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Validation of a canopy gas exchange model and derivation of a soil water modifier for transpiration for sugar maple (*Acer saccharum* Marsh.) using sap flow density measurements

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Abstract

Hourly plot-level transpiration measurements were carried out in a stand of sugar maple (*Acer saccharum* Marsh.) near Quebec City, Canada, during one summer using radial flow meters installed in selected trees. The measurements were used to validate transpiration estimates obtained from a multi-layer gas exchange model that included the modeling of the within-canopy radiation regime and the thermal balance of the leaves. The comparison between modeled and measured hourly transpiration showed no bias in the predictions, and an r^2 value of 0.80. Because of the close coupling between transpiration and photosynthesis built in the model, these results suggest that modeled estimates of photosynthesis should also be well-related to actual rates at the stand-level. The transpiration data were also used to adjust an empirical transpiration model based on the Penman–Monteith equation in which the canopy conductance term was replaced by a function of global radiation, vapor pressure deficit and soil water depletion. This empirically-fitted model captured 85% of the variation observed in the data, including the effect of soil water depletion during a late-season drought. The soil water modifier included within this equation was compared with other soil water modifier functions obtained from the literature. The comparison highlights two difficulties in the derivation of soil water modifiers applicable outside experimental areas. The first is in the determination of rooting depth so that mass balances of soil water content can be carried out. The second is in the determination of soil physical properties so that absolute values of moisture contents can be translated into relative values of water availability.

Keywords: Canopy conductance; Field capacity; Gas exchange; Permanent wilting point; Soil water depletion

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1. Introduction

Photosynthesis and transpiration of canopies are linked through a number of mechanisms. The most direct linkage involves stomatal closure and a reduction of CO_2 availability for photosynthesis. Such closure can result from increasing vapor pressure deficit (VPD) in the air, although the mechanism relating VPD to stomatal functioning is still unclear (Monteith, 1995). Hormonal signals from roots in drying soil also cause stomatal closure (Davies et al., 1990), which is usually paralleled by reduced photosynthesis in seedlings (Kubiske and Abrarns, 1992; Stewart et al., 1995) and trees (Arneth et al.,

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1999; Eamus et al., 1999). When simulating gas exchanges in canopies through process-based models, these linkages are usually explicitly recognized. The most common manner in which this is modeled is either through a functional link between relative humidity and photosynthetic rate (Ball et al., 1987), or through a VPD-mediated closure of the stomata. An additional refinement consists in linking transpiration and photosynthesis to a leaf energy budget, and iteratively seeking the equilibrium temperature of the leaf through calculations and the resulting transpiration and photosynthetic rates (Leuning et al., 1995).

The corollary of this close functional linkage between transpiration and photosynthesis in most process-based models is that a successful validation of the model using transpiration data should be a valid proxy for the validation of modeled photosynthesis. This is particularly useful considering that measurements of canopy-level exchanges of CO_2 are much more difficult to obtain than canopy-level measurements of transpiration. Whereas measurements of CO_2 uptake at the plot or stand scale require flux tower apparatus, estimates of plot-level transpiration can be obtained using sap flux density or sap flow measurements on sample trees.

We have recently developed a multi-layer canopy gas exchange model of sugar maple (Raulier et al., 2000) and are currently using it to parameterize a coarser landscape-level model of forest productivity based on the 3PG model of Landsberg and Waring (1997). In order to validate the absolute gas exchange values obtained from the multi-layer model, we measured transpiration in the stand from which the original leaf-level gas exchange data used to parameterize the model were obtained. The first objective of this work was therefore to validate the multi-layer canopy gas exchange model using hourly estimates of plot-level transpiration data.

In addition, depletion of soil water by transpiration provides an additional linkage between stomatal regulation and photosynthesis, and this important feedback is usually represented in most process-based models of forest productivity. During the summer in which the measurements were taken, short drought episodes were of sufficient magnitude to bring about a drop in canopy transpiration. An additional objective was therefore to develop from that data a soil water modifier for canopy conductance that could be applied within the coarser landscape-level model to capture the impact of soil water depletion on transpiration and on forest productivity.

2. Material and methods

2.1. Experimental site

The experiment was carried out in a stand of sugar maple (*Acer saccharum* Marsh.) at Saint-Gilles-de-Lotbinière during the summer of 1999. The Saint-Gilles site is located about 50 km south of Quebec City, Canada (longitude 71°25′00″W; latitude 46°26′30″N), in the Saint-Gilles-de-Beaurivage forest property of Daishowa Inc. The mature hardwood site lies within the Sugar Maple—Yellow Birch domain, ecological region 2C of Thibault and Hotte (1985), with 1660–1780 °C days above 5 °C. Slope is nil as the site rests on a gentle rise in the land, above poorly drained forested wetlands. The total basal area is 28.15 $m^2\ ha^{-1}$. Percent composition of stand total basal area is 72% for sugar maple, 17% for American beech (*Fagus grandifolia* Ehrh.), 6% for ironwood (*Ostrya virginiana* [Mill.] K. Koch.), 5% for yellow birch, and less than 1% for basswood (*Tilia americana* L.). The stand originates from a nearly complete cut dating from the 1930s. Trees form a closed, homogeneous canopy with very few gaps. Tree height ranges from about 22 to 27 m. Live crown depth is about 5 m. There are very few trees of intermediate height. Maple regeneration forms a nearly continuous single-leaf cover at a height of about 50 cm. The site is underlain by deposits of alluvial origin. The texture of the different soil horizons (Table 1) favors rapid drainage of excess water.

Environmental measurements were obtained from a suite of instruments positioned along a tower on the

Table 1
Soil properties of the Saint-Gilles experimental site

Depth (cm)	0–30	30–60
Percent stone (diameter > 2 mm) volume	20.0	44.9
Sand (vol.%)	53.6	39.7
Silt (vol.%)	17.6	9.9
Clay (vol.%)	8.8	5.5
Total porosity (cm^3/cm^3)	0.46	0.23
Percent fine root content	82	18

experimental site. All measurements were recorded on a 30 min basis unless otherwise noted. Air temperature and relative humidity were measured at mid-canopy (Campbell Scientific, Logan, UT, USA, 207 probe). Global incoming radiation was measured above the canopy (LICOR, Lincoln, NE, USA, LI200S sensor). During part of the summer of 1999, net radiation was measured above the canopy using a REBS net radiometer (Radiation Energy Balance System, Seattle, WA, USA). At the end of the growing season, the lower sun angle and the relative position of dominant trees caused partial daily shading of the net radiation sensor. For those periods, the net radiation was estimated from global radiation measurements using a quadratic function adjusted to data registered earlier in the growing season. Wind speed was measured 5 m above the canopy (Campbell Scientific-modified RM Young Wind Monitor). Above-canopy precipitation was measured using a tipping bucket raingauge. Soil water content of the upper 30 cm of soil was measured with a Campbell Scientific water content reflectometer probe (model CS615) at a single point within the plot on a continuous basis. A four-segment time domain reflectometry (TDR) probe (Environmental Sensors, Victoria, BC, type K probe), located about 1 m from the CS615 probe, was read on 14 occasions at irregular intervals using the MP-917 unit (Environmental Sensors). This probe provided readings at 15 cm intervals down to a depth of 60 cm.

2.2. Measurement of sap flux

Five trees were selected randomly within a rectangular 1100 m^2 plot. For the random selection, each tree received a weight equal to its basal area. This weighing was performed as in the weighed sampling scheme of Gregoire et al. (1995) so as to bias sampling towards the size classes that contribute the most to plot-level transpiration. This sampling technique improves the accuracy of plot-level estimations when scaling up from the sample trees to the plot by improving sap flux estimation in the largest diameter classes. From 14 June until the end of the seasonal measurements, Granier radial flowmeters (Granier, 1987) were used in these trees to obtain measurements of sap flux densities. As the sensor length is only 20 mm, i.e. much shorter in sugar maple than the sapwood thickness, a preliminary experiment consisted in measuring the sap flux density variation according to its depth in the trunk. This experiment was performed with three trees of different diameters (DBH 22–46 cm). A linear decrease in sap flux density according to the depth below cambium (data not shown) was evident in each of the studied trees. This relationship was used to estimate total sap flow in each of the five trees measured during the season. A 0.5 h lag in sap flow response to changes in environmental variables was verified prior to the analysis by comparing measured transpiration rates to potential rates to which various lags were applied. The scaling up from the single tree measurements to the plot-level transpiration was performed by multiplying the total sap flow measured in all five trees by the ratio of sapwood area in these trees to that of the whole plot.

2.3. The canopy gas exchange model

Raulier et al. (2000) developed a multi-layer canopy gas exchange model for sugar maple in which the layers are classes of foliage of similar mass per unit leaf area (LMA) rather than horizontal layers of the canopy. This arrangement is made possible by the strong relationships between average light environment, physiological properties of the leaves and LMA. The representations of gas exchanges were based on the equations of Farquhar et al. (1980) which were parameterized on instantaneous gas exchange data obtained in situ on leaves from different canopy positions in mature maple trees. For this particular exercise, two components of the model were modified. First, the Ball et al. (1987) linkage between relative humidity and stomatal conductance built in the original model was replaced with the more complete iterative procedure of Leuning et al. (1995). In this procedure, leaf energy balance is affected by latent heat loss through transpiration. The resulting leaf temperature in turn affects leaf photosynthesis, whose rate is used to compute the stomatal conductance which in turn affects transpiration. Iterative calculations usually converge quickly to equilibrium rates of gas exchanges for each hourly time step. A second modification to the model was to consider that the leaf distribution is spherical within each LMA layer l, and that each layer therefore has to be further stratified into classes of similar leaf zenithal (θ_l) and azimuthal (α_l)

angles. This particular modification was drawn from a second modeling exercise that extended the model of Raulier et al. (2000) to conifers (Bernier et al., in press). In the final model, the net canopy photosynthesis was estimated as

$$A_{\mathrm{c}} = L^{*}\sum_{i=l}^{n}\left[v_i\sum_{\theta_l}\sum_{\alpha_l}[v_{\theta,\alpha}(v_{\mathrm{b}}A_{\mathrm{n}}(\bar{I}_{l.\mathrm{b0}} + \bar{I}_{l.\mathrm{d}}) + (1 - v_{\mathrm{b}})A_{\mathrm{n}}\bar{I}_{l.\mathrm{d}})]\right] \tag{1}$$

where A_{c} is canopy net photosynthesis (mol (m^2 ground)$^{-1}$ s^{-1}), L^{*} the leaf area index of the canopy, v_i the distribution frequency of leaf area within a class i of LMA, $v_{\theta,\alpha}$ the distribution frequency of leaf area within an angular class, v_{b} corresponds to the fraction of sunlit leaf area in a given LMA layer, $A_{\mathrm{n}}(\bar{I}_{\mathrm{s}})$ is net leaf photosynthesis for a mean intercepted irradiance $\bar{I}_{\mathrm{s}}, \bar{I}_{l.\mathrm{b0}}$ the direct (beam) radiation reaching the LMA layer l, and $\bar{I}_{l.\mathrm{d}}$ is the diffuse radiation reaching the LMA layer l. Sixty leaf angular classes were considered (5 for the zenith and 12 for the azimuth). The derivation of the various terms can be found in Raulier et al. (2000) and in Bernier et al. (in press). The estimation of parameter values for application of the Farquhar et al. (1980) photosynthesis equations is described in Raulier et al. (2000).

2.4. The soil water modifier

Canopy transpiration can be estimated from climatic and vegetation variables using the Penman–Monteith equation (Monteith, 1973):

$$E_{\mathrm{c}} = \frac{e'(R_{\mathrm{n}} - G) + \rho C_p \mathrm{VPD} g_{\mathrm{a}}}{\lambda[e' + \gamma(1 + (g_{\mathrm{a}}/g_{\mathrm{c}}))]} \tag{2}$$

where E_{c} is the canopy transpiration (kg m^{-2} s^{-1}), g_{c} the canopy conductance (m s^{-1}), g_{a} the aerodynamic conductance (m s^{-1}), e' the slope of the saturated water vapor pressure curve (Pa °C^{-1}), R_{n} the net radiation above the stand (W m^{-2}), G the sensible heat storage in the biomass (W m^{-2}), VPD the vapor pressure deficit (Pa), C_p the specific heat of dry air (1010 j kg^{-1} °C^{-1}), ρ the density of the air (1.204 kg m^{-3}), γ the psychrometric constant (66.1 Pa °C^{-1}), and λ is the latent heat of vaporization (2.454 j kg^{-1}).

The canopy conductance, g_{c}, can be expressed as a function of global radiation R_{g}, VPD and a function of soil water availability, expressed in terms of relative available water θ_{r} (Granier and Loustau, 1994):

$$g_{\mathrm{c}} = a_0 + f(R_{\mathrm{g}}, \mathrm{VPD})f(\theta_{\mathrm{r}}) \tag{3}$$

in which a_0 is a parameter to be adjusted that absorbs any residual bias in the relationship between the environmental variables and the conductance. Several formulations have been used to represent g_{c} as a function of either R_{g} or VPD (Dye and Olbrich, 1993; Granier and Loustau, 1994; Granier and Bréda, 1996; Cienciala et al., 1998; Granier et al., 2000). We chose to use a derivation of the Ball et al. (1987) relationship proposed by Leuning (1995) and simplified by Landsberg and Gower (1997):

$$f(R_{\mathrm{g}}, \mathrm{VPD}) = a_1\frac{A_{\mathrm{n}}}{1 + (\mathrm{VPD}/a_2)} \tag{4}$$

in which a_1 and a_2 are parameters to be adjusted, and A_{n} is the net photosynthesis. Furthermore, A_{n} can be made a function of R_{g} as in Granier and Bréda (1996) to represent the relationship between R_{g} and g_{c}:

$$f(R_{\mathrm{g}}, \mathrm{VPD}) = a_1\frac{R_{\mathrm{g}}/(R_{\mathrm{g}} + a_3)}{1 + (\mathrm{VPD}/a_2)} \tag{5}$$

in which a_3 is a parameter to be adjusted.

For inclusion of soil water availability effects, we tested several soil water modifier functions proposed in the literature. Best fits were achieved with the two-parameter sigmoid function proposed by Landsberg and Waring (1997) in which the value of the modifier was allowed to vary between 0 (no transpiration) and 1 (optimal soil water content). The two parameters of this function were, however, highly correlated, resulting in convergence problems when adjusting the model. We finally chose a simple, three-segment model:

$$f(\theta_{\mathrm{r}}) = 0 \le (a_4 + a_5\theta_{\mathrm{r}}) \le 1 \tag{6}$$

where θ_{r} is relative available water, and a_4 and a_5 are parameters to be adjusted. The values of $f(\theta_{\mathrm{r}})$ between 0 and 1 are produced across the range of θ_{r} values above which water supply is still abundant enough not to limit the physiological activity of the tree, and below which the low unsaturated hydraulic conductivity of the soil prevents significant water uptake from occurring. This simple linear modifier provided a fit similar to that obtained with the modifier function proposed by Landsberg and Waring (1997), but its two parameters made the function much more robust for estimating the value of its parameters. Substituting Eqs. (5) and (6) into Eq. (3) yields a representation of g_c which is then substituted into Eq. (2) to produce a complete empirical representation of E_c. Adjustment of this function yields values of a_0 to a_5, which minimize the estimation errors on E_c.

2.5. Data processing

Hourly values of the various variables used in Eqs. (2), (3), (5) and (6) were obtained as follows. All measurements of field variables were obtained as described above, but all hours with a relative humidity above 95% were rejected in order to remove hours during which the foliage was likely to be wet. Measurements beyond 15 September were also removed from the analysis to eliminate any foliage senescence effect. All other records were used for the empirical fit. The hourly sensible heat storage in the biomass (G) was computed from an estimate of above-ground biomass, and the hourly change in air temperature (Stewart, 1988). Heat storage in the ground was considered negligible.

The aerodynamic conductance was estimated as in Thom (1972):

$$g_a = \frac{k^2 u}{\ln^2((z-d)/z_0)} \tag{7}$$

where k is von Karman's constant (0.41), u is above-canopy wind speed (m s^{-1}), z is measurement height (m), d is displacement height (m), and z_0 is roughness height (m). Since values of d and z_0 are dependent on wind speed, both were estimated hourly from functions fitted to the data presented by Rauner (1976; his Fig. 9), using a 25 m stand height.

The water content of the soil profile was obtained as follows: field excavations had revealed an increasing stone content down to 60 cm of depth, at which depth an impenetrable till layer was usually reached. A parallel study had shown that root density decreased dramatically with depth, but that some roots reached into the deepest portion of the 60 cm profile (Gilles Robitaille, pers. comm.). Measurements of volumetric soil moisture performed by the manual TDR unit in the 0–30 cm portion of the profile were strongly proportional to those obtained at the same depth by the automatic soil moisture probe ($r^2 = 0.91$). The 14 manual measurements also showed a strong ($r^2 = 0.86$) quadratic relationship between 0–30 cm soil moisture and 30–60 cm readings (function not shown). This relationship was applied to the continuous soil moisture readings of the automatic soil moisture probe to obtain an hourly record of the 0–60 cm soil water content. Relative available water (θ_r) was computed as

$$\theta_r = \frac{\theta - \theta_w}{\theta_{fc} - \theta_w} \tag{8}$$

where θ is the 0–60 cm average soil water content, and θ_w and θ_{fc} represent water content at permanent wilting point and field capacity, respectively. These two values were obtained from site-determined sand and clay contents (Table 1) using the equations of Saxton et al. (1986). This procedure yielded values of 0.09 and 0.22 for θ_w and θ_{fc}, respectively, which were then multiplied by 0.68 to correct for the average 32% stone content (Table 1) of the profile. This procedure yielded a potential usable water content of 0.09%, which, for the 60 cm soil profile, represented a water reserve of 5.3 cm, or enough water to sustain an average transpiration for about 10 days. The value of θ_r was not allowed to exceed 1, although the value occasionally rose to 1.5 after heavy rainfalls. θ_{fc} is a theoretical value which should be attained by the soil after a period of free drainage. Water contents above θ_{fc} should also result in non-limiting conditions for T and g_c, unless the soil should become waterlogged.

Eq. (2), with the complete empirical representation of g_c, was adjusted to the hourly field data using the PROC NLIN function of the SAS software (SAS Institute, Cary, NC). Initial values of the parameters were estimated from *a priori* analysis of the data.

3. Results and discussion

The summer of 1999 was characterized by an uneven precipitation regime with two dry periods. The first, in early June, caused a large drop in values of θ that were still very high from the April snowmelt. In spite of the large drop in θ, values of θ_r dipped only to about 0.8, indicating that there was still ample water available in the profile. The second drought period which took place from late August to early September started when the soil water content was lower than it

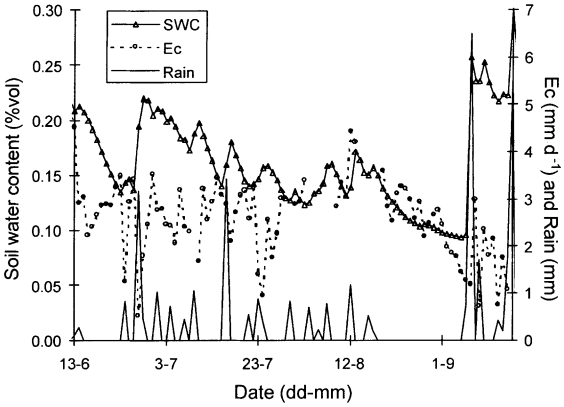

Fig. 1. Soil water content (SWC) of the 0–60 cm profile, daily canopy transpiration (E_c, mm per day) and daily rainfall amounts (mm) between 14 June and 16 September 1999 at the Saint-Gilles experimental site.

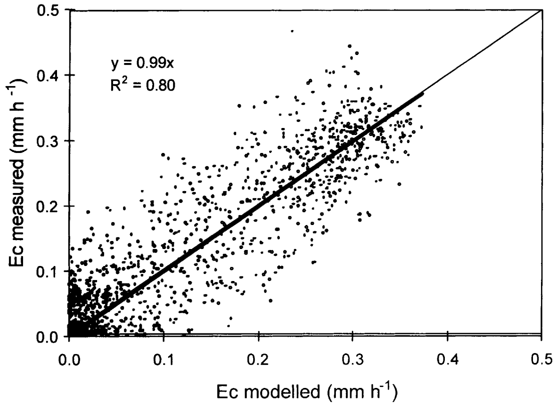

Fig. 2. Comparison of measured and modeled hourly values of sugar maple transpiration. Modeled estimates are obtained from the multi-layer canopy gas exchange model of Raulier et al. (2000), modified to include a leaf energy balance function. Only hours during which the foliage is assumed to be dry are included. The intercept component of the linear fit (dark line) between observed and predicted transpiration was non-significant ($\alpha - 0.05$). Also shown is the 1:1 line.

had been at the start of the June dry spell. As a result, its impact on the vegetation was pronounced, with transpiration losses dropping sharply during this period (Fig. 1). Heavy rainfall in early September re-established the transpiration stream to its former rates until leaf senescence occurred in late September (Fig. 1).

Hourly simulations were performed with the multi-layer canopy model of Raulier et al. (2000) (Eq. (1)) between 14 June and 30 August. Fig. 2 shows a comparison of hourly values of measured transpiration to modeled values for the canopy. The relationship between measured and modeled canopy transpiration shows no significant offset from the origin, a very small deviation from the 1:1 slope, and a R^2 of 0.80 over the complete range of temperature, humidity and light conditions encountered during the modeling period. As mentioned above, transpiration and net photosynthesis are closely coupled in trees, and this coupling is captured in the multi-layer model through the iterative procedure of Leuning et al. (1995), linking transpiration rates, leaf energy balance, photosynthesis and stomatal conductance. The ability of the model to simulate the transpiration dynamics at the canopy level with no apparent bias therefore suggests that the dynamics of net photosynthesis should also be well captured during the active growing season by the multi-layer model. Prior analysis of the data had revealed that the drought periods had reduced transpiration for only a few days in early September, which is why the simulations were terminated before this period. The multi-layer model of Raulier et al. (2000) does not account for soil water deficits.

Transpiration was also modeled empirically using the Penman–Monteith approach. Adjustment of the full evapotranspiration model (Eqs. (2), (3), (5) and (6)) to the field data provided a very good correspondence between predicted and observed stand-level transpiration, with an r^2 value of 0.85. Values of parameters a_0 to a_5 are provided in Table 2. All were highly significant. Analysis of residuals (measured minus predicted E_c) showed no apparent bias with respect to either predicted E_c, or any of the three limiting variables, R_g, VPD and θ_r (Fig. 3a–d). However, a bias was observed with respect to the day of year (Fig. 3e), with the model overestimating transpiration early in the season, and particularly during the June measurements. Because of this bias, the small depression in transpiration induced by the reduced relative available water during the June drought was not captured by the model (Fig. 4a). The much stronger depression in transpiration, with reductions in transpiration of up to 30% for a few days, resulting from the more pronounced August–September drought, was well captured (Fig. 4b). This bias in the prediction of E_c with the day of the year means that, for similar values

Table 2
Values of the parameters of the empirically-fitted transpiration model[a]

Parameters	Values	Standard error	Confidence (95%) interval	
a_0	−0.002007	0.00088	−0.00374	−0.000272
a_1	0.01860	0.000614	0.0174	0.0198
a_2	3.644	0.728	2.215	5.0723
a_3	1255.139	244.55	814.64	1695.63
a_4	−0.9301	0.340	−1.597	−0.263
a_5	4.596	0.860	2.908	6.284

[a] Also presented are their standard errors as well as the lower and upper bounds of the 95% confidence interval.

of R_g, VPD and θ_r, computed transpiration in June was lower than computed transpiration later in the summer. One possible explanation for this seasonal bias is a gradual change in the ability of the tree to extract water from the soil. Observations made with a minirhizotron system at the experimental site show that the fine root production increased more than three-fold, from a low in early June to a peak in mid-September (Gilles Robitaille, pers. comm.). Deep root production in sugar maple is also stimulated by water demand (Hendrick and Pregitzer, 1996), a response which should enhance the water uptake capacity of the trees in the drier portions of the late summer.

Fig. 5 shows the relationship between θ_r and the ratio of measured E_c to E_c estimated from Eq. (3), but sets $f(\theta_r)$ to 1 (as though water was never limiting). Superimposed are the values of our soil water modifier (Eq. (6)), as well as those obtained from a number of studies, using their original parameter values. Except for that of Landsberg and Waring (1997), the parameters for all modifiers in these studies were obtained, like ours, by postulating a function which was empirically fitted to a data set. In all cases, the stands were on predominantly sandy soils, and most were for coniferous species, except Granier and Bréda (1996) and Granier et al. (2000) who studied *Quercus* and *Fagus*, respectively. The modifier drawn from the 3PG model of Landsberg and Waring (1997) is different in that it is a function whose parameters are simply suggested for different soil types, and that it is used as a modifier both for reducing canopy conductance and absorbing photosynthetically active radiation. Not all modifiers are based on the θ_r concept as some use a soil water depletion value based on a difference between field capacity and soil water content (Stewart, 1988; Van Wijk et al., 2000). Data conversions were performed accordingly. Presentation of these modifiers against the ratio of actual to potential canopy conductance yields a virtually identical representation because aerodynamic conductance is much larger than canopy conductance, making E_c nearly directly proportional to g_c (Monteith, 1973; Phillips and Oren, 1998). An additional modifier, used by Aber and Federer (1992) in PnET was tested but is not shown here. This is a very different modifier in that it is based on the assumption that constraints on water use appear when potential transpiration rates per day exceed a fixed fraction of the available water. This fraction is called the soil release parameter by Aber and Federer (1992) and is set at 0.04 per day. For available water contents below this threshold, transpiration becomes the product of the available soil water and the soil release parameter. The "feedback strategy" equation of Berninger et al. (1996) (not included in this analysis) also uses an estimation of potential transpiration to compute the drought-induced reduction in g_c. When tested against our field data, the modifier proposed by Aber and Federer (1992) shows a very irregular response that bears little resemblance to our observations.

Perfect prediction of E_c using our empirical model would have resulted in ratios of actual to potential E_c of 1 in all cases where water was not limiting. This is obviously not the case, as can be seen in Fig. 5, as the seasonal bias and other effects not accounted for in the model result in a relatively large variability in values of the ratio of measured to potential E_c. However, the overall model did account for 85% of the variation in the measured values of E_c, and the use of a ratio representation amplifies errors on small absolute values, resulting in much of this large spread. It is interesting to note, however, that the range of values in the measured to potential E_c ratio is strongly dependent on soil water content, with the range

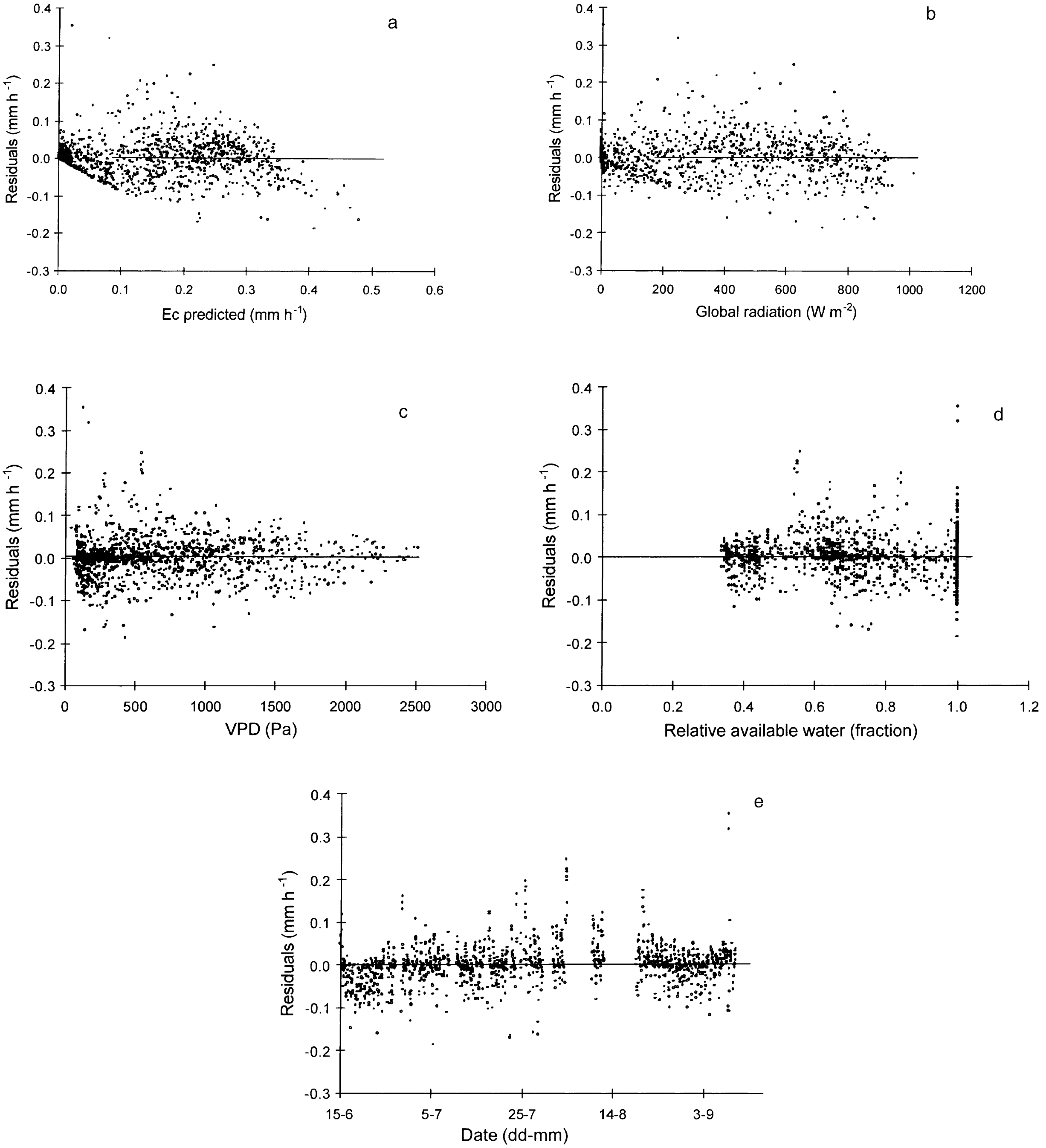

Fig. 3. Residuals (measured—modeled canopy transpiration E_c) as a function of (a) predicted E_c; (b) global radiation; (c) vapor pressure deficit; (d) relative available water and (e) day of year. E_c is modeled using the empirically adjusted Penman–Monteith equation.

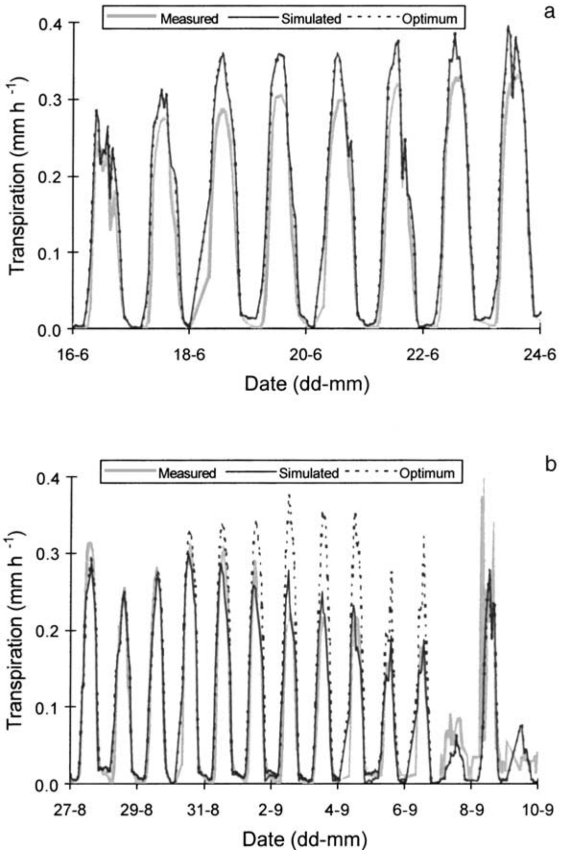

Fig. 4. Time course of measured, simulated and optimum canopy transpiration (E_c): (a) during a June drought and (b) during a late summer drought. E_c was modeled using the Penman–Monteith equation. Optimum E_c is the same as the modeled value, except that the soil moisture modifier is maintained at 1 (optimal). In figure (a), optimum and simulated are superimposed.

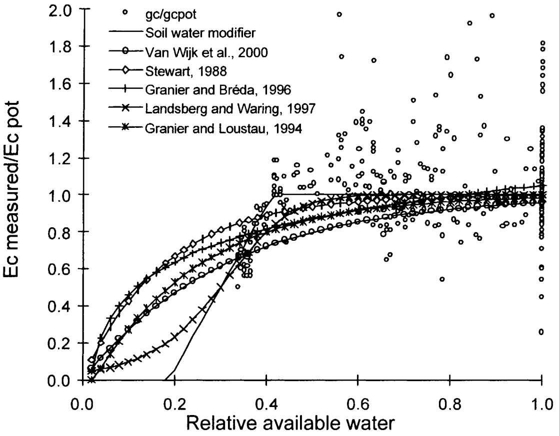

Fig. 5. Soil water modifier from this study as well as that from other studies as a function of relative available water. Data points are the ratio of measured to potential canopy transpiration (E_c/E_{cpot}) plotted against relative available water. E_{cpot} is obtained using the empirically-fitted Penman–Monteith equation, but assuming that soil water is optimal. Data are 11.00 to 14.00 h readings on rain-free days.

decreasing sharply as water becomes increasingly limiting.

Fig. 5 also shows that our soil water modifier (Eq. (6)) apparently predicts a transpiration of 0 when the relative available water is still above 0, which is contrary to the definition of relative available water. This observation highlights two problems inherent to the inclusion of soil water as a modifier of transpiration. The first is in the determination of rooting depth for the computation of water balance. If the depth chosen is shallower than the actual extension of the roots, the trees will appear resistant to low soil water content. If the depth chosen is deeper than the actual rooting depth, the trees will appear overly responsive to a drop in soil water content. Hendrick and Pregitzer (1996) have shown a climate-related response in the exploration of deeper soil layers in sugar maple. Field studies in a range of environments have also shown that rooting depth depends on species, on the climate and on physical soil properties, and values range from many meters in dry environments to a few centimeters in the tundra (Canadell et al., 1996). Studies of rooting profile are important in determining this rooting depth, but effective rooting depth for water extraction is determined not only by the root density profile, but also by the unsaturated hydraulic conductivity properties of this profile (Plamboeck et al., 1999). In most models, the standard rooting depth is set at 1 m (Kleidon and Heimann, 1998). Canadell et al. (1996) suggest a 2 m rooting depth for the boreal forest, but the 0.6 m used in our study was justified by the extremely compact layer found at that depth as well as minirhizotron observations. Rooting depths of many meters in dry areas with very deep soils further complicate the application of soil water modifier functions. We believe that field values generalized across their ecosystems of origin are likely the only manner in which realistic rooting depths can be obtained for non-experimental areas. Such an application to a larger area is the final purpose of the current exercise.

The second difficulty with the use of soil water in the computation of transpiration lies in the determination of fixed soil properties for converting measured or modeled soil water contents to a more general representation of soil water availability such as water deficit or relative available water. This problem is further compounded by the significant volume of stones in many forest soils. This is an important consideration for applying the soil moisture functions to areas outside the experimental sites as values of wilting point and field capacity have to be chosen to transform the water content data. The choice of these variables influences the scale of θ_r and therefore the apparent sensitivity of the trees to drought. For example, using a lower field capacity and a higher value of permanent wilting point in the computation of relative available water (Eq. (8)) would have lowered the slope of the soil water modifier in Fig. 5 and brought it more in line with the functions obtained from the literature. Most past studies (e.g. Stewart, 1988; Granier and Loustau, 1994; Granier and Bréda, 1996; Granier et al., 2000) have used field data to determine maximum and minimum soil water contents, with the purpose of achieving the best modeled fit to measured transpiration. In this study, we compute θ_r using values of wilting point and field capacity (θ_w and θ_{fc}) derived from the soil texture, the empirical equations of Saxton et al. (1986), and the stone content. This approach might not be optimal for an experimental site on which θ_w and θ_{fc} can actually be measured. However, it allows for the calculation of soil water depletion for sites and areas for which detailed information of soil properties is not available, provided that soil texture is known.

The comparison shown in Fig. 5 cannot be used to determine the most "universal" soil water modifier as all are used with the parameters derived empirically from data obtained under different local field conditions. However, from the data presented in Fig. 5 and the various modifiers plotted in that figure, we can draw a number of conclusions. First, the drop in canopy conductance and transpiration becomes noticeable only below a certain threshold value of relative available water. In this study, this value was 0.42, which corresponds to a soil water content of 0.12 (v:v) for our 60 cm profile. Granier and Bréda (1996) observed a similar threshold at a θ_r of 0.60. Secondly, when soil water does become limiting, the variability in the ratio of measured to potential transpiration (or of measured to potential canopy conductance) drops sharply. A similar pattern is reported in Granier and Bréda (1996) and in Granier and Loustau (1994). This pattern shows the strength of the soil water modifier function in helping to explain transpiration during episodes of low soil water, and therefore the importance of its inclusion in a predictive model. The last point, which stems from the diversity of the modifier functions, is the need to derive a more universal approach to estimating the impact of soil moisture depletion on transpiration. We feel that the use of texture-derived values of field capacity and of permanent wilting point, instead of locally-derived values, is a step in this direction. Estimates of average effective rooting depths for different environments and species functional groups could also help us reach this goal.

The soil modifier function was derived for application at the canopy scale and for a time interval of a day, and cannot be applied at will to smaller spatial scales or longer time intervals. Environmental (Niinemets and Tenhunen, 1997) and hydraulic (Yang and Tyree, 1994) gradients found within deciduous canopies are likely to cause stomatal limitations to appear at different levels of relative available water at different positions within the canopy. In multi-layer canopy models such as that of Raulier et al. (2000), the within-canopy variability in the limitation of gas exchanges caused by soil water depletion cannot be properly computed without taking into consideration these environmental gradients. The constraint on time steps comes from the non-linearity of the soil water depletion effects. Application to longer time steps can be achieved only by integrating the effect over the required time period, using probable soil water depletion scenarios. The resulting function should show a more gradual decline in canopy conductance with soil water depletion than what is shown in this study for daily measurements. On a monthly time step, initial effects of soil water depletion would therefore be observed at higher relative available water contents.

4. Conclusions

The results presented in this work show that the multi-layer model of Raulier et al. (2000) produces estimates of transpiration that match those measured with only minimal bias. Although photosynthesis requires a complex biochemical mechanism that is absent from the process of transpiration, the two gas exchange streams are well coupled. This well-demonstrated coupling and the close match between modeled and actual transpiration suggests that the modeled rates of canopy photosynthesis from this model would also be quite close to actual values.

The soil moisture modifier derived in this study contributed to explaining transpiration during a period of limiting soil water. However, the bias of the transpiration with the day of year model suggests our ability to capture the relationship between soil depletion and transpiration could be improved somewhat by considering time-related processes such as root growth.

Also shown in this work is the variability in the soil moisture modifiers presented in the literature, and the limits imposed upon their use by the specificity of the soil properties used in their derivation. Although soil water-related constraints are part of most ecophysiological models of forest productivity, the databases for documenting such an effect on trees and for developing and validating appropriate functions at the correct spatial and temporal scales are sparse. Given the importance of soil water balances in studies of climate change impact on forests, we suggest that more effort be put into the acquisition of transpiration and soil water datasets for forests.

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