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CARRY-OVER EFFECTS OF WATER AND NUTRIENT SUPPLY ON WATER USE OF *PINUS TAEDA*

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Abstract. A study of the effects of nutrients and water supply (2 × 2 factorial experiment) was conducted in a 12-yr-old stand of loblolly pine (*Pinus taeda* L.) during a period in which soil moisture was not augmented by irrigation because of frequent rain events. Information on the responses of sapwood-to-leaf area ratio and early-to-late wood ratio, to four years of treatments led to the hypothesis that the combination of increased nutrient and water supply (IF treatment) will increase tree transpiration rate per unit leaf area ($E_{C,l}$) above $E_{C,l}$ in the control (C), as well as increasing $E_{C,l}$ above that when either the supply of water (I) or of nutrients (F) is increased. We further hypothesized that canopy transpiration (E_C) will rank IF > F > I = C, based on the ranking of leaf area index (L) and assuming that the ranking of $E_{C,l}$ is as first hypothesized. We rejected our first hypothesis, because F had lower $E_{C,l}$ than the other treatments, rather than IF having higher values. We could not reject the second hypothesis; the ranking of average daily E_C was 1.8 mm for IF, 1.2 mm for F, and 0.7 mm for both C and I (SE < 0.1 mm for all treatments). Thus, it was the lower $E_{C,l}$ of the F treatment, relative to IF, that resulted in ranking of E_C similar to that hypothesized. Lower $E_{C,l}$ in F trees was found to relate to lower canopy stomatal conductance, even though soil moisture conditions during the time of the study were similar in all treatments. Only trees in the F treatment absorbed a substantial amount of water (25%) below 1 m in the soil. These results indicate a "carry-over" effect of irrigation when combined with fertilization that increases E_C in irrigated trees, relative to unirrigated trees, even under conditions when soil moisture is high and similar in all treatments.

Key words: local water balance; Pinus taeda; *sapflux; stand transpiration; water and nutrient supply.*

INTRODUCTION

In the past several decades, both the demand for wood products and society's demand for ecologically sound land management practices have increased dramatically (Binkley 1986). Fertilization is becoming an important silvicultural option to help meet increased requirements for wood production per unit land area (Allen et al. 1990). While irrigation is rarely used as a silvicultural option, the depth of the water table is managed in some plantations of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Englm.) on the southeast coastal plain of the United States (Ralston 1965). Thinning is more commonly used to increase water availability to the residual stand through increases in throughfall and lower stand water use (Stogsdill et al. 1989). Silvicultural alteration of whole-stand water use may change forest hydrology, giving rise to potentially large effects on the water table (Calder et al. 1993), water yields downstream (Vose and Swank 1994), and biosphere–atmosphere exchange of mass and energy (Sellars et al. 1997).

Numerous studies have found increases in canopy transpiration (E_C) with increasing leaf area index (L; Oren et al. 1986, Meinzer and Grantz 1991, Köstner et al. 1992, Hatton et al. 1995, Vertessey et al. 1995, Arneth et al. 1996, Oren et al. 1996, Sala et al. 1996, Teskey and Sheriff 1996). These studies quantified the effect of L on E_C, by thinning stands to specified levels, or by using natural variation in L due to variation in site quality, but not in response to manipulation of L by controlled supplies of water and nutrients. Other studies investigated the effect of site quality on other variables that may also affect E_C, including hydraulic conductance (k; Whitehead et al. 1983, Yang et al. 1988, Coyea and Margolis 1992) and sapwood-to-leaf area ratio (A_S:A_L; Whitehead et al. 1984, Mencuccini and Grace 1995). Thus, in most cases, variation in E_C may be interpreted in terms of variation in variables affected by site quality, an ambiguous quantity at best, but not by specific factors that control site quality. This study investigates the responses of E_C to differences in site fertility and water availability, two important determinants of site quality, under otherwise similar site characteristics.

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TABLE 1. Response of one block of the four experimental treatments (C, control; I, irrigated; F, fertilized; and IF, irrigated/fertilized) at Scotland County, North Carolina, USA.

Treatment	A_B† (m^2/ha)	A_B (m^2/ha)	L‡ (m^2/m^2)	$A_S:A_G$‡ (m^2/ha)	Early-wood/late-wood§	$A_S:A_L$§ (m^2/cm^2)	Number of rings: Outer 20 mm	Number of rings: Inner 20 mm
C	11.2	13.6	1.79 (100)	9.0 (100)	0.98[a]	5.0[a]	4	4
I	11.6	12.9	1.96 (109)	9.0 (100)	1.30[a]	4.5[a]	4	4
F	19.6	20.0	3.32 (185)	15.2 (165)	1.48[a]	4.3[a]	2	2
IF	25.9	23.9	3.64 (203)	21.9 (244)	2.34[b]	5.8[b]	2	2

Notes: Stand basal area, including bark (A_B), sapwood area per unit of ground area ($A_S:A_G$), leaf area index (L), and sapwood area per unit of leaf area ($A_S:A_L$) are reported when L is at its seasonal maximum. The number of growth rings is reported for the outer 20 mm and inner 20 mm of xylem.

† Whole plot measurements; all other variables reflect subplot values.

‡ Values in parentheses are percentage increases relative to control (C).

§ Letters a and b indicate significant differences within a column at the $P = 0.05$ level.

In general, E_C increases asymptotically with L because of decreasing water availability with increasing rates of water use. Water availability is further reduced in stands with high L because of increased interception losses (Stogsdill et al. 1989). Besides increasing L (Brix 1981), fertilization increases biomass partitioning to aboveground and decreases soil exploration by fine roots (Linder and Axelsson 1982, Axelsson and Axelsson 1986, Linder et al. 1987). While fertilization may increase E_C with L when water is available, other consequences of fertilization, which include higher interception, lower ratio of fine root mass to L, and, perhaps, a root system not thoroughly occupying the soil, may alter the amount and pattern of stand water use between rain events.

Morphological and physiological effects of fertilization may affect vapor phase conductance through the stomata and liquid phase conductance to the stomata. At the leaf level, fertilization may increase photosynthetic enzyme levels, resulting in lower internal CO_2 concentration and causing stomatal conductance to increase (Willmer and Fricker 1996). Higher stomatal conductance will increase transpiration rate per unit leaf area ($E_{C,l}$) in fertilized stands, if higher L does not attenuate light to the point that stomatal conductance in the lower layers is strongly reduced. Within the plant–soil continuum, $E_{C,l}$ is a function of liquid phase conductance and A_S:A_L at a given path length and water potential difference (Whitehead and Jarvis 1981). Thus, the equation of Whitehead and Jarvis (1981) is rearranged:

$$E_{C,l} = \frac{E_C}{A_L} = \frac{k \cdot A_S}{A_L} \cdot \left(\frac{n\rho_W \Delta\Psi}{l\eta} \right) \quad (1)$$

where k is hydraulic conductivity, n is number of stems, ρ_w is the density of water, $\Delta\Psi$ is the water potential gradient between the soil and the plant, l is the path length of the water potential gradient, and η is the viscosity of water. Based on Eq. 1, $E_{C,l}$ may increase with fertilization as a result of increases in hydraulic conductance and A_S:A_L, as long as $\Delta\Psi$ is unaffected.

While the effect on water use of several of the aforementioned variables can be isolated in field studies, variation in water availability greatly complicates the analysis, and results are less conclusive. Recently, a network of sites has been established to investigate the effects of experimentally controlled water and nutrient availability on the growth and water use of trees and stands (Teskey et al. 1994). We used one of these sites, in a *P. taeda* plantation, to investigate the water use dynamics of *P. taeda* subjected to controlled supply of water and nutrients since 1992 (Albaugh et al. 1998). The treatments include the following: control, irrigation, fertilization, and irrigation–fertilization (referred to hereafter as C, I, F, and IF, respectively).

Responses to treatments in terms of stand structure and morphology (Table 1; Albaugh et al. 1998) and physiology (Murthy et al. 1996) were used to propose hypotheses regarding the water use of *P. taeda* trees under fertilization and irrigation, during a period in which soil water was not limiting (>60% field capacity; Bassett 1964). Using this period permitted us to quantify the effect of changes in tree, stem, and leaf characteristics induced by the long-term effect of irrigation and fertilization on water use characteristics, unconfounded by the availability of soil moisture during the study. In this study, n, η, ρ_w, and l (Eq. 1) do not vary between treatments. Moreover, measurements of predawn and midday leaf Ψ (the difference is a proxy of $\Delta\Psi$ [Fahey and Young 1984]) did not vary between treatments during the summer of 1995 (Laviner 1997), and the soil during the study had a similar supply of water from precipitation in all treatments. Thus, differences in $E_{C,l}$ among treatments may be influenced by k and A_S:A_L.

While actual measurements of k are preferable, a qualitative index of k can be inferred from early-to-late wood ratio, because the proportions of large lu-

mens increase with the ratio of early-to-late wood (Tyree and Ewers 1991, Pothier et al. 1993*a*,*b*, Sellin 1993). Based on the responses to treatments (Table 1), our first hypothesis is that IF, which has the highest early-to-late wood ratio and A_S:A_L, will have the highest $E_{C,l}$. Furthermore, because $E_C = E_{C,l} \times L$, and, given that L is higher in both fertilized plots (Table 1), our second hypothesis is that E_C will rank as IF > F > I = C.

Materials and Methods

Study site and treatments

The Southeast Tree Research and Education Site (SETRES) was established in the Sandhills of North Carolina, USA (35° N, 79° W), on infertile, well drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series) in 1992. The soil has an available water holding capacity of 0.16–0.20 m in the upper 2 m of the profile. Annual precipitation averages 1210 mm, with occasional growing season water deficits. Sixteen 50 × 50 m treatment plots, with 30 × 30 m measurement plots centered in the treatment plot and separated by 10 m buffers, were established in 1992, in a mixed-families stand of North Carolina Piedmont *P. taeda* planted in 1984. Treatments were a 2 × 2 factorial combination of nutrition and water additions, replicated four times. Nutrient treatments have been maintained since March 1992, and water addition treatments have been maintained since April 1993. Nutrient treatments consisted of optimal nutrition, which was defined as maintaining nitrogen concentration of 1.3% in upper canopy foliage, with phosphorus, potassium, calcium, and magnesium balanced with nitrogen levels. Boron was also added to maintain foliar levels >12 ppm. Foliar nutrient status was monitored monthly and applied annually to meet target values. Water additions were made to keep available soil moisture between field capacity and 40% of available soil water in the upper 50 cm of the soil profile, corresponding to 3.0 cm soil water content in the surface 50 cm of soil, as measured with time domain reflectometry. For details of nutrition and water treatments, see Albaugh et al. (1998) and Murthy et al. (1996).

Sap flux measurements

We measured the flux of water in stem xylem of eight trees in a 6 m diameter subplot, within each of the four main effect treatment plots (C, I, F, IF), in one block of the experimental site from 29 August–23 October 1996. No irrigation was applied during the time of water flux measurements, due to frequent rain events that maintained the available soil water >60%. Water flux in the xylem (J_S, measured in $g_{H_2O} \cdot m^{-2}_{sapwood} \cdot s^{-1}$) was estimated using the constant heat method of Granier (1987). Measurements were made in three positions, two below the live crown and one ~1 m from the terminal bud. The lower sensors were installed at two depths within the xylem to permit scaling of flux to stand transpiration (Phillips et al. 1996, Oren et al. 1998*a*). The upper sensor was used to assess time lags between transpiration and water uptake, in order to facilitate evaluation of diurnal fluxes (Loustau et al. 1996).

In each treatment, J_S was measured at three stem positions, upper (height of ~7 m), and outer and inner xylem of the lower stem (height of 1.4 m). We installed outer xylem sensors in all eight trees of each treatment, with inner sensors in a subset of five of the eight trees, and upper sensors in the other three trees of each treatment. The upper stem measurements were carried out using 10 mm sensors installed at a point where the upper stem diameter was 40 mm (J_{Sup}). Lower stem measurements were made using two 20 mm sensors, one in the outer 20 mm of xylem (J_{Sout}) and one at a depth of 20–40 mm from the cambium (J_{Sin}). To avoid thermal gradients from direct radiation, all sensors were shielded with plastic covers; longitudinal stem temperature gradients, which may introduce error in estimating flux (Goulden and Field 1994), were <0.1°C throughout an entire sunny day (or ~7% of a diurnal minimum temperature difference between the heated and unheated probes of the sensor).

Analyses of daily water use were performed on sums of J_S for 24 h periods beginning at 0500, which approximately corresponded to the time of zero flow and, therefore, accounts for nighttime recharge (Phillips and Oren 1998). We calculated E_C using the hydroactive xylem area as a scaling variable (Oren et al. 1998*b*). Sapwood area per ground area (A_S:A_G) was calculated using the diameter of all trees in the subplot and subtracting bark thickness measured on cores taken from the eight measurement trees and two additional trees from each subplot. Based on visual inspection of the cores, no heartwood was present. The calculation of $E_C = J_S \times (A_S:A_G)$ and its standard error was slightly modified from Oren et al. (1998*b*), because J_{Sin} was monitored continuously. When scaling J_{Sin} to the stand, it was assumed that water flux of the entire inner xylem area (inward of 20 mm depth) was represented by the sensor installed in the inner xylem.

Environmental measurements

Vapor pressure deficit (D; calculated from relative humidity and temperature, based on Goff and Gratch [1946]), soil volumetric water content (θ), and overstory photosynthetically active radiation (PAR) were also monitored. A relative humidity and temperature probe (Vaisala HMP 35C, Campbell Scientific, Logan, Utah, USA) was positioned at a height of 7 m in the center of each subplot and provided data for calculating D. To evaluate the use of D as the driving force for transpiration, leaf temperatures were measured with infrared thermometry (Everest Interscience, Palo Alto, California, USA) on several clear days. Leaf-to-air temperature differences were always <+0.1°C. Diurnal

average of D was calculated by averaging daytime D values only, the period in which D affects canopy transpiration, and therefore uptake (Phillips and Oren 1998), and normalized by the number of daylight hours (determined as all half-hour intervals in which PAR > 0) divided by 24 (D_Z; Oren et al. 1996). This facilitates comparisons over seasons in which day length changes substantially. PAR above the canopy was monitored using a quantum sensor (Li-190s, Li-Cor, Lincoln, Nebraska, USA).

Soil volumetric moisture content (θ) was measured using automated time domain reflectometry (TDR) probes with 6 cm long steel rods (Theta Probe, Delta-T Devices, Cambridge, UK). Detailed studies of horizontal and vertical soil moisture content in a clay soil showed that the horizontal variability can be very large but that that the vertical variability in soil moisture is much larger (Todd 1995, Katul et al. 1997, Oren et al. 1998*a*). In the sandy soils in this study, we expect horizontal variability to be small relative to the vertical variability. Furthermore, our interest lies in the change in soil moisture between measurement times (ΔS), excluding times of free drainage after rain and irrigation events. The variability in ΔS is very small (Katul et al. 1997). We therefore selected to install the TDR probes vertically, in order to capture the maximum variability in soil moisture change. In order to install the probes with minimal disturbance to the monitored soil volume, a soil pit was dug to 1.0 m depth in the center of the four subplots, probes were inserted horizontally to 12 cm from the wall of the pit, and the pit was refilled. The probes were arrayed vertically at 5, 10, 25, 50, and 100 cm depths. Laboratory calibration of the TDR probes showed a large deviation from the constants provided by the manufacture, so constants were adjusted.

Xylem flux and all environmental sensors except PAR were sampled every 30 s, and 30 min average values were logged (DL2, Delta-T Devices, Cambridge, UK). PAR was sampled every 1 s and averaged every hour using a separate data logger (CR7, Campbell Scientific, Logan, Utah, USA).

Stand structural measurements

Structural and morphological measurements were generally conducted in the entire study area and then corrected if necessary for subplot deviation (Table 1). Tree leaf areas were calculated using allometric relationships with tree basal area, derived from winter biomass harvests (Albaugh et al. 1998). Leaf area estimates for each tree were corrected for seasonality, using the relative increase in L from winter to the sampling period as determined with a leaf area meter (LAI-2000, Li-Cor, Lincoln, Nebraska, USA) and litterfall. To estimate L (projected), "winter equivalent" leaf area of each tree in each subplot was estimated from its diameter, and the treatment-specific allometric relationships. Leaf area of all individuals in each subplot was summed, divided by the plot area (133 m^2), and corrected for seasonal leaf area dynamics. Using the bark thickness measured from the cores (12.6 $\pm$ 1.2, 10.4 $\pm$ 0.9, 11.0 $\pm$ 0.9, and 9.0 $\pm$ 0.9 mm for C, I, F, and IF respectively, $P < 0.05$ for C vs. IF only), A_S:A_L was calculated for each tree, based on estimated leaf area and inside-bark sapwood area. Early-to-late wood ratios were estimated from cut discs of harvested trees, using cell diameter change as the criterion for the transition (A. Sampson, *personal communication*). For comparisons between J_S in the lower stem and tree- or stand-averaged A_S:A_L, L, and early-to-late wood ratios, an average J_S weighted by the sapwood area at each sensor depth was calculated as tree averaged sap flux (hereafter J_S).

Statistical analyses

Technical limitations and cost preclude a truly replicated study. While studies based on sap flow measurements have used individual plants clustered within a treatment plot as replicates; this, in fact, represents pseudoreplication, much the same as individual plants in a growth chamber or a greenhouse, and may cause erroneous conclusions (Evans et al. 1984, Hurlbert 1984). However, while the scope of this study is constrained by the design, the apparent impact of the treatments was very large in comparison to the natural variation within treatments (Table 1), ensuring that the results reflect treatment rather than random effects. All statistical analyses were made using SAS, Verson 6 (1989). Analyses of variance (ANOVAs) on all daily data were conducted as repeated measures analysis with days as the repeated measure (Hicks 1993). Preplanned comparisons were conducted on single-classification ANOVAs using the following hypotheses: (1) F and IF are different from C and I, (2) F is different from IF, and (3) C is different from I. All ANOVA assumptions were met (Sokal and Rohlf 1995), except for days with rain events when water flux was low and not normally distributed (4 of 53 d) and the lack of independence in the data inherent to time series. However, we feel that using daily values of water flux for ANOVAs largely removes the dependence of one value of a variable on the next, as values change drastically (up to three-fold) with stochastic variation in the weather. For heterogeneity of slope analyses, J_S of each tree was multiplied by the average A_S:A_G of that treatment to obtain within-group error terms for each day.

Analyses of difference between treatments without regard to weather relied on a two-way ANOVA, using fertilization and irrigation as main effects. If interaction between fertilization and irrigation was significant, we followed with a single classification ANOVA and used preplanned contrasts to separate means, recognizing that interaction effects are present between irrigation and fertilization (Sokal and Rohlf 1995). In addition, we performed tests of slope difference among treat-

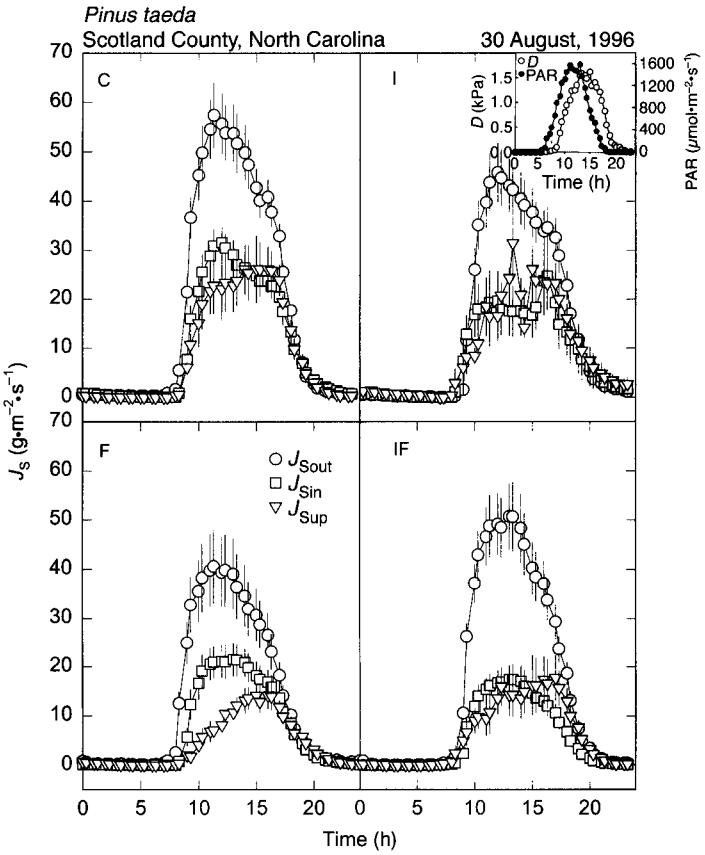

FIG. 1. Diurnal pattern of half-hour average water flux in the xylem for the control (C), irrigated (I), fertilized (F), and irrigated/fertilized (IF) treatments for a representative sunny day. Key to symbols: circles, outer 20 mm of xylem at 1.4 m height (J_{Sout}; n = 8 individuals); squares, the next 20 mm of xylem (J_{Sin}; n = 5 of the eight individuals); and triangles, upper xylem at approximately 7 m (J_{Sup}; n = 3 of the eight individuals). Inset figure is a diurnal pattern of vapor pressure deficit (D) and photosythetically active radiation (PAR). Vertical lines indicate ±1 SE of the means.

ments on water flux, in relation to D_Z, in order to decrease the unexplained variability in the data.

RESULTS

Diurnal patterns in J_S and environmental variable

In Fig. 1, we depict the diurnal course of water flux on a representative, sunny day. In each treatment, J_{Sout} is approximately double J_{Sin} and J_{Sup} at its maximum value. On this day, maximum J_{Sout} was 57.4, 45.8, 40.6, and 50.7 g·m^{-2}·s^{-1}; while J_{Sin} was 31.6, 24.7, 24.0, and 20.0 g·m^{-2}·s^{-1}, for C, I, F, and IF, respectively. Maximum J_{Sup} was comparable to J_{Sin} at 26.1, 31.5, 14.1, and 17.7 g·m^{-2}·s^{-1} for C, I, F, and IF, respectively. Comparing the patterns in all sensor positions with patterns of D (Fig. 1, and inset) it appears that the J_{Sup} followed closely the pattern in D, while J_S of the lower two sensors followed a pattern that peaked between the pattern of PAR and D.

Fig. 2 depicts water flux data, from the same day as Fig. 1, plotted against D to assess time lags caused by hysteresis between these variables. Hysteresis in J_{Sin} and J_{Sup} was smaller than that in J_{Sout}. The little hysteresis in J_{Sout} in IF treatment, and its absence in I relative to C and F, demonstrate that J_{Sout} was more correlated with D in IF and I. Evaluated in terms of the greatest difference between the ascending and descending parts of the hysteresis curve, hysteresis in J_{Sout} was 30% greater in F than C treatment for all clear days ($P < 0.001$ for all clear days; $P < 0.01$ for the day shown in Fig. 2).

Daily pattern in environmental and water use variables

Fig. 3 summarizes environmental variables over the entire measurement period. Missing data correspond to a loss of power during and after hurricane Fran from day-of-year 249–254. The precipitation values (P) were unusually high and frequent for that time of year, with a maximum of 78.9 mm/d and a total of 358.5 mm (Fig. 3a); therefore, irrigation was not applied to I and IF plots during the measurement period. Each rain event caused a large, transient increase in θ (up to 0.12 m^3 H_2O/m^3 soil), as a front rapidly moving down the profile. We note that the percent change in θ, once the wave of water passed through the profile, is less than the manufacturer's stated probe accuracy, but the time series of θ indicated that changes of 0.002 m^3 H_2O/m^3 soil can be readily discernible, even if the absolute value may contain an error. The rate of soil moisture depletion was similar for all depths in C, I, and F, and lower in these treatments than all depths in the IF, except for during the initial large decrease in θ, due to gravitational drainage, immediately after large rain events. There was also no systematic pattern in θ with

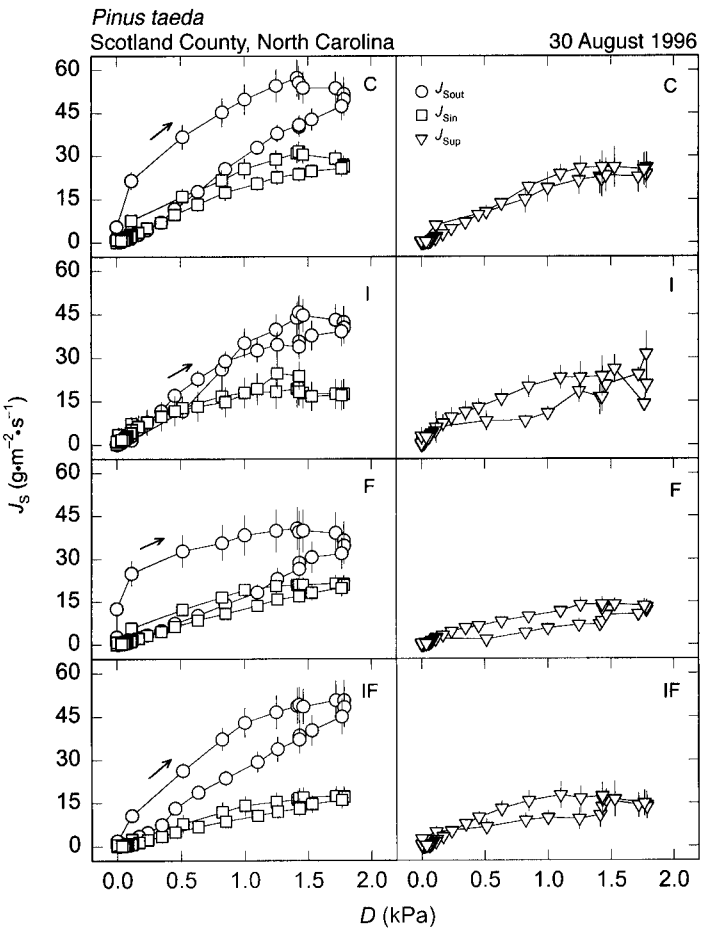

FIG. 2. Diurnal relationship between vapor pressure deficit (D) and water flux in outer (J_{Sout}) and inner xylem (J_{Sin}) of the lower stem, and the outer xylem of the upper stem (J_{Sup}) for each treatment. Treatments are control (C), irrigated (I), fertilized (F), and irrigated/fertilized (IF). Arrows show direction of hysteresis.

depth for ten randomly selected days ($P > 0.05$). Averaging θ to daily values across the profile (θ_D) reduced the effect of the moving front. θ_D was similar in C, I, and F treatments ($P > 0.1$; multiple comparisons), all of which were lower than IF ($P < 0.05$). Thus, θ_D was averaged for C, I, and F treatments ($\langle\theta_D\rangle$) for further analysis (Fig. 3b).

There was no difference in D_Z among treatments ($P > 0.1$), which ranged 0.05–1.5 kPa (Fig. 3c). Daily sums of PAR ranged 5.2–47.3 mol·m^{-2}·d^{-1} (Fig. 3d). While D_Z and PAR were generally positively correlated ($R = 0.84$), for day-of-year 257–259 PAR was relatively high while D_Z was low. This was due to rain events at predawn or postdusk, which caused small changes in daily average PAR, but resulted in high humidity, which depressed D_Z below that expected based on the PAR values.

The effect of interaction between fertilization and irrigation was significant on J_{Sout}, J_{Sin}, J_{Sup}, and E_C ($P < 0.001$ for each), so preplanned contrasts followed (Table 2). The average of daily J_{Sout} over the study period of trees in C treatment was higher (101.5 g·cm^{-2}·d^{-1}) than that of I, F, and IF, which showed similar values (84.0 g·cm^{-2}·d^{-1}; Table 2). The average of daily J_{Sin} over the study period in trees of C and I treatments were similar (59.6 g·cm^{-2}·d^{-1}) and higher than that of F (49.2 g·cm^{-2}·d^{-1}), which was higher still than that of IF (30.3 g·cm^{-2}·d^{-1}; Table 2). The average of daily J_{Sup} over the study period was lower for F (27.7 g·cm^{-2}·d^{-1}) than the other treatments (56.5 g·cm^{-2}·d^{-1}; Table 3). Analysis of J_S (the sapwood area-weighted average of J_{Sin} and J_{Sout}) showed no interaction ($P > 0.05$) or treatment effects (Table 2).

The average of daily E_C over the study period was the same in C and I, but was higher in F and higher still in IF (Tables 2 and 3, Fig. 4a). However, when E_C was normalized by L to $E_{C,l}$, F was lower than in the other treatments ($P < 0.001$; Fig. 4b).

Response of J_S, E_C, and $E_{C,l}$ to D_Z

We investigated the responses of J_S, E_C, and $E_{C,l}$ to D_Z, in order to account for some of the variability in the data and further evaluate treatment effects (Fig. 5, Table 4). Three days were excluded from analyses in F and IF. On each of these days, day-of-year 257–259, rain events occurred during the night, but not during the day, causing D_Z to be substantially lower than expected, based on PAR (Fig. 2), and keeping the canopy wet during a large part of the day. These events caused a relatively large daily sum of J_S, due to a predawn

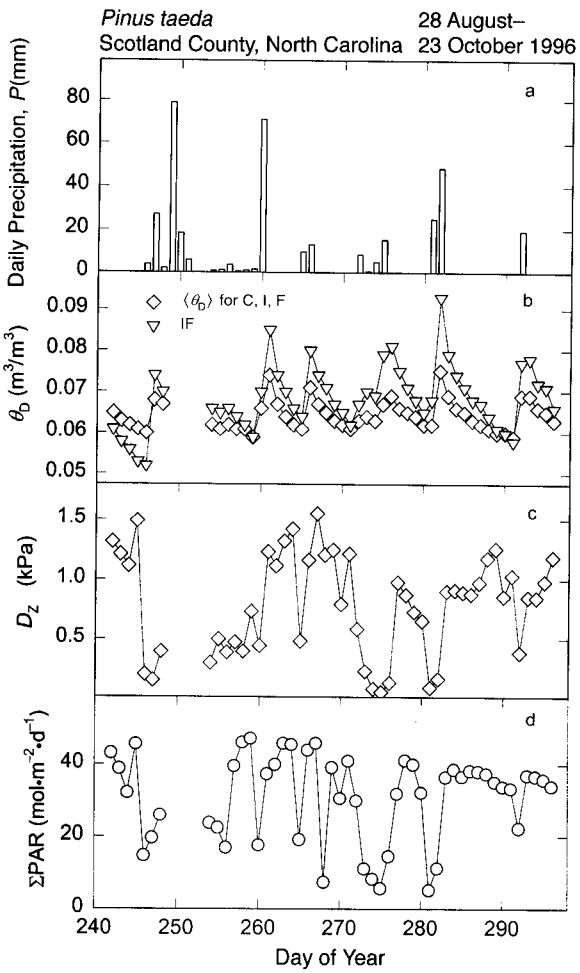

FIG. 3. Time series of (a) daily precipitation (P), (b) daily average soil volumetric water content to 1 m (θ_D), (c) daily light-hours averaged vapor pressure deficit normalized by day length (D_Z), and (d) daily average photosynthetically active radiation (PAR). Error bars were less than the symbol size for D_Z and θ. Treatments are control (C), irrigated (I), fertilized (F), and irrigated/fertilized (IF). Combination of treatments into diamond symbols indicates no significant difference at $\alpha = 0.05$.

TABLE 2. P values for planned contrasts between fertilized and nonfertilized treatments, and between irrigated and unirrigated treatments within each of the fertilization treatments.

Variable	Fertilized vs. nonfertilized	Within fertilized	Within nonfertilized
J_{Sout}	0.0001	0.9122	0.0001
J_{Sin}	0.0001	0.0002	0.8768
J_S	0.2567	0.6789	0.1345
J_{Sup}	0.0169	0.0001	0.7236
E_C	0.0001	0.0001	0.3336

Notes: Contrasts were done for sap flux density of the outer 20 mm xylem (J_{Sout}) and inner 20 mm xylem (J_{Sin}) of the lower stem (1.4 m), and upper stem xylem (J_{Sup}; 7 m). Lower stem weighted water flux is the average of J_{Sout} and J_{Sin}, weighted by their sapwood areas (J_S). Canopy transpiration is E_C.

TABLE 3. Average daily canopy transpiration (E_C) and canopy transpiration normalized by leaf area index ($E_{C,l}$) over the study period, 28 August–23 October 1996, for $n = 54$ d.

Treatment	E_C (1 SE) (mm/d)	$E_{C,l}$ (1 SE) (mm/d)
C	0.7 (0.04)	0.37 (0.03)
I	0.7 (0.04)	0.36 (0.03)
F	1.2 (0.05)	0.29 (0.02)
IF	1.8 (0.09)	0.36 (0.04)

and postdusk recharge of stem storage in F and IF. The recharge became evident as a sharp increase in flux at night in the two fertilized treatments, when diurnal J_S was normalized by D during these days (data not shown). Regression on untransformed water flux data resulted in an uneven distribution of residuals in the relationships of J_S, E_C, and $E_{C,l}$ with D_Z. Linear regression on the log-log (base e) transformed data resulted in an even distribution of residuals. Untransformed data and regression lines are shown in Fig. 5, but results are discussed based on analyses of transformed data.

There was no treatment effect on the response of J_S to D_Z (data not shown; Table 4). When water use was expressed as E_C and regressed against D_Z, E_C of the fertilized stands was higher than the E_C in unfertilized stands, and that of IF was higher than that of F, es-

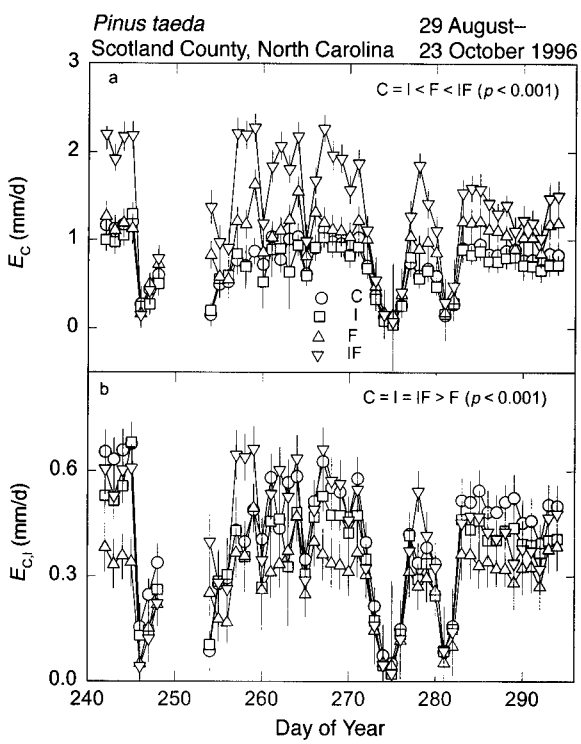

FIG. 4. Time series of (a) daily canopy transpiration (E_C) and (b) daily canopy transpiration normalized by leaf area index ($E_{C,l}$). Error bars are ±1 SE with $n = 8$. Treatments are control (C), irrigated (I), fertilized (F), and irrigated/fertilized (IF).

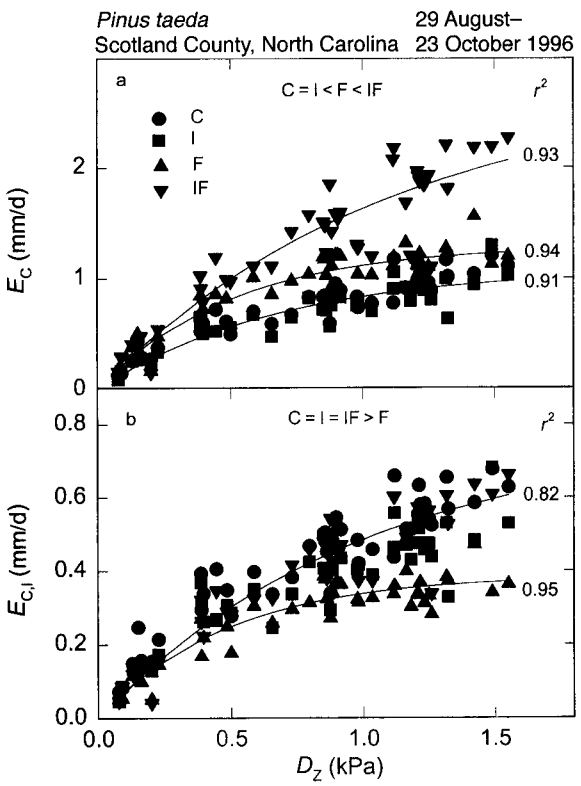

FIG. 5. Regression analysis of (a) daily canopy transpiration (E_C) and (b) daily canopy transpiration normalized by leaf area index ($E_{C,l}$) vs. daily average vapor pressure deficit normalized by daylight hours (D_Z).

pecially on high D_Z days (Fig. 5a, Table 4). Normalizing E_C by L resulted in lower $E_{C,l}$ in F than in the other treatments (Table 4, Fig. 5b). Generally, treatment effects are clearly discernible at high D_Z values and are undetectable at low D_Z values.

DISCUSSION

Long-term nutrient and water additions could alter tree water relations by modifying several tree structural properties (Table 1). Following the formulation of Whitehead and Jarvis (1981; see also Eq. 1), we hypothesized that $E_{C,l}$ will be higher in IF than in the other treatments, due to its higher early-to-late wood ratio (as an indication of k) and A_S:A_L. Contrary to our hypothesis, IF did not show higher $E_{C,l}$ (Figs. 4 and 5). Instead, F showed lower $E_{C,l}$ than all the other treatments. We further hypothesized that stand level E_C would reflect both $E_{C,l}$ and L, such that E_C will rank from highest to lowest as IF > F > C = I. The observed ranking of E_C was in fact as hypothesized (Tables 2, 3, and 4, Figs. 4 and 5), although not entirely for the reasons stipulated.

Treatment effects on $E_{C,l}$

Early-to-late wood ratio has been used as an indicator of hydraulic conductance, because higher ratios indicate a greater number of large diameter tracheids (Pothier et al. 1993*a*,*b*, Tyree and Ewers 1991, Sellin 1993). Because tracheid diameter increases with fertilization (Megraw 1985), it follows that hydraulic conductivity should also increase. However, bordered pits between tracheids (Schulte and Gibson 1987) exert the greatest resistance to water flow in stems of conifers, such that shorter tracheids reduce hydraulic conductivity (Siau 1984). Fertilization decreases tracheid length (Yang et al. 1988), potentially increasing the contribution of bordered pits to water flow resistance, thus negating the effect of the concurrent increase in tracheid diameter on flow. Consequently, when nutrition is altered, early-to-late wood ratio may become a poor index of hydraulic conductivity. High stem growth rates may also indicate increased hydraulic conductivity (Coyea and Margolis 1992). However, F trees, which grew faster than I trees (both treatments had similar A_S:A_L and early-to-late wood ratio; Table 1), displayed lower $E_{C,l}$ (Figs. 4 and 5). Thus, morphological traits that serve well as indicators of hydraulic conductivity in studies on trees growing at different rates due to site quality (Coyea and Margolis 1992) or canopy position (Sellin 1993) may be poor indicators of hydraulic conductivity of trees growing at different rates due to fertilization or irrigation.

TABLE 4. Comparisons between treatment pairs of the regression slopes between daily average vapor pressure deficit (D_Z) and sapwood weighted average sap flux density (J_S), stand transpiration (E_C), and transpiration per unit leaf area ($E_{C,l}$; Fig. 5). Matrix elements are P values for comparisons among treatment pairs.

Variable	Treatment	I	F	IF
J_S	C	0.222	0.146	0.074
	I	...	0.929	0.113
	F	...	...	0.232
E_C	C	0.246	0.001	0.001
	I	...	0.001	0.001
	F	...	...	0.010
$E_{C,l}$	C	0.234	0.001	0.543
	I	...	0.001	0.603
	F	...	...	0.001

Alternatively, providing fertilizers only may have affected both k and A_S:A_L in F, such that leaf specific conductivity (LSC = $k \cdot A_S/A_L$) decreased, resulting in a lower stomatal conductance (g_S) and $E_{C,l}$. Murthy et al. (1996) found no treatment effect on maximum g_S of current-year or one-year-old foliage during one growing season at this study site, except in one-year-old foliage in September when leaves of the F treatment had lower maximum g_S than the other treatments. We perform a post facto analysis of the responses of canopy stomatal conductance to the treatments.

Canopy conductance

We calculated an index of daily mean canopy stomatal conductance ($G_{C,l}$; Phillips and Oren 1998) using an inversion of the Penman–Monteith equation (Gran-

ier and Loustau 1994, Martin et al. 1997) and L. This approach to calculating $G_{C,I}$ is particularly suitable when conductance is calculated from sap flux data in *P. taeda* trees, which may have large storage of water in the stem (Phillips et al. 1997, Phillips and Oren 1998). We calculated ensemble daytime average boundary layer conductance (n = 54 d at 60 min intervals; Grace 1989) from wind speed that was measured in a small clearing and reduced to 50% to reflect air movement inside canopy. Boundary layer conductance was 33-fold total conductance, thus indicating that total conductance is similar to canopy stomatal conductance (Jarvis and McNaughton 1986). This was supported by the small difference in temperature between the surface of leaves and the air in the canopy ($<+0.1$°C). Our maximum $G_{C,I}$ value for F (0.09 $mol \cdot m^{-2} \cdot s^{-1}$) was lower ($P < 0.001$) than that of the other treatments (average of 0.13 $mol \cdot m^{-2} \cdot s^{-1}$). Based on Kinerson (1974), *P. taeda* in this area in September carries equal proportions of current-year and one-year-old foliage. We averaged the maximum g_S of current and one-year old foliage measured with a porometer in each treatment from Murthy et al. (1996) and obtained 0.12 $mol \cdot m^{-2} \cdot s^{-1}$ for F and an average of 0.16 $mol \cdot m^{-2} \cdot s^{-1}$ for C, I, and IF. Thus, $G_{C,I}$ was 75–80% of the maximum g_S obtained during the same season two years earlier; both methods show the conductance of F at ~70% of the other treatments. It is possible that the foliage of F trees developed under conditions of relative soil drought in comparison to (1) C and I trees, because higher L in F stands would increase interception losses and lead to a faster use of available soil water (Stogsdill et al. 1992); and (2) IF trees, because these were irrigated such that drought conditions were not permitted to develop as in F stands. If foliage developing under drought has a lower maximum leaf conductance (Whitehead et al. 1983), a more conservative water use rate may reduce $E_{C,I}$ even when soil moisture is not limiting, indicating a carry-over effect.

Carry-over effect of irrigation

Further evidence of carry-over effects of irrigation is apparent in the diurnal J_S pattern. Although during the study period soil moisture was similar in all treatments and was relatively high (Fig. 3), diurnal behavior of J_S appeared to differ between the irrigated and non-irrigated treatment pairs, as evident especially when J_{Sout} is evaluated against D (Fig. 2). Both the inner 20 mm xylem in the lower position, and the upper xylem had developed under direct influence of the crown, and thus represent juvenile wood of different morphological characteristics from the mature wood in the lower, outer xylem (Panshin and DeZeeuw 1980, Megraw 1985, Shelburne and Hedden 1996). Shorter tracheids in juvenile wood of *P. taeda* cause water to traverse more walls for a given distance and increase resistance to water flow, as well as reduce J_S relative to that in mature wood, as found in this study (juvenile $J_S \sim 0.5$ mature J_S; Phillips et al. 1996). Lower J_{Sup} values may also reflect lower A_S:A_L in the upper crown (Oren et al. 1986).

A typical response of J_S to D is a counterclockwise hysteresis when a large amount of water is taken out of storage above the sensor, or no hysteresis when the amount of moisture taken out of storage is very little (Pataki et al. 1998). The small departure from linearity in the relationships between J_S and D in the juvenile xylem (Fig. 2; J_{Sup} and J_{Sin}), and the lack of hysteresis in this xylem, indicate both unchanging resistance to water flow during the day and relatively little water storage capacity (Pataki et al. 1998), or a balance between increasing resistance (clockwise hysteresis) and decreasing storage (counterclockwise hysteresis). In contrast, J_S in mature xylem show a clear nonlinear response to D with clockwise hysteresis developing in both C and, to a greater extent, F trees (Fig. 2; J_{Sout}). The observed patterns indicate a higher diurnal buildup of resistance to water flow in the soil–plant–atmosphere pathway in the unirrigated treatments. Because soil moisture and leaf water potential (Laviner 1997) were similar in all treatments during this study (Fig. 3), the greater resistance generated in trees that had not received water supplements during dry periods in the preceding four treatment years further demonstrates a carry-over effect.

We do not know the cause for the difference in hysteresis size between irrigated and unirrigated treatment pairs (Fig. 2), but the difference between F and C trees indicates that changes in root system characteristics may be involved. The greater hysteresis seen in F than C trees (Fig. 2) may reflect the higher E_C in the F treatment (Figs. 4 and 5). Higher E_C would cause a faster use of soil moisture in the volume immediately adjacent to each fine root, thus increasing the soil-to-root hydraulic resistance (North and Nobel 1996, Stirzaker and Passioura 1996). Fertilization has been shown to decrease soil exploration by roots (Linder et al. 1987). While fine root mass per unit of leaf area is reduced by fertilization (Linder and Rook 1984, Axelsson and Axelsson 1986), rooting depth, at least in terms of tap root length and the vertical pattern of emanating lateral roots, is a more species-specific characteristic (Fowells 1965, Rutter 1968). On our site, the taproot of *P. taeda* was shown to reach a depth of 3 m (T. Albaugh, *unpublished data*); however, fine root density was lower in F than the other treatments (J. King, *unpublished data*). Thus, low g_S in F trees might reflect stomatal response to a hydraulic limitation to water uptake imposed by coincident low root density and coarse-textured soil (Sperry et al. 1998). We evaluate treatment effects on E_C, and the likelihood that the carry-over effect was caused by a treatment-related change in access to deep water.

Treatment effects on E_C

Because J_S did not differ among treatments (Tables 2 and 4), differences in E_C reflected differences in A_S:

A_G (Table 1). Our second hypothesis was based on the assumption that the first hypothesis (i.e., IF trees will have higher $E_{C,l}$) was correct. Combining low $E_{C,l}$ in F trees with high L in both fertilized treatments led to a ranking in E_C of IF > F > I = C (Figs. 4 and 5). In fact, this was the ranking expected for E_C, but for a different reason: a lower $E_{C,l}$ in F trees rather than a higher $E_{C,l}$ in IF trees. Nevertheless, the hypothesized effect of L on E_C (Oren et al. 1986, Granier and Loustau 1994) was demonstrated, as is obvious when comparing IF to both I and C treatments, all of which showed a similar $E_{C,l}$ (Table 3). The ranking of E_C among treatments was dominated by differences which became clear only on days of high evaporative demand: E_C increased with D_Z in the IF stand, while E_C of the other treatments reached a plateau at high D_Z, with F having a higher plateau than I and C (Fig. 5).

Mean daily E_C over the treatment period was the same for C and I, higher for F, and highest for IF (Table 3). Thus, the effect of nutrient addition was to increase L sufficiently to nearly double the latent heat flux from the stand (comparing F to I and C); while the effect of providing water during dry periods, in addition to nutrient, was to increase water use by 50%, when soil moisture was sufficiently high (comparing IF to F). Providing water without nutrients did not affect L or E_C, only changing the diurnal pattern of canopy transpiration. In *P. taeda* stands of higher basal area (25 m^2/ha), evapotranspiration rates were higher during the same season (1.5–3.6 mm/d; Stogsdill et al. 1992). However, in stands of lower basal area, but higher L, than IF on a clayey soil, mean daily E_C was 1.2 mm/d during the same time period as this study (Oren et al. 1998*a*); and, in a stand of *Pinus radiata* with similar L (3.7 m^2/m^2) to the IF treatment, late growing season E_C was comparable at 1.7 mm/d (Teskey and Sherriff 1996).

Fertilization may alter root distribution and, thus, access to deep water. Fine roots in F treatment declined in density with depth less than the other treatments, thus showing a more uniform vertical distribution of fine roots (from root profile maps on walls of soil pits to a depth of 0.8 m; J. King, *unpublished data*). This indicates that a larger proportion of fine roots may be found at depths below 0.8 m in F. We used a local water balance approach (Oren et al. 1998*a*,*b*) to assess whether water is absorbed in the same soil volume by all treatments. Specifically, we estimated the amount of water taken up by roots to a depth of 1 m and compared this value to E_C in each treatment, in order to estimate the amount of water taken from deeper soil.

We modified the local water balance method for use in this sandy site by excluding rain days and the one following day, so that free water could drain from the upper 1 m. Within a day after a precipitation event, drainage was negligible, as θ at all depths declined below 0.07 m^3 H_2O/m^3 soil, a value close to that at zero drainage for a theoretical sandy soil (Jury et al. 1991). We related cumlative ΔS during each drying cycle to the E_C estimated from sap flux measurements in each treatment (Fig. 6). The 95% confidence interval between E_C and ΔS included the 1:1 line for C, I, and IF, but not for F (Fig. 6). E_C of F exceeded ΔS, by an average of 0.2 mm indicating that only 75% of E_C was absorbed in the top 1 m of soil. We plan to use stable isotopes of hydrogen and oxygen in the xylem sap, soil water, and both rain and irrigated water, in order to obtain information on water sources and on pattern of water use with depth (Dawson and Ehleringer 1991, Ehleringer and Dawson 1992). We also plan to quantify treatment effects on hydraulic conductance (Sperry and Pockman 1993). In this way, the sources of the carryover effects on E_C and $E_{C,l}$ may be further isolated and quantified.

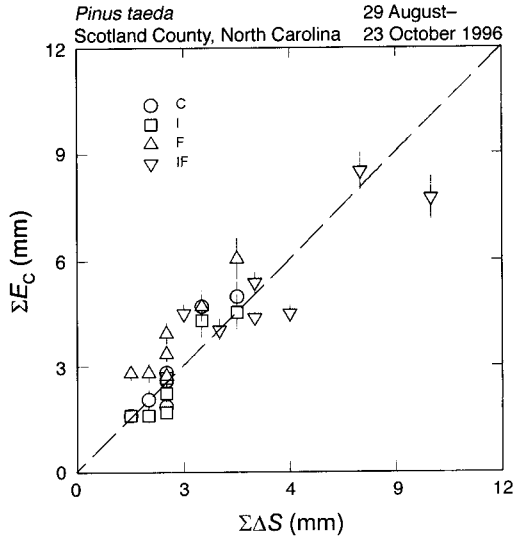

FIG. 6. Sums of daily transpiration (ΣE_C) plotted against sums of soil moisture depletion ($\Sigma \Delta S$) for each drying cycle during the measurement period (n = 6; cycle length, 2–8 d). The dashed line indicates the 1:1 line. Error bars are ±1 SE with n = 8 calculated for each drying cycle.

CONCLUSION

Site quality has been shown to affect several key variables important to determining $E_{C,l}$ and E_C, including L, k, and A_S:A_L (Whitehead et al. 1984, Yang et al. 1988, Coyea and Margolis 1992, Menuccini and Grace 1995). Studies isolated the effect of site fertility on these variables, but did not quantify E_C. Here we describe the effect that manipulations of site fertility and water availability have on E_C, under otherwise similar site and atmospheric conditions. Thus, results from this study may be employed to explain variation in E_C among sites of different qualities, caused by factors that control the availability of nutrient and water, and, in-turn, affect the development of L and A_S:A_L.

Lower supply of water over the 4-yr duration of the project altered certain tree characteristics (either not indicated by A_S:A_L or those associated with early-to-

late wood ratio or growth rate), such that even when water availability in this sandy soil was relatively high, greater resistance to water uptake developed diurnally (C and F treatments). It is therefore possible that acclimation to low levels of water stress (low L without water addition, as in C treatment) produced trees that are slightly more conservative water users than those supplied with ample water. A further increase in water stress (high L without water addition, as in F treatment) produced trees with even more conservative water use strategy and altered spatial distribution of water uptake. These responses to chronic levels of water stress affect the rate and vertical distribution of water uptake even when water is available, reflecting a carry-over effect of site fertility and water availability on E_C.

Applications

Manipulation of water availability to loblolly pine stands is practiced on a limited scale. However, even where only fertilizers are used, similar differences in response to fertilizer application, as found here, may occur between regions that receive frequent precipitation during the growing season, in comparison to drier regions. Thus high nutrient supply alone (dry regions) and the combination of high nutrient and water supply (moist regions) may support similar leaf area indices and produce a similar aboveground biomass. However, carry-over effects of continuously high water supply may result in higher transpiration rates than expected, based on leaf area index alone, during periods in which soil moisture is similar in both regions.

Overfertilization was shown to cause leaching of nutrients, especially nitrogen in the form of nitrate, into ground water and towards downstream ecosystems (Sands 1984). To reduce loss of nutrients to below the rooting zone, the supply of fertilizers must be based on the demand of trees throughout the growing season (Ingestad 1991). However, cost limitations usually prohibit tailoring fertilization regimes so precisely, so fertilizers are applied annually, based, at best, on target foliage nutrient concentrations (Allen et al. 1990). This study shows that trees supplied with additional nutrients, in sites where water availability is low (here due to low soil water-holding capacity, but elsewhere due to low precipitation), may access deeper soil water. To the extent that the uptake of nutrients is coupled to that of water (Kramer and Boyer 1995), such a response to fertilization in dry sites may increase access to deeply stored nutrients, perhaps leading to lower nutrient losses from leaching during rainy periods. However, in regions of high precipitation, especially in sites of course soils, land managers must exercise caution when fertilizing stands, because the combination of shallower root systems and high leaching rates may result in excessive nutrient losses into ground water.

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