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Seedling water stress response of two sandplain *Banksia* species differing in ability to tolerate drought

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Abstract

Effects of water stress on xylem water potential, stomatal conductance and growth were assessed experimentally on 7-month-old seedlings of *Banksia menziesii* R.Br. (Firewood Banksia) and *Banksia littoralis* R.Br. (Swamp Banksia) (Proteaceae) grown in 1 m deep tubes filled with course sand and subjected to 140 days of drought. Both are tree species of the sandplains of mediterranean southwestern Australia. *B. littoralis* is restricted to low-lying, winter damp areas, including the fringe of seasonal and permanent wetlands, whereas *B. menziesii* inhabits a range of habitats ranging from mid-upper slopes of deep, sandy dunes to dune crests. It was hypothesised that differences in their water relations and growth responses would reveal drought adaptation attributes that relates to their contrasting habitat preferences. For both species drought caused significant decreases in stomatal conductance and predawn xylem water potential. *B. menziesii* seedlings had a low stomatal conductance (< 0.1 mol m^{-2} s^{-1}) and exhibited a desiccation avoidance response to drought by maintaining relatively higher water potential. In comparison, *B. littoralis* seedlings sustained higher stomatal conductance (0.2-0.3 mol m^{-2} s^{-1}), until volumetric soil moisture content decreased to approximately 2%, avoiding drought by means of desiccation tolerance. Drought affected *B. littoralis* seedlings had lower relative growth rates (based on shoot dry weight) than well-watered controls. For *B. menziesii* there was no difference in relative growth rates between control and drought affected seedlings. Overall the two *Banksia* species displayed drought responses consistent with their current habitat preferences.

Introduction

Desiccation (or dehydration) avoidance and tolerance contribute to a plant's drought tolerance in different ways and varying proportions (Kramer, 1983; Turner, 1986). Species which exhibit a desiccation avoidance response have the ability to survive periods of drought by maintaining a relatively high water potential. In contrast, species decreasing their water potential during drought exhibit a desiccation tolerance response. The ability of plant species to avoid or tolerate desiccation depends on their response to water stress via stomatal regulation, turgor maintenance and other physiological mechanisms (Turner, 1986). Differences in seedling's drought tolerance have been used to explain the natural distribution of species co-occurring in environments that differ in water availability (e.g. Richards *et al.*, 1995; Fotelli *et al.*, 2000).

Of the five *Banksia* tree species dominating the woodlands of the sandplains immediately north of Perth, southwestern Western Australia, *Banksia littoralis* R.Br. (Swamp Banksia) is considered to be the most drought-prone (Havel, 1968), as this species is restricted to low-lying, winter damp areas, including the fringe of seasonal and permanent wetlands. *Banksia menziesii* R.Br. (Firewood Banksia) is considered to be one of the more drought-tolerant tree species, inhabiting both relatively shallow sandy sites (~2m depth to groundwater) and dune crest on deep sands (> 30 m depth to groundwater) (Havel, 1968). Based on their current distribution within the sandplain landscape, it is postulated that these two species differ in ability to tolerate extended periods of drought.

In this sandplain environment, a shift towards xeric types of vegetation has been observed in recent years, resulting in a loss, and sometimes replacement, of adult *Banksia littoralis* trees, and an increase in the number of *B. attenuata* R.Br. and *B. menziesii* trees (Heddle, 1980; Dodd & Heddle, 1989; Groom *et al.*, 2001a). Monitoring of this groundwater-dependent vegetation over a 20-30 year period has shown a reduction in vigour of overstorey species and soil moisture levels (Heddle, 1980), which has been attributed to decreasing groundwater levels caused by many years of below-average rainfall, and in some cases, combined with the effects of groundwater abstraction (Aplin, 1976; Groom *et al.*, 2000).

The ability of *Banksia* overstorey species to successfully establish in the nutrient-poor sandplain environments of southwestern Australia may be directly related to their seedlings' ability to tolerate and survive (summer) drought (Enright & Lamont, 1989, 1992b). It is hypothesised that water stress would promote significant changes in the ecophysiological and growth responses of *Banksia littoralis* and *B. menziesii* at the seedling stage, and that these differences should reveal drought adaptation attributes between the two species that relates to their contrasting habitat preferences. To compare drought response strategies of the two *Banksia* species, this paper details the changes in shoot xylem water potential, transpiration and stomatal conductance of seedlings subjected to a prolonged period of drought. In the sandplain environments of southwestern Australia, a species ability to survive extensive periods of (summer) water stress is an important factor influencing recruitment patterns and may ultimately affect a community's species composition (Enright & Lamont, 1992a; Richards & Lamont, 1996; Groom *et al.*, 2001b)

Materials and Methods

Experimental design

Seeds of *Banksia littoralis*, and *B. menziesii* were obtained from a commercial seed supplier (Kimseed Environmental Pty Ltd, Perth, Western Australia). Two hundred seeds of each species were soaked in tap water for 30 min and transferred to petri dishes lined with moist filter paper. Petri dishes were placed in a constant temperature cabinets maintained at 15˚C, the optimal germination temperature for other southwest Australian *Banksia* species (Cowling & Lamont, 1987). Once germinated, seeds were transferred to shallow seedling trays containing washed course white sand, a growth medium low in nutrients and free of organic matter (Stock *et al.*, 1990), because both species naturally occur in low-nutrient, sandy soils. Seedlings were grown in these trays for 2-3 months in an unheated glasshouse. In December 1999, seedlings were transferred to custom made experimental tubes. Tubes were constructed from 0.1 m diameter PVC pipes, cut into 1 m lengths. To allow free drainage, a PVC cap, with four 1 cm diameter holes, was glued to the lower ends of each tube. Each tube was then filled with 10 cm of course pea gravel, and the rest of the tube filled with course white sand. All tubes were held upright in a wire frame along the east wall of the glasshouse. Seedlings were grown in these tubes for 4 months before the experiment commenced, and watered twice daily from overhead sprinklers. Seedlings were randomly allocated to each tube. Two months after transplantation, all seedlings were fed with a iron chelate solution (13% w/w Fe as a complex of EDTA) to prevent leaf yellowing, caused by growing seedlings in sandy soils. Approximately 150 seedlings of both species were transplanted into these tubes.

The experiment commenced in early April 2000 and was completed by August 2000. During this period the tubes undergoing drought received no additional water. All overhead sprinklers immediate above the tubes were capped and sealed to prevent water leakage. To prevent water from the remaining overhead sprinklers from reaching the seedlings, clear plastic sheeting was hung from the roof. This created a 'dry' area, isolating the experimental tubes from the rest of the glasshouse. Control plants (20 seedlings) were individually watered every 14-20 days throughout the experiment. Because of the limited number of control plants available, measurements for control plants were recorded towards the beginning (April) and end (July) of the experiment. Some seedlings were rewatered after 120 days of water stress, and their ecophysiological and soil moisture data recorded 7 days later. All data was collected from 3-4 individuals.

Xylem water potential

For the experimental plants xylem water potential (WP) data was measured either weekly or fortnightly, depending on how quickly the soil profile dried. Predawn (0500-0630 h local time) (WP_{pd}) and midday (1200-1330 h) (WP_{md}) xylem water potential were measured on entire shoots (cut up to a centimetre below the cotyledons) using a pressure chamber (Model 3005, Soil Moisture Equipment Co., Santa Barbara, California, USA).

Soil moisture content

Soil moisture measurements were recorded for all tubes sampled for WP_{pd}. To retain soil stratigraphy tubes was carefully emptied onto a groundsheet. Soil samples were collected at 20 cm intervals from the top of the soil profile and immediately weighed. Soil samples were then dried at 60˚C for 48 h and reweighed. Gravimetric soil moisture content was calculated as (fresh weight – dry weight)/dry weight. Data was converted on a volumetric basis by multiplying gravimetric data by the soil's dry density.

Porometry and growth parameters

Porometry data was measured every 3-4 weeks, on the same day as a WP_{pd} measurement was recorded, or the next day if conditions were too cloudy. Transpiration (*E*) and stomatal conductance (*g*) were measured between 1130-1230 h (local time) on recently formed, fully-expanded leaves using a portable gas exchange analyser (LCi, ADC Bioscientific Ltd, Hoddesdon, England). Measurements were taken at ambient humidity and CO_2 concentrations, and recorded within 1 min of enclosing the leaf within the chamber. Air flow through the chamber was 5 mL s^{-1}. All data was collected on relatively cloud-free, sunny days when light intensity (PAR) was at it's maximum and greater than 1000 µmol m^{-2} s^{-1}. The glasshouse used ambient light conditions (midday PAR between 900 - 1200 µmol m^{-2} s^{-1}) with midday air temperatures varying between 23-27˚C, resulting in leaf chamber temperatures of 25-30˚C .

It has been shown that ventilated leaf chambers may alter boundary layer conductance and leaf temperatures (McDermitt, 1990) and hence porometry parameters. To minimise differences caused by the leaf chamber environment, measurements were made on similar sized (2-3 cm^2) and shaped broad leaves of each species. Ambient relatively humidity was also low (<30%) making it the dominant factor determining the evaporative gradient from leaf to air.

Using seedlings harvested for WP readings (at the beginning and end of the experiment), relative growth rates (based on shoot dry weight) were calculated according to equations given in McGraw and Garbutt (1990). Total leaf areas were measured on these seedlings using a digital image analyser (DIAS II, Delta-T Devices, Cambridge, UK).

Data analysis

Analysis of variance were calculated using the SuperANOVA (Abacus Concepts, Berkeley, CA) computer package. Homogeneity of variances was checked by residual plots and transformed as necessary by log or square roots, with data presented as untransformed means. Tukey's HSD test was used for comparisons between means at the 0.05 significance level.

Results

Soil moisture

It has been suggested that soil moisture becomes unavailable to plants in Perth's sandplain environment between 2-3% (volumetric) (Carbon *et al.*, 1982), relying on more plentiful soil moisture reserves during periods of summer drought. Assuming this was also the case for our study species in their experimental tubes, it was decided to use maximum volumetric soil moisture content as a measure of relative water availability to examine comparative drought responses between species. Both species had access to soil moisture reserves throughout the entire soil profile, having developed a 1 m deep root system (i.e reaching the bottom of the growing tubes) within 4 months of transplantation. As the soil profile dried out, the maximum soil moisture content typically occurred towards the bottom of the tube (Fig. 1A-B).

For the two *Banksia* species volumetric soil moisture decreased within the experimental tubes (Fig. 1) from a maximum (within the soil profile) of 4.5-6.1% to 0.2-0.3% over a 120 day period. *Banksia menziesii's* sand dried out the fastest, with the entire soil profile drying out to less than 1% volumetric moisture content by 54 days (Fig. 1A). The experimental tubes of *B. littoralis* attained a maximum volumetric moisture content of <1% by 110 days (Fig. 2D). After 22 days without water, *B. menziesii* was the only species to have a significant difference (*P*<0.01) in maximum soil moisture content between the experimental tubes and watered controls. After 120 days without water, both species displayed significant differences (*P* = 0.0063 to 0.0245) between drought affected and well watered tubes. There was no significant difference in maximum soil moisture contents between the first 3 sampling days (day 7, 15 and 22) for either species (Fig. 1C-D).

Xylem water potential

Predawn xylem water potential (WP_{pd}) for both species became more negative as the number of days without water increased (Fig. 1E-F), with predawn values remaining above -1 MPa for 110 days. After 22 and 120 days without water there was significant

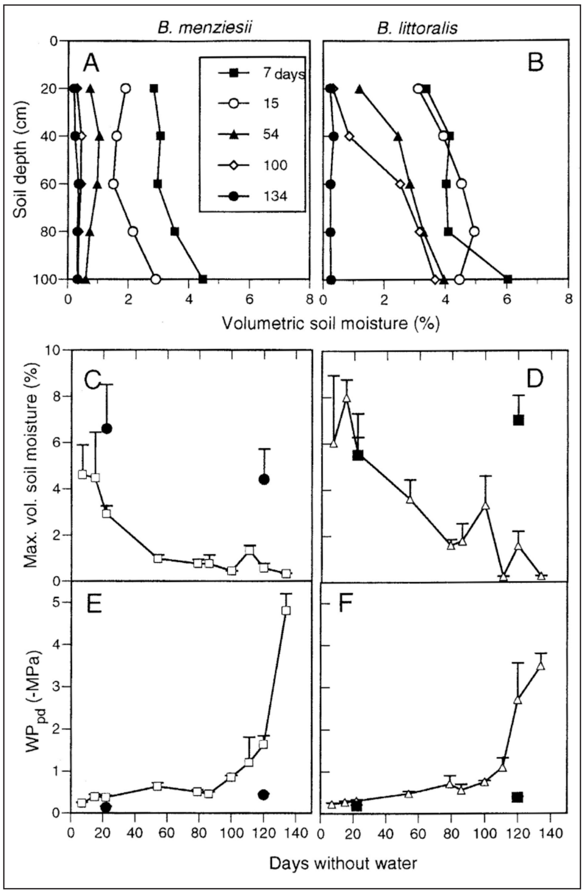

Figure 1. (A-B) Changes in volumetric soil moisture profiles in the experimental tubes as the sandy soil dries out over a 134 day period. (C-D) Maximum soil moisture content and (E-F) predawn WP as the number of days without water increase. Data are mean ± SE for 3-4 replicates for drought affected (open symbols) and well-watered (solid symbols) seedlings (C-F only). Graphs on the left are for *B. menziesii*; graphs on the right are for *B. littoralis*.

differences (Table 1) in WP$_{pd}$ and WP$_{md}$ between the watered controls and the experimental tubes, with the drought affected plants experiencing the lowest WP. Plants rewatered a fortnight after day 120, and their water relations examined 7 days later, displayed similar WP values to the well-watered controls.

For seedlings undergoing drought, both species displayed an inverse relationship when maximum soil moisture content was plotted against WP$_{pd}$ (Fig. 2A-B). Based on these relationships, the estimated maximum volumetric soil moisture content required to attain a WP$_{pd}$ of –1 MPa for *B. menziesii* was 0.75%, in contrast to *B. littoralis* where maximum soil moisture content was 1.64%. This occurred when stomatal conductance was 0.02 mol m^{-2} s^{-1} for *B. menziesii* and approximately 0.15 mol m^{-2} s^{-1} for *B. littoralis* (as interpreted from Fig. 2E-F).

Stomatal conductance and transpiration

After 22 days of drought conditions, there were significant differences in the midday transpiration rate (*E)* and stomatal conductance (*g)* between the watered controls and experimental *B. menziesii* seedlings ($P<0.044$), but not for *B. littoralis* (Table 1). By 120 days *E* of drought affected *B. menziesii* were significantly lower than that of well-watered seedlings ($P<0.024$). This was reflected in the *g* values recorded, which were calculated as less than the minimum detectable limit of the gas exchange analyser (<0.01 mol m^{-2} s^{-1}). On day 120, *E* and *g* of drought affected *B. littoralis* seedlings was also significantly different from the control ($P<0.0090$). Between the two species there was no significant difference in porometry parameters measured after 22 days of drought for either the well-watered or drought affected seedlings. After 120 of drought, *B. littoralis* had significantly higher rates of transpiration ($P=0.0058$) compared with *B. menziesii* (Table 1). Following rewatering at 120 days,

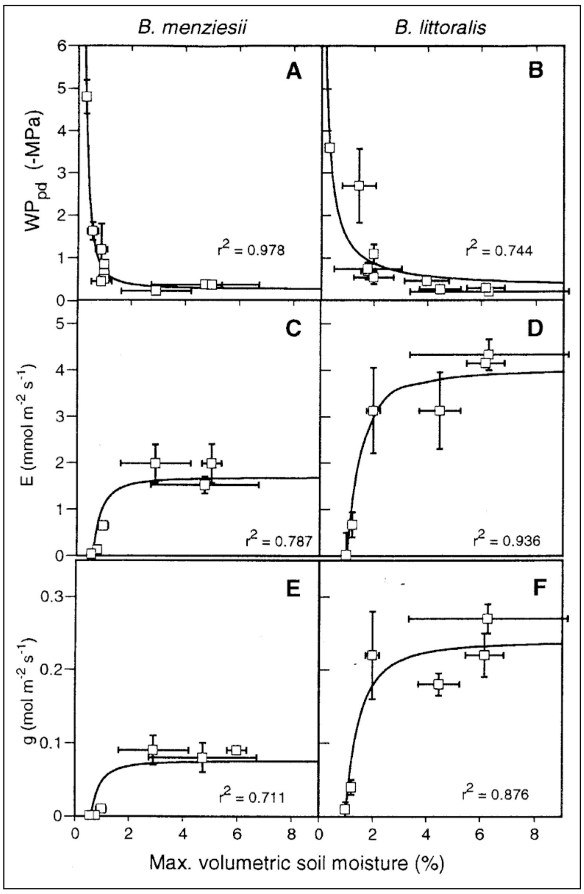

Figure 2. Relationship between maximum soil moisture content and predawn WP (A-B), transpiration (C-D) and stomatal conductance (E-F) for *B. menziesii* (left graphs) and *B. littoralis* (right graphs) seedlings. Data are mean ± SE for 3-4 replicates.

Table 1. Xylem water potential (WP) and porometry data for the two *Banksia* seedlings under well-watered and drought conditions after 22 and 120 days of water stress. Seedlings were rewatered after 120 days of drought and data collected 7 days later. Data is mean ± SD for 3-4 seedlings; ns = not significant ($P>0.05$). Different superscript letters indicate significant differences between treatment means (Tukey's HSD test), with day 22 and day 120 (including rewatering) data analysed independently.

	22 days			**120 days**		**Rewatered**	
	Well-watered	**Drought**	***P***	**Well-watered**	**Drought**		***P***
WP_{pd} (-MPa)							
B. menziesii	0.13 ± 0.04^{b}	0.38 ± 0.08^{a}	0.0138	0.43 ± 0.04 ^{b}	1.63 ± 0.43 ^{a}	0.13 ± 0.04 ^{c}	0.0002
B. littoralis	0.18 ± 0.04^{b}	0.30 ± 0.00^{a}	0.0340	0.38 ± 0.04 ^{b}	2.70 ± 1.51 ^{a}	0.40 ± 0.14 ^{b}	0.0250
WP_{md} (-MPa)							
B. menziesii	0.50 ± 0.00^{b}	1.15 ± 0.07^{a}	0.0390	0.45 ± 0.07 ^{b}	2.00 ± 0.50 ^{a}	0.67 ± 0.11 ^{b}	0.0010
B. littoralis	0.75 ± 0.14^{b}	1.28 ± 0.04^{a}	0.0360	1.33 ± 0.18 ^{b}	3.03 ± 0.25 ^{a}	1.03 ± 0.15 ^{b}	0.0019
E (mmol m^{-2} s^{-1})							
B. menziesii	3.91 ± 1.26 ^{a}	1.98 ± 1.00 ^{b}	0.0085	0.99 ± 0.55 ^{a}	0.04 ± 0.01 ^{b}	0.75 ± 0.33 ^{a}	0.0003
B. littoralis	5.51 ± 1.49	4.15 ± 1.87	ns	4.45 ± 0.94 ^{a}	0.67 ± 0.14 ^{b}	0.93 ± 0.24 ^{b}	0.0005
g (mol m^{-2} s^{-1})							
B. menziesii	0.18 ± 0.07 ^{a}	0.09 ± 0.04 ^{b}	0.0437	0.06 ± 0.01	<0.01	0.04 ± 0.02	-
B. littoralis	0.34 ± 0.17	0.22 ± 0.15	ns	0.23 ± 0.07 ^{a}	0.04 ± 0.02 ^{b}	0.04 ± 0.02 ^{b}	0.0090

there was no significant difference in E or g between drought and rewatered treatments for *B. littoralis* (Table 1). For *B. menziesii*, rewatered E and g values were similar to that of the well-watered controls.

Plotting transpiration and stomatal conductance against soil moisture content (Fig. 2C-F) both species showed significant saturation-type curves. *B. littoralis* retained a relatively high stomatal conductance (0.2-0.3 mol m^{-2} s^{-1}) until volumetric soil moisture content dropped below 2%; *B. menziesii* maintained a lower stomatal conductance (~0.09 mol m^{-2} s^{-1}) until volumetric soil moisture content dropped below 1.5%.

Relative growth rate

Relative growth rates (based on shoot dry weight) for *B. menziesii* did not differ between well-watered (2.4 mg g^{-1} day^{-1}) and drought affected (2.2 mg g^{-1} day^{-1}) seedlings over a 98 day period. Drought affected *B. littoralis* seedlings had lower relative growth rates (3.3 mg g ^{1} day^{-1}) than well-watered seedlings (5.5 mg g^{-1} day^{-1}). There was no significant increase in total leaf area after 98 days drought for either species, although there was a significant different between well watered (*B. menziesii*: 7.3 ± 0.4 cm^{2}, *B. littoralis*: 2.3 ± 0.3 cm^{2}) and drought affected (*B. menziesii*: 5.4 ± 0.8 cm^{2}, *B. littoralis*: 1.4 ± 0.3 cm^{2}) seedlings.

Discussion

B. menziesii is a common component of the woodlands on the deep sandy soils north of Perth, Western Australia (George, 1984), inhabiting all locations within the topographical gradient (Lamont *et al.*, 1989), excluding sites where the groundwater depth is less than 2 m (Groom *et al.*, 2001a). Our study shows that as seedlings, *B. menziesii* exhibits a desiccation avoidance response to drought (maintaining relative high WP_{pd}) and maintained a relatively low conductance, even during well-water conditions. This response to prolonged drought stress, whilst maintaining a relative growth rate equivalent to well-watered plants, supports the xerophytic nature of this species. *B. menziesii* seedlings are 'water savers' (after Levitt, 1972) in response to drought, with seedlings displaying full recovery (water relations similar to well-watered controls; WP_{pd} > controls) seven days after rewatering.

In contrast, *Banksia littoralis* is a species confined to low-lying seasonally wet areas (George, 1984). *B. littoralis* seedlings displayed a desiccation tolerance response to drought by maintaining relatively low WP_{pd}. This was achieved despite *B. littoralis* sustaining relatively high g and E in the presence of a depleting water source. *B. littoralis* seedlings are 'water spenders' (after Levitt, 1972) in response to drought, capable of transpiring at 3-4 mmol m^{-2} s^{-1}, until soil moisture reached 2% volumetric water content, when *E* dropped to < 1 mmol m^{-2} s^{-1}. This was associated with a greater decrease in WP_{pd} in comparison to *B. menziesii*. Seven days after rewatering *E* and *g* values were significantly less than those of well-watered controls. This suggests that at least in the short-term, an inability of *B. littoralis* to recover from severe water stress at the stomate level, despite a recovery in shoot water potential.

Species differences in water-dependent mortality may be consistent with the species distributions across landscape gradients of soil water availability, as has been documented for saplings of forest communities in northeastern USA (Caspersen & Kobe, 2001). Because of its occurrence in low-lying habitats, it is assumed that *B. littoralis* prefers shallow groundwater sites, the most mesic of all sites within a sandplain landscape. Species inhabiting these sites are the most likely to be affected by lengthy periods of drought during the summer and autumn (Dec-Apr), when soil moisture and groundwater levels are at their lowest (Heddle, 1980). Declining tree numbers in *B. littoralis* populations occupying these sites and poor seedling recruitment in recent years has been attributed to decreasing soil moisture levels (up to 2 m depth) and total winter rainfall since the mid-1970's (Heddle, 1980; Groom *et al.*, 2001a). *B. littoralis* seedlings were able to tolerate soil moisture contents down to 2%, as indicated by insignificant changes in their WP_{pd} and *g* values, however it is unlikely that this species would be able to tolerate/recover from volumetric soil moisture contents <1%, a scenario which may occur during late summer (Feb) or early autumn (April) (up to 5 m soil depth) (Dodd *et al.*, 1984), especially if there has been no summer rainfall. Although no information is available on the root growth of *B. littoralis* seedlings in their natural habitat, this species was capable of accessing soil moisture at the bottom of their experimental tubes, growing a 1 m deep root system within 4 months of transplantation. The water relations of *B. littoralis* trees in response to seasonal water stresses is also unknown, but would be closely linked to their reliance on groundwater resources (Groom *et al.*, 2001a).

During their first summer, Enright and Lamont (Enright & Lamont, 1992b) found that for the drought-tolerant *B. attenuata,* seedling occurring on the dune crests had more negative WP_{pd} and lower *g* than seedlings occurring on interdunal habitats, as dune crest species are unlikely to access groundwater sources at depth during their first summer, instead relying on limited soil moisture reserves (Zencich *et al.*, 2002). The preference of *B. menziesii* for crests and mid-upper slopes of deep, sandy dunes may be a result of competition pressures and ability to tolerate their first summer drought, as has been shown for other xeric *Banksia* species (Lamont *et al.*, 1989). *B. menzesii* seedlings may avoid drought stress by developing deep root systems (> 2 m) in their first year (Rokich *et al.*, 2001) increasing their likelihood of accessing groundwater or soil moisture sources at depth during the summer drought. This and the ability of *B. menziesii* seedlings to avoid desiccation when soil moisture content is < 2% enables *B. menziesii* to survive in the more xeric parts of a sandplain landscape. *B. menziesii* trees avoids summer drought by maintaining access with groundwater sources or utilizing soil moisture reserves at depth (Lamont & Bergl, 1991; Dodd & Bell, 1993).

Past studies that have compared seedling water relations of drought tolerant and intolerant species, or species inhabiting mesic and xeric habitats, have shown that the most mesic species usually displayed the greatest sensitivity of *g* to water stress, often developing very low WP (e.g. Abrams *et al.*, 1990; Ni & Pallardy, 1991; Fotelli *et al.*, 2000). In our study species were subjected to extremely xeric growing conditions, reflecting the soil moisture environment experienced by southwestern Australian sandplain species during a typical summer-autumn drought. For the most mesic of the species (*B. littoralis*), the ability to retain higher stomatal conductance when soil moisture was relatively more abundant, may reflect this species intolerance of very low soil moisture contents, and thus its requirements for a readily accessible water source. The relatively low stomatal conductance of the more xeric *B. menziesii* reflects it's greater tolerance to drought. For sandplain *Banksia* tree species of Mediterranean southwestern Australia, the ability of seedlings to resist drought when soil moisture contents and groundwater levels are naturally at their lowest is critical to ensure successful recruitment of both xeric and mesic species, particularly after the first or second drought period following establishment.

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