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Relative importance of transpiration rate and leaf morphological traits for the regulation of leaf temperature

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Running title: Leaf traits and temperature regulation

19 **Summary text for the Table of Contents**

20

21 Ability of plants to provide cooling in the urban environment is increasingly recognised.

22 Plants use various mechanisms to regulate leaf temperature, so we investigated how several

23 leaf traits (hairiness, colour, thickness) and processes (leaf water loss) rank in their

24 contribution to the leaf temperature regulation. We showed that the relative importance of

25 water loss and leaf traits for leaf temperature varied with plant genera. This can lead to

26 different plant types having significantly different potentials for cooling in applications such

27 as green roofs.

28

29

30

31 **Abstract**

32 Urban greening solutions such as green roofs help improve residents' thermal comfort and
33 building insulation. However, not all plants provide the same level of cooling. This is
34 partially due to differences in plant structure and function, including different mechanisms
35 that plants employ to regulate leaf temperature. Ranking of multiple leaf/plant traits involved
36 in the regulation of leaf temperature (and, consequently, plants' cooling 'service') is not well
37 understood. We therefore investigated the relative importance of water loss, leaf colour,
38 thickness and extent of pubescence for the regulation of leaf temperature, in the context of
39 species for semi-extensive green roofs. Leaf temperature were measured with an infrared
40 imaging camera in a range of contrasting genotypes within three plant genera (*Heuchera*,
41 *Salvia* and *Sempervivum*). In three glasshouse experiments (each evaluating three or four
42 genotypes of each genera) we varied water availability to the plants and assessed how leaf
43 temperature altered depending on water loss and specific leaf traits. Greatest reductions in
44 leaf temperature were closely associated with higher water loss. Additionally, in non-
45 succulents (*Heuchera*, *Salvia*), lighter leaf colour and longer hair length (on pubescent
46 leaves) both contributed to reduced leaf temperature. However, in succulent *Sempervivum*,
47 colour/pubescence made no significant contribution; leaf thickness and water loss rate were
48 the key regulating factors. We propose that this can lead to different plant types having
49 significantly different potentials for cooling. We suggest that maintaining transpirational
50 water loss by sustainable irrigation and selecting urban plants with favourable morphological
51 traits is the key to maximising thermal benefits provided by applications such as green roofs.

52 **Key words:** Leaf colour; Leaf hairs; Leaf temperature; Leaf thickness; Water deficit; Water

53 loss

54 **Introduction**

55 Green infrastructure (i.e. street trees, parks and gardens, green roofs and walls) in the urban
56 environments is being increasingly recognised for a number of services it provides, including
57 its role in regulation of air temperatures, particularly during periods of hot dry weather (Taha
58 1997; Wong *et al.* 2003; Bowler *et al.* 2010). Green, vegetated, roofs in particular are gaining
59 prominence for their ability to improve residents' thermal comfort and building insulation
60 (along with energy savings from the reduced use of air conditioning) (Saiz *et al.* 2006; Rowe
61 2011; Peng and Jim 2013). Plant species choice on extensive and semi-extensive green roofs,
62 which are designed with lower maintenance in mind, usually revolves around low growing
63 plants such as *Sedum* or grass mixes (Getter and Rowe 2006; Oberndorfer *et al.* 2007). Our
64 previous work, however, suggested that by choosing an alternative to *Sedum*, substrate
65 temperatures (and even air temperatures at times) can be consistently significantly lowered
66 (Blanusa *et al.* 2013). More broadly, little is known about how different plants compare in
67 their potential for these 'temperature regulation' services and what are the mechanisms/traits
68 that underpin those differences.

69 Certain leaf traits and physiological processes can influence the amount of radiation absorbed
70 by the leaf and how the absorbed heat is later dissipated. Individual morphological traits such
71 as leaf colour, the extent of leaf hairiness and structure of leaf hairs (if leaves are pubescent)
72 and leaf thickness, are known to affect leaf temperatures (Ansari and Loomis 1959; Ferguson
73 *et al.* 1973; Ehleringer and Mooney 1978). Leaves, however, exhibit these multiple traits
74 simultaneously (e.g. a *Stachys byzantina* leaf is light-coloured as well as pubescent), but the
75 relative contribution of multiple traits to leaf temperature regulation, and how do they 'rank'
76 in importance, in various types of leaves, is not understood.

77 Leaf colour is defined by leaf hue, chroma and lightness (Voss 1992); leaf lightness is
78 directly linked to its reflectance. A lighter leaf colour of a similar hue (i.e. light vs dark green
79 leaves) increases short-wave reflectance (Billings and Morris 1951) and thus reduces leaf
80 temperature (Ferguson *et al.* 1973). Leaf pubescence too can be associated with higher visible
81 reflectance (Billings and Morris 1951), but not in all cases as hairs can vary considerably in
82 their structure and colour (Gausman and Cardenas 1969). Additionally, leaf hair density may
83 affect leaf convection and transpiration (and thus leaf temperature) by affecting the leaf
84 boundary layer resistance (Schuepp 1993) and/or by influencing the number of stomata
85 present in a leaf (Skelton *et al.* 2012). Pubescence characteristics may also influence
86 irradiance parameters, including the degree of shading on the epidermis, as these structures
87 will act as a shield, reducing the radiation input onto the leaf itself (Lewis and Nobel 1977).
88 Finally, an increase in leaf thickness (succulence) is linked to an increased capacity for leaf
89 heat storage, but slower heat dissipation (Lewis and Nobel 1977) thus leading to increased
90 leaf temperatures.

91 Leaf temperatures are also largely dependent on substrate moisture (Grant *et al.* 2007). Plants
92 respond to periods of water deficit by closing their stomata and reducing transpiration loss
93 (Hsiao 1973; Jones 1998; Chaves *et al.* 2002), consequently increasing leaf temperature. This
94 might be of importance for plants grown on green roofs where summertime drying is
95 routinely experienced (Nagase and Dunnett 2010). Not all plants respond to substrate drying
96 in the same manner, however, with variations in stomatal behaviour during drying (Cameron
97 *et al.* 2008; Campbell *et al.* 2010). Plants also employ a range of additional mechanisms to
98 continue to function when subjected to long periods of water deficit. Plants/leaves with traits
99 that promote reflectance adapt fairly well to prolonged water deficiency. For instance, the
100 percentage of white, highly-reflective, hairs on certain xerophytes increases substantially

101 when they are experiencing prolonged water deficits (Ehleringer 1982). An increase in leaf
102 hairiness augments reflectance and so leaf temperatures of those plants can be maintained
103 close to the temperature of the air around them (Ehleringer and Mooney 1978). Other genera
104 possessing thick and fleshy succulent leaves or stems have the ability to store water within
105 specific water reserving cells and therefore can thrive in intense water deficit conditions. The
106 effectiveness of these water reserves is evident from a study which showed that apical leaves
107 of plants from *Sedum rubrotinctum* growing in a glasshouse environment were turgid for at
108 least two years without supplemental water (Teeri *et al.* 1986). Many succulents are also
109 facultative or compulsory Crassulacean Acid Metabolism (CAM) plants, and therefore
110 significantly reduce CO₂ uptake during the day, and hence reduce stomatal opening, during
111 periods of water deficiency without compromising their functioning (Kluge and Ting 1978).
112 However, a strategy like this will not allow plants to remain cool, as heat storage within their
113 leaves will also increase compared to thin-leaved plants.

114 The understanding of the relative importance of each of those morphological traits and
115 physiological processes becomes relevant, when attempting to rank plant genotypes in their
116 potential for ecosystem service delivery with respect to urban cooling. To elucidate this we
117 have studied three plant genera, each with a number of genotypes with contrasting leaf
118 attributes (dark *vs* light-coloured, thick *vs* thin-leaves, smooth *vs* pubescent, and pubescent
119 leaves with short *vs* long hairs) when exposed to two contrasting water availability regimes.
120 The following hypotheses were tested:

- 121 • Leaf water loss is key for leaf temperature regulation: a decrease in leaf stomatal
122 conductance increases leaf temperature in all plant-types.

123 • Genotypes with light-coloured leaves, thin leaves and/or longer leaf hairs (in
124 pubescent genotypes) have lowest leaf temperatures, even when subjected to water
125 deficit.

126 Genera selected were all evergreen perennials or sub-shrubs which are commonly found in
127 gardens. Although the key objective of this paper was to assess the relative contribution of
128 multiple leaf traits to leaf temperature regulation, the choice of plants was based on their
129 potential to also be used on semi-extensive green roofs. Low to medium growing perennials
130 can be easily incorporated in such systems, providing cooling without occupying the
131 restricted ground-level urban footprint.

132 **Materials and methods**

133 *Plant material*

134 Three plant genera, each with a number of genotypes, were selected for the experiments,
135 carried out in a ventilated glasshouse located at the University of Reading (UK) experimental
136 grounds. Genotypes were selected to include a range of contrasting leaf colour, pubescence
137 (presence and length of hairs) and leaf thickness (Table 1/ Figure 1).

138

139 [Insert Table 1]

140 [Insert Figure 1]

141 *Heuchera*, *Sempervivum* and *Salvia* genotypes were tested in three separate phases starting on
142 21 March, 2 June and 21 June 2011, respectively; each phase lasting 15-17 days. Plants were
143 purchased as six months old plugs. *Heuchera* and *Salvia* were transplanted into a peat-based

144 growing medium (SHL, 'William Sinclair', Lincoln, UK) one month before the start of each
145 experiment into 2 L containers (round, d = 17 cm, 10 cm of substrate). *Sempervivum* were
146 transplanted at the same time, but to 1 L containers (round, d = 13 cm, 8 cm of substrate);
147 here, the substrate was mixed with sand (v/v 50:50) to increase drainage and minimise risk of
148 root pathogens (*Pythium* and *Phytophthora* spp.) in this xerophytic genus.

149 Each irrigation treatment/genotype combination was represented by either seven (*Heuchera*
150 and *Salvia*) or eight (*Sempervivum*) replicate plants. For *Heuchera* and *Salvia*, containers
151 were arranged on two benches within a single glasshouse compartment using a randomized
152 two-block design (each bench contained three to four containers of each treatment). For
153 *Sempervivum*, all containers were arranged on one bench using a randomized design.

154 *Watering treatments*

155 On the morning of Day 0 of each experiment, containers were watered to full capacity. From
156 Day 1 onwards containers were either kept at full substrate water holding capacity (100%,
157 wet regime - 'WR') or subjected to regulated deficit irrigation (dry regime - 'DR') (Cameron
158 *et al.* 2006). Irrigation was carried out manually, based on a proportion of evapo-transpiration
159 (ET) over the preceding 24 h period; thereby accounting for daily variations in evapo-
160 transpirational demand. For *Heuchera* and *Salvia*, 'WR' plants received daily 100% of
161 moisture lost in the preceding 24 h period, whereas 'DR' plants received 50% of this volume.
162 For the succulent *Sempervivum*, due to naturally low ET rates, 'WR' plants received all the
163 water lost by evapotranspiration in 48 h cycles, rather than daily, and the 'DR' plants
164 received no irrigation for the duration of the experiment. Moisture loss was determined by
165 weighing containers on Adam CBK 32 Bench Scale (Scales and Balances, Thetford, Norfolk,
166 UK).

167 *Plant and substrate measurements*

168 The air temperature and relative humidity within the glasshouse compartment in each of the
169 experiments was recorded every 30 minutes by a screened Tinytag logger Plus 2 – TGP-4500
170 (Gemini Data Loggers Ltd., Chichester, West Sussex, UK; -25 to 85 °C and 0-100% RH
171 range and an accuracy of 0.4 °C and 3.0% RH at 25°C). Air temperatures during the
172 experiment are presented in the Results section; mean daily relative humidity in the
173 glasshouse compartment was relatively constant within each experiment and averaged 68 %
174 for the *Salvia* experiment and 70% for the *Heuchera* and *Sempervivum* experiments.

175 Substrate moisture content (SMC) was measured using a SM200 capacitance-type probe
176 connected to a HH2 Moisture Meter (Delta-T Devices, Cambridge, Cambridgeshire, UK; 0 –
177 100% range and an accuracy of 3%). Measurements were made regularly throughout the
178 experiment, as moisture availability decreased in the ‘DR’ treatment (with four dates that
179 represent different phases of the drying process being shown - see Figures 3-5). Two
180 measurements per container were made in *Heuchera* and *Salvia* and one measurement per
181 container in *Sempervivum*, between 09:30 - 11:30 h on each date. Probes were inserted into
182 the substrate vertically, as far away as possible from the container edge, to minimise edge
183 effects.

184 Water loss in *Heuchera* and *Salvia* was inferred by the measurement of their leaf stomatal
185 conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) using an LCI infra-red gas analyser (ADC Bioscientific,
186 Hoddesdon, Hertfordshire, UK) with ambient CO_2 concentration at $400 \pm 10 \text{ mm}^3 \text{ dm}^{-3}$.
187 During measurements, photosynthetic photon flux density was supplemented to $2000 \mu\text{mol}$
188 $\text{m}^{-2} \text{s}^{-1}$ by an external halogen source (50 W, 12 V). Stomatal conductance was measured at
189 the four dates when SMC was measured too, reflecting the different phases of drying in ‘DR’

190 treatments. At each date, two young, fully expanded leaves per container were measured
191 between 11.00 - 13.00 h (with measurements made on different treatments being spread out
192 evenly through the evaluation time on each date). In *Sempervivum*, however, the small leaf
193 size precluded the use of the gas analyser, so transpiration rates were estimated at a plant
194 level from container water loss between consecutive weight measurements instead. As at
195 least 90% of the substrate was completely covered by the low growing *Sempervivum* plants
196 (see Figure 1), we assumed that evaporation from the substrate surface was minimal and that
197 the recorded water loss corresponded mainly to plant transpiration.

198 Leaf thickness was estimated using the methodology proposed by Vile *et al.* (2005):

$$199 \quad \mathbf{LT} = \frac{\mathbf{1}}{\rho} \frac{\mathbf{1}}{(\mathbf{SLA} \times \mathbf{LDMC})} \quad (1)$$

200 Where: LT = Leaf thickness; ρ = Density of the leaf (assumed to be similar to water i.e. 1 g
201 cm^{-3}); SLA = Specific leaf area (ratio of area to dry mass, $\text{m}^2 \text{kg}^{-1}$); LDMC = Leaf dry matter
202 content (ratio of dry to fresh mass, mg g^{-1}).

203 SLA and LDMC were calculated based on the protocol of Garnier *et al.* (2001) with one
204 young fully expanded leaf per plant being assessed at the beginning and end of experiments.
205 Leaves were hydrated for 6 h at 4 °C in the dark, before fresh weight and area were
206 determined (Leaf Area Meter, Delta-T Devices, Cambridge, Cambridgeshire, UK). Leaf dry
207 weight was assessed after drying at 70 °C for 48 h.

208 Leaf colour was evaluated visually (Table 1) and the relative luminance parameter Y (here
209 presented as ‘leaf lightness’) was measured with a SP52 portable sphere spectrometer (X-
210 Rite, Poynton, Cheshire, UK), which measures the percentage of reflectance in the visual
211 spectral range of 400 to 700 nm. This parameter was measured, on the upper side of on one

212 leaf per container, at the beginning and end of the experiments for *Heuchera* and *Salvia* and
213 mid-experiment for *Sempervivum*.

214 In addition to the visual description of pubescence in all genera, length of leaf hairs was
215 determined in *Salvia*. Three cross sections on three leaves per treatment (one each of young,
216 medium and old leaves) were captured using an Axioskop 2 microscope (Carl Zeiss,
217 Cambridge, Cambridgeshire, UK). Hair length was then measured using the software Image J
218 (National Institutes of Health, Bethesda, Maryland, USA). Six fully visible hairs were
219 measured in each cross section to obtain average hair length values.

220 Thermal images of all individual containers were recorded using an infrared imaging camera
221 Thermo Tracer TH7800 (NEC San-ei Instruments Ltd., Tokyo, Japan; -20 to 250 °C range
222 and an accuracy of 0.1 °C) at the four dates SMC was measured, within one hour in the early
223 afternoon of each date. Containers were randomly selected for imaging to minimise the
224 impact of air temperature differences within the measurement hour on leaf temperatures.
225 Images were recorded from a consistent angle and distance on plants placed out of direct
226 sunlight. Plants were kept in the shade for 5 minutes before being measured so that the effect
227 of previous heat load differences on leaf temperature was minimized. For each individual
228 plant, temperatures were calculated in four separate sections of the canopy covering approx.
229 10 cm² (*Heuchera* and *Salvia*) or 5 cm² (*Sempervivum*). Leaf emissivity was determined on a
230 sub-sample of leaves in thin-leaved genotypes using the technique described by López et al.
231 (2012). Emissivity of *Sempervivum* was not measured due to its leaf morphology not being
232 conducive to the technique employed. Mean emissivity values ranged between 0.974 for
233 purple *Heuchera* and 0.968 for grey *Salvia*. Therefore a standard emissivity of 0.97 was used
234 for all genera when analysing the thermal images.

235 *Statistical analysis*

236 Data were analysed using GenStat (16th Edition, VSN International Ltd., Hemel Hempstead,
237 Hertfordshire, UK). Analysis of variance (ANOVA) was used to assess the effect of watering
238 regime and plant genotype on measured parameters; variance levels were checked for
239 homogeneity (where necessary data were transformed – e.g. leaf lightness in the *Heuchera*
240 experiment) and values are presented as means with associated least significant differences
241 (LSD, $P = 0.05$). Data for each day of the experiment were analysed separately.

242 In addition to ANOVA analyses, multiple regressions were performed to identify which leaf
243 factors contributed the most to leaf temperature differences in the three genera for the
244 selected four experimental days representing different phases of drying in ‘DR’ treatments.
245 Each daily regression had leaf temperature (averaged at the container level) as dependent
246 variable and the mean container’s g_s /water loss, leaf lightness and leaf thickness as
247 independent variables. In *Salvia*, hair length was also included as an independent variable.
248 When more than one plant factor was significant for the regression model, their measure of
249 importance was established using a dominance analysis, as described by Budescu (1993).

250 **Results**

251 *Heuchera: The influence of genotype and substrate moisture on leaf temperature, stomatal*
252 *behaviour, leaf lightness and leaf thickness*

253 *Heuchera* plants were evaluated on Days 0, 7, 12 and 16 of the experiment. Maximum air
254 temperatures within the glasshouse on Days 0 and 16 were above 30 °C. On the remaining
255 days, maximum air temperature was approximately 25 °C (Figure 2.A).

256 Leaf temperatures were lowest for the yellow genotype throughout the experiment. ‘WR’
257 yellow plants had significantly cooler leaves than all other treatments, and ‘DR’ yellow plants
258 had significantly cooler leaves than all purple and purple-white plants on all selected dates
259 (e.g. plant differences on Days 0 and 16, both $P < 0.001$) (Figure 2.D). On the last day of the
260 experiment, yellow plants were on average 2.8 °C cooler than purple plants under ‘WR’ and
261 1.9 °C under ‘DR’. Additionally, substrate moisture content (SMC) influenced leaf
262 temperatures significantly once the difference in watering regimes was introduced (e.g.
263 moisture differences on Days 7 and 16, both $P < 0.001$). From Day 7, leaf temperatures in the
264 ‘DR’ plants were significantly higher than their respective ‘WR’ controls (Figure 2.D).

265 Leaf stomatal conductance (g_s) also appeared to be strongly linked to the genotypes’ leaf
266 colour (e.g. differences on Days 0 and 16, both $P < 0.001$). In the ‘WR’, plants mean values
267 were: 286 (yellow), 248 (green), 191 (purple/white) and 187 $\text{mmol m}^{-2} \text{s}^{-1}$ (purple). Yellow
268 and green foliage plants had significantly higher g_s values than purple or purple/white
269 genotypes on all days when g_s was measured (Figure 2.C). Water deficits too had a dramatic
270 effect on g_s , with all ‘DR’ plants bar the yellow demonstrating significant reductions in g_s by
271 Day 7 (e.g. moisture differences on Days 7 and 16, both $P < 0.001$) (Figure 2.C). On that day
272 the g_s of the ‘DR’ purple plants had declined by 27% compared to the ‘WR’ ones, whilst for
273 the yellow one the g_s reduction was 13%. However, by Day 12, SMC was $< 0.20 \text{ m}^3 \text{ m}^{-3}$
274 across all the ‘DR’ treatments (Figure 2.B), and g_s correspondingly was significantly lower
275 for each genotype in comparison to their ‘WR’ controls. On the last day, the ‘DR’ yellow and
276 purple plants were both showing a 45-50% reduction in their g_s values.

277 As expected, leaf lightness was highest in the yellow foliage, being approximately 4-fold
278 greater than the other foliage colours (plant differences: Day 0 (data not shown) and Day 16,

279 (Table 2), both $P < 0.001$). Furthermore leaves from green *Heuchera* were 0.08 mm thicker
280 than those from the other genotypes (plant differences: Day 0 (data not shown) and Day 16
281 (Table 2), $P < 0.001$).

282 [Insert Figure 2]

283 [Insert Table 2]

284 *Salvia: The influence of genotype and substrate moisture on leaf temperature, stomatal*
285 *behaviour, leaf lightness and leaf thickness*

286 *Salvia* plants were evaluated on Days 0, 6, 13 and 17 of the experiment. Maximum air
287 temperature within the glasshouse on Days 6 and 13 was approximately 35 °C, whilst
288 maximum air temperatures on Days 0 and 17 were approximately 30 °C (Figure 3.A).

289 Throughout the experiment, leaf temperatures of ‘WR’ plants were significantly higher in the
290 purple genotype compared to the grey and green ones (e.g. plant differences on Days 0 and
291 17, both $P < 0.001$) (Figure 3.D). At the end of the experiment the difference between purple
292 and grey genotypes’ temperatures was on average 1.5 °C under ‘WR’ and 2.1 °C under ‘DR’
293 (Figure 3.D). Water deficit increased temperature, with leaf temperatures of all ‘DR’
294 treatments becoming significantly higher than their respective ‘WR’ controls from Day 6
295 onwards (e.g. moisture differences on Days 6 and 17, both $P < 0.001$). In the ‘WR’, plants of
296 the green and grey genotypes had similar temperatures, but from day 6 onwards in the ‘DR’
297 the grey was significantly cooler (e.g. 0.8 °C on the last day of the experiment) than the green
298 genotype (Figure 3.D).

299 When well watered, g_s values in the green genotype were significantly greater than those in
300 the purple ones, with the g_s values of grey plants being intermediate at all dates tested (e.g.

301 plant differences on Day 0, $P < 0.001$ and Day 17, $P = 0.006$) (Figure 3.C). Water deficit
302 reduced g_s , and from Day 6 onwards all genotypes in the 'DR' treatments (where SMC was
303 reduced to around $0.2 \text{ m}^3 \text{ m}^{-3}$ – Figure 3.B) had significantly lower g_s compared to the
304 respective 'WR' controls (e.g. moisture differences: Day 6, $P = 0.013$ and Day 17, $P < 0.001$)
305 (Figure 3.C). However not all genotypes showed a similar rate of g_s decrease as on the last
306 day the g_s of the 'DR' green plants were reduced by 45% compared to their 'WR' control,
307 whilst for the grey, the g_s reduction was 26%.

308 No differences in leaf thickness were detected, but genotypes with different leaf colour
309 differed significantly in their leaf lightness (plant differences: Day 0, (data not shown) and
310 Day 16, (Table 3), both $P < 0.001$). At the end of the experiment, leaf lightness of the grey
311 genotype was around 4% greater than that of the purple genotype. Leaf hair length was
312 significantly longer with the grey genotype too (0.96 mm) as compared to green or purple
313 genotypes (both averaging 0.63 mm) ($P < 0.001$, data not shown).

314 [Insert Figure 3]

315 [Insert Table 3]

316 *Sempervivum: The influence of genotype and substrate moisture on leaf temperature, plant*
317 *water loss, leaf lightness and leaf thickness*

318 *Sempervivum* plants were evaluated on Days 0, 7, 11 and 15 of the experiment. Maximum air
319 temperatures within the glasshouse on Days 0, 7 and 11 were approximately 30 °C and on
320 Day 15 maximum air temperature was approximately 25 °C (Figure 4.A).

321 Leaf temperature was highest with the green genotype, when plants were well watered (e.g.
322 plant differences: Day 0, $P < 0.001$ and Day 15, $P = 0.01$) (Figure 4.D). Imposing water

323 deficiency increased temperatures most markedly in the hairy genotype in the first instance,
324 and by Day 11 temperature differences between ‘DR’ and ‘WR’ hairy plants of this genotype
325 reached 2.8 °C. Water status also had a significant effect on temperature of the other two
326 genotypes by this time (Day 11, $P < 0.001$).

327 Differences in plant water use between ‘WR’ and ‘DR’ were significant from Day 7 for all
328 genotypes (Figure 4.C) (Day 7, $P = 0.008$), when all ‘DR’ treatments had a mean SMC of
329 around $0.10 \text{ m}^3 \text{ m}^{-3}$ (Figure 4.B). When well watered, hairy plants lost the highest amount of
330 water, but when water was withdrawn, the daily water loss of the hairy genotype plants was
331 similar to the other ones (Figure 4.C).

332 There were significant genotype differences in both leaf thickness (plant differences: Day 0,
333 $P < 0.001$ (data not shown) and Day 15, $P = 0.002$ (Table 4)) and leaf lightness ($P < 0.001$
334 (Table 4)). Green leaves were on average at least 0.3 mm thicker and had around 10% greater
335 leaf lightness than the red leaves.

336 [Insert Figure 4]

337 [Insert Table 4]

338 *Multiple regressions*

339 For *Heuchera*, g_s and leaf lightness (unlike leaf thickness) were significantly related with leaf
340 temperature at all times (Table 5.A). When plants were under well watered conditions (Day
341 0), leaf lightness contributed 9% more than g_s to the overall temperature variation. However,
342 when differences in g_s between ‘WR’ and ‘DR’ plants became significant, g_s was the largest
343 determinant of leaf temperature (accounting for 19% more of the variation than leaf lightness
344 on the last day) (Table 5.A).

345 In *Salvia*, only leaf lightness was significantly related with leaf temperature on Day 0, when
346 all plant factors (i.e. leaf lightness, hair length, leaf thickness as well as g_s) were considered
347 simultaneously (Table 5.B). However, on Day 6, g_s and hair length also contributed
348 significantly to leaf temperature, with g_s being the greatest determinant (54% more than leaf
349 lightness). On Days 13 and 17, leaf lightness was no longer significantly related with leaf
350 temperature when considered simultaneously with g_s and hair length. On the last day, g_s was
351 a more significant determinant of leaf temperature than hair length, with g_s contributing 6%
352 more to the overall variation in temperature (Table 5.B).

353 Unlike the other genera, in *Sempervivum*, leaf thickness was the only factor significantly
354 related with temperature on Days 0 and 7 (Table 5.C). Plant water loss played a significant
355 role in the leaf temperature variation as well but only when the SMC differences between
356 ‘WR’ and ‘DR’ treatments became apparent. By Day 13, the contribution of water loss
357 accounted for 10% more of the temperature variation than that of leaf thickness and by Day
358 15 it was the only significant factor (Table 5.C).

359 [Insert Table 5]

360 **Discussion**

361 All the leaf traits and physiological processes considered here (leaf lightness, extent of
362 pubescence, leaf thickness and stomatal conductance/water loss) influenced significantly leaf
363 temperature. This led to significant differences in leaf temperature between genotypes of the
364 same genera. Additionally, the extent of each factor’s contribution varied between genera and
365 was also dependent on substrate moisture content.

376 It is well established that leaf temperature and g_s are strongly linked. This relationship has
377 been shown in numerous studies on a range of species under different substrate moisture
378 conditions, in glasshouses or in the field. For example, in a glasshouse experiment with
379 *Phaseolus vulgaris*, g_s was accurately predicted from leaf thermal images using reference
380 surfaces with known water vapour conductance (Jones 1999). Furthermore, in an experiment
381 with *Fragaria ×ananassa* cultivars analysed under wet and dry conditions, g_s estimated from
382 thermal images of leaves placed horizontally were strongly related with direct g_s
383 measurements made with a porometer (Grant *et al.* 2012).

384 In our experiments, lower g_s (or lower plant water loss, in *Sempervivum*) was also always
385 strongly related with higher leaf temperatures. The increase in temperature was largely
386 controlled by the watering regime implemented. Leaf temperature differences between ‘WR’
387 and ‘DR’ plants became significant as soon as g_s /water loss decreased, due to less water
388 being given to the dry treatments. The only exception was *Sempervivum*, where the red and
389 green genotypes’ water losses were significantly reduced by Day 7 but a significant increase
in their leaf temperature was only apparent later, on Day 11. A study comparing thick,
succulent *Graptopetalum* leaves to other thinner leaves (in which the leaf mass of
Graptopetalum was at least 472 mg cm⁻² greater than the leaf mass of all other leaves
considered), identified that *Graptopetalum* leaves took the longest to heat up or cool in
response to changes in environmental conditions (in this case changes in sun/shade light
intensities) (Ansari and Loomis 1959). This suggests that succulent leaves’ temperatures are
more decoupled from environmental conditions than thinner leaves and this could explain
why some of the *Sempervivum* genotypes reacted more slowly to a significant change in their
daily water losses. Nevertheless, even for *Sempervivum*, water loss was related with leaf
temperature at the end of the experiment, when SMC was substantially reduced.

390 Inherent g_s /water losses differences between the genotypes of the same genera, however, also
391 contributed to differences in leaf temperature on some occasions. *Heuchera* and *Salvia*
392 genotypes with yellow or green leaves had higher g_s than genotypes with purple leaves
393 (Figures 2, 3). Consequently, and particularly in the *Heuchera* genotypes, differences in g_s
394 contributed to leaf temperature differences between genotypes even before SMC was reduced
395 in the dry treatments.

396 Leaf lightness was used to quantify genotype differences in leaf colour. Some studies
397 recognized the importance of light leaf colour to achieve high visible reflectance and
398 decrease plant temperature (Ferguson *et al.* 1973). In our study, the contribution of leaf
399 lightness to temperature regulation was significant only among the thin-leaved non-succulent
400 genera (*Heuchera* and *Salvia*) (Table 5). In both genera, leaf lightness was the factor that
401 contributed to temperature regulation most strongly before water deficit was introduced.
402 Furthermore, even when water deficit developed, leaf lightness significantly influenced leaf
403 temperature on some occasions, although less than g_s . More specifically, in the *Heuchera*
404 experiment the yellow genotype had lowest leaf temperature, even though its g_s was similar
405 to that of darker genotypes (e.g. ‘WR’ yellow *vs* ‘WR’ green or ‘DR’ yellow *vs* ‘WR’ purple
406 – Figure 2). With *Salvia*, a lighter leaf colour also led to lower leaf temperatures, even when
407 there were no differences in g_s (e.g. ‘DR’ green and purple genotypes, on the last day of the
408 experiment, with green genotype being cooler – Figure 3).

409 Similarly, leaf hair length also contributed to temperature differences in thin, pubescent
410 *Salvia* leaves, but only in water deficit conditions. When comparing the grey to the green
411 genotype, the ‘DR’ grey genotype – which has longer hairs - was always cooler than ‘DR’
412 green (Figure 3). This supports earlier work arguing that the presence of leaf hairs may

413 increase the leaf's time-scale of response to water deficit, compared to other non-hairy or less
414 hairy leaves (França *et al.* 2012; Blanusa *et al.* 2013). This may be linked to the effect that
415 the size and density of leaf pubescence can have on the leaf boundary layer thickness
416 (Schuepp 1993). Hairs in *Salvia* are relatively sparse (Table 1), so a small increase in their
417 length may enhance air turbulence (via an increased roughness) close to the leaf surface
418 leading to reduced boundary layer resistance to heat and water vapour transfer. This could
419 reduce leaf temperature, even when substrate moisture (and thus g_s) is restricted. It can also
420 be linked to the fact that highly pubescent leaves can have a higher number of stomata per
421 leaf area than glabrous/less pubescent leaves (Skelton *et al.* 2012). The number of stomata
422 was not assessed in this study but a possible increase in stomatal density could explain why,
423 on the last day, g_s of 'DR' grey *Salvia* was still only marginally lower than g_s of 'WR' purple
424 *Salvia*; this uncharacteristically small difference in g_s , along with the greater visible
425 reflectance of the grey leaves, may have contributed to 'DR' grey *Salvia* having slightly
426 lower leaf temperatures than 'WR' purple *Salvia* on Day 17.

427 Leaf thickness was only important for leaf temperature differences in succulent
428 genera/genotypes (Table 5). Thick leaves store more heat than thin leaves and consequently
429 have typically higher leaf temperatures (Lewis and Nobel 1977). In extreme cases, as for
430 thick desert cacti such as *Opuntia*, surface plant temperatures can rise up to 13 °C above
431 surface leaf temperatures shown by other surrounding desert plants with smaller thinner
432 leaves (Gates *et al.* 1968). Temperature differences between different *Sempervivum*
433 genotypes were not as large but still green *Sempervivum* – with thicker leaves - had higher
434 leaf temperature than the red, despite its highest visible reflectance among *Sempervivums*
435 (Table 4). In *Sempervivum*, along with leaf thickness, only differences in water loss between
436 the genotypes influenced leaf temperatures.

437 These results suggest therefore that different plant genera may depend on different
438 processes/traits to effectively regulate the temperature of their leaves and this is also
439 dependent on substrate moisture availability (summarized in Figure 5). Under water deficit
440 conditions, maintenance of transpiration (here approximately determined by leaf g_s or plant
441 water loss) was the key process for temperature regulation in all genera considered.
442 Temperature of thin leaves, however, was additionally dependent on leaf colour and, in
443 pubescent leaves, the length of leaf hairs (with lighter leaf colour and longer hair length being
444 associated with lower temperatures). Conversely, in succulent leaves, temperature was mostly
445 controlled by leaf thickness, with other simultaneously measured factors (such as leaf
446 hairiness and darker colour) not being significant.

447 [Insert Figure 5]

448 This knowledge can be valuable to identify potential differences in plant effects on
449 temperature of the surrounding environment. Genera/genotypes that normally heat up more
450 (i.e. with darker or thicker leaves) and/or that possess low typical g_s will inevitably re-radiate
451 more and release more heat by convection to the surrounding environment than others. In
452 highly urbanized areas, where temperatures can be considerably higher than in rural
453 environments (Oke 1987; Grimmond 2007), the increase of green space has been suggested
454 to be an effective way of reducing local air temperatures (Akbari et al., 2001; Gill et al.,
455 2007). Green roofs in particular have a potential to influence air temperatures as well as
456 building insulation, improving thermal comfort of residents (Saiz *et al.* 2006; Peng and Jim
457 2013). Based on the results discussed here we suggest that different genera and even
458 genotypes within the one genus may potentially have different cooling capacities, and thus
459 different benefits, when used on green roofs. Additionally, optimal substrate moisture is also

460 critical for keeping leaves cool. Consequently we suggest that maintaining transpirational
461 water loss by sustainable irrigation and selecting urban plants with advantageous
462 physiological/morphological traits are essential to maximize the thermal benefits (i.e.
463 increase latent heat loss, reduce convection and long wave emissions and reduce the heat
464 transferred into the buildings) provided by urban vegetation on green roofs and elsewhere.
465 Confirmatory findings to this effect will be presented in our follow-up papers.

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570 garden in the tropical environment. *Building and Environment* **38**, 261–270.
- 571

573 **Table 1. Plant genotypes with key traits (colour, extent of pubescence and leaf**
 574 **thickness) used in glasshouse experiments.**

Plant genus/species	Plant genotype	Leaf colour (visual perception)	Leaf pubescence (visual perception of length and density)	Leaf thickness	Referred to as
<i>Heuchera</i>	‘Electra’	yellow	no	Thin	Yellow <i>Heuchera</i>
	‘Café Olé’	dark green	no	Thin	Green <i>Heuchera</i>
	‘Geisha’s Fan’	variegated purple/white	no	Thin	Purple/ white <i>Heuchera</i>
	‘Obsidian’	purple	no	Thin	Purple <i>Heuchera</i>
<i>Salvia officinalis</i>	Common form	green	yes (short and sparse)	Thin	Green <i>Salvia</i>
	‘Berggarten’	green/grey	yes (long and sparse)	Thin	Grey <i>Salvia</i>
	‘Purpurascens’	green/purple	yes (short and sparse)	Thin	Purple <i>Salvia</i>
<i>Sempervivum</i>	‘Reinhard’	green	no	thick/ succulent	Green <i>Sempervivum</i>
	‘Red Shadows’	red	no	thick/ succulent	Red <i>Sempervivum</i>
	‘Lively Bug’	green	yes (long and sparse)	thick/ succulent	Hairy <i>Sempervivum</i>

576 **Table 2. *Heuchera*: The effect of genotype and irrigation regime ('WR' vs 'DR') on**
 577 **mean leaf lightness and leaf thickness on the last day of the experiment. Data are a**
 578 **mean of seven containers of each genotype per treatment; different letters correspond to**
 579 **statistically significant differences between means.**

Measurements	Purple 'WR'	Purple 'DR'	Yellow 'WR'	Yellow 'DR'	Green 'WR'	Green 'DR'	Purple/ White 'WR'	Purple/ White 'DR'	LSD
Leaf lightness (%)	5.55 a	5.60 a	35.30 c	37.81 c	9.42 b	8.87 b	8.87 b	9.45 b	A
Leaf thickness (mm)	0.21 ab	0.20 a	0.20 a	0.21 ab	0.28 d	0.27 d	0.24 c	0.23 bc	0.022

580 ^A LSD not shown as it relates to transformed data.

581

582 **Table 3. *Salvia*: The effect of genotype and irrigation regime ('WR' vs 'DR') on mean**
 583 **leaf lightness and leaf thickness on the last day of the experiment. Data are a mean of**
 584 **seven containers of each genotype per treatment; different letters correspond to**
 585 **statistically significant differences between means.**

Measurements	Green 'WR'	Green 'DR'	Purple 'WR'	Purple 'DR'	Grey 'WR'	Grey 'DR'	LSD
Leaf lightness (%)	12.93 b	12.69 b	9.61 a	10.06 a	14.16 b	13.89 b	1.669
Leaf thickness (mm)	0.29 a	0.30 a	0.28 a	0.30 a	0.30 a	0.29 a	0.023

586

587 **Table 4. *Sempervivum*: The effect of genotype and irrigation regime ('WR' vs 'DR') on**
 588 **mean leaf lightness on the middle of the experiment and leaf thickness on the last day of**
 589 **the experiment. Data are a mean of seven containers of each genotype per treatment;**
 590 **different letters correspond to statistically significant differences between means.**

Measurements	Red 'WR'	Red 'DR'	Green 'WR'	Green 'DR'	Hairy 'WR'	Hairy 'DR'	LSD
Leaf lightness (%)	7.52 a	7.52 a	17.57 b	17.20 b	16.67 b	16.11 b	1.826
Leaf thickness (mm)	2.17 ab	2.10 a	2.46 c	2.49 c	2.45 c	2.40 bc	0.271

591

592 **Table 5. Leaf temperature variation accounted for by the multiple regressions for four**
 593 **different days of each experiment (DOE) representing different stages of drying. The**
 594 **regression relates leaf temperature to all significant predictors (with $P < 0.05$) from leaf**
 595 **stomatal conductance (g_s)/daily water loss, leaf lightness, hair length and leaf thickness.**
 596 **Individual contributions of significant plant factors were determined by dominance**
 597 **analysis and are reported on the right side of the table.**

Plant types	DOE	Variation accounted for by the multiple regression (%)	Individual contributions of significant plant factors (%)			
			g_s / daily water loss	Leaf lightness	Hair length	leaf thickness
<i>A. Heuchera</i>	0	57.6	24.5	33.1		
	7	53.5	31.0	22.5		
	12	38.7	21.5	17.2		
	16	56.5	38.0	18.5		
<i>B. Salvia</i>	0	34.6		34.6		
	6	86.3	64.7	11.0	10.7	
	13	77.5	71.6		6.0	
	17	58.4	32.0		26.4	
<i>C. Sempervivum</i>	0	24.5				24.5
	7	14.1				14.1
	11	23.0	16.6			6.4
	15	30.3	30.3			

598

599 **Figure legends**

600 Figure 1. Images of all plant genotypes used for the experiments.

601 Figure 2. *Heuchera*: A. air temperature profile within the glasshouse over the full extent of
602 the experiment and B. substrate moisture content (SMC) C. leaf stomatal conductance (g_s)
603 and D. leaf temperature of different genotype/irrigation treatments on four days of the
604 experiment (DOE). Data for SMC, g_s and leaf temperature are a mean of seven containers of
605 each genotype per treatment. LSD values (5%) were calculated for each day separately and
606 are shown at the top of the figures; different letters on top of bars correspond to statistically
607 significant temperature differences between means.

608 Figure 3. *Salvia*: A. air temperature profile within the glasshouse and B. substrate moisture
609 content (SMC). C. leaf stomatal conductance (g_s) and D leaf temperature of different
610 genotype/irrigation treatments on four days of the experiment (DOE). Data for SMC, g_s and
611 leaf temperature are a mean of seven containers of each genotype per treatment. LSD values
612 (5%) were calculated for each day separately and are shown at the top of the figures; different
613 letters on top of bars correspond to statistically significant temperature differences between
614 means.

615 Figure 4. *Sempervivum*: A. air temperature profile within the glasshouse and B. substrate
616 moisture content (SMC). C. daily plant water loss and D. leaf temperature of different
617 genotype/irrigation treatments on four days of the experiment (DOE). Data for SMC, plant
618 water loss and leaf temperature are a mean of eight containers of each genotype per treatment.
619 LSD values (5%) were calculated for each day separately and are shown at the top of the

620 figures; different letters on top of bars correspond to statistically significant water loss and
621 temperature differences between means.

622 Figure 5. Factors influencing leaf temperature in various leaf types in our experiments when
623 substrate moisture content is optimal (dark blue) or low (light blue).

624