

## Defining phreatophyte response to reduced water availability: preliminary investigations on the use of xylem cavitation vulnerability in *Banksia* woodland species

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**Abstract.** The consideration of phreatophyte response to changes in water availability is important in identifying ecological water requirements in water-resource planning. Although much is known about water-source partitioning and intra- and interspecific variability in groundwater use by *Banksia* woodland species, little is known about the response of these species to groundwater draw-down. This paper describes a preliminary study into the use of xylem cavitation vulnerability as a measure of species response to reduced water availability. A response function and critical range in percentage loss of conductance is identified for four *Banksia* woodland overstorey species. Similarity in the vulnerability curves of *B. attenuata* R.Br. and *B. menziesii* R.Br. at low tensions supports the notion that they occupy a similar ecohydrological niche, as defined by their broad distributions relative to depth to groundwater. *B. ilicifolia* R.Br., however, as an obligate phreatophyte, has a range restricted to environments of higher water availability and shallower depth to groundwater and this is reflected in greater vulnerability to cavitation (relative to other *Banksia*) at lower tensions. The wetland tree *Melaleuca preissiana* Schauer generally expressed a greater vulnerability at any given xylem water potential ( $\Psi_x$ ). This paper identifies the range in  $\Psi_x$  within which there is an elevated risk of tree mortality, and represents a first step towards quantifying the critical thresholds in the response of *Banksia* woodland species to reduced water availability.

### Introduction

Underlying the northern Swan Coastal Plain (SCP) in the south-west of Western Australia (WA) is the Gngangara groundwater mound, a shallow, unconfined aquifer where a trend of lowered water tables has been observed since the mid-1970s (Davidson 1995). This trend is attributed to reduced rainfall recharge in addition to the abstraction of groundwater for Perth's scheme water supply, industrial and agricultural use, and plantation forestry (Groom 2003). As a result, negative impacts have been noticed in a diverse array of groundwater-dependent ecosystems including phreatophytic *Banksia* woodland (Groom *et al.* 2001).

There has been considerable research on identifying the water requirements and, in particular, the degree of groundwater dependency of SCP *Banksia* woodlands in WA. The majority of this work has used the proximity of a shallow, unconfined aquifer to plant rhizospheres as an inferential measure of potential groundwater dependency. Although a number of early researchers have recognised the *Banksia* woodlands of the SCP as phreatophytic (Farrington *et al.* 1989; Dawson and Pate 1996), these studies have not identified the variability in groundwater use and the

relative importance of groundwater in meeting vegetation water requirements. Recent work has concentrated on the identification of indicator species' ecohydrological ranges (niches) and the characterisation of their distribution in terms of depth to water table and the proportional importance of groundwater as a plant water source. Zencich *et al.* (2002) found the use of groundwater by *Banksia* species varied interspecifically, temporally and with topography and/or depth to groundwater. This variability in groundwater use and relative importance were assessed through the adoption of a simplified model of the zones of plant-available moisture, categorising potential water sources as either groundwater or the unsaturated zone, within uniform deep sands. Understanding this variability is significant to water-resource management as it can be used to spatially differentiate vegetation according to inferred susceptibility (from relative proportion of groundwater in total plant water uptake) to changes in groundwater availability.

Although the determination of the relative importance of groundwater to total plant water use contributes to our understanding of phreatophyte susceptibility, it tells

us little about phreatophyte response to changing water availability (beyond seasonal fluctuation). The development of species response curves to reduced water availability would significantly enhance our understanding of water requirements and perhaps lead to the identification of response thresholds (Eamus *et al.* 2006). Such thresholds could be used to identify the limits of reduction in water-source availability, a useful parameter for characterising water requirements for resource and conservation management. However, there have been no *in situ* drought experiments to measure *Banksia* woodland species response to separation from the water table. Such experimentation, while testing groundwater dependency and the physiological (plant water status) thresholds to long-term changes in groundwater availability, are expensive and difficult to maintain over the long term. A possible surrogate for manipulative, *in situ* whole-tree experimentation is the assessment of species hydraulic vulnerability curves over a range of water availability. The loss of hydraulic conductivity in the xylem has been recognised as playing an important role in drought response (Tyree and Sperry 1989). Xylem cavitation (Zimmermann 1983) under negative xylem pressure and subsequent embolism results in a conduit being unavailable for water transport, thus reducing hydraulic conductivity. Pockman and Sperry (2000) suggested that a high cavitation resistance results in a higher tolerance to water deficit, and that vulnerability to embolism formation has a significant influence on patterns of species survival and distribution within areas and during periods of water limitation.

Lam *et al.* (2004) suggested the use of species vulnerability curves as an alternative method to long-term field experimentation, for characterising the response of *Banksia* species to changes in water availability from all sources. Measurement of the loss of xylem conductance under increasingly stressful conditions could facilitate the quantification of water availability conditions at which plant vigour is likely to be significantly reduced or mortality occurs. Numerous authors have used plant water potential at 50% loss of conductivity (PLC<sub>50</sub>) as a comparative measure of vulnerability (Sperry *et al.* 1988; Cochard *et al.* 1994; Machado and Tyree 1994). It may be argued that variability in phreatophyte dependency on groundwater will be reflected in different xylem vulnerability response functions and therefore critical plant water potential thresholds. Therefore, *Banksia* species regarded as facultative phreatophytes (Zencich *et al.* 2002), such as *B. attenuata* and *B. menziesii*, may demonstrate lower PLC<sub>50</sub> values than obligate species such as *B. ilicifolia*, which is restricted to shallow depths to groundwater and is highly dependent on summer groundwater (Groom 2004).

This paper outlines a preliminary study at Gngangara into the determination and application of xylem vulnerability

functions as a measure of *Banksia* woodland species susceptibility to change in water availability. Specifically, we aim to determine whether vulnerability to xylem cavitation and critical plant water potential thresholds varies between obligate and facultative phreatophytes.

## Materials and methods

### *Study-site description and study design*

The Gngangara study site is situated on the Gngangara groundwater mound on the north-eastern fringe of the metropolitan area of the city of Perth, WA. The Swan Coastal Plain (SCP) on which the study area lies, experiences a Mediterranean-type climate with warm to hot, dry summers and mild, wet winters (Gentili 1972). On the basis of the length of the summer dry season, the climate type of the SCP can be further classified as warm Mediterranean (Bagnouls and Gaussen 1957), with 5–6 dry months between November and April. Gngangara receives a mean annual rainfall of 868 mm, a pan evaporation rate of ~2000 mm annually and mean maximum temperature during summer of 31°C (data sourced from Perth Bureau of Meteorology 2005). Rainfall normally exceeds evaporation in 3 months of the year (June–August).

Soils and vegetation at the site are typical of the Bassendean Dunes (Speck 1952; McArthur and Bettenay 1960; Havel 1968), with a deep sand profile underlying a low woodland dominated by species of *Banksia*. Part of the site was covered with remnant wetland vegetation, indicating an old wetland that had become colonised by terrestrial species through long-term reduction in water availability (Heddl 1980). The overstorey included *Banksia attenuata* R.Br., *B. menziesii* R.Br. and *B. ilicifolia* R.Br., with scattered *Melaleuca preissiana* Schauer. The latter two species are indicative of lower positions in the subdued landscape and shallow (<6 m) depths to groundwater (Heddl 1980). Depth to the water table under most of the vegetation was at 8 m at the time of sampling, while the *M. preissiana* present was believed to be restricted to soil profiles of remnant wetlands with higher water-holding properties owing to the presence of perched iron-rich hardpans within the soil profile (McArthur and Bettenay 1960; Glassford and Semeniuk 1989).

The site was selected because of the typical soil type and presence of four overstorey species representing a range in groundwater dependency. The most common *Banksia* species on the SCP, *B. attenuata* and *B. menziesii*, were included to represent facultative phreatophytes that occupy a similar ecohydrological niche (Zencich *et al.* 2002), inhabiting landscape positions with shallow (4 m) to deep (>20 m) water tables. *B. ilicifolia* was also included, representing an obligate phreatophyte restricted to shallow to moderate (<8 m) depths to groundwater. A fourth species, *Melaleuca preissiana*, was included in the study to reflect a typical wetland tree species, with an ecohydrological niche restricted to wetland fringes and depths to groundwater of <2 m.

Data from a previous unpublished study at Cooljarloo are used for comparison with vulnerability curves and suggested critical leaf water potentials. This study assessed the response of *B. attenuata* and *B. menziesii* to rapid, sustained declines in groundwater availability caused by proximity (200–300 m) to production bores at a mine site. A control site removed from the influence of the borefield (1 km) was included to allow comparisons of tree response. The Cooljarloo study area, also located on the SCP ~170 km north of Perth, has similar soils and vegetation to the Gngangara site. Owing to its northerly location relative to Gngangara, Cooljarloo receives a lower mean annual rainfall of 612 mm, higher pan evaporation rates of 2300 mm annually and mean maximum temperatures during summer of 33°C (data sourced from Perth Bureau of Meteorology 2005). Rainfall normally exceeds evaporation in only one month of the year (August). Pre-draw-down

depths to water table at both the affected and control sites at Cooljarloo were the same as at Gngangara, i.e. ~8 m.

#### Plant water status

Pre-dawn and midday leaf water potentials of the study species were also monitored from September 2003 to March 2004 at the Gngangara site to identify plant water status over the preceding drying phase (prior to vulnerability measurements). The leaf water potential was determined ( $n = 3$  leaves for each tree, 3 trees per species) with a Scholander-type pressure chamber (Model 3005, Soil Moisture Equipment, Santa Barbara, CA). Of the species assessed, *B. attenuata* represented the facultative phreatophyte species, although the obligate species *B. ilicifolia* and the wetland species *M. preissiana* were also included.

The same methods were employed at the Cooljarloo study sites from October 2000 to March 2001 and measurement continued until mortality occurred (March 2001). Only the two facultative phreatophytic species *B. attenuata* and *B. menziesii* were assessed.

#### Species vulnerability curves

Intact branches ~0.3–0.4 m in length were collected from four individuals of each species ( $n = 2$  branches for each individual tree) prior to sunrise in March 2004. Branches were double bagged, humidified and immediately transported to the laboratory. All sampled plants were considered to be close to full hydration at the time of collection, mean pre-dawn leaf water potential ( $\Psi_{pd}$ ) at this time was  $-0.20 \pm 0.02$  MPa ( $n = 32$ ).

Vulnerability to xylem embolism was determined as the relationship between percentage loss of hydraulic conductivity (PLC) and xylem water potential ( $\Psi_x$ ) (Sperry *et al.* 1988). Branches were removed from bags and allowed to dehydrate under laboratory conditions ( $20 \pm 3^\circ\text{C}$ ;  $50 \pm 10\%$  RH) to induce a given  $\Psi_x$ . The time frame for this process was 0–5 days. Twelve hours prior to the determination of  $\Psi_x$  and PLC, each branch was sealed in a plastic bag to equilibrate water potential ( $\Psi$ ) across all organs (leaves and stems). The xylem water potential of the branch was then determined from measurements of leaf water potential ( $n = 3$  leaves for each branch) with a Scholander-type pressure chamber (Model 3005). Maximum vessel lengths were determined by passing gaseous nitrogen at a pressure of 5 kPa through a length of stem, and cutting sections back from the distal end until gas flow was detected (by dipping the end in distilled water and watching for small bubbles). A stem segment (10% longer than the longest measured vessel and ~0.01 m in diameter) was then excised under distilled water for subsequent measurement of PLC. This was determined with a steady-state flow meter (SSFm) filled with a perfusion solution of 0.01 M KCl and degassed double-distilled water in accordance with hydrogel control of hydraulic conductance (Zwieniecki *et al.* 2001):

$$\text{PLC} = 100(k_{\text{max}} - k_h)/k_{\text{max}},$$

where  $k_h$  is the volume flux density at  $\Psi_x$  and  $k_{\text{max}}$  is the maximum volume flux density after flushing segments with the perfusion solution for 15 min at 100 kPa. Briefly, the SSFM was similar to that used by Feild *et al.* (2001), incorporating the pressure drop across a section of Peek<sup>TM</sup> resistance tubing (length = 0.407 m, internal diameter =  $1.96 \times 10^{-7}$  m<sup>2</sup>) with a known conductance ordered in series with the excised stem segment. This system allowed the use of small head pressures (<50 kPa) to determine volume flux through the stem segment.

Vulnerability curves were generated for each species as plots of PLC v.  $\Psi_x$ . Data were then fitted with exponential–sigmoidal functions:

$$\text{PLC} = 100/[1 + \exp\{a(\Psi_x - b)\}],$$

where  $a$  = the gradient of a linear transformation and  $b = \Psi_x$  where PLC = 50 (Pammenter and Vander Willigen 1998).

## Results and discussion

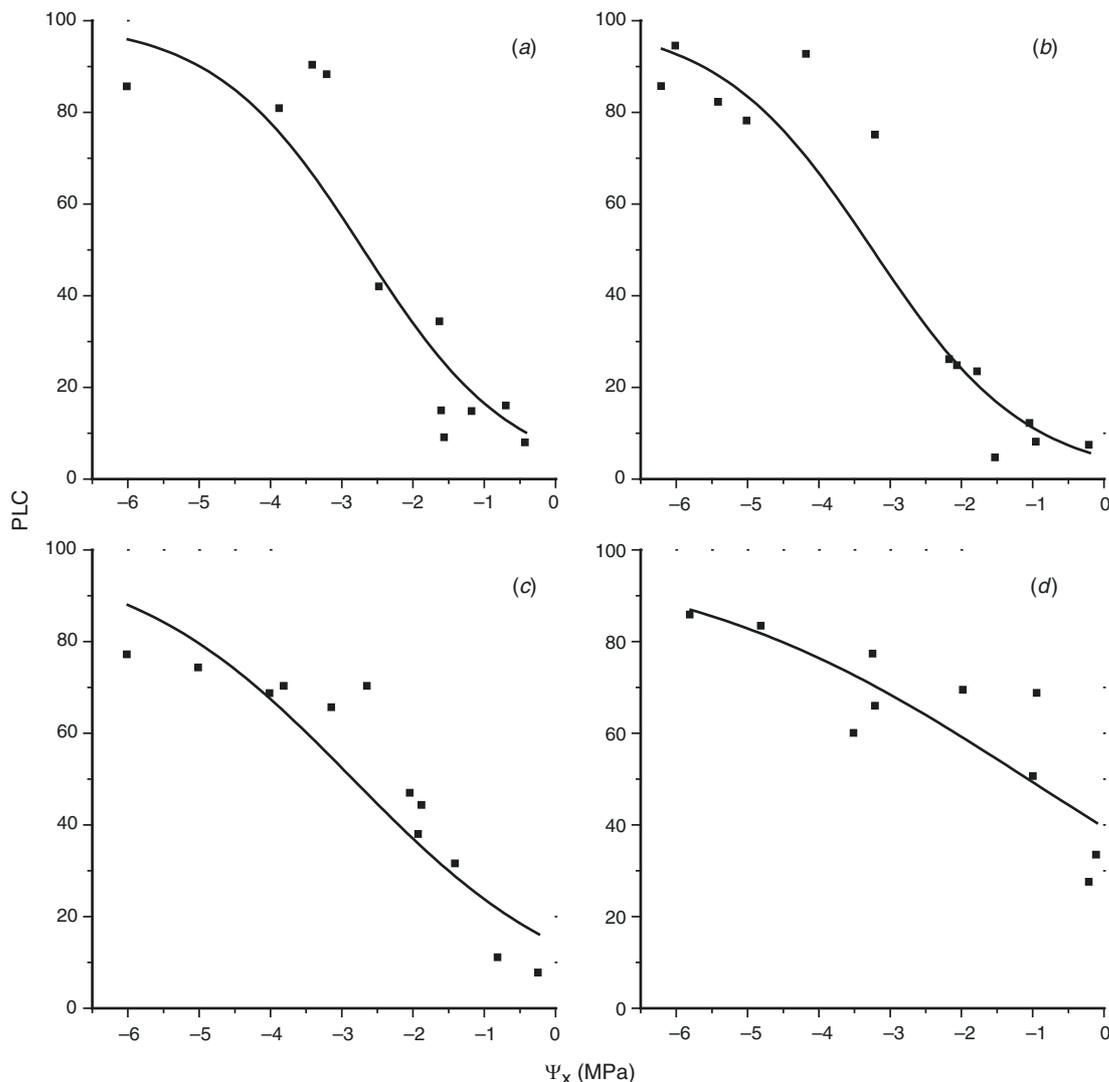
### Species vulnerability curves

Data collected from the Gngangara study were used to construct vulnerability curves for *B. attenuata*, *B. menziesii*, *B. ilicifolia* and *M. preissiana*. The results (Fig. 1) confirm previous assumptions about interspecific differences in physiological drought tolerance, with *B. attenuata* and *B. menziesii* maintaining better xylem function for a given tension than *B. ilicifolia*, and *M. preissiana* showing the poorest xylem function for the same pressure. Specifically, coefficient  $a$  (Table 1), related to the slope of a vulnerability curve, tended to be higher in *B. attenuata* and *B. menziesii* than in *B. ilicifolia* and *M. preissiana*. The gentle slope exhibited by these latter two obligate phreatophytes indicates that cavitation events occur over a much wider range of water potentials than in the former two facultative phreatophytes. Hence, despite the similarity in coefficient  $b$  ( $\Psi_x$  at 50% PLC, a widely used measure of embolism vulnerability; Table 1) between *B. ilicifolia* and the two facultative phreatophytic *Banksia* species of this study, the susceptibility to cavitation at water potentials characteristic of a normal dry season ( $> -1.5$  MPa) was greater in *B. ilicifolia*. By this rationale,  $\Psi_x$  at 20% PLC (PLC<sub>20</sub>) would appear to be a more appropriate means of separating the cavitation susceptibility of the obligate phreatophyte *B. ilicifolia* from the facultative phreatophytes. Similarity in the vulnerability curves of *B. attenuata* and *B. menziesii* at low tensions supports the notion that they occupy a similar ecohydrological niche, as defined by their broad distributions relative to depth to groundwater. *B. ilicifolia*, however, as an obligate phreatophyte, has a range restricted to environments of higher water availability and shallower depth to groundwater and this is reflected in lower tension at PLC<sub>20</sub> (Table 1). The wetland tree *M. preissiana* generally expressed a greater PLC at any given  $\Psi_x$ , which is consistent with a constraint in ecological range to very moist habitats.

Both *B. menziesii* and *B. attenuata* occur in all topographic locations except wetland fringes (Havel 1968; Heddle 1980). However, vulnerability (PLC<sub>20</sub> and PLC<sub>50</sub>) appears to be lowest in *B. menziesii*, supporting evidence on water relations (Groom *et al.* 2000) that the species is more drought-tolerant than *B. attenuata*.

### Plant water status relative to PLC

Assessment of field leaf water potential at Gngangara over the seasonal drying phase (spring to autumn) preceding the sampling for vulnerability measurement, provides an insight into the water status of the plants and the likelihood of xylem cavitation during the previous seasons. Evidence of significant water stress will have an impact on interpretation of the vulnerability curves.



**Fig. 1.** Vulnerability curves for (a) *Banksia attenuata* ( $r^2 = 0.85$ ), (b) *Banksia menziesii* ( $r^2 = 0.91$ ), (c) *Banksia ilicifolia* ( $r^2 = 0.81$ ) and (d) *Melaleuca preissiana* ( $r^2 = 0.72$ ). Fitted curves are exponential–sigmoidal functions:  $PLC = 100/[1 + \exp\{a(\Psi_x - b)\}]$ , where  $a$  is the gradient of a linear transformation and  $b$  is  $\Psi_x$  where  $PLC = 50$  (Pammenter and Vander Willigen 1998).

**Table 1.** Values for coefficients  $a$  (gradient) and  $b$  ( $PLC_{50}$ ) of the vulnerability curves and  $PLC_{20}$  ( $\Psi_x$  where  $PLC = 20\%$ ) for stem segments from each of the study species  
 $PLC_{20}$  for *Melaleuca preissiana* was not measurable

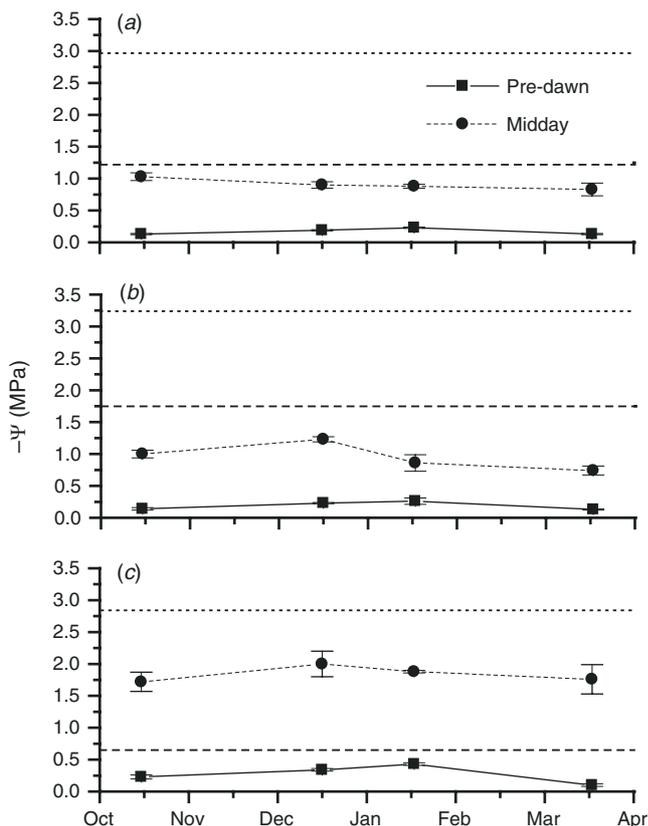
Species	$a$	$b$	$PLC_{20}$
<i>Banksia attenuata</i>	0.96	-2.69	-1.22
<i>Banksia menziesii</i>	0.92	-3.24	-1.74
<i>Banksia ilicifolia</i>	0.63	-2.84	-0.63
<i>Melaleuca preissiana</i>	0.40	-1.07	-

Pre-dawn ( $\Psi_{pd}$ ) and midday ( $\Psi_{md}$ ) leaf water potentials of both the obligate and facultative phreatophytes (*B. ilicifolia* and *B. attenuata*, respectively) did not exceed their respective  $PLC_{50}$  values during the course of the drying phase

(Fig. 2). Values were maintained well below  $PLC_{50}$ , indicating that water availability during the period was high and that the plants were not under water stress. The range between pre-dawn and midday values varied little during the period, with *B. ilicifolia* showing the greatest difference during summer.

A difference was observed between the species in  $\Psi_{md}$  proximity to  $PLC_{50}$  during summer. By using their respective response functions to estimate PLC, *B. ilicifolia*  $\Psi_{md}$  during December and January represented a possible 22–30% loss of conductance compared with 15% for *B. attenuata*. Although not significant with regard to total loss of conductance and water stress, the closer proximity to  $PLC_{50}$  of  $\Psi_{md}$  in *B. ilicifolia* during summer indicates a higher vulnerability of the species and that site water availability during the

dry season may have resulted in a greater PLC than that for *B. attenuata*. The greatest difference between  $\Psi_{pd}$  and  $\Psi_{md}$  was observed in *M. preissiana* during the drying phase, with no significant increase in tension during summer. In contrast with the *Banksia* species, *M. preissiana*  $\Psi_{md}$  was maintained at higher tensions than  $PLC_{50}$  throughout the period of study, including the wetter spring months. Although there was no physical evidence to suggest the *Melaleuca* trees were under drought stress, the population may have been situated at the dry end of the species' ecohydrological range, given the depth to groundwater and that the site included remnant wetland vegetation. Alternatively, there is increasing evidence that suggests xylem embolism acts as a water-loss control mechanism, together with stomatal control (Sperry *et al.* 2003). Maintenance of  $\Psi_{md}$  near or above  $PLC_{50}$  may indicate regulation of transpiration to avoid the positive feedback that would promote further loss of hydraulic conductivity and runaway embolism (Vilagrosa *et al.* 2003); hence, the persistence of a wetland tree species in a drying environment that now supports terrestrial species. With further change (drying) in water availability, it is likely



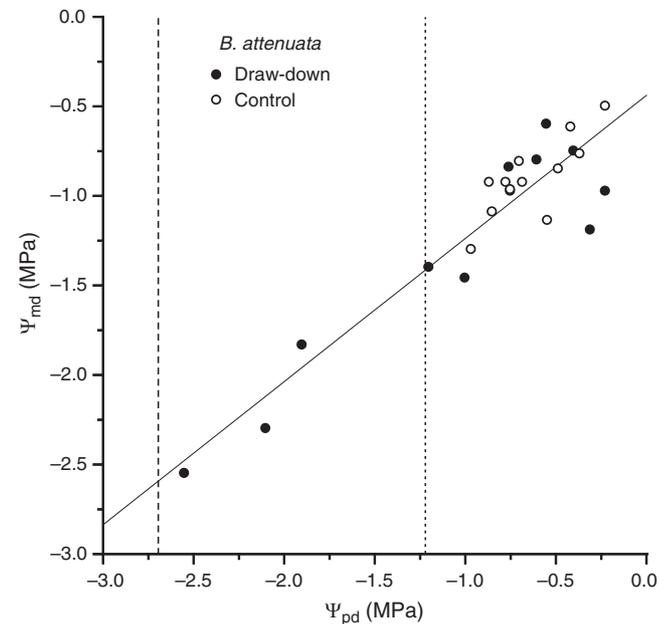
**Fig. 2.** Pre-dawn and midday leaf water potentials for (a) *Banksia attenuata*, (b) *Banksia ilicifolia* and (c) *Melaleuca preissiana* at Lexia wetland over the annual dry season. The dotted and dashed lines in each graph represent  $\Psi_x$  where PLC = 50% and  $\Psi_x$  where PLC = 20%, respectively.

that *M. preissiana* will be lost from the site, as evidenced by long-term monitoring of vegetation change on the Gngangara groundwater mound (Groom *et al.* 2000).

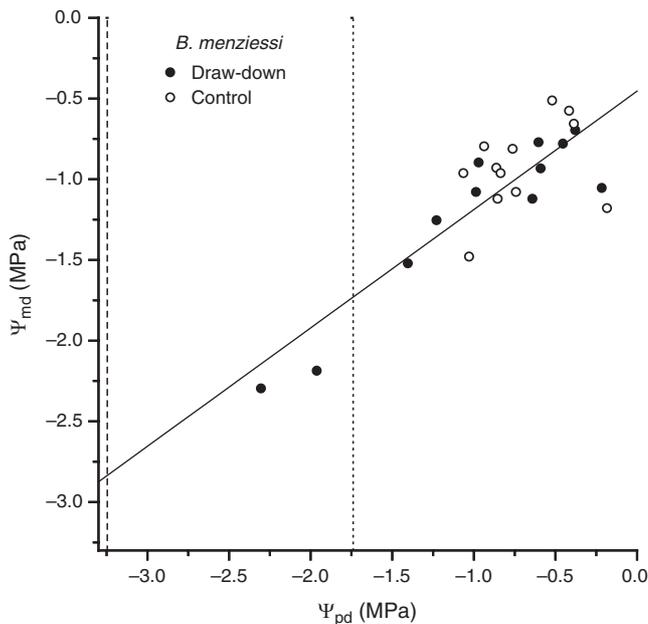
#### Critical shoot water potential

Critical leaf water potential ( $\Psi_{critical}$ ) can be defined as an *in situ* quantitative physiological threshold of drought tolerance. In other words, the critical shoot potential represents a 'point of no return', beyond which a plant rapidly declines towards death. An opportunity to measure *in situ* *Banksia* response to reduced water availability and possibly define critical shoot water potential was provided by measurements on *Banksia* woodlands at the Cooljarloo mine site. The resulting dataset captured the decline in leaf water potential with worsening drought stress, until tree death.

Leaf water potential declined to a minimum of  $-2.55$  MPa at the draw-down site before mortality occurred. In contrast, study trees at the control site, where depth to groundwater did not alter, had water potentials that remained above  $-0.97$  MPa over the course of the drying phase. In order to establish the responses to intense drought stress and investigate possible  $\Psi_{critical}$  values,  $\Psi_{md}$  as a function of  $\Psi_{pd}$  was analysed for *B. attenuata* and *B. menziesii* and these were compared to  $PLC_{20}$  and  $PLC_{50}$  values determined from the Gngangara vulnerability assessment (Figs 3, 4). Individuals of



**Fig. 3.** Relationship between midday and pre-dawn leaf water potential for *Banksia attenuata* (linear fit:  $y = a + bx$ , where  $y = \Psi_{md}$  and  $x = \Psi_{pd}$ ,  $r^2 = 0.86$ ) at Cooljarloo. In this example, pre-dawn leaf water potential at the draw-down site fell below  $\Psi_x$  where PLC = 20% (dotted vertical line), after which mortality was observed. Control sites did not breach this value and showed no signs of mortality. Xylem water potential at PLC = 50% is represented by the dashed vertical line.



**Fig. 4.** Relationship between midday and pre-dawn leaf water potential for *Banksia menziesii* (linear fit:  $y = a + bx$ , where  $y = \Psi_{md}$  and  $x = \Psi_{pd}$ ,  $r^2 = 0.71$ ) at Cooljarloo. In this example, pre-dawn leaf water potential at the draw-down site fell below  $\Psi_x$  where PLC = 20% (dotted vertical line), after which mortality was observed. Control sites did not breach this value and did not show signs of mortality. Xylem water potential at PLC = 50% is represented by the dashed vertical line.

both species at the draw-down site died from drought when tensions exceeded PLC<sub>20</sub> and progressed towards (but prior to reaching) their respective PLC<sub>50</sub> values. Plants of both species at the control site maintained tensions well under PLC<sub>20</sub> and survived.

Even though an absolute  $\Psi_{critical}$  value cannot be determined without an assessment of minimum  $\Psi_x$  values from which recovery is observed, the results do suggest that  $\Psi_{critical}$  is between PLC<sub>20</sub> and PLC<sub>50</sub> for each species. With this information, changes in water availability that result in these species exceeding PLC<sub>20</sub> may be used as a threshold of elevated risk to plant survival or vigour. In the absence of similar data for the obligate phreatophyte, *B. ilicifolia*, a contrast between different ecohydrological types cannot be made; however, one may infer from this species' PLC<sub>20</sub> and coefficient  $a$  (Table 1) that its risk threshold would be at lower tensions.

Although the mechanisms for embolism formation as a result of cavitation are well understood, the reverse repair processes remain understudied (Salleo *et al.* 2004). This is particularly important in species that operate close to critical threshold water potentials for loss of xylem function. Such species generally appear not to express specific adaptations to avoid such critical water potentials and hence must be capable of repairing dysfunctional xylem conduits. Studies of phreatophyte vulnerability to embolism

under typical wet–dry cyclic soil-moisture regimes should therefore also evaluate embolism recovery and cavitation fatigue-induced change to any subsequent exposure to critical water potentials.

## Conclusion

The outcomes of this study, although preliminary, do provide some physiological confirmation that the order of increasing drought vulnerability among the study species is *B. menziesii*, *B. attenuata*, *B. ilicifolia* and *M. preissiana*; representing a progression of ecohydrological types with increasing water requirements. In addition, the quantification of the range in PLC values (and corresponding leaf water potentials) within which there is an elevated risk of tree mortality, represents the first step towards identifying the critical thresholds in the response of *Banksia* to reduced water availability. Additional sampling and analysis of *Banksia* woodland species vulnerability curves will increase accuracy and certainty in the response parameters described in this study.

These trends should be considered provisional and not necessarily applicable to all *Banksia* woodland where the study species are found. The assumption inherent in using vulnerability curves from one site is that the shape of the response function is not influenced by differences in site conditions (i.e. depth to groundwater) and preconditioning of tree hydraulic vulnerability by the water availability during tree development (i.e. no intraspecific variability in xylem vulnerability), an assumption that is as yet untested. Further analysis of populations of the same species at different depths to groundwater is required to ascertain whether vulnerability to catastrophic hydraulic failure is greater where water availability is more consistent (e.g. accessible, shallow depths to groundwater).

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