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1 Plant and Soil

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

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1 **Abstract**

2

3 In water-limited systems, pulses of rainfall can trigger a cascade of plant physiological responses.
4 However, the timing and size of the physiological response can vary depending on plant and
5 environmental characteristics, such as rooting depth, plant size, rainfall amount, or antecedent soil
6 moisture. We investigated the influence of pulses of rainfall on the response of sap flow of two
7 dominant evergreen tree species, *Eucalyptus crebra* (a broadleaf) and *Callitris glaucophylla* (a
8 needle leaved tree), in a remnant open woodland in eastern Australia. Sap flow data were collected
9 using heat-pulse sensors installed in six trees of each species over a 2 year period which
10 encompassed the tail-end of a widespread drought. Our objectives were to estimate the magnitude
11 that a rainfall pulse had to exceed to increase tree water use (i.e., define the threshold response),
12 and to determine how tree and environmental factors influenced the increase in tree water use
13 following a rainfall pulse. We used data filtering techniques to isolate rainfall pulses, and analysed
14 the resulting data with multivariate statistical analysis. We found that rainfall pulses less than 20
15 mm did not significantly increase tree water use ($P > 0.05$). Using partial regression analysis to
16 hold all other variables constant, we determined that the size of the rain event ($P < 0.05$, $R^2 = 0.59$),
17 antecedent soil moisture ($P < 0.05$, $R^2 = 0.29$), and tree size (DBH, cm, $P < 0.05$, $R^2 = 0.15$), all
18 significantly affected the response to rainfall. Our results suggest that the conceptual Threshold-
19 Delay model describing physiological responses to rainfall pulses could be modified to include
20 these factors. We further conclude that modelling of stand water use over an annual cycle could be
21 improved by incorporating the T-D behaviour of tree transpiration.

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1 **Introduction**

2

3 Much of the eastern seaboard of Australia experienced a prolonged drought from
4 approximately 2002 to 2005, which has severely limited water availability for native vegetation,
5 agriculture, industry, and domestic use. Managing scarce fresh surface water resources is becoming
6 an increasingly important environmental, social and economic issue across many regions of the
7 world (Jackson et al. 2001). An understanding of the patterns and behaviour of water use of native
8 vegetation can contribute to the effective management of these water resources.

9 Pulses of rainfall are particularly pivotal in controlling plant physiological processes in low
10 rainfall systems (Ivans et al. 2006). Rainfall pulses can trigger a cascade of ecosystem responses
11 that affect plant nutrient-, water- and carbon cycling. These responses ultimately affect the balance
12 of ecosystem respiration and production in low rainfall systems (Huxman et al. 2004). Plant
13 nutrient, carbon and water assimilation are directly affected by plant and soil water status, however,
14 and may explain why plant responses to rainfall pulses can be temporally and spatially
15 heterogeneous, or deviate significantly from predicted or modelled responses (Meiresonne et al.
16 2003; Zeppel 2006). For example, in a recent study predictions from a temperature-dependent
17 respiration model did not agree well with measured responses immediately after rain events (Zhao
18 et al. 2006). This suggests that a deeper understanding of plant and soil water relations immediately
19 after rain events is required to make accurate predictions of ecosystem function in low rainfall
20 systems.

21 Various factors may interact to influence plant water relations following pulses of rain. For
22 example, plant functional type or species (BassiriRad et al. 1999; Cheng et al. 2006), landscape
23 position (Burgess 2006; Eberach and Burrows 2006), antecedent and ensuing environmental
24 conditions (e.g., season) (Ivans et al. 2006), evaporative demand, days since rain event (Sponseller
25 2007)), and soil properties all translate precipitation into plant available water (Fravolini et al.
26 2005; Potts et al. 2006a). Plant functional type or life form, e.g., trees or grasses, in particular can

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1 impart differences that may affect plant water relations following a rainfall pulse. These differences
2 include rooting depth (Jackson et al. 1996; Ogle and Reynolds 2004), and intrinsic differences in
3 the rates at which stomatal conductance, photosynthesis, and leaf area development increase
4 (Gebauer et al. 2002; Schwinning et al. 2002; Ignace et al. 2007).

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

20 While previous research has focused on shrubs, herbaceous plants, and bunchgrasses in arid
21 or semi-arid systems (BassiRad et al. 1999; Schwinning and Sala 2004; Ivans et al. 2006;
22 Sponseller 2007), trees in temperate, rainfall-limited systems can offer unique insight into
23 responses of plant water relations to rainfall pulses. First, trees not only have greater internal water
24 stores and potential water use, but also generally have deeper functional rooting profiles than non-
25 woody species (Jackson et al. 1996). One previous study showed that at least four different types of
26 plant water use responses to summer rainfall pulses existed in a low rainfall, temperate woodland

1 system (Burgess 2006). Second, tree-dominated, rainfall-limited systems currently represent
2 structural and climate conditions that will likely increase under several climate change scenarios
3 (e.g., unpredictable and sporadic rainfall of variable intensity) (Chesson et al. 2004; Eamus et al.
4 2006). Understanding the responses of tree water use to pulses of rain in these systems will likely
5 increase the predictive ability of climate change models to produce scenarios of future productivity
6 and water use in temperate forested systems. Finally, an understanding of responses of tree water
7 use to pulses of rain is relevant to a number of ecological problems mediated by deforestation,
8 including the salinisation of cleared agricultural land in temperate Australia (Burgess 2006).

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

17

1 **Materials and Methods**

2

3 Site description

4

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

14

15 Weather data

16

17 Rainfall data and aspirated wet and dry bulb air temperatures, and total solar radiation were
18 obtained from an open-field weather station (Envirodata Pty Ltd, Australia) located approximately
19 500 m from the study site. Air vapour pressure deficit (VPD) was calculated from wet and dry bulb
20 air temperatures. Potential evaporation (E_{pot}) was estimated as a function of the Penman-Monteith
21 equation (Lu et al. 2003).

22

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1 Soil moisture

2

3 Volumetric soil moisture content was measured in three plots with an array of frequency domain
4 reflectometry sensors which measure soil moisture by measuring the dielectric constant of soil
5 (Theta Probe, ML2-X, Delta-T devices, Cambridge). Theta probes were buried horizontally at 10,
6 40 and 50 cm in two plots, and at 10 and 40 cm in one plot. Total soil moisture storage was
7 calculated by multiplying the soil depth by the percent of moisture contained by the soil. Then the
8 water contained in each layer was summed (Fig. 1). Relative water content was estimated by
9 dividing actual daily soil moisture content by maximum soil moisture content measured over the
10 entire season.

11

12 Sap flow measurement

13

14 Sap velocity was measured using the heat pulse technique with commercial sap flow sensors
15 (Greenspan Technology Pty Ltd., Warwick, Australia). The methods of measuring sap flow and
16 scaling to whole tree water use are described fully in Zeppel et al. (2004). A brief description is
17 provided here. Two probe sets (4 sensors) were inserted into each tree at 1/3 and 2/3 of the
18 sapwood depth, separated circumferentially by 90°. A preliminary Monte Carlo simulation showed
19 that two probe sets per tree was adequate to capture circumferential variation in sap flow (Zeppel et
20 al. 2004). A minimum of seven and a maximum of 15 trees were instrumented for each species at
21 each sampling time.

22 The sap velocities were monitored at 15-minute intervals over a two-week period during
23 July-August 2002 (winter), January-February 2003 (summer) July-August 2003 (winter) and
24 February-March 2004 (summer). Tree water use was calculated for each sensor for twelve
25 consecutive days after allowing two days for development of the wound that results from drilling

1 into the wood (Olbrich 1991). The weighted averages technique of Hatton et al. (1995) was used to
2 convert sap velocities to whole tree water use (Q , L d⁻¹).

3 Sapwood depth was measured twice for each tree at the beginning of the study. We
4 extracted an increment core, and visually estimated sapwood depth from the clear colour change
5 observable at the boundary between sapwood and heartwood. Volume fractions of wood and water
6 in the sapwood were determined gravimetrically on 5 mm diameter cores taken from 10 trees of
7 each species on two occasions. In *E. crebra* the mean (\pm s.e.) wood fraction was 0.55 ± 0.03 and
8 0.50 ± 0.04 in winter and summer respectively. The water fraction was 0.23 ± 0.02 and 0.28 ± 0.01
9 in winter and summer respectively. In *C. glaucophylla* wood fraction was 0.34 ± 0.01 in winter and
10 0.34 ± 0.04 in summer. The water fraction was 0.52 ± 0.01 in winter and 0.48 ± 0.03 in summer.

11

12 Radial sapflow profiles and wound width

13

14 Radial profiles of sap velocity through the sapwood of each species were determined prior to the
15 study (Zeppel 2006) in order to calculate the regions of maximum flow across the sapwood. Sap
16 flow was measured at a minimum of 6 depths across the sapwood, replicated 3 or 4 times in
17 different aspects in each tree. Knowledge of the region of maximum sap flow across the sapwood
18 was used to calculate the depth to insert the sap flow sensors. The full method is described by
19 O'Grady et al. (2000) and Zeppel (2006).

20 The width of the wound around the holes used to insert the probes was measured twice in
21 seven trees of each species, using a binocular microscope to measure the wound (Olbrich 1991),
22 using the technique described by O'Grady et al. (2000). A wound width of 2.5 mm for *C.*
23 *glaucophylla* and 3.7 mm for *Eucalyptus crebra* was used to correct velocity estimates.

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1 Leaf xylem pressure potential

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3 Xylem pressure potential was measured on each of three leaves of three replicate trees of both
4 species. Measurements were made in summer 2002/3, winter 2003, and summer 2003/4, on at least
5 one, sometimes three, days, using a Scholander-type pressure bomb (Plant Water Status Console,
6 Soil Moisture Equipment Corporation, USA). Fully expanded, sunlit, mature leaves were sampled
7 in the outer canopy between 2 – 8 m height (using a hydraulic platform for access) between pre-
8 dawn and 17:00 h.

9

10 Statistical analyses

11

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

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

1 Previous research on plant responses to rain pulses has examined antecedent soil moisture
2 (Potts et al. 2006a) and we examined other variables that are known to influence sap flow, such tree
3 size (DBH, cm) (Zeppel 2006), days since previous rain event, size of rain event, and potential
4 evapotranspiration, E_{pot} (mm). A linear regression showed that the mean E_{pot} 5 days after the rain
5 event explained more variability (52%) in the dependent variable than 3 (18%) and 7 days (22%)
6 after the rain event.

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

1 **Results**

2 3 Meteorology and soil moisture

4
5 Average annual rainfall for the Liverpool Plains is 680 mm, with approximately 50% of this
6 occurring between October and February and 50% occurring from March to September (Fig. 1).
7 However, during the study period rainfall (300 mm) was significantly lower than this long-term
8 average due to a prolonged drought which occurred from approximately 2002 to 2004 at the study
9 site. Maximum soil water content during the study period was 40%. Rainfall influenced the relative
10 water content (RWC) of soil at 10 cm depth more frequently than soil at 40 cm depth (Fig. 1). Soil
11 RWC at 10 cm depth responded to rain events if the cumulative rainfall total over a 4 – 7 day
12 period exceeded 10 – 15 mm. Thus, a number of small (> 10mm) rain events on consecutive days
13 impacted soil RWC, as well as large (> 20 mm) rain events. Single rain events of less than 10 mm
14 had no effect on soil RWC at 10 cm or 40 cm depth. Soil at 40 cm responded to rain events larger
15 than 20 mm, yet the response time was slower, and soil at 40 cm depth retained moisture for longer
16 than soil at 10 cm, possibly reflecting a higher clay content at 40 cm, and a more sandy soil at 10
17 cm (Fig. 1).

18 Peak net radiation was about $4 \text{ MJ m}^{-2} \text{ h}^{-1}$ in summer and half of this in winter (Fig. 2).
19 Vapour pressure deficit was similarly larger in summer (2.1 kPa) than winter (1.1 kPa) and peaked
20 later in the afternoon in summer than in winter (Fig. 2).

21 22 Xylem pressure potential

23
24 Pre-dawn xylem pressure potential for the *E. creba* was low (approximately -2.8 MPa) in summer
25 2002/3, reflecting the impact of the prolonged drought on plant water relations (Fig. 3). During the
26 daylight period, xylem pressure potential (ψ_w) declined to a minimum of -4.0 MPa (Fig. 3). Pre-

1 dawn water potential data are not available for *C. glaucophylla* because of equipment problems.

2 However, in summer 2002/3, ψ_w of *C. glaucophylla* reached -5.0 MPa in late afternoon.

3 Pre-dawn xylem pressure potential of the *E. creba* was higher (closer to zero) in winter
4 2003 than summer 2002/3. Similarly, ψ_w throughout the day were higher for both species in winter
5 2003 than summer 2002/3 (Fig. 3). In the summer of 2003/4, after significant rains in the 3 months
6 prior to measurement of ψ_w , pre-dawn ψ_w for both species was higher than that observed in winter
7 2003 (Fig. 3). However, the daily range of ψ_w in summer 2003/4 was similar to that observed in
8 winter 2003, for both species. Generally, ψ_w of the *C. glaucophylla* was higher than that of the *E.*
9 *creba*, although this was not true for summer 2002/3. The difference in ψ_w between the two species
10 was typically 0.5 to 1.0 MPa throughout the day, but the difference was generally smaller at the
11 start or end of the day.

12

13 Rainfall response threshold

14

15 Most of the rainfall events were small, with the majority (56%) being less than 5 mm (Fig. 4). As
16 rainfall amounts increased, rainfall frequency decreased (Fig. 4). The percentage increase in tree
17 water use was significantly smaller ($p < 0.05$) for the 0-5 mm class than for rainfall in the 20-50 and
18 51-150 mm rainfall classes (Fig. 5), indicating that at this site 20 mm of rain is required before tree
19 water use increases significantly.

20

21 Determinants of the tree water use response to rainfall

22

23 Of the factors that we examined— tree size, antecedent soil moisture, potential evapotranspiration,
24 the size of the rain event (mm) and the number of days since the previous rain event—no single
25 factor alone explained the response of tree water use to rain pulses. There was no significant
26 relationship between antecedent soil moisture and the percent increase in tree water use after rain.

1 Similarly, there was no significant relationship between tree size, five day E_{pot} after rain event or
2 size of the rain event and increasing tree water use after rain. When antecedent soil moisture was
3 high (> 45 mm) the percentage increase in Q was always small, typically 0 – 50 %. In contrast,
4 when antecedent soil moisture was low (< 40 mm) the percentage increase could be large (> 200
5 %) but not always, indicating the influence of other factors (for example, E_{pot} or rain size) which
6 vary. Similarly, when E_{pot} after the rain event was low (< 6 mm), the percentage increase was
7 always small (< 100 %). In contrast, when E_{pot} after the rain event was high (> 6.5 mm), the
8 percentage increase could be large (> 200 %). Due to the apparent interactions of environmental
9 factors in determining the response of Q to pulses of rain, we analysed all factors simultaneously.

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

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

20

21 **Discussion**

22

23 Determinants of the size of the response to rainfall

24

25 Previous research has demonstrated a relationship between the size of rain events and plant
26 responses (Burgess 2006; Fravolini et al. 2005). For example, the increase and persistence of soil

1 respiration pulses and the time constant of the decay in respiration after rain are positively
2 correlated with the amount of precipitation (Mission et al. 2006; Xu et al. 2004). The method
3 applied in the present study, for identifying the threshold size of a rainfall event required to produce
4 a significant increase in tree water use (Q , $L d^{-1}$) is statistically simple but is an effective method
5 that has been used for many years in ecotoxicology research (Crane and Newman 2000).

6
7 In the present study, the threshold that rain events needed to exceed in order to elicit an increase in
8 Q was 20 mm; (Fig. 5). Consequently the majority of rain events, 77% of which were less than 20
9 mm (Fig. 4), lead to no significant increase in Q . We conclude that this value represents the effect
10 of two features of this woodland: canopy and litter interception losses, and competition for water
11 between trees and understory species. Losses arising from the tree and understorey canopies and
12 leaf litter intercepting rain and subsequent evaporation render rainfall amounts less than 20 mm
13 being unavailable to the roots. Previous studies report 1 – 4 mm of rainfall being intercepted by the
14 tree canopy and 1 – 2 mm by the litter in an open eucalypt woodland (Crockford and Richardson
15 2000). Including understory interception losses, total interception losses likely ranged 4 – 8 mm in
16 our study. This explains why rainfall events less than 8 mm (e.g., our 0 – 10 mm rainfall class) did
17 not elicit a significant response in tree water use. Rainfall amounts ranging 10 – 20 mm also failed
18 to elicit a significant response in tree water use. Two mechanisms may explain this result.

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

25 There were no clear relationships amongst tree size, soil moisture, days since rain event or
26 E_{pot} after the rain event and percentage increase in Q . However, when antecedent moisture is ample

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1 (>42 mm) or E_{pot} after rain is low (< 6.5 mm) the percentage increase was always small (typically
2 less than 50 %). In contrast, when antecedent moisture is low (< 42 mm) or E_{pot} after rain is large
3 (> 6.5 mm) the percentage increase in Q could be large (>100 %). Presumably this reflects the
4 impact of soil moisture content and E_{pot} on the ability of roots to supply water to the canopy and the
5 atmosphere to drive evaporation from the canopy. Large values of E_{pot} occur when radiation and
6 temperature levels are high and this can drive large increases in Q following rain. Conversely, when
7 soil moisture levels are high, the impact of additional rain on Q is likely small because soil
8 moisture is not limiting at this time. This difficulty in making generalisations regarding specific
9 responses to moisture pulses was also described by Reynolds et al. (2004), who noted the strong
10 effects of and interactions between precipitation, antecedent soil moisture and plant responses.

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

22

23 Future modelling directions

24 We propose a modification of the original T-D conceptual model that can describe the rate of daily
25 tree water use (y_t) as it is affected by (a) rainfall events above a minimum (R^L) and maximum
26 threshold (R^U); (b) the previous daily tree water use rate (y_{t-1}); and (c) is constrained by the

Comment [JaC1]: A or b?

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1 maximum daily potential evapotranspiration rate (E_{pot_t}). Incorporating climatic conditions such as
2 radiation and vapour pressure deficit, which are used to calculate potential evapotranspiration (Lu
3 et al. 2003), is the major modification of the T-D model. Potential evapotranspiration and y_t are
4 often highly correlated (Santiago et al. 2000; Infante et al. 2003; Lu et al. 2003; Meiresonne et al.
5 2003), thus incorporating daily potential evapotranspiration may allow better prediction of y_t . As
6 proposed, the modified y_t would not necessarily decrease over time in the absence of rainfall
7 (although the ratio of actual water use to potential water use (k) would), rather it would be a
8 function of climatic conditions. As in the original T-D model, and as supported by our results, the
9 response of y_t to rainfall (δ) would increase linearly with the amount of rainfall above some lower
10 threshold, R^L , until an upper threshold, R^U , was reached. The response of y_t to rainfall would also
11 be proportional to, but not in excess of the maximum potential rate (E_{pot_t}). Although our results
12 indicate that antecedent soil moisture is important in determining the response to rainfall, the
13 modified model does not have a separate parameter for soil moisture. However, as antecedent tree
14 water use is proportional to soil moisture, then our model indirectly incorporates this effect and
15 retains the potential for a delay in the physiological response (τ), as in the original model.

16

17

18 Conclusion

19

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

24 In conclusion, this work has shown that a threshold of 20 mm rainfall is required to induce a
25 response in tree water use. This suggests that when estimating the water balance of this site, the

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1 annual rainfall received might be significantly more than the effective rainfall, where effective is
2 defined as rainfall that influences tree water use. This has important implications when estimating
3 recharge to aquifers, which is often estimated by the difference between vegetation water use and
4 rainfall (where run-on and run-off are negligible; Zeppel 2006), since the majority of rainfall events
5 at sites with similar climate and vegetation have a size that is less than this.

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2

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10

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1 **Figures and tables**
2

3 **Fig. 1** Average daily soil moisture (shown as relative water content at 10 and 40 cm depths) and
4 total daily rainfall (mm) from June 2003 to January 2005. Sap flux was measured continually in 4
5 trees from December 2002 till March 2004 and intensively in from 7 to 15 trees in campaigns
6 during January-February 2003, July-August 2003, and February-March 2004.

7 **Fig. 2** Diurnal patterns of solar radiation ($\text{MJ m}^{-2} \text{h}^{-1}$) and 9 am VPD (kPa). Data shown represent
8 the mean and s.e. of 4 cloud-free days during each season. Summer data represent the mean and s.e.
9 of 25 – 28 February 2003 and winter data represent the mean and s.e. of 16 to 18 June 2002. Data
10 collected by the Department of Agriculture, Tamworth.

11 **Fig. 3** The diurnal time course of xylem pressure potential (MPa) for *E. crebra* (closed circles) and
12 *C. glaucophylla* (open circles) during summer 2002/3, winter 2003 and summer 2003/4. Mean (s.e.)
13 of all leaves measured over two or three cloud free days are shown. Dashed and dotted lines
14 represent 95 % confidence intervals for *E. crebra* and *C. glaucophylla*, respectively.

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

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

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

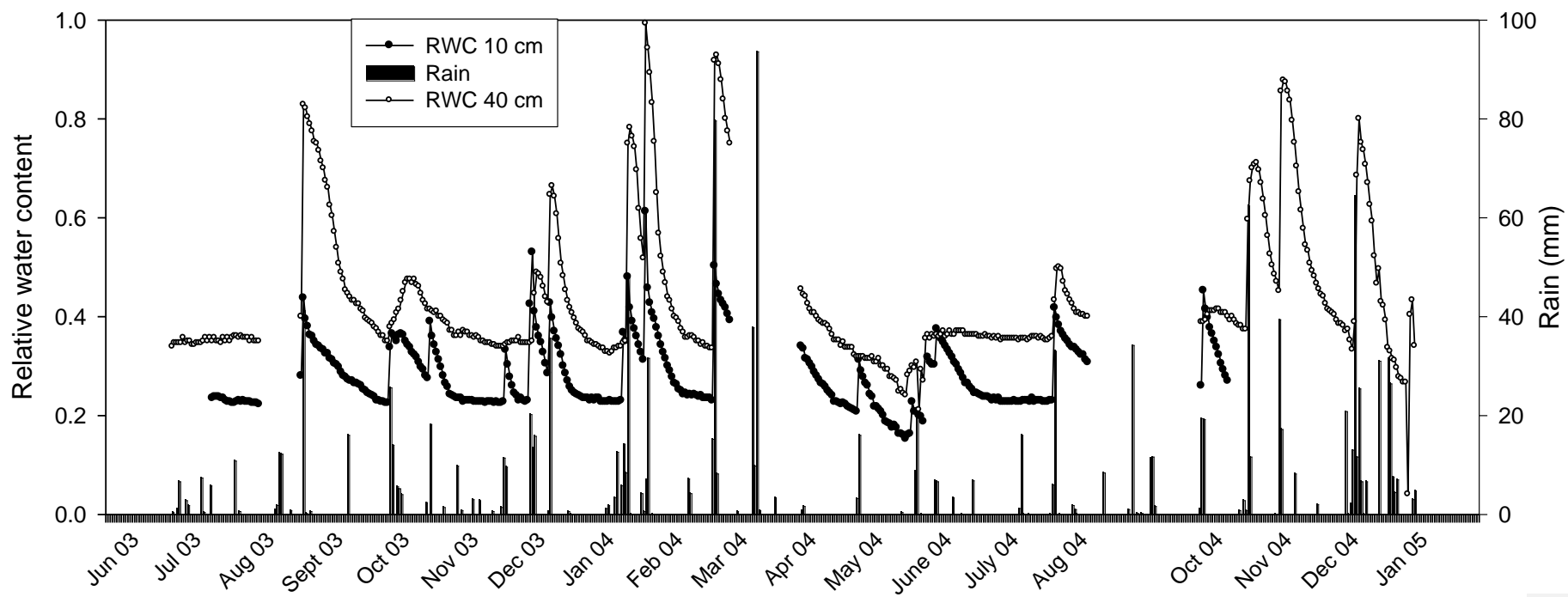


Figure 1

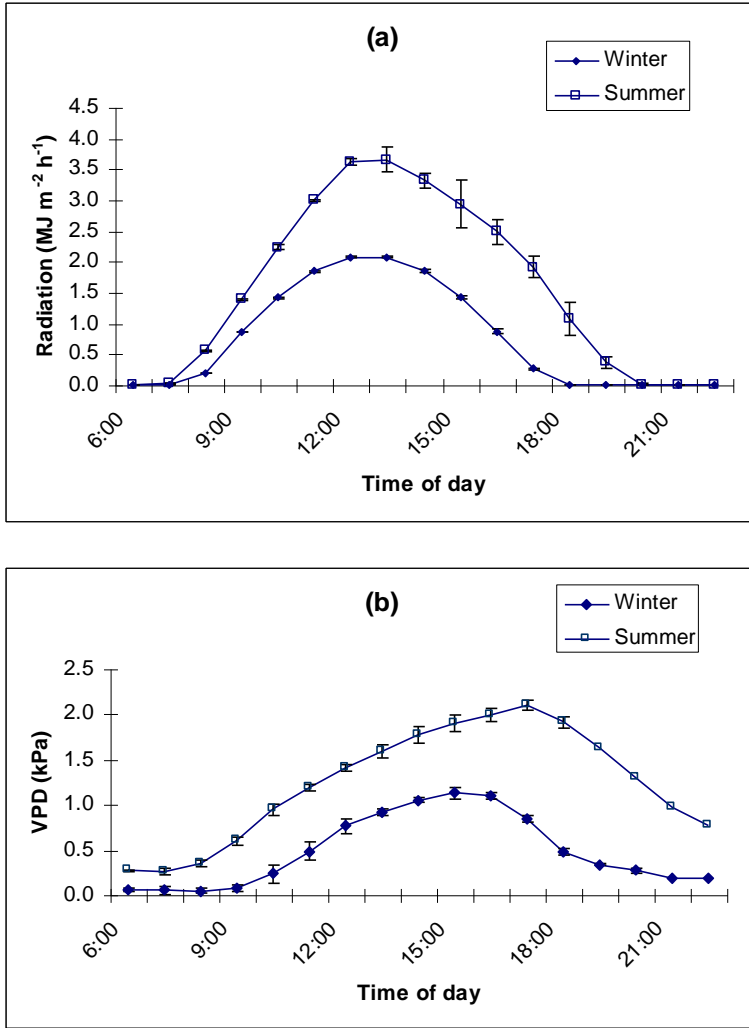


Figure 2

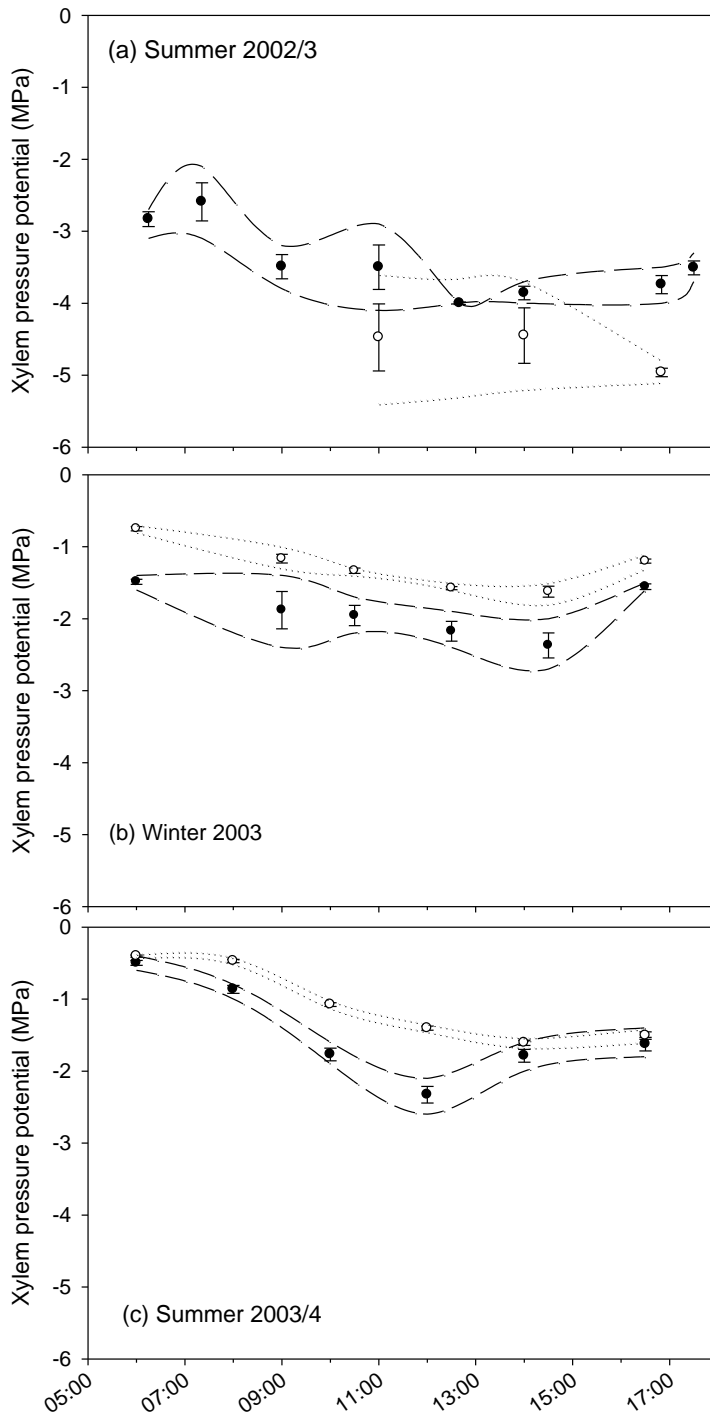


Figure 3

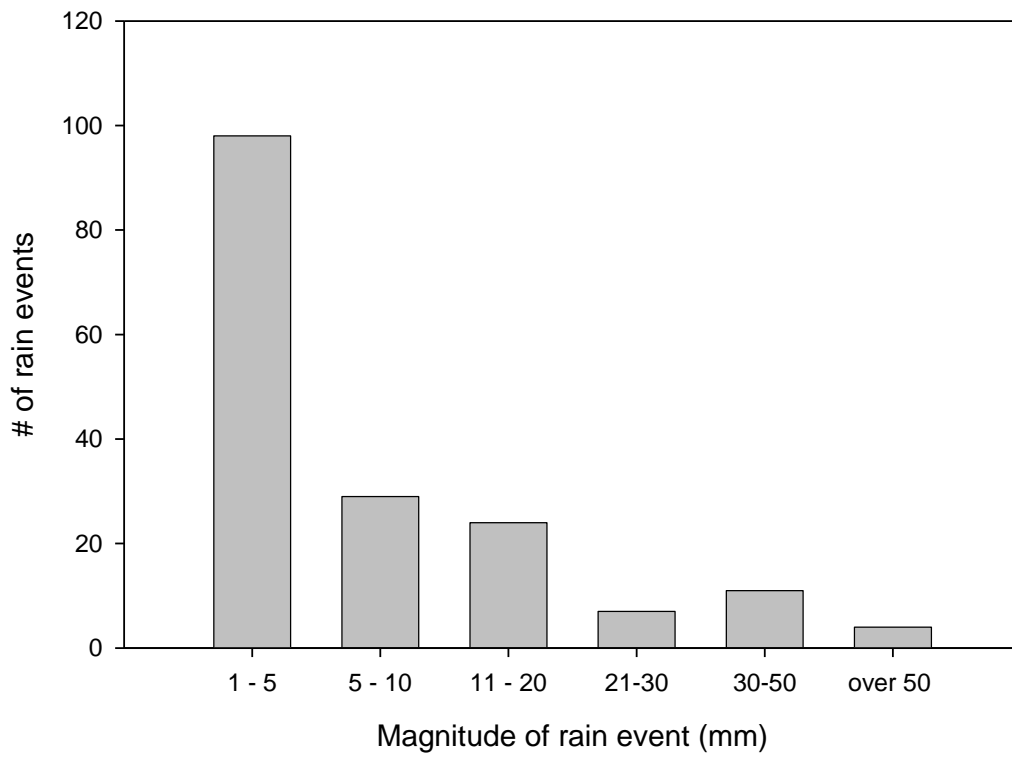


Figure 4

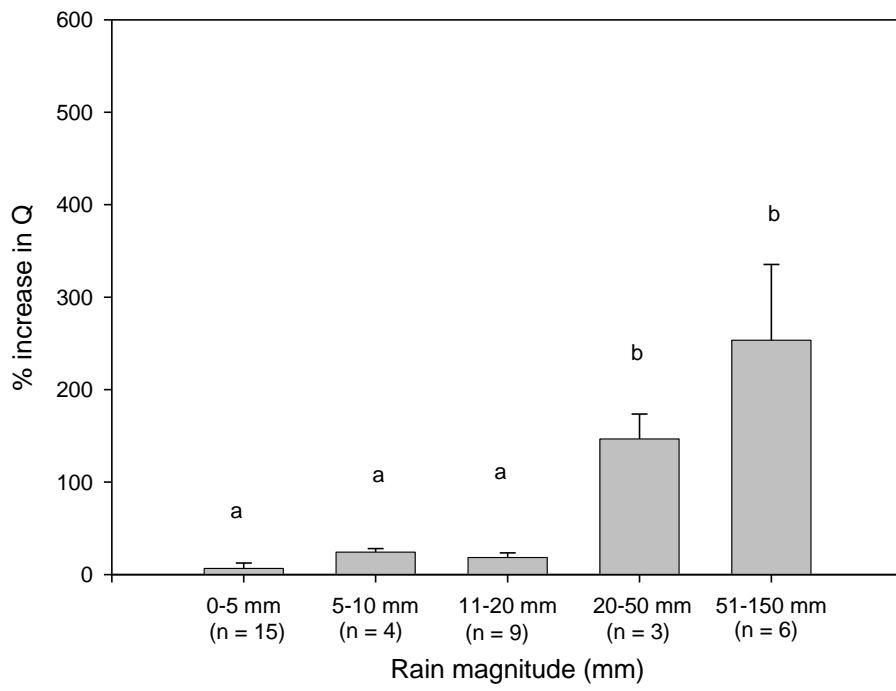


Figure 5

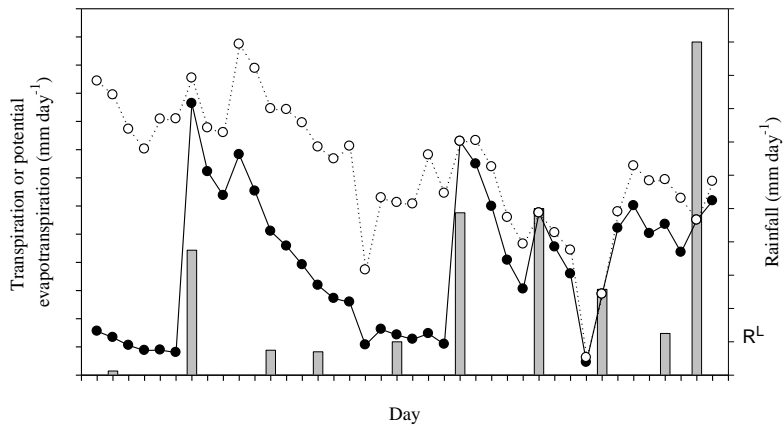


Figure 6

Table 1 Results from multiple linear regression analysis. Significant values ($P < 0.05$) in bold.

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