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Separating foliar physiology from morphology reveals the relative roles of vertically structured transpiration factors within red maple crowns and limitations of larger scale models

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Abstract

A spatially explicit mechanistic model, MAESTRA, was used to separate key parameters affecting transpiration to provide insights into the most influential parameters for accurate predictions of within-crown and within-canopy transpiration. Once validated among *Acer rubrum* L. genotypes, model responses to different parameterization scenarios were scaled up to stand transpiration (expressed per unit leaf area) to assess how transpiration might be affected by the spatial distribution of foliage properties. For example, when physiological differences were accounted for, differences in leaf width among *A. rubrum* L. genotypes resulted in a 25% difference in transpiration. An *in silico* within-canopy sensitivity analysis was conducted over the range of genotype parameter variation observed and under different climate forcing conditions. The analysis revealed that seven of 16 leaf traits had a $\geqslant$5% impact on transpiration predictions. Under sparse foliage conditions, comparisons of the present findings with previous studies were in agreement that parameters such as the maximum Rubisco-limited rate of photosynthesis can explain ~20% of the variability in predicted transpiration. However, the spatial analysis shows how such parameters can decrease or change in importance below the uppermost canopy layer. Alternatively, model sensitivity to leaf width and minimum stomatal conductance was continuous along a vertical canopy depth profile. Foremost, transpiration sensitivity to an observed range of morphological and physiological parameters is examined and the spatial sensitivity of transpiration model predictions to vertical variations in microclimate and foliage density is identified to reduce the uncertainty of current transpiration predictions.

Key words: Boundary layer conductance, leaf width, modelling, sensitivity analysis, stomatal conductance, transpiration, water vapour transfer, wind.

Introduction

Plants affect the land surface water and energy budgets by controlling the passage of water vapour through their stomata, thus exerting feedback on climate by regulating transpiration. One of the largest uncertainties in land surface climate prediction is from the representation of moisture exchanges (e.g. energy and water budgets) (e.g. Koster *et al.*, 2004; Henderson-Sellers *et al.*, 2008). Fortunately, most state-of-the-art land surface models try to describe the terrestrial vegetation transfer of water vapour to the atmosphere by accounting for water and energy budgets and plant physiological processes such as stomatal conductance (g_s) (e.g. Sellers *et al.*, 1997; Oleson *et al.*, 2008). However, water vapour exchanges over a range of temporal and spatial scales are complex functions, usually requiring simplifications of biological, chemical, and physical processes. Thus, there remains a need to understand the relative interactions among canopy controls over water loss and which parameters are most influential in the exchange of water vapour.

To capture feedbacks that span multiple temporal and spatial scales, land surface models must simulate transpiration sensitivity to changes in atmospheric conditions. The predominant technique is for land surface models to couple the g_s scheme (e.g. the g_s model of Ball *et al.*, 1987) to a biochemical photosynthesis model (e.g. Cox *et al.*, 1998; Yu *et al.*, 2004; Alton *et al.*, 2009; Niyogi *et al.*, 2009). The resultant g_s estimate then determines the conductance in the transpiration calculation. Amongst existing land surface models, however, the role and parameterization of transpiration vary widely (e.g. Hickler *et al.*, 2006; Fisher *et al.*, 2008; Henderson-Sellers *et al.*, 2008; Wei *et al.*, 2010). For instance, the maximum Rubisco-limited rate of photosynthesis (V_{cmax}) indirectly influences transpiration and surface energy fluxes via the linkage between g_s and photosynthesis, and, therefore, some consider it a key prognostic variable that couples biophysics, hydrology, and biogeochemistry (Harley and Baldocchi, 1995; Leuning *et al.*, 1995; Williams *et al.*, 1996; Alton *et al.*, 2007; Bauerle *et al.*, 2009; Houborg *et al.*, 2009). Alternatively, others simply infer transpiration by subtraction of runoff from precipitation (e.g. Eltahir and Bras, 1996; Ford *et al.*, 2007; Fisher *et al.*, 2008).

Although some of the most complex land surface schemes combine physical processes with biophysical exchanges (e.g. Cox *et al.*, 1999), only a few analyses have focused on the within-canopy spatial relevance of biophysical parameters specific to transpiration (Leuning *et al.*, 1995; Williams *et al.*, 1996; Bauerle *et al.*, 2009; Houborg *et al.*, 2009). In this study their findings are built on by taking account of potential within-canopy spatial interactions and by broadening the investigated parameters, linked output estimates, and climate forcing scenarios. Specifically, the microclimate conditions that pertain to canopy position are separated to test the sensitivity of 16 leaf morphological and/or physiological parameters at the intraspecific level in a common eastern biome continuously flushing species (*Acer rubrum* L.). The primary objective was to assess the vertical profile of leaf-to-atmosphere sensitivity of transpiration to independent variation in leaf morphology and physiology parameters among genotypes of a forest tree species with known differences in leaf morphology and physiology in an attempt to better understand key parameters for larger scale transpiration models. To do so, a model (MAESTRA) that simultaneously solves for leaf-scale g_s, net photosynthesis (A_{net}), and energy balance as a function of leaf position within the canopy was first parameterized and validated. Once validated, the sensitivity of predicted g_s, boundary layer conductance to water vapour (g_{bv}), leaf temperature (T_l), canopy coupling coefficient (Ω), A_{net}, absorbed net radiation (R_{na}), and scaled up leaf transpiration (E_l) estimates to independent variation in 16 leaf trait parameters was assessed. Two hypotheses were tested: (i) that the sensitivity of transpiration model predictions to vertical variations in microclimate and foliage density changes along a canopy vertical microclimate gradient; and (ii) that an increase in leaf width (L_w) within red maple considerably moderated transpiration.

Two model systems were used to separate key parameters affecting transpiration. *Acer rubrum* L. (red maple), the plant model system, was chosen to tease apart the interactions of foliage morphological versus physiological factors on transpiration for the following reasons: (i) red maples vary substantially in leaf morphology and physiology (Huff *et al.*, 2003; Royer *et al.*, 2005, 2008, 2009; Bauerle *et al.*, 2007, 2009; Weston and Bauerle, 2007; Weston *et al.*, 2007; Shahba and Bauerle, 2009); (ii) red maples have distinct leaf gas exchange differences in natural populations from contrasting hydrological (Abrams and Kubiske, 1990; Bauerle *et al.*, 2003b) and thermal habitats (Bauerle *et al.*, 2007; Weston and Bauerle, 2007; Weston *et al.*, 2007), as well as among genetically defined genotypes (Sibley *et al.*, 1995; Bauerle *et al.*, 2003a, 2006, 2007); and (iii) leaf morphology and physiology vary among ecotypes and clonally propagated red maple, suggesting that the intraspecific variation within the genus provides a good model in which to investigate morphological and physiological traits affecting transpiration (e.g. Abrams and Kubiske, 1990; Bauerle *et al.*, 2003a; 2009; Royer *et al.*, 2008). MAESTRA, a three-dimensional array model which couples g_s, photosynthesis, and leaf energy balance, provided the mathematical modelling framework. MAESTRA's spatially explicit approach deals with energy and leaf properties at multiple scales (leaf, whole canopy, and stand). Therefore, MAESTRA was parameterized and validated to establish a link from the leaf to canopy scale, and an attempt was made to isolate and control the interplay among variation in morphological and physiological variables affecting transpiration. The study was carried out with a three-dimensional model to take into account the sources and sinks for water vapour and heat along a vertical canopy depth profile for three forest leaf area densities (LAI=1, 5, and 10). However, the results have implications for larger scale global and regional one- and two-dimensional canopy models because the biophysical parameters, representation of processes (e.g. coupling a g_s model to a biochemical photosynthesis model), and performance of the different types of models are comparable (Hanson *et al.*, 2004; Alton *et al.*, 2007; Bauerle *et al.*, 2007).

Materials and methods

Site and plant material

Measurements were carried out during the 2003 and 2004 growing seasons in Clemson, South Carolina, USA (latitude 34°40'8''; longitude 82°50'40''). A full description of the site is given in Bauerle *et al.* (2002). In 2003 (experiment 1), two red maple genotypes, cv. 'October Glory' (OG) and cv. 'Summer Red' (SR), were shipped to Clemson and transplanted into oversized 114.0 l plastic pots containing a mixture of 20:1 pine bark:sand (v/v) with 8.3 kg m^3 of 10N-3P-8.3K Nutricote (type 360; Chisso-Asahi Fertilizer Co., Tokyo). In 2003, cultivars were chosen for climate of origin temperature differences and similar precipitation, and in 2004 the experiment was expanded to include differences in leaf size within a similar climate of origin (Sibley *et al.*, 1995). The clonal parents are summarized in Table 1. Trees were placed in a completely randomized design and spaced 1.5 m centre-to-centre.

Table 1. Genotypes of red maple in the study, cultivar selector, site of origin, latitude and longitude, mean annual maximum air temperature (MAMT), and mean annual precipitation (MAP) of the site of origin.

Experiment number (1 or 2) in parentheses next to the genotype depicts its involvement in experiment 1, 2, or both. Leaf widths are reported in Table 3. The climate data were derived from the meteorological stations closest to that of the site of origin.

Genotype	Cultivar selector	Site of origin	Latitude and longitude	MAMT	MAP
Autumn Blaze (2)	Jeffers Nursery	Fostoria, OH, USA	41°18' N 83°45' W	16.7 °C	1144 mm
October Glory (1, 2)	Princeton Nurseries	Princeton, NJ, USA	40°38' N 74°65' W	16.7 °C	1139 mm
Autumn Flame (2)	A. McGill and Sons Nursery	Fairview, OR, USA	45°53' N 122°44' W	15 °C	1211 mm
Red Sunset™ (2) 'Franksred'	Frank J. Schmidt and Son Co.	Troutdale, OR, USA	45°32' N 122°23' W	16.7 °C	1139 mm
Summer Red (1, 2) 'HOSR'	Head Ornamentals, Inc.	Tifton, GA, USA	31°27' N 83°30' W	26.7 °C	1361 mm

The continuous stand consisted of ~3.5 m tall equal age saplings ($n=100$, 50 per genotype). In 2004 (experiment 2) growing conditions were as for 2003, except the site plant material was replaced with 100 ~3 m tall equal age saplings of five genotypes ($n=20$ trees per genotype) to assemble a gradient in leaf size. Two genotypes were the same as the previous year, while cv. 'Autumn Flame', 'Franksred', and one Freeman maple cultivar 'Jeffersred' were included in the completely randomized design. At the start of the experiment (after 45 d under well-watered conditions), all pots were watered to container capacity and permitted to drain for 24 h. Thereafter, each tree was watered three times daily to near container capacity with 360 ° pressure-compensating microemitters (ML Irrigation Inc., Laurens, SC, USA). 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 ($0.4–0.5$ m^3 m^{-3}).

Experiment 1 (2003): within-crown spatial variation

Micrometeorology measurements outside and within the canopy: Meteorological data [air temperature (T_{air}), precipitation, relative humidity (RH), photosynthetic active radiation (PAR), and wind speed 0.3 m above the canopy (U_t)] were collected using a Campbell Scientific Weather Station located on the north side immediately adjacent to the experimental plot. Additionally, the vertical gradient of horizontal wind speed [$U_{(d)}$], RH, and T_{air} were measured in the canopy of each genotype at three 0.5 m intervals from the top. R.M. Young 03101-L wind sentry anemometers and Hobo® Pro Series™ loggers continuously monitored every minute, and 15 min averages were computed (CR21X, Campbell Scientific, Inc., Logan, UT and Onset Computer Cooperation, Polaset, MA, USA, respectively).

Crown layer sap flow measurements

Crown layer transpiration (E_{cl}) was measured with heat balance sap flow gauges (Dynamax Inc., Houston, TX, USA). Three gauges were installed on the main stem of each tree, one immediately upstream of each crown layer (three layers per tree crown). In total, 12 gauges were placed on four trees in each genotype comprising two 50 d continuous E_{cl} measurements, one period per genotype. Along the vertical stem height gradient, the heating elements were operated at constant power and the sheath conductance for each gauge (models SGB13-WS, SGB16-WS, and SGB19-WS) was determined during the night following a late day rain event (i.e. when E_l was assumed to be zero under dark wet-leaf conditions). Data were collected by a CR10X data logger

(Campbell Scientific) coupled to multiplexers (AM416, Campbell Scientific) every 30 s, and 15 min means were logged. Additional sap flow gauge installation and operation protocols are described in detail elsewhere (Bauerle *et al.*, 2002).

Leaf-level physiological measurements: Twice weekly throughout the growing season, leaf gas exchange was measured on a fully expanded, south-oriented and fully exposed leaf at each crown layer on four trees per genotype using a portable steady-state gas exchange system (CIRAS-I, PP Systems, Amesbury, MA, USA) equipped with a light-, humidity-, and temperature-controlled cuvette [model PLC5 (B); PP Systems]. Leaf A_{net} versus CO_2 response curves ($A_{net}–C_i$ curves, where A_{net} is net photosynthetic rate in µmol m^{-2} s^{-1} and the C_i is internal CO_2 concentration expressed as the mol fraction of CO_2] and temperature–response curves were constructed. To ensure steady-state activation of Rubisco before measurement by the CIRAS-I gas analyser, the leaf in the cuvette was acclimated to a CO_2 concentration of 370 µmol mol^{-1} and a saturating photosynthetic photon flux (PPF; 1200 µmol m^{-2} s^{-1}) for ~10 min. Each $A_{net}–C_i$ response measurement was stabilized for $\geqslant 2$ min, and each A_{net}–temperature response measurement was stabilized for $\geqslant 5$ min. Genotype physiological parameters and calculations followed Bauerle *et al.* (2007).

After each gas exchange measurement, five leaf reflectance, transmittance, and absorption estimates were quantified with a Minolta SPAD 502 meter (Minolta Camera, Ramsey, NJ, USA) and averaged as described in Bauerle *et al.* (2004a). The reflectance, transmittance, and absorption estimates were used for the calculation of quantum yield (Bauerle *et al.*, 2004a).

Leaf area and width measurements: Weekly, individual genotype leaf area was randomly measured on four replicate trees ($n=4$ trees per genotype) within each of the three crown layers ($n=12$ total layers for each genotype) with a LI-3000 leaf area meter (Li-Cor, Lincoln, NE, USA). A preliminary study of the red maple cultivars used and 15 red maple cultivars in the literature revealed a 1:1 relationship between L_w and length (Sibley *et al.*, 1995). Therefore, spherical leaf geometry with a uniform distribution of leaf area across the surface was assumed and L_w was calculated from leaf area per genotype. MAESTRA does not use a more detailed description of individual leaves; however, this technique was adequate for genotypic parameterization in red maple. Also, the spherical geometry allows equal boundary layer resistance to be assumed at any direction of air flow (Gates and Papian, 1971). The average L_w, therefore, determined the leaf dimension in the direction of air flow, calculated from individual leaf surface area measurements ($n=168$ per genotype) (Gates and Papian, 1971). At

the end of each 50 d measurement period, all trees with sap flow sensors were felled and leaves were removed from each crown layer and bagged separately. Crown layer leaf area was measured with a LI-3100 leaf area meter (Li-Cor). This permitted transpiration to be expressed on a unit leaf area per crown layer basis.

Model description: E_l was estimated with a crown subvolume derivative of the MAESTRA model. MAESTRA is a three-dimensional model that uses an array of tree crowns where radiation absorption, photosynthesis, and transpiration are calculated from leaf sunlit and shaded fractions by considering direct beam, diffuse, and scattered beam irradiance (Norman and Welles, 1983). MAESTRA includes leaf-level submodels for energy balance—described below (Leuning *et al.*, 1995)—g_s (e.g. Ball *et al.*, 1987; Leuning, 1995), and photosynthesis (Farquhar and von Caemmerer, 1982). Each submodel is applied to each subvolume within the canopy based on the unique distribution of environmental conditions at the specific subvolume. Therefore, whole crown transpiration estimates are merely the sum of each individual subvolume estimate. Previously, MAESTRA was validated against three independent PAR measurement techniques and found to predict within-crown PAR interception (Bauerle *et al.*, 2004*b*) and E_l in response to variation in T_l accurately (Bauerle *et al.*, 2007, 2009). In addition, MAESTRA performed well when compared with whole crown transpiration measurements (Bauerle *et al.*, 2002; Bowden and Bauerle, 2008) and whole tree CO_2 exchange rates (Reynolds *et al.*, 2009) in deciduous species, including red maple. Here, descriptions of MAESTRA specifics pertinent to the present study on changes in scaled-up E_l induced by genetic differences in leaf traits are given; however, interested readers are referred to a list of MAESTRA equation references (Supplementary data available at *JXB* online) and freely available code provided elsewhere (www.bio.mq.edu.au/maestra/).

Calculations were performed separately on sunlit and shaded leaf fractions per crown grid point, where volume and leaf area are calculated through the crown at grid point x, y, and z co-ordinates. The spatial algorithmic approach used by MAESTRA was key to synthesize knowledge of single leaf morphology and physiology, and account for physics of energy balance, where the grid point leaf energy budget and boundary layer conductance was computed with an iterative scheme (Leuning *et al.*, 1995). Specifically, to take into account the sources and sinks for water vapour and heat along a vertical canopy depth profile for the isometric hypostomatous leaves of red maple, boundary layer conductance for forced convection (g_{bhF}) was calculated as a function of L_w (m) (Monteith, 1973) and internal canopy wind speed:

$$g_{bhF} = 0.003[U_{(d)}/L_w]^{1/2} \qquad (1)$$

where $U_{(d)}$ (m s^{-1}) is a wind speed value exponentially less than U_t at a location inside the canopy, expressed as follows:

$$U_{(d)} = U_t \exp^{(-ad)} \qquad (2)$$

where d is the internal depth (m) from the top of the canopy and a is a dimensionless extinction coefficient. The coefficient was derived from measured values of wind speed above and inside the canopy based on the principals of accumulating leaf area above the grid point (Leuning *et al.*, 1995). In addition, Monteith (1973) demonstrated that the boundary layer conductance for free convection (g_{bhf}) can be expressed using the following equation:

$$g_{bhf} = 0.5 H_d Gr^{1/4}/L_w \qquad (3)$$

where H_d is the molecular diffusivity for heat and Gr is the Grashof number calculated as:

$$Gr = 1.6 \times 10^8 |T_l - T_{air}|L_w^3 \qquad (4)$$

The radiation conductance (g_r) is given by:

$$g_r = 4\varepsilon\sigma T_k^4 t_d exp^{-t\,C + exp^{-t\,(L-C)}_d}_{d} \qquad (5)$$

where ϵ is leaf emissivity (assumed to be 0.95), σ is the Stefan–Boltzmann constant (W m^{-2} K^{-4}), t_d is the transmittance of diffuse radiation to the grid point, C is the cumulative leaf area above the grid point, and L is total leaf area. To arrive at the isothermal form, g_{bhF} and g_{bhf} can then be nested in series with g_r as follows:

$$g_{bhr} = g_{bhF} + g_{bhf} + g_r \qquad (6)$$

where g_{bhr} is the total boundary layer conductance to heat. The g_{bhr} is converted to the total boundary layer conductance to vapour (g_{bv}) on a hypostomatous leaf by a factor of 1.075.

The isothermal form of the Penman–Monteith combination equation (Monteith, 1965) was then applied to each grid point and the sum of contributions from sunlit and shaded leaf fractions was used to derive grid point, crown layer, and whole crown transpiration estimates. Specific to E_l estimates in this study, the isothermal form of the Penman–Monteith combination equation for a hypostomatous leaf was defined as:

$$E_l = \frac{SR_{nr} + \rho_a C_p VPD g_{bhr}}{\lambda[S + \gamma(g_{bhr}/g_{bv})]} \qquad (7)$$

where S is the slope of the saturation vapour pressure deficit versus temperature at T_{air} (kPa K^{-1}), R_{nr} is the isothermal net radiation (W m^{-2}), ρ_a is the density of dry air (kg m^{-3}), C_p is the specific heat capacity of air (J kg^{-1} K^{-1}), VPD is the vapour pressure deficit (kPa), λ is the latent heat of evaporation of water (J kg^{-1}), and γ is the psychrometer constant (kPa K^{-1}). For interested readers, a detailed description of how MAESTRA links E_l of individual grid points to the whole crown and the subsequent leaf energy balance calculations can be found in Medlyn *et al.* (2007).

Model parameterization: The crown was divided into three layers, with each layer forming 124 equal subvolumes in an attempt to simulate the radial distribution of PAR per crown layer more accurately. To facilitate leaf-to-crown layer scaling, MAESTRA was set to spatially sum output estimates of all subvolumes per layer (Fig. 1). Leaf area density throughout the crown was assumed uniform based on evenly distributed measured leaf area in each crown layer (data not shown). Tables 2 and 3 list the primary model parameter values used in the simulations, and Supplementary Tables S1–S4 at *JXB* online list the full parameter sets (together with sources). Wind speed measurements were compared (Equation 2) at three canopy layers to derive 2003 and 2004 a values (Table 3). The wind speed in the canopy as a whole was verified to decay exponentially with canopy depth. Morphological and physiological attributes were parameterized on a genotype basis. Thus, MAESTRA scaled up each genotypes' genetic difference with genotype-specific leaf-level values and control equations.

Model input and output: Meteorological data to drive MAESTRA were collected on a 15 min time step as described previously. The model output the sunlit and shaded leaf area spatial distribution of absorbed direct, diffuse, and scattered PAR, R_{na}, A_{net}, g_s, T_l, E_l, E_{cl}, and g_{bv} per 15 min. Estimated wind speed was output per canopy depth.

Model application: Within MAESTRA, a simulated plot was created with site-descriptive, tree growth, and spacing data. Individual tree simulations were performed using tree-specific dimensions (radii of the crown in both the x and y direction, height of the crown, length of the trunk, stem diameter, and leaf area).

Experiment 2 (2004): whole crown and canopy genotype temporal variation

Except as otherwise indicated, micrometeorology measurements outside and within the canopy, gas exchange, SPAD values, and model validation tests were as in Experiment 1.
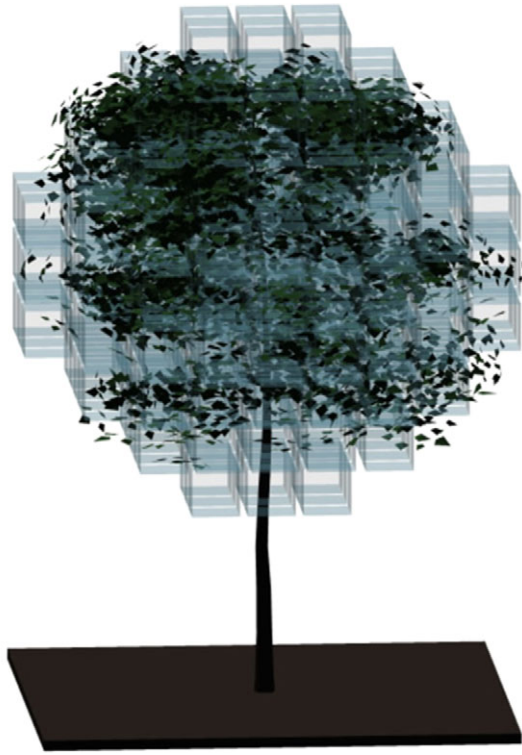
Fig. 1. Three-dimensional representation of discrete within-crown vegetation calculations. The crown is divided into grid cell volumes with known x, y, and z direction, i.e. grid point calculations with the spatial position relative to the tree crown.

Table 2. Physiological and biophysical parameters used amongst all genotypes for MAESTRA parameterization and transpiration predictions in 2003 and 2004

Parameter	Unit	*Acer rubrum* L.
Respiration reference temperature	°C	25
Deactivation energy temperature response of J_{max}	mol^{-1}	220000
Sensitivity of stomata to vapour pressure deficit	Pa	1500
Leaf NIR transmittance	%	32
Leaf IR transmittance	%	1
Leaf NIR reflectance	%	48
Leaf IR reflectance	%	5

IR, infrared; J_{max}, maximum rate of electron transport; NIR, near infrared.

Whole crown transpiration measurements: The sap flow system described in Experiment 1 was used for whole crown transpiration measurements. Gauges (15 total) were distributed evenly but randomly among the five cultivars ($n=3$ replicate trees per cultivar). The sap flow system installation and operation were as above, except that the sap flow gauges were installed one per tree, below the first branch, ~60 cm above the container soil surface. Whole crown transpiration measurements were compared against MAESTRA estimates.

Allometric measurements: Weekly, three-dimensional tree canopy characteristics (listed in the 'model application' section of 'Experiment 1') were measured on all study trees. Monthly, the total number of leaves on each study tree was counted.

Leaf area ratio: Total crown leaf area was measured along with a subset of leaves of each tree ($n=100$ leaves per genotype) (model 3100, LiCor Inc.). A 1:1 L_w versus length ratio was again observed on the subset, thus average L_w was calculated from leaf area and individual tree leaf area was scaled monthly throughout the course of the season (Gates and Papian, 1971).

Model parameterization and application: Unless otherwise indicated, the model was parameterized on a genotype basis and applied as in Experiment 1. Leaf area per crown was calculated from allometric measurements described above with uniform leaf area distribution divided by the volume of the crown using an oblate spheroid crown approximation. Linear interpolation of leaf area development across the season was applied.

Validation tests: In 2003, genotype daily mean E_{cl} estimates were compared with mean layer sap flow. In 2004, genotype daily mean whole crown transpiration estimates were compared with mean whole crown sap flow. Model performance for both experiments was evaluated by comparing observed values with predicted values. Root mean square error (RMSE) for differences in transpiration between measured and predicted values of each genotype were used to test the null hypothesis that the average of the differences between measured and predicted paired observations is zero at a $\alpha=0.05$. Note that specific to transpiration estimates among species at foliage densities less than or equal to an LAI of 10, MAESTRA has previously been validated (Bowden and Bauerle, 2008).

Separating the morphological versus physiological E_l factors: MAESTRA was used to scale up E_l and describe crown layer, whole crown, and canopy transpiration. To separate the influence of the coupled photosynthesis (Farquhar and von Caemmerer, 1982), g_s (Leuning, 1995), radiation (Norman and Welles, 1983), and leaf energy balance (Leuning *et al.*, 1995), an independent parameter variation sensitivity analysis was performed to quantify the relative effects model parameters have on E_l estimates as well as the coupled estimates of A_{net}, g_s, T_l, g_{bv}, R_{na}, and Ω (degree of canopy coupling; Jarvis and McNaughton, 1986). Since calculations are conducted at the leaf scale, MAESTRA was an ideal model for determining sensitivities among physiological and morphological parameters to transpiration because all non-linearities are maintained at the leaf level, therefore sensitivities to fluxes are additive (e.g. Leuning *et al.*, 1995). Hence, the effect of varying each parameter independently of other parameters was tested. The parameters were varied within their measured range of variability, an ideal situation according to White *et al.* (2000). The independent response to wind, T_{air}, PAR, and RH (e.g. Fig. 2; see also Houborg *et al.*, 2009) was tested for each parameter. Although the sensitivity percentages of all seven response variables under different climatic forcing conditions were tested and are provided, the focus is primarily on transpiration in this study for the reason that water vapour is the Earth's dominant greenhouse gas and the role and parameterization of transpiration varies widely among existing land surface models (e.g. Hickler *et al.*, 2006; Fisher *et al.*, 2008; Henderson-Sellers *et al.*, 2008; Wei *et al.*, 2010). Nonetheless, for readers interested in the other six linked estimates (A_{net}, g_s, T_l, g_{bv}, R_{na}, and Ω), note that the sensitivity analysis methodology was consistent. Below, the sensitivity analysis framework using E_{cl} as the output estimate is described.

In silico, a representative 20 m tall deciduous forest canopy was vertically stratified into 10 equal layers and E_l was estimated according to the Leuning (1995) g_s submodel. To investigate the vertical effects of different amounts of canopy leaf area under forced and mixed convection, canopies were compared across a representative range of naturally occurring LAI values (1, 5, and 10). The sensitivity analysis was used to assess the variability in E_l along a vertical profile caused by variation in parameter values over the measured genotypic range and among different representative LAI values. The parameters tested included the following

Table 3. Genotype-specific morphological and physiological parameters used for MAESTRA parameterization and transpiration predictions.

Parameter and units	AB	AF	OG	RS	SR	BC ±sensitivity range
L_t (%)	5.32	4.24	4.63	4.02	5.23	4.69±1.21
L_r (%)	9.64	8.5	8.92	8.25	9.54	8.97±1.39
L_w (cm)	10.18	6.35	8.76	8.15	3.98	7.48±6.2
a (dimensionless)	0.521	0.521	0.705	0.521	0.698	0.59±0.18
θ (dimensionless)	0.89	0.92	0.86	0.92	0.95	0.908±0.09
J_{max} (μmol m^{-2} s^{-1})	149.36	174.18	125.9	190.63	140.8	175.22±64.73
E_j (J mol^{-1})	5 1500	49 000	52 300	54 200	53 400	52 080±6200
τ_j (K^{-1} mol^{-1})	640	639	640	637	638	639±3
α (mol e– mol^{-1} PAR$_a$)	0.2404	0.2496	0.2244	0.2492	0.2872	0.2502±0.0628
V_{cmax} (μmol m^{-2} s^{-1})	65.03	66.37	70.1	64.04	79.8	69.06±15.76
E_v (J mol^{-1})	56 400	56 600	52 200	48 700	46 300	52 040±10Â300
τ_v (K^{-1} mol^{-1})	640	639	640	637	630	637±10
R_d (μmol m^{-2} s^{-1})	4.14	3.74	3.52	3.3	3.21	3.58±0.94
Γ (μmol m^{-2} s^{-1})	99.44	104.08	102.1	103.66	88.9	99.64±15.18
g_1 (mol m^{-2} s^{-1})	5.56	6.17	5.68	7.14	7.52	6.41±1.96
g_o (mol m^{-2} s^{-1})	0.041	0.048	0.046	0.035	0.043	0.0426±0.013

Genotype abbreviations: AB, Autumn Blaze; AF, Autumn Flame; OG, October Glory; RS, Red Sunset; SR, Summer Red; BC, base case. Parameter abbreviations: L_t, leaf PAR transmittance; L_r, leaf PAR reflectance; L_w, leaf width; a, wind speed extinction coefficient; θ, convexity parameter of the light response; J_{max}, the maximum rate of electron transport; E_j, activation energy temperature response of J_{max}; τ_j, entropy term in temperature response of J_{max}; α, quantum yield of electron transport (PAR$_a$; absorbed PAR); V_{cmax}, the maximum Rubisco-limited rate of photosynthesis; E_v, activation energy temperature response of V_{cmax}; τ_v, entropy term in temperature response of V_{cmax}; Γ, CO_2 compensation point; R_d, dark respiration; g_1, genotype slope coefficient; g_o, minimum stomatal conductance.
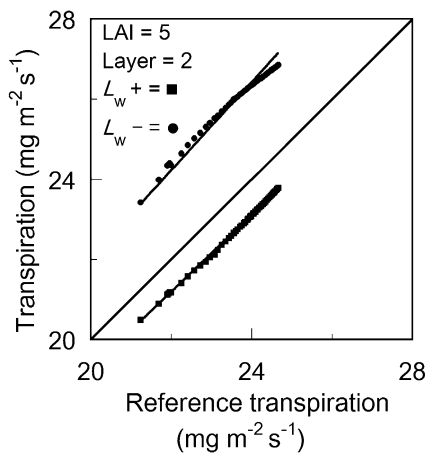
Fig. 2. The sensitivity of canopy layer transpiration simulations by the MAESTRA model to variations in leaf width (L_w) at an LAI=5 and middle (layer 2) position. The x-axis represents the reference base case transpiration estimate and the y-axis represents the relative change in transpiration in response to the applied L_w changes (± 6.2 cm). The estimates were generated using the following environmental conditions: air temperature=25 °C, relative humidity=60%, photosynthetic active radiation=1500 μmol m^{-2} s^{-1}, and wind speed=0.2–10 m s^{-1}.

full complement of MAESTRA leaf-level input that could potentially affect E_l: PAR transmittance, PAR reflectance, L_w, convexity parameter of the light response (θ), the maximum rate of electron transport (J_{max}), activation energy of the temperature response of J_{max} (E_j), the entropy term of the J_{max} temperature response (τ_j), the quantum yield of electron transport (α), V_{cmax}, activation energy of the temperature response of V_{cmax} (E_v), the

entropy term of the V_{cmax} temperature response (τ_v), dark respiration (R_d), CO_2 compensation point (Γ), genotype g_s slope coefficient (g_1), minimum g_s (g_o), and a. Specifically, the MAESTRA model was used to simulate the E_l response to variation in each parameter independently while the morphological and physiological variables were held constant at the mean [hereafter base case (BC); Table 3]. The parameters were varied over the range of observed genotype variation, where each parameter was increased to the maximum and decreased to the minimum. The vertical distribution of leaf energy balance was explicitly considered when predicting E_{cl} rates on an m^2 leaf area basis per crown layer. The positive and negative percentage changes for each run were calculated by linearly regressing BC estimates against the parameter increase or decrease estimates, where regression slopes were used to assess the average response of the parameter change relative to the BC (e.g. Fig. 2; see also Houborg *et al.*, 2009). To investigate the main and interacting effects of variation in specific environmental conditions, each parameter was tested over a range of individual atmospheric conditions while holding the others fixed (e.g. 0.2–10 m s^{-1} wind speed, 60% RH, 1500 μmol m^{-2} s^{-1} PAR, and 25 °C). Regression analysis provided the most comprehensive sensitivity measure (for a review of techniques for parameter sensitivity analysis specific to environmental models, see Hamby, 1994). Supplementary Tables S5–S8 at *JXB* online report the sensitivity for L_w, J_{max}, α, V_{cmax}, R_d, g_1, and g_o at solar noon and in response to LAI and canopy depth position. Although increases and decreases to all parameters were tested (resulting in 8064 runs of parameter percentage change regression contrasts), only those with ≥5% change in E_{cl} are reported (Supplementary Tables S5–S8). Based on the spatial sensitivity analysis results and the potential for relatively easy remote sensing quantification, the L_w parameter was examined further to assess its significance in predicting canopy transpiration among observed morphological variation. The maximum observed L_w difference (3.98 cm versus 10.18 cm) at contrasting T_{airs} (20 °C versus 35 °C) was compared along a vertical canopy depth profile for three representative forest leaf area densities (LAI=1, 5, and 10).

Results

Crown position versus E_cl *prediction within the crown*

The model was able to reproduce the measured E_{cl} for both genotypes at three crown spatial positions in 2003 (Fig. 3). RMSEs were small and ranged from 0.12 kg m^{-2} d^{-1} to 0.19 kg m^{-2} d^{-1} for both genotypes across crown position and were greater at upper crown layers coinciding with greater rates of E_{cl}. SR had greater daily E_{cl} than OG at all crown positions. The MAESTRA model also predicted the whole crown 81 d mean transpiration rate on a genotype-specific basis in 2004, with only a slight overestimation occurring in four of the five genotypes (Fig. 4). The relationship between genotype L_w and crown transpiration rate was linear and occurred along a gradient in L_w (Fig. 4). There was no difference in the average RMSE (0.16) across three crown layers for the two genotypes in the 2003 study or at the crown level for the five genotypes tested in 2004. Therefore, observed differences in genotypic crown transpiration under common garden conditions can be reliably captured using the genotype-specific morphological and physiological parameters.

Effects of genotype morphology and physiology on the E_l *within a crown*

The genotype with the smallest L_w (SR) transpired more water than the genotype with the largest [Autumn Blaze (AB)] (Fig. 4). Under inherent morphology and physiology conditions, SR was estimated to transpire ~36 mg m^{-2} s^{-1} more than AB. However, when the SR L_w was increased to simulate SR E_l at an AB L_w, the physiological variation alone indicated that E_l remains ~27 mg m^{-2} s^{-1} greater in SR as compared with AB (data not shown). Although physiological factors appear to add to the greater crown transpiration in SR as compared with AB at equal L_w, model isolation of L_w differences resulted in an additional 25% separation in SR versus AB crown transpiration under moderate wind speed conditions (~5 m s^{-1}) (data not shown).

Relationship between L_w, T_air, U_(d), *and transpiration*

The model was used to assess the influence of $U_{(d)}$ on the distribution of E_{cl} along a vertical canopy depth profile at three representative LAIs and two contrasting T_{airs} and L_ws. The E_{cl} differences among changes in canopy position, LAI, and L_w manifest as L_w effects on boundary layer conductance and subsequent effects on radiative conductance, where the divergent L_ws in red maple caused ~50% difference in boundary layer conductance at wind speeds of ~5 m s^{-1} and thus a more efficient heat transfer in the smaller leaf (Fig. 5). Figure 5 further illustrates that as E_{cl} increases the influences of differences in L_w become progressively more important. Between the observed differences in red maple L_w and under the T_{airs} simulated, T_{air} and L_w interactions caused the small warm leaf to behave like the cool large leaf at an LAI of ≥5 (Fig. 5b, c).
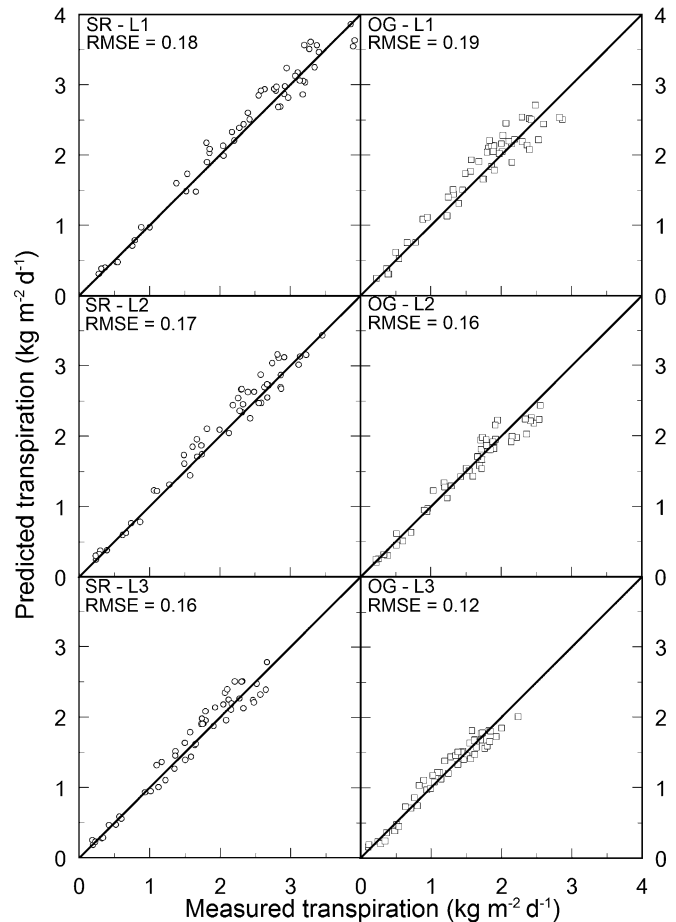

Fig. 3. The ability of the scaled-leaf MAESTRA transpiration model to predict genotype-specific transpiration at three vertical crown layers in 2003. Summer Red (SR; open circles and left column of panels) and October Glory (OG; open squares and right column of panels) mean measured versus predicted transpiration at three crown layers (designated alpha-numerically) in 2003 (e.g. SR–L1, SR–L2, and SR–L3). The 45 ° 1:1 line through the origin represents perfect prediction of observations by the model. Each symbol represents the mean daily transpiration of four replicate trees over a 50 d time period. The root mean square error (RMSE; kg m^{-2} d^{-1}) per genotype layer is reported in each panel.

Sensitivity analyses

The sensitivity of scaled up A_{net}, g_s, E_l, Ω, T_l, g_{bv}, and R_{na} model estimates to genotype-specific parameters was examined over the range of observed genotypic variation. Of the 16 parameters tested, L_w, J_{max}, α, V_{cmax}, R_d, g_1, and g_o had a ≥5% impact (i.e. higher or lower values of E_l) on estimates (Fig. 6). Within the range of variation in the red maple genotypes, the modelled A_{net}, g_s, E_l, Ω, T_l, g_{bv}, and R_{na} variables were found to be insensitive to PAR transmittance, PAR reflectance, θ, E_j, τ_j, E_v, τ_v, Γ, and a parameters. The sensitivity of E_l is shown graphically in Fig. 6a–d for each atmospheric condition (wind, PAR, RH, and T_{air}). The sensitivity of A_{net}, g_s, Ω, T_l, and g_{bv} to separate environmental forcings (wind, PAR, RH, and T_{air}) are presented in Supplementary Tables S5–S8 at *JXB* online, respectively. In addition, Tables S5–S8 contain the
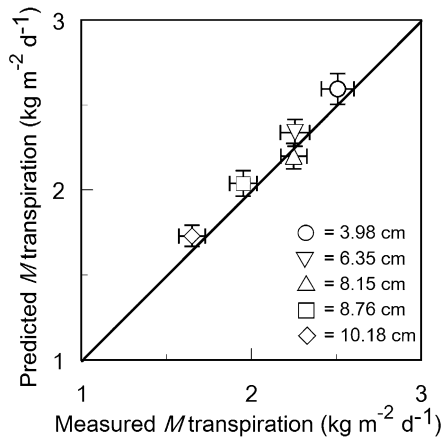
Fig. 4. The ability of the scaled-leaf MAESTRA transpiration model to predict genotype-specific whole crown seasonal daily mean (*M*) measured versus predicted transpiration of 2004 well-watered red maple genotypes Summer Red (SR; open circle), Autumn Flame (AF; inverted open triangle), Red Sunset (RS; open triangle), October Glory (OG; open square), and Autumn Blaze (AB; open diamond). The 45 ° 1:1 line through the origin represents perfect prediction of observations by the model. Each symbol represents the mean daily transpiration of three replicate trees over 81 d (Julian day 122–203) with standard error bars (*n*=81). The root mean square error (RMSE; kg m^{-2} d^{-1}) per genotype is as follows: SR=0.17, AF=0.15, RS=0.15, OG=0.19, and AB=0.16. The key reports genotype leaf widths for comparative purposes.

sensitivity to each variable's canopy spatial position for parameters with a ≥5% impact. Absorbed net radiation is omitted from the tables due to <5% sensitivity across all parameters tested. Specific to canopy transpiration, the parameters g_1 and V_{cmax} had the largest effect. However, the sensitivity of g_1 and V_{cmax} only persisted in upper canopy and lower LAI conditions. Similarly, J_{max} showed no spatial variation and was only sensitive (~15%) when decreased at an LAI=1; it is therefore omitted from Fig. 6. Over the range of observed genotype variation, the g_s parameters g_1 and g_o had the greatest influence on canopy transpiration estimates. However, they had an opposite outcome, where g_1 was more responsive in the upper canopy when vegetation was sparse, whereas g_o was more sensitive at greater LAI and lower canopy positions (Fig. 6). Considering the canopy as a whole, the response of E_l to L_w parameter value changes was consistently ≥5%, with the largest influence in the middle and lowest canopy position at an LAI=5. The sensitivity to the L_w parameter, however, was not symmetric, emphasizing the non-linear characteristic of the response. Hence, the model sensitivity to L_w increased more as L_w was decreased as opposed to increased. When considering parameters that are involved in the leaf energy balance, L_w had the largest influence on g_{bv} across all LAI and crown layer positions (Fig. 5). The changes in g_{bv} ranged from a 10–226% change at the lowest canopy layer to 20–226% at the top of the canopy (Supplementary Tables S5–S8 at *JXB* online). Depending on the canopy position and LAI, other variables such as A_{net}, g_s, Ω, and T_l were also
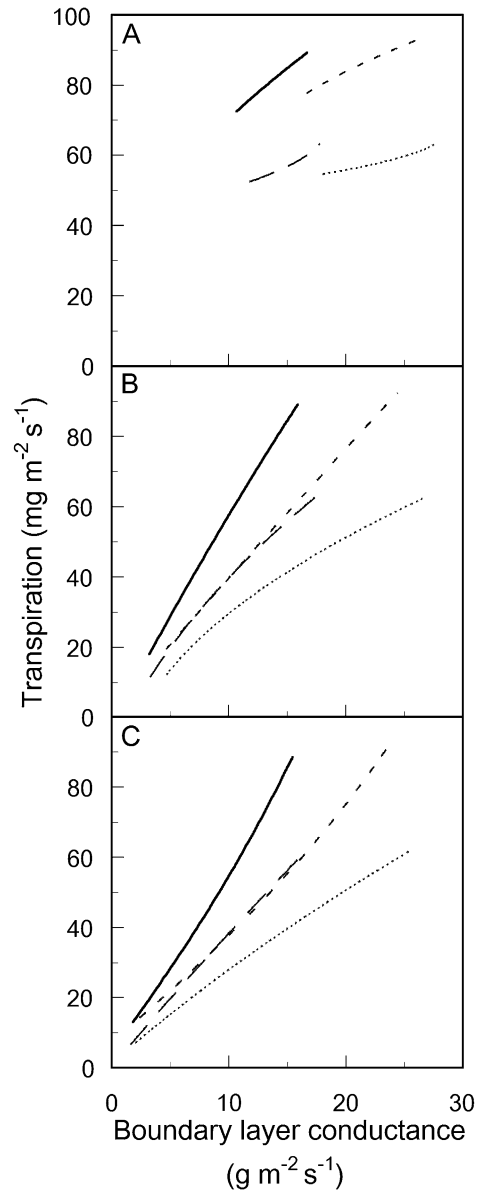

Fig. 5. *In silico* vertically stratified 20 m tall deciduous forest canopy predicted transpiration as a function of air temperature and leaf width (L_w) versus predicted boundary layer conductance at three representative canopy LAI values. (a) LAI=1, (b) LAI=5, and (c) LAI=10 at the top of canopy, wind speed=5 m s^{-1}, constant conditions of relative humidity=60%, and photosynthetic active radiation=1500 μmol m^{-2} s^{-1}. Boundary layer conductance is calculated for two contrasting air temperatures at different 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.

significantly impacted across canopy positions by L_w (Supplementary Tables S5–S8). Overall, the largest L_w influence on E_{cl} appeared at the middle to lower crown positions, whereas parameter sensitivity to g_1 and V_{cmax} only persisted at the top of the canopy.

Among environmental conditions, each parameter's response was relatively similar across LAI and canopy position (cf. Supplementary Tables S5–S8). A notable
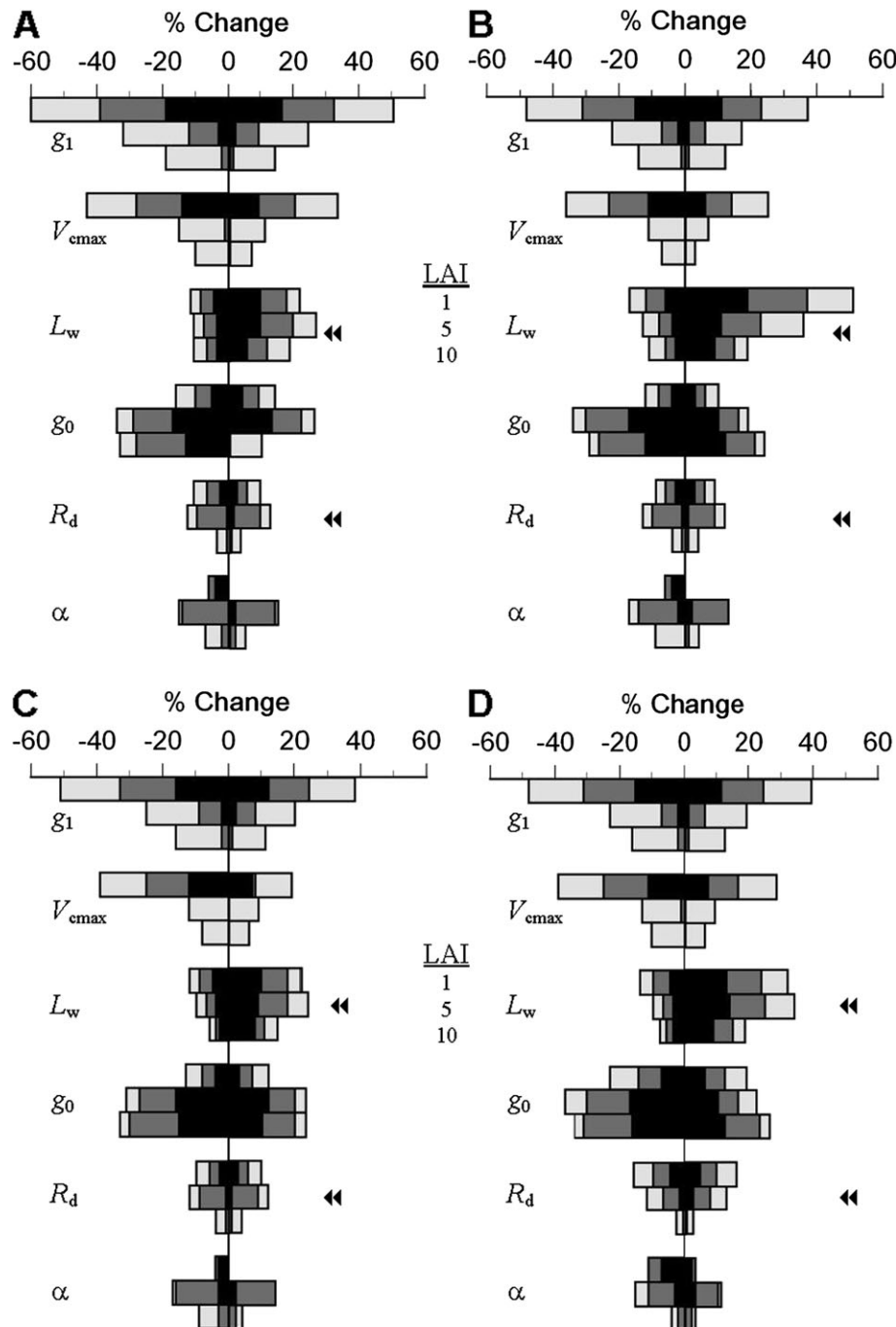
Fig. 6. Parameter sensitivity analysis results for the MAESTRA model transpiration estimate applied to the *Acer rubrum* L. genotypes under different climate forcing scenarios. Parameter abbreviations: genotype slope coefficient (g_1), the maximum Rubisco-limited rate of photosynthesis (V_{cmax}), leaf width (L_w), minimum stomatal conductance (g_o), dark respiration (R_d), and quantum yield of electron transport (α; absorbed PAR). Canopy vertical position (upper, middle, and lower) results are indicated by shaded bars: the light shaded area indicates upper, medium shaded indicates middle, and dark shaded indicates the bottom; the longer the bar, the more sensitive the parameter. In the case of L_w and R_d the ◄◄ symbol indicates a reversed response direction from all other parameters (i.e. an increase in L_w results in a decrease in transpiration). LAI results (1, 5, and 10) are indicated by the three separate horizontal bars within a parameter (e.g. L_w labelled). (A) Results for variation in microclimate wind speed (0.2–10 m s^{-1}), (B) photosynthetic active radiation (0–1500 µmol m^{-2} s^{-1}), (C) relative humidity (5–100%), and (D) air temperature (20–40 °C). One microclimate condition (e.g. wind speed) was varied per panel (see above) while all others were fixed as follows: wind speed (5 m s^{-1}), photosynthetic active radiation (1500 µmol m^{-2} s^{-1}), relative humidity (60%), and air temperature (25 °C).

exception was the L_w sensitivity to PAR across all canopy positions at an LAI of 1 and 5 (Fig. 6). In general, g_o was more sensitive in dense vegetation (LAI=10) and in lower

canopy positions. One additional notable trend was that α was most sensitive at the middle canopy position and an LAI of 5.

Discussion

Accurate predictions of the morphology and physiology spatial distribution influence on E_l within a canopy required a model (e.g. MAESTRA) that simultaneously solved for leaf-scale g_s, A_{net}, and energy balance as a function of leaf position. This study tested the ability of MAESTRA to predict within-crown and genotype-specific transpiration and, once validated, it was used to separate intraspecific differences in E_l brought about by morphological and physiological variation in leaf attributes. The spatial algorithmic approach used by MAESTRA was key to synthesize knowledge of single leaf morphology and physiology, and account for physics of energy balance. These results support the capability of MAESTRA to predict genotype-specific E_{cl} spatially. Aside from the spatial transpiration investigation on a single species of conifer (Wang and Jarvis, 1990) and a clone of hybrid poplar (Kim et al., 2008), to our knowledge no detailed simulation studies have looked at the effect of leaf morphological versus physiological constraints on transpiration within canopies. Moreover, the lack of intraspecific parameter differences prevented those studies from investigating either the full suite of parameters presented in this study or their effects along a vertical canopy depth profile. Thus, the present study is unique in that five genetically distinct genotypes that differ in their leaf-level effects on transpiration were examined. Simulation estimates and sensitivity analyses indicated that E_{cl} increased with decreasing L_w and vice versa at all canopy positions, whereas other parameters had a minimal impact (θ, E_j, τ_j, E_v, τ_v, Γ, and a). It was found that the L_w effect on transpiration at both the crown and canopy scale and among genotypes was not trivial. In effect, it was observed that the genotype with the smallest L_w (SR) had the greatest rate of transpiration across scales and among all the genotypes, and SR originated from the warmest climate. Moreover, when red maple genotypes were compared within a similar climate of origin, the crown transpiration differences among genotypes still fell along a gradient in L_w. Therefore, the results support the hypothesis that in a warmer climate the red maple genotype with smaller leaves may have an advantage over larger leaved genotypes as a result of an increased boundary layer conductance and the ability to prevent T_l from rising well above ambient T_{air}. The findings also suggest that on exposed warm sites, L_w will have a substantial effect on transpiration. This L_w attribute would seem highly adaptive for a plant occupying well-watered open sites such as the irrigated habitats of urban areas.

Within this study, a representation of parameter values that could be assigned on a plant functional type, provenance, ecotype, and/or genotype basis for a scaled-leaf model was evaluated. For instance, Royer et al. (2008) quantified leaf size changes in a study of red maple along a north to south T_{air} gradient. They found the smallest L_w in the warmest climate and formulated the hypothesis that variations in leaf sizes within red maple are an evolutionary adaptation that reduces the boundary layer to modify both

transpiration and sensible heat exchange in response to warmer site T_{airs}. Undoubtedly, changes in the thickness of the boundary layer have dramatic impacts on gas exchange and energy transport (for a recent review, see Vogel, 2009). The present results support the hypothesis of Royer et al. (2008) and also support the theoretical computer-based simulation study performed by Roth-Nebelsick (2001) who found leaf shape in *Acer* species to have a considerable influence on T_l across a wide array of wind speeds. It has now been demonstrated that leaf morphology, specifically L_w, should be considered when estimating transpiration among genotypes of red maple. Operating under boundary layer theory, this finding would be immediately applicable to better account for variation in the effects of L_w on transpiration among plant functional types, provenance, and/or ecotypes when scaling transpiration flux.

The exchange processes at the leaf level have important implications at much larger scales—such as the mesoscale flow pattern dynamics in the planetary boundary layer (e.g. Mascart et al., 1991; Giorgi and Avissar, 1997; Fraedrich et al., 1999). Although they were found to be important among genotypes of red maple, currently the majority (if not all) of land surface models do not use genotype-specific parameters in the water flux simulation process. It is common for them, however, to divide plants into functional types (e.g. Oleson et al., 2008) or vegetation classes (e.g. Houborg et al., 2009) when considering the different vegetation regimes across the globe. In so doing, some models standardize model parameters such as V_{cmax} or L_w across several vegetation classes or among different species (e.g. Houborg et al., 2009) or blanket all plant functional types with a general L_w value (e.g. Oleson et al., 2010). It is acknowledged that it may be impractical for regional- and global-scale terrestrial vegetation models to use genotype-specific parameters. However, L_w parameterization between grasslands versus broadleaf forests or coniferous versus broadleaf forests should be manageable at large spatial scales. Overall, the present data support the incorporation of leaf size effects into parameter sets of larger scale models for improved estimates of transpiration flux.

Wilson and Meyers (2007) in a study on seasonal variability in vegetation LAI, found that grasslands, deciduous forests, and croplands can have an LAI $\leqslant 2$ for ~50% of the year or more. In addition, large open gaps commonly occur in coniferous forests due to management or site conditions (Bladon et al., 2006; Wilson and Meyers, 2007). Relative to the present findings at the canopy scale, the lower the LAI, the greater the importance and impact of parameters such as V_{cmax} and g_1 on transpiration. However, to generalize the sensitivity of the output in the present study it must be asked if the variation within red maple morphology and physiology is different from that found in a deciduous forest or the range of variation used in previous assessments. Although others have not assessed global transpiration estimates at the intraspecific level, focusing instead on plant functional types, species, or vegetation classes, they have found the parameter V_{cmax} to account for 10–20% of the variability

in predicted transpiration (Alton *et al.*, 2007; Houborg *et al.*, 2009). The present results are similar and indicate uncertainties in predicted transpiration of up to ~20% within the red maple species alone. Although variation within red maple may be larger than other forest tree species, the present within-species investigation should be considered conservative in comparison with those performed across a wider array of genetics (e.g. among species or plant functional types). Moreover, the parameterization scheme used here would be considered one that does not amplify the response sensitivity along a vertical canopy depth profile by altering variation in a parameter such as leaf-N profiles (Alton *et al.*, 2007). The results, therefore, could reduce the uncertainty of models that estimate with either a standardized or omitted parameter specific to those which were found to be of less importance (e.g. those associated with the photosynthetic temperature response). Nevertheless, it does not preclude the importance of models accounting for temperature acclimation (Bauerle *et al.*, 2007; Houborg *et al.*, 2009).

Although the present findings support other studies that suggest that V_{cmax} and/or α are important transpiration model parameters (Harley and Baldocchi, 1995; Leuning *et al.*, 1995; Williams *et al.*, 1996; Alton *et al.*, 2007; Bauerle *et al.*, 2007, 2009; Houborg *et al.*, 2009), the study appears to be the first to illustrate that the sensitivity of transpiration model estimates to g_1 and V_{cmax} diminishes below the uppermost canopy layer. In addition, the results indicate that model estimate variation may arise due to intracanopy and intraspecific variability from L_w, R_d, g_o, and α as a result of leaf morphology, respiratory behaviour, stomatal physiology, or PAR capture characteristics, respectively. Usually, transpiration is less sensitive than photosynthesis to changes in those physiological parameters known to affect photosynthesis; however, transpiration is responsive to energy balance parameters. For example, transpiration is sensitive to L_w given that it has a direct effect on free and forced convection (Equations 1 and 3). Thus, the change in transpiration results from the wind speed and temperature interactions with L_w and leaf g_{bhF} and g_{bhf}. Alternatively, some photosynthesis model parameters are primarily responsible for characterizing the temperature effects on Rubisco kinetics and are not so important for determining water fluxes (e.g. E_j, τ_j, E_v, and τ_v). Thus, sensitivity analyses comparing the canopy spatial changes in E_{cl} provide insight into how L_w changes the within-canopy energy budget.

Similar to transpiration sensitivity, the separation of climate forcings on g_s, T_l, g_{bv}, Ω, and A_{net} estimates resulted in the same seven parameters (L_w, J_{max}, α, V_{cmax}, R_d, g_1, and g_o) having a ⩾5% impact. The continued response of model estimates to the seven parameters, regardless of a change in any one of the climate forcings (wind, PAR, RH, and T_{air}) independent of the others, indicates that the effects of the seven input parameters remains critical and responsible for most of the output variation. White *et al.* (2000), in an investigation of parameter sensitivity for net primary production prediction, also found a consistent and limited number of physiological variables to cause a change in estimates of net primary production. The study by White *et al.* (2000) did not investigate the spatial variation in parameter influences within a canopy but found that sensitivity to parameters would change based on climatic variation across biomes. The present results suggest that sensitivity to parameters varies within a canopy and interacts with foliage density. Additional research on predicting parameter spatial variability within canopies is warranted to reduce uncertainty of large-scale estimates. As a first attempt to quantify the spatial interactions of important parameters, future work should investigate the potential interacting effects of morphological and physiological parameter variation.

Conclusions

Spatial analyses revealed seven leaf traits that were influential on leaf, crown layer, and canopy transpiration estimates. Leaf transpiration was particularly sensitive to L_w along a vertical canopy depth profile. Given the magnitude of the transpiration changes caused by L_w from the leaf to canopy scale within red maple, it is expected that adding L_w to land surface models (e.g. Climate Land Model; Oleson *et al.*, 2010) will be a relatively easy means to alleviate one current parameterization inconsistency. In addition, the results indicate that the use of genotype-specific leaf morphology response functions may improve canopy-scale transpiration estimates.

Supplementary data

Supplementary data are available at *JXB* online.

Table S1. Leaf physiological parameters.
Table S2. Canopy structure parameters.
Table S3. Site-specific model parameters.
Table S4. Meteorological input parameters.
Table S5–S8. Sensitivity of MAESTRA within canopy estimates to variations in leaf morphology and physiology parameters.

Acknowledgements

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