Scientific Paper

Modelling maximum canopy conductance and transpiration in *Eucalyptus grandis* stands not subjected to soil water deficits

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SYNOPSIS

There is much current interest in predicting the maximum amount of water that can be transpired by *Eucalyptus* trees. It is possible that industrial waste water may be applied as irrigation water to eucalypts and it is important to predict the maximum transpiration rates of these plantations in an attempt to dispose of this contaminated water. It is also useful to have a reference against which to compare evapotranspiration at any *Eucalyptus* site to estimate the degree of reduction in potential water use caused by soil water deficits. This paper proposes a simple model that can be used to predict maximum rates of daily transpiration by short-rotation *Eucalyptus grandis* plantations experiencing no significant soil water deficits or fertility limitation. Daily sap flow data recorded in a single average tree in an irrigation and fertilisation trial at Came plantation in the KwaZulu-Natal Midlands were used to estimate mean daily canopy conductance. Analysis of daily and seasonal variation in conductance confirmed that solar radiation and vapour pressure deficit are the dominant factors reducing canopy conductance below potential values, when soil water availability is high. A simple canopy conductance model based on these data was then used with the Penman-Monteith equation to predict daily transpiration rates by *E. grandis* trees at a second site situated on Frankfort plantation in the vicinity of Sabie, Mpumalanga. These model predictions were compared to a mean daily sap flow rate recorded in four sample trees over a full year. Transpiration estimated using the Penman-Monteith equation and canopy conductance model agreed well with the observed daily sap flow (R^2 = 0.79). The total observed annual sap flow at Frankfort was equivalent to 1320 mm, with a mean daily rate of 46 ℓ tree^{-1}. The corresponding modelled annual sap flow was 1226 mm. A seasonal change in the relationship between canopy conductance and vapour pressure deficit, observed in a previous study on *E. grandis*, was again apparent from the Came plantation data.

Keywords: *Eucalyptus grandis*, heat pulse velocity, sap flow, Penman-Monteith equation, canopy conductance, model predictions

INTRODUCTION

There are growing concerns that deep-rooted trees, such as *Eucalyptus*, lower water tables and interfere with regional hydrology (Landsberg, 1997). In South Africa, the water use of *E. grandis* remains a controversial issue due to the perception that eucalypt plantations have the greatest impact on catchment water yields. It is important to obtain good data, and to be able to simulate water use at any given plantation, as only accurate measurements will provide a foundation on which decisions regarding regional ecology and human welfare can be made (Landsberg, 1997). Water use data are also required to evaluate the efficiency with which trees use water. High water use efficiency will be an important feature in increasing plantation yields and returns on investment (Dye, 2000). There is considerable information on the rates of water use by *E. grandis*, from both national (Dye, 1987; Dye and Olbrich, 1993; Olbrich *et al*., 1993; Dye, 1996; Dye *et al*., 1997), and international studies (Myers *et al*., 1996; Kallarackal and Somen, 1997a; Soares and Almeida, 2001). However, due to variations in site quality, there are still insufficient data to predict water use over the full range of growing conditions.

It is particularly important to be able to predict maximum rates of transpiration under conditions of non-limiting soil water availability, as

- Increasingly, fast-growing plantations are being investigated for their potential in disposing of industrial effluent from mines and other industries. It is essential to match applied waste water to the capacity of *Eucalyptus* trees to take up and transpire this water.
- Insufficient information exists on a) how soil fertility and water availability influence water use through canopy development, and b) the acclimation of the whole-tree water transport system to the long-term availability of soil water at a given site. Some recent evidence from Zululand suggests that these physiological changes may give rise to high rates of transpiration (Dye *et al*., 2004).
- Soil water deficits are the most common limitation to growth and water use in South African forestry plantations. In order to model these, it is important to know what the potential rate of stomatal conductance (g_s) and transpiration is.

Modelling is the best approach to explore the effects of climate and soil conditions on the water use of *E. grandis,* as the various factors affecting transpiration can be taken into account. Transpiration rates are influenced by atmospheric evaporative demand, soil moisture availability, and canopy conductance (g_c), which in turn is controlled by g_s and leaf area (Waring and Schlesinger, 1985; Beadle 1997; Landsberg and Gower, 1997). The three predominant environmental controls on stomatal conductance at the canopy level are light intensity, vapour pressure deficit (D), and the water status of the leaves (Landsberg and Gower, 1997). Models have been developed to describe stomatal and/or canopy conductance in response to two of the major environmental influences, light and D (Warrit *et al*., 1980; Thorpe *et al*., 1980; Kaufmann, 1982a,b; Dye and Olbrich, 1993; Granier *et al*., 2000). Model estimates of canopy conductance are often used in conjunction with the Penman-Monteith (P-M) equation (Monteith, 1965; 1981) to predict rates of evapotranspiration (Dye, 1987; Green, 1993; David *et al*., 1997; Landsberg and Waring, 1997; Soares and Almeida, 2001). This equation combines the two environmental drivers of evaporation, i.e. net radiation and dryness of the air, with a physical control (boundary layer conductance), and a physiological control (canopy g_s) (Landsberg and Gower, 1997; Waring and Running, 1998).

Predictions of water use by trees must be verified against actual measurements of sap flow, which are commonly conducted using the heat pulse velocity (HPV) technique. Experimental trials in the summer rainfall region of South Africa provided a valuable opportunity to measure sap flows under conditions of no soil water deficit, and to investigate the daily variation in g_c and transpiration. A simple model was constructed to predict g_c from the season of year, D and solar radiation data collected at one of the sites. The model was tested against g_c calculated from the P-M equation and measured sap flow rates at the second site.

MATERIALS AND METHODS

Site descriptions

Came

The experiment at Came in the KwaZulu-Natal Midlands (Lat. 29° 14' S, long. 30° 33' E, alt. 1113 m a.s.l.), was designed to determine the responses of *E. grandis* to irrigation and fertilisation. The soil is classified as a Kranskop (Soil Classification Working Group, 1991) and is derived from shale parent material. This highly weathered soil is well-drained and grades into weathered shale at approximately 0.95 m depth. The mean annual precipitation is 919 mm, with pronounced seasonal rainfall occurring predominantly during the summer months of November to March. The mean annual temperature is 16.6 °C. *E. grandis* seedlings were planted in March 1999 at a 2.0 x 3.0 m espacement and sap flow measurements were initiated in August 2001. Only irrigated trees were considered in this particular study; water was applied by drip irrigation and aimed to maintain soil water at 70% of the field capacity. The irrigated treatment received a total of 291 mm water during the August to November measurement period; 243 mm were received as rainfall, and 48 mm were applied as irrigation.

Frankfort

The Frankfort trial is located in the vicinity of Sabie, Mpumalanga (Lat. 24° 49' S, long. 30° 43' E, alt. 950 m a.s.l.). This trial investigated the relationship between soil water availability and transpiration rates of *E. grandis* plantations, and was initiated in June 1992 in a stand of three-year-old trees planted at a spacing of 3.5 x 3.5 m. The well-drained soil is of granitic origin and is classified as a Hutton (Soil Classification Working Group, 1991). Deep drilling showed the permeable subsoil at this site to extend beyond 30 m (Dye, 1996; Dye *et al*., 1997). The mean annual rainfall is 1459 mm, most of which falls in the summer months. The mean annual temperature is 18.1 °C. Plastic sheeting was laid out in a 30 x 30 m area centred on four sample trees, with the aim of preventing soil water recharge and inducing a progressive drying of the soil by tree roots. See Dye (1996) and Dye *et al*. (1997) for further details.

Weather data

The weather data for Came were collected from an automatic weather station situated at a nearby research site in the Seven Oaks district (Lat. 29° 11' S, long. 30° 40' E, alt. 1110 m a.s.l.). The distance from the trial site is 12.5 km and the altitude difference is 3 m. Sensors at the Seven Oaks weather station recorded temperature and relative humidity (Campbell Model 207 temperature and relative humidity sensor; Campbell Scientific, Inc., 815W. 1800 N., Logan, UT

84321-1784, USA), total solar irradiance (Kipp and Zonen solarimeter, Mercuriusweg 1, 2624 BC Delft, Holland), and rainfall (Rimco tipping bucket rain gauge; Selbys Scientific Ltd., 352 Ferntree Gully Road, Notting Hill, Victoria, Australia 3168). A Campbell 21X data logger was programmed to log data at 20 minute intervals, which were averaged or totalled over a 12 hour period each day. At the Frankfort site, an automatic weather station was mounted on the highest frame of a scaffholding tower erected near the centre of the experimental plot. The height of the tower was periodically increased to a maximum height of 23 m, to maintain it at approximately 1 m above the tallest adjacent tree. Sensors recorded temperature (MCS174 probe; Mike Cotton Systems (Pty.) Ltd., P.O. Box 73, Steenberg 7947, South Africa), relative humidity (Vaisala Humicap sensor; Vanha Nurmijarventie 21, 01670 Vantaa, Finland), solar radiation (pyranometer; LI-200S, LI-COR Inc., Lincoln, Nebraska, USA) and rainfall (Rimco rain gauge). An MCS datalogger was programmed to record hourly means of one minute instantaneous measurements.

Pre-dawn xylem pressure potential

Pre-dawn xylem pressure potential (XPP) measurements were performed with a Scholander pressure chamber (Ritchie and Hinckley, 1975). At the Came site, sample twigs were cut from the upper third of the canopy of six randomly located trees in the irrigated treatment. At Frankfort, a sample leaf was taken at mid-canopy position from each of five trees within reach of a centrally located scaffholding tower. Dates on which pre-dawn XPP was measured are listed in **Table 1**.

TABLE 1. Dates on which pre-dawn XPP measurements were conducted at the Came and Frankfort sites.

Came	Frankfort	
2001	**1992**	**1993**
7 Jun	2 Jun	13 Jan
26 Sep	16 Jun	4 Feb
24 Nov	30 Jun	9 Mar
	14 Jul	2 Apr
	28 Jul	18 May
	11 Aug	1 Jun
	25 Aug	15 Jun
	10 Sep	
	22 Sep	
	6 Oct	
	20 Oct	
	3 Nov	
	17 Nov	
	1 Dec	

Sap flow measurements

Heat pulse velocity was used to monitor hourly sap flow rates in two adjacent sample trees at Came, and four adjacent sample trees at Frankfort, located at the centre of each site. This technique has been verified on *E. grandis* using the cut-tree method (Olbrich, 1991). Sap flow was measured over a six month and 12 month time period at the Came and Frankfort sites, respectively. Four sets of heat pulse probes were implanted in each sample tree at various positions around the trunk. Using a 20 mm-thick drill jig, three vertically aligned holes were drilled radially into the sapwood at each position, using a 1.85 mm drill bit. A line heater was inserted into the central hole, while a teflon tube containing a single thermistor sensor was implanted in each of the other two holes, 10 mm above and 5 mm below the heating probe. Each sensor probe pair gave a point estimate of sapwood temperature. Paired thermistor probes were inserted into the sapwood to depths of 4, 9, 16 and 24 mm below the cambium at the Came site, and to depths of 5, 13, 23 and 35 mm at Frankfort. Each thermistor pair was connected in a Wheatstone bridge configuration and automatically zeroed before each heat pulse initiation. The logger was programmed to apply a current of 30 amperes lasting 0.5 seconds to each heater probe. HPV (u) was measured using the compensation technique (Huber and Schmidt, 1937; Swanson, 1974). The temperature rise was measured at distances X_u upstream and X_d downstream from the heater, and u was calculated as follows:

$$u = (X_u + X_d) / 2t \quad (1)$$

where t is the time delay for the temperatures at points X_u and X_d to become equal.

Heat pulse velocities were corrected for sapwood wounding caused during the drilling procedure. Swanson and Whitfield's (1981) wound correction coefficients were used to derive corrected heat pulse velocities (u'). The correction takes the form:

$$u' = \rho + qu + r(u)^2 \quad (2)$$

where ρ, q and r are the correction coefficients appropriate to the measured wound size, diameter of teflon probes, and probe separation distances, respectively. The size of the wound at each probe set location was measured at the end of the experiment. The four sections of the tree trunk containing the probe implantation holes were excised and re-cut longitudinally at the particular radial depth below the cambium where the thermistor was originally positioned. The exposed, fresh face was shaved smooth using a microtome to allow precise measurements of wound widths which were measured to the nearest 0.1 mm using a 7x scale loupe. These measurements were taken midway between the line heater position and both the upper and lower thermistors. A single mean wound width was calculated for each tree. The corrected heat pulse velocities were converted to sap flux (*v*) using the following equation (Marshall, 1958):

$$v = \rho_b (m_c + c_{dw})\ u' \qquad (3)$$

where ρ_b is dry wood density, m_c is the moisture fraction of sapwood, and c_{dw} is the specific heat of dry wood, assumed constant at 0.33 (Dunlap, 1912). In calculating wood density, the volume of a fresh sample of sapwood was determined by immersion in water and the application of Archimedes' principle. Moisture fraction was calculated as (fresh mass – dry mass) / dry mass, while basic wood density was calculated as the dry mass / volume of the freshly excised section of wood. Each of the four sap flux measurements recorded in each tree were considered to be representative of a ring of sapwood centred on the probe depth. Total sap flow was then calculated as the sum of the partial areas multiplied by their associated sap flux. Daily sap flows were calculated from hourly sap flow rates summed over the logging period between 04h30 and 19h30 each day.

Leaf area

Leaf areas of the sample trees at Came were estimated from regression analysis following destructive harvesting of 16 trees representative of the range of diameters at breast height (DBH). These trees were felled at 2.8 years of age and the foliage sub-sampled for fresh mass, and leaf area determination using the LI-3100 Leaf Area Meter (LI-COR Inc.). DBH values were regressed against leaf area measurements and this relationship was used to derive leaf area estimates of the sample trees. Mean leaf areas at the Frankfort site were estimated by stripping all leaves from the sample trees and estimating total area from the total mass using the relationship determined from a sub-sample of leaves.

Canopy conductance

Using transpiration data from HPV measurements, daily estimates of g_c were obtained by inverting the P-M equation:

$$g_c = DL\ (g_a\ E\ \lambda\gamma / (s\ A + \rho\ C_p\ D\ g_a - \lambda\ E\ (s + \gamma))) \qquad (4)$$

where:

DL = daylength (s);

g_a = boundary layer conductance (m s^{-1}). The P-M equation is not sensitive to g_a (Raupach and Finnigan, 1988; Landsberg, 1999), and this was fixed at 0.2 m s^{-1}, a representative value for forest canopies (see Kelliher *et al*., 1993; Landsberg and Gower, 1997; Waring and Running, 1998);

E = total daily transpiration (mm) derived from the sap flow data;

λ = latent heat of vaporisation of water (2450000 J kg^{-1});

γ = the psychrometric constant (0.0658 kPa $^oC^{-1}$);

s = slope of the curve relating saturated vapour pressure to temperature (0.13 kPa $^oC^{-1}$);

A = net radiation (W m^{-2}). Mean daily net radiation was estimated from daily solar radiation using a relationship recommended by Landsberg and Gower (1997):

$$A = 0.85 * \text{solar radiation} - 55\ W\ m^{-2} \qquad (5);$$

ρ = air density (1.204 kg m^{-3});

C_p = specific heat of air at constant pressure (1010 J kg $^oC^{-1}$);

D = the vapour pressure deficit (kPa). D was averaged over daylight hours 06h00 to 18h00.

RESULTS

Sample trees

Characteristics of the trees sampled for sap flow measurements are presented in **Table 2**.

Pre-dawn XPP

Pre-dawn XPP measurements at Came ranged from –0.03 to –0.08 MPa over the period June to November 2001, and indicated that these trees were not water stressed at any time during the sap flow measurement period. At the Frankfort site, pre-dawn XPP data showed that the lowest potentials in the trees under plastic barely exceeded –0.7 MPa. Prevention of soil water recharge resulted in more negative water potentials compared to nearby control trees where normal soil water recharge occurred, but the greatest

TABLE 2. A summary of the salient properties of the sample trees at Came and Frankfort, recorded at the conclusion of each study. Values presented are means and (standard deviation).

Site	Came	Frankfort
Age (years)	2.8	4.0
DBH (cm)	9.2 (1.5)	14.7 (1.2)
Height (m)	9.4 (0.8)	14.7 (1.0)
Leaf area per tree (m^2)	29.6 (7.7)	62.0 (11.8)
Sapwood moisture fraction	2.01 (0.33)	1.37 (0.16)
Sapwood density (g cm^{-3})	0.33 (0.03)	0.45 (0.04)
Wound width (mm)	2.9 (0.07)	2.8 (0.29)

difference only amounted to approximately –0.3 MPa, leading to the conclusion that these trees only experienced a mild degree of stress towards the end of the monitoring period (Dye, 1996; Dye *et al.*, 1997). The failure of the trees to respond to the imposed soil water deficit was attributed to their ability to abstract soil water to a depth of at least 8 m (Dye, 1996; Dye *et al.*, 1997).

Came

Good quality HPV data were available from 15 August to 7 November 2001. Due to the very limited data record for the second sample tree at Came (owing to persistent data logger problems and frequent theft of equipment), only data from one tree were used. This single tree was representative of the remaining trees in the plot, with DBH, height and leaf area of 10.3 cm, 10.0 m and 35.1 m^2, respectively, compared to plot-level values of 9.5 ± 3.3 cm (DBH), 9.2 ± 2.2 m (height), and 30.1 ± 17.2 m^2 (leaf area).

Estimates of g_c obtained from Equation 4 were plotted against mean daily D (**Figure 1**).

There is a dominant overall non-linear response to D, with g_c decreasing with increasing D. In view of the results of a previous study of *E. grandis* g_c patterns, where a distinct seasonal shift in the relationship between g_s and D occurred in early spring and late autumn (Dye and Olbrich, 1993), these data were investigated to ascertain whether such a seasonal change was observable. A clearly defined trend was found for the September – November data (open squares, **Figure 1**). Points significantly below this trend were associated with conditions of low solar radiation (< 6.3 MJ m^{-2} day^{-1}). These data points were removed before a reciprocal function was fitted to the remaining data. Data recorded during August (solid squares) were found to define a different and lower trend and a separate function was fitted to these data points. A reciprocal function of the form y = 1/(a*x+b) was fitted to the September – November data (a = 43.474, b = 10.695) and the August data (a = 80.781, b = 10.337), respectively.

We used a simple hyperbolic function to describe the relationship between solar radiation and maximum g_c (**Figure 2**), as defined by the trend lines in **Figure 1**.

Parameter a was adjusted to return a value of 1 under conditions of maximum solar radiation. An optimising algorithm was used to optimise the parameter b to best fit the calculated g_c. Daily g_c was then calculated over the entire Came data record as the product of the two functions relating g_c to mean daily D and to total solar radiation. These estimates were compared to those calculated from the P-M equation and measured transpiration (**Figure 3**). The apparent outliers in **Figure 3** were from data collected on days where the solar radiation did not exceed 6.3 MJ m^{-2} day^{-1}.

Modelled g_c was then used to estimate daily transpiration with the P-M equation. The correspondence to measured transpiration by HPV is shown in **Figure 4**.

The transpiration rates determined by the two methods were well correlated (R^2 = 0.76). Days where the fit between measured and modelled transpiration was not particularly good were again related to conditions of low solar radiation.

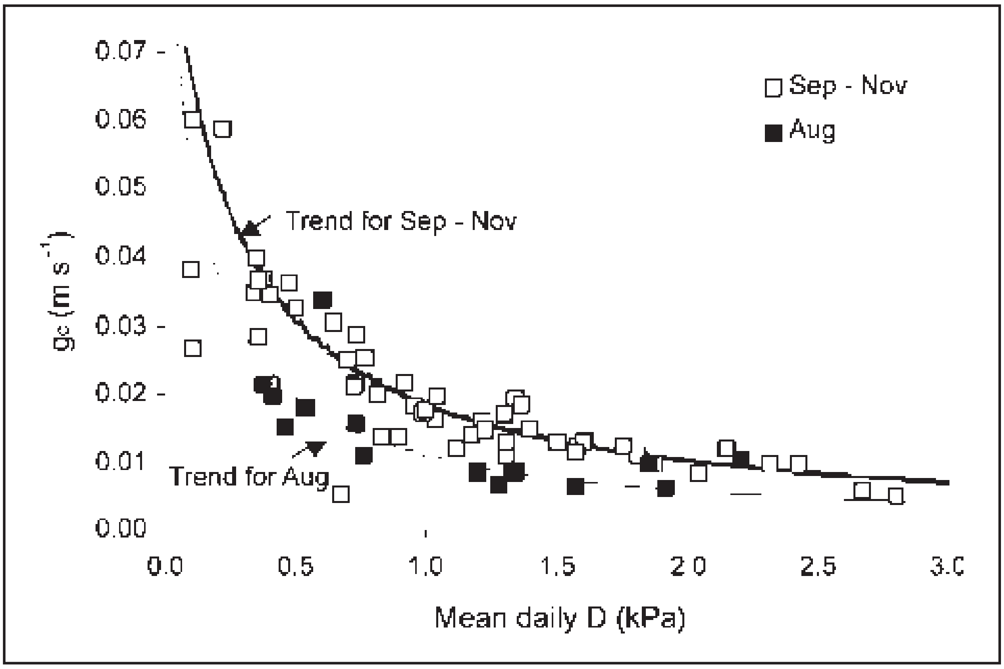


*FIGURE 1. The relationship between mean daily vapour pressure deficit (D) and canopy conductance (g_c) at Came, calculated using Equation 4. A reciprocal function of the form y = 1/(a*x+b) was fitted to the September – November data (a = 43.474, b = 10.695) and the August data (a = 80.781, b = 10.337).*

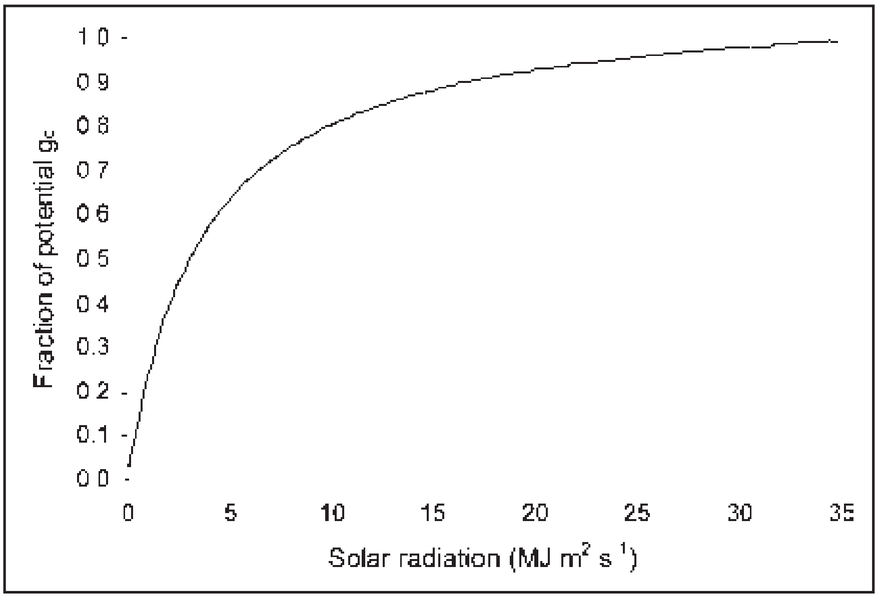
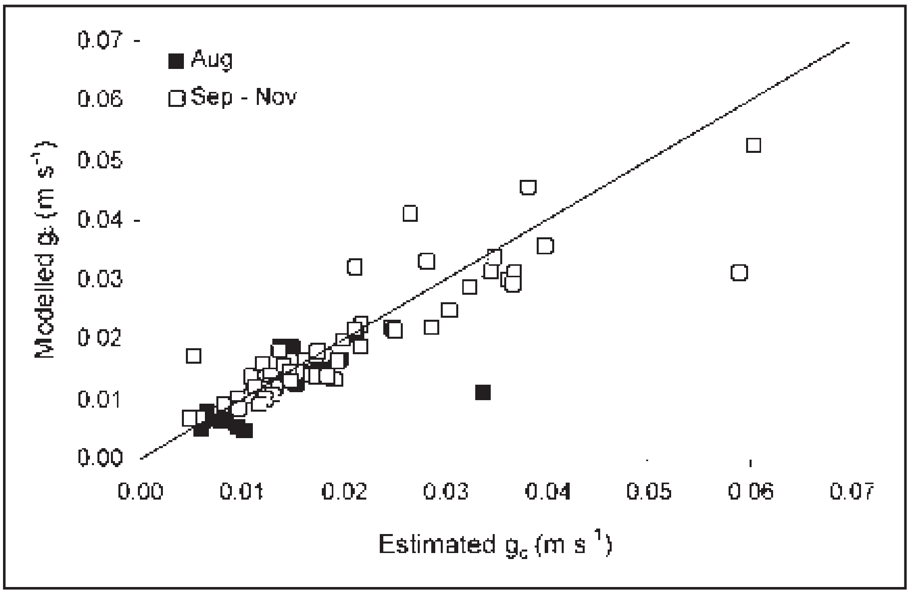


*FIGURE 2. The relationship between daily solar radiation and the fraction of potential canopy conductance (g_c) at Came. The function and parameter values adopted were as follows: y = a*b*SR/(a+b*SR) ; a = 1.1, b = 0.3.*

FIGURE 3. The relationship between estimated and modelled canopy conductance (g_c) for the Came site. Estimated g_c was obtained from the P-M equation and measured transpiration rates, and the modelled g_c was derived from the functions described in Figures 1 and 2.



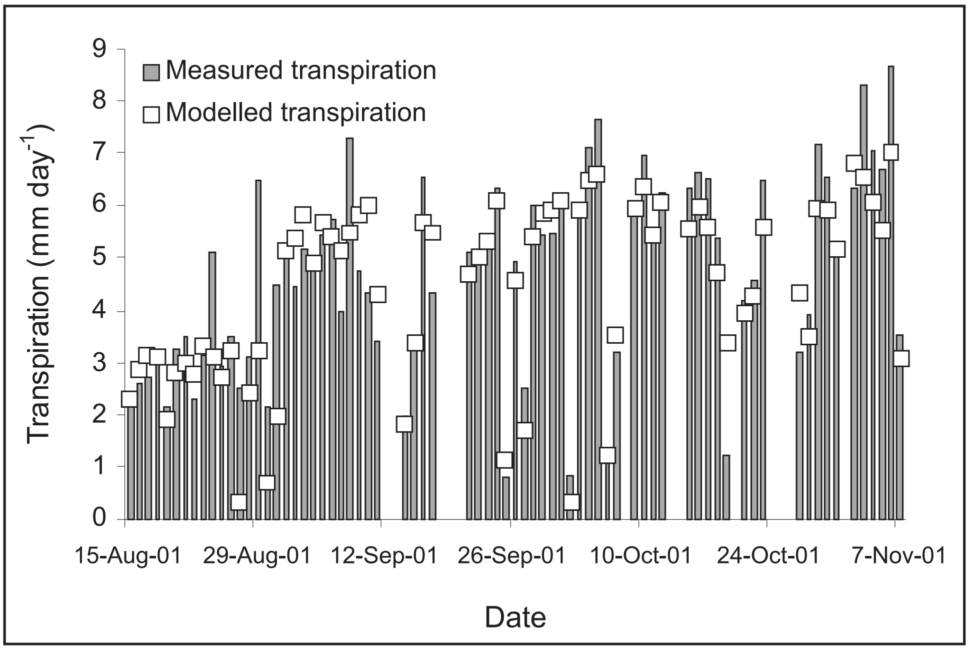


FIGURE 4. The relationship between modelled and measured daily transpiration at the Came site.

Frankfort

The g_c model derived from the Came data was tested against the measured transpiration and associated weather data recorded at Frankfort. On the basis of an earlier porometer-based study (Dye and Olbrich, 1993), the summer g_c function was initially applied from September to April, while the winter function was applied from May to August. However, a better fit of the data was obtained when the summer g_c function was applied from September to May, and the winter function from June to August. This may be related to the development of mild water stress by the trees after a year of no soil water infiltration. The correlation between modelled g_c and g_c values based on the P-M equation using measured mean daily transpiration is shown in **Figure 5.**

Predicted g_c was then used to estimate daily transpiration with the P-M equation. The correlation between modelled and measured daily transpiration is given in **Figure 6**.

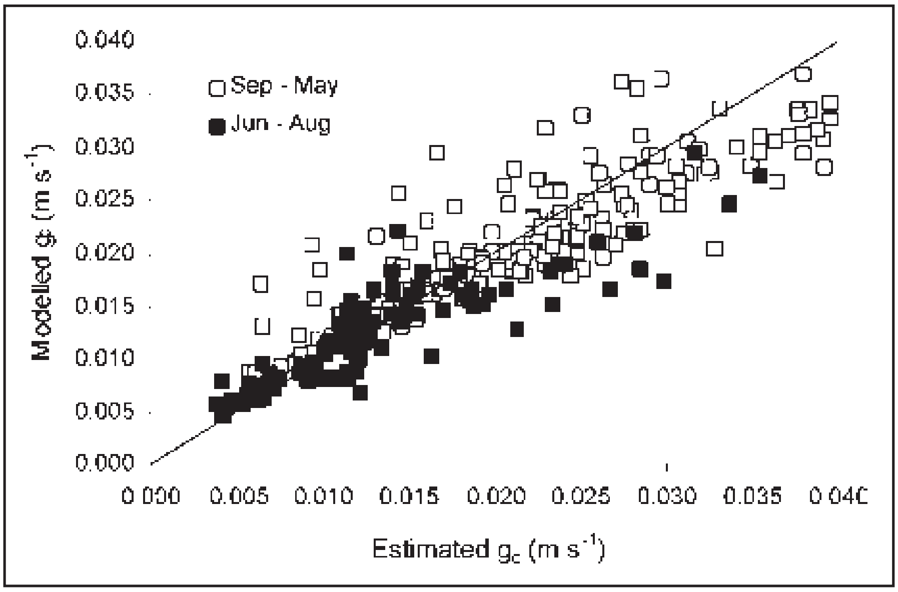


FIGURE 5. The relationship between estimated and modelled canopy conductance (g_c) for the Frankfort site. Estimated g_c was obtained from the P-M equation and measured transpiration rates, and the modelled g_c is derived from the functions described in Figures 1 and 2.

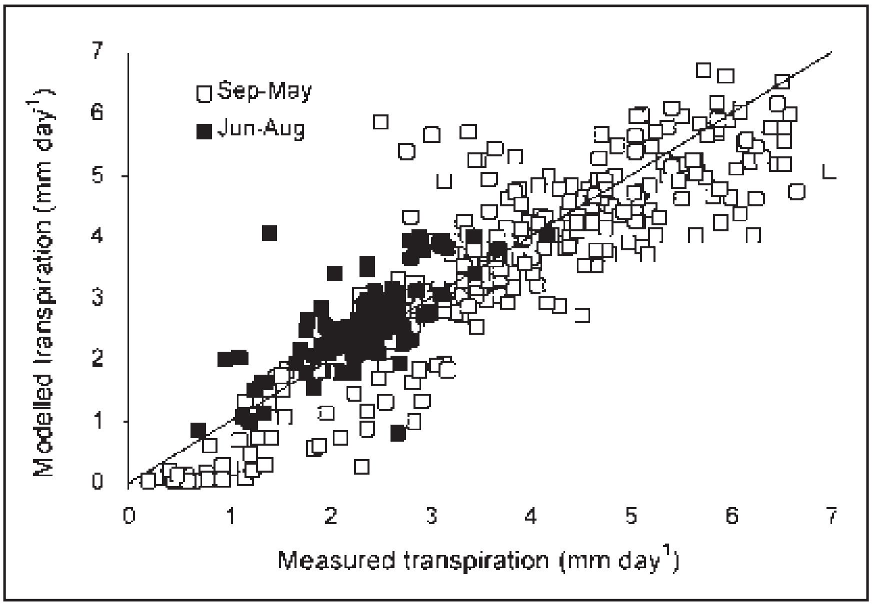


FIGURE 6. The relationship between modelled and measured daily transpiration at the Frankfort site.

DISCUSSION AND CONCLUSION

Canopy conductance was modelled as a function of D and solar radiation from data collected for the Came site. Many other studies point to these two environmental factors as being the major determinants of g_c and transpiration rates (Dunn and Connor, 1993; Dye and Olbrich, 1993; Green, 1993; Leuning, 1995; Kallarackal and Somen, 1997b; Granier *et al*., 2000; Soares and Almeida, 2001) where there is no soil water limitation or change in leaf area.

A similar seasonal shift in the g_c-D relationship, as observed in **Figure 1**, was recorded in an earlier porometer-based study of the g_s patterns in a single *E. grandis* tree (Dye and Olbrich, 1993). A seasonal shift in the relationship between D and g_c of *E. grandis* in Mpumalanga was also observed by Dye (1987), at the low end of the D range, but this could not be attributed to differences in soil moisture availability or micro-climate factors. Dye (1987) hypothesised that this pattern may be caused by substantial osmotic adjustment in the guard cells during springtime. We hypothesise that the marked changeover in the relationship between g_c and D at the end of August is due to a change in the osmotic potential of the leaf, and may be related to the accumulation of sugars at low water availability.

The model constructed to predict g_c from D, solar radiation and the season of year generated from observations at Came was tested against an independent data set collected at Frankfort. On a daily basis, a good agreement was observed between the transpiration predicted by the model and that obtained from sap flow measurements (**Figure 6**).

A regression line through the data points yields $y = 0.91x + 0.1264$ (R^2 = 0.79). It is evident that the model underpredicts transpiration on days of low sap flow (**Figure 6**). There were relatively few days in the Came data record on which sap flow was below 2 mm. In view of the known overestimation of low sap flows by the HPV technique when based on the compensation principle (Becker, 1998; Burgess *et al.*, 2001), we believe that the model should be used in its current form until the low flow measurement problem is investigated using an alternative methodology.

The cumulative transpiration measured by HPV over a one-year period at Frankfort was 1320 mm, as compared to 1226 mm estimated from modelled g_c and the P-M equation, resulting in a difference of 7.7%. Other studies have also indicated a good agreement between transpiration rates estimated by the P-M equation and those based on sap flow measurements (Edwards and Warwick, 1984; Green, 1993; David *et al.*, 1997). Mean daily transpiration at the Frankfort site was 3.4 mm, with a maximum of 6.8 mm. These values lie well within the range of water use estimates cited for *E. grandis* (Dye, 1987; Dye, 1996; Myers *et al.*, 1996; Dye *et al.*, 1997; Kallarackal and Somen, 1997a).

The g_c model developed from the Came data and subsequent use of the P-M equation, using inputs from the Frankfort data set, provided accurate estimates of transpiration compared to sap flow rates measured by HPV. This simple model, requiring inputs of standard weather data, is useful to estimate the potential transpiration rate of a young *Eucalyptus* stand under conditions of non-limiting soil water availability.

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