

# Interannual Invariability of Forest Evapotranspiration and Its Consequence to Water Flow Downstream

A. Christopher Oishi,<sup>1\*</sup> Ram Oren,<sup>1,2</sup> Kimberly A. Novick,<sup>1</sup> Sari Palmroth,<sup>1</sup> and Gabriel G. Katul<sup>1,2</sup>

<sup>1</sup>Nicholas School of the Environment and Earth Sciences, Duke University, Box 90328, Durham, North Carolina 27708, USA;

<sup>2</sup>Department of Civil and Environmental Engineering, Pratt School of Engineering, Duke University, Durham, North Carolina 27708, USA

## ABSTRACT

Although drought in temperate deciduous forests decreases transpiration rates of many species, stand-level transpiration and total evapotranspiration is often reported to exhibit only minor interannual variability with precipitation. This apparent contradiction was investigated using four years of transpiration estimates from sap flux, interception–evaporation estimates from precipitation and throughfall gauges, modeled soil evaporation and drainage estimates, and eddy covariance data in a mature oak-hickory forest in North Carolina, USA. The study period included one severe drought year and one year of well above-average precipitation. Normalized for atmospheric conditions, transpiration rates of some species were lower in drought than in wet periods whereas others did not respond to drought. However, atmospheric conditions during drought periods are unlike conditions during typical growing season periods. The rainy days that are required to maintain drought-free periods are characterized by low atmospheric vapor pressure deficit, leading to very low transpiration. In contrast, days

with low air vapor pressure deficit were practically absent during drought and moderate levels of transpiration were maintained throughout despite the drying soil. Thus, integrated over the growing season, canopy transpiration was not reduced by drought. In addition, high vapor pressure deficit during drought periods sustained appreciable soil evaporation rates. As a result, despite the large interannual variation in precipitation (ranging from 934 to 1346 mm), annual evapotranspiration varied little (610–668 mm), increasing only slightly with precipitation, due to increased canopy rainfall interception. Because forest evapotranspiration shows only modest changes with annual precipitation, lower precipitation translates to decreased replenishment of groundwater and outflow, and thus the supply of water to downstream ecosystems and water bodies.

**Key words:** broadleaf; deciduous; drainage; drought; precipitation; transpiration; water yield.

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\*Corresponding author; e-mail: acoishi@duke.edu

## INTRODUCTION

Evapotranspiration is a large component of the hydrological budget of forests, exerting great influence on the flow of water to downstream users, including aquatic ecosystems and human populations. Forest transpiration in temperate regions has shown remarkable consistency as stands develop, regardless of the accompanying increases in canopy

leaf area and changes in species composition (Roberts 1983; Phillips and Oren 2001). This “conservative” behavior (Roberts 1983) is achieved in some forests through relatively low transpiration rates (compared to precipitation or potential evapotranspiration) and compensatory behavior among canopy strata or species. However, some forests decrease canopy transpiration during periods of limited water availability through large reduction of average canopy stomatal conductance (Oren and others 1998; Bréda and others 2006; Köecher and others 2009). In these forests, large interannual variation of precipitation is reflected in variation of annual transpiration (for example, a pine plantation in Stoy and others 2006). More difficult to reconcile are observations in stands where transpiration of a number of dominant species decreases with water availability, yet stand-level annual transpiration remains relatively unaffected (Wullschleger and Hanson 2003; Bovard and others 2005; Sinclair and others 2005; Wullschleger and Hanson 2006).

Total evapotranspiration is also affected by precipitation ( $P$ ), which indirectly affects transpiration by influencing soil moisture ( $\theta$ ) and directly affects evaporation by influencing surface wetness (Wilson and others 2000). Like transpiration, the amount of interannual variation of evapotranspiration differs among forests. For example, the variation of annual evapotranspiration data from the pine plantation mentioned above was higher and more sensitive to changes in  $P$  than that of an adjacent hardwood stand (Stoy and others 2006).

The objective of this study was to resolve the apparent contradictions between the observed drought response of the individual components of evapotranspiration (reduced transpiration of drought-sensitive species and evaporation) and the lack of response of total canopy transpiration ( $E_C$ ) and evapotranspiration. To accomplish this, we focused on a mature, southeastern bottomland hardwood stand, which contains drought-sensitive species (Pataki and Oren 2003) but exhibits little variation in annual evapotranspiration (Stoy and others 2006). The soil is frequently saturated in the dormant season, but the relatively thin, well-drained rooting zone regularly dries to the hygroscopic point in the growing season (Oosting 1942). This type of mesic site, which makes up 16% of forested land in the southern U.S. (Wear and Greis 2002), represents an ideal setting to examine drought response of components of the hydrologic budget because the trees, species, and stands are not specifically adapted to xeric or hydric extremes (for example, Addington and others 2006). Using

data collected over four years (2002–2005), including years with mild and severe droughts as well as an uncharacteristically wet year, we produced component-based evapotranspiration ( $ET_{\text{comp}}$ ), combining  $E_C$  from scaled sap flux measurements, measured canopy-intercepted precipitation ( $I_C$ ), and modeled soil evaporation ( $E_S$ ). Previous work described in Oishi and others (2008) demonstrated an excellent agreement between eddy covariance estimates of latent heat flux of evapotranspiration ( $LE$ ) and  $ET_{\text{comp}}$ . (For clarity of terminology,  $ET_{\text{comp}}$  and  $LE$  shall refer to estimates of evapotranspiration based on component sums and eddy covariance, respectively.)

Using  $ET_{\text{comp}}$ , we first investigated whether drought led to decreases in species-level transpiration at reference atmospheric conditions. Provided that drought affects transpiration of enough trees within a forest, and given that drought persists through a sizable portion of the growing season, we would expect to observe reductions in annual transpiration. However, drought periods are characterized by sunny (that is, high radiation loads) and dry (that is, high atmospheric demand for water) weather, leading to favorable conditions for both evaporation and transpiration (Juang and others 2007). Indeed, atmospheric demand for water vapor is much greater during drought periods than in the frequently cloudy and rainy weather characteristic of wet growing seasons. We therefore hypothesized that conservative annual transpiration can be achieved if drought-induced reductions in transpiration are similar to the reductions caused by weakened atmospheric demand during non-drought years. (See Supplemental Appendix for a theoretical basis for this hypothesis.) Furthermore, to achieve conservative evapotranspiration at the site, we hypothesized that during dry years lower  $I_C$  is compensated for by higher  $E_S$ .

The mechanisms leading to the observed invariance in evapotranspiration in some forests not only regulate ecosystem productivity, dynamics, and resilience, but also have consequences for ecosystem services that rely on water draining from forests such as maintaining stream flow for downstream aquatic ecosystems and recharging groundwater and reservoirs for human consumption. Therefore, we completed our analysis by producing modeled estimates of the remaining components of the hydrologic budget, drainage ( $Q$ ) and surface runoff ( $F_O$ ). We assessed how variability in precipitation affects these components and how forest outflow ( $O = Q + F_O$ ) compares to water supply to downstream users.

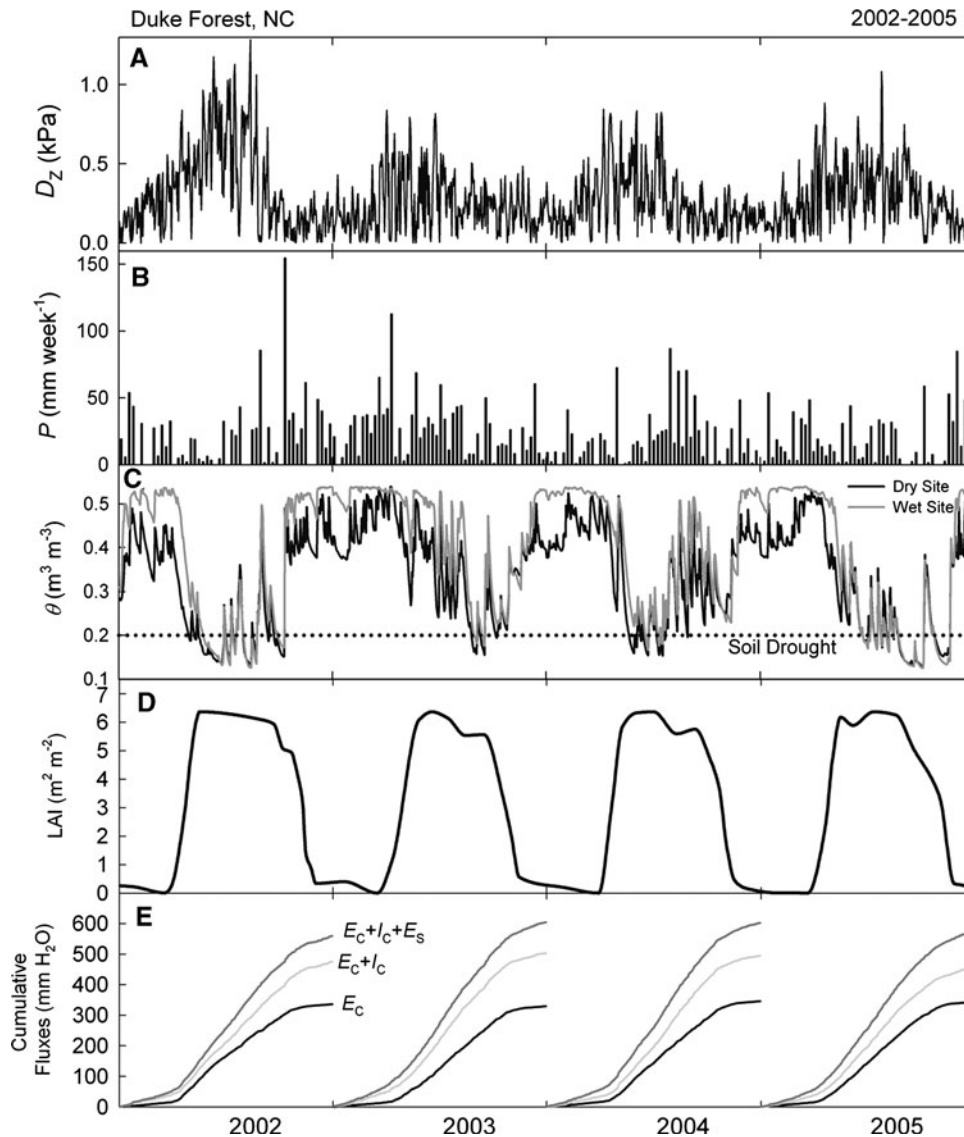
## MATERIALS AND METHODS

### Study Site

The study was conducted at the Duke Forest Ameriflux Hardwood site, Orange County, North Carolina (36°58'41.430"N, 79°05'39.087"W). This bottomland forest stand is described in other studies (Pataki and Oren 2003; Stoy and others 2006; Oishi and others 2008). Briefly, it is an 80- to 100-year-old mixed broadleaved deciduous forest dominated by hickories (*Carya tomentosa*, *C. glabra*), yellow poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), and oaks (*Quercus alba*, *Q. michauxii*, *Q. phellos*). Mean canopy height is 25 m with emergent crown tops extending above 35 m. Peak leaf area index (LAI) is approximately 7.0 m<sup>2</sup> m<sup>-2</sup>, occurring from mid-May until early-September (Figure 1D). Stand characteristics, including

stand basal area and sapwood area per unit ground area ( $A_S$ ), were taken in a one-hectare area surrounding the Ameriflux tower and two subplots of approximately 25 m radius (hereinafter the "wet and dry sap flux plots"). These data were scaled up to the 6.25 ha area surrounding an eddy covariance tower (hereinafter the "eddy covariance footprint") (Table 1; for methodological details, see Oishi and others 2008). The growing season was defined as April through October (DOY 91-304), a period characterized by LAI above 2.0 m<sup>2</sup> m<sup>-2</sup>.

With 3° slope, the site is nearly flat. The soil is an Iredell gravelly loam, with the upper 0.35 m a clay loam overlying a clay pan with low hydraulic conductivity that inhibits the rooting zone (Oren and others 1998). Soil depth can be 2 m which overlays bedrock (D. Richter, unpublished data).



**Figure 1.** Environmental variables measured at the studied broadleaf-deciduous forest. (A) day-length normalized vapor pressure deficit ( $D_z$ ), (B) weekly totals of precipitation ( $P$ ), (C) soil moisture ( $\theta$ ) measurements from dry and wet sap flux plots, with the value at which stomatal closure begins (0.20 m<sup>3</sup> m<sup>-3</sup>) indicated as horizontal dashed line, (D) canopy leaf area index (LAI), (E) canopy transpiration from scaled sap flux measurements ( $E_c$ ), estimated canopy interception ( $I_c$ ), and total component-based evapotranspiration ( $ET_{comp}$ ).

**Table 1.** Coefficients of the Relationship Between Sapwood Area ( $A_S$ ) and Basal Area ( $A_B$ ) for the Equation in the Form  $A_S = a \times A_B^b$  where Both Variables are in  $\text{cm}^2$  per  $\text{m}^2$  Ground Area

Species	$a$	$b$	$A_S$	LAI
<i>L. tulipifera</i>	0.382	2.010	3.18	0.83
<i>L. styraciflua</i>	0.246	2.202	2.96	0.69
<i>Carya</i> spp.	1.499	1.669	3.41	1.27
<i>Q. alba</i>	0.612	1.737	0.52	0.57
<i>Q. michauxii</i>	0.612	1.737	0.59	0.59
<i>Q. phellos</i>	0.284	1.932	0.27	0.11
Other species	0.246	2.202	2.78	2.11
Total			13.71	6.17

The stand-level mean of  $A_S$  and leaf area index (LAI) is in  $\text{m}^2 \text{m}^{-2}$  represents an average over the four study years (after Oishi and others 2008).

## Environmental Measurements

Air temperature ( $T_a$ ) and relative humidity (RH) were measured at two-thirds canopy height using HMP35C  $T_a$ /RH probes (Campbell Scientific, Logan, UT, USA) and were used to calculate the vapor pressure deficit ( $D$ ). Photosynthetically active radiation (PAR) and net radiation ( $R_n$ ) were measured above the canopy at 38.9 m (see Stoy and others 2006). Precipitation ( $P$ ) was measured daily with a rain gauge and partitioned over half-hourly values using data from tipping bucket gauges (TR-525USW, Texas Electronics, Dallas, TX, USA) positioned at the Duke FACE site, less than 1 km away. Long-term (115-year) mean annual  $P$  for the area is 1146 (standard deviation (SD) = 166) mm, with 654 (SD = 183) mm occurring during the growing season ([www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)).

Soil moisture ( $\theta$ ,  $\text{m}^3 \text{m}^{-3}$ ) was measured with 12 sensors (ThetaProbe, Delta-T Devices, Cambridge, UK), four in each of the wet and dry sap flux sites and four next to the eddy covariance tower, half installed from 0.05–0.10 m and half installed at 0.20–0.25 m. Values were rescaled based on periods when  $\theta$  reached saturation (set to  $0.54 \text{ m}^3 \text{m}^{-3}$ ) or the hygroscopic minima (set to  $0.125 \text{ m}^3 \text{m}^{-3}$ ), based on procedure and soil characteristics described in Oishi and others (2008). With these estimates of saturated and hygroscopic soil moisture states, the maximum amount of plant extractable water in a 0.30 m root-zone is approximately 125 mm.

## Hydrologic Balance

The forest hydrologic budget can be framed using a simple equation balancing outputs with precipitation:

$$P = I_C + E_S + E_C + Q + F_O + \Delta S \quad (1)$$

where  $\Delta S$  is change in soil water storage. Stemflow was estimated to contribute less than 1% of annual precipitation and excluded from further consideration (Oishi and others 2008).

Precipitation passing through the canopy and reaching the forest floor as throughfall ( $P_T$ ) was measured manually once or twice weekly with six rain gauges positioned on the forest floor.  $I_C$  was estimated as  $P - P_T$  between measurement periods, partitioned proportionately with the time-series of  $P$ . Occasional periods in which no  $P_T$  was recorded were gapfilled using linear relationships between  $P$  and  $P_T$  (Oishi and others 2008).

Methods for generating half-hourly estimates of  $E_C$  are described in Oishi and others (2008). Briefly, sap flux ( $J_S$ ) measurements were made using 20 mm length, thermal dissipation probes (Granier 1987) on 40 trees. Five trees each of *C. tomentosa* and *Q. alba* were measured in the dry sap flux plot and five each of *Q. michauxii* and *Q. phellos* were measured in the wet sap flux plot. Additionally, five trees each of *L. tulipifera* and *L. styraciflua* were measured in both the wet and dry plots. Probes were installed at 20 mm depth intervals to the maximum depth of active sapwood (up to 60 mm) to account for radial variability in flow rates (Phillips and others 1996). In total, 84 sensors were deployed at breast height in the forty sample trees. Flow of water through the trunk during the night, either resulting from nighttime conductance or recharge of stored water to the trunk and branches, has been shown to occur across a variety of species and climates (Oren and others 1999, 2001; Daley and Phillips 2006; Dawson and others, 2007) and, if not adequately identified, can lead to substantial underestimations in  $E_C$  (Kim and others 2008; Oishi and others 2008; Ward and others 2008). We assumed that nighttime flux did not occur in times in which simultaneously (1) the average 2-h  $D$  was less than 0.05 kPa and (2) the coefficient of variation (CV = standard deviation/mean) of the four temperature differential values ( $\Delta T$ ) from the heat dissipation sensor was less than 0.5% (Oishi and others 2008). These conditions were used to set the baseline for converting the output signal to water flux (Granier 1987).

No differences in  $J_S$  were observed between the populations of the same species from the wet and dry sap flux plots (that is, *L. tulipifera* and *L. styraciflua*), or among species of the genus *Quercus* (minimum  $P$ -value > 0.1) so the mean  $J_S$  from all monitored trees of a given genera ( $J_{Si}$ , where

subscript  $i$  represents an individual genera) was applied to all trees of that genera in the stand. All *Carya* species were assumed to behave like *C. tomentosa*. Tree-level  $J_{Si}$  estimates were scaled to canopy transpiration of each genera ( $E_{Ci}$ ) based on estimates of sapwood area in the eddy covariance footprint (Table 1). Estimates of  $A_S$  were generated for each genera based on linear relationships between leaf area (collected in litter baskets) and  $A_S$  from the one-hectare and two sap flux plots. These relationships were then applied to 29 litter baskets distributed throughout a 300 m × 300 m area representing approximately 95% of the daytime footprint of the eddy covariance instruments (for details, see Oishi and others 2008).

Half-hourly estimates of  $E_S$  previously described in Oishi and others (2008) based on the relationship between  $D$  and wintertime LE measured using eddy covariance were used after filtering out days following recent rain events and subtracting water vapor losses through bark. Oishi and others (2008) investigated the causes of the often-observed lack of agreement between  $ET_{comp}$  and LE, but did not assess how the components of evapotranspiration respond to interannual variation in weather nor the effect on forest water outflow.

Total evapotranspiration measured by the eddy covariance system as LE is described in Stoy and others (2006). The 35% lack of closure in the energy balance at the site was due largely to convective conditions influencing sensible heat flux more than LE. The error in the annual LE component ranged 7–14%.

A Richards' equation was used to estimate vertical water movement in the soil using standard retention and hydraulic conductivity functions (Clapp and Hornberger 1978). Water redistribution between 7.5 mm soil layers up to 0.50 m depth was calculated at 4-s intervals, with soil physical properties taken from Oren and others (1998). At each time step,  $P_T$  (if any precipitated) was added to the soil surface and estimated  $E_S$  was subtracted from the top soil 5 layers (37.5 mm). In addition,  $E_C$  was subtracted from the soil profile based on root distribution data and the relative amount of available water (see Katul and others 1997). Diagnostic soil pits (0.40 m × 0.40 m,  $n=3$ ) showed that root biomass in the upper 0.40 m of soil was 426 g m<sup>-2</sup>; 0.015 (SD = 0.007), 0.017 (0.009), 0.008 (0.011), and 0.002 (0.002) g m<sup>-2</sup> at 0.00–0.05, 0.05–0.10, 0.10–0.20, and 0.20–0.30 m, respectively (K. Johnsen, unpublished). Over 75% of the root mass was in the upper 0.12 m whereas root biomass between 0.30 and 0.40 m was less than 5% of the total for these pits, indicating that the clay pan

severely restricted rooting below 0.30 m. Although evidence of roots up to 2 m have been found near this site (D. Richter, unpublished), the sparseness of deep roots, along with the low hydraulic conductivity of this soil makes water availability in the upper 0.30 m the most important for trees. Therefore,  $Q$  was equated to water draining below 0.30 m.

To determine  $F_O$ , the maximum ponding height ( $h_{max}$ ) was calculated based on Paul and others (2003) as

$$h_{max} = 0.5v \left( \frac{\sin^2(\zeta - s)}{\sin \zeta} \right) \times \left( \frac{\cot(\zeta + s) + \cot(\zeta - s)}{2 \cos \zeta \cos s} \right) \quad (2)$$

where  $v$  is litter depth (25 mm),  $\zeta$  is clod angle (30°), and  $s$  is the average site slope (3°). Based on this  $h_{max}$  at the site was estimated at 10 mm. When  $P_T$  exceeded the infiltration rate estimated from the drainage model, water accumulated up to 10 mm, with the excess designated as  $F_O$ .

## RESULTS

### Site and Environmental Variables

The severe 2002 growing season drought, preceded by the milder 2001 growing season drought, ended with heavy, late-summer rainfall (Figure 1B). Thus, despite a severe summer drought, annual  $P$  in 2002 was only slightly lower than the long-term mean (Table 2). In contrast, 2003 presented the second wettest growing season in the 115-year local record. Both 2004 and 2005 were relatively dry, close to one standard deviation below the mean annual precipitation; however, 2004 was characterized by a relatively wet growing season and dry dormant season, whereas 2005 experienced a dryer than normal growing season and typical dormant season.

The primary force driving daily evapotranspiration at the site, day-length normalized vapor pressure deficit ( $D_Z$ ), was higher during the dry 2002 growing season than in other years of the study (Figure 1A). Potential evapotranspiration (PET) was estimated based on the Priestley-Taylor method, recommended for the southeastern US (Lu and others 2005). Annual PET was typically close to annual  $P$  (Table 2), although  $P$  was greater than PET in the wet year of 2003. Cumulative daily values of  $P$ -PET showed a deficit ( $P$ -PET < 0) for the majority of the growing season in 2002 (DOY 120 until the end of the year) and 2005 (DOY 129 through 345).

**Table 2.** Flux Components of the Annual Hydrologic Budget for Each Year and Partitioned to Growing Season (April–October), and Dormant Season (January–March and November–December)

Year	<i>P</i>	PET	<i>I<sub>C</sub></i>	<i>E<sub>C</sub></i>	<i>E<sub>S</sub></i>	ET <sub>comp</sub>	LE	<i>F<sub>O</sub></i>	<i>Q</i>	<i>O</i>	<i>R</i>
Annual											
2002	1092	1156	189	336	84	610	577	62	400	462	20
2003	1346	1107	236	329	102	668	618	134	600	734	−56
2004	992	972	181	346	108	635	618	36	352	388	−31
2005	934	933	157	343	119	619	605	20	325	345	−30
Mean	1091	1042	191	339	103	633	605	63	419	482	−24
SD	182	106	33	8	15	26	19	50	124	175	32
Growing season											
2002	610	932	80	306	68	453	505	59	82	141	16
2003	859	873	123	299	69	491	531	97	294	391	−23
2004	720	805	145	311	72	529	525	36	196	232	−41
2005	426	819	34	311	88	433	517	5	33	38	−45
Mean	654	857	96	307	74	477	520	49	151	201	−23
SD	183	58	49	6	9	42	11	39	117	150	28
Dormant season											
2002	482	224	109	30	16	157	72	3	318	321	4
2003	487	234	113	30	33	177	87	37	306	343	−33
2004	272	167	36	35	36	106	93	0	156	156	10
2005	508	114	123	32	31	186	88	15	292	307	15
Mean	437	185	95	32	29	157	85	14	268	282	−1
SD	111	56	40	2	9	36	9	17	75	85	22

Precipitation (*P*), potential evapotranspiration (PET), canopy interception (*I<sub>C</sub>*), transpiration (*E<sub>C</sub>*), soil evaporation (*E<sub>S</sub>*), evapotranspiration (ET<sub>comp</sub>), latent heat flux (LE), overland flow (*F<sub>O</sub>*), drainage (*Q*), outflow (*O* = *F<sub>O</sub>* + *Q*), residual (*R* = *P* − (ET<sub>comp</sub> + *O*)) (all values in mm).

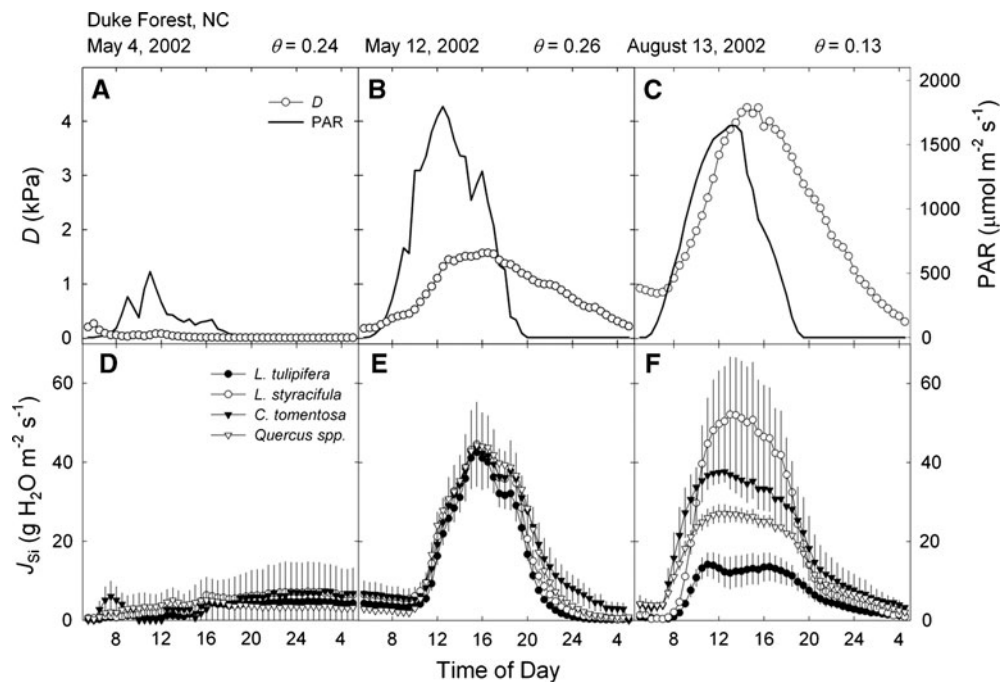
Soil water storage, represented by  $\theta$ , was high during the dormant season and declined substantially during the growing season (Figure 1C). Differences in  $\theta$  between the wet and dry sap flux plots were most evident in winter months when either within-stand *F<sub>O</sub>* or horizontal soil moisture redistribution drained the dry plot and accumulated in the wet plot, keeping it near saturation for a longer period. During the growing season of any year, differences in  $\theta$  between the two plots were small owing to high evapotranspiration.

The presence of a clay pan restricts more than 95% of fine root mass to the upper 0.30 m; however, roots up to 10 mm diameter can occasionally penetrate as deep as 2 m (D. Richter, unpublished data). For the purposes of this analysis, we define drought as periods in which soil moisture in the upper 0.30 m drops below  $0.20 \text{ m}^3 \text{ m}^{-3}$ , a value shown to limit stomatal conductance in pine and hardwood forests in the study area and in a nearby grass/hay field (Oren and others 1998; Pataki and Oren 2003; Novick and others 2004; Stoy and others 2006). Based on this definition, drought days represent 15% of growing season days over the entire study period. During the wet years of 2003 and 2004,  $\theta$  dropped below  $0.20 \text{ m}^3 \text{ m}^{-3}$  for only 14 and 18 growing season days, respectively.

However, the forest experienced some degree of soil water limitation during nearly half of the growing season in 2002 (90 days or 42% of the growing season) and 2005 (98 days or 47% of the growing season). Thus, the duration of drought in 2002 and 2005 should provide an adequate contrast to the wetter growing seasons of 2003 and 2004. The reliability of this definition of drought is considered in the “Discussion” section.

## Transpiration

At a daily time-scale, marked differences in transpiration were observed among species. To illustrate these differences, we focus on three sample days from the 2002 growing season (Figure 2): an early growing season day that received 14.8 mm of precipitation distributed throughout the day (May 4), an early growing season day with no precipitation but relatively high  $\theta$  (May 12), and a mid-summer day with similar PAR to May 12, but at the peak of the drought (August 13). Precipitation on May 4 resulted in low PAR and *D*, as well as low *J<sub>Si</sub>* for all species. On May 12, ample soil moisture and favorable atmospheric conditions resulted in high and similar *J<sub>Si</sub>* in all species. The reduction of *J<sub>Si</sub>* at the peak of the drought was greatest in *L. tulipifera*,



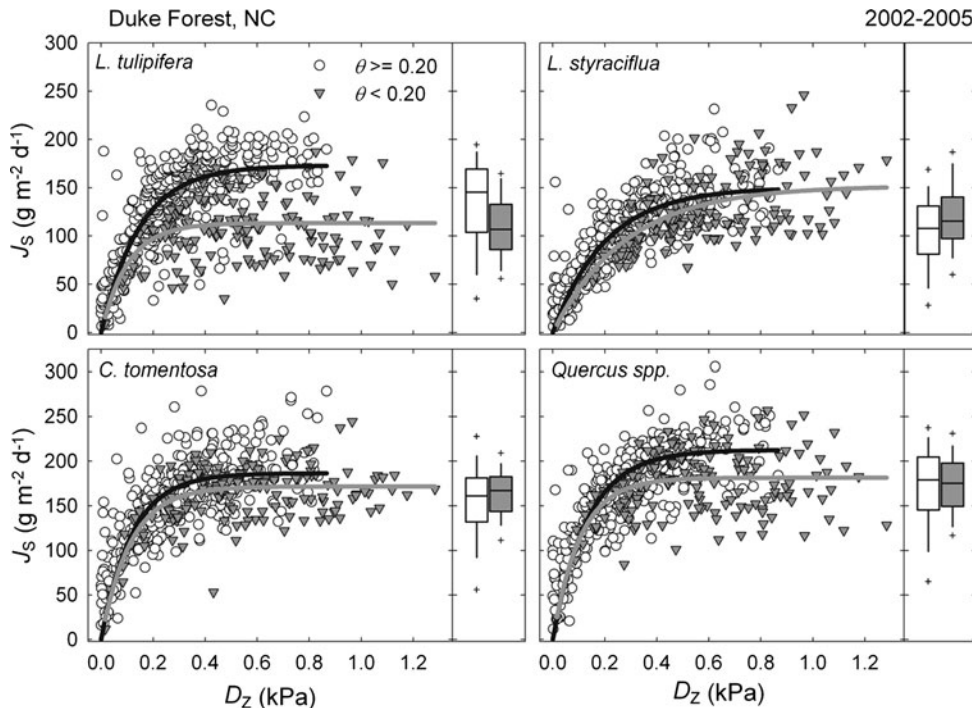
**Figure 2.** Time series from three example days representing an early growing season day receiving 14.8 mm in a rain event lasting most of the day (**A, D**), an early growing-season dry day with ample soil moisture (**B, E**), and a late growing-season day under drought conditions (**C, F**). Half-hourly values of vapor pressure deficit ( $D$ ) and above-canopy photosynthetically active radiation (PAR) (**A, B, and C**); sap flux density ( $J_{Si}$ ) for the outer 20 mm of xylem for the observed species (error bars represent 1 s.e.).

followed by *Quercus*, and *C. tomentosa*; the average flux of *L. styraciflua* was unaffected by the drought although the variance increased.

Examined at a daily time-scale for the entirety of the study period, drought sensitivity was consistent with the diurnal pattern (Figure 3, Table 3). Daily  $J_{Si}$  followed the commonly observed relationship with  $D_Z$ , increasing rapidly at low  $D_Z$  and tending to saturate with increasing  $D_Z$  (Pataki and Oren 2003; Bovard and others 2005; Ewers and others 2007; Köecher and others 2009). At a given  $D_Z$ , *L. tulipifera*, *C. tomentosa*, and *Quercus* spp. exhibited lower  $J_{Si}$  when  $\theta$  was less than  $0.20 \text{ m}^3 \text{ m}^{-3}$  (see Table 3 for information on regression statistics). However, although maximum  $J_{Si}$  in *L. tulipifera* and *Quercus* spp. decreased during drought by 59 and 31  $\text{g H}_2\text{O m}^{-2} \text{ d}^{-1}$  (34% and 15%), respectively, *C. tomentosa* exhibited a decrease of only 15  $\text{g H}_2\text{O m}^{-2} \text{ d}^{-1}$  (8%). The drought response of  $J_{Si}$  to  $D_Z$  in *L. styraciflua* was significant ( $P$ -value  $< 0.001$ ) leading, nevertheless to only a slight decrease in  $J_{Si}$  at intermediate  $D_Z$  (0.2–0.6 kPa), with negligible differences in the maximum transpiration at high  $D_Z$ . The relationship between  $D_Z$  and species-level  $J_{Si}$  kept its features upon scaling to stand-level  $E_C$  (Figure 4, Table 3).

## Seasonal Patterns of Transpiration

When examining daily trends in transpiration throughout the four growing seasons, it was found that, at a given  $D_Z$ , maximum  $J_{Si}$  and  $E_C$  (the asymptotic values in Figures 3 and 4) decreased when  $\theta$  was low; however, under dry soil conditions we also observed the expected absence of very low  $D_Z$  conditions, conditions that are common in the wetter periods (Figure 5). Thus, comparing daily means of growing season transpiration rates over the entire study period show that average  $J_{Si}$  (and thus  $E_{Ci}$ ) did not differ greatly between drought and non-drought periods (see box plots in Figures 3 and 4). Aggregating transpiration rates during drought and non-drought periods across all four years demonstrates that mean transpiration of *L. tulipifera* decreased appreciably during drought periods (19%;  $P$ -value  $< 0.001$ ), but less than the 34% decrease reflected in the asymptotic maximum values. Despite a decrease in maximum  $J_{Si}$ , no significant decrease in mean transpiration was observed in *Quercus* spp ( $P$ -value  $> 0.5$ ). In contrast, transpiration of *C. tomentosa* increased slightly under drought (5%;  $P$ -value  $< 0.04$ ), whereas average  $J_{Si}$  of *L. styraciflua* increased by 14% ( $P$ -value  $< 0.001$ ). It is important to note that this



**Figure 3.** Response of daily species-specific sap flux ( $J_{Si}$ ) to day-length normalized vapor pressure deficit ( $D_z$ ) under non-limiting soil moisture conditions ( $\theta \geq 0.20 \text{ m}^3 \text{ m}^{-3}$ , open circles) and limiting conditions ( $\theta < 0.20 \text{ m}^3 \text{ m}^{-3}$ , closed triangles) during growing seasons 2001–2005. Corresponding box plots of  $J_{Si}$  for normal (white box) and drier (grey box) conditions show median, 25th/75th percentile, 10th/90th percentile, and 5th/95th percentile with the center line, box, whiskers and +, respectively. See Table 3 for information on regression statistics.

apparent increase in the average  $J_{Si}$  of *C. tomentosa* and *L. styraciflua* during the drought was not due to an increase in the sensitivity of transpiration to  $D_z$ , but rather from a similar sensitivity to  $D_z$  coupled with continuously high  $D_z$  days. This trend is even

more apparent when comparing the sensitivity of stand-level  $E_C$  to  $D_z$  during the drought because drought-insensitive species buffered the response of drought-sensitive species (Figure 4). The overall effect is that  $J_{Si}$  and  $E_C$  on any given drought day can be similar to that of a non-drought day.

**Table 3.** Regression Information for Figures 3 and 4

Species	$\theta$	$a$	$b$	$r^2$
<i>L. tulipifera</i>	Non-limiting	173.0803	6.7442	0.61
	Limiting	113.5015	3.0316	0.15
<i>L. styraciflua</i>	Non-limiting	150.2446	4.9187	0.65
	Limiting	151.7859	3.5586	0.49
<i>Carya</i> spp.	Non-limiting	186.5391	8.4670	0.54
	Limiting	171.7235	8.8670	0.36
<i>Quercus</i> spp.	Non-limiting	212.6332	7.5055	0.67
	Limiting	181.4982	9.4501	0.27
$E_C$	Non-limiting	2.0791	6.9150	0.71
	Limiting	1.7708	7.5950	0.42

Equations relating day-length normalized vapor pressure deficit ( $D_z$ ; kPa) to water flux based on either limiting ( $\theta < 0.20 \text{ m}^3 \text{ m}^{-3}$ ) or non-limiting ( $\theta \geq 0.20 \text{ m}^3 \text{ m}^{-3}$ ) soil moisture conditions. Data were fit with an exponential rise to maximum function;  $y = a(1 - e^{-b \times D_z})$  where  $y$  is  $J_{Si}$  ( $\text{g H}_2\text{O m}^{-2}$  sapwood area  $\text{d}^{-1}$ ) for individual genera or  $E_C$  ( $\text{mm H}_2\text{O d}^{-1}$ ). All regressions and the effect of  $\theta$  (extra sum of squares F-test) are significant ( $P$ -value  $< 0.001$ ).

Growing season (April–October)  $E_C$  was very consistent among years (Table 2), despite large differences in the amount and timing of precipitation. Over the growing season, *Quercus* spp. comprised 38% (SD = 2% among the four years) of total  $E_C$ . Groups making the next largest contributions were *Carya* spp., *L. styraciflua*, and *L. tulipifera* at 19 (SD = 2), 16 (SD = 1), and 11 (SD = 1) %, respectively. Other species, which included most understory and some overstory trees, accounted for the remaining 17 (SD < 1) % of  $E_C$ .

### Evapotranspiration

Atmospheric and soil conditions interact to affect components of evapotranspiration. Conditions that lead to drought, and thus high resistance to water flux from the biosphere to the atmosphere, are also associated with high atmospheric demand for biospheric moisture (Figure 5).



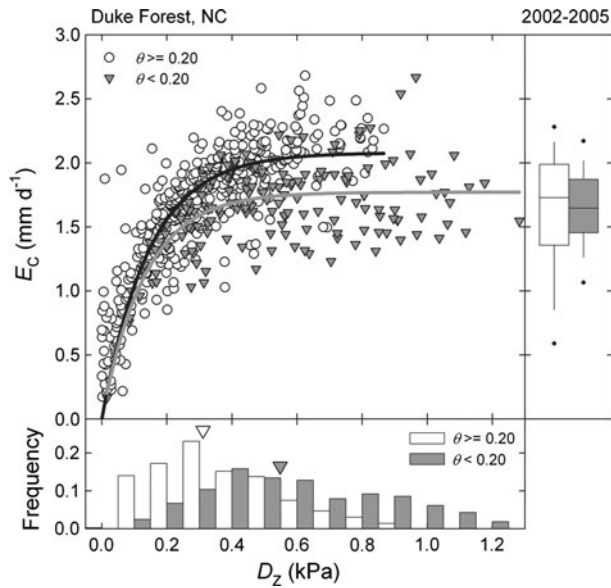


Figure 4. Response of daily stand-level transpiration ( $E_C$ ) to day-length normalized vapor pressure deficit ( $D_Z$ ) under non-limiting soil moisture conditions ( $\theta \geq 0.20 \text{ m}^3 \text{ m}^{-3}$ , open circles) and limiting conditions ( $\theta < 0.20 \text{ m}^3 \text{ m}^{-3}$ , closed triangles) during growing seasons 2001–2005. Corresponding box plots of  $E_C$  for normal (white box) and drier (grey box) conditions show median, 25th/75th percentile, 10th/90th percentile, and 5th/95th percentile with the center line, box, whiskers and +, respectively. PDF of  $D_Z$  during limiting and non-limiting soil moisture conditions; triangles are positioned at mean values. See Table 3 for information on regression statistics.

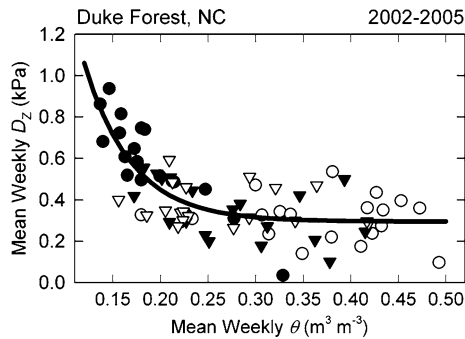


Figure 5. Relationship between mean weekly soil moisture ( $\theta$ ) during the four growing seasons and day-length normalized vapor pressure deficit ( $D_Z$ ). See Table 4 for information on regression.

The components of evapotranspiration along the range of soil moisture are shown in Figure 6 not to imply causality, but to provide a frame of reference for atmosphere-soil conditions. Regression lines in Figure 6 were selected based on  $r^2$  and distribution of residuals. In cases where no regression was significant, the mean value is depicted as a horizontal dashed line (Table 4).

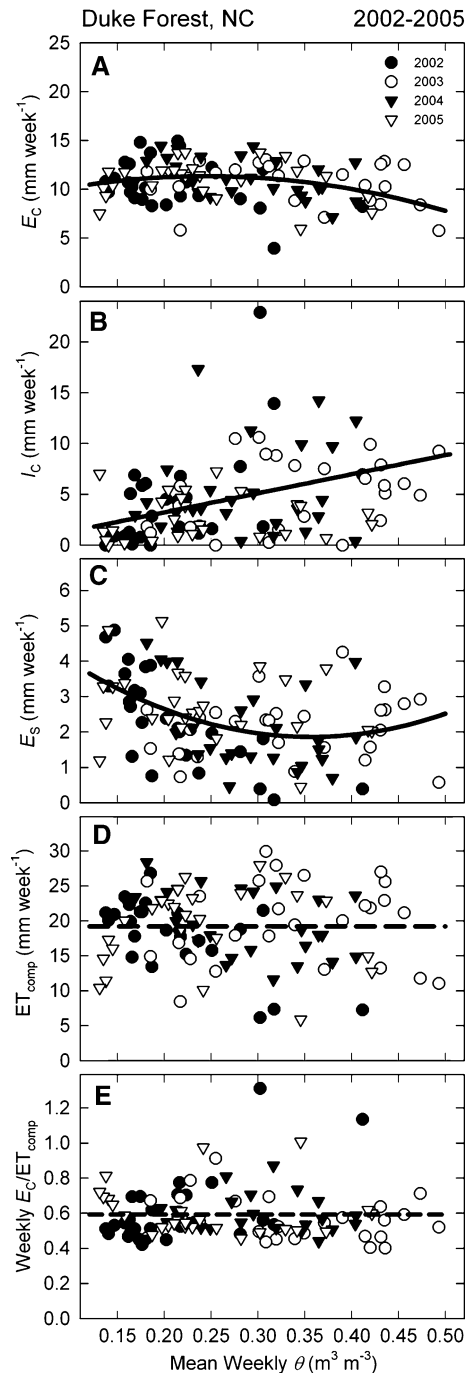


Figure 6. Relationship between mean weekly soil moisture ( $\theta$ ) during four growing seasons and (A) canopy transpiration ( $E_C$ ), (B) canopy interception ( $I_C$ ), (C) soil evaporation ( $E_S$ ), (D) component-based evapotranspiration ( $ET_{\text{comp}}$ ), and (E) ratio of  $E_C$  to  $ET_{\text{comp}}$ . See Table 4 for information on regressions.

Despite reductions in daily  $J_{\text{Si}}$  at low  $\theta$ , when sap flux was scaled to the canopy-level, weekly  $E_C$  during the growing season was weakly related to  $\theta$ , declining slightly at very high or low  $\theta$  values

**Table 4.** Regression Information for Figures 5 and 6

Variable	Equation	$r^2$	P-value
$D_Z$	$0.30 + 8.47e^{-20.02 \times \theta}$	0.54	<0.0001
$E_C$	$8.06 + 26.75\theta - 54.64\theta^2$	0.09	0.0070
$I_C$	$18.76\theta - 0.52$	0.18	<0.0001
$E_S$	$5.92 - 22.78\theta + 31.94\theta^2$	0.16	0.0001
$ET_{comp}$	19.21	–	0.30
$E_C/ET_{comp}$	0.593	–	0.73

Equations relating mean weekly soil moisture ( $\theta$ ;  $m^3 m^{-3}$ ) for 2002–2005 growing seasons and day-length normalized vapor pressure deficit ( $D_Z$ ; kPa), canopy transpiration ( $E_C$ ; mm), canopy interception ( $I_C$ ; mm  $H_2O$ ), soil evaporation ( $E_S$ ; mm  $H_2O$ ), component-based evapotranspiration ( $ET_{comp}$ ; mm  $H_2O$ ), and the ratio of  $E_C$  to  $ET_{comp}$ . Regressions were selected based on  $r^2$  and distribution of residuals. In cases where regressions were not significant ( $P$ -value > 0.01), the mean value is given.

(Figure 6A). Weekly  $E_C$  typically ranged from 5 to 15 mm, although high  $E_C$  (> 12 mm  $week^{-1}$ ) was not observed at the lowest  $\theta$ .

$I_C$  was closely related to  $P$  from daily to annual time scales. Thus, increasing  $P$  led to a positive correlation between  $I_C$  and  $\theta$  at a weekly time scale (Figure 6B). This linear relationship did not vary seasonally, despite large changes in LAI (Oishi and others 2008). Annually,  $I_C$  was 17.5 (SD = 0.6) % of  $P$  (Table 2) and was the most variable component of  $ET_{comp}$ .

Daily  $E_S$  varied with atmospheric conditions ( $P$ ,  $D$ , and  $R_{net}$ ), reaching the highest daily maximum values during the summer months (Oishi and others 2008). The majority of annual  $E_S$  occurred during the growing season and was invariable among years (Table 2). Winter  $E_S$  was more variable, but was a small portion of the hydrologic budget. Examining growing season trends, weekly  $E_S$  was fairly invariable along the range of  $\theta$ , with a slight increase at low  $\theta$  (Figure 6C) reflecting the corresponding increase of  $D_Z$  (Figure 5). Our method for estimating  $E_S$  as a function of  $D$  is rather simplistic, yet the daily values were similar to those obtained based on the difference between LE and  $E_C + I_C$  (Oishi and others 2008).  $D$  at the floor of deciduous forests has been shown to be similar to that above the canopy and understory evaporation is better related to  $D$  than to net radiation (Baldocchi and Meyers 1991; Wilson and others 2000), making  $D$  the driver of choice for estimating  $E_S$ . Confidence in our estimates of  $E_S$  is further enhanced noting that they were within the range observed by a sub-canopy eddy covariance system in a similar southeastern deciduous forest (Wilson and others 2000).

Daily  $ET_{comp}$ , the sum of  $E_S$ ,  $E_C$ , and  $I_C$ , varied widely mostly depending on the occurrence of rain

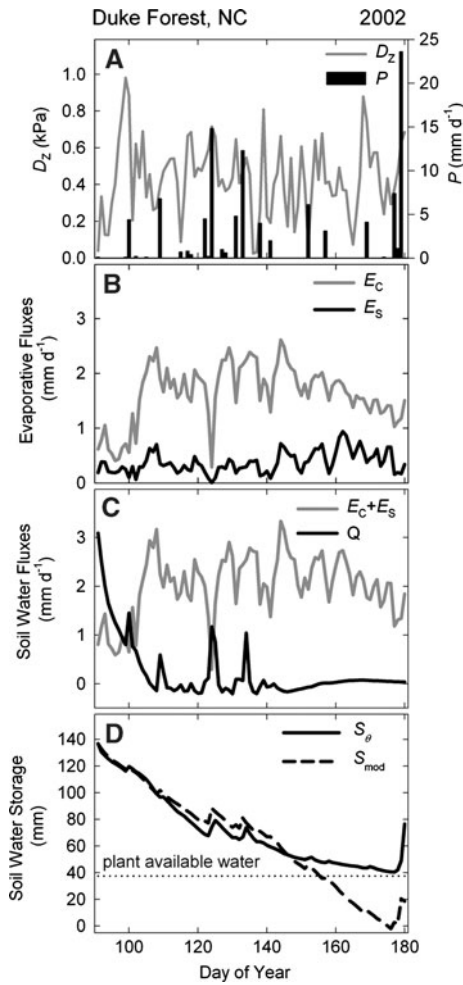
events. Variability in growing season  $ET_{comp}$  was still apparent when integrated weekly, ranging from about 5 to 30 mm  $week^{-1}$  (Figure 6D). However, similar to the weekly variations in  $E_C$  and  $E_S$  (Figure 6A and C), the variation in growing season  $ET_{comp}$  was unrelated to  $\theta$ .

Annual  $ET_{comp}$  averaged 633 mm  $y^{-1}$ , 4.8% (SD = 2.6%) higher than LE but well within the uncertainty of LE estimates (Stoy and others 2006; Oishi and others 2008). Growing season  $ET_{comp}$  was fairly consistent amongst years. If we consider the moderately-wet year of 2004 as 'normal', growing season  $ET_{comp}$  in the dry years of 2002 and 2005 was approximately 16% lower than normal and was about 7% lower than normal in the very wet growing season of 2003 (Table 2). Annual  $ET_{comp}$  was not as consistent as weekly growing season data (Figure 6D) due to the incorporation of winter  $I_C$  and the distribution of environmental variables (for example,  $P$  and  $D$ ).  $E_C$  was consistently about 60% of  $ET_{comp}$  throughout the growing season and this ratio showed little variability across the range of  $\theta$  (Figure 6E). The sum of  $E_C$  and  $E_S$  ranged only 42 mm (from 420 to 462 mm  $y^{-1}$ ) or 7% of mean annual  $ET_{comp}$ .  $I_C$  varied 79 mm among years, or 12% of annual mean  $ET_{comp}$ .

## Drainage and Runoff

$Q$  was estimated as water draining below 0.30 m, the depth delineating the active rooting zone.  $Q$  occurred only when soil was sufficiently wet, greater than about 0.40  $m^3 m^{-3}$ , conditions more frequently observed in winter months. Consequently, during the winters (2002, 2003, and 2005),  $Q$  comprised a large portion of the seasonal hydrologic budget (Table 2).  $P$  in winters of these years was similar, producing fairly similar  $Q$ . The dry winter of 2004 had approximately half the  $Q$  of other years. Regardless of the total winter precipitation, low evaporative demand during this period allowed rainfall to fully recharge soil water to the point of saturation prior to each growing season.

Similar to winter months, growing season  $Q$  followed trends of  $P$ . Seasonal  $F_O$  generally increased with  $P$ ; however, because overland flow requires rain falling on saturated soil surface, these events depended primarily on the timing of precipitation events, as opposed to the seasonal total.  $F_O$  exceeding 5 mm occurred on only 5 days in the wettest year (2003) and only once in 2002. Although this site is fairly flat and  $F_O$  is not expected to be high, the combination of frequently saturated soil in the winter and micro-topographic features can

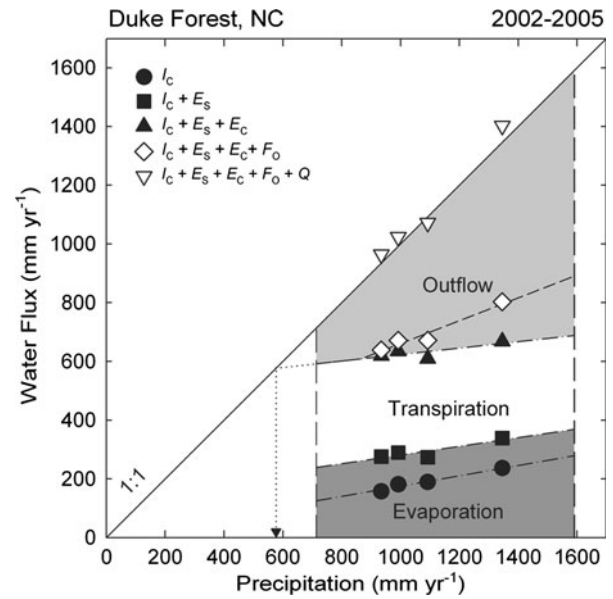


**Figure 7.** Time series from the driest growing season of (A) day-length normalized vapor pressure deficit ( $D_z$ ) and precipitation ( $P$ ), (B) evaporative fluxes of canopy transpiration ( $E_c$ ) and soil evaporation ( $E_s$ ), (C) soil water fluxes from the top 0.30 m of soil from  $E_s + E_c$  and drainage ( $Q$ ), (D) soil water storage in the top 0.30 m of soil based on scaled soil moisture probe values ( $S_\theta$ ) and estimated based on throughfall precipitation ( $P_T$ ) minus  $E_s + E_c + Q$  ( $S_{mod}$ ).

result in redistribution of water either out of the stand or into low-lying areas within the stand where it is inaccessible to most trees, thus continuing to feed drainage.

### Site Water Balance

Figure 7 illustrates environmental drivers and the soil water budget over the beginning of the 2002 growing season, a time period characterized by high evapotranspiration and low  $P$ . Early growing season  $E_c$  quickly increases during leaf expansion, and then follows a similar pattern to  $E_s$  (Figure 7B). These fluxes and their sum (Figure 7C)



**Figure 8.** A comparison of annual precipitation with additive components of hydrologic budget. Closed symbols represent components of evapotranspiration whereas open symbols represent components of water outflow. The dashed vertical lines represent the lowest (714 mm) and highest (1591 mm) annual precipitation in the past 115 years. Dashed diagonal lines represent linear regressions approximating the sensitivity of components of the hydrologic budget to precipitation. Dotted line and arrow indicate the level of annual precipitation where drainage is theoretically equal to zero (577 mm).

show daily variation consistent largely with variations in the atmospheric drivers associated with  $D_z$  and  $P$  (Figure 7A), but ultimately decline as the soil dries towards the end of the growing season. Daily  $Q$  quickly declines to near-zero 20 days after the onset of the growing season, briefly punctuated by higher flows after rain events. However, because  $P$  must first partially recharge soil water storage ( $S$ ) before drainage can occur and available soil water is quickly used for evapotranspiration, very little  $P$  is converted to  $Q$  during the growing season. In Figure 7D, modeled soil water storage in the upper 0.30 m was defined as  $S_{mod} = P - (I_c + E_c + E_s + Q)$  (no  $F_o$  occurred during this period). Although  $S_{mod}$  follows  $S$  estimated from soil moisture probes ( $S_\theta$ , scaled for the upper 0.30 m) during the beginning of this period,  $S_{mod}$  exceeds the amount of plant available water in that layer by DOY 155. This illustration demonstrates that without adequate precipitation, soil water storage in the upper 0.30 m was not sufficient to meet growing season water demands and water extraction from deeper soil must be invoked.

The full hydrologic balance, based on measured  $P_T$ , estimated  $E_C$  and  $E_S$ , and modeled  $Q$  and  $F_O$  is displayed as cumulative totals in Figure 8. As previously mentioned, annual  $E_S$  was generally insensitive to  $P$  ( $P$ -value  $>0.50$ ). Annual  $E_C$  showed a relationship with  $P$  ( $P$ -value = 0.064), but the low-significance of the slope ( $-0.038$ ) shows only a small decrease in transpiration with increasing  $P$ . Annual  $I_C$  does exhibit a linear increase with  $P$  ( $I_C = 0.175 \times P$ ;  $P$ -value  $<0.001$ , intercept not significant). Averaging the four years, our hydrologic budget overestimated total  $P$  by less than 5% (SD = 3%). Hence, with the modeled estimates of  $Q$  and  $F_O$ , we demonstrate a nearly balanced annual hydrologic budget (lack of closure not significantly different than zero,  $P$ -value=0.85; Table 2). Although  $I_C$  increased with  $P$ , after accounting for  $E_S$  and  $E_C$ , changes in  $P$  did not appear to lead to changes in  $ET_{comp}$ . Consequently, the variability in annual  $P$  matched well the variability in outflow ( $O = Q + F_O$ ).

## DISCUSSION

We found that the transpiration rate of certain species was greatly reduced by drought when compared under similar atmospheric conditions at diurnal and daily time scales. However, no drought effects were noticeable when transpiration was integrated seasonally or annually. At these longer periods, large interannual variation in precipitation was accompanied by much smaller variation in transpiration as well as in total evapotranspiration. We first discuss the processes responsible for producing conservative interannual transpiration and evapotranspiration, followed by an analysis of the implication to downstream water users.

### Species Differences of Drought Sensitivity and Conservative Stand Transpiration

Among the species investigated in this study, *L. tulipifera* showed the strongest  $J_S$  sensitivity to drought, similar to previous findings for this species which experiences premature leaf loss during prolonged droughts (Pataki and Oren 2003). In contrast, *L. styraciflua* in our study did not show the level of sensitivity observed in that study. We confirmed that *Carya* is one of the most drought-tolerant genera in southeastern hardwood stands (Oren and Pataki 2001; Wullschleger and Hanson 2003). However, although *Quercus* species typically exhibit low degrees of drought-sensitivity in this region (Oren and Pataki 2001; Wullschleger and

Hanson 2003), often attributed to deeper rooting than co-occurring species (Bovard and others 2005), our study showed that once  $\theta$  in the upper rooting zone of our stand dropped below  $0.20 \text{ m}^3 \text{ m}^{-3}$ , species of this genus exhibited a pronounced sensitivity to drought (Figure 3D).

Had the distribution of tree species been such that drought-insensitive species were concentrated in the dry plot and drought-sensitive species in the wet plot, an *apparent* stand-level drought-insensitivity of transpiration could have been attributed to within-site differences in species composition. However, the most drought-sensitive species (*L. tulipifera*) represented a greater proportion of sapwood area in the dryer site (Oishi and others 2008). Similarly, the drought-sensitive understory species *Cornus florida* and *Acer rubrum* (Wullschleger and Hanson 2006) were present in both plots. These results suggest that conservative annual  $E_C$  can be achieved through a mechanism other than shifts in species composition.

One-third of the total sapwood area in the stand belonged to drought-sensitive species. During our example drought day, their  $J_{Si}$  decreased, leading to a lower  $E_C$  than on the reference non-drought day ( $1.51 \text{ mm d}^{-1}$  versus  $2.12 \text{ mm d}^{-1}$ ; compare Figure 2E, F), even though  $D$  was 2.5 times greater (Figure 2B, C), providing a greater force to drive evapotranspiration. However, the very low  $D$  on the rainy day led to much greater reductions in  $E_C$  than the drought, declining to  $0.21 \text{ mm d}^{-1}$  (Figure 2A, D). The effect of rainy days goes beyond drastically reducing  $D$  in the same day; rain events keep soil moist and  $D$  low for several days. Indeed, over the four growing seasons, weekly  $D_Z$  remained low as long as precipitation kept  $\theta$  above  $0.20 \text{ m}^3 \text{ m}^{-3}$ ; however, as  $\theta$  dropped below this threshold,  $D_Z$  increased rapidly (Figure 5). Based on these results, rainy conditions with moist soil can lead to depressed  $E_C$  on time scales ranging from diurnal to seasonal (Table 2) and even annual. Indeed,  $E_C$  was lowest in 2003, the wettest year in our study period, causing a slightly declining trend in transpiration with  $P$  (reflected in the narrowing of the white band in Figure 8 with increasing  $P$ ; Table 2).

Although  $E_C$  across all times scales was sensitive to precipitation, the sensitivity decreased with integration time. The decrease in sensitivity of  $E_C$  despite changing soil moisture is driven by the interactions between  $\theta$  and  $D_Z$  (Figure 5) and modulated by the stomatal response to  $D$  (Oren and others 1999, see Supplemental Appendix). For example, the long-term, daytime, growing season mean  $D$  at the site is  $0.75 \text{ kPa}$ ; however, mean growing season daytime  $D$  during the drought year

of 2002 was 1.37 kPa, theoretically maintaining annual  $E_C$  at 95% of the average rate (see Supplemental Appendix). Based on the analysis shown in the Appendix, average  $D$  over the growing season would have to be approximately 1.54 kPa for the atmospheric demand to fully compensate for drought-induced reductions in conductance.

Because low  $D_Z$  days are not present during drought periods, the average stand-level transpiration rates may remain similar to the rates during wet periods regardless of species composition. To examine the maximum possible influence species composition could have over  $E_C$  under drought conditions, we ran simulations assuming all trees in our stand were a single species, either the most drought sensitive *L. tulipifera*, or the least sensitive *L. styraciflua* using  $D_Z$  and  $P_T$  from the drought year 2002 as inputs. Trees within the one-hectare plot surrounding the tower were assigned sapwood area depending on the characteristics of either species.  $E_S$  as a function of  $D$ , and  $I_C$  as a function of  $P$  remained the same.  $E_C$  was estimated using functions from Table 3 (after scaling  $J_{Si}$ ), thus allowing for different responses to  $D_Z$  depending on our dynamic  $\theta$  calculations. Our hypothetical forest comprised exclusively of *L. tulipifera* resulted in a decrease of only 7% (21 mm) of the annual  $E_C$  in 2002 relative to the actual forest. When the characteristics of *L. styraciflua* were assigned to all trees, annual  $E_C$  in 2002 was practically unaffected (+4 mm). Thus, regardless of species composition, the high  $D$  conditions during the drought period are sufficient to maintain average  $E_C$  similar to that of wet periods.

Clearly, this conclusion cannot be generalized to a long series of drought years. For example, a similar hardwood forest in this region (Wilson and others 2001), also exhibited small interannual variability in  $E_C$  (C.V. = 10%) with no apparent response to annual  $P$ ; however, in a long-term experiment where throughfall was manually reduced by a third, growing season  $E_C$  was reduced an average of 23% (SD = 8%) compared to ambient plots (Wullschleger and Hanson 2006). These results suggest that droughts of increasing severity and frequency could ultimately result in mortality of certain species and a change in the forest's species composition.

Because we estimated the components of the hydrologic budget over the majority of the eddy covariance footprint (Oishi and others 2008) and positioned sensors in one of the wettest micro-sites, it is not likely that spatial variation in the hydrological budget is responsible for the apparent water deficit in the upper 0.30 m soil (Figure 7). Instead,

the results suggest that trees were accessing water beneath the depth of the lower soil moisture probes even though the majority of fine roots were concentrated in the upper 0.30 m. Uptake from deeper soil can sustain transpiration in hardwood species during drought, albeit at a reduced rate (Wullschleger and Hanson 2006). Based on the modeled drainage, this water extraction was estimated to range from 23 mm (3% of  $ET_{comp}$ ) during the wet year of 2003 to 53 mm (9%) during the dry year of 2002.

## Evaporation and Drought

Although we have shown how species' sensitivities to soil moisture and atmospheric conditions, combined with the frequency distributions of these conditions, can help stabilize annual  $E_C$ , we must also consider other evaporative losses to explain the observed invariability in evapotranspiration.

Again, let us consider the example drought and non-drought days (Figure 2). Rain did not occur for several days prior to either of these days, so  $I_C$  can be assumed zero.  $E_C$  decreased with drought but eddy covariance-based LE increased from 3.05 mm to 3.28 mm, suggesting that  $E_S$  compensated for the reduction in  $E_C$ . Approximating  $E_S$  using LE- $E_C$ , evaporation increased by 0.81 mm from the non-drought to the drought day (from 0.95 to 1.76 mm), similar to the difference between these days in the  $D$ -based estimates of  $E_S$  (0.85 mm; 0.27 and 1.12 mm, respectively).

Roots that extended below 0.30 m are able to tap into deeper pools of water when the upper layers are exhausted, supplying not only  $E_C$ , but also potentially  $E_S$  through hydraulic redistribution (Emerman and Dawson 1996; Caldwell and others 1998). According to a modeling study for this soil type and shallow rooting depth, hydraulic redistribution is at its maximum when  $\theta$  is between 0.15 and 0.20  $m^3 m^{-3}$  (Siqueira and others 2008). Under peak drought conditions in our study ( $\theta < 0.20 m^3 m^{-3}$ ), several  $\theta$  sensors positioned at 0.05–0.10 m depth exhibited nightly increases of 0.0075  $m^3 m^{-3}$ . When these increases are scaled to the upper 0.15 m soil, they translate to 1.125  $mm d^{-1}$ , approaching the 2  $mm d^{-1}$  of  $E_S$  estimated during these periods. Because water is simultaneously added to the top soil layer through hydraulic redistribution and subtracted through evaporation, the pattern observed by the soil moisture sensors represents only a portion of the hydraulic lift.

Daily, drought conditions which reduced  $E_C$  corresponded with increased  $E_S$ . Weekly, as  $\theta$  decreased, no changes were observed in weekly

$ET_{\text{comp}}$  or the ratio of  $E_C$  to  $ET_{\text{comp}}$  (Figure 6, Table 4), suggesting that evaporative losses were fairly consistent through the growing season. Integrated over the growing season or annually, the relatively high rates of  $E_S$  during droughts did not completely compensate for the reduction in the other component of evaporation,  $I_C$ , though they weakened the relationship between  $ET_{\text{comp}}$  and  $P$  (Figure 8). These processes, driven by the inverse, non-linear relationship between  $D$  and  $\theta$ , produce annual stand evapotranspiration that is a fairly conservative quantity ( $CV = 4\%$ ) in comparison to average annual  $P$  (17%) or PET (10%). The annual precipitation in the driest year of this study exceeded  $ET_{\text{comp}}$ , and extrapolation of the observed patterns (Figure 8) suggests that the evapotranspiration demands of the forest would likely be met even in the driest year on record.

### Downstream Implications

At an annual time-scale, each component of the hydrologic budget showed a different sensitivity to changes in  $P$  (Figure 8). Assessing the annual hydrologic budget (Eq. 1) in terms of changes in precipitation can be done based on

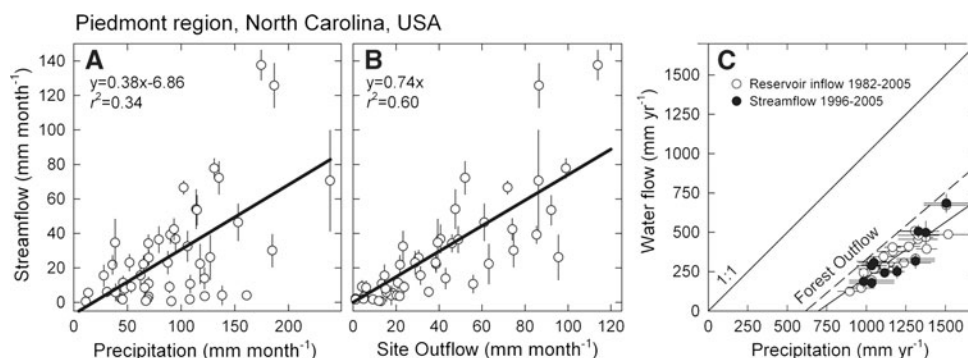
$$\delta P \approx \delta I_C + \delta E_S + \delta E_C + \delta Q + \delta F_O \quad (3)$$

(Changes in annual storage ( $\Delta S$ ) are less than  $15 \text{ mm y}^{-1}$  due to ample winter precipitation and can be neglected.) The combination of these terms based on the information in Figure 6 results in  $\delta I_C + \delta E_S + \delta E_C \approx 0$  with respect to  $\delta P$  ( $P$ -value  $> 0.20$ ), allowing Eq. (3) to be expressed as

$\delta P \approx \delta Q + \delta F_O$ . Thus, once precipitation (reasonably well-distributed throughout the growing season) exceeds the annual minimum used by the forest for evapotranspiration ( $\sim 577 \text{ mm}$ , indicated by the dotted line in Figure 8), each millimeter increase of  $P$  should lead to a millimeter increase of outflow ( $O = Q + F_O$ ) from this forest stand, augmenting the supply to groundwater and downstream water bodies.

To estimate long-term mean outflow from our site, we linearly regressed annual outflow versus  $P$  and employed the long-term average  $P$  at the site (1146 mm). Based on the regression for our site ( $O = 0.881 \times P - 478$ ,  $r^2 = 0.99$ ,  $n = 4$  years), long-term mean outflow was 535 mm, close to (only 8% lower) the outflow from a similar Tennessean forest ( $O = 0.720 \times P - 317$ ,  $r^2 = 0.85$ ,  $n = 8$  years; after Hanson and others 2003, 2004). Although species composition can alter outflow if it leads to differences in  $E_C$  (Hornbeck and others 1997), and certain species are indeed so sensitive to drought that a strong reduction is observed in evapotranspiration in years of low  $P$  (Stoy and others 2006), the simulated annual water budgets based on the most drought-sensitive broadleaved species in this study resulted in only small changes in  $E_C$  and thus  $Q$ . Our results support the notion that forest transpiration can be interannually conservative, largely independent of precipitation or exact species richness, making downstream outflow the most sensitive hydrologic flux to variations in  $P$ .

Drainage and runoff from forests depend not only on precipitation, but also evapotranspiration



**Figure 9.** Comparisons of monthly stream flow from seven local gauging stations with (A) precipitation and (B) water outflow (drainage + runoff) from the study site (volume per unit time per unit watershed area) from 2002–2005. The relationship with precipitation has a significant negative intercept ( $P$ -value  $< 0.05$ ) whereas that with outflow is not significant (0.44). (C) Comparisons of annual precipitation from seven meteorological stations in the watershed with estimated watershed outflow (based on combined broadleaf and pine forest outflow; dashed line) and with stream-flow (closed circles) and inflow to a nearby reservoir (open circles). Annual downstream water flow varied linearly with precipitation ( $r^2 = 0.77$ ,  $P$ -value  $< 0.0001$ ). Error bars represent 1 standard deviation. Stream flow was highly correlated with inflow rate to local reservoirs ( $r^2 = 0.91$ ,  $P$ -value  $< 0.0001$ , data not shown).

and soil moisture. We compared streamflow from seven watersheds to precipitation and our estimate of outflow. Although this type of broadleaf stand represents on average 44% of the watershed area, outflow from such forests is similar to that estimated from pine covered areas (Schäfer and others 2002; Kim 2009), so our estimate of outflow represents approximately two-thirds of the area, with the remainder covered mostly by agriculture and pasture fields. Assuming that our forest outflow rates represent the rates from the entire watersheds, we find that the variation in monthly streamflow was explained appreciably better by outflow than precipitation (Figure 9A, B). Annually, the estimated outflow set an upper limit for water flow in nearby streams, and by extension to inflow of a reservoir fed by these streams (Figure 9C). The upper limit represents the maximum potential drainage to downstream water supply, excluding other water losses from the system such as subsurface flow, deep infiltration, groundwater withdrawal, and additional evaporation from locally impounded water, together producing an average offset of 143.8 (SD = 69.5) mm  $y^{-1}$ . Figure 9C illustrates that water supply downstream is not proportionate to precipitation, but is offset by a relatively consistent evapotranspiration demand (nearly 700 mm  $y^{-1}$  in this area) and then receives nearly all subsequent precipitation. Clearly, different dominant mechanisms and evapotranspiration responses can be expected in different biomes, further complicated by land-cover conversions. However, our analysis shows that in areas dominated by forests, tree physiology and forest hydrology extract a tax on precipitation before allowing water to move on to downstream water users.

## SUMMARY

Species-level reductions in transpiration during drought often result in lower-than-maximum canopy-level transpiration observed under comparable atmospheric conditions. However, on the annual time scale, even severe growing season droughts may not lead to reductions in annual transpiration because the magnitude and duration of drought-induced reductions of canopy transpiration are similar to the magnitude and frequency of reductions in transpiration associated with rain events in wet years. Furthermore, evapotranspiration can remain consistent among years because atmospheric conditions associated with drought (that is, high radiation and atmospheric vapor deficit) provide a strong driving force for both

canopy transpiration and soil evaporation, compensating for reduced canopy interception losses. The resulting conservative behavior of evapotranspiration means that changes in annual precipitation lead to similar changes in the amount of water that flows from forests to streams and reservoirs.

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