Measuring and modeling the variation in species-specific transpiration in temperate deciduous hardwoods

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Summary We investigated which parameters required by the MAESTRA model were most important in predicting leaf-area-based transpiration in 5-year-old trees of five deciduous hardwood species—yoshino cherry (*Prunus × yedoensis* Matsum.), red maple (*Acer rubrum* L. 'Autumn Flame'), trident maple (*Acer buergeranum* Miq.), Japanese flowering cherry (*Prunus serrulata* Lindl. 'Kwanzan') and London plane-tree (*Platanus × acerifolia* (Ait.) Willd.). Transpiration estimated from sap flow measured by the heat balance method in branches and trunks was compared with estimates predicted by the three-dimensional transpiration, photosynthesis and absorbed radiation model, MAESTRA. MAESTRA predicted species-specific transpiration from the interactions of leaf-level physiology and spatially explicit micro-scale weather patterns in a mixed deciduous hardwood plantation on a 15-min time step. The monthly differences between modeled mean daily transpiration estimates and measured mean daily sap flow ranged from a 35% underestimation for *Acer buergeranum* in June to a 25% overestimation for *A. rubrum* in July. The sensitivity of the modeled transpiration estimates was examined across a 30% error range for seven physiological input parameters. The minimum value of stomatal conductance as incident solar radiation tends to zero was determined to be eight times more influential than all other physiological model input parameters. This work quantified the major factors that influence modeled species-specific transpiration and confirmed the ability to scale leaf-level physiological attributes to whole-crown transpiration on a species-specific basis.

Keywords: MAESTRA, species-specific transpiration, vapor pressure deficit.

Introduction

Accurate computation of transpiration is necessary to forecast forest water use (e.g., Gordon and Famiglietti 2004, Morales et al. 2005) and to investigate scientific questions such as the effects of forest management on groundwater recharge (e.g., Walker et al. 2002, Lasch et al. 2005, Vano et al. 2006). Water-use patterns of individual species add uncertainty and variability to the transpiration component of the hydrological cycle (Oren and Pataki 2001, Pataki and Oren 2003, Ford et al. 2007). Therefore, understanding vegetation influences on transpiration is critical for predicting the transpiration response of forest ecosystems. There is a paucity of information on reliable approaches for predicting species-specific transpiration per unit leaf area; however, failure to account for physiological traits that influence species differences in transpiration could lead to large errors in transpiration estimates (Wullschleger et al. 2001, Ewers et al. 2002, Pataki and Oren 2003). Consequently, reliable methods are needed for predicting species-specific physiological transpiration constraints for use in mechanistic models.

We measured and modeled species-specific transpiration rates in five deciduous tree species. We used a three-dimensional (3-D) spatially explicit individual tree process model (MAESTRA) to investigate and explain transpiration constraints among species. The model has been validated previously for CO_2 exchange with eddy covariance measurements (Wang et al. 1998), transpiration based on comparison with sap flux (Bauerle et al. 2002), and deciduous tree light absorption estimates made by fiber optic assessment (Bauerle et al. 2004*a*). In this study, we parameterized the model on a species-specific basis with measurements made over the 2005 growing season. We compared scaled-up model estimates of leaf transpiration with whole-tree or branch measurements of sap flow. With this approach, we evaluated model estimate sensitivity to species-specific physiological trait parameterization, and determined which model components are fundamental for differentiating species-specific differences in transpiration. We tested two hypotheses: (1) variation in leaf-level physiological traits among species translates to variation at the whole-tree level when scaling from the leaf to the tree; and (2) stand-level transpiration is influenced by underlying species-specific responses to climate.

Materials and methods

Site description

In May 2005, a 1950 m^2 (65 × 30 m) experimental plot was

chosen in the center of a 16,800 m² (120 × 140 m) mixed deciduous stand at King Sunset Nursery, Liberty, SC (34°47′16″ N, 82°41′33″ W). Trees were spaced at 2 × 4 m in rows oriented from northeast to southwest. Each month, growth of 182 trees was followed by measuring mean stem diameter at 0.20 m from the soil surface (mm), mean crown radius (m), total tree height (m), height of stem to the first branch (m) and length of crown (m).

Plant material

Yoshino cherry (*Prunus × yedoensis* Matsum.), red maple (*Acer rubrum* L. 'Autumn Flame'), trident maple (*Acer buergeranum* Miq.), Japanese flowering cherry (*Prunus serrulata* Lindl. 'Kwanzan') and London plane-tree (*Platanus × acerifolia* (Ait.) Willd.) were studied. Four replicates per species were randomly selected within a 30 m radius of the plot center for the intensive study (described below). Soil water content was measured adjacent to all the study trees.

Meteorology data

Photosynthetic photon flux (PPF), air temperature (T_{air}), relative humidity (RH), and wind speed (V_{wind}) were measured once per minute and averaged every 15 minutes. On a single wind pole within the experimental plot, V_{wind} measurements were made at 1.5, 2.0, and 2.5 m from the soil surface with R.M. Young 03101-L wind sentry anemometers (Campbell Scientific, Logan, UT). We measured PPF with a quantum sensor placed above the canopy about 3.0 m from the soil surface to avoid shade from the neighboring trees. Both T_{air} and RH were measured at five locations across a 100-m transect through the stand at 1.5 m from the soil surface. Three of the T_{air}/RH sensors (Onset Computer Corporation, Pocasset, MA) were placed inside the experimental plot, and two were located immediately adjacent to it.

Sap flow

Sap flow was measured on 20 trees (four replicates per species) with Dynagage™ heat balance branch and trunk collars (Dynamax, Houston, TX) as described by Bauerle et al. (2002), unless otherwise noted. Trunk gauges were installed at 0.50 m from the soil surface on 17 trees (SGB25-WS, SGB35-WS and SGB50-WS) and branch gauges (SGB19-WS) were placed on a single dominant branch within the crown of an *A. rubrum*, *Prunus × yedoensis* and *Prunus serrulata*. All gauges were read once per minute and 15-min means were logged. The gauges were adjusted for every 5 mm of caliper growth to prevent stem girdling and to determine sheath conductance (K_{sh}), which was calculated about every 3 weeks from zero-flow measurements collected between 1 and 2 h after a precipitation event. The sap flow system was shut down at 2200 h throughout the rest of the growing season. *Platanus × acerifolia* were not measured during the last two months of the growing season because of gauge failures.

Gas exchange

The relationships between photosynthesis (*A*, μmol m⁻² s⁻¹) and intercellular CO_2 concentration (C_i; expressed as the mol fraction of CO_2) and PPF were determined with a CIRAS-1 CO_2/H_2O infrared gas analyzer with a PLC (B) temperature, humidity and light controlled cuvette (PP Systems). For the *A*–C_i curves, cuvette CO_2 concentration was set at 380, 200, 150, 100, 50, 380, 400, 600, 800, 1000 and 1200 ppm consecutively at 1200 μmol m⁻² s⁻¹ PPF. For the photosynthetic light response curves, PPF was set at 1200, 1000, 800, 600, 425, 200, 100, 50 and 0 μmol m⁻² s⁻¹ consecutively with a CO_2 concentration of 380 ppm. Both curve types were measured at 25 °C and 60% RH. Measurements were taken monthly on two fully expanded leaves between nodes three and seven from the branch terminal tip on each tree measured for sap flow. Maximum rate of carboxylation (V_{cmax}) and maximum rate of electron transport (J_{max}) were estimated from the *A*–C_i curves. Quantum efficiency (φ), dark respiration (R_d) and curvature of the light response (θ) were calculated from the photosynthetic light response curves for each species as described by Bauerle et al. (2003). From the gas exchange data, we calculated the empirical slope coefficient of the Ball-Berry equation (g_1) and the *y*-intercept parameter (g_0) from the linear relationship between photosynthesis and stomatal conductance (g_s) for each species and month. In addition, leaf absorptance and greenness were measured with a SPAD 502 meter (Minolta) immediately after the gas exchange measurements for use in the quantum yield calculations (Bauerle et al. 2004*b*).

Soil water content

Soil volumetric water content was monitored with twenty 20-cm ECH₂O soil moisture probes (Decagon Devices) inserted at an angle of 45° to the vertical under the drip line of each tree instrumented for sap flow. The lead wire–probe interface was set at 5 cm below the soil surface. A copper-constantan thermocouple dipped in liquid electrical tape was buried adjacent to the probes to account for temperature sensitivity of the ECH₂O probes. Campbell Scientific data loggers recorded the data obtained by the ECH₂O and thermocouple sensors.

Destructive harvest

At the end of the growing season, all trees instrumented with sap flow sensors were felled above the root collar. For trees with gauges attached to the trunk, the crown was divided into vertical 1-m sections from the dominant leader. For trees instrumented with branch gauges, trees were divided into two sections; one being the measured branch, the other being the unmeasured portion of the crown. Leaves were removed from each section and bagged separately. Individual crown sections were immediately brought to the laboratory, stored at 5 °C and scanned between 1 and 4 days after harvest with an LI-3100 leaf area meter (Li-Cor). Leaves were dried at 70 °C for 10 days, and dry masses were measured for each crown section. Leaf area was estimated by allometric relationships be-

tween whole-crown leaf area and stem basal area on a species basis for all unharvested trees.

Model description and parameterization

A modified version (Bauerle et al. 2002, 2004*a*, 2007) of an individual tree 3-D model for calculating transpiration, photosynthesis and absorbed radiation, MAESTRA (see Medlyn 2004 for a retrospective of the MAESTRA process model), was parameterized for the experimental site. The updated version of MAESTRA operates on a 15-min time step, responds to soil water content with a response function that was validated on deciduous trees based on measurements of leaf-level stomatal conductance, sap flow, photosynthetic rates, crown transpiration and light interception, and incorporates thermal acclimation response functions (Bauerle et al. 2007). In our study, we divided the crown into five layers, resulting in 12 sectors of 30°, with each layer forming 12 equal sub-volumes.

Physiological attributes were parameterized on a species basis. Thus, we parameterized each species' genetic difference with species-specific leaf-level values and control equations based on process-based physiological models such as the Ball-Berry (Ball et al. 1987) or the Farquhar and von Caemmerer (1982) model. Specific to this version of MAESTRA, we updated the g_s response by incorporating physical drought-response functions (Bauerle et al. 2002).

Model application

Within MAESTRA, a simulated plot was created with site description, tree growth and tree spacing data. The model was parameterized for each species on a monthly basis (June–September). Transpiration estimates were output on a 15-min time step and averaged across the four gauged trees per species. Mean model estimates per species were compared with mean species sap flow measurements on 15-min, daily and monthly time steps.

Sensitivity analysis

Physiological parameters (J_{max}, V_{cmax}, R_d, g_0, g_1, φ and θ) were analyzed over a 30% error range to quantify their influence on transpiration predictions. Each parameter was increased and decreased by 15% from the parameterized model value for each species and month. The positive and negative percent changes for each run were calculated and divided by fifteen. The absolute value of each value was averaged to generate an importance value.

Stomatal conductance and soil water deficit

The g_0 parameter was examined further to assess its significance in predicting transpiration. The model was run at five g_0 values (0.25, 0.15, 0.05, 0.005 and 0.0 mol m^{-2} s^{-1}) across five soil water deficits (0.0, 0.3, 0.5, 0.75 and 1.0, representing the wettest to driest soil conditions) for all species to determine how variations in soil water content affected transpiration predictions in relation to g_0.

Results

Variations in leaf area, total tree height, crown length, stem diameter, crown width, trunk length and leaf width were observed among the study species (Table 1). Figure 1 illustrates the meteorological data over the course of a representative week for each month of the study. Vapor pressure deficit (VPD) and PPF were highly variable during June–August; however, VPD and PPF were relatively constant in September. Extreme soil water deficits were never observed during the study and ranged from 0.25 to 0.59. The 2005 growing season was characterized by frequent minor rains. Starting May 1, 39 of 153 days had 2 cm of precipitation or less, and only 10 days in the season had more than 2 cm of precipitation. All study species had similar seasonal trends in J_{max}, V_{cmax} and R_d, with maximum values for each parameter occurring in July with the exception of *Prunus serrulata*, which reached its highest V_{cmax} in August; however, the August value was not significantly different ($\alpha = 0.05$) from the July value (Table 2). In all species, g_0 was highest in August and ranged from 0.075 to 0.384 mol m^{-2} s^{-1} throughout the study (Table 2). Although the seasonal pattern in g_0 was variable and differed among species, the seasonal mean g_0 for all species was 0.2072 ± 0.0045 mol m^{-2} s^{-1}. The species-specific slope parameter for the Ball-Berry stomatal conductance sub-model, g_1, remained constant throughout the season for all species (Table 2).

Model performance was evaluated against diurnal sap flow for each study species (Figure 2) and corresponds to the meteorological data illustrated in Figure 1. Mean seasonal differ-

Table 1. Mean (± standard error) leaf area, total tree height, crown length, stem diameter (measured at 20 cm above soil surface), crown width, trunk length, leaf width and the resultant allometric leaf area equation (y = leaf area (m^2); x = basal area (m^2)) for the five deciduous gauge tree species over the study period. ($n = 16$, except for *Platanus × acerifolia* where $n = 8$; a double asterisk (**) indicates standard error < 0.01).

| Species	Leaf area (m^2)	Tree height (m)	Crown length (m)	Stem diameter (cm)	Crown width (m)	Trunk length (m)	Leaf width (cm)	Leaf area equation
Prunus × yedoensis	5.96 ± 0.54	3.64 ± 0.06	2.28 ± 0.10	5.1 ± 0.0 **	1.51 ± 0.10	1.36 ± 0.16	8.9	$y = 2700.4x$
Acer rubrum	28.26 ± 2.08	4.69 ± 0.14	3.34 ± 0.31	5.8 ± 0.0 **	1.36 ± 0.31	1.35 ± 0.06	8.9	$y = 9123.1x$
Acer buergeranum	6.83 ± 0.32	2.67 ± 0.05	1.71 ± 0.10	3.3 ± 0.0 **	0.82 ± 0.10	0.96 ± 0.03	6.4	$y = 7540.8x$
Prunus serrulata	7.70 ± 0.40	3.95 ± 0.02	2.28 ± 0.11	4.6 ± 0.0 **	1.29 ± 0.11	1.67 ± 0.07	6.4	$y = 4379.4x$
Platanus × acerifolia	30.74 ± 2.17	5.60 ± 0.04	4.00 ± 0.08	6.3 ± 0.0 **	1.57 ± 0.08	1.60 ± 0.04	16.5	$y = 9906.5x$
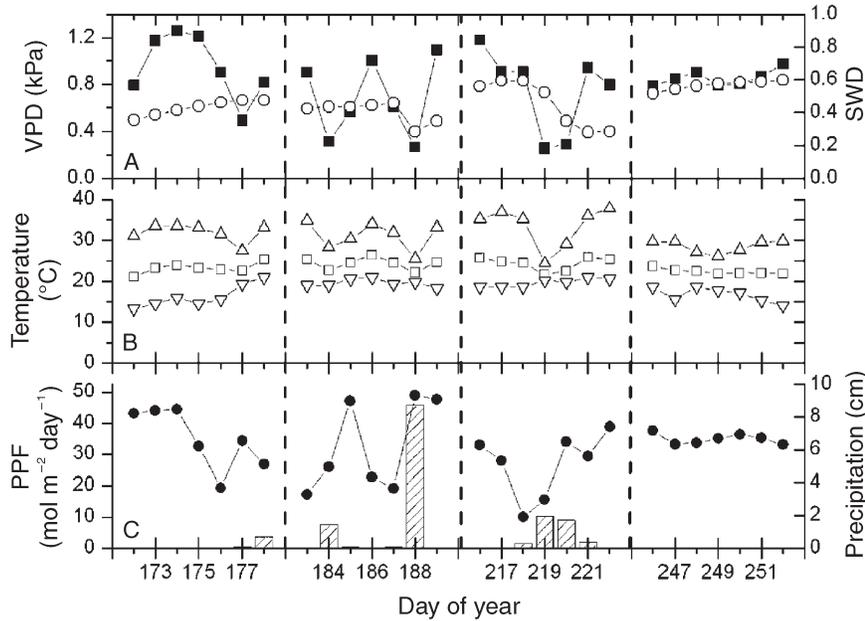
Figure 1. Meteorological data for seven consecutive days per month during the study period. (A) Mean daily vapor pressure deficit (VPD, ■) and mean daily soil water deficit (SWD, ○). (B) Maximum (△), mean (□) and minimum (▽) daily air temperatures. (C) Daily cumulative photosynthetic photon flux (PPF, ●) and daily cumulative precipitation (bars) ($n = 96$ for all mean daily values; vertical dashed lines separate the months).

Table 2. The $A–C_i$ derived parameters were maximum rate of carboxylation (V_{cmax}) and maximum rate of electron transport (J_{max}). Light response derived parameters were dark respiration (R_d), quantum efficiency (φ), the curvature of the light response (θ), stomatal conductance empirical slope coefficient (g_1), and the minimum value of stomatal conductance as light tends to zero (g_0). Inputs used to parameterize MAESTRA monthly per species ± standard error.

Parameter	Month	*Prunus × yedoensis*	*Acer rubrum*	*Acer buergeranum*	*Prunus serrulata*	*Platanus × acerifolia*
V_{cmax}	June	47.4 ± 2.5	40.0 ± 1.8	44.6 ± 5.5	54.6 ± 3.5	33.9 ± 4.1
(μmol m^{-2} s^{-1})	July	74.5 ± 3.9	72.8 ± 1.9	52.0 ± 8.5	68.9 ± 4.1	78.6 ± 5.8
	August	64.7 ± 5.3	61.8 ± 3.3	45.7 ± 3.6	69.3 ± 6.6	–
	September	53.1 ± 8.6	49.5 ± 3.5	12.0 ± 1.7	43.1 ± 6.7	–
J_{max}	June	153.0 ± 17.4	106.9 ± 11.4	105.4 ± 8.9	138.2 ± 18.3	90.9 ± 10.6
(μmol m^{-2} s^{-1})	July	239.3 ± 21.6	185.4 ± 11.1	138.2 ± 27.7	196.4 ± 10.1	241.6 ± 26.3
	August	149.4 ± 8.9	166.0 ± 15.4	93.4 ± 5.2	180.0 ± 17.7	–
	September	116.3 ± 23.8	175.3 ± 17.0	21.3 ± 3.8	111.5 ± 10.8	–
R_d	June	2.34 ± 0.49	4.04 ± 0.27	5.68 ± 0.67	5.66 ± 0.39	1.36 ± 0.34
(μmol m^{-2} s^{-1})	July	2.34 ± 0.99	9.01 ± 1.90	8.44 ± 1.73	8.20 ± 0.85	4.56 ± 1.34
	August	1.00 ± 0.87	8.61 ± 1.36	6.16 ± 0.52	0.72 ± 0.55	–
	September	1.25 ± 2.12	8.52 ± 1.26	7.23 ± 0.18	2.09 ± 3.96	–
φ	June	0.058 ± 0.009	0.058 ± 0.004	0.080 ± 0.013	0.057 ± 0.002	0.056 ± 0.244
	July	0.076 ± 0.003	0.059 ± 0.003	0.065 ± 0.014	0.082 ± 0.020	0.066 ± 0.147
	August	0.071 ± 0.007	0.060 ± 0.004	0.053 ± 0.014	0.068 ± 0.006	–
	September	0.079 ± 0.018	0.069 ± 0.005	0.055 ± 0.011	0.039 ± 0.008	–
θ	June	0.816 ± 0.067	0.793 ± 0.078	0.360 ± 0.146	0.891 ± 0.018	0.837 ± 0.050
	July	0.875 ± 0.035	0.972 ± 0.006	0.488 ± 0.118	0.891 ± 0.030	0.878 ± 0.022
	August	0.858 ± 0.056	0.971 ± 0.019	0.986 ± 0.007	0.863 ± 0.032	–
	September	0.790 ± 0.134	0.951 ± 0.049	0.945 ± 0.232	0.974 ± 0.011	–
g_1 (mol m^{-2} s^{-1})	June– September	4.5 ± 0.7	6.2 ± 1.6	10.0 ± 2.9	13.8 ± 1.7	13.0 ± 1.6
g_0	June	0.231 ± 0.017	0.231 ± 0.013	0.082 ± 0.013	0.233 ± 0.023	0.131 ± 0.030
(mol m^{-2} s^{-1})	July	0.261 ± 0.032	0.159 ± 0.054	0.117 ± 0.030	0.229 ± 0.027	0.210 ± 0.065
	August	0.288 ± 0.048	0.249 ± 0.051	0.211 ± 0.019	0.384 ± 0.050	–
	September	0.260 ± 0.008	0.167 ± 0.056	0.075 ± 0.010	0.213 ± 0.017	–

ence between the measured and modeled estimates ranged from 6.8 ± 4.5 to $-26.0 \pm 6.6\%$ for *Prunus serrulata* and *Platanus × acerifolia*, respectively; however, *Acer rubrum* had the highest correlation coefficient ($r = 0.876$) and *Platanus × acerifolia* had the lowest ($r = 0.809$). Monthly percent differences between mean daily leaf-area-based transpiration estimates and mean daily measured sap flow ranged from a 35% underestimation for *A. buergeranum* in June to a 25% overestimation for *A. rubrum* in July (Table 3). The most accurate estimates were for *Prunus × yedoensis*, with an absolute mean daily percent error of 13%. *Platanus × acerifolia* had the low-

est estimate precision with an absolute mean daily percent error of 26%.

Prunus × yedoensis had the highest daily transpiration rate and mean seasonal transpiration ($\alpha = 0.05$, Table 3). No significant differences were detected between the *Prunus* species until September, and all species had similar transpiration rates in August. The greatest differences in species-specific water use were during September, and the species separated into three distinct groups (Table 3). *Prunus serrulata* was characterized by similar monthly water use throughout the entire study period.
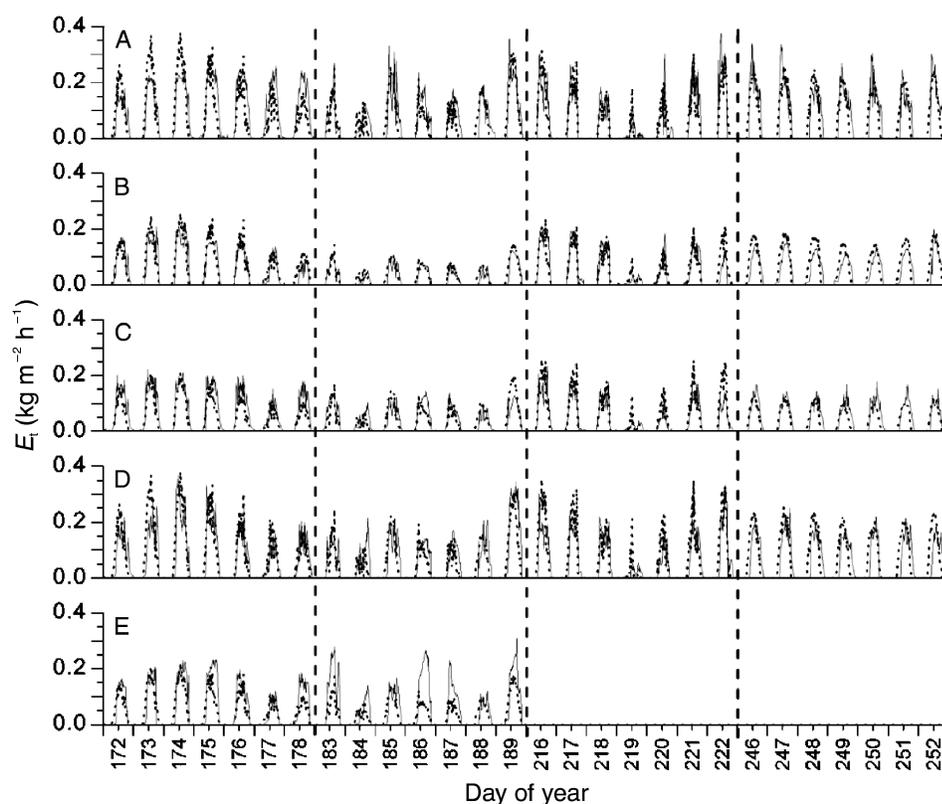

Figure 2. Diurnal time series of measured (solid line) versus modeled (dashed line) transpiration (E_t) over seven consecutive days within the months of June–September 2005 for (A) *Prunus × yedoensis*, (B) *Acer rubrum*, (C) *Acer buergeranum*, (D) *Prunus serrulata* and (E) *Platanus × acerifolia*.

Table 3. Sap flow monthly differences in mean daily transpiration (E_t) compared with MAESTRA model estimates ($\pm$ standard error) for each species. Different lowercase letters indicate significant differences in E_t among months within a species, and different uppercase letters delineate differences in E_t among species within each month ($\alpha = 0.05$).

Month	*Prunus × yedoensis*	*Acer rubrum*	*Acer buergeranum*	*Prunus serrulata*	*Platanus × acerifolia*
Sap flow E_t (kg m^{-2} day^{-1})					
June	1.98 ± 0.14 a A	1.22 ± 0.18 a B	1.52 ± 0.13 a AB	1.57 ± 0.18 a AB	1.37 ± 0.17 a B
July	1.37 ± 0.18 b A	0.56 ± 0.10 b B	0.87 ± 0.10 b AB	1.37 ± 0.24 a A	1.37 ± 0.22 a A
August	1.25 ± 0.21 b A	0.93 ± 0.19 ab A	0.90 ± 0.16 b A	1.18 ± 0.19 a A	–
September	1.69 ± 0.08 ab A	1.05 ± 0.03 a C	1.00 ± 0.04 b C	1.31 ± 0.05 a B	–
MAESTRA modeled E_t (kg m^{-2} day^{-1})					
June	1.67 ± 0.10	1.33 ± 0.07	1.05 ± 0.06	1.74 ± 0.10	1.09 ± 0.06
July	1.13 ± 0.10	0.67 ± 0.07	0.80 ± 0.06	1.09 ± 0.09	0.81 ± 0.05
August	1.11 ± 0.09	0.95 ± 0.06	1.04 ± 0.08	1.33 ± 0.10	–
September	1.57 ± 0.02	1.31 ± 0.02	0.81 ± 0.01	1.61 ± 0.02	–

Among the parameters tested, modeled daily transpiration rates were most sensitive to changes in g_0 (Figure 3). The sensitivity of transpiration predictions displayed no clear seasonal trend with any parameter except g_0. Among species, mean seasonal g_0 had the greatest effect on modeled transpiration rate in *A. buergeranum*, where a 1% change in g_0 resulted in a change of ~0.5% in modeled transpiration rate. The g_0 parameter also had a dramatic effect on *Prunus × yedoensis* modeled transpiration rates in June across a range of SWD values (Figure 4A), with modeled transpiration rate increasing with g_0 in the non-water limiting portions of the curve; however, the effect of declining SWD was reduced at high g_0 values. All species showed similar trends to that of *Prunus × yedoensis* in response to high g_0 values, indicating that differences in transpiration rates among species were significantly affected by changes in g_0 (Figures 4B and 4C). At values of g_0 of 0.25 mol m^{-2} s^{-1} or greater, the species separated into two groups based on water use with the lowest rates of transpiration in *Platanus × acerifolia* (Figure 4B). When g_0 was reduced to 0.005 mol m^{-2} s^{-1}, the species separated into another two groups based on water use; however, under these circumstances *Platanus × acerifolia* exceeded the transpiration rates of three of the study species but it did not differ significantly from *Prunus × yedoensis*, which had the highest water use.

Discussion

The mechanistic use of inherent physiological traits allows characterization of species-specific responses to environmental conditions (Kosugi et al. 2003). MAESTRA integrates leaf-level sub-models (e.g., Farquhar and von Caemmerer (1982) for photosynthesis and Ball-Berry (Ball et al. 1987) for stomatal conductance) within a 3-D spatially explicit frame-
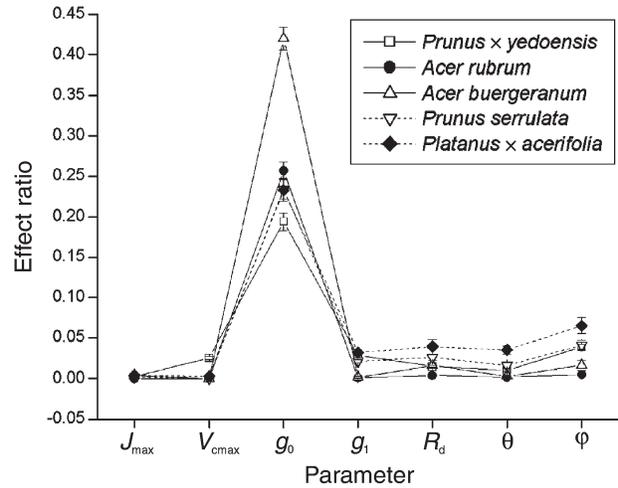

Figure 3. Seasonal mean effect ratio of the maximum rate of electron transport (J_{max}), maximum rate of carboxylation (V_{cmax}), empirical slope (g_1) and intercept (g_0) coefficients of the Ball-Berry equation, dark respiration (R_d), curvature of the light response (θ) and quantum efficiency (φ) for each species.

work to account for interactions between physiological phenomena and environmental stimuli. Thus, MAESTRA can be parameterized to account for species-specific physiological responses, and the physiological parameters responsible for describing inherent species-specific differences afford the model the capacity to predict transpiration in a physiologically diverse hardwood plantation. Although there have been numerous reports on differences in species-specific sap flux (Cienciala et al. 1997, Oren and Pataki 2001, Wullschleger et al. 2001, Ewers et al. 2002, Lagergren and Lindroth 2002, Ford et al. 2004), stomatal conductance (Gao et al. 2002,
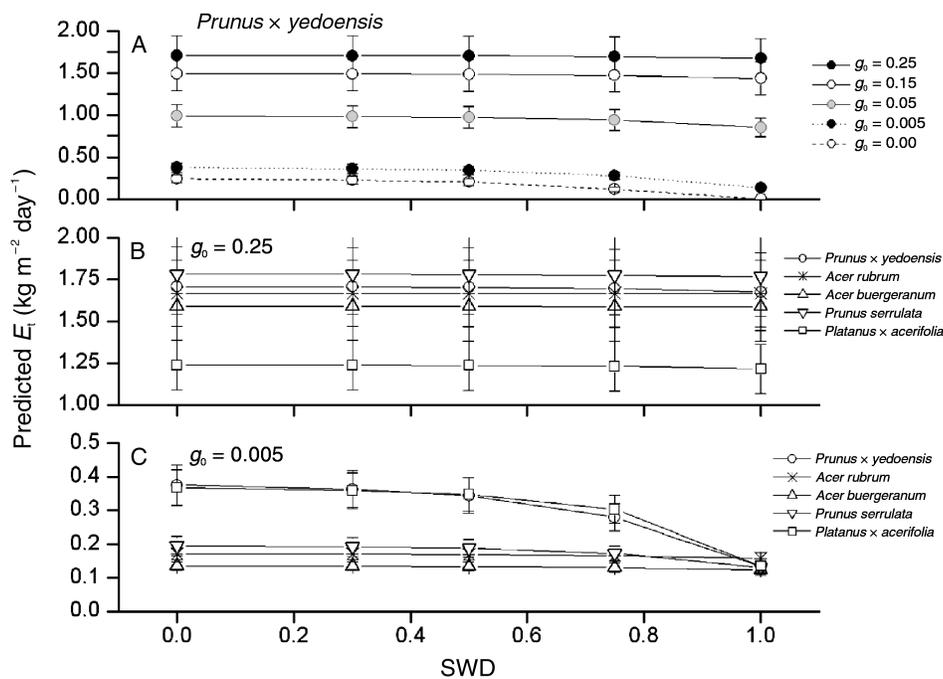

Figure 4. Effect of different Ball-Berry intercept coefficient (g_0) values at varying soil water deficits (SWD) on predicted mean daily transpiration (E_t, ± standard error, $n = 96$). (A) *Prunus × yedoensis* at five values of g_0. (B) Comparison among species at $g_0 = 0.25$ mol m^{-2} s^{-1}. (C) All species at $g_0 = 0.005$ mol m^{-2} s^{-1}. The y-axis scale differs among panels to separate the influences of both g_0 and species.

Kosugi et al. 2003, Pataki and Oren 2003, Bunce 2004), transpiration among functional groups (e.g., Gao et al. 2002) and whole-tree transpiration (Wullschleger et al. 1998, 2001, Misson et al. 2002, Sinclair et al. 2005), few experiments have quantified species-specific differences in diurnal transpiration rates among species under standardized leaf area and environmental conditions. More importantly, little information exists on modeling interspecific differences in transpiration among deciduous hardwoods. Variation among species may not always warrant individual species parameterization. In such cases, classification into functional groups would capture the majority of variation by grouping species with similar physiological responses. Quantification of physiological response parameters is a helpful first step for distinguishing between these scenarios.

Transpiration of trees is commonly measured with sap flow sensors. The heat balance method requires zero sap flow at night to calculate an accurate K_{sh}. Therefore, we calculated K_{sh} the morning after a precipitation event and corrected for zero-sap flow at the end of the season. This approach allowed us to quantify the variation among species. During 89% of the season, there were differences in species-specific mean hourly and daily diurnal transpiration per unit leaf area ($\alpha = 0.05$). Although all study species had mean tree heights and diameters less than those of the 67 species reviewed by Wullschleger et al. (1998), *Acer rubrum*, *Prunus serrulata* and *Platanus × acerifolia* had mean whole-tree daily transpiration rates greater than 10 kg tree^{-1} day^{-1}, which is the minimum daily whole-tree transpiration value reported by Wullschleger et al. (1998). Mean daily whole-tree transpiration rates of *Prunus × yedoensis* and *A. buergeranum* were slightly less (9.29 and 6.69 kg tree^{-1} day^{-1}) at mean tree heights of 3.64 m and 2.67 m, respectively. MAESTRA, parameterized on a species-specific basis, made possible the prediction of the variation in transpiration among the study species.

Differential rates of mean daily diurnal water use were observed over the growing season, August being anomalous. Over three days (days of year 216–218), we observed no variation in transpiration rate among species, at a time when soil water deficits were 21–30% higher than the mean daily soil water deficit in the study. The driest soils occurred on day of year 217 (0.63 m^3 m^{-3}). Additionally, mean daily diurnal VPD for the three consecutive days was higher than the seasonal daily mean. These data indicate that differences in mean daily diurnal transpiration among species could converge as soil water deficit increases to a critical value (Sinclair et al. 2005). But although reductions in transpiration are commonly observed when soil water becomes limiting, increases in VPD can still result in high transpiration provided that concurrent stresses do no exceed a species-specific threshold for stomatal closure (Bond and Kavanagh 1999). Because most species have feedback mechanisms that regulate stomata as VPD increases to reduce water loss or embolism, or both (e.g., chemical, hydraulic, or both), neither the feedback sensitivity nor the magnitude is uniform across species (Oren et al. 1999, Bond and Kavanagh 1999). However, all our study species had a strong positive correlation ($r > 0.73$) between mean daily diurnal

transpiration and VPD. Unlike Pataki and Oren (2003), we observed no characteristic decrease in canopy stomatal conductance in response to VPD. Our site, however, did not experience a severe drought which might have elicited a reduction in transpiration with increasing VPD.

Sensitivity analyses are commonly used to test the effects of parameters on model predictions. We conducted a sensitivity analysis for transpiration, similar to that conducted for gross primary production by Luo et al. (2001). We found that g_0 was the most influential parameter across all months and species, and was the only physiological parameter that affected transpiration by more than 0.5% per 1% change in parameter value. The connection between leaf conductance and transpiration is consistent with the mechanics of stomatal regulation of water loss. Recently, this parameter has received attention because of its relationship with dark transpiration (Daley and Phillips 2006, Marks and Lechowicz 2007, Kavanagh et al. 2007). The g_0 parameter has been shown to vary significantly (i.e., $0.43–0.00$ mol m^{-2} s^{-1}) between functional types, species, and changing soil water regimes—most notably, g_0 can decrease as much as 96% from a wet to dry season within a species (Gao et al. 2002). We found that g_0 varied considerably throughout the season and between species. For all species, 11 of 18 g_0 measurements differed by more than 15% from the mean seasonal g_0 value. In MAESTRA, increases in g_0 cause increases in hourly diurnal transpiration for all species across the range of soil water deficits tested. Although MAESTRA uses light as the primary driving factor in stomatal regulation and does not account for transpiration under dark conditions, the g_0 parameter nonetheless influenced daytime transpiration estimates. Because of the influence of g_0 on transpiration estimates, its accurate estimation is essential. Increased sample size, accurate gas exchange measurement and a wide range of stomatal conductance versus photosynthetic values would increase g_0 prediction accuracy. Our model estimate validation for daytime conditions indicates that our g_0 estimates were precise. The finding that g_0 values were higher than zero indicates that nighttime transpiration occurred.

In conclusion, the differences in species-specific physiology were paired with meteorological data in a 3-D spatially explicit model, MAESTRA, to estimate differences in species-specific transpiration rates. MAESTRA was capable of predicting significant differences in species transpiration on 89% of the study days. Model parameterization of species-specific transpiration rates provided estimates that were precise and acceptably accurate. Although there are several methods for predicting transpiration using the water balance equation, our study documents MAESTRA's ability to estimate species-specific transpiration at the scale of the whole tree and the potential to scale transpiration to the stand and watershed based on leaf-level measurements. The modeled transpiration rates were highly sensitive to small percentage changes in g_0, indicating the importance of both precise measurement of this parameter and the need to capture seasonal variation in all physiological attributes when predicting the seasonal course of transpiration. The variation in water use among species indicates a need to further investigate the Ball-Berry stomatal

conductance model parameters and the physiological basis underlying the species-specific differences in transpiration rates.

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