

Drought constraints on transpiration and canopy conductance in mature aspen and jack pine stands

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Abstract

Half-hourly mean values of transpiration measured by eddy covariance over the course of six growing seasons in two boreal forest sites were used to develop stand-level relationships between transpiration and soil water content. The two sites were an aspen site on fine-textured soil and over five growing seasons for a jack pine site on coarse-textured soil in Saskatchewan, Canada. About half of the data record covered a multi-year drought that was more severe at the aspen site than the jack pine site. Measurements of transpiration and environmental variables were used to adjust a transpiration model to each site, with environmental variables retained in the model based on their capacity to improve the model adjustment. The model was also used to produce estimates of maximum canopy conductance (g_{cMAX}). The fit of the model to the aspen half-hourly transpiration is better than to the jack pine data (r^2 of 0.86 versus 0.60). Relative soil water content explains more of the variability in half-hourly transpiration at the aspen site (46%) than at the jack pine site (10%). The relationships between transpiration and environmental variables are stable throughout the drought suggesting an absence of acclimation. Published soil water modifier curves for loamy clay soils compare well with the modifier function we obtained for a similar soil at the aspen site, but the agreement between the published curve and our curve is poor for the sandy soil of the jack pine site. Values of g_{cMAX} computed at the half-hourly scale are greater at the aspen site (14.3 mm s^{-1}) than at the jack pine site (10.2 mm s^{-1}), but we hypothesize that the coarse soil and perennially lower water content of the jack pine site may cause this difference. Finally, we also present values of g_{cMAX} computed at the daily and monthly scales for use in models that operate at these time steps.

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1. Introduction

Soil water content can exert an important control over forest surface or canopy conductance (Stewart, 1988) which directly affects transpiration and tree growth by limiting the supply of CO_2 to the leaf

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mesophyll cells. In the boreal forest of western Canada, periodic droughts already affect the growth of aspen (Hogg et al., 2005), and future climate change is predicted to increase drought frequency, with direct impact on the growth and survival of trees in these regions (Hogg, 2001). Proper prediction of current and future growth of forests in such regions therefore requires an understanding of soil water controls on physiological processes.

Empirical evidence has shown the strong coupling between transpiration and photosynthesis, and the effect that drought can have on both processes (e.g., Roth et al., 1997), and most models that attempt to predict forest productivity from basic growth processes incorporate, either implicitly or explicitly, some form of soil water-based constraint. Running et al. (2000) present a model used to map global net primary productivity in near-real time, and in which soil drought is accounted for simply by postulating a long-term impact of soil water content on the observed leaf area index. In predictive models, canopy conductance and carbon uptake are often coupled through feedback that may or may not include a functional link to soil water content. The leaf-level model of Leuning (1995), for example, explicitly links stomatal conductance to photosynthesis through an energy balance-related feedback process. Katul et al. (2003) also show, through a modelling analysis of CO₂ uptake and water use, the coupling between maximum carboxylation capacity and soil–plant hydraulic properties. Such studies demonstrate the need to explicitly incorporate into models the conductance–soil water relationship in order to properly capture the transient impacts of short-term drought on tree growth.

The derivation of appropriate conductance–soil water response functions presents the particular challenge of obtaining such a function at the appropriate spatial and temporal scales. Attempts to produce drought response have been made in natural environments with limited success (e.g., Phillips et al., 2001), or in controlled environments on seedlings in pots (e.g., Saliendra et al., 1995) with limited ability to scale up to natural ecosystems. Whole tree lysimeter studies, such as that by Dunin et al. (1985) on eucalypts, have provided good approximations of normal tree response to drought but were again limited by constraints inherent to such studies, i.e., the limited number of trees, the perturbed soil profile and the limited soil volume accessible to the trees. Stand-level determination of canopy conductance response functions to soil water have been derived in a number of studies (Grassi and Magnani, 2005; Lagergren and Lindroth, 2002;

Bernier et al., 2002; Granier et al., 2000), but mostly using single years of data. Granier et al. (2000), in particular, have used data from five sites each supporting different species to propose a generic function describing the response of canopy conductance to soil water. Further analysis of canopy-level measurements of transpiration under conditions of drought is required to strengthen the current empirical relationships and extend their applications to untested species and soil conditions. Analysis over multi-year periods is also required to determine longer term responses of trees to drought.

In addition, the shape of the function linking environmental variables to canopy conductance is likely dependent on the time scale for which it is to be used. For example, Raulier et al. (2000) have shown that the shape of the temperature response function of photosynthesis is influenced by the size of the time interval over which the input variables are averaged, with the response becoming more linear with aggregation to coarser time steps. A similar scaling phenomenon likely applies to the determination of canopy conductance and to the various environmental response functions, meaning that different parameter sets must be used in models with different time steps. Usual scales for models of ecosystem productivity are daily (e.g., Running et al., 2000; Liu et al., 2002) and monthly (Landsberg and Waring, 1997), and response functions must therefore be offered at such time steps.

From 2001 to 2003, the Canadian Prairies and the adjacent boreal forest were subjected to a severe drought. This drought affected some of the sites over which continuous measurements of ecosystem exchanges of CO₂ and water vapour had been made for a number of years, along with measurements of environmental variables, thereby providing the necessary data to conduct an ecosystem-level study of drought impacts on canopy conductance. The primary objectives of this work were (1) to quantify the relationship between canopy conductance and soil water content for two forested sites of contrasting soil properties, and (2) to determine whether these relationships depend on the temporal scale at which they are determined. We also wanted verify the applicability of the simple relationship proposed by Landsberg and Waring (1997) for quantifying the impact of drought on radiation use efficiency. Although the present work focuses on the transpiration process and the canopy conductance to water vapour, the inference drawn from it also applies to the conductance to CO₂ and, as a result, to carbon uptake by the trees.

2. Material and methods

2.1. Sites and measurements

The data used in this analysis were obtained at the Old Aspen (OA) and Old Jack Pine (OJP) flux tower sites of the Boreal Ecosystem Research and Monitoring Sites (BERMS) program (<http://berms.ccrp.ec.gc.ca>), two sites that are now also part of the Fluxnet-Canada Research Network (<http://www.fluxnet-canada.ca/>). Both sites originated as part of the Boreal Ecosystems Atmosphere Study (BOREAS) project (Sellers et al., 1997).

The OA site is located at the southern fringe of the boreal forest (53°7'N, 106°2'W; Fig. 1) and is covered by a 21-m-tall, 85-year-old aspen (*Populus tremuloides* Michx) stand with a small balsam poplar (*Populus balsamifera* L.) component and a dense understory of hazelnut (*Corylus cornuta* Marsh.) and green alder (*Alnus crispa* (Alt.) Pursch). The leaf area index (LAI) of the stand, measured with a plant canopy analyzer (PCA) (model LAI 2000, LICOR Inc., Lincoln, NE, USA) ranged from 4.0 to 5.2 during the period of this study (Barr et al., 2004), with 56% on average contained in the aspen. The elevation is 600 m. The soil is an orthic gray luvisol. Average textural composition of the 120-cm-deep profile over which soil moisture measurements are made is 50% sand, 28% silt and 21% clay, making this soil a sandy clay loam (Anderson, 2000; Newcomer et al., 2000). There is also a surface organic layer of about 8–10 cm in depth.

The OJP stand is also within the southern fringe of the boreal forest (53°9'N, 104°7'W), and is about 100 km east of the OA site (Fig. 1). The stand is composed of 13-m-tall, 90-year-old mature jack pine (*Pinus banksiana* Lamb.) with a very sparse green alder understory and a lichen ground cover. Both optical and allometric measurements produced LAI estimates of about 2.5 (Chen et al., 1997). The elevation is 579 m. Average textural composition of the 150-cm-deep profile over which soil moisture measurements are made is 92% (mostly medium to fine) sand, 5% silt and 2% clay, making this soil a sand, with a very thin surface organic layer (Anderson, 2000; Newcomer et al., 2000).

Mean annual air temperature and precipitation (1971–2000 Canadian Climate Normals) at the nearest long-term weather station (Waskesiu Lake, 53°92'N, 106°07'W) are 0.4 °C and 467 mm, respectively. Additional details on the sites and their climate can be found in Griffis et al. (2003) and Barr et al. (2004). Continuous evapotranspiration data were obtained from an eddy covariance (EC) system mounted 39 m above the ground

for the OA site, and 28 m above the ground for the OJP site. The EC systems consisted of a three-dimensional sonic anemometer (models R2 and R3, Gill Instruments Ltd., Lymington, UK at the OA site, and model CSAT3, Campbell Scientific Inc. (CSI), Logan, UT, USA at the OJP site) and a temperature-controlled infrared (CO₂/H₂O) gas analyzer (LI-6262, LI-COR Inc., Lincoln, NE, USA). Air was drawn through a 3.5-m-long heated sample tube at about 10 L min⁻¹ to ensure there was turbulent flow. For details, see Griffis et al. (2003). The EC system at the OA site has been in continuous operation since March 1996, while the OJP site has been in continuous operation since August 1999. The analysis was based on the 1998–2003 time series for the OA site, and on the 1999–2003 time series for the OJP site.

Incoming solar radiation (K_d) was measured above the canopies with pyranometers (model CM11, Kipp & Zonen, Delft, The Netherlands). Air temperature and relative humidity were measured within and above the canopies using temperature/relative humidity probes (model HMP45C, Vaisala Oyj, Helsinki, Finland) mounted in 12-plate radiation shields (R.M. Young Co., Traverse City, MI, USA) at heights of 37, 24, 18, 4 and 1 m at OA, and at heights of 28, 16, 10, 5 and 1 m at OJP. Wind speed was measured above the canopies at a height of 38 m at OA and 29 m at OJP using wind monitors (model 05103, R.M. Young Co., Traverse City, MI, USA). Soil moisture was measured using soil moisture reflectometer probes (model CS615, CSI) horizontally oriented in the organic surface layer at OA at depths of 2.5 and 7.5 cm, and vertically oriented at 0–15, 15–30, 30–60, 60–90, 90–120 cm at OA and OJP, and at 120–150 cm at OJP. In addition, multi-segmented time domain reflectometry probes (MoisturePoint, Environmental Sensors Inc., Victoria, BC, Canada) were installed in the mineral soils at OA, with measurements taken at 0–15, 15–30, 30–60, 60–90 and 90–120 cm.

2.2. Modelling transpiration

Transpiration was modelled as in Phillips and Oren (1998), using the Monteith and Unsworth (1990) equation for vegetation well coupled to the atmosphere, i.e., vegetation with aerodynamic conductance much higher than its canopy conductance as in the case of forest stands:

$$E_c = g_c D_a \frac{c_p \rho}{\gamma \lambda} \quad (1)$$

where E_c is the canopy transpiration (mm h⁻¹), g_c the canopy (or surface) conductance (m h⁻¹), D_a the vapour

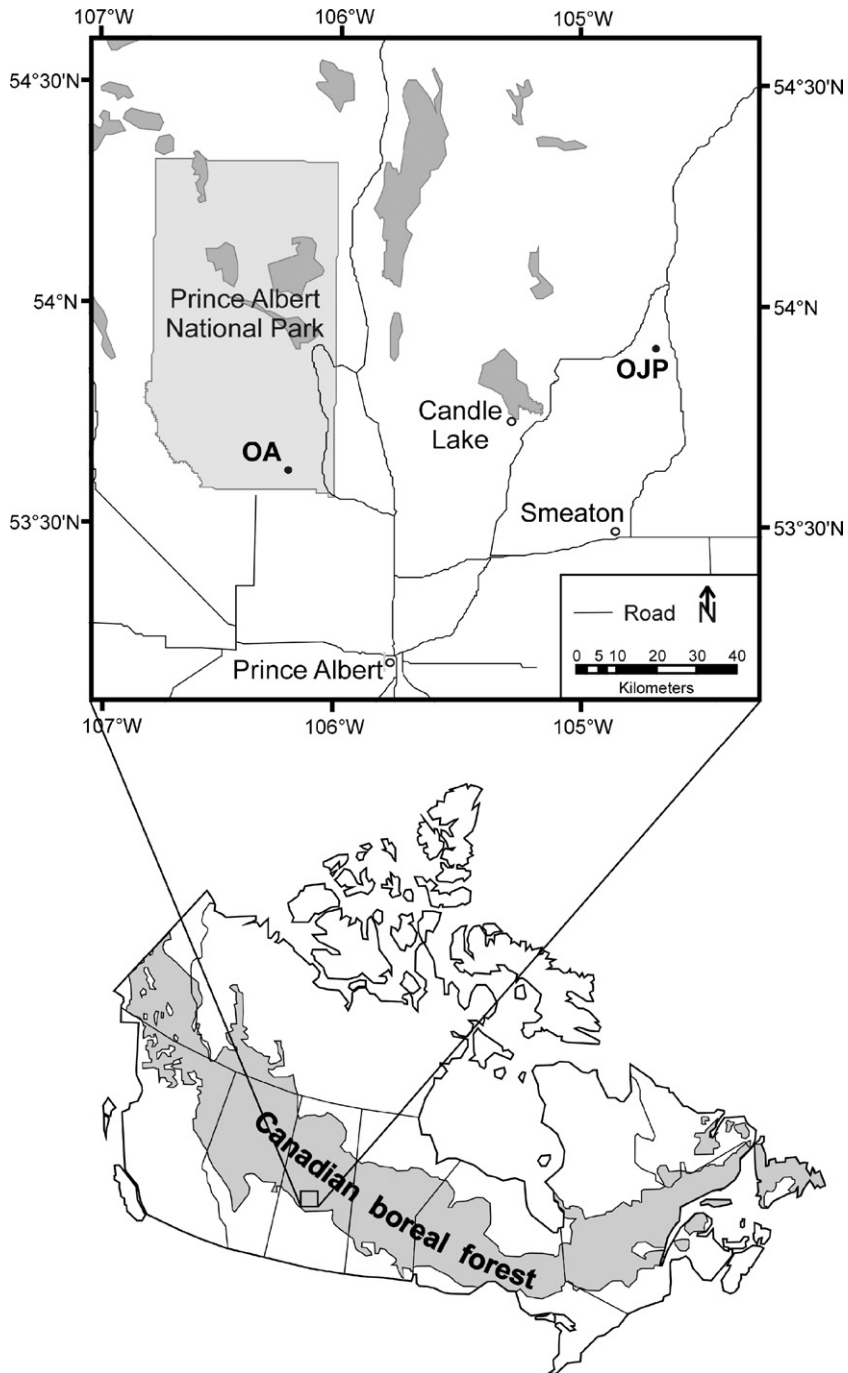


Fig. 1. Location of the experimental sites.

pressure deficit (Pa), c_p the specific heat of dry air ($\text{J kg}^{-1} \text{C}^{-1}$), ρ the density of the air (kg m^{-3}), γ the psychrometric constant (Pa K^{-1}) and λ is the latent heat of vaporization (kJ kg^{-1}). We used an approach to modelling of environmental effects on the canopy conductance term based on the work of Raulier et al. (2000) in

which they modelled environmental effects on the quantum use efficiency for estimating gross primary productivity. The canopy conductance term, g_c , was defined as:

$$g_c = \bar{g}_c \prod f_x \quad (2)$$

where \bar{g}_c is a fitted parameter representing the average canopy conductance (m s^{-1}) over the course of the measurement period, and $\prod f_x$ refers to the product of modifiers for environmental variable x that are computed as in Raulier et al. (2000). The modifier f_x is given by:

$$f_x = 1 + \alpha_{l,x} \left(\frac{x - \bar{x}}{\bar{x}} \right) + \alpha_{q,x} \left(\frac{x - \bar{x}}{\bar{x}} \right)^2 \quad (3)$$

where \bar{x} is the mean value of this variable for the observation dataset, and $\alpha_{l,x}$ and $\alpha_{q,x}$ are parameters to be estimated along with \bar{g}_c . Variables tested to be incorporated as modifiers can be for any quantifiable environmental variable (e.g., temperature, radiation, wind speed) or measurement of time (e.g., time of day, day of year). This methodology departs from the approach of Jarvis (1976) and Stewart (1988) in which g_c is computed as the product of the maximum g_c ($g_{c\text{MAX}}$) and of response functions in which a value of 1 represents optimum conditions. Our use of an average term, \bar{g}_c , facilitates model adjustment compared with the use of an optimum term ($g_{c\text{MAX}}$) that may be unobserved during the course of the measurements. In the approach described by Eqs. (2) and (3), a value of 1 for a modifier represents average conditions within the experimental dataset. In addition, the quadratic form of the modifier function in Eq. (3) provides a flexible adjustment to the data, permitting linear and non-linear effects to be expressed. Finally, normalizing variables as in Eq. (3) yields parameter values that are of equal magnitude among variables, which makes for easy comparison and independence of units. All environmental variables were treated in this manner except soil water content for which the modifier was derived using natural values of either relative (θ_r , Eq. (5)) or absolute water contents in a simple quadratic function:

$$f_{\theta_r} = \alpha_0 + \alpha_{l,\theta_r} \theta_r + \alpha_{q,\theta_r} \theta_r^2 \quad (4)$$

This special treatment for soil water was done to facilitate the comparison with the Landsberg and Waring (1997) functions.

2.3. Data preparation

Direct comparisons of spatially-averaged transpiration measurements and point measurements of soil water content are always uncertain because of the difference in spatial representativeness of the two measurement sets, but we carried out a water balance analysis to confirm the consistency of our data and the conservation of mass water balance in our measurements. We found that soil

water lost within the 1.2 m measurement profile at OA during 10 rain-free periods (from 2 to 14 days in duration) during the 6-year measurement period was only 82% of the transpiration estimates obtained from the EC measurements. To obtain mass balance, we assumed that the water content in the soil below the 1.2 m depth was equal to the values measured within the 0.9–1.2 m layer, and gradually lowered the bottom of this layer until the volume of water lost in the full profile equalled the transpiration values measured by the EC. A slope of 1.009 between soil water losses and EC measurements was reached with a profile depth of 2 m. This modified average profile water content was used in the remainder of the analysis.

For the OJP site, the soil water depletion in the 0–1.5 m profile was only weakly related to the measured transpiration for the same period, with no apparent bias (Fig. 2). Jack pine tap roots extend beyond 1.5 m, and it is likely that water was withdrawn from deeper soil layers in the driest periods. However, we found no reason in our dataset to adjust the 0–1.5 m profile downwards in order to obtain conservation of mass.

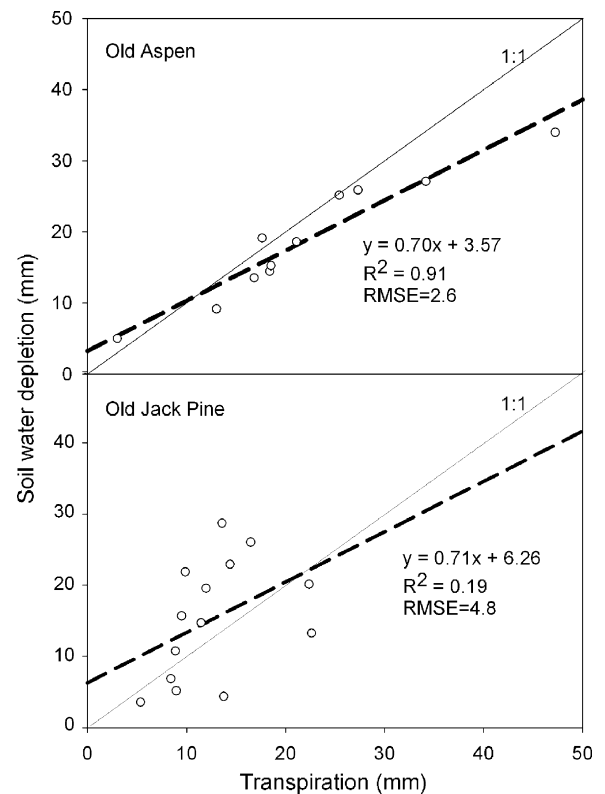


Fig. 2. Soil water depletion over the 120 cm (Old Aspen) or 150 cm (Old Jack Pine) soil profiles during periods of multiple days without rain, plotted against the measured transpiration losses for the same periods.

The measured average volumetric water content of the soil profile (θ_m) was obtained from the water content measurements by summing up the depths of water per layer and expressing the result as a fractional depth of the complete profile. The relative water content (θ_r) was computed as:

$$\theta_r = \frac{\theta_m - \theta_{wp}}{\theta_{fc} - \theta_{wp}} \quad (5)$$

where θ_{fc} is water content at field capacity, and θ_{wp} is water content at the permanent wilting point. Theoretical estimates of θ_{fc} ($0.25 \text{ m}^3 \text{ m}^{-3}$ for the OA site, and $0.11 \text{ m}^3 \text{ m}^{-3}$ for the OJP site) were obtained from soil texture using the equations of Saxton et al. (1986) (OA = 47% sand, 20% clay; OJP = 95% sand, 3% clay). However, water contents at the OA site exceeded the theoretical value of θ_{fc} for about 65% of the measurement period. We therefore relied on field observations for the estimation of θ_{fc} , as in Lagergren and Lindroth (2002). The value of θ_{fc} was estimated for each site as the average of the top 5% of the water content observations during the complete measurement period, while that of θ_{wp} was estimated for each site using textural information and the equations of Saxton et al. (1986). Final values of θ_{fc} and of θ_{wp} used for the OA site are $0.36 \text{ m}^3 \text{ m}^{-3}$ and $0.14 \text{ m}^3 \text{ m}^{-3}$, while those used for the OJP site are $0.102 \text{ m}^3 \text{ m}^{-3}$ and $0.04 \text{ m}^3 \text{ m}^{-3}$, respectively.

We used only daytime half-hourly eddy covariance (EC) measurements of water vapour flux made during the growing season, with daytime defined by observed incoming solar radiation larger than 5 W m^{-2} . To obtain the transpiration component of the water vapour flux, we used only data from periods during which the evaporation component was judged to be minimal. This entailed removing data for: (i) all half hours with measured rainfall, (ii) half hours within 12 h after rainfall events, and (iii) all half hours during which relative humidity was above 95%. Based on our observations in boreal forest stands, 12 h appears long enough following rainfall to dry the canopy. The soil surface and litter may undergo a longer drying period, but the removal of periods in which relative humidity was above 95% ensures elimination of the wettest periods where evaporation from wet surfaces would dominate the water vapour flux. We also removed periods when the Bowen ratio was negative because as such a condition is indicative of periods of negligible transpiration, or evaporation from a wet canopy. Further evidence for a low contribution of soil evaporation to the water vapour flux comes from Blanken et al. (2001) who report contributions of this term of less than 5% of

total evapotranspiration at the OA site. Baldocchi et al. (1997), on the other hand, report a daily average contribution of soil evaporation at the OJP site of between 5 and 25 W m^{-2} or 10–40% of the total latent heat flux. However, examination of their results shows the soil evaporation component to be conservative near 10 W m^{-2} , and the overall responsiveness of the total water vapour flux appears dominated by the canopy transpiration. In the remainder of this document, we therefore use the term “canopy conductance” or g_c to describe the proportionality coefficient that relates water vapour flux to vapour pressure deficit.

An initial analysis revealed that the period of leaf expansion usually lasted until about June 24 at the OA site, as also reported by Barr et al. (2004). We therefore used only data gathered between that date and September 1 in the analysis for both sites in order to remove phenological effects that would confound the modelling approach. Once all filtering was done, Eqs. (1)–(3) were fitted using the remaining half-hourly measurements ($n = 3368$ for OA and $n = 4948$ for OJP). For the daily analysis, we used the half-hourly model to estimate the transpiration for all half-hourly periods between June 24 and September 1 of all years of measurements. Using modelled values enabled us to produce more complete time series of transpiration estimates since the only periods rejected in this analysis were those for which instrumental data were missing. The environmental data and modelled transpiration amounts were then either averaged (e.g., soil water content) or summed (e.g., transpiration) at the daily time step. We estimated the daily mean value of D_a from the daily minimum and maximum temperatures as in Hogg (1999). Only days with 24-h records of all environmental variables were retained ($n = 334$ for OA and $n = 416$ for OJP).

A further analysis was carried out on data aggregated to monthly time periods. The monthly analysis was carried out on the OA data only as it contained more data points (9 versus 6 for OJP). The analysis was carried out on the monthly summation (E_c) or average (K_d , D_a , θ_r) of the data used in the daily analysis. Transpiration was the sum of the half-hourly values modelled for the full period for which environmental data were available using the model developed from the half-hourly analysis. We accepted months missing at most 3 days of data. In the case of months with missing data, transpiration was pro-rated to the full 30 or 31 days of the month by multiplying the partial transpiration estimate by the ratio of the number of days in the month to the number of measurement days.

Eqs. (1)–(4) were adjusted to the half-hourly, daily or monthly data using the PROC MODEL function of the

SAS software (SAS Institute, Cary, NC), a standard procedure that provides least-squares adjustment to equation systems. Modifier variables were included in a forward fashion. In this method, the variables are first tested individually for their contribution to the variation in measured transpiration. The variable with the largest contribution (best model adjustment) is retained in the model, and the remaining variables are tested again for their contribution to the residual variation in measured transpiration for a new round of modifier variable inclusion. Variables were retained only if they accounted for more than 5% of the variability in observed transpiration rates. No other provision was made to account for the repeated nature of the measurements.

For the half-hourly model, the variables tested were wind speed, air temperature, K_d , D_a , time of day, day of year, day number in the time series, and θ_r measurements of the various depths or thickness of the soil profile. For the daily model, we tested profile θ_r (see below), K_d , D_a , and date variables (day of year, day number in the time series). For the monthly model, we tested only the variables that were retained as significant in the daily model.

Following model adjustment, we also computed values of g_{cMAX} for each site by first modelling the values of half-hourly g_c for the complete summer time series using Eq. (2), in which the significant environmental modifiers were inserted along with the fitted value of \bar{g}_c . We then defined maximum canopy conductance as the average of the top 5% of all values of computed values of g_c . Values of g_{cMAX} were also computed for the daily (OA and OJP sites) and monthly (OA site only) values by aggregating the half-hourly g_c values to either the day or the month, and again by computing the average of the top 5% values.

3. Results and discussion

3.1. Soil water

The drought at OA started with a drop in summer precipitation in 2001, and lasted through 2002 and 2003 (Fig. 3). The drought at the OJP site was not as pronounced (Fig. 3). Although located only 100 km to the east of the OA site, the OJP stand received substantially more precipitation during the summer of 2002 because of a few strong storms that rewetted the area. Soil water content measurements from the OA site show the impact of drought from the summer of 2001 onwards (Fig. 3). The high soil water content in early 2001 following snowmelt dropped throughout the summer and remained low for the following 2 years.

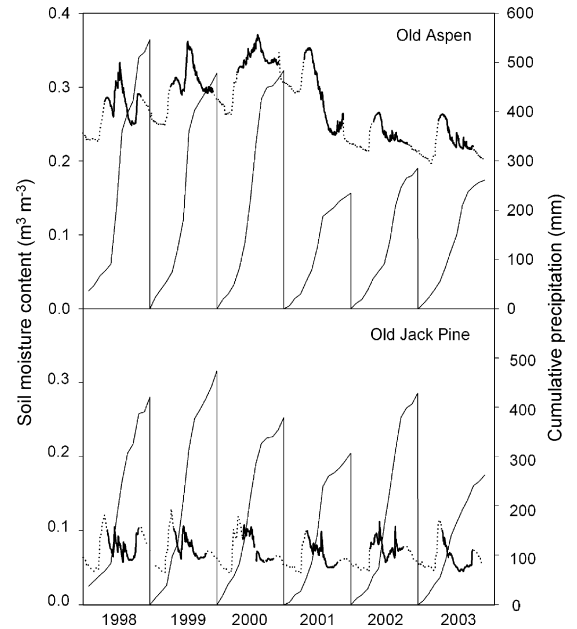


Fig. 3. Time course of soil water content (circles) and cumulative precipitation (solid line) at the Old Aspen and Old Jack Pine sites. Cumulative precipitation is reset to 0 on January 1. The dashed portion of the soil moisture time course represent periods when part of the soil water is ice and thus invisible to the reflectometry-based probes.

Soil water content at the OJP site, however, showed no trend over the same measurement period for two reasons (Fig. 3). First, summer precipitation in 2002 helped lessen the impact of the drought. Second, because of the coarse nature of the soil at the OJP site, water contents are always very low compared with those of the OA site, even when the OA site is under a severe drought constraint.

Initial analysis revealed that soil water was an important variable for explaining the observed variations in transpiration at the half-hourly level at both the OA and OJP sites. This initial analysis also revealed that there was no difference among any of the soil water variables tested in their power to explain this variation in observed transpiration. Tested variables included θ_m and θ_r , by layer, and averaged over the full profile.

3.2. Modelling half-hourly transpiration

Application of Eqs. (1)–(4) to the half-hourly environmental and transpiration data from the OA site yielded an excellent fit of the model, with an r^2 of 0.86 and a minimal prediction bias (Fig. 4a). This fit was achieved by including three environmental modifiers in Eq. (2), θ_r , K_d and D_a (Fig. 5a–c). These three modifiers capture 46, 18 and 13%, respectively, of the variability in the transpiration. The dependence on K_d and D_a is

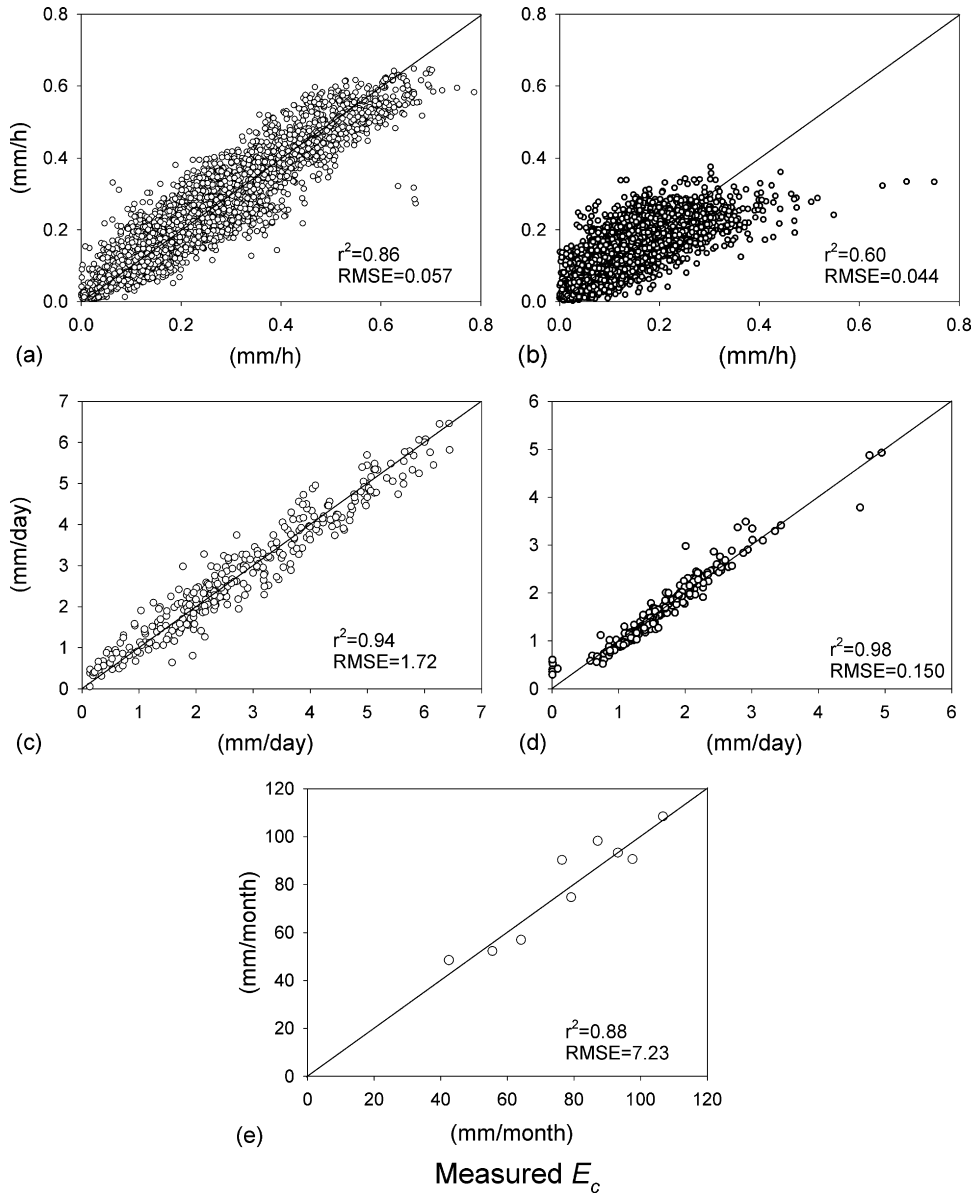


Fig. 4. Predicted values of transpiration (E_c) plotted against "measured" values of transpiration. The predictions are done for two sites, Old Aspen (a, c and e) and Old Jack Pine (b and d), and three time scales, half-hourly (a and b), daily (c and e) and monthly (e). For the daily and monthly graphs, the "measured" transpiration rates are values predicted from the half-hourly model summed up to the appropriate scale. Also shown are values of the coefficient of determination (r^2) and of the root mean square error (RMSE) for the individual model adjustments.

similar to that reported by Wu et al. (2000) for OA in conditions of non-limited soil water supply. All values of adjusted parameters, including \bar{g}_c , are presented in Table 1, along with the mean values of the variables in the present dataset (required in the calculation of the modifier in Eq. (3)). Other variables (wind speed, air temperature, time of day, day of year and day number) in the time series failed to explain 5% or more of the residual unexplained variation in measured transpiration and are left out of the final equation. Visual analysis

of the residuals plotted against all environmental variables and against time variables (not shown) showed no particular bias.

Results from the OJP site were not as good, with an r^2 value of 0.60, and a slight bias that resulted in a tendency to under-predict at high evaporation rates (Fig. 4b). We tested an asymptotic function to represent the D_a modifier in replacement of Eq. (3), but this formulation improved the fit by only 2% and was not retained. Visual analysis of the residuals plotted against all environmental variables

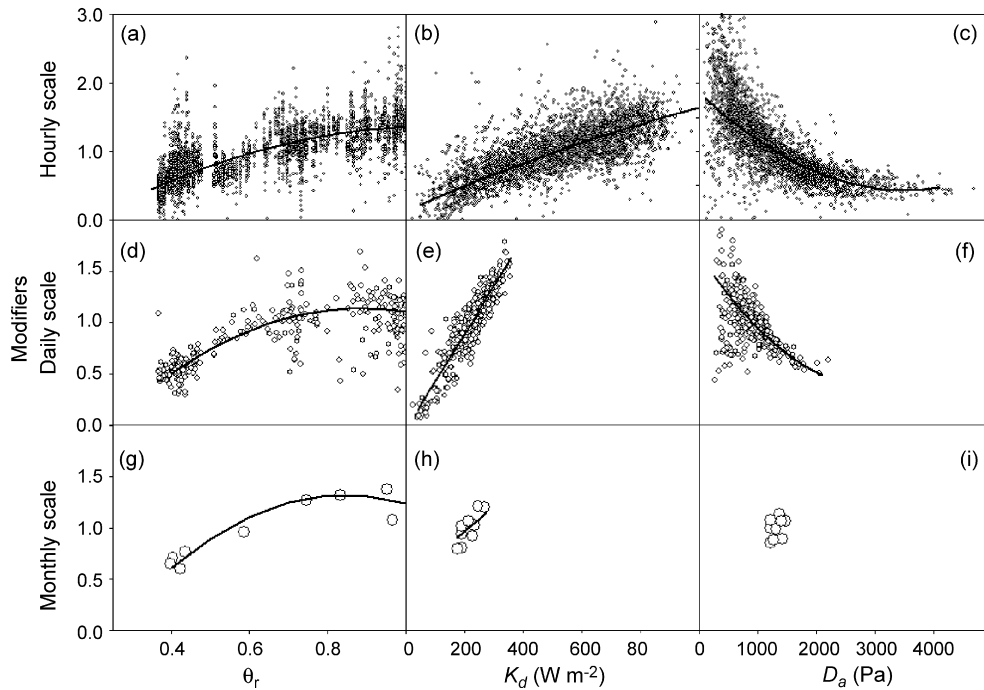


Fig. 5. Environmental modifiers (solid lines) for relative water content (θ_r), vapour pressure deficit (D_a , Pa) and global incoming solar radiation (K_d , W m^{-2}) derived from Eqs. (4) or (5), and values from Table 1 and used in Eq. (3) to estimate transpiration at the half-hourly (a–c), daily (d–f) and monthly (g–i) scales for the Old Aspen site. The data points represent the ratio values of transpiration modelled without using the specific modifier to “measured” values of transpiration. The definition of “measured” is as in Fig. 4. Summaries of modifier coefficients are in Table 1.

Table 1

Values of mean canopy conductance (\bar{g}_c) and of empirical parameters a_0 , a_L and a_Q necessary to compute canopy conductance (g_c) and transpiration using Eqs. (1)–(4)

Variable	Old Aspen (OA)			Old Jack Pine (OJP)			$g_{c\text{MAX}}$ (mm s^{-1})	
	Mean or α_0	α_L	α_Q	Mean or α_0	α_L	α_Q	OA	OJP
Half-hourly scale ^a								
θ_r	−0.64	3.7	−1.71	0.65	0.78	–	14.3	10.2
D_a	1316	−0.67	0.20	1310	−0.95	0.31		
K_d	515	0.77	−0.10	440	0.73	−0.17		
Daily scale ^b								
θ_r	−0.96	4.71	−2.65	0.66	0.85	–	9.3	5.9
D_a	902	−0.54	0.116	867	−0.86	0.37		
K_d	224	1.03	–	193	0.55	–		
Monthly scale ^c								
θ_r	−1.23	6.022	−3.56	–	–	–	3.4	–
K_d	215	0.53	–	–	–	–		

The graphical representation of the modifiers is found in Fig. 5 (Old Aspen) and Fig. 6 (Old Jack Pine). Symbols and units for the environmental variables are D_a (Pa) for vapour pressure deficit, K_d (W m^{-2}) for global radiation, and θ_r for relative soil water content. All parameters are significant ($\alpha < 0.001$). Also shown are the values of $g_{c\text{MAX}}$ computed as the average of the top 5% values of g_c estimated for the full observation time series (six growing seasons for OA and five growing seasons for OJP) using Eq. (2).

^a \bar{g}_c : OA = 31 m h^{-1} , OJP = 18 m h^{-1} .

^b \bar{g}_c : OA = 490 m day^{-1} , OJP = 280 m day^{-1} .

^c \bar{g}_c : OA = $8260 \text{ m month}^{-1}$.

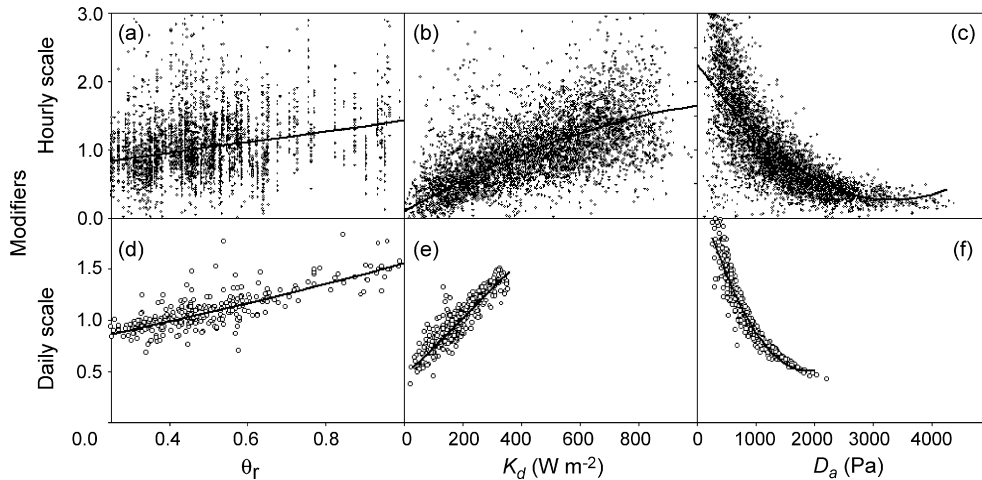


Fig. 6. Environmental modifiers (solid lines) for relative water content (θ_r), vapour pressure deficit (D_a , Pa) and global incoming solar radiation (K_d , $W m^{-2}$) derived from Eqs. (4) or (5), and values from Table 1 and used in Eq. (3) to estimate transpiration at the half-hourly (a–c) and daily (d–f) scales for the Old Jack Pine site. The data points represent the ratio values of transpiration modelled without using the specific modifier to “measured” values of transpiration. The definition of “measured” is as in Fig. 4. Summaries of modifier coefficients are in Table 1.

and against time variables failed to reveal the source of the bias. The fit was achieved using the same variables as for the OA site: θ_r , D_a and K_d (Fig. 6a–c). These three modifiers capture 10, 13 and 30%, respectively, of the variability in transpiration. The modifier relationship to D_a in Fig. 6c is similar to branch-level relationships for jack pine obtained by Dang et al. (1997a) near Thompson, Manitoba using a LI-COR model LI-6200 portable photosynthesis system. All values of adjusted parameters, including mean canopy conductance (\bar{g}_c), are presented in Table 1, along with the mean values of the variables in the present dataset (required in the calculation of the modifier in Eq. (3)). Other variables (wind speed, time of day, day of year, day number in the time series) failed to explain 5% of the residual unexplained variation in measured transpiration and were left out of the final model.

The θ_r modifier was the most important environmental modifier in the OA dataset, explaining by itself about 46% of the variation in measured transpiration. The non-linear shape of this modifier shows a plateau at the higher values of θ_r when water is non-limited, and a rapid drop as θ_r falls below about 0.7 (Fig. 5a). Similarly shaped responses of transpiration to θ_r or θ have been found in other studies (Granier et al., 2000; Granier and Loustau, 1994; Granier and Bréda, 1996; Bernier et al., 2002) for a variety of tree species.

For the OJP dataset, θ_r explained only about 10% of the observed variation in the transpiration dataset. The best fit to the dataset for θ_r is achieved with a simple linear model, with no plateau at high θ_r (Fig. 6a). This lack of plateau suggests that θ had limited transpiration

throughout the 5 years of measurements, whatever the rainfall conditions. The very low values of θ at the OJP site when compared with the OA site (Fig. 2) support this interpretation of the θ_r modifier. The lack of plateau also suggests that the maximum value of g_c reached by this jack pine stand during the five summers of measurements is still water limited.

An increase in D_a generated a strong and highly non-linear drop in canopy conductance at both sites (Figs. 5c and 6c). Aspen is known for its stomatal sensitivity to D_a (Lieffers et al., 2001), and the pattern reported here is very similar to that presented by Hogg and Hurdle (1997) for the OA site, except that it lacks the initial plateau proposed by these authors. The difference in our modifiers from those of Hogg and Hurdle (1997) may result from differences between their modelling approach and that of the current work. The D_a modifier derived by Wu et al. (2000) is quite similar to the one derived in the current exercise as both cause g_c to be halved as D_a rises from about 500–2500 Pa. In their study near Thompson, Manitoba, Dang et al. (1997a) found the relative sensitivity of g_s to D_a in jack pine to be slightly greater than in aspen, an observation that is supported by the present study (Figs. 5c and 6c).

K_d also contributed significantly to explain the variation in measured transpiration rates at both sites (Figs. 5b and 6b). The significance of K_d as a modifier for half-hourly transpiration may result either from an energy limitation to the transpiration process or from a direct effect of radiation on stomatal closure.

Wind speed was not a significant environmental variable at either the OA site or the OJP site, and the

analysis of residuals revealed an absence of bias with respect to wind speed at either site (analysis not shown). This result validates the use of the Monteith and Unsworth (1990) simplification of the Penman–Monteith model of transpiration for forest canopies with their strong coupling to the atmosphere. A similar absence of relationship between transpiration and wind speed has also been found for balsam fir (*Abies balsamea* L.) in eastern Canada (P.Y. Bernier, unpublished results).

There was also a notable absence of any relationship between residuals and time since the beginning of the measurement sequence for the two stands (analysis not shown), indicating a constancy in the relationships between g_c and environmental variables between the non-drought and the drought periods'. A similar constancy in the relationship between evapotranspiration and photosynthesis throughout the drought period has also been observed by Kljun et al. (in press) on the OA site. Measurements of leaf area index (Barr et al., 2004) show a drop in the leaf area of the aspen trees at the OA site from a pre-drought (1998–2001) average of 2.69 to a low of 1.95 in 2003, indicating that some acclimation to drought has taken place at this site through canopy-level modifications. Why this drop in LAI does not show as a change in the residuals of Fig. 5 may result from the confounding effect of θ_r , whose effect is captured in the model (Fig. 5a).

Values of half-hourly g_{cMAX} were computed, as described earlier, as the average of the top 5% of modelled g_c values. This procedure yielded a value of 14.3 mm s^{-1} for the half-hourly analysis of OA data, a value close to the 15 mm s^{-1} ($600 \text{ mmol m}^{-2} \text{ s}^{-1}$) reported by Blanken and Black (2004) from 1994 eddy covariance data for the same site. The g_{cMAX} value obtained for the OJP site is 10.2 mm s^{-1} . The lower g_{cMAX} of jack pine as compared with aspen may reflect intrinsic species differences but, as discussed above, may also result from a near-permanent water stress caused by the very low soil water contents at the OJP site. The lack of a plateau in the water content modifier in the highest water contents for the OJP site (Fig. 6a) supports this interpretation. Additional analysis (not shown) reveals that over all measurement years, total yearly evapotranspiration was nearly constant at the OJP site at about 230 mm, in spite of large year-to-year variations in rainfall, from a low of 262 mm in 2003, to a high of 429 mm in 2002. Again, this suggests that water drains very rapidly from the soil profile and is rapidly unavailable to the pine for transpiration.

The parameter values reported in Table 1, together with Eqs. (1)–(4), make it possible to estimate half-hourly g_c and transpiration for years other than those

used in the analysis. The only caveat is that extrapolation outside the domain of an independent variable used in the adjustment must be done with care if the modifier is non-linear. A case in point is the non-linear modifier for D_a for both the OA (Fig. 5c) and OJP (Fig. 6c) sites that increases when D_a increases beyond about 3500 Pa. The values of the parameter \bar{g}_c presented in Table 1 are dependent on the dataset used in the model adjustment and thus have little significance outside their use in generating modelled values of g_c and E_c . Modellers preferring to use g_{cMAX} rather than \bar{g}_c (two constants) can simply replace \bar{g}_c in Eq. (2) by $(g_{cMAX} - \Delta)$, where Δ is the difference between g_{cMAX} and \bar{g}_c .

3.3. Changing the temporal scale

Application of Eqs. (2)–(4) to the daily environmental data yields an excellent agreement between predicted and measured E_c with an r^2 of 0.94 for the OA site, and 0.98 for the OJP site (Fig. 4c and d). This good agreement is not surprising since the daily model was adjusted to modelled half-hourly transpiration aggregated up to the day. Only daily θ_r , D_a and K_d were retained as modifiers in both cases, using the 5% contribution criteria. It is to be noted, however, that we used values of daily D_a computed from daily maximum and minimum temperatures rather than a daily average of the measured values, as most modellers would have to do. The three environmental modifiers are shown in Fig. 5d–f for OA and in Fig. 6d–f for OJP, while the parameter values are shown in Table 1.

The shape of both daily D_a and K_d modifiers shows the linearization effects of moving from a semi-hourly to a daily time step. For both sites, the quadratic term of the K_d modifier is non-significant in this daily analysis, while that of the D_a modifier is still significant, but far less important than in the half-hourly model. The θ_r modifier, on the other hand, is identical in both the half-hourly and daily models (Fig. 5), an expected result since dry-down is a slow process that generates little within-day variability in soil water content. Instantaneous measurements of θ on any given day are therefore similar to the daily average value, which is quite different from that of the rapidly varying K_d and D_a .

Maximum canopy conductance at the daily time step is computed by applying Eq. (2) and the appropriate parameter values of Table 1 to the daily-level environmental variables, and averaging the top 5% values. The result for the OA site is a daily g_{cMAX} of 9.3 mm s^{-1} , or just over 60% of the value found when using half-hourly data. For the OJP site, the daily g_{cMAX} is

5.9 mm s^{-1} , also about 60% of the half-hourly value. This drop in daily $g_{c\text{MAX}}$ is partly due to the model-to-model least-square fit, which tends to eliminate extreme values. However, most of the difference between the half-hourly and the daily $g_{c\text{MAX}}$ values is a result of the change in temporal scale. Whereas the maximum half-hourly values are for periods of high conductance only, the maximum daily values necessarily incorporate a mixture of conditions found during the diurnal cycle that are not all favourable to high conductance.

The monthly analysis of the OA data yielded an excellent agreement ($r^2 = 0.88$, Fig. 4d). Again, the good fit is expected since this is a model-to-model adjustment, and the number of parameters (6) is high in comparison to the number of data points (9). At this temporal scale, only the K_d and θ modifiers still contribute to explain more than 5% of the variation in measured transpiration (Fig. 5g and h). The D_a modifier fails to explain the 5% of variation necessary to be included in the final model (Fig. 5i). A monthly value of daily $g_{c\text{MAX}}$ is derived from the monthly analysis by applying Eq. (2) and the appropriate parameters from Table 1 to the monthly measurements of K_d and θ . The application of the top 5% rule for getting the maximum value is more approximate in this case than it is for the half-hourly or the daily model since only nine monthly values are available, and the top 5% contains a single value. Nevertheless, at 3.4 mm s^{-1} , the monthly-level estimate of $g_{c\text{MAX}}$ shows the clear trend of a drop in daily $g_{c\text{MAX}}$ values with an increase in the coarseness of the temporal resolution.

It is clear from this exercise that the value of $g_{c\text{MAX}}$ and environmental modifiers used in any model has to be derived using a temporal resolution similar to the one used to define the environmental variables. Studies have shown that similar care must be taken with respect to changes in the spatial scale. Dang et al. (1997b) showed that the estimated photosynthetic capacity of boreal jack pine, black spruce and aspen canopies was strongly affected by the method used to scale from the leaf-level, with linear scaling based on LAI producing the largest estimates. Bartlett et al. (2003) found that branch level g_s scaled by LAI overestimated g_c by a factor of 2, based on comparisons of modelled fluxes with eddy covariance measurements in a highly clumped boreal black spruce stand. Rambal et al. (2003) examined two big-leaf scaling methods and found their performance limited with respect to g_c derived from tower measurements. They argued that clumping should be accounted for because tower measurements integrate fluxes from foliage elements clumped at the branch, tree and ecosystem scales.

3.4. Comparing with other soil water modifier functions

We compare in Fig. 7 the soil water modifiers obtained using the half-hourly OA and OJP data to the soil water modifiers proposed by Landsberg and Waring (1997; LW curves) for radiation use efficiency, and to the soil water modifier of Granier et al. (2000) for transpiration. We transformed our modifiers to fit the common framework in which a value of 1 represents optimum conditions, not average ones. As can be seen, the agreement between the LW sandy clay loam curve and the OA curve is very good. However, the LW curve for sand bears no resemblance to that derived from the OJP dataset. Neither the OA nor the OJP curve compares very well to that empirically determined by Granier et al. (2000), although the Granier curve and our OA have similar shapes.

One of the problems plaguing a comparison of soil water modifiers is the basis on which the volumetric water contents are transformed into relative water contents. For example, the LW curves are expressed as a function of the “soil moisture ratio”, a transformation of θ that is somewhat different from that of Eq. (5) for θ_r (see Waring and Major (1964) for the basis of available water for the LW curves). And even when the relative water content is calculated as in Eq. (5), the manner in which water contents at field capacity and at wilting point (or maximum and minimum available water) are obtained may vary, thereby creating differences in scales. As mentioned above, this scaling effect could explain the difference between the Granier and the OA

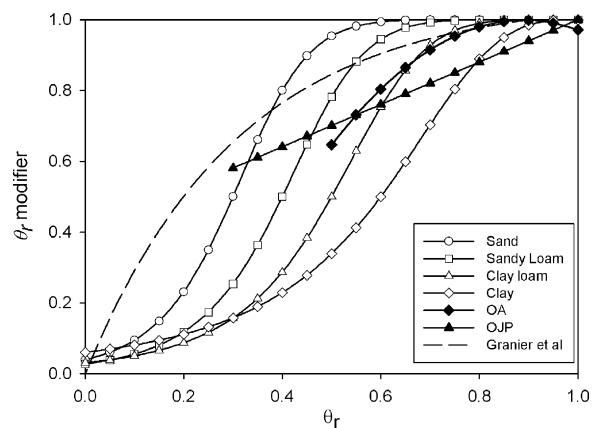


Fig. 7. Comparison of the family of curves proposed by Landsberg and Waring (1997) to capture the effect of soil water content on light use efficiency, and of the soil water modifier to transpiration obtained by Granier et al. (2000) and those obtained in this study for the sandy clay loam soil of the Old Aspen (OA) site and the sandy soil of the Old Jack Pine (OJP) site.

curves in Fig. 7. Attention must be paid to such an issue if widely applicable curves are to be proposed.

The OJP soil water modifier obtained on a site with very coarse soil is very different from both the LW and Granier curves. Landsberg and Waring (1997) attempted to capture the differences in the hydraulic properties of the soils with different proportions of clay, and implicitly assumed that the absence of clay extends the range of θ over which water can be extracted without affecting physiological processes. This was done while recognizing a lack of empirical evidence and a need for improvement. Our results show that the link between clay content and the soil water modifier is not monotonic. In very coarse soils, low unsaturated hydraulic conductivity decreases plant water absorption under most circumstances, so that optimum conditions are seldom met. As a second approximation to the LW curves, we suggest using the clay, clay loam and sandy loam functions in unmodified form, but using the curve for sand as presented in Fig. 7.

4. Conclusion

The results presented in this analysis show that the relationship between canopy conductance and soil water content is significantly affected by soil texture, mostly because texture determines the amount of water that will be retained in the root zone and made available to the trees. The analysis also shows the effect of scale on the shape and significance of response functions. Increasing coarseness in time tends to linearize physiological responses to environmental variables (e.g., global radiation) and makes non-significant some that are critical at finer scales (e.g., D_a). At the monthly scale, solar irradiance (or energy) and soil moisture (or wetness) are the significant variables for modelling transpiration during the growing season. We hypothesize that a similar linearization will occur with increased spatial averaging, particularly for soil water.

The relationship between scale and parameter values demonstrated for g_{cMAX} in this study likely applies to all parameters that are derived from variables whose domain is scale-dependent. The scale across which the changes are most important varies with independent variables, as shown in Fig. 5, with values of parameters for the soil water modifier being stable from the half-hour to the month, while those of D_a change dramatically over the same time scales. This point is of particular importance when parameters obtained from the literature are used in models, and underlines the necessity to verify the correspondence in temporal and spatial resolution between the experiment from

which the parameters were derived and the resolutions in the model to which the parameters will be applied.

Finally, this empirical analysis validates proposed soil water modifiers that are necessary to predict the impact of present and future droughts on physiological processes and tree growth. Our results for a sandy clay loam (Old Aspen site) are in approximate agreement with those of Landsberg and Waring (1997), but a different relationship was found for a sand with rapid drainage (Old Jack Pine site). The numbers of flux towers around the world offers increased opportunity for carrying out such analysis for other species and soil textures.

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