

Full Length Research Paper

Characteristics and modelling of canopy conductance and transpiration of *Platycladus orientalis* (L.) Franco in Loess Plateau of China

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Estimating plant water use is an important step in assessing the effects of increasing vegetation cultivation on the hydrological cycle especially in arid and semi-arid regions. In this study, meteorological measurements combined with sap flow techniques provided a low-cost option to study the canopy physiological transpiration of *Platycladus orientalis* response to environmental factors on a continuous basis. Canopy transpiration (E_c) was measured by thermal dissipation method of Granier, and canopy conductance (g_c) was calculated by inverting the Penman-Monteith equation. The results showed that the transpiration of *P. orientalis* was strongly controlled by stomatal conductance, and g_c was a comprehensive and compounded environmental variable. An improved Jarvis-type model, based on a series of environmental control functions, explained 85% of the variation observed in g_c . Cross validation showed that this model provided good predictions of canopy conductance and transpiration for *P. orientalis*. Such a methodology offers a reasonable estimation of water use in the determination of water balance for land water resources planning, vegetation management and impact assessments of rehabilitation.

Key words: Sap flow, canopy transpiration, canopy conductance, model, Penman-Monteith equation, *Platycladus orientalis*, semi-arid region.

INTRODUCTION

Water is becoming an increasingly scarce resource and has become one of the increasing threats to the growth of artificial forests in the semi-arid Loess Plateau of China (Chen et al., 2008). Although tree planting can temporarily increase catchment water yield in some circumstances (Bosch and Hewlett, 1982; Hornbeck et al., 1993), regrowth of tall, dense forests consumes more water, with the result that catchment yield may decline and even soil desiccation occurred (Cornish and Vertessy, 2001; Vertessy et al., 2001; Li et al., 2008; Macfarlane et al., 2010). Therefore it is necessary to determine water use and requirements as well as assessing the effects of increasing artificial forest cultivation on the hydrological cycle.

Given it is an important component of the water balance in forests, transpiration of whole forests canopies has been experimentally measured in a wide range of environments, from boreal to tropical, using different methodologies. In this study meteorological measurements combined with sap flow techniques provide a low-cost option to study the canopy physiological transpiration response to environmental factors on a continuous basis. Sap flow technique based on thermal dissipation method has helped to measure transpiration from different species or a single component of mixed vegetation (Granier et al., 1996; Evers et al., 2002; Rana et al., 2005; Oguntunde et al., 2007; Gebauer et al., 2008).

Canopy conductance (g_c) is a key parameter in controlling energy and water exchanges between canopy and the atmosphere (Wang et al., 2009). Measured sap flows have successfully been used to derive canopy conductance (g_c) by inversion of the Penman-Monteith

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equation (Ewers et al., 2002; Chuang et al., 2006; Krauss et al., 2007; Gebauer et al., 2008). In this approach, the bulk behaviour of stomata is represented by the canopy conductance. Stomatal behaviour could be conveniently inferred from continuous monitoring g_c . This provided the basis for exploring ways of modelling tree water use with available mechanistic models. An analytical model of Jarvis (1976), which was further developed by Stewart (1988) and Wright et al. (1995) was one of the most important representations of stomatal controls, and hence prediction of transpiration. The advantage of the Jarvis-type model for hydrologic processes is that it directly addresses plant response to vapour pressure deficit from canopy to air, which means it works best when the rate of water loss is high and hence hydrologically significant.

Platyclusus orientalis (L.) Franco belongs to the Cupressaceae Family, is synonym to *Thuja orientalis* L., *Platyclusus stricta* Spach., *Thuja acita* Moonch., *Biota orientalis* (L.) Endl. This species is native to China and Korea. The seeds, leaves and branches of this plant have long been used as a traditional Chinese medicine to cure haemorrhaging, palpitations, ephidrosis, asthma and bronchitis. Since 1980, it has been widely cultivated as ornamental in America (Dirr and Heuser, 1987). So far, studies on physiological responses of *P. orientalis* to environmental factors were limited among water use efficiency, transpiration in leaves, spatial variation pattern of stem sap flow and nighttime sap flow (He et al., 2003; Tian et al., 2005; Wang et al., 2006). Apart from these studies, little is known about the canopy physiological response to changing environments in *P. orientalis*. Therefore, the aim of this study is to (1) characterize the response of sap flow and canopy conductance to meteorological variables, (2) use sap flow based transpiration measurements to parameterize the improved Jarvis-type models of canopy conductance, and (3) simulate the canopy transpiration using the Penman-Monteith equation for *P. orientalis*.

MATERIALS AND METHODS

Study site

This study was conducted in a *P. orientalis* plantation at Tuqiaogou watershed of Fangshan County in Shanxi Province on the Loess Plateau of China (37°36' N, 110°02' E, altitude:1200 m). The *P. orientalis* trees (spacing of 1.5 × 4 m giving a density of 1666 trees ha⁻¹) established in 1993 from four year old bare root seedling has an average height of 6.5 m and average trunk diameter (DBH) of 6.2 cm. Basal area and DBH of all trees were measured in five replicate 20 × 20 m plots. Mean annual temperature (1975 to 1992) at the study site was 7.3°C and annual rainfall averaged 416 mm, concentrated in the June to September period with the soil texture within the plot as generally medium loam.

Incoming solar radiation (R_s), air temperature (T_a), relative humidity (RH), wind speed (u) and rainfall were recorded as 15 min averages with an automatic weather station (Vantage Pro 2, Davis Inc., USA) installed about 200 m away from the plot.

Sap flow measurements

Fifteen sample trees covering the range size distribution at the stand (mean tree height 6.5±0.2 m and sapwood area 44.1±6.17 cm²) were selected for measurements of sap flow using thermal dissipation method of Granier (1987). Two cylindrical sensor probes (TDP 50, Dynamax, USA) about 2 mm in diameter, each containing a copper-constantan thermocouple, were inserted in the sapwood of the tree trunks with one probe about 10 cm above the other. The probes were installed in the trunk at a point halfway between the soil surface and the lowest actively growing branch, then the trunk was shielded with aluminium foil, to minimize the effect of thermal fluctuation on the measurements (Lu et al., 2004). Measured transpiration (E_c^{meas} , mm h⁻¹) of an individual tree was calculated as the product of weighted sap flux density and the ratio of sapwood area (A_{sw}) and the projected canopy area (A_c):

$$E_c^{meas} = f \frac{A_{sw}}{A_c} \quad (1)$$

Sapwood area was determined with an increment borer (5 mm in diameter) which is a specialized tool used to extract a section of wood tissue from a living tree with relatively minor injury to the tree. The length of the core sample can be measured with diameter tape, for the boundary line between the sapwood and the heartwood was identified based on the different colors. Samples were taken at breast height. Whole tree sap flux density (f , cm s⁻¹) was computed through an empirical relation validated and confirmed for many species (Granier, 1987; Braun and Schmid, 1999) as:

$$f = 0.0119 \left(\frac{\Delta T_{max} - \Delta T}{\Delta T} \right)^{1.231} \quad (2)$$

where ΔT is the temperature difference between the two probes and ΔT_{max} is the baseline (maximum) temperature difference for the dataset of the day. Sap flow measurements, sampled at 15 min intervals in step with the weather data, were made between 20 June [Day of Year (DOY) 171] and 16 (DOY 259) September 2009.

Calculation of canopy conductance

Assuming an aerodynamically well mixed canopy and similar leaf and air temperature, mean canopy stomatal conductance (g_c) can be calculated as a simplified form of the Penman-Monteith equation (Monteith and Unsworth, 1990; Bosveld and Bouten, 2001) as:

$$g_c = \frac{\gamma E_c^{meas}}{\rho C_p D_e} \quad (3)$$

where γ is the psychrometric constant (kPa K⁻¹), λ is the latent heat of water vaporization (J kg⁻¹), E_c^{meas} is the measured canopy transpiration by TDP method, ρ is the density of dry air (kg m⁻³), C_p is the specific heat of dry air (J kg⁻¹ K⁻¹), D_e is the vapour pressure deficit of air (kPa).

Equation 3 has been shown to be valid especially when the vegetation canopy is well coupled with the atmosphere, with D_e mainly controlling the canopy process resulting to the decoupling factor of ≤ 0.2 (Granier et al., 1996; Bosveld and Bouten, 2001) and had been tested against the form inverted directly from Equation 8 by Oguntunde et al. (2007), the predicted pattern was near perfect ($r^2=0.98$).

Canopy conductance modelling

Predicted canopy conductance (g_c^{pred} , $m\ s^{-1}$) is modeled by as a product of response functions (f , $0 \leq f \leq 1$). In present study, g_c is assumed to be determined by D_e , R_s and T_a (Jarvis, 1976; Stewart, 1988):

$$g_c^{pred} = g_{cmax} f(D_e) f(T_a) f(R_s) \quad (4)$$

$$f(D_e) = \exp(-k_1 D_e) \quad (5)$$

$$f(T_a) = \exp[-k_2 (T_a - T_{opt})^2] \quad (6)$$

$$f(R_s) = R_s (1000 + k_3) / 1000 (R_s + k_3) \quad (7)$$

where g_{cmax} is a theoretical maximum stomatal conductance under optimal environmental and leaf conditions. T_{opt} is the optimum temperature limit to transpiration. Parameters k_1 – k_3 were optimized using the Levenberg-Marquardt algorithm (Marquardt, 1963).

Canopy transpiration prediction

The prediction of *P. orientalis* canopy transpiration (E_c^{pred}) was made based on widely used Penman–Monteith equation (Monteith and Unsworth, 1990):

$$E_c^{pred} = \frac{\Delta(R_n - G) + \rho C_p D_e g_a}{\lambda \left[\Delta + \gamma(1 + g_a / g_c^{pred}) \right]} \quad (8)$$

where Δ is the slope of saturation vapour pressure with temperature ($kPa\ ^\circ C^{-1}$), R_n is the net radiation above canopy ($W\ m^{-2}$), G is the heat flux to soils ($W\ m^{-2}$), g_a is the aerodynamic conductance ($m\ s^{-1}$), g_c^{pred} is the predicted canopy conductance ($m\ s^{-1}$), λ is the latent heat of water vaporization ($J\ kg^{-1}$), γ is the psychrometric constant ($kPa\ K^{-1}$).

The R_n is the difference between the incoming net shortwave radiation (R_{ns}) and the outgoing net longwave radiation (R_{nl}). R_{ns} resulting from the balance between incoming and reflected solar radiation is given by $R_{ns} = (1 - \alpha) R_s$, where R_s is the solar radiation recorded by the automatic weather station and α is albedo measured by sun photometer (MI-110, China) in 2009. The R_{nl} is expressed quantitatively by Stefan-Boltzmann law (Allen et al., 1998). The hourly albedo (α) was estimated as ($R^2 = 0.864$, $n = 132$, $P < 0.001$):

$$\alpha = 0.08629 + 0.0002825 D - 0.04054 T - 7.0 \times 10^{-6} D^2 + 1 \times 10^{-6} DT + 1.62 \times 10^{-3} T^2 \quad (9)$$

where D is the day sequence and T is the time sequence.

Statistical analysis and cross validation

The statistical analysis was carried out with the SPSS software (version 17.0). Daily measurements of sap flow were filtered to exclude rainfall events to eliminate wet-canopy conditions. To determine the extent to which canopy transpiration is controlled by stomatal aperture in response to micrometeorological changes, a dimensionless decoupling coefficient (Ω) was calculated according to Jarvis and McNaughton (1986):

$$\Omega = \frac{1 + \Delta / \gamma}{1 + \Delta / \gamma + g_a / g_c} \quad (10)$$

where the g_a has been derived, following the formulation described by Thom and Oliver (1977). The decoupling factor ranges from zero to one. Stomatal control of transpiration grows progressively stronger as Ω approaches zero because the vapour pressure at the canopy surface becomes increasingly coupled to that in the bulk air.

To validate the selected model, the whole data was divided into two groups, covering the odd days (Database A) and even days (Database B) of measurement respectively. The selected model was then fitted separately to each of the two groups and cross-validated on each other. For each group, predicted g_c was then used to predict E_c using Equation 8. These predicted E_c values were compared graphically with the measured E_c values measured from sap flow, as was done for g_c . This type of validation procedure has been described as robust and consistent (Stewart, 1988; Lu et al., 2003). Root mean square error ($RMSE$) was used to weight the deviation between the i th experimental value (y_i) and the i th predicted value (\hat{y}_i) of g_c and E_c . Where we express the $RMSE$ as:

$$RMSE = \left[\frac{1}{n} \sum (y_i - \hat{y}_i)^2 \right]^{1/2} \quad (11)$$

RESULTS AND DISCUSSION

Transpiration

As results shown in Figure 1a, the correlation between *P. orientalis* canopy transpiration and solar radiation could be described by a simple linear model ($R^2 = 0.829$, $P < 0.001$) during 6:00 to 13:00 h and a *Sigmoidall–Hill* curve ($R^2 = 0.74$, $P < 0.001$) in the afternoon (13:00 to 20:00 h) respectively. A hysteresis loop was clearly demonstrated in Figure 1b, which indicates a time lag between sap flow and climatic variables, had been reported in cashew (Oguntunde and van de Giesen, 2005), and *Caragana korshinskii* (Dang et al., 2010). *P. orientalis* showed the greatest tendency towards efficiency, similarly in aspen by Mackay et al. (2003), indicating that it has high E_c under low vapour pressure deficit conditions ($D_e < 1.2\ kPa$), but with the highest E_c , would also show the greatest decline at the highest levels of D_e . This follows from the argument that stomatal closure would more than offset the increased evaporative demand, as first suggested by Jarvis (1980) and shown empirically by Pataki et al. (2000).

Canopy conductance

Highest g_c values ($0.003\ m\ s^{-1}$) were observed between 10:00 and 11:00 h before declining, which subsequently decreased in response to increasing evaporative demand but later recovering in late afternoon (Figure 2). This behaviour was explained by stomatal conductance declining as D_e increased. We shall show later that there is also a negative relationship between g_c and D_e . Figure 2 also shows the mean diurnal trends in transpiration and it is evident that this reflects the diurnal patterns in R_s and D_e . However, it is not possible at this point to determine,

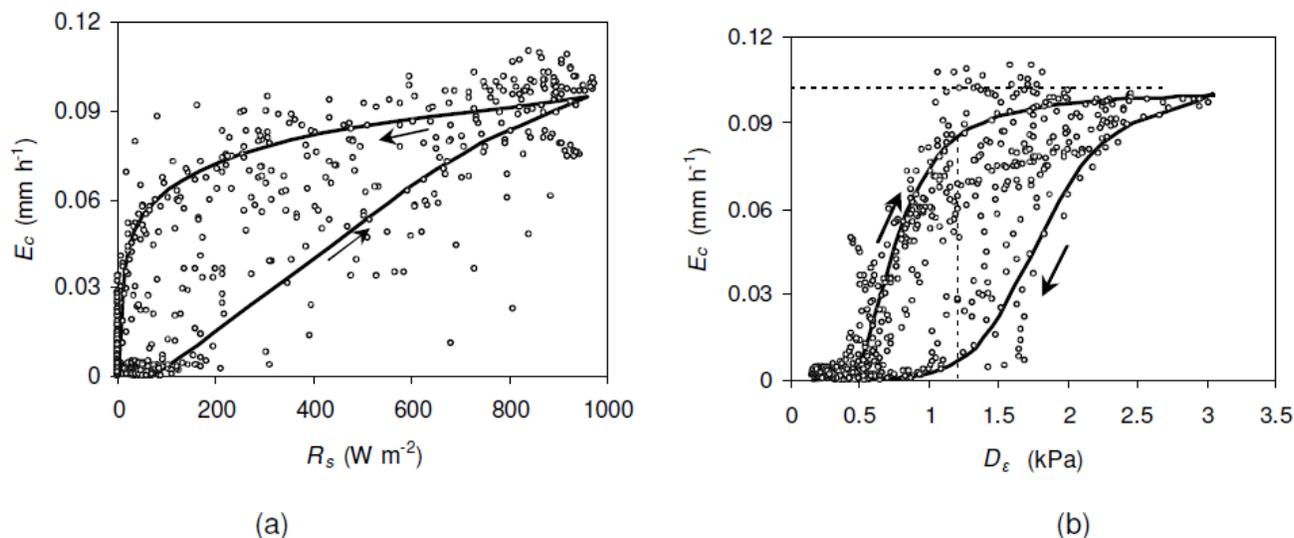


Figure 1. Canopy transpiration (E_c) as function of solar radiation (R_s) and vapour pressure deficit (D_e). The arrow up and down represents morning and afternoon separately.

which of these two variables has most effect on transpiration. Solar radiation reached very high values (722 W m^{-2}) around midday whereas D_e only peaked at about 1.9 kPa, reflecting the relatively high relative humidity conditions that existed at this site.

Values of Ω followed a similar pattern to g_c (Figure 2c). The mean daytime Ω observed over the whole period was 0.025 ± 0.008 . These low values were smaller than those reported by Granier et al. (1996) (that is, 0.2) and Kumagai et al. (2004) (0.1 to 0.4) and were characteristic of vegetation that transpiration of *P. orientalis* in this trial was strongly controlled by stomatal conductance, and that the canopy was highly coupled to the atmosphere (McNaughton and Jarvis, 1983).

From the above results, and previous studies of various other tree species transpiration (e.g. Granier et al., 1996; Roberts et al., 2001; Kumagai et al., 2004; Wallace and McJannet, 2010), it appears that canopy conductance variation is strongly related to atmospheric vapour pressure deficit and solar radiation and only weakly related to air temperature. As was shown in Figure 3a, canopy conductance declined with increasing D_e and the location of this relationship only varies slightly with solar radiation, was in agreement with the findings of Oguntunde et al. (2007). This type of stomatal response to D_e would avoid excessive water loss at high D_e and prevent leaf water potential from falling to a dangerous level. The correlation with R_s was shown in Figure 3b, where it could be described by a *Sigmoidal-Hill* curve ($R^2 = 0.747$, $P < 0.001$) in despite of large scatter in the data. The flat trends of g_c corresponding increase in R_s may further confirm that high sensitivity of *P. orientalis* leaves to changing atmospheric variations and hence the regulation of its transpiration at the canopy level.

Modelling canopy conductance

The three stomatal control functions of R_s , D_e and T_a explained about 85% of variation in g_c with an overall error of 0.001 m s^{-1} (Table 1). This is a better result compared to those with a linear model: $\ln(g_c) = a_0 + a_1 D_e + a_2 T_a + a_3 R_s$ (Oguntunde et al., 2007) and a negative exponential model: $g_c = [R_s / (R_s + d)] [a + b(c^{D_e})]$ described by Lu et al., (2003), in which 67 and 83% of the variability in conductance was explained respectively.

Some research indicated that removal of the temperature seemed to improve the predictive ability of Jarvis-type model (Oguntunde et al., 2007; Li et al., 2010) while in this study, model excluded T_a resulted a lower correlation ($R^2 = 0.834$) and a slight increase in *RMSE* (4.05×10^{-4}). The values of g_{cmax} ranging from 0.004 to 0.006 m s^{-1} , were found to be low compared to 0.01 m s^{-1} in jack pine (Bernier et al., 2006), which is evidently connected to the fact that *P. orientalis* presents a very high resistance to flow compared to several other species. The optimum temperature for *P. orientalis* transpiration was average $27.9 \pm 3.48^\circ\text{C}$ compared to 28.5°C (Wright et al., 1995), and 25.5°C (Oguntunde et al., 2007).

Cross validation

Database A and B were used for cross-validation which is seemed to be a more stringent test of the model than selecting random subsets (Stewart, 1988). The 1:1 plots in Figure 4 showed a good agreement ($R^2 > 0.85$, $P < 0.001$) between predicted and measured g_c and E_c for the two subsets. However, the scattered values (grey symbols) in Figure 4a shows that the model did not work well in

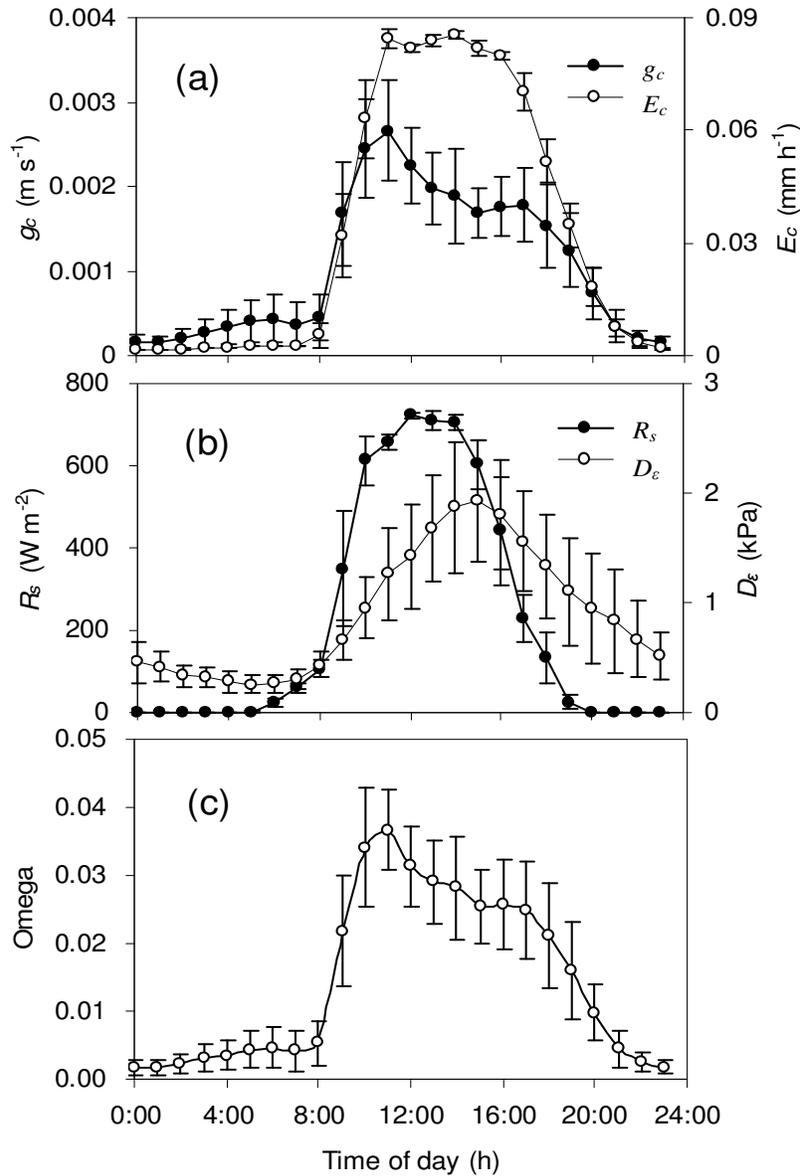


Figure 2. Diurnal courses of (a) calculated canopy conductance (g_c) and average canopy transpiration (E_c) (b) solar radiation (R_s) and vapour pressure deficit (D_e), and (c) the decoupling factor (Ω). Vertical bars on point are \pm S.E. of the mean.

certain time of day with D_e and R_s fluctuated dramatically especially when clouds increased suddenly. For example, in late afternoon (17:30 to 19:45 h) of DOY 201 when the scattered values (closed grey symbol in Figure 4a) appeared, D_e , R_s , and T_a were all much lower than those in the same time of other days. The resulting measured g_c values were higher than other days actually, but amplification of values was much less than that of being predicted from model.

As for g_c , there was a broad agreement between predicted and measured E_c (Figure 4b), but comparison with the line of equality shows that in some places (such

as grey symbols in Figure 4b which represented E_c values estimated from the same time scattered g_c values appeared) over the range of transpiration where the points were mostly on one side of the line but not noticeable further away from the line of equality. Predicted hourly E_c followed closely those measured (Figure 5). Though there was a little nighttime sap flow, in this study, we estimated no canopy transpiration of *P. orientalis* when zero values appeared in R_s , based on the hypothesis of a transport distance delay between stem and leaves (Cermak et al., 2007) and nocturnal sap flow supply for tissue water deficit by daytime great transpiration (Senock and

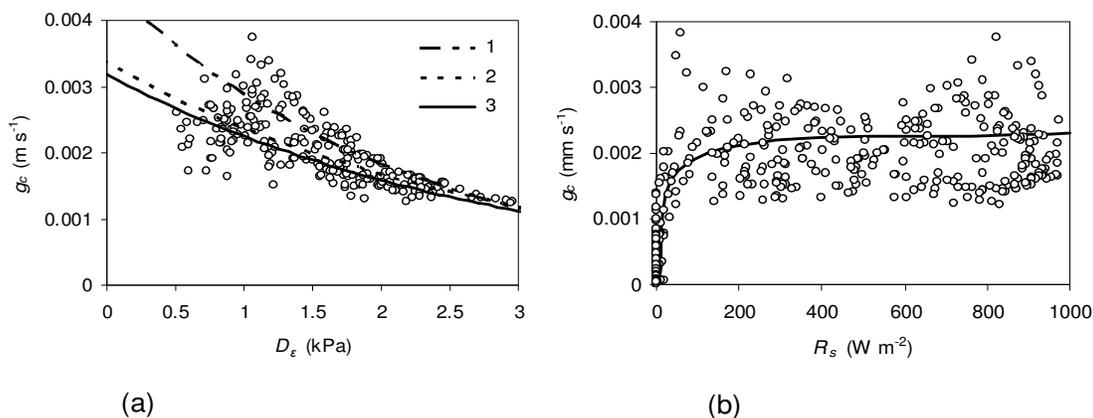


Figure 3. (a) Canopy conductance (g_c) as function of vapour pressure deficit (D_e) under different radiation condition with negative exponential curves: 1) $R_s=800$ W m⁻², $R^2=0.776$, 2) $R_s=600$ W m⁻², $R^2=0.832$, and 3) $R_s=300$ W m⁻², $R^2=0.633$. (b) Relationships between g_c and solar radiation (R_s).

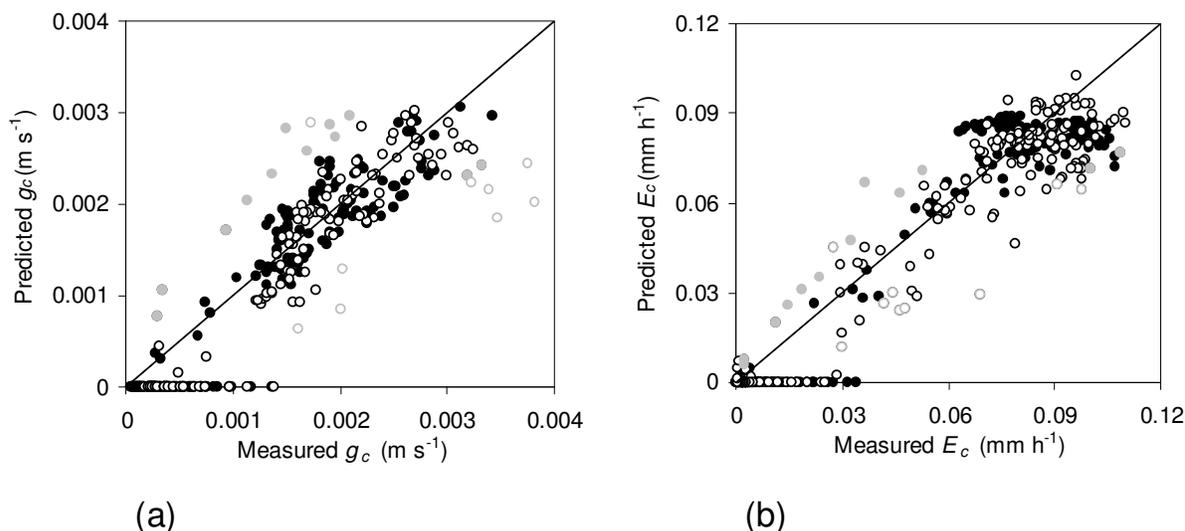


Figure 4. Predicted compared with measured g_c and E_c using independent dataset A (closed symbols) and dataset B (open symbols).

Table 1. Fitted values of parameters for Jarvis-type model optimized to predict the *P. orientalis* canopy conductance (g_c) with vapour pressure deficit (D_e), solar radiation (R_s) and air temperature (T_a) as response functions respectively.

Parameter	All data, n=454	Database A, n=223	Database B, n=231
g_{cmax}	0.005 (0.000)	0.004 (0.000)	0.006 (0.001)
k_1	0.468 (0.036)	0.405 (0.043)	0.627 (0.057)
k_2	0.006 (0.001)	0.007 (0.002)	0.005 (0.002)
k_3	21.360 (3.096)	43.148 (7.109)	10.875 (2.761)
T_{opt}	26.969 (0.692)	24.911 (0.685)	31.078 (2.046)
R^2	0.848	0.859	0.862
RMSE in g_c	3.98×10^{-4}	3.54×10^{-4}	3.80×10^{-4}
RMSE in E_c	1.01×10^{-2}	1.08×10^{-2}	1.01×10^{-2}

Values in brackets are standard errors.

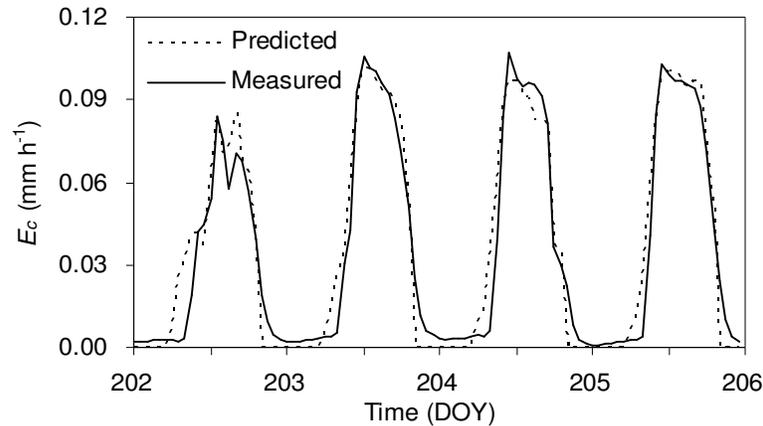


Figure 5. Diurnal courses of predicted and measured hourly E_c over the random four consecutive days (DOY 202–205). Note a good prediction of E_c for the day (DOY 202) with a light rain event around noon.

Leuschner, 1999; Fisher et al., 2007; Dang et al., 2010).

Conclusions

This study characterizes the impacts of main environmental variables on canopy conductance and transpiration of *P. orientalis*. *P. orientalis* in this trial is strongly controlled by stomatal conductance and presents a very high resistance to water flux. The parameterized Jarvis-type canopy conductance model based on a series of functions of vapour pressure deficit, solar relation and air temperature is suitable for prediction of *P. orientalis* transpiration using the Penman-Monteith equation and explains 85% of the variation observed in g_c . Cross validation shows that this model provided good predictions of canopy conductance and transpiration for *P. orientalis*. Such a methodology offers a reasonable estimation of water use in the determination of water balance for land water resources planning, forest and agriculture water management.

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