International Journal of Phytoremediation: Vol. 2, No. 1, pp. 53–73 (2000)

Leaf Water Relations and Sapflow in Eastern Cottonwood (*Populus deltoides* Bartr.) Trees Planted for Phytoremediation of a Groundwater Pollutant

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ABSTRACT

Plants that remediate groundwater pollutants may offer a feasible alternative to the traditional and more expensive practices. Because its success depends on water use, this approach requires a complete understanding of species-specific transpiration patterns. The objectives of this study were (1) to quantify tree and stand-level transpiration in two age classes (whips and 1-year-old seedlings) of eastern cottonwoods (*Populus deltoides* Bartr.), and (2) to determine climatic and physiological driving variables at the Carswell Air Force Base in central Texas, USA. Trichloroethylene (TCE) was detected in shallow (2 to 3 m) groundwater in the early 1980s. Cottonwood whips and 1-year-old potted seedlings were planted in two separate 0.15-ha plantations in spring 1996. Sapflow gauges determined sapflow on 14 to 16 trees in May, June, July, August, and October 1997. Without adjusting for differences in tree size, sapflow rates were greater for 1-year-old trees than whips (peak values were 0.75 and 0.53 kg hr^{-1} $tree^{-1}$, respectively). When adjusted for tree size, the pattern reversed, with whips having significantly greater sapflow rates than 1-year-old trees (peak values were 0.053 and 0.045 kg cm^{-2} hr^{-1}, respectively). Temporal variation (diurnal and seasonal) in sapflow rates was principally related to VPD, solar radiation, and leaf conductance. Extrapolating to the stand and across the growing season, the plantations transpired ~25 cm of water. Early attainment of high levels of transpiration indicates that the stands will transpire considerably more water as leaf area and root exploitation increases with stand development.

KEY WORDS: abiotic controls, leaf conductance, stand-level transpiration

1522-6514/00/$.50
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I. INTRODUCTION

Phytoremediation of ground and soil water contaminants is an attractive alternative to conventional methods, such as pump and treat, because costs are low and potential alternative products include short rotation wood culture (SRWC). Vegetation at the majority of hazardous waste sites across the U. S. is native, but the potentially positive impacts of these and planted species has only recently been advanced as a site clean-up tool (Flathman and Lanza, 1998). In the case of soil and ground water pollutants, a key factor in phytoremediation is choosing plant species that will transpire a substantial quantity of water and subsequently metabolize or accumulate the contaminant. Hence, the successful application of phytoremediation technology requires a thorough and accurate assessment of water use patterns (e.g., transpiration rates, depth of soil water uptake, interactions with climate, and soil water availability) in plant species that are known to be effective metabolizers of the specific pollutant. Accurate determination of stand- or tree-level transpiration in field conditions has been difficult and estimates have only recently been reported in the literature (e.g., Hinckley *et al.,* 1994; Hogg and Hurdle 1997; Martin *et al.,* 1997) Typically, four methods have been used: (1) precipitation minus runoff (P-RO) relationships on gaged watersheds, (2) energy balance (e.g., Penman-Montieth), (3) hydrologic models, and (4) direct sapflow measurement. The first two methods are integrated estimates of the entire system and do not partition water losses based on transpiration vs. evaporation. Hydrologic models vary considerably in complexity and data requirements, but usually only detailed physiologically based models that link vegetation, soils, and the atmosphere provide accurate assessments of transpiration (Vose and Swank, 1992). Unlike these indirect measurements, sapflow measurements provide an opportunity to directly measure transpiration on an individual tree basis under field conditions (Hinckley *et al.,* 1994; Martin *et al.,* 1997). Modeling or other scaling approaches can then be used to extrapolate tree-level measurements to the stand.

Native vegetation is commonly found in the presence of hazardous contaminants in soil and ground water at many locations. While relying on native vegetation to remediate polluted soil and ground water is potentially important, planting species that are known to metabolize pollutants and have high growth and transpiration rates may be an even more effective alternative. In this project, we assess the use of planted eastern cottonwood (*Populus deltoides* Bartr.) to accelerate the remediation of shallow groundwater contaminated with trichloroethylene (TCE), a common degreasing agent. *Populus* has high rates of transpiration (Pallardy and Kozlowski, 1981; Heilman *et al.,* 1996), rapid establishment and dry matter production (Heilman *et al.,* 1996), and the ability to take-up, metabolize, and mineralize TCE (Newman *et al.,* 1997, Gordon et al. 1998). This combination of attributes makes *Populus* an ideal candidate for a combined approach of phytoremediation and SRWC; however, stand level determinations of water use, and the abiotic factors that regulate water use at stand scales needs to be more completely understood. We had two objectives: (1) to quantify tree- and stand-level transpiration (estimated by sapflow) rates in two age classes (whips and 1-year-old seedlings) of eastern cottonwoods, and (2) to deter-

mine climatic and physiological driving variables. Large differences in the cost of whips vs. seedlings, as well as differences in planting costs, make the comparison of whips vs. 1-year-old seedlings particularly important from an implementation standpoint.

II. METHODS

A. Site Description

The study site is located in north-central Texas in Tarrant County, about 15 km west of Fort Worth. Study plots are located on the Naval Air Station (formerly Carswell Air Force Base), which adjoins U.S. Air Force Plant 4 (AFP4) on the west and the Carswell Golf Club on the south. AFP4 was constructed in 1942 and currently is operated by Lockheed, producing F–16 aircraft, radar units, and various aircraft and missile components. Historically, the manufacturing processes at AFP4 generated an estimated 2.5 to 2.7 tonnes of waste per year, including solvents, oils, fuels, paint residues, and miscellaneous chemicals. Before the 1970s, AFP4's waste oil, solvents, and fuels were disposed of in onsite landfills or were burned in fire training exercises. Chemical wastes were discharged to the sanitary sewer system, which drained to the city of Fort Worth sewer treatment system. In the 1970s, chemical wastes were treated onsite using a chemical treatment system, before discharge to the sanitary sewer system. Currently, waste oils and solvents are disposed of by a contractor and chemical wastes are treated onsite before discharge to the sanitary sewer system.

The hydrogeologic system at AFP4 consists of four primary components: (1) the terrace alluvial aquifer, (2) the Goodland-Walnut confining unit, (3) the Paluxy aquifer, and (4) the Glenn Rose Formation and the Twin Mountains aquifer. The terrace alluvial aquifer (TAA) is the uppermost hydrogeologic unit at AFP4 and consists of silt, clay, sand, gravel, and fossiliferous limestone. Recharge to the TAA occurs as infiltration of precipitation, and leakage from water supply lines, sewer lines, and fire protection lines. Potential contamination of the groundwater in the vicinity of AFP4 was first noticed in 1982, and intensive sampling began in 1985. A plume containing trichloroethylene (TCE) was detected in the TAA extending eastward from APF4 through our study site. Subsequent analysis of groundwater samples beneath our study site indicated the presence of two groundwater contaminants: trichloroethylene and dichloroethylene, with maximum concentrations (1996 sampling) of 960 and 131 $\mu g\ L^{-1}$, respectively (AFP4 Technology Demonstration Plan, 1996).

Surface soils are characterized as clayey in the top 50 cm, clay to silty clay from 50 to 130 cm, and clay, silty clay, to clayey loam from 130 to 200 cm (USDA Soil Survey, 1981). The topography of the site is generally flat except for a gentle slope toward Farmer's Branch Creek. AFP4 and the Naval Air Station are located within the Grand Prairie Section of the Central Lowland Physiographic region. Groundwater depth varies from 2 to 3.4 m across the study area, and aquifer thickness varies from 0.2 to 1.4 m. The climate is characterized as subhumid, with mild winters and hot and humid summers. Average annual precipitation is 80 cm yr^{-1}, with most

rainfall occurring between May and October. Average annual temperature is 18.6°C. The number of annual frost-free days ranges from 220 to 240 days.

B. Tree Planting

Trees were planted and the irrigation system was installed in April 1996. Trees were planted in two plantations located within 30 m of each other. One plantation was planted with 440 eastern cottonwood vegetative cuttings (whips) comprised of a mixture of 11 clones derived from local sources, and the other with 224 nursery grown 1-year-old eastern cottonwood (Soiuxland variety) seedlings. Each plantation was approximately 80 × 20 m and located perpendicular to groundwater flow in the alluvial aquifer. Trees were planted in approximately 2.4-m-wide rows trenched to a depth of 1 m for the length of the plantation. Whips were planted approximately every 1.2 m within rows, and 1-year-old trees were planted approximately every 2.4 m. To ensure establishment, both plantations were liberally irrigated every other day during the spring and summer of 1996. Summer 1996 was one of the driest on record in Texas. Sapflow and other physiological measurements (described below) were initiated during the second growing season (1997). Table 1 displays pre- (winter 1997) and post-measurement (fall 1997) stand characteristics.

C. Sapflow Measurements

Sapflow was measured using sap flow gauges (Dynagage, Dynamax Inc., Houston, TX[1]) on 14 to 16 trees (divided equally between whips and 1-year-old trees) in May, June, July, August, and October 1997. Variation in the number of trees sampled during each sample period was the result of faulty gauges. Gauges consist of a flexible heating element and thermocouples located above and below the heating element, both of which are pressed firmly against the outside of the stem (Baker and van Bavel, 1987; Steinberg *et al.*, 1989). Sapflow is calculated using the heat-balance principle based on the difference in temperature between thermocouples above and below the heated stem section, after subtracting for heat loss due to conduction by stemwood. Standard procedures for calculating sapflow from heat balance principles (Baker and van Bavel, 1987, Dynagauge Operators Manual, Houston, TX[1]) were field tested in 1997 using the "cut-tree" method (Landsberg *et al.*, 1976; Vertessey *et al.*, 1997) for trees representing a range of sizes in the plantation. Results showed

TABLE 1. Stand Characteristics of the Whip and 1 year Plantation

Plantation	Density (# ha^{-1})	Initial mean diameter[a] (range) (cm)	Final mean diameter[a] (range) (cm)
Whips	3 144	2.8 (1.6–4.0)	4.7 (2.7–8.2)
1-yr	2 019	4.6 (3.3–5.9)	7.6 (6.2–9.8)

[a]Diameter measured at 10 cm above ground level.

excellent agreement between "cut-tree" and sapflow-based transpiration estimates (within +/- 5%). These results are consistent with other studies that indicate good agreement between sapflow and independent transpiration estimates (e.g., Steinberg *et al.,* 1990; Vertessey *et al.,* 1997; Zhang *et al.,* 1997).

Sap flow gauges were installed on stems at approximately 5 cm above ground level and below all branches. Sapflow trees were selected to span the range of diameters, and the same trees were used for each measurement period (Table 1). Stem diameters at the location of the heating strip were recorded at each measurement period. In some cases, diameter growth through the year required the installation of a larger gauge in the later sampling periods. Before gauge installation, stems were lightly sanded to remove loose bark and ensure good thermal contact. Trees with irregular bark or with branches near the ground were not selected because adequate thermal contact could not be assured. The heating element and thermocouples were wrapped tightly against the stem and covered with 2.5-cm-thick insulation, a radiation shield, and caulking to minimize external variation in temperature and prevent rainfall (either directly or from stemflow) from getting beneath the sapflow gauge. During each monthly measurement period, sapflow measurements were taken every minute for 2 to 3 consecutive days and stored as 15-min averages using a Campbell CR10 datalogger (Campbell Scientific Inc., Logan, UT[1]).

D. Leaf Level Physiological Measurements

Leaf conductance (g_l in cm s^{-1}) was measured on sapflow trees with a steady-state porometer (LI–1600, LI-COR Instruments, Lincoln, NE[1]). While *Populus deltoides* has approximately equal stomata distribution on both sides of the leaf, reported values are for stomata on the bottom side of the leaf only. Daily measurements were taken in late morning (0900 to 1100), early afternoon (1200 to 1400), and late afternoon (1500 to 1700) from leaves in the lower-half and upper-half of the crown (one per location) and averaged to estimate mean daily g_l for each sample tree. Fewer measurements were obtained in the October sample period because afternoon rains were frequent. Measurements were taken under ambient conditions, and photosynthetically active radiation (PAR), leaf temperature, and relative humidity incident on each leaf were recorded. In addition, pre-dawn (0600) and mid-day (1300 to 1400) leaf water potential (MPa) were measured on sapflow trees with a Scholander Pressure Bomb (PMS Instruments, Corvallis, Oregon[1]) on leaves sampled (one per tree) from the mid-crown.

E. Climatic Measurements

Rainfall (cm), wind speed (m s^{-1}), solar radiation (W m^{-2}), temperature (°C), and relative humidity (%) were measured from a climate station on the site. Relative humidity and air temperature were used to calculate vapor pressure deficit (VPD in kPa). Beginning in June, soil moisture (%) in the top 30 cm of soil was measured with time domain reflectometry (TDR) at eight random locations (four within each plantation) in the vicinity of the sample trees during each measurement period. In addition, soil moisture was measured continuously in an open field near the climate station using TDR (Campbell Scientific, Logan, UT[1]).

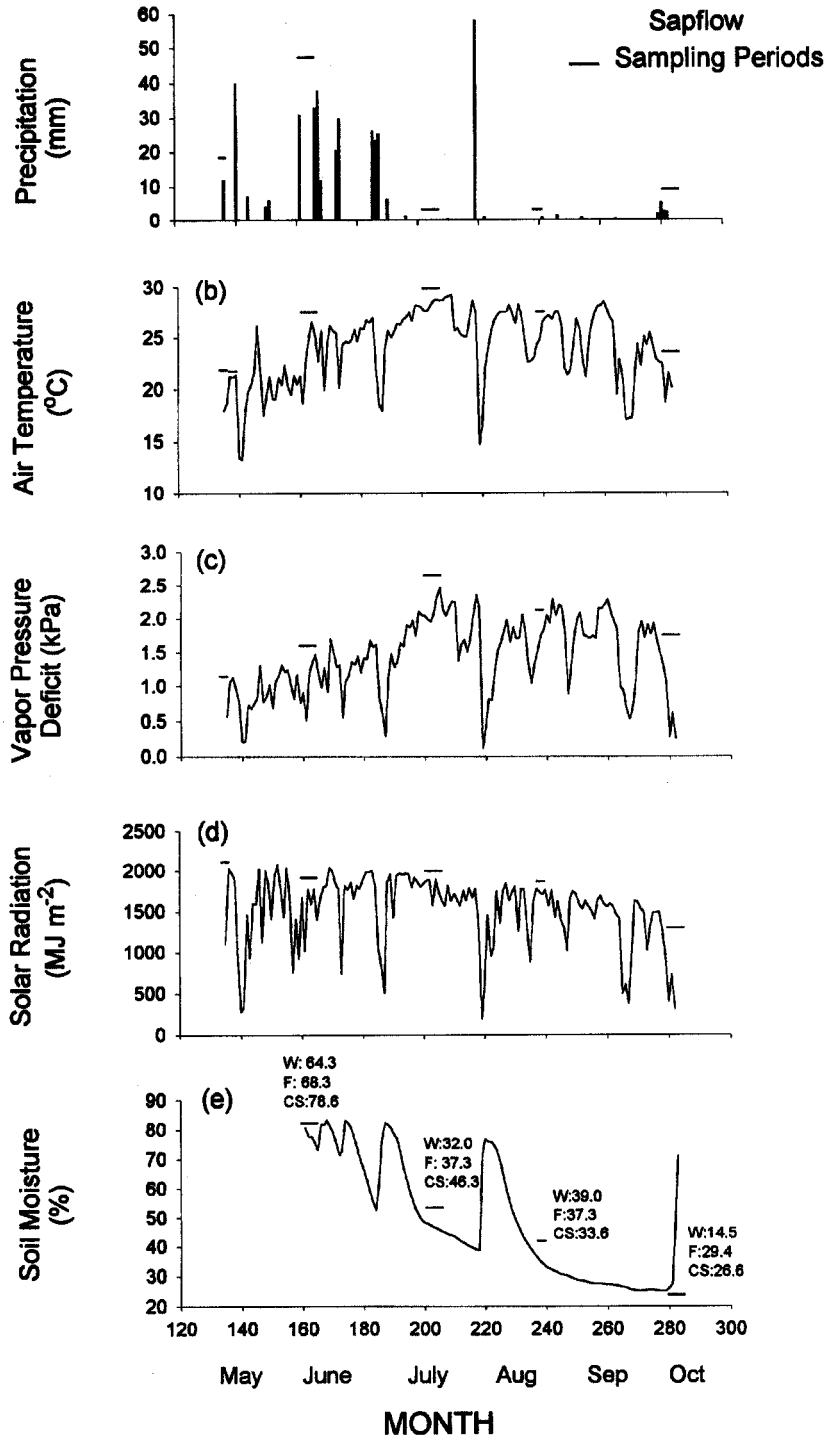
Precipitation (mm)
Sapflow
Sampling Periods
Air Temperature (°C)
(b)
Vapor Pressure Deficit (kPa)
(c)
Solar Radiation (MJ m-2)
(d)
Soil Moisture (%)
(e)
W: 64.3
F: 68.3
CS:78.6
W:32.0
F: 37.3
CS:46.3
W:39.0
F:37.3
CS:33.6
W:14.5
F:29.4
CS:26.6
May
June
July
Aug
Sep
Oct
MONTH

FIGURE 1. Variation in climate over the measurement period. Values are 24-h means for air temperature (b), vapor pressure deficit (c), and soil moisture (e), and 24-h totals for precipitation (a) and solar radiation (d). For soil moisture (e) represents 24-h means of continuous measurements at the climate station, W = mean soil moisture within the whip plantation for each measurement period, F = mean soil moisture within the 1-year-old plantation for each measurement period, and CS = mean soil moisture at the climate station for each measurement period.

F. Statistical Analyses

Analysis of variance (PROC ANOVA, SAS, 1987) was used to test for differences in g_l among canopy positions (by measurement period, whips and 1-year-old analyzed separately) and for differences between whips and 1 year old trees in g_l, $\Psi_{am/pm}$, and sapflow (by measurement period). All analyses were conducted at the tree level. Linear (PROC REG, SAS, 1987) and nonlinear (PROC NLIN, SAS, 1987) regressions were used to examine relationships among sapflow rate, leaf-level physiological variables, and climate. For all statistical tests an $\alpha = 0.05$ significance level was used.

III. RESULTS

A. Climate and Soil Moisture

Precipitation patterns over the measurement period (May through October) were characterized by frequent, but relatively small (< 40 mm) rain events in May, June, and early July, with less frequent rain from mid-July through October (Figure 1a). The largest rainfall event (58 mm) occurred in August. Total precipitation for the measurement period was 331 mm. Average daily temperature ranged from ~13 to 29°C with the highest temperatures occurring in July and August (Figure 1b). Mean daily VPD ranged ~0.2 to 2.4 kPa, with the largest VPD generally occurring from mid-June to September (Figure 1c). Solar radiation ranged from 216 to 2088 MJ m^{-2} and varied in response to cloud cover (i.e., lowest values usually occurred during rainy periods) (Figure 1d). Soil moisture (%) varied considerably (range 26.6 to 80.1%) throughout the measurement period (Figure 1e), responding to rainfall and evapotranspiration. Soil moisture was generally plentiful (> 50%) in the spring and early summer when precipitation inputs were frequent and declined through the summer as rainfall declined and evapotranspiration increased.

B. Leaf-Level Water Relations

The effect of canopy position on g_l differed throughout the measurement period and between whips and 1-year-old trees. For whips, significant canopy position effects on g_l were observed only in June and July, when g_l was significantly ($p < 0.05$) greater in the upper canopy (Figure 2). In contrast, g_l did not differ significantly between canopy positions for 1-year-old trees. Mean g_l (averaged across trees, canopy position, and sample days within a month) and $\Psi_{am/pm}$ varied considerably

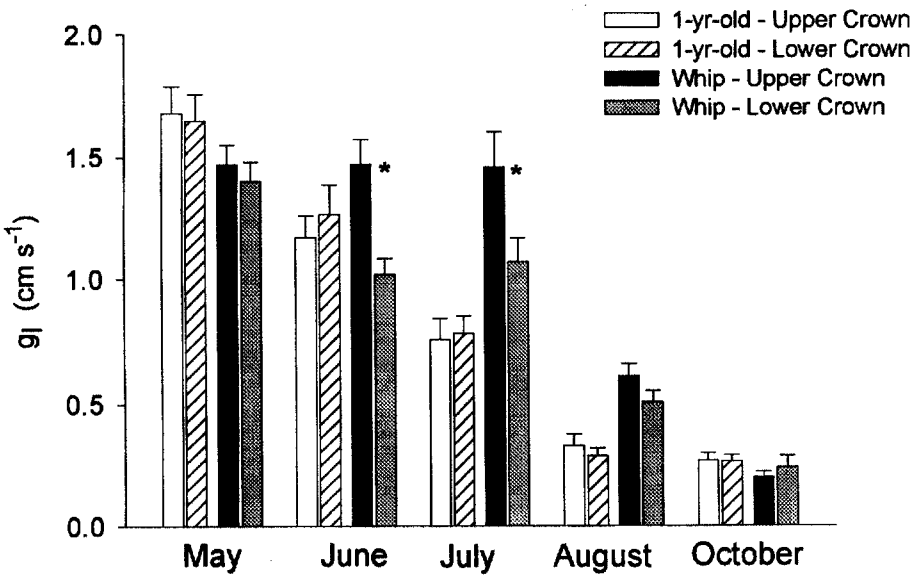

FIGURE 2. Mean measurement period leaf conductance (g_l) by canopy position for whips and 1-year-old trees. Statistically significant ($p < 0.05$) differences (within measurement periods and age classes) between upper and lower canopy positions are denoted by *. Vertical lines on all bars represent standard errors.

across measurement periods and between whips and 1-year-old trees (Figure 3a and b). For both whips and 1-year-old trees, g_l declined during the growing season with the greatest g_l in May (1.7 and 2.1 cm s^{-1}, respectively) and the lowest g_l in October (0.25 and 0.22 cm s^{-1}, respectively). Averaged across measurement periods, g_l for whips and 1-year-old trees were nearly equal (1.1 cm s^{-1} and 1.0 cm s^{-1}, respectively); however, g_l for whips was significantly greater ($p < 0.05$) in July and August, and g_l for 1-year-old trees was significantly ($p < 0.05$) greater in May (Figure 3a).

Ψ_{am} was greatest in May and October and decreased substantially in midsummer. The lowest Ψ_{am} values for both whips and 1-year-old trees occurred in July (–0.51 and –0.40 MPa for whips and 1-year-old trees, respectively). Ψ_{am} was significantly lower for whips in May and June than for 1-year-old trees (Figure 3b). Ψ_{pm} also varied considerably across measurement periods and followed a pattern similar to Ψ_{am}. Lowest values for whips occurred in July and August (–1.42 and –1.59 MPa, respectively) and lowest values for 1-year-old trees occurred in June and July (–1.19 and –0.95 MPa, respectively). Highest values for both age classes occurred in May (–0.48 and –0.56 MPa for whips and 1-year-old trees, respectively). Ψ_{pm} values were significantly lower for whips than for 1-year-old trees in July and August.

There were no statistically significant relationships between mean Ψ_{am} and mean daily g_l for either whips or 1-year-old trees (Figure 4b). However, there was a general

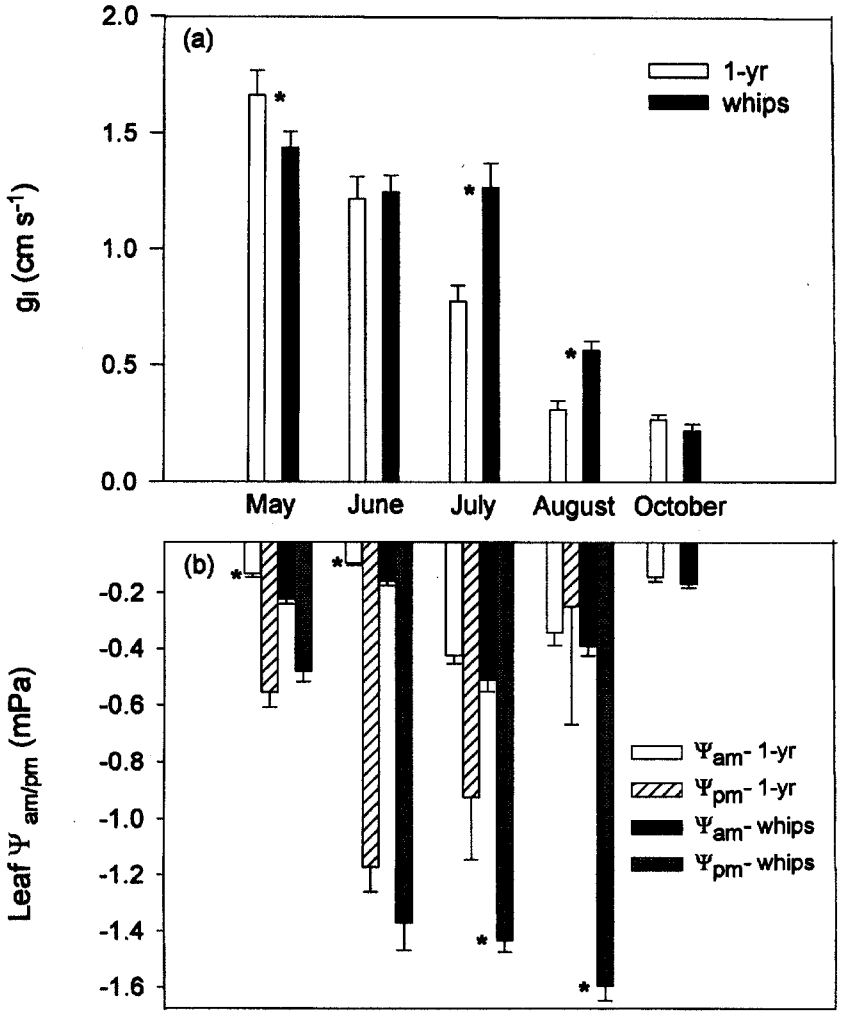

FIGURE 3. Mean measurement period leaf conductance (g_l) (a), and predawn and mid-day leaf water potential ($\Psi_{am/pm}$) (b) for whips and 1-year-old trees. Statistically significant ($p < 0.05$) differences (within measurement periods) in mean values between whips and 1-year-old trees are denoted by *. For Figure 3b, differences in May and June are for Ψ_{am} values only, and differences in July and August are for Ψ_{pm} values only. Vertical lines on all bars represent standard errors.

trend of decreased g_l with decreased Ψ_{am}, especially for 1-year-old trees. In contrast, there were significant linear relationships between Ψ_{pm} and mean g_l for both whips ($r^2 = 0.51$; $p < 0.05$) and 1-year-old trees ($r^2 = 0.93$; $p < 0.05$) (Figure 4a).

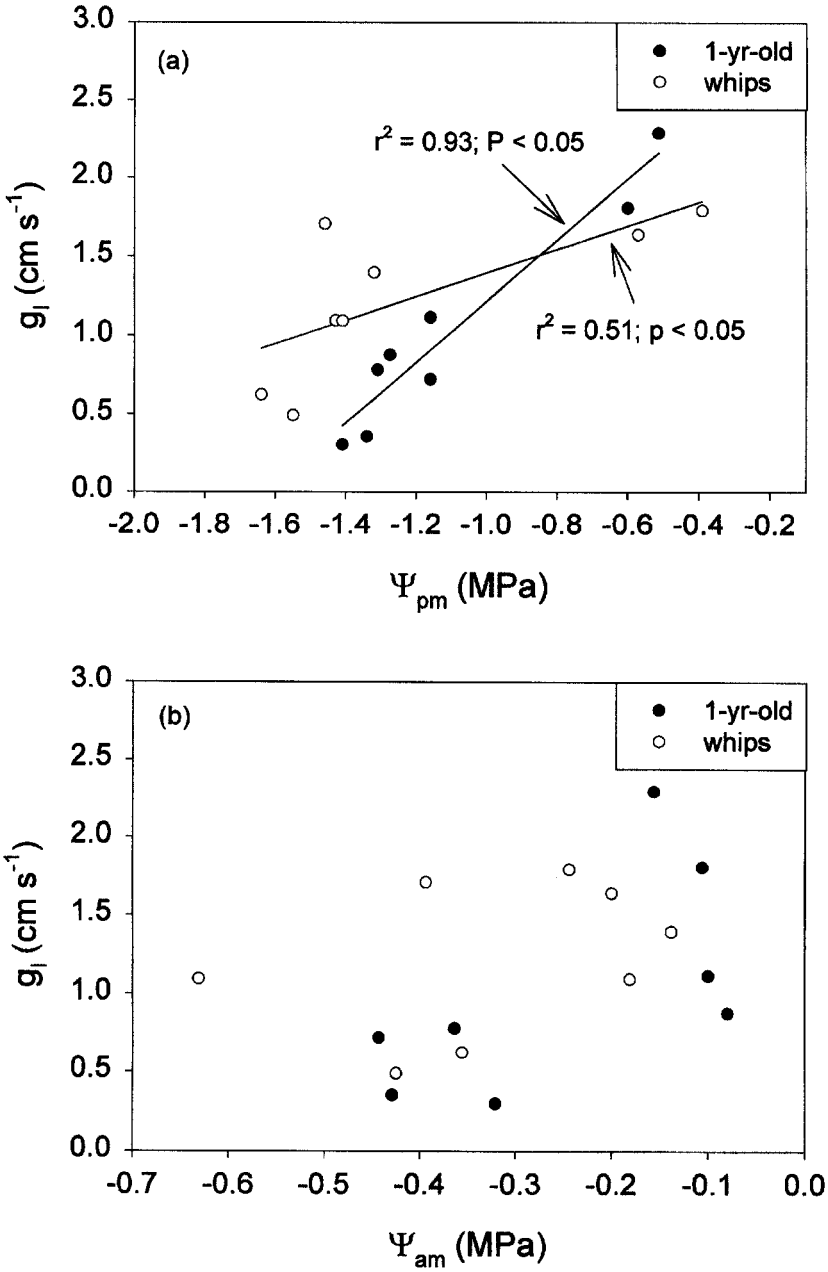

FIGURE 4. Relationship between mean daily g_l and Ψ_{pm} (a) and Ψ_{am} (b).

C. Sapflow

Average (i.e., averaged across trees and sample days within the month) monthly sapflow rates (kg hr^{-1} $tree^{-1}$) varied considerably through the growing season and

between whips and 1-year-old trees (Figure 5a). For both whips and 1-year-old trees, the greatest sapflow (0.53 and 0.75 kg hr^{-1} $tree^{-1}$, respectively) occurred in June and the lowest occurred in October (0.13 and 0.16 kg hr^{-1} $tree^{-1}$, respectively). Sapflow was significantly ($p < 0.05$) greater for 1-year-old trees than whips for all measurement periods except October. Averaged across the growing season, 1-year-old trees show a sapflow rate two times greater than that of the whips (0.61 kg hr^{-1} $tree^{-1}$ vs. 0.34 kg hr^{-1} $tree^{-1}$ for 1 year old vs. whips, respectively).

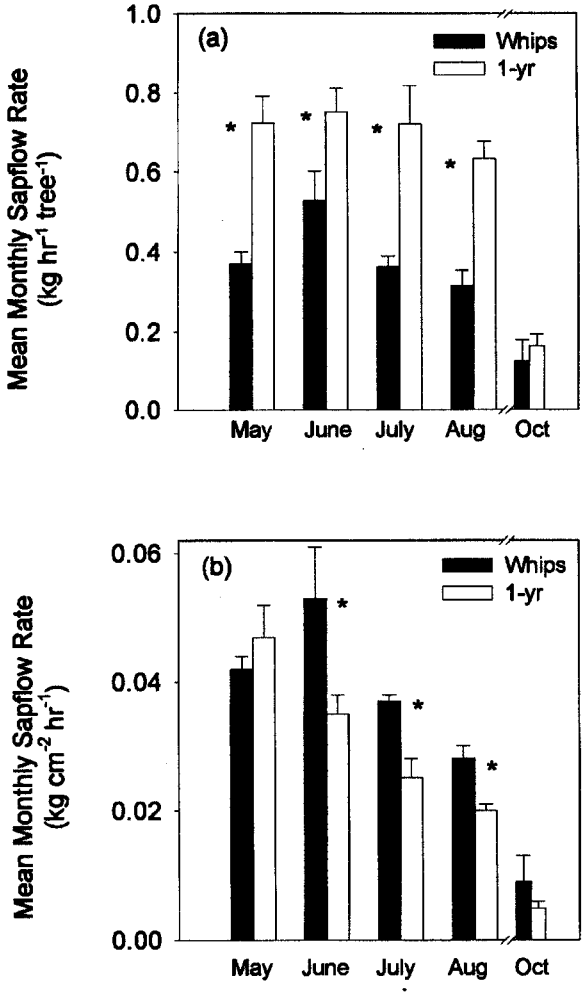

FIGURE 5. Variation in mean hourly sapflow rate expressed on a per tree (a) or per unit basal area (b) basis. Data are sample period means for all months sampled. Statistically significant ($p < 0.05$) differences between whips and 1-year-old trees are denoted by *. Vertical lines on all bars represent standard errors.

Because whips and 1-year-old trees were considerably different in size (and presumably leaf area), sapflow estimates were divided by basal area of each measurement tree. Leaf area is directly proportional to tree basal area, because nearly all the stemwood in young (< 5 years old) *Populus* is sapwood (Telewski *et al.,* 1996) and numerous studies have found strong relationships between sapwood area and foliar biomass and/or area (Waring *et al.,* 1982; Vertessey *et al.,* 1997). When expressed on a per unit basal area basis (kg cm^{-2} hr^{-1}) (Figure 5b), mean monthly transpiration rates were generally greater in whips than 1-year-old trees, with statistically significant ($p < 0.05$) differences occurring in June, July, and August; however, averaged across the growing season, rates were only slightly greater in whips (0.033 kg^{-1} cm^{-2} hr^{-1}) than 1-year-old trees (0.027 kg^{-1} cm^{-2} hr^{-1}).

D. Hourly Climate vs. Hourly Sapflow

We analyzed the relationship between mean hourly climatic variables and sapflow rate for May through August. Best fits were obtained when sapflow data were lagged 1 hour to account for the time lag between transpiration and waterflux through the stem (Schulze *et al.,* 1985; Phillips *et al.,* 1997). October was excluded from the analyses because of the confounding effects of leaf senescence. For both whips and 1-year-old trees, VPD and hourly sapflow rate across measurement periods showed an aysmptotic relationship (Table 2, Figure 6a and b). In most cases, sapflow rate became unresponsive to VPD at values greater than approximately 1.5 kPa. The sapflow rate obtained at the asymptote varied considerably across the season. In May and June, when Ψ_{am} was > –0.20, the parameter estimating the asymptote (β_0) was

TABLE 2. Parameters for Nonlinear Model Relating Mean Hourly Vapor Pressure Deficit (VPD) to Mean Hourly Sapflow Rate (Lagged 1 h)

		Parameter	
Plantation	**Month**	β_0	β_1
Whips	May	0.071 (0.009)	–1.559(0.469)
	June	0.110 (0.011)	–0.806 (0.164)
	July	0.057 (0.0042)	–0.643(0.120)
	August	0.035(0.0024)	–1.164 (0.308)
1-year	May	0.047 (0.010)	–1.218 (0.573)
	June	0.056 (0.006)	–1.504 (0.464)
	July	0.042 (0.003)	–1.042 (0.300)
	August	0.0303 (0.006)	–0.906 (0.511)

Note: Model is of the form: sapflow = β_0*(1-$e^{(\beta 1*VPD)}$), where sapflow is in kg cm^{-2} hr^{-1} and VPD is in kPa. Values in parentheses are standard errors. All parameters are significant at $p < 0.05$.

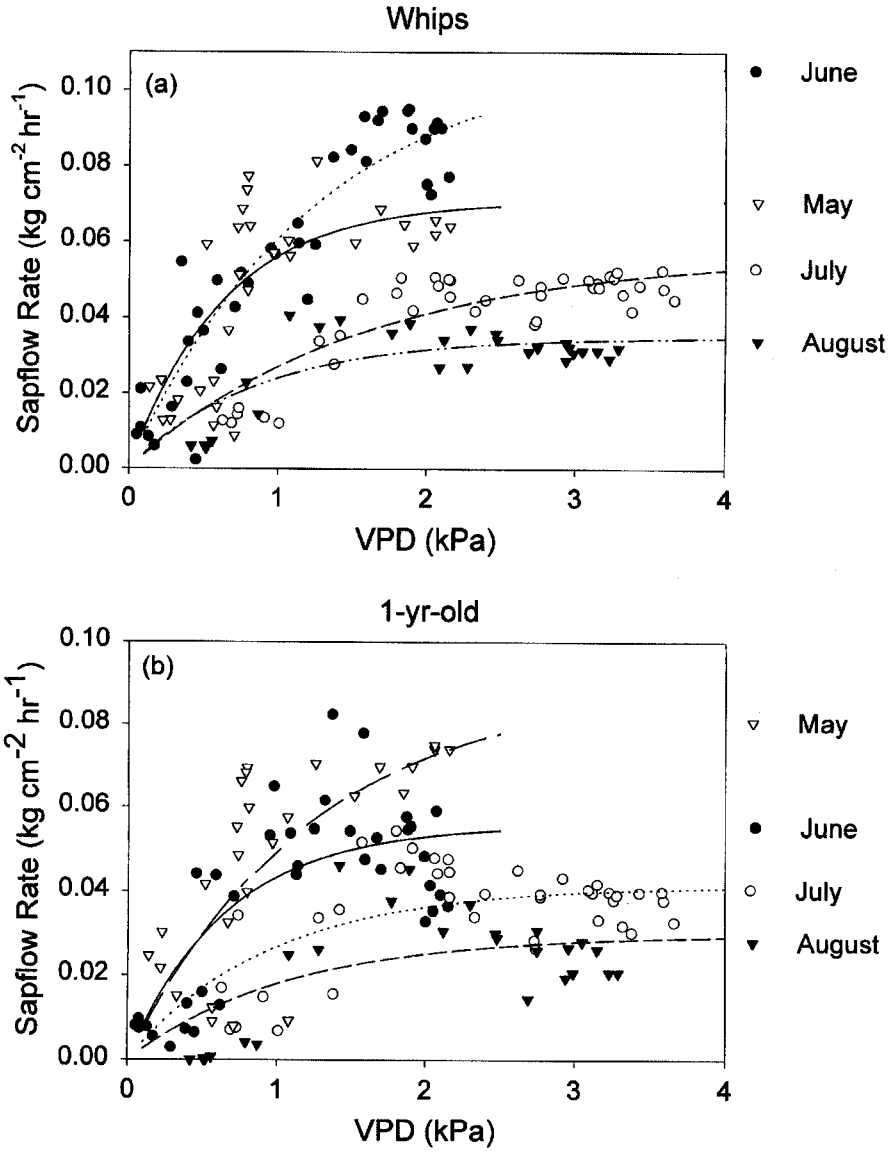

FIGURE 6. Nonlinear relationships between mean hourly VPD (kPa) and mean hourly sapflow rate (kg cm^{-2} hr^{-1}) for May, June, July, and August for whips (a) and 1-year-old (b) trees. Parameters for the curves are given in Table 2.

0.071 (May) and 0.110 (June) for whips and 0.090 (May) and 0.056 (June) for 1-year-old trees. In July and August, Ψ_{am} decreased to as much as –0.51, and β_o parameters decreased to 0.057 to 0.035 for whips and 0.047 to 0.030 for 1-year-old trees. In

addition, both whips and 1-year-old trees were more responsive to changes in VPD in May and June, as shown by the steeper slope of the relationship between sapflow rate and VPD during those months (Figures 6a and b). Sapflow rate was linearly related to solar radiation, with r^2 values ranging from 0.52 to 0.70 for whips and 0.57 and 0.78 for 1-year-old trees (Fig. 7a and b). For whips, the slopes of the linear relationship were generally greater in May and June than in July and August. In contrast, the slope of the relationship between solar radiation and sapflow rate did not differ for 1-year-old trees.

E. Mean Daily Leaf Conductance vs. Mean Daily Sapflow

A strong and significant linear relationship ($r^2 = 0.75$; $p < 0.05$; $n = 20$) appeared between mean daily g_l (averaged across canopy positions) and mean daily sapflow rate (kg cm^{-2} hr^{-1} $tree^{-1}$) when g_l was < 1.5 cm s^{-1} (Figure 8). However, at $g_l > 1.5$ cm s^{-1} no relationship was found between g_l and sapflow rate, and sapflow was lower or equal to that observed at considerably lower g_l. For both whips and 1-year-old trees, $g_l > 1.5$ occurred in May, and for whips alone in July.

F. Stand Level Water Use

Mean total daily transpiration ranged from 14.7 kg $tree^{-1}$ day^{-1} (July 23) to 0.92 kg $tree^{-1}$ day^{-1} (October 9) for 1-year-old trees and from 9.2 kg $tree^{-1}$ day^{-1} (June 12) to 1.6 kg $tree^{-1}$ day^{-1} (October 9) for whips. We extrapolated these values to stand level (kg ha^{-1} day^{-1}) using a mean tree approach where we assumed that the sapflow values obtained from the sample trees were representative of the population. Averaged across all measurement periods, stand-level sapflow was 16 637 kg ha^{-1} day^{-1} for the 1-year-old tree plantation, and 15 560 kg ha^{-1} day^{-1} for the whip plantation. To place these averages in broader terms of water use, we extrapolated mean daily values to the growing season (May 1 to September 30 = 153 days). Total growing season transpiration was estimated to be 25.5 and 23.8 cm for 1-year-old trees and whips, respectively.

IV. DISCUSSION

A. Leaf-Level Water Relations

Vertical gradients in leaf-level water relations are a common phenomena in closed canopied *Populus* stands. For example, Hinckley *et al.*, (1994) observed a considerable decline in leaf conductance from top to bottom branches. In their study, differences were attributed to a strong gradient in light availability between upper and lower canopy positions. In our study, responses were inconsistent, with differences in g_l between upper and lower crown positions observed only in June and July and only for whips. Because the canopies of both plantations were open (leaf area index visually estimated at 1.5 to 2.0), gradients in light availability were unlikely causal factors for the differences observed. During these months, mean PAR in the lower canopy was only 17% lower (approximately 1000 mmol m^{-2} s^{-1} at full sunlight) than that in the upper canopy. Instead, we speculate that lower g_l in leaves in the lower

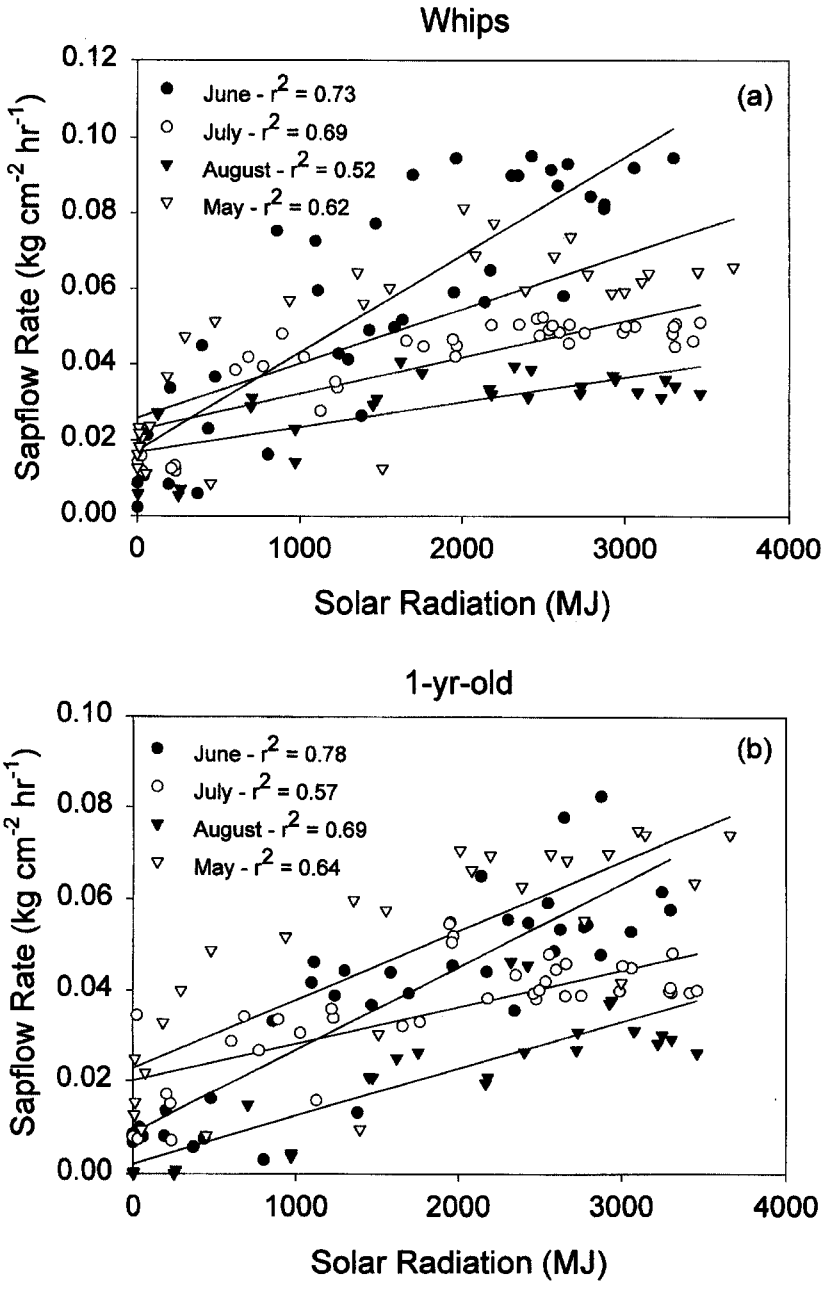

FIGURE 7. Linear relationships between mean hourly solar radiation (MJ) and mean hourly sapflow rate (kg cm^{-2} hr^{-1}) for May, June, July, and August for whips (a) and 1-year-old (b) trees.

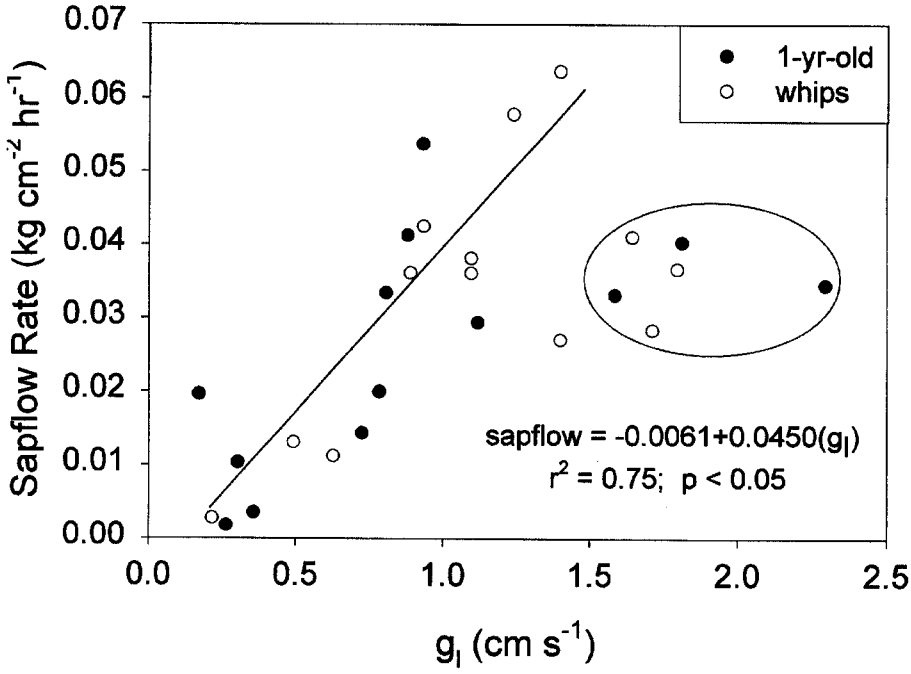

FIGURE 8. Relationship between mean daily sapflow rate (kg cm^{-2} hr^{-1}) and mean daily g_l for whips and 1-year-old trees. Linear regression was applied to the combined whip and 1-year-old tree data. Data in the circle were excluded from analyses for reasons described in the text.

canopy was indicative of the onset of leaf senescence in response to drought, because most drought-induced leaf fall occurred in the lower canopy.

Variation in climatic conditions across the measurement period resulted in substantial variation in leaf-level water relations. In general, g_l and $\Psi_{am/pm}$ were greatest in the early growing season (May) and declined as precipitation decreased and temperature and VPD increased (June to August), with lowest values occurring near the onset of leaf senescence (October). Although leaves were responsive to climatic variation, g_l and Ψ_{am} values were not indicative of severe water stress. In previous studies examining leaf-level water relations in *Populus* tremendous genetic variation has been found in responses to water stress (Braatne *et al.*, 1992; Pezeshki and Hinkley, 1988; Pallardy and Kozlowski, 1981). In our study (excluding October), g_l values were generally greater than reported for other *Populus* clones (Hinckley *et al.*, 1994; Zhang *et al.*, 1997). However, Braatne *et al.*, (1992), found g_l values comparable to those found in our study. Similarly, Ψ_{am} was never < –0.7 MPa on any measurement day and most measurement periods were > –0.5 MPa, which is comparable to Ψ_{am} values observed under well-watered conditions (Steinberg *et al.*,

1990; Zhang *et al.,* 1997). Stomatal conductance is related to Ψ in *Populus*; however, this response has been reported to only occur after Ψ falls below threshold values ranging from –1.2 MPa to –2.0 Mpa (Zhang *et al.,* 1997). Furthermore, genetic variation affects responses (Foster and Smith, 1991; Pezeshki and Hinkley, 1988). Stomata of *Populus deltoides* are reported to be more sensitive to declining leaf water potential than many other *Populus* species and clones (Pallardy and Kozlowski, 1981; Braatne et al., 1992). In our study, g_l was related to Ψ_{pm} across a range of –0.40 to –1.65 Mpa. The finding that the slope of the relationship was considerably steeper for 1-year-old trees than for whips (Figure 3a and b) may reflect genetic differences in their ability to withstand drought.

At least two factors may be responsible for lack of severe water stress under the conditions of low precipitation, high air temperature and high VPD characteristic of our study site. First, observations from another study on our site indicated that some *Populus* roots (whips and 1 year old) had reached the shallow groundwater (2 to 3 m below surface) aquifer by the end of the 1997 growing season (R. L. Hendrick, personal communication). Hence, severe water stress may have been alleviated by partial water uptake from the groundwater. Moderate water stress clearly occurred as indicated by decreased stomatal conductance and leaf senescence (see below). However, increased rooting volume with stand development should further offset the effects of high evaporative demand and low precipitation, as other studies have shown that access to a shallow groundwater source minimizes the effects of soil water deficit and high evaporative demand (Zhang *et al.,* 1997). Second, in July we observed a substantial amount of premature leaf fall (approximately 1/2 the total leaf area) from the whips — a common response in *Populus* and other tree species to avoid the effects of prolonged drought by reducing their transpiration surface area (Parker, 1968; Levitt, 1972).

B. Sapflow

Sapflow rates (kg tree^{-1} day^{-1}) for both whips and 1-year-old trees appeared to be greater than observed for *Populus* in other regions when normalized for tree size. For example, Hinckley *et al.,* (1994) observed sapflow rates of 20 to 26 kg tree^{-1} day^{-1} for *Populus* trees measuring 12 cm DBH in eastern Washington, USA. In our study, trees ranging from 2.75 to 7.61 cm diameter at ground level had maximum sapflow rates of 15 kg tree^{-1} day^{-1}. These differences in tree-level transpiration rates may be primarily related to climate, because conditions (higher solar radiation and high VPD) at our study site are more conducive to high transpiration rates than those in western Washington. With canopy closure and subsequent leaf area development at the Texas site in future years, there is potential for substantially greater stand-level transpiration at the site. Currently, observed sapflow rates are far below those observed for other species in well-watered conditions with comparable climatic conditions. Steinberg *et al.,* (1990) measured sapflow rates of 100 to 150 kg tree^{-1} day^{-1} for 7.9 cm diameter *Carya illinoensis* in central Texas, USA, under greenhouse conditions. This tenfold difference between what we observed in the field and what is obtainable under ideal conditions indicates that far greater transpiration rates might

be possible at our study site if water stress was alleviated. We anticipate that as more roots reach the ground water and leaf area increases, substantially greater tree and stand-level transpiration rates will be observed.

Greater sapflow rates in 1-year-old trees relative to the whips probably resulted from higher leaf area because sapflow rate was greater in whips when expressed per unit basal area. The slightly greater (measurement period average) rate of sapflow per unit basal area for whips relative to 1-year-old trees could be a result of several factors: (1) greater leaf area per unit sapwood area, (2) higher stomatal conductance, and (3) greater access to soil water. We have no data on differences in leaf area per unit sapwood between the whips and 1-year-old trees, but genetic differences could be an explanatory factor. For example, whips were collected from local sources while the 1-year-old trees were from nursery stock ("Siouxland" variety) indicative of a more northern source. Whips had significantly greater g_l than 1-year-old trees in July and August, but only slightly greater g_l when averaged over the measurement period. In addition, it is possible that the whips had greater access to groundwater because the depth to groundwater was approximately 0.5 m closer to the surface (as determined by groundwater wells located on site) in the whip plantation than in the 1-year-old plantation. Because of differences in genetics, age, and access to groundwater, extrapolating the results of sapflow comparisons between 1-year-old trees and whips to other sites and genotypes must be done with caution.

C. Sapflow vs. Climate and g_l

Transpiration is driven by the combined influences of climate driving variables, leaf area index, and stomatal opening. The curvilinear relationship observed between mean hourly sapflow rate and VPD indicates stomatal closure at high VPD, with an apparent threshold at approximately 1.5 kPa VPD. In *Populus tremuloides*, Hogg and Hurdle (1997) also found a curvilinear response between sapflow and VPD, with a threshold value of 1-kPa VPD. Variation in the slope and asymptote of the sapflow vs. VPD curves reflects the sensitivity of stomata to changing Ψ and soil water availability. As conditions became drier, the slope of the sapflow-VPD relationship declined and the asymptote was considerably reduced.

The high degree of stomatal control of transpiration is supported by the strong linear relationship between mean daily sapflow rate and mean g_l (Figure 8). It is interesting to note that the data points ($n = 6$) that did not fit the overall relationship came from the time periods when leaf area index was not fully developed (May for both whips and 1 year old) or was substantially reduced due to drought related leaf abscission (July for whips). Hence, there appears to be tight coupling between stomatal response to climatic driving variables, plant water status, and sapflow rate under the conditions of low stand LAI and drought observed in this study. However, as the stand develops the relationship between individual leaf g_l and tree or stand-level sapflow could change due to shifts in the relative importance of stomatal vs. boundary layer conductance to total vapor phase conductance (Heilman *et al.*, 1996). For example, Martin *et al.*, (1999) demonstrated that microenvironmental conditions within the canopy influence the degree of coupling in *Abies amablis*, with branches in the lower canopy generally having a lower coupling than upper canopy branches.

Crown development and increased leaf area will substantially alter microenvironmental conditions in the *Populus* stands studied here, which could decrease the strength of the relationship between g_l and sapflow.

V. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The high sapflow rate and stem diameter growth in both the whips and 1-year-old *Populus deltoides* indicates great potential for the dual use of this species for phytoremediation and fiber production. Even under the extreme drought and high evaporative demand conditions characteristic of our study site, both the whips and 1-year-old trees survived, transpired, and grew considerably in the year following planting. Because sapflow rates in the whips were equal to or greater that the 1-year-old trees when expressed per unit sapwood, there was no apparent advantage to planting the 1-year-old trees. This conclusion must be made cautiously, however, because differences in genetics and access to groundwater may have strongly influenced the results we observed. From an economic standpoint, lower costs for whips ($0.20 each vs. $8 each for 1-year-old trees) and easier planting may make them the preferred alternative.

Preliminary estimates of ~25 cm of growing season transpiration for the first year after planting is about one-third to one-half the amount of transpiration for mature hardwood forests in other regions of North America (Vose and Swank, 1992). These results indicate that substantially greater transpiration will occur as trees within the plantations increase leaf area and root volume.

ACKNOWLEDGMENTS

This work was supported by the Department of Defense's Environmental Security Technology Certification Program Project E95BRAB004, Gregory J. Harvey, Program Manager. We thank Dr. Katherine Elliott and Patsy Clinton for help in the field, and Dr. Kurt Johnson and Chris Geron for helpful reviews of early drafts of the manuscript.

REFERENCES

Baker, J. M., and van Bavel, C. H. M. 1987. Measurement of mass flow of water in stems of herbaceous plants. *Plant Cell Environ.* **10,** 777–782.

Braatne, J. H., Hinckley, T. M., and Stettler, R. F. 1992. Influence of soil water on the physiological and morphological components of plant water balance in *Populus trichocarpa, Populus deltoides* and their F1 hybrids. *Tree Phys.* **11,** 325–339.

Flathman, P.E. and Lanza, G.R. 1998. Phytoremediation: current views on an emerging green technology. *J. Soil. Contam.* **7(4),** 415–432.

Foster, J. R. and Smith, W. K. 1991. Stomatal conductance patterns in high elevation phreatophytes of Wyoming. *Can. J. Bot.* **69,** 647–655.

Gordon, M., Choe, N., Duffy, J., Ekuan, G., Heilman, P., Muiznieks, I., Ruszaj, M., Shurtleff, B. B., Strand, S., Wilmoth, J., and Newman, L. A. 1998. Phytoremediation of trichloroethylene with hybrid poplars. *Environ. Health Perspet.* **106,** 1001–1004.

Heilman, P. E., Hinckley, T. M., Roberts, D. A., and Ceulemans, R. 1996. Production physiology. In: R. F. Stettler, H. D. Bradshaw, Jr., P. E. Heilman, and Hinckley, T. M., Eds., *Biology of Populus and Its Implications for Management and Conservation.* NRC Research Press, Ottawa, Canada, pp. 459–489.

Hinckley, T. M., Brooks, J. R., Cermak, J., Ceulemans, R., Kucera, J., Meinzer, F. C., and Roberts, D. A. 1994. Water flux in a hybrid poplar stand. *Tree Phys.* **14,** 1005–1018.

Hogg, E. H. and Hurdle, P. A. 1997. Sapflow in trembling aspen: implications for stomatal responses to vapor pressure deficit. *Tree Phys.* **17,** 501–509.

Landsberg, J. J., Blanchard, T. W. and Warrit, B. 1976. Studies on the movement of water through apple trees. *J. Exp. Bot.* **27,** 579–596.

Levitt, J. 1972. *Plant Responses to Environmental Stress.* Academic Press, New York.

Martin, T. A., Brown, K. J., Cermak, J., Ceulemans, R., Kucera, J., Meinzer, F. C., Rombold, J. S., Sprugal, D. G., and Hinckley, T. M. 1997. Crown conductance and tree and stand transpiration in second-growth *Abies amabilis* forest. *Can. J. For. Res.* **27,** 797–808.

Martin, T. A., Hinckley, T. M., Meinzer, F. C., and Sprugal, D. S. 1999. Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. *Tree Phys.* **19,** 435–443.

Pallardy, S. G. and Kozlowski, T. T. 1981. Water relations of *Populus* clones. *Ecology* **62,** 159–169.

Parker, J. 1968. Drought resistance mechanisms. In: T. T. Kozlowski, Ed. *Water Deficits and Plant Growth,* Vol. 1. Academic Press, New York, pp. 195–234.

Pezeshki, S. R. and Hinckley, T. M. 1988. Water relations characteristics of *Alnus rubra* and *Populus trichocarpa*: responses to field drought. *Can. J. For. Res.* **18,** 1159–1166.

Phillips, N., Nagchaudhuri, A., Oren, R. and Katul, G. 1997. Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* **11,** 412–419.

SAS Institute. 1987. SAS/STAT Guide for Personal Computers, Version 6. SAS Institute, Inc. Cary, NC, USA.

Schulze, E.-D., Cermak, J., Matyessek, R., Penka, M., Zimmermann, R., Vasicek, F., Gries, W., Kucera, J. 1985. Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea*—a comparison of xylem flow, porometer and cuvette measurements. *Oecologia* **66,** 475–483.

Steinberg, S. L., Van Bavel, C. H. M., and McFarland, M. J. 1989. A gauge to measure mass flow of sap in stems and trunks of woody plants. *J. Amer. Soc. Hort. Sci.* **114,** 466–472.

Steinberg, S. L., McFarland, M. J., and Worthington, J. W. 1990. Comparison of trunk and branch sapflow with canopy transpiration in pecan. *J. Exp. Bot.* **41,** 653–659.

Telewski, F. W., Aloni, R., and Sauter, J. J. 1996. Physiology of secondary tissues of *Populus*. In: R. F. Stettler, H. D. Bradshaw, Jr., P. E. Heilman, Hinckley, T. M., Eds.), *Biology of Populus and Its Implications for Management and Conservation.* NRC Research Press, Ottawa, Canada, pp. 301–330.

USDA Soil Survey. 1981. Soil Survey of Tarrant County, Texas. USDA Soil Conservation Service Report.

Vertessey, R. A., Hatton, T. J., Reece, P., O'Sullivan, S. K., and Benyon, R. G. 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Phys.* **17,** 747–756.

Vose, J. M. and Swank, W. T. 1992. Water balances. In: D. W. Johnson, Lindberg, S. E., Eds. *Atmospheric Deposition and Forest Nutrient Cycling: A Synthesis of the Integrated Forest Study.* Ecological Studies 91, Springer-Verlag, New York, pp. 27–49.

Waring, R. H., Schroeder, P. E. and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* **12,** 556–560.

Zhang, H., Simmonds, L. P., Morison, J. I. L., and Payne, D. 1997. Estimation of transpiration by single trees: comparison of sapflow measurements with a combination equation. *Agric. For. Met.* **87,** 155–169.