Measuring transpiration responses to summer precipitation in a Mediterranean climate: a simple screening tool for identifying plant water-use strategies

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Rainfall utilization by vegetation is a complex function of the timing and magnitude of rain events, soil properties, evaporative demand and aboveground and belowground plant functioning. Understanding these interactions is highly relevant to a number of ecological problems, including salinization of cleared agricultural land in southern Australia. Ameliorative revegetation efforts require information on plant water-use strategies; we used sap-flow recordings to screen a range of species and identify four types of response to a large summer rainfall event: (1) no response, (2) delayed response, (3) small, rapid response and (4) large, rapid response. Proteaceous shrub species (e.g. *Isopogon gardneri*) rapidly increased transpiration up to five-fold. Other shrubs such as *Allocausarina campestris* (Casuarinaceae) only increased transpiration two-fold due to partial summer dormancy. Deep-rooted *Eucalyptus* species (Myrtaceae, e.g. *E. wandoo*) were sufficiently reliant on antecedent soil water that they did not respond to summer precipitation. One hemi-parasite species *Nuytsia floribunda* (Loranthaceae) required over 2 weeks to fully respond to rainfall, possibly due to water storage and changes to the hydraulic pathway. We discuss these results in terms of the 'threshold-delay' model and the role of this screening method in assisting revegetation strategies.

Introduction

Vegetation covers 70% of the Earth's surface (Costanza et al. 1997) and both influences (e.g. Huang et al. 1995, Raddatz 1998) and is strongly influenced by (e.g. Schulze et al. 1996, Weltzin and McPherson 1997, Hanson and Weltzin 2000, Chesson et al. 2004) patterns of precipitation. The way plants use rainfall has a profound impact on both plant productivity (Fischer and Turner 1978, Horton and Hart 1998) and the hydrological cycle (Clothier and Green 1997, Feddes et al. 2001). The factors which affect rainfall utilization by vegetation are numerous and extend into all compartments of the soil–plant atmosphere continuum. Ignoring the minor contribution of the metabolic water budget (Kozlowski and Pallardy 1996), the primary driver of any water 'used' by plants is evaporative demand. Solar and atmospheric conditions that drive evaporation are often strongly seasonal and can be out of phase with patterns of precipitation to the point where extremes of either waterlogging or drought can result. Precipitation patterns themselves can vary from regular, small events to torrential episodic pulses. Such variability affects rates of interception, evaporation, runoff and the penetration of wetting fronts into the soil (Noy-Meir 1973, Wallace 1996). Of course, penetration of water into the

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Abbreviations – V_h, heat pulse velocity.

soil is also strongly affected by soil properties, and the overall depth of soil contributes to the volume of stored soil water that is available to plant roots.

The depth to which plant roots explore soil water resources varies greatly among species and life forms, with a tendency toward deeper rooted species in water-limited environments (Schenk and Jackson 2002): extensive root systems are better at scavenging scarce resources. Dimorphic root systems (shallow and deep roots) are prevalent in strongly seasonal environments (e.g. in Mediterranean ecosystems) and can facilitate redistribution of soil water, as its relative availability in deep and shallow layers fluctuates seasonally (e.g. Burgess et al. 1998, Burgess et al. 2000). Aboveground plant form and function also affects rainfall utilization in numerous ways. Adaptations in leaf geometry and display angle can either minimize or maximize interception of solar radiation; scleromorphic, scale-like or needle-like leaves hold advantage for water conservation (Wright and Westoby 2002). Drought deciduousness is an extreme leaf trait that minimizes water loss (Yoder and Nowak 1999, Stratton et al. 2000). Stomatal regulation of water loss is a key physiological function where plants can actively adjust hydraulic conductance to water vapour at the leaf surface to preserve leaf water status. Conductance of other parts of the hydraulic pathway can also vary through active and passive mechanisms, including changes to ion concentrations, xylem cavitation and repair (Holbrook et al. 2002) and fine root dynamics (Cermak et al. 1993, Magnani et al. 2000).

In any given ecosystem, plants may exhibit a range of functional characteristics that dictate patterns of water use: indeed, co-existence of multiple species in floristically diverse communities, such as the global biodiversity hot spot of southwestern Australia (Myers et al. 2000, Hopper and Gioia 2004), presupposes a diversity of water-use strategies to permit niche differentiation and reduce competition. One of the classic studies on this theme was Walter's (1971) effort to explain the co-existence of grasses and trees in savannahs: his 'two-layer' hypothesis suggested that these functional types co-exist by a vertical stratification in rooting habit. If the roots of grasses are confined to upper soil layers, while the roots of trees exploit deep layers, this permits vertical partitioning of soil water resources. Although follow-up studies have provided some support for this model, they also indicate that it is too simplistic (Dodd et al. 1998, Ludwig et al. 2004). Resource partitioning and overlap can vary considerably, both within and among species, due to a range of other factors such as tree size and phenology (Meinzer et al. 1999). Additionally, the timing and magnitude of resource

availability strongly influences how it is used and partitioned. Beatley (1974) discussed the importance of 'critical' rain events that exceed certain thresholds in determining plant responses, e.g. the responses of shallow- and deep-rooted plants will depend on how deep rain penetrates into the soil. The timing of rain events may also affect how plants respond: Snyder et al. (2004) reported that growth responses differ depending on whether rain falls during summer or winter.

In recognition of the complex interactions between plants and their environment in determining patterns of resource use, Ogle and Reynolds (2004) recently developed a composite model, which draws on earlier paradigms of resource partitioning (e.g. Walter 1971), thresholds (Beatley 1974) and pulse responses (e.g. the Westoby-Bridges model described in Noy-Meir 1973) to describe the response of different plants to rainfall in terms of a 'threshold-delay' model. This model permits the effect of individual pulses of rain to be analysed according to a physiological response of plants. It incorporates how quickly a plant responds (e.g. delays), the magnitude of response, duration of response (rate of decay) and thresholds below or above which no response, or no further response, is evident (Fig. 1). This model lends itself to simple parameterization of the above components which then permits comparisons to be made between different plant functional types.

Comparing the water-use physiology of different plant functional types has received increasing research attention in response to emerging environmental issues such as climate change (Ehleringer et al. 1991), land-use change and degradation of agricultural land (Pate and Dawson 1999). In southern Australia, conversion of native vegetation, which contained a rich assemblage of plant functional types, to European style agricultural systems has led to serious hydrological imbalance and secondary salinization of soils and waterways (Eberbach 2003, Taylor and Hoxley 2003, Turner 2004). Native vegetation included perennial species, which could
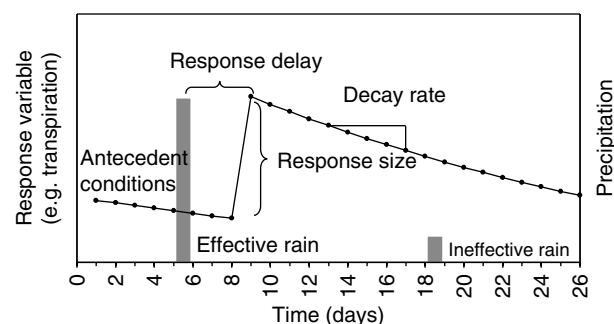

Fig. 1. A conceptual diagram of the threshold-delay model (adapted from the original presentation of Ogle and Reynolds 2004).

deplete winter-derived soil moisture reserves at rapid rates associated with peak summer evapotranspiration; this perennial vegetation could also draw on summer precipitation (Turner 2004). In contrast, most agricultural crops used in this environment are short-lived annuals, which use water when evaporative demand is low. Native vegetation also included deep-rooted species, which could access deep water reserves created by large winter pulses that recharge deep into the soil profile. Agricultural crops, by contrast, are mostly shallow-rooted and best suited to utilizing the small regular pulses that fall during their growing season.

Understanding how different plant functional types use water and how assemblages of plants together produce hydrologically balanced ecosystems is key to designing agricultural systems suitable for areas at risk of salinization through excessive groundwater recharge. A large number of techniques are available to study plant water use, at a range of different scales. Aboveground techniques such as eddy correlation (e.g. Silberstein et al. 2001) or Bowen ratio (Malek and Bingham 1993) are useful for studying assemblages of vegetation as a whole but usually do not provide sufficient detail about the different functional types that comprise a plant community. Belowground techniques, such as measuring soil moisture depletion, can suffer similar ambiguities, except where species mixes are relatively simple (e.g. Lefroy et al. 2001). Measurements of soil moisture must be combined with the knowledge of rooting patterns, and both the installation of moisture meters and excavation of root systems can be exceptionally challenging in substrates such as the lateritic soils common to agricultural regions of Western Australia. Plant-based measurements can provide detailed information on the functioning of individual species or functional types. However, such measurements are invariably labour- or equipment-intensive. In species-rich communities such as those in southwestern Australia (Beard 1990, Myers et al. 2000, Hopper and Gioia 2004), there are many hundreds of species from among which species of considerable promise for improved agricultural systems may be identified. Improved screening tools for characterizing the water-use strategies of native plants could therefore be very valuable in this regard.

In recent decades, some of the more popular methods to measure how plants respond to rain have included measurement of leaf water potentials, leaf-level gas exchange or tracing water uptake using stable isotopes (Ehleringer et al. 1991, Leffler et al. 2004, Snyder et al. 2004). These types of measurements usually require repeated sampling, before and after rain events, to gather the information needed to understand plant responses to rain, and this can be quite labour-intensive. In the present study, we focused on the widely applied technique of thermometric xylem sap-flux measurement as a simple means to gather data on the response of different species to rain. We hypothesized that insights into the various traits that dictate water use (e.g. rooting depth, leaf behaviour; see above) could be gained by simply measuring the timing and magnitude of change in xylem sap flow following a dry season rain event. For example, Zeng et al. (in press) recently inferred the rooting depth and water sources of desert tree species by measuring patterns of sap flow in response to irrigation. The lack of response to irrigation identified these trees as deep-rooted phreatophytes that lack superficial roots capable of responding to episodic rain events. In this study, we monitored 11 sympatric sclerophytes in semiarid southwestern Australia for their response to a natural summer rain event to learn more about variation in water-use strategies among the diverse mixture of endemic species and functional types.

Methods

Site description

The research was conducted at the Corrigin Water Reserve approximately 2 km west of Corrigin, Western Australia (32°19′-S, 117°52′E). This reserve consists of 1096 ha of remnant vegetation containing a range of plant communities typical to Western Australia's wheat-belt region. Vegetation and soils follow a catenary sequence down the landscape, where canopy height increases with soil depth towards valleys (Beard 1990). As is typical for this ancient landscape, the topography is relatively flat, with a difference in elevation at our site of 20–30 m from ridge to valley over a horizontal relief of approximately 2 km. Soils in 'elevated' areas are very shallow (approximately 10 cm) sand over very hard laterite. Exploratory drilling indicated increasingly compressed and weathered laterite to at least 5 m. These lateritic soils support mixed heath vegetation comprising chiefly Proteaceae, Myrtaceae and Casuarinaceae. The species we investigated at this site are summarized in Table 1.

Midslope the soils are 'duplex', comprising approximately 1-m sand over clay to at least 5 m. These duplex soils support 'mallee' vegetation. Mallees are multi-stemmed eucalypts; the mallee vegetation type also includes a mixture of other trees and erect shrubs of generally taller stature than those found in the mixed heath described above. For specific species studied, see Table 1.

Table 1. List of the habit, soil type and landscape position of 11 sclerophytic species studied at Corrigin, Western Australia

Family/species	Habit
Heath vegetation on lateritic soils	
Casuarinaceae: *Allocasuarina campestris* (Diels) L.A.S. Johnson	Erect shrub
Proteaceae: *Dryandra cirsioides* A.S. George	Shrub
Proteaceae: *Isopogon gardneri* D. Foreman	Shrub
Proteaceae: *Hakea subsulcata* Meisn.	Erect shrub
Proteaceae: *Banksia sphaerocarpa* R.Br. var. *sphaerocarpa*	Shrub
Mallee vegetation on duplex soils	
Cupressaceae: *Actinostrobus arenarius* C. A. Gardner	Tree
Myrtaceae: *Eucalyptus albida* Maiden and Blakely	Mallee
Proteaceae: *Dryandra sessilis* Knight Domin var. *sessilis*	Erect shrub
Loranthaceae: *Nuytsia floribunda* (Labill.) Fenzi	Hemiparasitic tree
Woodland vegetation on clay-loam	
Myrtaceae: *Eucalyptus wandoo* Blakely	Tree
Myrtaceae: *Eucalypus salmonophloia* F.Muell.	Tree

Lower lying areas have heavy soils and are sparsely wooded. Our study site comprised chiefly a mixture of wandoo (*Eucalyptus wandoo* Blakely) and salmon gum (*Eucalyptus salmonophloia* F. Muell.) trees ranging in height from 10 to 30 m, with a scattered dwarf scrub understorey (e.g. *Olearia axillaris* DC. Benth., *Grevillea patentiloba* F.Muell.). At this site, we focused on the dominant two species, *E. wandoo* and *E. salmonophloia* (Table 1). Salmon gum/wandoo woodland is widespread throughout the semiarid region of southwestern Australia, but little information is available on rooting habit (Hobbs and O'Connor 1999). Lamont (1985) recorded that the *E. wandoo* saplings have root systems dominated by a taproot, whereas mature trees are dominated by an extensive system of lateral roots in the 20–40-cm zone which extend approximately 10 m. These findings agree with our excavations of both wandoo and salmon gum saplings and observations of wind-thrown mature specimens.

Superficially, soils at our woodland site were a light brown sandy loam, which transitioned rapidly (approximately 50 cm) to a heavy clay loam subsoil. We did not detect a water table after drilling to 11 m. The long-term (since 1910) average annual rainfall for Corrigin is 376 mm, with an annual pan evaporation of 1817 mm (Bureau of Meteorology, Australia). A Mediterranean climate prevails with most rain falling in the cooler winter months.

Sap-flow measurements

We used the heat ratio method (Burgess et al. 2001a, Burgess et al. 2001b) to measure sap flow in stems of 2–3 individuals from 11 different shrub and tree species.

All sap-flow sensors were routed via AM 16/32 multiplexers to CR10X dataloggers (Campbell Scientific Inc., Logan, UT). Burgess and Dawson (2004) provide a more detailed description of the physical layout of the system. Zero-offset values for sensor calibration were estimated from night-time minimum values, rather than by the usual method outlined by Burgess et al. (2001b) of severing the plant to guarantee zero-flow conditions. For purposes of this investigation, estimates from night-time minimum values were deemed sufficiently accurate. Heat-pulse velocities (V_h) were used as a simple proxy for 'transpiration', because they are an index of the rate of water flux through woody tissues. Our chief interests were to characterize the relative changes in transpiration rate for individual species in response to season and rain events. For these purposes, V_h is a simple but robust index of transpiration, and therefore the latter term is used throughout this paper in discussing the results.

Meteorological measurements

A tipping bucket rain gauge (CS701), quantum sensor (QSO-SUN, Apogee Instruments, Logan, UT) and temperature/relative humidity sensor (CS500) were also attached to a CR10X datalogger (devices other than quantum sensor are Campbell Scientific Inc.) to monitor weather conditions.

Species

A full list of the 11 species included in this investigation, including their growth habit and soil type is summarized in Table 1. All were dominant species for each of the three basic soil types and landscape positions typical to this region. Overall, these species represent a broad cross-section typical of the Mediterranean-type vegetation common throughout the wheatbelt region of southwestern Australia (Beard 1990).

Results

The water-use responses of 11 species of trees and shrubs to a 34-mm summer rain event ranged from essentially nil to a greater than five-fold increase in transpiration, with a tendency for greater responses in plants growing higher in the landscape (Fig. 2). Although responses might be considered as varying along a continuum, we categorized responses into four distinct types and present detailed data for four species to illustrate these. *E. wandoo* showed almost no response to summer rain (Figs 3A and 4B). Total daily sap flow was decreased by the rain event itself (i.e. wet
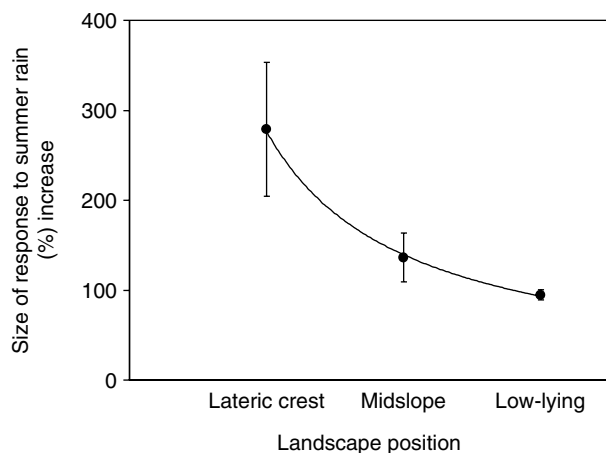
Fig. 2. Average increase in transpiration in response to a 34-mm summer rain event for 11 species on three landscape positions/soil types (elevations between positions differed only by a few meters).

leaves prevented transpiration; note also small flow reversals (Fig. 3A) believed due to hydraulic redistribution process (SSO Burgess and TM Bleby unpublished data). Relative to the decreased transpiration caused by rain (note again the dip in transpiration in Fig. 4B that coincides with the 34-mm rain event on day 363, Fig. 4A), transpiration increased dramatically following rain in the ensuing fine weather. However, relative to the overall course of sap flow, the increase was small (Fig. 4B). Prior to the summer rain, rates of sap flow did not decrease as summer drought conditions progressed but instead increased in proportion to the total amount of solar radiation (Fig. 4B).

Isopogon gardneri showed the largest response to summer rainfall of any species: transpiration increased approximately five-fold within hours of rainfall (Figs 3B and 4C). Prior to rain, rates of sap flow had decreased steadily since the last rains of spring. Note that small rain events (4 mm on day 330, 2 mm on day 350, Fig. 4A) had no effect on rates of sap flow (Fig. 4C). The response to 34 mm of rain lasted approximately 1 month, after which sap-flow rates steadily decayed to prerainfall values (Fig. 4C).

The erect shrub *Allocasuarina campestris* showed a similar speed of response to *I. gardneri*, but the size of the response was much smaller: only an approximately two-fold increase in transpiration (Figs 3C and 4D). Overall, rates of sap flow were much slower than those for the other species measured. The small rain events on days 330 and 350 appeared to increase transpiration slightly, in contrast to the absence of any response in *I. gardneri*.

Finally, *Nuytsia floribunda*, a hemiparasitic tree, showed a delayed response to summer rain, with a peak increase of approximately two-fold occurring
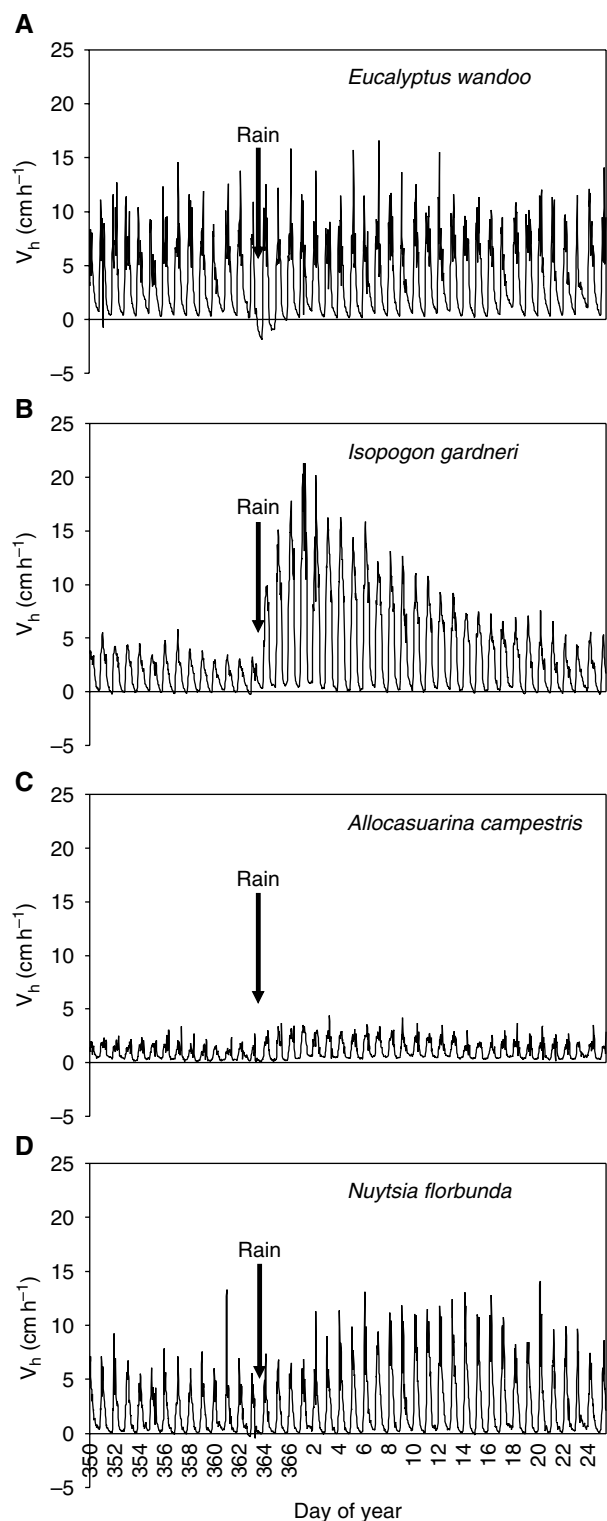

Fig. 3. (A–D) Diurnal patterns of transpiration before and after a summer-rain event (day 363) in *Eucalyptus wandoo*, *Isopogon gardneri*, *Allocasuarina campestris* and *Nuytsia floribunda* (a root hemiparasite) using heat-pulse velocity, V_h, as a proxy.
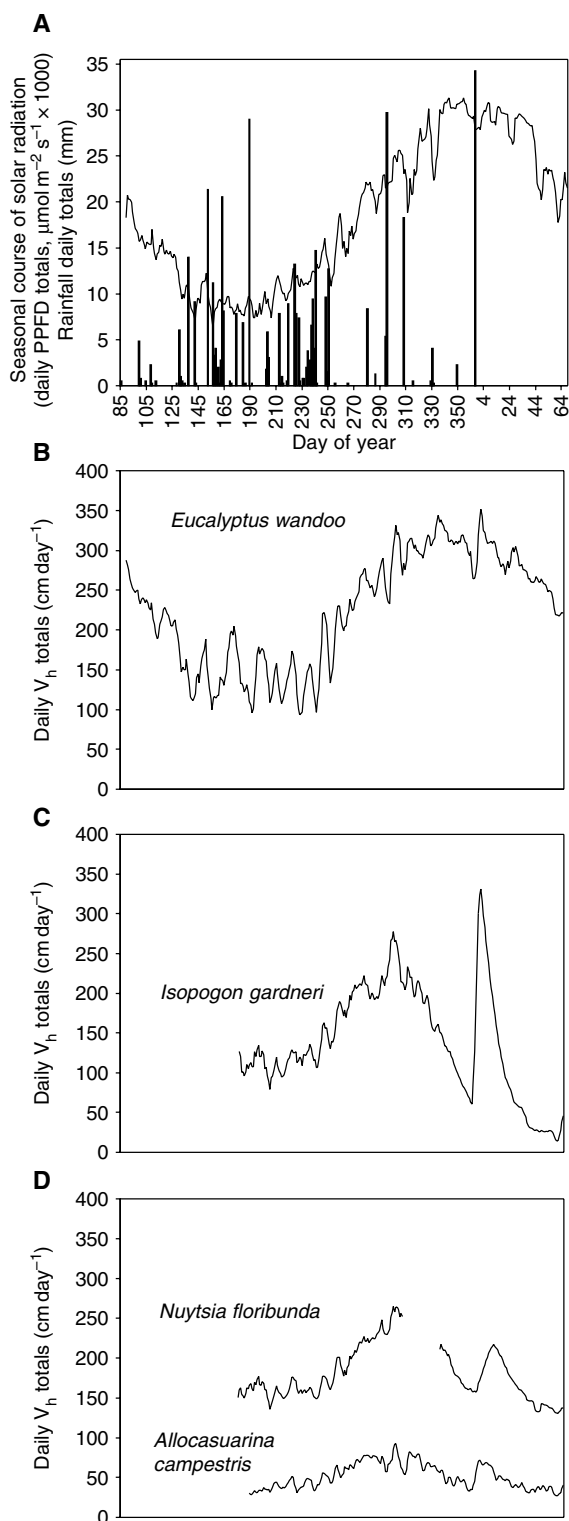
Fig. 4. (A) Seasonal course of solar radiation (daily totals of photosynthetic flux density, PPFD) and rainfall (daily totals, mm). (B–D) Seasonal course of transpiration in *Eucalyptus wandoo*, *Isopogon gardneri*, *Allocasuarina campestris* and *Nuytsia floribunda* (a root hemiparasite) using heat-pulse velocity, V_h, as a proxy.

around 2 weeks after rain (Figs 3D and 4D). Small rain events did not elicit a response (either immediate or delayed) (Fig. 4D).

Discussion

Summer rainfall produced markedly different responses in the transpiration rate of the 11 species we monitored, with a tendency toward larger responses higher in the landscape. Variability among responses was also greatest higher in the landscape (see error bars in Fig. 2), but the greater number of dominant species we were able to measure due to greater species diversity on shallower soils is obviously a factor here.

Low in the landscape, woodland eucalypt species showed almost no change in the seasonal trajectory of transpiration. Transpiration by *E. wandoo* tracked with the seasonal course of solar radiation, suggesting that energy, rather than water availability was the main determinant of transpiration. The deeper soils lower in the landscape apparently contain sufficient antecedent soil water reserves built up from winter precipitation (or possibly groundwater resources beyond our 11-m drilling range) to permit transpiration to increase in proportion to evaporative demand. This is in contrast to other species on shallow soils which showed dramatic decreases in transpiration with the onset of summer drought. From a related study which measured sap flow in roots (SSO Burgess and TM Bleby unpublished data), we know lateral roots of *E. wandoo* did absorb summer rain and redistribute it to other parts of the soil profile. Given that water available to the root system increased without increasing transpiration, this argues for a possible rate limitation to transpiration in *E. wandoo* at the level of stomatal or hydraulic conductance. Eamus et al. (2000) suggested that hydraulic conductance in certain eucalypts is determined by dry season conditions: xylem that is built to avoid dysfunction during drought yields conductance limitations during periods of higher water availability (via a safety–efficiency trade-off, see Tyree et al. 1994). Finally, it is worth pointing out that although the acquisition and redistribution of summer rain by *E. wandoo* roots (SSO Burgess and TM Bleby unpublished data) did not contribute immediately to transpiration, such a process may contribute to deep soil water stores and increase overall annual transpiration.

Higher in the landscape, where soils are shallower and more 'hostile' to root penetration, antecedent water reserves (or rooting depths) were clearly inadequate to sustain transpiration in response to summer demand. Species at this site showed marked decreases in transpiration rates with the progression of summer drought. Responses to summer rainfall were quite variable,

averaging approximately three-fold increases in transpiration: this variability suggests considerable variation in either rooting depth or degree of summer dormancy. Partial excavations of root systems at this site demonstrated that although roots were generally very superficial (<30 cm), some individual roots exploited cracks or macropores in the compressed laterite, and this may have contributed to the variability in responses (P. Mitchell unpublished data)

Species growing midslope on duplex soils showed a mix of responses that indicated transition between the other two sites. This was evident with *Eucalyptus albida*, which responded similarly (therefore data not shown) to the woodland eucalypt species, but with slight reductions in transpiration with progression of summer drought, and, as might be expected, a slight response to summer rain. One species at this site was unique among all other species: *N. floribunda* required approximately 2 weeks to fully respond to summer rainfall. *N. floribunda* is a root hemiparasitic tree, and one might expect its response to mirror that of its hosts. *N. floribunda* is capable of attaching to a wide range of host species (Calladine et al. 2000). None of the putative hosts (surrounding plants) we measured showed a delay in their response to rainfall. This suggests that the delayed response of *N. floribunda* had physiological origins. One possibility is the necessity to form new haustorial connections with well-hydrated neighbours (Calladine and Pate 2000). Another possibility is very slow repair of cavitated vessels. A further, and related, possibility that is currently under investigation is the refilling of stem water storage reservoirs. This species has very soft, pulpy wood of low density and high water content (P. Mitchell unpublished data). The exact mechanism of the delay warrants further investigation.

Using sap-flow responses to parameterize the threshold-delay model

Sap-flow recordings provided clear information on how rates of transpiration in different plant species changed in response to rain events. Response patterns closely resembled the idealized response predicted by Ogle and Reynolds (2004) (Fig. 1), and thus the sap-flow data could easily be used to measure all the parameters relevant to the threshold-delay model. For example, 4-mm and 2-mm summer-rain events were generally below the minimum threshold to generate a response, except for a very small response in *A. campestris*. Root excavations indicated that this species had a mass of very superficial roots, which may explain why it showed a response to such small rain events. In terms of maximum thresholds, it could be argued that the lack of

response of *E. wandoo* fits into this category: antecedent soil water conditions were sufficient to meet the requirements of species such that the 34-mm summer-rain event caused effectively no increase in transpiration. For most species, response delays were minor, but they could be clearly identified in the hemiparasite *N. floribunda*. Decay rates can also be easily calculated from the sap-flow traces. Typically, the water reserve created by the 34-mm rain event was used within approximately 30 days or at an average rate of approximately 1 mm per day. Instantaneous rates of water use obviously vary greatly due to species differences and the exponential nature of the decay in response. In the latter case, this likely reflects soil moisture-release properties and the changing driving force between leaf water potential and soil water potential as soil dries out.

Concluding remarks

In summary, using the threshold-delay model in conjunction with continuous sap-flow records yields an easy method to characterize the different water-use strategies of sympatric species. Further work using 'artificial' rain events of different sizes (i.e. by irrigation) should allow more specific details on thresholds and other response parameters to be gathered. From our simple screening exercise using a single summer rain event, we readily recognized the superior ability of *I. gardneri* to use summer rainfall compared with *A. campestris*, which shows a greater degree of summer leaf dormancy (P. Mitchell, unpublished data). Also, the ability of the *Eucalyptus* species to tap into deep antecedent soil water derived from winter precipitation was easily recognized. This type of information is valuable for species selection in plantings designed to maximize water use and prevent the excessive groundwater recharge, which threatens to degrade soils and waterways through secondary salinity.

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