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Title

High water users can be drought tolerant: using physiological traits for green roof plant selection

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Abstract

Background and aims: Green roofs are often installed to reduce urban stormwater runoff. To optimally achieve this, green roof plants need to use water when available, but reduce transpiration when limited to ensure survival. Succulent species commonly planted on green roofs do not achieve this. Water availability on green roofs is analogous to natural shallow-soil habitats including rock outcrops. We aimed to determine whether granite outcrop species could improve green roof performance by evaluating water use strategies under contrasting water availability.

Methods: Physiological and morphological responses of 12 granite outcrop species with different life-forms (monocots, herbs and shrubs) and a common green roof succulent were compared in well watered (WW) and water deficit (WD) treatments.

Key results: Granite outcrop species showed a variety of water-use strategies. Unlike the green roof succulent all of the granite outcrop species showed plasticity in water use. Monocot and herb species showed high water use under WW but also high water status under WD. This was achieved by large reductions in transpiration under WD. Maintenance of water status was also related to high root mass fraction.

Conclusions: By developing a conceptual model using physiological traits we were able to select species suitable for green roofs. The ideal species for green roofs were high water users which were also drought tolerant.

Keywords: Granite outcrop, shallow soil, geophyte, water relations, trait, *Sedum*

Introduction

Green or vegetated roofs have great potential to restore ecosystem services to cities by reducing stormwater runoff (Carter and Jackson 2007; VanWoert et al. 2005), mitigating the urban heat island effect (Bass and Baskaran 2003) and increasing biodiversity (Brenneisen 2006). Although reduced stormwater runoff is only one of the benefits of green roofs, it is the driver of green roof implementation, with cities internationally legislating or incentivising green roofs for stormwater retention runoff reduction (Getter and Rowe 2006). Restoration of ecosystem services at a city-scale requires establishment of green roofs on existing buildings, which may not have the structural capacity to support heavy loads. Consequently, substrate (growing media) depths are generally shallow (< 20 cm), making green roofs extremely difficult environments for plant growth and survival as water availability fluctuates dramatically (Nagase and Dunnett 2010) and is often limiting between rain events (Oberndorfer et al. 2007). As plant performance will ultimately determine the effectiveness of green roofs in restoring ecological function, appropriate plant selection is essential.

The most common plant species used on European and North American green roofs are *Sedum* species (Oberndorfer et al. 2007). The genus is typically selected for its drought tolerance that is conferred by leaf succulence and high water use efficiency due to physiological adaptations such as CAM photosynthesis (Durhman et al. 2007; Sayed 2001). Although the conservative water use of *Sedum* species increases their survival under drought (Farrell et al. 2012), it means they may not be very effective at reducing stormwater runoff (Nagase and Dunnett 2010; Wolf and Lundholm 2008). Effective stormwater runoff reduction is determined by the water holding capacity of green roof substrates and their water content prior to rainfall (Berndtsson 2010). Consequently, species with low transpiration rates may not dry out green roof substrates sufficiently between rain events, reducing rainfall storage capacity and increasing runoff (Oberndorfer et al. 2007). Designing green roofs to maximise reductions in urban stormwater runoff therefore requires plants that are tolerant of extremes in water availability and can balance survival under drought conditions with effective water use after rain events.

One way to improve green roof performance is to select plant species from natural habitats with similar environmental conditions to green roofs (Lundholm 2006). Seasonal and diurnal extremes of water availability are common on granite outcrops, also known as inselbergs (Hopper 2000), making them ideal habitats for identifying potential green roof plants. Plant species on granite outcrops, particularly in shallow soil-filled depressions, are exposed to drought stress due to rapid runoff of rainfall, and high irradiance and temperatures (Barthlott and Porembski 2000a; Baskin and Baskin 1988; Hopper 2000). Soil moisture can be depleted from field capacity to zero in under a week under such conditions (Gaff and Churchill 1976). Soil depth in depressions varies between 2-20 cm, with plant longevity (Porembski et al. 2000), species richness (Collins et al. 1989) and survival (Phillips 1981) tending to increase with depth. Although granite outcrop vegetation has limited structural diversity there are a broad range of life-forms (Barthlott and Porembski 2000b). Perennial vegetation on rock outcrops generally consists of xerophytes adapted to water scarcity, either through stomatal control of water loss or xeromorphic features such as sclerophyllous leaves, succulence, leaf hairs or thickened cuticles (Kluge and Brulfert 2000). Geophytes commonly die back to persistent underground storage organs as a drought avoidance strategy (Biedinger et al. 2000; Hopper 2000), resprouting when conditions are favourable (Parsons and Hopper 2003). Monocots with a hemicryptophyte life-form can also have underground storage organs such as rhizomes and are also common on outcrops (Hopper 2000). However, unlike geophytes, these plants do not necessarily die back completely every year (Parsons 2000).

The various life-forms on granite outcrops are likely to respond differently to drought. Several studies from Mediterranean climates have shown distinct differences in the ability of species to cope with seasonal drought (Galmés et al. 2007; Hernández et al. 2010; Valladares and Sánchez-Gómez 2006). Specific mechanisms by which plants can survive drought include short-term physiological changes such as stomatal closure, and longer-term morphological changes in biomass allocation. These include reducing light interception by reducing leaf biomass and leaf rolling and increasing access to water through increased root biomass (Chaves et al. 2003; Poorter and Nagel 2000; Poorter et al. 2012). Species which have a higher capacity to undergo shifts in physiological and morphological adaptation are considered to have superior fitness and enhanced capacity to cope with short-and long-term changes in climate (Nicotra et al. 2010). However, an in-depth investigation of the physiological and morphological responses of different plant species and life-forms from granite outcrops to drought is lacking (Kluge and Brulfert 2000).

For effective stormwater management, green roof plants need high transpiration rates following rainfall yet need to down-regulate water use when water is limiting to maintain water status. We aimed to determine whether granite outcrop plants could achieve both high water use and drought tolerance and therefore be suitable for green roofs. To achieve this we compared the physiological and morphological responses of 12 granite outcrop species of different life-forms (monocot, herb and shrub) and a commonly used green roof succulent to contrasting water availability (well watered and water deficit) under glasshouse conditions. Specifically, we had four objectives: (1) determine the water-use strategies of granite outcrop species/life-forms and a succulent under well watered and drought stress conditions; (2) determine the water status (level of drought stress) of granite outcrop species/life-forms and a succulent under well watered and drought stress conditions; (3) determine whether plasticity in physiological and/or morphological traits is responsible for drought adaptation in granite outcrop plant species; and (4) assess if physiological traits can be used to develop a conceptual model for plant selection for green roof plants.

Materials and methods

Species selection

Twelve species which grow on granite outcrops in south-eastern Australia (chosen from Victorian Ecological Vegetation Class (EVC) characteristic species lists) along with a succulent commonly used on green roofs (*Sedum pachyphyllum*) were selected for this study. The 12 granite outcrop species were from three life-forms: 4 grass-like monocots; 4 herbs and 4 small shrubs (Table 1). They were obtained as six-month old seedlings from a commercial nursery; while *S. pachyphyllum* was propagated from cuttings and grown for six months. In early summer (December), 20 plants of uniform size of each species were planted into 4 L black plastic pots (200 mm diameter, 190 mm height) containing 4.4 kg (added by weight) of a scoria-based green roof substrate (60% aerolite black scoria 7 mm minus blockmix; 20% 7 mm red scoria aggregate and 20% coir). The scoria substrate has a water holding capacity of 46% and a bulk density of 1.26 g cm^{-3} (Farrell et al. 2013). Twelve grams of low phosphorous slow release fertiliser (Osmocote® plus, Scotts Australia Pty Ltd.; 16 nitrogen (N):1.3 phosphorus (P):9.1 potassium (K)) was added to the surface of each pot one month post-planting. Plants were grown in a glasshouse at the Burnley Campus, University of Melbourne. Glasshouse temperatures ranged from 9 to 42.5 °C, with an average temperature of 18.7 °C during the experiment. All plants were watered to pot capacity twice a week prior to the start of the experiment.

Experimental design

The experiment ran for 50 days, commencing on the 7th of February (Mid-summer) and finishing on the 28th of March (Mid-autumn), 2011. Five plants of each species were randomly allocated to two treatments: well watered (WW) and water deficit (WD). An additional 10 substrate-only pots were used to determine evaporation rates from WW and WD treatments during the experiment (5 pots per treatment). Pots were arranged in a complete randomised block design (5 blocks). All plants were watered twice weekly (Monday and Thursday). WW plants were watered to pot capacity (2 L per pot) while the WD treatment was watered with 20% of the water used by well watered plants (determined gravimetrically) in the 3-4 days preceding each watering event. This WD treatment was designed to stress each species relative to its well watered control and was used in preference to a terminal drought treatment to allow sufficient time for each species to adjust both physiological and morphological traits to low water availability.

Growth and biomass measurements

At the start of the experiment, 5 plants of each species were harvested to determine initial biomass (root, stem and leaf mass) and leaf area. At the conclusion of the experiment, on the 30 March all WW and WD plants were harvested to determine total plant, leaf, stem and root masses. Leaf areas on a subsample of leaves of all species were measured using a LI3100 area meter (Li-Cor, Lincoln, NE, USA). Dry weights were determined after oven drying samples at 70 °C for one week (until a constant weight was reached). Dry weights and leaf areas were used to determine root mass fraction (RMF, g root g^{-1} total plant), leaf area ratio (LAR, m^2 leaf kg^{-1} plant) and specific leaf area (SLA m^2 kg^{-1} leaf).

Soil water content over time

Soil water content (SWC) was determined from pot weights pre- (WD and WW) and post- (WW only) watering. SWC was calculated by first correcting pot weight for estimated plant weight at each weighing; estimated as: initial mean fresh weight + daily biomass gain; where daily biomass gain = (final fresh weight – initial fresh weight) / number of days in experiment. SWC was then calculated as: (corrected pot weight – substrate dry weight) / substrate dry weight. Substrate dry weight was determined by drying the substrate from the 10 bare pots (5 per treatment) at the end of the experiment to a constant weight in a 70ºC oven.

Transpiration

Transpiration (E) was determined by weighing pots before and after each watering event. Transpiration was calculated by subtracting evaporation (determined from substrate only pots) from total water lost from each pot at each weighing event. Cumulative transpiration was calculated as the sum of transpiration over the 50 days of the experiment. Daily transpiration per pot and per unit final leaf area were then calculated from cumulative transpiration.

Plant water status

Plants received their final watering event mid-morning on day 50. Pre-dawn (Ψ_{PD}) and midday (Ψ_{MD}) leaf water potential were determined the following day (Day 51) on five replicates of each species from WW and WD treatments. Leaf water potentials of fully-expanded leaves were measured using a Scholander-type pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA, USA). Due to short petiole lengths, some water potentials were measured on apical branches with 2-3 leaves. Some difficulty was encountered in identifying the balancing pressure for *Isotoma axillaris* and *Arthropodium milleflorum* due to production of latex (*I. axillaris*) or mucilage (*A. milleflorum*) from the cut surface. Applying pressure as per normal confused the signal between expression of wound-response fluid and the water column. This was overcome by maintaining the section at a low pressure (0.1 MPa) in the chamber to promote expression of wound-response fluid. Once all fluids were expressed and wiped from the cut surface (which generally took <1 minute), pressure in the chamber was then increased as per normal to reach the balancing point. Leaf water potential measurements of *S. pachyphyllum* were not captured in this experiment due to high leaf succulence.

Leaf pre-dawn relative water contents (RWC) were also determined at the end of the experiment (Day 51) on five replicates of each species from WW and WD treatments. RWC was determined as: RWC = (fresh weight – dry weight)/(saturated weight- dry weight) x 100. Fresh weights were weighed immediately after re-cutting the stem/petiole under water before placing the leaf/small apical branch (as per leaf water potential measurements) in 50 ml centrifuge tubes with deionised water. Saturated weights were measured after samples had rehydrated in darkness at room temperature which ranged from 21 to 24 ºC. Samples were then oven dried at 70 °C to a constant weight to determine dry weight.

Relating transpiration, biomass allocation, leaf morphology and plant water status

Species in the WD treatment were stressed relative to their WW control and therefore each species received a different amount of water over the experiment. To standardise the effect of the WD treatment on rates of water use and water status and therefore make species/life-form comparisons, transpiration of WD plants was expressed as a percentage of WW plants. Transpiration of WD as a percentage of WW was then related to capacity of plants to maintain water status (predawn water potential) in response to the WD treatment. Shifts in biomass allocation (RMF and LAR) and leaf morphology (SLA) of WD plants were expressed as a percentage of WW plants as well as in absolute terms and related to predawn water potential.

Statistical analysis

Differences in soil water content between days were analysed within species using one-way ANOVA. The day where SWC (before watering) was not significantly different from the previous day was identified as the point at which stored water in the pot was considered depleted and plants relied solely on water delivered by the WD treatment (indicated by an arrow in Fig. 1). Treatment differences within and between species and treatments were analysed using one-way ANOVA. Relationships between predawn water potential and transpiration, biomass allocation and leaf morphology were analysed using simple linear regression. Data were transformed where necessary to ensure univariate normality. All data presented in figures and tables are non-transformed data. Significant differences between species means were determined by Tukey's post hoc test ($P < 0.05$). All data analyses used GenStat 12.1 (2009, VSN International Ltd.).

Results

Soil water content and transpiration

Species differed dramatically in rates of water use per pot under WW conditions, with *I axillaris* and *Derwemtia perfoliata* (herbs), transpiring 125.7 and 92.7 g H_2O d^{-1}, compared to the species average of 52.1 g H_2O d^{-1} (Table 2). In contrast, *S. pachyphyllum*, commonly used on green roofs used only 4.3 g H_2O pot^{-1} d^{-1}. Two shrubs, *Grevillea alpina* and *Hibbertia obtusifolia* showed similarly low transpiration rates on a pot basis (Table 2). However, when transpiration was expressed per unit final leaf area, all monocots, all shrubs (except *Calytrix tetragona*) and the herb *D. perfoliata* showed similar rates of water use (Table 2). *C. tetragona* and *I. axillaris* showed the highest rate of water use on a per unit leaf area basis (more than two-fold higher than the mean for all species). Granite outcrop species transpired 9.6 - 58.8 times more than *S. pachyphyllum* per unit leaf area.

Species differed in the time taken to deplete soil water status to the minimum level maintained by the WD treatment (Fig. 1) due to differences in transpiration rate on a pot basis (Table 2). *I. axillaris* and *D. perfoliata* depleted stored water after 14 days on account of high transpiration rates per pot. In contrast, *G. alpina* and *H. obtusifolia* took 38 days to deplete pot water capacity in the WD treatment due to relatively low transpiration rates on a per pot basis. *S. pachyphyllum* showed the lowest transpiration rates of all species on a per pot basis under WD conditions and was the only species to not show a statistically significant difference in transpiration rate between watering treatments (Table 2).

Shrubs did not show a significant difference in transpiration between watering treatments, when expressed per unit final leaf area (Table 2). Of the remaining species, *A. milleflorum* (monocot), *B. multifida* and *C. semipapposum* (herbs) and *S. pachyphyllum* (succulent) also showed no significant difference in transpiration per unit leaf area between treatments (Table 2). The remaining herbs (*D. perfoliata* and *I. axillaris*) and monocots (*D. admixta*, *Lomandra filiformis* and *Stypandra glauca*) showed statistically lower transpiration per unit leaf area under WD conditions compared with WW.

Plant water status

At the end of the experiment (day 51) species differed in their predawn water potential (Ψ_{PD}) and leaf relative water content (RWC) in response to the WD treatment (Table 3). All species showed a lower Ψ_{PD} for the WD compared with the WW treatment, with the exception of *A. milleflorum* (Table 3). Species differed in Ψ_{PD} within the WW treatment, with *H. obtusifolia*, *L. longifolia*, *I. axillaris*, *S. glauca* and *A. milleflorum* maintaining higher Ψ_{PD} (-0.30 to -0.34 MPa) compared with *C. semipapposum* and *Correa reflexa* (-0.65 to -0.70 MPa). Aside from *A. milleflorum*, *S. glauca*, *D. admixta* and *I. axillaris* all showed the smallest difference in Ψ_{PD} between treatments (82-109%) reduction between WW and WD treatments). Under WD conditions, *G. alpina* showed the lowest Ψ_{PD} (-5.23 MPa) although not significantly lower than *C. semipapposum* (-4.61 MPa) or *B. multifida* (-3.70 MPa). All monocotyledonous species and *I. axillaris* maintained Ψ_{PD} > -1.5 MPa under WD conditions.

A. milleflorum, *L. longifolia*, *S. glauca* and *I. axillaris* showed no difference in Ψ_{MD} between the WW and WD treatments while all other species showed a lower Ψ_{MD} for WD (Table 3). *I. axillaris* and *H. obtusifolia* had the highest Ψ_{MD} under WW conditions (-0.92 MPa), significantly higher than *D. admixta* (-1.44 MPa), *L. longifolia* (-1.58 MPa) and *D. perfoliata* (-1.86 MPa). *I. axillaris* showed the highest Ψ_{MD} for the WD treatment (-1.03 MPa) which was higher than all other herbs and the shrubs. Under WD conditions, *C. semipapposum* and *G. alpina* showed the lowest Ψ_{MD} (-5.76 and -5.32 MPa).

There was no difference between treatments in pre-dawn leaf relative water content (RWC) for *A. milleflorum*, *L. longifolia*, *S. glauca* and *S. pachyphyllum* (Table 3). All other species showed lower RWC in the WD treatment compared with WW. The largest difference in RWC between treatments was shown in *B. multifida* and *C. semipapposum* (34 and 30% lower for the WD treatment). *I. axillaris* had the highest RWC in the WW treatment (101.7%) which was higher than the other herbs, the shrubs except for *C. tetragona* and *S. glauca*. *C. semipapposum* and *B. multifida* had the lowest RWCs in response to the WD treatment (61.2 and 61.8%) but were not significantly different from *G. alpina* (65.7%) or *H. obtusifolia* (72.6%).

Biomass allocation, leaf area ratio and specific leaf area

Proportion of biomass allocated to roots (root mass fraction; RMF) increased by 18-133% for monocots (except *L. longifolia*), shrubs (except *C. tetragona*) and *S. pachyphyllum* in response to the WD treatment (Table 4). *A. milleflorum* (geophytic monocot) showed the highest RMF under WW and WD conditions; significantly higher than all species except *D. admixta*. Despite RMF increasing by the greatest proportion in *G. alpina* in response to the WD treatment (133%), it showed the lowest RMF under WD conditions (0.28 g g^{-1}) compared with species which did not differ between WW and WD conditions, including: *C. semipapposum* (0.46 g g^{-1}) and *L. longifolia* (0.50 g g^{-1}).

Leaf area ratio (LAR) was significantly lower under WD conditions for all species except *D. perfoliata* and *I. axillaris* (Table 3). *A. milleflorum* showed the highest LAR under WW conditions, 3.5-fold greater than the lowest (*C. tetragona*). *C. tetragona* also showed the lowest LAR under WD conditions (0.88 m^2 kg^{-1}) while *D. perfoliata* showed the highest (4.73 m^2 kg^{-1}).

Specific Leaf Area (SLA) was significantly lower under WD conditions than in WW plants for all species except *D. perfoliata, I. axillaris* and *G. alpina* (Table 3). *C. tetragona* showed the largest difference between WW and WD (52% reduction); while *L. longifolia* showed the smallest significant difference (15% reduction). *A. milleflorum* had a substantially higher SLA than all other species regardless of treatment (125% greater than the mean of all other species).

Relationships between transpiration, biomass allocation and plant water status

In the WD treatment there was a significant but weak negative relationship ($R^2 = 0.40$; $P = 0.028$) between transpiration on a per pot basis (WD as a % of WW) and plant water status (predawn water potential) across all species and life-forms at the end of the experiment (Fig. 2a). There was, however, no significant relationship between transpiration per unit leaf area or transpiration per unit final biomass and predawn water potential (Fig. 2b and 2c).

There was no significant relationship between the change in root mass fraction (RMF) and predawn water potential between WW and WD conditions (Fig. 3a); however, species with a high RMF in absolute terms typically showed a high water status under WD conditions (Fig. 3b; $R^2 = 0.36$; $P = 0.039$). There was no relationship between leaf area ratio (LAR) or specific leaf area (SLA), on a relative or absolute basis, and predawn water potential at the end of the experiment in the WD treatment (Fig. 3c-3f).

Water use strategy and water status

Table 5 categorises the water use strategies and water status of each species into one of three arbitrary categories to summarise key physiological traits. Ideal physiological traits for selecting green roof plants are highlighted and include (i) high water users under well watered conditions, (ii) low water users under water deficit and (iii) species able to maintain high water status under water deficit. No one species achieved all three ideal physiological traits; however, in general the monocots and *I. axillaris* (herb) achieved both the capacity to use high rates of water under well watered conditions as well as the capacity to maintain water status under water deficit.

Discussion

This paper determined the suitability of granite outcrop species for use on green roofs. For green roofs to effectively reduce stormwater runoff, vegetation must not only use high amounts of water when available post rainfall to reduce runoff, but also persist and survive extended periods of drought.

Water-use strategies of granite outcrop species under well watered and drought stress conditions

We observed large differences between granite outcrop species in the rates of water use under well watered conditions on a per pot basis. Species could be allocated to one of three water use strategies when water supply was not limiting: high, medium and low water users (Table 5). Most species achieved moderate-high transpiration rates, using substantially more water than the commonly planted green roof succulent, *Sedum pachyphyllum.* These results suggest that, despite the variety of water use strategies observed, granite outcrop species are better able to reduce stormwater runoff than highly conservative exotic succulent species (Wolf and Lundholm 2008). Monocots and herbs tended to use more water than shrubs, which is likely to be related to their ecological strategies as early colonisers on shallow soil accumulations on granite slopes (Beadle 1981). When water use was expressed on a per unit leaf area basis rather than per pot, rates of water use were similar for 8 of the 12 granite outcrop species. For example, on a pot basis two of the smallest shrubs, *G. alpina* and *H. obtusifolia*, showed similar transpiration rates to *S. pachyphyllum* and depleted soil moisture at a slower rate. However, their rates of water use were much higher on a leaf area basis than *S. pachyphyllum*, suggesting that smaller size, rather than conservative water use, delayed depletion of soil moisture. As our plants were all the same age, this indicates that plant size (most likely leaf area), rather than inherent differences in rate of water loss per unit leaf, was the key driver of water use. Size of mature plants is therefore a critical design consideration for green roofs if high water use is a desired trait.

Granite outcrop species also showed a range of responses to the water deficit treatment which effectively mimicked their water use strategies under well watered conditions (Table 5). This is not surprising as the volume of water delivered to plants under water deficit was dependent on rates of water use of well watered plants; thus exposing each species to the same level of drought stress relative to its own control. The reduction in transpiration of plants under water deficit relative to their well-watered control was, however, independent of this experimental design. Three of the shrubs (*G. alpina, H. obtusifolia* and *C. reflexa*) and the herb *B. multifida* showed the smallest reductions in transpiration from well watered to water deficit conditions. This response is often observed in evergreen shrubs from dry environments which typically show conservative rates of water use with low plasticity, low hydraulic efficiency and low vulnerability to xylem embolism (Galmés et al. 2007; Hacke et al. 2000; Mitchell et al. 2008; Sperry and Hacke 2002). In contrast, the shrub *C. tetragona* showed a large reduction in transpiration from WW to WD deficit conditions, indicating high sensitivity to drought (Chaves et al. 2002; Sperry 2000). Inconsistencies in water-use strategies of similar life-forms are common in comparative physiological studies and highlight the need to describe species by physiological behaviour (Cooke and Suski 2008). The remaining species (monocots and herbs) showed high sensitivity to water deficit through large reductions in transpiration as soil moisture status declined. High sensitivity to declining water status is typical of perennial non-woody species from water-limited environments which must balance the need to maximise carbon assimilation when soil moisture is high; yet retain the capacity to survive short periods of intense water deficit (Chaves et al. 2002).

Water status of granite outcrop species under well watered and drought stress conditions

In addition to high water use following rainfall, green roof plants need to be able to tolerate periods of drought due to low water storage capacity of the shallow substrate. We considered species to have a higher relative level of drought tolerance if they were able to maintain water status (Ψ_{PD}) above -1.5 MPa when they received 20% of the water used by their well watered control. Four monocot species (*S. glauca*, *D. admixta*, *L. longifolia* and *A. milleflorum*) and one herb (*I. axillaris*), maintained high water status under this regime. These species typically occupy the shallowest soil-filled depressions on granite outcrops (Bayly 1999; Hunter and Clarke 1998) where abiotic stresses are severe (Parsons and Hopper 2003; Shure and Ragsdale 1977), therefore it is not surprising that these species are well-adapted to drought stress. The mechanisms by which they achieve the high water status are less clear. However, of these 5 species, all except *D. admixta* showed no difference in Ψ_{MD} between treatments. This result indicates that, relative to other species studied here, *A. milleflorum*, *L. longifolia*, *S. glauca* (monocots) and the herb *I. axillaris* showed isohydric behaviour by maintaining similar midday water status under both well watered and water deficit conditions (Tardieu and Simonneau 1998).

Isohydric behaviour is typically facilitated through high stomatal sensitivity to increasing evaporative demand/transpiration rate (Flexas et al. 2006; Mott and Parkhurst 1991) or leaf water status (Davies and Zhang 1991; Tardieu and Davies 1993) regardless of soil moisture status (Tardieu and Simonneau 1998). Although we did not measure stomatal conductance during this experiment, it is likely that the isohydric species closed stomata and reduced water-use to a minimum when soil moisture conditions became unfavourable. This would explain relatively high water-use in the drought treatment and a high water status. High stomatal sensitivity to drought is a desirable physiological trait for plants on green roofs; however, extended periods without gas exchange have the potential to cause damaging leaf temperatures (West et al. 2012), particularly on green roofs where surface temperatures can exceed 60º C (Szarzynski 2000; Wong et al. 2003). Hence, it is possible that these species may suffer heat stress and aboveground parts may not survive extended periods of drought stress. However, a reduction or loss of aboveground organs is part of the ecological strategy of these species as they are likely to survive extended periods of drought due to fleshy and succulent belowground organs (Pate and Dixon 1981).

Of the species which did not maintain a relatively high water status under water deficit, all showed a large reduction in Ψ_{MD} from well watered to water deficit conditions which typically suggests anisohydric behaviour (Tardieu and Simonneau 1998). These results must be interpreted with caution, as the Ψ_{PD} values for these species (-2.20 to -5.23 MPa) indicate these plants were under a high level of drought stress (Jacobsen et al. 2009). It is therefore unclear whether these plants are physiologically plastic and facilitating reductions in Ψ_{MD} through elastic or osmotic adjustments (Sanders and Arndt 2012), or whether they have lost turgor and were effectively dead or dying. It is possible that the behaviour of these species was affected by the nature of the water deficit treatment and that our classifications of isohydry and anisohydry may not hold in alternative (e.g. terminal) drought treatments (Pou et al. 2012).

Plasticity in physiological and/or morphological traits

Maintenance of water status (Ψ_{PD}) in response to the water deficit was related to the degree to which species reduced whole plant transpiration relative to their well watered control. The five granite outcrop species which maintained a high water status during water deficit reduced rates of transpiration to 23-28% of their well watered control. This indicates an enhanced capacity to survive periods of low water availability and was most likely achieved through high stomatal sensitivity to declining water supply (Jarvis and McNaughton 1986).

Whole plant responses to drought stress can also involve changes in plant biomass allocation to avoid dehydration (Cowan 1981; Poorter and Nagel 2000). Most species we exposed to water deficit increased allocation to roots and reduced leaf area ratio and SLA. However, there were no significant relationships between changes in morphological traits and maintenance of water status in response to water deficit. For example, RMF of the shrub *G. alpina* increased by 133% in response to water deficit but this was insufficient to maintain water status.

Importantly, plants with inherently high RMF maintained water status when water was limited. High RMF is common in plants from areas with low precipitation (Poorter et al. 2012). In our experiment the species with the highest RMF were the four monocots, where high RMF was due to underground storage organs: *S. glauca*, *D. admixta*, *L. longifolia* had fleshy rhizomes while *A. milleflorum* has tubers (Parsons 2000; Pate and Dixon 1981). The shrubs and herbs in our study also had relatively high RMF when compared with a range of drought-adapted species from Mediterranean environments (Hernández et al. 2010). However, with the exception of *I. axillaris,* these shrub and herb species were all severely affected by water limitations and none were able to maintain water status despite relatively high RMF. High RMF in shrubs from shallow soil habitats is thought to increase plant available water through increased access to cracks and fissures and deeply stored water in underlying bedrock (Poot and Lambers 2003; Sternberg 1996). In our study root foraging was limited by pot size, negating the benefits of high RMF for maintaining water status.

The species which maintained water status under WD conditions all possessed some degree of succulence, which is likely to have enhanced their capacity to maintain water status as soil moisture declined (Eggli and Nyffeler 2009). In true succulents, such as *S. pachyphyllum* water stored in stems and leaves is redistributed around the plant to maintain physiological activity (Eggli and Nyffeler 2009). Similarly, plants which store water in underground storage organs and use it for growth or flowering before the onset of rain are also considered succulents (Eggli and Nyffeler 2009). *I. axillaris* has succulent stems (Nikulinsky and Hopper 1999) and the monocots (*S. glauca*, *D. admixta*, *L. longifolia* and *A. milleflorum*) all have fleshy underground storage organs (Parsons 2000; Pate and Dixon 1981). Kluge and Brulfert (2000) suggest that underground storage organs of hemicryptophytes may help to maintain homeostasis in plant water budgets and explain the prevalence of this life-form on granite outcrops. Rhizopoulou et al. (1997) also reported that the summer dormant geophyte *Asphodelus aestivus* from the east Mediterranean showed high root water potential relative to soil water status, due to below-ground water storage in tubers. In our study, it is likely that the high water content capacity of *A. milleflorum's* tubers (up to 88%; Incoll et al. 1989) facilitated maintenance of leaf water status under water deficit.

Physiological traits can be used to develop a conceptual model for plant selection for green roof plants.

Plant selection for green roofs needs to consider trade-offs between low water use for survival and high water use for stormwater mitigation (MacIvor et al. 2011). In order to evaluate these potential trade-offs, we developed a conceptual model where species were categorised according to (i) water use strategy under WW conditions, (ii) rate of water use under water deficit and (iii) maintenance of water status under water deficit (Table 5). Across the 12 granite outcrop species there were differences in response to water availability. Preferred species for green roofs are those with high water use under well watered conditions for effective stormwater mitigation and can maintain water status under water deficit (Category 1 species) (Table 5). It is also generally assumed that species with slow rates of water use under water deficit conditions (Category 3 species; Table 5) will be more drought tolerant. However, we did not find this as shrubs were unable to maintain water status despite slow rates of water use under water deficit. The monocots and *I. axillaris* (herb) had high rates of water use when available and maintained water status under water deficit. These species also had high rates of water use under water deficit but were presumably able to tolerate drought stress and maintain water status through stomatal closure or access to stored water in underground tubers and rhizomes.

Life-form differences in water use strategies and drought tolerance reflect differences in species distribution across granite outcrop habitats. Soil depth and water availability determine vegetation structure and composition across rock outcrops (Shure and Ragsdale 1977). In our study the most drought tolerant species, the four monocots and the herb *I. axillaris*, all occupy shallow depressions on southern Australian outcrops (Michael and Lindenmayer 2012) (Beadle 1981; Hopper et al. 1997; Hunter and Clarke 1998). Globally, monocots are relatively abundant and diverse on rock outcrops (Ornduff 1987; Pérez-García and Meave 2005) making up 32-45% of all species, compared with 26% as the 'normal spectrum' of Raunkiaer (Walters and Wyatt 1982). In shallow depressions abiotic conditions are both extreme and highly variable (Shure and Ragsdale 1977; Szarzynski 2000) and the ability to cope with unpredictable or seasonal drought is an important strategy for survival (Hopper 2000). Facultative dormancy in monocots with underground storage enables these species to survive severe drought but also make the most of unpredictable rainfall for growth or reproduction (Kluge and Brulfert 2000). Stem succulence in herbs such as *I. axillaris* (Nikulinsky and Hopper 1999) would also facilitate persistence in shallow depressions. Shrubs generally occur in deeper soil depressions or in cracks (Biedinger et al. 2000; Porembski and Barthlott 2000) and may avoid water stress by accessing deeper stored water in the underlying bedrock (Poot et al. 2012; Schwinning 2010). While this is successful strategy on outcrops, access to water on green roofs is limited by the shallow profile and therefore the high water potentials and anisohydric response of shrubs to water deficit is a risky strategy. These species also had inherently low water use under well watered conditions and would not be very useful for stormwater mitigation.

Potentially rates of water use under water deficit may be a consequence of our experimental design. Although all species were exposed to the same level of drought stress relative to the control, species which used more water under well watered conditions also received more water under water deficit. This additional water may have been sufficient to maintain water status in the high water users under water deficit. However, species behaved similar under a subsequent experiment under terminal drought (data not shown). Further, as previously mentioned, under terminal drought, species would not have had sufficient time for morphological changes to occur in response to drought as they did under water deficit.

Conclusions

By using physiological traits as a screening tool we identified several potential granite outcrop species, which were drought tolerant high water users. These species optimize green roof performance by using high amounts of water when it is available and reduce runoff, but they will also persist and survive periods of drought. Unlike the green roof succulent (*S. pachyphyllum*), all of the granite outcrop species showed plasticity in water use. However, the best species for green roof selection in our study were the monocots (*A. milleflorum*, *S. glauca*, *D. admixta*, *L. longifolia*) and the herb *I. axillaris* which had the highest rates of transpiration under well watered conditions and could also maintain water status under water deficit. This was achieved through reduced transpiration and/or high inherent RMF and demonstrates that high water users can also be drought tolerant making them the most suitable species tested for green roofs. These species all had some degree of root, stem or leaf succulence and future plant selection for green roofs should prioritise these traits in non-*Sedum* species. Our conceptual model provides a framework for green roof plant selection based on physiological traits and future research should validate this approach, particularly in regard to stormwater runoff from extensive green roofs. Further, although it is tempting to plant roofs with these optimal species, we believe that green roofs should still be planted with a diversity of life-forms and drought avoidance strategies to ensure both performance and resilience (Lundholm et al. 2010; MacIvor et al. 2011). Other criteria such as plant form and aesthetics may also be important considerations for plant selection on highly designed green roofs. This approach of species selection based on physiological response to water availability also has great potential for improving ecosystem services provided by green infrastructure beyond green roofs.

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Figure captions

Fig. 1 Soil water content (SWC) over time for well watered (WW; open symbols) and water-deficit (WD; closed symbols) treatments over the course of the experiment (50 days) for grass-like monocotyledons (left), herbs (centre) and shrubs (right). Values represent mean SWC before and after re-watering events every 3-4 days. Arrows for the WD treatment indicate the day after which there was no significant difference (one-way ANOVAs) in preor post-watering SWC between days; thereby differentiating between the initial drying phase to the left of the arrow and the steady-state phase to the right. *Sedum pachyphyllum* is not shown here as it did not reach a steady-state SWC by day 50 in the WD treatment. Bars on values represent mean standard error (n=5)

Fig. 2 Relationship between pre-dawn water potential on the final day of the experiment (Ψ_{PD}) and transpiration (E) under water deficit (expressed as a proportion of the well watered (WW) control for each species). E is calculated both on a per pot basis (A) and per unit leaf area (LA) at final harvest (B). Different symbols indicate life-form, where white squares = monocots, black triangles = herbs and grey circles = shrubs. Bars represent standard error of the mean (n=5)

Fig. 3 Relationship between pre-dawn water potential on the final day of the experiment (Ψ_{PD}) and root mass fraction (RMF), leaf area ratio (LAR) and specific leaf area (SLA) under water deficit. RMF, LAR and SLA are expressed relative to the well watered (WW) control (A, C and E) and in absolute terms (B, D and F) for each species. Different symbols indicate life-form, where white squares = monocots, black triangles = herbs and grey circles = shrubs. Bars represent standard error of the mean (n=5)

Table 1 Life-forms and descriptions of granite outcrop species used in drought screening experiment

Family	Species	Raunkiaer (1934) Life-form Classification
Monocots		
Antheraceae	*Arthropodium milleflorum*	Geophyte
Phormiaceae	*Dianella admixta*	Graminoid Hemicryptophyte
Lomandraceae	*Lomandra longifolia*	Graminoid Hemicryptophyte
Phormiaceae	*Stypandra glauca*	Graminoid Hemicryptophyte
Herbs		
Asteraceae	*Brachyscome multifida*	Hemicryptophyte
Asteraceae	*Chrysocephalum semipapposum*	Hemicryptophyte
Scrophulariaceae	*Derwentia perfoliata*	Hemicryptophyte
Lobeliaceae	*Isotoma axillaris*	Hemicryptophyte
Shrubs		
Proteaceae	*Grevillea alpina*	Chamaephyte
Dilleniaceae	*Hibbertia obtusifolia*	Chamaephyte
Rutaceae	*Correa reflexa*	Chamaephyte
Myrtaceae	*Calytrix tetragona*	Chamaephyte

Geophyte = persistent buds buried to a depth of 2-3 cm;
Hemicryptophyte = persistent buds are in the immediate vicinity of the soil surface only, maximum height of 1 cm;
Chamaephyte = persistent buds greater than 1 cm and less than 20-30 cm above ground surface.

Table 2 Average daily transpiration (E) per pot and per square metre of final leaf area for well watered (WW) and water deficit (WD) treatments. Values in parentheses show mean standard error (n=5). P-values indicate significant differences between treatments within species. Different letters indicate significant differences between species within treatments (all P-values <0.001). Transpiration of water deficit plants is also expressed as a percentage of well watered plants (WD% of WW) for species with a significant difference between treatments

	E (g H_2O pot^{-1} d^{-1})				E (g H_2O m^{-2} d^{-1})			
Species	**WW**	**WD**	**P-value**	**WD% of WW**	**WW**	**WD**	**P-value**	**WD% of WW**
Monocots								
A. milleflorum	49.8^{cde} (8.0)	13.5^{d} (0.01)	0.002	27	401^{b} (72)	489^{abc} (44)	0.326	-
D. admixta	71.0^{efg} (7.6)	17.5^{e} (0.2)	<0.001	25	605^{bc} (32)	315^{ab} (29)	<0.001	52
L. longifolia	39.9^{bcde} (3.0)	11.3^{c} (0.2)	<0.001	28	782^{bc} (42)	547^{abcd} (36)	0.003	70
S. glauca	85.1^{fg} (7.8)	21.9^{f} (0.4)	<0.001	26	710^{bc} (79)	384^{ab} (28)	0.005	54
Herbs								
B. multifida	36.3^{bcd} (6.0)	10.8^{c} (0.5)	0.003	30	1339^{c} (224)	1375^{d} (148)	0.895	-
C. semipapposum	46.7^{bcde} (4.9)	11.4^{c} (0.2)	<0.001	24	1116^{c} (148)	846^{abcd} (92)	0.159	-
D. perfoliata	92.7^{gh} (10.9)	24.1^{g} (0.3)	<0.001	26	608^{b} (83)	245^{a} (31)	0.003	40
I. axillaris	125.7^{h} (9.4)	28.5^{h} (0.1)	<0.001	23	1843^{d} (108)	1092^{bcd} (144)	0.003	59
Shrubs								
G. alpina	14.4^{ab} (2.2)	7.9^{b} (0.2)	0.018	55	779^{bc} (91)	920^{abcd} (131)	0.459	-
H. obtusifolia	19.2^{abc} (2.4)	7.1^{b} (0.4)	0.001	37	788^{bc} (51)	1267^{cd} (65)	0.054	-
C. reflexa	34.0^{bcd} (5.1)	10.7^{c} (0.1)	0.002	31	852^{bc} (119)	675^{abcd} (71)	0.283	-
C. tetragona	58.5^{def} (9.6)	14.3^{d} (0.1)	0.002	24	2272^{d} (489)	2276^{e} (518)	0.996	-
Succulents								
S. pachyphyllum	4.3^{a} (3.6)	5.2^{a} (0.2)	0.807	-	38^{a} (30)	90^{a} (8)	0.131	-

Table 3 Mean leaf water potential at pre-dawn (Ψ_{PD}) and midday (Ψ_{MD}) and leaf relative water content at pre-dawn (RWC) for well watered (WW) and water deficit (WD) treatments on day of harvest (Day 51). Values in parentheses show mean standard error (n=5). P-values indicate significant differences between WW and WD treatments within species. Different letters indicate significant differences between species within treatments (all P-values <0.001). Water potential was not determined (n.d) for *S. pachyphyllum* due to high leaf succulence

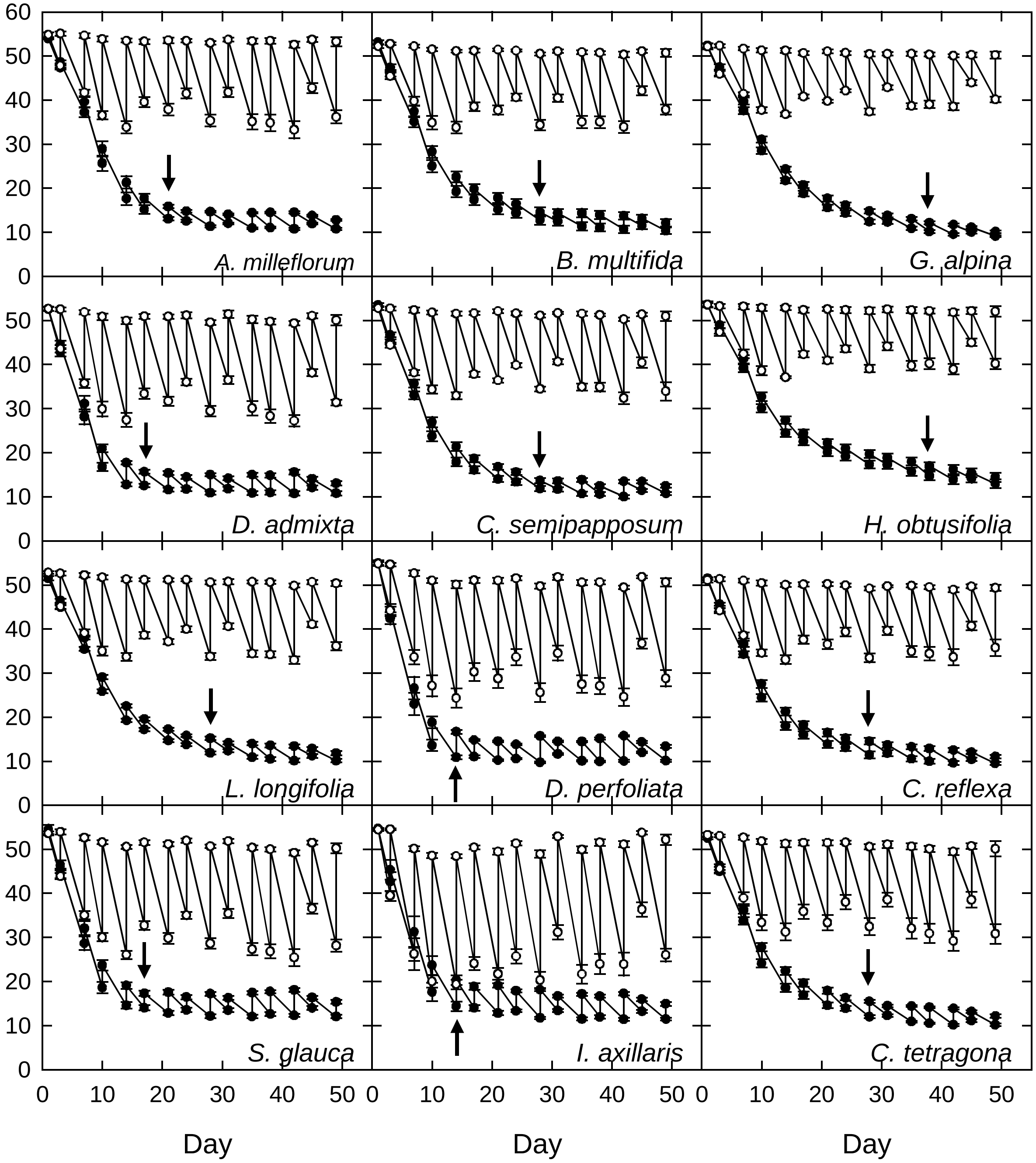
	Ψ_{PD} (MPa)			**Ψ_{MD} (MPa)**			**RWC (%)**		
Species	**WW**	**WD**	**P-value**	**WW**	**WD**	**P-value**	**WW**	**WD**	**P-value**
Monocots									
A. milleflorum	-0.39 ^{cd}	-0.50 ^{e}	0.084	-1.04 ^{cde}	-1.20 ^{ef}	0.450	98.5 ^{bcd}	96.8 ^{e}	0.117
	(0.03)	(0.04)		(0.10)	(0.17)		(0.4)	(0.8)	
D. admixta	-0.53 ^{abcd}	-1.05 ^{de}	0.026	-1.44 ^{abcd}	-2.42 ^{cdef}	<0.001	98.5 ^{bcd}	95.0 ^{de}	<0.001
	(0.10)	(0.17)		(0.12)	(0.10)		(0.5)	(0.2)	
L. longifolia	-0.31 ^{d}	-1.18 ^{de}	0.007	-1.58 ^{ab}	-1.85 ^{def}	0.384	99.7 ^{cd}	98.0 ^{e}	0.622
	(0.05)	(0.24)		(0.20)	(0.21)		(0.4)	(2.9)	
S. glauca	-0.34 ^{cd}	-0.62 ^{e}	<0.001	-1.11 ^{bcde}	-1.36 ^{def}	0.128	91.8 ^{ab}	90.8 ^{cde}	0.473
	(0.02)	(0.05)		(0.09)	(0.12)		(1.2)	(0.4)	
Herbs									
B. multifida	-0.49 ^{abcd}	-3.70 ^{abc}	<0.001	-1.17 ^{bcde}	-3.82 ^{bc}	0.005	93.5 ^{abc}	61.8 ^{a}	<0.001
	(0.02)	(0.63)		(0.07)	(0.69)		(1.6)	(5.1)	
C. semipapposum	-0.65 ^{ab}	-4.61 ^{ab}	<0.001	-1.52 ^{abc}	-5.76 ^{a}	<0.001	87.5 ^{a}	61.2 ^{a}	<0.001
	(0.07)	(0.27)		(0.09)	(0.26)		(2.4)	(5.7)	
D. perfoliata	-0.40 ^{bcd}	-2.20 ^{cd}	<0.001	-1.86 ^{a}	-3.63 ^{bc}	<0.001	92.0 ^{ab}	80.6 ^{bcde}	0.002
	(0.02)	(0.24)		(0.15)	(0.31)		(0.4)	(2.4)	
I. axillaris	-0.34 ^{cd}	-0.71 ^{e}	0.004	-0.92 ^{e}	-1.03 ^{f}	0.350	101.7 ^{d}	95.5 ^{e}	0.045
	(0.04)	(0.08)		(0.08)	(0.08)		(1.2)	(2.3)	
Shrubs									
G. alpina	-0.50 ^{abcd}	-5.23 ^{a}	<0.001	-1.04 ^{cde}	-5.32 ^{ab}	<0.001	90.5 ^{a}	65.7 ^{ab}	<0.001
	(0.08)	(0.60)		(0.04)	(0.26)		(3.2)	(3.9)	
H. obtusifolia	-0.30 ^{d}	-2.97 ^{bc}	<0.001	-0.92 ^{e}	-3.83 ^{bc}	0.002	91.3 ^{ab}	72.6 ^{abc}	<0.001
	(0.03)	(0.49)		(0.03)	(0.67)		(1.2)	(3.3)	
C. reflexa	-0.70 ^{a}	-3.07 ^{bc}	<0.001	-1.29 ^{bcde}	-2.96 ^{cd}	0.008	91.2 ^{ab}	77.1 ^{bcd}	0.018
	(0.04)	(0.36)		(0.09)	(0.47)		(1.3)	(4.6)	
C. tetragona	-0.57 ^{abc}	-2.49 ^{cd}	0.002	-1.00 ^{de}	-2.80 ^{cde}	<0.001	90.4 ^{abcd}	81.3 ^{bcde}	0.011
	(0.05)	(0.36)		(0.09)	(0.09)		(1.7)	(2.1)	
Succulents									
S. pachyphyllum	n.d.	n.d.		n.d.	n.d.		94.6 ^{abcd}	95.8 ^{e}	0.337
							(0.7)	(1.2)	

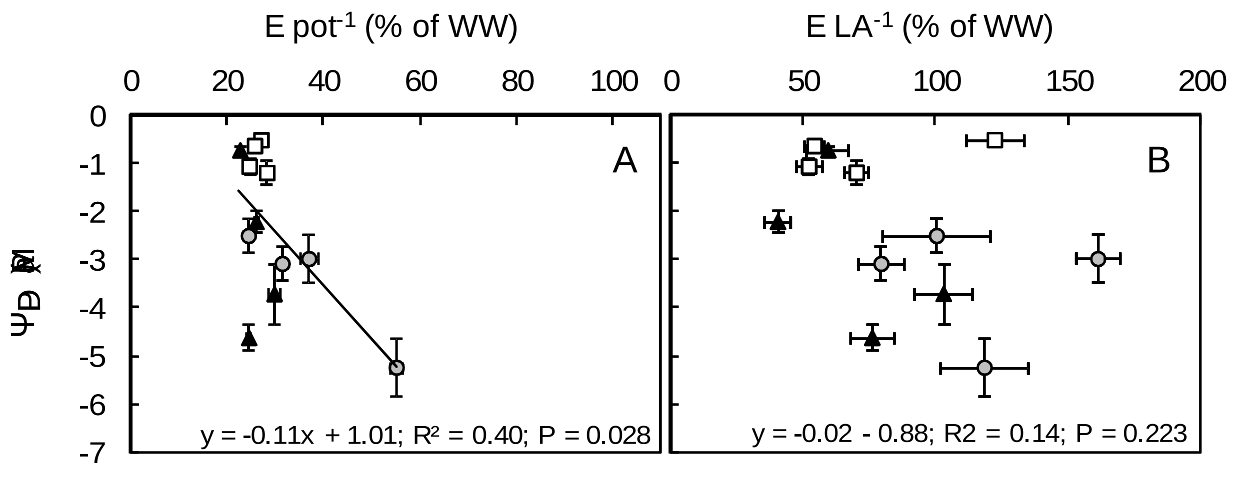
Table 4 Root mass fraction (RMF), leaf area ratio (LAR) and specific leaf area (SLA) for well-watered (WW) and water-deficit (WD) treatments. Values in parenthesis represent mean standard error (n=5). P-values indicate significant differences between WW and WD treatments within species and different letters denote significant differences between species within WW or WD treatments (all P values <0.001)

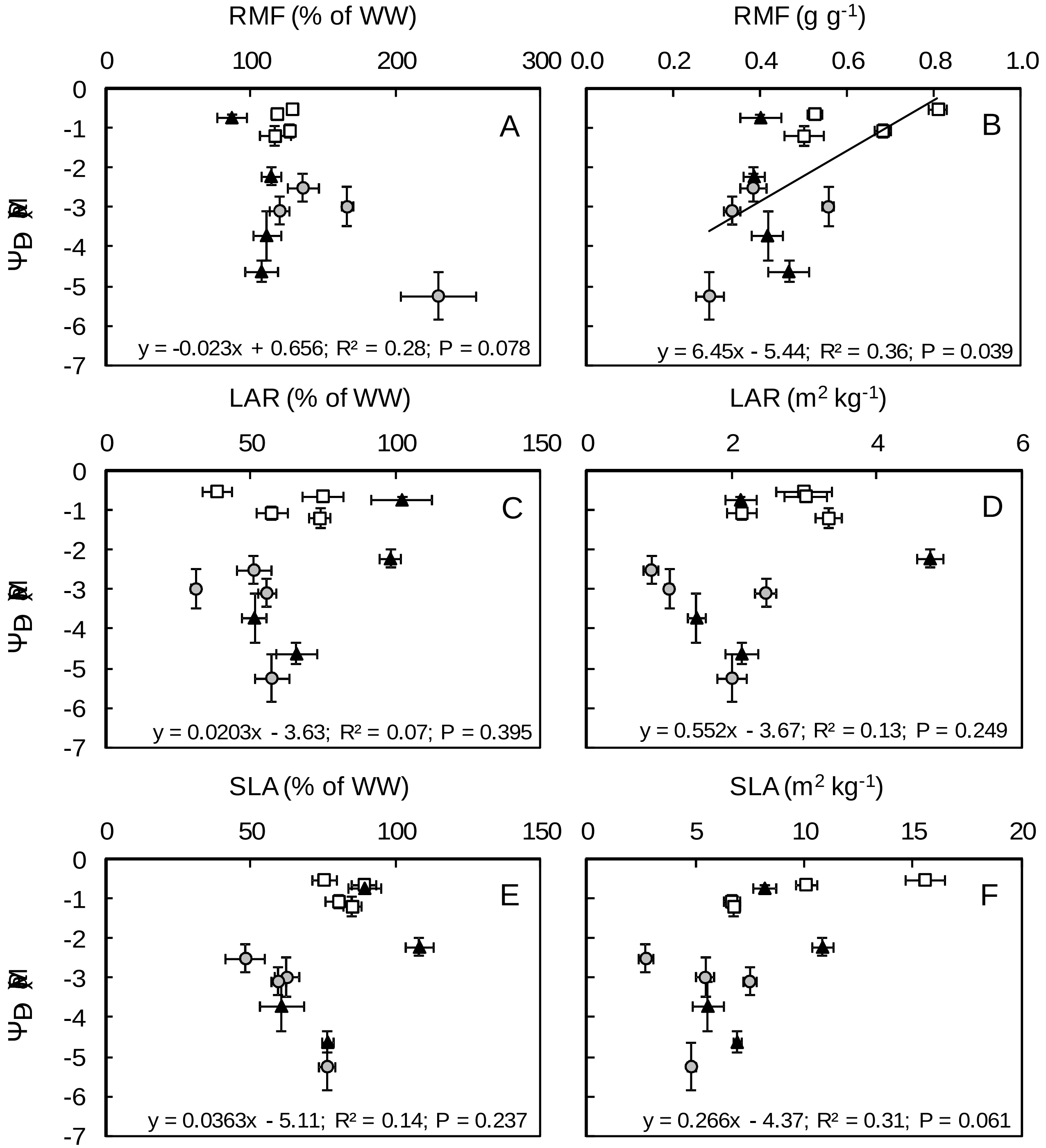
	RMF (g g^{-1})			**LAR (m^{2} kg^{-1} plant)**			**SLA (m^{2} kg^{-1} leaf)**		
Species	**WW**	**WD**	**P-value**	**WW**	**WD**	**P-value**	**WW**	**WD**	**P-value**
Monocots									
A. milleflorum	0.63^{f} (0.05)	0.81^{g} (0.02)	0.009	7.81^{e} (1.36)	2.99^{def} (0.38)	0.009	20.7^{e} (1.1)	15.5^{h} (0.9)	0.006
D. admixta	0.54^{ef} (0.04)	0.69^{fg} (0.01)	0.004	3.63^{abc} (0.32)	2.18^{cde} (0.23)	0.007	8.3^{abc} (0.4)	6.6^{bcde} (0.4)	0.021
L. longifolia	0.43^{de} (0.02)	0.50^{cde} (0.04)	0.196	4.52^{bcd} (0.22)	3.33^{f} (0.17)	0.003	7.9^{abc} (0.4)	6.7^{bcde} (0.3)	0.035
S. glauca	0.44^{de} (0.02)	0.52^{de} (0.02)	0.016	4.04^{abcd} (0.35)	3.02^{def} (0.29)	0.046	11.3^{cd} (0.7)	10.1^{fg} (0.5)	0.174
Herbs									
B. multifida	0.38^{cd} (0.02)	0.42^{abcde} (0.04)	0.379	2.96^{abc} (0.36)	1.51^{abc} (0.13)	0.005	9.2^{abcd} (1.0)	5.5^{bcd} (0.7)	0.016
C. semipapposum	0.43^{de} (0.03)	0.46^{bcde} (0.05)	0.613	3.25^{abc} (0.41)	2.13^{bcde} (0.22)	0.045	9.0^{abcd} (0.9)	6.9^{bcde} (0.2)	0.043
D. perfoliata	0.34^{bcd} (0.03)	0.39^{abcd} (0.02)	0.219	4.83^{cd} (0.40)	4.73^{g} (0.17)	0.828	10.0^{bcd} (0.4)	10.8^{g} (0.5)	0.247
I. axillaris	0.46^{de} (0.02)	0.40^{abcde} (0.05)	0.259	2.07^{ab} (0.26)	2.11^{bcde} (0.21)	0.907	9.2^{abcd} (0.3)	8.2^{ef} (0.5)	0.142
Shrubs									
G. alpina	0.12^{a} (0.01)	0.28^{a} (0.03)	0.005	3.50^{abc} (0.43)	2.00^{bcd} (0.20)	0.029	6.3^{ab} (0.7)	4.8^{ab} (0.3)	0.120
H. obtusifolia	0.33^{bcd} (0.02)	0.56^{ef} (0.01)	<0.001	3.64^{abc} (0.76)	1.13^{ab} (0.05)	<0.001	8.7^{abcd} (0.2)	5.4^{bc} (0.4)	0.001
C. reflexa	0.28^{bc} (0.01)	0.33^{ab} (0.02)	0.047	4.45^{bcd} (0.61)	2.46^{cdef} (0.14)	0.026	12.6^{d} (1.5)	7.5^{cde} (0.3)	0.024
C. tetragona	0.28^{bc} (0.02)	0.38^{abcd} (0.03)	0.082	1.73^{a} (0.16)	0.88^{a} (0.10)	0.002	5.6^{a} (0.26)	2.7^{a} (0.4)	<0.001
Succulents									
S. pachyphyllum	0.21^{ab} (0.01)	0.36^{abc} (0.04)	0.013	6.50^{de} (0.32)	3.09^{ef} (0.19)	<0.001	12.2^{d} (0.7)	7.8^{def} (0.4)	<0.001

Table 5. Synthesis of key results categorising species according to: (1) water use strategy under well watered (WW) conditions (daily transpiration rate), (2) rate of water use under water deficit (WD), i.e. time taken to effectively deplete soil moisture content and (3) water status (predawn water potential; Ψ_{PD}) under water deficit at the end of the experiment. Life-form indicated in parentheses with M = monocot, H = herb, S = shrub and Su = succulent. Categories are arbitrarily assigned and shading represents desirable characteristics for green roof plant species. '*' indicates that although Ψ_{PD} was not measured for *Sedum pachyphyllum*, leaf relative water content data (see Table 3) suggests it maintained a high water status under water deficit.

Characteristic	Category 1	Category 2	Category 3
Water use strategy when well-watered (WW)	**High water users** **(>70 g H_2O pot^{-1} d^{-1})** *D. admixta* (M) *S. glauca* (M) *D. perfoliata* (H) *I. axillaris* (H)	**Moderate water users** **(30-50 g H_2O pot^{-1} d^{-1})** *A. milleflorum* (M) *L. longifolia* (M) *B. multifida* (H) *C. semipapposum* (H) *C. reflexa* (S) *C. tetragona* (S)	**Low water users** **(<20 g H_2O pot^{-1} d^{-1})** *G. alpina* (S) *H. obtusifolia* (S) *S. pachyphyllum* (Su)
Water use strategy under water deficit (WD)	**High water users** **(>20 g H_2O pot^{-1} d^{-1})** *S. glauca* (M) *D. perfoliata* (H) *I. axillaris* (H)	**Moderate water users** **(10-20 g H_2O pot^{-1} d^{-1})** *A. milleflorum* (M) *D. admixta* (M) *L. longifolia* (M) *B. multifida* (H) *C. semipapposum* (H) *C. reflexa* (S) *C. tetragona* (S)	**Low water users** **(<10 g H_2O pot^{-1} d^{-1})** *G. alpina* (S) *H. obtusifolia* (S) *S. pachyphyllum* (Su)
Water status (Ψ_{PD}) under water deficit (WD)	**High water status** **(Ψ_{PD}<-1.5 MPa)** *A. milleflorum* (M) *D. admixta* (M) *L. longifolia* (M) *S. glauca* (M) *I. axillaris* (H) **S. pachyphyllum* (Su)	**Moderate water status** **(Ψ_{PD} -1.5 to -3.0 MPa)** *D. perfoliata* (H) *C. tetragona* (S)	**Low water status** **(Ψ_{PD}>-3.0 MPa)** *B. multifida* (H) *C. semipapposum* (H) *G. alpina* (S) *H. obtusifolia* (S) *C. reflexa* (S)


A. milleflorum
B. multifida
G. alpina
D. admixta
C. semipapposum
H. obtusifolia
L. longifolia
D. perfoliata
C. reflexa
S. glauca
I. axillaris
C. tetragona
0
10
20
30
40
50
60
Day


E pot^{-1} (% of WW)
0
20
40
60
80
100
E LA^{-1} (% of WW)
0
50
100
150
200
Ψ D
0
-1
-2
-3
-4
-5
-6
-7
A
B
y = -0.11x + 1.01; R² = 0.40; P = 0.028
y = -0.02 - 0.88; R2 = 0.14; P = 0.223


RMF (% of WW)
0
100
200
300
0
-1
-2
-3
-4
-5
-6
-7
ΨD
A
y = -0.023x + 0.656; R² = 0.28; P = 0.078
RMF (g g-1)
0.0
0.2
0.4
0.6
0.8
1.0
B
y = 6.45x - 5.44; R² = 0.36; P = 0.039
LAR (% of WW)
0
50
100
150
C
y = 0.0203x - 3.63; R² = 0.07; P = 0.395
LAR (m2 kg-1)
0
2
4
6
D
y = 0.552x - 3.67; R² = 0.13; P = 0.249
SLA (% of WW)
0
50
100
150
E
y = 0.0363x - 5.11; R² = 0.14; P = 0.237
SLA (m2 kg-1)
0
5
10
15
20
F
y = 0.266x - 4.37; R² = 0.31; P = 0.061