Water Deficit Stress Responses of Three Native Australian Ornamental Herbaceous Wildflower Species for Water-wise Landscapes

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Abstract. Perennial wildflower species are important but not well-understood elements in water-wise landscaping that anchors urban water conservation programs in arid climates. Comparative growth and physiological responses to soil substrate drying of three herbaceous Australian ornamental species from habitats of variable moisture regimes were investigated in the context of isohydric and anisohydric behavior. Clonal *Orthosiphon aristatus*, *Dianella revoluta* ‘Breeze’, and *Ptilotus nobilis* plants were container-grown individually and competitively together in two separate studies. In both studies, plants were water-stressed through cyclical dry downs. We measured stomatal conductance (g_s), soil water content, and water potential during each study and osmotic adjustment estimated from pressure-volume data and plant biomass at the end of each study. *O. aristatus*, a rainforest species, fit a general anisohydric model of high water use and more negative water potential during soil drying until stomatal closure and leaf wilting. *D. revoluta* and *P. nobilis*, indigenous to Australia’s dry interior, fit a general isohydric, drought-tolerant model of stomatal closure from water deficits that moderates leaf water potential but through different mechanisms. *P. nobilis* and *D. revoluta* moderate water use and maintain acceptable aesthetic performance under water stress, suitable for mixed low-water landscape plantings. *O. aristatus* would not be suitable for low-water urban landscapes, either isolated or in mixed plantings, because of high soil water depletion and wilting.

Drought is an increasing problem in many parts of the world (IPCC, 2007). Australia is the driest inhabited continent with the vast majority of the land receiving less than 600 mm of rain each year (Bowman, 2000) and declining as a result of climate change. Although Australia’s population is mostly concentrated in major urban zones along the higher rainfall seaboard, even these areas are affected by drought (McWilliams, 1986). Similarly, the rapidly growing western United States is being affected by drought

and climate change (Barnett et al., 2004). In both Australia and the western United States, up to half of municipal water supplies are applied to urban landscapes (AWRA, 2000); thus, areas such as irrigated urban parks, gardens, and sports fields are increasingly targeted for water conservation.

Low water-requiring or “water-wise” urban landscaping is an increasingly important policy tool in arid/semiarid and water-limited areas in Australia and the western United States (Hurd et al., 2006; Kjelgren et al., 2000). Water-wise landscaping can maintain acceptable appearance during drought when designed with more drought-tolerant plants than turf and when irrigation is zoned by plant water needs (Mee et al., 2003). Appropriate species selection for water-wise landscaping can be improved with knowledge of drought tolerance and water stress response mechanisms among candidate species (Kjelgren et al., 2000).

Drought and water stress response mechanisms have been well studied in woody forest (Crombie et al., 1988) and annual crop species (Subbaro et al., 1995). This general knowledge provides the physiological framework (Maseda and Fernandez, 2006) for understanding drought and water stress responses when combined with appropriate measures of performance for specific urban landscape species (e.g., He and Joyce, 2007).

Herbaceous perennial wildflowers dominate arid regions of Australia (Johnston and Joyce, 2006) and the western United States (Mee et al., 2003), and thus are a rich source of drought-tolerant plants for water-wise landscaping. Characterizing herbaceous wildflower water deficit stress response mechanisms can inform selection of drought-tolerant herbaceous perennial species appropriate for urban landscapes (Chapman and Auge, 1994). Herbaceous perennials that avoid drought through wilting, dormancy, or dieback are less acceptable than species that tolerate drought by maintaining intact foliage (Zollinger et al., 2006). Some drought tolerance responses are better suited to urban landscapes. Deep-rooted, drought-avoiding species that become stressed and lose visual quality in shallow urban soils would be less suitable than species that withstand drought through stomatal closure and dehydration tolerance (Stewart et al., 2004).

Integrating the overall drought responses and performance measures in the context of duration and severity of urban drought is an important consideration on a species or even a cultivar level (Maseda and Fernandez, 2006). The isohydric/anisohydric model provides a potentially useful conceptual framework for understanding different drought response strategies (Schultz, 2003) in assessing performance and enhancing herbaceous species selection for low water-requiring landscapes. Anisohydric species tolerate greater soil water depletion by maintaining open stomata and generating more negative internal water potential while scavenging soil water under water stress, particularly if deep-rooted (West et al., 2007). However, during prolonged drought, anisohydric species risk cavitation damage and are slow to recover and can outcompete and suppress adjacent species (West et al., 2008). Isohydric species maintain less negative internal water potentials through partial stomatal closure during drought to avoid cavitation (West et al., 2007) but at the cost of reduced photosynthesis (West et al., 2008). Isohydric species may be a more conservative and hence appropriate choice for low-water landscapes with variable soil and water conditions.

Australia has an abundance of seemingly drought-tolerant native wildflower species in its vast interior arid zones. Many of these species have desirable ornamental qualities and apparent drought tolerance and are thus candidates for water-wise landscaping in Australia and overseas (Johnston and Joyce, 2006). However, little is known about the water stress response mechanisms and performance of these species. We investigated

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water deficit stress in three herbaceous Australian native ornamental species, two originating from dry regions and one common to southeast Asia rainforests, in terms of isohydric/anisohydric behavior under isolated and competitive growing environments.

Materials and Methods

Two experiments were conducted to comparatively characterize the water deficit stress responses of three herbaceous native Australian ornamental plants: *Orthosiphon aristatus* (cats whiskers; Lamiaceae), a tropical rainforest species (Shibuya et al., 1999) likely to have little drought tolerance; *Dianella revoluta* 'Breeze' (flax lily; Liliaceae), a species indigenous to dry sclerophyll woodlands in southeastern Australia (Cunningham, 2000); and *Ptilotus nobilis* (mulla mulla; Amarantaceae) collected in arid western Queensland (Lee et al., 2007). The first experiment compared plant responses during successive dry downs in individual containers. The second experiment compared plant response under variable irrigation (under shade to slow substrate drying) of the three species in direct competition with each other within a single container. These experiments were conducted at The University of Queensland's Gatton plant nursery unit (long. 27°33' S, lat. 152°17' E) in a subtropical region characterized by dry austral winters (June to August) and high-precipitation monsoonal summers (December to January) from south-moving tropical weather systems.

Rooted cuttings of each species were transplanted in late winter (early Sept. 2006) into 120-mm diameter containers containing a 75% composted pine bark/25% sphagnum peat growing (potting) medium. Each container was top-dressed with a 20:0:15 slow-release nitrogen, phosphorus, and potassium Osmocote™ fertilizer (Scott's Company, Marysville, OH) plus micronutrients (5 g × per container) at planting and grown for 5 weeks in an open-ventilated shadehouse under 30% shade. Well-established plants were transplanted in early Oct. 2006 into 200-mm diameter (7-L) pots containing a red ferrosol clay-loam soil (Biggs et al., 2001). This approach was to simulate transplanting into the landscape. This clay-loam soil has a high water-holding capacity (0.2 mm water/mm soil at field capacity), thereby reducing potentially confounding effects from rapid root zone drying in organic potting substrate.

Weather conditions differed substantially between the two experiments detailed subsequently (full data set not presented). Temperatures during the first experiment in midspring were initially hot (30 to 36 °C maximum) with humidity from 20% to 30%. A frontal system with clouds then moved through and cooled temperatures down to 21 to 25 °C for several days. For the last 4 d of the experiment, temperatures rose to near 30 °C with similar low humidity. Characteristic of a subtropical summer monsoonal climate, partly cloudy and hot conditions prevailed through the dry down of the second

experiment. Maximum temperatures were between 30 and 33 °C with humidities from 40% to 60%.

Study 1. Two treatments were imposed on plants growing outside, well-watered (control) and water withheld variably over a 12-d stress cycle during Nov. 2006. Each watering-treatment-by-species combination involved 10 single-plant replicates for a total of 60 plants. The experiment was laid out on a concrete pad in a completely randomized design. All plants were irrigated daily for 15 min with two 4-L·h⁻¹ drip emitters per container during their establishment in October as they acclimated to full sun conditions.

Before starting the dry-down cycle, dawn-to-dusk stomatal conductance (g_s) was measured with a porometer (model SC-1; Decagon Devices, Pullman, WA). A four-plant subsample was measured on two representative mature full-sun leaves per plant every 2 h during the day for each species × treatment combination. This dawn-to-dusk data helped identified peak conductance as midday with no midday depression under well-watered conditions, timing that was used for subsequent daily measurement (Zollinger et al., 2006). Subsequently, all plants were watered by hand at the start of the dry-down cycle in addition to routine drip irrigation to ensure growing substrate was at field capacity. Drip emitters were then withdrawn from plants in the no-water treatment, which were allowed to deplete soil water until visible water stress symptoms, wilting, or leaf curling, were evident in at least half of the individual plants within the stress treatment. At this point, all plants within that species were rewatered to return the substrate to field capacity. Thus, each species had dry-down periods of different durations.

Stomatal conductance was measured as described previously either each day or every other day during dry-down periods. Substrate volumetric water content was recorded concurrently using a time-domain reflectometer (HydroSense CS620; Campbell Scientific, Logan, UT) probe with 200-mm long prongs that reached from the substrate surface to near the container bottom. Because the HydroSense is a low-frequency general use sensor, we calibrated it to both the pine bark and field substrates. Two soil water measurements were taken, one through the original pine bark substrate and the other wholly in the field soil to determine depletion in the original rooting and transplanted root volume. The two measurements for every plant were averaged to yield a representative measure of substrate water status.

Internal plant water status was measured with a pressure chamber during the dry-down periods just before rewatering of the species, then currently exhibiting the most drought-stressed symptoms. A four-plant subsample was selected for measurement from each species × treatment combination. A single leaf on each plant was wrapped individually in plastic film and then with aluminum at dawn on the day of measurement to eliminate transpiration and approximate whole-plant

water potential (McCutchan and Schackel, 1992). Leaves were then excised after conductance readings were taken and immediately moved indoors for measurement. Leaf water potential was measured in a custom Scholander-type pressure chamber (Ritchie and Hinckley, 1975) constructed at the University of Queensland and fitted with a digital readout.

Osmotic adjustment in terms of accumulation of organic solutes was estimated using the pressure volume curve analysis method as described by Robichaux (1984) at the end of the last drying cycle for each study. Pressure volume curves were run over 3 d, one species per day starting with *Orthosiphon* and ending with *Dianella*. The night before measurement, three plants from each treatment were watered thoroughly, allowed to drain, and then were taken indoors. One leaf from each plant was excised early the next morning, weighed, immediately covered in plastic wrap and aluminum foil to eliminate confounding transpiration effects on leaf water potential, and then sealed into the pressure chamber for measurement of balance pressure. Leaves were then uncovered and allowed to bench-dry under paper to minimize drying too quickly until the next measurement.

After pressure volume data measurements were completed, all leaves were harvested from each of the plants, a representative 10-leaf subsample removed from mature mid-canopy leaves, and the remaining leaves dried at 60 °C for 24 h and then weighed. The subsample was measured for average leaf area and then dried. We used the leaf area:weight ratio (specific leaf area) to calculate total leaf area from total dried leaf mass. The root system of each plant was also harvested, the substrate washed away, dried, and then the roots were dried at 60 °C for 24 h and weighed.

Study 2. We compared the drought responses of the three species under within-container competition during early Jan. 2007. In early Dec. 2006, 18 plants of each species remaining from Expt. 1 still growing in 120-mm diameter containers were used for this study. One plant of each of the three species was transplanted into a 285-mm diameter 18-L container and backfilled with the same red ferrosol clay-loam soil. The plants were allowed to grow and establish together under well-watered conditions outside under full sun for 2 weeks, at which time inspection showed roots had grown to the container walls. The plants were not fertilized after transplanting as per the same procedure described in the first study.

Three irrigation treatments were applied to plants: well-watered (control), intermediate dry down (plants irrigated when any one species showed visible signs of water stress), and full dry-down (plants irrigated when all three species showed visible signs of water stress), in which water stress was indicated by wilting and leaf curling. The treatments were applied while plants were under exposed outside conditions for 2 weeks after

establishment but before data collection. We observed that plants in intermediate and dry treatments showed stress signs after 1 to 2 d, respectively, of water being withheld as a result of high temperatures. On 10 Jan. we transferred plants to a ventilated structure under 30% shade and applied the treatments for 10 d. Shading at 30% light reduction allowed for slower root zone drying and better resolution of plant drought responses under reasonably nonlimiting light levels. At that point, water was withheld from all the plants and they were allowed to slowly deplete soil moisture. The plants were arranged beneath a suspended clear plastic tent to avoid potential confounding effects of frequent summer rainfall.

Midday g_s was measured daily during the dry-down period, concurrent with substrate water content as previously described, and midday water potential was measured at the start and end of the dry down following the same procedure as the first study. Pots were again arranged in a completely randomized design. The analysis was a split plot design,

in which containers were the main irrigation treatment plots and species were the subplots. Leaf osmotic potential (ψ_s) was estimated from analysis of pressure volume curves at the end of the dry down as per the first study. Each species was measured on sequential days, three plants per treatment starting with *Orthosiphon* and ending with *Dianella*. Containers of the remaining species were kept outside and well-watered until they could be measured. Again, benchtop drying was slowed and resolution of the leaf weight–balance pressure relationship increased by placing leaves under paper between measurements. Finally, total leaf area and specific leaf area were measured as previously described. Root biomass was not collected because of the difficulty of separating the roots of the three species.

Data analysis. g_s , water potential, daily high temperature, and substrate water content data with SES were initially plotted against time for each study. Further graphic analysis assessed the relationship between g_s and substrate water content for both first and second experiments. g_s was regressed on

substrate water content (Table curve 2-D ver 5.01). Where initial analysis showed a non-straight line regression with an inflection point based on F-statistic, separate regression lines were calculated on either side of the inflection point. The extent to which g_s controlled leaf water potential was graphically assessed with data from the first experiment through regression analysis (Table curve 2-D Version 5.01; Systat Inc., Chicago, IL). We regressed the ratio of dry to wet treatment water potential against the ratio of wet to dry treatment g_s for data from the first study (there were not enough water potential measurements to include the second study) to filter confounding day-to-day meteorological effects.

In the first study, we analyzed differences among treatments in ψ_s , biomass, and leaf and specific leaf area data using a simple two-way, species $\times$ irrigation treatment, analysis of variance for a completely randomized design (SigmaStat 3.0; Systat Inc., Richmond, CA). When the species term was significant, Fisher's least significant difference

Fig. 1. Stomatal conductance, midday enclosed water potential, daily high air temperature, and media water content for container-grown *Dianella revolata*, *Orthosiphon aristata*, and *Ptilotus nobilis* under well-watered and water-stressed irrigation treatments conducted outside under full sun at the University of Queensland campus in Nov. 2006. Arrows indicate days of irrigation for dry treatments.

(LSD) test was used to separate significant differences among means using $P = 0.05$. For the second study, because species was a subplot of irrigation main plot treatments, PROC MIXED (Version 9.1; SAS Inc., Raleigh, NC) was used to analyze the biomass, specific leaf area, and ψ_s data as fixed effects in a split plot design with main plots completely randomized. Again, species means were separated using Fisher's LSD test with $P = 0.05$ when the species term was significant.

Results and Discussion

Orthosiphon exhibited a more sensitive response to drought than either *Dianella* or *Ptilotus*, whereas the latter two species appeared to differ in their drought tolerance mechanisms over both studies. In the first study, substrate water contents for all three species decreased to $\approx 5\%$ after 4 d of drying under maximum temperatures of ≈ 33 to 36°C (Fig. 1). Although stomata of all three species were nearly closed at this point, *Dianella* showed no visible signs of water

stress and no detectable differences in mid-day water potential and thus was allowed to continue drying for 2 d further. *Ptilotus* showed more signs of water stress, as leaves had started to curl, displaying a visible loss of turgor and water potential was nearly 1 MPa more negative compared with the well-watered control (Fig. 1). By contrast, *Orthosiphon* was severely stressed with leaves completely wilted and water potential 2 MPa more negative than the control. Both of these species were rewatered after the initial 4 d of drying. Daily high air temperatures on the subsequent 2 d of drying were also in excess of 30°C , resulting in moderate but visible water stress symptoms again in both *Ptilotus* and *Orthosiphon*. Although water potential differences were not as great as those initially, these species were again rewatered. *Dianella*, after 6 d without water under high temperatures, had visible leaf curling and was rewatered.

The remaining 6 d in Study 1 were cooler and somewhat cloudy, progressively increasing in air temperature maxima from 21 to 29°C . Cooler temperatures and lower evapo-

transpiration were evidently manifested in reduced g_s which would have in turn reduced plant water use (Fig. 1). Visible signs of water stress in *Dianella* and *Ptilotus* during this period were minimal until the last 2 d, and so the plants were not rewatered. Interestingly, g_s of *Dianella* subjected to the dry down did not fully recover even after rewatering, and water potential differences between the stressed versus control treatments were minimal. By contrast, g_s in *Ptilotus* increased to near well-watered levels after rewatering with a corresponding large water potential difference. *Ptilotus* g_s then rapidly declined in the dry plants during the remainder of the study, moderating water potential to levels similar to the well-watered plants.

The relative pattern of water stress response among species was similar during Study 2 (Fig. 2). In the intermediate and dry treatments, substrate water contents were depleted to near 4% for *Ptilotus* and to 7% to 10% for *Dianella* and *Orthosiphon*. *Dianella* and *Ptilotus* g_s in the dry treatment declined rapidly to levels lower than the

Fig. 2. Stomatal conductance, midday enclosed water potential, daily high air temperature, and media water content for *Dianella revoluta*, *Orthosiphon aristata*, and *Ptilotus nobilis* grown together in 200-mm containers without irrigation previously subjected to dry, intermediate, and wet irrigation treatments. The study was conducted under 30% shade cloth at the University of Queensland campus in Jan. 2007.

intermediate and wet treatments. However, *Dianella* and *Ptilotus* intermediate and wet treatment plants also declined. This decline could possibly be the result of air temperatures reaching up to 37 °C by the fourth day, suggesting an impact of leaf temperature-mediated saturation deficit effect on g_s (Choudhury and Monteith, 1986).

Alternatively, *Orthosiphon* may have simply suppressed g_s of the other two species by outcompeting them for water, even in the well-watered treatment as a result of higher water use rate and greater leaf area (Stewart et al., 2005). Similar to the first experiment, *Dianella* water potential did not differ among watering treatments at the end of the drying cycle, whereas wet *Ptilotus* water potential was ≈ 0.5 MPa less negative than that of the dry and intermediate treatments. By contrast, dry and intermediate *Orthosiphon* g_s declined rapidly after 2 to 3 d of soil drying, resulting in water potential nearly 1 MPa more negative than the wet plants that maintained more open stomata even under the highest temperatures. Temperatures during the last 2 d of the drying cycle in the greenhouse fell to near 30 °C, moderating the atmospheric saturations deficit, whereupon *Dianella* recovered somewhat but *Orthosiphon* and *Ptilotus* did not.

Water stress response characteristics were more evident when g_s was plotted against substrate water content (Fig. 3). In the first experiment, variability in g_s was greater in well-watered plants, but generally *Orthosiphon* had overall higher g_s compared with the other two species. *Dianella* and *Ptilotus* g_s averaged 240 and 260 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with a minimal relationship to root zone water content above 20% and 17%, respectively. By contrast, *Orthosiphon* g_s was, on average, 340 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ down to 13.5% water content and then fell by almost half at 11% water content. Compared with the other two species, *Ptilotus* g_s exhibited more open stomata at lower water contents. Three ostensibly outlying *Ptilotus* g_s values at 14% to 17% water content impacting the relationship may be somewhat anomalous as a result of osmotic adjustment. The high value, ≈ 300 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ water content, was the very first measurement of the drying cycle unaffected by substrate drying. The two low values, ≈ 100 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, were after the last rewatering, suggesting acclimation that may have constrained stomatal aperture (Sanchez-Blanco et al., 2004), the overall effect being something of a hysteresis curve for g_s versus substrate moisture. Similarly, post rewatering g_s in *Dianella*, at 28% root zone water content, was approximately one-third less than values for wet plants at similar root zone water contents again suggesting some degree of acclimation to drought stress that limited stomatal opening.

In Study 2, the g_s -substrate water content relationships for the slow drying cycle conducted under shade showed a similar pattern to the first experiment (Fig. 3B). *Orthosiphon* had higher g_s that decreased sharply $\approx 15\%$ substrate water content. *Dianella* and *Ptilotus*

Fig. 3. (A; top). Expt. 1 stomatal conductance (g_s) versus media water content for well-watered (wet) and water-stressed (dry) *Dianella revolata*, *Orthosiphon aristata*, and *Ptilotus nobilis* growing in separate containers. Curve fits for each species are separated by values above 20% root zone water content (wet) and those below (dry): *Dianella* dry $50.1 + 10.6 \cdot X$ ($r^2 = 0.67$), wet $534 - 8.62 \cdot X$ ($r^2 = 0.41$); *Orthosiphon* dry $190 + 35 \cdot X$ ($r^2 = 0.88$), wet $238 + 3.1 \cdot X$ ($r^2 = 0.01$); *Ptilotus* dry $30.2 + 9.5 \cdot X$ ($r^2 = 0.41$), wet $374 + 3.4 \cdot X$ ($r^2 = 0.07$). (B; bottom). Expt. 2 g_s versus media water content well-watered (wet) and water-stressed (dry) *Dianella revolata*, *Orthosiphon aristata*, and *Ptilotus nobilis* growing together competitively in one container. Curve fits were separated by wet and dry responses for *Orthosiphon*, but not for *Dianella* and *Ptilotus* in which a straight-line response gave the highest fit: *Dianella* combined $69 + 3.1 \cdot X$ ($r^2 = 0.76$); *Orthosiphon* dry $136 + 21.4 \cdot X$ ($r^2 = 0.71$), wet $200 + 3.0 \cdot X$ ($r^2 = 0.41$); *Ptilotus* combined $11.4 + 3.8 \cdot X$ ($r^2 = 0.70$).

g_s declined more linearly and gradually as substrate water was depleted. This decline fit an isohydric pattern, initial stomatal closure at higher substrate water contents than in *Orthosiphon*, which fit a more anisohydric pattern. Also similar to the first experiment, but more pronounced, *Ptilotus* was able to maintain open stomata at lower substrate water contents, $\approx 4\%$, than the other two species. *Dianella* maintained open stomata down to 8% substrate water content but with a range of values. This range was the result of g_s increasing, whereas substrate water content stayed the same, during the last 2 d of the

drying cycle as air temperatures moderated as a result of increased cloudiness.

By normalizing g_s and water potential of stressed relative to well-watered plants, we observed that g_s appeared to control leaf water potential as much as it was controlled by substrate water content (Fig. 4). Particularly for dry *Dianella*, near complete g_s closure moderated leaf water potential to within 40% well-watered (wet) values. *Ptilotus* stomata did not initially moderate leaf water potential as much, because it fell to three times more negative as well-watered plants as stomata closed during the first

drying cycle. Otherwise, partial stomatal closure in *Ptilotus* maintained water potential within 40% of well-watered levels. *Orthosiphon* stomata maintained less control in a more anisohydric pattern. Leaf water potential fell to four times more negative than well-watered plants as stomata completely closed during the first drying cycle. Partial stomatal closure still allowed *Orthosiphon* water potential to decline to nearly twice as negative as well-watered plants.

Growth performance and osmotic data reinforced the relative pattern of water deficit stress responses among the three species. Comparing among species, *Ptilotus* exhibited greater osmotic adjustment, lowering its ψ_s

to a greater degree than the other two species, whereas *Dianella* osmotically adjusted the least (Tables 1 and 2). Indeed, ψ_s values were nearly identical for each of the two species in both studies, although differences between the wet and dry *Ptilotus* treatments observed in the first study were not observed in the second.

Biomass changed substantially among species between the two experiments (Tables 1 and 2). In the first, *Dianella* produced the least leaf biomass and had a specific leaf area intermediate between *Ptilotus* and *Orthosiphon* plants (Table 1). In Study 2, *Dianella* growth was dramatically more vigorous than the other two species. It was particularly

greater than *Ptilotus*, although their specific leaf areas were the same (Table 2). Greater growth may be attributable in part to mature *Dianella* being similar in size to *Orthosiphon* and, anecdotally, a typically larger plant than mature *Ptilotus*, which, being smaller, would be less competitive (see Tables 1 and 2).

Orthosiphon response to water stress was consistent with anisohydric behavior. However, anisohydric behavior does not a priori predict drought tolerance. A “use-it-or-lose-it” strategy is successful for rainforest species such as *Orthosiphon* surviving brief dry periods, but equally successful for *Juniperus osteosperma* surviving 250 mm of rainfall by falling back on deep rooting (West et al., 2007). Drought intolerant anisohydric species such as *Orthosiphon* are unsuited to low water landscapes, higher plant density plantings in particular. Under minimal or no landscape irrigation, a species like *Orthosiphon* would have visually unacceptable wilting and reduced leaf and root biomass. *Orthosiphon* did not appear to be particularly competitive with a normally similar-sized (≈ 1 to 1.5 m high) species like *Dianella* even when well watered, its height increasing only 25% from the first to the second study. However, *Orthosiphon*’s apparent use-it-or-lose-it water use could deplete root zone water in dense plantings and cause adjacent species to become water-stressed more quickly than when both were grown with wider spacing (Likowse and Lawn, 2008). Wet habitat and high specific leaf area (thin, papery leaves) may be a species predictor and screening criteria of not only a propensity for drought intolerance, but also anisohydric water scavenging that makes for bad neighbors in competitive landscape plantings.

Dianella and *Ptilotus* by comparison are both drought-tolerant compared with *Orthosiphon* and suitable for low-water landscapes but differ in adaptive mechanisms. *Dianella* stomatal sensitivity, which moderated internal water potential triggered by initial root zone drying, is consistent with the “save-it-for-a-rainy-day” isohydric water use model (Schultz, 2003). Also consistent with this conservative model is lower g_s in *Dianella* after being rewatered, possibly as a result of abscisic acid (ABA) accumulation. ABA signaling from the roots has been well documented to reduce g_s under mild-moderate water stress (Miyashita et al., 2005), a signal that can persist for a period of time (Davies et al., 2005). The conservative isohydric model would be suitable in *Dianella*’s slightly more mesic habitat, compared with *Ptilotus*, for survival between rainfall, assuming minimal scavenging for water by competing plants.

Ptilotus did not fit the iso- and anisohydric models as well. Initial soil drying in the first study did not moderate water potential to the same degree as *Dianella*, but did appear to trigger osmotic adjustment, consistent with the observed more negative midday leaf water potentials. Osmotic adjustment would increase turgor potential and allow stomata to close more slowly, and to greater depletion

Fig. 4. Relationship between the ratio of water-stressed (dry treatment) to well-watered (wet) water potential versus stomatal conductance for *Dianella revolata*, *Orthosiphon aristata*, and *Ptilotus nobilis* grown in individual containers conducted outside under full sun at the University of Queensland campus, Australia, in Nov. 2006. Black lines represent linear relationship of leaf water potential to stomatal closure at $y = 1.25 - 0.53x$ ($r^2 = 0.54$) (*Dianella*), $y = 2.18 - 1.17x$ ($r^2 = 0.93$) (*Orthosiphon*), and $y = 1.3 - 0.245x$ ($r^2 = 0.50$) (*Ptilotus*). Gray lines for *Ptilotus* and *Orthosiphon* represent the decline to the lowest conductance and water potential ratios at the end of the first drying cycle in the first experiment.

Table 1. Osmotic potential (n = 3), total leaf weight, specific leaf area, and root weight (n = 10 for each variable) for *Dianella revolata*, *Orthosiphon aristata*, and *Ptilotus nobilis* grown in individual containers under well-watered (wet) and water-stressed (dry) irrigation treatment conducted outside under full sun at the University of Queensland campus in Nov. 2006.

		Osmotic potential (-MPa) ^z	Total leaf wt (g)	Specific leaf area (cm ² ·g ⁻¹)	Root wt (g)
Species ^z		***	***	***	***
Irrigation		**	**	NS	**
Species × treatment		**	***	NS	**
Species ^y					
<i>Dianella</i>		0.98 c	3.5 c	220 b	3.0 b
<i>Orthosiphon</i>		1.32 b	8.9 a	278 a	25.6 a
<i>Ptilotus</i>		1.98 a	5.3 b	152 c	4.4 b
Species × irrigation ^x					
<i>Dianella</i>	Wet	0.95	3.8	—	2.8
<i>Dianella</i>	Dry	1.01	3.3	—	3.3
<i>Orthosiphon</i>	Wet	1.17 b	10.6 a	—	35.2 a
<i>Orthosiphon</i>	Dry	1.47 a	7.2 b	—	16.0 b
<i>Ptilotus</i>	Wet	1.63 b	5.0	—	6.0
<i>Ptilotus</i>	Dry	2.34 a	5.7	—	2.8

^zNS, *, **, ***Nonsignificant or significant at $P \leq 0.1$, 0.05, or 0.01, respectively.

^yMean separation among species by lowercase letters for a given variable column using Fisher’s multiple range test at $P \leq 0.05$.

^xMean separation between wet and dry treatments within a species by lowercase letters for a given variable column using Fisher’s multiple range test at $P \leq 0.05$.

Table 2. Osmotic potential (n = 3), total leaf weight and specific leaf area (n = 10 for both variables) for container-grown *Dianella revoluta*, *Orthosiphon aristata*, and *Ptilotus nobilis* grown together in 200-mm containers under dry, intermediate, and wet irrigation treatments conducted under 30% shade outside at the University of Queensland campus, Australia, in Jan. 2006.

		Osmotic potential (–MPa) ^z	Total leaf wt (g)	Specific leaf area (cm ² ·g ^{–1})
Species ^z		***	***	***
Treatment		NS	***	NS
Species times treatment		NS	*	NS
Species ^y				
<i>Dianella</i>		1.00 c	30.0 a	143 b
<i>Orthosiphon</i>		1.34 b	12.8 b	186 a
<i>Ptilotus</i>		2.04 a	5.02 c	150 b
Species × treatment ^x				
<i>Dianella</i>	Wet	—	35.3 a	—
<i>Dianella</i>	Moderate	—	27.8 b	—
<i>Dianella</i>	Dry	—	26.8 b	—
<i>Orthosiphon</i>	Wet	—	15.4 a	—
<i>Orthosiphon</i>	Moderate	—	12.2 ab	—
<i>Orthosiphon</i>	Dry	—	10.8 b	—
<i>Ptilotus</i>	Wet	—	—	—
<i>Ptilotus</i>	Moderate	—	—	—
<i>Ptilotus</i>	Dry	—	—	—

^zNS, *, **, ***Nonsignificant or significant at $P \leq 0.10$, 0.05, or 0.01, respectively.

^yMean separation among species by lowercase letters for a given variable column using Fisher's multiple range test at $P \leq 0.05$.

^xMean separation between wet and dry treatments for a given species by lowercase letters for a given variable column using Fisher's multiple range test at $P \leq 0.05$.

levels, during root zone drying. Somewhat more open stomata and more negative internal water potentials would allow more aggressive water extraction (Lenz et al., 2006). This less conservative, moderately isohydric behavior would be consistent with its native range in the driest areas of Australia where extracting as much water as possible while tolerating desiccation would be key to survival.

Morphology may also play a role in the different mechanisms of drought tolerance in *Dianella* and *Ptilotus*. *Dianella* had upright and narrow grass-like leaves that tended to reduce radiation interception (Zollinger et al., 2006). *Ptilotus* had observably more glaucous leaves that reflect more radiation (Johnson et al., 1983), but also larger and thicker (i.e., lower specific leaf area) leaves in a greater variety of orientations that would resist desiccation better and moderate light interception, particularly under drought stress (Lampinen et al., 2004). This latter leaf presentation would intercept more radiation than upright leaves, suggesting greater tolerance for midday radiation loading and drought tolerance (Martinez-Ferri et al., 2000).

Ostensible root morphology differences would appear to be consistent with different drought tolerance strategies. Root mass was unaffected by water stress in both *Dianella* (the only monocot) and *Ptilotus* in the first study, but based on anecdotal observations, root structure did appear to differ. *Dianella* ostensibly had a coarser, more deeply penetrating root system that concentrated at the container bottom based on observations made during transplanting. Deep rooting is a trait consistent with species who forestall drought by extracting water deeper in the soil profile (Stewart et al., 2004), an advantage in a woodland habitat (Cunningham, 2000). We also observed that *Ptilotus* (a dicot) had a finer root system that filled the entire con-

tainer, suggesting it may exploit water closer to the soil surface. Such a rooting pattern would probably not be advantageous in forestalling drought but would be able to exploit infrequent surface rainfall in its desert habitat in interior Australia (Lee et al., 2007) and be particularly suitable for landscapes with shallow soils in a way *Dianella* might not.

Both *Ptilotus* and *Dianella* are suited to low-water Australian landscapes, whereas *Orthosiphon* is not. Although *Ptilotus* was apparently more affected by competition than *Dianella*, the similar stomatal sensitivity of both these species to substrate drying suggests somewhat isohydric behavior (Schultz, 2003) that would preserve more root zone moisture. Thus, based on our observations, if their root zones are complementary rather than overlapping, *Dianella*, with a deeper root system, could coexist in landscapes with the ostensibly more shallow-rooting *Ptilotus* in a "water-wise" urban landscape (Crombie et al., 1988; He and Joyce, 2007).

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