	0.05	0.06	nc
<i>Carya</i> sp.	0.02	0.02	nc
<i>Cornus florida</i>	0.62	0.49	-
<i>Fagus grandifolia</i> J.F. Ehrh.	0.03	0.05	nc
<i>Nyssa sylvatica</i>	0.36	0.30	-
<i>Oxydendrum arboreum</i>	0.29	0.30	nc
<i>Prunus serotina</i>	0.19	0.15	-
<i>Quercus</i> sp.	0.14	0.12	nc
<i>Quercus alba</i>	0.04	0.04	nc
<i>Quercus prinus</i>	0.01	0.01	nc
<i>Rhamnus</i> sp.	0.16	0.11	-
<i>Sassafras albidum</i> (Nutt.) Nees	0.05	0.03	nc
Miscellaneous	0.03	0.02	nc
Total saplings	2.97	2.64	-
C. Total basal area	23.93	25.44	

¹ A total of 18 individual tree species were present in the > 0.1 m DBH size range, but some groups were combined for presentation.

² A total of 20 individual sapling species were present, but some groups were combined for presentation.

soil water potentials for the 0–0.35-m soil depth for the water stress integral. Water stress integrals were estimated using a combination of measured soil water potential data and modeled interpolations for periods without data. Modeled interpolations were executed with a revised version of the TEHM/PROSPER model (Huff et al. 1977, Luxmoore 1983) coded using “Ithink” modeling software (High Performance Systems, Hanover, NH).

Weather data (Table 2) including air temperature, relative humidity and soil temperatures (at 0.1- and 0.35-m soil depths) were logged hourly on each treatment plot. Rainfall, solar irradiance (pyranometer sensor, LI-2005A, Li-Cor Inc., Lincoln, NE) and photosynthetic photon flux density (Li-Cor quantum sensor, LI-1915A) were also measured continuously and logged as hourly means.

Measurements of tree growth and mortality

Diameter growth and mortality of all trees greater than 0.1 m

DBH was recorded annually. *Quercus alba*, *Q. prinus*, *Acer rubrum*, *Liriodendron tulipifera*, and *Nyssa sylvatica* trees greater than 0.2 m DBH were fitted with dendrometer bands ($n = 170$) for biweekly measurements of stem circumference during each growing season. These species made up almost 80% of the basal area of the experimental area (Table 1). Although most species were uniformly distributed across the plots, the distribution of *Q. alba* and *Q. prinus* was not uniform. *Quercus alba* dominated in the wet plot, and *Q. prinus* dominated in the dry plot. Because of this nonuniformity, the two *Quercus* species were combined for analyses of treatment effects. The two *Quercus* species were kept separate for regression analysis of intra-annual growth differences as a function of soil water potential.

A single dendrometer measurement consists of duplicate digital caliper measurements (0.01 mm resolution) of the distance between two reference holes in stainless steel dendrometer bands (25.4 mm wide × 0.2 mm thick) installed around

Table 2. Weather and soil water variables for each year of the study including: (A) mean air temperature for the year and growing season; (B) cumulative radiation for the full year and the growing season; (C) total annual precipitation; (D) minimum soil water potential by treatment; and (E) water stress integrals by treatment. The growing season (GS) is defined as the May through September period.

Variable	Year of observations							Mean ¹
	1993	1994	1995	1996	1997	1998	1999	
A. Air temperature (°C)								
Annual	14.3	14.4	14.4	13.6	14.1	15.8	15.0	14.5
GS	22.9	21.6	22.7	22.0	21.5	23.6	22.2	22.3
B. Cumulative radiation (MJ m⁻²)								
Annual	4724	4737	4960	4824	4849	4928	5600	4946
GS	2830	2643	2717	2777	2765	2928	3155	2831
C. Control precipitation (mm)								
Annual	1139	1675	1135	1638	1462	1225	1152	1352
GS	383	569	394	783	650	333	522	534
D. Minimum daily soil water potential (MPa)²								
Wet plot	–	–0.19	–1.47	–0.35	–0.34	–1.69	–1.84	–0.98
Control plot	–2.08	–0.27	–2.30	–0.64	–0.55	–2.20	–1.90	–1.31
Dry plot	–	–1.07	–2.80	–1.12	–1.05	–2.89	–2.04	–1.83
E. Water stress integral (MPa day)²								
<i>Control plot</i>								
Jan–Jul	–61	–14	–48	–13	–11	–20	–21	–27
Aug–Dec	–11	–9	–62	–16	–15	–73	–77	–38
Annual	–72	–23	–110	–29	–26	–93	–98	–65
<i>Dry plot</i>								
Jan–Jul	–	–23	–72	–15	–12	–26	–40	–31
Aug–Dec	–	–10	–96	–30	–25	–149	–120	–72
Annual	–	–33	–168	–45	–37	–175	–160	–103
<i>Wet plot</i>								
Jan–Jul	–	–12	–27	–13	–11	–16	–14	–15
Aug–Dec	–	–9	–38	–12	–12	–31	–57	–27
Annual	–	–21	–65	–25	–23	–47	–71	–42

¹ The mean for annual precipitation is the 50-year mean based on data gathered since 1949. All other means are for the years shown.

² Values for the integrated water stress integral and minimum daily soil water potential are estimates from a model of the water budget for these stands.

the circumference of each tree (McLaughlin and Downing 1996). Measured changes in the circumference of each tree were used to calculate change in stem basal area over time (mm² day⁻¹ or mm² year⁻¹). Dendrometer bands were installed on the *Q. alba*, *Q. prinus*, and *A. rubrum* trees prior to the 1993 growing season and bands for *L. tulipifera* and *N. sylvatica* were added in February of 1994. All dendrometer bands were installed during the dormant season, ahead of the initial growth measurements, to eliminate potential first year bias in the dendrometer band measurements (Keeland and Sharitz 1993).

Winter stem shrinkage (Winget and Kozlowski 1964, 1965) or stem shrinkage coincident with bud break was observed to varying degrees for all species measured. Therefore, cumulative growth or biweekly growth rate integrals, or both, were calculated only after recovery from shrinkage. Because the incremental basal area changes over 2 weeks were large compared with reported diurnal shrink–swell patterns for our tree

species (Haasis 1934, Kozlowski 1971, Kramer and Kozlowski 1979, Kozlowski 1982), diurnal patterns of stem shrinkage were assumed to be unimportant to this study.

Measurements of sapling growth and mortality

In February and March 1994, 10 transects for observations of sapling growth and mortality were established across the three plots from lower- to upper-slope positions. Although other species were considered for these measurements, only *A. rubrum* and *C. florida* were distributed across the TDE in sufficient numbers for inclusion. Saplings ranged from 10 to 60 mm DBH with the majority from 10 to 40 mm DBH. Height measurements were not included because the crowns were broad, without predominant main shoots, and because height growth was minimal in the low light understory environment of our closed canopy stand. Starting at the time of spring bud break each year, biweekly measurements of stem diameter at a permanently marked location on each sapling's main stem

(typically between 1 and 1.5 m above ground) were conducted until sapling growth had ceased for that year. Each stem caliper measurement was the mean of three replicate diameter measurements made with a digital caliper (0.01 mm resolution) from three different angles around the marked point of measurement. The mean of replicate measurements from different angles was required to minimize the impact of noncircular stem cross sections. Sapling stem diameters were converted to basal area to express mean daily sapling growth rates per plant in $\text{mm}^2 \text{day}^{-1}$, or integrated annual sapling growth in $\text{mm}^2 \text{year}^{-1}$.

Statistical analyses

The unreplicated nature of the TDE is not ideal, but the resulting pseudoreplication is recognized as a reasonable approach when such costly experimental field designs are undertaken (Eberhardt and Thomas 1991). Nevertheless, dealing with the issue of pseudoreplication in our sampling design is critical (Hurlbert 1984). Eberhardt and Thomas (1991) recommended that unreplicated experiments be supported by adequate sampling of site environmental parameters (including climatic conditions), comparable control areas and pretreatment sampling. Hanson et al. (1998) showed that the individual $8 \times 8 \text{ m}$ resolution soil water measurements across the TDE plots were not correlated with each other and could, therefore, be treated as independent measurements. Because this was true, we treated individual, spatially separated plants as being independent with respect to soil water conditions. Recognizing that extensive horizontal rooting of large trees would impact this assumption, trees in buffer zones were not used in our analyses. With these considerations in mind, analyses of covariance were used to test for wet, control, and dry plot effects on growth of large trees and saplings. Each covariate analysis of variance was executed as a two-way design with main effect and interaction tests for plot and vertical slope position. However, slope was left out of the analysis for species that did not occupy the full range of slope positions (e.g., *L. tulipifera* occurred only on the lower third of the plot). Repeated measures analysis of variance was also conducted to determine if the treatment effects were consistent with time.

To account for bias in growth as a result of pretreatment plant size, initial basal area of individual saplings was used as a covariate in analysis of variance tests of treatment effects. Similarly, for the large trees, pretreatment annual growth rates (*Acer* and *Quercus*) or their initial basal area (*Liriodendron* and *Nyssa*) were used as covariates. All covariates were highly significant and, therefore, appropriate for their intended purpose. Chi-square analyses were used to test for treatment effects on sapling mortality rates. Nonlinear regression was used to evaluate relationships between growth rate, phenology and soil water potential using a modified form of the crop development equation of Yin et al. (1995). All statistical analyses were conducted with SPSS 6.1 for the Macintosh (SPSS, Inc., Chicago, IL).

Results

1993–1999 Climate

Weather and soil water data showed substantial interannual variation from 1993 through 1999 (Table 2). Lower than average annual precipitation was measured in 1993 (–16%), 1995 (–16%), 1998 (–9%), and 1999 (–15%), and above average precipitation was observed in 1994 (+24%), 1996 (+21%) and 1997 (+8%). Growing season precipitation was near normal in 1994 and 1999, but it was 26 to 38% less than normal during the drought years of 1993, 1995 and 1998. Growing season precipitation was 47 and 22% higher than normal in 1996 and 1997, respectively (Table 2). Mean annual air temperature and annual incident solar radiation were not as variable as annual precipitation (Table 2), but mean annual air temperatures in 1998 and 1999 were higher than in previous years.

Cumulative annual incident solar radiation at the site was similar across years. Cumulative growing season radiation inputs ranged from 2643 to 3155 MJ m^{-2} from 1993 through 1999, but showed no trends with annual or growing season precipitation, even though dry years (1993, 1995, 1998, 1999) tended to have greater growing season radiation inputs than wet years.

Minimum daily soil water potentials showed that significant drought occurred in 1993, 1995, 1998, and 1999 (sustained values below -0.7 MPa in Figure 1). However, the annual water stress integrals (Table 2) demonstrated that the 1993 drought (-72 MPa day) was not sustained as long as the droughts in 1995, 1998, and 1999 (-110 , -93 and -98 MPa day , respectively). In the wet growing seasons of 1994, 1996, and 1997, control soil water potentials never fell below -0.7 MPa , but the dry plot soil water potentials reached substantially lower values (Figure 1, Table 2). Although control precipitation inputs during the dry 1995 growing season were comparable with dry plot precipitation inputs in 1994 (394 versus 379 mm), the minimum control soil water potential differed from the minimum dry plot soil water potential (-2.3 versus -1.1 MPa , respectively) because of the timing of rainfall events.

Calculated water stress integrals for the January through July periods versus the August through December periods further demonstrated year-to-year differences in the characteristics of the droughts (Table 2). The droughts of 1995, 1998 and 1999 were most severe in the second half of the growing season (i.e., exhibited the most negative soil water potentials), whereas the drought of 1993 was most severe during the earlier half of the growing season.

The throughfall displacement manipulations have been maintained continuously since July 1993. Soil water measurements showed that the TDE produced significantly different hydrologic budgets for the wet, control and dry plots in years having either high or low precipitation during a growing season (Hanson et al. 1995, 1998). In addition, because of interannual variation in growing season rainfall inputs, we obtained a much broader range of treatments than originally anticipated. The combination of treatment manipulations and

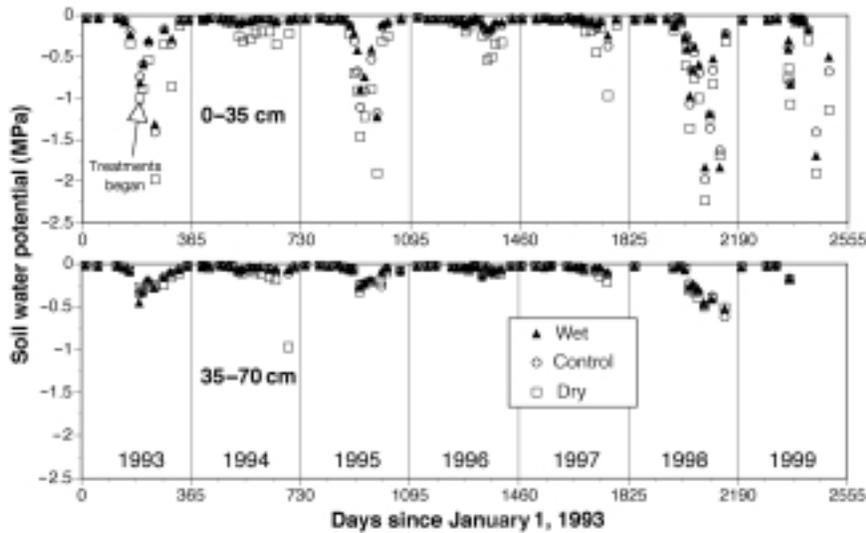


Figure 1. Soil water potentials between 0 and 0.35 m (A) and between 0.35 and 0.7 m (B) from 1993 through 1996. Data are the mean values for the wet, control, and dry plots. Throughfall displacement treatments were initiated on July 14, 1993. Because of the large number of replicate samples contributing to each treatment, mean standard errors about the mean are smaller than the graph symbols.

variable annual and growing season precipitation (Table 2) has allowed us to test not only the impact of a constant $\pm 33\%$ alteration of throughfall resulting from all incoming rainfall events, but also to determine the influence of sustained droughts as well.

Basal area growth of saplings

Over the 6-year period, mean annual basal area increment of *A. rubrum* saplings was significantly higher in the wet plot compared with the control and dry plots (Table 3). Mean annual basal area increment of *C. florida* saplings was significantly higher in the wet plot and significantly lower in the dry plot compared with the control plot. The highest annual growth for *A. rubrum* was observed in 1996 and 1997, but the highest growth rates for *C. florida* were measured in 1994,

which was the year of lowest growth for *A. rubrum*. The lowest growth rates for *C. florida* were measured in 1997, which was one of the wet growing seasons.

Stem growth of *A. rubrum* and *C. florida* saplings was largely limited to the first half of the growing seasons in 1994, 1995 and 1996 (Figure 2). Thus, most stem diameter growth of the saplings occurred before the development of late-season water deficits (e.g., 1995).

Basal area growth of large trees

In contrast to the growth responses of saplings, growth of large trees was unaffected by treatment (Table 4). Analyses of treatment responses for small trees (< 0.1 m DBH) versus large trees (> 0.1 m DBH) was conducted to determine if tree size had an impact on tree sensitivity, but no significant differences

Table 3. Mean annual sapling growth by species and treatment (\pm SE) for the 1994 through 1999 growing seasons. The mean number of trees per treatment block (n) is also shown for each year of the study. The P -values provided are for covariate analyses of variance of treatment main effects within a year. Abbreviation: ns = non-significant.

Species	Year	n	Annual growth ($\text{mm}^2 \text{ year}^{-1}$)			P -Value
			Wet	Control	Dry	
<i>Acer rubrum</i>	1994	42	19 \pm 3	11 \pm 2	9 \pm 2	ns
	1995	61	26 \pm 4	13 \pm 2	17 \pm 2	0.01
	1996	60	50 \pm 6	28 \pm 5	31 \pm 6	0.01
	1997	55	52 \pm 9	28 \pm 4	26 \pm 4	0.03
	1998	55	34 \pm 5	24 \pm 5	15 \pm 3	ns
	1999	48	22 \pm 7	10 \pm 4	7 \pm 5	ns
	Mean			33	18	18
<i>Cornus florida</i>	1994	45	58 \pm 12	51 \pm 7	25 \pm 5	ns
	1995	60	50 \pm 10	38 \pm 6	21 \pm 4	0.00
	1996	57	48 \pm 10	31 \pm 4	40 \pm 6	0.01
	1997	51	12 \pm 4	12 \pm 4	15 \pm 4	ns
	1998	45	25 \pm 9	18 \pm 5	16 \pm 4	ns
	1999	29	28 \pm 13	19 \pm 7	9 \pm 9	ns
	Mean			33	25	18

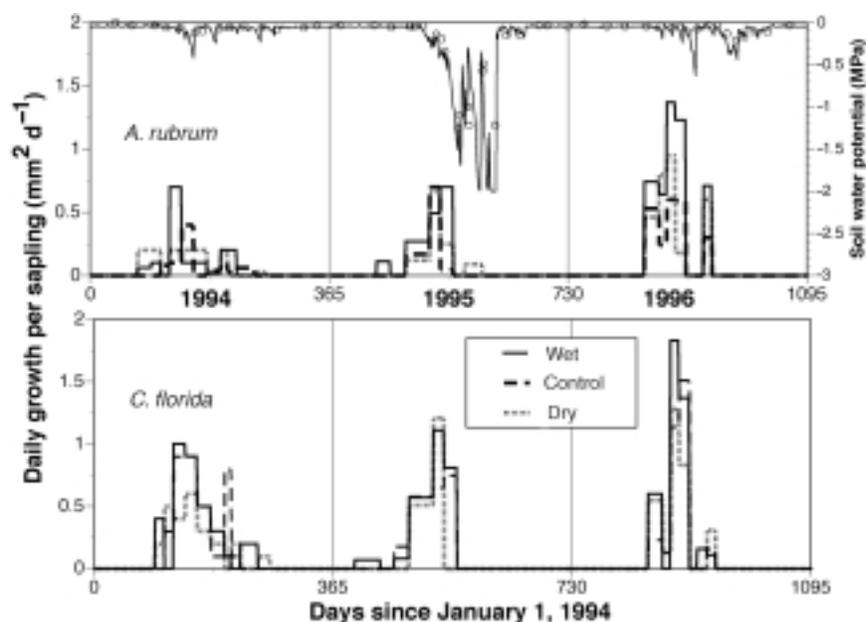


Figure 2. Daily growth rates averaged over 14–20 day periods for *A. rubrum* and *C. florida* saplings on the wet, control and dry plots throughout 1994, 1995 and 1996. Mean, daily, control plot soil water potentials between 0 and 0.35-m are shown to indicate periods of water stress in each year (open symbols are the means of 100 observations and the solid line is a model prediction for unmeasured periods).

Table 4. Annual mean tree (stems > 0.1 m DBH) basal area growth by species and TDE treatment (\pm SE) for the 1994 through 1999 growing seasons. The mean number of trees per treatment block (n) is also shown for each year of the study. The P -values provided are for covariate analysis of variance based on pretreatment annual basal area growth. Abbreviation: ns = non-significant.

Species	Year	n	Annual growth (mm ² year ⁻¹)			P -Value
			Wet	Control	Dry	
<i>Acer rubrum</i>	1994	15	2420 \pm 510	3355 \pm 520	1947 \pm 410	ns
	1995	15	1254 \pm 210	1625 \pm 230	1239 \pm 260	ns
	1996	16	2349 \pm 390	3154 \pm 450	2007 \pm 340	ns
	1997	16	2108 \pm 370	3035 \pm 460	1744 \pm 300	ns
	1998	16	1654 \pm 320	2451 \pm 360	1475 \pm 320	ns
	1999	16	1531 \pm 280	2755 \pm 520	1508 \pm 290	ns
<i>Nyssa sylvatica</i>	1994	9	679 \pm 230	728 \pm 170	663 \pm 150	ns
	1995	10	720 \pm 200	860 \pm 170	842 \pm 250	ns
	1996	10	1077 \pm 190	1126 \pm 220	1002 \pm 290	ns
	1997	11	998 \pm 250	836 \pm 180	935 \pm 250	ns
	1998	11	997 \pm 300	784 \pm 170	742 \pm 210	ns
	1999	11	1153 \pm 270	931 \pm 160	811 \pm 220	ns
<i>Liriodendron tulipifera</i>	1994	7	290 \pm 190	437 \pm 160	307 \pm 420	ns
	1995	7	228 \pm 170	436 \pm 130	334 \pm 140	ns
	1996	8	985 \pm 210	908 \pm 190	817 \pm 150	ns
	1997	8	1581 \pm 350	1315 \pm 220	1078 \pm 380	ns
	1998	8	2560 \pm 490	2096 \pm 430	1851 \pm 290	ns
	1999	8	3265 \pm 940	2504 \pm 630	2127 \pm 410	ns
<i>Quercus alba</i>	1994	17	2473 \pm 270	2952 \pm 460	3195 \pm 630	ns
	1995	17	1870 \pm 220	1850 \pm 280	2478 \pm 430	ns
	1996	17	2818 \pm 340	2907 \pm 380	3506 \pm 740	ns
	1997	17	1745 \pm 190	1944 \pm 210	2438 \pm 510	ns
	1998	17	2202 \pm 250	2548 \pm 310	2878 \pm 550	ns
	1999	17	2640 \pm 310	2765 \pm 370	2753 \pm 660	ns
<i>Quercus prinus</i>	1994	18	3623 \pm 430	5529 \pm 690	3415 \pm 280	ns
	1995	18	2956 \pm 390	4659 \pm 800	3144 \pm 290	ns
	1996	18	4318 \pm 550	6723 \pm 950	4371 \pm 400	ns
	1997	18	3023 \pm 350	4404 \pm 670	3096 \pm 270	ns
	1998	18	3019 \pm 380	4415 \pm 830	2549 \pm 230	ns
	1999	18	3402 \pm 360	5074 \pm 710	3538 \pm 130	ns

were found (data not shown). Although insensitive to the imposed treatments, tree growth showed significant interannual variation (Figures 3 and 4). *Acer rubrum*, *Q. alba*, and *Q. prinus* all exhibited their highest growth rates during the 1994 and 1996 wet seasons and low growth rates during droughts in 1995 and 1998. Low and high growth rates in 1997 and 1999, respectively, were unrelated to measured soil water status.

Growth rates of individual species varied widely in proportion to that species' mean basal area (Figures 3 and 4). *Quercus prinus* had the highest annual growth rate among species, but *Q. alba* and *A. rubrum* were nearly as productive. Annual growth of *N. sylvatica* was less than half that of *Quercus* and *Acer*. For all species, except *Liriodendron*, maximum annual growth occurred during 1994 or 1996 and minimum annual growth occurred during 1993 or 1995 (Figure 3). In the drought years of 1993 and 1995, annual basal area growth was reduced with respect to growth in the wet growing seasons of 1994 and 1996, but severe late-season droughts in 1998 and 1999 had little impact on current basal area growth. *Liriodendron tulipifera* showed increasing growth rates from 1994 through 1999.

Mean daily growth rates of all species showed a similar pattern for each year of the study (Figure 4). Maximum growth rates occurred before the end of June in each year (i.e., before Day 180), and all basal area growth was completed before late September (i.e., Day 270) in both wet and dry years.

Growth rate and soil water potential

Because of the absence of drought conditions during the 1994, 1996 and 1997 growing seasons (Figure 1), growth rates during those years could be interpreted as the seasonal pattern of growth to be expected in the absence of water stress. With this growth pattern as a reference, the influence of growth reduc-

tions during periods with water stress (i.e., late-season growth in 1995, 1998, and 1999) was quantified. Figure 5 shows the relationship between mean basal area growth, phenology (i.e., day of the year), and soil water potential for the five large tree species. Equation 1 describes a response surface indicated by these data:

$$BA_{\text{growth}} = \exp(c)(DOY - S)^a (E - DOY)^b \left(\frac{WP_{\text{min}} - SWP}{WP_{\text{min}}} \right), \quad (1)$$

where BA_{growth} is mean daily basal area increment of an individual tree, DOY is day of the year, SWP is observed soil water potential in the surface horizon (0–0.35 m depth), a , b and c are model constants that control the shape and magnitude of the growth rate under no water stress, S is the day on which measurable stem growth begins, E is the day when growth ceases and WP_{min} is the soil water potential needed to preclude growth. Table 5 summarizes the regression estimates of these constants for each species and the mean of all five species averaged across all years of the study. Although there was substantial variation in the magnitude of growth rates for each species, the overall pattern of the response surface was consistent across species.

Sapling and tree mortality

By the end of the 1999 growing season, mortality of *C. florida* saplings was more than double that of *A. rubrum* saplings, but both species showed a similar long-term trend (Table 6). Greatest annual mortality of both *A. rubrum* and *C. florida* was observed in 1998. Significant treatment effects on annual mortality of *A. rubrum* were found only in 1998 and 1999, but

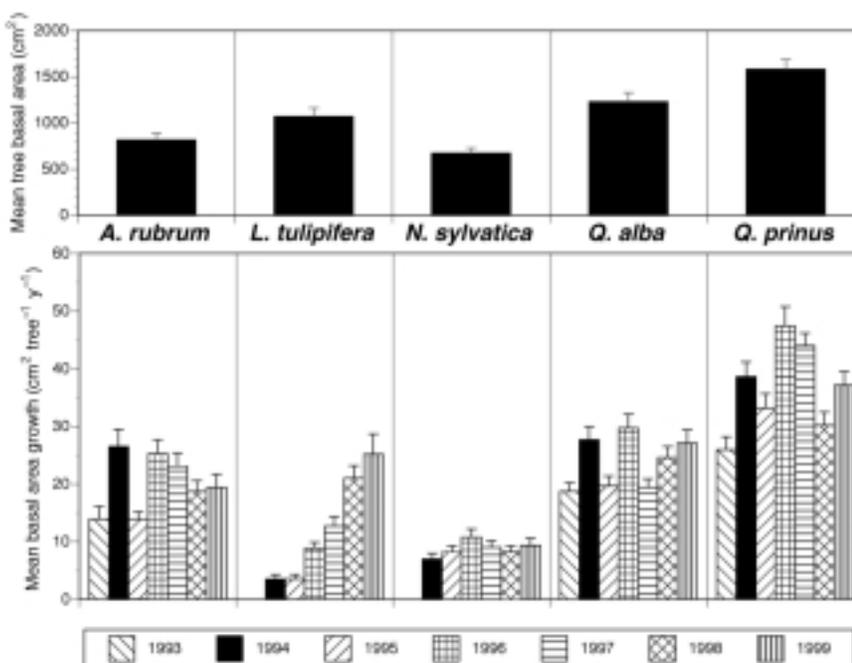


Figure 3. Mean annual basal area growth of large trees by species averaged across treatments compared with the mean tree basal area for each species.

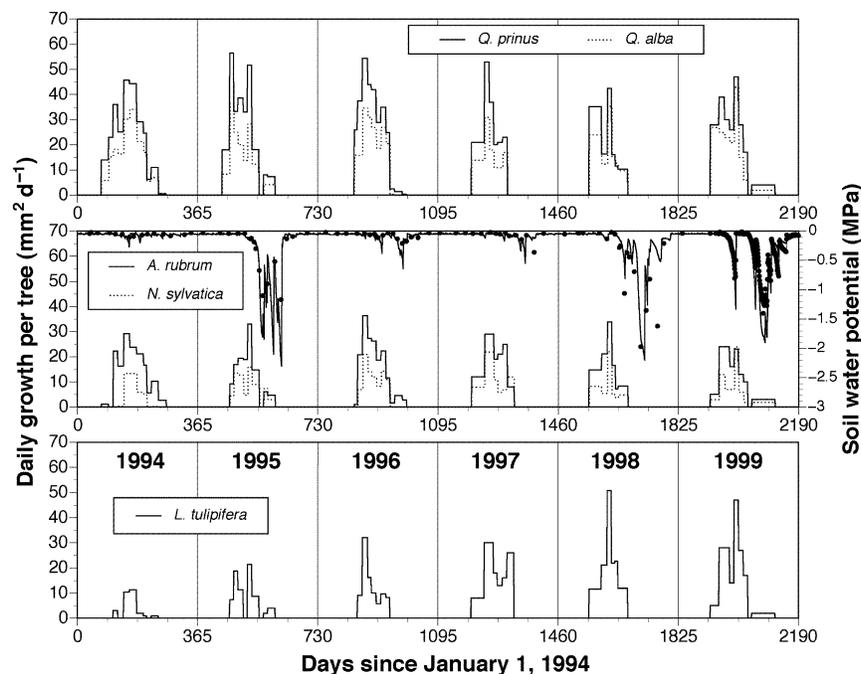


Figure 4. Daily growth rates of *Quercus alba* (top), *Q. prinus* (top), *A. rubrum* (middle), *N. sylvatica* (middle), and *L. tulipifera* (bottom) for each year of TDE precipitation manipulations. Data are the means of individual tree observations across all three TDE treatment areas. Mean control plot soil water potentials for the 0–0.35-m soil depth are provided in the middle graph to indicate periods of water stress in each year (symbols are measured soil water potentials and the line is a model-derived integration between observations).

C. florida mortality showed significant treatment effects in all years except 1994. At the end of 1999, cumulative mortality on the wet treatment plot was significantly lower than cumulative mortality on the control and dry plots for both species. In the first 3 years of the study, the pattern of mortality differed with respect to treatments. Following the drought of 1995, mortality of *C. florida* was significantly enhanced by the dry treatment, whereas there was little mortality in *A. rubrum* in any of the plots (Table 6).

Over the period 1993 through 1999, 63 out of 762 trees with stems greater than 0.1 m DBH died for a mean annual mortality rate of approximately 1.2% per year. Sixteen trees died from known causes unrelated to the imposed treatments (i.e., wind throw or lightning). For the remaining trees, annual mortality rates showed little change by TDE treatment or year (Table 6), reaching cumulative mortality of 11.2, 6.3 and 8.3% in the wet, control and dry plots, respectively, at the end of 1999. Differences in mortality rate among treatments were not significant.

Discussion

Saplings

Observed basal area growth rates during 6 years of throughfall manipulation support our hypothesis that small-stature vegetation is more sensitive to reductions in precipitation and soil water content than large trees. Although *A. rubrum* and *C. florida* saplings had comparable aboveground stem and branch structure and foliar physiology (Gebre et al. 1998, Tschaplinski et al. 1998), *C. florida* had a higher mortality rate than *A. rubrum* in most years (Table 6). Differences in rooting depth are one possible cause for this difference. *Cornus*

florida has a shallow root system (Hinckley et al. 1979, 1981, Bahari et al. 1985) and, therefore, may be sensitive to drought leading to high mortality rates. Alternatively, because *Cornus* anthracnose symptoms (Hiers and Evans 1997) were ubiquitous across the plots (data not shown), it is possible that *Cornus* mortality resulted from the fungal pathogen *Discula destructiva* (Redlin.), with possible interactions with drought. Reduced mortality of *C. florida* and *A. rubrum* saplings on the wet plot indicate that a wetter future climate would sustain establishment and survival of trees in the understory, but a drier future climate might reduce understory success of susceptible species.

Large trees

The treatments did not affect basal area growth of large trees through six growing seasons, but growth of large trees was two to three times greater in wet years than in dry years (Table 4). Although it is commonly assumed that large trees have many deep roots that provide protection against periodic droughts (Kozłowski 1982, Abrams 1990), reductions in growth of large trees during drought periods in 1993, 1995, 1998 and 1999 were apparently driven by reduced soil water potentials in the upper 0.35 m of the soil horizon (Figure 1). Growth reductions associated with shallow soil drying indicate that the number or conductivity, or both, of deep roots may be insufficient to support growth.

Slow growth of the large *L. tulipifera* trees in the first 3 years of the study was probably a result of intense herbivory by the yellow-poplar weevil (*Odontopus calceatus* (Say)) (Burns and Gibson 1968) in those years (authors' unpublished observations). However, the small crown diameters of the *L. tulipifera* trees (~6.8 m) compared with those of *Acer* and

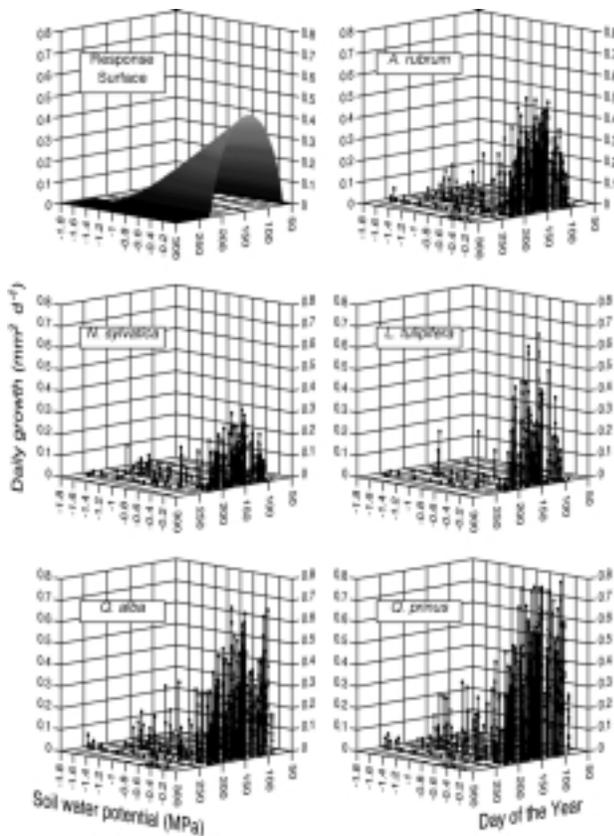


Figure 5. Relationships between basal area tree growth rate, time of the year and soil water potential (0–0.35 m soil depth) for *Acer rubrum*, *Nyssa sylvatica*, *Liriodendron tulipifera*, *Quercus alba*, and *Q. prinus*. The mean fitted response surface for all five species is provided. Variable estimates for fitted response surfaces for each species and the combined data set are in Table 5.

Quercus trees (~9 to 10 m) may have contributed to the low growth rates (*L. tulipifera* is commonly considered the fastest growing tree in the southeastern USA).

Previous publications have documented that TDE treatments affect forest physiological processes (Gebre et al. 1998, Tschaplinski et al. 1998, Wullschleger et al. 1998); however, we found no strong relationship between variation in growing

season precipitation and annual basal area growth of large trees. This discrepancy can be explained on the basis of the relative timing of basal area growth and the drought periods. In years without soil water deficits (i.e., 1994, 1996, and 1997) basal area growth of saplings and trees was complete by late July (Figure 4) even though canopy foliage remained physiologically active throughout the late summer (Wilson et al. 2000a). Thus, basal area growth (a spring phenomenon) was nearly complete before the onset of late-summer droughts. Similar patterns were reported by Buell et al. (1961) for eastern hardwoods, and by Bréda and Granier (1996) who concluded that early wood development in *Q. petraea* L. ex Liebl. was independent of soil water deficits. Phipps (1961) concluded that soil water content was never low enough in Ohio deciduous forests to limit the development of early sapwood. Conversely, severe spring droughts (if they occurred) might represent a significant water stress event with direct impact on current-year basal area growth. In support of this conclusion, Robbins (1921) reported that the amount of March–June precipitation was positively correlated with *Quercus* growth in Missouri. Explanations for mid-season growth reductions of eastern hardwood trees are uncertain, but reduced day lengths, internal growth regulator changes, and limited nutrient supply rates may all play a role. Reductions in late-season carbohydrate supplies are not the cause of the late-season slow down of diameter growth on the TDE site, because net carbon gain remained high late in the growing seasons of the wet years 1994, 1996, and 1997 (Wilson et al. 2000b and authors' unpublished data).

Other studies of hardwood tree growth responses to drought

Early studies dealing with tree growth responses to soil water deficits relied on interannual differences in rainfall patterns. Hursh and Haasis (1931) reported defoliation and mortality of large trees in the southern Appalachians during the 1925 drought when May–August precipitation was 32% below the long-term mean, and soil water contents (~0.3-m depth) declined to 8 to 11% (v/v). They also reported that foliar browning (i.e., wilting) was severe for *Cornus florida*, *Oxydendrum arboreum* and *Quercus prinus*, whereas species of *Fraxinus*, *Robinia*, and *Carya* showed less injury. Small (1961) reported

Table 5. Species-specific regression coefficients for the relationship between daily basal area tree growth, day of the year, and soil water potential in the 0–0.35 m portion of the soil profile for five tree species and their mean. Equation 1 (see text) has six constants: three control the shape and magnitude of the growth rate under no water stress (a , b , c), and the other three are the day of growth initiation (S), day on which growth stops (E), and the soil water potential at which growth ceases (WP_{\min}).

Species	Regression coefficients						R^2
	a	b	c	S (day)	E (day)	WP_{\min} (MPa)	
<i>Acer rubrum</i>	1.31 ± 0.46	2.44 ± 1.36	-17.9 ± 8.8	98 ± 5	257 ± 30	-1.5 ± 0.2	0.46
<i>Liriodendron tulipifera</i>	1.09 ± 0.51	1.21 ± 0.56	-11.0 ± 4.5	98 ± 8	226 ± 10	-1.2 ± 0.2	0.29
<i>Nyssa sylvatica</i>	0.72 ± 0.15	0.88 ± 0.19	-8.7 ± 1.4	101 ± 1	225 ± 3	-2.0 ± 0.5	0.28
<i>Quercus alba</i>	0.70 ± 0.4	0.72 ± 0.2	-7.0 ± 2.7	70 ± 21	226 ± 3	-1.5 ± 0.2	0.33
<i>Quercus prinus</i>	0.16 ± 0.1	0.22 ± 0.1	-3.0 ± 0.6	86 ± 0.3	217 ± 0.3	-1.6 ± 0.1	0.15
All species	1.55 ± 0.6	1.35 ± 0.4	-14.2 ± 4.7	65 ± 16	233 ± 7	-1.6 ± 0.1	0.21

Table 6. Annual mortality (%) by year and treatment and cumulative mortality through 1999 by treatment for understory *A. rubrum* and *C. florida* saplings and canopy trees (all species). The number of measured individuals living in all treatments at the beginning of each year (*n*) is also provided. The *P*-value for a Chi square test on the mortality data is provided. *P*-Values < 0.05 were considered significant treatment responses.

Species/Status	Year	<i>n</i>	Annual mortality (%)			<i>P</i> -Value
			Wet	Control	Dry	
<i>Acer rubrum</i>	1994	195	0	0	1.8	ns
	1995	194	2.8	5.9	3.6	ns
	1996	186	1.4	7.8	1.9	ns
	1997	179	2.9	6.8	9.6	ns
	1998	168	7.6	20.0	12.8	0.02
	1999	146	0	2.3	7.3	0.01
	Cumulative	–	14.1	36.8	32.1	0.01
<i>Cornus florida</i>	1994	205	1.9	0	1.3	ns
	1995	203	5.9	7.9	22.4	0.01
	1996	177	4.2	10.0	11.9	0.01
	1997	161	8.7	19.0	13.5	0.03
	1998	138	19.0	41.0	37.8	0.04
	1999	88	3.3	3.3	7.1	0.04
	Cumulative	–	44.2	61.8	66.2	0.01
Canopy trees	1994	762	0.9	0.4	0.4	ns
	1995	753	0	0	0	ns
	1996	743	1.9	1.5	1.9	ns
	1997	731	0.5	0.8	0.4	ns
	1998	721	2.9	0.4	2.3	ns
	1999	709	0.5	0.4	3.2	ns
	Cumulative	–	11.2	6.3	8.3	ns

foliar wilting and subsequent mortality for several hardwoods growing on shallow soils of the New Jersey Piedmont in 1957, when summer rainfall (May–August) was only 52% of the long-term mean. Buell et al. (1961) contrasted tree growth of several tree species growing on shallow soils in a normal (1956) versus a dry year (1957) with 48% less rainfall, and measured dramatic midsummer stem shrinkage during drought. However, the shrinkage was reversible and total growth was similar in the wet versus dry years because growth occurred before the late-season droughts. Comparison of these results with our study must be made with caution because: (1) Hirsch and Hassis (1931) worked on forest plots that were “conspicuously affected by drought;” and (2) the soils in these other studies were characterized as shallow, whereas the TDE site has very deep soils.

Orwig and Abrams (1997) analyzed annual radial growth responses from tree rings of *Quercus alba*, *Q. velutina* Lam., *Liriodendron tulipifera*, *Carya glabra* (Mill.) Sweet and *Nyssa sylvatica* in Virginia over the 1900–1993 period to determine how each species responded to severe droughts recorded in 1930, 1942, 1954 and 1966. Those years had growing season precipitation between 54 and 82% of the 60-year mean (557 mm), which is similar to the manipulated rates of precipitation in the TDE study. With the exception of *Q. alba*, Orwig and Abrams (1997) found no significant difference in the growth of these species for any of the targeted drought years, but they concluded that growth in years following severe drought episodes was reduced relative to the

long-term trend. Based on tree ring analysis, Jenkins and Pallardy (1995) found a significant correlation between annual basal area increment of *Quercus coccinea* Muenchh. and *Q. velutina* in the Missouri Ozarks and measures of drought severity. This finding contrasts with our results; however, their observations were made in a region of substantially lower precipitation, and it is reasonable to anticipate stronger relationships between growth and soil water deficits in areas where rainfall is more limiting. During an unusually severe drought in central Missouri in 1976 (34% of normal rainfall), when mean soil water potential in the upper 0.45 m of soil declined to –2.6 MPa, Hinckley et al. (1979) reported 19% reductions in stem circumference growth of dominant white oaks. Hanson and Weltzin (2000) pointed out that forests near the prairie–forest border (i.e., Missouri) may be at a higher risk of drought impacts than forests further east where rainfall is more abundant.

Tree ring studies of hardwoods that correlate annual growth increment with climate also support the idea that spring drought conditions produce larger growth effects than late-season droughts of similar magnitude (Fritts 1960, Buell et al. 1961, Phipps 1961, Fritts 1962, Penninckx et al. 1999). Borchert (1998) described a similar phenomenon for tropical rain forests. Our observations of growth of large trees indicate that differences in seasonal timing of rainfall will have a greater impact on basal area growth than percentage changes in rainfall applied to all events throughout a year.

Pedersen (1998) hypothesized that severe drought years

may represent “inciting stresses” that lead to eventual mortality of large trees; however, analysis of mortality of mid-western overstory oaks in Arkansas, Illinois, Indiana and southern Ohio did not show increased mortality of overstory oaks in the first year following an inciting stress (Pedersen 1999). Mortality of large trees on the TDE was rather conservative at about 1% per year, with little evidence of accelerated mortality following the severe droughts of 1995 and 1998. It is possible that inciting stresses may take some years to be expressed in large trees.

Response functions

Although annual basal area growth of large trees was insensitive to late season drought, early season daily growth rates were related to soil water potential (Figure 5). *Quercus* species initiated basal area growth several weeks earlier than the other species, and *Acer* sustained growth longer than the four other study species. The soil water potential required to inhibit growth completely ranged from -1.2 MPa for *Liriodendron* to -2.0 MPa for *Nyssa*. The WP_{\min} for *Acer* and *Quercus* was intermediate at -1.5 MPa, which is the traditionally accepted value for the wilting point of vegetation (Brady 1974). The linear decline in growth with decreasing soil water potential (Figure 5) was consistent with the annual basal area growth response to mean growing season soil water potential in *Pinus strobus* L. (Vose and Swank 1994, McNulty and Swank 1995).

The response surfaces (Figure 5) and their coefficients (Table 5) may be applied to growth models, but only with caution. The soil water potential values used in the regressions in Table 5 were for the upper 0.35 m of the soil. If other studies use soil water measurements at other depths to represent different rooting zones, the relationships will most likely be different. Relationships might also change with soil nutrient availability and stand age. Notwithstanding these cautions, model estimates of the soil water potential leading to total basal area growth inhibition (WP_{\min} from Table 5) indicate that, of the species investigated, *L. tulipifera* is the most sensitive to soil water stress with a WP_{\min} of -1.2 MPa. Limited data for *N. sylvatica* indicate that it might be the least sensitive to soil drying. The WP_{\min} values for *A. rubrum* and the two *Quercus* species were all centered on the traditionally accepted permanent wilting point of -1.5 MPa. The relative sensitivity of *L. tulipifera* growth to soil water potential is consistent with interspecies observations of foliar conductance sensitivity to soil water potential (Hinckley et al. 1979, Hinckley et al. 1981, Bahari et al. 1985). It also agrees with interspecific rankings of drought sensitivity based on saturated foliar osmotic potential (Tschaplinski et al. 1998).

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