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Coping with drought: root trait variability within the perennial grass *Dactylis glomerata* captures a trade-off between dehydration avoidance and dehydration tolerance --Manuscript Draft--

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| Abstract: | <p>Background and Aims. Understanding plant adaptation to drought is a crucial challenge under climate change. This study aimed at investigating root traits and water use among plants exhibiting a range of dehydration avoidance and tolerance strategies to cope with drought.</p> <p>Methods. Sixteen populations of the perennial grass <i>Dactylis glomerata</i> originating from Mediterranean to Scandinavian biogeographical regions were grown in long tubes to measure root depth potential under irrigation and root adaptation under severe drought. Water uptake under drought was used as proxy for dehydration avoidance. Root depth, biomass, and morphological traits of the deep roots were measured. We assessed plant survival after severe drought as a measure of dehydration tolerance.</p> <p>Results. All populations had similar maximum rooting depth and specific root length. Compared to Northern and Temperate populations, Mediterranean populations had twice lower total and deep root biomass, thinner and denser deep roots. They were less affected by drought. This syndrome was associated with lower water uptake (lower dehydration avoidance) but higher survival to severe drought (dehydration tolerance).</p> <p>Conclusion. The intraspecific variability in root traits captured a trade-off between dehydration avoidance and dehydration tolerance which illustrates contrasting adaptive plant and root strategies according to the biogeographical origins of populations.</p> | |
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3 **Coping with drought: root trait variability within the perennial grass *Dactylis glomerata* captures a trade-**
4 **off between dehydration avoidance and dehydration tolerance**

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34 **SUMMARY**

35 *Background and Aims.* Understanding plant adaptation to drought is a crucial challenge under climate change.
36 This study aimed to investigate root traits and water use of grass populations exhibiting a range of dehydration
37 avoidance and tolerance strategies to cope with drought.

38 *Methods.* Sixteen populations of the perennial grass *Dactylis glomerata* originating from three biogeographical
39 origins (Northern, Temperate and Mediterranean) were grown in long tubes. Plant biomass, rooting depth and
40 morphological traits of deep roots were measured both under full irrigation and under severe drought. Water uptake
41 under drought was used as a proxy for dehydration avoidance. Plant survival after severe drought was a measure
42 of dehydration tolerance.

43 *Results.* All populations had similar maximum rooting depth and specific root length. Compared to Northern and
44 Temperate populations, Mediterranean populations had half total and deep root biomass but thinner and denser deep
45 roots. They were less affected by drought. These traits were associated with less water uptake (lower dehydration
46 avoidance) but greater survival to severe drought (enhanced dehydration tolerance).

47 *Conclusion.* The intraspecific variability in root traits revealed a trade-off between dehydration avoidance and
48 dehydration tolerance which illustrates contrasting adaptive plant and root strategies associated with the
49 biogeographical origins of populations.

50

51

52 **Key words:** cocksfoot; orchardgrass, drought; functional trade-off; intraspecific variability; root traits; plant
53 strategies; water acquisition.

54

55 INTRODUCTION

56 According to several climatic models, drought risk will dramatically increase during the century (Dai 2011;
57 Sherwood and Fu 2014). Improving our understanding of the adaptive mechanisms underlying the response of
58 wild and cultivated plant species to drought is a priority research avenue in both ecology and agronomy (e.g.,
59 Volaire et al., 2014; Kooyers, 2015).

60 To cope with drought, plants exhibit a range of physiological strategies that are defined as combinations
61 of mechanistically linked responses and traits that lead to a particular type of behavior during a period of water
62 deficit (Ludlow, 1989). Under moderate drought, a ‘dehydration avoidance’ strategy is expected, with plants
63 characterized by roots able to reach moisture, and thereby to sustain growth (Brown et al. 2005). In this case, the
64 main mechanism to maintain enough tissue water content for turgor is based on the optimization of water uptake,
65 notably through a deep and efficient root system (Garwood and Sinclair 1979; Comas et al. 2013). Under more
66 severe drought, a ‘dehydration tolerance’ strategy is linked to the maximization of the probability of survival rather
67 than maintenance of growth rate (Levitt, 1972; Levitt *et al.*, 1980). As such, plants display low tissue water content
68 and preserve cells of surviving organs such as meristems from critical dehydration consequences by osmotic
69 adjustment (West and Wullschleger 1990). In addition, under chronic severe summer droughts (e.g., around the
70 Mediterranean Basin: Volaire et al. 2009), some perennial herbaceous plants exhibit a summer dormancy strategy
71 that enhances their dehydration tolerance (Voltaire and Norton, 2006; Gillespie and Voltaire, 2017). However the
72 role of root traits in regulating these strategies has been little examined (Zwicke *et al.*, 2015). Measuring
73 dehydration avoidance as the ability of plants to extract soil water during a drought and dehydration tolerance as
74 the ability of plants to survive at a low soil water content (Voltaire et al., 2014), the present study aims to investigate
75 whether root traits and plant water use significantly differ among plants that exhibit a range of dehydration
76 avoidance and tolerance.

77 The adaptive meaning of plant traits to drought can be usefully explored through the link between eco-
78 physiological and ecological strategies (Voltaire, 2018). As a general pattern, resource poor environments are likely
79 to select for plants characterized by resource conservation strategies and ‘slow traits’, i.e. traits associated with
80 slow growth rate, while resource rich environments select for opposite strategies, so-called resource acquisition
81 strategies and ‘fast’ traits (Reich 2014). This framework identified root traits associated to water acquisition to
82 tradeoff with root traits associated with water conservation (Prieto et al. 2015; Weemstra et al. 2016; Roumet et
83 al. 2016; Fort et al. 2017). As a general rule, water acquisitive plants are expected to exhibit a deep root system
84 with low carbon investment (i.e., high specific root length, low root tissue density, and small diameter; e.g., White
85 and Snow, 2012; Freschet et al., 2017) allowing extensive soil exploration. At the other extreme, water
86 conservative plants are expected to exhibit ‘slower traits’ such as thicker roots with high root tissue density,
87 associated with longer root life span (McCormack et al. 2012). As underlined in former studies (Hernández et al.
88 2010; Lelièvre et al. 2011; Pérez-Ramos et al. 2013; Zwicke et al. 2015; Balachowski et al. 2016), it is then
89 assumed that plants characterized by a dehydration avoidance strategy should have ‘faster’ root traits associated
90 with efficient water acquisition. Conversely, it is hypothesized that plants characterized by a dehydration tolerance
91 strategy should have ‘slower’ root traits associated with water conservation.

92 To investigate the response of plants to drought, latitudinal gradients are considered as natural laboratories
93 (De Frenne et al. 2013; Violle et al. 2014) since they allow comparing plants from contrasting environments.
94 Perennial herbaceous species are an interesting model to explore drought response strategies since their perennial
95 habit requires them to survive many successive years even under harsh conditions such as drought prone
96 environments. In addition, as they dominate most grassland ecosystems, they have developed adaptive strategies
97 to cope with different intensity and duration of droughts (Levitt 1980; Ludlow 1989; Turner 1997). The perennial
98 grass species *Dactylis glomerata* has a very broad biogeographic distribution across most of Eurasia and northern
99 Africa (Lumaret 1988; Borrill 1991). Previous work on this species showed a large intra-specific variability in
100 above-ground traits and seasonal growth potential using a range of populations of *D. glomerata* originating from
101 a large latitudinal gradient (Mediterranean to Scandinavia; Bristiel et al. 2018). Notably, the Mediterranean
102 populations were summer dormant and survived severe drought with thinner and more lignified leaves, while
103 Temperate and Northern populations were more summer active, drought sensitive with larger leaves. (Bristiel et
104 al., 2018). However, the intra-specific variability in root systems has not been described in this species, although
105 their large climate range likely relates to marked differences in root trait values and water use strategies.

106 In this study, sixteen populations of *D. glomerata* representative of three biogeographical origins
107 (Northern, Temperate and Mediterranean) were grown in long tubes. Plant biomass and root traits were measured
108 both under full irrigation and under severe experimental drought in order to investigate 1) the intraspecific
109 variability in plant and root traits among populations from the three biogeographic origins, 2) the response of these
110 traits to drought, 3) the relationships between traits and water use and finally 4) the relationship between
111 dehydration avoidance and dehydration tolerance. We focus on rooting depth and on traits of deep roots
112 (morphological traits, root mass and length densities), that have been little explored so far, since they are less
113 accessible although they drive water uptake from the deepest soil layers where water remains available for a longer
114 time during a severe drought (Maeght et al. 2013; Prieto et al. 2015; Fort et al. 2016, 2017). The water use during
115 the drought period was used as a proxy of dehydration avoidance. Plants were grown in 2 m long tubes in order to
116 determine rooting depth and deep root trait response to minimize rooting depth constraints. The biogeographic
117 origin of populations should be associated with contrasting root traits when plants grow under non-limiting water
118 supply while rooting depth and root biomass allocation are expected to increase under drought in order to enhance
119 water uptake. In addition, we assumed that root traits should be associated to water use. According to the root
120 economics framework (Roumet et al. 2016; Weemstra et al. 2016), ‘slow’ root traits such as a high root tissue
121 density and a low specific root length should result in low water uptake and therefore water conservation.
122 Conversely, ‘fast’ root traits, such as abundant and thin roots with high specific root length and low tissue density
123 would enhance water acquisition and dehydration avoidance. These relationships between root traits and water use
124 have rarely been explored using contrasting intra-specific populations. Ultimately, since populations originating
125 from Mediterranean drought prone environment are more dehydration tolerant than Temperate and Northern
126 populations less adapted to severe drought (Bristiel et al., 2018), a trade-off between dehydration avoidance and
127 dehydration tolerance might exist in *D. glomerata*.

128

129 MATERIAL AND METHODS

130 The experiments were carried out at the CNRS (Centre National de la Recherche Scientifique) experimental field
131 in Montpellier, southern France (43°38'N, 3°51'E, 100 m a.s.l.). The climate is Mediterranean subhumid (Daget,
132 1977), with cool to cold winters, frequent frosts in winter and severe water deficits in summer.

133 **Plant material**

134 Sixteen tetraploid populations of *Dactylis glomerata* L. (cocksfoot), were chosen from germplasm banks to be
135 representative of three biogeographical origins (Northern, Temperate and Mediterranean) within a large latitudinal
136 gradient (Norway to Morocco), with contrasting annual precipitation patterns ranging from 246 to 893 mm (Table
137 S1). They were therefore expected to express various adaptive strategies, particularly regarding water use (Cooper
138 1964; Eagles 1967, 1971).

139 **Experimental design**

140 Two experiments were carried out in order to determine the dehydration avoidance and dehydration tolerance of
141 the same *D. glomerata* populations.

142 **Dehydration avoidance experimentation: Long tube design**

143 Dehydration avoidance was assessed by determining the ability of the contrasting populations to take up water
144 under non-limiting rooting depth conditions (2 m long tubes). Long transparent PVC tubes (6 cm diameter, 2 m
145 long) were filled with 9 kg of substrate (75 % sand and 25 % local soil). The local soil is a clay loam with 2.8%
146 organic matter and pH 8.1. Water content of the substrate at field capacity and wilting point were 24.1 and 2.9 g
147 H₂O per 100 g⁻¹ dry soil respectively (measurements made on 3 replicates of substrate with standard saturation
148 under vacuum, at INRA Orléans, France). PVC tubes were directly filled (without transparent plastic containing
149 the soil) with three successive soil layers of decreasing density (density of 1.85, 1.70 and 1.6 g cm⁻³ respectively
150 from the bottom third to the top third of the column) to simulate a natural gradient of soil density with denser soil
151 at the bottom. They were covered with an opaque and insulating film to protect roots from solar radiation and
152 inclined at 25° to allow root development to be visible against the transparent tube wall (Fig 1). These 2 m long
153 tubes allowed the comparison of the maximum rooting depth of all populations since only one reached 197 cm at
154 the end of the experiment. The large tube volume (5.6 L) avoids a pot size effect on plant growth. Indeed according
155 to Poorter et al (2012) an appropriate pot size is one in which the total plant biomass does not exceed 1 g L⁻¹. In
156 our study at the end of experiment, the ratio between the total plant biomass and the pot volume was much lower
157 than this threshold: it ranged from 0.09 g L⁻¹ (Mediterranean populations) to 2.5 g L⁻¹ (Northern and Temperate
158 populations). However, the small diameter of the tubes may have constrained root architecture especially the lateral
159 and vertical root distribution and therefore may not reflect the distribution of roots in field soil (Hodgkinson et al.
160 2017). Despite these constraints, the tubes used remain appropriate for comparative studies.

161 Seeds from each *D. glomerata* population were sown in February 2013 and maintained fully irrigated and fertilized
162 in pots. On the 10th of February 2015 (day 0), one ramet of each population (with 5 cm root length and 5 cm shoot
163 length) was transplanted into each tube with 6 replicates per population (total of 96 tubes). Tubes were placed
164 outside and arranged as a randomized complete blocks, under a transparent roof to avoid natural precipitation and
165 allow the experimental control of water supply (Fig. 1a). During the experiment, mean daily air temperature ranged
166 from 14.5 to 28.5°C while maximum temperature reached 35.2°C in July. Plants were grown under optimal

167 irrigation and fertilization for all populations during 5 months. On 5 June 2015 (day 114), when visible roots of
168 all populations reached 140 ± 18 cm, the foliage of each plant was cut at 3 cm from soil level to determine the
169 above-ground dry biomass (spring AGB, g DM plant⁻¹, weighed after oven dried at 65°C for 48h) before the onset
170 of the drought/irrigated summer treatments. The same day, all tubes were irrigated to field capacity (24.1%
171 gravimetric soil moisture). Then, the experimental treatments started: irrigation was stopped on half of the tubes
172 to simulate an intensifying drought, the other half of the tubes were kept fully irrigated, as a control treatment.

173 174 *Plant sampling*

175 On the 20th of July 2015 (day 159 and 45 days after the onset of the drought/irrigated summer treatments), when
176 full senescence of the foliage was reached for all populations, the whole soil column was carefully extracted from
177 each tube and placed horizontally on wire netting. Shoots of each plant were cut at root insertion, oven-dried at
178 65°C for 48h, and weighed, to determine the summer above-ground biomass (summer AGB, g DM plant⁻¹)
179 produced by plants after the onset of the drought/irrigated summer treatments. In order to characterize root biomass
180 distribution with depth, each soil column was divided into eight soil layers of 25 cm depth (Fig. 1b). Samples of
181 soil (without roots) were immediately collected for each 25 cm soil layer depth and weighed. These soil samples
182 were reweighed after oven-drying for 48 h at 105°C in order to obtain the soil water content of each soil layer. The
183 remaining soil was gently brushed away from roots, taking care not to disturb root depth distribution, to measure
184 the maximum rooting depth (cm). Roots of each soil layer were then carefully washed free of soil in water (Fig.
185 1c). Roots from the soil layer above the deepest soil layer including roots, were frozen into plastic bags filled with
186 water for further root morphological trait measurements (see Fig. 1, and the following section of material and
187 methods). All other root samples were oven-dried at 65°C for 48h and weighed.

188 At the whole plant level, the total root biomass was calculated as the sum of the root dry mass in each soil layer;
189 the root: shoot ratio was the ratio between total root biomass and total AGB (sum of spring and summer AGB);
190 the 95% rooting depth (cm), i.e. the soil depth that contains 95% of the total root biomass, was calculated according
191 to Schenk and Jackson (2002).

192 For the tubes that were not irrigated during 45 days, the total water used (Total WU; g H₂O day⁻¹ plant⁻¹) during
193 this period was used as a proxy of the 'dehydration avoidance'. This was calculated as the difference between the
194 initial soil water content in the tube at field capacity (soil volume exploited by roots x soil density x 24,1 g H₂O
195 per 100 g⁻¹ dry soil which is soil moisture at field capacity) and the remaining water in the soil explored by the
196 roots for each tube (soil volume exploited by roots x soil density x soil moisture measured once at the final
197 sampling on day 159). Similarly, the 'deep soil water use' (Deep soil WU; g H₂O day⁻¹ plant⁻¹) was calculated as
198 the difference between the initial soil water reserve at field capacity in the deep soil layers (100 cm- rooting
199 depth) and the remaining water in this layer of soil explored by the roots measured on day 159. Due to the small
200 column surface, and to the plant foliage covering most of the soil surface, even when plants were senescent at the
201 end of the drought, we assumed that atmospheric demand was similar for each tube allowing the comparison of
202 overall transpiration between populations.

203 Water use efficiency was not calculated since plants of the summer dormant Mediterranean populations have
204 senescent foliage even under irrigation in summer.

205 *Deep root trait measurements*

206 For each plant, root morphological traits were measured on deep roots from the last but one soil layer including
207 roots (n-1; Fig. 1b). We thus focused on deep roots that are localized in the moistest soil layers and avoided the
208 roots from the deepest soil layer (n) which were often not fully developed and composed of a single axis without
209 branching. The frozen root samples were thawed and a representative sub-sample of roots (one representative 10
210 cm root axis) was scanned in water at 600 dpi (Fig. 2). The resulting images were analyzed using WinRHIZO Pro
211 software (ver. 2009, Regent Instrument Inc., Quebec, Canada) to determine mean root diameter (mm), length (m)
212 and volume (cm³). Root volume was calculated by Winrhizo as the product of root length times π times the square
213 of root diameter/2, assuming a cylindrical shape of roots. After scanning, the sub-samples and the remaining roots
214 were oven-dried for 48 h at 65°C and weighed. On these deep roots scanned, a number of variables were calculated
215 for each root sub-samples: root tissue density (RTD; ratio of subsample root dry mass to rootvolume, g cm⁻³),
216 specific root length (SRL; ratio of root length to root dry mass g⁻¹) and mean root diameter (mm). Deep root
217 biomass (corresponding to the n-1 soil layer) was calculated as the sum of biomass of the scanned sub-sample and
218 remaining roots (g DM plant⁻¹), and deep root length density (RLD; m cm⁻³) as (SRL x deep root dry mass)/soil
219 layer volume.

220 **Dehydration tolerance experimentation: Short pot design**

221 To test for the existence of a trade-off between dehydration avoidance and dehydration tolerance, we used the data
222 from a previous study which measured dehydration tolerance on the same *D. glomerata* populations grown in short
223 pots by recording plant survival after a drought period (Bristiel et al., 2018). As roots were equally limited in depth
224 for all the populations in short pots, plant drought survival mirrored plant dehydration tolerance under a similar
225 soil water availability (Volaire 2008). It allowed us to discount the effect of rooting depth associated mainly with
226 dehydration avoidance (Volaire & Lelievre, 2001; Pérez-Ramos *et al.*, 2013). This experiment is briefly described
227 below.

228 In May, plants of each *D. glomerata* population were transplanted into 4L, 23 cm-high, 18cm-diameter pots (4
229 individuals per pot; 12 pots respectively per population) under an open-ended clear plastic tunnel and kept fully
230 irrigated and fertilized. Pots were filled with a substrate composed of 65% local loamy-clay soil and 35% compost.
231 In summer 2014, the soil moisture was raised to field capacity (60% soil moisture) and irrigation was ceased
232 thereafter. Pots were weighed every 2-5 days throughout the experiment to monitor the decrease in soil water
233 content. Once full leaf senescence was reached in all populations, and when soil water content in the pots decreased
234 to near 12% (27 to 35 days after irrigation cessation), plants were harvested at 3 cm height, then pots were
235 rehydrated, thus ending the severe drought. All pots were re-watered at the same soil water content to ensure that
236 plant survival corresponded to an identical final soil dehydration for all populations irrespective of their growth
237 potential. The plants were kept rehydrated for 15 days after which dehydration survival was measured. Plants that
238 had not produced new shoots after 15 days of rehydration were considered as dead. The survival rate was measured
239 as the number of living plants divided by the total number of plants and is a proxy for dehydration tolerance.

240

241 **Data analysis**

242 All statistical analyses were conducted using the R environment (version 0.99.879; RStudio Team, 2015). Linear
243 mixed models were used to estimate the effect of origin of *D. glomerata* (i.e., Northern, Temperate or
244 Mediterranean), treatment (irrigated versus drought), and their interaction, on total above-ground biomass, total
245 root biomass, root: shoot ratio, summer above-ground biomass, maximum rooting depth, 95% rooting depth, deep
246 root biomass, mean root diameter, root tissue density, specific root length, and root length density. The above-
247 ground biomass, root: shoot ratio, root tissue density, and root length density were log transformed, and total water
248 use and deep soil water use underwent an arcsin transformation to fit model requirements. Population accounted
249 for random effect. Linear models were followed by post-hoc tests using Tukey's correction for multiple
250 comparisons ('lsmeans' package; Lenth, 2016). Dehydration survival differences among origins were tested using
251 a non-parametric Kruskal-Wallis test followed by post-hoc comparisons ('kruskalmc' in 'pgirmess' package;
252 Siegel and Castellan, 1988). Bivariate correlations among traits were calculated using Pearson's correlation tests.

253 A principal component analysis (PCA; 'ade4' package) was performed using eight variables measured on
254 irrigated plants: total above-ground biomass and seven root traits (total root biomass, deep root biomass, maximum
255 root depth, root tissue density, specific root length, root length density, root diameter). Total water use and deep
256 soil water use that were measured under drought were used as supplementary variables in the PCA. The
257 relationship between total water use in long tubes (used as a proxy of dehydration avoidance) and drought survival
258 in short pots (dehydration tolerance) was explored to quantify a possible trade-off between the two strategies of
259 dehydration avoidance and tolerance in these species.

260 **RESULTS**

261 *Intraspecific variability under summer irrigation*

262 Under full summer irrigation, the sixteen populations of *D. glomerata* exhibited a large range of above-ground and
263 root trait values (Fig. 3; Table S2). The total above-ground biomass ranged from 0.69 g to 3.20 g DM plant⁻¹ (Fig.
264 3A) while total root biomass ranged from 1.68 to 5.97 g DM plant⁻¹ (Fig. 3B; Table S2). The maximum rooting
265 depth ranged from 160 to 197 cm and the 95% rooting depth varied from 115 to 161 cm (Fig. 3E, F; Table S2).
266 The root tissue density of deep roots, varied 3.5 fold among populations and their specific root length ranged from
267 115 to 429 m g⁻¹ (Fig. 3I, J; Table S2).

268 As a general pattern, under full summer irrigation, Mediterranean populations differed from both Northern and
269 Temperate populations (Fig. 3). Mediterranean populations produced significantly less above-ground biomass
270 (total and in summer) and lower root biomass (approximately 54% less), resulting in a root: shoot ratio double
271 that of the other populations (Fig. 3A, B, C, D). The very low summer above-ground biomass under irrigation of
272 Mediterranean populations confirmed that these populations were summer dormant (Fig. 4D). Their root biomass
273 and root length density in deep soil layers were also 2.4 and 2 times lower respectively (Fig. 3G, K). Deep roots
274 of Mediterranean populations had a 16% lower mean diameter but double the tissue density (Fig. 3H, I) of both
275 Northern and Temperate populations. However, the maximum rooting depth and specific root length were similar
276 across all origins (Fig. 3E, J).

277 *Response to drought*

278 Moisture deficit affected above-ground and root traits differently according to the population of *D. glomerata*
279 considered (Fig. S1, S2) and to their origin as illustrated by the significant origin x treatment interactions detected
280 for 7 of the eleven traits studied (Table 1). The Northern and Temperate populations were more affected by drought
281 than Mediterranean populations (Fig. 4). In comparison to irrigated plants, the overall growth of plants of
282 Temperate and Northern populations was reduced under drought. They showed a greater root: shoot ratio (Fig 4C).
283 Their above-ground biomass in summer was markedly reduced (26% on average; Fig 4D) as a response of foliage
284 senescence; they also showed lower 95% rooting depth (minus 16 cm on average; Fig. 4F) as compared to irrigated
285 plants. Conversely, the root: shoot ratio, summer above-ground biomass and 95% rooting depth of Mediterranean
286 populations were not affected by drought (Fig. 4C, D, F). Overall, the total and deep root biomass and the
287 maximum rooting depth of the three population origin groups were not affected by drought (Fig. 4B, E). Deep root
288 morphological traits (root tissue density, specific root length as well as the root length density) were unaffected by
289 drought across all origins except the mean root diameter of Temperate populations which was 0.04 mm less under
290 drought (Fig. 4 H).

291 *Water use under drought*

292 The total water use (Fig. 5A), used here as a proxy for dehydration avoidance, as well as the deep soil water use
293 (Fig. 5B) were significantly lower in Mediterranean populations which took up 12 % less water during the drought
294 period than the Northern and Temperate populations.

295 The PCA performed on plant traits measured under irrigation and with total and deep soil water use under drought
296 as supplementary variables (Fig. 6), captured 72.5% of the total variance in the first two axes (56.4% on the first
297 axis). The first PC axis opposed Mediterranean populations with high root: shoot ratio and root tissue density to
298 both Northern and Temperate populations which had higher summer above-ground and root biomasses, higher
299 root length density and larger root diameter, associated with higher water consumption under drought (high water
300 use). The second PC axis (PC2: 16.1%) which opposed the specific root length on one side and the maximum root
301 depth on the other side, did not discriminate populations according to their origin. The total water use measured
302 under drought was positively correlated with above-ground biomass, total and deep root biomass, mean deep root
303 diameter, and root length density, and negatively correlated with the root: shoot ratio, maximum root depth and
304 root tissue density, all measured under irrigation (Table S3). The relationships between the total water use and
305 traits both measured under drought showed similar patterns but stronger relationships. Interestingly, the
306 relationship between total water use measured under drought and maximum root depth was negative when
307 maximum root depth was measured under irrigation but non-significant when measured under drought (Table S3).

308 *Relationship between total water use during drought (dehydration avoidance) and drought survival (dehydration* 309 *tolerance)*

310 The dehydration tolerance measured by the plant survival after severe drought in short pots, was on average 3 fold
311 higher for Mediterranean populations of *D. glomerata* than for both Northern and Temperate populations (Fig. S3;
312 Bristiel et al. 2018). It was strongly negatively related ($r=-0.82$, $P < 0.001$) to the dehydration avoidance estimated
313 by the total water use measured under drought in long tubes (Fig. 7). Figure 7 also showed that Mediterranean
314 populations of *D. glomerata* expressed a lower water use but a higher dehydration tolerance after severe drought
315 as compared to Northern and Temperate populations.

316

317 **DISCUSSION**

318 When grown in deep soil in tubes and under irrigation, the sixteen populations of *D. glomerata* showed
319 considerable variation in root traits. We identified marked trait variation between origins, with Mediterranean
320 populations showing highly contrasting traits as compared to both Northern and Temperate populations.
321 Mediterranean populations of *D. glomerata* were characterized by a lower plant biomass, a higher root: shoot ratio,
322 and thinner deep roots with a higher tissue density than Northern and Temperate populations. This suite of traits
323 was associated with a lower water use and therefore a lower dehydration avoidance although Mediterranean
324 populations exhibited a higher dehydration tolerance when they were subjected to severe drought in short pots.

325

326 **Variability in plant traits among populations from different biogeographic origins**

327 The reduced aerial growth and early leaf senescence induced by summer dormancy in Mediterranean populations
328 even under irrigation, contribute to reduce plant evapotranspiration rate, and thereby soil water uptake (Volaire et
329 al. 1998; Pérez-Ramos et al. 2013; Volaire 2018). Interestingly, Mediterranean populations of *D. glomerata* had
330 a similar maximum rooting depth both in irrigated and drought conditions and their root mass and length densities
331 in deep soil layers were much lower than those of Northern and Temperate populations. This genetic difference
332 was unexpected since rooting depth comparisons between species across ecosystems showed that dry
333 environments select for deeper root systems than wetlands (Canadell et al. 1996; Jackson et al. 1996; Schenk and
334 Jackson 2002, 2005; Collins and Bras 2007). A deep root system is assumed to promote water uptake by allowing
335 the roots to collect the resource where it still remains in the deepest soil layers, enhancing growth and drought
336 resilience (Ho et al. 2005; Nardini et al. 2016; Yang et al. 2017). Further, even a small proportion of roots in deep
337 and moist soil layers may be sufficient to sustain water absorption (Jackson et al. 1996; Nicotra et al. 2002). In
338 another perennial grass (*Phalaris aquatica*), which exhibits summer dormancy like Mediterranean populations of
339 *D. glomerata* used in this study, a deep root system was crucial for dehydration tolerance and plant survival since
340 plants died when roots were severed (McWilliam and Kramer 1968). In Mediterranean populations of *D.*
341 *glomerata*, increasing the root: shoot ratio and decreasing the shoot transpiration requirements rather than foraging
342 deeper underground appears to be the preferred strategy. Moreover, the clearest difference in deep root morphology
343 between Mediterranean populations and Northern and Temperate populations of *D. glomerata* was in their higher
344 root tissue density. A high root tissue density has also been found in plants grown under stressful, resource poor
345 environments (Craine et al. 2001; Kramer-Walter et al. 2016; Ostonen et al. 2017), at high latitude (Ostonen et al.
346 2017), and at high mean annual temperature (Freschet et al. 2017). Higher root tissue density might be due to
347 narrower, more numerous xylem vessels (Wahl and Ryser 2000; Hummel et al. 2007) and higher lignification
348 conferring a greater longevity (Ryser 1996) and drought resistance (Wahl and Ryser 2000; Fitter 2002), although
349 it might negatively impact their hydraulic conductivity (Mapfumo et al. 1993). Deep roots of Mediterranean
350 populations were also thinner than those of Northern and Temperate populations, although the opposite pattern
351 has been observed both within three woody species located along a latitudinal gradient from temperate to subarctic
352 boreal forest (latitudes 48°N and 69°N) (Ostonen et al. 2017) and among 1115 species from contrasting growth
353 forms and climatic areas (Freschet et al. 2017) in which mean root diameter, often measured on shallow roots,

354 increased with increasing mean annual temperature. In our study, the thinner roots of the Mediterranean
355 populations might allow extensive soil exploration for water per unit of biomass invested, with low biomass
356 investment, efficient hydraulic conductance (Hernández et al. 2010; Comas et al. 2012) and a higher resistance to
357 embolism of roots with smaller xylem vessel diameter (Fitter 1987; Alameda and Villar 2012). Although they
358 were thinner and had a higher tissue density, deep roots of the Mediterranean populations of *D. glomerata* had
359 similar specific root length (SRL) than those of Northern and Temperate populations. The unforeseen association
360 of thin but dense roots in Mediterranean populations and thick roots with low tissue density in Northern and
361 Temperate populations blurred variations in SRL in this study. As a consequence, variation of SRL among
362 populations was independent from variation of root tissue density and mean root diameter, as already reported for
363 seedlings of 66 tree species (Kramer-Walter et al., 2016). Conversely, the root system of Northern and Temperate
364 populations was characterized by greater root biomass and deeper roots with lower tissue density. These trait
365 values can be associated with wider vessels and higher hydraulic conductivity, but also to higher vulnerability to
366 drought-induced embolism (McElrone et al. 2004; Wang et al. 2016). Although with a lower root: shoot ratio than
367 Mediterranean populations, the greater deep root length density of Northern and Temperate populations reflected
368 a ‘water acquisitive’ root trait strategy conferring greater ability to collect soil resources, notably water, as long as
369 it remains accessible (Lobet et al. 2014).

370

371 **Response of plant traits to experimental drought**

372 Compared to Mediterranean populations, the Northern and Temperate populations were more affected by drought
373 with a decrease of above-ground biomass, and an increase in root: shoot ratio. This is a well-known response to
374 drought that allows plants to improve water foraging capacity ((Skinner and Comas 2010; Olmo et al. 2014;
375 Markesteijn and Poorter 2009). Northern and Temperate populations also had more shallow roots (lower 95%
376 rooting depth) under drought than the control irrigated plants. The opposite pattern has been observed for different
377 species, for which drought stress increased the proportion of deep roots compared to controls (Padilla and Pugnaire
378 2007; Skinner and Comas 2010; Olmo et al. 2014). Surprisingly, drought did not affect the values of any deep root
379 morphological traits. Two reviews (Ostonen et al. 2007; Olmo et al. 2014) also reported no clear effect of drought
380 on specific root length (SRL), but rather a great variability in the SRL response across species due to the contrasting
381 response of the two components of SRL, i.e. the root tissue density (RTD) and the mean root diameter. In many
382 studies, drought was associated with a greater RTD but a lower root diameter leading to a nil effect of drought on
383 SRL. In our growth conditions, root morphological traits of the populations of *D. glomerata* are less plastic than
384 in other species, maybe because we measured root traits in deep soil layers whereas they are more commonly
385 measured in the driest shallow soil layers. In Mediterranean populations, the lack of response of above-ground and
386 root traits to drought might be associated with summer dormancy and suggests that these populations are
387 genetically adapted to severe drought, which contributes to prevent opportunistic plant re-growth after episodic
388 summer rain, which may be fatal to the non-adapted plant under severe extended drought (Laude 1953; Norton et
389 al. 2009).

390 **Relationships between water use under drought and plant traits**

391 The total water use under drought was closely related to plant traits measured both under irrigation and under
392 drought. In both cases, water use was positively correlated with the summer above-ground biomass and thus the
393 evaporative demand during the drought period. Greater water use was also positively related to the capacity of
394 roots to acquire water especially in deep soil layers (deep soil water use). Both total and deep water use increased
395 with greater root biomass and root length densities in deep soil layers and with thicker deep roots but not with
396 deeper root systems. Conversely, lower water use was associated with high root: shoot ratios and high root tissue
397 density, two traits related to resistance to drought and root longevity and thus to resource conservation in long
398 lived tissues. These relationships confirm those obtained on twelve Mediterranean rangeland species grown in a
399 common garden experiment (Fort et al. 2017). The first PC axis thus opposed traits related to water acquisition
400 and those related to resource conservation. Contrary to the conceptual root economics framework (Roumet et al.
401 2016; Weemstra et al. 2016) suggesting that a high rate of soil resource acquisition is associated with high SRL
402 (fine roots with low tissue density) this study showed that at the intraspecific level, plants with coarser roots can
403 take up more water than plants with thinner roots. In addition, SRL and maximum rooting depth were unrelated to
404 water use and independent from the water acquisition - conservation axis. This questions the role of SRL for water
405 acquisition and suggests that root diameter and root tissue density are better predictors of plant water use than SRL
406 or maximum root depth for *D. glomerata* at intraspecific level.

407 **A trade-off between dehydration avoidance and dehydration tolerance**

408 This study shows that the populations of *D. glomerata* that best tolerate dehydration, by surviving well at low soil
409 water content under similar access to water in short pots, take up less water when this resource is accessible in
410 long tubes. These results highlight that, at the intraspecific level, a strong trade-off exists between dehydration
411 tolerance and dehydration avoidance strategies. The dehydration tolerance strategy can mainly be associated with
412 some water conservative ('slow') root traits values while the dehydration avoidance can mainly be associated to
413 water acquisitive ('fast') root traits values (Reich, 2014). Although counterintuitive, these results confirm our
414 hypothesis that populations that invest least in water acquisition, survive water stress better when the soil water
415 resource is limited. Former studies have also shown that plants exhibiting fast above-ground growth rate during a
416 drought period also expressed low dehydration tolerance (Pearson et al., 2003; Volaire et al., 2014; Benavides et
417 al., 2015; Bristiel et al. 2018). Above-ground, 'fast' traits (Reich 2014) are associated with poor survival of
418 environmental stress. This study revealed the same pattern below ground, underlining that, in *D. glomerata*, root
419 traits favoring access to water do not primarily contribute to dehydration tolerance. In their natural environments,
420 Northern and Temperate populations of *D. glomerata* have developed a root strategy to uptake water, avoid
421 dehydration and keep the plant growing under the moderate droughts they typically face. In contrast, within the
422 same species, the Mediterranean populations have developed summer dormancy, dehydration tolerance and deep
423 roots with high tissue density to maintain a minimum water uptake to sustain plant survival under chronic, intense
424 and extended summer droughts.

425 Finally, this exploration of plant and root traits of a range of populations of *D. glomerata* grown in long tubes
426 showed that all traits except specific root length and maximum rooting depth discriminated the populations
427 according to their biogeographical origins.

428 In the field, rooting depth was similar within a few summer dormant and summer active cultivars of *D. glomerata*
429 (Lelièvre et al. 2011; Barkaoui et al. 2016). Summer dormant Mediterranean populations outperformed Temperate
430 populations for survival to severe drought in deep soils and for all tested climate scenarios (Poirier et al. 2012).
431 Our results showing that Northern and Temperate populations exhibit root traits associated with dehydration
432 avoidance tend to confirm that this strategy is not adapted to limit plant mortality under severe drought in shallow
433 soils. Conversely, dehydration tolerance associated with lower water use during a drought, can be the most efficient
434 strategy to promote drought survival (Norton et al. 2014). This pattern should be tested further on more populations
435 and species in order to select traits in the context of greater occurrence of intense drought under climate change.

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443 CONSTRAINTS].
444

- 445 Alameda D, Villar R (2012) Linking root traits to plant physiology and growth in *Fraxinus angustifolia* Vahl.
446 seedlings under soil compaction conditions. *Environ Exp Bot* 79:49–57.
- 447 Balachowski JA, Bristiel PM, Volaire FA (2016) Summer dormancy, drought survival and functional resource
448 acquisition strategies in California perennial grasses. *Ann Bot* 118:357–368. doi: 10.1093/aob/mcw109
- 449 Barkaoui K, Roumet C, Volaire F (2016) Mean root trait more than root trait diversity determines drought
450 resilience in native and cultivated Mediterranean grass mixtures. *Agric Ecosyst Environ*. doi:
451 10.1016/j.agee.2016.06.035
- 452 Benavides R, Escudero A, Coll L, et al (2015) Survival vs. growth trade-off in early recruitment challenges
453 global warming impacts on mountain trees. *Perspect Plant Ecol Evol Syst* 17:369–378. doi:
454 10.1016/j.ppees.2015.06.004
- 455 Bohnert HJ, Nelson DE, Jensen RJ (1995) Adaptations to Environmental Stresses. *Plant Cell* 7:1099–1111. doi:
456 10.1105/tpc.7.7.1099
- 457 Borrill M (1991) Evolution and genetic resources in cocksfoot. In: Tushiya & Gupta (ed) *Chromosome*
458 *Engineering in Plants: Genetics, Breeding, Evolution, Part B*. Elsevier Science Publishers, pp 379–398
- 459 Bristiel P., Gillespie L., Østrem L, Balachowski J., Violle C., Volaire F. (2018) Experimental evaluation of the
460 robustness of the growth-stress tolerance trade-off within the perennial grass *Dactylis glomerata*.
461 *Functional Ecology* 32: 1944–1958. DOI: 10.1111/1365-2435.13112
- 462 Brouwer R (1963) Some aspects of the equilibrium between overground and underground plant parts. *Meded*
463 *van het Inst voor Biol en Scheikd Onderz van Landbouwgewassen* 213:31–39.
- 464 Brown H, Moot D, Pollock K (2005) Herbage production, persistence, nutritive characteristics and water use of
465 perennial forages grown over 6 years on a Wakanui silt loam. *New Zeal J Agric Res* 48:423–439. doi:
466 10.1080/00288233.2005.9513677
- 467 Canadell J, Jackson RB, Ehleringer JB, et al (1996) Maximum rooting depth of vegetation types at the global
468 scale. *Oecologia* 108:583–595. doi: 10.1007/BF00329030
- 469 Collins DBG, Bras RL (2007) Plant rooting strategies in water-limited ecosystems. *Water Resour Res* 43:1–10.
470 doi: 10.1029/2006WR005541
- 471 Comas LH, Becker SR, Cruz VM V, et al (2013) Root traits contributing to plant productivity under drought.
472 *Front Plant Sci* 4:442. doi: 10.3389/fpls.2013.00442
- 473 Comas LH, Mueller KE, Taylor LL, et al (2012) Evolutionary Patterns and Biogeochemical Significance of
474 Angiosperm Root Traits. *Int J Plant Sci* 173:584–595. doi: 10.1086/665823
- 475 Cooper JP (1964) Climatic variation in forage grasses I. *J Appl Ecol* 1:45–61.
- 476 Craine JM, Froehle J, Tilman DG, et al (2001) The relationships among root and leaf traits of 76 grassland

477 species and relative abundance along fertility and disturbance gradients. *Oikos* 93:274–285. doi:
478 10.1034/j.1600-0706.2001.930210x

479 Daget P (1977) Le bioclimat méditerranéen: caractères généraux, modes de
480 caractérisation. *Vegetatio* 34: 1–20.

481 Dai A (2011) Drought under global warming: A review. *Wiley Interdiscip Rev Clim Chang* 2:45–65. doi:
482 10.1002/wcc.81

483 De Frenne P, Graae BJ, Rodriguez-Sanchez F, et al (2013) Latitudinal gradients as natural laboratories to infer
484 species' responses to temperature. *J Ecol* 101:784–795. doi: 10.1111/1365-2745.12074

485 Eagles CF (1967) The effect of temperature on vegetative growth in climatic races of *Dactylis glomerata* in
486 controlled environments. *Ann Bot* 31:31–39.

487 Eagles CF (1971) Effect of photoperiod on vegetative growth in two natural populations of *Dactylis glomerata* L.
488 *Ann Bot* 35:75–86.

489 Fitter A (2002) Characteristics and Functions of Root Systems. In: Waisel Y, Eschel A, Kafkafi U (eds) *Plant*
490 *Roots, The hidden half, Third Edit.* CRC Press, New York, pp 15–32

491 Fitter AH (1987) An Architectural Approach To The Comparative Ecology Of Plant Root Systems. *New Phytol*
492 106:61–77. doi: 10.1111/j.1469-8137.1987.tb04683.x

493 Fort F, Cruz P, Lecloux E, et al (2016) Grassland root functional parameters vary according to a community-
494 level resource acquisition-conservation trade-off. *J Veg Sci* 27:749–758. doi: 10.1111/jvs.12405

495 Fort F, Volaire F, Guillioni L, et al (2017) Root traits are related to plant water-use among rangeland
496 Mediterranean species. *Funct Ecol*. doi: 10.1111/1365-2435.12888

497 Freschet GT, Valverde-Barrantes OJ, Tucker CM, et al (2017) Climate, soil and plant functional types as drivers
498 of global fine-root trait variation. *J Ecol* 1–15. doi: 10.1111/1365-2745.12769

499 Garwood EA, Sinclair J (1979) Use of water by six grass species. 2. Root distribution and use of soil water. *J*
500 *Agric Sci* 93:25. doi: 10.1017/S0021859600086081

501 Gillepsie L, Volaire F (2017) Are winter and summer dormancy symmetrical seasonal adaptive strategies? The
502 case of temperate herbaceous perennials. *Ann. Bot.* 119: 311-323, doi:10.1093/aob/mcw264

503 Hernández EI, Vilagrosa A, Pausas JG, Bellot J (2010) Morphological traits and water use strategies in seedlings
504 of Mediterranean coexisting species. *Plant Ecol* 207:233–244. doi: 10.1007/s11258-009-9668-2

505 Hodgkinson L, Dodd IC, Binley A, Ashton RW, White RP, Watts CW, Whalley WR. (2017). Root growth in
506 field-grown winter wheat: Some effects of soil conditions, season and genotype. *European Journal of*
507 *Agronomy*, 91: 74-83.
508

509 Ho MD, Rosas JC, Brown KM, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus
510 acquisition. *Funct Plant Biol* 32:737. doi: 10.1071/FP05043

511 Hummel I, Vile D, Violle C, Devaux J, Ricci B., Blanchard A, Garnier E, Roumet C (2007). Relating root
512 structure and anatomy to whole plant functioning in 14 herbaceous Mediterranean species. *New Phytologist*,
513 173: 313-321.

514 Jackson RB, Canadell J, Ehleringer JR, et al (1996) International Association for Ecology A Global Analysis of
515 Root Distributions for Terrestrial Biomes A global analysis of root distributions for terrestrial biomes.
516 Source: *Oecologia* 108:389–411. doi: 10.1007/BF00333714

517 Kooyers NJ (2015) The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Sci*
518 234:155–62. doi: 10.1016/j.plantsci.2015.02.012

519 Kramer-Walter KR, Bellingham PJ, Millar TR, et al (2016) Root traits are multidimensional: specific root length
520 is independent from root tissue density and the plant economic spectrum. *J Ecol* 104:1299–1310. doi:
521 10.1111/1365-2745.12562

522 Laude HM (1953) The Nature of Summer Dormancy in Perennial Grasses. *Bot Gaz* 114:284–292. doi:
523 10.1086/335770

524 Lelièvre F, Seddaiu G, Ledda L, et al (2011) Water use efficiency and drought survival in Mediterranean
525 perennial forage grasses. *F Crop Res* 121:333–342. doi: 10.1016/j.fcr.2010.12.023

526 Lenth R V. (2016) Least-Squares Means: The *R* Package **lsmeans**. *J Stat Softw*. doi: 10.18637/jss.v069.i01

527 Levitt J (Jacob) (1980) Responses of plants to environmental stresses. Academic Press

528 Li H, Liu B, McCormack ML, Ma Z, Guo D. (2017), Diverse belowground resource strategies underlie plant
529 species coexistence and spatial distribution in three grasslands along a precipitation gradient. *New Phytol*,
530 216: 1140-1150.

531 Lobet G, Couvreur V, Meunier F, et al (2014) Plant Water Uptake in Drying Soils. *Plant Physiol* 164:1619–
532 1627. doi: 10.1104/pp.113.233486

533 Ludlow MM (1989) Strategies of response to water stress. *Struct. Funct. Responses to Environ. Stress* 269–81.

534 Lumaret R (1988) Cytology, genetics, and evolution in the genus *Dactylis*. *CRC Crit Rev Plant Sci* 7:55–91.

535 Maeght J-L, Rewald B, Pierret A (2013) How to study deep roots-and why it matters. *Front Plant Sci* 4:299. doi:
536 10.3389/fpls.2013.00299

537 Malik RS, Dhankar JS, Turner NC (1979) Influence of soil water deficits on root growth of cotton seedlings.
538 *Plant Soil* 115:109–115.

539 Mapfumo E, Aspinwall D, Hancock T, Sedgley M (1993) Xylem development in relation to water uptake by

540 roots of grapevine (*Vitis vinifera* L.). *New Phytol* 125:93–99. doi: 10.1111/j.1469-8137.1993.tb03867.x

541 Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in
542 relation to drought- and shade-tolerance. *J Ecol* 97:311–325. doi: 10.1111/j.1365-2745.2008.01466.x

543 McCormack LM, Adams TS, Smithwick EAH, Eissenstat DM (2012) Predicting fine root lifespan from plant
544 functional traits in temperate trees. *New Phytol* 195:823–831. doi: 10.1111/j.1469-8137.2012.04198.x

545 Mcelrone AJ, Pockman WT, Martínez-vilalta J, et al (2004) Variation in xylem structure and function in stems
546 and roots. *New Phytol* 163:507–517.

547 McWilliam J, Kramer P (1968) The nature of the perennial response in Mediterranean grasses. I. Water relations
548 and summer survival in *Phalaris*. *Aust J Agric Res* 19:381. doi: 10.1071/AR9680381

549 Nardini A, Casolo V, Dal Borgo A, et al (2016) Rooting depth, water relations and non-structural carbohydrate
550 dynamics in three woody angiosperms differentially affected by an extreme summer drought. *Plant, Cell*
551 *Environ* 39:618–627. doi: 10.1111/pce.12646

552 Nicotra A, Babicka N, Westoby M (2002) Seedling root anatomy and morphology: an examination of ecological
553 differentiation with rainfall using phylogenetically independent contrasts. *Oecologia* 130:136–145. doi:
554 10.1007/s004420100788

555 Norton MRA, Lelièvre FB, Volaire FB (2014) Measuring dehydration tolerance in pasture grasses to improve
556 drought survival. *Crop Pasture Sci* 65:828–840.

557 Norton MR, Volaire F, Lelièvre F, Fukai S (2009) Identification and measurement of summer dormancy in
558 temperate perennial grasses. *Crop Sci* 49:2347–2352. doi: 10.2135/cropsci2009.06.0319

559 Olmo M, Lopez-Iglesias B, Villar R (2014) Drought changes the structure and elemental composition of very
560 fine roots in seedlings of ten woody tree species. Implications for a drier climate. *Plant Soil* 384:113–129.
561 doi: 10.1007/s11104-014-2178-6

562 Ostonen I, Lohmus K, Helmisaari H-S, et al (2007) Fine root morphological adaptations in Scots pine, Norway
563 spruce and silver birch along a latitudinal gradient in boreal forests. *Tree Physiol* 27:1627–1634. doi:
564 10.1093/treephys/27.11.1627

565 Ostonen I, Truu M, Helmisaari H-S, et al (2017) Adaptive root foraging strategies along a boreal-temperate
566 forest gradient. *New Phytol* 215:977–991. doi: 10.1111/nph.14643

567 Padilla FM, Pugnaire FI (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival
568 during drought. *Funct Ecol* 21:489–495. doi: 10.1111/j.1365-2435.2007.01267.x

569 Pearson TRH, Burslem DFRP, Goeriz RE, Dalling JW (2003) Regeneration niche partitioning in neotropical
570 pioneers: Effects of gap size, seasonal drought and herbivory on growth and survival. *Oecologia* 137:456–
571 465. doi: 10.1007/s00442-003-1361-x

572 Pérez-Ramos IM, Volaire F, Fattet M, et al (2013) Tradeoffs between functional strategies for resource-use and
573 drought-survival in Mediterranean rangeland species. *Environ Exp Bot* 87:126–136. doi:
574 10.1016/j.envexpbot.2012.09.004

575 Poirier M, Durand J-LL, Volaire F (2012) Persistence and production of perennial grasses under water deficits
576 and extreme temperatures: Importance of intraspecific vs. interspecific variability. *Glob Chang Biol*
577 18:3632–3646. doi: 10.1111/j.1365-2486.2012.02800.x

578 Poorter H, Fiorani F, Stitt M, Schurr U, Finck A, Gibon Y, Usadel B, Munns R, Atkin OK, Tardieu F, Pons TL.
579 (2012) The art of growing plants for experimental purposes: a practical guide for the plant biologist
580 Review. *Functional Plant Biology*, 39: 821-838.
581

582 Prieto I, Roumet C, Cardinael R, et al (2015) Root functional parameters along a land-use gradient: Evidence of
583 a community-level economics spectrum. *J Ecol* 103:361–373. doi: 10.1111/1365-2745.12351

584 Reich PB (2014) The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *J Ecol* 102:275–301.
585 doi: 10.1111/1365-2745.12211

586 Roumet C, Birouste M, Picon-Cochard C, et al (2016) Root structure-function relationships in 74 species:
587 evidence of a root economics spectrum related to carbon economy. *New Phytol* 210:815–826. doi:
588 10.1111/nph.13828

589 Ryser P (1996) The Importance of Tissue Density for Growth and Life Span of Leaves and Roots: A
590 Comparison of Five Ecologically Contrasting Grasses. *Funct Ecol* 10:717. doi: 10.2307/2390506

591 Schenk HJ, Jackson RB (2002) The global biogeography of roots. *Ecol Monogr* 72:311–328. doi: 10.1890/0012-
592 9615(2002)072[0311:TGBOR]2.0.CO;2

593 Schenk HJ, Jackson RB (2005) Mapping the global distribution of deep roots in relation to climate and soil
594 characteristics. *Geoderma* 126:129–140. doi: 10.1016/j.geoderma.2004.11.018

595 Sherwood S, Fu Q (2014) A drier future ? *Science* (80-) 343:737–739.

596 Siegel S, Castellan NJ (1988) *Nonparametric statistics for the behavioral sciences*. McGraw-Hill

597 Skinner RH, Comas LH (2010) Root distribution of temperate forage species subjected to water and nitrogen
598 stress. *Crop Sci* 50:2178–2185. doi: 10.2135/cropsci2009.08.0461

599 Tjoelker MG, Craine JM, Wedin D, et al (2005) Linking leaf and root trait syndromes among 39 grassland and
600 savannah species. *New Phytol* 167:493–508. doi: 10.1111/j.1469-8137.2005.01428.x

601 Turner NC (1997) Further Progress in Crop Water Relations. *Adv Agron* 58:293–338. doi: 10.1016/S0065-
602 2113(08)60258-8

603 Violle C, Reich PB, Pacala SW, et al (2014) The emergence and promise of functional biogeography. *Proc Natl*
604 *Acad Sci* 111:13690–13696. doi: 10.1073/pnas.1415442111

605 Volaire F (2008) Plant traits and functional types to characterise drought survival of pluri-specific perennial
606 herbaceous swards in Mediterranean areas. *Eur J Agron* 29:116–124. doi: 10.1016/j.eja.2008.04.008

607 Volaire F. (2018) A unified framework for plant adaptive strategies to drought: across scales and disciplines.
608 *Global Change Biology*, 00:1-10. <https://doi.org/10.1111/gcb.14062>

609 Volaire F., Norton M. (2006) Summer dormancy in perennial temperate grasses. *Ann Bot* 98, 5: 927-933.

610 Volaire F, Barkaoui K, Norton M (2014) Designing resilient and sustainable grasslands for a drier future:
611 Adaptive strategies, functional traits and biotic interactions. *Eur J Agron* 52:81–89. doi:
612 10.1016/j.eja.2013.10.002

613 Volaire F, Norton MR, Lelièvre F (2009) Summer Drought Survival Strategies and Sustainability of Perennial
614 Temperate Forage Grasses in Mediterranean Areas. *Crop Sci* 49:2386. doi: 10.2135/cropsci2009.06.0317

615 Volaire F, Thomas H, Lelièvre F (1998) Survival and recovery of perennial forage grasses under prolonged
616 Mediterranean drought: I. Growth, death, water relations and solute content in herbage and stubble. *New*
617 *Phytol* 140:439–449. doi: 10.1046/j.1469-8137.1998.00288.x

618 Wahl S, Ryser P (2000) Root tissue structure is linked to ecological strategies of grasses. *New Phytol* 148:459–
619 471.

620 Wang Y, Dong X, Wang H, et al (2016) Root tip morphology, anatomy, chemistry and potential hydraulic
621 conductivity vary with soil depth in three temperate hardwood species. *Tree Physiol* 36:99–108. doi:
622 10.1093/treephys/tpv094

623 Weemstra M, Mommer L, Visser EJW, et al (2016) Towards a multidimensional root trait framework: a tree root
624 review. *New Phytol*. doi: 10.1111/nph.14003

625 West CP, Wullschleger SD (1990) Osmotic adjustment in tissues of tall fescue in response to water deficit.
626 *Environ Exp Bot* 30:149–156.

627 White TA, Snow VO (2012) A modelling analysis to identify plant traits for enhanced water-use efficiency of
628 pasture. *Crop Pasture Sci* 63:63–76. doi: 10.1071/CP11250

629 Yang F, Feng Z, Wang H, et al (2017) Deep soil water extraction helps to drought avoidance but shallow soil
630 water uptake during dry season controls the inter-annual variation in tree growth in four subtropical
631 plantations. *Agric For Meteorol* 234–235:106–114. doi: 10.1016/j.agrformet.2016.12.020

632 Zwicke M, Picon-Cochard C, Morvan-Bertrand A, et al (2015) What functional strategies drive drought survival
633 and recovery of perennial species from upland grassland? *Ann Bot* 116:1001–1015. doi:
634 10.1093/aob/mcv037

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640 Table 1. Results of linear mixed models testing the effect of origin, treatment (irrigated or drought) and their
 641 interaction on above ground and root variables of 16 populations of *Dactylis glomerata* from three climatic
 642 origins. The effect of origin on dehydration survival was tested using a Kruskal Wallis test.

| Model variables | Unit | Origin | | | | Treatment | | | Interaction | | |
|-----------------------------------|---|----------|------|----------|----------|-----------|----------|----------|-------------|----------|----------|
| | | <i>n</i> | d.f. | <i>F</i> | <i>P</i> | d.f. | <i>F</i> | <i>P</i> | d.f. | <i>F</i> | <i>P</i> |
| Total above ground biomass (log) | g DM plant ⁻¹ | 95 | 2 | 149,1 | <0.001 | 1 | 19,2 | <0.001 | 2 | 5,1 | 0,008 |
| Total root biomass | g DM plant ⁻¹ | 95 | 2 | 31,2 | <0.001 | 1 | 0,1 | 0,80 | 2 | 3,8 | 0,02 |
| Root : shoot (log) | - | 95 | 2 | 45,3 | <0.001 | 1 | 30,2 | <0.001 | 2 | 0,2 | 0,76 |
| Summer above ground biomass (log) | g DM plant ⁻¹ | 95 | 2 | 59,4 | <0.001 | 1 | 15,2 | <0.001 | 2 | 6,0 | 0,003 |
| Maximum root depth | cm | 95 | 2 | 2,4 | 0,09 | 1 | 6,1 | 0,01 | 2 | 1,7 | 0,19 |
| 95% rooting depth | cm | 95 | 2 | 5,0 | 0,008 | 1 | 9,4 | 0,002 | 2 | 7,7 | <0.001 |
| Deep root biomass | g DM plant ⁻¹ | 95 | 2 | 22,6 | <0.001 | 1 | 0,4 | 0,55 | 2 | 1,6 | 0,21 |
| Mean root diameter | mm | 95 | 2 | 12,3 | <0.001 | 1 | 1,4 | 0,24 | 2 | 9,5 | <0.001 |
| Root tissue density (log) | g cm ⁻³ | 95 | 2 | 15,5 | <0.001 | 1 | 4,3 | 0,04 | 2 | 4,3 | 0,01 |
| Specific root length | m g ⁻¹ | 95 | 2 | 0,9 | 0,41 | 1 | 6,9 | 0,01 | 2 | 1,5 | 0,22 |
| Root length density (log) | m cm ⁻³ | 95 | 2 | 43,9 | <0.001 | 1 | 1,5 | 0,22 | 2 | 5,3 | 0,01 |
| Total water use | g plant ⁻¹ day ⁻¹ | 47 | 2 | 27,6 | <0.001 | - | - | - | - | - | - |
| Deep soil water use | g plant ⁻¹ day ⁻¹ | 47 | 2 | 42,8 | <0.001 | - | - | - | - | - | - |
| | | <i>n</i> | d.f. | χ^2 | <i>P</i> | | | | | | |
| Dehydration tolerance | % | 16 | 2 | 6,8 | 0,03 | | | | | | |

643

644 Legend

645 **Figure 1.** a) Experimental design of the long tube experiment comparing above and below ground traits of
646 sixteen populations of *Dactylis glomerata* grown under drought and irrigation; b) diagram illustrating the
647 plant harvest protocol and the variables measured or calculated; soil depth (cm) is indicated on the left side
648 of the soil column which was divided into eight sections represented by dotted lines. Variables in italics
649 were measured on roots harvested in the last but one soil layer (n-1) including roots. Total and deep soil
650 water use were measured for plants grown under drought; c) picture of roots harvested in a 25 cm soil
651 layer; d) picture of a 10 cm root axis used for morphological trait measurement.

652

653 **Figure 2.** Illustration of root axes differences between the three origins of *Dactylis glometata* and between
654 treatments (IR: irrigated; DR: drought). Images were obtained from the root scans at 600 dpi used to
655 perform root morphological trait analysis. For comparative purposes, roots of the same populations (for
656 each origin) are presented. Each picture represents one 10 cm long-root axis.

657 **Figure 3.** Boxplots of above ground and root traits measured under irrigation on 16 populations of *D. glomerata*.
658 Total above ground biomass (Total AGB), total root biomass (Total RB), summer above ground biomass
659 (Sum. AGB), deep root biomass (Deep RB), root tissue density (RTD), specific root length (SRL), root
660 length density (RLD). Each point represents a mean value by population according to their origin:
661 Northern in blue, Temperate in green and Mediterranean in red. Small letters indicate significant
662 differences among origins (Tukey's post hoc test, $P < 0.05$).

663 **Figure 4.** Mean values and standard error of eleven traits measured on 16 populations of *D. glomerata* from
664 three bioclimatic regions: Northern in blue, Temperate in green and Mediterranean in red. Traits were
665 measured under irrigated (\square) and drought (Δ) conditions. Total above ground biomass (Total AGB), total
666 root biomass (Total RB), summer above ground biomass (Sum. AGB), deep root biomass (Deep RB), root
667 tissue density (RTD), specific root length (SRL), root length density (RLD). Small letters indicate
668 significant differences between both origins and treatments (i.e., irrigated or drought; Tukey post hoc test;
669 $P < 0.05$)

670 **Figure 5.** Mean values with standard errors of (A) total water use and, (B) deep soil water use measured at the
671 end of the drought period on 16 populations of *D. glomerata* from different origins, Northern in blue,
672 Temperate in green and Mediterranean in red. Small letters indicate significant differences between origins
673 (Tukey test; $P < 0.05$).

674 **Figure 6.** Principal component analysis performed on ten above ground and root traits of 16 populations of *D.*
675 *glomerata*, measured under irrigation. Total root biomass (Total RB), deep root biomass (Deep RB),
676 maximum root depth, 95% rooting depth, root tissue density (RTD), specific root length (SRL), mean root
677 diameter, summer above ground vegetative biomass (summer AGB), root length density (RLD), and root:
678 shoot ratio (Root: Shoot), contributed to the analysis (solid arrows on the correlation circle (A)). Total
679 water use (total WU), and deep soil water use (deep soil WU), were measured at the end of the drought

680 period as a proxy of dehydration avoidance, and were used as supplementary variables (orange arrows). In
681 figure 6 (B), populations (points) were grouped by origin (NOR: northern in blue, TEMP: temperate in
682 green, MED: Mediterranean in red) according to their barycenter.

683 **Figure 7.** Relationship between dehydration tolerance (%) and dehydration avoidance. Triangles represent
684 population mean values displayed by origin: Northern in blue, Temperate in green and Mediterranean in
685 red. Regression lines show linear relationship, R^2 with associated P-value (***) < 0.001) is represented.

686

687 **Table S1.** List of the 16 populations of *Dactylis glomerata*. Climatic data associated with their origins were
688 collected from the WorldClim data set (<http://www.worldclim.org>; Hijmans *et al.*, 2005). Seeds from
689 Northern populations were provided by the Nordic Genetic Resource Center (NordGen). Temperate
690 ecotypes and cultivars, and population 'Porto', were provided by the plant genetic resources information
691 system of the National Institute for Agronomical Research (INRA, France, Lusignan). The Sicilian ecotype
692 came from University of Catania, Italy. The Moroccan ecotypes came from INRA Rabat, Morocco.

693 **Table S2.** Mean and range of the traits measured under irrigation or under drought on 16 populations of *D.*
694 *glomerata*.

695 **Table S3.** Root biomass distribution in soil columns (0-200 cm): Mean and standard deviation of root biomass
696 for each 25cm layer for Northern, Temperate and Mediterranean populations of *D. glomerata* under
697 drought or irrigation.

698 **Table S4.** Correlations between the total water use measured under drought and eleven traits measured under
699 irrigation or under drought. The R coefficient of Pearson correlations were represented with associated P-
700 value (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns: not significant).

701

702 **Figure S5.** Mean values and standard errors of dehydration tolerance (plant survival rate in short pots after
703 severe drought) measured on 16 populations of *D. glomerata* from different origins: Northern in blue,
704 Temperate in green and Mediterranean in red. Letters indicate significant differences between origins
705 (Kruskal-Wallis test; $P < 0.05$).

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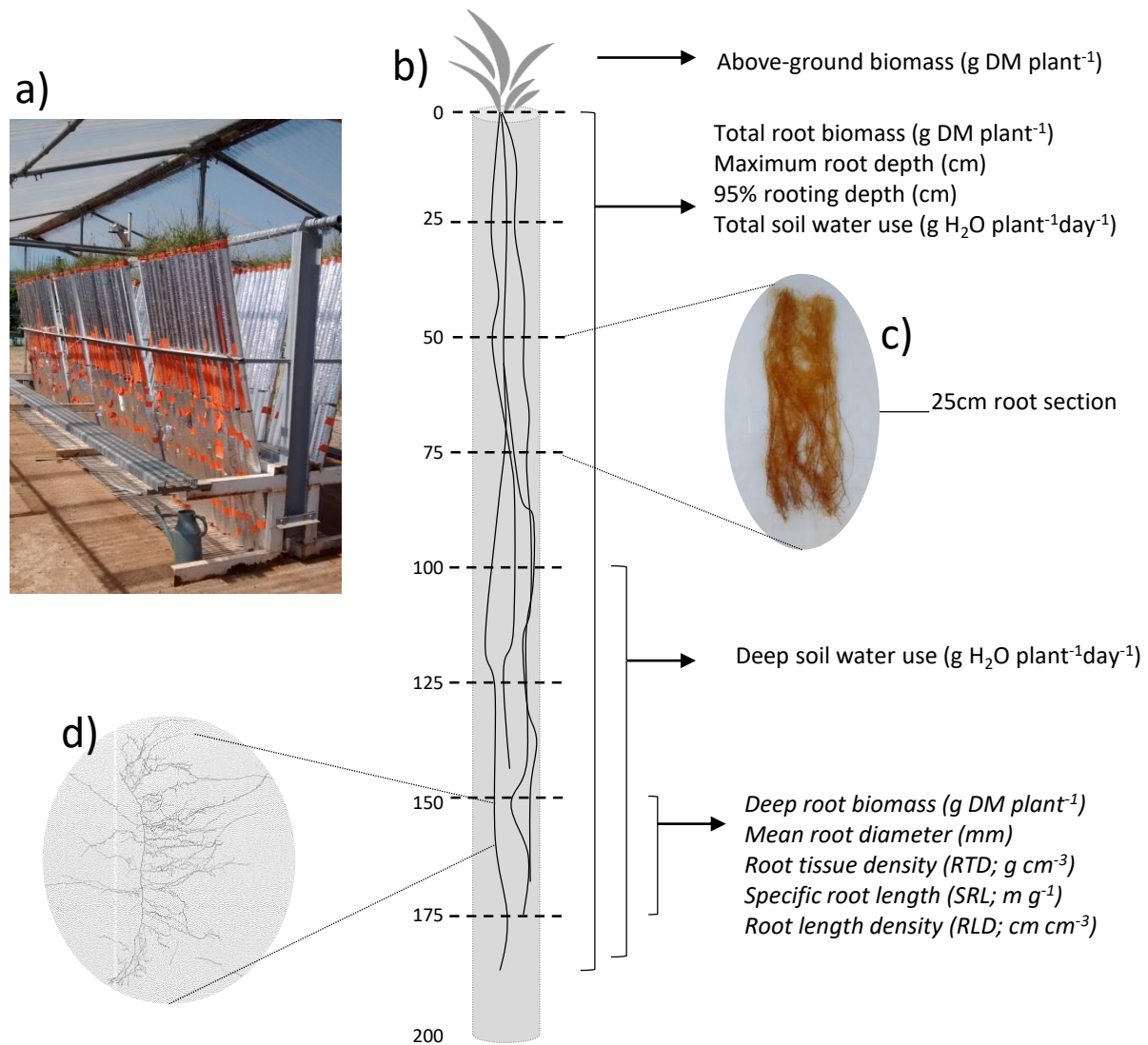
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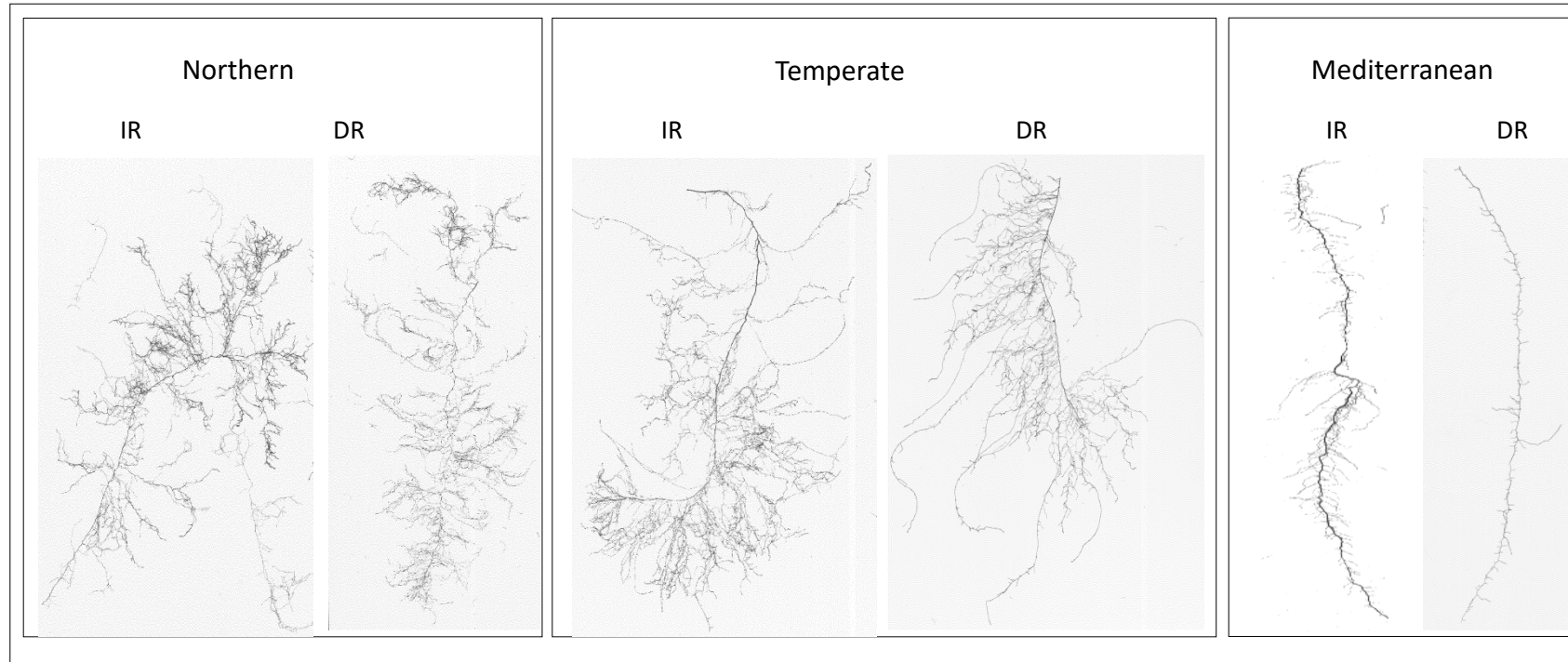
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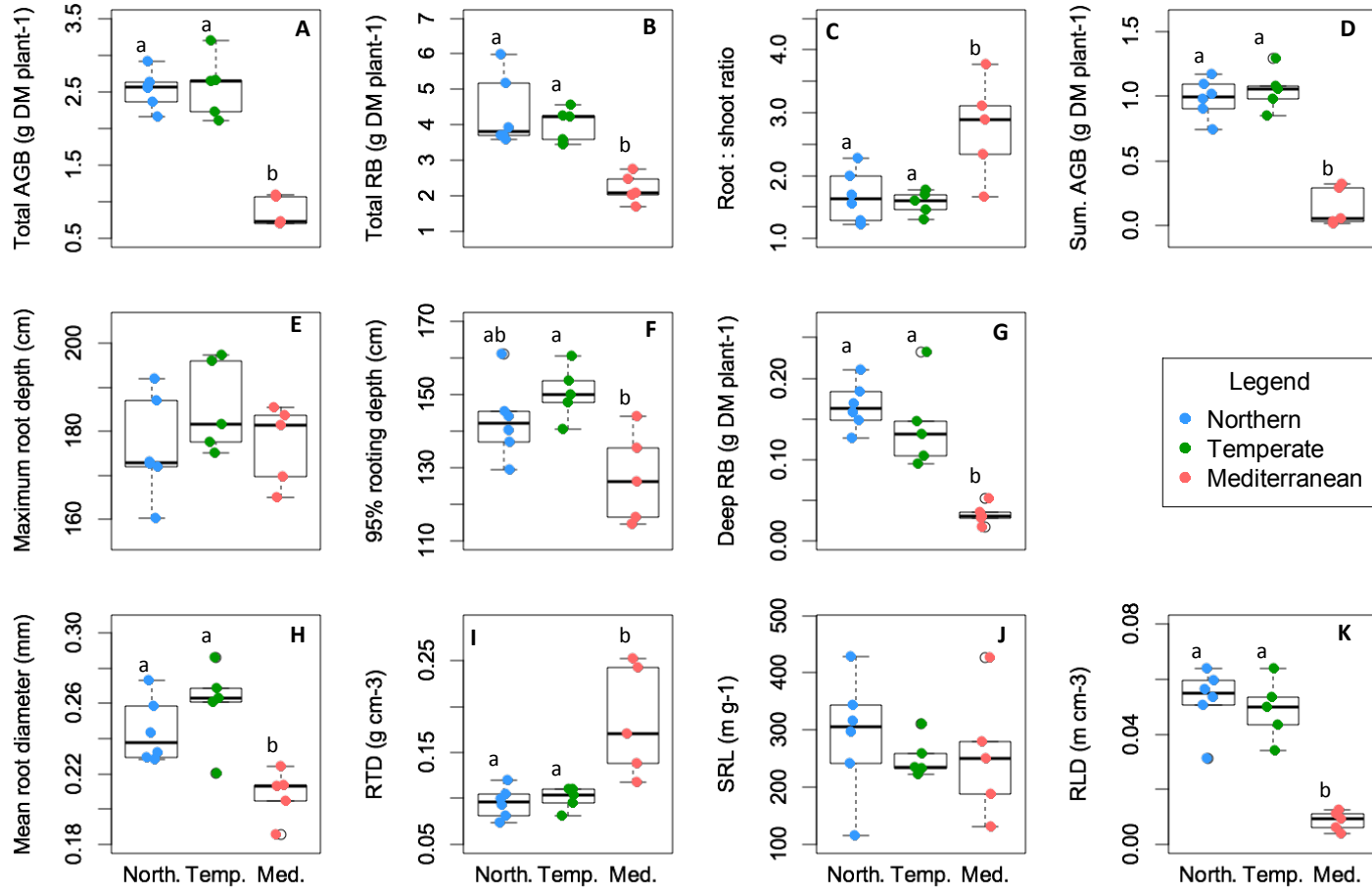
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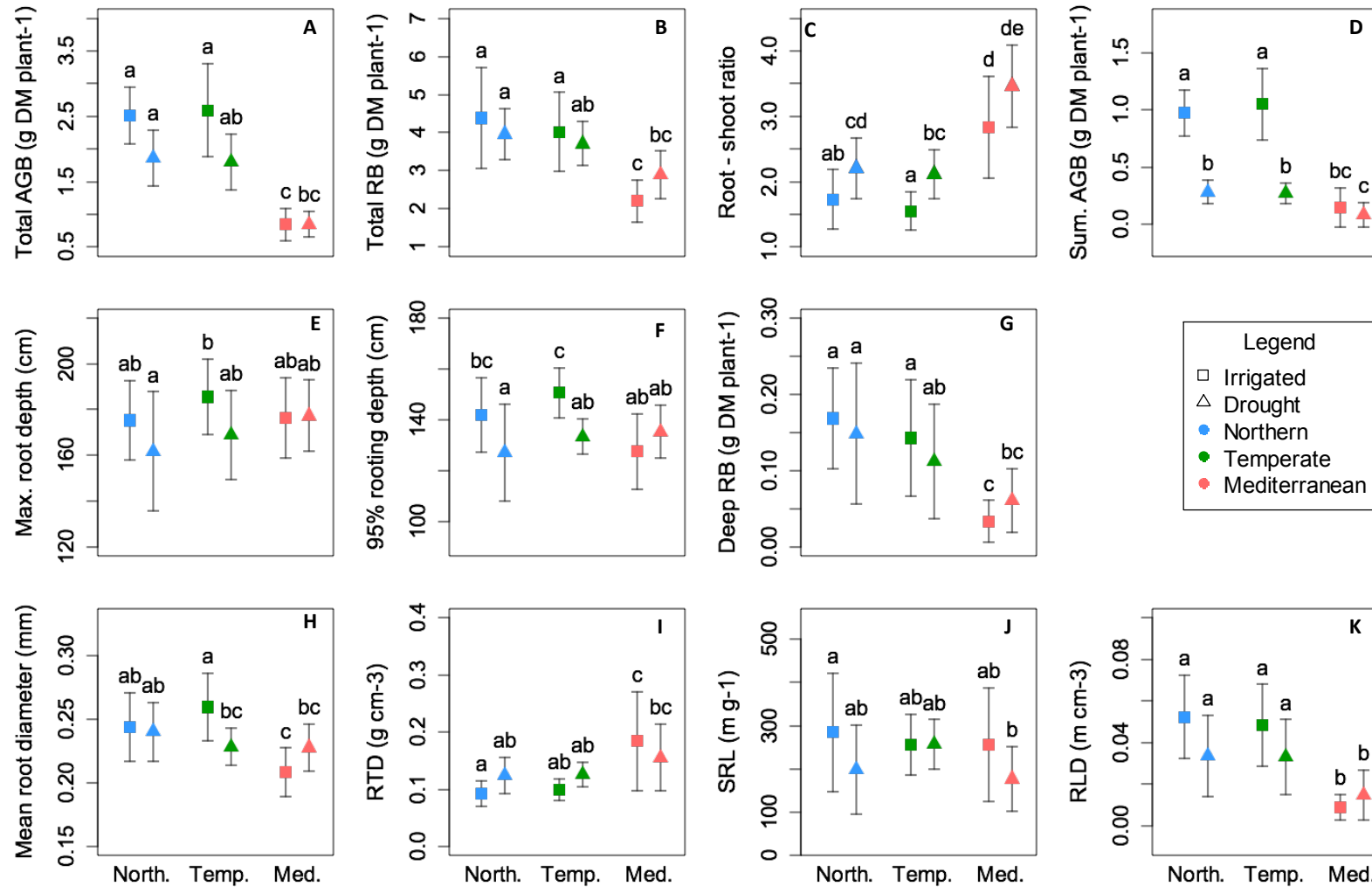
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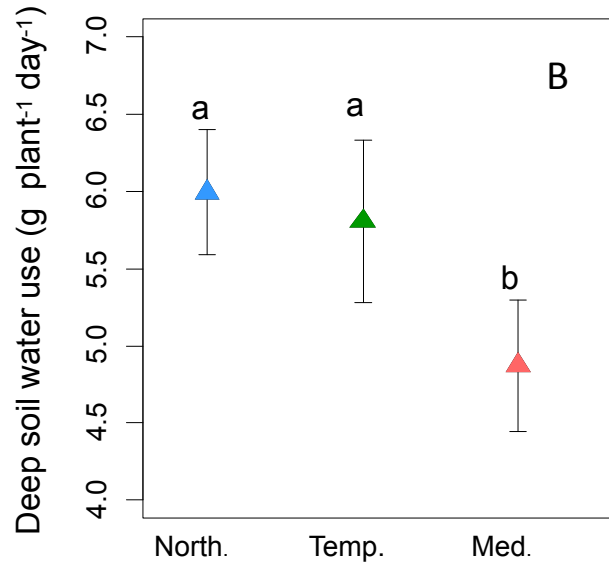
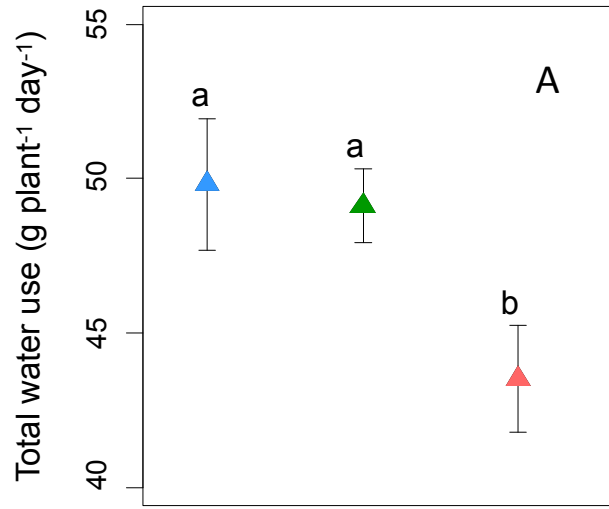
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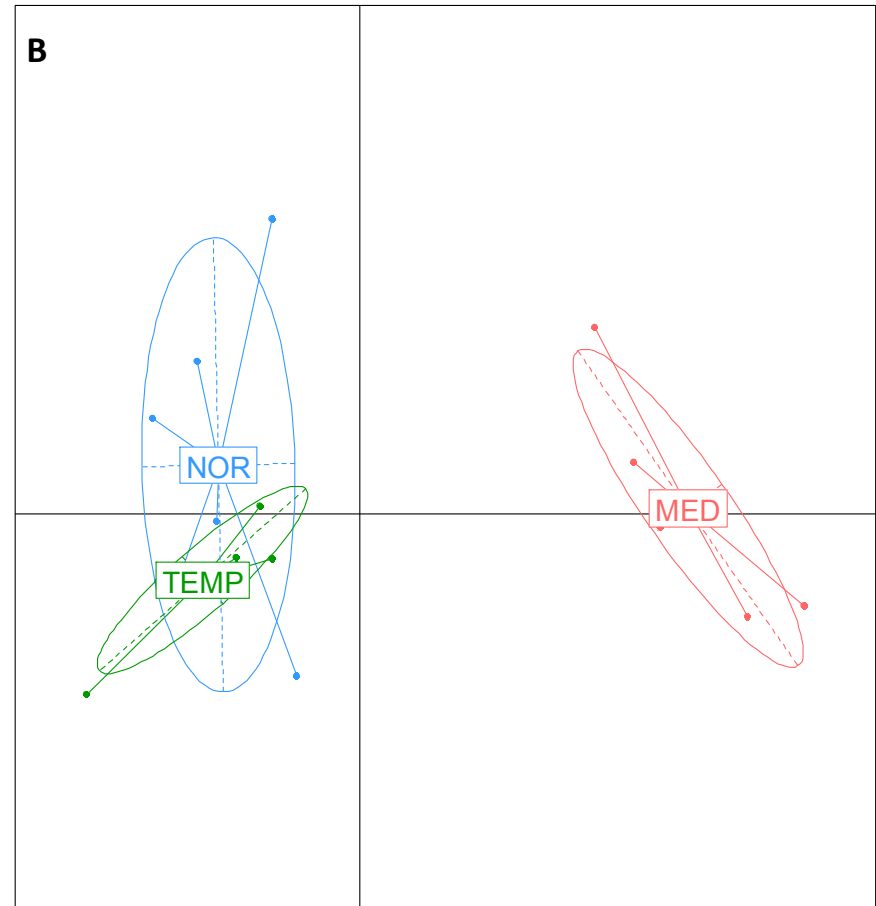
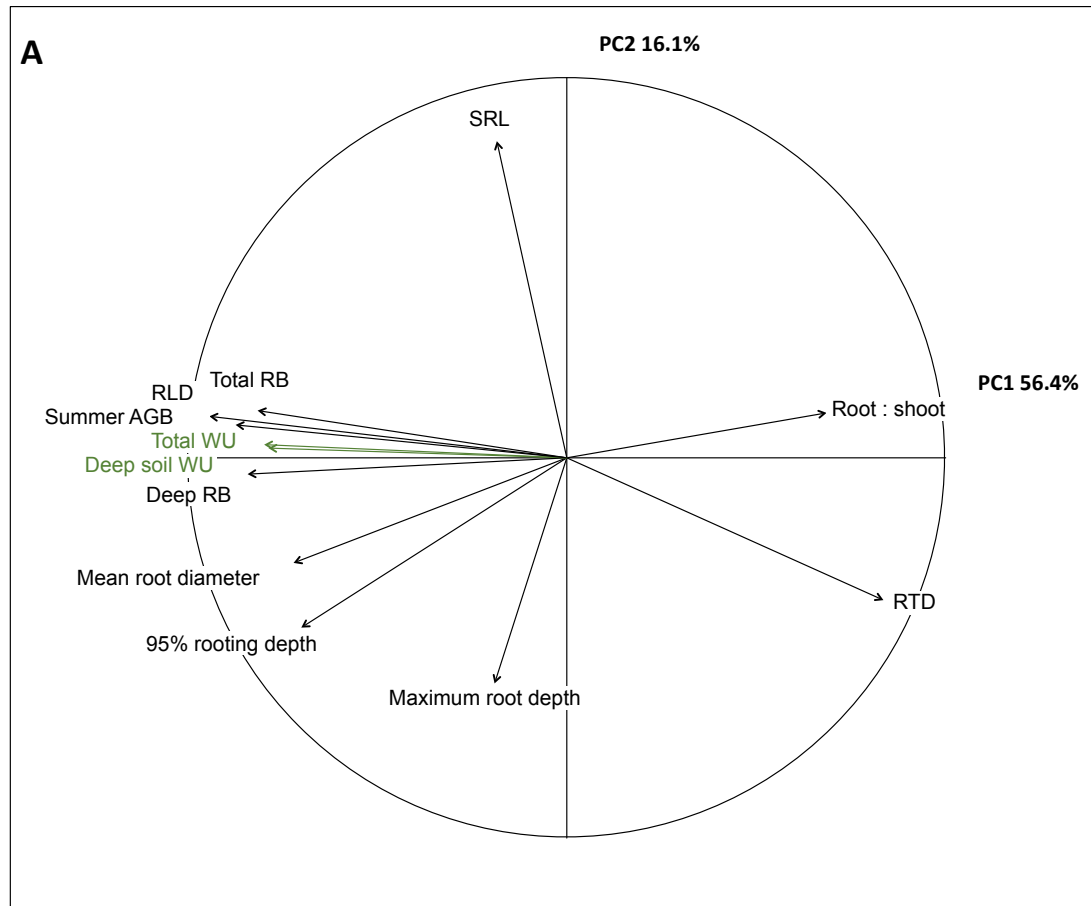


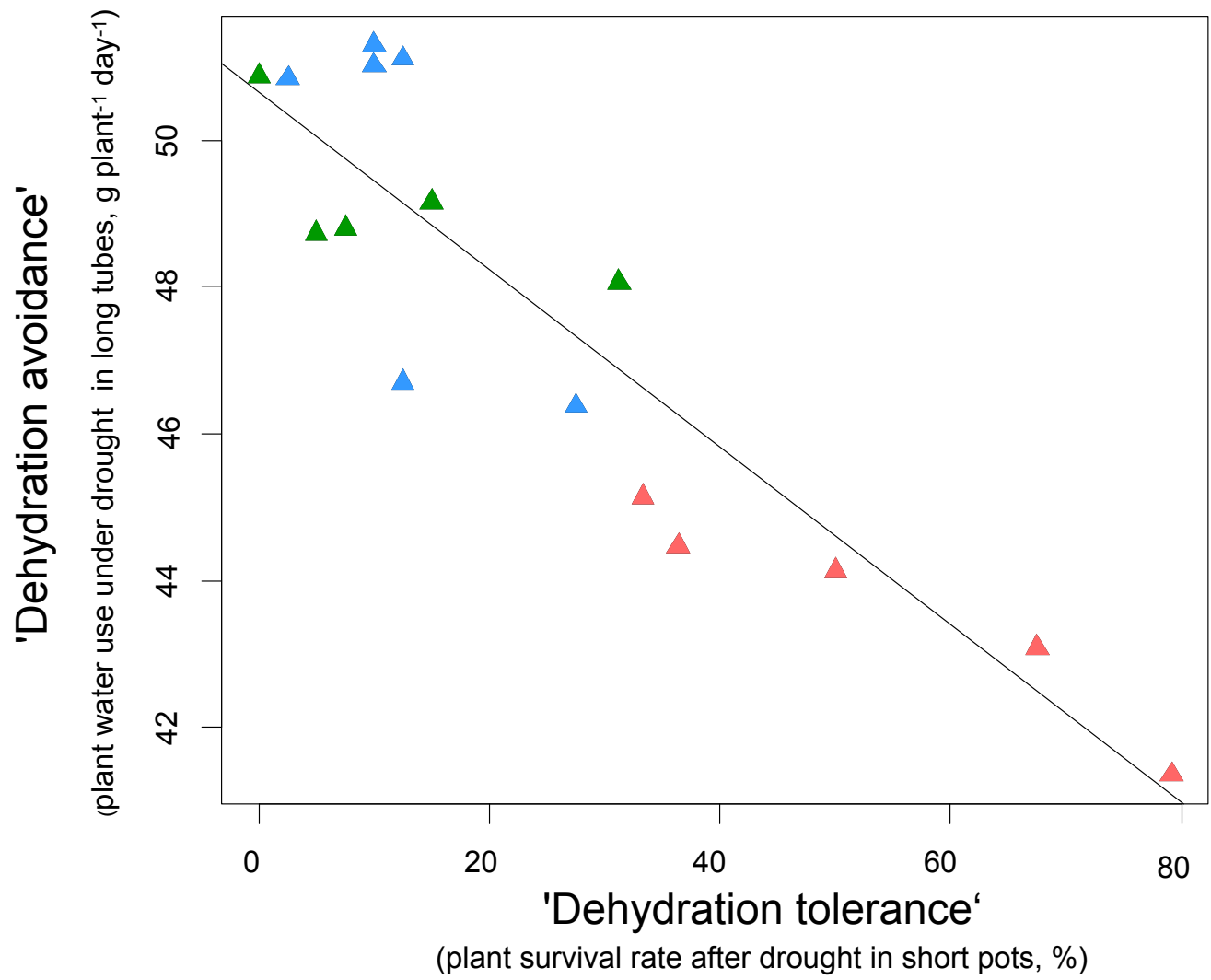












| Population | Country | Type | Origin | Latitude | Longitude | Mean annual temperature (°C) | Mean annual rainfall (mm/year) | Rainfall of the driest month (mm/month) |
|---------------------|----------|----------|---------------|----------|-----------|------------------------------|--------------------------------|---|
| Sweden | Sweden | Native | Northern | 60.5 | 24.22 | 4.8 | 613 | 93 |
| Norway | Norway | Native | Northern | 60.25 | 9.68 | 1.9 | 768 | 118 |
| Denmark | Denmark | Native | Northern | 56.46 | 8.66 | 7.8 | 809 | 134 |
| St Michel | France | Native | Temperate | 48.63 | -1.51 | 11.5 | 731 | 149 |
| Fourchette | France | Native | Temperate | 48.17 | -2.75 | 10.8 | 857 | 153 |
| Carnac | France | Native | Temperate | 47.58 | -3.07 | 11.7 | 893 | 153 |
| Sicily | Italy | Native | Mediterranean | 37.48 | 14.5 | 16.2 | 246 | 1 |
| Morocco 14 | Morocco | Native | Mediterranean | 33.59 | -5.36 | 14.7 | 725 | 30 |
| Morocco 1 | Morocco | Native | Mediterranean | 33.1 | -8.08 | 18 | 346 | 4 |
| Morocco 9 | Morocco | Native | Mediterranean | 29.71 | -8.96 | 16.2 | 246 | 5 |
| Hattfjelldal | Norway | Cultivar | Northern | - | - | - | - | - |
| Tammisto | Finland | Cultivar | Northern | - | - | - | - | - |
| Loke | Sweden | Cultivar | Northern | - | - | - | - | - |
| Ludac | France | Cultivar | Temperate | - | - | - | - | - |
| Porto | Portugal | Cultivar | Temperate | - | - | - | - | - |
| Kasbah | Morocco | Cultivar | Mediterranean | - | - | - | - | - |

Table S1. List of the 16 populations of *Dactylis glomerata*. Climatic data associated with their origins were collected from the WorldClim data set (<http://www.worldclim.org>; Hijmans *et al.*, 2005). Seeds from Northern populations were provided by the Nordic Genetic Resource Center (NordGen). Temperate ecotypes and cultivars, and population 'Porto', were provided by the plant genetic resources information system of the National Institute for Agronomical Research (INRA, France, Lusignan). The Sicilian ecotype came from University of Catania, Italy. The Moroccan ecotypes came from INRA Rabat, Morocco.

Table S2. Mean and range of the traits measured under irrigation or under drought on 16 populations of *D. glomerata*.

| Variable | Unit | Irrigated | | Drought | |
|-----------------------------|-----------------|-----------|-------------|---------|-------------|
| | | Mean | Range | Mean | Range |
| Total above ground biomass | g DM plant-1 | 2,02 | 0.69-3.20 | 1,53 | 0.69-2.38 |
| Total root biomass | g DM plant-1 | 3,57 | 1.68-5.97 | 3,55 | 2.52-4.56 |
| Root : shoot | - | 1,98 | 1.26-3.75 | 2,54 | 1.69-3.77 |
| Summer above ground biomass | g DM plant-1 | 0,74 | 0.01-1.29 | 0,21 | 0.02-0.39 |
| Maximum root depth | cm | 179 | 160-197 | 169 | 139-188 |
| 95% rooting depth | cm | 140 | 114-160 | 131 | 113-148 |
| Deep root biomass | g DM plant-1 | 0,11 | 0.01-0.23 | 0,1 | 0.03-0.24 |
| Mean root diameter | mm | 0,23 | 0.18-0.28 | 0,23 | 0.21-0.26 |
| Root tissue density | g cm-3 | 0,12 | 0.07-0.25 | 0,13 | 0.10-0.21 |
| Specific root length | m g-1 | 267 | 114-428 | 212 | 81-289 |
| Root length density | m cm-3 | 0,037 | 0.003-0.064 | 0,027 | 0.007-0.057 |
| Total water use | g plant-1 day-1 | - | - | 47,3 | 41.3-51.3 |
| Deep soil water use | g plant-1 day-1 | - | - | 5,6 | 4.5-6.3 |

| <i>D. glomerata</i> populations | Summer Treatment | Root biomass distribution (g DM plant ⁻¹) per soil layers in 2m long tubes | | | | | | | |
|------------------------------------|---------------------|--|-------------|-------------|-------------|-------------|-------------|-------------|---------------|
| | | 0-25 cm | 25-50 cm | 50-75 cm | 75-100 cm | 100-125 cm | 125-150 cm | 150-175 cm | 175-200 cm |
| Northern | irrigation | 1.89 ± 0.67 | 1.01 ± 0.30 | 0.57 ± 0.16 | 0.36 ± 0.16 | 0.27 ± 0.11 | 0.20 ± 0.09 | 0.07 ± 0.07 | 0.012 ± 0.024 |
| | drought | 2.10 ± 0.38 | 0.79 ± 0.23 | 0.46 ± 0.15 | 0.30 ± 0.09 | 0.20 ± 0.10 | 0.10 ± 0.07 | 0.02 ± 0.02 | 0.002 ± 0.003 |
| Temperate | irrigation | 1.52 ± 0.44 | 0.86 ± 0.26 | 0.62 ± 0.21 | 0.37 ± 0.11 | 0.29 ± 0.09 | 0.21 ± 0.09 | 0.10 ± 0.08 | 0.024 ± 0.038 |
| | drought | 1.82 ± 0.32 | 0.77 ± 0.17 | 0.49 ± 0.11 | 0.29 ± 0.10 | 0.21 ± 0.07 | 0.08 ± 0.05 | 0.02 ± 0.02 | 0.003 ± 0.005 |
| Mediterranean | irrigation | 1.08 ± 0.42 | 0.67 ± 0.26 | 0.42 ± 0.17 | 0.26 ± 0.12 | 0.17 ± 0.09 | 0.10 ± 0.08 | 0.04 ± 0.04 | 0.007 ± 0.012 |
| | drought | 1.42 ± 0.36 | 0.66 ± 0.20 | 0.43 ± 0.17 | 0.25 ± 0.10 | 0.19 ± 0.08 | 0.08 ± 0.06 | 0.02 ± 0.03 | 0.003 ± 0.004 |

Table S3. Root biomass distribution in soil columns (0-200 cm length, 6 cm diameter): Mean (\pm standard deviation) of root biomass (g DM plant⁻¹) for each 25cm soil layer for Northern, Temperate and Mediterranean populations of *D. glomerata* under drought or irrigation.

Table S4. Correlations between the total water use measured under drought and eleven traits measured under irrigation or under drought. The *R* coefficient of Pearson correlations were represented with associated P-value (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns: not significant).

| | | Traits measured under | | | |
|-----------------------------|---|-----------------------|----------|------------------|----------|
| | | Irrigation | | Drought | |
| | | <i>R</i> Pearson | <i>P</i> | <i>R</i> Pearson | <i>P</i> |
| Total above ground biomass | g DM plant ⁻¹ | 0,76 | *** | 0,76 | *** |
| Total root biomass | g DM plant ⁻¹ | 0,64 | ** | 0,84 | *** |
| Root : shoot | - | -0,64 | ** | -0,73 | *** |
| Summer above ground biomass | g DM plant ⁻¹ | 0,77 | *** | 0,85 | *** |
| Maximum root depth | cm | -0,59 | ** | -0,06 | ns |
| 95% rooting depth | cm | 0,21 | ns | 0,56 | * |
| Deep root biomass | g DM plant ⁻¹ | 0,77 | *** | 0,85 | *** |
| Mean root diameter | mm | 0,51 | * | 0,80 | *** |
| Root tissue density | g cm ⁻³ | -0,53 | * | -0,75 | *** |
| Specific root length | m g ⁻¹ | -0,47 | ns | 0,07 | ns |
| Root length density | m cm ⁻³ | 0,83 | *** | 0,89 | *** |
| Deep soil water use | g plant ⁻¹ day ⁻¹ | | | 0,97 | *** |

