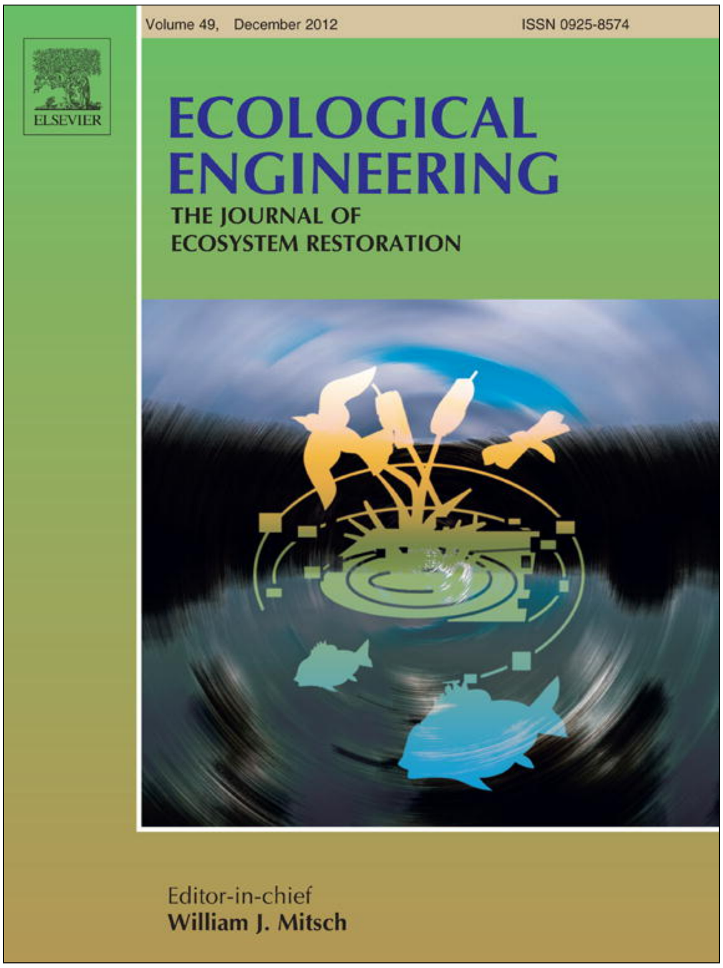
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Green roofs for hot and dry climates: Interacting effects of plant water use, succulence and substrate

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ABSTRACT

Green roofs are increasingly being constructed in urban environments to provide a range of environmental benefits. However, little is known about how they will perform in hot and dry climates where water is often limiting and drought tolerance determines plant survival. We evaluated the effects of severe drought (113 days without water) on growth, water use and survival of five succulent species (*Sedum pachyphyllum*, *S. clavatum*, *S. spurium*, *Disphyma crassifolium* and *Carpobrotus modestus*) planted in three different green roof substrates (growing media) differing in water holding capacity. Plants survived 12 days longer in substrates with higher water holding capacity. Water use determined survival under severe drought with species with higher water use (*D. crassifolium* and *C. modestus*) dying at least 15 days earlier than *Sedum* species which were conservative water users. Increased survival was not related to increased leaf succulence but was related to reduced biomass under drought. Under well-watered conditions, water use was greatest in species with lower leaf succulence in substrates with increased water holding capacity. To maximise survival, green roofs in year round or seasonally hot and dry climates should be planted with species that have high leaf succulence and low water use in substrates with high water holding capacity.

1. Introduction

Green roofs are increasingly being built to provide a diverse range of environmental benefits. These include energy conservation through improved building insulation and energy efficiency (Sailor, 2008), mitigation of the urban heat island effect (Bass and Baskaran, 2003), noise attenuation (Van Renterghem and Botteldooren, 2009), biodiversity habitat provision (Brenneisen, 2006) and urban stormwater management (Berndtsson, 2010; VanWoert et al., 2005). Green roofs are constructed profiles made up of layers including water-proofing, drainage (gravel or proprietary system) and substrate (growing media) layers in which plants are grown. Weight loading restrictions on buildings limit the depth of substrate (often <20 cm) on retrofitted green roofs. This makes green roofs difficult environments for plant growth and survival as water availability fluctuates dramatically between rain events (Nagase and Dunnett, 2010; Oberndorfer et al., 2007). Consequently, survival during drought periods determines plant species suitability for green roofs (Bousselot et al., 2011), especially in hot and dry climates.

Survival on green roofs is determined by substrate depth and physical properties, particularly water holding capacity. Drought tolerance of *Sedum* species in response to substrate depth has been widely investigated, with increased survival in greater depths (Durhman et al., 2007; Getter and Rowe, 2009; VanWoert et al., 2005). However, there has been little comparison of species performance under drought conditions in different substrates with different physical properties. For long term success, green roof substrates need to balance a number of competing and sometimes contrasting properties. Good aeration and low bulk density are needed to ensure the substrate is free draining, lightweight and facilitates plant respiration, yet this must be balanced against sufficient water retention for plant growth and survival (Nektarios et al., 2004; Rowe et al., 2006; Thuring et al., 2010). These properties can be achieved with light weight components; however, many components, particularly organic materials, shrink and/or decompose over time, therefore green roof substrates are largely mineral based. Mineral based substrate composition differs according to local availability and cost, and many include recycled or waste products to maximise the environmental benefits of green roofs (Molineux et al., 2009). Most green roof substrates are developed according to specified performance guidelines and standards, notably the widely used German FLL guidelines (FLL 2008) or the more recent American Standard Testing Methods (ASTM 2009a,b,c, ASTM 2010). Both specify value ranges and limits for different substrate properties and the required testing methodologies.

The plants most commonly used on European and North American green roofs in temperate climates are succulents from the

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genus *Sedum* (Oberndorfer et al., 2007; Snodgrass and Snodgrass, 2006). *Sedum* species are considered ideal for green roofs due to their low spreading habit, providing good lateral cover, and drought tolerance (Nagase and Dunnett, 2010; VanWoert et al., 2005). Their drought tolerance is largely due to high leaf succulence and physiological adaptations such as CAM (Crassulacean Acid Metabolism) photosynthesis (Butler, 2012; Durhman et al., 2006). CAM plants have greater water use efficiency than C3 plants as transpiration per unit CO_2 fixed is reduced due to stomata opening at night for CO_2 uptake (Sayed, 2001). Some *Sedum* species are also considered facultative CAM (Kluge, 1977), shifting from C3 to CAM photosynthesis under stressful conditions such as drought, salinity or elevated temperature (Sayed, 2001). Leaf succulence enables plants to survive periodic drought by providing usable water when soil water conditions prevent uptake by roots (von Willert, 1992). Many *Sedum* species used on green roofs have been selected from alpine areas for their frost tolerance and enhanced survival during winter (Durhman et al., 2007), including *Sedum album*, *S. acre, S. reflexum* and *S. spurium*. As a consequence of higher frost tolerance, these species exhibit reduced leaf succulence (Osmond et al., 1975; Teeri et al., 1981). As the degree of leaf succulence directly influences drought tolerance (von Willert, 1992), these *Sedum* species may be less suitable in hot and dry climates than species with greater succulence (Williams et al., 2010b).

Despite widespread implementation in cooler northern hemisphere climates, there are very few extensive green roofs in hot and dry climates (Williams et al., 2010b). Successful implementation of green roofs in hot and dry climates is important as the environmental benefits are likely to be far greater in than in temperate climates (Alexandri and Jones, 2008). However, it is problematic to rely on temperate northern hemisphere green roof practices without scientific testing (Williams et al., 2010b), due to climatic differences, access to suitable substrate and plants and limited information on plant performance under drought conditions (Bousselot et al., 2011). To date little research has been done to determine drought tolerance of green roof succulents and the suitability of different substrates in year round or seasonally hot and dry climates.

This paper describes an experiment that determined the effects of drought on plant growth, survival and water use of five succulent species, with varying degrees of leaf succulence, grown in three different substrates that were developed according to the FLL guidelines. This drought experiment had two objectives: (i) to determine how substrate water holding capacity affects plant water use and survival; and (ii) to determine whether leaf succulence affects plant survival.

2. Materials and methods

Five succulent species were evaluated, three introduced *Sedum* species (*S. pachyphyllum* Rose, *S. clavatum* Clausen and *S. spurium* Marshall von Bieberstein) and two Australian species (*Carpobrotus modestus* S.T. Blake and *Disphyma crassifolium* L.) (Table 1). The Sedum species are likely to be obligate CAM plants, however little is known about their CAM strategies. Butler (2012) found that although *S. spurium* showed nocturnal CO_2 accumulation they did not show nocturnal CO_2 uptake. The two Australian species are facultative CAM plants when water is limiting (Winter et al., 1981). Three month-old cuttings of each species were planted on December 1, 2010 into 200 mm diameter pots containing one of the three substrates (160 mm deep substrate). As Cuttings had been grown in commercial potting mix, as much of this mix as possible was removed prior to planting to reduce the effects of this media on the water holding capacity of the green roof substrates. These were comprised of 80% readily available mineral components, either scoria, crushed roof tiles or bottom ash from coal fired power stations and 20% horticultural grade coir (Rayner et al., unpublished data). Table 2 shows the aggregate sizes of the mineral components for the three green roof substrates. Scoria and crushed roof tile components were sourced locally from Melbourne, Victoria, while the bottom ash was sourced from coal-fired power stations in New South Wales. Whilst conforming to the FLL guidelines (2008), the three growing media differed in physical and chemical properties (Table 2), including water holding capacity (WHC). Bottom ash had a significantly higher WHC than either scoria or roof tile. Low WHC of the substrates was related to a higher air-filled porosity (AFP) in scoria but not in roof tile, which has a similar AFP to bottom ash.

As the three substrates differed in bulk densities, substrates were added by weight to pots to ensure the same volume (equivalent oven dried weight = 2702.8 g scoria; 3904.6 g roof tile; and 2051.2 g bottom ash substrate). This diameter pot approximates planting density on established green roofs in Melbourne (25 plants m^{-2}). Fine mesh squares were placed in the bottom of pots to prevent loss of substrate. One month post-planting 12 g of 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.

2.1. Experimental design

The drought experiment ran for 113 days (25 January to 17 June, 2011) and was conducted in a temperature controlled glasshouse at The University of Melbourne's Burnley campus, Melbourne, Australia (−37.828472, 145.020883). Daytime temperature ranged between 6 and 49 °C with a mean of 21.4 °C, and night-time temperatures ranged between 6 and 28 °C with a mean of 15.7 °C. We used a factorial randomised block design with substrate and watering regime (drought or well-watered) as treatments, with five replicates. All plants were watered weekly until the start of experiment (25 January 2011) when they were considered well established. Plants were considered well established when above ground growth was sufficient to cover the pot's surface. Two treatments were implemented: well-watered (WW) and droughted (D). Well-watered plants were watered once a week to pot capacity from days 1 to 85, then fortnightly until day 113 as evaporative demand declined. Droughted plants were watered to pot capacity at the start of the experiment then received no further watering.

2.2. Plant growth, biomass, leaf succulence and survival

At the start of the experiment, five plants of each species were harvested to determine initial biomass (root and shoot mass). During the experiment plant survival was determined by visual assessment. Plants were considered dead when all leaves were dry and shrivelled. They were then harvested to determine plant biomass. Fallen leaves were retained and added to shoot biomass. On June 17 (day 113) all surviving plants were harvested to determine total plant, shoot and root masses. Root mass was determined by thoroughly washing substrate away from plant roots over a sieve to ensure minimal root loss. Any substrate still adhering to roots was removed after drying roots in the oven. Dry weights were determined after oven drying samples at 70 °C to a constant weight. Dry weights were used to determine shoot to root ratio (g shoot g^{-1} root). Ten leaves from well-watered plants of each species were sampled to determine leaf succulence, determined as: Leaf succulence = water content of leaf/surface area of leaf (Jones, 2011). Leaf areas of individual leaves were measured using ImageJ 1.43 software (NIH, USA).

Table 1
Species descriptions of the five perennial green roof succulents evaluated in the glasshouse experiment.

Species	Origin	Habitat	Life-form
Sedum pachyphyllum	Mexico	Mountain cliffs	Evergreen upright succulent
S. clavatum	Mexico	Volcanic soils	Rosette succulent
S. spurium	Caucasus	Sub-alpine meadows	Short herbaceous semi-evergreen succulent
Carpobrotus modestus	Australia	Coastal dunes, shallow rocky soils and inland deep sands	Trailing succulent
Disphyma crassifolium	Australia	Coastal saltmarsh or sea cliffs	Prostrate trailing succulent

Table 2
Physical and chemical properties (mean ± SE; $n = 3$) of three green roof substrates evaluated. Air filled porosity (AFP), bulk density at pot capacity, water holding capacity (WHC) and electrical conductivity ($EC_{1:5}$). Values highlighted meet the FLL guideline recommendations (FLL 2008). There are no recommended FLL ranges for bulk density at pot capacity.

Substrate	pH	$EC_{1:5}$ dSm^{-1}	WHC %	AFP %	Bulk density gcm^{-3}
Scoria mix 60% scoria 8 mm minus, 20% 7 mm scoria aggregate and 20% coir	6.9^c (± 0.03)	0.14^a (± 0.003)	45.9^b (± 0.3)	13.8^b (± 0.5)	1.26^b (± 0.01)
Crushed roof tile mix 80% 8 mm minus crushed roof tile and 20% coir	6.4^a (± 0.01)	0.15^a (± 0.004)	44.0^a (± 0.8)	7.14^a (± 0.3)	1.56^c (± 0.01)
Bottom ash mix 60% bayswater sand (less than 2 mm diameter), 20% eraring filter (less than 10 mm diameter) and 20% coir	6.7^b (± 0.03)	0.48^b (± 0.004)	51.7^c (± 0.4)	7.65^a (± 0.6)	1.11^a (± 0.01)

Note: To compare EC to the FLL guidelines EC μS cm^{-1} was converted to g L^{-1} using the conversion formula g L^{-1}/ = μS cm^{-1} × 0.00156. AFP was tested according to Australian standard for Potting Mixes (AS 3743) and compared against the FLL (2008) air content at full water capacity.

2.3. Plant water use and water use efficiency

Plant evapotranspiration was determined from the difference in pre- (drought and well-watered treatments) and post-watering (well-watered treatments only) pot weights at every watering. Cumulative evapotranspiration (ET) was the total amount of water lost from each pot during the experiment while plants were still alive. Water lost from five bare pots of each substrate was used to determine evaporation and was subtracted from ET to determine cumulative transpiration. Transpiration per unit biomass (E) was determined by dividing cumulative transpiration by final biomass (dry weight) at the end of the experiment.

2.4. Soil water content

Soil water content (SWC) was determined from pot weights pre- (drought and well-watered) and post- (well-watered only) watering every 7 days until day 85 then every 14 days thereafter. SWC was calculated by first correcting pot weight for estimated plant weight at each weighing, estimated as initial fresh weight + daily biomass gain (final fresh weight−initial fresh weight/113). 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 (five drought and five well-watered) at the end of the experiment to a constant weight in a 70 °C oven. SWC of drought plants was expressed as a proportion of well-watered plants.

2.5. Statistical analyses

Treatment differences in biomass allocation at harvest were analyzed using two-way ANOVA within species (substrate × watering treatment). Relative growth rate and survival (days until death) were analyzed with one-way ANOVA within substrate under drought or well-watered conditions. Two-way ANOVAs were used to determine differences in cumulative evapotranspiration (ET) and transpiration per unit harvest biomass (E): within species between substrate and watering treatment and within watering treatment between species and substrate. One-way ANOVAs were used to determine when SWC reached a constant level (within species × substrate; between days) and to determine differences in SWC (within day; between species × substrate). Data were transformed where necessary to ensure univariate normality. All data presented in figures and tables are non-transformed. Significant differences were determined by Tukey's post hoc test ($P < 0.05$). All data analyses were performed in GenStat 12.1 (2009, VSN International Ltd.). For clarity, all P-values are presented in the results text.

3. Results

3.1. Effects of substrate and watering regime on plant biomass, allocation and survival

With the exception of *D. crassifolium*, total biomass was always higher under well-watered conditions (Table 3). *C. modestus* ($P = 0.01$), *S. clavatum* ($P < 0.001$) and *S. spurium* ($P < 0.001$) had 16, 56 and 79% greater biomass in well-watered substrates. Total biomass of *C. modestus* also differed between substrates ($P = 0.003$) with at least 10% greater biomass in bottom ash substrate. There was no difference in total biomass between substrates for *S. clavatum* and *S. spurium*.

In *D. crassifolium* and *S. pachyphyllum* there was an interaction between substrate and watering regime and biomass differed between substrates under well-watered conditions. *D. crassifolium* biomass was significantly greater in well-watered roof tile than in scoria (interaction $P = 0.01$). Conversely, total biomass of *S. pachyphyllum* was higher in well-watered scoria and bottom ash substrates, with 35% and 43% greater biomass than in well-watered roof tile respectively (interaction $P = 0.001$).

Table 3
Effects of substrate and watering regime (drought; D and well-watered; WW) on total plant biomass, allocation (dry weight) and survival (days until death) (mean ± SE; $n = 5$) of five green roof succulent species.

Species	Substrate	Total (g)		Shoot:root ($g\,g^{-1}$)		Survival (days)	
		D	WW	D	WW	D	WW
C. modestus	Scoria	$^{A}9.55^{a}$ (±0.85)	$^{B}11.77^{a}$ (±0.76)	$^{A}5.77^{a}$ (±1.65)	$^{B}10.25^{a}$ (±4.22)	$^{A}72.4^{a}$ (±3.4)	101.8^{b} (± 5.2)
	Roof tile	$^{A}10.05^{a}$ (±0.98)	$^{B}12.41^{a}$ (±1.28)	$^{A}4.47^{a}$ (±0.88)	$^{B}6.13^{a}$ (±1.92)	$^{A}82.2^{ab}$ (±1.7)	100.4^{b} (± 6.4)
	Bottom ash	$^{A}13.13^{b}$ (±1.31)	$^{B}13.84^{b}$ (±0.79)	$^{A}3.48^{a}$ (±0.55)	$^{B}13.98^{a}$ (±3.13)	$^{A}99.0^{b}$ (±8.9)	107.4^{b} (± 3.4)
D. crassifolium	Scoria	7.58^{a} (±1.05)	4.81^{a} (±0.08)	$^{A}1.12^{a}$ (±0.12)	$^{B}2.47^{a}$ (±0.16)	$^{A}66.8^{a}$ (±1.7)	64.0^{a} (± 0.0)
	Roof tile	8.23^{a} (±1.58)	11.72^{b} (±2.36)	$^{A}1.95^{a}$ (±0.55)	$^{B}4.08^{a}$ (±1.80)	$^{A}80.8^{ab}$ (±8.7)	103.2^{b} (± 6.9)
	Bottom ash	8.59^{a} (±1.33)	18.09^{ab} (±3.21)	$^{A}1.54^{a}$ (±0.14)	$^{B}3.34^{a}$ (±0.87)	$^{A}80.8^{b}$ (±8.7)	110.2^{b} (± 2.8)
S. pachyphyllum	Scoria	9.94^{a} (±0.47)	25.94^{c} (±1.30)	2.58 (±0.41)	3.37 (±0.36)	$^{B}113.0^{a}$ (±0.0)	113.0^{b} (± 0.0)
	Roof tile	9.18^{a} (±0.69)	16.95^{b} (±1.42)	2.49 (±0.26)	2.76 (±0.54)	$^{B}113.0^{ab}$ (±0.0)	113.0^{b} (± 0.0)
	Bottom ash	10.79^{a} (±1.55)	29.64^{c} (±1.89)	3.04 (±0.73)	4.29 (±1.21)	$^{B}113.0^{b}$ (±0.0)	113.0^{b} (± 0.0)
S. spurium	Scoria	$^{A}7.55^{a}$ (±1.28)	$^{B}31.92^{a}$ (±2.76)	2.46 (±0.66)	3.78 (±0.91)	$^{B}101.8^{a}$ (±8.2)	113.0^{b} (± 0.0)
	Roof tile	$^{A}6.14^{a}$ (±0.87)	$^{B}28.23^{a}$ (± 3.35)	2.72 (±0.80)	2.92 (±0.57)	$^{B}94.8^{ab}$ (±11.2)	113.0^{b} (± 0.0)
	Bottom ash	$^{A}6.90^{a}$ (±0.54)	$^{B}39.27^{a}$ (±3.13)	3.10 (±0.62)	4.31 (±0.68)	$^{B}103.2^{b}$ (±6.9)	113.0^{b} (± 0.0)
S. clavatum	Scoria	$^{A}6.25^{a}$ (±0.64)	$^{B}15.51^{a}$ (±0.93)	2.97 (±0.80)	4.83 (±1.32)	$^{B}94.8^{a}$ (±11.2)	113.0^{b} (± 0.0)
	Roof tile	$^{A}6.99^{a}$ (±1.41)	$^{B}13.96^{a}$ (±1.13)	3.76 (±0.83)	5.37 (±0.96)	$^{B}113.0^{ab}$ (±0.0)	113.0^{b} (± 0.0)
	Bottom ash	$^{A}7.39^{a}$ (±0.38)	$^{B}17.41^{a}$ (±1.87)	6.42 (±2.15)	3.85 (±0.82)	$^{B}113.0^{b}$ (±0.0)	113.0^{b} (± 0.0)

For total biomass and shoot:root ratios, lower case letters show differences between substrates and upper case letters between D and WW within species. Where only lower case letters are given these indicate a significant interaction between substrate and watering treatments and no letter indicates no significant difference within species. For survival under D, lower case letters show differences between substrates and upper case letters differences between species. Under WW, lower case letters show the interaction between substrate and species. All two-way ANOVA; see results 3.1 for *P*-values.

Shoot:root ratios (Table 3) were unaffected by substrate for all species. However drought reduced shoot:root ratios at least 2-fold in *D. crassifolium* ($P = 0.025$) and *C. modestus* ($P = 0.002$).

Generally, drought reduced survival (days until death; Table 3), relative to well-watered conditions. Survival under drought conditions differed between the five succulent species ($P < 0.001$) with *C. modestus* and *D. crassifolium* dying at least 15 and 23 days earlier than the three *Sedum* species, which were not significantly different. Survival under drought conditions also differed between substrates ($P = 0.017$) with mean survival (all species pooled) 12 days longer in bottom ash substrate than in scoria. Mean survival in bottom ash was not significantly different from survival in roof tile substrate. For survival under well-watered conditions, there was a significant interaction between substrate and species ($P < 0.001$), with *D. crassifolium* in scoria substrate dying at least 36 days earlier than all other species and substrate combinations.

3.2. Effects of substrate and watering regime on cumulative evapotranspiration and transpiration per unit biomass

Cumulative transpiration (ET) was always greater in well-watered plants for each species (Table 4). Under well-watered conditions, ET in bottom ash planted with *C. modestus* ($P = 0.003$), *D. crassifolium* ($P < 0.001$) and *S. spurium* ($P = 0.003$) was at least 6 times higher than droughted plants. The greatest difference between well-watered and droughted *S. clavatum* ($P = 0.002$), and *S. pachyphyllum* ($P = 0.001$) occurred in the roof tile substrate, with 3.6 and 4.0 times higher ET in WW.

Under drought conditions, cumulative evapotranspiration was significantly different between substrates, with bottom ash > roof tile > scoria ($P < 0.001$) (Table 4). There were no species differences in ET under drought, but all species lost more water than from evaporation (bare pots) alone ($P < 0.001$). Under well-watered conditions there was a significant interaction between species and substrate ($P < 0.001$), with *S. spurium* in bottom ash losing the most water (105.8 g $H_2O\,d^{-1}$; 11.96 kg H_2O in total) and *D. crassifolium* in scoria losing the least (37.5 g $H_2O\,d^{-1}$; 4.24 kg H_2O in total). In scoria substrates, only *S. spurium* lost more water than from evaporation (bare pots) in scoria alone. With the exception of *S. clavatum*, where water use did not differ between substrates and was no different from evaporation, water use was greater in roof tile and bottom ash substrates than in scoria. However, water lost from bottom ash planted with *S. pachyphyllum* was less than evaporation.

When transpiration was considered on a per unit biomass basis (E) (Table 4), E was lower under drought conditions in all species except *S. clavatum* and *S. pachyphyllum*, which had significantly higher E under drought. Within the drought treatment there were no significant differences in transpiration per unit biomass between the five succulent species.

Under well-watered conditions there was an interaction between substrate and species (interaction $P < 0.001$) with *C. modestus* and *D. crassifolium* in bottom ash and roof tile substrates using 1.1–2.2 times more water per unit biomass than *S. spurium*

Table 4
Effects of substrate and watering treatment (drought, D and well-watered, WW) on cumulative evapotranspiration (ET) and cumulative transpiration (E) per unit harvest biomass (mean ± S E; $n=5$) of five green roof succulents.

Species	Substrate	Cumulative ET (g H_2O)		Cumulative E (g H_2O g biomass^{-1})	
		D	WW	D	WW
Bare	Scoria	$^{A}1029^{a}$ (±12)	$^{C}6555^{bc}$ (±73)	–	–
	Roof tile	$^{AB}1130^{b}$ (±12)	$^{D}7029^{bcde}$ (±101)	–	–
	Bottom ash	$^{B}1389^{c}$ (±2)	$^{E}7811^{cdef}$ (±108)	–	–
C. modestus	Scoria	$^{A}1388^{a}$ (±152)	$^{B}7704^{cdef}$ (±303)	$^{A}22.3$ (±2.8)	$^{B}133.3^{de}$ (±14.0)
	Roof tile	$^{A}1341^{b}$ (±10)	$^{B}9058^{efg}$ (±638)	$^{A}22.2$ (±2.6)	$^{B}215.1^{ef}$ (±41.1)
	Bottom ash	$^{A}1527^{c}$ (±50)	$^{C}10723^{gh}$ (±565)	$^{A}9.5$ (±2.7)	$^{B}221.9^{ef}$ (±21.8)
D. crassifolium	Scoria	$^{A}1209^{a}$ (±16)	$^{B}4239^{a}$ (±35)	$^{A}25.8$ (±1.9)	$^{B}47.8^{bcd}$ (±7.8)
	Roof tile	$^{A}1323^{b}$ (±21)	$^{C}9271^{fg}$ (±815)	$^{A}28.2$ (±5.8)	$^{B}231.5^{f}$ (±33.4)
	Bottom ash	$^{A}1536^{c}$ (±13)	$^{D}11759^{h}$ (±749)	$^{A}20.2$ (±4.2)	$^{B}227.4^{ef}$ (±22.1)
S. pachyphyllum	Scoria	$^{A}1285^{a}$ (±13)	$^{B}6088^{abc}$ (±149)	$^{B}22.9$ (±2.2)	$^{A}-11.4^{ab}$ (±5.9)
	Roof tile	$^{A}1363^{b}$ (±26)	$^{C}6804^{bcd}$ (±133)	$^{B}25.6$ (±2.4)	$^{A}-13.2^{abc}$ (±7.9)
	Bottom ash	$^{A}1606^{c}$ (±19)	$^{D}7499^{bcdef}$ (±246)	$^{B}26.0$ (±5.5)	$^{A}-17.9^{abc}$ (±9.0)
S. spurium	Scoria	$^{A}1230^{a}$ (±23)	$^{B}8798^{defg}$ (±266)	$^{A}29.4$ (±6.1)	$^{B}71.6^{bcd}$ (±8.7)
	Roof tile	$^{A}1287^{b}$ (±8)	$^{B}9221^{fg}$ (±314)	$^{A}28.6$ (±3.9)	$^{B}78.3^{cd}$ (±9.4)
	Bottom ash	$^{A}1550^{c}$ (±19)	$^{C}11964^{h}$ (±893)	$^{A}23.2$ (±1.7)	$^{B}101.7^{d}$ (±19.3)
S. clavatum	Scoria	$^{A}1284^{a}$ (±19)	$^{C}5540^{ab}$ (±73)	$^{B}43.5$ (±6.1)	$^{A}-67.1^{a}$ (±7.5)
	Roof tile	$^{AB}1327^{b}$ (±13)	$^{D}6168^{abc}$ (±131)	$^{B}-10.4$ (±5.8)	$^{A}-65.3^{a}$ (±13.1)
	Bottom ash	$^{B}1631^{c}$ (±24)	$^{D}6112^{abc}$ (±94)	$^{B}32.9$ (±3.5)	$^{A}-103.4^{a}$ (±13.8)

Lower-case letters indicate significant differences within watering treatment (two-way ANOVA) and upper-case letters indicate significant differences within species (two-way ANOVA; see results 3.2 for *P*-values).

(all substrates). In scoria substrates, *D. crassifolium* and *C. modestus* transpired 79% and 38–40% less water per unit biomass compared with bottom ash and roof tile substrates. Across all substrates, E in WW plants was highest in *C. modestus* and *D. crassifolium*, followed by *S. spurium*, *S. pachyphyllum* and *S. clavatum*.

3.3. Leaf succulence

The five succulent species differed in terms of mean leaf succulence (g H_2O cm^{-2} leaf) ($P<0.001$). *S. spurium* was the least succulent species (0.05 g cm^{-2}), while *S. pachyphyllum* and *S. clavatum* were equally the most succulent species (0.50 and 0.52 g cm^{-2}, respectively). Leaf succulence of *D. crassifolium and C. modestus* were 0.18 and 0.31 g cm^{-2}, respectively.

3.4. Soil water content

Initial depletion of soil water in the drought treatment was rapid for all species and substrates, with 53–92% declines in SWC after 15 days (Fig. 1; all *P*-values < 0.001). Soil water content in the drought treatment took longer to reach its minimum level in scoria compared with bottom ash and roof tile substrates for all species, with the exception of *S. clavatum* in the bottom ash substrate which reached its minimum on the same day as scoria (day 64). In the drought treatment *C. modestus* and *D. crassifolum* depleted soil water 121–191% faster than *S. clavatum*, 95–127% times faster than *S. pachyphyllum* and 64–72% faster than *S. spurium* depending on substrate.

4. Discussion

Substrates with increased water holding capacity showed greater plant survival. Survival was on average 12 days longer in bottom ash substrate than in scoria, presumably as it had a greater water holding capacity (WHC). This reflects other green roof studies where increased water availability due to deeper substrates (Durhman et al., 2007) or increased substrate WHC (Thuring et al., 2010) increased plant survival. Greater WHC in the bottom ash substrate resulted in greater total evapotranspiration compared with roof tile and scoria substrates, regardless of watering regime. Although all species took longer to reach minimum soil water contents in scoria, they also tended to have lower survival than in bottom ash. This indicates that the additional time to deplete soil water in scoria was due to poor plant performance rather than an enhanced capacity to sustain plants under drought conditions. Higher water use by *C. modestus* and *D. crassifolium* is also likely to have reduced their survival compared with the three *Sedum* species.

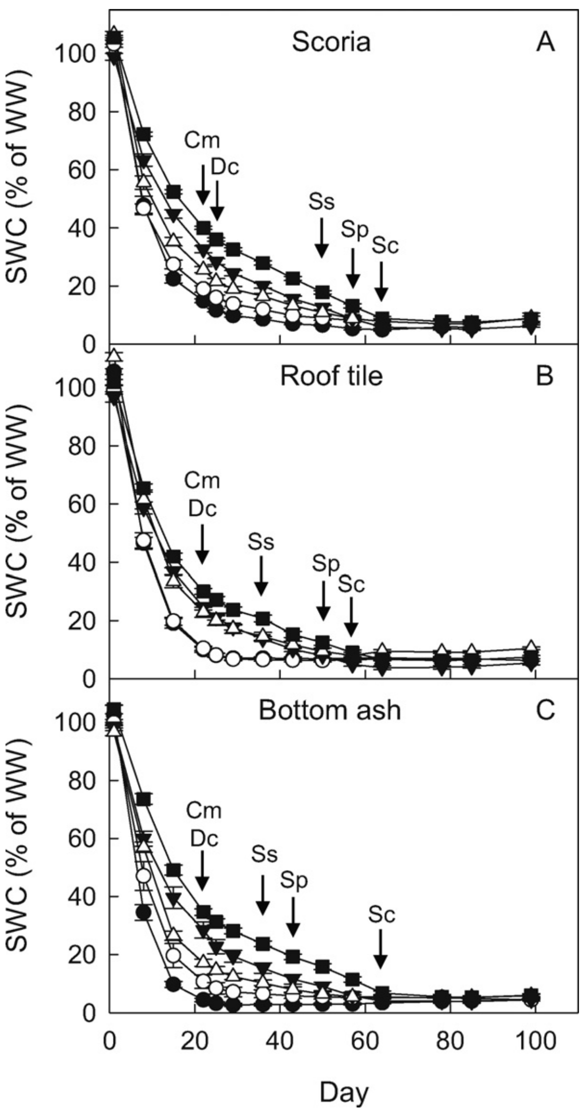

Fig. 1. Soil water content (SWC) over time of droughted *C. modestus* (Cm; ●), *D. crassifolium* (Dc; ○), *Sedum pachyphyllum* (Sp; ▾), *S. spurium* (Ss; △) and *S. clavatum* (Sc; ■) in each of three substrates: scoria (A), roof tile (B) and bottom ash (C). Arrows indicate the day on which SWC was depleted, i.e. on which SWC was no longer significantly different from the previous day (one-way ANOVA; all *P*-values < 0.001). Symbols represent means (*n* = 5) and bars represent mean standard error.

Both *C. modestus* and *D. crassifolium* depleted substrate water contents to effectively zero within 22–36 days, compared with 36–71 days for the *Sedum* species. Water use per unit biomass was, however, similar between all species and substrates under drought conditions. This is most likely because *C. modestus* and *D. crassifolium* lost shoot biomass over the drought period. Greater water use by the Australian species in this experiment is comparable with the results of Williams et al. (2010a) who found that *D. crassifolium* and *Carpobrotus rossii* used 8 and 12 times the amount of water that *Sedum acre* used in a 10-day period after watering. Voyde et al. (2010) found that although daily water use of *Disphyma australe* and *Sedum mexicanum* were not significantly different during the first nine days without water, *S. mexicanum* subsequently decreased water use enabling it to survive longer. This contrasts with our study where *C. modestus* and *D. crassifolium* depleted substrate water contents at a much faster rate in the first 20 days of drought than *Sedum* species.

Greater survival of the three *Sedum* species was related to reduced biomass under drought conditions. In other green roof studies, low water availability due to limited substrate depth (Durhman et al., 2007; Getter and Rowe, 2009) or increased time between watering (VanWoert et al., 2005) has resulted in reduced biomass in *Sedum* species. Drought did not change allocation patterns in the three *Sedum* species in our study, although *D. crassifolium* and *C. modestus* reduced shoot to root ratios in all substrates under drought conditions. However, as *C. modestus* and *D. crassifolium* died at least two weeks earlier than the *Sedum* species, changes in allocation were not as important as total biomass reduction for plant survival.

Differences in survival between species when water was no longer available may also have been due to leaf succulence. We hypothesized that species with greater leaf succulence would have greater survival than those with limited succulence under severe drought conditions. However, the relationship between survival and leaf succulence was not straightforward. *S. pachyphyllum* and *S. clavatum* had the highest degree of succulence and showed high survival in all substrates under drought conditions. However, *S. spurium*, which had the least succulence, was equally drought tolerant and lived almost two weeks longer than *C. modestus* and *D. crassifolium* which had greater leaf succulence. *S. spurium* has variable drought tolerance reported in the literature. Nagase and Dunnett (2010) reported poor survival (20%) after 21 days without water, Bousselot et al. (2011) reported no visible shoot dieback until 127 days without water and VanWoert et al. (2005) reported 100% survival after 88 days without water. As it is the amount of utilizable water which determines the length of time succulent plants can survive (von Willert, 1992), it is possible that water from *S. spurium* leaves was more available to the plant than water in *C. modestus* or *D. crassifolium* leaves. *S. spurium* sheds leaves to maintain actively growing terminal shoots (Stephenson, 1994). *C. modestus* may not have been able to redistribute water from old to new leaves to maintain turgor, as Rabas and Martin (2003) found in *Carpobrotus edulis*, a species with similar morphology and succulence to *C. modestus*. Rapid initial depletion of substrate water by *C. modestus* and *D. crassifolium* would also have meant that they needed to draw on water stored in leaves earlier than *S. spurium*, despite similar ET over the course of the experiment.

Higher survival of *Sedum* species was not associated with lower water use per unit biomass in our study. Lower water use per unit biomass, along with leaf succulence, has been attributed to higher survival in CAM plants (Herrera, 2009; Sayed, 2001), although Gravatt and Martin (1992) found no relationship between water use efficiency and photosynthetic pathway in five *Sedum* species. Both Australian succulents (*C. modestus* and *D. crassifolium*) are facultative CAM plants, shifting to dark CO_2 fixation when soil water is limiting and reversing back to C3 photosynthesis when re-watered (Winter et al., 1981). However, there was no difference in water use per unit biomass between the Australian native species and the *Sedum* species in our study.

The importance of selecting substrates and plant species which are climate appropriate was highlighted by the poor survival of *D. crassifolium* growing in scoria under well-watered conditions. *D. crassifolium* had higher evapotranspiration in well-watered scoria substrate than in droughted scoria; however, well-watered plants used less water than was lost from evaporation. Given *D. crassifolium* performed well in other substrates, this suggests that scoria may be an unsuitable substrate for this species. Biomass did not differ between watering regimes suggesting that another factor, such as higher air-filled porosity, may have reduced growth and survival in scoria.

This study exposed plants to extreme drought for a duration of 113 days. While it is unlikely that green roofs in Mediterranean climates will be exposed to this degree of water limitation, it is useful to determine the limits of species survival to maximize relevance to different climates and applications. In hot and dry climates, water availability from rainfall and substrate properties will determine plant and substrate selection. Green roofs in year round or seasonally hot and dry climates should be planted with species that have high leaf succulence and low water use to ensure plant survival. Lightweight substrates with high water holding capacity should continue to be developed to improve plant survival rates and broaden the range of species suitable for these harsh conditions.

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