

# The response of sap flow to pulses of rain in a temperate Australian woodland

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Received: 30 March 2007 / Accepted: 5 July 2007 / Published online: 3 August 2007  
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**Abstract** In water-limited systems, pulses of rainfall can trigger a cascade of plant physiological responses. However, the timing and size of the physiological response can vary depending on plant and environmental characteristics, such as rooting depth, plant size, rainfall amount, or antecedent soil moisture. We investigated the influence of pulses of rainfall on the response of sap flow of two dominant evergreen tree species, *Eucalyptus crebra* (a broadleaf) and *Callitris glaucophylla* (a needle leaved tree), in a remnant open woodland in eastern Australia. Sap flow data were collected using heat-pulse sensors installed in six trees of each species over a 2 year period which encompassed the tail-end of a widespread drought. Our objectives were to estimate the magnitude that a rainfall pulse had to exceed to increase tree water use (i.e., define the threshold response), and to determine

how tree and environmental factors influenced the increase in tree water use following a rainfall pulse. We used data filtering techniques to isolate rainfall pulses, and analysed the resulting data with multivariate statistical analysis. We found that rainfall pulses less than 20 mm did not significantly increase tree water use ( $P > 0.05$ ). Using partial regression analysis to hold all other variables constant, we determined that the size of the rain event ( $P < 0.05$ ,  $R^2 = 0.59$ ), antecedent soil moisture ( $P < 0.05$ ,  $R^2 = 0.29$ ), and tree size (DBH, cm,  $P < 0.05$ ,  $R^2 = 0.15$ ), all significantly affected the response to rainfall. Our results suggest that the conceptual Threshold-Delay model describing physiological responses to rainfall pulses could be modified to include these factors. We further conclude that modelling of stand water use over an annual cycle could be improved by incorporating the T-D behaviour of tree transpiration.

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Responsible Editor: Stephen S.O. Burgess

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**Keywords** Rain pulses · Sap flow · Soil moisture ·  
Threshold-delay model · Transpiration rate

## Introduction

Much of the eastern seaboard of Australia experienced a prolonged drought from approximately 2002 to 2005, which has severely limited water availability for native vegetation, agriculture, industry, and domestic use. Managing scarce fresh surface water

resources is becoming an increasingly important environmental, social and economic issue across many regions of the world (Jackson et al. 2001). An understanding of the patterns and behaviour of water use of native vegetation can contribute to the effective management of these water resources.

Pulses of rainfall are particularly pivotal in controlling plant physiological processes in low rainfall systems (Ivans et al. 2006). Rainfall pulses can trigger a cascade of ecosystem responses that affect plant nutrient-, water- and carbon cycling. These responses ultimately affect the balance of ecosystem respiration and production in low rainfall systems (Huxman et al. 2004). Plant nutrient, carbon and water assimilation are directly affected by plant and soil water status, however, and may explain why plant responses to rainfall pulses can be temporally and spatially heterogeneous, or deviate significantly from predicted or modelled responses (Meiresonne et al. 2003; Zeppel 2006). For example, in a recent study predictions from a temperature-dependent respiration model did not agree well with measured responses immediately after rain events (Zhao et al. 2006). This suggests that a deeper understanding of plant and soil water relations immediately after rain events is required to make accurate predictions of ecosystem function in low rainfall systems.

Various factors may interact to influence plant water relations following pulses of rain. For example, plant functional type or species (BassiriRad et al. 1999; Cheng et al. 2006), landscape position (Burgess 2006; Eberbach and Burrows 2006), antecedent and ensuing environmental conditions (e.g., season; Ivans et al. 2006), evaporative demand, days since rain event (Sponseller 2007), and soil properties all translate precipitation into plant available water (Fravolini et al. 2005; Potts et al. 2006a). Plant functional type or life form, e.g., trees or grasses, in particular can impart differences that may affect plant water relations following a rainfall pulse. These differences include rooting depth (Jackson et al. 1996; Ogle and Reynolds 2004), and intrinsic differences in the rates at which stomatal conductance, photosynthesis, and leaf area development increase (Gebauer et al. 2002; Schwinning et al. 2002; Ignace et al. 2007).

These various factors have long been recognized to potentially influence plant physiological responses to pulses of rainfall (Walter 1971; Noy-Meir 1973). The

paradigms of resource partitioning such as the Westoby–Bridges theme of ‘triggering pulses’ (Noy-Meir 1973) and rooting patterns and resource acquisition (Walter 1971), have been integrated into a conceptual Threshold-Delay (T-D) model, proposed by Ogle and Reynolds (2004). The T-D model is conceptually simple, and allows plants to exhibit a range of physiological rates (e.g., respiration or tree water use) following rainfall pulses (Ogle and Reynolds 2004). Rates of plant response to rainfall pulses can potentially differ depending on species or plant functional types, a delay in timing of physiological responses, the effect of antecedent moisture and physiologic conditions, or precipitation thresholds. For example, the model can allow that if the size of the pulse is below a threshold, there will be no response evident. Alternatively, if the pulse exceeds the threshold, a response is observed, increasing to some maximum rate, and then declining over time. A weakness of the model is that it is empirical rather than mechanistic. Thus, no single parameterised T-D model can be expected to describe every system; the model needs to be parameterised for each site. However, the model provides a useful framework for evaluating plant responses to rainfall pulses.

While previous research has focused on shrubs, herbaceous plants, and bunchgrasses in arid or semi-arid systems (BassiriRad et al. 1999; Schwinning and Sala 2004; Ivans et al. 2006; Sponseller 2007), trees in temperate, rainfall-limited systems can offer unique insight into responses of plant water relations to rainfall pulses. First, trees not only have greater internal water stores and potential water use, but also generally have deeper functional rooting profiles than non-woody species (Jackson et al. 1996). One previous study showed that at least four different types of plant water use responses to summer rainfall pulses existed in a low rainfall, temperate woodland system (Burgess 2006). Second, tree-dominated, rainfall-limited systems currently represent structural and climate conditions that will likely increase under several climate change scenarios (e.g., unpredictable and sporadic rainfall of variable intensity; Chesson et al. 2004; Eamus et al. 2006). Understanding the responses of tree water use to pulses of rain in these systems will likely increase the predictive ability of climate change models to produce scenarios of future productivity and water use in temperate forested systems. Finally, an understanding of responses of

tree water use to pulses of rain is relevant to a number of ecological problems mediated by deforestation, including the salinisation of cleared agricultural land in temperate Australia (Burgess 2006).

Using the T-D model as a conceptual framework, we evaluated the seasonal and diurnal water use patterns of two dominant tree species in an open woodland in eastern Australia. Our objectives were to address the following questions: (1) what is the threshold that a rain event must exceed to elicit an increase in tree water use, (2) does the size of the response vary under different conditions, and (3) what factors have the strongest influence on this response? Specifically, we examine the influence of tree size, antecedent soil moisture, potential evapotranspiration, the size of the rain event (mm) and the number of days since the previous rain event on the size of the response of tree water use to rain pulses.

## Materials and methods

### Site description

The study site was located in remnant woodland on the Liverpool Plains, (about 90 km south of Tamworth) in the northwest of New South Wales, Australia (31.5°S, 150.7°E, elevation 390 m). Vegetation at the site consisted of open woodland, with an average height of 14 m, dominated by *Eucalyptus crebra* F. Muell. and *Callitris glaucophylla* J. Thompson and L.A.S. Johnson. These two species account for approximately 75% of the tree basal area. The understorey was dominated by grasses including *Stipa* and *Aristida* species, which were comparatively shallow rooted compared to the trees. Soils were well drained acidic lithic bleached earthy sands (Banks 1998) with pockets of clay. Mean ( $\pm$ SE) tree basal area for the site was  $23.8 \pm 3.4 \text{ m}^2 \text{ ha}^{-1}$  and leaf area index was generally about 1.0 to  $1.2 \text{ m}^2 \text{ m}^{-2}$  throughout the year.

### Weather data

Rainfall data and aspirated wet and dry bulb air temperatures, and total solar radiation were obtained from an open-field weather station (Envirodata Pty Ltd, Australia) located approximately 500 m from the study site. Air vapour pressure deficit (VPD) was calculated from wet and dry bulb air temperatures.

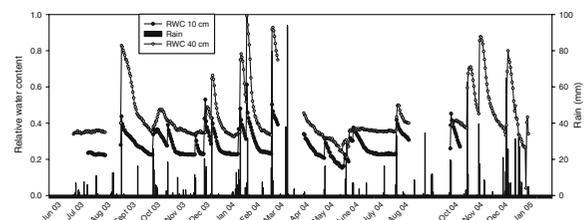
Potential evaporation ( $E_{\text{pot}}$ ) was estimated as a function of the Penman–Monteith equation (Lu et al. 2003).

### Soil moisture

Volumetric soil moisture content was measured in three plots with an array of frequency domain reflectometry sensors which measure soil moisture by measuring the dielectric constant of soil (Theta Probe, ML2-X, Delta-T devices, Cambridge). Theta probes were buried horizontally at 10, 40 and 50 cm in two plots, and at 10 and 40 cm in one plot. Total soil moisture storage was calculated by multiplying the soil depth by the percent of moisture contained by the soil. Then the water contained in each layer was summed (Fig. 1). Relative water content was estimated by dividing actual daily soil moisture content by maximum soil moisture content measured over the entire season.

### Sap flow measurement

Sap velocity was measured using the heat pulse technique with commercial sap flow sensors (Green-span Technology Pty Ltd., Warwick, Australia). The methods of measuring sap flow and scaling to whole tree water use are described fully in Zeppel et al. (2004). A brief description is provided here. Two probe sets (four sensors) were inserted into each tree at one third and two thirds of the sapwood depth, separated circumferentially by 90°. A preliminary Monte Carlo simulation showed that two probe sets per tree was adequate to capture circumferential variation in sap flow (Zeppel et al. 2004). A minimum



**Fig. 1** Average daily soil moisture (shown as relative water content at 10 and 40 cm depths) and total daily rainfall (mm) from June 2003 to January 2005. Sap flux was measured continually in four trees from December 2002 till March 2004 and intensively in from 7 to 15 trees in campaigns during January–February 2003, July–August 2003, and February–March 2004

of 7 and a maximum of 15 trees were instrumented for each species at each sampling time.

The sap velocities were monitored at 15-min intervals over a 2-week period during July–August 2002 (winter), January–February 2003 (summer) July–August 2003 (winter) and February–March 2004 (summer). Tree water use was calculated for each sensor for 12 consecutive days after allowing 2 days for development of the wound that results from drilling into the wood (Olbrich 1991). The weighted averages technique of Hatton et al. (1995) was used to convert sap velocities to whole tree water use ( $Q$ ,  $1 \text{ day}^{-1}$ ).

Sapwood depth was measured twice for each tree at the beginning of the study. We extracted an increment core, and visually estimated sapwood depth from the clear colour change observable at the boundary between sapwood and heartwood. Volume fractions of wood and water in the sapwood were determined gravimetrically on 5 mm diameter cores taken from ten trees of each species on two occasions. In *E. crebra* the mean ( $\pm$ SE) wood fraction was  $0.55 + 0.03$  and  $0.50 + 0.04$  in winter and summer respectively. The water fraction was  $0.23 + 0.02$  and  $0.28 + 0.01$  in winter and summer respectively. In *C. glaucophylla* wood fraction was  $0.34 + 0.01$  in winter and  $0.34 + 0.04$  in summer. The water fraction was  $0.52 + 0.01$  in winter and  $0.48 + 0.03$  in summer.

#### Radial sapflow profiles and wound width

Radial profiles of sap velocity through the sapwood of each species were determined prior to the study (Zeppel 2006) in order to calculate the regions of maximum flow across the sapwood. Sap flow was measured at a minimum of six depths across the sapwood, replicated 3 or 4 times in different aspects in each tree. Knowledge of the region of maximum sap flow across the sapwood was used to calculate the depth to insert the sap flow sensors. The full method is described by O'Grady et al. (2000) and Zeppel (2006).

The width of the wound around the holes used to insert the probes was measured twice in seven trees of each species, using a binocular microscope to measure the wound (Olbrich 1991), 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.

#### Leaf xylem pressure potential

Xylem pressure potential was measured on each of three leaves of three replicate trees of both species. Measurements were made in summer 2002/2003, winter 2003, and summer 2003/2004, on at least 1, sometimes 3, days, using a Scholander-type pressure bomb (Plant Water Status Console, Soil Moisture Equipment Corporation, USA). Fully expanded, sunlit, mature leaves were sampled in the outer canopy between 2–8 m height (using a hydraulic platform for access) between pre-dawn and 17:00 h.

#### Statistical analyses

The threshold rainfall size was determined using ANOVA and Tukey's HSD test (after testing for homogeneity of variance and normal distribution). The threshold was identified as the lowest rainfall event to be significantly different from the 0–5 mm rainfall class (Statistica version 8), conceptually similar to a method commonly used in ecotoxicology studies to identify the lowest observed effect concentration (Crane and Newman 2000).

Data were filtered to exclude the following situations: when rain free and continuous tree water use data were not available for 2 days before and 7 days after the rain event; days where the rain event lasted longer than 5 days (we considered that this was not a 'pulse'). In addition, solar radiation, evaporative demand and potential evaporation rates were all generally declining in autumn and winter, which meant that the tree water use was also declining regardless of rain and the resulting soil moisture content. This meant that the decay curve after rain events was not declining, consequently we excluded the months of May to August. Of a possible 44 rain events during the study period, 16 were suitable for analysis (37% of the data) and up to seven trees were analysed for each rain event. For this study site, data from both species were pooled as there was no significant difference ( $P > 0.05$ ) between the size of the response of the two species.

Previous research on plant responses to rain pulses has examined antecedent soil moisture (Potts et al. 2006a) and we examined other variables that are known to influence sap flow, such tree size (DBH, cm; Zeppel 2006), days since previous rain event, size of rain event, and potential evapotranspiration,  $E_{\text{pot}}$

(mm). A linear regression showed that the mean  $E_{\text{pot}}$  5 days after the rain event explained more variability (52%) in the dependent variable than 3 (18%) and 7 days (22%) after the rain event.

Influences on the response of tree water use to rainfall were first investigated using non-linear regression analysis. This analysis showed that no one variable was able to explain a large proportion of the variation. Non-linear regressions determined that rain size explained 43% of the variation of increase in tree water use, antecedent soil moisture explained 13%,  $E_{\text{pot}}$  5 day mean explained 8%, and tree size explained 9%. Thus, in order to determine which variables most influenced the dependent variable (response of tree water use to rain pulses) the following multivariate analysis was conducted. Interactions between influences on tree water use responses to rainfall were assessed with multiple linear regression (MLR). We used multiple regressions (SPSS v12.0 for Windows) to explore the unique contribution of each predictor in explaining the variance of the dependant variable. The unique relationship of each predictor was assessed in terms of a partial slope and “partial  $r^2$ ” value. A partial slope is the slope of the relationship between predictor  $x$  and dependent variable  $y$ , after the effects of other independent variables in the model are held constant. A partial  $r^2$  value is a measure of the variance in the dependent variable that is explained by an independent variable (predictor), over and above the effects of other independent variables in the model (Murray and Hose 2005). The use of multiple regression allowed us to look at the unique relationship between two variables while holding potentially confounding effects of other variables constant (Hair et al. 2006). For example, we looked at the relationship between increase in tree water use and rain size while holding tree size and  $E_{\text{pot}}$  after rain event constant.

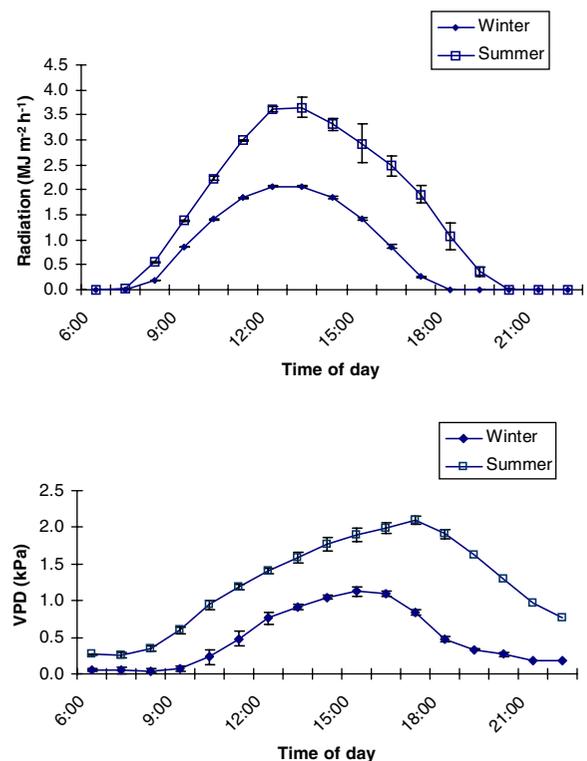
## Results

### Meteorology and soil moisture

Average annual rainfall for the Liverpool Plains is 680 mm, with approximately 50% of this occurring between October and February and 50% occurring from March to September (Fig. 1). However, during the study period rainfall (300 mm) was significantly lower than

this long-term average due to a prolonged drought which occurred from approximately 2002 to 2004 at the study site. Maximum soil water content during the study period was 40%. Rainfall influenced the relative water content (RWC) of soil at 10 cm depth more frequently than soil at 40 cm depth (Fig. 1). Soil RWC at 10 cm depth responded to rain events if the cumulative rainfall total over a 4–7 day period exceeded 10–15 mm. Thus, a number of small (>10 mm) rain events on consecutive days impacted soil RWC, as well as large (>20 mm) rain events. Single rain events of less than 10 mm had no effect on soil RWC at 10 cm or 40 cm depth. Soil at 40 cm responded to rain events larger than 20 mm, yet the response time was slower, and soil at 40 cm depth retained moisture for longer than soil at 10 cm, possibly reflecting a higher clay content at 40 cm, and a more sandy soil at 10 cm (Fig. 1).

Peak net radiation was about  $4 \text{ MJ m}^{-2} \text{ h}^{-1}$  in summer and half of this in winter (Fig. 2). Vapour pressure deficit was similarly larger in summer



**Fig. 2** Diurnal patterns of solar radiation ( $\text{MJ m}^{-2} \text{ h}^{-1}$ ) and 9 A.M. VPD (kPa). Data shown represent the mean and SE of four cloud-free days during each season. Summer data represent the mean and SE of 25–28 February 2003 and winter data represent the mean and SE of 16 to 18 June 2002. Data collected by the Department of Agriculture, Tamworth

(2.1 kPa) than winter (1.1 kPa) and peaked later in the afternoon in summer than in winter (Fig. 2).

### Xylem pressure potential

Pre-dawn xylem pressure potential for the *E. crebra* was low (approximately  $-2.8$  MPa) in summer 2002/2003, reflecting the impact of the prolonged drought on plant water relations (Fig. 3). During the daylight period, xylem pressure potential ( $\psi_w$ ) declined to a minimum of  $-4.0$  MPa (Fig. 3). Pre-dawn water potential data are not available for *C. glaucophylla* because of equipment problems. However, in summer 2002/2003,  $\psi_w$  of *C. glaucophylla* reached  $-5.0$  MPa in late afternoon.

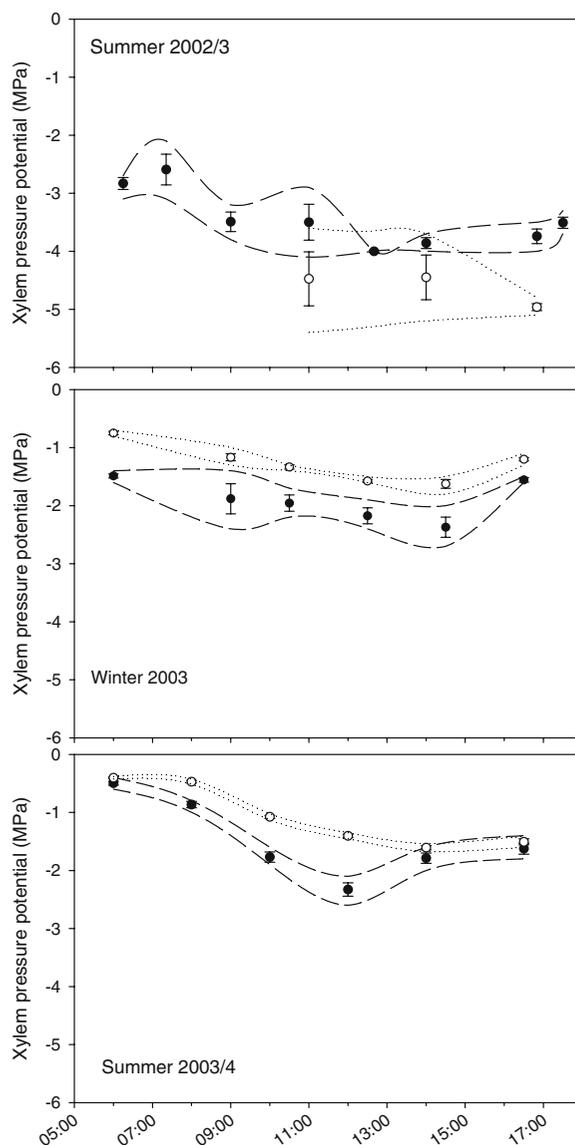
Pre-dawn xylem pressure potential of the *E. crebra* was higher (closer to zero) in winter 2003 than summer 2002/2003. Similarly,  $\psi_w$  throughout the day were higher for both species in winter 2003 than summer 2002/2003 (Fig. 3). In the summer of 2003/2004, after significant rains in the 3 months prior to measurement of  $\psi_w$ , pre-dawn  $\psi_w$  for both species was higher than that observed in winter 2003 (Fig. 3). However, the daily range of  $\psi_w$  in summer 2003/2004 was similar to that observed in winter 2003, for both species. Generally,  $\psi_w$  of the *C. glaucophylla* was higher than that of the *E. crebra*, although this was not true for summer 2002/2003. The difference in  $\psi_w$  between the two species was typically 0.5 to 1.0 MPa throughout the day, but the difference was generally smaller at the start or end of the day.

### Rainfall response threshold

Most of the rainfall events were small, with the majority (56%) being less than 5 mm (Fig. 4). As rainfall amounts increased, rainfall frequency decreased (Fig. 4). The percentage increase in tree water use was significantly smaller ( $p < 0.05$ ) for the 0–5 mm class than for rainfall in the 20–50 and 51–150 mm rainfall classes (Fig. 5), indicating that at this site 20 mm of rain is required before tree water use increases significantly.

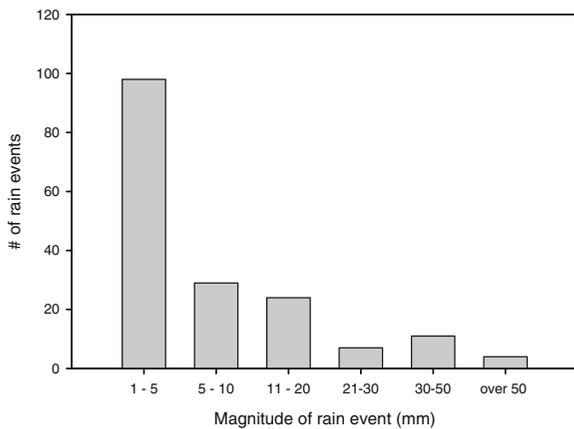
### Determinants of the tree water use response to rainfall

Of the factors that we examined – tree size, antecedent soil moisture, potential evapotranspiration, the size of the rain event (mm) and the number of



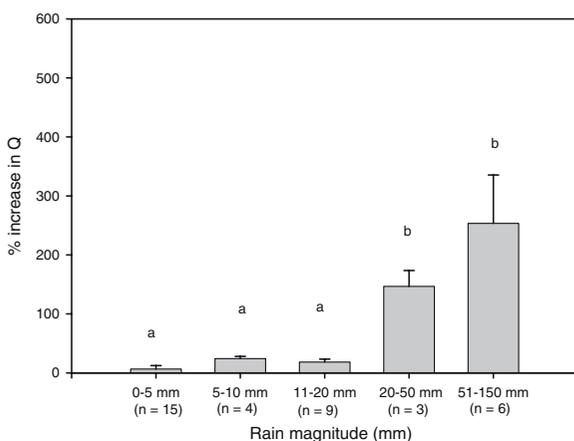
**Fig. 3** The diurnal time course of xylem pressure potential (MPa) for *E. crebra* (closed circles) and *C. glaucophylla* (open circles) during summer 2002/2003, winter 2003 and summer 2003/2004. Mean (SE) of all leaves measured over two or three cloud free days are shown. Dashed and dotted lines represent 95% confidence intervals for *E. crebra* and *C. glaucophylla*, respectively

days since the previous rain event – no single factor alone explained the response of tree water use to rain pulses. There was no significant relationship between antecedent soil moisture and the percent increase in tree water use after rain. Similarly, there was no significant relationship between tree size, 5 day  $E_{pot}$  after rain event or size of the rain event and increasing



**Fig. 4** Frequency distribution of size of rainfall events during the study period

tree water use after rain. When antecedent soil moisture was high (>45 mm) the percentage increase in  $Q$  was always small, typically 0–50%. In contrast, when antecedent soil moisture was low (<40 mm) the percentage increase could be large (>200%) but not always, indicating the influence of other factors (for example,  $E_{pot}$  or rain size) which vary. Similarly, when  $E_{pot}$  after the rain event was low (<6 mm), the percentage increase was always small (<100%). In contrast, when  $E_{pot}$  after the rain event was high (>6.5 mm), the percentage increase could be large (>200%). Due to the apparent interactions of environmental factors in determining the response of  $Q$  to pulses of rain, we analysed all factors simultaneously.



**Fig. 5** Percentage increase in tree water use, ( $Q$ ,  $l\ day^{-1}$ ) from the day before rain to the day of peak tree water use, in response to different rainfall size classes. Different letters above columns represent significantly different treatments (Tukey's HSD test,  $P<0.05$ )

The fact that non-linear regressions showed no strong relationships, but partial regressions showed significant relationships, demonstrates the interactive nature of responses of tree water use to the many independent variables which are revealed using the partial regression methodology.

When using partial regressions, which held all other factors constant, rainfall amount significantly influenced the increase in tree water use (Fig. 5). Rainfall amount was the most influential factor in determining the size of the response to rainfall, accounting for 59% of the variation in the data (Table 1). The next most influential predictor was antecedent soil moisture, followed by tree size, together accounting for 44% of the variation in the data (Table 1). The negative partial slopes of these two predictors indicate that as antecedent soil moisture and tree size increase, the size of the response of tree water use to rainfall decreased.

## Discussion

### Determinants of the size of the response to rainfall

Previous research has demonstrated a relationship between the size of rain events and plant responses (Burgess 2006; Fravolini et al. 2005). For example, the increase and persistence of soil respiration pulses and the time constant of the decay in respiration after rain are positively correlated with the amount of precipitation (Misson et al. 2006; Xu et al. 2004). The method applied in the present study, for identifying the threshold size of a rainfall event required to produce a significant increase in tree water use ( $Q$ ,  $l\ day^{-1}$ ) is statistically simple but is an effective method that has been used for many years in ecotoxicology research (Crane and Newman 2000).

**Table 1** Results from multiple linear regression analysis

Predictor	Partial slope	Partial $r^2$ (%)
Size of rain event (mm)	<b>0.77</b>	59
Antecedent soil moisture (mm)	<b>-0.54</b>	29
Tree size (DBH, cm)	<b>-0.39</b>	15
$E_{pot}$ for 5 days after rain event (mm)	<b>-0.27</b>	7
Days since previous rain event	<b>-0.05</b>	1

Significant values ( $P<0.05$ ) in bold.

In the present study, the threshold that rain events needed to exceed in order to elicit an increase in  $Q$  was 20 mm; (Fig. 5). Consequently the majority of rain events, 77% of which were less than 20 mm (Fig. 4), lead to no significant increase in  $Q$ . We conclude that this value represents the effect of two features of this woodland: canopy and litter interception losses, and competition for water between trees and understorey species. Losses arising from the tree and understorey canopies and leaf litter intercepting rain and subsequent evaporation render rainfall amounts less than 20 mm being unavailable to the roots. Previous studies report 1–4 mm of rainfall being intercepted by the tree canopy and 1–2 mm by the litter in an open eucalypt woodland (Crockford and Richardson 2000). Including understorey interception losses, total interception losses likely ranged 4–8 mm in our study. This explains why rainfall events less than 8 mm (e.g., our 0–10 mm rainfall class) did not elicit a significant response in tree water use. Rainfall amounts ranging 10–20 mm also failed to elicit a significant response in tree water use. Two mechanisms may explain this result.

First, the possibility exists that the sap probes were insufficiently sensitive to detect small increases in  $Q$ . The Greenspan sensors used in the present study are known to have relatively poor sensitivity to low flows. Second, it is highly likely that competitive uptake of water by roots of understorey species will have been significant and therefore the availability of water to the trees that were examined was much reduced. And therefore a significant increase of  $Q$  at very low rainfall is unlikely.

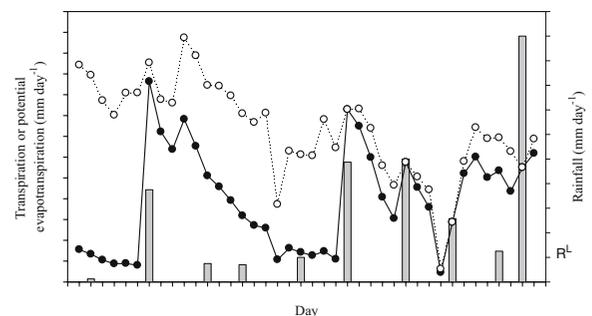
There were no clear relationships amongst tree size, soil moisture, days since rain event or  $E_{pot}$  after the rain event and percentage increase in  $Q$ . However, when antecedent moisture is ample (>42 mm) or  $E_{pot}$  after rain is low (<6.5 mm) the percentage increase was always small (typically less than 50%). In contrast, when antecedent moisture is low (<42 mm) or  $E_{pot}$  after rain is large (>6.5 mm) the percentage increase in  $Q$  could be large (>100%). Presumably this reflects the impact of soil moisture content and  $E_{pot}$  on the ability of roots to supply water to the canopy and the atmosphere to drive evaporation from the canopy. Large values of  $E_{pot}$  occur when radiation and temperature levels are high and this can drive large increases in  $Q$  following rain. Conversely, when soil moisture levels are high, the impact of additional rain on  $Q$  is likely small because soil moisture is not limiting at this time. This difficulty in making

generalisations regarding specific responses to moisture pulses was also described by Reynolds et al. (2004), who noted the strong effects of and interactions between precipitation, antecedent soil moisture and plant responses.

Most previous research on the impact of pulses of rain on plant responses has been conducted in arid and semi-arid vegetation such as grasses and shrubs (BassiriRad et al. 1999; Fravolini et al. 2005; Ivans et al. 2006; Potts et al. 2006a, b; Xu and Li 2006), rather than in temperate woodlands (but see Burgess 2006). The present study is the first to estimate the threshold of rain pulses that lead to an increase in tree water use. We found that the strongest influence on the response of  $Q$  was the size of the rain event, followed by, in decreasing order of impact, antecedent soil moisture, tree size,  $E_{pot}$  for 5 days after the rain event, and number of days since the rain event. We are not aware of any previous attempt to rank these influences although the amount of rain (Misson et al. 2006), antecedent soil moisture (Fravolini et al. 2005; Potts et al. 2006a), landscape position (Eberbach and Burrows 2006; Burgess 2006) and soil type (Burgess 2006; Sperry and Hacke 2002) have been identified as important influences on plant responses to pulses of rain.

#### Future modelling directions

We propose a modification of the original T-D conceptual model that can describe the rate of daily tree water use ( $y_t$ ) as it is affected by (a) rainfall



**Fig. 6** Illustration of modified T-D model using simulated data where the daily transpiration rate (filled symbols, solid line) is a function of rainfall (bars) above some lower threshold ( $R^L$ ) and potential evapotranspiration (open symbols, dotted line). In addition to  $E_{pot}$  series above, parameters used for above illustrated data were  $k=0.9$ ,  $\delta=0.8$ ,  $R^L=4$ ,  $\tau=0$ ,  $y_0=1.5$

events above a minimum ( $R^L$ ) and below a maximum threshold ( $R^U$ ); (b) the previous daily tree water use rate ( $y_{t-1}$ ); and (c) is constrained by the maximum daily potential evapotranspiration rate ( $E_{pot_t}$ ). Incorporating climatic conditions such as radiation and vapour pressure deficit, which are used to calculate potential evapotranspiration (Lu et al. 2003), is the major modification of the T-D model (Fig. 6). Potential evapotranspiration and  $y_t$  are often highly correlated (Santiago et al. 2000; Infante et al. 2003; Lu et al. 2003; Meiresonne et al. 2003), thus incorporating daily potential evapotranspiration may allow better prediction of  $y_t$ . As proposed, the modified  $y_t$  would not necessarily decrease over time in the absence of rainfall (although the ratio of actual water use to potential water use ( $k$ ) would), rather it would be a function of climatic conditions. As in the original T-D model, and as supported by our results, the response of  $y_t$  to rainfall ( $\delta$  would increase linearly with the amount of rainfall above some lower threshold,  $R^L$ , until an upper threshold,  $R^U$ , was reached. The response of  $y_t$  to rainfall would also be proportional to, but not in excess of the maximum potential rate ( $E_{pot_t}$ ). Although our results indicate that antecedent soil moisture is important in determining the response to rainfall, the modified model does not have a separate parameter for soil moisture. However, as antecedent tree water use is proportional to soil moisture, then our model indirectly incorporates this effect and retains the potential for a delay in the physiological response ( $\tau$ ), as in the original model.

## Conclusion

Variation in frequency and magnitude of rain events may cause lasting and perhaps irreversible changes to ecosystem structure and function (Schwinning et al. 2005). Thus, knowledge of tree responses to rain pulses will allow better prediction of how ecosystems may respond to changes in rain regimes resulting from climate change (Potts et al. 2006a).

In conclusion, this work has shown that a threshold of 20 mm rainfall is required to induce a response in tree water use. This suggests that when estimating the water balance of this site, the annual rainfall received might be significantly more than the effective rainfall, where effective is defined as rainfall that influences tree water use. This has important implications when

estimating recharge to aquifers, which is often estimated by the difference between vegetation water use and rainfall (where run-on and run-off are negligible; Zeppel 2006), since the majority of rainfall events at sites with similar climate and vegetation have a size that is less than this.

**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 thank 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. We are grateful to Daniel Taylor, Tony O'Grady, and Stephen Burgess for useful discussion and helpful comments from two anonymous reviewers.

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