

# THE RESILIENCE OF UPLAND-OAK FOREST CANOPY TREES TO CHRONIC AND ACUTE PRECIPITATION MANIPULATIONS

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**Abstract**—Implications of chronic ( $\pm 33$  percent) and acute (-100 percent) precipitation change were evaluated for trees of upland-oak forests of the eastern United States. Chronic manipulations have been conducted since 1993, and acute manipulations of dominant canopy trees (*Quercus prinus*; *Liriodendron tulipifera*) were initiated in 2003. Through 12 years of chronic manipulations tree growth remained unaffected by natural or induced rainfall deficits even though severe drought conditions dramatically reduced canopy function in some years. The resilience of canopy trees to chronic-change was the result of a disconnect between tree growth phenology and late-season drought occurrence. Acute precipitation exclusion from the largest canopy trees also produced limited growth reductions from 2003 through 2005. Elimination of lateral root water sources for the acute treatment trees, via trenching midway through the 2004 growing-season, forced the conclusion that deep rooting was a key mechanism for large-tree resilience to severe drought.

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## INTRODUCTION

Changes in regional precipitation expected to result from increasing global temperatures are predicted to have a major effect on the composition, structure and productivity of forest ecosystems (Houghton and others 2001). Such predicted changes raise concerns about terrestrial ecosystem productivity, biogeochemical cycling, and the availability of water resources (Kirschbaum and Fischlin 1996, Melillo and others 1990) and the IPCC Working Group II Third Assessment Report (McCarthy and others 2001) requested further research on the response of ecosystems to multiple stresses (e.g., increased temperature and drought). Unfortunately, the direction and magnitude of expected changes in precipitation remain highly uncertain (Houghton and others 2001). Given this uncertainty, manipulative field experiments can play a powerful role in the identification of gradual and threshold ecosystem responses that might result from future precipitation changes. This paper describes the results of multi-year chronic and acute precipitation manipulations designed to evaluate the sensitivity of upland-oak forest tree species to natural and manipulated water deficits. The paper summarizes the responses for large trees, which are defined as trees having a dbh greater than 0.1 m. Sapling growth is described elsewhere (Hanson and others 2001, 2003b).

## EXPERIMENTAL SITE

The experiments were located on the Walker Branch Watershed (35°58' N and 84°17' W), a 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 was 1352 mm and mean annual temperature was 14.2 °C. The soils are primarily Typic Paleudults derived from dolomitic bedrock. Plant extractable water (water held between 0 and -2.5 MPa) for the upper meter of soil is approximately 183 mm. A large fraction of this water (44 percent) is held in the upper 0.35 m of the soil profile, which is the location of 60 percent of all fine roots in the 0-0.90 m soil profile (Joslin and Wolfe 1998). The soils are highly weathered and very deep (> 10m) on ridge tops and therefore retain little evidence of their carbonate parent material. Deep rooting may be a source of some water. Early aerial photographs show that the study area was forested in the late 1930's (<http://tde.ornl.gov/landuse.html>), but several large dominant trees show open growth characteristics suggesting some harvesting before that time. The forest on Walker Branch Watershed is a centrally located example of the eastern broadleaf forest province

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as defined by Bailey (1983) and historically has been characterized as a *Quercus/Carya* forest. Insect outbreaks in the early 1980s, however, decimated the *Carya* populations (Dale and others 1990), and the current forests are better termed upland oak forests.

*Quercus* spp. and *Acer* spp. are the major canopy dominants across all slope positions. *Liriodendron tulipifera* L. is a canopy dominant on the lower slope positions, and *Acer rubrum* L., *Nyssa sylvatica* Marsh. and *Oxydendrum arboreum* (L.) DC are the predominant species occupying mid-canopy locations. In March of 1994, stand basal area averaged 21.1 m<sup>2</sup>/ha (Hanson and others 2001). By April 2004, the mean basal area across all plots had increased to 25.4 m<sup>2</sup>/ha (table 1). The number of saplings (trees < 0.1 m dbh) across the study area averaged 3079 trees/ha in 1994 falling to 1881/ha in April of 2005. Saplings contributed an additional 3, 2.6, and 2.5 m<sup>2</sup>/ha to total stand basal area in 1994, 1999, and 2005, respectively (table 1). In 1994, *Acer rubrum* L. and *Cornus florida* L. made up 59 percent of all saplings and 53 percent of the sapling basal area (Hanson and others 2001).

## PROCEDURES

### Chronic Precipitation Manipulation

The Throughfall Displacement Experiment (TDE) is a multi-year chronic precipitation manipulation study. It was constructed across a 2-ha portion of an upper sub-catchment of the Walker Branch Watershed in 1992 and 1993. The site was chosen because of its uniform slope, consistent soils, and a reasonably uniform distribution of vegetation. The TDE system and its performance are described in detail by Hanson and others (1995, 1998, 2003a). Early aerial photographs show that the TDE study area was forested in 1935, but several large dominant trees show open-growth characteristics, confirming that selective cutting along the ridge had been done before that time (Dale and others 1990).

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 x 80 m) experimental plots: one wet, one dry, and one ambient. Each plot was divided into 100 8 x 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 ~1900 below-canopy troughs (0.3 x 5 m) made of greenhouse grade polyethylene that was suspended at an angle above the forest floor (~33 percent of the ground area was covered). The intercepted throughfall was transferred by gravity flow across the ambient plot and distributed onto the wet treatment plot through paired drip holes spaced approximately 1 m apart.

The experimental area was located at the upper divide of the watershed so that lateral flow of water into the plots from upslope did not occur. The site had a southern aspect. Reductions in soil moisture anticipated from the experimental removal of 33 percent of the throughfall were designed to be comparable to the growing season having the lowest recorded rainfall during the dry 1980s decade (Cook and others 1988).

### Acute Precipitation Manipulation

Because results of the TDE study (Hanson and others 2001) showed greater than expected resilience of tree growth in response to chronic drought, a follow up study was conceived to quantify responses to acute soil water deficits. This study termed the 'TARP' study used understory tents for the removal of 100 percent of the growing-season throughfall and stem flow from large, individual canopy trees. Two species representative of two distinct plant functional types *L. tulipifera* (yellow-poplar) and *Q. prinus* (chestnut oak) were manipulated (n = 4 for each species treatment combination). Each treatment ambient plot area was the same, and exceeded the projected canopy spread for the largest trees. Each tent covered an area with a minimum circular radius of 10 m from the target tree bole. The TARP tents and water collection gutters were installed before leaf-out in March of 2003 and have been left in place through the 2005 growing season. Photographs of the experimental system are available at the following web site: <http://tarp.ornl.gov>.

**Table 1—Cumulative basal area of (A) individual tree species > 0.1 m d.b.h. and (B) saplings for the Throughfall Displacement Experimental area in March 1994, December 1999, and April 2005<sup>a</sup>**

Species	Cumulative basal area		
	March 1994	December 1999	April 2005
	----- m <sup>2</sup> ha <sup>-1</sup> -----		
(A) Trees > 0.1 m d.b.h.			
<i>Acer rubrum</i> L.	2.40	2.92	3.39
<i>A. saccharum</i> Marsh.	0.56	0.66	0.72
<i>Carya</i> sp.	0.44	0.42	0.46
<i>Cornus florida</i> L.	0.16	0.13	0.11
<i>Liriodendron tulipifera</i> L.	1.64	1.62	1.82
<i>Nyssa sylvatica</i> Marsh.	2.97	3.07	3.26
<i>Oxydendrum arboreum</i> [L.] D.C.	0.77	0.83	0.86
<i>Prunus serotina</i> Ehrh.	0.11	0.16	0.22
<i>Quercus alba</i> L.	4.17	4.95	5.04
<i>Q. prinus</i> L.	5.72	6.02	7.09
<i>Q.</i> sp.	2.04	1.83	2.18
Misc. conifers	0.15	0.15	0.17
Misc. hardwoods	0.00	0.04	0.08
Total trees	21.15	22.80	25.40
(B) Saplings are plants > 1 m and < 0.1 m d.b.h.			
<i>Acer rubrum</i> L.	0.97	0.96	1.11
<i>A. saccharum</i> Marsh.	0.05	0.06	0.07
<i>Carya</i> sp.	0.02	0.02	0.06
<i>Cornus florida</i> L.	0.62	0.49	0.31
<i>Fagus grandifolia</i> J.F. Ehrh.	0.03	0.05	0.07
<i>Nyssa sylvatica</i> Marsh.	0.36	0.30	0.22
<i>Oxydendrum arboreum</i> [L.] D.C.	0.29	0.30	0.25
<i>Prunus serotina</i> Ehrh.	0.19	0.15	0.14
<i>Quercus</i> sp.	0.14	0.12	0.10
<i>Q. alba</i> L.	0.04	0.04	0.04
<i>Q. prinus</i> L.	0.01	0.01	< 0.01
<i>Rhamnus</i> sp.	0.16	0.11	0.03
<i>Sassafras albidum</i> (Nutt.) Nees	0.05	0.03	0.03
Miscellaneous	0.03	0.02	0.03
Total saplings	2.97	2.64	2.47
(C) Total basal area	23.93	25.44	27.87

<sup>a</sup>A total of 18 tree species and 20 sapling species were present on the measurement plots, but some groups were combined for presentation in this table.

Trenching of the TARP plots was not done initially to avoid the artifacts of root severing and to allow external tree roots to continue to extract water from the target dry plots. In July of 2004 (following limited tree response to the acute treatments) the TARP treatment plots were trenched with a ditcher to a depth of 50 to 60 cm and width of 20 cm to eliminate potential lateral root water sources. This process severed 100 percent of the lateral roots over this depth representing more than 80 percent of the total known root population at this site (Joslin and Wolfe 1998).

### **Soil Water Content, Water Potential and Weather**

Soil water content (percent, v/v) was measured in both studies with a time domain reflectometer (TDR; Soil Moisture Equipment Corp., Santa Barbara, California) following the procedure of Topp and Davis (1985) as documented for soils with high coarse fraction content (Drungil and others 1987). On the TDE, Three hundred ten sampling locations were installed at an 8 x 8 m spacing across the site giving more than 100 soil water monitoring locations per plot. For the TARP study, each experimental tree was instrumented with four TDR locations within the canopy drip line. Each of these TDR measurement sites consisted of two pairs of TDR waveguides installed in a vertical orientation (0-0.35 and 0-0.7 m). The surface (0-0.35 m) TDR measurements coincide with the zone of maximum root density in these soils. TDR measurements were obtained biweekly during the growing season and approximately monthly during the dormant season on the TDE study, and periodically during physiological campaigns for the TARP study. Automated hourly observations of soil water status were also logged using heat-dissipation probes (CS615 water content reflectometer; Campbell Scientific, Logan, Utah) installed in vertical profiles within each of the TDE and TARP treatment plots.

The TDR soil water content measurements were adjusted for the coarse fraction of these soils (mean coarse fraction of 14 percent) and converted to soil water potentials using laboratory derived soil moisture retention curves for the A, A/E and E/B horizons (Hanson and others 2003a). To facilitate comparisons of the severity of soil water deficits between years, the minimum soil water potential (MPa) and calculate a water stress integral (units of MPa d; Hanson and others 2003a) were measured or estimated for all years and treatments.

Weather data including air temperature, relative humidity, and soil temperatures (0.1 and 0.35 m) were logged hourly on each treatment plot. Rainfall, solar irradiance (Pyranometer sensor, LiCor Inc., Lincoln, NE) and photosynthetic photon flux density (Quantum sensor, LiCor Inc.) were also measured continuously and logged as hourly means for one above-canopy location in the vicinity of both experiments.

### **Measurements of Tree Growth**

Diameter measurements of all individual trees greater than 0.1 m dbh and a record of their presence/mortality were recorded annually for the TDE experiment. *Quercus alba* L., *Q. prinus* L., *A. rubrum*, *L. tulipifera*, and *Nyssa sylvatica* trees greater than 0.2 m dbh were fitted with dendrometer bands (170 trees) for biweekly measurements of stem circumference during each growing season as described by Hanson and others (2001). These five species made up almost 80 percent of the basal area of the experimental area (table 1). Similar dendrometer band measurements were conducted for all *Q. prinus* and *L. tulipifera* trees manipulated as a part of the TARP study.

Measured changes in the circumference of each tree were combined with information on its initial stem diameter to obtain the change in stem basal area over time (cm<sup>2</sup> per year). 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). This paper focuses on cumulative annual tree growth data and shrink/swell patterns capable of being measured by dendrometer bands are not important to the current discussion.

### **Statistical Analyses**

The unreplicated nature of the TDE is not ideal (Hurlbert 1984), but the resulting pseudoreplication is recognized as a reasonable approach when costly large-scale experimental field designs are undertaken

(Eberhardt and Thomas 1991). To minimize the possibility that spatial variation would be confounded with treatment effects, the TDE observations were preceded by judicious selection of homogeneous sites (considering aspect, vegetation, and soils), detailed characterization of site environmental parameters, and pretreatment measurements for key response variables (Hanson and others 2001). Growth responses on the TDE were analyzed using individual trees growth ( $n = 200$  to  $250$ ) as the experimental unit. In support of the use of individual trees as the experimental unit, Hanson and others (1998, 2001, 2003a) demonstrated that the individual  $8 \times 8$  m resolution soil water measurements across the TDE plots were not correlated with each other and could therefore be treated as independent measurements. Nevertheless, to further account for bias in growth rates caused by pretreatment plant size and growth rate, the initial basal area of individual saplings was used as a covariate in analysis-of-variance tests of treatment effects. Such covariates were significant and appropriate for their intended purpose.

The TARP study was conducted on fully replicated mature trees with randomly assigned ambient or dry-plot treatments. One-way analysis of variance with covariates based on initial basal area was used to evaluate significant annual growth responses in the TARP study. Additional regression analyses relating individual tree responses to tree-specific soil water content data are planned for a future paper. Statistical analyses were conducted with SPSS 6.1 for Macintosh (SPSS, Inc.).

## **RESULTS AND DISCUSSION**

### **Interannual Weather 1993 to 2005**

Weather conditions exhibited substantial interannual variation from 1993 through 2005 (Hanson and others 2003, <http://tde.ornl.gov/tdedata.html>). Lower-than-average annual precipitation was measured in 1993 (-16 percent), 1995 (-16 percent), 1998 (-9 percent), 1999 (-15 percent), 2000 (-11 percent), and 2001 (-27 percent). Above-average precipitation was observed in 1994 (+24 percent), 1996 (+21 percent), 1997 (+8 percent), 2003 (+13 percent), and 2004 (+7 percent). Growing-season precipitation (May to September) was near normal in 1994, 1999, 2000, 2002, and 2004, but it was 26 to 38 percent less during the drought years of 1993, 1995, and 1998. Growing-season precipitation was 47, 22, and 29 percent higher than normal in 1996, 1997, and 2003, respectively. Mean annual air temperature and annual incident solar radiation were not as variable as annual precipitation, but mean annual air temperatures in 1993, 1998 and 2002 were warmer than in the other years. Cumulative annual incident solar radiation at the site was similar across years ranging from 2643 to 3155 MJ m<sup>-2</sup>.

### **Observed Patterns of Soil Water Potential**

The seasonal patterns of mean TDR soil water potential by treatment in the 0 to 0.35 and 0.35 to 0.7 m depth increments from 1993 through August of 2005 are shown for the TDE and TARP manipulations in figures 1 and 2, respectively. Minimum daily soil water potentials for the 0 to 0.35 m depth showed that significant ambient drought occurred in 1993, 1995, 1998, 1999, 2000, and 2002 (sustained values below -0.7 MPa in figure 1). In years with significant dry periods (1993, 1995, 1998, 1999, and 2002), long periods without rainfall caused treatment differentials to be minimized. Following the depth of drought, treatment differences redeveloped as the soils refilled at a faster and slower rate on the wet and dry plots, respectively. No treatment differences were ever observed during the dormant seasons when all soils returned to field capacity.

Water in the 0.35 to 0.7 m depth remained available for plant use throughout the drought periods in all years with consistent evidence of reduced water availability at depth observed only during the severe late-season droughts of 1998 and 2002. Annual water stress integrals (Hanson and others 2001, 2003a), which account for the duration of drought, demonstrate that the 1993, 1999, and 2002 droughts (-92, -31 and -114 MPa d, respectively) were not sustained as long as those occurring in 1995 and 1998 (-168 and -217 MPa d, respectively).

Acute soil moisture treatments associated with the TARP study diverged from ambient plot conditions within one month after the initiation of treatments in 2003 and 2004 (fig. 2). Surface soils were allowed

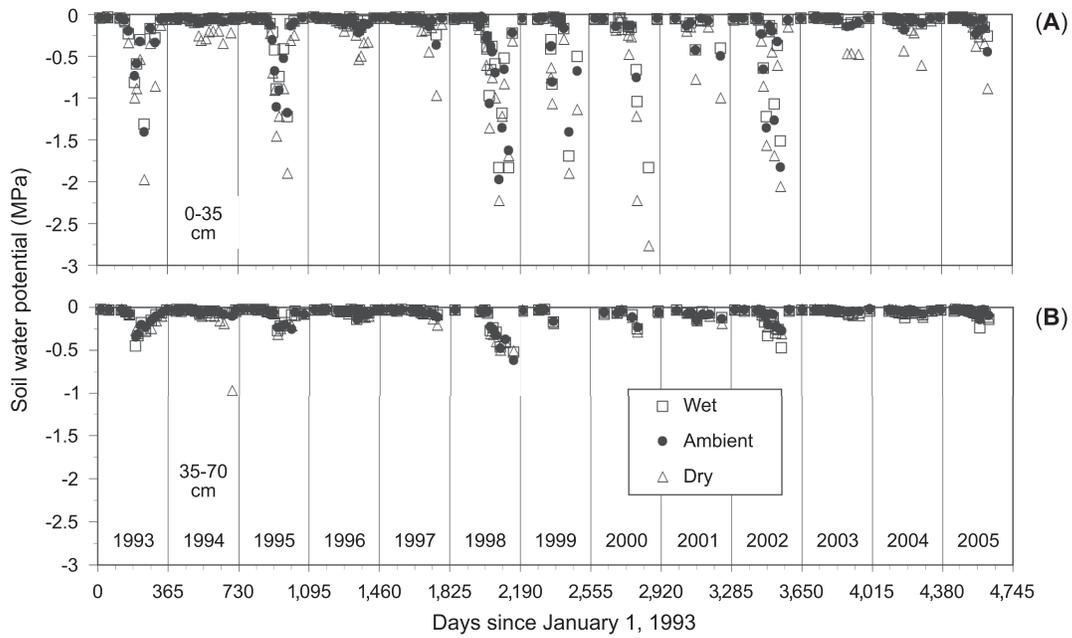


Figure 1—(A) Soil water potentials for the 0- to 0.35-m and (B) 0.35- to 0.7-m soil depth from 1993 through 2005. Data are the mean values (n = 100 or 30 starting in 2001) for the wet, ambient, and dry plots of the throughfall displacement experiment (TDE). Treatments were initiated on July 14, 1993.

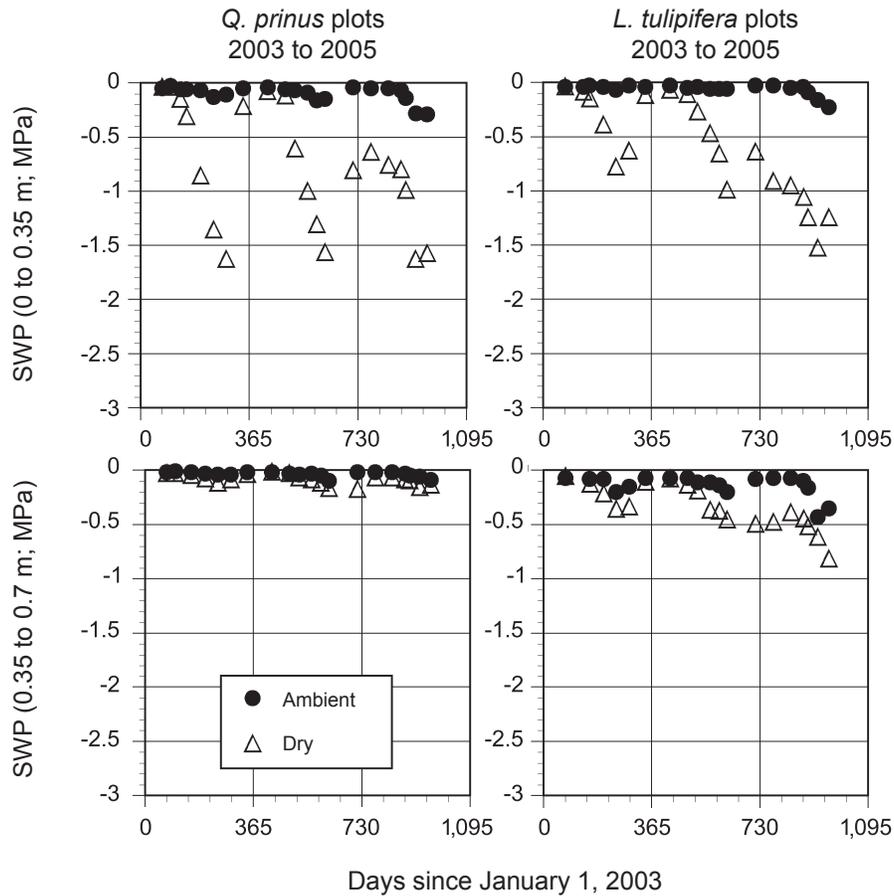


Figure 2—Pattern of soil water potential in the 0- to 0.35-m and 0.35- to 0.7-m for the TARP study from 2003 through 2005.

to return to field capacity during the winter of 2003/2004, but were maintained at acute drought levels throughout the winter of 2004/2005. Partial refilling of surface-soil water stocks in February and March of 2005 was evident the dry plots of the *Quercus* plots and was presumed to result from hydraulic redistribution (Burgess and others 1998) via roots having access to deep water supplies.

### Responses to Chronic Precipitation Change

Through 12 years of chronic manipulations, individual tree annual growth, measured on a subset of trees with dendrometer bands, remained unaffected by natural or induced rainfall deficits even though severe drought conditions were observed to dramatically reduce canopy function in some years (Wilson and Hanson 2003). Hanson and others (2001, 2003b) showed that the observed resilience of these upper-canopy *Acer*, *Nyssa*, *Liriodendron*, and *Quercus* trees was the result of a disconnect between their early-summer growth phenology and normal late-season occurrence of drought.

Analysis of cumulative tree basal area growth over the entire experimental period from 1993 through 2005, however, showed a significant influence of the TDE precipitation treatments (fig. 3). Dry plot tree growth was lower than both the ambient and wet treatments, but wet plot growth did not exceed ambient growth. Tree size did not have a dramatic influence on the response to chronic precipitation manipulations. Although not justified in this paper, current analyses of element cycles for the TDE suggest that long-term chronic increases in precipitation may increase leaching of beneficial base cations (Johnson and others 2002), and drought conditions may lead to immobilization of mineral elements (Paul J. Hanson, unpublished data). Both processes could lead to reductions in growth over time.

### Responses to Acute Precipitation Change

Results from the TDE study led us to hypothesize that an acute early spring precipitation deficit would force drought conditions to overlap tree growth phenology on Walker Branch and lead to significant current-year growth reductions. The acute precipitation exclusion in the TARP experiment, however, produced limited growth (fig. 4) or physiology effects through three consecutive growing seasons (data not shown). The TARP growth data provide further evidence of the resilience of upland-oak canopy trees to drought on Walker Branch.

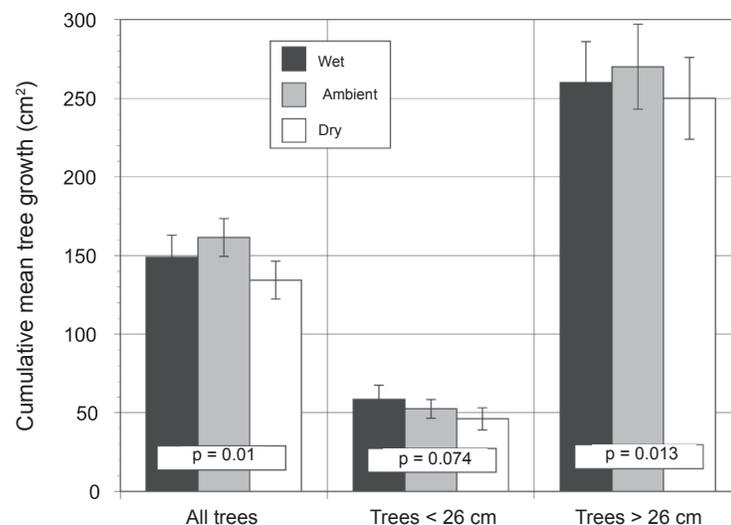


Figure 3—Cumulative individual tree basal area growth ( $\text{cm}^2 \pm 95$  percent C.I.) from 1994 through 2005 as a function of the chronic throughfall displacement experiment (TDE) treatments for all defined trees (woody plants > 10 cm d.b.h.), and the same analysis for defined trees < or > 26 cm d.b.h.

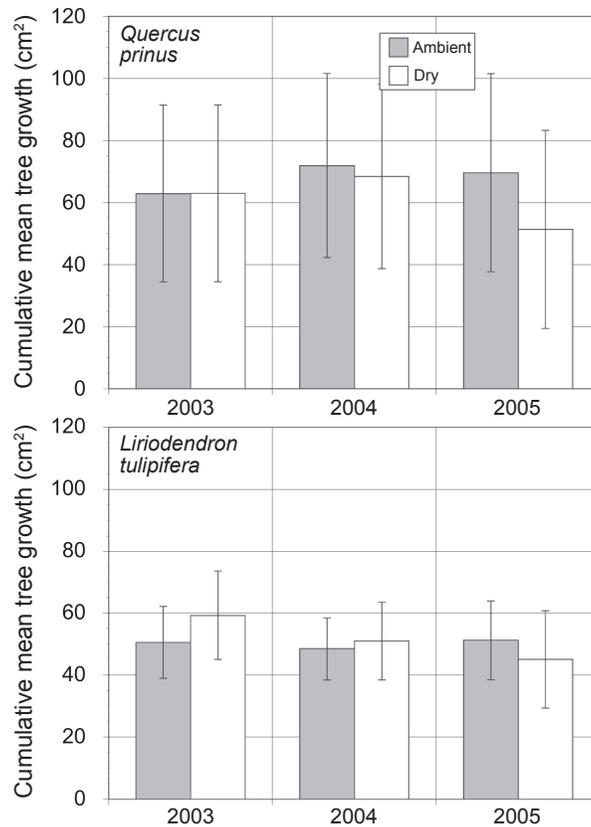


Figure 4—Annual cumulative tree growth ( $\text{cm}^2 \pm 95$  percent C.I.) for *Quercus prinus* (upper box) and *Liriodendron tulipifera* (lower box) trees in response to the acute precipitation manipulations (100 percent growing-season removal) of the TARP study in 2003, 2004, and 2005.

Trenching around each dry-plot tent midway through the 2004 growing season was conducted to determine if lateral root water sources were responsible for the resilience of the trees exposed to acute droughts. The manipulation showed no negative influence on continuous observations of water use by the sapflow method (Wullschleger and Hanson, in press) and allowed for the conclusion that deep rooting must be a key mechanism for large-tree resilience to severe drought. Although such a conclusion is common for woody plants in dryland ecosystems of the western United States and deep roots are known for oak forests (Phillips 1963, Stringer and others 1989, Canadell and others 1996), such a conclusion was unexpected for the upland-oak forest of Walker Branch for two reasons (1) measured root densities at depth were very low at this site, and (2) dramatic canopy physiological effects and leaf senescence were observed during the drought of 1998 when deep soil moisture was non-limiting. The TARP manipulations, however, clearly demonstrate that the largest individual *Q. prinus* and *L. tulipifera* trees in this forest have an effective mechanism for the extraction of deep soil water resources. Observations to quantitatively evaluate the presence and water transport capacity of roots below 90 cm for the Walker Branch forest are underway.

### Conclusions Relevant To Ecosystem Modeling

In their current form, ecosystem models used for assessments of the impacts of climatic change on eastern forests overestimate the severity and influence of precipitation deficits on the upland forests of Walker Branch (Hanson and others 2004). The precipitation manipulation experiments on Walker Branch demonstrate the following needed improvements to ecosystem models of eastern deciduous forests: an understanding of the timing of growth phenology and drought, an improved characterization

of root hydraulic architecture and soil water supplies with depth, and the need to understand how stored nonstructural carbohydrate (Tschaplinski and Hanson 2003) and element reserves vary from year to year and when such pools become limiting to current-year growth.

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# Proceedings

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