

Measurement and modeling of the transpiration of a temperate red maple container nursery

William L. Bauerle^{a,*}, Christopher J. Post^b, Michael F. McLeod^c, Jerry B. Dudley^a,
Joe E. Toler^d

^a Department of Horticulture, Clemson University, Clemson, SC 29634-0375, USA

^b Department of Forest Resources, Clemson University, Clemson, SC 29634, USA

^c Department of Agricultural and Biological Engineering, Clemson University, Clemson, SC 29634, USA

^d Department of Experimental Statistics, Clemson University, Clemson, SC 29634, USA

Received 25 April 2002; received in revised form 13 August 2002; accepted 14 August 2002

Abstract

This study was designed to estimate transpiration in a container nursery under both irrigated and water stressed conditions using a biologically based canopy model. The model, MAESTRA, was parameterized with a suite of physiological measurements and an explicit response function for soil moisture deficit was incorporated. The model was validated against transpiration measurements monitored by the stem heat balance method in both irrigated and non-irrigated plots. Distinct disconnects between estimated and measured values were found at high soil moisture deficits. The data justify the incorporation of a soil moisture component to simulate transpiration of plants with root zones in limited soil volumes. The agreement between measured and modelled canopy transpiration separated at a soil moisture deficit of 0.85 or greater, however, estimates of daily transpiration simulated by the model were in agreement with sap-flow measurements when water was not limiting. The data indicate that cuticular conductance at soil moisture deficits ≤ 0.85 may explain the separation in model estimates and actual plant water loss.

© 2002 Elsevier Science B.V. All rights reserved.

Keywords: Stomatal conductance; Modeling; Transpiration; Red maple

1. Introduction

It is well known that water management is essential for the survival and growth of crops. Just as important, if not more so, is successful water man-

agement in limited soil volumes such as containerized plants. Either over watering or under watering plants can have negative consequences. Over watering can lead to leaching of nutrients that affect environmental quality, while water deficit can deleteriously affect potential growth. Management practices with nursery crops tend toward excessive water use due to fears of a decline in growth and production. Models to predict potential transpiration add to this fear by often over-estimating transpiration rates in water-stressed trees. One possible explanation for this over-estimation is not taking into account the

* Corresponding author. Tel.: +1-864-656-7433;

fax: +1-864-656-4960.

E-mail addresses: bauerle@clemson.edu (W.L. Bauerle),

cpost@clemson.edu (C.J. Post), mmcleod@clemson.edu

(M.F. McLeod), jerry_dudley@ncsu.edu (J.B. Dudley),

jtoler@clemson.edu (J.E. Toler).

water balance in the soil profile. Another explanation includes inadequate representation of canopy parameters.

Recent studies emphasize the need to go beyond whole-tree measurements of sap flow into stands of plants (e.g. Wullschleger et al., 2000), a necessary component of nursery scale water use modeling. Aerodynamically rough, well-ventilated canopies such as forests, orchards, or nurseries are well coupled to their environment. When aerodynamically rough conditions are present, stomatal conductance (g_s) can cause an increase in canopy conductance that is nearly proportional to transpiration (Jarvis and McNaughton, 1986). Micrometeorological techniques such as estimates using Bowen ratio, however, are not very feasible under nursery conditions because they require large amounts of fetch, whereas, the expense and logistics of monitoring individual tree sap flow does not lend itself to nursery conditions. Modeling synthesis of experimental measurements offers another viable approach to estimate water use in both well-watered and drought stressed canopies. To date, simplified forms of the Penman-Monteith equation are often used to estimate rates of canopy transpiration from atmospheric humidity deficits in aerodynamically well-coupled canopies (Phillips and Oren, 1998). Numerous models have been employed to estimate evapotranspiration (ET) from meteorological data in an attempt to relate the climatic conditions to a reference crop such as the Penman-Monteith well-irrigated short-green grass based equation (Schuch and Burger, 1997). The next step in this scenario is to develop a crop coefficient to compare the water use of a specific crop to that of a reference crop. Lost in this common procedure are a number of plant morphological and physiological features of both the crop canopy as a whole and the individual tree within the canopy. Furthermore, the assumption that adequate water exists in the soil profile can lead to overestimates of transpiration in water-stressed trees (Dye, 1996).

Water supply limits evaporation in dry environments when demand is independent of supply, and meteorological measurements and modeling become irrelevant when demand exceeds supply (Calder, 1998). The evaporation process primarily depends on six types of potential limits: advection, radiation, soil water, tree physiology, tree size, and raindrop size.

Tree physiologists attempt to account for these limits through biophysical models that have become increasingly complex and difficult to apply to real-world water resource problems (Calder, 1998). Alternatively, oversimplification can misrepresent crop parameters, especially when primary controls are not well defined. Dynamic ET factors can complicate the problem. For example, under semiarid conditions, Calder et al. (1993) found soil water availability and plant physiological controls to limit evaporation; whereas, in a wet UK upland, atmospheric demand through advection and radiation controls were the prominent evaporative drivers. Robust model estimates, therefore, rely on identification and parameterization of controlling limits to accurately estimate water use under inadequate supply of one or more limiting factors.

Leaf transpiration and photosynthesis are related to radiation flux density in a non-linear fashion that can be overestimated if averaged over a long time period and large spatial area (Smolander and Lappi, 1985). Alternatively, MAESTRO, a model originally developed by Norman and Jarvis (1974, 1975) and validated by Wang and Jarvis (1990a), takes into account canopy radiation and photosynthesis of single trees at relatively short time intervals. The model holds potential advantages for nursery, forest, and orchards in that structural parameters such as tree position, crown shape, and dimensions are specified. Moreover, specific physiological values of the species under study are incorporated into model calculations, potentially yielding a more accurate estimate of water use for a specific crop.

The model MAESTRO has been described and applied by Wang and Jarvis (1990a,b) and recently updated and renamed MAESTRA (Medlyn et al., 1999). The aim of this paper is to parameterize and analyze the ability to model water use using the canopy model MAESTRA (Medlyn et al., 1999) in response to water deficits under nursery conditions. The MAESTRA model parameters were estimated from leaf scale gas exchange measurements and validated against whole-plant flux data at ambient atmospheric CO_2 . The validity of the model will be compared to whole-plant flux data (E) under both well-watered and water stress conditions. Finally, the model will be used to simulate below-potential transpiration rates.

2. Materials and methods

2.1. Plant material

In August 2001, South Carolina grown *Acer rubrum* (red maple) cultivars were shipped to Clemson University, transferred to an outdoor gravel pad of open terrain, and fit with pressure-compensating micro emitters (ML Irrigation Inc., Laurens, SC). Prior to arrival, cultivars were transplanted into 15 gal Spin Out treated plastic pots containing a mixture of pine bark and sand (20:1 (v/v)), fertilized with 8.3 kg m^{-3} of Nutricote™ 20N-3.0P-8.3 K type 360 (Chiso-Asahi Inc., Japan). Upon arrival, all pots were watered to saturation and permitted to drain for 18 h.

2.2. Water measurements

After drainage and thereafter on alternate days, bulk volumetric water content of each container was measured in four locations with a Theta Probe type ML2 (Delta-T Devices, Cambridge, England) at 10 and 20 cm below the rooting medium surface. The readings were taken in pre-drilled locations on opposite sides of the pot. Drilled holes were large enough to allow the probe adequate movement and contact with the soil surface within the container. The readings were then averaged in order to estimate bulk volumetric water content for each container.

We undertook a preliminary experiment to construct soil moisture release curves on representative soil samples ($n = 6$). Our pressure plate apparatus was capable of 1500 kPa. In order to relate soil moisture to plant water relations, we paired a sub-sample of leaf water potential (Plant Moisture Status Console, Soil Moisture Equipment Corp., Santa Barbara, CA) to bulk moisture content of the rooting medium. For water potential readings, one leaf per tree was selected on the south side and covered with aluminum foil 24 h prior to the reading. At solar noon, the leaf water potential was measured in parallel with soil moisture. For leaf water potential readings, a leaf was removed and, while still covered with foil, its water potential measured. This measurement provided an estimate of the xylem stream water potential under conditions in which mid-afternoon (13:00–15:00) transpiration is minimized (Bauerle et al., 1999).

2.3. Sap-flow measurements

Commercially available sap-flow gauges (Dynamax Inc., Houston, TX) were used for all measurements. The gauges have been described in detail elsewhere (Steinberg et al., 1990). Briefly, a flexible heating element surrounds the stem and heat is accounted for with a thermopile for radial heat loss and thermocouples above and below the heater for vertical conductive heat loss. A one-layer thick 5 cm piece of Saran Wrap® (Dow Brands, Indianapolis, IN) encircled the stem to exclude moisture from the heater element. A thin coat of silicone-based waterproof grease (Dow Corning 64, Dow Corning, Midland, MI) was applied to the Saran wrapped stem segment to facilitate gauge contact. The sap-flow gauges (Models SLD 13, 16, and 19, Dynamax) were installed between the two foam insulation rings, approximately 60 cm above the container soil surface. Also, a weather shield encased the gauge and rubber sealant circled the stem–gauge interface at both the upper and lower stem extrusion points. Lastly, aluminum foil was placed over the gauge assembly and sealed to the stem with Parafilm (American National Can™, Greenwich, CT) and white elastic cord. The foil continued from the base of each gauge to the plastic skirt for a distance of about 50 cm. Power supply for the heaters were set between 3.5–4 V (Model AVRDC, Dynamax), a manufacturer recommended setting. At times when sheath conductivity was not estimated for radial heat loss, heating elements were operated from 4:00 a.m. to 8:00 p.m. to minimize overheating of the stem during night time low flow conditions. Gauge signals were monitored by a CR10X data logger (Campbell Scientific, Logan, UT) equipped with a multiplexer (AM416, Campbell Scientific, Logan, UT) every 30 s; and 15-min averages were computed and stored in a storage module (SM4M, Campbell Scientific, Logan, UT). Thermal conductivity was assumed to be constant with an average value of $0.42 \text{ W m}^{-1} \text{ }^\circ\text{C}^{-1}$ (Steinberg et al., 1989). Sheath conductivity (K_{sh}), was computed as the average of the measured K_h values between 02:00 and 04:00 h, four times over the course of the experiment.

2.4. Nursery experiments

Sixty containerized red maple saplings were spaced 1.5 m center-to-center. Plants were irrigated six

times daily to container capacity prior to imposing drought. For each cultivar, treatments consisted of a well-watered control and a drought treatment where water was withheld. Randomly selected plants from each source and treatment combination were chosen for continuous sampling of sap flow. To eliminate evaporation from the soil surface and/or water penetration in case of rain, white plastic bags were cut and sealed to the stem with Parafilm (American National Can™, Greenwich, CT). The bottom ends of the bags were left open and secured to the pots with an elastic fit. Wrapping the exterior of each container with aluminum foil reduced radiation load on containers.

Sixteen sap-flow gauges were installed on the trunks of red maple. Trunk diameter at the point of gauge attachment ranged from 13.7 to 24.9 mm. Of the gauges employed, six were on well-watered control plants and eight were on plants subjected to a drought stress and well-watered recovery cycle. Two additional trees with unheated gauges were continuously monitored to check for environmentally induced fluctuations in the stem temperature difference across the heater. The gauges were evenly distributed between two red maple cultivars, Summer Red and October Glory®, in both the well-watered ($n = 3$) and drought stressed ($n = 4$) treatments.

When the media of an individual replicate of a given cultivar reached a bulk volumetric water content of $0.090 \text{ m}^3 \cdot \text{m}^{-3}$, a timed drought and recovery cycle was initiated. Plants were re-watered to container capacity the evening of the 5th day and tracked for recovery responses. When a plant completed its cycle, it was removed from the study.

Whole-tree sap-flow rates and microclimatic conditions were measured simultaneously. Meteorological data (air temperature, precipitation, humidity, photosynthetic photon flux density (PPFD), wind speed, wind direction, and direct and diffuse solar radiation) were collected at a height of 3 m using a Campbell Scientific Weather Station located on the north side immediately adjacent to the experimental plot and within 0.25 m of canopy level.

2.5. Gas exchange determinations of leaf transpiration

During the experiment, transpiration measurements were taken twice daily in conjunction with

soil moisture. Transpiration was measured on the first fully expanded leaf using a portable steady state gas-exchange system (CIRAS-I, PP Systems, Haverhill, MA) equipped with a light and temperature controlled cuvette (Model PLC5 (B); PP Systems). Measurements were taken on the youngest fully expanded and undamaged leaf from 09:00 to 12:30 h. The leaves were tagged and daily measurements were taken in random order to compensate for any effects caused by time of sampling. All leaves were naturally south oriented and fully exposed to incoming radiation to reduce environmental interactions. Leaf temperature was controlled at 25°C ; PPFD was maintained at $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ with the cuvette light source; and vapor pressure deficit in the cuvette was kept at $1.3 \pm 0.4 \text{ kPa}$. Measurements at saturating PPFD were recorded after reaching steady state.

2.6. Model parameterization

In this study, MAESTRA—a 3D model of forest canopy radiation absorption, photosynthesis, and transpiration—was parameterized for an experimental containerized *Acer rubrum* site near Clemson, SC, USA (latitude, $34^\circ 40' 8''$; longitude, $82^\circ 50' 40''$). Model structure and parameterization followed that of Luo et al. (2001). Briefly, the canopy is represented by an array of semi-ellipsoidal tree crowns in an area of 90 m^2 . The trees were evenly spaced in nursery drip irrigated rows. Leaf area of all trees was measured at the end of the study by a destructive harvest with an LI-3100 leaf area meter (Li-Cor Inc., Lincoln, NE). Parameter values used by the photosynthesis and stomatal conductance models are listed in Table 1. Unless otherwise noted, parameter values were not changed from that of the Luo model (Luo

Table 1

Summary of CO_2 exchange and stomatal conductance model parameters on *Acer rubrum* (red maple) taken from Bauerle (2001)

Parameter	Units	<i>A. rubrum</i>
V_{cmax} (25°C)	$\mu\text{mol m}^2 \text{ s}^{-1}$	77.3 ± 2.9
J_{max} (25°C)	$\mu\text{mol m}^2 \text{ s}^{-1}$	189.1 ± 5.0
R_d (25°C)	$\mu\text{mol m}^2 \text{ s}^{-1}$	1.7 ± 0.1

Maximum carboxylation rate (V_{cmax}) and estimates of the potential electron transport rate (J_{max}) were calculated from the biochemical model of von Caemmerer and Farquhar (1981), incorporating the parameter values of Kirschbaum and Farquhar (1984).

et al., 2001). Leaf area index was assumed to be constant during each simulation.

2.7. Modeling the stomatal canopy conductance

We followed the approach of Jarvis (1976), modified by Granier and Loustau (1994) for a maritime pine canopy. Parameter estimates for k_{s1} and k_{s2} , derived and validated by Granier and Loustau (1994), were used to parameterize the effect of soil drought on stomatal function within MAESTRA by constraining water loss as soil water depleted. We made the following changes to their approach: the mean bi-daily value of soil moisture deficit was substituted for the leaf water potential (Schulze et al., 1987). We substituted PPFd into the Granier and Loustau (1994) equation, shown to be of primary importance in modeling the response of stomatal conductance (Massman and Kaufmann, 1991). The final form of the model was as follows:

$$g_s = k_1 \left(\frac{P_s}{P_s + k_r} \right) \left(\frac{1 - k_{d1} \delta q}{1 + k_{d2} \delta q} \right) [1 - k_{s1} \exp(k_{s2} \delta M)] \quad (1)$$

where k_1 , k_r , k_{d1} , k_{d2} , and k_{s2} are estimated parameters (Table 2), P_s is the PPFd ($\mu\text{mol m}^{-2} \text{s}^{-1}$), δq the water vapor deficit (g kg^{-1}), and δM is the soil moisture deficit. Soil moisture deficit (δM) was estimated by

$$\delta M = \frac{(M_{\max} - M)}{(M_{\max} - M_{\min})} \quad (2)$$

where M_{\max} , M_{\min} and M are the maximal, minimal and actual root zone volumetric soil moisture, respectively.

Other functions of these variables were tested (e.g. Ogink-Hendriks, 1995), but the estimates derived by Granier and Loustau (1994) gave the best fit between predicted and observed values of E . We compared the

estimates to the stomatal response of both sap flow and gas exchange measurements. A negative exponential function fit to our data agreed well with the response function derived in the Granier and Loustau (1994) dataset; therefore, we used those estimates in our model.

2.8. Validation tests

Using the physiological and physical parameters, the E values were computed and compared with the observed values. Predicted transpiration values were also compared to potential evapotranspiration of both the Penman-Monteith with zero canopy resistance and van Bavel combination equations. These values were compared with MAESTRA estimates and observed values of transpiration calculated from sap flow and gas exchange measurements on both a 15-min and daily basis.

The Penman-Monteith equation for a leaf with stomata just on the lower surface only can be defined as

$$E_{\text{crown}} = \frac{SR_n + \rho_a C_p D g_a}{\lambda [s + \gamma (1 + g_a / g_{\text{crown}})]} \quad (3)$$

where E_{crown} is transpiration ($\text{kg m}^{-2} \text{s}^{-1}$), s the slope of the saturation vapor pressure deficit versus temperature at air temperature (kPa K^{-1}), R_n net radiation (W m^{-2}), ρ_a the density of dry air (kg m^{-3}), C_p the specific heat capacity of air ($\text{J kg}^{-1} \text{K}^{-1}$), D the vapor pressure deficit (kPa), g_a the boundary layer conductance (m s^{-1}), λ the latent heat of evaporation of water (J kg^{-1}), γ the psychrometer constant (kPa K^{-1}), and g_{crown} is the crown conductance (m s^{-1}).

The transpiration rate of individual trees is known in our study and in that situation, crown conductance can be calculated by substituting E_{crown} , g_a , and weather station data into the inverted Penamn-Monteith equation. We used the inverse form given in Granier and Loustau (1994):

$$\frac{1}{g_{\text{crown}}} = \left[\frac{s}{\gamma} \left(\frac{R_n - \lambda E_{\text{crown}}}{\lambda E_{\text{crown}}} \right) - 1 \right] \frac{1}{g_a} \frac{\rho_a}{E_{\text{crown}}} \frac{C_p}{\lambda \gamma} \quad (4)$$

The combination model of potential evaporation was a formulation given in van Bavel (1966):

$$LE_0 (\text{m}^2/\text{s}^{-1}) = - \frac{\Delta/\gamma H + LB_v d_\alpha}{\Delta/\gamma + 1} \quad (5)$$

Table 2
Estimates of the model parameters, taken from Granier and Loustau (1994)

Parameter	Estimates	Units
k_1	0.02017	mm s^{-1}
k_r	497.791	W m^{-2}
k_{d1}	0.0360	kg g^{-1}
k_{d2}	0.389	kg g^{-1}
k_{s1}	0.0156	–
k_{s2}	4.269	–

where L is the latent heat of vaporization, E_0 the potential evaporation rate, Δ/γ a dimensionless number dependant on the air temperature at the elevation above the surface, H the sum of energy inputs at the surface other than those of latent heat and sensible heat, B_v the turbulent transfer coefficient, and d_α is the saturation vapor pressure deficit of air.

The change in observed and predicted transpiration values (y) with increased soil moisture deficit (x) was characterized by the exponential function

$$y(x) = \alpha + \beta e^{-\lambda x} \quad (6)$$

where response declines at an ever decreasing rate, according to shape parameter λ toward asymptotic value α as $x \rightarrow \infty$, parameter β shifts the location of the curve along the x -axis by determining the intercept, $y(0) = \alpha + \beta$. The above relationships was fitted by non-linear least squares using an iterative process to obtain parameter estimates.

3. Results

3.1. Whole-tree sap flux

Stem diameters of the 14 sap flow measured trees at gauge height (approximately 60 cm above the container surface) ranged from 13.7 to 24.9 mm, leaf area

from 1.1 to 2.85 m², and length of canopy from 1.07 to 1.5 m (Table 3). Fig. 1 depicts sap flow of four representative trees (Fig. 1b) in relation to potential transpiration of both the Penman-Monteith and van Bavel combination equations (Fig. 1a) and soil moisture deficit (Fig. 1c) for the period Julian day 245 to 262. Potential evapotranspiration calculated by the Penman-Monteith and van Bavel combination equations was nearly identical, leaving different symbols undecipherable (Fig. 1a). It is important to note that container-to-container variation in soil water content prevented aggregating trees and, therefore, sap flow and soil moisture deficit is expressed for individual trees in Fig. 1b and c. In addition, Fig. 1b illustrates the variation in water loss among irrigated trees and trees subjected to progressive water stress within the plot at similar soil moisture deficit. First, for irrigated trees, transpiration rate calculated on a unit leaf area basis varied from day-to-day in parallel with potential transpiration. Second, as soil moisture deficit increased in trees subjected to water deficit, sap flow declined and became disconnected from the other environmental variables that drive transpiration. In measurement trees subjected to water deficit when soil moisture deficit rose above 0.5, sap-flow measurements began to deviate from those of potential transpiration (Fig. 1b).

Fig. 2 illustrates the relationship between measured and modeled water loss under irrigated conditions.

Table 3

Above ground biometric characteristics of the *A. rubrum* trees used for sap-flow measurements

Treatment	Tree no.	Diameter at gauge height (cm)	Length of canopy (m)	Leaf area (m ²)	x-radii (m)	y-radii (m)
Irrigated	1	1.73	1.22	1.79	0.61	0.74
	2	1.73	1.50	1.56	0.61	0.74
	3	1.88	1.44	2.61	0.39	0.44
	4	2.0	1.19	2.34	0.43	0.58
	5	2.13	1.27	2.85	0.41	0.64
	6	1.67	1.42	2.03	0.41	0.71
Drought	7	1.43	1.27	1.10	0.36	0.64
	8	2.20	1.35	2.84	0.48	0.66
	9	2.49	1.07	2.64	0.46	0.53
	10	2.09	1.12	2.30	0.43	0.56
	11	1.94	1.09	2.25	0.41	0.53
	12	1.78	1.32	1.31	0.28	0.66
	13	1.85	1.37	1.75	0.36	0.69
	14	1.87	1.12	1.42	0.36	0.56

An average measure of the south and north x -radii direction was taken with a flexible meter tape. The y -radii was measured from a ladder using a flexible meter tape.

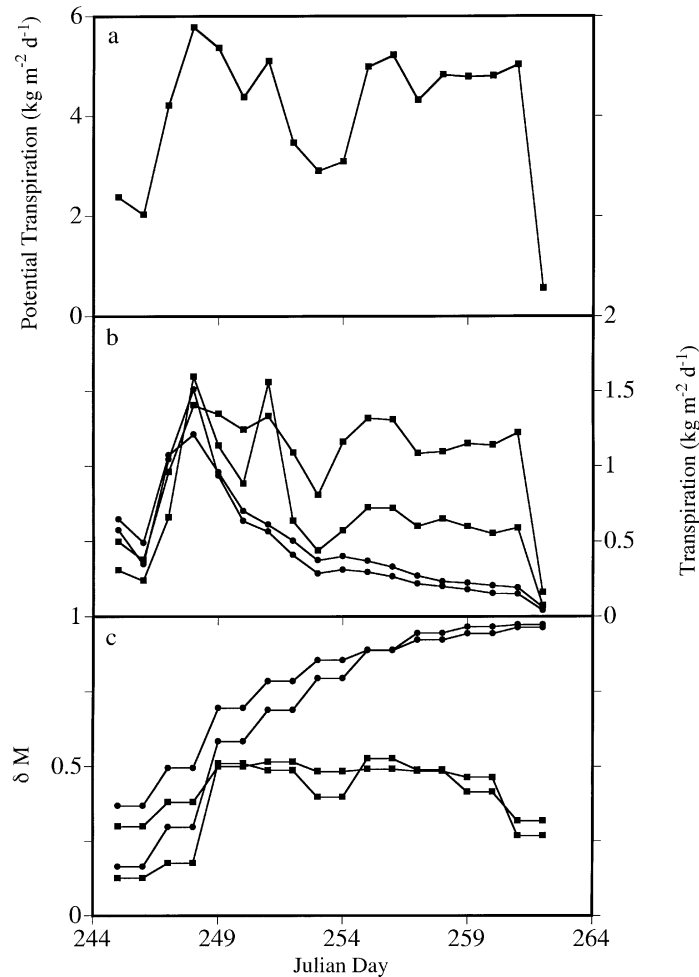


Fig. 1. Variation of (a) potential evapotranspiration calculated by the Penman-Monteith combination equation (solid squares) and the van Bavel combination equation (open squares), which is not distinguishable due to the similar estimate, (b) actual transpiration of two representative irrigated individual trees (trees 1 and 6; solid squares) and two representative drought stressed individual trees (trees 7 and 12; solid circles) on a m^2 crown projection area basis, (c) soil moisture deficit (δM) of the respective trees from Julian day 245 to 262.

Measured water loss of a representative tree (tree 4) and that predicted by MAESTRA on a 15-min basis from Julian day 248–259 agree under various daily environmental conditions at δM values below 0.5. Again, it is important to note that individual representative trees are presented due to the container-to-container variation in soil moisture values. Soil moisture deficit was relatively low (below 0.4) and did not appear to influence either measured or predicted E . Overall, the model agreed well with measured sap flow under these conditions and appeared to be sensitive enough to es-

timate the highest and lowest transpiration rates. The response to rapidly changing environmental variables, however, was generally underestimated by the model, which resulted in a water loss estimate higher than that measured by sap flow.

In comparison to irrigated measured and modeled values, Fig. 3 illustrates a representative drought stressed tree for the same period as shown in Fig. 2. Based on Eq. (2), soil moisture deficit was calculated for each individual tree and date. The model appeared to be sensitive enough to estimate the lowest rates

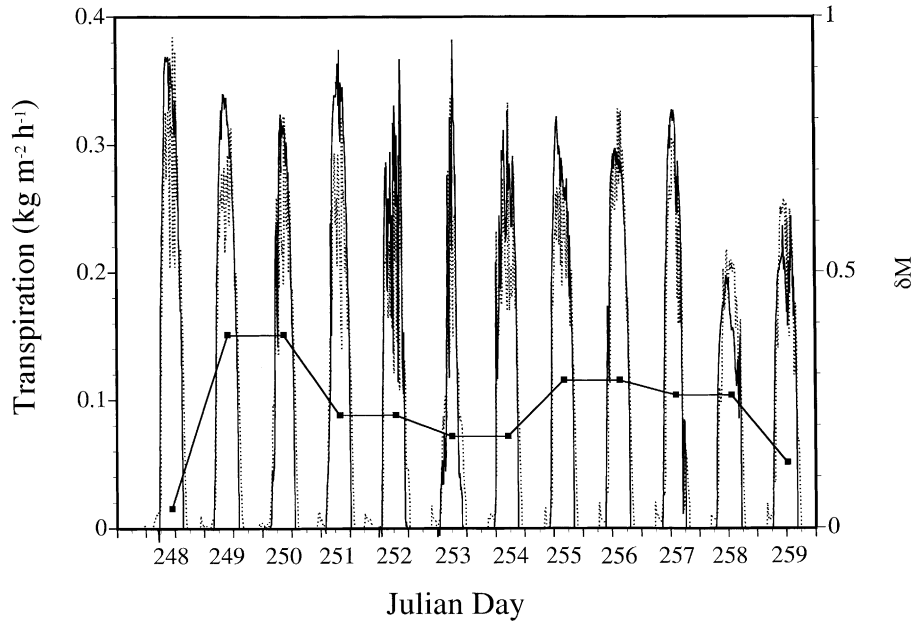


Fig. 2. Comparison of transpiration evolution for a representative irrigated tree (tree 4; broken line) to estimated transpiration using the canopy transpiration model (solid line) from Julian day 248 to 259. The daily soil moisture deficit is depicted by solid squares connected by a solid line.

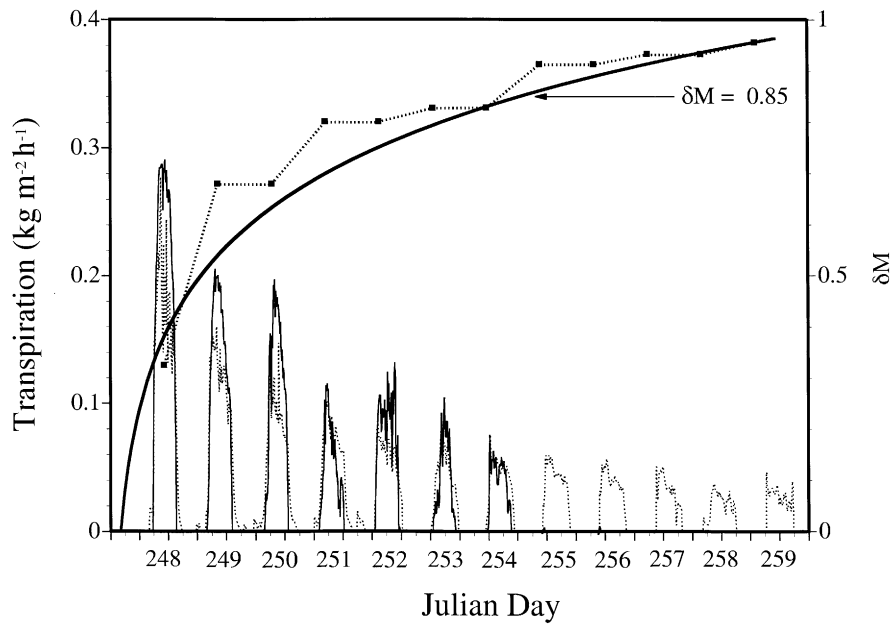


Fig. 3. Comparison of transpiration evolution for a representative drought stressed tree (tree 13; broken line) to estimated transpiration using the canopy transpiration model (solid line) from Julian day 248 to 259. The daily soil moisture deficit (δM) is depicted by solid squares connected by a broken line. The non-linear curve indicates the soil moisture deficit stomatal function response in the model.

of transpiration unless soil moisture deficit exceeded 0.85. A moisture deficit of this magnitude equates to volumetric water content slightly below $0.11 \text{ m}^3 \cdot \text{m}^{-3}$, a laboratory calculated estimate performed on our soil. Beyond the threshold of 0.85, model predictions became unreliable and underestimated water loss in comparison to both sap-flow and gas exchange measurements. As long as soil moisture deficit remained below 0.85, the stomatal function developed for maritime pine by Granier and Loustau (1994) worked well for our red maple container nursery. The non-linear stomatal function of the Granier and Loustau function and that of our measured values are similar, as might be expected from physical parameter derivations (Fig. 3).

Sap-flow measurements (kg per day) and information on the biometric characteristics of individual trees were used to estimate daily water use in relation to soil moisture deficit (Fig. 4). For the 14 measurement trees, there was a clear relationship between soil moisture deficit and water used (Fig. 4). The intercept of this relationship came close to crossing zero in the measured trees but fell short of zero in the model predictions. Other than soil moisture deficits above 0.85, model and measured mean water loss estimates were comparable and roughly equivalent.

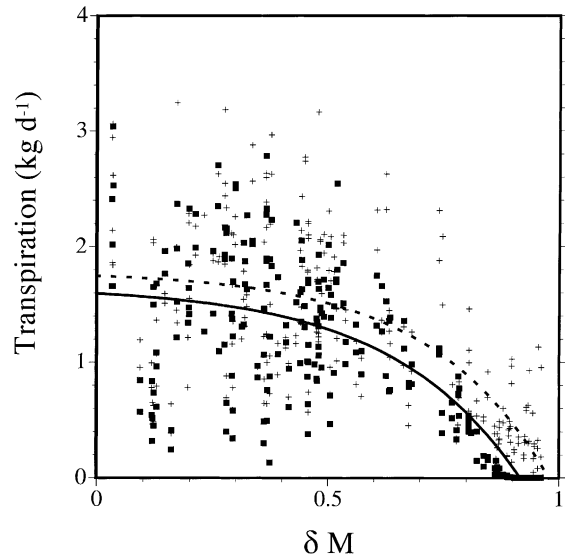


Fig. 4. Daily mean predicted transpiration (solid squares) and actual mean transpiration (crosses) in relation to soil moisture deficit. The non-linear curves indicate the soil moisture deficit stomatal function response in the model (solid line) and measured (broken line).

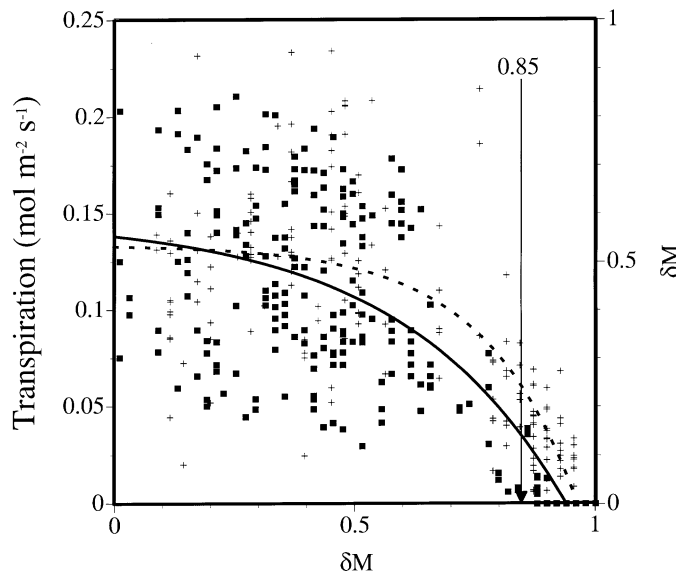


Fig. 5. Predicted transpiration (E ; solid squares) and actual transpiration (crosses) at PPFD $1000\text{--}1020 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in relation to soil moisture deficit. Arrow indicates soil moisture deficit at which predicted values become erroneous.

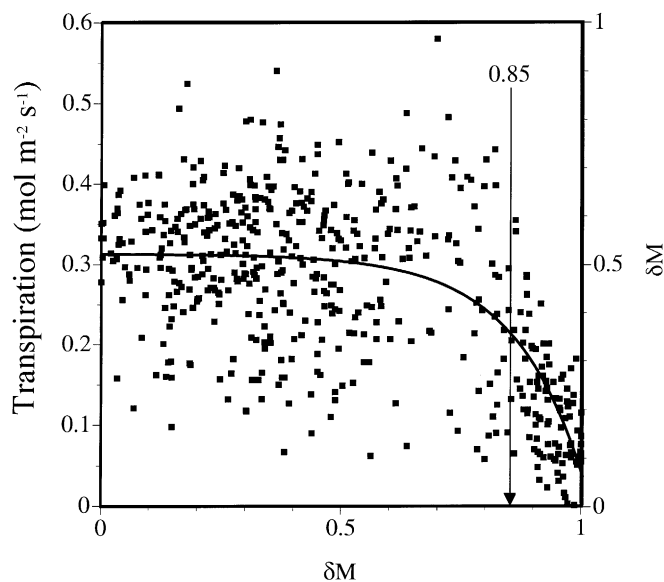


Fig. 6. Leaf level transpiration (solid squares) measured with the gas exchange unit at PPFD 1000–1020 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The data is expressed in relation to soil moisture deficit. Arrow indicates soil moisture deficit at which predicted values become erroneous.

3.2. Comparison between leaf and canopy transpiration

Transpiration, measured and modeled from sap-flow data collected every 15 min were selected at a PPFD 1000–1020 $\mu\text{mol m}^{-2} \text{s}^{-1}$, a value shown to saturate the red maple photosynthetic apparatus in a prior study (Bauerle, 2001), is illustrated as shown in Fig. 5. The negative exponential function, fit to modeled and measured transpiration independently, described the negative influence of soil moisture deficit. The effect of soil moisture deficit increased dramatically above 0.70; δM did not appear to exert a strong influence below this value. At a threshold δM value of 0.85, the model underestimated transpiration and did not agree with measured trends of potential transpiration derived from environmental meteorological parameters. The curvatures of measured and modeled negative exponential functions were slightly different due to underestimated water loss at high soil moisture deficits (>0.85).

To provide an independent measure of transpiration, gas exchange estimates of leaf level transpiration are as shown in Fig. 6. The measured values were taken under similar light levels of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and again the curvature of the negative exponential

function, fit to measured transpiration, described the negative influence of soil moisture deficit. Gas exchange values of E , however, were nearly twice those of either measured or modeled estimates.

4. Discussion

Internal tree physiological and biometrical conditions, as well as external atmospheric and soil water status, provide the framework for tree transpiration. Using the MAESTRA biological process model, estimated transpiration of a red maple container nursery was validated with measured transpiration rates. The scale of the study was appropriate to identify the need for stomatal response functions, where our results indicate that the incorporated parameterizations effectively capture the important PPFD, temperature, and soil moisture dependences of water loss from individual trees of red maple in a container nursery. On a quarter hourly basis, the model overestimates at high evaporation rates and underestimates at low soil moisture, a possible result of soil water depletion around the roots (Bosveld and Bouten, 2001). Although soil moisture deficit may influence estimated transpiration under low soil moisture conditions, the extreme

water deficits experienced in this study are not likely under managed nursery conditions. Nonetheless, they explicitly uncover a possible model limitation at low soil moisture conditions.

The ability of a tree to adjust H₂O exchange with the ambient atmosphere is primarily a function of stomatal response. Good parameterization and general use of a model require the inclusion of a wide range of environmental conditions. The soil moisture manipulation period in the study contained extreme wet, cloudy, dry and warm days. Additionally, with the exception of flooded conditions, the variation from container capacity to extreme soil water deficit spanned the breadth of all possible soil moisture deficits. Clearly, including a soil moisture function in the model enhances the general applicability. This may be relevant when models are used to schedule irrigation or when used to model photosynthetic response. During drought, water absorption by roots from the soil seemed to continue across the full range of observed soil moisture deficits in measured water loss. In contrast, modeled estimates indicated little to no water loss at soil moisture deficits above 0.85. Similar to forest trees in a plantation, where the relationship between soil water in the upper meter of soil and daily stand water use identifies the effect of water availability in the upper soil horizons on transpiration (Teskey and Sheriff, 1996), containerized nursery trees show a close correspondence between the rate of evapotranspiration and soil water content.

Independent measures of both sap flow and leaf gas exchange indicated that water loss still occurs above 0.85. In unstressed vascular plants, stomatal transpiration represents approximately 90% of total water losses (Monneveux and Belhassen, 1996). One possible explanation of transpirational water loss at extreme water deficits, when stomata are likely closed, is the effect of cuticular transpiration. Cuticular transpiration is a well known phenomena in leaves (Boyer et al., 1997) and identifies an incomplete part of the MAESTRA model. The known root system depth and rain shielded soil volume made it possible to predict the occurrence and severity of soil water deficits from the relationship between transpiration rate and available soil water within the rooting zone, thus eliminating the potential uncertainty of soil water recharge mechanisms. Evaluating the cuticular contribution to gas exchange is relatively unexplored

in intact leaves and difficult due to stomata in the epidermis (Boyer et al., 1997). In grape leaves, Boyer et al. (1997) found the cuticular conductance to be 5.7% of that of the total conductance for water vapor. Our findings on containerized red maple indicate that under severe water stress, when stomata are likely closed, transpirational water loss can reach approximately 10% of the water vapor loss under conditions of high evaporative demand and small water deficit.

The need for complex, multilayer models increases as the scale diminishes from the region to the forest allowing for within canopy allocation of parameters appropriate to different foliage (Whitehead, 1998). Incorporation of detailed process information, common to the bottom-up approach, facilitates prediction under conditions other than those in which the model was derived. Crop coefficients are commonly used to estimate water use in woody ornamental nurseries (Schuch and Burger, 1997). Crop coefficients were originally developed for uniform canopies such as alfalfa, but containerized plants in nursery production situations have more similarities to stands of vegetation. Moreover, “universally valid” crop coefficients are nonexistent, even in fully developed canopies, because the values are subject to solar radiation, air temperature, air vapor density, and wind speed (Annandale and Stockle, 1990). An integrated biological process approach, without the use of a crop coefficient, can further refine water balance models and predict evapotranspiration directly from Penman-Monteith. Leaf level simulation models of CO₂ and H₂O exchange have been successfully parameterized and applied to a deciduous forest (e.g. Harley and Baldocchi, 1995; Baldocchi and Harley, 1995). No model closely matches experimental data in all situations and errors must be expected. MAESTRA, an integrated multilayer biological process model, can synthesize the complex and non-linear forcing of environmental variables on biological systems, as well as predict container nursery water use without the uncertainties of crop coefficients.

4.1. Concluding remarks

The results indicate that when soil water is extractable, measured and modeled transpiration follows that of atmospheric demand. In contrast, when soil water becomes limiting during progressive drought,

transpiration is not only reduced, but diverges from atmospheric driving variables. Surprisingly, water loss continued even under severe water deficit, cuticular conductance being one possible explanation. As all the parameters of the model can be measured directly, it can be applied without calibration. However, in its present state, the model does not consider the effect of cuticular transpiration on evapotranspiration and is, therefore, not applicable to severe soil water stress conditions. Transpiration can vary between plants at the same site (e.g. Hatton and Wu, 1995); however, the model is spatially explicit and allows for assessment of positional variation in evaporation. Further work is required to evaluate containerized plants in different conditions, such as abnormal precipitation and temperature, and to check whether modeling the water balance in the soil profile would then permit prediction of the fraction of potential transpiration taking place both spatially and temporally.

Acknowledgements

We thank B. Medlyn for technical assistance with the model, E. Bauerle for earlier reviews of this manuscript, and T. Owino for helpful discussions. The State of South Carolina Research and Experiment Station funded this research.

References

- Annandale, J.G., Stockle, G.O., 1990. Sensitivity analysis of evapotranspiration crop coefficients fluctuation with climate. *Trans. ASAE* 90, 2645.
- Baldocchi, D.D., Harley, P.C., 1995. Scaling carbon dioxide and water vapor exchange from leaf to canopy in a deciduous forest. Part II. Model testing and application. *Plant Cell Environ.* 18, 1157–1173.
- Bauerle, W.L., Hinckley, T.M., Cermak, J., Kucera, J., Bible, K., 1999. The canopy water relations of old-growth Douglas-fir trees. *Trees* 13, 211–217.
- Bauerle, W.L., 2001. The water relations of *Acer rubrum* L. ecotypes from contrasting hydrologic habitats. Ph.D. Dissertation, Cornell University, Ithaca, NY, pp. 152.
- Bosveld, F.C., Bouten, W., 2001. Evaluation of transpiration models with observations over a Douglas-fir forest. *Agric. For. Meteorol.* 108, 247–264.
- Boyer, J.S., Wong, S.C., Farquhar, G.D., 1997. CO₂ and water vapor exchange across leaf cuticle (epidermis) at various water potentials. *Plant Physiol.* 114, 185–191.
- Calder, I.R., 1998. Water use by forests, limits and controls. *Tree Physiol.* 18, 625–631.
- Calder, I.R., Hall, R.L., Prasanna, K.T., 1993. Hydrological impact of Eucalyptus plantation in India. *J. Hydrol.* 150, 635–648.
- von Caemmerer, S., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Plantation* 156, 376–387.
- Dye, P.J., 1996. Response of *Eucalyptus grandis* trees to soil water deficits. *Tree Physiol.* 16, 233–238.
- Granier, A., Loustau, D., 1994. Measuring and modeling the transpiration of a maritime pine canopy from sap-flow data. *Agric. For. Meteorol.* 71, 61–81.
- Harley, P.C., Baldocchi, D.D., 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. Part I. Leaf model parametrization. *Plant Cell Environ.* 18, 1146–1156.
- Hatton, T.J., Wu, H.I., 1995. Scaling theory to extrapolate individual tree water use to stand water use. *Hydrol. Proc.* 9, 527–540.
- Jarvis, P.G., 1976. The interpretations of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philos. Trans. R. Soc. London Ser. B* 273, 593–610.
- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15, 1–49.
- Kirschbaum, M.U.F., Farquhar, G.D., 1984. Temperature dependence of whole-leaf photosynthesis in *Eucalyptus pauciflora* Sieb. ex Spreng. *Aust. J. Plant Physiol.* 11, 519–538.
- Luo, Y., Medlyn, B., Dafeng, H., Ellsworth, D., Reynolds, J., Katul, G., 2001. Gross primary productivity in Duke Forest: modeling synthesis of CO₂ experiment and Eddy-flux data. *Ecol. Appl.* 11 (1), 239–252.
- Massman, W.J., Kaufmann, M.R., 1991. Stomatal response to certain environmental factors: a comparison of models for subalpine trees in the Rocky Mountains. *Agric. For. Meteorol.* 54, 155–167.
- Medlyn, B.E., Badeck, F.-W., De Pury, D.G.G., Barton, C.V.M., Broadmeadow, M., Ceulemans, R., De Angelis, P., Forstreuter, M., Jach, M.E., Kellomaki, S., Laita, E., Marek, M., Philippot, S., Rey, A., Strassmeyer, J., Laitinen, K., Liozon, R., Portier, B., Roberntz, P., Wang, K., Jarvis, P.G., 1999. Effects of elevated CO₂ on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant Cell Environ.* 22, 1475–1495.
- Monneveux, P., Belhassen, E., 1996. The diversity of drought adaptation in the wide. *Plant Growth Regulat.* 20, 85–92.
- Norman, J.M., Jarvis, P.G., 1974. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Part III. Measurements of canopy structure and interception of radiation. *J. Appl. Ecol.* 12, 375–398.
- Norman, J.M., Jarvis, P.G., 1975. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Part V. Radiation penetration theory and a test case. *J. Appl. Ecol.* 12, 839–878.
- Ogink-Hendriks, M.J., 1995. Modeling surface conductance and transpiration of an oak forest in The Netherlands. *Agric. For. Meteorol.* 74, 99–118.
- Phillips, N., Oren, R., 1998. A comparison of daily representations of canopy conductance based on two conditional time

- averaging methods and the dependence of daily conductance on environmental factors. *Ann. Sci. For.* 55, 217–235.
- Schuch, U.K., Burger, D.W., 1997. Water use and crop coefficients of woody ornamentals in containers. *J. Am. Soc. Hort. Sci.* 122 (5), 727–734.
- Schulze, E.D., Turner, N.C., Gollan, T., Schakel, K.A. 1987. Stomatal response to air humidity and to soil drought. In: Zeiger, E., Cowan, I., Farquhar, G.D. (Eds.), *Stomatal Function*. Stanford University Press, Stanford, CA, pp. 311–321.
- Smolander, H., Lappi, J., 1985. Integration of a non-linear function in a changing environment: estimating photosynthesis using mean and variance of radiation. *Agric. For. Meteorol.* 34, 83–91.
- Steinberg, S., van Bavel, C.H.M., McFarland, M.J., 1989. A gauge to measure mass flow rate of sap in stems and trunks of woody plants. *J. Am. Soc. Hort. Sci.* 114 (3), 466–472.
- Steinberg, S.L., van Bavel, C.H.M., McFarland, M.J., 1990. Improved sap-flow gauge for woody and herbaceous plants. *J. Agron.* 82, 851–854.
- Teskey, R.O., Sheriff, D.W., 1996. Water use by *Pinus radiata* in a plantation. *Tree Physiol.* 16, 273–279.
- van Bavel, C.H.M., 1966. Potential evaporation: the combination concept and its experimental verification. *Water Resources Res.* 2, 19–31.
- Wang, Y.P., Jarvis, P.G., 1990a. Description and validation of an array model—MAESTRO. *Agric. For. Meteorol.* 51, 257–280.
- Wang, Y.P., Jarvis, P.G., 1990b. Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka spruce: application of a model (MAESTRO). *Tree Physiol.* 7, 297–316.
- Whitehead, D., 1998. Regulation of stomatal conductance and transpiration in forest canopies. *Tree Physiol.* 18, 633–644.
- Wullschleger, S.D., Wilson, K.B., Hanson, P.J., 2000. Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees. *Agric. For. Meteorol.* 104, 157–168.