Predicting Transpiration Response to Climate Change: Insights on Physiological and Morphological Interactions that Modulate Water Exchange from Leaves to Canopies

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Abstract. Leaves are key factors in the global water exchange cycle. As the primary control interface involved in regulating water loss, understanding the relative influence of leaf morphological and physiological transpiration factors is critical to accurate evapotranspiration predictions. We parameterized a three-dimensional array model, MAESTRA, to establish a link from the leaf to canopy scale and attempted to isolate and understand the interplay among variation in morphological and physiological variables affecting transpiration. When physiological differences were accounted for, differences in leaf width (L_w) among *Acer rubrum* L. genotypes significantly affected leaf temperature and transpiration under slow to moderate wind velocities. In instances, L_w variation among genotypes resulted in a 25% difference in transpiration. This study demonstrates how simple morphological traits like L_w can provide useful selection criteria for plant breeders to consider in a changing climate.

The boundary layer governs the diffusion of gases between vegetation and the atmosphere at the leaf and whole crown scale. Although Prandtl is credited with the introduction of boundary layer theory in 1904 (Schlichting and Gersten, 2004), the first leaf model incorporating physically based boundary layer concepts was not introduced until 52 years later (Raschke, 1956). Raschke's pioneering work identified the influence of leaf size (e.g., leaf width) on the leaf energy budget through sensible heat and water exchange; however, consideration for boundary layer effects on the diffusion pathway of the leaf waxed and waned thereafter (Schuepp, 1993). Nonetheless, leaf size and within-crown spatial distribution affect the boundary layer conductance of the canopy and are a key element in modulating the soil–plant–atmosphere water transport process at the earth's surface (e.g., Monteith and Unsworth, 2008).

The thickness of the boundary layer interacts with stomatal conductance (g_s) to control transpiration. At scales larger than the leaf, however, the boundary layer control on transpiration can become more important than genotype-specific stomata expressions. For example, it is commonly accepted that under ventilated conditions at the leaf surface, stomata control transpiration in response to vapor pressure deficit (VPD) (e.g., Bunce, 1985; Katul et al., 2009). In contrast, it is the thickness of the boundary layer that often controls transpiration at the stand scale, a consequence of environment and canopy structure interactions (Hinckley et al., 1994; Jarvis and McNaughton, 1986; Meinzer et al., 1995). Thus, there remains a need to understand the relative interaction between canopy controls over water loss and how leaf morphology and physiology scale up to whole plant and canopy scales (Monteith, 1989).

Our objective was to assess the transpiration response among genotypes of a common horticulture tree crop through investigation of the leaf-to-atmosphere microclimate interactions in a changing climate. We used a three-dimensional spatially explicit individual plant process model, MAESTRA (Multi-Array Evaporation Stand Tree Radiation A) (Wang and Jarvis, 1990) to investigate and separate the contributions of morphological and physiological transpiration parameters in leaf and canopy scale transpiration predictions. We parameterized the model on a genotype-specific basis from measurements on commercially available *Acer rubrum* L. (red maple) cultivars. We tested the hypothesis that variation in L_w within red maple considerably modified boundary layer conductance, leaf temperature, and transpiration aside from physiological differences.

MATERIALS AND METHODS

Site and plant material. Measurements were taken on South Carolina grown red maple cultivars ['Summer Red' (SR), 'October Glory' (October Glory®) (OG), 'Autumn Flame' (AF), and 'Franksred' (Red Sunset®) (RS) and one Freeman maple cultivar, Jeffersred (Autumn Blaze®) (AB) and used to parameterize MAESTRA. Plants were grown in 114-L Spin Out-treated plastic pots containing a mixture of 20:1 pine bark to sand (by volume) fertilized with 8.3 kg·m^{-3} of Nutricote™ 20N–3.0P–8.3K Type 360 (Chisso-Asahi Inc., Tokyo, Japan) on an outdoor gravel pad. Trees were placed in a completely randomized design and spaced 1.5 m center to center in rows 1.5 m apart. The continuous stand consisted of ≈3 m tall equal age saplings of five genotypes (n = 20 trees per genotype). Each tree was watered three times daily to near container capacity with 360° pressure compensating micro-emitters (ML Irrigation Inc., Laurens, SC). Substrate volumetric water content was monitored daily in each container at 10 cm and 20 cm below the substrate surface in four pre-drilled locations on opposite sides of the container (Theta Probe Type ML2; Delta- T Devices, Cambridge, UK) to verify that root zone volumetric water content was maintained within a previously determined well-watered range (0.4 to 0.5 m^3·m^{-3}).

Measurements of leaf-level and whole tree morphology and physiology. Leaf physiology was quantified using a portable steady-state gas exchange system (CIRAS-I; PP Systems Inc., Amesbury, MA); cuvette conditions were controlled at 25 °C air temperature, 1.3 kPa VPD, saturating photosynthetic photon flux (1000 μmol·m^{-2}·s^{-1} or greater), and varied carbon dioxide (CO_2) levels. Photosynthetic activity was assessed by constructing net photosynthesis versus intercellular CO_2 concentration curves from which maximum carboxylation rates (μmol·m^{-2}·s^{-1}) and maximum electron-transport rates (μmol·m^{-2}·s^{-1}) were estimated. Leaf reflectance and transmittance were estimated with a SPAD meter for quantum yield calculations (Model 502 Minolta Camera Inc., Ramsey, NJ). Detailed descriptions of leaf-level morphology and physiology have been described in Bauerle et al. (2003, 2007). Whole-tree morphology and physiology are as described in Bauerle et al. (2009).

Model description. MAESTRA is a three-dimensional process-based model that computes transpiration, photosynthesis, and absorbed radiation within individual tree crowns. Specific to this study, a modified version previously validated to estimate deciduous tree transpiration (Bauerle et al., 2002; Bowden and Bauerle,

2008) and within-crown light interception (Bauerle et al., 2004) was used. Each genotype's leaf physiological and morphological difference was parameterized with clonal-specific parameters. During the scaling process, MAESTRA scaled up leaf-level biochemical and energy balance properties that were linked with stomatal gas regulation both spatially and temporally (Bowden and Bauerle, 2008). This characteristic was also used to scale up genotype-specific transpiration (E) responses and to analyze the physiological and morphological regulation of E among genotypes. A full description of the model is beyond the scope of this article; however, detailed descriptions and references to model components can be found in Emhart et al. (2007) and Reynolds et al. (2009).

Model validation tests. Predicting leaf to whole crown transpiration (Bauerle et al., 2002, 2009; Bowden and Bauerle, 2008), within-crown light interception (Bauerle et al., 2004), and whole-tree CO_2 exchange (Reynolds et al., 2009) with MAESTRA has been previously demonstrated in red maple cultivars.

Separating the morphologic versus physiologic leaf and canopy transpiration factors. MAESTRA was used to scale up leaf transpiration to the whole crown of a simulated 20-m tall mature deciduous canopy. The canopy was vertically stratified into 10 equal layers (2-m depth per layer) and g_s was estimated according to the Leuning (1995) submodel. We evaluated the vertical effects of horizontal wind speed, air temperature, and L_w on canopy transpiration profiles when forced convection is present. We held genotype physiological and morphological parameters constant at the mean (Table 1) and varied L_w. Simulations were conducted using the minimum and maximum L_ws (SR: 3.98 cm versus AB: 10.18 cm) at two different growth temperatures (20 versus 35 °C) to assess within-species L_w effects on transpiration. In addition, genotype-specific transpiration response curves were created from polynomial regressions over a range of possible broadleaf plant L_ws at genotype-specific physiology parameters reported in Table 1.

RESULTS

Simulated effects of air temperature, wind speed, and leaf width within the canopy. At moderate to slow canopy surface wind velocity (5 m·s^{-1} or less), L_w has greater influences on transpiration under higher (35 °C as opposed to 20 °C) air temperature conditions; however, L_w effects on transpiration are diminished in the upper portions of the canopy as air temperature decreases (Fig. 1A). The same holds true at slower wind velocities (0.2 m·s^{-1} or less), except, at lower air temperatures leaves with a smaller L_w still transpire more at all canopy depths (Fig. 1). The difference between a 5 m·s^{-1} versus 0.2 m·s^{-1} wind velocity at the canopy surface can cause transpiration to increase by ≈0.75 mmol·m^{-2}·s^{-1} (compare Figs. 1A and 1B). However, regardless of air temperature, L_w effects on transpiration are greater at lower wind speeds (compare Figs. 1A and 1B).

Table 1. Species mean (n = 5 ± SE of genotypes with genotypic range; each genotype value was derived from the mean of five replicate trees) parameter values used in MAESTRA.

Parameter and units	Mean	Range
L_t (%)	4.69 ± 0.23	1.21
L_r (%)	8.97 ± 0.25	1.39
L_w (cm)	7.48 ± 0.96	6.2
W_e (dimensionless)	1.0 ± 0.04	0.2
θ (dimensionless)	0.908 ± 0.01	0.09
J_{max} (µmol·m^{-2}·s^{-1})	175.22 ± 10.41	64.73
E_j (J·mol^{-1})	52,080 ± 802.69	6200
τ_j (K^{-1}·mol^{-1})	639 ± 0.52	3
α (mol e– mol^{-1} PAR$_a$)	0.2502 ± 0.01	0.0628
V_{cmax} (µmol·m^{-2}·s^{-1})	69.06 ± 2.57	15.76
E_v (J·mol^{-1})	52,040 ± 1,832.29	10,300
R_d (µmol·m^{-2}·s^{-1})	3.58 ± 0.15	0.94
Γ (µmol·m^{-2}·s^{-1})	99.64 ± 2.51	15.18
g_1 (mol·m^{-2}·s^{-1})	6.41 ± 0.35	1.96
g_o (mol·m^{-2}·s^{-1})	0.0426 ± <0.00	0.013

Parameter abbreviations: L_t = leaf PAR transitivity; L_r = leaf PAR reflectance; L_w = leaf width; W_e = wind speed extinction coefficient; θ = convexity parameter of the light response; J_{max} = the maximum electron transport rate; E_j = activation energy temperature response of J_{max}; τ_j = entropy term in temperature response of J_{max}; α = absorbed PAR – PAR$_a$ = quantum yield of electron transport; V_{cmax} = the maximum rate of carboxylation; E_v = activation energy temperature response of V_{cmax}; Γ = carbon dioxide compensation point; R_d = dark respiration; g_1 = genotype slope coefficient; g_o = minimum stomatal conductance.
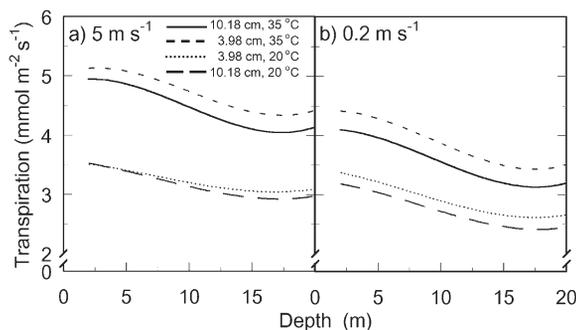

Fig. 1. Vertical depth from the canopy surface versus predicted transpiration profiles as a function of air temperature and leaf width (L_w) at two canopy surface wind speeds: (**A**) 5 m·s^{-1} and (**B**) 0.2 m·s^{-1}. Transpiration is calculated for two different air temperatures and L_w where the solid line depicts a 10.18-cm L_w at 35 °C, the line with short dashes is 3.98 cm L_w at 35 °C, the line with long dashes is 10.18 cm L_w at 20 °C, and the dotted line is 3.98 cm L_w at 20 °C. Simulations were conducted under constant conditions of relative humidity = 60% and photosynthetic photon flux = 1500 µmol·m^{-2}·s^{-1} at a leaf area index = 1.

Relationship among leaf width, leaf minus air temperature, horizontal wind speed, and transpiration. The model was used to assess the influence of horizontal wind speed on the distribution of transpiration along a vertical canopy depth profile at three different leaf area indexes (LAIs) and two different air temperatures using the narrowest and widest L_ws among the five genotypes. The simulation showed the impact of changes in LAI and how the leaf–air temperature difference is lowered as wind speed increases (compare Figs. 2A–C and 2D–F). As a result of elevated temperature effects on VPD and wind speed effects on boundary layer conductance, transpiration increased with temperature and wind speed. Faster wind velocities also increased leaf heat dissipation rates. Hence, L_w effects on the leaf–air temperature difference were larger at lower wind speeds and elevated temperature (compare Figs. 2C and 2F). Clearly, these differences illustrate L_w and within-canopy depth effects on transpiration at contrasting air temperatures but

identical physiological profiles (Fig. 2). The transpiration differences among changes in canopy position, LAI, and L_w effects on leaf–air temperature differences and subsequent effects on long wave re-radiation as a function of leaf temperature, in which the divergent L_ws in red maple caused ≈25% difference in transpiration at wind speeds of ≈5 m·s^{-1} and thus a more efficient heat transfer in the smaller leaf (compare Fig. 2 and Fig. 3). Figure 3 further illustrates that the leaf–air temperature difference and, hence, loss of long-wave radiation by the leaves is non-linearly related to wind speed.

Effects of genotype morphology and physiology on the transpiration within a crown. The transpiration responses to changes in L_w were unique to each genotype across a range of simulated L_w sizes (Fig. 4). The genotype with the smallest L_w (SR) transpired more water than the genotype with the largest (AB) under identical environmental conditions (Fig. 4). Under inherent morphology and physiology conditions, SR was estimated to transpire
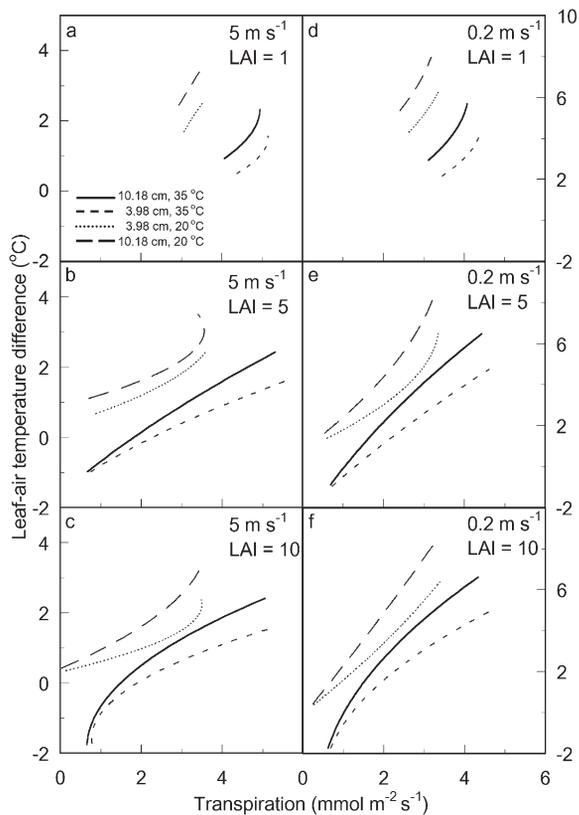
Fig. 2. Predicted transpiration crown profiles as a function of air temperature and leaf width (L_w) versus the predicted leaf temperature to measured air temperature difference at two different wind speeds and three canopy leaf area index (LAI) values. (**A–C**) Wind speed = 5 m·s⁻¹ and (**D–F**) 0.2 m·s⁻¹. (**A, D**) LAI = 1, (**B, E**) = 5, and (**C, F**) = 10 at constant environmental conditions (relative humidity = 60% and photosynthetic photon flux = 1500 μmol·m⁻²·s⁻¹). Transpiration is calculated for two different temperatures and L_w where the solid line depicts a 10.18 cm L_w at 35 °C, the line with short dashes is 3.98 cm L_w at 35 °C, the line with long dashes is 10.18 cm L_w at 20 °C, and the dotted line is 3.98 cm L_w at 20 °C. Please note differences in y-axis scale between **A–C** versus **D–F**.
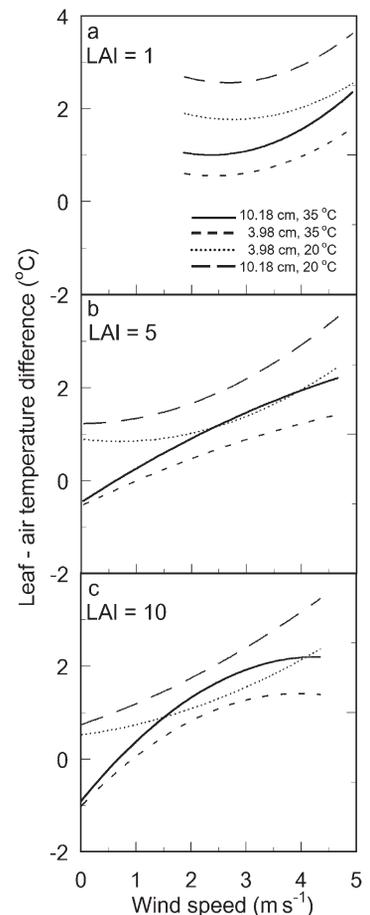

Fig. 3. Predicted leaf temperature to measured air temperature difference crown profiles as a function of wind speed, air temperature, and leaf width (L_w) at three different canopy leaf area index (LAI) values. (**A**) LAI = 1, (**B**) = 5, and (**C**) = 10 at constant environmental conditions (relative humidity = 60% and photosynthetic photon flux = 1500 μmol·m⁻²·s⁻¹). Leaf temperature to measured air temperature difference is calculated for two different air temperatures and L_w in which the solid line depicts a 10.18-cm L_w at 35 °C, the line with short dashes is 3.98 cm L_w at 35 °C, the line with long dashes is 10.18 cm L_w at 20 °C, and the dotted line is 3.98 cm L_w at 20 °C.

≈2 mmol·m⁻²·s⁻¹ more than AB. However, when the SR L_w was increased to match that of AB, the physiological variation between genotypes indicated that transpiration remains ≈1.5 mmol·m⁻²·s⁻¹ greater in SR as compared with AB (Fig. 4). Although physiological factors appear to add to the greater transpiration in SR as compared with AB at equal L_w, L_w differences alone cause an additional 25% increase/decrease in SR versus AB transpiration under moderate wind speed conditions (≈5 m·s⁻¹). Alternatively, other genotypes converge to approximate equal transpiration rates when L_w is uniform (e.g., cv. AF and RS). Thus, the genotypes AB, RS, and OG illustrate the phenomenon termed equifinality (Franks et al., 1997) in that a similar simulation result can be achieved with different parameter combinations. Nonetheless, the simulation results illustrate that physiological parameters can counterbalance morphological and vice versa to yield similar transpiration estimates.

DISCUSSION

Our model results indicate that the aerodynamic and physiological controls on transpiration interact. Model simulations showed that variation in physiological attributes can counterbalance morphological transpiration controls (Fig. 4). Alternatively, morphology

and physiology attributes can work in the same direction to elevate or depress transpiration (e.g., SR versus AB) because leaf morphology and physiology often vary together (Niinemets et al., 1998). Changes in both morphology and physiology may occur in plants where adaptations are required to deal with potential evapotranspiration in very different climates. Nevertheless, multiple factors appear to be involved in regulating transpiration.

Simulation estimates indicated that transpiration increased with decreasing L_w and vice versa; however, physiological factors can also add to the transpiration differences among genotypes (Fig. 4). Nonetheless, we found that the L_w effect on transpiration was important at both the crown and canopy scale and among genotypes. The genotype with the smallest L_w (SR) had the greatest rates of transpiration among all the genotypes and perhaps not consequently SR originated from the warmest climate. Moreover, when red maple genotypes were compared at their inherent physiology, the transpiration differences among genotypes still fell along a gradient in L_w (Fig. 4). Therefore, our results support the hypothesis that in a warmer climate, the red maple genotype with smaller leaves may have an advantage over larger-leaved genotypes resulting from an increased boundary layer con-

ductance and the ability to prevent leaf temperature from rising well above ambient in non-limiting soil moisture conditions (Royer et al., 2008). This L_w attribute would seem highly adaptive for a tree with a canopy more exposed to solar radiation, like in home landscapes or intensive production horticulture sites. Additionally, smaller leaves could be viewed as an easily identifiable trait when breeding for improved productivity in agricultural crops for a future warmer world.

Microclimate influences leaf size through a variety of environmental cues at multiple scales (Granier and Tardieu, 2009). At the leaf scale, cell number or size can change in response to environmental conditions, whereas at the whole-plant level, leaf size is more likely to change than leaf number (e.g., Aguirrezabal et al., 2006; Hovenden and Vander Schoor, 2004; Karamanos et al., 1982; Oleksyn et al., 1998). Relative to our findings at the canopy
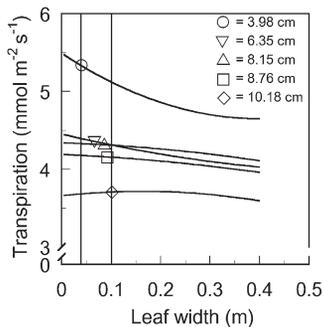
Fig. 4. Predicted leaf-level transpiration response for five genotypes to variations in leaf width (L_w). Results were generated using individual genotype-specific physiology parameters at constant environmental conditions (air temperature = 25 °C, relative humidity = 60%, photosynthetic photon flux = 1500 μmol·m^{-2}·s^{-1}, and wind speed = 5 m·s^{-1}). Symbol locations depict the genotype transpiration at inherent L_w (reported in legend) and physiology. The non-linear lines that intersect each symbol illustrate the predicted genotype transpiration response to alterations in L_w. Vertical bars bracket the range of L_w observed across the genotypes in this study. Red maple genotype symbols are as follows: 'Summer Red' (○), 'Autumn Flame' (▽), 'Red Sunset' (△), 'October Glory' (□), and 'Autumn Blaze' (◇).

scale, the lower the LAI and slower the wind speed, the greater the L_w impact on transpiration. Thus, changes to leaf size can mediate transpiration in response to environmental stimuli (e.g., Gates, 1968). In addition, changes in L_w can have a dramatic impact on both transpiration (assuming no changes in g_s) and leaf–air temperature differences. Our findings suggest that on exposed warm sites, L_w will have a substantial effect on transpiration to the extent that it may provide a means to prevent the leaf temperature from rising to a harmful level. Hence, changes in L_w can play a substantial part in modulating leaf temperature and transpiration.

CONCLUSIONS

Increases in temperature resulting from climate change will impact plant transpiration and water use. Selection of trees with smaller leaves will be a better fit for hotter climates. Smaller leaves have a higher boundary layer conductance that increases the rate of water vapor and heat transport, appreciably influencing leaf temperature in favor of a smaller leaf in warmer climates.

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