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Title:
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Date:
2022-01-01

Citation:
Chu, H. H. & Farrell, C. (2022). Fast plants have water-use and drought strategies that balance rainfall retention and drought survival on green roofs. Ecological Applications, 32 (1), https://doi.org/10.1002/eap.2486.

Persistent Link:
https://hdl.handle.net/11343/299279

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Article type : Article

Journal: Ecological Applications

Manuscript type: Articles

Running Head: Selecting green roof plants using traits

Fast plants have water-use and drought strategies that balance rainfall retention and drought survival on green roofs

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Manuscript received 22 October 202; revised 5 May 2021; accepted 26 May 2021; final version received 11 October 2021.

Open Research:

Data (Chu 2021) are available on Figshare at: https://doi.org/10.26188/5ebce2c3c57bd

Abstract

Green roofs can improve ecosystem services in cities, however this depends on appropriate plant selection. For stormwater management, plants should have high water-use to maximise retention and also survive dry periods. Plants adapted to wetter habitats develop ‘fast’ traits for growth, whereas plants from drier habitats develop ‘slow’ traits to conserve water-use and survive drought. Therefore, we hypothesised that (1) plants with ‘fast’ traits would have greater water-use, (2) plants with ‘slow’ traits would have greater drought tolerance, (3) ‘fast-slow’ traits would be consistent across the plant, and (4) ‘fast’ plants with greater water-use could avoid drought stress. We evaluated 14 green roof species in a glasshouse experiment under well-watered (WW) and water-deficit (WD) conditions to determine relationships between ‘fast-slow’ traits, water-use, and drought resistance. Traits measured were: shoot dry weight, specific leaf area (SLA), root mass fraction (RMF), and specific root length (SRL). Daily evapotranspiration per shoot dry weight was used to describe water-use. Drought resistance was represented by: (1) days to stomatal closure; (2) cumulative ET before stomatal closure; and (3) degree of iso-anisohydry (difference between midday leaf water potential (Ψ_{MD}) of WW and WD plants; $\Delta\Psi_{MD}$). Plants with greater water-use had ‘fast’ above-ground traits (greater shoot biomass and SLA). Plants with ‘slow’ traits had greater drought tolerance as plants with lower shoot dry weight closed their stomata later under WD, and plants with greater root allocation were more anisohydric. ‘Fast-slow’ traits were not consistent across the plant. Although SLA and SRL were positively related, SRL was not related to water-use or drought resistance. Shoot dry weight was inversely related to SLA and had a stronger influence on stomatal closure. Though plants with greater water-use under well-watered conditions closed their stomates earlier to avoid drought stress, they were not more isohydric (smaller $\Delta\Psi_{MD}$) and did not necessarily use more water under WD. ‘Fast’ above-ground traits can be used to select green roof plants with high water-use

that avoid drought stress to optimise rainfall retention without jeopardising drought survival. This will facilitate rapid plant selection using trait information from online databases.

Key words: anisohydry; drought-avoidance; drought-tolerance; evapotranspiration; fast-slow plant economics spectrum; isohydry, trait

Introduction

Urbanisation increases impervious surface cover quicker than population growth, leading to negative environmental impacts such as reduced rainfall infiltration and increased stormwater runoff (Meyer et al. 2005). Green roofs can reduce stormwater runoff as they reduce imperviousness without using additional space at ground level (Berndtsson 2010). However, to reduce stormwater runoff to pre-urbanisation levels, green roofs need to retain 60 to 80% of annual rainfall, comparable to the evapotranspiration of natural forests and grasslands (Zhang et al. 2001). Globally, green roofs have been shown to achieve rainfall retention between 30 to 86% (Li and Babcock 2014), depending on green roof design and plant selection (Yang et al. 2015).

Plants improve green roof rainfall retention through evapotranspiration and plants that use more water can dry out substrates more efficiently between rain events (Farrell et al. 2013b), thereby restoring storage capacity and increasing retention (Oberndorfer et al. 2007, Berndtsson 2010). However, green roofs typically have shallow substrates which are designed for efficient drainage (Ampim et al. 2010), making it difficult for plants with greater water-use to survive dry periods, which is exacerbated by high rooftop temperatures (Rayner et al. 2016). Therefore, though seemingly contradictory, green roof plants should have greater water-use during rain events to increase rainfall retention capacity, but also survive dry periods to remain functional until the next rain event (Farrell et al. 2013b).

Plant functional traits may be useful to select suitable plants and simplifies plant selection as many traits can be measured rapidly and consistently using standardised protocols (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2016). Functional traits, both morphological and physiological, reflect the ecological strategies that plants use to achieve optimal growth or survival in natural ecosystems (Violle et al. 2007, Mitchell et al. 2008, Poorter et al. 2009, Volaire 2018) depending on resource-availability (Grime 1988, Wright et al. 2004). One trait-based framework which could be used to select green roof plants is the ‘fast-slow plant economics spectrum’ (Reich 2014), which suggests that plants adapted to resource-rich environments have ‘fast’ traits that support rapid resource-acquisition for growth. Conversely, plants adapted to resource-poor environments have ‘slow’ traits and conservative resource-use to ensure survival (Reich 2014, Volaire 2018). For optimal rainfall retention on green roofs, we hypothesise that plants should have ‘fast’ traits for greater water-use to absorb more rainfall. However, ‘slow’ traits associated with drought tolerance are likely to be beneficial for surviving dry periods between rainfall events.

For above-ground traits, greater shoot dry weight and SLA are ‘fast’ traits that relate to rapid water-uptake (Xie et al. 2018) and lower drought tolerance (Reich 2014). For below-ground traits, greater root allocation (RMF) and lower SRL are ‘slow’ traits that relate to conservative water-use and greater drought tolerance (Markesteijn and Poorter 2009, Reich 2014). Though less studied, SRL has been proposed as the below-ground equivalent of SLA and therefore greater SRL is also associated with ‘fast’ resource-use (Cornelissen et al. 2003). Following this, studies have suggested that traits should be coordinated across the entire plant (Liu et al. 2010, Reich 2014, de la Riva et al. 2016) to improve the ability of plants to adjust to changes in resource availability (Du et al. 2019a). Some studies have shown relationships between above- and below-ground traits such as SLA and SRL (Wright and Westoby 1999, Fort et al. 2012, Cheng et al. 2016), while others have shown no co-ordination, or inconsistent co-ordination between above- and below-ground traits (Craine et al. 2005, Weemstra et al. 2016). For instance, in a study that sampled 90 grass species from 67 sites across four grassland regions, Craine et al. (2005) showed that leaf and root traits were not correlated either within and across the grassland regions. However, where trait coordination occurs between above- and below-ground traits, it provides the potential to use a single, well-studied trait to represent other traits, making trait approaches for plant selection more practical (Reich 2014).

Physiological approaches have also been used to select plants for green roofs which have greater water-use and drought resistance (Szota et al. 2017, Du et al. 2018). For example, Farrell et al. (2013b) showed that non-woody plants originating from rocky outcrops had greater water-use when water was abundant, but were able to maintain water-status (pre-dawn leaf water potential) under water-deficit. Physiologically, plants resist drought through either avoiding or tolerating drought stress (Levitt 1980). Drought-avoiders have greater stomatal sensitivity and close their stomates more rapidly to maintain their leaf water status (midday leaf water potential; Ψ_{MD}) in response to water-deficit (Tardieu and Simonneau 1998, Delzon 2015, Henry et al. 2019). Therefore, these plants maintain their leaf water status and have smaller differences between Ψ_{MD} under well-watered and water-deficit conditions ($\Delta\Psi_{MD}$) and are more isohydric (Franks et al. 2007, Farrell et al. 2013b, Delzon 2015, Farrell et al. 2017). On the other hand, drought-tolerators have lower stomatal sensitivity and are more anisohydric as they reduce their Ψ_{MD} in response to water-deficit and endure greater degree of tissue dehydration (Tardieu and Simonneau 1998, Farrell et al. 2017). Under water-deficit, isohydric plants are thought to use less water as they close their stomates earlier than anisohydric plants (West et al. 2008, Skelton et al. 2015).

We investigated whether morphological traits could indicate plant water-use and drought resistance and be used to help select green roof plants that can optimise rainfall retention through greater water-use without jeopardizing drought survival. We hypothesised that: (1) WW plants with 'fast' traits would have greater water-use; (2) plants with 'slow' traits would have greater drought tolerance (anisohydric and lower stomatal sensitivity) under WD; and (3) above- and below-ground traits would be coordinated, i.e. plants with greater SLA would also have greater SRL. In addition, we investigated whether plants with greater water-use (WW) could also avoid drought stress and maintain water status under WD through isohydry and greater stomatal sensitivity.

Methods

Species selection

We selected 14 species (mostly C3 plants) used in Mediterranean-type climate green roofs based on their SLA to represent a gradient of 'fast-slow' plants (Table 1). Plants with C3 photosynthetic pathway are better suited in Mediterranean-type climates with wet winters and less annual rainfall (Gurevitch et al. 2006). However, C3 plants have lower instantaneous water-use efficiency compared to C4 and CAM plants (Gurevitch et al. 2006), i.e. C3 plants gain less carbon for every unit of water used in photosynthesis. SLA data were obtained from the TRY Plant Trait Database (Kattge et al. 2020). Fifteen plants of each species were obtained as sixmonth old seedlings from local nurseries. In early December (summer) 2018, the seedlings were potted into 4-L black plastic pots (200 mm diameter, 190 mm height), containing 3 kg of a scoria-based green roof substrate (60% scoria 8 mm minus, 20% 7 mm scoria aggregate, 20% composted coir; water-holding capacity (WHC) = 45.9%; air-filled porosity (AFP) = 13.8%; bulk density = 1.26 g cm^{-3} (Farrell et al. 2012)) that is designed based on the FLL (2008) guideline recommendations for extensive green roofs. The substrate design is commonly used on Australian green roofs as the components are readily available with minimal variation in composition and properties (Conn et al. 2020). After potting, 12 grams of low-phosphorous slow-release fertiliser (14 N:1.3P:14.9K, Osmocote® Pro, Scotts Australia Pty Ltd.) was applied evenly to the surface of each pot. For the next two months, plants were grown outdoors and watered by automated sprinklers for 7 minutes twice daily (06:45 and 13:45 h).

Experimental Design

The experiment took place at the Burnley Campus, University of Melbourne, Australia (37°470 S; 144°580 E). In mid-February (summer) 2019, plants were moved into a glasshouse, with daily temperatures ranging from 8.5 to 28.6 °C and an average temperature of 17.5 °C during the experiment. This temperature range was on average lower than that of green roof surfaces in Melbourne, which have been shown to range from 15 to 65 °C from summer to winter, with average maximum temperatures in summer reaching up to 35 °C (Rayner et al. 2016). All plants were watered to pot-capacity three times a week until the start of the experiment. The experiment ran for 72 days, from 20th March to 31st May (autumn) 2019. Three plants of each species were harvested before the watering treatments began to determine initial plant mass. Their mean initial biomass was assumed to be representative of their species in the treatment blocks for calculation of soil water content (SWC). Plants were arranged in a complete randomised block design with five blocks. Each block comprised 28 plants; each species had one pair of similar-sized plants randomly assigned to either well-watered (WW) or water-deficit (WD) treatments. All pots were weighed before each watering session, and pots that were watered were weighed again after pots drained (45 minutes after watering) to determine evapotranspiration (ET). Throughout the experiment, WW plants were watered to pot-capacity three times a week (Monday, Wednesday, and Friday). For the first 42 days of the experiment, WD plants were watered on the same day as WW plants, but only when their gravimetric SWC was below 20%, to gradually induce drought stress. Water-deficit plants received their final watering on day 42 and were then left to dry-down. During the dry-down phase, ET and midday water potential (Ψ_{MD}) of all plants were measured daily until stomatal closure (when ET of WD was < 20% of WW plants) (Somerville et al. 2019) (see Appendix S1: Figure S1 for figures showing the relationship between Ψ_{MD} and SWC for each species). WW and WD plants were harvested in replicate pairs, based on the dry-down rate of WD plants. Final plant biomass (shoot and root), SLA, SRL were measured during the final harvest for WW plants only.

Soil water content

Soil water content (SWC) of WD plants was determined before each watering session based on the mass of the potted plants before watering, and calculated as:

$$\text{SWC (\%)} = \frac{\text{Current mass of potted plant - initial plant mass - substrate dry mass - empty pot mass}}{\text{substrate dry mass}} \times 100$$

(Farrell et al. 2013b).

Substrate dry weight was determined from oven-drying five 3 kg samples at 80 °C for one week.

Evapotranspiration

Evapotranspiration (ET) was calculated based on the difference in pot weights between two watering sessions: ET = post-watering weight (session *n-1*) – pre-watering weight (session *n*). When WD plants were not yet watered (SWC > 20% of WW plants), their ET was calculated as: ET = weight (session *n-1*) – weight (session *n*). Total ET for the experiment was determined by summing up ET until stomatal closure (ET of WD plants < 20% of that of WW plants). Total ET was then used to calculate daily ET both on a per pot basis (g d^{-1}) and per shoot dry weight (g g^{-1} d^{-1}).

Drought resistance metrics

This study used three metrics to indicate drought resistance. (1) The number of days until stomatal closure: the duration from the start of dry-down period (day 43) to the day when the ET of WD plants reached 20% of WW ET. (2) Cumulative ET: total ET until stomatal closure. (3) The degree of iso-anisohydry ($\Delta\Psi_{MD}$): difference between mean midday leaf water potential (Ψ_{MD}) of WW plants and WD plants ($\Delta\Psi_{MD}$) (Franks et al. 2007, Farrell et al. 2013b, Delzon 2015, Farrell et al. 2017). For each pair of WW and WD plants, Ψ_{MD} was measured on the day that WD plants reached stomatal closure (ET of WD plant < 20% of the WW plant pair). A fully expanded leaf was cut from each plant at midday (12:00-13:00 h) and sealed in a zip-lock bag prior to determining leaf water potential with a Scholander-type pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA, USA). For leaves with short petioles, leaf water potential was measured on apical branches with 2-3 leaves.

Morphological traits

Morphological traits were measured only for WW plants at the end of the experiment using standardised protocols (Perez-Harguindeguy et al. 2016). Shoot dry weight included above-ground stems and leaves and was recorded after drying in an 80 °C oven until constant mass. SLA (leaf area per unit leaf dry mass; $m^2\ kg^{-1}$ leaf) was determined for three youngest fully expanded leaves for each plant using individual leaf area measured using ImageJ (version 1.52a; Wayne Rasband, National Institutes of Health, USA) and the dry mass of sampled leaves. Where present, the petiole was included in SLA measurements. Roots were washed free of soil and weighed before storing in 1-L plastic containers filled with 50% ethanol and stored at 4 - 5 °C to preserve them for root-scanning. Three replicates of washed roots were scanned at 2400 dpi to determine root length using WinRHIZO (version 2016; Regent Instruments Inc., Quebec, QC, Canada). All root samples were then oven-dried at 80 °C until constant mass to calculate SRL (total root length per unit root dry mass; $m\ g^{-1}$ root) ($n = 3$) for scanned samples and RMF (root dry mass per unit total plant dry mass; $g\ g^{-1}$) ($n=5$).

Statistical analyses

Relationships between plant traits, water-use, and drought resistance were analysed using Pearson's correlations in R, version 1.3.959 (RStudio Team 2019) and the significance threshold is set at $p < 0.005$. Data for each species were averaged across 5 replicates, except for SRL measurements (3 replicates). All data not normally distributed were transformed to ensure univariate linearity (log-transformed: RMF, Ψ_{MD}; square-root-transformed: daily ET per shoot dry weight, days to stomatal closure, shoot dry weight, SLA; square-transformed: cumulative ET) for relationship analysis. All figures were plotted with non-transformed data for easy comparison with values in other studies.

Results

Relationships between water-use and morphological traits

Under WW conditions, water-use (ET) was significantly and positively related to above-ground traits (shoot dry weight and SLA), but not to below-ground traits (RMF and SRL). Plants with greater shoot dry weight used more water per day on a pot basis ($r^2 = 0.42$; $p < 0.001$; Fig. 1A), but water-use was not related to root allocation ($r^2 = 0.01$; $p = 0.40$; Fig. 1B). When daily ET was adjusted for shoot dry weight, plants with greater SLA had greater water-use ($r^2 = 0.10$; $p = 0.01$; Fig. 1C), but water-use was not related to SRL ($r^2 = 0.02$; $p = 0.34$; Fig. 1D).

Relationships between drought-resistance metrics and morphological traits

There were no consistent relationships among the three drought-resistance metrics and morphological traits. Days to stomatal closure during the dry-down period was related to above-ground traits (shoot dry weight and SLA). Plants with lower shoot dry weight ($r^2 = 0.32$; $p < 0.001$; Fig. 2A) and those with greater SLA ($r^2 = 0.16$; $p < 0.001$; Fig. 2C) took longer to close their stomates under WD. The amount of water used by WD plants during the dry-down period (cumulative ET until stomatal closure) was not related with any morphological traits (Fig. 2E-H). However, when *Olearia axillaris* was omitted from the analysis as an outlier, there was a significant positive relationship between cumulative ET until stomatal closure and SLA ($r^2 = 0.06$; $p = 0.05$; data not shown). The degree of iso-anisohydry was significantly related to RMF, where plants with greater root allocation were more anisohydric ($r^2 = 0.33$; $p = 0.03$; Fig. 2J).

Coordination among morphological traits

There was a significant negative relationship between shoot dry weight and SLA ($r^2 = 0.09$; $p = 0.014$; Fig. 3A), i.e. plants with lower shoot dry weight had greater SLA. There was no significant relationship between shoot dry weight and root allocation ($r^2 = 0.05$; $p = 0.06$; Fig. 3B). SLA was significantly and positively related to SRL for all plants ($r^2 = 0.36$; $p < 0.001$; Fig. 3C).

Relationships between water-use (WW) and drought-response metrics and the relationship amongst the drought-response metrics

Water-use on a pot basis (WW) was negatively related to days until stomatal closure (WD); i.e. plants that used more water under WW conditions closed their stomates quicker under WD ($r^2 =$

0.37; $p < 0.001$; Fig. 4A). However, cumulative ET of WD plants during the dry-down period ($r^2 < 0.01$; $p = 0.75$; Fig. 4B) and the degree of iso-anisohydry ($r^2 < 0.01$; $p = 0.91$; Fig. 4C) were not related to water-use (WW).

During the dry-down period, plants that were more anisohydric (greater $\Delta\Psi_{MD}$) used more water than isohydric plants ($r^2 = 0.41$; $p = 0.01$; Fig. 4E). However, days to stomatal closure was not related to either the degree of iso-anisohydry ($r^2 = 0.09$; $p = 0.30$; Fig. 4D) or cumulative ET of WD plants under water-deficit ($r^2 < 0.01$; $p = 0.92$; Fig. 4F).

Discussion

We undertook a glasshouse experiment to determine whether ‘fast-slow’ above- and below-ground plant traits could be used to help select green roof plants that can optimise rainfall retention through greater water-use without jeopardizing drought survival. We hypothesised that: (1) plants with ‘fast’ traits would have greater water-use (WW); (2) plants with ‘slow’ traits would have greater drought tolerance (anisohydric and lower stomatal sensitivity to WD); and (3) above- and below-ground traits would be coordinated, i.e. plants with greater SLA would also have greater SRL. In addition, we investigated whether plants with greater water-use (WW) could also avoid drought stress and maintain water status under WD through isohydry and greater stomatal sensitivity.

Water-use was positively related to ‘fast’ above-ground traits

Under well-watered conditions, plant water-use was positively related to shoot dry weight, i.e. in plants of the same age, plants with greater shoot dry weight used more water. Further, when water-use was adjusted for shoot dry weight, plants with greater SLA also showed greater water-use. This is consistent with other studies that showed positive relationships between water-use, shoot dry weight, and SLA (Mitchell et al. 2008, Markesteijn and Poorter 2009, Farrell et al. 2013b, Du et al. 2018). For instance, Nagase and Dunnett (2012) showed that for 12 species (forbs, sedums and grasses) commonly planted on extensive green roofs in England, plants with greater shoot dry weight were more efficient at retaining rainfall, with bigger plants retaining close to 80% of the stimulated high-intensity rainfall. The plants in our experiment had greater shoot dry weight compared to Nagase and Dunnett (2012) (10 to 20-fold difference), so it is highly possible that the plants in our study, if used on green roofs, could reduce stormwater retention to pre-urbanisation levels. In modular green roofs under maritime climatic conditions, taller plants with greater SLA used more water, across 21 species selected from natural habitats with similar conditions to green roofs (Lundholm et al. 2015). Therefore, for green roofs, selecting plants with greater shoot dry weight and SLA can improve stormwater management, as they have a greater potential to dry out substrates more effectively after rainfall.

In contrast, water-use under non-limiting conditions was not related to below-ground traits: root mass allocation (RMF) and SRL. This is inconsistent with previous studies showing that plants with lower root mass allocation and greater SRL have greater water-use (Markesteijn and Poorter 2009, Larson and Funk 2016). While SLA was positively related to SRL in our study, water-use (WW) was not related to SRL. This is surprising, as the two traits tend to be coordinated (Craine and Lee 2003, Freschet et al. 2010, Fort et al. 2012, Reich 2014), and greater SLA and SRL tend to indicate 'faster' water-uptake as opposed to lower SLA and SRL (Cheng et al. 2016, Balachowski and Volaire 2018). In our study, the lack of relationship between below-ground traits and water-use might have been due to the pots restricting root growth and hence might not reflect the way these plants access and use water in their natural habitats (Poot and Lambers 2003, Fort et al. 2017, Xie 2019), though other pot-based studies have shown positive relationships between SRL and water-use (Hernández et al. 2010, Balachowski and Volaire 2018). However, as green roofs also have limited substrate depth (often less than 20 cm depth), our results will likely reflect plant water-use under green roof conditions. However, other root traits such as root diameter, root tissue density, and rooting architecture, which were not investigated in this study, might be better related to water-use (Markesteijn and Poorter 2009, Fort et al. 2012, Nagase and Dunnett 2012). Though this study showed a positive relationship between SLA and SRL, this relationship is not always straightforward in the literature, as unlike leaves, roots are responsible for the uptake of multiple resources, which complicates the relationships between above- and below-ground traits (Weemstra et al. 2016). Based on our results, root allocation and SRL are less useful than above-ground traits for selecting green roof plants for stormwater mitigation.

Drought tolerance was related to shoot dry weight, SLA, and root allocation but not consistently with 'slow' traits

Apart from having greater water-use after rainfall, green roof plants need to tolerate dry conditions between rainfall events, due to water limitations of shallow substrates (Farrell et al. 2013b, Rayner et al. 2016). This study used three metrics to represent drought-resistance: (1) days to stomatal closure, (2) cumulative ET under WD, and (3) the degree of iso-anisohydry ($\Delta\Psi_{MD}$).

Days to stomatal closure was only related to above-ground traits, though not consistently with 'slow' traits. Plants with lower shoot dry weight ('slow') and greater SLA ('fast') closed their stomates later during the dry-down and were more drought-tolerant. On green roofs, it has been suggested that larger plants will be more vulnerable to drought due to their greater demand for water (Lundholm et al. 2015), consistent with the results of our glasshouse study. Generally, plants with greater SLA have lower drought tolerance (Farrell et al. 2017, Xie et al. 2018) and come from more mesic natural environments (Mitchell et al. 2008, Poorter et al. 2009), so it was surprising that plants with greater SLA closed their stomata later during the dry-down (Lundholm et al. 2015). However, 'fast' traits (faster growth rates) were also related to lower stomatal sensitivity to water deficit (more negative leaf water potentials) for six deciduous tree species (Aasamaa and Sõber 2011). Other studies have also shown that stomatal regulation was not related to 'fast' leaf traits such as greater SLA (Kröber and Bruelheide (2014). In our study, shoot dry weight had a stronger influence on stomatal response to drought than SLA, and smaller plants had greater SLA. This indicates that the relationships between leaf traits and stomatal response to drought are not straightforward.

Plants with greater root allocation ('slow') were more anisohydric. This relationship is expected, as plants adapted to drought-prone environments tend to be anisohydric (McDowell et al. 2008) with greater root allocation to access more water in drying soils (Gurevitch et al. 2006). Although this is in contrast with Du et al. (2018) who observed no significant relationship between root allocation and water status (Ψ_{MD}) under water deficit for 20 Australian shrub species. SRL was not related with drought-tolerance in our study. This contradicts previous studies showing relationships between SRL and drought-resistance (Wright and Westoby 1999, Markesteijn and Poorter 2009, Fort et al. 2012, Larson and Funk 2016). For instance, Balachowski and Volaire (2018) showed that plants with greater SRL avoided drought stress by absorbing water rapidly from shallow soil layers. As mentioned previously, rooting depth was restricted in our experiment due to our focus on using traits to select plants for shallow green roofs. In nature, deep-rooted plants can access water from fissures and deep soil profiles, helping the plants to maintain water status during drought (Sternberg et al. 1996, Poot and Lambers 2003, Xie 2019). While SRL may not be a useful trait for green roof plant selection due to restricted rooting depths, RMF can be useful for indicating iso-anisohydric behaviours.

Though drought resistance was related to shoot dry weight, SLA, and root allocation, there was no consistent relationship across the three metrics. In particular, cumulative ET (WD) was not related to any of the traits measured, i.e. plants with ‘fast’ traits did not use more water than plants with ‘slow’ traits under WD conditions. This inconsistency in relationships not only reflects the complicated nature of drought-resistance strategies but also supports that for some species, drought-avoiders can survive as well as drought-tolerators on green roofs (Du et al. 2019b). This is likely, as in addition to physiological responses, drought responses on green roofs can also be influenced by plant succulence (Farrell et al. 2013b), substrate depth (Thuring et al. 2010), and substrate water holding capacity (Farrell et al. 2013a). As drought-resistance is influenced by multiple factors and ecological processes (Kissel et al. 2015, Garcia-Forner et al. 2016), it is still unclear which drought metric can consistently represent drought resistance to select green roof plants.

Plants with greater water-use (WW) could avoid drought through greater stomatal sensitivity.

Consistent with previous studies (West et al. 2012, Henry et al. 2019), anisohydric plants in our study had greater water-use under WD than isohydric plants, supporting that drought tolerant plants continued to use water under drought conditions. However, contrary to other studies (Klein 2014, Farrell et al. 2017, Henry et al. 2019), anisohydric plants did not take longer to close their stomates under WD, implying that iso-anisohydric behaviour was not related to stomatal sensitivity (Martínez-Vilalta and Garcia-Forner 2017). Our study also showed no relationship between stomatal closure and water-use under WD, which contradicts West et al. (2008) who showed that plants with lower stomatal sensitivity continued gas exchange, and therefore water-use, longer during drought. These results imply that the greater water-use exhibited by anisohydric plants during drought was not a function of lower stomatal sensitivity nor greater root allocation but may reflect other traits not evaluated in this paper. This also suggests that greater root allocation may be more responsible for structural support or storage rather than water-use. Of the three drought response metrics, only stomatal closure was related to water-use under WW. In our study, plants with greater water-use (WW) closed their stomates faster (WD) and avoided drought stress. This is supported by Henry et al. (2019), who showed that plants with greater stomatal conductance when water was available, had greater stomatal sensitivity and maintained higher water-potential under WD, across 15 Californian woody angiosperms. Therefore, while our study supports other research which shows a trade-off between water-use and drought-tolerance (Comas et al. 2013, Du et al. 2018), plants with high water-use are more likely to survive on green roofs through drought-avoidance strategies.

Conclusion

We were able to use morphological traits to help identify green roofs plants for stormwater management and drought survival. Higher water-use was related to 'fast' above-ground traits and plants with greater shoot dry weight and SLA are likely to maximise rainfall retention on green roofs by drying out substrates after rainfall. Plants with 'slow' traits were generally more drought tolerant, as plants with lower shoot dry weight closed their stomata later and plants with greater root allocation were more anisohydric. Plants with greater water-use (WW) could technically avoid drought stress by closing their stomates faster but were neither more isohydric nor used more water under WD. Therefore, 'fast' above-ground traits can be used to select green roof plants with high water-use that can rapidly uptake water during pulses of rainfall and avoid drought stress to optimise rainfall retention without jeopardising drought survival.

Although SLA and SRL were co-ordinated, SRL was not related to water-use or drought-resistance. Though roots are primarily in charge of water-uptake, it seems that root traits that reflect tissue longevity (SRL) might not reflect water-use strategies when rooting depth is limited, as occurs in green roofs with shallow substrates. However, RMF can indicate iso-anisohydric behaviors. Given the complicated nature of plant adaptations to drought, other root traits such as root diameter, root tissue density, and root architecture might better reflect drought response strategies and should be investigated in future studies.

Though morphological traits are useful for selecting green roof plants to maximise rainfall retention, it is still important to consider the original habitat and select plants from natural habitats with conditions like green roofs. Ideal habitats include coastal dunes and rock outcrops, which are exposed to high temperatures with shallow soils (Lundholm 2006). As Balachowski and Volaire (2018) suggested, it is better to consider both climate of origin and plant traits when selecting plants, as the former indicates the environment that a plant is adapted to, but the latter helps to predict the likely ecological strategies that the plants employ in response to resource limitations. As SLA and SRL were coordinated, future green roof plant selection could focus solely on using above-ground traits which would facilitate rapid plant selection as above-ground traits are readily available from online databases (e.g. TRY Plant Trait Database).

Acknowledgments

We would like to thank Burnley nursery staff Brett Hough and Rowan Berry for technical assistance throughout the experiment. We are also thankful to Christopher Szota for demonstrating the use of pressure chamber for water potential measurements and his feedback on our draft manuscript. Many thanks to Pei-Wen Chung and Vicky J. McGimpsey for their suggestions on data collection procedures. We thank the reviewers for their time and effort in helping us improve our manuscript. Authors' contributions: Hsiao-Hsuan Chu and Claire Farrell conceived the ideas and designed the experiment; Hsiao-Hsuan Chu collected and analysed the data and led the writing of the manuscript; both authors contributed critically to drafts and gave final approval for publication.

Literature Cited

Aasamaa, K., and A. Sõber. 2011. Stomatal sensitivities to changes in leaf water potential, air humidity, CO2 concentration and light intensity, and the effect of abscisic acid on the sensitivities in six temperate deciduous tree species. Environmental and Experimental Botany **71**:72-78.

Ampim, P. A., J. J. Sloan, R. I. Cabrera, D. A. Harp, and F. H. Jaber. 2010. Green roof growing substrates: types, ingredients, composition and properties. Journal of Environmental Horticulture **28**:244-252.

Balachowski, J. A., and F. A. Volaire. 2018. Implications of plant functional traits and drought survival strategies for ecological restoration. Journal of Applied Ecology **55**:631-640.

Berndtsson, J. C. 2010. Green roof performance towards management of runoff water quantity and quality: A review. Ecological Engineering **36**:351-360.

Cheng, J., P. Chu, D. Chen, and Y. Bai. 2016. Functional correlations between specific leaf area and specific root length along a regional environmental gradient in Inner Mongolia grasslands. Functional Ecology **30**:985-997.

Chu, H.-H. 2021. Data for figures.xlsx. University of Melbourne. Dataset. https://doi.org/10.26188/5ebce2c3c57bd

Comas, L. H., S. R. Becker, V. M. V. Cruz, P. F. Byrne, and D. A. Dierig. 2013. Root traits contributing to plant productivity under drought. Frontiers in Plant Science **4**:442.

Conn, R., J. Werdin, J. P. Rayner, and C. Farrell. 2020. Green roof substrate physical properties differ between standard laboratory tests due to differences in compaction. Journal of environmental management **261**:110206.

Cornelissen, J., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. Gurvich, P. B. Reich, H. Ter Steege, H. Morgan, and M. Van Der Heijden. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of botany **51**:335-380.

Craine, J., and W. Lee. 2003. Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. Oecologia **134**:471-478.

Craine, J. M., W. G. Lee, W. J. Bond, R. J. Williams, and L. C. Johnson. 2005. ENVIRONMENTAL CONSTRAINTS ON A GLOBAL RELATIONSHIP AMONG LEAF AND ROOT TRAITS OF GRASSES. Ecology **86**:12-19.

de la Riva, E. G., A. Tosto, I. M. Pérez-Ramos, C. M. Navarro-Fernández, M. Olmo, N. P. Anten, T. Marañón, and R. Villar. 2016. A plant economics spectrum in Mediterranean forests along environmental gradients: is there coordination among leaf, stem and root traits? Journal of Vegetation Science **27**:187-199.

Delzon, S. 2015. New insight into leaf drought tolerance. Functional Ecology **29**:1247-1249.

Du, L., H. Liu, W. Guan, J. Li, and J. Li. 2019a. Drought affects the coordination of belowground and aboveground resource-related traits in Solidago canadensis in China. Ecology and Evolution **9**:9948-9960.

Du, P., S. K. Arndt, and C. Farrell. 2018. Relationships between plant drought response, traits, and climate of origin for green roof plant selection. Ecological Applications: A Publication Of The Ecological Society Of America **28**:1752-1761.

Du, P., S. K. Arndt, and C. Farrell. 2019b. Is plant survival on green roofs related to their drought response, water use or climate of origin? Science of the Total Environment **667**:25-32.

Farrell, C., X. Q. Ang, and J. P. Rayner. 2013a. Water-retention additives increase plant available water in green roof substrates. Ecological Engineering **52**:112-118.

Farrell, C., R. Mitchell, C. Szota, J. Rayner, and N. Williams. 2012. Green roofs for hot and dry climates: interacting effects of plant water use, succulence and substrate. Ecological Engineering **49**:270-276.

Farrell, C., C. Szota, and S. K. Arndt. 2017. Does the turgor loss point characterize drought response in dryland plants? Plant, Cell & Environment **40**:1500-1511.

Farrell, C., C. Szota, N. S. G. Williams, and S. K. Arndt. 2013b. High water users can be drought tolerant: Using physiological traits for green roof plant selection. Plant and Soil **372**:177-193.

FLL, F. L. L. 2008. Guidelines for the planning, Construction and Maintenance of Green Roofing. Landscape, Research, Development & Construction Society, Bonn, Germany.

Fort, F., C. Jouany, and P. Cruz. 2012. Root and leaf functional trait relations in Poaceae species: implications of differing resource-acquisition strategies. Journal of Plant Ecology **6**:211-219.

Fort, F., F. Volaire, L. Guilioni, K. Barkaoui, M. L. Navas, and C. Roumet. 2017. Root traits are related to plant water-use among rangeland Mediterranean species. Functional Ecology **31**:1700-1709.

Franks, P. J., P. L. Drake, and R. H. Froend. 2007. Anisohydric but isohydrodynamic: seasonally constant plant water potential gradient explained by a stomatal control mechanism incorporating variable plant hydraulic conductance. Plant, Cell & Environment **30**:19-30.

Freschet, G. T., J. H. Cornelissen, R. S. Van Logtestijn, and R. Aerts. 2010. Evidence of the ‘plant economics spectrum’in a subarctic flora. Journal of Ecology **98**:362-373.

Garcia-Forner, N., A. Sala, C. Biel, R. Savé, and J. Martínez-Vilalta. 2016. Individual traits as determinants of time to death under extreme drought in Pinus sylvestris L. Tree Physiology **36**:1196-1209.

Grime, J. P. 1988. The CSR model of primary plant strategies—origins, implications and tests. Pages 371-393 Plant evolutionary biology.

Gurevitch, J., S. M. Scheiner, and G. A. Fox. 2006. The ecology of plants. 2nd ed. edition. Sinauer Associates.

Henry, C., G. P. John, R. Pan, M. K. Bartlett, L. R. Fletcher, C. Scoffoni, and L. Sack. 2019. A stomatal safety-efficiency trade-off constrains responses to leaf dehydration. Nature communications **10**:1-9.

Hernández, E. I., A. Vilagrosa, J. G. Pausas, and J. Bellot. 2010. Morphological traits and water use strategies in seedlings of Mediterranean coexisting species. Plant Ecology **207**:233-244.

Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D. Werner, T. Aakala, and M. Abedi. 2020. TRY plant trait database–enhanced coverage and open access. Global Change Biology.

Kissel, E., P. Van Asten, R. Swennen, J. Lorenzen, and S. Carpentier. 2015. Transpiration efficiency versus growth: exploring the banana biodiversity for drought tolerance. Scientia Horticulturae **185**:175-182.

Klein, T. 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Functional Ecology **28**:1313-1320.

Kröber, W., and H. Bruelheide. 2014. Transpiration and stomatal control: a cross-species study of leaf traits in 39 evergreen and deciduous broadleaved subtropical tree species. Trees **28**:901-914.

Larson, J. E., and J. L. Funk. 2016. Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. New Phytologist **210**:827-838.

Levitt, J. 1980. Responses of plants to environmental stresses. 2nd ed. edition. New York : Academic Press.

Li, Y., and R. W. Babcock. 2014. Green roof hydrologic performance and modeling: a review. Water Science and Technology **69**:727-738.

Liu, G., G. T. Freschet, X. Pan, J. H. Cornelissen, Y. Li, and M. Dong. 2010. Coordinated variation in leaf and root traits across multiple spatial scales in Chinese semi-arid and arid ecosystems. New Phytologist **188**:543-553.

Lundholm, J. 2006. Green Roofs and Facades: A Habitat Template Approach. Urban Habitats **4**:87-101.

Lundholm, J., S. Tran, and L. Gebert. 2015. Plant functional traits predict green roof ecosystem services. Environmental science & technology **49**:2366-2374.

Markesteijn, L., and L. Poorter. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought-and shade-tolerance. Journal of Ecology **97**:311-325.

Martínez-Vilalta, J., and N. Garcia-Forner. 2017. Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. Plant Cell and Environment **40**:962-976.

McDowell, N., W. T. Pockman, C. D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. G. Williams, and E. A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytologist **178**:719-739.

Meyer, J. L., M. J. Paul, and W. K. Taulbee. 2005. Stream ecosystem function in urbanizing landscapes. Journal of the North American Benthological Society **24**:602-612.

Mitchell, P. J., E. J. Veneklaas, H. Lambers, and S. S. Burgess. 2008. Using multiple trait associations to define hydraulic functional types in plant communities of south-western Australia. Oecologia **158**:385-397.

Nagase, A., and N. Dunnett. 2012. Amount of water runoff from different vegetation types on extensive green roofs: Effects of plant species, diversity and plant structure. Landscape and Urban Planning **104**:356-363.

Oberndorfer, E., J. Lundholm, B. Bass, R. R. Coffman, H. Doshi, N. Dunnett, S. Gaffin, M. Köhler, K. K. Liu, and B. Rowe. 2007. Green roofs as urban ecosystems: ecological structures, functions, and services. BioScience **57**:823-833.

Perez-Harguindeguy, N., S. Diaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. Bret-Harte, W. K. Cornwell, J. M. Craine, and D. E. Gurvich. 2016. Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. Australian Journal of botany **64**:715-716.

Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist **182**:565-588.

Poot, P., and H. Lambers. 2003. Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. Journal of Ecology **91**:58-67.

Rayner, J. P., C. Farrell, K. J. Raynor, S. M. Murphy, and N. S. Williams. 2016. Plant establishment on a green roof under extreme hot and dry conditions: The importance of leaf succulence in plant selection. Urban Forestry & Urban Greening **15**:6-14.

Reich, P. B. 2014. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. Journal of Ecology **102**:275-301.

RStudio Team. 2019. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA.

Skelton, R. P., A. G. West, and T. E. Dawson. 2015. Predicting plant vulnerability to drought in biodiverse regions using functional traits. Proceedings of the National Academy of Sciences of the United States of America **112**:5744-5749.

Somerville, P. D., C. Farrell, P. B. May, and S. J. Livesley. 2019. Tree water use strategies and soil type determine growth responses to biochar and compost organic amendments. Soil and Tillage Research **192**:12-21.

Sternberg, P., M. Anderson, R. Graham, J. Beyers, and K. Tice. 1996. Root distribution and seasonal water status in weathered granitic bedrock under chaparral. Geoderma **72**:89-98.

Szota, C., C. Farrell, N. S. G. Williams, S. K. Arndt, and T. D. Fletcher. 2017. Drought-avoiding plants with low water use can achieve high rainfall retention without jeopardising survival on green roofs. Science of the Total Environment **603-604**:340-351.

Tardieu, F., and T. Simonneau. 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: Modelling isohydric and anisohydric behaviours. Journal of experimental botany **49**:419-432.

Thuring, C. E., R. D. Berghage, and D. J. Beattie. 2010. Green roof plant responses to different substrate types and depths under various drought conditions. HortTechnology **20**:395-401.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos **116**:882-892.

Volaire, F. 2018. A unified framework of plant adaptive strategies to drought: Crossing scales and disciplines. Global Change Biology **24**:2929-2938.

Weemstra, M., L. Mommer, E. J. W. Visser, J. van Ruijven, T. W. Kuyper, G. M. J. Mohren, and F. J. Sterck. 2016. Towards a multidimensional root trait framework: a tree root review. New Phytologist **211**:1159-1169.

West, A., K. Hultine, J. Sperry, S. Bush, and J. Ehleringer. 2008. Transpiration and hydraulic strategies in a piñon–juniper woodland. Ecological Applications **18**:911-927.

West, A. G., T. Dawson, E. February, G. Midgley, W. Bond, and T. Aston. 2012. Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. New Phytologist **195**:396-407.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature **428**:821-827.

Wright, I. J., and M. Westoby. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. Journal of Ecology **87**:85-97.

Xie, G. 2019. Root traits influence stormwater performance in a green roof microcosm. Saint Mary's University, Halifax, Nova Scotia.

Xie, G., J. T. Lundholm, and J. S. MacIvor. 2018. Phylogenetic diversity and plant trait composition predict multiple ecosystem functions in green roofs. Science of the Total Environment **628**:1017-1026.

Yang, W.-Y., D. Li, T. Sun, and G.-H. Ni. 2015. Saturation-excess and infiltration-excess runoff on green roofs. Ecological Engineering **74**:327-336.

Zhang, L., W. R. Dawes, and G. R. Walker. 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. Water Resources Research **37**:701-708.

Table 1. The 14 Mediterranean green roof species used in the glasshouse experiment to determine their water-use and drought response strategies, listed in order of mean SLA values (Trait ID 11) with their leaf photosynthesis pathways (Trait ID 22) obtained from the TRY Plant Trait Database (Kattge et al. 2020; https://www.try-db.org).

Family	**Species**	**SLA (m^2 kg^{-1} leaf)**	**Photosynthetic Pathways**
Asteraceae	*Chrysocephalum apiculatum*	1.2	C3
Asteraceae	*Olearia axillaris*	2.0; 4.3	-
Asteraceae	*Brachyscome multifida*	9.0	-
Fabaceae	*Indigofera australis*	10.8	C3
Fabaceae	*Hardenbergia violacea*	13.2	C3
Asteraceae	*Achillea millefolium*	18.0	C3
Plumbaginaceae	*Armeria maritima* subsp. *maritima*	20.3	-
Lamiaceae	*Hyssopus officinalis*	20.6	C3
Lamiaceae	*Rosmarinus officinalis*	21.3; 22.6	C3
Lamiaceae	*Nepeta cataria*	31.9	C3
Asteraceae	*Jacobaea maritima*	59.3	C3
Lamiaceae	*Teucrium fruticans*	116.0	-
Convolvulaceae	*Convolvulus sabatius*	133.0	-
Lamiaceae	*Origanum vulgare*	144.0	C3

Figure 1. Relationships of daily ET per pot with shoot dry weight (A) and RMF (B) and daily ET per unit shoot dry weight with SLA (C) and SRL (D), for 14 species under well-watered (WW) conditions. Bars represent standard error of the mean ($n = 3$ for SRL; $n = 5$ for others).

Symbol colours represent the range of SLA measured in this experiment for WW plants; from lower SLA = yellow (lighter shade) to greater SLA = purple (darker shade).

Figure 2. Relationships of morphological traits with days to stomatal closure (A-D), cumulative ET (E-H), and the degree of iso-anisohydry (I-L) for all plants. Traits were measured under well-watered (WW) conditions, whereas days to stomatal closure, cumulative ET, and the degree of iso-anisohydry were measured under water-deficit (WD) conditions. Bars represent standard error of the mean (*n* = 3 for SRL; *n* = 5 for others); not shown for the degree of iso-anisohydry as it was calculated from mean values. Symbol colours represent the range of SLA measured in this experiment for WW plants; from lower SLA = yellow (lighter shade) to greater SLA = purple (darker shade).

Figure 3. Correlation among above- and below-ground traits for 14 species measured under well-watered (WW) conditions. Grey dashed line indicates 1:1 relationship. Bars represent standard error of the mean (*n* = 5 for A; *n* = 3 for C). Symbol colours represent the range of SLA measured in this experiment for WW plants; from lower SLA = yellow (lighter shade) to greater SLA = purple (darker shade).

Figure 4. Relationships between daily whole-plant water-use under well-watered (WW) conditions and drought-response strategies (A-C), and relationships between drought-response strategies (D-F). Daily water-use was recorded under well-watered (WW) conditions and drought-response strategies were measured under water-deficit (WD) conditions. Bars represent standard error of the mean (*n* = 5); standard errors not shown for the degree of iso-anisohydry as it was calculated from mean values. Symbol colours represent the range of SLA measured in this experiment for WW plants; from lower SLA = yellow (lighter shade) to greater SLA = purple (darker shade).

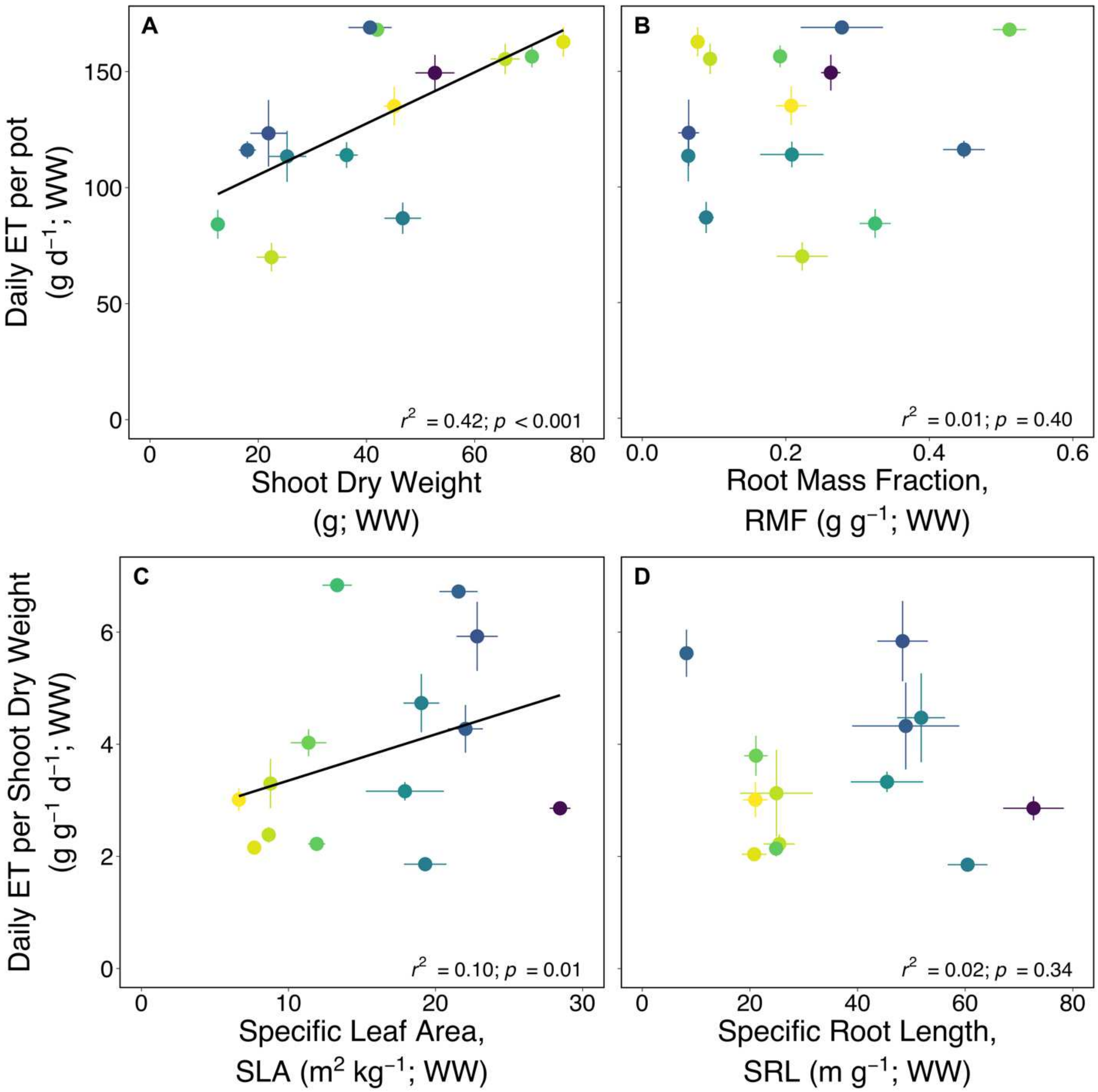
A
B
C
D
Daily ET per pot
(g d^{-1}; WW)
Daily ET per Shoot Dry Weight
(g g^{-1} d^{-1}; WW)
r^2 = 0.42; p < 0.001
r^2 = 0.01; p = 0.40
r^2 = 0.10; p = 0.01
r^2 = 0.02; p = 0.34
Shoot Dry Weight
(g; WW)
Root Mass Fraction,
RMF (g g^{-1}; WW)
Specific Leaf Area,
SLA (m^2 kg^{-1}; WW)
Specific Root Length,
SRL (m g^{-1}; WW)
0
50
100
150
0
2
4
6
0
20
40
60
80
0.0
0.2
0.4
0.6
0
10
20
30
0
20
40
60
80

Figure 1.

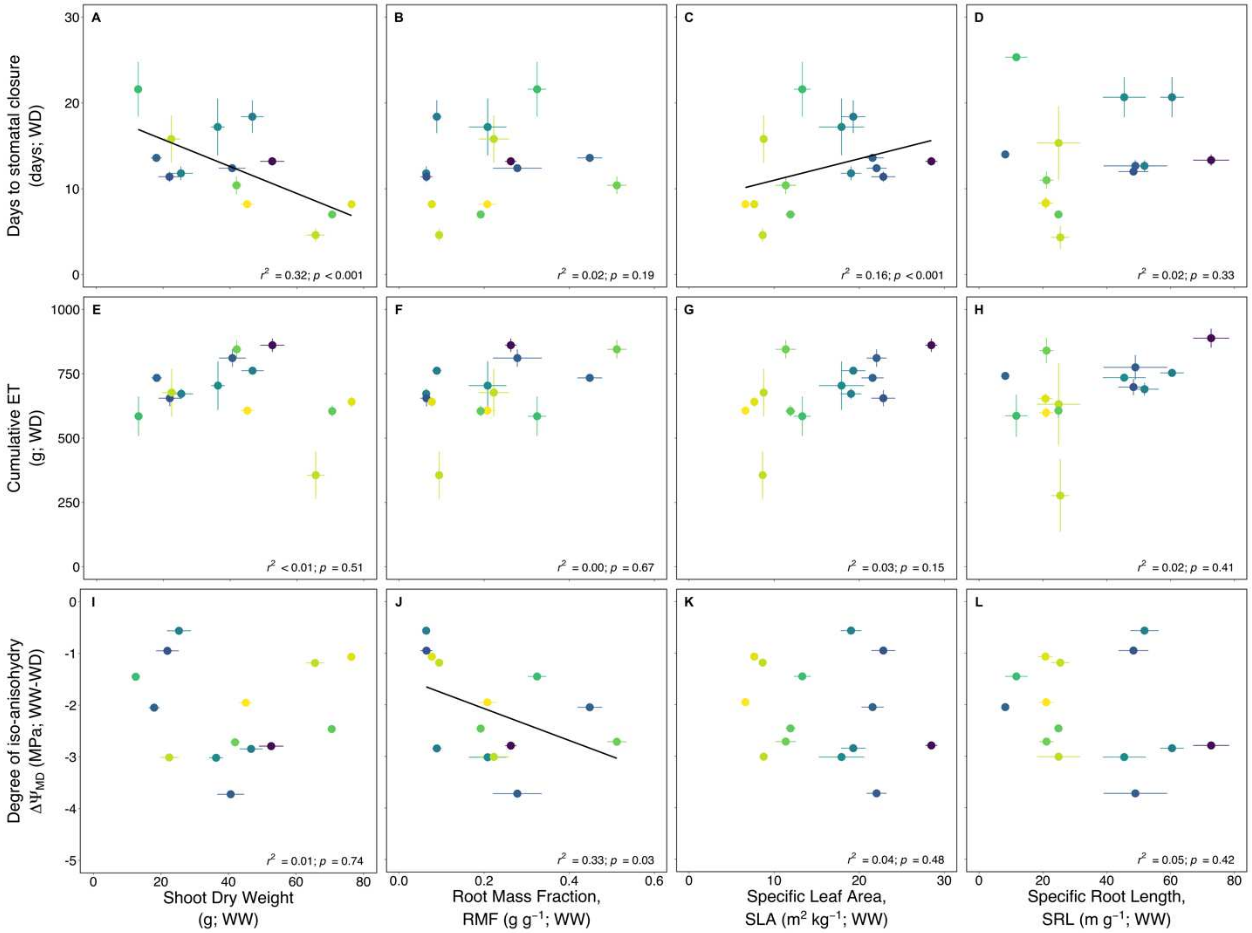
A
B
C
D
E
F
G
H
I
J
K
L
Days to stomatal closure
(days; WD)
Cumulative ET
(g; WD)
Degree of iso-anisohydry
$\Delta\Psi_{MD}$ (MPa; WW-WD)
r^2 = 0.32; p < 0.001
r^2 = 0.02; p = 0.19
r^2 = 0.16; p < 0.001
r^2 = 0.02; p = 0.33
r^2 < 0.01; p = 0.51
r^2 = 0.00; p = 0.67
r^2 = 0.03; p = 0.15
r^2 = 0.02; p = 0.41
r^2 = 0.01; p = 0.74
r^2 = 0.33; p = 0.03
r^2 = 0.04; p = 0.48
r^2 = 0.05; p = 0.42
0
10
20
30
0
250
500
750
1000
0
-1
-2
-3
-4
-5
0
20
40
60
80
0.0
0.2
0.4
0.6
0
10
20
30
0
20
40
60
80
Shoot Dry Weight
(g; WW)
Root Mass Fraction,
RMF (g g^{-1}; WW)
Specific Leaf Area,
SLA (m^2 kg^{-1}; WW)
Specific Root Length,
SRL (m g^{-1}; WW)

Figure 2.

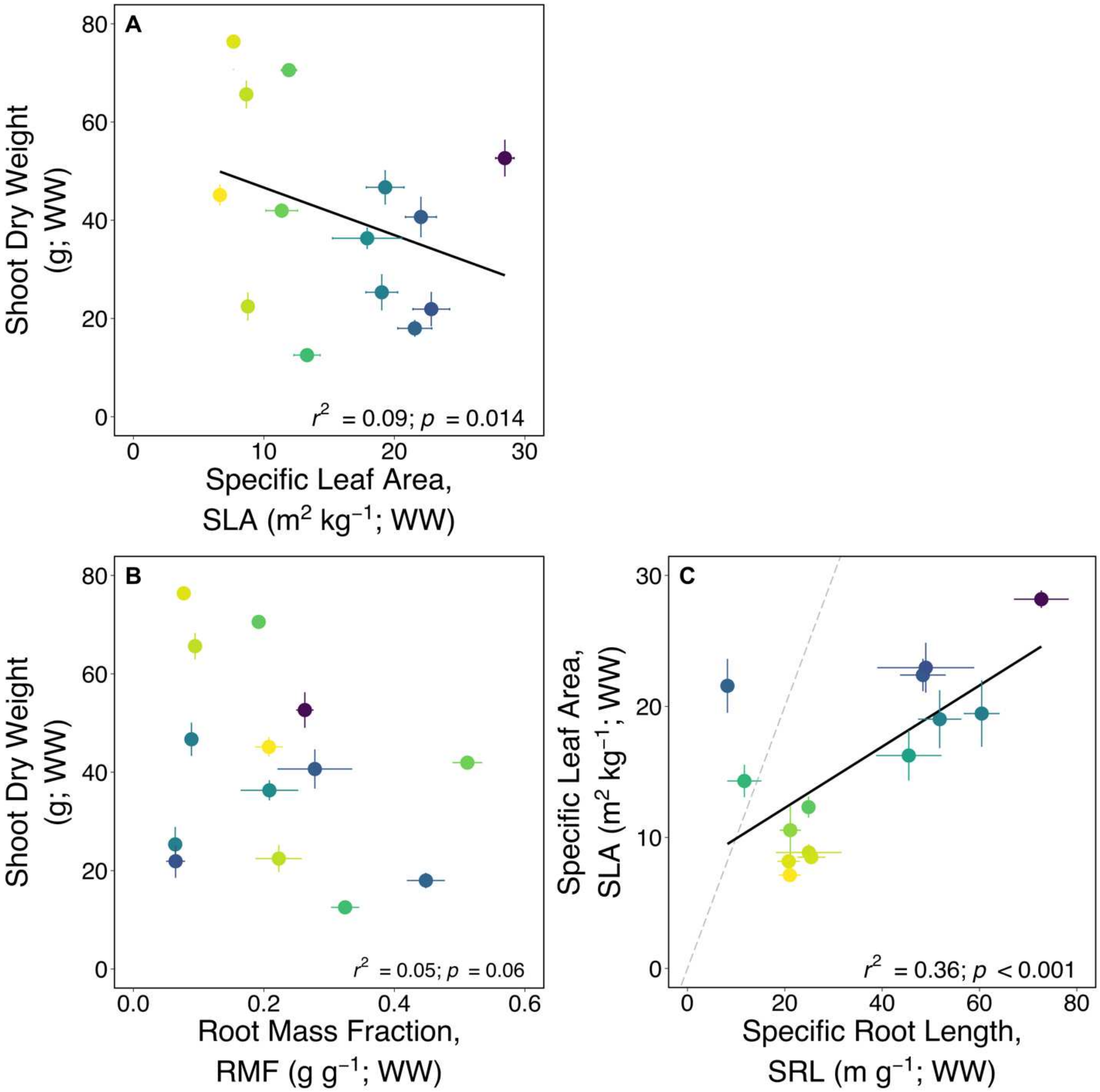
A
Shoot Dry Weight (g; WW)
80
60
40
20
0
0
10
20
30
Specific Leaf Area, SLA (m^2 kg^{-1}; WW)
r^2 = 0.09; p = 0.014
B
Shoot Dry Weight (g; WW)
80
60
40
20
0
0.0
0.2
0.4
0.6
Root Mass Fraction, RMF (g g^{-1}; WW)
r^2 = 0.05; p = 0.06
C
Specific Leaf Area, SLA (m^2 kg^{-1}; WW)
30
20
10
0
0
20
40
60
80
Specific Root Length, SRL (m g^{-1}; WW)
r^2 = 0.36; p < 0.001

Figure 3.

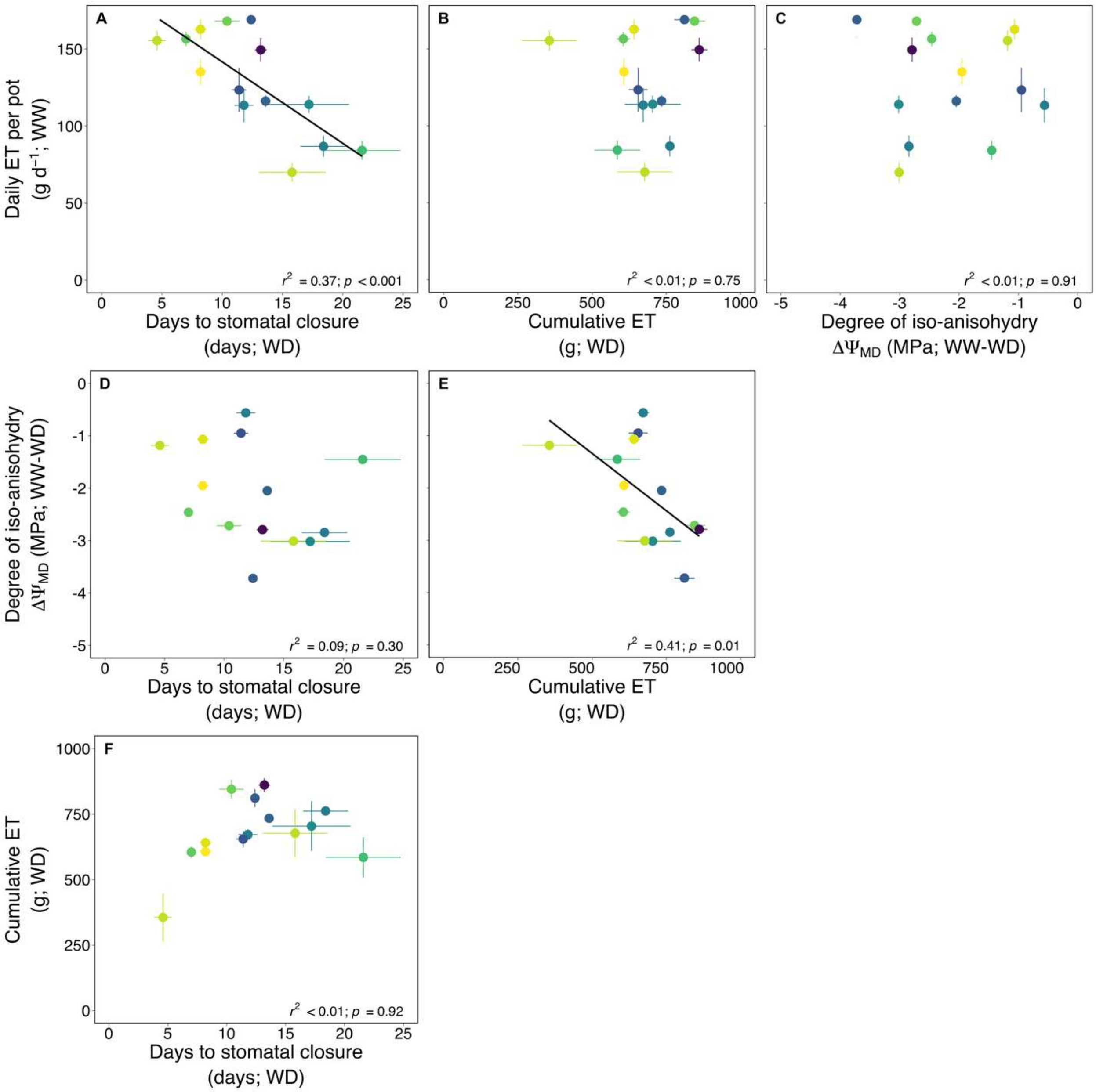
A
B
C
D
E
F
Daily ET per pot
(g d^{-1}; WW)
Degree of iso-anisohydry
$\Delta\Psi_{MD}$ (MPa; WW-WD)
Cumulative ET
(g; WD)
Days to stomatal closure
(days; WD)
Cumulative ET
(g; WD)
Degree of iso-anisohydry
$\Delta\Psi_{MD}$ (MPa; WW-WD)
r^2 = 0.37; p < 0.001
r^2 < 0.01; p = 0.75
r^2 < 0.01; p = 0.91
r^2 = 0.09; p = 0.30
r^2 = 0.41; p = 0.01
r^2 < 0.01; p = 0.92
0
50
100
150
0
5
10
15
20
25
0
250
500
750
1000
-5
-4
-3
-2
-1
0

Figure 4.