

# Identifying Critical Thresholds for Acute Response of Plants and Ecosystems to Water Stress (TARP): 1-Year Results

A progress report to the United States Department of Energy,  
Office of Science, Biological and Environmental Research (BER),  
Program for Ecosystem Research (PER)

Submitted March 5, 2004

Paul J. Hanson<sup>1</sup>, Stan D. Wullschleger<sup>1</sup>, Timothy J. Tschaplinski<sup>1</sup>, and Robert M. Augé<sup>2</sup>  
<sup>1</sup>Oak Ridge National Laboratory, Oak Ridge, Tennessee  
<sup>2</sup>University of Tennessee, Knoxville, Tennessee

---

Contents	
Item	Page(s)
Summary bullets	
Operational progress and scientific conclusions	2
Plans for FY2004	2
Publications and presentations	2
TARP Background and task-specific progress	3-11
Purpose	3
Objectives	3
Experimental approach	4
Experimental performance	5
Whole-tree water use	8
Storage carbohydrates	8
Canopy and seedling physiology	9
Tree growth	10
Modeling water stress propagation	11
A new manipulation	12

---

## First Year Summary

### Progress and Scientific Conclusion for FY2003

- TARP treatments were initiated on schedule (just prior to leaf emergence) for all *Quercus prinus* and *Liriodendron tulipifera* trees.
- The experimental system was able to produce statistically significant differences in soil water status after only a few weeks of manipulation, and those differences were sustained without interruption throughout the growing season.
- Higher than average ambient precipitation in 2003 hampered the speed of development of soil water deficits and limited the magnitude of the deficits attained late in the summer.
- Late-season reductions in whole-tree water use under the acute manipulation were observed for *L. tulipifera* but not *Q. prinus*. Furthermore, no significant changes in leaf photosynthesis, conductance or water potential were observed for either species on the dates measured.
- Storage carbohydrates for terminal branches, bole sapwood, and surface fine roots were measured for all trees starting in June 2002, and periodically throughout 2003. No consistent effects of acute drought were observed, but tissue concentrations of storage carbohydrates showed minimum levels for stems suggesting that sapwood is a logical point of observation for early indications of drought-induced carbohydrate limitations.
- No significant growth reductions with soil drying were observed for either *Q. prinus* or *L. tulipifera* suggesting that late-season droughts did not overlap with critical growth periods.
- The lack of physiological and growth responses to the imposed droughts in 2003 suggests that lateral or deep roots connected to the 'dry' treatment trees might have been responsible for supplying water to sustain normal physiological functions. Model calculations suggest that only 10 percent of the root system would need to reside in surface soils beyond the treatment-tent perimeter, or in deep soils, to provide water supplies sufficient to sustain physiological function during wet conditions like we had in 2003.

### Plans for FY2004

- Ambient precipitation was allowed to refill the soil water storage pool during the winter of 2003/2004, and acute manipulations will be reinitiated prior to leaf out in 2004. To avoid artifacts that would make extrapolations difficult we will not trench these plots in 2004.
- A separate trenching study on newly selected mature *Q. prinus* trees will be conducted in May/June 2004 to evaluate the importance of lateral surface roots for whole-tree function. Further details are provided below.

### TARP Publications and Presentations

After just one year of field manipulation, manuscripts are still being developed from the results of this study. We anticipate a completed initial manuscript detailing the influence of lateral roots on whole-tree water by the end of the 2004 growing season, and several others characterizing tree growth responses to the acute moisture treatments early in 2005.

## TARP Background, Approach and Task Specific Progress

Biogeography models and dynamic ecosystem simulation models used in the assessment of climatic change routinely predict species displacement and population migration following mortality. Although such predictions are based on reasonable hypotheses regarding plant response to warming and associated inter-specific competition, predicted mortality rates driving current models and mechanisms remain largely untested. We are conducting a manipulative field study to provide data on the impact of acute drought on mechanisms responsible for growth and mortality of deciduous forest canopy trees representative of common plant functional types (*Liriodendron* and *Quercus*). We have deployed replicated understory canopies for the removal of 100 percent throughfall and stem flow around mature trees to allow the artificial introduction of a spring drought. Such droughts overlap the period of optimum stem growth and have a greater potential to disrupt plant function. Key measurements include weekly dendrometer band observations, periodic evaluation of plant nonstructural carbohydrates status, automated measurements of sapflow, periodic observations of foliar photosynthesis and conductance, and observations of soil moisture status by depth and horizontal extent of the tree root zone. A primary goal of this research will be to translate such data into mechanistic expressions of the threshold levels of moisture stress responsible for limiting plant function and growth and the inclusion of mechanistic expressions in biogeochemical and biogeography models to enhance their usefulness for assessments of climatic change. While the ongoing field experiments and observations are limited to acute precipitation manipulations, interactions between acute drought, future warming, elevated CO<sub>2</sub> and increasing tropospheric ozone will be addressed with stand-level ecosystem models to evaluate the potential for mitigating (CO<sub>2</sub>) or exacerbating (temperature, ozone) impacts.

### *Purpose of the TARP Project*

We proposed a two phase study designed to (1) provide data on the impact of spring droughts on current year growth of common deciduous forest canopy trees (*Liriodendron* and *Quercus*) and (2) evaluate the threshold and timing of acute moisture stress required to introduce catastrophic drought responses (i.e., cessation of current year growth, critical reductions in dormant season carbohydrate supplies and reductions in post-drought leaf production). We are using understory canopy roofs for 100 percent throughfall and stem flow removal to induce acute drought conditions at increasing levels of severity over three years so that we can characterize soil moisture deficit thresholds associated with reduced plant physiological function and ultimately senescence. Key measurements to address the following hypotheses will include weekly dendrometer band observations, periodic evaluation of plant nonstructural carbohydrates status (January and maximum drought), and sapflow as an integrated measure of whole-tree physiological response, and continuous hourly observations of soil moisture status by depth and horizontal extent of the tree root zone.

### *Objectives*

- 1) Demonstrate that a late spring/early summer drought will have a direct impact on current year growth due to reductions in development of functional sapwood.
- 2) Identify the level and extent of drought needed to induce reduce stored carbohydrate and nutrient reserves, accelerate canopy senescence, and lead to reduced canopy production in subsequent years for two common plant functional types.

- 3) Translate these observations into appropriate algorithms for inclusion in biogeochemical and biogeography models being used for assessments of climatic change impacts.

### *Experimental Approach*

Although manipulative studies of tree seedlings and saplings are expedient and cost effective, recent studies have shown that they produce physiological and growth responses that differ from those of mature trees. Therefore, to gain an understanding of mature forest response to scenarios for future environmental change, direct experiments on large trees or forested catchments are warranted. We are quantifying the impact of early spring and acute drought conditions on two mature tree species which represent key functional plant types common to the eastern deciduous forest ecosystem: *Liriodendron tulipifera* L. (yellow-poplar) and *Quercus prinus* L. (chestnut oak). *Liriodendron tulipifera* is an early successional species exhibiting drought avoidance mechanisms with diffuse porous sapwood and leaves with high stomatal conductance. *Quercus prinus* is a late successional species exhibiting drought tolerance characteristics (osmotic adjustment) with ring porous sapwood and leaves with low conductance. These two species are well represented in established eastern deciduous forest stands and their responses should reflect the broader response of an entire closed-canopy forest.

Extended droughts will be imposed on mature canopy trees through the use of a reusable understory roof elevated above the forest floor. Ground level tarpaulins, which act as a surface mulch layer, have been shown to be ineffective at producing rapid soil drying. The roof will be constructed from commercially available canopies joined together and installed around the target trees with a custom designed tarp, gutter and tree sleeve system. The understory roof will be capable of removing 100 percent of throughfall and stem flow from the rooting zone of mature trees. Observations from the TDE experiment suggest that manipulations reaching beyond the tree crown should be adequate to contain the effective horizontal rooting distribution of the target mature canopy trees under typical conditions. Treatment canopies were assigned to 8 of the 16 experimental trees in a random manner and the experimental unit for all analyses of variance or covariance will be the individual tree. The a priori tests suggested are: treated vs. untreated trees, *Quercus* vs. *Liriodendron*, and the interaction between species and treatment.

A priori hydrologic modeling of the Walker Branch forest suggested that 100% throughfall exclusion starting on or about April 15 of a mean year would be required for a minimum of 40 days to be effective at producing soil water deficits sufficient to reduce plant water use, foliar photosynthetic function, and stem growth (Stage 1). The occurrence of acute drought conditions in late spring and early summer appears to be a prerequisite for substantial growth reductions in eastern forest trees. Total exclusion for at least 70-80 days would be required to force premature leaf senescence and cavitation of the hydraulic pathways (Stage 2). We propose to induce increasing levels of acute moisture stress over three years to experimentally mimic this simulation. In 2002 100% throughfall removal treatments will only be left in place until Stage 1 drought conditions are reached. Throughfall removal in years 2 and 3 will be sustained 4 and 8 additional weeks further into the summer, respectively, to exacerbate the acute drought in an attempt to bring on Stage 2 drought conditions.

Microclimate differences at the forest floor level should be minimized because the height of the canopies above the forest floor (2-3 meters) is sufficient to allow normal air movement. However, because stagnant conditions commonly occur in this area (especially at night) some

changes may occur, and air and surface soil temperature monitoring of treated and untreated plots is planned.

### **Experimental Manipulations**

Paul Hanson and Donald E. Todd

The TARP treatment system was designed to exclude 100% of ambient precipitation over an area extending to (or beyond) the drip line of the individual canopy trees (~310 m<sup>2</sup> per tree). Eight independent ‘treatment-tents’ were installed and operational for 4 *Quercus prinus* L. and 4 *Liriodendron tulipifera* L. trees on 31 March 2003 prior to canopy leaf out. Eight additional control trees (4 *Q. prinus* and 4 *L. tulipifera* trees) were also instrumented. The experimental treatment plots were not trenched to avoid the artifact of root removal and to allow roots from adjacent trees to function to accelerate drying within the dry plots.

During the first year of operation, local weather conditions yielded the 7<sup>th</sup> wettest growing season (April-October) and the 2<sup>nd</sup> wettest April to June period over the last 55 years (1949 to 2003). The April to June period coincides with the period of maximum tree growth, and the above-average rainfall during this period hampered the first-year goals of the TARP project. Nevertheless, we successfully produced significantly lower soil water contents and water potentials under all treatment trees within the boundaries of the ‘treatment tents.’ Significant drying of soils to a depth of 35 cm was observed as early as day 150 for both species, and both species showed water contents in the surface 10 cm to reach ~5% (v/v) by the end of the growing season (day 288). At 10 to 35 cm the dry treatment soils under *Q. prinus* attained lower soil water contents than *L. tulipifera* by day 288. The pattern was the opposite for the 35 to 55 cm depths where soils were the driest for *L. tulipifera*. Dry plot soil water potentials showed a continuous decline throughout the growing season reaching depth-averaged minimums around -0.8 and -1.4 MPa for *L. tulipifera* and *Q. prinus*, respectively. A sharp boundary between drought conditions under the tent versus ambient conditions away from the tents was also observed.

Growing-season rainfall was sufficient to keep ambient plot soils near field capacity throughout most of 2003, however, during the period from day 230 to 300 the ambient soils showed transient drying at all soil depths. The late-season transient drying throughout the soil profile in the presence of abundant rainfall inputs suggests that available soil water storage pools for these large trees were indeed being drawn down. Had we received typical precipitation inputs in 2003 we expect that the dry treatments would have become more extreme earlier in the growing season, and have reached more extreme levels of water deficit by the late growing season.

We expect that lateral roots extending beyond the treatment tents and deep roots reaching deep within the soil profile were actively involved in the hydraulic redistribution of soil moisture into the drying zone underneath the tents. In the absence of such a process, measured water-use by these trees would have led to greater soil water draw-down than we observed. Additional manipulations (see below) are proposed in 2004 to determine the relative importance of lateral vs. deep roots to this process.

Air temperature and relative humidity at 1 m above the soil surface under the treatment tents did not differ from the ambient plots, but soil temperatures at ~10 cm were 2-3 °C warmer under the tents during the middle of the growing season. Later in the year when the solar angle was reduced these differences were minimized.



Figure 1. Photographs of one 'dry-plot' *Liriodendron tulipifera* L. tree.

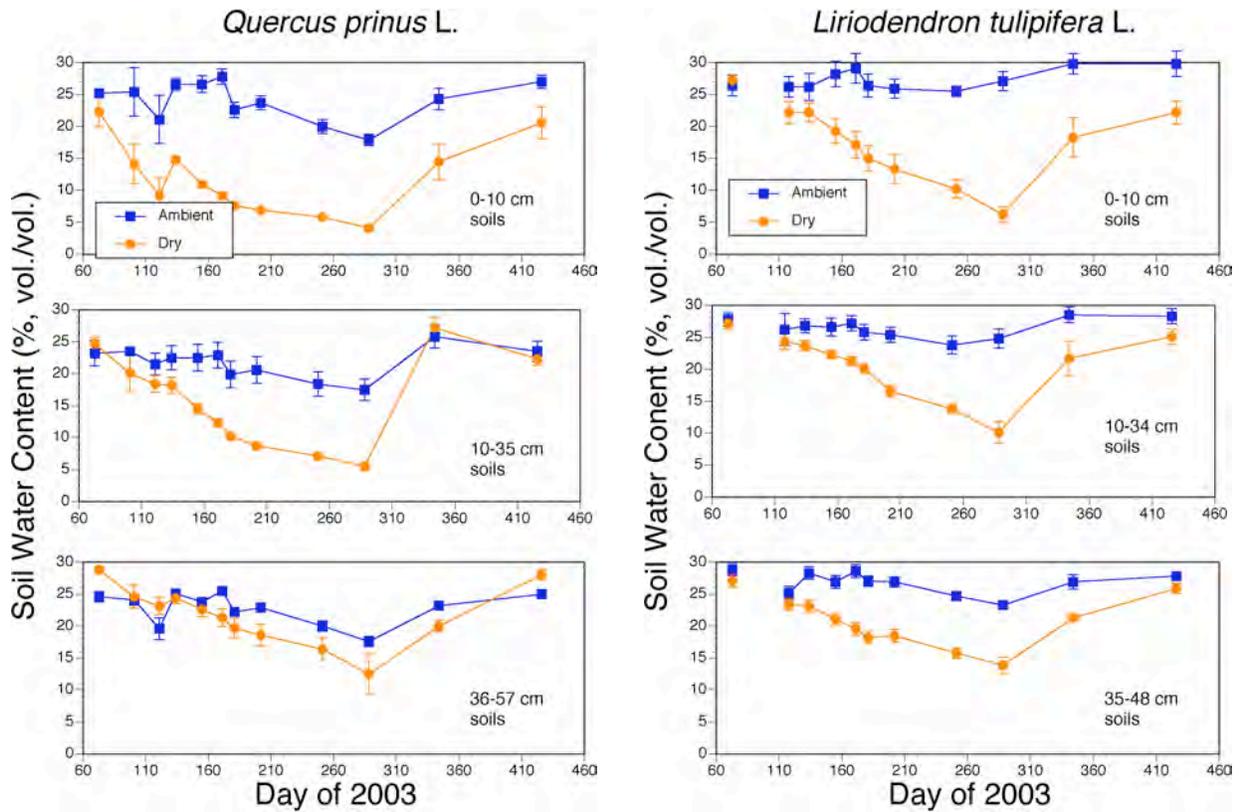
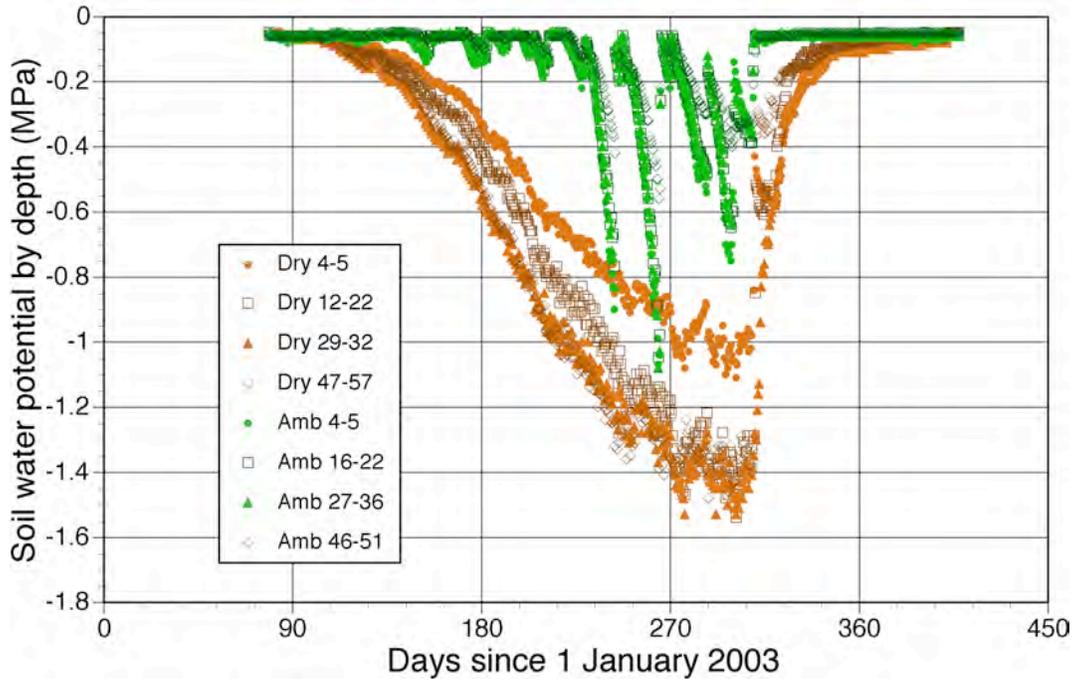


Figure 2. Soil water content by species, treatment and soil depth throughout 2003.

*Quercus prinus* L.



*Liriodendron tulipifera* L.

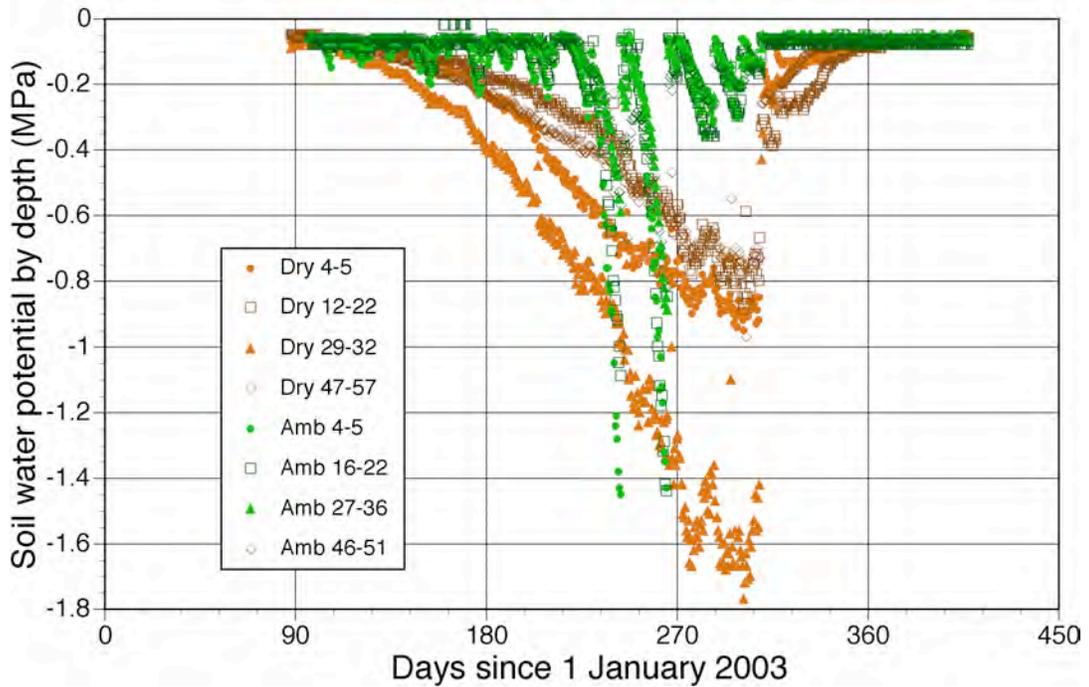


Figure 3. Approximate soil water potentials by species, treatment and soil depth throughout 2003. These values will be modified as we proceed with additional laboratory measurements of site-specific soil moisture release curves.

## Whole-tree Water Use

Stan D. Wullschlegel

Hourly rates of sap velocity were measured for *Q. prinus* and *L. tulipifera* trees from March 26 to October 31, 2003. Seasonal patterns of sap velocity for both species showed considerable day-to-day variation. Much of this could be explained by daily variation in radiation, vapor pressure deficit, and longer-term changes associated with canopy leaf area development and senescence. Average rates of sap velocity and whole-tree water use were higher for *L. tulipifera* than for *Q. prinus*. *Quercus prinus* trees transpired approximately 90 kg/d compared to 120 kg/d for *L. tulipifera* trees. Few differences in rates of sap velocity or whole-tree water use were observed between *Q. prinus* trees from either the control or rainfall-exclusion treatments. In contrast, treatment differences were observed for *L. tulipifera* trees, with early-season rates of sap velocity being 15 to 20% lower in the rainfall-exclusion treatments. Beginning in early- to mid-August, rates of whole-tree water use for *L. tulipifera* trees as calculated from measured sapwood area were 25 to 30% lower in the rainfall-exclusion treatment compared to that of the control trees. These differences continued throughout the remainder of the season.

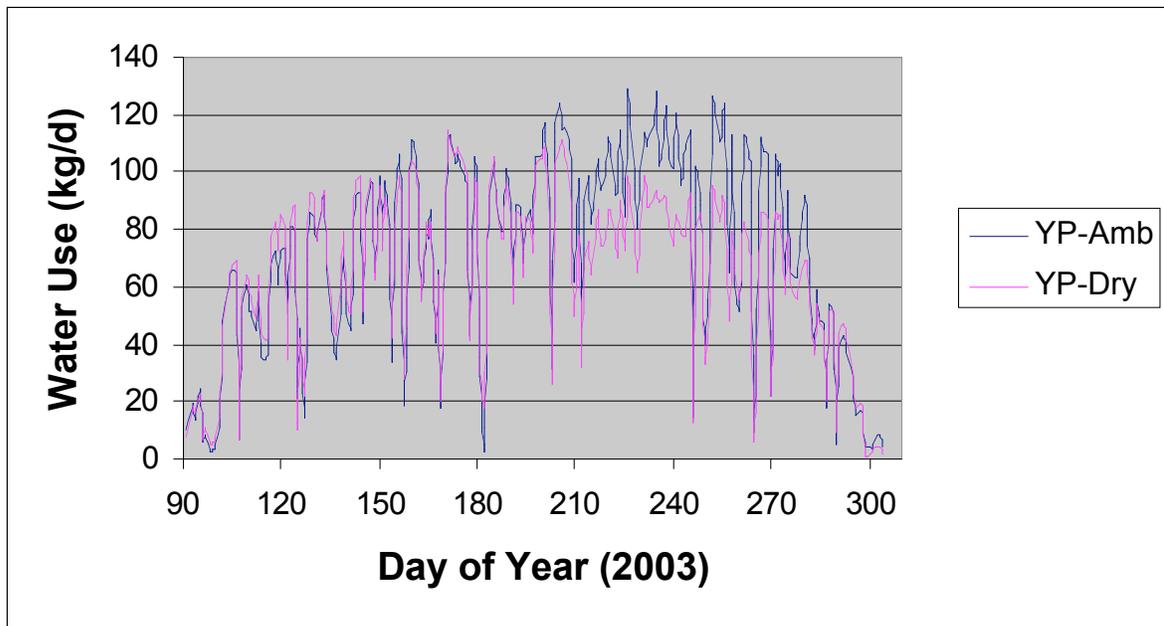


Figure 4. Whole-tree water use of *Liriodendron tulipifera* L. trees throughout 2003 showing 'dry-treatment' induced reductions between days 210 and 270.

## Storage Carbohydrates

Timothy J. Tschaplinski and Ramie Wilkerson

Stem, branch, and fine roots of *L. tulipifera* and *Q. prinus* were analyzed for soluble sugars and starch to determine total nonstructural carbohydrate (TNC) concentrations over the course of 2003. The only statistically significant treatment difference occurred in branches of *Q. prinus* in June, when starch was increased by 9% in the dry treatment, resulting in a 12%

increased in TNC. The increase in branch starch concentrations was correlated with the early season dry period that was alleviated by a subsequent wetter-than-average summer. Carbohydrate concentrations were somewhat reduced in July versus June, but there were no treatment differences. September values were again elevated back to the same high levels observed the previous January. More pronounced treatment differences are likely to be expressed in a normal to dry growing season. It is of interest to note that the lowest tissue TNC concentration was in stem tissues, which may suggest that any treatment-induced limitation in carbon availability may be evident in stems. Stem TNC concentration of *L. tulipifera* declined to as low as 1.7% in June of the pretreatment year when growth was most active. We will sample stem cores more frequently to determine the seasonal trend in stem TNC, rather than solely the dormant season sampling that was done this year.

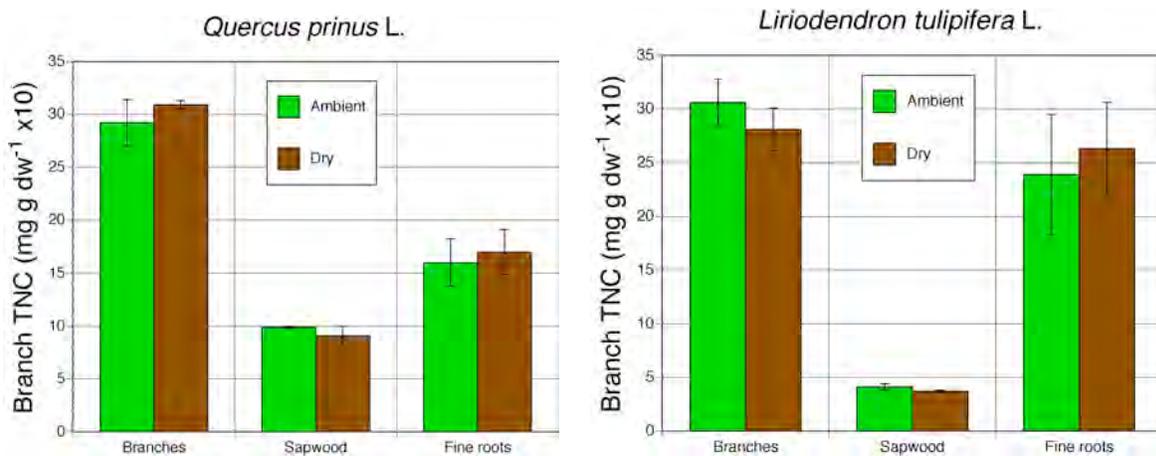


Figure 5. Total nonstructural carbohydrate levels for *Quercus prinus* and *Liriodendron tulipifera* in September of 2003 showing the importance of tissue-type.

## Canopy and Seedling Physiology

Robert M. Augé

Leaf water potential, osmotic potential, carbon exchange rate (CER), transpiration and stomatal conductance ( $g_s$ ) of *L. tulipifera* and *Q. prinus* in the ambient and dry treatments were measured on clear days in early June, the fourth week of July and early September in 2003. Foliage near the tops of trees was sampled with a shotgun from the ground, with samples rapidly collected and placed into measurement instruments within 30-80 s of the shotgun blast. There were no significant differences between dry and ambient trees in any of these parameters in either tree species on any measurement day, nor were there significant drought treatment x species interactions. Gas exchange parameters were mostly lower in *Q. prinus* than in *L. tulipifera* on the July and September dates. On the three measurement dates, average daily CER was about 11 to 12  $\mu\text{mol}^{-2} \text{s}^{-1}$ , transpiration 4 to 6  $\text{mmol}^{-2} \text{s}^{-1}$  and  $g_s$  225 to 340  $\text{mmol}^{-2} \text{s}^{-1}$ , for ambient and dry trees. Leaf osmotic potentials were higher in *L. tulipifera* than in *Q. prinus* on all measurement days, with daily averages between about -1.7 and -2.0 MPa. Leaf water potential remained between about -0.6 and -1.0 MPa for the June, July and September measurement days.

## Tree Growth

Paul J. Hanson

Patterns of stem growth of both *Q. prinus* and *L. tulipifera* followed the seasonal phenology demonstrated on the Walker Branch Throughfall Displacement Experiment (TDE) in years with minimal water stress. Maximum stem growth rates for both species ranged from 60 to 80 mm<sup>2</sup> d<sup>-1</sup> during the period between days 140 to 180, and growth ceased around day 260. Had the growth of the dry-treatment trees only been exposed to the soil water conditions measured under the treatment tents we would have expected a 20% reduction in annual growth. The presence of abundant precipitation in adjacent ambient plots, and the likely presence of roots of the target trees extending outside of the treatment zone, is hypothesized to have precluded a growth response by the treatment trees.

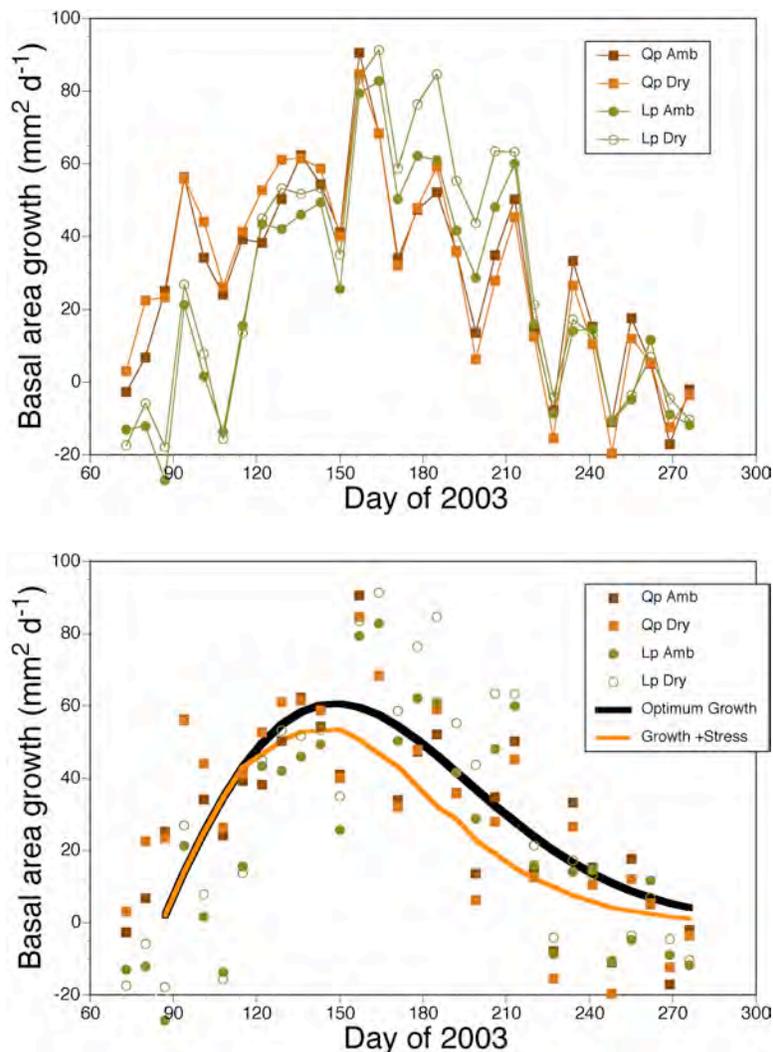


Figure 6. Observed annual tree basal area growth by species and treatment throughout 2003 (upper graph), and the superimposed optimum tree growth pattern (black line-upper graph) and the tree growth pattern expected if all roots for this tree had ‘seen’ water potentials consistent with soils beneath the treatment tent (brown line – lower graph).

## Modeling Water-Stress Propagation

Paul J. Hanson

Answer the question:

What percent of the water-conducting root system would need to extend to regions of low soil water potential to account for observed water use patterns in 2003? The INTRASTAND model was used to estimate the influence of the contribution of perimeter roots to tree/stand water use to help explain the lack of physiological and growth responses to the imposed droughts in 2003. Model calculations suggest that as little as 10 percent of the root system would need to reside in surface soils beyond the treatment-tent perimeter, or in deep soils, to provide water supplies sufficient to sustain physiological function during wet conditions like we had in 2003. In an average year when the surrounding soils dry at a faster rate, perimeter roots would be less efficient at supplying water to the target trees.

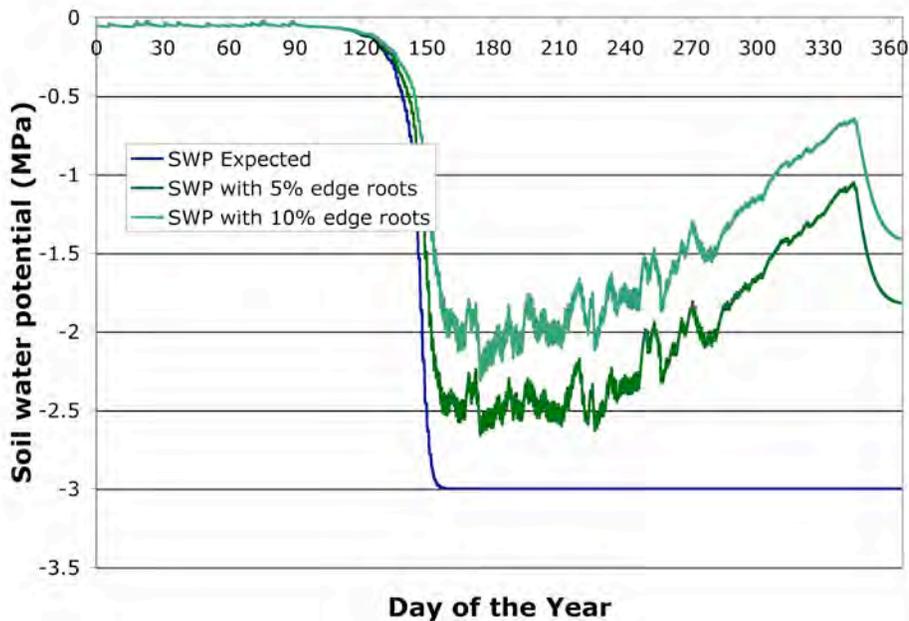


Figure 7. Simulated soil water potentials for a mature oak tree/forest if all roots were exposed to acute drought starting on day 90 (SWP Expected), and the same scenario where 5% or 10% of the roots for that tree/forest were located in soils (lateral or deep)

## **A Manipulation to Resolve Root Distribution Questions**

During the 2004 growing season we will manipulate a limited number of *Q. prinus* trees using sequential, circumferential root removal to determine the importance of lateral root connections as a function of distance from a tree's main stem. During the period from mid-May to mid-June after canopy leaf expansion, but before significant ambient soil water loss, we will use sapflow velocity measurements of 2 to 3 target trees as an indicator of root hydraulic connections while trimming their roots in sequentially smaller circles surrounding the main stem. We will start with a circle having a radius 2x the distance to the canopy drip line and work inwards in 2 m increments at regular intervals. We will need to allow enough time at each stage in the trimming process for near-optimum radiation and atmospheric conditions to be attained so that diurnal patterns of pre- and post-treatment sapflow velocity can be interpreted as a treatment response and not variation driven by cloudy conditions or variable vapor pressure deficit. When combined with data on root density with depth measurements in progress, these observations should allow us to estimate the effective influence of soil water supply areas at known distances from target trees with the water use at the whole-tree level.