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MEASURING AND MODELING SPECIES SPECIFIC

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MEASURING AND MODELING SPECIES SPECIFIC
TRANSPIRATION IN A MIXED HARDWOOD PLANTATION

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Plant and Environmental Science

by
Joseph David Bowden
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Accepted by:
Dr. William L. Bauerle, Committee Chair
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Dr. G. Geoff Wang

ABSTRACT

Differences in transpiration have been reported in tree species over the last several decades; however, few studies have teased out the environmental component with a common garden. Species specific transpiration was measured via sap flow on twenty trees from five deciduous hardwood species, *Prunus x yedoensis* Matsum., *Acer rubrum* L. ‘Autumn Flame’, *Acer buergeranum* Miq., *Prunus serrulata* Lindl. ‘Kwanzan,’ and *Platanus x acerifolia* (Ait.) Willd., throughout the 2005 growing season in a plantation. In addition, monthly growth and gas exchange measurements were collected for each species and used to parameterize a three dimensional spatially explicit transpiration model, MAESTRA. The model estimates predicted differences in species mean daily and hourly diurnal transpiration and we validated the model predictions against measured sap flow. Throughout the growing season, *Prunus x yedoensis* had the highest mean daily diurnal transpiration, $1.54 \text{ kg m}^{-2} \text{ d}^{-1}$, while *Prunus serrulata* had the single highest diurnal daily rate, $2.72 \text{ kg m}^{-2} \text{ d}^{-1}$. A sensitivity analysis was conducted to determine the effect that individual parameters have on predicting differences in transpiration and to focus model parameterization efforts. The dark stomatal conductance parameter was the most physiologically significant and was more than eight times more sensitive than the next closest importance parameter.

DEDICATION

This thesis is dedicated to my parents Cathy and Archie Jones who provided unyielding encouragement and inspiration long before this project was started and continues today.

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While there are many people who deserve thanks, first and foremost I would like to thank Dr. William L. Bauerle for his guidance and inspiration through this process. He has been a friend and mentor and for that I am grateful.

I would also like to thank my committee, Dr. Victor B. Shelburne and Dr. G. Geoff Wang for their advice and criticisms which have aided in advancing this writing. I owe many thanks to the Clemson horticulture department professors which have endured many conversations and discussions particular to this work.

I wish to express my deepest gratitude to my wife, Jennie, for her support and encouragement as well as her willingness to listen to my ramblings over the years. I would not have been able to accomplish this undertaking without her.

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LIST OF ABBREVIATIONS

Abbreviation	Units	Definition
A	$\mu\text{mol m}^{-2} \text{s}^{-1}$	net photosynthetic rate
A_{max}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	maximum net photosynthetic rate
C_i	$\text{mol m}^{-2} \text{s}^{-1}$	intercellular CO_2 concentration
DOY	day	cumulative day of the year
E_t	$\text{kg m}^{-2} \text{h}^{-1}$	hourly transpiration
	$\text{kg m}^{-2} \text{d}^{-1}$	daily transpiration
g_0	$\text{mol m}^{-2} \text{s}^{-1}$	empirical intercept coefficient of the Ball-Berry eqn.
g_1	$\text{mol m}^{-2} \text{s}^{-1}$	empirical slope coefficient of the Ball-Berry eqn.
I_c	$\mu\text{mol m}^{-2} \text{s}^{-1}$	light compensation point
J_{max}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	maximum electron transport rate
K_{sh}	dimensionless	sheath conductance
LAI	$\text{m}^2 \text{m}^{-2}$	leaf area index
PAR	$\mu\text{mol m}^{-2} \text{s}^{-1}$	photosynthetically active radiation (400 – 700 nm)
Q_{app}	%	apparent quantum efficiency
R_d	$\mu\text{mol m}^{-2} \text{s}^{-1}$	dark respiration
RH	%	relative humidity
SMD	%	soil moisture deficit
T_{air}	° Celcius	air temperature
V_{cmax}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	maximum RuBP carboxylation activity
VPD	kPa	vapor pressure deficit
V_{wind}	m s^{-1}	wind speed
θ	dimensionless	the curvature of the light response
Γ	$\text{mol m}^{-2} \text{s}^{-1}$	CO_2 compensation point

INTRODUCTION

Over the next century, the global mean annual temperature and atmospheric carbon dioxide concentration are predicted to increase as much as 5 – 7 °C and 320 ppm respectively (IPCC 2001). Consequently, forest canopy transpiration flux will be affected by the change in climate, which will undoubtedly also affect physiological responses and biological systems, i.e. the soil-plant-atmosphere continuum (IPCC 2007). The vegetation-atmosphere interactions in deciduous broad-leafed gas exchange, therefore, need to be quantified in order to obtain primary information for canopy-scale long-term estimates (Kosugi and Matsuo 2006).

While numerous studies have investigated the physiological differences among deciduous tree species (e.g., Sullivan et al. 1996, Wullschleger et al. 2001, Misson et al. 2002) and intraspecific variation (e.g., Bauerle et al. 2003, Mohan et al. 2004), there remains a paucity of results applicable to species specific transpiration and the specific parameters which influence species differences (Wullschleger et al. 2001, Sinclair et al. 2005). The effect of impending climate change on species survival will likely vary as species utilize different strategies within their environmental stress tolerance range (Davis and Shaw 2001). For instance, the correlation between vapor pressure deficit and stomatal behavior or sap flux and subsequently transpiration has been made known for a variety of different species (Granier and Loustau 1994, Bauerle et al. 1999, Oren et al. 1999, Wullschleger et al. 2001, Lagergren and Lindroth 2002, Misson et al. 2002, Bauerle et al. 2004a, Kumagai et al. 2007). Although none of these authors deny the reality of adaptive differentiation among species, the matching of process-based model

transpiration flux predictions to observed species specific physiological variation still requires additional experimental examination to decipher physiologically distinct species response to climate change.

Due to the size and structure of trees, a formidable scaling challenge exists, where model validation at scales higher than the leaf can easily become a tremendous task. In fact, even though mechanistic models are primarily built from known leaf scale physiological and biochemical reactions, e.g., the Farquhar and von Caemmerer (1982) leaf level photosynthesis model, it is common to make assumptions in the attempt to integrate from small-scale process level phenomena to the forest-stand (Hanson et al. 2004). Traversing scales also opens up the potential to propagate error, thus increasing the difficulty of rigorously validating the leaf-tree-stand response of a model against measurements at all scales. That said, mechanistic models are a widely accepted means to investigate tree response to climate change (e.g., Constable and Friend 2000, Hanson et al. 2004). At the species level, the ability to predict species specific transpiration response then depends on both accurate physiological parameterization and resolution and measurement precision.

In this study, we measured and modeled five deciduous tree species to determine differences in transpiration rates. We used a three dimensional process model (MAESTRA) to investigate and explain controls on transpiration. The model has been validated previously with eddy covariance (Wang et al. 1998), sap flow (Bauerle et al. 2002), and light transfer (Bauerle et al. 2004b) on temperate deciduous trees. We parameterized the model on a species specific basis from measurements made over the

course of the 2005 growing season. Few studies have tested and calibrated a fine-scale process model among deciduous temperate species in a common garden environment (Bauerle et al. 2002, 2004b). With this approach, we evaluated the following: 1) the sensitivity to species-specific physiological trait parameterization on model estimates, 2) the ability to predict within crown and whole crown transpiration across deciduous species, 3) the extent to which species physiological variation alters variable sensitivity, and 4) what model components are fundamental to differentiate species differences in transpiration. We test the hypotheses that i) variation in physiological traits among species causes variation in scale transition sensitivity and ii) stand-level transpiration is influenced by the underlying species specific response to climate.

MATERIALS AND METHODS

Site description. In May of 2005 a 1950 m² (65m x 30m; 0.195 ha) experimental plot was chosen in the center of a 16800 m² (120m x 140m; 1.68 ha) mixed deciduous stand, which contained 11.6 % of the total production area at King Sunset Nursery, Inc. (Liberty, SC, USA. 34° 47' 16" N, 082° 41' 33" W). All trees were spaced ca. 2 x 4 m in rows oriented northeast to southwest. Monthly, non-destructive growth was measured on the 182 plot trees as follows: average stem caliper at 0.20 m from the soil surface (mm), average crown radius (m), total tree height (m), height of stem to the first branch (m), and length of crown (m). In addition, five times over the course of the growing season (May 31, 2005 – August 16, 2005) leaf area index (LAI) was measured on uniformly overcast or clear sky days (LAI-2000, Li-Cor, Lincoln, NE).

Plant material. Five species, Yoshino Cherry (*Prunus x yedoensis* Matsum.), red maple (*Acer rubrum* L. 'Autumn Flame'), trident maple (*Acer buergerianum* Miq.), kwanzan cherry (*Prunus serrulata* Lindl. 'Kwanzan'), and London planetree (*Platanus x acerifolia* (Ait.) Willd.), were chosen for intensive investigation of leaf gas exchange, sap flow, and soil moisture. Four replicates of each species were randomly selected within a 30 m radius of the plot center.

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 on a fifteen minute time-step. Within the plot, V_{wind} was collected 1.5, 2.0, and 2.5 m from the soil surface with R.M. Young 03101-L wind sentry anemometers (Campbell Scientific, Inc., Logan, UT). In addition, T_{air} and RH were measured in five

locations (Onset Computer Cooperation, Polaset, Mass., U.S.A.) across a transect through the plot. Three of the air temperature/relative humidity sensors were placed inside the experimental plot and two were located immediately adjacent in a surrounding block.

Sap flow measurements. Sap flow was measured on twenty experimental trees (four replicates of each study species) using Dynagage™ heat balance branch and trunk collars (Dynamax, Inc., Houston, TX). Unless otherwise noted, protocols followed Bauerle et al. (2002). Trunk gauges were outfitted at 0.50 m from the soil surface and branch gauges were placed on a dominant branch within the canopy. All gauges were read once per minute and a 15 minute average was logged. The gauges periodically were adjusted at every 5 mm of caliper growth to prevent stem girdling and to recalculate sheath conductance (K_{sh}). Due to partial mechanical failure of the sap flow system in early August, followed by a subsequent early leaf drop of all *Platanus x acerifolia* trees, potentially initiated from plane tree anthracnose, *Platanus x acerifolia* was not measured in the last two months of the measurement period.

Gas exchange measurements. For each sap flow tree, the relationship between photosynthesis and internal CO₂ concentration (A-C_i curves, where A is net photosynthetic rate $\mu\text{mol m}^{-2} \text{s}^{-1}$ and C_i is internal CO₂ concentration expressed as the mol fraction of CO₂) was determined monthly on two fully expanded leaves between nodes three and seven from the branch terminal tip. In addition, each sap flow tree was subjected to two light response curves using a CIRAS-1 CO₂/H₂O infrared gas analyzer with a PLC (B) temperature, humidity, and light controlled cuvette (PP Systems, Amesbury, MA). From the curves, the maximum rate of carboxylation (V_{cmax}),

maximum rate of photosynthetic electron transport (J_{\max}), CO_2 and light compensation point (Γ and I_c , respectively), and dark respiration (R_d) were estimated as described in Bauerle et al. (2003). In addition, leaf absorptance and greenness were measured with a SPAD 502 meter (Minolta Corp., Ramsey, NJ) immediately after gas exchange measurements and used in quantum yield calculations (Bauerle et al. 2004c). The leaves were analyzed for total leaf nitrogen content (LECO model FP528 nitrogen combustion analyzer (LECO Corporation, St. Joseph, MI, USA)) and a linear regression was developed to estimate total leaf nitrogen from leaf greenness on a species basis.

Soil moisture measurements. Soil volumetric water content was monitored with twenty 20 cm ECH₂O soil moisture probes (Decagon Devices, Inc., Pullman, WA). Probes were inserted at a 45° angle, where the lead wire/probe interface was buried five cm below the soil surface. Probes were placed within the canopy drip-line and paired with sap flow trees. A copper-constantan thermocouple dipped in liquid electrical tape was buried adjacent to the probes to account for ECH₂O temperature sensitivity. Campbell Scientific data loggers (Campbell Scientific, Inc., Logan, UT) were used to read and log ECH₂O and thermocouple sensors. Field soil samples were randomly collected using a cylindrical soil corer (230 cm³) for analysis of bulk density and soil volumetric water content characteristics.

Destructive harvest. At the end of the growing season, all gauge trees were cut just above the root collar. In the case of trunk measurement, the canopy was divided into vertical one meter sections from the dominant leader. Branch gauge trees were divided into two sections; one corresponded with the measured branch, while the other portion of

the canopy was treated as the second section. Leaves were removed for each section and bagged separately. Individual canopy sections were immediately brought to the lab, stored in a walk in cooler at 5 °C for less than four days from harvest, and scanned using a Li-3100 leaf area meter (Li-Cor, Lincoln, NE). Leaves were then dried at 70°C for 10 days and oven dry weights were measured for each crown section. Leaf area was estimated by allometric relationships between whole crown leaf area and stem basal area on a species by species basis for all unharvested trees.

Model description and parameterization. The essence of this study is a species specific modeling analysis that aims to quantify the differences in transpiration among deciduous species. In this study, MAESTRA (see Medlyn 2004 for a retrospective of the process model), a three-dimensional model for calculating photosynthesis, transpiration, and absorbed radiation was parameterized for the experimental site. MAESTRA is an updated version of MAESTRO (Wang & Jarvis, 1990a) and is available on-line at www.maestra.unsw.edu.au. Originally, MAESTRA was developed and validated on coniferous trees (Wang and Jarvis 1990a,b). However, Bauerle et al., (2002; 2004b) updated the model to run on a 15 minute time step, incorporated a soil moisture response function, and validated the model on deciduous trees using measurements of leaf-level g_s , sap flow, photosynthetic rates, crown transpiration, and crown light interception.

Specific to this study, the models spatial explicitness was critical, where MAESTRA allows canopy description at the individual crown and sub crown level. The transpiration response of a “target crown”, therefore, depends on the structure of the crown and the distribution of environmental parameters over the crown. Spatial

characteristics are accounted for with a Cartesian coordinate system. To integrate PAR absorption over temporal and spatial distributions of irradiance, each crown layer is treated as unifacial and the assimilating leaf area is defined as one-sided. The positions and dimensions of the trees surrounding the target crown are used to calculate the sunlit and shaded fractions of leaf area after passing through the neighboring tree canopies, where the canopy is represented by an array of geometric (ellipsoidal, half-ellipsoidal, spherical, cubical, conical, inverted conical) user defined tree crowns. In our study, the crown was divided into five layers, resulting in 12 sectors of 30° with each layer forming 72 equal sub-volumes.

Another critical aspect of the model is the detailed ability to parameterize the physiological genetics on a species by species basis. Thus, our sampling structure and measurements allowed us to describe each species genetic difference with species-specific parameters and control equations using process-based physiological models such as the Ball-Berry (Ball et al. 1987) and the Farquhar and von Caemmerer (1982). The response of a species to an environmental condition was thus represented by ‘meta-mechanisms’ that represent quantitative variation in species differences via species specific experimental response curve parameters (e.g., Reymond et al., 2003; Tardieu, 2003). Specific to our 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 descriptive, tree growth, and tree spacing data. Monthly, the model was parameterized for each species. Within a species, transpiration rate estimates were output on a fifteen

minute time step for all four replicate gauge trees and the estimates per species were averaged and compared against mean species sap flow measurements on a 15-minute, daily, and monthly time step.

Sensitivity analysis. A suite of different physiological parameters (J_{\max} , V_{cmax} , R_d , g_0 , empirical slope coefficient of the Bally-berry equation (g_1), apparent quantum yield (Q_{app}), and curvature of the light response (θ) were analyzed for their sensitivity in predicting transpiration. Each parameter was increased and decreased by fifteen percent from the parameterized model value for each species per month. The positive and negative percent change for each run was then calculated and divided by fifteen to get a parameter effect ratio. The absolute value of the two importance values was then averaged to directly compare their significance to each other with regard to transpiration estimates.

Dark stomatal conductance and soil moisture deficit. The g_0 parameter was examined in further detail due to its sensitivity in predicting transpiration. The model was run at five different g_0 values 0.25, 0.15, 0.05, 0.005, 0.0 $\text{mol m}^{-2} \text{s}^{-1}$ across five different soil moisture deficits 0.0, 0.3, 0.5, 0.75, 1.0 (wettest – driest soil conditions, respectively) for all species to determine how variations in soil moisture effected transpiration predictions in relation to g_0 .

RESULTS

Variability in leaf area, crown height, crown length, stem diameter, crown width, trunk length, and leaf width were observed for the five study species. Mean tree dimensions were calculated for each species by averaging the measurements from all gauged trees within a species for all study months. Relative to an even aged field grown monoculture, the mixed deciduous species variability in leaf area, leaf width, and crown length was substantial (Table 1).

Figure 1 illustrates the pattern among the environmental variables of vapor pressure deficit (VPD), temperature, PAR, precipitation, and soil moisture deficit (SMD) during a representative week of each study month. The data matches the Julian days of measured and modeled E_t illustrated in Figure 2. In addition, Figure 1 shows the gamut of meteorological events that were used in validating model estimates of species specific water use. Often, VPD and PAR were highly variable during June-August; however, VPD and PAR were relatively constant in September. Extreme soil moisture deficits were never observed during the study period and ranged from 0.25 to 0.59; however, the longest consecutive time span without precipitation occurred in September between days 243 and 270. In addition, the 2005 growing season was characterized by frequent minor rains. In fact starting on May 1, 39 out of 153 days had two cm of precipitation or less and only ten days had two cm or more. Only one relatively high volume rain event occurred (day 188) prior to sun rise; interestingly, the highest accumulation of PAR throughout the entire growing season also occurred on the same day. Atmospheric

Table 1. Mean (n=16) leaf area, crown height, crown length, stem diameter (*measured at 20 cm above soil surface), crown width, trunk length, and leaf width for the five deciduous gauge tree species over the study period. († n=8)

Species	Leaf area (m ²)	Crown height (m)	Crown Length (m)	Diameter* (cm)	Crown width (m)	Trunk length (m)	Leaf width (cm)
<i>Prunus x yedoensis</i>	5.96	3.64	2.28	5.1	1.51	1.36	8.9
<i>Acer rubrum</i>	28.26	4.69	3.34	5.8	1.36	1.35	8.9
<i>Acer buergernaum</i>	6.83	2.67	1.71	3.3	0.82	0.96	6.4
<i>Prunus serrulata</i>	7.70	3.95	2.28	4.6	1.29	1.67	6.4
<i>Platanus x acerifolia</i> [†]	30.74	5.60	4.00	6.3	1.57	1.60	16.5

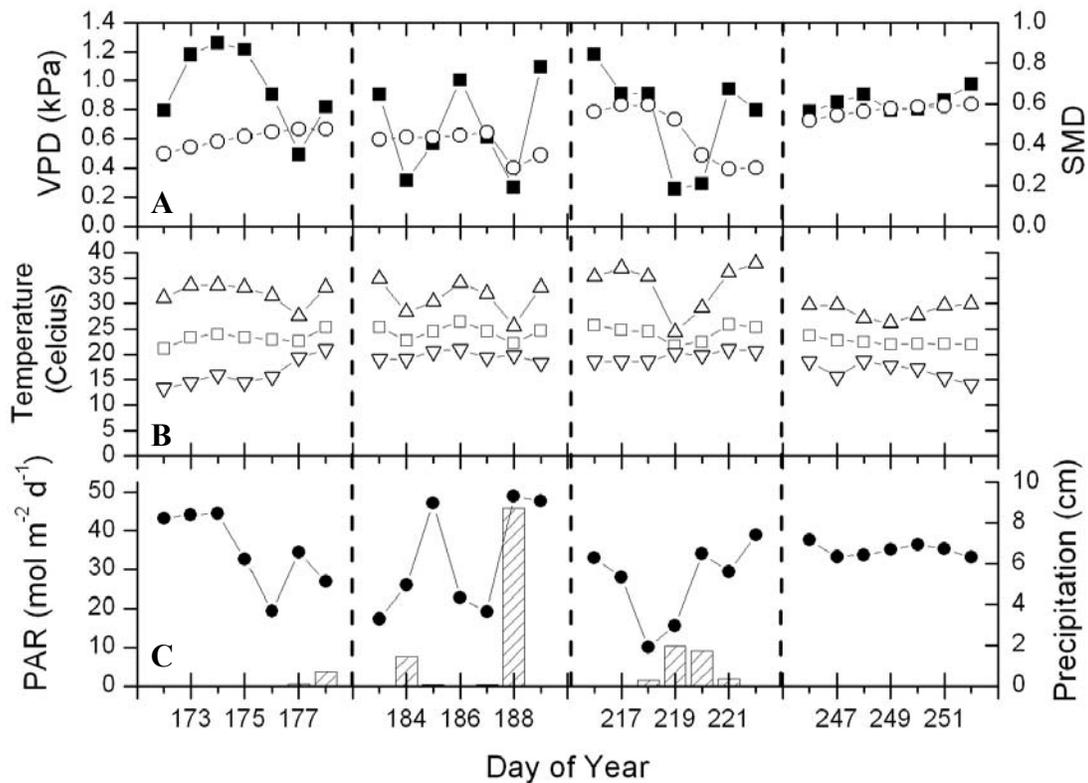


Figure 1. Meteorological data for seven consecutive days per month during the study period. Top panel (A) shows average daily vapor pressure deficit (VPD) (■) and average daily soil moisture deficit (SMD) (○); middle panel (B) depicts maximum (△), average (□), and minimum (▽) daily air temperatures; bottom panel (C) shows daily cumulative photosynthetic active radiation (PAR) (●) and daily cumulative precipitation (bars) (n=96 for all average daily values; vertical broken lines separate each month)

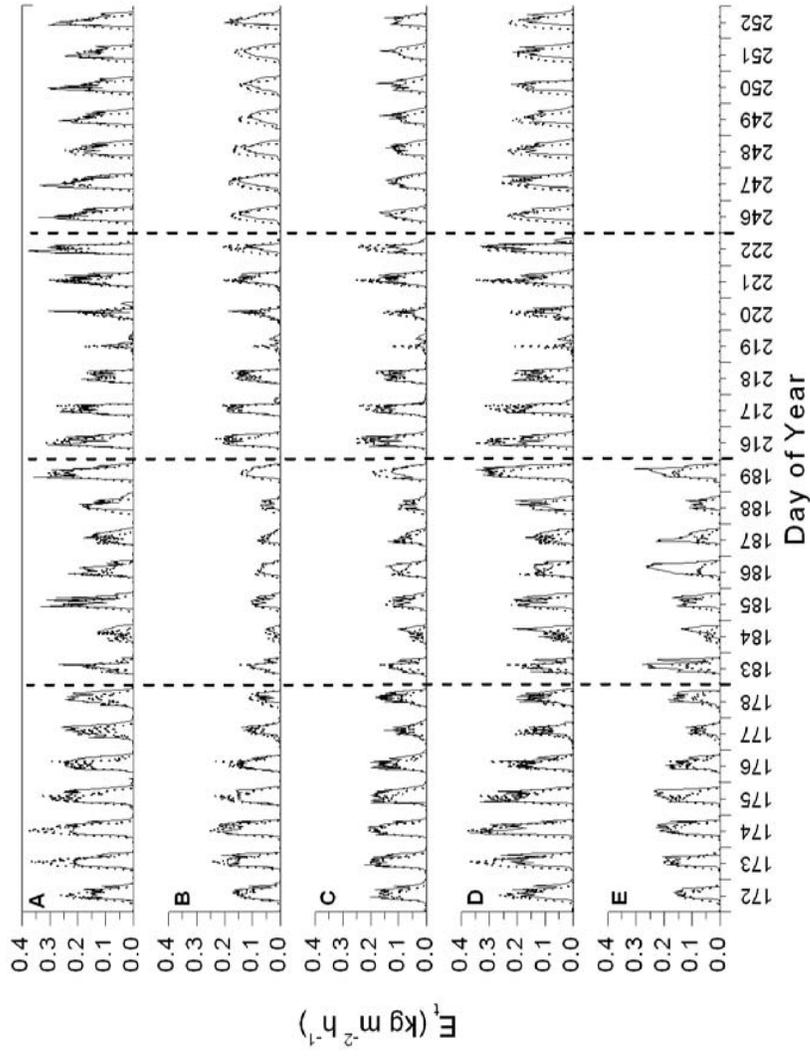


Figure 2. Diurnal time series measured (solid) versus modeled (broken) transpiration (E_t) for five study species over seven consecutive representative days within the months of June-September, 2005. A) *Prunus x yedoensis*; B) *Acer rubrum*; C) *Acer buergerianum*; D) *Prunus serrulata*; and E) *Platanus x acerifolia*.

evaporative demand was relatively minimal throughout the study period and rarely exceeded values above 1.0 kPa.

MAESTRA was originally developed for use on monoculture conifer plantations. All parameters were within the range of values previously reported in other work on hardwood species (Table 2) (Bauerle et al. 2003, Gao et al. 2002, Luo et al. 2001). All five species demonstrate similar seasonal trends for J_{\max} , V_{\max} , and R_d where the maximum values for each parameter occurred in July with exception of *Prunus serrulata*, which reached its highest V_{\max} value in August; however, the V_{\max} value was not significantly different ($\alpha=0.05$) from its July value. *Prunus x yedoensis* also had the same value for R_d in July as in June. The minimum value for stomatal conductance, g_0 , was highest for all measured species in August. The species specific slope parameter for the Ball-Berry stomatal conductance sub-routine, g_1 , remained constant throughout the season for each species.

Model performance was evaluated against measured sap-flow for each study species. Figure 2 and Figure 3 illustrate observed transpiration from sap-flow compared to MAESTRA predicted transpiration on a diurnal basis over twenty-eight days. Figure 2 shows seven consecutive representative days in each study month (June-September), whereas Figure 3 illustrates the strong positive linear correlation on a species basis between the estimated and measured values. Average seasonal percent difference from the model estimates ranged from 6.76 ± 4.46 to -25.99 ± 6.58 for *Prunus serrulata* and *Platanus x acerifolia*, respectively; however, *Acer rubrum* had the highest correlation coefficient ($R = 0.876$) and *Platanus x acerifolia* had the lowest ($R = 0.809$). The percent

Table 2. Physiological parameters for each species and month used in for transpiration predictions in MAESTRA.

Parameter	Month	<i>Prunus x yedoensis</i>	<i>Acer rubrum</i>	<i>Acer buergerianum</i>	<i>Prunus serrulata</i>	<i>Platanus x acerifolia</i>
V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	June	47.38	39.97	44.60	54.55	33.87
	July	74.51	72.77	51.98	68.94	78.61
	August	64.71	61.77	45.67	69.32	---
	September	53.07	49.45	12.02	43.12	---
J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	June	153.00	106.91	105.39	138.18	90.88
	July	239.25	185.43	138.18	196.42	241.60
	August	149.42	166.00	93.36	180.03	---
	September	116.33	175.25	21.29	111.49	---
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	June	2.34	4.04	5.68	5.66	1.36
	July	2.34	9.01	8.44	8.20	4.56
	August	1.00	8.61	6.16	0.72	---
	September	1.25	8.52	7.23	2.09	---
Q_{app} (dimensionless)	June	0.058	0.058	0.080	0.057	0.056
	July	0.076	0.059	0.065	0.082	0.066
	August	0.071	0.060	0.053	0.068	---
	September	0.079	0.069	0.055	0.039	---
Θ (dimensionless)	June	0.816	0.793	0.360	0.891	0.837
	July	0.875	0.972	0.488	0.891	0.878
	August	0.858	0.971	0.986	0.863	---
	September	0.790	0.951	0.945	0.974	---
g_1 ($\text{mol m}^{-2} \text{s}^{-1}$)	June	4.5	6.2	10.0	13.8	13.0
	July	4.5	6.2	10.0	13.8	13.0
	August	4.5	6.2	10.0	13.8	---
	September	4.5	6.2	10.0	13.8	---
g_0 ($\text{mol m}^{-2} \text{s}^{-1}$)	June	0.2309	0.2312	0.0823	0.2326	0.1310
	July	0.2605	0.1588	0.1168	0.2291	0.2098
	August	0.2880	0.2493	0.2106	0.3839	---
	September	0.2598	0.1674	0.0750	0.2134	---

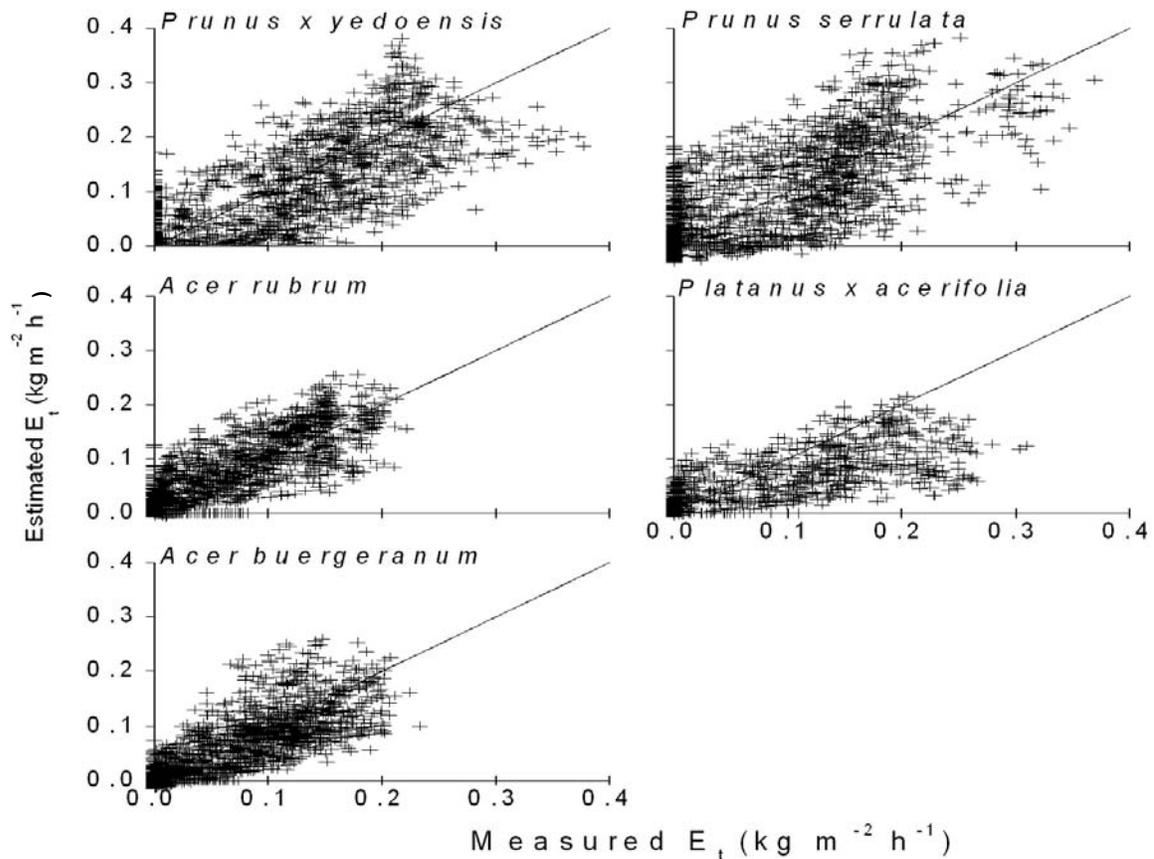


Figure 3. Seasonal correlation between measured and estimated diurnal hourly transpiration (E_t) for the five study species.

differences between mean daily transpiration estimates ($\text{kg m}^{-2} \text{d}^{-1}$) per month and mean daily measured sap flow ($\text{kg m}^{-2} \text{d}^{-1}$) per month ranged from 35% underestimation for *Acer buergeranum* in June to 25% overestimation for *Acer rubrum* in July. *Prunus x yedoensis* had the highest degree of estimation precision with an absolute mean daily percent error of 13%. *Platanus x acerifolia* had the lowest estimation precision with an absolute mean daily percent error of 26%.

Prunus x yedoensis had the highest daily transpiration rate and was the highest water user throughout the study (Table 3; $\alpha=0.05$). No significant differences were detected between both of the *Prunus* spp. until September and all species had similar transpiration rates in August. September resulted in the most difference in species specific water use, separating into three distinct groups (Table 3). *Prunus serrulata* was characterized by similar monthly water use throughout the entire study period.

Differences in seasonal average daily transpiration rates for all five study species are illustrated in Figure 4. *Prunus x yedoensis* had the highest seasonal daily average E_t and was significantly different than *Acer rubrum* ($\alpha=0.05$) and *Acer buergeranum* ($\alpha=0.01$). Interestingly, within the species of *Prunus* and *Acer*, there were no significant differences in seasonal E_t .

Meteorological variables can greatly influence species transpiration rates. Figure 5 illustrates the effect of vapor pressure deficit on transpiration and the species specific separation among transpiration rates. Day 175 had a higher daily average VPD and VPD range, (1.21 ± 0.12 ; $0.02 - 3.31$ kPa) and was significantly different ($\alpha=0.01$) than day 184 (0.32 ± 0.03 ; $0.02 - 1.13$ kPa). Average temperature and PPF were similar on both days and not significantly different ($\alpha=0.01$). Within a species, *Prunus x yedoensis* had the highest transpiration rate at elevated VPD, whereas *Prunus serrulata* was higher at lower VPD (Figure 5). Overall, *Acer rubrum* was most affected by changes in VPD with a 679% reduction in transpiration rate on day 175 compared to 184.

The minimum stomatal conductance parameter, g_0 , was the most sensitive in predicting daily transpiration for all study species (Table 4). No clear seasonal trends in

Table 3. Monthly differences in mean daily transpiration (E_t) \pm standard error for each species and species specific differences (right) in E_t for each month. Means with the same letter are not significantly different at $\alpha=0.05$.

Species	Month	E_t ($\text{kg m}^{-2} \text{d}^{-1}$) \pm se	Month	Species
<i>Prunus x yedoensis</i>	June	1.984 \pm 0.136	June	<i>Prunus x yedoensis</i>
	July	1.369 \pm 0.178		<i>Acer rubrum</i>
	August	1.254 \pm 0.214		<i>Acer buergeranum</i>
	September	1.687 \pm 0.081		<i>Prunus serrulata</i>
<i>Acer rubrum</i>	June	1.220 \pm 0.179	July	<i>Platanus x acerifolia</i>
	July	0.559 \pm 0.097		<i>Prunus x yedoensis</i>
	August	0.925 \pm 0.194		<i>Acer rubrum</i>
	September	1.047 \pm 0.026		<i>Acer buergeranum</i>
<i>Acer buergeranum</i>	June	1.522 \pm 0.134	August	<i>Prunus serrulata</i>
	July	0.866 \pm 0.096		<i>Platanus x acerifolia</i>
	August	0.896 \pm 0.164		<i>Prunus x yedoensis</i>
	September	0.999 \pm 0.036		<i>Acer rubrum</i>
<i>Prunus serrulata</i>	June	1.567 \pm 0.183	August	<i>Acer buergeranum</i>
	July	1.367 \pm 0.235		<i>Prunus serrulata</i>
	August	1.180 \pm 0.194		<i>Platanus x acerifolia</i>
	September	1.306 \pm 0.054		<i>Prunus x yedoensis</i>
<i>Platanus x acerifolia</i>	June	1.373 \pm 0.166	September	<i>Acer rubrum</i>
	July	1.369 \pm 0.223		<i>Acer buergeranum</i>
	August	-----		<i>Prunus serrulata</i>
	September	-----		<i>Platanus x acerifolia</i>

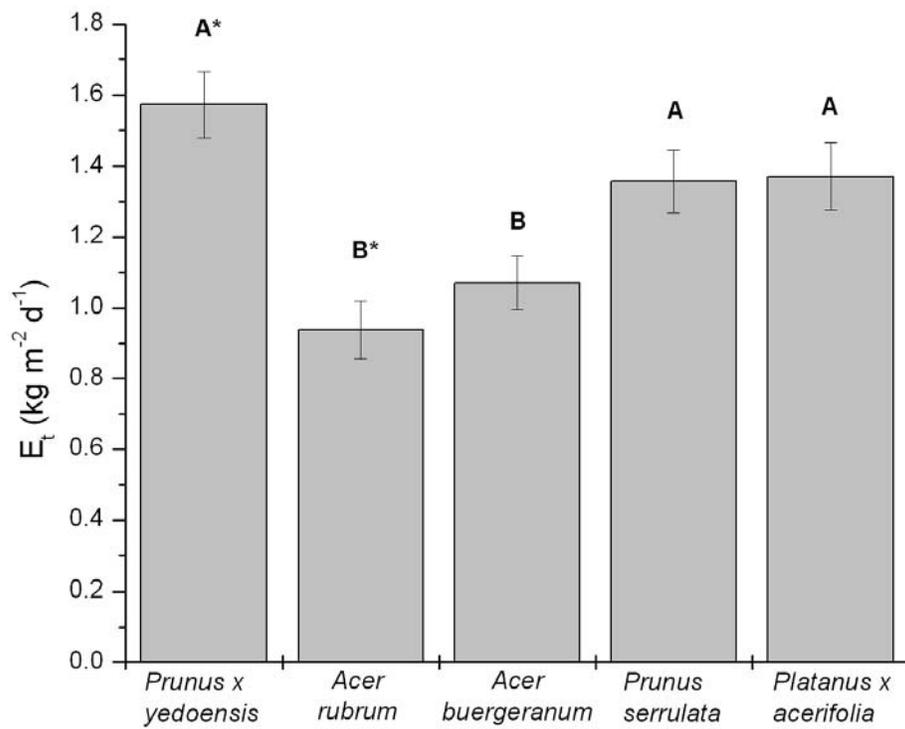


Figure 4. Seasonal mean daily transpiration (n=28) for the five study species \pm standard error. Means with the same letter are not significantly different at 0.05 level of significance (* Indicates $\alpha=0.01$).

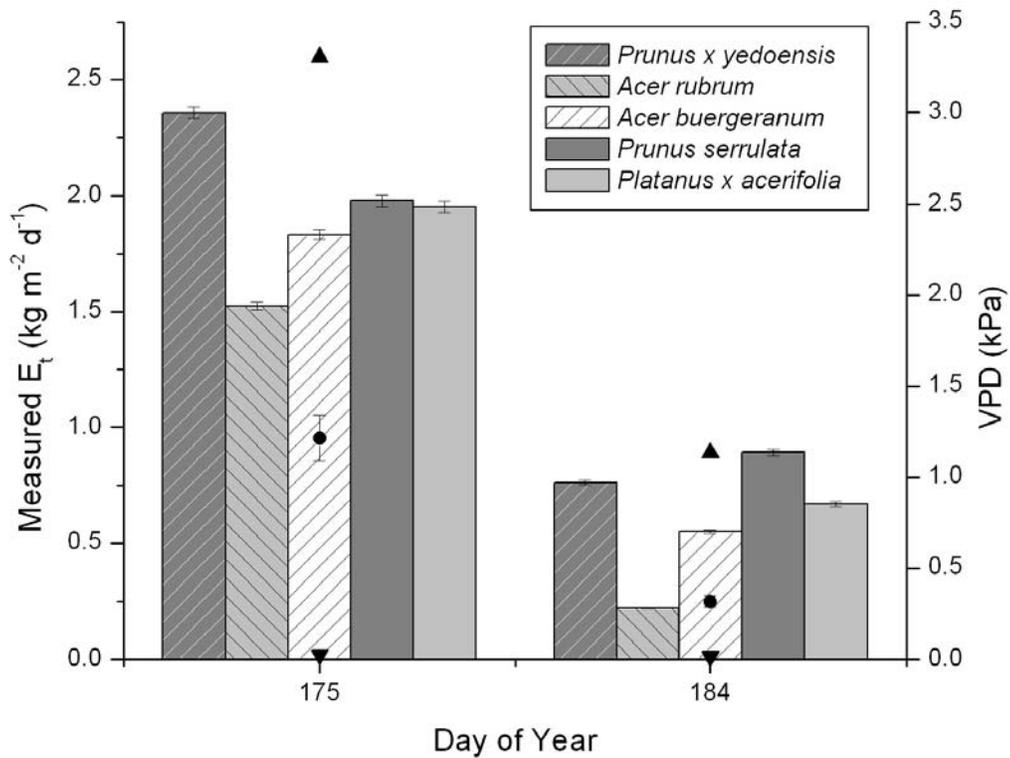


Figure 5. Effect of vapor pressure deficit (VPD) on measured daily transpiration (\pm standard error) for the five study species on two selected days with disparate VPD but similar temperature and PAR (June 24 and July 3). Daily VPD range for each day is shown by maximum (\blacktriangle), minimum (\blacktriangledown), and mean daily VPD \pm standard error (\bullet ; $n=96$) for both days.

Table 4. Sensitivity of physiological parameters on a species basis for June - Sept.

Parameter	Month	<i>Prunus x yedoensis</i>	<i>Acer rubrum</i>	<i>Acer buergerianum</i>	<i>Prunus serrulata</i>	<i>Platanus x acerifolia</i>
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	June	0.005	0.005	0.045	0.033	0.039
	July	0.001	0.001	0.005	0.015	0.023
	August	0.002	0.002	0.008	0.007	---
	September	0.008	0.008	0.007	0.049	---
Q_{app} (dimensionless)	June	0.006	0.006	0.037	0.023	0.065
	July	0.001	0.001	0.003	0.013	0.055
	August	0.002	0.002	0.004	0.091	---
	September	0.009	0.009	0.010	0.091	---
Θ (dimensionless)	June	0.002	0.002	0.005	0.023	0.035
	July	0.000	0.000	0.001	0.007	0.021
	August	0.001	0.001	0.008	0.008	---
	September	0.004	0.004	0.005	0.027	---
g_1 ($\text{mol m}^{-2} \text{s}^{-1}$)	June	0.017	0.001	0.006	0.007	0.032
	July	0.037	0.000	0.000	0.001	0.012
	August	0.023	0.000	0.001	0.032	---
	September	0.037	0.002	0.007	0.049	---
g_0 ($\text{mol m}^{-2} \text{s}^{-1}$)	June	0.241	0.231	0.491	0.280	0.233
	July	0.139	0.263	0.369	0.255	0.245
	August	0.170	0.202	0.267	0.119	---
	September	0.255	0.333	0.552	0.283	---

parameter sensitivity were found except for g_0 , which had the highest importance in predicting daily transpiration rates for all species in September. *Acer buergeranum* had the highest seasonal average g_0 importance level, where every one percent change in the g_0 parameter resulted in a 42 percent change in transpiration.

The g_0 parameter had a dramatic effect on *Prunus x yedoensis* transpiration estimates in June across a spectrum of soil moisture deficits (Figure 6A). Higher g_0 values increase the transpiration rate within a species on the non-moisture limiting portions of the curve; however, the effect of declining soil moistures is reduced at higher values. All species show similar trends as *Prunus x yedoensis* in response to higher g_0 values. Differences in transpiration rates among species were significantly affected with changes in g_0 (Fig. 6B and 6C). g_0 values of $0.25 \text{ mol m}^{-2} \text{ s}^{-1}$ separate species into two different groups of water use with lowest rates of transpiration in *Platanus x acerifolia* (Fig. 6B). When the g_0 value is reduced to $0.005 \text{ mol m}^{-2} \text{ s}^{-1}$ two distinct groups of water use also emerge; however, under these circumstances *Platanus x acerifolia* exceeds the transpiration rates of three species but is not significantly different from *Prunus x yedoensis*, the highest water user.

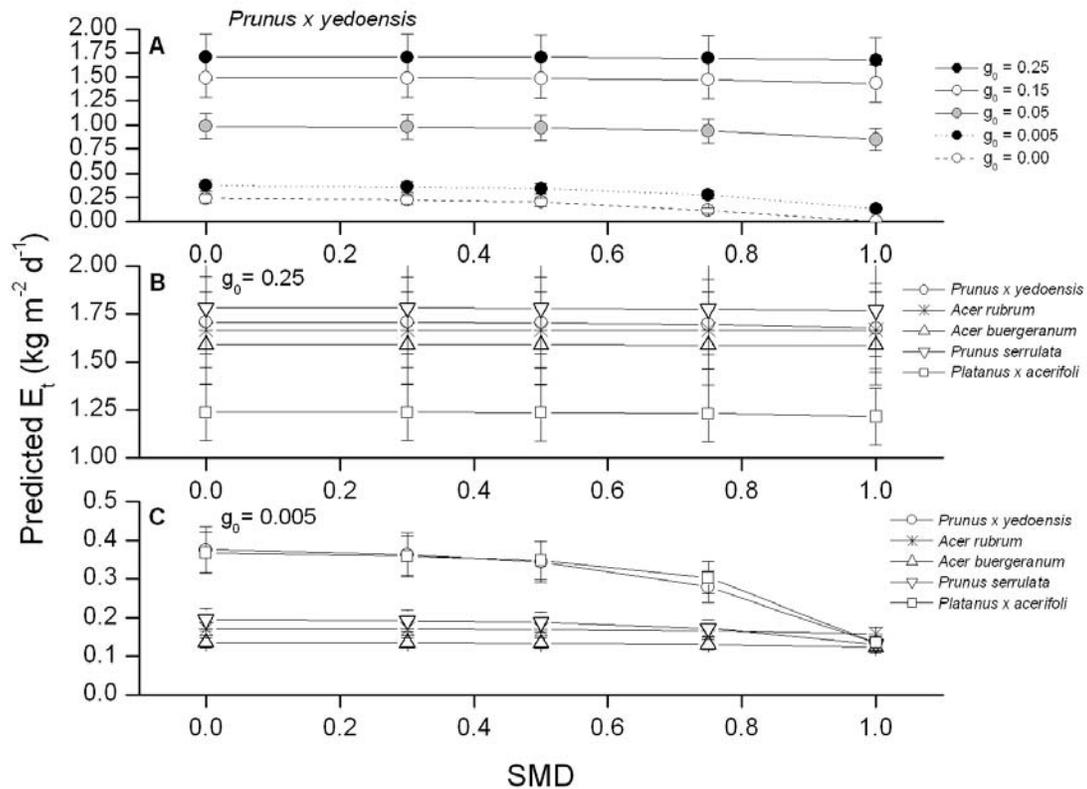


Figure 6. Effect of different g_0 values at varying soil moisture deficits (SMD) on predicted mean daily transpiration \pm standard error ($n=96$). Top panel (A) shows *Prunus x yedoensis* at five levels of g_0 , middle panel (B) compares all five study species at $g_0 = 0.25 \text{ mol m}^{-2} \text{ s}^{-1}$, and (C) depicts all five study species at $g_0=0.005 \text{ mol m}^{-2} \text{ s}^{-1}$. The y-axis scale among panels is specifically not uniform to separate both the influence of g_0 and species.

DISSCUSSION

Changes in climate affect species existence and distributions directly through specific interactions with the environment and indirectly through changes in population dynamics (e.g. herbivory, competition, etc.) (Hijmans and Graham 2006). Species distribution models (SDM) are used to predict geographic shifts in species distribution in response to climate changes. These models are limited by the future climate predictions used in the model as well as understanding how species respond to different environmental variables, therefore, quantifying differences in species specific responses such as transpiration will aid species distribution modeling (Pearson and Dawson 2003).

The climate change rate will be a large determinate of survival, however, the plasticity of a species also will greatly influence its existence. Although single variable predictions of species distribution in response to climate change do not capture the true complexity of their occurrence, it is likely that *Acer rubrum* will survive increases in temperature and changes in water distribution due to its naturally variable genotypic population (Bauerle et al. 2003, Bauerle et al. 2004a, Bauerle et al. 2007). *Acer rubrum* had the lowest mean daily transpiration rate in this study under non-stress conditions indicating its conservative approach to resource utilization.

The results of this study clearly demonstrate that differences in species specific transpiration can be accounted for with the MAESTRA model. Moreover, the physiological parameters, which are responsible for accounting for underlying species specific differences, allow it to predict transpiration in a physiologically diverse hardwood plantation. While there have been numerous reports on diurnal 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, Kosugi et al. 2003, Bunce 2004), transpiration among functional groups (i.e. pines, broad-leaf, shrubs, etc.) (Gao et al. 2002), and whole tree transpiration (Wullschleger et al. 1998, Wullschleger et al. 2001, Misson et al. 2002, Sinclair et al. 2005), a review of the literature reveals that few experiments have quantified species specific differences in diurnal transpiration that is standardized by leaf area and environment. Other important issues, such as the prediction of transpiration among species, have received relatively little attention.

On 89% of the 28 study days, we report differences in species specific mean hourly and daily diurnal transpiration per unit leaf area ($\alpha = 0.05$). Although all five species in this experiment had mean tree heights and diameters less than the 67 species reviewed by Wullschleger et al. (1998), *Acer rubrum*, *Prunus serrulata*, and *Platanus x acerifolia* each had mean daily whole tree transpiration rates greater than $10 \text{ kg tree}^{-1} \text{ d}^{-1}$ - the minimum daily whole tree transpiration value reported by Wullschleger et al. (1998). *Prunus x yedoensis* and *Acer buergeranum*, on the other hand, had mean daily whole tree rates that were slightly less (9.29 and $6.69 \text{ kg tree}^{-1} \text{ d}^{-1}$) at mean tree heights of 3.64 m and 2.67 m , respectively. In fact, *Prunus x yedoensis* had the highest mean daily diurnal transpiration rate at $1.54 \text{ kg m}^{-2} \text{ d}^{-1}$ which was 68% higher than the lowest species (*Acer rubrum*, $0.92 \text{ kg m}^{-2} \text{ d}^{-1}$) in the study. *Prunus serrulata*, however, achieved the highest seasonal maximum daily diurnal transpiration rate per unit leaf area ($2.72 \text{ kg m}^{-2} \text{ d}^{-1}$ on

day 189). To our knowledge, transpiration rates for our study species, other than *Acer rubrum* have not been reported elsewhere.

Differential rates of mean daily diurnal water use were not detected on three consecutive days in August, 216 – 218, where soil moisture deficits were between 21% and 30% higher than the mean daily soil moisture deficit in the study. The driest soil moisture conditions throughout the season were observed on day 217 ($0.63 \text{ cm}^3/\text{cm}^3$). Additionally, mean daily diurnal deficits in atmospheric vapor pressure for the three consecutive days were higher than seasonal mean daily diurnal vapor pressure deficit. The stomata closure threshold in response to elevated vapor pressure deficits (2.0 kPa) reported for *Prunus dulcis* grown in Spain (Romero and Botia 2006) was higher than the mean daily diurnal vapor pressure deficit for each day, 216 – 218. These data indicate that differences among species in mean daily diurnal transpiration will become negligible as soil moisture deficit increases below some critical level (Sinclair et al. 2005). It is of considerable interest however, that while reductions in transpiration are commonly observed when soil moisture becomes limiting, increased vapor pressure deficit can still cause substantial transpiration rates as long as the paired stresses are not beyond a species specific threshold which causes stomata closure (Bond and Kavanagh 1999).

Most species have some type of feedback mechanism which regulates stomata as VPD increases in an attempt to reduce water loss and/or embolism (e.g. chemical, hydraulic, or both). Though the feedback sensitivity and magnitude are not uniform across species (Oren et al. 1999, Bond and Kavanagh 1999), all species in our study had a strong positive correlation ($r > 0.73$) between mean daily diurnal transpiration and VPD. In

fact, significant increases ($\alpha=.05$) in diurnal daily transpiration rates occurred when VPD increased significantly ($\alpha=.05$, Fig. 6) but other environmental variables were held constant (i.e. PAR, Tair, SMD). Interestingly, due to the species VPD response differences, we witnessed a species-specific increase in transpiration.

Currently genomic techniques are not capable of being incorporated into models that quantify hardwood specific transpiration. However, physiologically based models are a mechanistic means of quantifying inherent responses and have shown to be capable of modeling species specific differences in transpiration. The mechanistic use of genetically inherent physiological traits, thus allow them to characterize the species specific environmental response (Kosugi et al. 2003). Similarly, empirical models indirectly capture the physiology response of species with response parameters. MAESTRA combines these two approaches with multiple leaf level sub-models (e.g. Farquhar and von Caemmerer photosynthesis and Ball-Berry stomatal conductance model) to account for the interactions between physiological phenomena and environmental stimuli in predicting differences in species transpiration. We found that the ability to capture species specific differences in a modeling environment is directly related to the measured variation in specific physiology. In other words two species with identical physiological profiles will transpire similarly at equal size (i.e. height, leaf area, leaf area distribution, etc.) under the same environmental conditions. Ultimately, process models such as MAESTRA separate species by their physiological function and not by arbitrary taxonomic or ecological terms.

Sensitivity analyses are commonly utilized to test the effects different parameters have on prediction, this study is the first to report the sensitivity of MAESTRA model parameters that influence transpiration prediction. A similar analysis has been conducted for the MAESTRA model but for gross primary production (Luo et al. 2001). We found that the minimum value of stomatal conductance, g_0 , was the most sensitive parameter for all months and species, and was the only physiological parameter which effected transpiration by more than 5%. The connection between leaf conductance and transpiration is consistent with the mechanics of stomatal regulation of water loss.

Although changes in g_0 had the greatest effect on transpiration estimates, only recently has this empirical parameter begun to receive attention in the literature. In fact, it is reported in an indirect fashion at the species level as dark transpiration (Daley and Phillips 2006, Marks and Lechowicz 2007, Kavanagh et al. 2007). In MAESTRA, increases in g_0 , within a biologically relevant range cause increases in hourly diurnal transpiration for all species across the array of soil moisture deficits. MAESTRA, however, uses light as the major driving factor behind transpiration and currently does not account for dark transpiration.

While it is well known that water management is essential for the survival and growth of crops, unfortunately little information is available on woody ornamental water use (Bauerle et al. 2002). Few studies in the ornamental literature have provided any accurate, long-term water or nutrient-use efficiency data. To date, irrigation of ornamentals tends to be excessive, and water and nutrient use is very inefficient (Bauerle et al. 2002; Bilderback 2002). If the nursery and landscape industry expects to counter

legislation that restricts water use, it is imperative that they are able to quantify and document the water use requirements of ornamentals in both nursery and landscape situations. Our study, therefore, provides a first step towards quantification of water use in ornamentals.

On a national level, recent federal water management regulations are increasing awareness of inefficient water applications in the United States, particularly when plants are grown in intensive, out-of-ground container-nursery and greenhouse operations. Much of the water applied through overhead irrigation systems falls between containers and drip or micro irrigation can cause nutrient leaching which contributes to non point source nutrient runoff (Environmental Protection Agency, 2004). The economic, environmental and social benefits of improving and protecting water sources are substantial. The situation has placed the grower in a position to preemptively address the critical need to accurately quantify water use for nursery and landscape situations, and to document water use requirements of plant material in both the nursery and landscape setting.

CONCLUSION

In conclusion, differences in hourly and daily diurnal transpiration were found in five deciduous hardwood species on 89% of the study days in the 2005 growing season. The differences in growth and species specific physiology were paired with meteorological data in a three dimensional spatially explicit model, MAESTRA, to estimate differences in transpiration for each species. Model estimates were accurate and had acceptable precision due to the detailed model parameterization and inclusion of individual physiological characteristics. While several methods exist for predicting transpiration using the water balance equation, this study indicates the significance of species specific transpiration differences and MAESTRA's ability to estimate them at scales of the whole tree, stand, and watershed.

The dark stomatal conductance parameter, g_0 , was highly sensitive to small percent changes in parameter values suggesting the importance of its precise measurement. In addition, this and other parameters change across the season and it is important to capture their seasonal variation when attempting to predict transpiration across the season. Moreover, the variation indicates a need to further investigate the variation of the Ball-Berry stomatal conductance model parameters and the physiological basis of the species specific differences. Although there is evidence that a combination of small scale perturbations can cause divergence in species specific water use, this work indicates that the species variation in stomatal regulation under similar environmental conditions are the source of the difference in transpiration among species.

APPENDICES

Appendix A

Soil moisture and precipitation

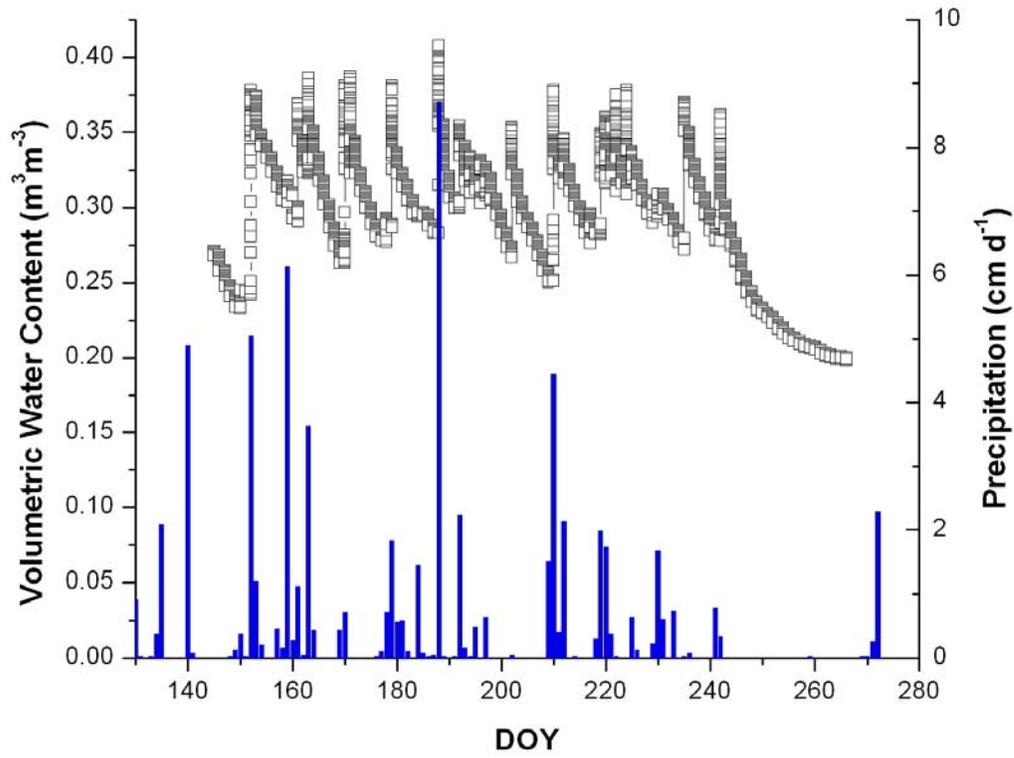


Figure 7. Daily precipitation (bars; cm d⁻¹) and mean daily volumetric soil moisture content (□; m³ m⁻³) during the 2005 growing season.

Appendix B

Modeling transpiration at small time scales

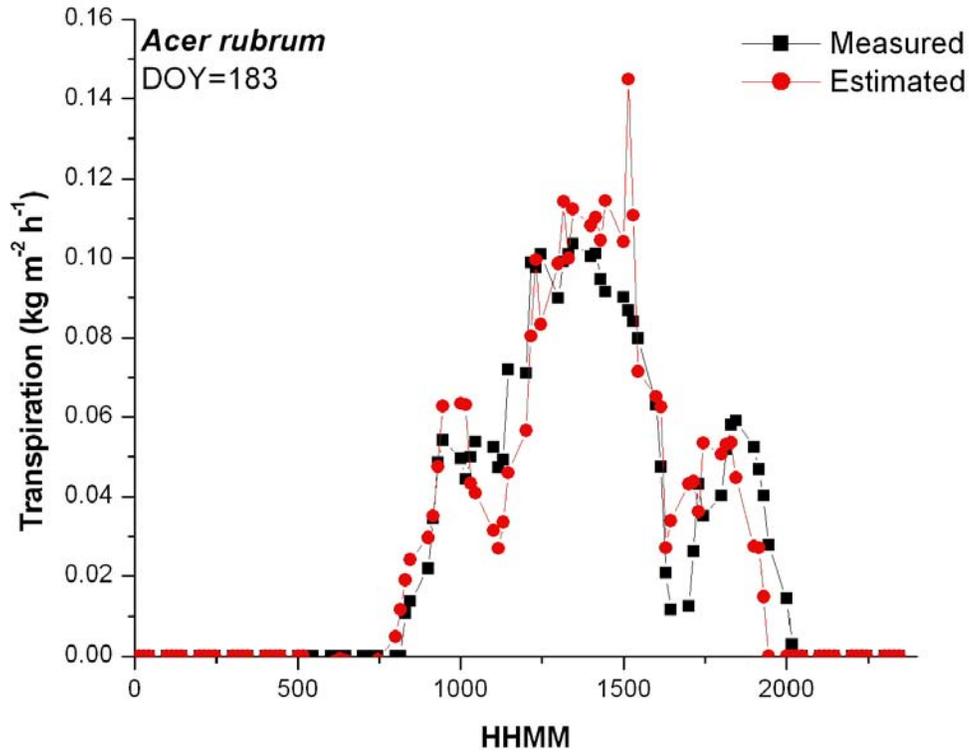


Figure 8. A representative day (183) between measured transpiration ($\text{kg m}^{-2} \text{h}^{-1}$) and MAESTRA estimated transpiration ($\text{kg m}^{-2} \text{h}^{-1}$) for *Acer rubrum* on an hourly time step (HHMM=hour minutes)

Appendix C

Seasonal mean sensitivity of model parameters

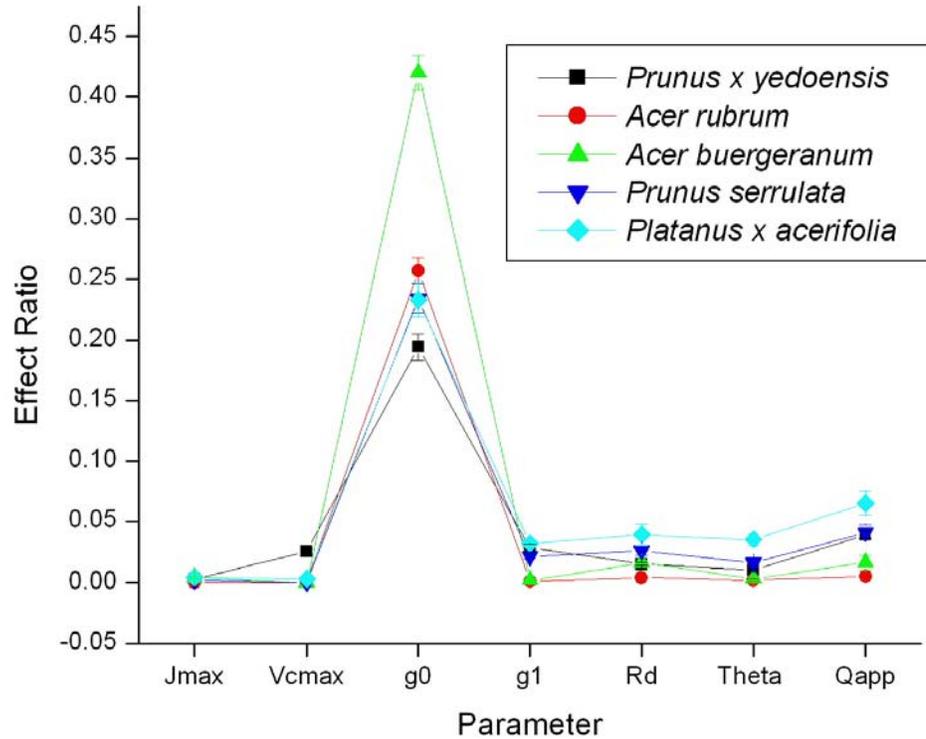


Figure 9. Seasonal mean effect ratio of the maximum rate of electron transport (J_{max}), maximum rate of carboxylation (V_{cmax}), empirical slope coefficient of the Ball-Berry equation (g_0), empirical intercept coefficient of the Ball-Berry equation (g_1), dark respiration (R_d), curvature of the light response (θ), and quantum efficiency (Q_{app}) for all five study species.

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