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Influence of irrigation and fertilization on transpiration and hydraulic properties of *Populus deltoides*

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Summary Long-term hydraulic acclimation to resource availability was explored in 3-year-old *Populus deltoides* Bartr. ex Marsh. clones by examining transpiration, leaf-specific hydraulic conductance (G_L), canopy stomatal conductance (G_S) and leaf to sapwood area ratio (A_L:A_S) in response to irrigation (13 and 551 mm year^{-1} in addition to ambient precipitation) and fertilization (0 and 120 kg N ha^{-1} year^{-1}). Sap flow was measured continuously over one growing season with thermal dissipation probes. Fertilization had a greater effect on growth and hydraulic properties than irrigation, and fertilization effects were independent of irrigation treatment. Transpiration on a ground area basis (E) ranged between 0.3 and 1.8 mm day^{-1}, and increased 66% and 90% in response to irrigation and fertilization, respectively. Increases in G_L, G_S at a reference vapor pressure deficit of 1 kPa, and transpiration per unit leaf area in response to increases in resource availability were associated with reductions in A_L:A_S and consequently a minimal change in the water potential gradient from soil to leaf. Irrigation and fertilization increased leaf area index similarly, from an average 1.16 in control stands to 1.45, but sapwood area was increased from 4.0 to 6.3 m^2 ha^{-1} by irrigation and from 3.7 to 6.7 m^2 ha^{-1} by fertilization. The balance between leaf area and sapwood area was important in understanding long-term hydraulic acclimation to resource availability and mechanisms controlling maximum productivity in *Populus deltoides*.

Keywords: canopy stomatal conductance, leaf area to sapwood area ratio, leaf specific hydraulic conductance, water potential.

Introduction

Exploration of relationships between hydraulic and physiological traits can provide insights into regulation of water use and limitations to stand growth (Magnani et al. 2000, Köstner et al. 2002). Transpiration and leaf water status are coordinated with tree architectural features to minimize plant water loss and avoid hydraulic failure (Sperry et al. 2002, Tyree 2003, Whitehead and Beadle 2004). This balance can be described as:

$$\frac{A_L}{A_S} = \frac{G\Delta\Psi}{G_S D} \quad (1)$$

where A_L:A_S is the ratio of leaf area to sapwood area, G is whole-tree conductance per unit sapwood area, G_S is canopy stomatal conductance, $\Delta\Psi$ is the gradient in water potential between the soil and leaf, and D is bulk air vapor pressure deficit (Whitehead et al. 1984*a*, Whitehead et al. 1984*b*, Whitehead 1998). Stomatal conductance (g_S) and leaf-specific hydraulic conductance (whole-tree conductance per unit leaf area, G_L) are also positively linked:

$$g_S = \frac{G_L\Delta\Psi}{D} \quad (2)$$

and G_L and D are important in understanding the regulation of stomatal conductance and plant water status (Whitehead 1998, Sperry 2000, Hubbard et al. 2001, Tyree 2003). Oren et al. (1999) demonstrated that stands with a high stomatal conductance at low D show greater stomatal sensitivity to D to regulate Ψ_L, and stomatal response to D has been shown to be correlated to changes in G_L in mature trees (Addington et al. 2004).

Transpiration is often proportional to stand growth and leaf area index (LAI) (LeMaitre and Versfeld 1997), but the long-term acclimation of the hydraulic system to resource availability is unclear. For example, based on a meta-analysis of different plant forms that included only a few long-term studies of trees, Mencucinni (2003) proposed that hydraulic efficiency decreases, defined by decreasing G_L, with increasing resource availability. In theory, low G_L at high nutrient availability would facilitate greater stomatal control of water loss during episodic drought, and high G_L during prolonged drought would maintain leaf water status as water potential declined. Reductions in G_L and G_S in response to fertilization were demonstrated in *Pinus taeda* L.; however, irrigation and irrigation plus fertilization had no influence on G_L and G_S (Ewers et al. 2000). Similarly, Samuelson and Stokes (2006) observed no influence of long-term irrigation and fertilization plus irrigation on G_L and G_S of *Pinus taeda*. The seemingly in-

consistent responses of G_L to resource availability may be unified by considering changes in leaf and sapwood areas. For instance, in the study by Ewers et al. (2000), when irrigation was applied with fertilization, sapwood area increased. Similarly, in the study by Samuelson and Stokes (2006), the large increase in LAI of *Pinus taeda* stands observed in response to fertilization plus irrigation was balanced by large increases in sapwood area. Leaf-specific hydraulic conductance is linked to changes in A_L:A_S, but this relationship is complicated by resource availability (Addington et al. 2006).

Our overall goal was to test the hypothesis that long-term hydraulic acclimation to increased resource availability is defined by a reduction in G_L. Our specific objective was to explore hydraulic and physiological relationships described by Equations 1 and 2 in 3-year-old *Populus deltoides* Bartr. ex Marsh. clones in response to a factorial combination of irrigation and fertilization. Although cause and effect could not be tested directly, we hypothesized that changes in G_L and sensitivity of G_S to D in response to irrigation and fertilization are negatively correlated with A_L:A_S.

Materials and methods

Study site

The 24.4-ha experimental plantation was located on the U.S. Department of Energy Savannah River Site, a National Environmental Research Park, located near Aiken, SC, in the Carolina Sand Hill physiographic region (33°23′ N, 81°40′ E). Mean annual temperature and precipitation are 20 °C and 1190 mm, respectively, with extended droughts common throughout the growing season. The soil is a loamy, siliceous, semiactive and thermic Grossarenic Paleudult (Blanton series). The site was farmed until the 1950s and then converted to *Pinus palustris* Mill. and *Pinus taeda* stands harvested in 1999. Soil and small debris from the harvest were homogenized to a depth of 30 cm and dolomite lime was applied at 3.4 Mg ha^{-1} to increase soil pH to 6.5.

Two native male *Populus deltoides* clones were studied: one from an east Texas population (S7C15: Brazos County, TX) and the other from Mississippi (ST66: Issaquena County, MS). Clonal material was provided by Crown Vantage Corp. (Filter, MS). Cuttings were planted at a 2.5 × 3 m spacing (density of 1333 trees ha^{-1}) in February 2000. The 0.22-ha clonal plots were divided into four treatment plots with the central 0.04-ha plot considered the measurement plot.

The experimental design was a 2 × 2 factorial combination of irrigation and fertilization replicated in three blocks. In 2002, drip irrigation was on average 1.9 cm week^{-1} (551 mm total during the growing season in addition to ambient precipitation) and designed to meet evaporative demand. Liquid fertilizer solution of 7:0:7 (N:P:K) plus micronutrients (0.001% B, 0.01% Cu, 0.05% Mn, 0.001% Mo and 0.03% Zn) and separate P additions were applied through the drip irrigation system. Lime application during site preparation met Ca and Mg requirements. Nitrogen, P and K were applied at a rate of 120, 53 and 99 kg ha^{-1} year^{-1}, respectively, in 2002 in 26 weekly applications using enough water to dispense the fertilizer and flush the lines (about 0.5 cm week^{-1} of water alone, for a total of 13 mm). Control plots also received the 0.5 cm week^{-1} of water but no fertilizer applications. Weeds were controlled on all plots with the pre-emergent oxyfluorfen and glyphosate as needed. An on-site standard weather station recorded environmental data (Dynamet, Dynamax, Houston, TX) and included software to calculate potential evapotranspiration following Van Bavel (1966). See Coyle and Coleman (2005) for more details on treatments and experimental design.

Stand biometric data for the third growing season were reported by Coyle and Coleman (2005) and are summarized in Table 1. Irrigation and fertilization increased ground-line diameter, height, basal area and aboveground woody biomass and productivity. In general, fertilization had a larger impact on growth than did irrigation. No significant clonal differences in growth were observed, and no statistical interactions among treatments and clones were detected for the majority of growth variables.

Transpiration

There was no canopy closure in any plots during the study. Two sample trees in each plot (a total of 48 trees) representing the mean plot stem diameter were selected for sap flow measurements. Thermal dissipation probes (Granier 1987) with a 20-mm integrating length were inserted into the sapwood about 30 cm above the ground line on the north aspect of each tree by removing the outer bark and drilling small holes (1.6 mm in diameter) into the sapwood. Insulated constantan wire and a thermally conducting paste were wrapped around

Table 1. Mean ground-line stem diameter, total height, basal area estimated from ground-line diameters, aboveground woody (stem + branch) biomass at the end of the third growing season and aboveground woody productivity during the third growing season in *Populus deltoides* in response to irrigation (I-0 no irrigation, I-1 irrigation), fertilization (F-0 no fertilization, F-1 fertilization) and clone (ST66 and S7C15) (data from Coyle and Coleman 2005). An asterisk (*) indicates a significant (P = 0.05) difference between irrigation treatments, fertilization treatments or clones.

Variable	I-0	I-1	F-0	F-1	ST66	S7C15
Diameter (cm)	5.7*	7.2	5.4*	7.5	6.5	6.5
Height (m)	4.0*	5.6	3.7*	5.9	4.8	4.8
Basal area (m^2 ha^{-1})	4.0*	6.3	3.7*	6.7	5.1	5.2
Aboveground biomass	3.7*	6.8	3.1*	7.4	4.9	5.6
Aboveground productivity (Mg ha^{-1} year^{-1})	2.1*	4.1	1.5*	4.7	3.2	3.0

the heated probe, and aluminum shields were placed around both probes. Silicon was placed around the probes to seal out water, and the stem and probes were wrapped with porous insulation to reduce thermal gradients. Sap flux (linear dimension per unit time, as defined by Reid et al. 2005) was recorded every 30 s and the 30-min means stored on a data logger (Model DL2e, Delta-T Devices, Cambridge, U.K.). Sap flux was recorded continuously from June through August 2002.

Stem diameter at the probe location was measured monthly to calculate sapwood cross-sectional area. All wood was considered functioning sapwood because of the young age of the trees and because of the absence of visible evidence of a color transition from sapwood to heartwood in harvested buffer trees. Sample trees ranged in radius at probe locations from 2.5 to 4.4 cm, indicating that the probes sampled from 70 to 96% of the sapwood cross-sectional area. We assumed uniform sap flux across the sapwood area, because Edwards and Booker (1984) reported little reduction in sapwood conductivity up to a radial depth of 4.0 cm at a sampling height of 32 cm in *Populus deltoides* trees. Lambs and Muller (2002) also found no reduction in maximum sap flux to 4 cm depth in 10-year-old *Populus* hybrids and *Populus nigra* L.

Sap flow (volume flow per unit time, as defined by Reid et al. 2005) was calculated as the product of mean sap flux and sapwood area (Granier 1987). Stand-level transpiration on a ground area basis (E) was estimated by dividing sap flow by plot area and multiplying by the ratio of total plot basal area to mean sample tree basal area (Čermák et al. 2004). Stand-level transpiration per unit leaf area (E_L) was calculated by dividing E by LAI. The LAI of each plot was measured monthly with an LAI-2000 plant canopy analyzer (Li-Cor, Lincoln, NE.). The A_L:A_S ratio was calculated as the quotient of mean LAI over the three months and basal area based on ground-line diameters at the end of the growing season.

Canopy stomatal conductance

Mean canopy stomatal conductance of sample trees was calculated as:

$$G_S = \frac{\lambda E_L \gamma}{\rho c_p D} \quad (3)$$

where λ is the latent heat of vaporization of water (2465 J g^{-1}), γ is the psychometric constant (65.5 Pa K^{-1}), ρ is the density of air (1225 g m^{-3}), c_p is the specific heat of air (1.01 J g^{-1} K^{-1}) and E_L is in m^{-2} s^{-1} (Monteith and Unsworth 1990). Transpiration per unit leaf area was calculated by multiplying mean sap flux by A_L:A_S. Because the trees were small and canopies open, we assumed that the atmosphere and canopy were well coupled and that hydraulic capacity was negligible. Values were converted from m s^{-1} to mmol m^{-2} s^{-1} following Nobel (1991). To reduce errors from instrument limitations, G_S was calculated only when $D \geq 1.0$ kPa (Ewers and Oren 2000).

Hydraulic conductance

Whole-tree hydraulic conductance per unit sapwood area (G) and leaf-specific conductance (G_L) were calculated from the slope of the linear relationship between mean sap flux or E_L, respectively, of the two measurement trees per plot and leaf water potential (Ψ_L) (Wullschleger et al. 1998). Leaf water potential was measured with a pressure chamber (PMS Instrument Corp., Corvallis, OR) on three leaves collected from the upper third of the canopy of each sample tree at 0500, 0800, 1030, 1300 and 1600 h on June 18–20, July 23–25 and August 13–15, 2002. One block was randomly selected and measured over one day, and the order of plot measurements within a block was random. To estimate G and G_L for each plot, data were pooled by plot across the three measurement months (n = 15). The difference in Ψ_L between 0500 and 1300 h was used to calculate the gradient in water potential between the soil and leaf ($\Delta\Psi$). Volumetric soil water content to a depth of 15 cm at 30 cm from the tree in the northern and southern aspects was also measured diurnally by time domain reflectometry at each Ψ_L sampling session (Soilmoisture Equipment Co., Santa Barbara, CA). The drip line was located at the base of the trees at a southern aspect.

Foliar $\delta^{13}C$ and N concentration

Foliar $\delta^{13}C$ was measured on a composite sample of two leaves from each sample tree collected at the last sampling session. Between 1.8 and 2.2 mg of ground powder from each sample was combusted, and the resulting gases swept by a helium gas carrier into an isotope ratio mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany) operated by the University of Georgia Institute of Ecology. All carbon isotope ratios were expressed in delta notation ($\delta^{13}C$; ‰) relative to the PeeDee Belemnite standard ($\delta^{13}C = (R_{sample}/R_{standard} - 1)1000$).

Nutrient analysis was performed on one composite sample from each plot consisting of at least five leaves from each sample tree collected at each monthly Ψ_L sampling session. Leaves were stored in coolers and dried at 65–70 °C within 24 h of collection. Dried leaf tissue was ground in steel vials with a Spex ball mill 8000 (Metuchme, NJ) to a 0.2 mm particle size. Total foliar N was measured by LECO analysis (Jones and Case 1990).

Statistical analyses

All response variables were averaged across the two measurement trees in each plot and the plot was considered the experimental unit. Fertilization, irrigation, and clone main and interactive effects were tested by analysis of variance for a factorial split-plot design with treatments within clones. When variables were measured over time, repeated measures analysis of variance was used (Proc Mixed, SAS Inc., Cary, NC). Linear and nonlinear relationships between G_S and D were examined as described by Ewers et al. (2005). Effects were considered significant at $\alpha = 0.05$.

Results

Environmental conditions

Precipitation and potential evapotranspiration summed from June 1 through August 31, 2002 were 287 and 426 mm, respectively. Mean 24-h temperature over the period was 29.0 °C with a mean maximum of 32 °C and a mean minimum of 20 °C. Soil water data were averaged across locations within a plot and diurnal measurements within a sampling session. Soil water status was influenced by irrigation and month (Table 2). Irrigation increased soil water content (Table 3), and soil water content was higher in July (8.1%) and August (7.8%) than in June (6.2%) (data not shown).

Transpiration

Daily E ranged between 0.3 and 1.8 mm day^{-1} and was generally higher in fertilized and irrigated plots and in clone S7C15 (Figure 1). Summed by month, E was influenced by irrigation, fertilization, clone and month, and fertilization effects on E were independent of irrigation (Table 2). Irrigation increased monthly E by 66% and fertilization increased E by 90% (Table 3). Clone S7C15 had 39% higher monthly E than clone ST66. Monthly E was higher in July (32 mm month^{-1}) and August (30 mm month^{-1}) than in June (24 mm month^{-1}) (data not shown).

Daily E_L ranged between 0.2 and 1.7 mm day^{-1} (Figure 2) and when summed by month, E_L was influenced by irrigation, fertilization and month (Table 2). A significant interaction between clone and fertilization (Table 2) indicated that monthly E_L was higher in clone S7C15 than in clone ST66 only in the fertilization treatment (Figure 3). Irrigation and fertilization increased monthly E_L by 30 and 48%, respectively (Table 3), and fertilization effects on E_L were independent of irrigation treatment (Table 2). Monthly E_L decreased from July (31 mm month^{-1}) to August (17 mm month^{-1}), most likely because of increased LAI, which was higher in August (1.82) than in June (1.02) or July (1.06) (data not shown). Leaf area index varied with month and with irrigation and fertilization treatments, but not with clone (Table 2). Gains in LAI resulting from irrigation and fertilization were similar: 26% from irrigation and 23% from fertilization (Table 3).

Canopy stomatal conductance

The relationship between G_S (above a solar irradiance of 600 W m^{-2}) and D (Figure 4) was best described by $G_S = a + b(1/D)$ (Hogg and Hurdle 1997). The model was fit to each block treatment combination for the month of July, and treatment and clonal differences in slopes were tested. Sample sizes for each model were between 145 and 151 observations, and slopes were highly significant ($P < 0.0001$) for all models with R^2 ranging from 0.60 to 0.90. Sensitivity of G_S to D was influenced by fertilization and clone (Table 4). Fertilization increased sensitivity of G_S to D, and sensitivity to D was higher in Clone S7C15 than in Clone ST66 (Table 3). A reference maximum G_S (G_{Sref}) was calculated at a D of 1 kPa (Oren and Pataki 2001). Significant irrigation, fertilization and clone

Table 2. Observed probability values for main and interaction effects of irrigation (I), fertilization (F), clone (C) and month (M) on transpiration on a ground area (E) and leaf area (E_L) basis summed by month, leaf area index (LAI), soil water content (SWC), predawn leaf water potential (Ψ_L), and the gradient in water potential from soil to leaf ($\Delta\Psi$) in 3-year-old *Populus deltoides*.

Variable	Source ($P > F$)														
	I	F	C	M	I × F	I × C	F × C	I × F × C	I × M	F × M	C × M	I × C × M	F × C × M	I × F × M	I × F × C × M
E	0.004	< 0.001	0.010	0.001	0.154	0.389	0.137	0.854	0.757	0.390	0.067	0.171	0.634	0.851	0.609
E_L	0.049	0.006	0.120	< 0.001	0.326	0.585	0.036	0.600	0.895	0.995	0.439	0.702	0.545	0.914	0.177
LAI	< 0.001	0.002	0.661	< 0.001	0.909	0.885	0.294	0.740	0.438	0.366	0.976	0.745	0.471	0.872	0.642
SWC	< 0.001	0.608	0.982	< 0.001	0.683	0.486	0.959	0.411	0.913	0.654	0.760	0.324	0.999	0.675	0.449
Ψ_L	0.494	0.013	0.723	< 0.001	0.911	0.341	0.724	0.926	0.597	0.251	0.159	0.652	0.862	0.962	0.849
$\Delta\Psi$	0.126	0.039	0.745	< 0.001	0.633	0.484	0.717	0.216	0.258	0.675	0.853	0.903	0.324	0.528	0.952

Table 3. Mean (± 1 SE) leaf area to sapwood are ratio (A_L:A_S), transpiration on a ground area (E) and leaf area (E_L) basis, foliar $\delta^{13}C$ content, foliar nitrogen (N) concentration, whole-tree hydraulic conductance per unit sapwood area (G), leaf-specific hydraulic conductance (G_L), slope of the linear model ($y = a + b(1/D)$) describing the relationship between canopy stomatal conductance (G_S) expressed on a leaf area ($dG_S/d(1/D)$) or sapwood area ($dG_{S\text{-}SA}/d(1/D)$) basis and vapor pressure deficit (D), reference G_S expressed on a leaf area (G_{Sref}) or sapwood area ($G_{Sref\text{-}SA}$) basis at a D of 1 kPa, leaf area index (LAI), soil water content, predawn leaf water potential (Ψ_L) and the gradient in water potential from soil to leaf ($\Delta\Psi$) for 3-year-old *Populus deltoides* in response to irrigation (I-0 no irrigation, I-1 irrigation), fertilization (F-0 no fertilization, F-1 fertilization) and clone (ST66 and S7C15). An asterisk (*) indicates a significant ($P = 0.05$) difference between irrigation treatments, fertilization treatments or clones.

Variable	I-0	I-1	F-0	F-1	ST66	S7C15
A_L:A_S (m^2 cm^{-2})	0.316 (0.029)	0.255 (0.025)	0.347 (0.028) *	0.222 (0.011)	0.288 (0.028)	0.282 (0.029)
E (mm $month^{-1}$)	21.6 (2.2) *	35.8 (2.3)	19.8 (2.2) *	37.6 (2.2)	24.0 (2.2) *	33.4 (2.2)
E_L (mm $month^{-1}$)	21.0 (2.1) *	27.2 (2.4)	19.4 (2.3) *	28.8 (2.2)	20.4 (2.4)	27.7 (2.6)
Foliar $\delta^{13}C$ (‰)	–26.8 (0.2) *	–27.6 (0.1)	–27.5 (0.1) *	–26.9 (0.2)	–27.1 (0.2)	–27.3 (0.2)
Foliar N (mg g^{-1})	21.1 (1.2)	21.6 (1.6)	18.2 (0.9) *	24.5 (1.1)	19.3 (1.2) *	23.4 (1.3)
G (mol m^{-2} s^{-1} MPa^{-1})	2.5 (0.2)	3.0 (0.3)	2.6 (0.3)	2.9 (0.3)	2.4 (0.3)	3.1 (0.2)
G_L (mmol m^{-2} s^{-1} MPa^{-1})	0.63 (0.09) *	0.94 (0.2)	0.54 (0.07) *	1.03 (0.14)	0.64 (0.10) *	0.92 (0.14)
$dG_S/d(1/D)$ (mmol m^{-2} s^{-1} kPa^{-1})	76.2 (11.3)	95.1 (9.6)	63.0 (8.0) *	108.2 (8.8)	71.5 (7.0) *	99.8 (12.2)
$dG_{S\text{-}SA}/d(1/D)$ (mmol m^{-2} s^{-1} kPa^{-1})	30.0 (2.8)	31.8 (2.8)	30.5 (2.9)	31.2 (2.7)	26.9 (2.7)	34.8 (2.4)
G_{Sref} (mmol m^{-2} s^{-1})	80.0 (12.2) *	108.8 (13.6)	67.2 (10.0) *	121.6 (11.8)	74.5 (7.7)*	114.2 (15.5)
$G_{Sref\text{-}SA}$ (mmol m^{-2} s^{-1})	31.4 (3.2)	35.6 (3.4)	31.9 (3.1)	35.0 (3.4)	27.9 (2.8)	39.0 (3.0)
LAI (m^2 m^{-2})	1.15 (0.05)	1.45 (0.07)	1.16 (0.06)	1.43 (0.07)	1.32 (0.08)	1.28 (0.08)
Soil water content (%)	6.1 (0.4)*	8.6 (0.5)	7.6 (0.6)	7.2 (0.6)	7.4 (0.4)	7.4 (0.7)
Ψ_L (MPa)	–0.47 (0.02)	–0.45 (0.02)	–0.42 (0.01) *	–0.49 (0.02)	–0.45 (0.02)	–0.47 (0.02)
$\Delta\Psi$ (MPa)	0.98 (0.03)	1.04 (0.04)	0.96 (0.04) *	1.05 (0.03)	1.02 (0.03)	0.99 (0.04)

main effects on G_{Sref} were observed (Table 4). Irrigation and fertilization increased G_{Sref}, and G_{Sref} was higher in Clone S7C15 than in Clone ST66 (Table 3). To determine if sensitivity of G_S to D was dependent on intrinsic G_S (Oren and Pataki 2001, Ewers et al. 2005), data from all plots were pooled, and the relationship between $dG_S/d(1/D)$ and G_{Sref} explored. A linear relationship between $dG_S/d(1/D)$ and G_{Sref} was observed, with G_{Sref} explaining 92% of the variation in $dG_S/d(1/D)$ (Figure 4). When G_S was standardized by the A_L:A_S ratio (Meinzer 2003), no significant effects of treatment or clone on $dG_S/d(1/D)$ or G_{Sref} were detected (Tables 3 and 4).

Hydraulic traits

The linear relationship between sap flux or E_L and Ψ_L, the slope defined G and G_L, respectively, was significant for all plots with r^2 values between 0.60 and 0.97 (data not shown). Resource availability and clone had no significant influence on G (Table 4) and mean G was 2.8 mol m^{-2} s^{-1} MPa^{-1} (Table 3). In contrast, G_L was increased by irrigation and fertilization, and G_L was higher in Clone S7C15 than in Clone ST66 (Tables 3 and 4). The largest increase in G_L (91%) was in response to fertilization (Table 3). Fertilization effects on G_L were independent of irrigation treatment (Table 4).

Significant but small effects of fertilization on predawn Ψ_L and $\Delta\Psi$ were observed, and water relations varied with month (Table 2). Predawn Ψ_L decreased by 0.07 MPa, and $\Delta\Psi$ increased by 0.09 MPa in response to fertilization (Table 3). Predawn Ψ_L was highest in July (–0.39 MPa versus –0.49 MPa in June and –0.47 MPa in August), and $\Delta\Psi$ was greatest in August (1.20 MPa versus 1.02 MPa in June and 1.06 MPa in July) (data not shown). Predawn Ψ_L and $\Delta\Psi$ were unaffected by irrigation or clone, and the influence of fertilization on water relations was independent of irrigation treatment (Table 2).

The A_L:A_S ratio decreased from 0.347 to 0.222 m^2 cm^{-2} in response to fertilization (Table 3). Fertilization effects on A_L:A_S were independent of irrigation, and A_L:A_S was not significantly influenced by irrigation or clone (Table 4).

Foliar $\delta^{13}C$ and N concentration

Foliar $\delta^{13}C$ was influenced by irrigation and fertilization but was similar between clones (Table 4). Irrigation decreased and fertilization increased foliar $\delta^{13}C$ enrichment (Table 3). Foliar N concentration increased with fertilization from 18.2 to 24.5 mg g^{-1} and was higher in Clone S7C15 than in Clone ST66 (Table 3 and Table 4). Irrigation had no significant influence on foliar N concentration (Table 4).

Discussion

Transpiration on a ground area basis (E) was as high as 1.8 mm day^{-1} and averaged 37.6 mm $month^{-1}$ in 3-year-old *Populus deltoides* in response to fertilization. These values are comparable with other reports for *Populus* when differences in stand structure are considered. For example, Hinckley et al. (1994) reported a maximum E of 4.8 mm day^{-1} and a mean E of 113 mm $month^{-1}$ for 4-year-old hybrid *Populus* in the Pacific Northwest, but basal area was 21.4 m^2 ha^{-1} compared with 6.7 m^2 ha^{-1} in our study. Maximum E was 5 mm day^{-1} in a 13-year-old hybrid *Populus* plantation in Belgium with a basal area of 25.1 m^2 ha^{-1} (Meiresonne et al. 1999). Compared with our mean E of 36 mm $month^{-1}$ in irrigated stands, Vose et al. (2000) reported a mean E of 51 mm $month^{-1}$ in an irrigated

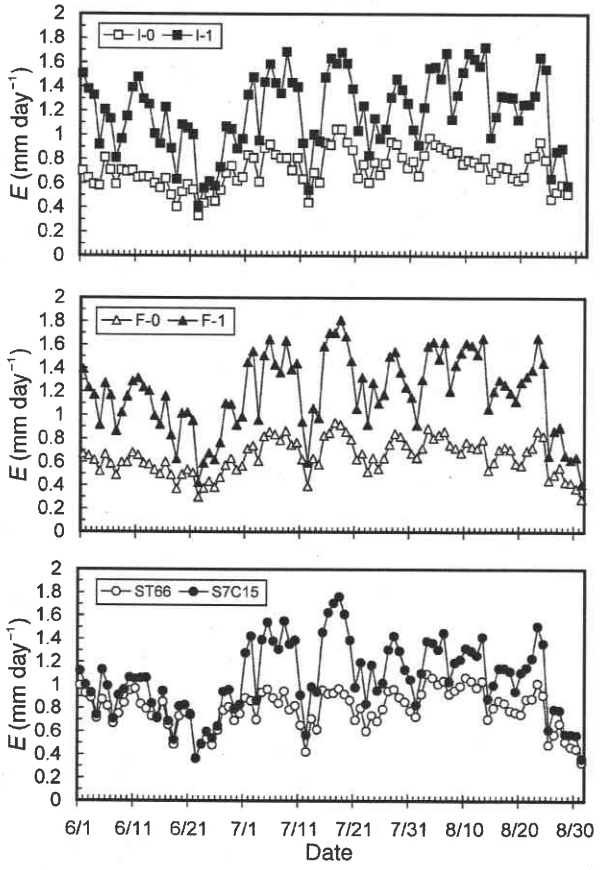

Figure 1. Mean daily transpiration on a ground area basis (E) in response to irrigation (I-0 no irrigation, I-1 irrigation), fertilization (F-0 no fertilization, F-1 fertilization) and clone (Clones ST66 and S7C15) in a 3-year-old *Populus deltoides* plantation from June through August 2002.

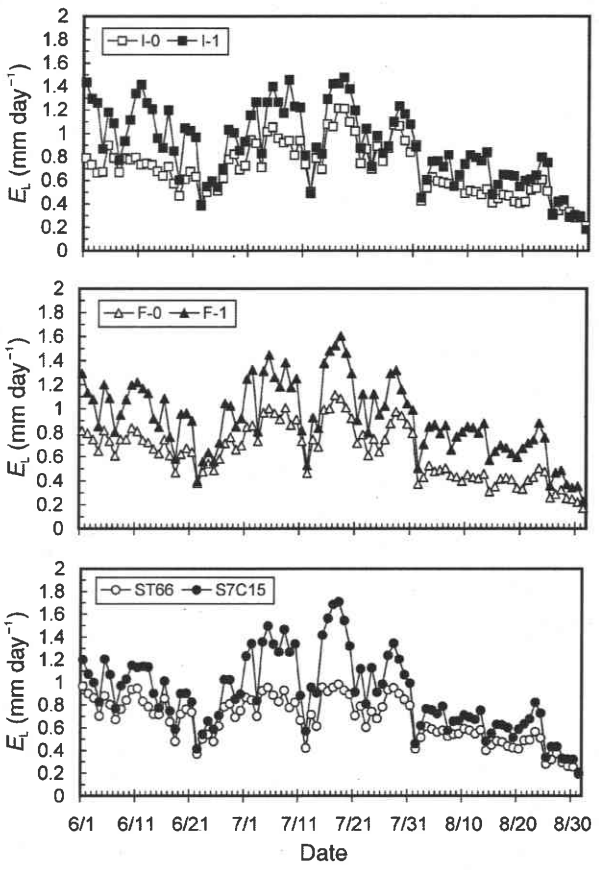

Figure 2. Mean daily transpiration on a leaf area basis (E_L) in response to irrigation (I-0 no irrigation, I-1 irrigation), fertilization (F-0 no fertilization, F-1 fertilization) and clone (Clones ST66 and S7C15) in a 3-year-old *Populus deltoides* plantation from June through August 2002.

1-year-old *Populus deltoides* plantation in Texas with a basal area of 9 m^2 ha^{-1}. Transpiration on a leaf area basis (E_L) was as high as 1.7 mm day^{-1} and averaged 28.8 mm $month^{-1}$ in fertilized stands, which is similar to the reported E_L values of *Populus deltoides* planted in New Zealand (36 mm $month^{-1}$) (Guevara-Escobar et al. 2000) and *Populus tremuloides* (33 mm $month^{-1}$) (Ewers et al. 2005).

Our goal was to examine the theoretical hydraulic and physiological relationships described by Equation 1 and the long-term hydraulic acclimation to increased resource availability in *Populus deltoides*. Based on the work of Mencuccini (2003), we hypothesized that increasing nutrient and water availability would decrease G_L and thus G_S, but we observed the opposite response, which may be explained by resource effects on A_L:A_S. Higher G_L was associated with reduced A_L:A_S in response to fertilization and with a trend ($P = 0.069$) toward lower A_L:A_S with irrigation, and consequently a minimal change in $\Delta\Psi$. Negative correlations between G_L and A_L:A_S were previously reported for Neotropical savanna trees (Bucci et al. 2005), *Coffea arabica* L. cultivars (Tausend et al. 2000) and tropical trees (Andrade et al. 1998). The inverse relationship between G_L and A_L:A_S can be described by replacing G in Equation 1 with sapwood permeability (K_S):

$$G_L = \frac{K_S A_S}{l\eta A_L} \quad (4)$$

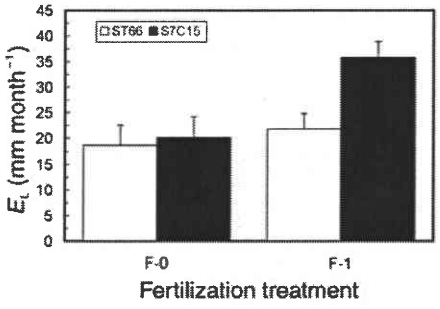

Figure 3. Variation in monthly transpiration per unit leaf area (E_L) between clones (clones ST66 or S7C15) in response to fertilization (F) in a 3-year-old *Populus deltoides* plantation. Bars represent 1 SE.

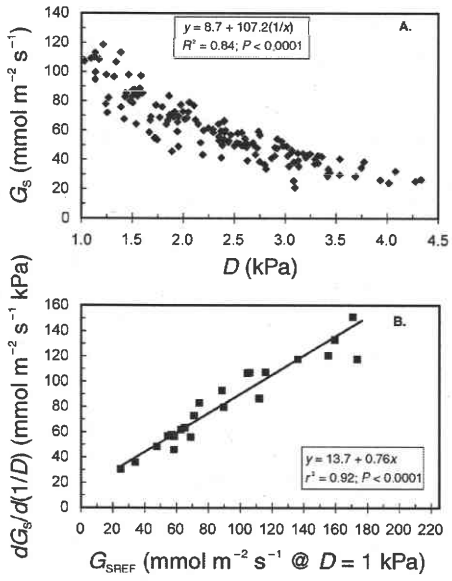

Figure 4. An example of the relationship between canopy stomatal conductance (G_S) and vapor pressure deficit (D) at high solar radiation (> 600 W m^{-2}) for one plot in July 2002 (A), and the linear relationship between sensitivity of G_S to 1/D ($dG_S/d(1/D)$) and reference G_S at a D of 1 kPa in 3-year-old *Populus deltoides* (B).

based on the relationship between K_S and G (Whitehead et al. 1984*b*, Hubbard et al. 2001, Simonin et al. 2006), where l is hydraulic path length and η is viscosity of water. Changes in G_L with resource availability are often related to A_L:A_S, although most studies including ours suffer from auto-correlation, because A_L:A_S is used to calculate G_L (Mencuccini 2003). To avoid auto-correlation, we examined the relationship between absolute whole-plant hydraulic conductance and A_L:A_S, and observed a significant but weak negative correlation (Figure 5). It is also possible that irrigation and fertilization increased K_S. Vessel size is positively related to site water supply in *Populus* (Schume et al. 2004), and fertilization increased vessel diameter in *Populus deltoides* even when water was limited (Harvey and van den Driessche 1999). Proportional increases in G_L with decreasing wood density in Panamanian forest canopy trees (Santiago et al. 2004) and the positive correlation between wood density and xylem resistance to cavitation support a link between xylem anatomy and G_L (Meinzer 2003). Although changes in xylem anatomy associated with fertilization may increase susceptibility to cavitation (Harvey and van den Driessche 1999), the positive effects of fertilization on growth were larger than the negative effects of fertilization on physiology and growth during periods of drought (Nilsen 1995).

We found a curvilinear relationship between G_S and D in *Populus deltoides*, similar to that reported for *Populus tremuloides* (Hogg and Hurdle 1997) and hybrid *Populus* (Meinzer et al. 1997*b*), that was related to resource availability and intrinsic G_S. An empirical analysis of stomatal sensitivity to D by Oren et al. (1999) demonstrated that stands with high stomatal conductance at low D show greater stomatal sensitivity to D to regulate Ψ_L, which our results support. Greater sensitivity of G_S to D with fertilization and in Clone S7C15 was a function not only of higher intrinsic G_S but also of hydraulic architecture, because G_{Sref} and sensitivity of G_S to D were similar between treatments and clones when G_S was expressed on a sapwood area basis (Meinzer 2003). When Meinzer et al. (1997*a*) standardized G_S by A_L:A_S, a common relationship between G_S and D emerged among different tropical tree species, demonstrating convergence in plant function (Andrade et al. 1998, Meinzer 2003). Likewise, standardizing G_S by A_L:A_S eliminated variation in stomatal response to humidity among *Coffea arabica* cultivars (Tausend et al. 2000).

Transpiration (E) followed the growth responses reported by Coyle and Coleman (2005) and others showing enhancement of growth of *Populus* with increasing water availability (Blake et al. 1996, Dickmann et al. 1996) and fertilization on nutrient-limited soils (Blackmon 1977, Czapowskyj and Safford 1993, Thorton et al. 2000). Analogous to productivity in the plantation studied by Coyle and Coleman (2005), we ob-

Table 4. Observed probability values for main and interaction effects of irrigation (I), fertilization (F), and clone (C) on the leaf area to sapwood area ratio (A_L:A_S), foliar $\delta^{13}C$ content, foliar nitrogen (N) concentration, whole-tree conductance per unit sapwood area (G), leaf-specific hydraulic conductance (G_L), the slope of the linear model ($y = a + b(1/D)$) describing the relationship between canopy stomatal conductance (G_S) expressed on a leaf area ($dG_S/d(1/D)$) or sapwood area ($dG_{S\text{-}SA}/d(1/D)$) basis and vapor pressure deficit (D), and reference G_S expressed on a leaf area (G_{Sref}) or sapwood area ($G_{Sref\text{-}SA}$) basis at a D of 1 kPa in 3-year-old *Populus deltoides*.

Variable	Source ($P > F$)						
	I	F	C	I × F	I × C	F × C	I × F × C
A_L:A_S	0.069	< 0.001	0.839	0.654	0.900	0.966	0.750
Foliar $\delta^{13}C$	< 0.001	< 0.001	0.476	0.112	0.964	0.446	0.460
Foliar N	0.560	< 0.001	0.038	0.216	0.335	0.605	0.824
G	0.260	0.443	0.210	0.257	0.528	0.281	0.967
G_L	0.036	0.003	0.019	0.154	0.831	0.308	0.793
$dG_S/d(1/D)$	0.075	< 0.001	0.012	0.586	0.469	0.140	0.492
$dG_{S\text{-}SA}/d(1/D)$	0.604	0.830	0.150	0.341	0.187	0.104	0.792
G_{Sref}	0.031	< 0.001	0.029	0.630	0.995	0.079	0.557
$G_{Sref\text{-}SA}$	0.267	0.395	0.110	0.961	0.542	0.058	0.695

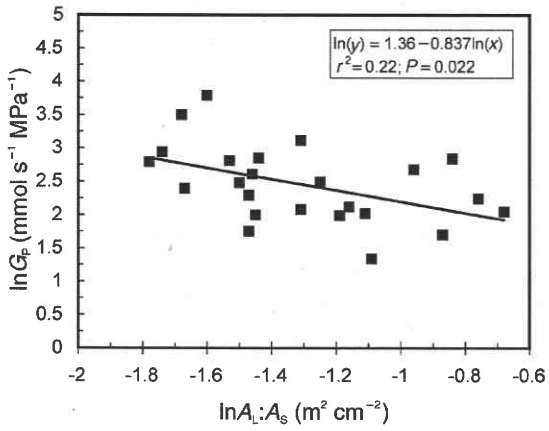

Figure 5. Relationship between absolute whole-plant hydraulic conductance (G_P) and the ratio of leaf area to sapwood area (A_L:A_S) in 3-year-old *Populus deltoides*.

served no interactive effects of nutrient and water availability on hydraulic properties. Although phenology, leaf morphology, crown structure, light interception efficiency and photosynthetic capacity influence growth of *Populus* (Ceulemans et al. 1992, Niinemets et al. 2004), the greatest gains in growth in young *Populus* are often achieved by management effects on leaf area (Cannell et al. 1988, Heilman et al. 1996, Harrington et al. 1997, van den Driessche 1999, Rae et al. 2004). For example, in 6-year-old *Populus deltoides* with a maximum LAI of 6.0, N fertilization doubled LAI and aboveground net primary productivity, leading Henderson and Jose (2005) to conclude that gains in leaf area alone were sufficient to maximize productivity. In our study, irrigation and fertilization doubled and tripled, respectively, aboveground biomass productivity in the third growing season, but LAI increased only 26% with irrigation and 23% with fertilization. Enhanced leaf-level net photosynthesis was likely important in maximizing growth, because fertilization and irrigation increased E_L, G_{Sref} and G_L. A direct link between G_L and net photosynthetic rate (Hubbard et al. 2001) and a positive relationship between maximum carboxylation capacity and G_{Sref} (Katul et al. 2003) have been proposed.

Leaf area index was increased similarly by irrigation and fertilization, but fertilization induced greater gains in growth than irrigation (Coyle and Coleman 2005), possibly because of greater enhancement of leaf-level net photosynthesis in response to fertilization. A strong correlation between foliar N concentration on a mass or area basis and photosynthetic capacity has been reported for *Populus* (Coleman et al. 1998, Ibrahim et al. 1998, Casella and Ceulemans 2002, Henderson and Jose 2005), and foliar N concentration increased with fertilization. Increased foliar $\delta^{13}C$ enrichment in response to fertilization may be related to increased photosynthetic capacity. Foliar nitrogen and $\delta^{13}C$ have been positively linked in *Populus fremontii* Wats and *Populus angustifolia* James (Sparks and Ehleringer 1997). In contrast, the greater foliar $\delta^{13}C$ enrichment that was observed in non-irrigated stands was likely in response to water stress and increased stomatal limitation of photosynthesis (Korol et al. 1999, Rood et al. 2003).

We speculate that the trends toward greater biomass in Clone S7C15 than in Clone ST66 observed by Coyle and Coleman (2005) were facilitated by higher leaf carbon gain. Clone S7C15 had higher E, G_L, G_{Sref} and foliar N concentration than Clone ST66, but LAI was similar between clones. The higher G_L in Clone S7C15, the clone from Texas, may be a result of ecotypic variation, with higher G_L in clones from hotter regions (Mencuccini 2003). For example, mean annual 24-h temperature and annual precipitation over the 1971–2000 period was 20.5 °C and 1008 mm, respectively, for the Brazos County region in Texas, the origin of Clone S7C15, and 17.7 °C and 1420 mm, respectively, for the Issaquena County region in Mississippi, the origin of Clone ST66 (Southeast Regional Climate Center). Potential variation in crown architecture (Michael et al. 1990, Marron et al. 2006) may also account for the clonal differences in G_{Sref}. Variations in drought tolerance (Liu and Dickman 1996, Tschaplinski et al. 1998) and nutrient-use efficiency (Heilman et al. 1996) have been reported for *Populus* clones, but, in our study, clonal differences in the majority of hydraulic traits were independent of resource availability.

In conclusion, irrigation and fertilization increased E, E_L, G_L, and G_S at a D of 1.0 kPa in a young *Populus deltoides* plantation. Fertilization had greater effects on growth and hydraulic properties than irrigation, and the influence of fertilization on hydraulic traits was independent of water supply. The A_L:A_S ratio was important in understanding long-term acclimation to resource availability, regulation of water loss and mechanisms controlling maximum productivity. Gains in aboveground biomass in *Populus deltoides* were achieved by increased leaf area and most likely enhanced leaf assimilation rate.

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