

Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians

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ABSTRACT

Recent studies have shown that planted pine stands exhibit higher evapotranspiration (ET) and are more sensitive to climatic conditions compared with hardwood stands. Whether this is due to management and stand effects, biological effects or their interaction is poorly understood. We estimated growing season canopy- and sap flux-scaled leaf-level transpiration (E_c and E_L) in five major overstory species over 3 years. Four hardwood species, *Liriodendron tulipifera*, *Carya* spp., *Quercus rubra* and *Quercus prinus*, were measured in an unmanaged watershed. *Pinus strobus* was measured in an adjacent planted pine watershed. We hypothesized that (1) species would differ in E_L and stomatal conductance (G_S), and their relationship with vapour pressure deficit (D); and (2) differences in growing season ET between the stands would result primarily from the differences in interception (E_i). Growing season ET in the planted pine stand exceeded hardwood ET by twofold during all 3 years. Transpiration and E_i contributed similarly to the ET difference, suggesting that physiological differences were equally as important as structural factors to the overall difference in ET. Among species, mean E_L and G_S differed significantly, as did their relationship with D . E_L and G_S of oaks and hickories were least responsive to changing D , while *L. tulipifera* and *P. strobus* were most responsive. This species-level understanding of variation in E_L and G_S and their interactions with climatic driving variables has important implications for predicting watershed-level responses to stand management, species invasion and loss, and climate variability. Published in 2010. This article is a US Government work and is in the public domain in the USA.

KEY WORDS evapotranspiration; sap flow; species; stomatal conductance; transpiration

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INTRODUCTION

Over the past century, rapid changes in species composition in forest ecosystems have occurred on a wide-spread scale. Often these changes have been associated with disturbances (e.g. non-native insects or diseases) that target individual species. In contrast to whole-basin vegetation changes (reviewed in Brown *et al.*, 2005; Farley *et al.*, 2005), the impacts of long-term changes in individual species composition on hydrology are less well known (Ellison *et al.*, 2005). Our ability to understand and predict how changes in forest species composition will impact hydrologic processes [e.g. evapotranspiration (ET), soil moisture dynamics, and stream flow] is an increasingly important issue (National Research Council of the National Academies, 2008), because of the accelerated pace of tree species losses (or gains) due to insects, diseases, native and non-native invasive plants, and afforestation projects.

Much of what is known about differences in water use among species has been inferred from the water yield studies on intensively managed forests that are

typically monospecific, fully stocked and have short rotations; thus, resulting in significant differences in forest structure, age and species composition relative to unmanaged stands. One example of these intensive management practices is the conversion of hardwood stands to coniferous stands, which often results in a reduced stream flow (Swank and Douglass, 1974; Komatsu *et al.*, 2008). A synthesis of the literature indicates that across many sites, for any given precipitation regime, annual ET from coniferous forests (both managed and unmanaged) is generally greater than hardwood forests (Figure 1). Mechanisms regulating the increase in ET for coniferous species compared with deciduous species have been postulated to include: (1) greater interception because of higher stocking density and year-round leaf area, (2) greater annual transpiration in moderate climates because of persistent leaf area and hence a longer growing season and (3) differences in leaf-level transpiration. Hence, differences in ET are driven by the physical factors (e.g. interception), biological factors (e.g. transpiration) or some combination of the two. The relative importance of physical versus biological controls varies throughout the year and interacts with climatic conditions. For example, in the growing season, species-specific variation in transpiration was the primary reason for differences between ET

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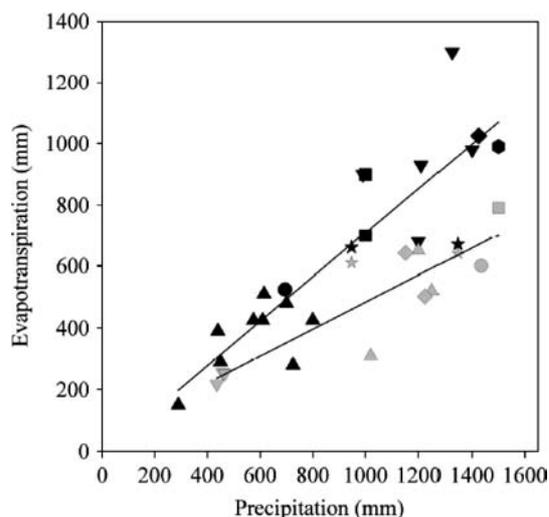


Figure 1. Relationship between ET and precipitation (P) for different forest biomes (in various countries) dominated by either conifers (black symbols) or hardwood (grey symbols) species. Data are from \blacktriangle Knight *et al.* (1985), \blacktriangledown Vose and Swank (1992), \bullet Ewel and Gholz (1991), \blacksquare Waring and Schlesinger (1985), \blacklozenge Grip *et al.* (1979), \bullet Whitehead and Kelliher (1991), \star \star Stoy *et al.* (2006); Vose and Swank (1992). IFS sites \triangle NC, \circ CAN, \square WA; ∇ Granier *et al.* (2000); \diamond Wilson *et al.* (2001). Regression lines and fits for conifer and hardwood data sets, respectively, are $ET = 0.72 \times P - 10.48$, $R^2_{adj} = 0.75$, $P < 0.001$; and $ET = 0.42 \times P + 46.35$, $R^2_{adj} = 0.74$, $P = 0.002$. All values are for annual ET except ∇ $\star\star$, which are growing season only.

in hardwood and coniferous stands (Stoy *et al.*, 2006); moreover, these species also differed in their sensitivity to climatic variation, with ET of hardwood stands being less sensitive to climate variability than coniferous stands.

Understanding the factors regulating transpiration among species within mixed stands is also important for quantifying the potential consequences of shifting species composition due to succession, introduction of invasive species, or selective loss of species due to invasive insects and disease. For example, large differences in transpiration among species exist in many forested systems (Wullschlegel *et al.*, 2001; Moore *et al.*, 2004; Ewers *et al.*, 2005). In addition, several studies also indicate that younger or shorter trees may have higher transpiration rates than older or taller trees because as trees grow taller, the path length of water flow from soil to leaf to atmosphere increases (Dunn and Connor, 1993; Hubbard *et al.*, 1999; Moore *et al.*, 2004; Ryan *et al.*, 2006; Novick *et al.*, 2009), and stomata can respond directly to this change in hydraulic conductance (Hubbard *et al.*, 2001). Young trees also may be more affected by climate variability than more mature ones, especially if the latter has a larger or deeper functional rooting zone than the former that could buffer it against transient droughts (Sperry *et al.*, 2002). Thus, age- and species-related changes in forest structure can also be important factors affecting forest ET.

The objectives of this research were to estimate and compare whole-tree water use of major canopy species in a native deciduous southern Appalachian hardwood forest and an adjacent planted pine forest. Using sap flux probes, we estimated growing season canopy transpiration (E_c)

and transpiration per unit leaf area (E_L) in five major overstory species over 3 years. Four hardwood species, *Liriodendron tulipifera*, *Carya* spp., *Quercus rubra* and *Quercus prinus*, were measured in the unmanaged reference watershed; and one coniferous species, *Pinus strobus*, was measured in the adjacent species-conversion treatment watershed. We hypothesized that E_L would vary by species, and that the relationship between E_L and stomatal conductance (G_s) with vapour pressure deficit (D) would vary by species. We also hypothesized that differences in growing season ET between the planted pine watershed and the hardwood watershed would be the result of structural differences (interception and tree height) and biological differences (E_c among species), with structural differences contributing more to the difference than E_c . Differences in interception were expected to be the result of management effects (e.g. stocking related differences in leaf, branch and bole surface area), whereas differences in E_c were expected to be largely species-specific effects (e.g. E_L and G_s).

MATERIALS AND METHODS

Study site

The study sites were located in watersheds 17 and 18 (WS17 and WS18), two adjacent, northwest-facing, steeply sloping (average 57 and 53% slopes, respectively), 13.5- and 12.5-ha catchments within the Coweeta Basin in the Nantahala Mountain Range of western North Carolina, USA. Climate in the Coweeta Basin is classified as marine, humid temperate (Swift *et al.*, 1988), and average annual precipitation is 2014 mm. WS17 elevation ranges from 742 to 1021 m, and WS18 elevation ranges from 726 to 993 m. Soils on both watersheds fall into two main series: the Saunook series, a fine-loamy, mixed, mesic Humic Hapludult, is present at streamside positions (~50-cm depth); and Cowee-Evard complex soils, a fine-loamy, mixed-oxidic, mesic, Typic Hapludult, typically present on ridges (~70-cm depth) (Knoepp and Swank, 1994).

WS18, a mixed hardwood reference watershed, has been undisturbed since being selectively logged in the early 1900s, with the exception of the chestnut blight which decimated American chestnut trees in the southern Appalachians in the 1920s (Kovner, 1955; Woods and Shanks, 1957; Elliott and Swank, 2008). Plant community composition in WS18 is closely associated with elevation, aspect and soil moisture (Day and Monk, 1974). A chestnut oak–hickory overstory and mountain laurel understory dominates the upper slopes and drier ridges, a northern red oak–red maple–tulip poplar overstory and rhododendron understory dominates the intermediate mid-slopes, and a birch–red maple–tulip poplar overstory and rhododendron understory dominates the mesic cove and riparian areas (Day and Monk, 1974).

Prior to 1941, WS17 was similar in species composition and forest age to that of WS18 (Hoover, 1944).

Table I. Characteristics of stands and tree species monitored for sap flux density in each watershed.

Species	LAI (m ² m ⁻²)*	BA (m ² ha ⁻¹)*	Density (stems ha ⁻¹)*	<i>N</i>	DBH (cm)	Height (m) [†]	<i>A</i> _{sw} (cm ²) [†]	<i>A</i> _L (m ²) [†]	<i>A</i> _L : <i>A</i> _{sw}
Hardwood reference watershed	6.2	39.1	558						
<i>Carya</i> spp.	0.9	5.5	50	9	38.6 (3.3) ^{b‡}	28.7 (1.5) ^b	491.1 (78.1)	194.3 (30.8) ^{bc}	0.40 (0.00) ^c
<i>L. tulipifera</i> L.	0.6	4.0	53	5	45.4 (2.2) ^{ab}	36.6 (1.8) ^a	725.9 (104.2)	219.0 (33.1) ^{bc}	0.30 (0.00) ^c
<i>Q. prinus</i> L.	2.2	13.5	81	12	51.2 (5.8) ^{ab}	27.9 (1.8) ^b	381.0 (63.0)	366.3 (74.5) ^{ab}	0.87 (0.05) ^b
<i>Q. rubra</i> L.	1.1	6.5	19	5	59.4 (9.3) ^a	30.2 (2.6) ^{ab}	305.5 (78.9)	505.6 (149.4) ^a	1.57 (0.09) ^a
Other	1.5	9.6	355						
Planted pine watershed	7.2	66.5	556						
<i>P. strobus</i> L.	7.2	66.5	556	42	40.5 (1.4) ^b	30.9 (0.5) ^b	498.3 (42.1)	149.5 (13.3) ^c	0.31 (0.03) ^c

Peak * LAI (projected for hardwoods and $\sim 2/3$ for pine), basal area (BA), and stem density of trees >5 cm in diameter at 1.3 m above the ground height. Values shown are integrated across all plots for each watershed during 2005. [†] Height, sapwood (*A*_{sw}), and leaf area (*A*_L) measurements or estimates are for 2006 growing season. Means (standard error) shown. [‡] Species not sharing the same lowercase letters within individual columns denote significant differences for that variable if a significant species effect was found in the full model.

In January to March 1941, all shrub and forest vegetation was cut in WS17 and left onsite. Thereafter, annual sprout growth was cutback most years until 1955. In 1956, WS17 was planted with eastern white pine (*P. strobus* L.) seedlings at a 2 × 2 m spacing to experimentally evaluate how hardwood-to-pine conversion affected catchment water yield (Swank and Douglass, 1974). The stand was unmanaged until 2001 when a small area of the watershed (~ 2 ha) was cut to stop the spread of southern pine beetle (*Dendroctonus frontalis* Z.).

Interception and transpiration estimates

Interception for the growing season was estimated using empirical equations developed on stands with similar species, stocking density, basal area and climate (Helvey and Patric, 1965; Helvey, 1967). The equation used for the growing season interception by the hardwood stand was based on a meta-analysis of over 12 studies that published interception equations, which included the hardwood stand in the present study. The general equation was developed by using a weighted average equation based on the number of throughfall gages used. Interception was estimated based on the total precipitation measured in the growing season, and the number of events [$\sum E_i = 0.083(\sum P) + 0.036(n)$, where E_i is interception, P the precipitation and n the number of events in the growing season] (all units in inches, Helvey and Patric, 1965). The equation used for the growing season interception by the pine stand was based on an empirical equation developed by Helvey (1967, Table III) for eastern white pine stands of similar age (60 years old) but lesser basal area (35 m² ha⁻¹ vs a mean basal area of 66 m² ha⁻¹ in the present study). The equation [$\sum E_i = 0.06(n) + 0.18(\sum P)$] predicted interception losses as a function of total growing season precipitation and the number (n) of storm events (all units in inches).

To estimate the transpirational water loss, we used constant heat dissipation probes (Granier, 1985) to monitor

a subset of trees in the two watersheds. Mid-slope on WS17, 42 trees in three plots (289, 292 and 203 m² in area), and on the mid-to-upper slopes on WS18, 31 trees in two plots (1295 and 1905 m² in area) were monitored for sap flux density throughout 2004–2006 (Table I). Plot locations and sizes in both watersheds were chosen to sample a range of comparable mid-slope conditions and sample the major overstory species present in WS18 (Day and Monk, 1974). However, they do not represent the full range of conditions (e.g. soils, topography, species composition for WS18, etc.) in either watershed.

Sap flux density (v , g H₂O m⁻² sapwood s⁻¹) was determined by installing probes in the outer 2 or 3 cm of the functional xylem. Probe length was determined based on the estimated sapwood depth: if 2 cm did not span at least 30% of the sapwood depth, a 3-cm probe was installed. For each tree monitored, we installed two sets of probes circumferentially at least 90° apart. Probes were installed, shielded from thermal gradients and wired to dataloggers as described by Ford and Vose (2007). Sensors were queried every 30 s and 15 min averages were logged. The temperature difference (ΔT) between the upper and lower probes was converted to v using the equation of Granier (1985), with the maximum temperature difference (ΔT_{\max}) between probes identified for each biweekly period. The ΔT_{\max} values were determined using this time step due to the positive relationship between ΔT_{\max} and rainfall events, and because at least one rainfall event typically occurred in a biweekly period (Lu *et al.*, 2004). In 7 of the 28 hardwood trees, corrections to ΔT values were made according to Clearwater *et al.* (1999) because probes were in contact with heartwood. For all trees, v estimates for the two replicate sets of sensors were averaged. Sensors were replaced in newly drilled holes each year. Within a year, sensors were replaced if null, out of range, erratic, or negative readings were recorded, or if probes were physically damaged. Probes typically performed well in the hardwood

trees for 6–8 months, and 10–12 months in the pine trees.

Scaling and allometry

Leaf areas for all trees and sapwood areas for the hardwood trees were estimated using species- and site-specific allometric equations (Martin *et al.*, 1998, B. D. Kloeppel and J. M. Vose, unpublished data). To estimate the sapwood area for the pine trees monitored, we visually estimated sapwood length based on the dye uptake at breast height (described in Ford and Vose, 2007). Diameter at breast height (DBH, 1.3 m above the ground height) was measured, and assuming circular symmetry we developed equations predicting sapwood area (A_{SW}) as a function of DBH on log-transformed data ($\log A_{SW} = \log DBH \times 2.27 - 1.11$, correction factor = 1.1015; Sprugel, 1983). In the dormant season following sap flux measurements, we measured DBH and bark thickness (T_b) on all trees and estimated A_{SW} .

To scale v in the outer 2 or 3 cm of sapwood to whole-tree sap flow (F , g H₂O s⁻¹), we developed general radial profile functions of v versus fraction of hydroactive sapwood depth for each species (methods presented in Ford *et al.*, 2007). We measured v at various depths in the sapwood of three *P. strobus* trees (45.6 cm mean DBH) (data presented in Ford *et al.*, 2007), two *L. tulipifera* trees (57.8 cm mean DBH), two *Carya* spp. trees (36.8 cm mean DBH), and two *Q. rubra* trees (46.5 cm mean DBH) (data not shown). Individuals monitored for radial profile functions were outside of the long-term sap flow plots and were monitored over several days during 2005 (*P. strobus*) or 2006 (hardwood spp.).

We estimated mean stomatal conductance (G_S , m s⁻¹) from E_L and D (vapour pressure deficit, kPa, measurements described below) using the following equation:

$$G_S = \frac{K_G(T) \cdot E_L}{D} \quad (1)$$

where K_G is a function of temperature ($115.8 + 0.4236T$; kPa m³ kg⁻¹), and accounts for the temperature effects on the psychrometric constant, latent heat of vapourization and the specific heat and density of air (Phillips and Oren, 1998). We converted to molar units following Pearcy *et al.* (1989). Several conditions must be met for Equation (1) to estimate G_S in conifers and hardwoods (discussed in Ewers and Oren, 2000). Specifically, (1) boundary layer conductance must be high so that atmospheric D approximates leaf-to-air D , (2) heterogeneity in canopy D must be low and (3) stem sap flow must represent the magnitude and timing of leaf fluxes from the canopy. For the hardwood stands, we used canopy D (as in Ewers *et al.*, 2007) while for the planted pine stands we used open-field D (measurements described below) to minimize errors due to (1). We used rain-free days and excluded days when $D < 0.6$ kPa to minimize errors due to (1) and (2). We used mean daytime E_L to minimize errors due to (3).

To make inferences about the relationship between G_S and D , we used a boundary line approach (Schafer *et al.*,

2000; Ewers *et al.*, 2005). This approach fit a nonlinear model through the greatest values of G_S for any level of D for each tree. Because many variables affect G_S [soil moisture, photosynthetically active radiation (PAR), etc.], there is typically a distribution of G_S values for any level of D . By only fitting a model through the upper values of G_S for any level of D , the constraints of other variables on G_S are minimized and the inference of the effect of D on G_S is maximized. For each tree, we therefore divided D into five bins (D_i), every 0.2 kPa, and excluded all G_S data less than the mean plus 1 standard deviation of G_S in bin D_i . The values falling above the mean plus 1 standard deviation were the values we fit a nonlinear model through (described below).

To estimate the plot transpiration per unit ground area (E_t , mm), we multiplied E_L for each species by the proportion of total leaf area index (for all trees >5 cm DBH, m² m⁻²) represented by that species. Sap flux gaged trees represented 74–79% of the species that occupy the overstory in the reference hardwood stand (Table I). Unrepresented species were *Acer rubrum* L., *Acer pensylvanicum* L., *Betula lenta* L., *Oxydendrum arboreum* (L.) DC. and *Nyssa sylvatica* Marsh. The A_L of unrepresented species >5 cm DBH was assigned a mean E_L of all species measured. Because we did not measure transpiration of either herbaceous or woody (<5-cm diameter), understory species, canopy transpiration (E_c) and plot transpiration (E_t) definitions are used interchangeably. Understory species are a minor component of overall stand leaf area [e.g. LAI for woody understory species <5-cm diameter in similar hardwood control watersheds averaged 0.4 m² m⁻² in 2007 (K. Elliott, unpublished data)]; and are likely to contribute little to plot-level transpiration. Values from all plots within a watershed were averaged.

Growing season E_t was estimated by summing daily scaled E_t during days of year 128–280. Across all years and plots, missing data averaged 26%. To estimate missing data, we developed time-series models predicting daily E_t from the climate variables (D , PAR and wind speed, measurements described below) according to the procedures in Ford *et al.* (2005). Missing data resulted from sap flux or data logging equipment malfunction, which typically occurred as a result of thunderstorms. Because missing data typically occurred on rainy days when sapflow was likely low, the significance of errors associated with predicting sap flux was assumed to be minor.

Environmental variables

An open-field climate station (CS17) was located mid-slope in WS17 (<200 m from the measured plots). CS17 measured precipitation (P , Belfort Instrument Co., Baltimore, MD, USA) every 1 min and logged 15 min totals, air temperature, and relative humidity (T_a and RH, model HMP45C, Campbell Scientific, Inc. Logan, UT, USA), solar radiation (model 8–48, Epply Lab Inc., Newport, RI, USA) and wind speed and direction

(Met One 014A anemometer, Campbell Scientific, Inc.) every 1 min and logged 15 min averages and totals. In WS18, a T_a and RH sensor (model CS500, Campbell Scientific, Inc.) was mounted in the canopy layer of the lower plot. We used T_a to calculate saturation vapour pressure (e_s) according to Lowe (1977). Actual vapour pressure (e_a) was calculated from fractional RH and e_s . Air vapour pressure deficit (D) was calculated as the difference between e_s and e_a . Barometric air pressure was recorded hourly in the valley floor (Chart No. 5–1071, Belfort Instrument Co.).

Volumetric soil water content (θ , v/v %) was estimated using time domain reflectometry probes (models CS615 and CS616, Campbell Scientific, Inc.). Two 30-cm long probes were inserted vertically into the soil in each plot spanning 0- to 30-cm soil depth on WS18. One probe in each of the three plots on WS17 spanned 0- to 30-cm soil depth. Probes were queried every 1 min, and 15 min averages were logged by dataloggers. We removed a soil monolith from the appropriate depth in soils adjacent to each plot and calibrated period output from the sensors to known volumetric water content in the laboratory.

Statistics

We tested for differences among tree species characteristics (A_{SW} , A_L , A_L : A_{SW} and DBH) in 2006 with a one-factor analysis of variance (ANOVA) (SAS v9.1, SAS Institute, Inc., Cary, NC, USA) using PROC GLM and Tukey's *post hoc* means separation test. The variable A_L : A_{SW} was transformed with a square root function prior to statistical analysis. We tested for differences in mean growing season E_L and G_S among all years and species using a two-factor repeated-measure ANOVA (PROC MIXED) with unstructured variance.

We tested for differences in the mean species E_L response to D and the mean species G_S response to D for each year by using a repeated-measure, mixed effects, nonlinear model (PROC NL MIXED) in the form:

$$y = f(x_{ij}, \beta, u_i) + e_{ij} \quad (2)$$

where f is a function of known vector covariates (x_{ij}), in our case, daytime D on the j th day for the i th tree; a vector of unknown fixed parameters (β); and a vector of unknown random effect parameters (u_i), in our case, u_0 and u_1 ; and e_{ij} is unknown random errors associated with the j th day for the i th tree (Peek *et al.*, 2002). For the E_L versus D relationship, the function had the following form:

$$E_L = \beta_0(1 - e^{-\beta_1 \cdot D}) \quad (3)$$

where E_L is transpiration per unit leaf area (mm day^{-1}), and β_0 and β_1 represent the maximum E_L and the initial increase in E_L with each unit D , respectively. For the G_S versus D relationship, the function had the following form:

$$G_S = -\beta_2 \cdot \ln(D) + \beta_3 \quad (4)$$

where G_S is the stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$), β_2 is the slope and represents the apparent sensitivity of G_S to D (sensu Oren *et al.*, 1999), and β_3 is the intercept and represents a reference stomatal conductance ($G_{S\text{ref}}$) at $D = 1$ kPa. We tested for significant differences among parameter estimates for each species using custom contrast statements. To compare response curve parameters among years for any species, if the upper and lower 95% confidence interval for each parameter estimate did not overlap, we interpreted this as a significant difference.

We tested for differences in the relationship between stomatal conductance at a reference D (i.e. $G_{S\text{ref}}$) and tree height among hardwood species. We excluded *P. strobus* from the analysis because of low variation in tree height within the species measured. We averaged the $G_{S\text{ref}}$ parameters for each tree across years. We fit a linear model to the $G_{S\text{ref}}$ versus height relationship using trees as individual replicates and species as a covariate (PROC GLM, SAS Institute, Inc.). We used contrast statements to test for differences among the slopes and intercepts of lines for each species.

RESULTS

Stand and species characteristics

Stand characteristics were markedly different between the two watersheds. The hardwood stand had lower LAI than the planted pine (Table I) and more than half of the LAI was contributed by two oak species. Although the planted pine stand had roughly 1.7 times the basal area of the hardwood stand, stem density was similar between the stands due to a large number of small stems in the understory of the hardwood stand. Tree diameter, height and tree-level leaf area all varied among species (Table I). Mean diameters of the *Q. rubra*, *L. tulipifera* and *Q. prinus* trees were the largest, and *P. strobus* and *Carya* spp. were the smallest trees ($F_{4, 68} = 4.23$, $P < 0.01$; Table I). Mean tree height ($F_{4, 68} = 4.37$, $P < 0.01$) and leaf area ($F_{4, 68} = 9.51$, $P < 0.01$) among species also varied. *L. tulipifera* and *Q. rubra* were significantly taller than the other species; tree heights among other species did not differ. *Q. rubra* trees supported the greatest and *P. strobus* trees supported the least amount of leaf area among all species. Individual species also supported significantly different amounts of leaf area for each unit of sapwood area ($F_{4, 68} = 82.15$, $P < 0.01$). The ranking among species was related to xylem anatomy: the two ring-porous sapwood species (*Quercus* spp.) supported significantly more leaf area per unit sapwood area than species with smaller conduits which included semi-ring porous (*Carya* spp.), tracheid (*P. strobus*) and diffuse porous (*L. tulipifera*) sapwood species.

Inter-annual climate

Total annual precipitation varied among the three study years, 2159, 2320 and 1691 mm, and was 7% higher,

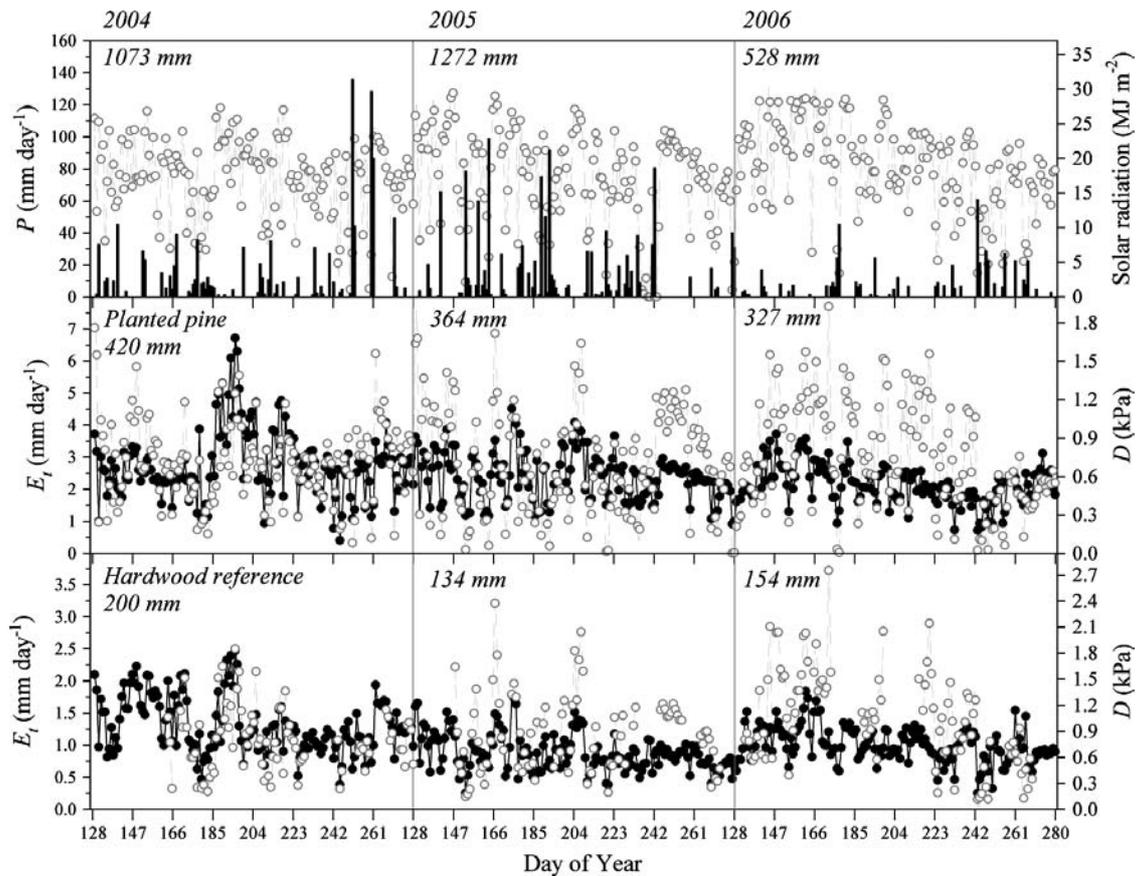


Figure 2. Daily growing season (days of year 128–280) precipitation (P , bars) and solar radiation (open symbols), and transpiration (E_L , solid symbols) and D (open symbols) for planted pine watershed (WS17) and hardwood reference watershed (WS18) during 2004–2006. Numbers in individual panels show P or E_L growing season totals.

15% higher and 16% lower than the long-term average (67-year average 2014 mm, SD \pm 312 mm). Growing season precipitation (1073, 1272 and 528 mm) was 32% higher, 46% higher and 33% lower than the long-term average (67-year average during May to October was 878 mm, SD \pm 210 mm; Figure 2).

Average soil moisture during the growing season in the planted pine plots did not vary considerably from year to year; the mean was 20, 23 and 19% for the three study years. In contrast, soil moisture in the hardwood plots was more variable among years. In the lower plot, the mean soil moisture for the three years was \geq 24%; however, in the upper plot, mean growing season soil moisture was 16, 21 and 12% in 2004, 2005 and 2006, respectively.

Variation in species E_L and G_S , and responses to climate

Growing season daily transpiration per unit leaf area (E_L) varied significantly among species ($F_{4, 65.6} = 17.94$, $P < 0.01$) and years ($F_{2, 65.3} = 5.91$, $P < 0.01$; Table II), and there was a significant species by year interaction ($F_{8, 89.2} = 2.89$, $P < 0.01$). Among species, *L. tulipifera* always had the highest E_L while *Q. rubra* always had the lowest. E_L rates were highest for all species in 2004. *P. strobus* and *Q. prinus* exhibited the greatest variation in E_L over the study period. In 2004 and 2005, *P. strobus* had E_L values similar to *L. tulipifera*; however,

Table II. Mean (standard error) growing season daily transpiration per unit leaf area (E_L , mm) for species in the two study watersheds.

Species	E_L		
	2004	2005	2006
Hardwood reference watershed			
<i>Carya</i> spp.	0.20 (0.03) ^{b,A*}	0.19 (0.02) ^{b,A}	0.18 (0.02) ^{c,A}
<i>L. tulipifera</i> L.	0.45 (0.05) ^{a,AB}	0.39 (0.07) ^{a,B}	0.46 (0.03) ^{a,A}
<i>Q. prinus</i> L.	0.21 (0.03) ^{b,A}	0.07 (0.01) ^{b,B}	0.10 (0.02) ^{cd,AB}
<i>Q. rubra</i> L.	0.10 (0.02) ^{b,A}	0.07 (0.02) ^{b,A}	0.07 (0.01) ^{c,A}
Planted pine watershed			
<i>P. strobus</i> L.	0.41 (0.02) ^{a,A}	0.36 (0.03) ^{a,B}	0.30 (0.02) ^{b,C}

* Within columns, species not sharing the same lowercase letters denote significant differences among species for that year. Within rows, years not sharing the same uppercase letters denote significant differences among years for that species.

in 2006 E_L of *P. strobus* was intermediate between *L. tulipifera* and *Carya* spp. During 2004, *Q. prinus* had a significantly higher E_L compared with 2005, and was similar to the *Q. rubra* and *Carya* spp. These three species were also similar in 2005, but only *Q. prinus* had a significantly lower E_L compared with the previous year. Species with significant variation in E_L among years were *L. tulipifera*, *Q. prinus* and *P. strobus*. By 2006, *P. strobus* E_L had declined 27% compared with E_L in

Table III. Parameter estimates for species' mean daily transpiration per unit leaf area (E_L , mm day⁻¹) response curves to daytime mean vapour pressure deficit (D , kPa).

Species	β_0^*			$-\beta_1^*$		
	2004	2005	2006	2004	2005	2006
Hardwood reference watershed						
<i>Carya</i> spp.	0.54 (0.14) ^{b,A†}	0.31 (0.10) ^{b,A}	0.26 (0.04) ^{c,A}	0.68 (0.19) ^{b,A}	1.16 (0.19) ^{b,A}	1.33 (0.22) ^{b,A}
<i>L. tulipifera</i> L.	1.19 (0.23) ^{a,A}	0.60 (0.14) ^{a,A}	0.74 (0.07) ^{a,A}	0.75 (0.24) ^{b,A}	1.33 (0.22) ^{b,A}	0.97 (0.24) ^{b,B}
<i>Q. prinus</i> L.	0.53 (0.19) ^{b,A}	0.10 (0.02) ^{c,A}	0.13 (0.05) ^{d,A}	0.72 (0.27) ^{b,A}	1.15 (0.28) ^{b,A}	1.40 (0.42) ^{b,A}
<i>Q. rubra</i> L.	0.26 (0.11) ^{c,A}	0.12 (0.06) ^{c,A}	0.09 (0.05) ^{d,A}	0.69 (0.27) ^{b,A}	1.13 (0.26) ^{b,A}	1.26 (0.40) ^{b,A}
Planted pine watershed						
<i>P. strobus</i> L.	0.76 (0.14) ^{b,A}	0.51 (0.09) ^{a,AB}	0.38 (0.04) ^{b,B}	1.18 (0.21) ^{a,A}	1.98 (0.20) ^{a,AB}	2.53 (0.24) ^{a,B}

Standard error of the parameter estimate given in parentheses. * Maximum E_L described by β_0 , and rate of increase in E_L per unit D described by β_1 . † Within columns, species not sharing the same lowercase letters denote significant differences among species for that year. Within rows, years not sharing the same uppercase letters denote significant differences among years for that species. Curves shown in Figure 3 use the parameter estimates given above.

2004. From 2004 to 2005, *Q. prinus* E_L declined by 67%. From 2005 to 2006, E_L had increased 18% in *L. tulipifera*.

For all species, E_L was significantly related to D (Table III and Figure 3). The model that described the relationship best was a nonlinear two-parameter exponential saturation model. These two parameters described the initial linear increase in E_L with increasing D (β_1), and the maximum E_L (β_0). Maximum E_L parameter estimates differed significantly among species. During 2004, *L. tulipifera* had the highest and *Q. rubra* had the lowest maximum E_L parameter estimate compared with all the other species, which were not significantly different from one another. In 2005 and 2006, species fell roughly into three groups: *L. tulipifera* had a significantly higher maximum E_L parameter estimate compared with *P. strobus* and *Carya* spp., and the *Quercus* spp. had the lowest parameter estimates. Parameter estimates for the initial increase in E_L with D had large standard errors, and thus did not differ significantly. The exception to this was *P. strobus*, in which E_L increased more sharply with initial D compared with all other species.

During the growing season, stomatal conductance (G_S) varied significantly among species ($F_{4, 68.5} = 17.44$, $P < 0.01$) and years ($F_{2, 68} = 11.86$, $P < 0.01$; Table IV). The ranking among species was not the same for all years (species \times year interaction $F_{8, 93} = 5.21$, $P < 0.01$). Similar to E_L , among species *L. tulipifera* maintained the greatest mean G_S while the two oak species always had the lowest. In the hardwood stand, stomatal conductance of *Carya* spp. and *Q. rubra* was consistent among years; however, stomatal conductance of two hardwood species (*L. tulipifera* and *Q. prinus*) was greater in 2004 compared with 2005 and 2006. Stomatal conductance of *P. strobus* was greatest in 2005 followed by 2004 then 2006.

The stomatal conductance response to D varied significantly among species, but was fairly consistent among years (Table V and Figure 4). The reference stomatal conductance parameter (β_3) was significantly higher in *L.*

Table IV. Mean (standard error) growing season daily stomatal conductance (G_S , mmol m⁻² s⁻¹) for species during daylight hours and times with no precipitation and $D > 0.6$ kPa in the two study watersheds.

Species	G_S		
	2004	2005	2006
Hardwood reference watershed			
<i>Carya</i> spp.	20.4 (3.3) ^{c,A*}	16.1 (1.7) ^{b,A}	15.1 (1.7) ^{c,A}
<i>L. tulipifera</i> L.	49.5 (4.6) ^{a,A}	37.8 (8.6) ^{a,B}	38.2 (1.9) ^{a,B}
<i>Q. prinus</i> L.	19.5 (2.8) ^{c,A}	5.9 (0.8) ^{c,B}	7.9 (1.1) ^{c,B}
<i>Q. rubra</i> L.	8.6 (1.3) ^{c,A}	4.9 (0.8) ^{c,A}	4.6 (0.5) ^{c,A}
Planted pine watershed			
<i>P. strobus</i> L.	31.8 (2.2) ^{b,B}	38.4 (2.7) ^{a,A}	27.5 (1.9) ^{b,C}

* Within columns, species not sharing the same lowercase letters denote significant differences among species for that year. Within rows, years not sharing the same uppercase letters denote significant differences among years for that species.

tulipifera and *P. strobus* compared with the other species, indicating that at low D , stomatal conductance was relatively high. The species with ring porous and semi-ring porous xylem anatomy consistently had the lowest modelled reference stomatal conductance among all species. Although the two species with the highest G_S at 1 kPa appeared to have the greatest sensitivity or decline in G_S with D , and the species with the lowest G_S at 1 kPa appeared to change G_S only slightly in response to D , this trend was not statistically significant due to large variance estimates in $-\beta_2$ among trees.

Among individual hardwood trees within a species, G_S at a reference D (i.e. β_3 or G_{Sref} , $D = 1$ kPa) was negatively related to tree height ($R^2 = 0.86$, $F_{5, 26} = 120.50$, $P < 0.001$; Figure 5). The rate of decline in G_{Sref} with height was consistent across species (test of slopes, $F_{3, 23} = 0.47$, $P = 0.70$); however, the intercepts of the lines varied significantly by species (test of intercepts, $F_{4, 26} = 39.39$, $P < 0.001$). At any tree height, *L. tulipifera* had the greatest G_{Sref} , followed by *Carya* spp., and then the two *Quercus* spp., which did not differ significantly ($F_{1, 26} = 2.42$, $P = 0.13$).

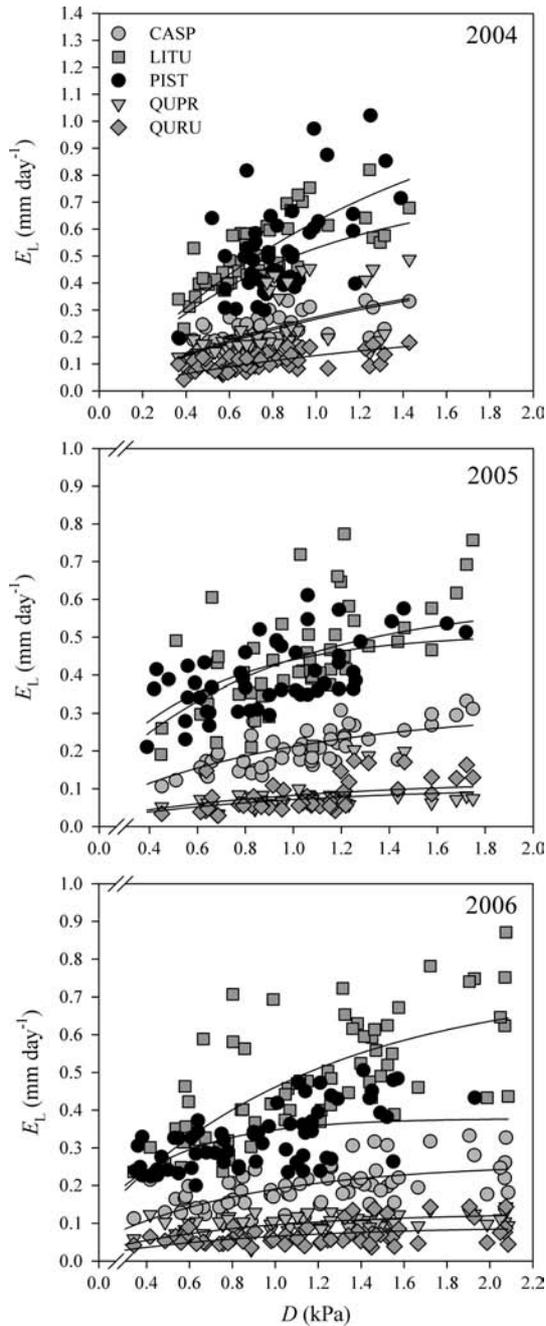


Figure 3. Daily transpiration per unit leaf area (E_L) versus vapour pressure deficit (D) for species measured. Points represent the mean of all individual trees in a species. Species abbreviations are LITU: *L. tulipifera*, CASP: *Carya* spp., PIST: *P. strobus*, QUPR: *Q. prinus* and QURU: *Q. rubra*. Curves represent a nonlinear mixed model fit to the population of individuals for each species. Parameters for curves are in Table III.

Comparison of growing season E_t and E_i between watersheds

When scaled to the plot, daily transpiration rates (E_t) were highly correlated in the two watersheds ($0.62 < R^2 < 0.81$) but varied significantly among years (Figures 2 and 6, Table VI). During the growing season, E_t in WS17 was consistently higher for the 3 years (420, 364 and 327 mm) compared with WS18 (200, 134 and 154 mm). E_t in WS17 was 52, 63 and 53% greater than WS18 in 2004, 2005 and 2006. From 2004 to 2005, E_t

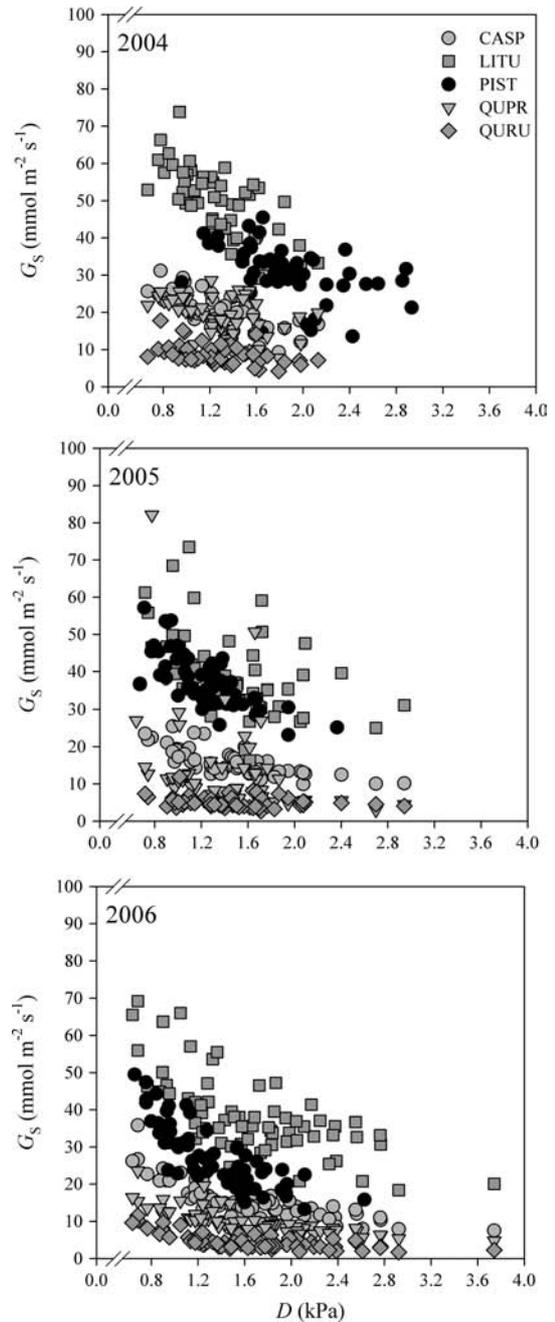


Figure 4. Relationship between stomatal conductance (G_S) and vapour pressure deficit (D) when $D > 0.6$ kPa. Individual points represent the daily mean of all trees within a species. Legend as in Figure 3.

in both watersheds declined; however, WS17 E_t declined by 13% while WS18 E_t declined by 33%. The pronounced decline in WS18 E_t from 2004 to 2005 was mainly attributable to one species—*Q. prinus*—during days of year 147–166 and 185–204. Differences in D and PAR, and the corresponding relationships between E_L and D for the different species during 2004 and 2005 were responsible for differences in E_t among watersheds for these years. In contrast, low precipitation and resulting low soil moisture restricted E_t in 2006. During the two wetter years, the E_t response to D was greater for the planted pine watershed compared with the hardwood

Table V. Parameter estimates for species' mean stomatal conductance (G_S , $\text{mmol m}^{-2} \text{s}^{-1}$) response to daytime mean vapour pressure deficit (D , kPa) when $D > 0.6$ kPa.

Species	$-\beta_2^*$			β_3^*		
	2004	2005	2006	2004	2005	2006
Hardwood reference watershed						
<i>Carya</i> spp.	7.6 (5.0) ^{b,A} ‡	10.6 (11.5) ^{a,A}	22.0 (6.1) ^{ab,A}	15.2 (3.3) ^{c,A}	28.9 (7.4) ^{bc,A}	28.3 (3.9) ^{c,A}
<i>L. tulipifera</i> L.	31.3 (8.3) ^{a,A}	12.4 (22.3) ^{a,A}	28.2 (10.7) ^{ab,A}	68.0 (5.3) ^{a,A}	54.0 (13.5) ^{ab,A}	65.5 (6.6) ^{a,A}
<i>Q. prinus</i> L.	13.5 (6.7) ^{b,A}	19.5 (15.6) ^{a,A}	14.2 (8.1) ^{b,A}	28.5 (4.3) ^{b,A}	16.6 (9.8) ^{c,A}	19.9 (5.2) ^{cd,A}
<i>Q. rubra</i> L.	10.7 (8.2) ^{b,A}	1.7 (19.7) ^{a,A}	5.3 (10.2) ^{b,A}	20.7 (5.4) ^{bc,A}	6.9 (12.3) ^{c,A}	8.9 (6.6) ^{d,A}
Planted pine watershed						
<i>P. strobus</i> L.	21.3 (7.2) ^{ab,A}	26.6 (12.9) ^{a,A}	27.9 (6.6) ^{a,A}	54.7 (4.5) ^{a,A}	57.9 (8.1) ^{a,AB}	44.1 (4.3) ^{b,B}

Standard error of parameter estimate given in parentheses. * The rate of decrease in G_S per unit D is described by $-\beta_2$, and stomatal conductance at $D = 1$ kPa (i.e. G_{Sref}) is described by β_3 . ‡ Within columns, species not sharing the same lowercase letters denote significant differences among species for that year. Within rows, years not sharing the same uppercase letters denote significant differences among years for that species.

Table VI. Estimates of growing season interception, transpiration and ET.

	Interception (E_i , mm)		Transpiration (E_t , mm)*		$E_i + E_t$ (ET, mm)		ΔET (mm)	$\Delta E_i / \Delta ET$ (%)	$\Delta E_t / \Delta ET$ (%)
	Planted pine	Hardwood reference	Planted pine	Hardwood reference	Planted pine	Hardwood reference			
2004	282	146	420 (23)	200 (9)	702	346	357	38	62
2005	324	166	364 (76)	134 (67)	687	300	387	41	59
2006	164	88	327 (90)	154 (59)	491	242	249	30	70
Average								36	64

* Transpiration value is the mean (standard deviation) among plots within the watershed.

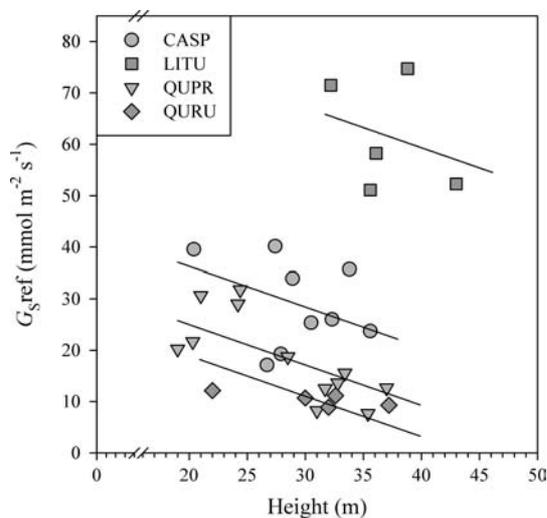


Figure 5. Relationship of G_S at $D = 1$ kPa (G_{Sref}) and tree height for the hardwood species. Symbols correspond to the mean G_{Sref} for a tree across the three study years. Lines correspond to a linear model with species as covariate: model $R^2 = 0.86$, $F_{5, 26} = 120.50$, $P < 0.001$. Parameter estimates (standard errors) for lines: slope = -0.786 (0.26); intercepts: $\bullet = 52.00$ (7.96); $\blacksquare = 90.77$ (10.18); $\blacktriangledown = 40.72$ (7.63); $\blacklozenge = 34.63$ (8.63). Legend as in Figure 3.

watershed (Figure 6), while in the drier year, the relationship between E_t and D was similar between watersheds.

Growing season interception (E_i) differed for the two watersheds within and among years (Table VI). Interception by WS17 (282, 324, 164 mm or 26, 25, 31% of growing season precipitation) exceeded interception

by WS18 (146, 166, 88 mm or 14, 13, 17% of growing season precipitation) by about twofold; however, the proportion of growing season ET (i.e. $ET = E_t + E_i$) contributed by E_i and E_t was remarkably similar between watersheds. Averaged over the 3 years of measurement, E_i was 40% of total ET for WS17 versus 45% of total ET for WS18; and E_t was 60% of total ET for WS17 and 55% of total ET for WS18.

DISCUSSION

Inter- and intra-annual differences among species in transpiration

Our data show considerable variation among species in their responsiveness to variation in climate. This supports our expectation that E_L would vary by species, and that the relationship between E_L and G_S with vapour pressure deficit (D) would also vary by species. The two species that responded most to climatic variation were *L. tulipifera* and *P. strobus*. Both of these species are among the fastest growing species in the southern Appalachians (Burns and Honkala, 1990; Mohan *et al.*, 2007), and also showed the greatest stomatal sensitivity to D , and the greatest response to soil moisture. *L. tulipifera* often reduces its leaf area by premature leaf senescence in response to severe drought, thereby increasing the sapwood area to leaf area ratio to increase specific leaf conductance, which allows maintenance of stomatal conductance and photosynthesis. Our estimates of canopy

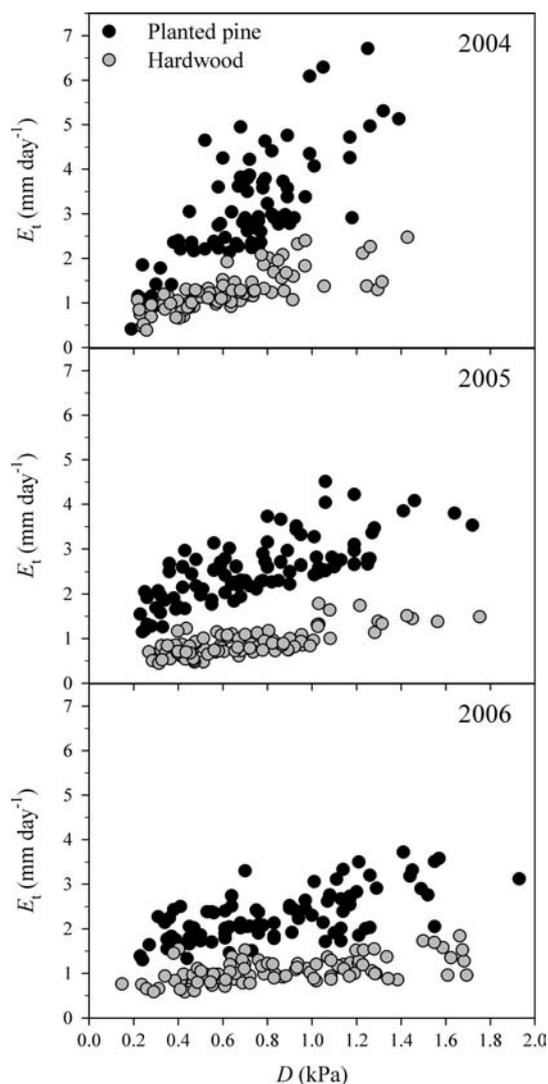


Figure 6. Daily plot transpiration (E_t) during the growing season versus mean daily vapour pressure deficit (D) for the three study years. Points represent the mean of all stands measured within a watershed. Days with precipitation events are also shown.

transpiration used constant growing season leaf area values, and thus we would have likely underestimated E_L and G_S if *L. tulipifera* exhibited premature leaf senescence; however, we did not see E_L of *L. tulipifera* decline in the driest year. Instead, *L. tulipifera* E_L increased from the wettest to the driest year. *P. strobus* showed the largest reduction in mean G_S (28%) from the wettest to the driest year, and also decreased E_L . In contrast, *Carya* spp. were the least responsive to inter-annual variation in climate. This species had similar G_S and E_L responses to D , and mean G_S and E_L among all years. *Carya* spp. are known to develop deep tap roots (the other species studied here are not) which may provide access to a more stable water source that buffers the effects of drought (Ford *et al.*, 2008).

The *Quercus* spp. were highly conservative in their water use; the majority of the oak trees in this study were found in the upper plot and not the lower plot. Consequently, soils were drier and hence had less available soil water. This reflects the typical distribution for oaks in the

southern Appalachians; they tend to occupy drier locations, such as the ridges and upper side slopes (Bolstad *et al.*, 1998). During exceptional droughts in the southern Appalachians in the mid-1980s, oak species experienced wide-spread mortality (Clinton *et al.*, 1993), with older trees being the most vulnerable to the interaction between drought and root pathogens. Interestingly, the *Quercus* spp. had the greatest amount of leaf area to support per unit sapwood; yet, they had the lowest transpiration per unit leaf area.

The oak and hickory spp. together were consistently the least responsive to D , a response noted previously in temperate hardwood forests by Oren and Pataki (2001). Similarly, Bush *et al.* (2008) found that E_L for well-watered oak species was relatively unresponsive to changes in D . They further found that this relationship held constant across three species with ring-porous xylem anatomy, while across three species with diffuse-porous anatomy, the relationship between E_L and D was linear. Our results conform to this pattern. Our data suggest that changes in D from year to year would have a lesser effect on E_t in hardwood forests dominated by oak and hickory species compared with forests dominated by diffuse-porous species, such as *L. tulipifera*. By extension, we hypothesize that the intra-annual variability in stream flow in forested catchments dominated by oaks would be lower during the growing season than that of a forest catchment dominated by diffuse-porous species, such as *L. tulipifera*.

Our results suggest that either managing to favour a particular species or suite of species in a watershed, or non-random species removal (e.g. as a result of pests and pathogens that remove single species) may affect forest E_t and the E_t response to climatic variation. While others have found similar patterns to what we observed, the consistency of response varies across ecosystems. For example, among native tropical forest species little variation in the relationships between E_c and climate is evident (Meinzer *et al.*, 2001; O'Brien *et al.*, 2004; Dierick and Holscher, 2009). In contrast, native temperate forest species exhibit considerable variation in the relationships between E_c and climate (Oren and Pataki, 2001; Wullschlegel *et al.*, 2001; Moore *et al.*, 2004; Ewers *et al.*, 2005). Interestingly, some of the greatest differences observed in E_c among species within either tropical or temperate forests has been between native and exotic species (Dierick and Holscher, 2009; Kagawa *et al.*, 2009).

Structural controls on ET

Differences in growing season ET between the planted pine watershed and the hardwood watershed were the result of structural differences, both in tree height and in interception. Morphological and physiological changes in water use that are directly or indirectly related to tree height can have important effects on water use (Ryan *et al.*, 2000; Woodruff *et al.*, 2007, 2010). Our results also show significant differences in stomatal conductance

with tree height: within any species, shorter trees had a higher conductance at 1 kPa compared with taller trees. Not accounting for the effects of species and tree height on E_t may have important implications for process-based streamflow models. For example, many process-based stream flow models estimate transpiration from the vegetation layer using a ‘big leaf’ approach, whereby all the leaf area in a catchment behaves the same way [e.g. BIOME-BGC and RHESSYS (Running and Hunt, 1993), PROSPER (Swift *et al.*, 1975)]. Unless the ‘big leaf’ approach adequately accounts for differences in physiology among individual species, as well as age-related changes with tree height within a species, our results suggest that species and size effects may have a large impact on modelled transpiration, and subsequently stream flow and stream flow dynamics. In some cases, it is likely that model calibration is accounting for some of these effects; however, our results suggest that calibrated models will not be particularly useful for examining responses to potential species changes or interactions with climate variability.

Early work on these stands indicated the interception was the primary driver of the differences in ET between the planted pine and hardwood stands, as modelled growing season estimated of E_t were similar (Swift *et al.*, 1975). Interestingly, this was not the case in our study, at least when comparing mid-slope locations. In fact our data suggest that across both wet and dry years, transpiration accounts for a larger proportion of the differences in ET than does interception. Interception accounted for more of the discrepancy in wet years compared with the dry year, while transpiration accounted for more of the discrepancy in dry years, similar to Oishi *et al.* (2010).

Although the pattern of response we observed agrees with annual precipitation minus runoff ($P - R_o$) estimates which indicate higher ET in the pine stands (Swank and Miner, 1968), the magnitude of the difference in ET is much greater than predicted by annual $P - R_o$ estimates. A few limitations of our approach may explain the difference. For example, understory transpiration in the hardwood watershed, while a minor component, was not estimated. Most notably, however, is that we do not capture hydrologic processes that occur outside of the growing season [e.g. winter time transpiration by *P. strobus* (Ford *et al.*, 2007)] or hillslope flow path dynamics that contribute to annual streamflow. In addition, by limiting our comparison to mid- and upper-slope positions, we do not fully capture the variation in species composition in WS18 that is driven by topographic position. For example, lower sites in the watershed (cove sites) are dominated by *L. tulipifera* (Elliott *et al.*, 1999), which had the greatest E_L of any of the hardwood species. Stand-based growing season ET estimates on WS18 would likely increase substantially if sites lower in the watershed, which have a high proportion of *L. tulipifera* were included in the scaling, further emphasizing the importance of species-level information.

CONCLUSIONS

We found substantial differences in E_L and G_S among major canopy species in the southern Appalachians. On per unit leaf area basis, species ranked *L. tulipifera* > *P. strobus* > *Carya* spp. > *Q. prinus* > *Q. rubra* for both E_L and G_S . Quantifying this variation in water use among species is useful for evaluating (either empirically or with process-based models) the hydrologic impacts of changes in species composition due to management, succession or invasive insects or diseases. Species also varied in their responses to inter-annual variation in climate. For example, E_L and G_S of oaks and hickories were least responsive to changing vapour pressure deficit, while *L. tulipifera* and *P. strobus* were most responsive. This species level understanding of variation in E_L and G_S and their interactions with climatic driving variables has important implications for predicting watershed-level responses to climate variability. For example, our data suggest that streamflow from forests dominated by oaks and hickories will be less impacted by drought (when comparing post-drought streamflow with pre-drought streamflow) than streamflow from forests dominated by *P. strobus* and *L. tulipifera*. At the plot scale, *P. strobus* growing season ET ($E_t + E_i$) was twofold greater than growing season hardwood ET. Contrary to our expectations, growing season E_t in the pine stand was about twofold greater than growing season E_t in the hardwood stand, suggesting that physiological differences between pine and hardwood species contributed as much to the overall difference in ET as did differences in structural factors (i.e. surface interception by leaf area, branch area, stem area) that influence E_i .

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