

# Sensitivity of canopy transpiration to altered precipitation in an upland oak forest: evidence from a long-term field manipulation study

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## Abstract

Climate-induced changes in regional precipitation could have important implications for the carbon, water, and nutrient cycles of forest ecosystems. However, few studies have examined the response of deciduous forests to increases or decreases in precipitation. Therefore, the throughfall displacement experiment (TDE) was established in 1993 near Oak Ridge, Tennessee to examine the sensitivity of an upland oak (*Quercus* spp.) forest to ambient, wet (+33%), and dry (−33%) precipitation regimes. Sap flux measurements on co-occurring tree species were scaled using species-specific estimates of stand sapwood area to derive daily and seasonal rates of canopy transpiration ( $E_C$ ) from 2000 to 2003. With the exception of 2003, which was an extremely wet year, daily  $E_C$  in the dry plot, and occasionally during extended droughts in the ambient and wet plots, declined as water potential in the upper 0.35 m soil profile approached −3.0 MPa. Seasonal patterns of soil water potential and treatment-specific differences in  $E_C$  were dependent on precipitation frequency and intensity. Supplemental precipitation added to the wet plot increased seasonal  $E_C$  on average by 9% (range −1% to 19%), whereas extended periods of drought on the dry plot in 2000, 2001, and 2002 were sufficient to reduce seasonal  $E_C$  by 26–30% compared with the ambient plot. There was a strong correlation between seasonal  $E_C$  and the water stress integral, a cumulative index of drought severity and duration. A polynomial fitted to these data indicated that reductions in seasonal  $E_C$  on the order of 40% were possible given TDE-imposed reductions in soil water potential. Application of this equation to all years of the TDE (1994–2003) revealed considerable interannual and treatment-specific variation in canopy transpiration. In general, a 33% removal of throughfall on the dry plot during 1995, 1998, and 2002 resulted in a 23–32% reduction in seasonal  $E_C$  compared with the ambient plot. While droughts in deciduous forests are often limited in duration and tend to occur late in the growing season, soil water deficits of the magnitude observed in this study have the potential to impact local and regional forest water budgets.

*Keywords:* evapotranspiration, global change, hydrology, sap flow, water balance, water cycle

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## Introduction

Predicted changes in global and regional climate associated with increasing concentrations of atmospheric CO<sub>2</sub> and other greenhouse gases have raised concerns about the potential impact of precipitation and temperature on the water budgets of terrestrial ecosystems (Vitousek, 1994; Hanson & Weltzin, 2000; Knapp *et al.*,

2001; Weltzin *et al.*, 2003). Increases and decreases in precipitation are expected to alter surface evaporation, transpiration, and soil water content, which, in turn, will have implications for plant function, catchment water yield, and hydrologic budgets across broad spatial scales. Increasing temperatures are also expected to intensify the hydrologic cycle at global and regional scales, resulting in increased winter precipitation at high latitudes, more hot days and fewer cold days, and changes in the frequency and intensity of droughts and floods (Houghton *et al.*, 2001).

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General circulation models indicate that some regions of the globe will experience increased precipitation, while others will face a greater likelihood of drought because of decreased precipitation or increased evaporative demand in a warmer climate (Giorgi & Francisco, 2000; Giorgi *et al.*, 2001; Mearns *et al.*, 2003). How projected changes in the frequency and intensity of droughts will impact terrestrial ecosystems is uncertain. Net primary production has been shown responsive to altered rainfall patterns in temperate prairies (Knapp *et al.*, 2001; Fay *et al.*, 2003), whereas in temperate savannas and Midwestern grasslands more frequent and severe droughts may alter resource acquisition and competitive interactions between coexisting trees and grasses (Weltzin & McPherson, 2000; Danner & Knapp, 2003). Likewise droughts are known to occur in nearly all forest ecosystems (Hanson & Weltzin, 2000) and Neilson *et al.* (1989) has concluded that forests could be severely impacted by climate-induced reductions in soil water availability. The potential impact of altered precipitation regimes on forest ecosystems can be inferred from studies with large trees (Bréda *et al.*, 1993; Cermák *et al.*, 1993; Cienciala *et al.*, 1994; Irvine *et al.*, 1998), seedlings and saplings (Abrams, 1990; Kubiske & Abrams, 1994), natural stands (Oren & Pataki, 2001; Phillips & Oren, 2001), and in computer simulations that model the long-term effects of drought on productivity, water use, species composition, and forest succession (Pastor & Post, 1988; Bugmann & Cramer, 1998; Wullschleger *et al.*, 2003b).

Because alterations in the quantity, intensity, and frequency of precipitation, and resulting changes in soil water availability could have important implications for terrestrial ecosystems, the throughfall displacement experiment (TDE) was established during 1993 in an upland oak (*Quercus* spp.) forest on the Walker Branch Watershed in east Tennessee (Hanson *et al.*, 2003a). The TDE was designed to passively impose ambient, wet, and dry treatments on three experimental plots with the goal of developing an improved understanding of how temperate forest ecosystems and their component organisms would respond to changes in precipitation resulting from a warming global climate (Hanson & Wullschleger, 2003).

This paper describes a 4-year (2000–2003) study conducted on the TDE during which the response of canopy transpiration ( $E_C$ ) to normal, above-normal (+33%), and below-normal (–33%) precipitation was characterized using sap flux techniques. Our primary objective was to evaluate treatment-specific responses in daily and seasonal water use, and to relate those responses to changes in soil water potential across the ambient, wet, and dry TDE treatments. We hypothesized that treatment-specific differences in  $E_C$  would

reflect not only the primary effect of precipitation on soil water potential, but also the secondary effects of soil water availability on leaf area development, leaf area index, canopy senescence, and vertical root distribution among the ambient, wet, and dry plots. In addition, the four-year record was used to assess inter- and intraannual variation in  $E_C$  and soil water potential as a function of precipitation quantity, frequency, and intensity. We are aware of no studies in which drought conditions have been imposed, as we have done here, for a temperate deciduous forest (see Cermák *et al.*, 1993). As a result, there is a lack of experimental data from which to predict impacts of climate-induced changes in precipitation on these ecosystems.

## Material and methods

### Site description

The TDE is located on the Walker Branch Watershed (35°58'N and 84°17'W), a part of the US Department of Energy's (DOE) National Environmental Research Park near Oak Ridge, Tennessee (Hanson *et al.*, 2003a). Large trees range in age from 65 to 120 years old. The basal area of the forest overstory (dbh > 0.10 m) is dominated by chestnut oak (*Q. prinus* L.), white oak (*Q. alba* L.), black gum (*Nyssa sylvatica* Marsh.), red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboretum* L.), northern red oak (*Q. rubra* L.), and yellow-poplar (*Liriodendron tulipifera* L.). Average canopy height is 24 m and density of overstory trees is 380 trees ha<sup>-1</sup> (Hanson *et al.*, 2001). Long-term measurements indicate a mean leaf area index (LAI) of 6.2 m<sup>2</sup> m<sup>-2</sup> (Hanson *et al.*, 2003b). Basal area averaged 23.9 m<sup>2</sup> ha<sup>-1</sup> over the 4 years reported in this paper (Table 1). Saplings contributed 2.6–3.0 m<sup>2</sup> ha<sup>-1</sup> to stand basal area. Red maple and flowering dogwood (*Cornus florida* L.) are the major understory species.

Long-term (50-year) mean annual precipitation at the study site is 1352 mm with a mean annual temperature of 14.2 °C. The acidic forest soils are typic Paleudults derived from Dolomitic bedrock. Plant extractable water (i.e. water held between 0 and –2.5 MPa) for the upper 1.0 m of soil is ca. 183 mm. A large fraction of this water (44%) is held in the upper 0.35 m of the soil profile which is the location of 60% or more of all fine roots in the 0–0.90 m soil profile (Joslin & Wolfe, 1998). Depth to bedrock is ca. 30 m (McMaster, 1967).

### Experimental system

The 1.92 ha TDE site has been described by Hanson *et al.* (1998, 2003a). Briefly, the study is situated on a south-east facing slope that extends 240 m along a ridge top. The experimental area was located specifically at the

**Table 1** Stand characteristics and selected environmental conditions for each year in which canopy transpiration was measured

Variable	Year of observation			
	2000	2001	2002	2003
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	23.1	23.8	24.1	24.6
Ambient	22.3	23.0	22.9	23.3
Wet	22.8	23.4	23.9	24.3
Dry	24.3	24.8	25.4	26.3
Sapwood area (m <sup>2</sup> ha <sup>-1</sup> )	11.8	12.0	12.2	12.4
Ambient	11.4	11.5	11.5	11.9
Wet	11.4	11.9	12.0	12.3
Dry	12.4	12.4	13.0	13.2
LAI (m <sup>2</sup> m <sup>-2</sup> )	7.0	6.7	5.5	5.8
Leaf area duration	233	234	230	248
PET (mm)	772	762	694	749
Precipitation (mm)	766	539	730	968

Data are provided for the entire throughfall displacement experiment area (1.92 ha) and, where appropriate, individually for the ambient, wet, and dry plots. Calculations of potential evapotranspiration and precipitation amount are for the growing season (April 1 to November 13; 227 days).

LAI, leaf area index; PET, potential evapotranspiration.

upper divide of the watershed so that lateral flow of water into the treatment plots from upslope positions did not occur. Manipulations of throughfall reaching the forest floor were made by passively transferring a fraction of the throughfall from one treatment plot to another. On the dry plot, throughfall was intercepted in ca. 1900 troughs (0.3 × 5.0 m) made of greenhouse-grade polyethylene that were suspended at an angle above the forest floor. Approximately 33% of the ground area in the dry plot was covered by troughs. Intercepted throughfall was transferred by gravity across the ambient plot and distributed onto the wet treatment plot. Uniform application of throughfall onto the wet plot was achieved using a series of pipes in which drainage holes spaced 1 m apart had been drilled. Troughs were arranged in 21 rows with ca. 80–90 troughs each. Hanson *et al.* (1998, 2003a) previously reported that troughs in the dry plot had little impact on the microclimate of the forest understory. Reductions in soil water content from the removal of 33% throughfall were designed to be comparable with the growing season having the lowest recorded precipitation during the historically dry 1980s (Cook *et al.*, 1988).

#### Sap flow measurements and scaling to stand transpiration

Instantaneous xylem sap flux ( $J_s$ ) was measured with 30 mm continuously heated thermal dissipation probes

(TDP-30, Dynamax, Houston, TX, USA; Granier, 1987). Each probe contained a copper-constantan thermocouple and the temperature difference between the two probes was influenced by sap velocity in the vicinity of the heated probe. TDP were installed in late March of each year (i.e. 2000–2003) and removed after visible signs of canopy senescence were apparent (usually after November 1). All probes were installed on the north side of trees to avoid direct solar heating and insulated with Styrofoam and shielded with aluminum foil to minimize temperature fluctuations in the sapwood. In cases where sapwood depth was less than the 30 mm probe length, the measured temperature differentials were corrected according to the procedures of Clearwater *et al.* (1999).

Twenty-four trees were selected across the three TDE plots for hourly measurements of sap flux in all years. Similar species were measured in each plot; chestnut oak, white oak, black gum, sourwood, red maple, and yellow-poplar. Trees were classified as canopy dominants and co-dominants, with diameters that ranged from 28.1 to 68.5 cm. Red maple and flowering dogwood growing in the understory of each TDE plot were also measured.

Sap flux densities for individual species were scaled to the stand level as previously described (Wilson *et al.*, 2001; Pataki & Oren, 2003):

$$E_{Ci} = J_{Si}A_{Si}/A_{GCi}, \quad (1)$$

where  $E_{Ci}$  is transpiration rate of species  $i$ ,  $J_{Si}$  is the hourly sap flux of the  $i$ th species,  $A_{Si}/A_G$  is the sapwood to ground area of species  $i$ , and  $C_i$  is a weighted average of sap flux ratios with depth in the sapwood (Zang *et al.*, 1996).  $E_{Ci}$  summed across species is equal to stand transpiration ( $E_C$ ; mm h<sup>-1</sup>); estimates include both over- and understory components. Errors likely to be encountered in the use of TDP and uncertainties associated with upscaling sap flux measured on individual trees to the scale of canopy transpiration in this or closely related studies are discussed elsewhere (Wilson *et al.*, 2001; Wullschleger *et al.*, 2001; Hanson *et al.*, 2004).

Sapwood area for individual species and the stand were calculated from species-specific allometric relationships between stem diameter at breast height (dbh) and sapwood area for trees and saplings on the TDE (Table 2). Individuals used to generate these equations were selected from across the Walker Branch Watershed and covered a dbh range representative of major tree species on the TDE. To estimate sapwood area for individual trees of a given species (i.e.  $A_{Si}$ ), stem diameter was first measured using a diameter tape. Bark and sapwood thickness were then determined at two to five locations around the stem circumference by drilling 1.3-cm holes through the bark and to

**Table 2** Allometric equations describing the relationship between cross-sectional sapwood area (m<sup>2</sup>) and stem diameter at breast height (m) for major tree species present on the TDE plots

Species	Regression coefficients			$A_{Si}/A_G$ (m <sup>2</sup> ha <sup>-1</sup> )	$C_i$
	$B_0$	$B_1$	$R^2$		
<i>Acer rubrum</i>	0.5174	1.9171	0.97	5.3	0.74
<i>Carya</i> spp.	0.1783	1.3754	0.89	0.2	0.71
<i>Liriodendron tulipifera</i>	0.4036	2.0561	0.93	0.8	0.66
<i>Nyssa sylvatica</i>	0.4050	1.7958	0.95	2.2	0.74
<i>Oxydendrum arboreum</i>	0.5422	2.0710	0.89	0.5	0.74
<i>Quercus alba</i>	0.1021	1.5483	0.89	0.9	na
<i>Quercus prinus</i>	0.1146	1.7154	0.92	1.2	na
<i>Quercus rubra</i>	0.0875	1.5075	0.77	0.4	na
Misc. species				0.6	na

Sapwood area per unit ground area ( $A_{Si}/A_G$ ) and the species-weighted sap flux ratios with depth in the sapwood ( $C_i$ ) for each of the species is also provided.

TDE, throughfall displacement experiment.

the bark-sapwood interface. An electronic caliper (Brown & Sharpe Mfg. Co., North Kingstown, RI, USA) was used to measure bark thickness, and sapwood thickness was measured with a ruler on a core extracted with a 5 mm increment borer. Sapwood areas (m<sup>2</sup>) were fitted to the equation (Vertessy *et al.*, 1995):

$$A_{Si} = B_0 dbh^{B_1}, \quad (2)$$

where  $dbh$  is the stem diameter (m), and  $B_0$  and  $B_1$  are species-specific coefficients as determined with regression techniques.

Stem diameters for all trees  $\geq 0.10$  m on the TDE were recorded each year. In addition, saplings with a  $dbh$  less than 0.10 m were measured in  $8 \times 8$  m subplots along three transects from lower- to upper-slope positions. These inventory data, together with the species-specific allometric equations, were used to estimate sapwood area per unit ground area (i.e.  $A_{Si}/A_G$ ) for all species at the study site.

The compensation heat pulse method (SF-300, Green-span Technology Pty. Ltd, Warwick, Queensland, Australia) was used to estimate the weighted average of sap flux ratios (i.e.  $C_i$ ) for multiple species on the TDE (Zang *et al.*, 1996). This calculation was necessary because sapwood thickness in red maple, *Carya* spp., yellow-poplar, black gum, and sourwood often exceeded the 30 mm length of the TDP. Calculation of  $C_i$  was not required for any of the *Quercus* species. Heat pulse velocity profiles were determined for probes implanted to four predetermined depths in the sapwood (Hatton

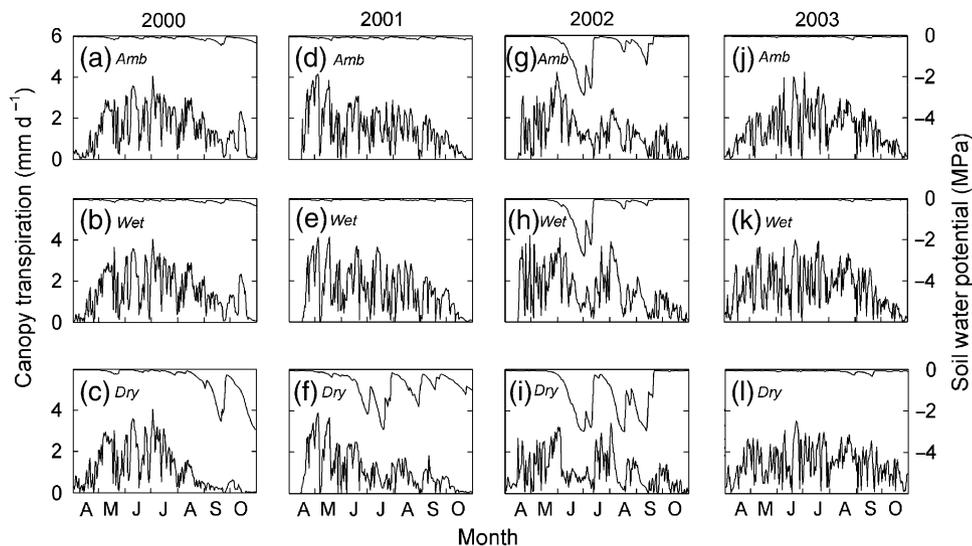
*et al.*, 1990; Wullschleger & King, 2000). A data logger was programmed to provide a heat pulse for 1.8 s and measurements at each sapwood depth were recorded every 20 min. All estimates of sap velocity were corrected for probe implantation effects (Swanson & Whitfield, 1981).

#### Soil water content, water potential, and environmental monitoring

Ambient, wet, and dry plots of the TDE were divided into 100 subplots ( $8 \times 8$  m), the intersections of which served as locations for measuring soil water content. Soil water content (% v/v) was measured with a time-domain reflectometer (TDR; Soil Moisture Equipment Corp., Santa Barbara, CA, USA) following procedures outlined by Topp & Davis (1985) as documented for soils with high coarse fraction content (Drungil *et al.*, 1987). At each grid location two pairs of vertical waveguides were installed (0–0.35 and 0–0.70 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 monthly during the dormant season. Soil water content measurements were adjusted for the coarse fraction of these soils (mean coarse fraction of 14%) and converted to soil water potentials using laboratory-derived soil moisture retention curves for the A, A/E, and E/B horizons (Hanson *et al.*, 1998, 2003a).

To facilitate comparisons of soil water deficits between years and among TDE treatments, two quantitative indices are reported; (1) the minimum annual soil water potential (MPa) and (2) a water stress integral (MPa days). The first is a direct measure of drought intensity, whereas the second provides a measure of cumulative drought intensity (Myers, 1988). This later index for the rooted soil profile (i.e. 0–0.35 m) has been shown to be a good index of soil water deficits (Hanson *et al.*, 2003a). Water stress integrals for all years and treatments were estimated using a combination of measured soil water potential data and modeled interpolations for periods of the season without data. Modeled interpolations were executed with a revised version of the TEHM/PROSPER model (Huff *et al.*, 1977; Luxmoore, 1983) coded with STELLA modeling software (isee systems, Lebanon, NH, USA).

Air temperature and relative humidity in the forest understory, and soil temperatures were logged hourly on the ambient, wet, and dry plots. Air temperature, relative humidity, precipitation, wind speed, solar irradiance, and photosynthetic photon flux density were also measured continuously at the top of a 26 m tower located on the ambient plot and logged as hourly



**Fig. 1** Seasonal patterns of daily canopy transpiration and soil water potential in the 0–0.35 m soil depth profile for ambient, wet, and dry plots on the throughfall displacement experiment. Data are shown for each of 4 years (2000–2003) during which measurements were taken.

means. Radiation, vapor pressure deficit, air temperature, and wind speed were used to calculate rates of potential evapotranspiration (PET) for the site using the Penman–Monteith equation (Stewart, 1988; Wullschlegler *et al.*, 2000). LAI was estimated from a series of litter baskets distributed across the experimental area. Litter collections were made periodically throughout the year, typically mid-May, late August, and biweekly from October 1 through December 1 of each year.

## Results

Canopy transpiration and soil water potential (i.e. 0–0.35 m) varied across years and among treatment plots of the TDE (Fig. 1). With the exception of the 2002 growing season, the quantity and frequency of precipitation received in the ambient plot was sufficient to maintain soil water potential above  $-0.60$  MPa (Table 3). Under these conditions, early to mid-season rates of daily  $E_C$  reached  $4.0 \text{ mm day}^{-1}$  and higher. Canopy transpiration and soil water potential in the wet plot for 2000, 2001, and 2003 were similar in magnitude and pattern to those observed in the ambient plot. However, in 2002, soil water potential in all TDE plots began to decline in mid- to late-May, reaching  $-3.0$  MPa during late-June (Fig. 1). In the dry plot, this early-season drought was followed by two additional periods of limited soil water availability, one in mid-August and another in mid-September. Canopy transpiration in each of the three treatment plots declined noticeably as soil water potential approached  $-3.0$  MPa during the first drought, and again during the later two droughts

**Table 3** Minimum soil water potential (MPa) for each season and TDE treatment

Variable/treatment plot	Year of observation			
	2000	2001	2002	2003
Ambient	−0.55	−0.28	−2.90	−0.20
Wet	−0.53	−0.18	−2.82	−0.16
Dry	−3.00	−2.91	−3.00	−0.33

in the dry plot. Although less extensive than those observed in 2002, similar droughts occurred in the dry plot during 2000 and 2001 (Fig. 1). Canopy transpiration declined during these droughts. Precipitation in 2003 was well above the long-term average and, as a result, soil water potential and daily  $E_C$  remained high in all treatments of the TDE (Table 3).

Variation in daily  $E_C$  was considerable for all TDE treatments, the cause of which was largely explained by variation in mean daily vapor pressure deficit and radiation (data not shown; see Wullschlegler *et al.*, 2000, 2001). There was a strong linear relationship between daily  $E_C$  and PET for many of the treatment plots, particularly the ambient and wet plots in 2000 and 2001, and for all three plots in 2003 (Fig. 2). Slopes of linear regressions fitted to these data indicated that  $E_C$  was on average 58% (range 0.50–0.64) of daily PET. However, linear relationships were less distinct during periods of limited soil water availability, especially for the dry plot in 2000 (Fig. 2c) and for all plots in 2002 (Fig. 2g, h, and i). This was largely because of the effect

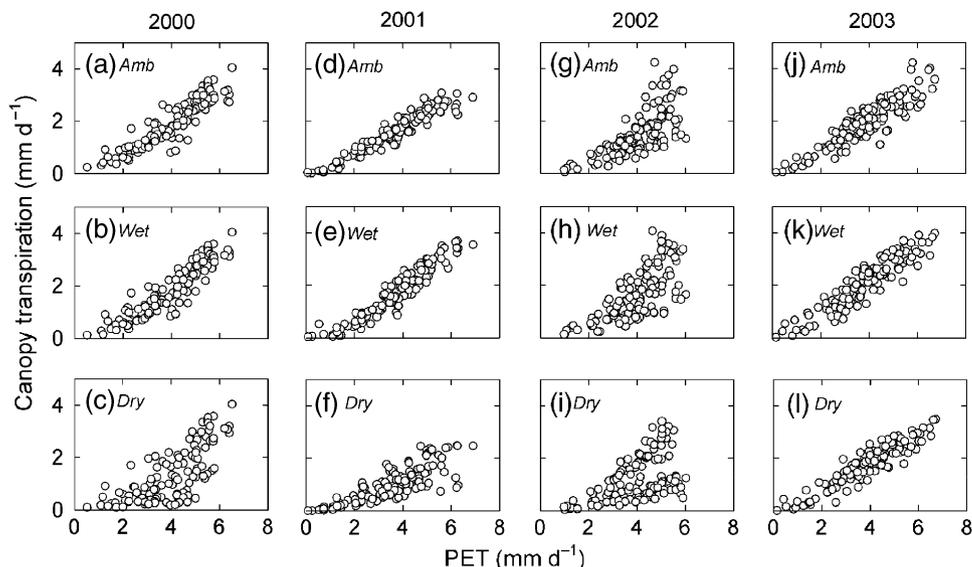


Fig. 2 Daily canopy transpiration plotted against potential evapotranspiration (PET) for each of the three throughfall displacement experiment plots in 2000–2003. Estimates of PET were calculated using the Penman–Monteith equation.

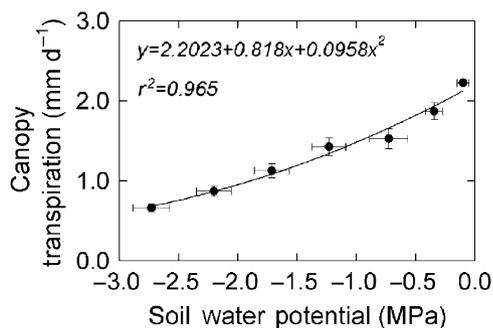


Fig. 3 Influence of soil water potential on daily rates of canopy transpiration in ambient, wet, and dry plots of the throughfall displacement experiment. Data for each year of the study (2000–2003) were combined and binned according to defined ranges of soil water potential. Standard error bars are shown for both soil water potential and canopy transpiration.

of soil water potential on daily  $E_C$  (Fig. 3). Across years and treatments of the TDE, average daily  $E_C$  declined from 2.2 to 0.6 mm day<sup>-1</sup> as soil water potential declined from -0.25 to -3.0 MPa.

Seasonal patterns of soil water potential and treatment-specific differences imposed by the TDE were dependent on precipitation quantity, frequency, and intensity. In 2001, a year in which 539 mm of precipitation was received during the growing season (Table 1), there was good separation among treatments, especially for soil water potential between the ambient and wet plots and the dry treatment plot (Fig. 4a). Soil water potential began to decline in the dry plot in early-May and continued to decline into mid-July. During this

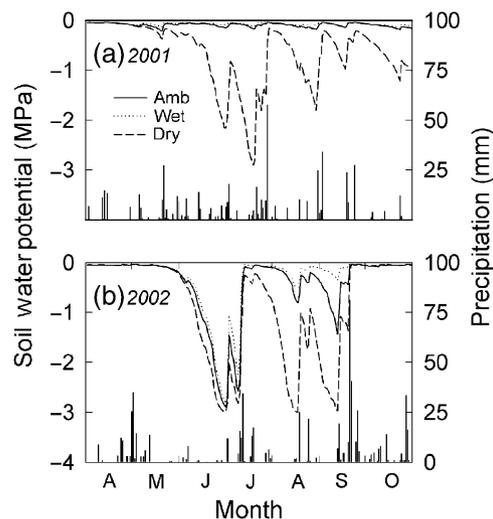
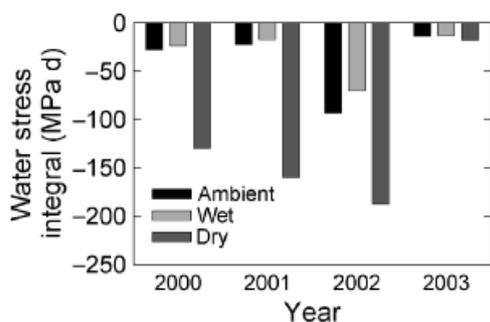


Fig. 4 Seasonal and throughfall displacement experiment-imposed patterns of soil water potential for the ambient, wet, and dry plots in 2001 and 2002. Ambient precipitation received on the ambient plot is shown for both years.

period, ambient precipitation totaled 196 mm, occurring in 30 events ranging from 1.1 to 27.4 mm (mean = 6.5 mm) per event. By contrast, in 2002 there was an extended period without precipitation that began again in early-May and continued until mid-June (Fig. 4b). During this period, ambient precipitation totaled only 57 mm in 11 events ranging from 1.0 to 13.6 mm (mean 4.9 mm) per event. As a result, soil water potential declined in all treatments of the TDE. Reductions in soil water potential on the dry plot, however, preceded



**Fig. 5** Annual water stress integral for each of the three throughfall displacement experiment treatments in 2000–2003. The water stress integral reflects the cumulative soil water potential as measured throughout the season for the ambient, wet, and dry plots.

those on the ambient and wet plots by several days. A late-season period of reduced soil water availability also occurred in 2002, during which soil water potential on the dry plot was more negative than that measured on the ambient and wet plots (Fig. 4b).

Although seasonal patterns of drought across years and TDE treatments were dynamic and complex, depending on timing and intensity of ambient precipitation, the water stress integral was a useful metric for capturing these patterns over time (Fig. 5). With the exception of 2003, water stress integrals for the dry plot were more negative than those calculated for either the ambient and wet plots. The water stress integral for the dry plot was  $-130$  MPa days in 2000,  $-160$  MPa days in 2001, and  $-189$  MPa days in 2002. In 2002, the water stress integrals for all plots were more negative than in other years. Compared to other years, growing season precipitation in 2003 (i.e. 968 mm) was the wettest year recorded in this study and one of the wettest on record for the Walker Branch Watershed. Thus, the water stress integral differed little among treatments of the TDE.

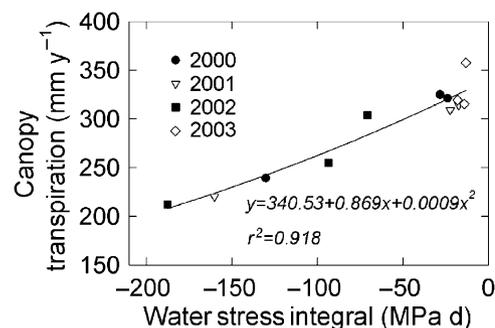
Interannual variation in seasonal  $E_C$  for the ambient plots ranged from 255 mm in the driest year of the study (2002) to 325 mm in 2000 (Table 4). As expected, differences among years were less marked for seasonal  $E_C$  of the wet plots (i.e. 304–358 mm). Seasonal  $E_C$  generally increased as a result of adding supplemental precipitation, with  $E_C$  in the wet plot increasing by up to 19% (in 2002) compared with the ambient plot. With the exception of 2003, the wettest year reported in this study, seasonal  $E_C$  of the dry plots (i.e. 212–239 mm) were considerably lower than rates recorded for the ambient and wet plots. Treatment-specific differences between dry and ambient plots were  $-11\%$  in 2003 and  $-30\%$  in 2001 (Table 4).

Across all years and treatments of the TDE there was a strong correlation between seasonal  $E_C$  and the water

**Table 4** Canopy transpiration for the ambient, wet, and dry plots of the throughfall displacement experiment during the 2000–2003 growing seasons

Year	Canopy transpiration (mm yr <sup>-1</sup> )			Change (%)	
	Ambient	Wet	Dry	Ambient to dry	Ambient to wet
2000	325	321	239	-26	-1
2001	309	314	220	-30	+3
2002	255	304	212	-26	+19
2003	315	358	319	-11	+14

Percent change in seasonal transpiration between the ambient and dry plot, and between the ambient and wet plot are calculated.



**Fig. 6** Relationship between seasonal canopy transpiration and the water stress integral for each of the throughfall displacement experiment plots in 2000–2003.

stress integral (Fig. 6). A polynomial fitted to these data indicated that reductions in seasonal  $E_C$  on the order of 40% were possible given TDE-imposed reductions in soil water potential. Application of this equation to water stress integrals reported here and in earlier years of the TDE experiment (Hanson *et al.*, 2003a) revealed considerable interannual variation and treatment-specific differences in seasonal  $E_C$  (Fig. 7). In general, between 1994 and 2003, seasonal  $E_C$  for the ambient plot varied from 219 mm in 1998 to 325 mm in 2000. In four of the wettest years (1994, 1996, 1997, and 2003) differences in  $E_C$  between the wet and the ambient treatments were small (Fig. 7). However, a 33% removal of throughfall on the dry plot during 1995, 1998, and 2002 resulted in a 23–32% reduction in seasonal  $E_C$  compared with the ambient plot. Interannual variation in seasonal  $E_C$  and the water stress integral were typically larger than TDE-imposed differences during any 1 year.

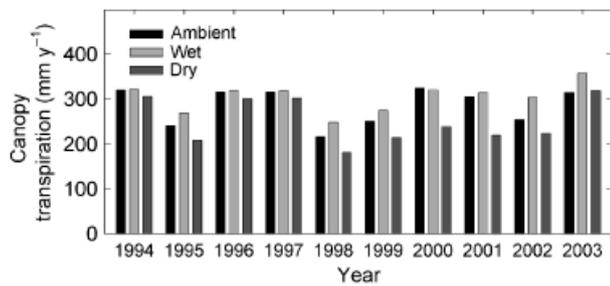


Fig. 7 Canopy transpiration estimated from the water stress integral for the ambient, wet, and dry plots in each year of the throughfall displacement experiment (1994–2003).

## Discussion

The long-term goal of the TDE is to develop an improved understanding of how deciduous forest ecosystems and their component organisms respond to changes in precipitation inputs (Hanson & Wullschleger, 2003). In the 11 years since the treatments were first imposed we have found that the temporal pattern of precipitation plays a complex role in determining the magnitude and direction by which tree growth, nutrient cycling, and  $E_C$  respond to soil water availability across the ambient, wet, and dry treatments. Similar conclusions have been reached in other manipulative experiments, including those that have used rain-exclusion shelters to assess the response of  $C_4$ -dominated grasslands to altered timing and quantity of precipitation inputs (Knapp *et al.*, 2001; Fay *et al.*, 2003) and in studies that have examined the response of temperate savannas to altered soil water availability using rainfall capture and redistribution systems (Weltzin & McPherson, 2000). Only in a few instances, however, have manipulative studies been conducted in other forest ecosystems (see Hanson, 2000), with the majority of these investigations addressing the response of either tropical (Nepstad *et al.*, 2002) or coniferous (Cienciala *et al.*, 1994; Irvine *et al.*, 1998; Cinnirella *et al.*, 2002) forests to altered precipitation regimes.

In the current investigation, adding precipitation to the wet plot resulted in only a modest enhancement of canopy transpiration. In contrast, the removal of precipitation on the dry plot contributed to more negative soil water potentials which, in turn, led to 70% reductions in daily  $E_C$  and 11–30% reductions in seasonal  $E_C$  compared with rates calculated for the ambient plot (Table 4). Interannual variation in soil water potential also contributed to year-to-year fluctuations in seasonal  $E_C$ , with coefficients of variation on the order of 10%, 7%, and 20% for the ambient, wet, and dry plots, respectively. Treatment-specific reductions in daily and seasonal  $E_C$  were similar in magnitude to those reported elsewhere. Daily  $E_C$  in 41-year-old Scots pine

(*Pinus sylvestris* L.) trees declined to 30% of the control value during a mid-summer imposition of drought (Irvine *et al.*, 1998), whereas in 35-year-old *Pinus laricio* Poiret trees exposed to a restricted supply of soil water fell to 50% or more that of unrestricted trees (Cinnirella *et al.*, 2002). Neither study provided a season-long integration of these effects. However, Cienciala *et al.* (1994) reported that seasonal  $E_C$  in Norway spruce (*Picea abies* L.) exposed to three water regimes was 380, 325, and 209 mm for the irrigated, control, and drought treatment, respectively. Relative differences among treatments in this study were similar to those measured in the wet, ambient, and dry plots of the TDE. Unfortunately, the study of Cienciala *et al.* (1994) was conducted only over a single growing seasons, thus, precluding the possibility of detecting long-term effects of altered soil water availability on seasonal  $E_C$  as characterized for the TDE.

Thermal dissipation probes and scaling based on measured sapwood area for several cooccurring tree species were used in this study to assess the magnitude by which  $E_C$  responds to interannual and TDE-imposed changes in soil water potential. Although adequate replication is always an issue in scaling sap flux measured on individual trees to that of the stand (Granier *et al.*, 1996; Cermák *et al.*, 2004), data collected at our field site (Wilson *et al.*, 2001) and elsewhere (Hogg *et al.*, 1997; Saugier *et al.*, 1997; Granier *et al.*, 2000) show that daily fluctuations in  $E_C$  calculated using sap flux techniques are qualitatively similar to rates of evapotranspiration derived from eddy covariance measurements. Several studies indicate, however, that the sap flux technique can, in some applications, systematically underestimate daily  $E_C$  compared with rates calculated from eddy covariance, soil water budgets, and catchment water balance (Wilson *et al.*, 2001; Bovard *et al.*, 2005). The source of this uncertainty has not been identified. Possibilities include failure to adequately sample tree-to-tree variation in sap flux (Cermák *et al.*, 2004), errors associated with radial gradients in sap flux and the perceived inability of TDP to adequately integrate observed rates of sap flux along their length (Clearwater *et al.*, 1999), uncertainties in estimating sapwood area for individual trees or the stand, and difficulties associated with incorporating a variable eddy covariance footprint into the scaling process (Wilson *et al.*, 2001). We have addressed some, but not all, of these concerns in the present investigation. Thus, the absolute magnitude of daily and seasonal  $E_C$  as calculated here should be viewed accordingly. Tree-to-tree variation in sap flux for species on the TDE is typically 10% or less (unpublished data) and we are confident that species-specific allometric estimates of sapwood area are not a significant source of uncertainty. It will

be important to thoroughly characterize uncertainties associated the measurement of sap flux in diffuse- and especially ring-porous species and to quantify errors likely to be encountered in the scaling process for mixed-hardwood forests (Clearwater *et al.*, 1999). Notwithstanding these areas of uncertainty, rates of seasonal  $E_C$  estimated here for the ambient TDE plot (i.e. 255–325 mm) are similar to growing season rates reported elsewhere for oak-hickory forests (278 mm; Oren & Pataki, 2001), bottomland oak-hickory forests (264 mm; Pataki & Oren, 2003), and mixed pine-hardwood forests (267–326 mm; Phillips & Oren, 2001) in the southeastern United States.

Reductions in daily and seasonal  $E_C$  as measured on the ambient, wet, and dry plots of the TDE reflect the cumulative response of large trees and smaller understory seedlings and saplings to soil water availability. Canopy transpiration estimated for saplings measured in this study ranged from 38 to 53 mm season<sup>-1</sup> in the ambient plot, 54 to 73 mm season<sup>-1</sup> in the wet plot, and 19 to 47 mm season<sup>-1</sup> in the dry plot. Earlier results published from the TDE have shown that red maple (Wullschleger *et al.*, 1998) and flowering dogwood (Wullschleger & Hanson, 2003) saplings growing in the forest understory display a marked sensitivity to seasonal and TDE-imposed periods of limited soil water availability. Sap flow decreased, for example, by 40–45% for red maple saplings on the dry plot in 1995 with leaf water potentials that ranged from -1.68 to -2.08 MPa (Wullschleger *et al.*, 1998).

Previous studies with both red maple and flowering dogwood have shown that restricted root development with soil depth may predispose seedlings and saplings of these species to negative impacts of drought (Bahari *et al.*, 1985), including reductions in whole-plant water use and stem diameter increment and, in severe cases, increased mortality (Hanson *et al.*, 2001). Joslin & Wolfe (1999) reported that 74% of total fine-root biomass on the TDE was distributed in the upper 0.30 m soil layer, and root distribution with depth has not changed across the wet, ambient, and dry treatments (Joslin *et al.*, 2000). More recently, Joslin and Wolfe (2003) indicate that some migration of fine roots to depth might be taking place on the dry plot, but note that differences in the vertical distribution of roots in the dry compared with the ambient plot are still not significant. Thus, soil water depletion in the upper soil layer is especially important in determining the sensitivity of seedlings, saplings, and mature trees to drought on this site, perhaps leading to increased seedling and sapling mortality and long-term changes in species composition (Bugmann *et al.*, 2001; Wullschleger *et al.*, 2003b).

Despite the known sensitivity of understory seedlings and saplings to drought, the majority of seasonal  $E_C$

(i.e. 76–94%) for the plots measured in this investigation was accounted for by large, canopy-dominant and codominant trees. Moreover, these trees were composed of multiple species, each with a potentially unique response to environmental variables and soil water potential. Few studies, however, have attempted to integrate the response of multiple species within a forest to altered precipitation regimes, despite the fact that interesting ecological insights might emerge from quantifying the response of co-occurring species to drought (Pataki *et al.*, 2000; Wullschleger *et al.*, 2001). Although we were able to only measure a limited number of individual trees in this investigation, an analysis of the 2000 data set indicated that the relative ranking of drought tolerance for trees of the forest overstory was *Carya* spp. > *Q. prinus* > *N. sylvatica* > *Q. alba* > *Q. rubra* > *A. rubrum* (Wullschleger *et al.*, 2003a). Species-specific sensitivities to soil water availability have been reported in several studies with deciduous tree species and sap flux techniques appear well-suited for assessing relationships between  $E_C$  and drought, as quantified in various ways. Oren & Pataki (2001) reported sap-flux scaled transpiration for two co-occurring species in upland eastern hardwood forests and concluded that transpiration in *A. rubrum* showed a greater response to soil moisture depletion than did that of *Q. alba*. In apparent support of these observations, Bovard *et al.* (2005) recently reported that among the species studied in a northern hardwood forest, *A. rubrum* showed the greatest degree of sensitivity to low soil water availability. These authors concluded that this sensitivity was largely because of the fact that red maple roots are located in the upper 0.25 m of the soil horizon, making seedlings, saplings, and even mature individuals of this species susceptible to the negative impacts of altered precipitation regimes. Given the abundance of red maple across the TDE, and the contribution of this species to stand basal area and, more importantly total sapwood area, we suggest that the drought sensitivity of this species contributed disproportionately to the stand-level effects we have observed in daily and seasonal  $E_C$  on the TDE.

The relationships between daily and seasonal  $E_C$  and soil water potential that we established in this study were for soil water potentials calculated in the upper 0–0.35 m of soil. Measurements of soil water potential were also made for the 0.35–0.70 m depth, but observations over the course of this study have indicated that soil water in this layer is readily available, with soil water potentials measured between 1993 and 2000 seldom falling below -0.5 MPa (Hanson *et al.*, 2003a). Soil water potentials measured in the 0.35–0.70 m depth profile between 2000 and 2003 never fell below -0.37 MPa and this occurred on the dry plot in 2002

(data not shown). The availability of water below the dominant rooting zone may be important in minimizing treatment related differences among the ambient, wet, and dry plots. Had this layer of soil dried to a greater extent, we expect that the relationships between daily  $E_C$  and soil water potential (Fig. 3) and season  $E_C$  and the water stress integral (Fig. 6) would be much different. Soil water depletion in the 0.35–0.70 m layer was observed on the TDE during 1998 (approaching  $-0.75$  MPa) and Wilson and Hanson (2003) showed that drying of soil at these depths had a marked effect on canopy processes (i.e. photosynthesis) across the ambient, wet, and dry plots.

Root systems may also be tapping supplies of water deep in the soil profile during dry periods (Joslin & Wolfe, 2003). Although a high bulk density ( $1.75 \text{ g cm}^{-3}$ ) in the zone of maximum clay accumulation and limited available nutrients appear to restrict most root growth to the upper 0.90 m of soil, some roots occupy this layer. The density of fine roots at this depth is low, but the presence of live fine-root mass at depth indicates that such penetration does occur and, therefore, could facilitate water uptake, especially during dry periods. Hanson *et al.* (2003c) note that the number and conductivity of deep roots of eastern deciduous forests may provide enough water to sustain low levels of leaf function and water use during severe droughts. It will be important to resolve uncertainties regarding the role of deep roots in growth and water use during periods of drought in temperate deciduous forests.

Sustained alterations in precipitation input on the TDE were originally hypothesized to impact carbon assimilation, growth, and leaf area development, with feedbacks on water use at the scale of leaves, trees, and the entire stand. Changes in stored carbohydrates and/or changes in current photosynthate available at the time of leaf production were predicted to increase canopy production with increasing water inputs and to decrease production with water removal. Over the 11 years of the TDE the observed patterns of leaf area development have not agreed with this hypothesis (Hanson *et al.*, 2003b). Temporal patterns of seasonal leaf area development, duration, and senescence have not shown reductions in response to precipitation removal. An analysis of early-season litter fall for 1994–2000 showed that no significant treatments effects were observed for 1995, 1996, 1997, or 2000. However, leaf-litter accumulation by mid-September on the wet plot was reduced relative to ambient and dry plot litter fall in both 1994 and 1999. Accelerated leaf senescence of the dry plot trees was only observed in 1998, when litter fall in the dry plot was 50% greater than in either the wet or ambient plots (Hanson *et al.*, 2003b). Contrary to our original hypothesis, annual litter production on the

TDE dry plot was higher than the ambient and wet plots starting in 1998. We suspect that this unexpected pattern is driven by feedbacks between precipitation input and elemental cycling. In a study of canopy-scale water loss in a bottomland deciduous forest, Pataki & Oren (2003) observed that for many of the species studied, which included *C. tomentosa*, *Q. alba*, *Q. rubra*, *Fraxinus americana*, and *Liquidambar styraciflua*, the primary effect of drought was not observed as reductions of sap flux, but rather in the initiation of early leaf senescence and abscission later in the growing season. Between 2000 and 2003, the period during which we have complete records of daily and seasonal  $E_C$  for the three TDE treatments, annual patterns of leaf area development, duration, and senescence have continued to show few responses to altered precipitation (Hanson, unpublished data).

Finally, seasonal patterns of ambient precipitation and soil water potential suggest that droughts representative of eastern Tennessee occur almost exclusively in the late summer and fall, with few periods of water-deficit occurring prior to mid-June. Hanson and Weltzin (2000) point out that there is commonly a disconnect between active growth periods and mid- to late-season droughts in eastern deciduous forests. Saplings and trees on the TDE generally show initiation of stem growth following canopy leaf development, maximum rates of stem growth in late May and early June, and the completion of stem growth by early August (Hanson *et al.*, 2001). Thus, basal area increment for trees on the TDE is usually completed before the onset of natural or TDE-imposed droughts. A consequence of this is that forest productivity and drought are uncoupled in terms of their seasonal dynamics. Severe spring droughts, however, if they were to occur, might represent a significant water stress event with the potential to directly impact current-year growth and forest water use. Large-scale field experiments that manipulate soil water content in early to mid-spring are underway (Hanson *et al.* unpublished data; <http://tarp.ornl.gov>) and such investigations should yield information complementary to the data reported here.

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