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Author/s:

Du, P.;Arndt, SK;Farrell, C

Title:

Relationships between plant drought response, traits, and climate of origin for green roof plant selection

Date:

2018-10-01

Citation:

Du, P., Arndt, S. K. & Farrell, C. (2018). Relationships between plant drought response, traits, and climate of origin for green roof plant selection. *Ecological Applications*, 28 (7), pp.1752-1761. <https://doi.org/10.1002/eap.1782>.

Persistent Link:

<https://hdl.handle.net/11343/284408>

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DR. CLAIRE FARRELL (Orcid ID : 0000-0002-5822-7529)

Article type : Articles

Running head: Green roof plant traits and drought

Title: Relationships between plant drought response, traits and climate of origin for green roof plant selection

List of authors:

Pengzhen Du

Department of Ecosystem and Forestry Science, University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia

Stefan K. Arndt

Department of Ecosystem and Forestry Science, University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia

Claire Farrell¹

Department of Ecosystem and Forestry Science, University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia

¹ Corresponding author email: c.farrell@unimelb.edu.au.

Other authors email: pengzhend@student.unimelb.edu.au; sarndt@unimelb.edu.au.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1002/eap.1782](https://doi.org/10.1002/eap.1782)

27 **Abstract**

28 The ideal species for green or vegetated roofs should have high water use after rainfall to
29 maximise stormwater retention but also survive periods with low water availability in dry
30 substrates. Shrubs have great potential for green roofs because they have higher rates of water
31 use, and many species are also drought tolerant. However, not all shrub species will be
32 suitable and there may be a trade-off between water use and drought tolerance. We conducted
33 a glasshouse experiment to determine the possible trade-offs between shrub water use for
34 stormwater management and their response to drought conditions. We selected 20 shrubs
35 from a wide range of climate of origins, represented by heat moisture index (HMI) and mean
36 annual precipitation (MAP). Under well-watered (WW) and water deficit (WD) conditions,
37 we assessed morphological responses to water availability; evapotranspiration rate (ET) and
38 midday water potential (Ψ_{MD}) were used to evaluate species water use and drought response.
39 In response to WD, all 20 shrubs adjusted their morphology and physiology. However, there
40 were no species that simultaneously achieved high rates of water use (high ET) under WW
41 and high drought tolerance (low Ψ_{MD}) under WD. Although some species which had high
42 water use under WW conditions could avoid drought stress (high Ψ_{MD}) used. Water use was
43 strongly related to plant biomass, total leaf area and leaf traits (SLA and LAR). Conversely,
44 drought response (Ψ_{MD}) was not related to morphological traits. Species' climate of origin
45 was not related to drought response or water use. Drought avoiding shrubs (high Ψ_{MD}) could
46 optimize rainfall reduction on green roofs. Water use was related to biomass, leaf area and
47 leaf traits, thus these traits could be used to assist the selection of shrubs for stormwater
48 mitigation on green roofs. The natural distribution of species was not related to their water
49 use or drought response, which suggests that shrubs from less arid climates may be suitable
50 for use on green roofs. Selecting species based on traits and not climate of origin could both
51 improve green roof performance and biodiversity outcomes by expanding the current plant
52 palette.

53

54 **Keywords:** Drought response strategies; ET; green roof; habitat template; heat moisture
55 index (HMI); plant selection; shrub; trait; water use

56

57 **Introduction**

58 Green or vegetated roofs are increasingly being built in cities because of the range of
59 ecosystem services they provide, including cooling, stormwater runoff reduction, habitat
60 provision for biodiversity and improved air quality (Oberndorfer et al. 2007, Berndtsson

61 2010, Williams et al. 2014). A prominent benefit of green roofs in cities is the reduction of
62 stormwater runoff (Teemusk and Mander 2007, MacIvor et al. 2016), which otherwise causes
63 degradation to aquatic ecosystems (Walsh et al. 2005). In some cases, green roofs can retain
64 up to 100% of rainfall (Berndtsson 2010). The reduction in runoff from green roofs is largely
65 result of substrate water holding capacity and depth, yet vegetation water use can increase the
66 ability of a roof to retain rainfall by drying out the substrate after rain events (Villarreal and
67 Bengtsson 2005). Maximizing transpiration by plants on the roof may thus increase the total
68 amount of water prevented from flowing off into waterways or sewer system. However,
69 plants with high transpiration rates may not be able to survive on green roofs due to the low
70 water holding capacity and shallow depth of many green roof substrates (Szota et al. 2017).

71
72 The extensive green roof environment can be highly stressful for plants, as they are exposed
73 to wind and high irradiance, large temperature fluctuations, low substrate water availability
74 and shallow substrate depths (<20 cm) (Nagase and Dunnett 2010, Walker and Lundholm
75 2017). Consequently, green roofs are often planted with succulent species such as *Sedum*
76 species, which are shallow-rooted and very drought tolerant due to water storage in their
77 fleshy leaves and/or stems (Sayed 2001, Durhman et al. 2006). However, in terms of
78 stormwater retention, succulent plants are not the best choice due to their reduced
79 transpiration (Wolf and Lundholm 2008, Farrell et al. 2012), which means they do not dry out
80 substrates sufficiently between rainfall events.

81
82 There has been an interest to expand the list of plant species used on green roofs (Lundholm
83 2015). A variety of different growth forms, including grasses, shrubs and herbs, have been
84 tested as they potentially provide greater stormwater retention than traditional *Sedum*
85 monocultures (Wolf and Lundholm 2008, Nagase and Dunnett 2012, Farrell et al. 2013).
86 There are several approaches that have been applied to select plants which will be suitable for
87 the green roof environment. Plant trait methods (Farrell et al. 2012, Nagase and Dunnett
88 2012, Lundholm et al. 2015) and habitat template approaches (Lundholm 2006, Farrell et al.
89 2013, Lundholm and Walker 2018) have been successful in selecting native species across a
90 range of life-forms for green roofs. More recently physiological approaches tested the ability
91 of plants to tolerate drought and use water as the main factors determining plant selection for
92 green roofs where stormwater management is important (Farrell et al. 2013). Another
93 potential method is the climate of origin approach, which has yet not been tested for green
94 roofs.

95

96 Climate is the ultimate driver of broad-scale ecosystem composition and structure, and
97 temperature and precipitation have large influences on the distribution of species (Birks et al.
98 2000, Birks and Birks 2014). Aridity indices, such as the mean heat moisture index (HMI),
99 can be useful measure as they represent the aridity of the environment and consider the
100 interaction between temperature and precipitation (Dobbs et al. 2014). Species from climates
101 with greater HMI endure drier and hotter conditions and this may indicate greater potential
102 for tolerance of water deficit conditions (Aspinwall et al. 2013). Although plants for green
103 roofs in hot and dry climates have often been selected from dry environments as part of the
104 habitat template approach (MacIvor et al. 2011, Farrell et al. 2013, Papafotiou et al. 2013),
105 the influence of a species climate of origin on plant performance on green roofs has not been
106 investigated.

107

108 In terms of diversifying the range of life-forms used on green roofs, shrubs are potentially of
109 interest because they can have higher rates of water use than commonly used succulent plants
110 and therefore improve stormwater retention (Wolf and Lundholm 2008). Shrubs can also be
111 very drought tolerant, for example, shrubs from dry rocky habitats were able to survive water
112 deficit conditions when growing in shallow green roof substrate (Farrell et al. 2013). While
113 several studies have evaluated the drought tolerance of shrubs from dry and semi-dry habitats
114 (Farrell et al. 2013, Papafotiou et al. 2013, Raimondo et al. 2015, Savi et al. 2016) there are
115 no studies which have assessed shrubs based on physiological and climate of origin
116 approaches. For stormwater retention, the ideal shrub species for green roofs would have high
117 evapotranspiration under well-watered conditions, but will also tolerate water deficit as
118 demonstrated by a more negative midday water potential (Farrell et al. 2013) (Fig 1). This
119 strategy has been demonstrated for monocot and herb species from rocky outcrops, which
120 showed high water use under well-watered conditions but also drought tolerance by reducing
121 water potentials under drought. However, it is unclear whether this ideal combination of high
122 water use and high drought tolerance also exists in shrubs as drought tolerance is often
123 negatively correlated with transpiration rate (Orians and Solbrig 1977, Tardieu 2005).

124

125 Drought avoidance, which is another drought response strategy differing from drought
126 tolerance (decrease ψ_{MD} under WD). Drought avoiding plants maintain water potentials (high
127 ψ_{MD}) during drought stress through deep root systems (water spenders) or stomatal closure,
128 leaf rolling or below-ground organs (water savers) (Levitt 1980, Price et al. 2002, Bodner et

129 al. 2015, Delzon 2015). As extensive green roof systems are designed with shallow
130 substrates, plants which avoid drought through deep roots will not be able to persist on green
131 roofs due to limited access to deep stored water (Raimondo et al. 2015, Szota et al. 2017), but
132 plants which avoid drought through stomatal closure have great potential to be used on green
133 roofs.

134
135 The first objective of this study was to determine whether shrubs on green roofs can provide
136 stormwater management benefits by a high-water use when water is available and avoidance
137 of drought stress when water is limiting. A second objective was to evaluate whether the
138 physiological response to water availability; water use (ET under WW conditions) and
139 drought response (ψ_{MD} under WD) is related to climate of origin (HMI) and morphological
140 traits.

141 142 **Methods**

143 *Plant material*

144 In this experiment, 20 shrubs were selected from different climates of origin based on their
145 Heat Moisture Index (HMI), across southern Australia (Table 1). We used species occurrence
146 records in the Atlas of Living Australia (ALA, www.ala.org.au) to determine the climate
147 envelope of each species. For each species, mean annual temperature (MAT) and mean
148 annual precipitation (MAP) were determined for each location that the species had been
149 recorded and these were used to calculate HMI for each location. HMI was calculated as,
150 $(MAT+10)/MAP \times 1000$. The mean HMI ranged from 20 to 98, and MAP from 280 mm to
151 1100 mm. Species with higher HMI were distributed in drier and hotter sites, while species
152 with lower HMI were from wetter and cooler regions.

153
154 Six-month old seedlings in tube-stock, 20 plants per species, were obtained from an
155 indigenous commercial nursery (Goldfields Revegetation). All plants were individually
156 potted into 6 l plastic pots (200 mm diameter and 190 mm height) containing green roof
157 substrate (3.8 kg per pot) consisting of 60% scoria 7 mm minus block mix, 20% 7 mm scoria
158 aggregate and 20% composted coir (Farrell et al. 2012). Low phosphorous slow release
159 fertiliser (12 g per pot; Osmocote plus, Scotts Australia Pty Ltd.) containing 61% nitrogen,
160 34% potassium and 5% phosphorus was added to the surface of each pot at planting. For the
161 establishment period, three months before the start of the experiment, plants were grown
162 outside and were watered automatically for 30 minutes twice a day (0600 h and 1800 h) to

163 ensure sufficient water availability. The experiment was conducted in the nursery at the
164 Burnley Campus, University of Melbourne, Australia (37°47'S; 144°58'E)

165

166 ***Experimental design***

167 In March 2016, plants were moved into a glasshouse and watered by hand for another week
168 before the experiment started. Five replicates of each of the 20 species with uniform size
169 were allocated randomly to two different watering treatments: well-watered (WW) and water
170 deficit (WD) and arranged in a complete randomised block design. The remaining 100 pots (5
171 replicates per species) were used for the initial harvest to determine plant biomass. WW
172 plants were watered to pot capacity at 1700 h three times per week (Monday, Wednesday and
173 Friday). The plants in the WD treatment were also watered at the same time with the quantity
174 of water added determined from the water use of each individual species under WW. That is,
175 50% of the water used by WW plants (calculated by the difference in pot weights of WW
176 plants after the last watering and before the current watering event) was added to WD plants
177 using a measuring cylinder. All pots were weighed before being watered and again after
178 watering to determine plant water use and soil water content (SWC). Watering treatments
179 continued until each plant in the WD treatment had experienced 30 days of SWC below 20%
180 to enable them to adjust physiologically to water stress conditions. Consequently, different
181 species were harvested on different days based on their dry-down rates.

182

183 ***Morphological traits***

184 Five replicates of 20 species were initially harvested prior to the watering treatments to obtain
185 total plant dry mass, total leaf dry mass and total leaf area. Leaf area was measured using a
186 LI3100 area meter (Li-Cor, Lincoln, NE, USA). Total leaf and stem dry mass was recorded
187 separately after drying in 70 °C oven for at least 48 hrs or until constant weight was reached.
188 Specific leaf area (SLA $\text{m}^2 \text{kg}^{-1}$ leaf) and leaf area ratio (LAR, $\text{m}^2 \text{leaf kg}^{-1}$ plant) were
189 calculated from leaf area and dry leaf/whole plant mass. These measurements were repeated
190 at the conclusion of the experiment on all WW and WD plants. The difference in mass
191 between the final and initial harvests was also used to calculate relative growth rate (RGR) of
192 WW and WD treatments and was determined as: (final dry mass- initial dry mass)/ (initial
193 dry mass/days).

194

195 **Whole plant water use and plant water status**

196 Cumulative evapotranspiration per pot was determined as the sum of evapotranspiration
197 (mentioned above) over the 42-81 days of the experiment, depending on each species dry-
198 down rate. Daily evapotranspiration rate ($\text{g H}_2\text{O pot}^{-1} \text{ day}^{-1}$) was then determined from
199 cumulative evapotranspiration.

200

201 At the conclusion of the dry-down for each species, leaf water potentials at pre-dawn (ψ_{PD} ;
202 0500-0530 h) and midday (ψ_{MD} ; 1230-1300 h) were measured using a Scholander-type
203 pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA, USA) on individual
204 leaves or terminal shoots for both WW and WD treatments.

205

206 **Statistical analyses**

207 Differences in species morphological and physiological response between WW and WD
208 treatments were analysed using one-way ANOVA. Pearson correlation analyses were used to
209 explore the relationships between morphological traits, HMI and physiological response.
210 Significant differences between species and treatment means were determined by Tukey's
211 post-hoc tests ($P < 0.05$). All analyses were performed using SPSS Statistics 22 (IBM SPSS
212 Statistics 22. Ink).

213

214 **Results**

215 **Whole plant water use and plant water status**

216 The rates of water use (ET) differed greatly among 20 shrubs under both WW and WD
217 treatments (both $P < 0.001$) (Table 2). Under WW conditions, ET ranged from 199.7 (*I.*
218 *australis*) to 59.1 (*C. linearis*) $\text{g H}_2\text{O pot}^{-1} \text{ day}^{-1}$, and under WD from 113.1 (*P. incisa*) to 31
219 (*C. linearis*) $\text{g H}_2\text{O pot}^{-1} \text{ day}^{-1}$. All species, except *D. stenozuga* significantly decreased ET
220 under WD and the change in ΔET (ranged from 28.1 (*C. linearis*) to 84.6 (*P.*
221 *aspalathoides*) $\text{g H}_2\text{O pot}^{-1} \text{ day}^{-1}$.

222

223 There were significant differences in the water potential of species at the end of the
224 experiment under both WW and WD conditions (Table 3). Under WW, predawn water
225 potential (ψ_{PD}) ranged from -0.24 to -0.98 MPa, while midday water potential (ψ_{MD}) ranged
226 from -0.64 to -2.02 MPa. All species had a significantly lower ψ_{PD} and ψ_{MD} in response to
227 WD compared with the WW treatment, with the exception of *C. linearis*. Under WD, the
228 largest decrease in ψ_{PD} was observed in *D. ulicifolia*, while *E. polyclada* did not significantly

229 lower its ψ_{PD} . For ψ_{MD} , *C. linearis* maintained leaf water potential, while *E. microphylla*
230 lowered its ψ_{MD} by 3.01 MPa under WD.

231

232 While the ideal shrub for green roofs was considered to have greater water use under WW
233 conditions and have greater drought tolerance, evapotranspiration rate (ET) under WW was
234 not significantly related to ψ_{MD} under WD ($R^2=-0.224$, $P=0.343$; Fig 2). However, by using
235 the relative position of the 20 shrubs on these axes, we could categorise the species according
236 to their drought response (ψ_{MD} under WD; x axis) and their water use (ET under WW; y axis)
237 (Fig 2). Using this categorisation, species in the top left corner were classified as having high
238 water use (high ET values) and high drought avoidance (high ψ_{MD} values), while species in
239 the bottom left corner were species with low water use and high drought avoidance. Species
240 in the bottom right corner were low water users with high drought tolerance. Hence, there
241 was a general trend that high water using plants tended to have higher water potentials with
242 lower drought tolerance. Therefore, high water users which were also drought tolerant were
243 not observed in our study.

244

245 ***Relationships between water use and drought tolerance with morphological traits and*** 246 ***climate of origin***

247 Water use (ET) under WW conditions was significantly correlated with all morphological
248 traits (measured under WW conditions), including: total shoot dry mass ($R^2=0.84$, $P<0.001$),
249 total leaf area ($R^2=0.66$, $P=0.001$), SLA ($R^2=-0.57$, $P=0.009$), LAR ($R^2=0.49$, $P=0.013$) and
250 RGR ($R^2=0.459$, $P=0.042$) (Fig 3). However, there were no statistically significant
251 relationships between drought response (ψ_{MD}) and any of the morphological traits measured
252 under WD conditions, including: total dry mass ($R^2=0.29$, $P=0.218$), total leaf area ($R^2=0.29$,
253 $P=0.209$), SLA ($R^2=0.34$, $P=0.144$), LAR ($R^2=0.35$, $P=0.129$) and RGR ($R^2=0.39$, $P=0.088$)
254 (Fig 3). In addition, there were no significant relationships between root mass fraction (RMF)
255 and ψ_{MD} under WD or ET under WW (data not shown).

256

257 Heat moisture index (HMI) was not related to water use (ET under WW; $R^2=-0.11$, $P=0.653$)
258 or drought response (ψ_{MD} under WD; $R^2=-0.03$, $P=0.898$) (Fig 4). There were also no
259 significant relationships between mean annual precipitation (MAP) or mean annual
260 temperature (MAT) and ET or ψ_{MD} (data not shown).

261

262 **Discussion**

263 The 20 shrubs showed considerable variation in their morphological and physiological
264 responses to the experimental water deficit, indicating a range of diverse behaviours and
265 adaptations in response to water deficit. This likely reflects the fact that species originate
266 from a range of different climates, which likely contributed to the evolution of a series of
267 different adaptive strategies (Valladares and Sánchez-Gómez 2006). For instance, in this
268 experiment some species reduced their above ground biomass, total leaf area, SLA or growth
269 in response to water limitations, while others also reduced transpiration or were able to lower
270 their water potentials as soil water deficit increased. Hence, there was no uniform response of
271 the shrubs to drought and as a consequence we did not observe relationships between climate
272 of origin and water use or drought tolerance.

273

274 ***Trade-off between high water use and drought tolerance***

275 We observed a trade-off between water use and drought tolerance in the 20 shrubs selected
276 from across a broad precipitation gradient. Shrubs that had high water use generally were not
277 very drought tolerant and we did not observe any shrubs which had high water use and high
278 drought tolerance. This result is in contrast with a previous study which evaluated the
279 physiological response of a range of life-forms for green roofs and showed that high water
280 users could also be drought tolerant (Farrell et al. 2013). However, in that study, it was the
281 grass-like monocots and one herb species which achieved this and not any of the four shrubs
282 species. The trade-off between drought tolerance and water use in shrubs may be related to
283 their woody nature. In woody plants, xylem vessel dimensions influence both the amount of
284 water that can be transported and the risk of cavitation under drought stress (Sperry and
285 Tyree 1988, Bartlett et al. 2016). Hence, woody plants with large vessels have more efficient
286 water transport at higher transpiration rates but are more likely to have lower cavitation
287 resistance under low water potentials (Dong and Zhang 2001, Christman et al. 2012).
288 Conversely, woody plants with narrow xylem vessels are not be able to transport water at
289 high rates but are likely more resistant to cavitation (Brodribb et al. 2003). As a consequence,
290 we mainly observed shrubs which had low water use (water savers) and high drought
291 tolerance or shrubs which had higher water use (water spenders) and low drought tolerance.
292 Shrubs which had low drought tolerance maintained relatively high midday water potentials
293 under water deficit, and avoided drought stress by minimizing water loss (decreasing ET)
294 during drought. These drought avoiding shrubs may be able to survive dry conditions on
295 green roofs through leaf area reduction and stomatal closure to postpone dehydration (Farrell

296 et al. 2013, Raimondo et al. 2015, Szota et al. 2017) and still achieve optimal water use for
297 stormwater management. In line with Szota et al. (2017), we suggest the drought avoiding
298 shrubs which can achieve high rainfall retention should be considered on future green roof
299 designs, especially in temperate climates, which have plentiful precipitation during summer
300 (Kottek et al. 2006).

301

302 ***Relationships between morphological traits, water use and drought tolerance***

303 We observed a number of significant correlations between water use and morphological traits.
304 Plants with higher water use generally had greater above-ground biomass, greater leaf areas,
305 and higher SLA in line with previous studies (Wolf and Lundholm 2008, Farrell et al. 2013).
306 For example, Nagase and Dunnett (2012) showed that taller species with higher dry shoot
307 mass had greater runoff retention compared with shorter species with lower dry shoot mass in
308 a simulated green roof study. In addition, Farrell et al. (2013) proposed that plant size or leaf
309 area is a key determinant of water use and should be an important consideration for green
310 roof design to mitigate stormwater. It is likely that positive correlations between above-
311 ground biomass and water use are observed because larger plants have greater surface area
312 and more stomata to transpire water back to the atmosphere (Vertessy et al. 1995, Nagase and
313 Dunnett 2012). Thus, to some extent, morphological traits could be used to determine water
314 use of plants for green roofs.

315

316 Although plant water use was coupled with leaf area, it is important to note that the reduction
317 in evapotranspiration rate (ΔET %) was not accompanied by a significant change in the leaf
318 area (ΔLA %) (Appendix S1: Figure S1), suggesting that leaf area adjustment was not the
319 main determinant of changes in plant water use in our study. Variation in wood anatomy,
320 especially xylem vessel diameters in leaves, stem or roots, may also influence shrub water
321 use and hydraulic conductance in response to extreme drought (Vasellati et al. 2001, Hacke et
322 al. 2009). In addition, conservative stomatal control can minimize plant water loss and
323 maintain water balance for efficient survival of the plant under extreme situations (Farquhar
324 and Sharkey 1982, Dong and Zhang 2001). Hence, the stomatal regulation can be a protective
325 mechanism to avoid plant complete hydraulic failure and xylem cavitation (Sperry 2000).
326 Therefore, it is likely to be another significant driver of vegetation water use for stormwater
327 reduction and should be taken into account in future green roof studies.

328

329 However, there were no relationships between drought response (midday water potential
330 under WD) and any of the measured morphological traits, suggesting that drought response
331 does not depend on plant size, shoot biomass, leaf structure, root mass or growth rate. This is
332 in contrast with Mitchell et al. (2008) which showed that there were significantly positive
333 relationships between ψ_{MD} and SLA and RMF, with species with lower ψ_{MD} having lower
334 SLA (smaller but thicker leaves) and smaller RMF. Furthermore, Farrell et al. (2013)
335 demonstrated that species with higher RMF maintained higher water status (ψ_{PD} , not ψ_{MD})
336 under water deficit conditions. The reason for the lack of relationships between
337 morphological traits and drought response in our study is still unclear. It may be due to
338 differences in rooting volume and access to stored water or due to differences in plant
339 phenology between glasshouse pot and field-based conditions (Kaspar et al. 1984).

340

341 ***Relationships between climate of origin, water use and drought tolerance***

342 Species from drier habitats are generally thought to be less susceptible to water limitation due to
343 greater physiological plasticity (Lázaro-Nogal et al. 2015). Strong relationships between
344 drought tolerance and the distribution of species have been reported (Mitchell and O'Grady
345 2015). In arid climates, species with greater drought tolerance often have a greater
346 survival, lower water potentials and lower turgor loss points (Baltzer et al. 2008, Kursar et al.
347 2009, Mitchell and O'Grady 2015). However, we observed no relationships between climate
348 of origin and either drought tolerance or water use. Under water deficit, not all species from
349 hotter and drier climates (higher HMI) showed greater drought tolerance (more negative ψ_{MD})
350 and not all species from wetter and cooler sites were high water users under WW. This is in
351 contrast to previous studies, which have suggested that drought tolerance measures such as
352 turgor loss point, can predict species distribution and mortality (Engelbrecht et al. 2007,
353 Bartlett et al. 2012). For example, Mitchell and O'Grady (2015) compiled a database for 174
354 woody species across a range of temperature and precipitation in Australia, and showed that
355 natural habitat water availability (precipitation and temperature) was significantly related to
356 plant drought tolerance, with species from drier and hotter regions having more negative
357 turgor loss points than species from cooler and wetter regions.

358

359 In our experiment the lack of a relationship between climate of origin and plant water use or
360 drought tolerance may be because under new studied environments, like the glasshouse,
361 plants may adjust their physiology according to water availability to a greater extent than
362 measured in their natural ecosystems. It is also possible that within shrubs, there may be more

363 drought tolerance and water use (water-spending and water-saving) strategies than previously
364 reported for trees (Dong and Zhang 2001). That is, species with different rooting depths may
365 respond differently to drought and have distinct water use patterns (Oberbauer and Billings
366 1981, West et al. 2012). Deep-rooted species often avoid drought (high Ψ_{MD}) and use large
367 amounts of water, like *Prosopis* sp. (Delzon 2015), or alternatively, are conservative water-
368 users (Wright et al. 1983, Hund et al. 2009). Some desert shrubs with shallower roots like
369 *Artemisia scopulorum* and *Hymenoxys grandiflora* have also been shown to be drought
370 tolerant (Hinckley et al. 1983) and use very little water because of their small plant size, due
371 to restricted growth or due to leaf adaptations like finely divided hairy leaves (Oberbauer and
372 Billings 1981, West et al. 2012). Alternatively, they may use a lot of water and have a low
373 drought tolerance (high Ψ_{MD}) because they have developed extreme phenotypic plasticity by
374 dropping all their leaves under WD and resprouting when conditions improve (drought
375 escape strategy) (Delzon 2015). Therefore, there are likely multiple drought resistance
376 strategies for plants growing in hot and dry climates and determining the drought tolerance of
377 shrubs by minimum water potential or turgor loss point is not the only criterion to assess
378 species real survival capabilities. On the other hand, stomata of mature field-grown trees or
379 shrubs may not respond to water deficit as dramatically and readily as those of the young
380 shrubs in pots or on green roofs with limited root systems and shallow substrates. This
381 indicates that unlike for tree studies in field conditions, climate of origin may not be a
382 suitable approach to select drought tolerant shrubs with high water use for stormwater
383 management on green roofs. However, future studies of plant cavitation resistance, safety
384 margin and anatomical measurements on shrub species with different climatic distributions
385 are still required to be certain that climate of origin has no influence on plant tolerance of
386 green roof conditions.

387

388 **Conclusion**

389 The results of this study demonstrate that mainly drought avoiding shrubs (high Ψ_{MD}), like
390 *Correa glabra*, *Derwentia perfoliata* and *Olearia axillaris*, can optimize stormwater
391 mitigation on green roofs. Unlike previous studies with monocots and geophytes, it was not
392 possible to identify drought tolerant shrubs (low Ψ_{MD}) that had high water use under well-
393 watered conditions. However, there were several drought avoiding shrubs which also had
394 high water use. These shrubs probably have greater potential for stormwater mitigation on
395 green roofs in temperate climates, which in summer have relatively high temperature but also
396 high precipitation (high water availability), rather than Mediterranean-type climates with

397 frequent extreme droughts. In addition, as the water use of shrubs under well-watered
398 conditions was related to their aboveground biomass and leaf traits like SLA, these are likely
399 to be useful traits to predict the ability of shrubs to mitigate stormwater on green roofs.
400 Finally, drought tolerance and water use of shrubs was not related to their climate of origin
401 (MAT, MAP and HMI). Therefore, climate of origin is not a useful approach for selecting
402 young woody shrubs for green roofs to reduce stormwater runoff from green roofs and
403 survive periods of water limitations.

404

405 **Acknowledgements**

406 We thank Guiqing Xu and Xiang Zhang for assistance planting and harvesting plants, and
407 Chris Szota for assistance with the use of the pressure chamber during this experiment.
408 Thanks also to Burnley nursery staff Nick Osborne and Sascha Andrusiak for technical
409 assistance during the experiment. The China Scholarship Council (CSC) funded P. Du with a
410 PhD fellowship.

411

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568 **DATA AVAILABILITY**

569 Data are available on Figshare: <https://doi.org/10.4225/49/5b0de625052f9>

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570 **Table 1.** Climate of origin (Köppen Classification) for the selected 20 shrubs: mean annual heat-moisture index (HMI), mean annual
 571 precipitation (MAP) and mean annual temperature (MAT). Rows are ordered by increasing HMI at the climate of origin.

Species	Family	HMI	MAP (mm)	MAT (°C)	Climate classifications	Habitat
<i>Derwentia derwentiana</i>	Plantaginaceae	20.31	1126.36	10.64	Csb, Cfa, Cfb	Moist forest ¹
<i>Prostanthera incisa</i>	Lamiaceae	23.69	1126.11	15.45	Cfa, Cfb	Moist forest ¹
<i>Derwentia perfoliata</i>	Plantaginaceae	25.53	923.59	11.21	Cfa, Cfb	Mosit forest ¹
<i>Daviesia ulicifolia</i>	Fabaceae	29.06	900.52	13.98	BWh, Csa, Csb, Cfa, Cfb	Hilly country ¹
<i>Hardenbergia violacea</i>	Fabaceae	29.17	922.08	15.42	Am, BWh, BSk, Csa, Csb, Cfa, Cfb	Dry forest ¹
<i>Indigofera australis</i>	Fabaceae	32.09	851.22	14.62	Am, Aw, BWh, BSh, BSk, Csa, Csb, Cfa, Cfb	Inland woodland ²
<i>Dillwynia sericea</i>	Fabaceae	35.75	719.97	14.18	BSk, Csb, Cfa, Cfb	Heathy woodland ¹
<i>Cheiranthra linearis</i>	Pittosporaceae	36.48	688.22	14.11	Cfa, Cfb	Dry forest ¹
<i>Grevillea alpina</i>	Proteaceae	36.86	695.10	13.53	Cfb	Dry sclerophyll forest ¹
<i>Grevillea rosmarinifolia</i>	Proteaceae	37.64	704.43	13.93	Csb, Cfb	Coastal dune ¹
<i>Calytrix tetragona</i>	Myrtaceae	44.29	816.54	14.43	Bsh, BSk, Csb, Cfa, Cfb	Dry sclerophyll forest ²
<i>Correa glabra</i>	Rutaceae	52.73	532.10	15.62	BSk, Csb, Cfa, Cfb	Rock outcrop ³
<i>Olearia axillaris</i>	Asteraceae	55.34	555.19	16.14	Bwh, Bsh, Csa, Csb, BSk, Cfb	Coastal dune ³
<i>Eremophila gibbifolia</i>	Myoporaceae	61.33	436.74	15.52	Csa, Csb, Cfb, Bwh	Inland woodland ¹
<i>Goodenia benthamiana</i>	Goodeniaceae	61.45	420.24	15.29	BSk, Cfb	Inland woodland ¹
<i>Eutaxia microphylla</i>	Fabaceae	63.79	438.96	15.84	Csa, Csb, Cfb, Bwh	Rocky grassland ³
<i>Prostanthera aspalathoides</i>	Lamiaceae	70.97	388.06	16.07	BSk, Csa, Cfa	Inland woodland ¹
<i>Dodonaea stenozyga</i>	Sapindaceae	90.87	306.62	17.11	Csa, BSk, Csb	Inland woodland ¹
<i>Eremophila polyclada</i>	Myoporaceae	96.57	348.38	21.20	BSh, BSk	Inland woodland ¹

Eremophila divaricata Myoporaceae 98.34 283.44 17.56 BSk, BSh

Floodplain¹

572 Climate classifications are based on species occurrence records in the Atlas of Living Australia (ALA, www.ala.org.au). Plant habitat based on
573 the information from ¹Flora of Victoria (<https://vicflora.rbg.vic.gov.au>), ²PlantNET (<http://plantnet.rbg.syd.nsw.gov.au>) and ³Farrell et al. (2017).

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574 **Table 2.** Mean daily evapotranspiration rate (ET) under well-watered (WW) and water deficit
 575 (WD) conditions and the change in ET (Δ ET) from WW to WD.

Species	ET (g H ₂ O pot ⁻¹ d ⁻¹)		P-Value	Δ ET
	WW	WD		
<i>Derwentia derwentiana</i>	173.65(17.54)ab	102.96(1.98)b	0.004	70.69
<i>Prostanthera incisa</i>	196.06(11.92)a	113.09(1.51)a	0.012	82.97
<i>Derwentia perfoliata</i>	154.48(8.54)abc	91.70(1.04)c	< 0.001	62.78
<i>Daviesia ulicifolia</i>	107.93(11.02)cde	55.98(0.94)h	< 0.001	51.95
<i>Hardenbergia violacea</i>	120.90(7.27)cde	75.68(0.57)e	< 0.001	45.22
<i>Indigofera australis</i>	199.65(49.52)a	99.86(2.00)b	0.038	99.79
<i>Dillwynia sericea</i>	88.37(11.20)def	46.28(1.18)jk	0.006	42.09
<i>Cheiranthera linearis</i>	59.09(3.53)f	31.04(2.52)m	< 0.001	28.05
<i>Grevillea alpina</i>	123.35(14.55)cd	58.81(0.72)gh	< 0.001	64.54
<i>Grevillea rosmarinifolia</i>	114.94(15.80)cde	58.81(1.43)gh	< 0.001	56.13
<i>Calytrix tetragona</i>	95.69(13.37)def	62.37(1.25)g	0.038	33.32
<i>Correa glabra</i>	195.55(8.25)a	111.81(0.66)a	< 0.001	83.74
<i>Olearia axillaris</i>	135.49(10.46)bcd	85.20(0.78)d	0.002	50.29
<i>Eremophila gibbifolia</i>	101.87(7.08)def	50.77(2.21)i	< 0.001	51.10
<i>Goodenia benthamiana</i>	90.35(10.97)def	47.75(1.36)ij	< 0.001	42.60
<i>Eutaxia microphylla</i>	73.99(8.94)ef	39.89(0.33)l	< 0.001	34.10
<i>Prostanthera aspalathoides</i>	195.61(9.31)a	111.04(1.54)a	0.010	84.57
<i>Dodonaea stenozyga</i>	94.10(25.54)def	42.88(1.15)kl	0.092	51.22
<i>Eremophila polyclada</i>	180.11(7.23)a	100.07(0.81)b	0.004	80.04
<i>Eremophila divaricata</i>	110.81(7.05)cde	70.42(0.67)f	< 0.001	40.39
P-Value	< 0.001	< 0.001	< 0.001	

576

577 Values in parentheses show mean standard error. Difference letters indicate significant
 578 differences between species within treatment and variable (one-way ANOVA; Tukey post

579 hoc test). *P*-values in table show significant differences among species and between WW and
580 WD treatments within each species (Tukey post hoc test).

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582 **Table 3.** Mean leaf water potential at pre-dawn (ψ_{PD}) and midday (ψ_{MD}) under well-watered (WW) and water deficit (WD).

Species	$\Psi_{PD}(-\text{Mpa})$			$\Psi_{MD}(-\text{Mpa})$		
	WW	WD	<i>P</i> -Value	WW	WD	<i>P</i> -Value
<i>Derwentia derwentiana</i>	0.50(0.04)bcde	2.17(0.33)bcd	0.001	0.86(0.08)defg	2.89(0.46)abcdef	0.002
<i>Prostanthera incisa</i>	0.47(0.05)cdef	1.68(0.13)bcde	< 0.001	0.94(0.08)cdefg	2.63(0.19)bcdef	< 0.001
<i>Derwentia perfoliata</i>	0.51(0.06)bcde	2.06(0.17)bcde	< 0.001	0.92(0.10)cdefg	3.13(0.22)abcd	< 0.001
<i>Daviesia ulicifolia</i>	0.33(0.03)def	3.42(0.44)a	< 0.001	0.98(0.10)cdefg	3.92(0.36)ab	< 0.001
<i>Hardenbergia violacea</i>	0.24(0.03)f	0.93(0.12)de	0.001	0.67(0.09)fg	1.67(0.23)ef	0.004
<i>Indigofera australis</i>	0.42(0.15)cdef	1.47(0.38)cde	0.032	1.13(0.20)bcde	2.62(0.43)bcdef	0.013
<i>Dillwynia sericea</i>	0.38(0.06)cdef	2.54(0.34)abc	< 0.001	0.77(0.10)efg	3.26(0.62)abcd	0.001
<i>Cheiranthra linearis</i>	0.37(0.05)cdef	1.18(0.31)de	0.033	1.18(0.19)bcd	1.58(0.31)f	0.307
<i>Grevillea alpina</i>	0.36(0.08)cdef	1.95(0.62)bcde	0.014	1.24(0.15)bc	2.90(0.55)abcdef	0.010
<i>Grevillea rosmarinifolia</i>	0.31(0.06)ef	2.90(0.70)ab	0.003	0.88(0.08)cdefg	3.82(0.78)abc	0.003
<i>Calytrix tetragona</i>	0.46(0.07)cdef	1.29(0.30)de	0.016	0.84(0.12)defg	2.51(0.39)cdef	0.002
<i>Correa glabra</i>	0.48(0.09)bcdef	1.54(0.14)cde	< 0.001	1.38(0.09)b	2.50(0.13)cdef	< 0.001
<i>Olearia axillaris</i>	0.51(0.05)bcde	1.69(0.19)bcde	< 0.001	1.03(0.05)bcdef	2.24(0.16)def	< 0.001
<i>Eremophila gibbifolia</i>	0.72(0.05)b	2.60(0.66)abc	0.022	1.09(0.09)bcde	3.30(0.81)abcd	0.027
<i>Goodenia benthamiana</i>	0.59(0.08)bc	2.17(0.40)bcd	0.002	1.19(0.10)bcd	3.03(0.31)abcde	< 0.001
<i>Eutaxia microphylla</i>	0.45(0.09)cdef	1.96(0.48)bcde	0.003	1.11(0.10)bcde	4.12(0.35)a	< 0.001

<i>Prostanthera aspalathoides</i>	0.58(0.10)bcd	1.86(0.07)bcde	< 0.001	1.07(0.12)bcde	2.88(0.14)abcdef	< 0.001
<i>Dodonaea stenozyga</i>	0.98(0.13)a	1.92(0.36)bcde	0.021	2.02(0.10)a	3.40(0.43)abcd	0.005
<i>Eremophila polyclada</i>	0.47(0.03)cdef	0.88(0.07)e	< 0.001	0.79(0.09)efg	2.04(0.09)def	< 0.001
<i>Eremophila divaricata</i>	0.40(0.04)cdef	1.65(0.21)cde	< 0.001	0.64(0.04)g	2.43(0.32)cdef	0.001
<i>P-Value</i>	< 0.001	< 0.001		< 0.001	< 0.001	

583 Values in parentheses show mean standard error. Difference letters indicate significant
584 differences between species within treatment and variable (one-way ANOVA; Tukey post
585 hoc test). P-values in table show significant differences among species and between WW and
586 WD treatments within each species (Tukey post hoc test).

587

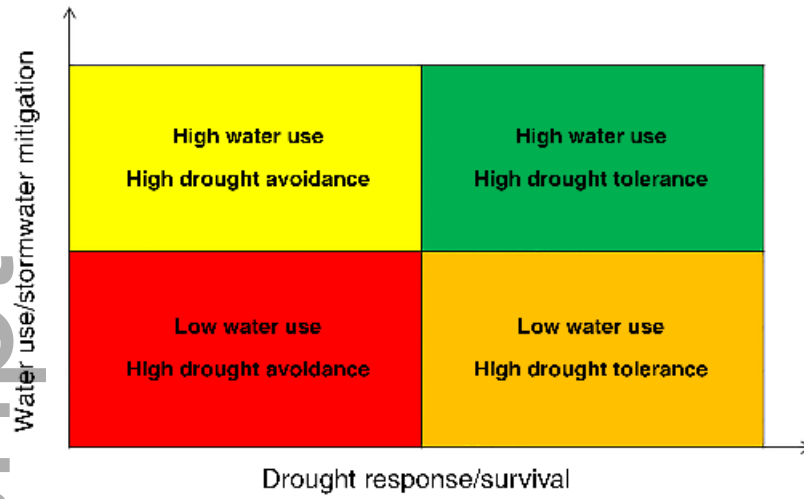
588 **Figure legends**

589 **Fig1.** The category of species based on the function of stormwater mitigation after rainfall
590 and survival under water deficit on harsh roof. Four categories were included, the green block
591 represents the ideal species for green roof, high water use when available and high drought
592 tolerance under stress; the yellow and orange ones represent species with high water use, high
593 drought avoidance and low water use and high drought tolerance. While the red block
594 represents species with low water use and high drought avoidance.

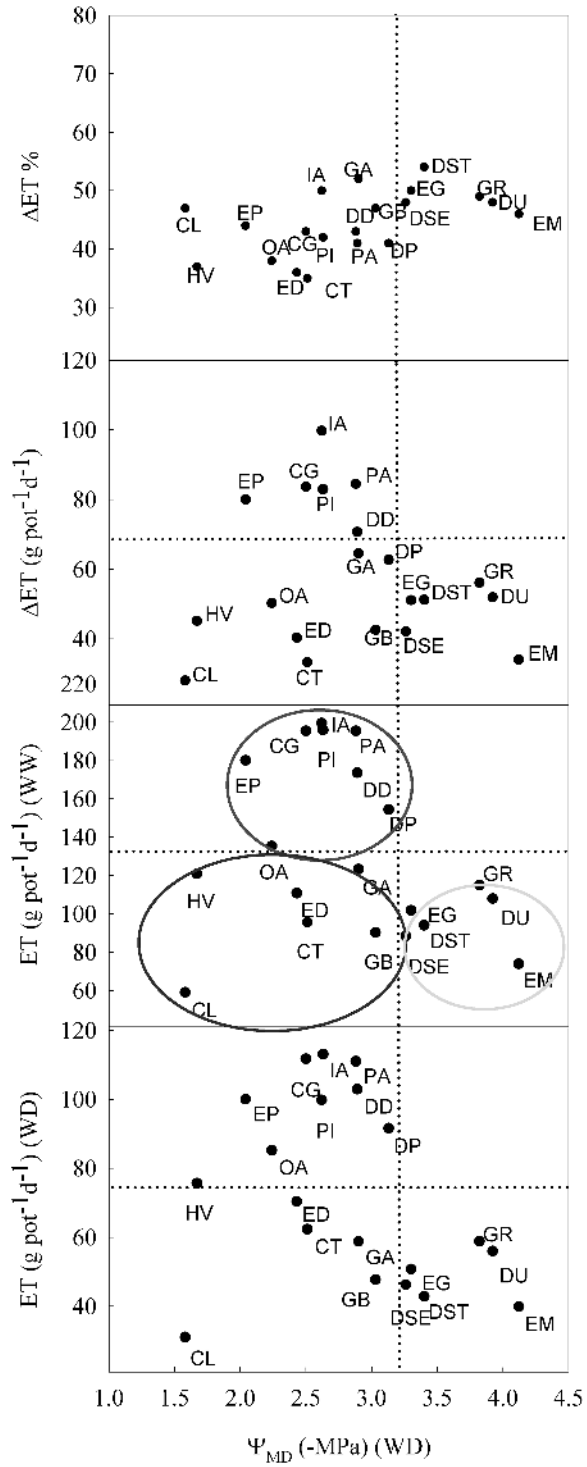
595 **Fig2.** Correlations between midday water potential (Ψ_{MD}) under WD and evapotranspiration
596 rate (ET) under WW, WD, and the change in ET from WW to WD. No high water users
597 which are drought tolerant were found among 20 shrubs.

598 **Fig3.** Correlations between ET/d under WW, Ψ_{MD} under WD and different morphological
599 traits for 20 shrub species. Solid line is the relationship that is significant across all species.
600 Bars represent standard error of the mean (n=5). ET/d was significantly correlated with all the
601 morphological traits under WW, but no correlations between Ψ_{MD} and morphological traits
602 under WD.

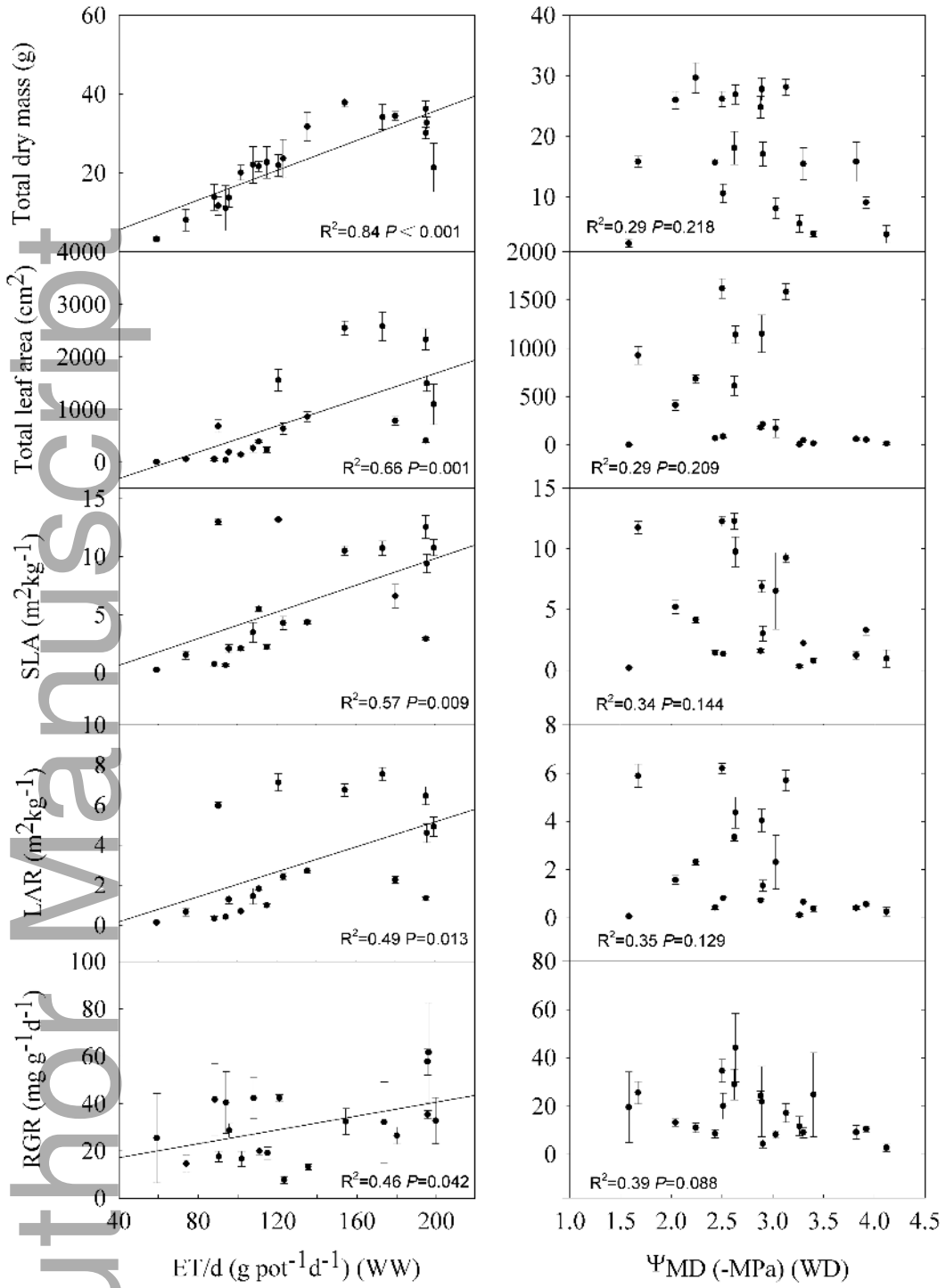
603 **Fig4.** Correlations between HMI and evapotranspiration rate (ET) under WW and midday
604 water potential (Ψ_{MD}) under WD for 20 shrub species. Bars represent standard error of the
605 mean (n=5). Both traits were not significantly correlated with HMI.



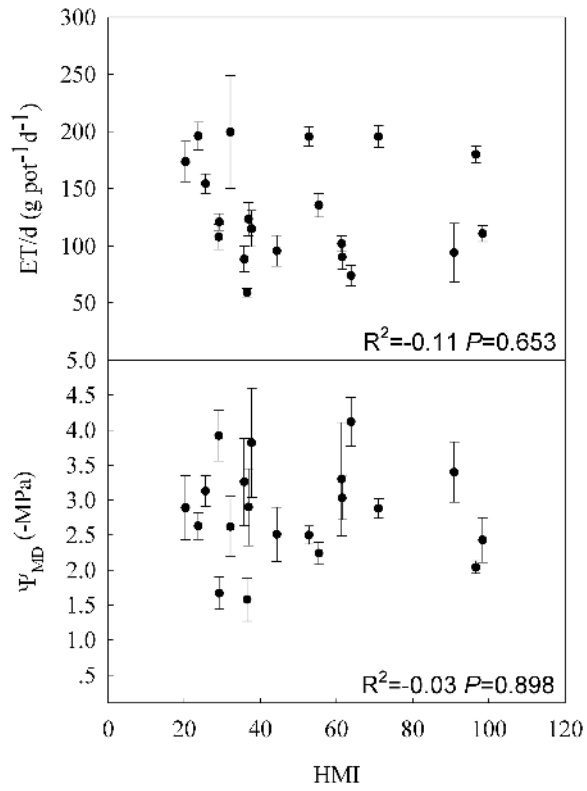
eap_1782_f1.tif



eap_1782_f2.tif



eap_1782_f3.tif



eap_1782_f4.tif