Long term trends of stand transpiration in a remnant forest during wet and dry years

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Running title: Long term trends of transpiration

Abstract

Daily and annual rates of stand transpiration in a drought year and a non-drought year are compared in order to understand the adaptive responses of a remnant woodland to drought. Two methods were used to estimate stand transpiration. In the first, the ratio of sap velocity of a few trees measured for several hundred days to the mean sap velocity of many trees measured during brief sampling periods (generally 6-7 trees for 5 or 6 days), called the E_{sv} method is used to scale temporally from the few intensive study periods. The second method used the Penman-Monteith (P-M) equation (called the E_{PM} method). Weather variables were used to predict canopy conductance, which in turn was used to predict daily and annual stand transpiration. Comparisons of daily transpiration estimated with the two methods showed larger values for the E_{PM} method during a drought year and smaller values for the E_{PM} when the rainfall was above average**.** Annual estimates of stand transpiration were similar using the two methods. The E_{sv} method produced an estimate of 318 mm (61 % of rainfall) in the drought year and 443 mm (42 %) in the year having above average rainfall. The E_{PM} method estimated stand transpiration as 379 mm (73 %) and 398 mm (37 %) respectively for the two years. Both estimates of annual stand transpiration demonstrated that the remnant forest showed resilience to an extreme and long-term drought. More importantly, the annual estimates showed that in dry years a larger proportion of rainfall was used as transpiration, and groundwater recharge was absent but in years with above average rainfall recharge was significantly increased. Changes in leaf area index were minimal between years and changes in stomatal conductance were the dominant mechanism for adapting to the drought. The remnant forest rapidly responded to increased water availability after the drought through a new flush of leaves and increased stomatal conductance.

Keywords: tree water use, stand transpiration, sap flow, heat pulse method, annual water use.

1. Introduction

Drought is a recurrent global phenomenon having significant impacts on surface water flows, the ecohydrology and productivity of forests and groundwater recharge (Breda et al. 2006, Eamus et al. 2006). Understanding how severe and long-term droughts, such as those that affected Europe in 2003 and eastern Australia between 2001 and 2003, influence seasonal and annual patterns of water use and how quickly forests are able to recover from drought, is central to the long-term successful management of both water and vegetation resources. However, there have been relatively few studies of the resilience of forests to drought and even fewer that incorporate studies of vegetation water fluxes both during and after a severe drought. A key aim of this paper is to present annual estimates of water use of a remnant native forest during and after a long-term and wide-spread drought and to determine whether changes in sensitivity of stomatal conductance to VPD or leaf area index were the dominant mechanisms employed by this remnant woodland to adapt to the impact of the drought (Maseda and Fernandez 2006).

Land clearing and land use change have altered the hydrologic balance of Australian landscapes. In particular, the replacement of trees by annual crops and pastures has decreased annual transpiration rates from vegetation and consequently increased the rate of recharge of aquifers (George et al. 1999, Hatton and Nulsen 1999, Hatton et al. 2003). Under remnant native vegetation, recharge rates can be as low as 0.1 to 20 mm y^{-1} (Allison et al. 1990, Dunin 1992, Knight et al. 2002) whilst recharge under crops and pasture may be an order of magnitude, or more, larger (Greenwood et al. 1985, Farrington et al. 1992). However, such estimates are based on relatively few measurements, in space and time and do not include comparisons of years receiving above- and below-average rainfall.

Reforestation of Australian landscapes may significantly alter catchment water budgets by increasing vegetation water use (compared to that of annual crops and pastures) and reducing recharge (Bari and Schofield 1992, Hatton and George 2001). However, a major problem in designing reforestation programs and estimating recharge has been the need to extrapolate spatially and temporally (Wullschleger et al. 1998, Host et al. 1996, Scott et al. 2004). A number of studies of tree water use have had insufficient data, spatially (Meiresonne et al. 2003) and/or temporally, to allow annual estimates of stand water use (Schafer et al. 2000, Wilson et al. 2001, Lundblad and Lindroth 2002), because of the difficulty in obtaining sufficient data across a site throughout a year or across years (Eamus et al. 2006).

Rates of tree water use are largely governed by environmental conditions, such as solar radiation, rainfall, soil water content and VPD, in addition to plant factors such as leaf area and whole-plant hydraulic conductance (Maseda and Fernandez 2006). Because environmental conditions and plant factors vary daily, seasonally (Hogg and Hurdle 1997; Lhomme et al. 2001; Scott et al. 2004) and annually (Leuzinger et al. 2005) measurements of temporal variation in tree water use need to include these daily, seasonal, annual, and stochastic (for example, drought) environmental changes. However, most studies using sap flow methods have been conducted during only one season, (Wullschleger et al. 1998, Schafer et al. 2000, Lundblad and Lindroth 2002) and consequently are unable to provide reliable annual estimates.

This manuscript discusses two methods of temporally scaling transpiration. The first method involves using the ratio of sap velocity of a few trees measured for hundreds of days to the mean sap velocity of many trees (6-7 trees) measured during short sampling periods (5-6 days), called the E_{sv} method. The second method uses the Penman-Monteith equation, using a number of site and climate variables to predict canopy conductance, from which stand transpiration was calculated.

The aims of this research were to first, examine the impact of a severe drought on seasonal patterns and annual budgets of water use, through a comparison of data obtained in a drought and non-drought year; second, to compare relationships among stand water use, vapour pressure deficit, solar radiation and potential evaporation for a drought and non-drought year; and third compare two methods of temporally scaling transpiration and describe the benefits and limitations of each method.

2. Materials and Methods

2.1Study site

The study was conducted in a remnant woodland within the Liverpool Plains, approximately 70 km south of Tamworth, in north-western NSW (31.5 ° S, 150.7 ° E, elevation 390 m), as described previously by Zeppel et al. (2004) and Zeppel and Eamus (2005). The open woodland had an average height of 15 m and was dominated by *Eucalyptus crebra* F. Muell. and *Callitris glaucophylla* Thompson and Johnson. These two species contributed approximately 75% of the tree basal area at the site. The total tree basal area at the site was 23.8 ± 3.4 m^2 ha^{-1}. The eucalypt population has a lower density than that of the *Callitris* (42 stems ha^{-1} compared to 212 stem ha^{-1}) but the eucalypt contributed about 56 % of the basal area of the site (versus about 19 % for *Callitris*) because its average diameter was much larger than that of the *Callitris* (Table 1). Grasses including Stipa and Aristida species dominated the understorey. Soils at the site were shallow (15 to 30 cm) with well drained acid lithic bleached earthy sands (Banks 1998) with occasional exposed sandstone.

The Liverpool Plains is characterised by summer dominant rainfall, and during the study period, rainfall was generally smaller than the long-term average during June 2002 to July 2003, and was generally larger than the long-term average for the period August 2003 to March

2004. Maximum daily radiation reached 35 MJ m^{-2} day^{-1} in summer, and 13 MJ m^{-2} day^{-1} in winter. Vapour pressure deficit (VPD) reached a peak of 1.1 kPa at 15:00 h in winter, and 3.1 kPa at 17:00 h in summer.

2.2 Instrumentation

2.2.1 Meteorological variables and soil moisture

Radiation, temperature and wet- and dry-bulb data were obtained from a weather station located in a cleared pasture approximately 100 m from the remnant woodland, maintained by the NSW Department of Agriculture, Tamworth. Wet and dry bulb data were used to calculate vapour pressure deficit. Potential evapotranspiration (E_o) was estimated using the Priestley-Taylor method (Priestley and Taylor 1972). Wind speed was obtained from a cup anemometer located approximately 3 m above the canopy (approximately 18 m above ground). Wind data were scanned every 15 seconds and the readings were averaged and logged at one hour intervals on a Star Logger (Measurement Engineering Australia, Adelaide).

Soil moisture content was measured with theta probes (Measurement Engineering Australia, Adelaide) implanted horizontally in the ground at depths of 10 cm, 40 cm and 50 cm at two locations, and at 10 cm and 40 cm at one location (8 Theta Probes in total). Relative soil water content (RWC) was estimated using measured (measured H_2O), minimum (H_2O_{min}) and maximum water (H_2O_{max}) content during the study period in the following equation:

$$RWC = (\text{measured } H_2O - H_2O_{min}) / (H_2O_{max} - H_2O_{min}) \qquad \text{Equation 1.}$$

2.3 Vegetation parameters

2.3.1 Leaf area index (LAI)

Leaf area index of the tree overstorey was measured using a Li-Cor 2000 Plant Canopy Analyser, with one wand used for both above- and below-canopy measurements (Cherry et al., 1998). Measurements of above-canopy light were taken in a large (4 ha) clearing next to the remnant forest, and the below-canopy estimates were measured in seven representative locations within the remnant forest. Measurements were taken in diffuse light, at dusk, so time limitations meant that no more than 7 measurements could be taken on one day, before light conditions became inappropriate. Measurements were collected approximately once every two months between March and September 2003, and then every six months until February 2005. Leaf area index of the canopy was 0.9 to 1.5 throughout the study period.

2.3.2 Stomatal conductance

A leaf diffusion porometer (AP4 Delta-T Devices, Cambridge) was used to measure stomatal conductance at the leaf scale. The porometer was calibrated four times each day immediately before use. Stomatal conductance of only *Eucalyptus crebra* was measured as the broad leaves of this species were able to cover the surface of the porometer, whereas the needle-leaves of *Callitris glaucophylla* did not. The leaves of the eucalypt were hypostomatous, and the sunlit surface of at least three leaves per tree was measured using a hydraulic platform. Three trees were measured in winter 2003, June 25th and 26th, and in summer 2003/4, March 16th, 18^{th,} and 19th, and summer 2004/5, December 6 to 8. Measurements were taken at 2 hourly intervals from 10:30 to 16:30 in winter, and at 7:30 and then at hourly intervals from 8:00 to 17:00 in summer. These sampling dates were representative of the seasons they were measured in as environmental data values were generally within one standard deviation of the mean for that particular season (Table 3).

2.3.3 Measuring water use by individual trees

The volume of water taken up by individual trees (Q; with units L day^{-1}) was measured using commercial sap flow sensors (Greenspan Technology, Pty Ltd, Warwick, Australia) following the procedures described previously (Zeppel et al. 2004). Briefly, two probe sets (four sensors) were positioned at right-angles in each tree. Sap flow loggers recorded the heat pulse at 15 min intervals throughout sampling. The weighted averages technique of Hatton and Wu (1995) was used to convert sap velocities to transpired water volume. During analysis of sapflow, data were corrected for the effects of wound, radial variability in flow, sapwood area and volumetric fractions of water and wood as reported previously (Zeppel et al. 2004). The width of the wound around the holes used to insert the probes was measured twice in seven trees of each species, using the technique described by O'Grady et al. (2000). A wound width of 2.5 mm for *C. glaucophylla* and 3.7 mm for *Eucalyptus crebra* was used to correct velocity estimates. For each species between 7 and 15 trees were chosen to cover the size distribution for each species at the site and were instrumented with 4 heat sensors (2 x SF100 probe-sets per tree). The sensors were stratified with depth to account for variation in sap flow across the radial profile of each tree (Medhurst et al. 2002). Sap flow was measured during 4 intensive field campaigns within contrasting periods that encompassed drought and post-drought periods: June-August 2002 (drought; winter), January-February 2003 (drought; summer), July-August 2003 (post-drought, winter), and February-March 2004 (post-drought, summer).

In addition to intensive field campaigns, 2 trees of each species were monitored longer-term over the study period (411 days out of 759 days). These 4 reference trees are defined as the ‘long-term trees’. Equipment failure meant that there were gaps in the sap flow data from long-term monitored trees (the remaining 348 days).

Basal area and diameter at breast height (DBH) of all trees were measured in seven plots of 50 m x 50 m, following previously described methods (Zeppel et al. 2004). A list of abbreviations used in the manuscript, and their derivations is given in Table 2.

2.3.3.1 Time lag between sapflow and meteorological variation

There can be a time lag between transpiration from the canopy, and sap flow in the tree stem measured at 1.3 m height above ground. This is due to the contribution of water stored in stems of trees (Schulze et al. 1985, Ewers and Oren 2000, Lhomme et al. 2001). In order to estimate the length of this time lag, regressions between hourly values of transpiration (mm^3 water h^{-1} mm^2 leaf area) and radiation (MJ m^{-2} h^{-1}) on clear sunny days were performed for time differences of -1, 0, 1 and 2 h. The regression with the highest r^2 was assumed to be the correct time lag, and regressions were performed for three trees (or one tree when equipment failure occurred in Summer 2003/4), for each sampling period (Winter 2002, Summer 2002/3, Winter 2003 and Summer 2003/4). Each season had a time lag of one hour, with the exception of Summer 2002/3, which had no time lag, possibly due to an extremely large rain event (93 mm) preceding the sampling period. Therefore a lag of one hour was used in all hourly time step calculations except Summer 2002/3.

2.4 Scaling from tree- to stand-scale water use

2.4.1 Using the sapwood area x sap velocity ratio method (E_{sv})

This method of scaling sap flux (mm^3 day^{-1} mm^{-2}), that is, sap velocity (mm day^{-1}) multiplied by sapwood area (mm^2) of a stand, from a field campaign lasting several days, to annual estimates of transpiration is hereafter called the E_{sv} method. This was used to calculate daily transpiration of the stand from the ratio of sap velocity of long term trees to the mean sap velocity of 6 trees measured during each of the intensive field campaigns over 2 years. This method used the mean ratio of the water use of the long-term reference trees (monitored for 411 days of 759 days) to the average water use of all the trees measured during the intensive field campaigns (4 campaigns over 2 years). This ratio was then multiplied by the water use of the reference trees for each day to obtain a daily value of stand water use. The E_{sv} method provides estimates of stand transpiration only for days where sap velocity of long term trees was measured (411 days out of 759 days).

To fill the gaps in stand transpiration, we used regression analysis to predict daily transpiration from RWC, VPD and solar radiation (Rn). The most accurate prediction was found by log transforming all the data and using linear regression analysis (SPSS, V12.0.1, SPSS Inc.) to derive the following equation:

$$\log E = 0.211 \log VPD + 0.921 \log Rn + 0.304 \log RWC - 1.067 \qquad \text{Equation 2}$$

The data were then back-transformed to obtain a daily estimate of transpiration for the days when equipment failed and these values were summed for an annual estimate of stand transpiration. The regression was significant ($p < 0.001$, $R^2 = 0.62$) and all terms had a significant effect on E ($p < 0.001$).

2.4.2 Using the Penman Monteith equation to estimate daily stand transpiration (E_{PM})

2.4.2.1 Calculating canopy conductance

Net radiation, temperature, VPD, and soil water content were used to model stomatal conductance (g_s) using a Jarvis (1976) type equation (equation 3):

$g_s = g_{smax} . fn (D). fn (R_n). fn (S)$ Equation 3.

where g_s is stomatal conductance (mm h^{-1}), G_{smax} is maximum stomatal conductance measured (mm h^{-1}), D is vapour pressure deficit (kPa), R_n is incident solar radiation (W m^{-2}), and S is soil water content. S was parameterised from a sensitivity analysis of measured stomatal conductance, where RWC is the ratio of actual volumetric soil water content to maximum soil water content.

$fn (S) = (RWC^{0.25})/2$ Equation 4.

In forests with discontinuous canopies, it may be necessary to account for the fraction of canopy cover when predicting stand transpiration using the Penman-Monteith equation (Medhurst et al. 2002). In order to convert leaf scale stomatal conductance (g_s) to canopy conductance (G_c), the following equation was used (Lu et al. 2003):

$G_c = g_s \times LAI_s$ Equation 5.

Sunlit leaf area index (LAI_s) is the fraction of total leaf area index that is sunlit (Cermak, 1989) and was estimated using the equation (Filho et al., 1998):

$LAI_s = 2\cos(\theta)*(1-\exp(-0.5*LAI/\cos(\theta)))$ Equation 6.

where θ is the zenith angle of the sun, which is a function of time of day, solar declination angle and latitude. LAI in winter was assumed to be 1.0 and in summer was 0.80 (based on data measured using a Li-Cor 2000 PCA, measured 8 times per year). Also,

$$\theta = \cos -1 (\sin\phi \sin\delta + \cos\phi \cos\delta \cos H)$$ Equation 7.

where ϕ is latitude, δ is solar declination angle and H is hour angle due to time of day, H =15° x (EST -12))(EST = Eastern Standard Time). Declination varies daily between a maximum value of 23.5 for the winter equinox and -23.5 for the summer equinox in the southern hemisphere (http://edmall.gsfc.nasa.gov).

After g_s was estimated from equation 3, G_c was calculated using equation 5. Using this estimate of G_c then allowed daily estimations of E_{PM} using the P-M equation (Equation 8). Mean daily weather variables were used to estimate daily E_{PM} over a two year period, in order to compare the two methods (E_{sv} and E_{PM}).

2.4.2.1 Applying the Penman-Monteith Equation

Using stomatal conductance derived from porometer measurements as an input to equation 5 to calculate G_c, transpiration ($E_{PM,}$ mm^3 h^{-1} mm^{-2}) was estimated using the equation (Lu et al. 2003):

●E_{PM} = [(☟.$R_{n.}$k) + (❒.C_p.D.G_a)] / [☟ + ✞(1+G_a/$G_{c)}$] Equation 8.

where ● is the latent heat of vaporisation (2.39 MJ kg^{-1}), ☟ is the slope of the relationship between saturation vapour pressure and temperature (kPa ⌖C^{-1}), R_n is net radiation above the forest canopy (MJ m^{-2} h^{-1}), ρ is air density (kg m^{-3}), C_p is the specific heat of air (1.013 MJ kg^{-1} $°C^{-1}$), D is the vapour pressure deficit (kPa), G_a is aerodynamic conductance (m s^{-1}), γ is the psychometric constant (0.066 kPa $°C^{-1}$), k is a conversion factor (3600 s h^{-1}) converting from hours to seconds, and G_c is canopy conductance estimated using the Jarvis (1976) type model (m s^{-1}).

A sensitivity analysis was conducted on the effect of change in temperature on γ and Δ. Varying temperature from 6 to 40 °C only changed transpiration by 2% and consequently a mean ambient temperature of 13.5 °C in winter and 27.5 °C in summer was assumed. Net radiation (R_n) (W m^{-2}) was estimated from total (short wave) radiation (R_{sw}) (W m^{-2}) using the equation estimated from a dataset of approximately 2000 radiation estimates (Hutley, pers. comm.):

$$R_n = (0.7965 * R_{sw}) - 57.6452 \qquad \text{Equation 9.}$$

A sensitivity analysis showed that varying net radiation by 20 % only changed transpiration by 5 %. Therefore, we used equation 9 to estimate R_n from R_{sw}.

G_a is the inverse of r_a, aerodynamic resistance (s m^{-1}), which was estimated from the following equation:

$$r_a = 4.72(\ln (Z/Z_o))^2 / (1+ 0.54U) \qquad \text{Equation 10.}$$

where Z is canopy height (m), Z_o is roughness height (1.95 m for this forest type, Hutley, pers comm), and U is windspeed (m s^{-1}) (Yunusa et al. 2000). A conversion factor that was dependent on air temperature was used to convert E_{PM} in mmol m^{-2} s^{-1} to mm h^{-1}.

2.5 Assessing the P-M-model

The P-M model was evaluated in two ways. First we used linear regression analysis to determine whether there was a significant relationship between measured stand transpiration (E_{sv}) and E_{PM}. Second, we plotted residuals to determine whether there was any bias in the model. This comparison was made by evaluating the weighted residuals and binning them to produce a histogram. This procedure provides both qualitative and quantitative assessment of the plausibility of the P-M-model relative to the experimental data.

The weighted-residuals were defined as

$$residual_i = \frac{Exp_i - Calc_i}{Exp_i}, \quad \forall i = 1, 2, 3, \ldots N \qquad \text{Equation 11}$$

where the standard deviations is assumed to be proportional to the experimental value, such that, $\sigma_i \propto Exp_i$; and N is the number of data points over the evaluated time period (Armstrong 2006). The weighted residuals were also plotted though time so changes in the bias of the model could be detected. Regression analysis was used to evaluate relationships between environmental conditions (solar radiation and VPD) and measured (E_{sv}) and calculated (E_{PM}) stand transpiration.

3. Results

For the entire year 2002 (data not shown) and for seven of the 12 months of 2003, rainfall at the site was significantly lower than the long-term average (Fig. 1), indicative of the widespread drought encompassing all of the eastern seaboard of Australia during this time. However, 2004 received above-average rainfall. Thus, the annual rainfall for 2003 was 522 mm (the long-term average is 604 mm) whilst in 2004, 1062 mm of rain was received.

Solar radiation and potential rates of evaporation show typical seasonal patterns, with maxima observed in summer and minima in winter (Fig. 2). Within season variation amongst days reflects daily variation in cloud cover, rainfall and the passage of associated weather fronts. Maximum daily solar radiation was approximately 35 MJ m^{-2} day^{-1} in summer and 13 MJ m^{-2} day^{-1} in winter whilst maximum rates of potential evaporation were 11 mm day^{-1} in summer and about 2 mm day^{-1} in winter. Rapid increases in soil RWC occurred after moderate and large rainfall events (Fig. 2) but not after small (< 20 mm) rainfall events.

The first method for calculating stand water use (E_{sv}; Fig. 3) used the mean ratio of the water use of the long-term trees (monitored for 411 days of 759 days) to the average water use of all the trees measured during the intensive field campaigns (4 campaigns over 2 years). Stand water use was less in winter (June – Aug) than summer (Fig. 3) because of the lower solar radiation levels and lower VPD in winter compared to summer (Fig. 2). The maximum rates of stand water use in the summer of 2002/3 were less than the maximum rates observed in the summer of 2003/4, which in turn were less than the maximum rates observed in the summer of 2004/5. Similarly, rainfall in December and January for these three periods increased from 99 mm (Dec 02-Jan 03), to 230 mm (Dec-Jan 03/04) and more than 280 mm (Dec-Jan 04/05).

The period Jan 2003 – March 2003, and the period March 2004 to June 2004 were characterised as periods of very low rainfall preceded by a week of significant rainfall. The decrease in daily water use observed during these two periods reflects the impact predominantly of declining soil moisture, although declining solar radiation in May and June 2004 will also have contributed to the decrease in the later period.

The second method of calculating daily stand water use (E_{PM}) was based upon the Penman-Monteith equation, and used weather data and assessments of stomatal conductance using a porometer. While the number of assessments was very limited, stomatal conductance values were collected on days with conditions representative of each particular season (Table 3).

Figure 3 shows variation in E_{PM} over the 2 year study period. As observed previously, rates of stand water use were lower in winter than in summer and daily fluctuations occurred as a function of solar radiation and vapour pressure deficit (see below). However, unlike E_{sv}, rates of stand water use calculated from the P-M equation during summer did not show a trend of increasing water use from summer 2002 through to the summer of 2005. Indeed, peak rates of water use in the summer of 2002/3 were larger than that observed in the summer of 2004/5 and the largest rates of stand water use in summer were observed in 2003/4 using the E_{PM} method (Fig. 3).

Agreement in estimates of stand water use were closest during periods of low rates of water use (winter predominantly, but also some of spring and autumn; Figs. 3 - 5). Despite the wide scatter around the regression, the slope of the regression was not significantly different from 1, indicating good agreement, on average, between the two methods of calculating daily stand water use (Fig. 4). The histogram of weighted residuals (Fig. 5) indicates that the P-M model was predominantly biased towards overestimating daily stand transpiration in comparison to the measured values (negative residual values indicate overestimation, equation 11). In comparison to a normal distribution, the histogram has a shift to the left because where overestimation of values occurred, it was further from the mean than when underestimation occurred (Fig. 5). If scatter in the weighted-residuals is normalised relative to the standard deviation, and assuming that the uncertainty is drawn from a normal distribution, approximately 68% of the data-points should lie in the ±1 region. This in turn corresponds to ± one standard deviation (σ) of a normal distribution. On the other hand, any systematic variation in the residuals points to underlying systematic errors that could be a result of biasing in the model or data collection. During low rainfall periods (2003, Fig. 1), the P-M model generally overestimated stand transpiration and during high rainfall periods, (2004, Fig. 1), the P-M model generally underestimated stand transpiration.

Irrespecitve of the method of calculation, cumulative transpiration in 2003 and 2004 increased rapidly during the early (summer) months of both years and then tended to an asymptote during winter before increasing again over summer (Fig. 6), consistent with the patterns described from Fig. 3. In 2003, both methods for calculating transpiration produced similar results until February when E_{PM} was larger than E_{sv}. The two estimates gradually diverged slightly more over the remainder of the year. In 2004, the values from the two methods were similar until April when E_{sv} became larger than E_{PM}. This difference occurred after a massive rain event in March 2004 of greater than 90 mm in 1 day (Fig. 2). The differences between the two methods remained consistent over the remainder of the year (Fig. 6).

Stand water use (E_{sv}) increased curvilinearly with increasing VPD, and increased linearly with increasing radiation or potential evaporation (E_{pot}) in both years (Fig 7a-c). In all three relationships, E_{sv} was smaller in the drought year (2003) than in the following, non-drought year, at all values of VPD, radiation or E_{pot}. Since leaf area index of the site was slightly larger in 2003 than 2004 (Zeppel 2006), it is apparent that stomatal conductance, which is proportional to the ratio of E_{sv} to D (Whitehead 1998) was larger in the non-drought year than the drought year, thereby allowing a larger rate of transpiration after the drought compared to during the drought.

.During 2003, total annual stand water use, estimated using sapflow data and meteorological data to fill in gaps in the data, was 317 mm, or 61 % of rainfall. In 2004, when rainfall doubled, stand water use increased to 443 mm and this represented only 42 % of rainfall. Similarly, the P-M method estimated stand water use to be 371 mm (71 % of rainfall) in 2003 and 398 mm (37 % of rainfall) in 2004 (Table 4). Recharge plus run-off was zero during the drought but was significant during the following year, with a maximum possible of 195 mm.

4. Discussion

4.1 Adaptive responses of canopy function

The contrast in rainfall between the two study years was very large,, with 86 % of the long-term average rainfall falling in 2003 but 176 % of the long-term average being received in 2004. These differences in rainfall were reflected in the pre-dawn leaf water potential of trees growing at this site. For example, *Eucalyptus crebra*, one of the two dominant species found at this site, exhibited pre-dawn leaf water potentials of -3.0 MPa in the summer of 2003 (Zeppel 2006). Such low values indicate a large degree of water stress. In contrast, pre-dawn leaf water potential in the summer of 2004 was -0.4 MPa, indicating well watered conditions. In comparison, pre-dawn leaf water potential of two evergreen eucalypt tree species measured at the end of the 6 month dry season in the Northern Territory of Australia ranged from -1.25 MPa to -1.4 MPa over a 2 year period, despite volumetric soil moisture content being approximately 6 % at 50 cm depth (Duff et al. 1997). Clearly the 2003 drought exerted a significant impact on the water relations of the trees at our study site.

There was also a clear impact of this difference in rainfall and leaf water relations between years on the functioning of the woodland. The relationship between stand water use (E_{sv}) and VPD was depressed in 2003 compared to 2004 such that at any value of VPD, water use in 2004 was significantly larger that in 2004 (Fig 7a). Since the slope of the relationship between E and VPD is proportional to stomatal conductance (Whitehead 1998) it can be concluded that the lower leaf water potential observed in 2003 compared to 2004 increased the sensitivity of stomata to VPD, thereby causing a reduced conductance over the entire range of VPD. Such an increase in stomatal sensitivity to VPD with declining leaf water potential has been observed previously (Thomas and Eamus 1999). It is caused by a combination of increased supply of abscisic acid to the leaf from roots and a decline in hydraulic conductance of the soil-to-leaf pathway arising from declining soil conductance (Thomas and Eamus 1999). Increasing xylem embolism as soil moisture declines and evaporative demand exceeds the capacity of the canopy to transpire water is also an important factor (Macinnis et al. 2004, McClenahan et al. 2004).

The slope of the relationship between tree water use and net radiation or potential evaporation was also found to be lower in 2003 than that observed in 2004, (Fig. 7b,c), further indicating that a down regulation of canopy water use was apparent at the end of the drought compared to after the break of drought. Because the leaf area index of the canopy in the summer of 2003 was 1.2 but in summer 2004 was almost 1.0, it is apparent that these reduced rates of E_{sv} observed in Fig. 7a-c are the result of changes in stomatal (and hence canopy) conductance (since canopy conductance is the product of stomatal conductance and leaf area index (Lu et al. 2003) and not merely because of a decline in leaf are per tree. The reason for the small decline in LAI between the summer of 2003 and summer 2004 was because of a significant and coordinated replacement of the old foliage that was present at the end of the summer of 2003, with a new cohort of younger leaves in the spring of 2003 in response to the increasing availability of soil moisture as the drought was broken (Zeppel 2006). These new leaves (with a reduced total LAI compared to 2003) exhibited a larger conductance and hence water use as functions of VPD, radiation and potential evaporation that the older leaves in the summer of 2003.

4.2 Annual stand water use and water budgest

Annual estimates of stand water use were remarkably similar between the two methods of calculation. Large differences in rainfall between the two years examined (522 mm *cf* 1062 mm) led to a greater proportion of rainfall being transpired in 2003 than 2004 (61 % vs. 42 % estimated using the E_{sv} method and 71 % vs. 37 % estimated using the E_{PM} method). These estimates pf the proportion of rainfall lost as transpiration are in agreement with those for a *Banksia* woodland in Western Australia (Dodd and Bell 1993) and an open wet schlerophyll forest in the Australian Capitol Territory (Leuning et al. 2005).

Despite the reduction in the proportion of rainfall used in transpiration when more rain occurred, the volume transpired increased with increasing rainfall (317 mm vs. 443 mm estimated using the E_{sv} method and 371 mm vs. 398 mm estimated using the E_{PM} method). The ability of the native vegetation at this site to rapidly increase transpiration in response to above-average rainfall following a 2 year drought, supports the view that the native woody vegetation of Australia has evolved to capture a large proportion of the available rainfall (Dunin 1999, Hatton et al. 2003) and thereby minimise leakage of water out of the system (Petheram et al. 2002).

Zhang et al. (1999) examined a large number of global datasets relating annual evapotranspiration to annual rainfall minus run-off. They observed that when rainfall minus run-off was less than 800 mm, evapotranspiration accounted for about 100 % of the available water. Alternatively, they show that when rainfall is less than 1000 mm per year, annual evapotranspiration was typically 80 % of rainfall. Estimates of understory water use and soil evaporation at the present site account for approximately 28-30 % of total rainfall (Zeppel et al. 2006); total evapotranspiration was therefore approximately 100 % of rainfall in the drought year but this declined significantly (to a minimum of about 80 %) in the year that received above-average rainfall. This highlights (a) the need for comparisons of water budgets across several years that differ in rainfall; and (b) the importance of occasional high-rainfall years in recharging deep stores of water.

4.3 Comparing the two scaling methods

Two methods of temporal scaling were applied. In the first the ratio of average daily water use of all trees measured during short, intensive, campaign trees, to average daily water use of a few trees measured over the long-term was used to derive daily rate of stand water use for 411 days across different seasons and various rainfall conditions over a 759 day period. Meteorological data (VPD, R_n) and soil RWC were then used to estimate stand water use for the remaining days. In the second, a modelled value of G_c was used as an input in the Penman-Monteith equation. Each method provides a daily estimate based on either the behaviour of trees measured 54% of days, or on weather data, measured every day. This makes both methods an improvement on some earlier studies, where annual stand water use was estimated by multiplying the mean daily stand water use measured over a short period, by 365 (Mahmood et al. 2001), or by multiplying two seasonal estimates by the number of days in each season (O'Grady 2000; Kelley, 2002). Such approaches do not take into account daily fluctuations in climate and soil moisture

The E_{sv} method has been used previously in Australia and overseas, in both natural forests (Barbour et al. 2005, Barbour and Whitehead 2003, Bernier et al. 2002), and plantations (Mahmood et al. 2001). This method assumes that sap velocity is not related to tree size, an assumption tested by some (Barbour et al. 2005, Barbour and Whitehead, 2003) but not others (Goodrich et al. 2000, Lhomme et al. 2001). In the present study, sap velocity was not a function of tree size (data not shown), making this method suitable to application at this site. To apply the E_{sv} method at least a few trees need to be continually monitored and field campaigns of intensive sampling of sap flow are also required. Intensive field campaigns are expensive (for labour and equipment), but necessary to provide data across the full range of tree sizes at a site , in order to allow spatial scaling to plot-scale (ha) estimates of stand water use. However, neither soil nor climate data are required.

Many authors have designed models to predict transpiration based on the Penman-Monteith equation using VPD, radiation and soil moisture content (Bernier et al. 2002, Bosveld and Bouten 2001, Lhomme et al. 2001, Rana et al. 2005, Takagi et al. 1998). Traditionally transpiration is used as an input into the Penman-Monteith equation to derive G_c. In contrast, in this study, a model was used to predict G_s (Thorpe et al. 1981) from climate and soil moisture parameters only. G_s and LAI_s were then used to predict G_c, and then the predicted G_c was used to calculate transpiration using the Penman-Monteith equation. Transpiration has been estimated using the Penman-Monteith equation with varying degrees of success. Lhomme et al. (2001) found much scatter in the relationship between predicted and measured transpiration. In contrast, a number of authors have reported a good degree of correlation between predicted and measured transpiration (Yunusa et al. 2000, Yunusa et al. 2004), generally in low-lying vegetation (but not always; David et al. 1997).

The P-M approach is practical and convenient because once G_s has been predicted from the Thorpe et al. (1981) model (which requires field measurements of maximum stomatal conductance) it does not require any subsequent measurements of either G_s or sap flow; only climate and soil moisture data are needed. However, a problem with the E_{PM} method is that stand water use appears to be underestimated compared to sap flow estimates when soil water is limiting. The Thorpe et al. (1981) model predicted canopy conductance to be high in the afternoon, in both summer and winter sampling periods, despite the trees exhibiting a low stomatal conductance in the afternoon for both periods, as soil moisture declined (data not shown). Similar over-estimates of transpiration in the afternoon by the Penman-Monteith equation, compared with sap flow estimates, were reported by Lhomme et al. (2001) and the correlation between sap flow estimates and P-M estimates of transpiration became weaker as soil water content declined (David et al., 1997). This may be explained by the fact that P-M equation does not explicitly account for features such as diurnal and seasonal changes in hydraulic conductance between soil and root (Williams et al. 1998, 2001) or the contribution of water stored within tree stems to transpiration (Meinzer et al. 2004) and the capacity of water stored in stems to contribute to transpiration may also lead to inaccurate estimates of G_s, G_c (Gao et al. 2005) and hence transpiration rate. We suggest that when soil moisture is limiting the P-M equation is less reliable. Thus, under limited soil moisture, the E_{sv} provides a more reliable estimate of daily and annual water use. In addition, a limitation of the present study was that soil moisture was measured to 50 cm in the present study, yet clearly roots access water in soil deeper than this, and measurement of soil moisture at deeper layers may provide better estimates of stand transpiration.

4.4 Conclusion

In drought years a larger proportion of rainfall was used as transpiration than occurred in wet years; recharge and run-off were zero in dry years but were substantial in wet years. Despite expectations, large differences in leaf area index were not observed between the two years and differences that did exist could not explain differences in water use by trees between years. Resilience of this forest was observed in the rapid increase in tree water use and this was mediated by decreased sensitivity of stomatal conductance to vapour pressure deficit in the non-drought year. Estimating the annual water budget of stands of trees is important to water, forest and catchment managers. Whilst the use of sap-flow sensors to quantify water use of individual trees is relatively common, scaling spatially and temporally from individual trees measured from over a few days to annual estimates of stand water use is less commonly undertaken. We conclude that a method based on the ratio of estimates of tree water use derived from few trees measured for hundreds of days to estimates derived from many more trees sampled for several days, provided a plausible estimate of annual stand water use

Acknowledgements

Weather data were provided by the NSW Department of Agriculture (Department of Industry and Primary Natural Resources). This project was conducted in collaboration with the State Forests of NSW and the NSW Department of Agriculture. We give thanks to the Cudmores for providing access to their property, Paringa. Funding was provided by the CRC for Greenhouse Accounting, State Forests of NSW, IWERM and MZ was funded by an APA(I) during this project.

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Table 1. Basal area, density and sapwood area of the dominant species.

Variable	*E. crebra*	*C. glaucophylla*
Basal area (m^2 ha^{-1})	14.5 ± 1.8	5.9 ± 3.6
Density (stems ha^{-1})	42.2 ± 22.6	212.2 ± 3.2
Total sapwood area (m^2 ha^{-1})	1.4	2.4

Table 2. Abbreviations and derivations used.

Symbol	*Meaning and units*	*Derivation*
E_{PM}	Penman-Monteith transpiration (mm^3 water h^{-1} mm^{-2} leaf area)	Penman-Monteith equation using G_c as an input
E_{sv}	Transpiration (mm h^{-1} or mm day^{-1})	Sap velocity multiplied by sapwood area
G_s	Canopy stomatal conductance of one tree (m s^{-1} or mm s^{-1})	Derived from a Jarvis (1976) type equation.
G_c	Canopy total conductance of the tree stand (m s^{-1} or mm s^{-1})	G_s x LAI
G_{smax}	Maximum stomatal conductance measured on all trees (mm h^{-1})	G_s measured using a porometer.

Table 3. Meteorological data for days when stomatal conductance was measured. Season means show means and standard deviations.

Date	Season	9 am VPD (kPa)	Total solar radiation (MJ m^{-2} day^{-1})	Potential evaporation (mm)	Rainfall (mm)
25th Jun 2003	Winter	0.3	9.3	1.7	0.0
26th Jun 2003	Winter	0.3	7.9	1.9	0.6
Season means	Winter 2003	0.2 ± 0.1	11.2 ± 3.4	2.2 ± 0.6	1.6 ± 5.1
16th Mar 2004	Summer	0.8	14.3	2.9	1.0
18th Mar 2004	Summer	0.9	22.7	5.1	0.0
19th Mar 2004	Summer	0.8	22.2	4.9	0.0
Season means	Summer 2003-04	1.4 ± 0.7	25.9 ± 8.4	6.8 ± 2.4	3.6 ± 12.1
6th Dec 2004	Summer	1.2	18.2	3.7	0.2
7th Dec 2004	Summer	1.2	27.0	6.2	2.4
8th Dec 2004	Summer	1.4	18.9	4.1	13.2
Season means	Summer 2004-05	1.3 ± 0.7	27.3 ± 7.7	6.5 ± 2.1	7.5 ± 13.6

Table 4. Annual water budget estimated using E_{sv} and E_{PM} methods. Understorey evapotranspiration and interception were crudely estimated as described in Zeppel *et al*., 2006. Run-off and deep drainage were estimated by difference.

	2003		2004	
	(mm)	(% of rainfall)	(mm)	(% of rainfall)
Rainfall	522		1062	
E_{sv}	317	61 %	443	42 %
E_{PM}	371	71 %	398	37 %
Interception (Zeppel et al., 2006).	52 -78	10-15 %	106 -159	10-15 %
Understorey evapotranspiration (Zeppel et al., 2006)	146	28 %	318	30 %
Run-off and deep drainage estimated using $E_{sv.}$	-19 to 7	-4 to1 %	142 -195	1-19 %

Figures

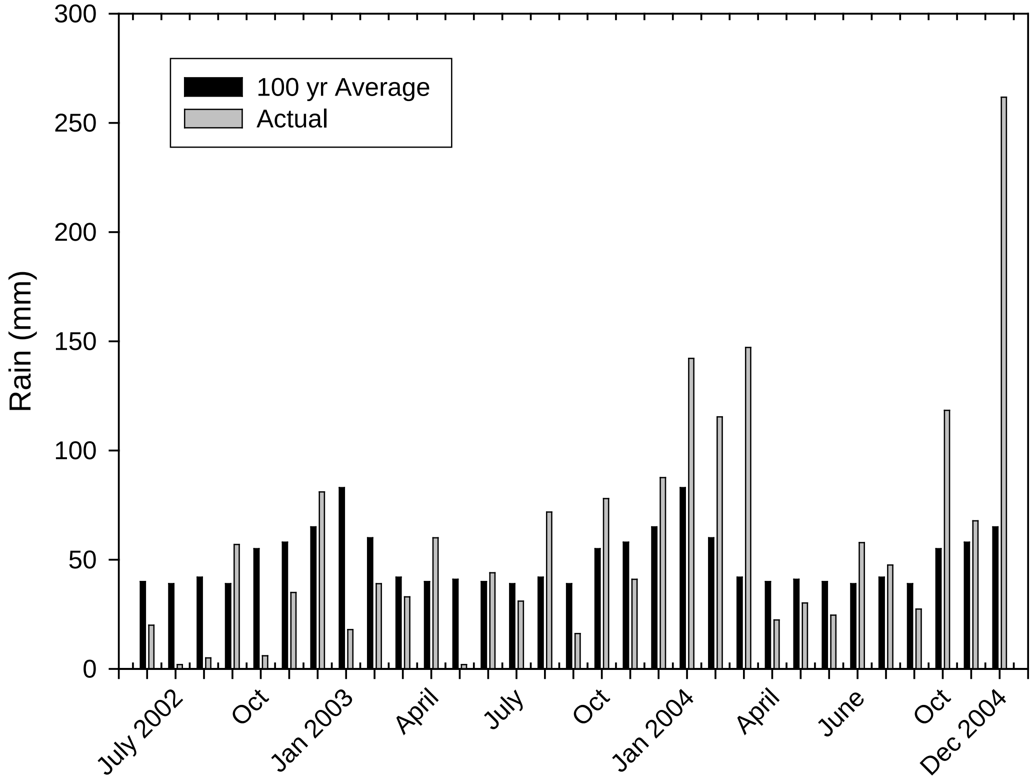

Figure 1. Rainfall over the study period, from June 2002 to December 2004, compared with 100 year average rainfall. Data collected by the Department of Agriculture, Tamworth and source of average rainfall data was the Australian Bureau of Meteorology (www.bom.gov.au).

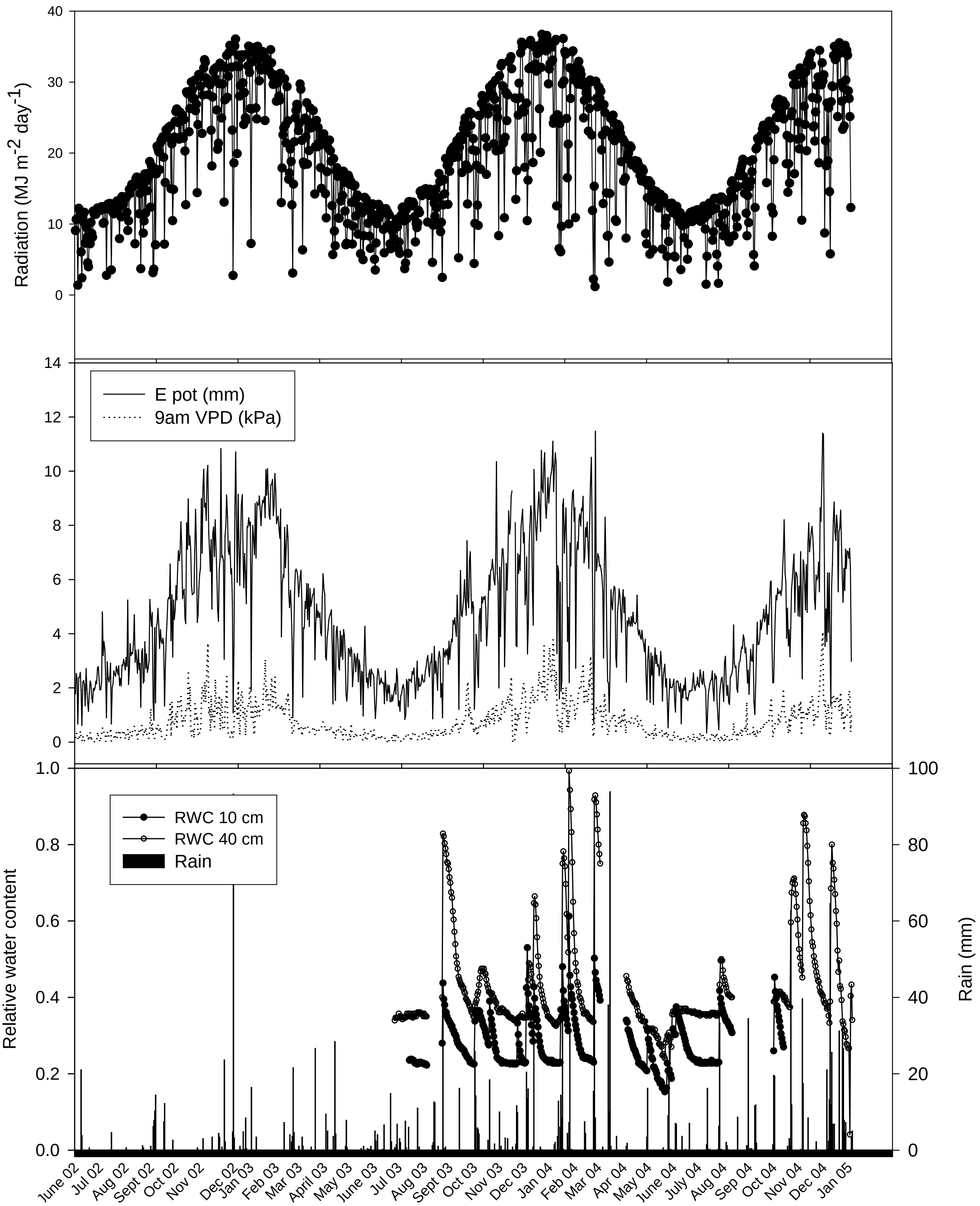

Figure 2. Seasonal patterns of radiation, potential evaporation (E_{pot}), VPD, relative water content (RWC) of soil and rainfall. VPD shown is VPD measured at 9:00 h. RWC of soil (%) was measured at 10 and 40 cm depths. All data (except RWC) collected by the Department of Agriculture, Tamworth.

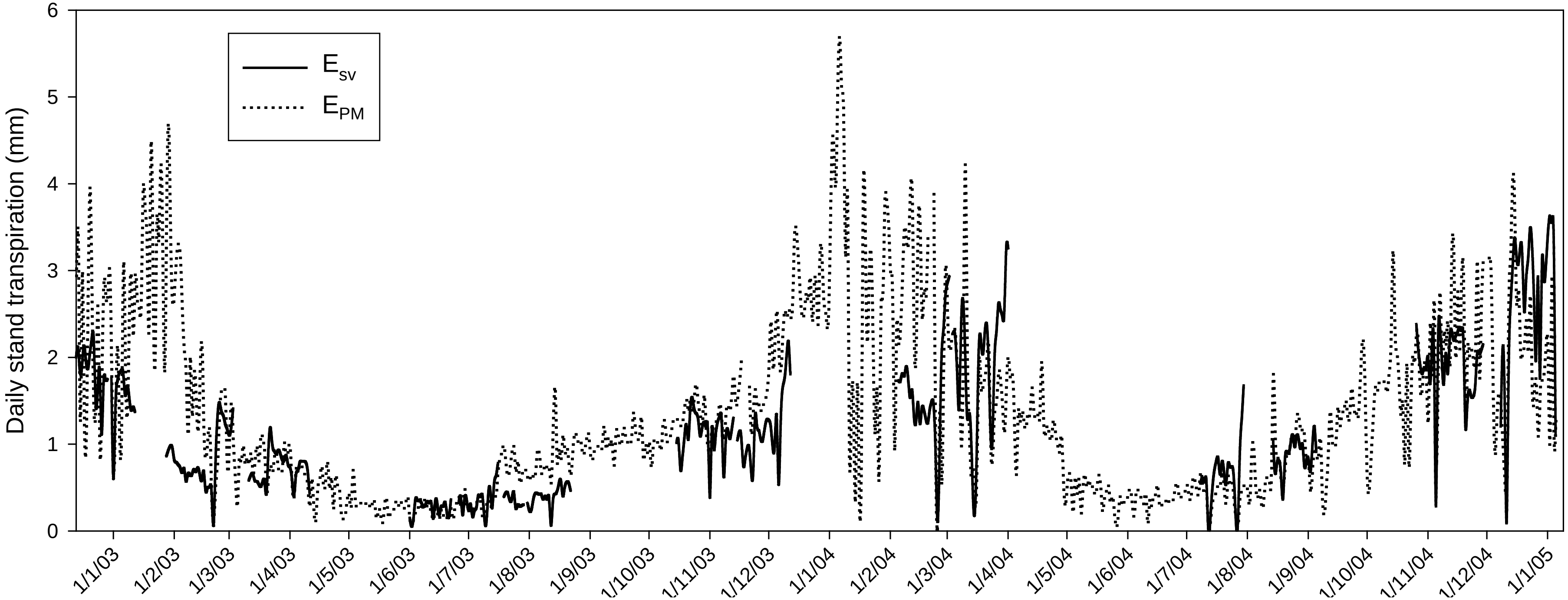

Figure 3. A comparison of E_{PM} and E_{sv} from December 2002 to January 2005. Gaps in E_{sv} method are due to equipment failure and batteries running low. E_{PM} estimates are continuous and based on continually monitored climate data.

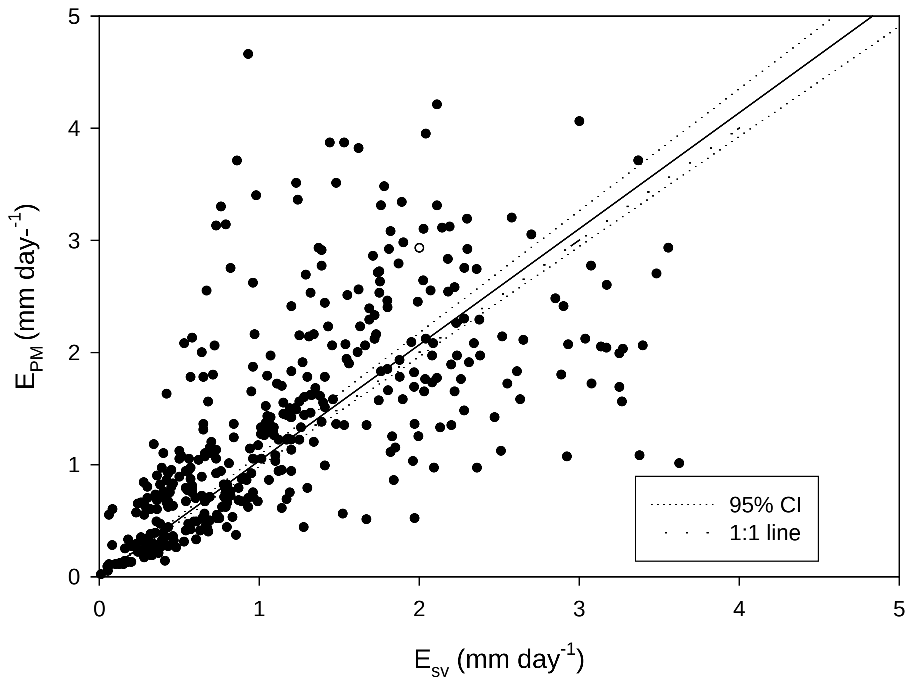

Figure 4. The relationship between daily transpiration estimated using E_{PM} and $E_{sv.}$ $y = 1.03x$; $r^2 = 0.41$

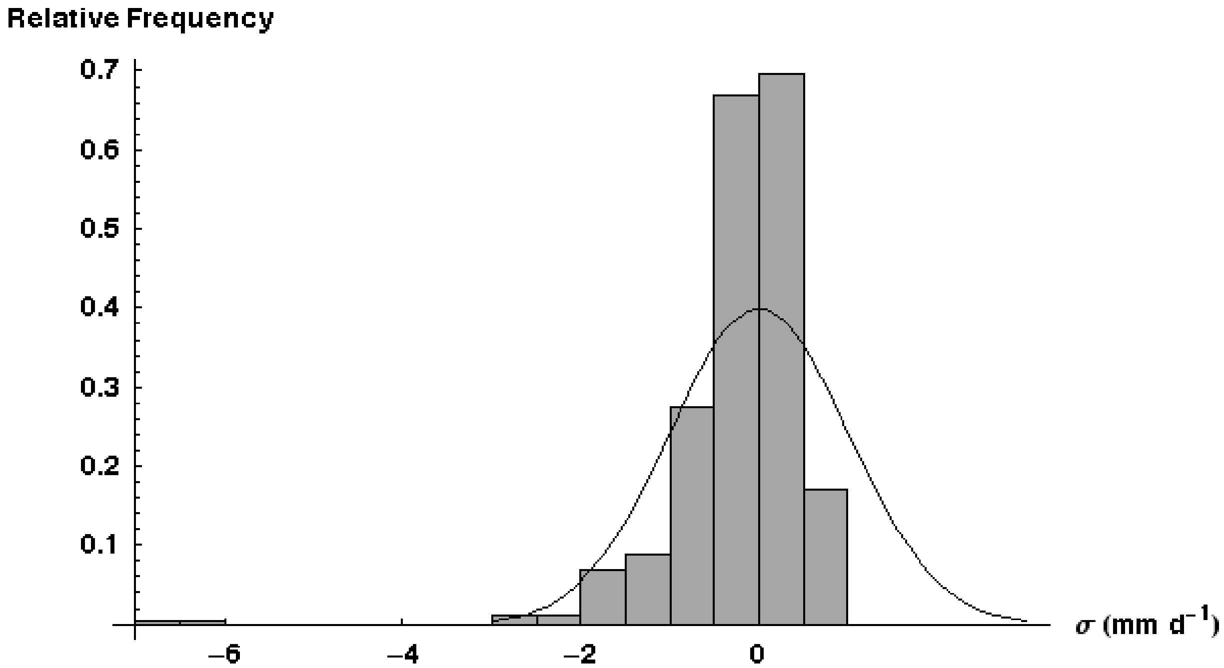

Figure 5. Frequency histogram of weighted residuals from comparison of transpiration estimated with E_{PM} and measured stand transpiration.

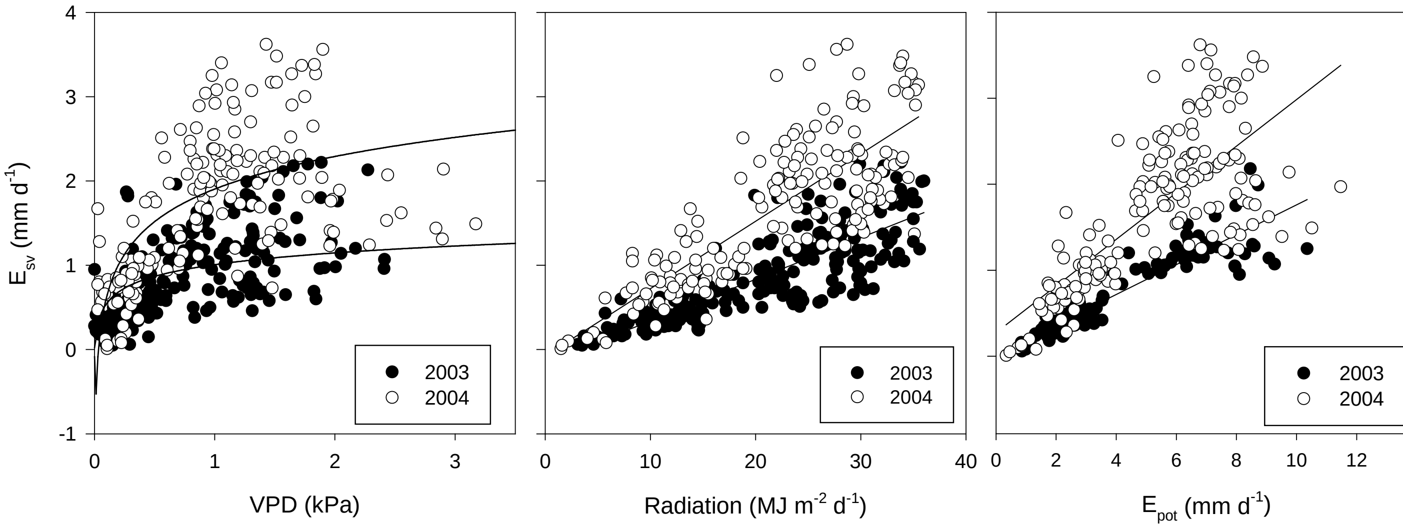

Figure 7 Rates of stand water use (Esv) increase curvilenearly with increasing VPD and increase linearly with increasing solar radiation and potential evaporation. For the drought year (2003) rates of E_{sv} were consistently lower than the rates observed in the following non-drought year.

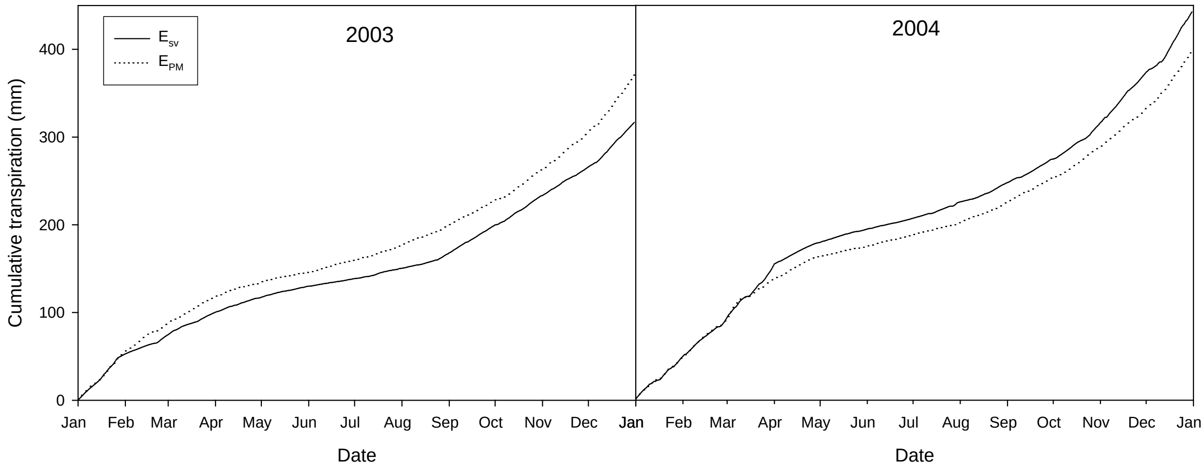

Figure 8. Cumulative transpiration in 2003 and 2004 calculated with the sap velocity (E_{sv}) and Penman-Monteith (E_{PM}) methods.

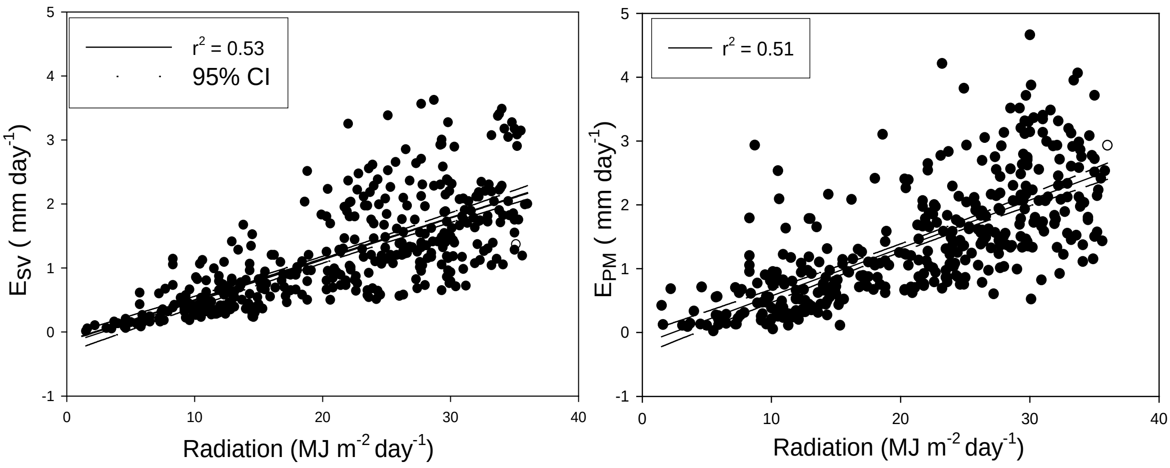

Figure 8. The relationship between daily transpiration and radiation determined with the sap velocity (E_{sv}) and Penman-Monteith (E_{PM}) methods. Days immediately following rainfall were excluded as they were outliers, because radiation was high and stand transpiration was low. For $E_{sv,}$ y = 0.064x - 0.15. For $E_{PM,}$ y = 0.070x - 0.13.

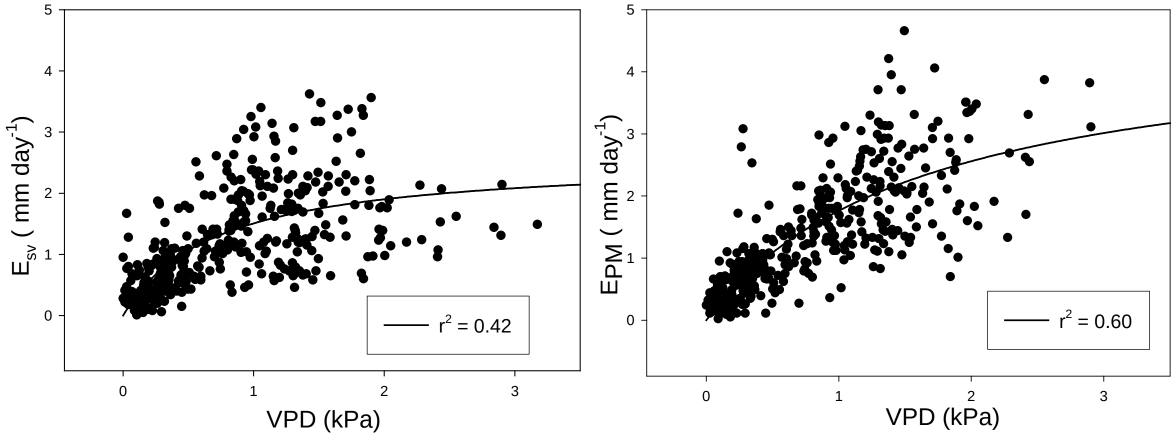

Figure 9. The relationship between daily transpiration and VPD determined with the sap velocity (E_{sv}) and Penman-Monteith (E_{PM}) methods. For E_{sv} y = 2.6x / (0.7 + x). For E_{pm} y = 4.7x / (1.6 + x)