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1 **Root foraging capacity depends on root system architecture and ontogeny in**
2 **seedlings of three Andean *Chenopodium* species**

3

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14 **Abstract**

15 *Aims* Morphological and ontogenetic variation in root system architecture holds ecological significance,
16 particularly in low-resource habitats where soil rooting is critical for both seedling establishment and water and
17 nutrient uptake. To assess this variation under contrasted agroecological backgrounds, root architecture and rooting
18 patterns were compared in Andean populations of *Chenopodium hircinum*, *Chenopodium pallidicaule* and two
19 ecotypes (wet- and dry-habitat) of *Chenopodium quinoa*.

20 *Methods* Seedlings were grown in rhizotrons under controlled water and nutrient availability. Root branching and
21 elongation dynamics were characterized during 6 weeks after germination, while leaf area, above and below-
22 ground biomass, and specific root length were determined at the end of the experiment.

23 *Results* Despite large differences in aboveground biomass, all populations showed similar herringbone root
24 systems. The dry-habitat *C. quinoa* had generally the highest root trait values, with fast taproot elongation, thick
25 roots and long root segments resulting in high total root length and deep root proliferation.

26 *Conclusion* Irrespective of their contrasting agroecological background, the studied chenopods displayed a similar
27 root system topology. However, from very early development stages, they showed differential root foraging
28 patterns with two extremes: fast and vigorous rooting at depth in the dry-habitat *C. quinoa*, and shallow and thin
29 root system in *C. pallidicaule* adapted to shallow-soil and high-altitude habitats.

30

31 **Keywords** *Chenopodium quinoa*; *Chenopodium hircinum*; *Chenopodium pallidicaule*; Ecotypes; Rhizotron; Root
32 traits; Root system topology

33 Introduction

34 Root system architecture considers the spatial structure, the geometric features and the branching complexity of
35 the roots of whole plants (Fitter 1987). It has profound implications for plant growth and species distribution,
36 enabling individual plants to cope with changing environmental conditions and plant species to thrive in different
37 ecological niches (Lynch 1995; White et al. 2013). Differences in root system architecture are associated with
38 differences in soil resource acquisition, not only between contrasting functional types (Paula and Pausas 2011;
39 Roumet et al. 2006; Taub and Goldberg 1996), but also among genera and species of the same growth form
40 originating from contrasted ecological habitats (Leva et al. 2009). *Chenopodium* is one of these genera that thrive
41 under strikingly contrasted environments, notably in South America where strong ecological gradients develop
42 from Amazonian or Southern Pacific lowlands of humid climate and nutrient-rich soil up to the Andean highlands
43 of dry and cold climate and nutrient-poor soil (Troll 1968; Di Castri and Hajek 1976). In these highly contrasted
44 habitats, annual chenopods have diversified, some of them as spontaneous chenopods (e.g. *C. hircinum* Schrad.,
45 *C. petiolare* Kunth, *C. carnosolum* Moq.), others as cultivated species like quinoa (*C. quinoa* Willd.) and cañahua
46 (*C. pallidicaule* Aellen) with many ecotypes (Kühn et al. 1993; Vargas et al. 2011). None of these chenopods show
47 the morphophysiological adaptations typical to dry or saline habitats environments, such as Kranz anatomy, C4
48 photosynthetic pathway, or succulence (Fuentes-Bazan et al. 2012). For surviving, these plants thus rely on
49 common plant and life-history traits that control the balance between resource capture and resource use, for which
50 root system architecture plays a key role (Singh et al. 2010).

51 Examining the various patterns of root system branching or topology, theoretical and experimental works
52 suggest that a root system consisting of only a main axis and primary laterals (herringbone topology) would favour
53 nutrient acquisition in low-resource habitats because it minimizes intraplant root competition (Fitter et al. 1991;
54 Taub and Goldberg 1996). Conversely, a dichotomous topology associated with shorter root links (the segments
55 of root between two nodes, or between a node and a root tip) and greater link number, would favour nutrient
56 capture in high-resource habitats (Fitter et al. 1991; Taub and Goldberg 1996). Most chenopods show a
57 herringbone root system (Fitter 1987), but detailed descriptions are lacking to appreciate differences among species
58 or among ecotypes of contrasted habitats. Regarding plant species adapted to cold and high altitude habitats, they
59 might develop a growth syndrome that includes short plant height and high root mass fraction (Poorter et al. 2011).
60 Growing at elevations up to 4.600 m, the small-sized *C. pallidicaule* is renowned as the hardest Andean chenopods
61 (Gade 1970) and yet the adaptive value of its morphophysiological traits remains unknown.

62 In a context of increasing scarcity of agricultural water and nutrients, improved root system functioning
63 could enhance crop productivity while decreasing crop input requirements (De Dordot et al. 2007; Lynch and
64 Brown 2012; White et al. 2013). Cultivated chenopod species such as *Ch. quinoa* and *Ch. pallidicaule* are
65 promising candidates for exploring plant ideotypes suited to low-input agriculture (Rojas et al. 2009). In fact, since
66 centuries, Andean farmers have selected several tens of local chenopod varieties for their hardiness under harsh
67 climate and poor soil conditions (Bonifacio 2003). As it happened in other crop species (Palta et al. 2011; Wasson
68 et al. 2012), unconscious selection for improved rooting capacity is likely to have occurred in these Andean
69 chenopod crops. Exploring the morphological variation in root architecture, and particularly the contrast between
70 wild and cultivated species, would help testing this hypothesis of unconscious selection as well as defining root
71 system ideotypes that optimize soil resource uptake.

72 Since root distribution and soil resource profiles are temporally dynamic, characterizing the root system

73 based on one time measurements cannot reveal the full range of plant responses to changing soil conditions
74 (Chesson 2004). In seedlings, in particular, the dynamics of root growth and branching is critical for the successful
75 establishment of the plants and the exploitation of the soil volume, especially in harsh and variable environments
76 where fast and early rooting is vital to capture ephemeral soil nutrients and deep water (León et al. 2011; Padilla
77 and Pugnaire 2007). An important factor for early root vigor is individual seed mass (Richards et al. 2007; White
78 et al. 2013), a trait showing extensive genetic variation, including in chenopods where natural polyploidization
79 and human selection have led to broad variation in seed mass (Bhargava et al. 2007; Fuentes-Bazan et al. 2012).

80 By means of a rhizotron experiment, the present study addresses the ontogenetic changes in root system
81 architecture of seedlings plants in three Andean *Chenopodium* species of different agroecological backgrounds.
82 The starting hypothesis is that *Chenopodium* plants from low-resource habitats have developed root traits that
83 enhance root foraging in deep soil layers. More specifically, it is expected that chenopods from low-resource
84 habitats would have faster root growth at early growth stage and greater root elongation at depth.

85 **Materials and methods**

86 Study site and plant populations

87 The study was conducted outdoor under a transparent rain shelter at the CEFÉ-CNRS experimental field
88 (Montpellier, France, 43°38'19''N, 3°51'46''E), from the 11th of March to the 22th of April 2011. Four
89 *Chenopodium* population samples from contrasting habitats were compared: *C. hircinum* and *C. pallidicaule* both
90 from semi-arid highlands with nutrient-poor soils, *C. quinoa* from temperate lowlands with nutrient-rich soils (wet
91 habitat), *C. quinoa* from arid and cold highlands with nutrient-poor soils (dry habitat) (Table 1). *C. hircinum* is a
92 wild tetraploid species, *C. pallidicaule* is a domesticated diploid, and *C. quinoa* is a domesticated tetraploid. The
93 wet-habitat *C. quinoa* pertains to the coastal quinoa ecotype of Chile while the dry-habitat *C. quinoa* is
94 representative of the Salar quinoa ecotype of Bolivia. The seeds of *C. quinoa* and *C. pallidicaule* were from local
95 landraces without pedigree. They were collected directly at the specified sites, as were the seeds of *C. hircinum*.
96 In the four studied populations, seeds were selected for their size homogeneity and sterilized with sodium
97 hypochlorite (1%) for 10 min before sowing in rhizotrons at 3 cm depth.

98 Rhizotrons

99 Rhizotrons measuring 85 x 34 x 2.3 cm were made of white PVC plates with a pane of glass on one side. The
100 windowpane was protected from light incidence with a mobile polystyrene plate 1.5 cm thick. Each rhizotron was
101 filled with 7 L of a soil substrate humidified at field capacity (see below), sown with two seeds of the same
102 population and then disposed outdoor under a transparent roof for rain protection. The rhizotrons were disposed
103 with a 15° inclination from the vertical to favor the root growth on the windowpane.

104 Soil substrate and growth conditions

105 The soil substrate was composed of 84.5 % of sand, 6.3 % of clay, 4.5 % of silt, 3.1 % of organic matter, with pH
106 8.08, CEC Metson 9.02 cmol+/kg, and C/N 11.2. Prior to the experiment, the substrate was dried and sterilized to
107 120 °C for 48 hours. Then, it was humidified using a nutritive solution (N: 16%, P: 10 %, K: 24 %, MgO: 3 %,
108 micro-elements: 2.5 g/L). When the experiment started, rhizotrons were at field capacity (0.12 cm³/cm³) and no

109 more water was applied until the end of the study. Over the course of the experiment, air temperature at 150 cm
110 height varied between 3.0 and 35.2 °C (mean = 15.5 °C ± 0.1), soil temperature at 25 cm depth varied between 4.8
111 and 35.2 °C (mean = 14.9 °C ± 0.05), and air relative humidity varied between 30 and 89 % (mean = 61 % ± 0.5).
112 These conditions of temperature and soil humidity grossly satisfied the optimal growth requirements of the studied
113 populations and no sign of plant physiological stress (e.g. leaf wilting, slow plant growth) was detected. Apart
114 from being a convenient substrate in a comparative study under controlled conditions, the sandy substrate fitted
115 the soil conditions commonly experienced by *C. pallidicaule* and the dry-habitat *C. quinoa* in their native
116 highlands. As regards *C. hircinum* and the wet-habitat *C. quinoa*, their natural environments show a range of soil
117 conditions, including sandy ones. The overall satisfactory growth of these plants in the present experiment
118 indicates that they did not suffer any physical or nutritional limitation due to the soil substrate.

119 Plant sampling and measurements

120 Three days after emergence, plants were thinned to one seedling per rhizotron, and five replicate plants per
121 population were followed weekly from 7 to 42 days after sowing (DAS) for non-destructive growth measurements.
122 Root growth of each replicate plant was recorded weekly by tracing on a transparent acetate sheet the root axes
123 visible through the windowpane of the rhizotron. The root system images were then scanned at a resolution of 400
124 dpi (Acer Scan 300F, 6684 03A) (Fig. 1) and analyzed with the morphological and architectural procedures of the
125 WinRHIZO Pro2009 software (Regent Instruments Inc., Quebec, Canada). The following root traits were
126 calculated: total tip number (TTN), total link number (TLN), total root length (TRL, m) and total root length per
127 link type (see Fig. 2a for a definition of root link types). The number of new lateral roots appearing on the taproot
128 in successive soil layers was also counted each week.

129 Following Glimskär (2000), two root topological indices were calculated. The topological quotient index
130 (TQI) for individual plants at 42 DAS was calculated as the ratio $\log(\alpha)/\log(\mu)$, with α representing the altitude of
131 the root system (i.e. the number of links of the longest path from the root collar to an external tip) and μ its
132 magnitude (i.e. the total number of tips in the root system). The topological slope index (TSI) was determined as
133 described by Fitter and Stickland (1991), calculating the slope of the regression of $\log(\alpha)$ on $\log(\mu)$ for the set of
134 altitude and magnitude values observed in each population during the time of the experiment. Both topological
135 indices vary between 0 and 1, with large values indicative of a more herringbone-like root system with branching
136 mostly confined to the main axis.

137 By the end of the experiment (42 DAS), after completing the non-destructive root growth measurements,
138 root collar diameter was measured with an electronic caliper (Mitutoyo, Andover, UK) and each individual plant
139 was cut at the level of the root collar. Plant height (PH, cm) was measured as the length of the main stem from the
140 root collar to the shoot apex. Leaves were separated from the stems, scanned at 400 dpi (CanonScan LIDE 100)
141 and the images were analyzed with the SigmaScan Pro 5 software (Systat Software Inc.) to determine the total leaf
142 area per plant (LA, cm²). Leaves and stems were then oven-dried at 65 °C for 48 h before dry mass weighting. The
143 substrate containing the root system was divided into six depth levels (0-5 cm, 5-20 cm, 20-35 cm, 35-50 cm, 50-
144 65 cm, 65-80 cm) and roots within each layer were washed, separating the roots growing onto the windowpane
145 from those growing inside the substrate. After drying at 65 °C for 48 hours, root dry mass was determined to
146 calculate: i) the specific root length (SRL, m/g) from the roots growing onto the windowpane, and ii) the root/shoot
147 ratio (R:S, g/g) from the bulk of the root system biomass.

148 Data analyses

149 Differences in plant traits among populations were tested using factorial analysis of variance (ANOVA) after log
150 transformation of the data when necessary to meet the normality and homoscedasticity assumptions. To avoid size
151 effects when comparing populations for TTN, TLN, MLL II, MLL EI and MLL EE, analyses of covariance
152 (ANCOVA) were performed, with TRL as the covariate, and testing for a possible interaction between the
153 covariate and the factor “populations”. Tukey’s HSD post-hoc tests were used to compare population means at P
154 < 0.05 . The dependence between selected variables was determined using Pearson's correlation analysis. Statistical
155 procedures were performed using STATISTICA v.7.1 (Statsoft Inc., Tulsa, USA).

156 Results

157 Plant size, biomass production and root/shoot ratio

158 Seedlings of dry-habitat *C. quinoa* showed the most vigorous growth, resulting in higher plant height and deeper
159 root system during the course of the experiment, and higher leaf area, root collar diameter and biomass production
160 at 42 DAS (Table 2). At that time, *C. pallidicaule*, the least vigorous of the studied populations, was only 6.5%
161 the size of dry-habitat *C. quinoa* in terms of total plant mass, 10% its size in terms of leaf area, and 20% its size in
162 terms of total root length. *C. hircinum* and wet-habitat *C. quinoa* showed intermediate values, with the wild *C.*
163 *hircinum* always less productive than the cultivated *C. quinoa*, essentially due to lower aboveground growth. These
164 differences in seedling growth among the studied populations were in relation with their respective mean seed
165 mass (SM, Table 2). Despite contrasted growth capacities, *C. pallidicaule* and dry-habitat *C. quinoa* showed
166 similar biomass allocation patterns with R:S ratios of 0.31 and 0.28 respectively, significantly lower than those
167 observed in wet-habitat *C. quinoa* (0.45) and *C. hircinum* (0.39).

168 Root system profile and branching dynamics

169 After six weeks of plant growth (42 DAS), the vertical distribution of the root system showed significant
170 differences among populations and among soil layers (Fig. 3). In each soil layer, the number of root tips was highly
171 correlated to the root length ($r = 0.97$, $P < 0.001$, $n = 24$) and both traits showed similar vertical distributions. *C.*
172 *quinoa* from dry and wet habitats had similar root profiles down to 65 cm depth, with maximum root development
173 in the 20-35 cm soil layer (ca. 5 m root length in that layer, equivalent to a root length density ca. 0.35 cm root/cm³
174 soil). Beyond a 65 cm depth, dry-habitat *C. quinoa* showed significantly higher root colonization than the wet-
175 habitat ecotype (ca. 4 m of root against 0.5 m respectively). Compared to *C. quinoa*, *C. hircinum* and *C.*
176 *pallidicaule* showed significantly less root development, although the former still colonized deep soil while the
177 latter was almost exclusively limited to the 35-50 cm layer (Fig. 3).

178 These patterns of vertical root distribution at 42 DAS resulted from the progressive proliferation of the
179 root system through the soil profile (Fig. 1). The sequential analysis of the number of new lateral branches
180 appearing on the taproot during the experiment revealed contrasted dynamics among the studied populations (Fig.
181 4). In *C. hircinum* and wet-habitat *C. quinoa*, root branching proceeded in a similar way, with new lateral roots
182 successively appearing in ever deeper soil layers down to 75 cm at 42 DAS. The main difference between these
183 two populations was in a more extended period of root proliferation in wet-habitat *C. quinoa*, starting one week

184 earlier than in *C. hircinum*. By contrast, in dry-habitat *C. quinoa*, root branching was maximum at 75 cm as soon
185 as 35 DAS, when none of the other populations had reached that depth yet. In *C. pallidicaule*, root branching
186 occurred over the same lapse of time than in the other populations but at a much lower rate, and it hardly passed
187 the 30 cm soil depth.

188 Root segment and root system morphology

189 The morphology of individual root segments varied greatly among the studied populations, with SRL in *C.*
190 *pallidicaule* showing roots three-fold finer on average than those of dry-habitat *C. quinoa*, the other two
191 populations having intermediate values (Table 2). With regard to the shape of the root system, the topological
192 slope index TSI showed statistical differences only among dry-habitat *C. quinoa* (0.72) and *C. hircinum* (0.87),
193 while the topological quotient index TQI did not show any difference among the four populations (Table 2). Such
194 high values of the topological indices are characteristic of a herringbone morphology for the root systems. The
195 regression of $\log(\alpha)$ on $\log(\mu)$ showed a strong, unique linear relationship ($r^2 = 0.96$) over the range of observed
196 plant sizes, irrespective of the species (Fig. 5). However, the plot also shows a tendency for the slope of the
197 regression to decrease sharply at high magnitude values (namely, $\log(\mu)$ close to 3).

198 Root system architecture

199 Despite a similar herringbone morphology, the studied populations differed greatly in the details of their root
200 system architecture: both *C. quinoa* ecotypes produced higher TRL and had significantly greater TLN and TTN
201 than *C. hircinum* which, in turn, showed nearly three times more root branches and root tips than *C. pallidicaule*
202 (Table 2).

203 A thorough analysis of the different kinds of root links reveals contrasted dynamics of root branching
204 among the studied populations (Figs. 6, 7, 8). Except in the first three weeks when the root system was essentially
205 limited to the taproot (see Fig. 1), EI links concentrated most of the total root length in the four populations (Fig.
206 6). Considering the cumulated root length per link type, the highest increase was observed between 28 and 35 DAS
207 in dry-habitat *C. quinoa*, particularly in EI links which, by the end of the experiment, totalized 8 m per plant on
208 average (53% of the total root length) (Fig. 6). In comparison, EI links in *C. pallidicaule* at the same stage totalized
209 only 2 m per plant on average, though they amounted to a similar proportion of the total root length. Decomposing
210 the total root length in its two components (namely: the mean number and the mean length of the different links,
211 Fig. 7 and 8), it appeared that temporal changes in total root length reflected mostly the changes in link number (r
212 $= 0.84$, $P < 0.001$, $n = 65$) and not those in mean link length ($r = 0.02$, $P > 0.1$, $n = 65$). The number of EI and EE
213 links increased progressively from 14 DAS on, with EI links always in a higher proportion than EE links in all
214 populations (Fig. 7). The appearance of new links reached its highest rate by the end of the experiment with wet-
215 habitat *C. quinoa* showing the highest rate of root branching.

216 Regarding the mean length of the different types of links, considerable variation was shown with maximal
217 values of nearly 7 cm observed in the young taproot of the dry-habitat *C. quinoa*, while the taproot of the other
218 populations was limited to about 2 cm at that early developmental stage (Fig. 8). From 14 DAS on, the mean length
219 of II links decreased rapidly as a consequence of the emergence of new lateral roots. While mean link length did
220 not show much time variations from 28 DAS on, it varied significantly among populations, with constantly longer
221 II and EI links in dry-habitat *C. quinoa* than in the other three populations (Fig. 8 and Table 2). This trait

222 compensated for lower or equal link numbers in this ecotype compared to that from wet habitat (Fig. 7 and Table
223 2), resulting in higher TRL in the dry-habitat *C. quinoa*, with a non-significant trend when considering the whole
224 plant root system (Table 2, $P = 0.12$) but a highly significant difference as regards the cumulated EI segments (Fig.
225 6, $P < 0.001$) which formed the major part of the entire root system.

226 **Discussion**

227 Root topology in different chenopod species: plant size and ontogenetic effects

228 This study found significant variation in initial seedling size (TPM or PH, Table 2) among three Andean
229 *Chenopodium* species, with *C. quinoa* producing two to five-fold more biomass than *C. hircinum* and up to fifteen-
230 fold more than *C. pallidicaule*. Among the two *C. quinoa* ecotypes, the one from the dry habitat showed the most
231 vigorous growth, which should give it a decisive advantage since initial seedling size strongly determines early
232 plant survival in arid environments (León et al. 2010). As observed in other wild and cultivated species (Coomes
233 and Grubb 2003; Bertholdsson et al. 2009), the ranking in plant vigor among the studied populations was related
234 to the differences in individual seed mass. This contrast between species did not affect the overall shape of the root
235 system: all showed similar root topological indices (Table 2) with values characteristic of herringbone root
236 systems, a feature commonly observed in chenopod species (Fitter 1987). Such similar topological indices could
237 reflect the phylogenetic closeness of the studied species. In fact, *C. quinoa* was probably domesticated from *C.*
238 *hircinum*, this latter being also a wild relative of *C. pallidicaule* (Gandarillas 1984). An alternative explanation to
239 this topological similarity arises when comparing our results to those of Glimskär (2000). In his study on forbs
240 and grasses grown at different nitrogen levels, a quite general relationship emerges between altitude (α) and
241 magnitude (μ) with a curvature in the $\log(\alpha) / \log(\mu)$ relation suggesting a general size effect. Interestingly, the
242 curvature in Glimskär's data appears at $\log(\mu)$ near 3, with $\log(\alpha)$ leveling near 2.4, both values which are quite
243 close to our own data for three chenopod species (Fig. 5). The leveling in the altitude / magnitude relationship as
244 plants grow could have an ontogenetic explanation related to the continued branching of a not strictly herringbone
245 root system. After an initial period of seedling growth dominated by the elongation and branching of the main
246 root, lateral roots begin to emerge from internal links, thus forming new external links (EI) which directly increase
247 the root system magnitude without necessarily increasing its altitude. In our study, such new lateral roots of second
248 and higher orders emerged in great number from 21 DAS on (Figs. 4 and 7). The generality of the altitude /
249 magnitude relation observed in forbs and grasses under different growth conditions (Arredondo and Jonhson 1991;
250 Fitter 1991; Glimskär 2000; Paula et al. 2011; Roumet et al. 2006; this study), suggests a general ontogenetic shift
251 in the root topology of annual plant species, with lateral roots emerging in ever greater numbers (increasing
252 magnitude) as soon as $\log(\alpha)$ exceeds a value of 2 approximately.

253 Due to this ontogenetic effect, the curvature in the altitude / magnitude relation points to a limitation of
254 the topological slope index (TSI) as proposed by Fitter and Stickland (1991). Assuming a linear relation over a
255 large size range, TSI overemphasizes small deviations from linearity (Glimskär 2000), which makes it a poorly
256 suited index to discriminate root branching patterns in growing seedlings (Paula and Pausas 2011). As an
257 alternative index, Glimskär (2000) proposed the TQI quotient calculated on individual plants, with a range of
258 values from 0.69 to 0.79 for five different species. Our chenopod species fall within this range with an estimate of
259 0.77 (Table 2). Considering our results together with those of Glimskär, we suggest a general ontogenetic shift as

260 a possible component of this size effect. Therefore, when evaluating species differences in root topology, we would
261 recommend comparing not only plants belonging to a narrow size interval (Glimskär 2000), but also plants of
262 similar developmental stages.

263 As for the ecological interpretation of this ontogenetic-size effect on root topology, Glimskär (2000) as
264 well as Paula and Pausas (2011) put forward that the more herringbone topology of young plants could be related
265 to the need to quickly reach deep soil layers, in a context of competition with other plants. This assumption
266 similarly applies to the growth of seedling plants in low-resource habitats where fast root growth at an early
267 developmental stage would secure soil resource capture and young plant survival (León et al. 2011; Palta et al.
268 2011; Richards et al. 2007). The following discussion on the root foraging traits observed in the studied species
269 brings more insights into this assumption.

270 Root foraging: a suite of traits significantly improved in the dry-habitat quinoa ecotype

271 While the herringbone topology remained virtually unchanged among the three Andean chenopods of the present
272 study, their root systems were quite different with regard to the branching architecture and the progressive
273 proliferation through the soil profile. *C. quinoa* produced higher total root length than *C. hircinum* and *C.*
274 *pallidicaule*, though the difference between the *C. hircinum* and wet-habitat *C. quinoa* appeared marginal (Table
275 2). The detailed analysis of root links revealed that external links (EI and EE) were not only in higher proportion
276 than internal links: they were also more abundant in wet-habitat *C. quinoa* and longer in dry-habitat *C. quinoa*
277 than in the other two species (Table 2, Figs. 7 and 8). As these external links are more absorptive than the suberified
278 internal root segments (Kramer and Boyer 1995), their relative abundance in *C. quinoa* should give this species a
279 physiological advantage for soil resource uptake.

280 Among the *C. quinoa* populations, the one from the dry habitat had statistically fewer root tips and
281 marginally fewer root links (Table 2) but consistently greater EI and EE link lengths (Table 2, Fig. 8), resulting in
282 marginally higher TRL values. Such compensation between link number and link length bears a general ecological
283 significance as shown by Nicotra et al. (2002) who found, comparing 11 phylogenetically independent contrasts,
284 that species originating from dry environments usually have fewer root links but with greater link length than
285 species from wetter environments. From a functional point of view, greater root link length reduces the overlap
286 between depletion zones of neighbouring branches and, thus, improves the root foraging efficiency particularly
287 for mobile resources like nitrate or water (Arredondo and Johnson 2011; Fitter et al. 1991b; Pagès 2011). In arid
288 habitats where soil water recharge occurs during the wet season and where deeper soil layers maintain higher soil
289 moisture, a fast elongation of the root system at depth seems more adapted to drought than multiplying root
290 branches in the upper soil layers (Bauerle et al. 2008; Padilla and Pugnaire 2007; Reader et al. 1993). The vertical
291 root growth allows the plants to access water resources at depth, while dense root colonization in the upper soil
292 would rapidly lead to root competition and complete water depletion in the absence of new rainfall events. For the
293 plant mineral nutrition, however, a dense root system in the superficial layers, where soil nutrients generally
294 accumulate, seems more favorable. In fact, most part of the root system in the three studied species was
295 concentrated between 5 and 50 cm depth, with a maximum in the 20-35 cm soil layer (Fig. 3). But in the filtrating
296 sandy soils typical of many arid and semi-arid areas, such a mobile element as nitrate moves easily to depth (Austin
297 et al. 2004). In this case, a dense and fast root growth beyond 50 cm depth would be useful to better capture water
298 as well as nitrate before they move beyond the root zone (Richards et al. 2007). This feature was indeed observed

299 in the dry-habitat *C. quinoa* which produced abundant lateral roots at 75 cm depth as early as the fifth week of
300 growth, when none of the other populations had reached that depth yet (Figs. 1b and 4). These observations
301 substantiate those made in an independent experiment conducted on the same species, where dry-habitat *C. quinoa*
302 reached 1 m taproot length between 42 and 49 DAS, one to two weeks earlier than wet-habitat *C. quinoa* and *C.*
303 *hircinum*, while *C. pallidicaule* remained limited to the first 40 cm soil layer (Alvarez-Flores et al. 2014).

304 Differences in root architecture among populations from dry and wet habitats suggest an adaptive
305 response of the plants for soil resource capture by means of an improved foraging capacity of the root system in
306 the dry-habitat populations (Reynolds et al. 2004). In fact, the greater root link length in dry-habitat *C. quinoa*,
307 particularly at the very beginning of the root system growth (Fig. 8), was associated with a fast and vigorous
308 growth of the taproot in the early days after seed germination, then relayed by greater elongation of II and EI links
309 in the subsequent weeks (Fig. 6). This elongation dynamics associated to a vigorous root branching at depth (Figs.
310 1b and 4) explains how the dry-habitat *C. quinoa* rapidly developed a higher root foraging capacity than the wet-
311 habitat ecotype. In several wild and cultivated species, fast and vigorous rooting at depth was found crucial for
312 early seedling survival in environments where water and nutrients are scarce and variable (León et al. 2011; Singh
313 et al. 2010). In the most arid Andean highlands, quinoa farmers take advantage of this rooting pattern:
314 traditionally, quinoa fields in these rainfed agrosystems are sown every other year, and only seedlings with a
315 vigorous foraging capacity are able to reach the water stored at depth during the fallow year preceeding the crop
316 year (Joffre and Acho 2008).

317 Specific root length is another trait of importance for root foraging capacity, as it influences the capacity
318 of the root system to proliferate through the soil, with thick roots (low SRL) penetrating more easily than fine
319 ones, specially into dry or compacted soil layers (Cornelissen et al. 2003). In a comparison of nine shrub species
320 of the Atacama desert, low SRL appeared linked to higher seedling survival rate (Léon et al. 2010). In general,
321 low SRL values are characteristic of species from dry habitats that tend to have a conservative strategy of water
322 use, with a lower absorptive surface per unit of root biomass (Nicotra et al. 2002; Wright and Westoby 1999). Low
323 SRL in *C. quinoa* should thus enhance its ability to penetrate deeply tough soil layers and withstand low soil
324 moisture, at the same time that it improves the anchoring of plants significantly taller than those of *C. hircinum*
325 and *C. pallidicaule* (see PH and RCD values in Table 2). On the opposite, high SRL in *C. pallidicaule* could
326 compensate for its low rooting capacity by a higher nutrient transport efficiency and relative low investment in
327 root dry matter (Picon-Cochard et al. 2012). High SRL associated to the small plant height and low plant
328 productivity typical of *C. pallidicaule* could be part of a plant growth syndrome adapted to cold, high altitude
329 habitats where shallow soils supply only limited water and nutrient resources (Gade 1970; Poorter et al. 2011).

330 **Conclusion and perspectives**

331 The present study brings the first detailed report of root system architecture and growth dynamics in three little-
332 known Andean species of *Chenopodium*, including two cultivated ecotypes of *C. quinoa*. As a whole, the fast root
333 elongation, with thicker roots allowing deep soil penetration, and abundant and long external links conferring an
334 efficient soil exploration, make a suite of root traits that significantly improve the root foraging capacity of *C.*
335 *quinoa* compared to *C. hircinum* and *C. pallidicaule*. This should be particularly true for the dry-habitat *C. quinoa*,
336 which showed the highest ranking in these root foraging traits, and which actually thrives in a region of poor but
337 frequently deep sandy soils under extremely dry and cold climate. As for *C. pallidicaule*, it exhibited a particular

338 plant growth syndrome adapted to shallow soils at very high altitude. In both situations, specific suites of
339 architectural root traits are expressed from very early developmental stages to support initial seedling growth and
340 establishment which are crucial for field performance. These contrasted rooting syndromes agree with two
341 differential foraging strategies in dry environments described by several authors, namely: shallow root systems
342 exploring topsoil layers to benefit from seasonal rainfalls, versus deep root systems with thick roots feeding
343 from water stored at depth (Bauerle et al. 2008; Paula and Pausas 2011).

344 These findings identify some key root system attributes of the studied chenopods, particularly of *C.*
345 *quinoa* which, despite growing scientific and economic interest (Rojas et al. 2009), remains up to now roughly
346 parameterized in the few crop models developed for this species (see AquaCrop by Geerts et al. 2007, or STICS
347 by Lebonvallet 2008). The integration of these root parameters into plant growth models could allow for a more
348 accurate description and understanding of the different capacities of root foraging and nutrient uptake in the related
349 species or ecotypes (Pagès 2011). Similarly, such root traits could be exploited in breeding for drought adaptation
350 or low-input agriculture, though this would require some complementary studies to verify whether improved
351 seedling root attributes translate into improved performance of mature plants in the field (Manshadi et al. 2008;
352 Singh et al. 2010).

353 From an evolutionary perspective, one should bear in mind that natural selection as well as crop
354 domestication both rely on phenotypic selection (Lynch and Brown 2012). Considering that the higher root
355 branching and foraging capacity of *C. quinoa* is associated to a higher seed mass and higher biomass production
356 than in its wild progenitor, *C. hircinum*, or its diploid relative, *C. pallidicaule*, we hypothesize that these root
357 system traits have been indirectly selected during the polyploidization and domestication processes. Recent works
358 on improved root systems in water-limited crops suggest that such indirect impacts on root branching and foraging
359 might indeed have occurred in several crop species (Palta et al. 2011; Wasson et al. 2012).

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365 the seeds of *C. pallidicaule* and *C. hircinum*, and to Ivan Prieto, Marie-Laure Navas and Florence Volaire for their
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483 species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* 87: 85-97

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485

486 **Table 1** Origin of the four studied *Chenopodium* populations.

487 **Table 2** Mean values of seed mass, and plant and root system traits of four *Chenopodium* populations at 42 DAS.

488 SM: individual seed mass (mg/seed), TPM: total plant mass (g/plant), LA: leaf area (cm²/plant), PH: plant height

489 (cm), R:S: root shoot ratio (g/g), RCD: root collar diameter (mm), SRL: specific root length (m/g), TRL: total root

490 length (m/plant), TTN: total tip number, TLN: total link number, TQI: topological quotient index, TSI: topological

491 slope index, MLL: mean link length (II: Internal–Internal links, EI: External–Internal links, EE: External–External

492 links). (data show mean ± standard error, n = 5 except for SM (n = 120), different letters within a row show

493 significant differences at P = 0.05)

494 **Table 1** Origin of the four studied *Chenopodium* populations.

Species	Code	Provenance	Latitude	Longitude	Altitude (m)	Rainfall mean (mm/year)	SOM range (%) ^a
<i>C. hircinum</i>	HI	Aranjuez, Bolivia	16°33'S	68°36'W	3.200	550	0.4 – 1.5
<i>C. pallidicaule</i>	PA	La Paz, Bolivia	17°30'S	68°36'W	3.600	550	0.4 – 1.5
<i>C. quinoa</i>	QB	Jirira, Bolivia	19°51'S	67°34'W	3.700	250	0.2 – 0.4
<i>C. quinoa</i>	QC	Cunco, Chile	38°56'S	72°03'W	200	1.200	7 – 29

495 SOM: soil organic matter

496 ^a sources: HI, PA and QB: Lebonvallet (2008); QC: Alvear et al. (2005) and Reyes et al. (2011).

497

498 **Table 2** Mean values of seed mass, and plant and root system traits of four *Chenopodium* populations at 42 DAS.

499 SM: individual seed mass (mg/seed), TPM: total plant mass (g/plant), LA: leaf area (cm²/plant), PH: plant height
 500 (cm), R:S: root shoot ratio (g/g), RCD: root collar diameter (mm), SRL: specific root length (m/g), TRL: total root
 501 length (m/plant), TTN: total tip number, TLN: total link number, TQI: topological quotient index, TSI: topological
 502 slope index, MLL: mean link length (cm; II: Internal–Internal links, EI: External–Internal links, EE: External–
 503 External links). (data show mean ± standard error, n = 5 except for SM (n = 120), different letters within a row
 504 show significant differences at P = 0.05).

505

Traits	<i>C. quinoa</i> (dry habitat)	<i>C. quinoa</i> (wet habitat)	<i>C. hircinum</i>	<i>C. pallidicaule</i>
SM	4.89 ± 0.10 a	2.09 ± 0.04 b	1.50 ± 0.04 c	0.6 ± 0.01 d
TPM	2.00 ± 0.37 a	0.87 ± 0.10 b	0.40 ± 0.08 c	0.13 ± 0.03 d
LA	98.0 ± 3.7 a	54.0 ± 1.3 b	21.7 ± 4.8 c	10.0 ± 2.3 d
PH	8.4 ± 0.5 a	5.9 ± 0.5 b	4.5 ± 0.4 bc	3.5 ± 0.4 c
R:S	0.28 ± 0.01 a	0.39 ± 0.02 b	0.45 ± 0.01 c	0.31 ± 0.03 ab
RCD	4.90 ± 0.49 a	3.47 ± 0.49 b	2.31 ± 0.28 c	1.34 ± 0.27 d
SRL	57.9 ± 3.82 a	75.1 ± 12.2 ab	106.5 ± 10.0 b	179.7 ± 15.3 c
TRL	24.1 ± 3.4 a	16.4 ± 2.6 ab	12.7 ± 2.0 b	4.8 ± 0.4 c
TTN	525 ± 14.3 a	663 ± 12.4 b	449 ± 11 c	140 ± 8.1 d
TLN	1122 ± 64.6 a	1398 ± 62 b	816 ± 61.2 c	283 ± 46.1 d
TQI	0.77 ± 0.01 a	0.77 ± 0.01 a	0.77 ± 0.01 a	0.77 ± 0.01 a
TSI	0.72 ± 0.04a	0.80 ± 0.04 ab	0.87 ± 0.03 b	0.85 ± 0.04 ab
MLL II	1.0 ± 0.03 a	0.6 ± 0.02 b	0.5 ± 0.01 c	0.6 ± 0.03 b
MLL EI	2.0 ± 0.05 a	1.2 ± 0.03 b	1.7 ± 0.04 c	1.6 ± 0.08 c
MLL EE	1.7 ± 0.09 a	1.8 ± 0.11 a	1.8 ± 0.15 a	2.4 ± 0.28 b

506

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508

509 **Fig. 1** Time course of the root system growth of two typical plants of *Chenopodium hircinum* (above) and
510 *Chenopodium quinoa* from dry habitat (below) as observed in the rhizotron (DAS: days after sowing).

511 **Fig. 2** Root system topology: (a) Link types: EE (External-External), EI (External-Internal), II (Internal-
512 Internal). (b) Maximally herringbone topology: magnitude = altitude = 8. (c) Maximally dichotomic topology:
513 magnitude = 8, altitude = 4. In (b) and (c), the first number in each pair is the altitude from the root collar and the
514 second the link magnitude (modified from Arredondo and Johnson 1999).

515 **Fig. 3** Total root length distribution in the soil profile at 42 DAS in dry-habitat *C. quinoa* (QB), wet-habitat *C.*
516 *quinoa* (QC), *C. hircinum* (HI) and *C. pallidicaule* (PA) (mean \pm standard error, n = 5, letters show statistical
517 differences between populations at a given depth, P < 0.05).

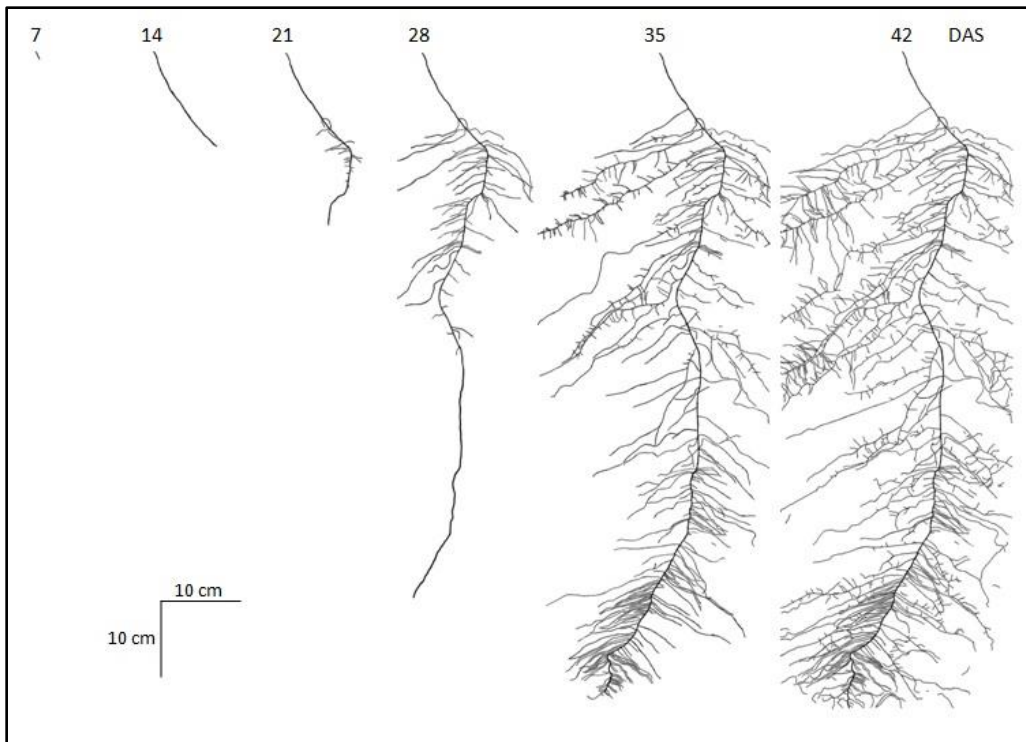
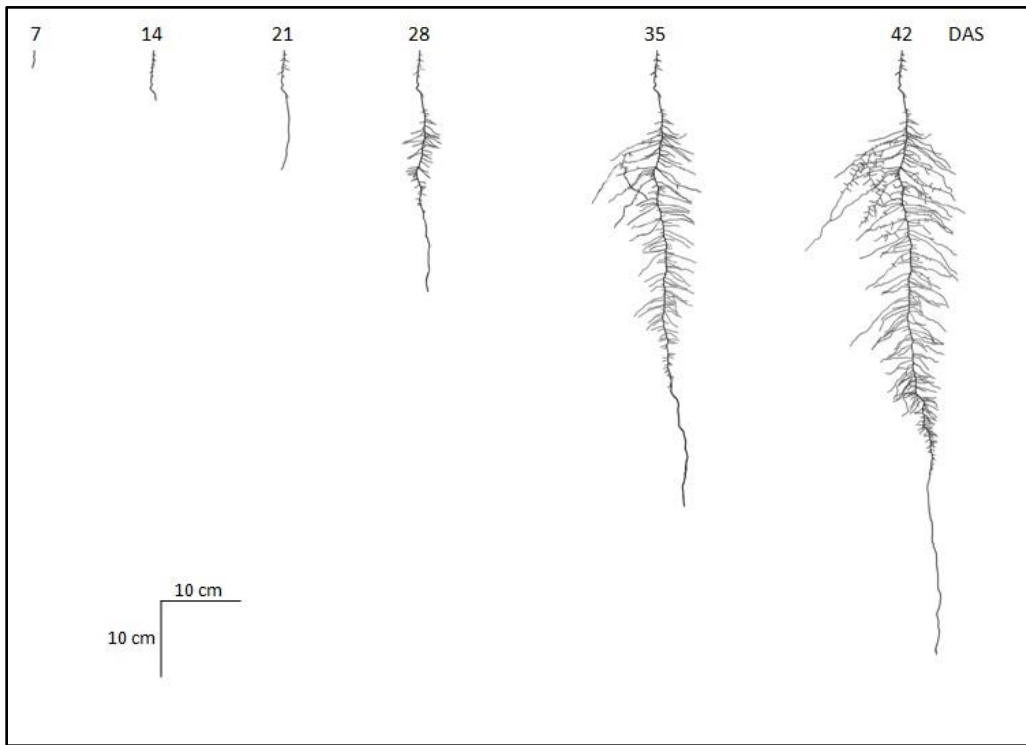
518 **Fig. 4** Vertical distribution of the mean number of new lateral roots appearing on the taproot during the
519 experiment in dry-habitat *C. quinoa* (QB), wet-habitat *C. quinoa* (QC), *C. hircinum* (HI) and *C. pallidicaule*
520 (PA) (each point is the mean of n = 5 plants).

521 **Fig. 5** Logarithmic regression of altitude (α) on magnitude (μ) of the root system observed during the experiment
522 in dry-habitat *C. quinoa* (Δ), wet-habitat *C. quinoa* (\blacktriangle), *C. hircinum* (\bullet) and *C. pallidicaule* (\circ) ($y = 0.81x +$
523 0.08 , $r^2 = 0.96$, n = 80 ; the dotted line corresponds to a maximally herringbone topology; see Material and
524 Methods for definitions of altitude and magnitude).

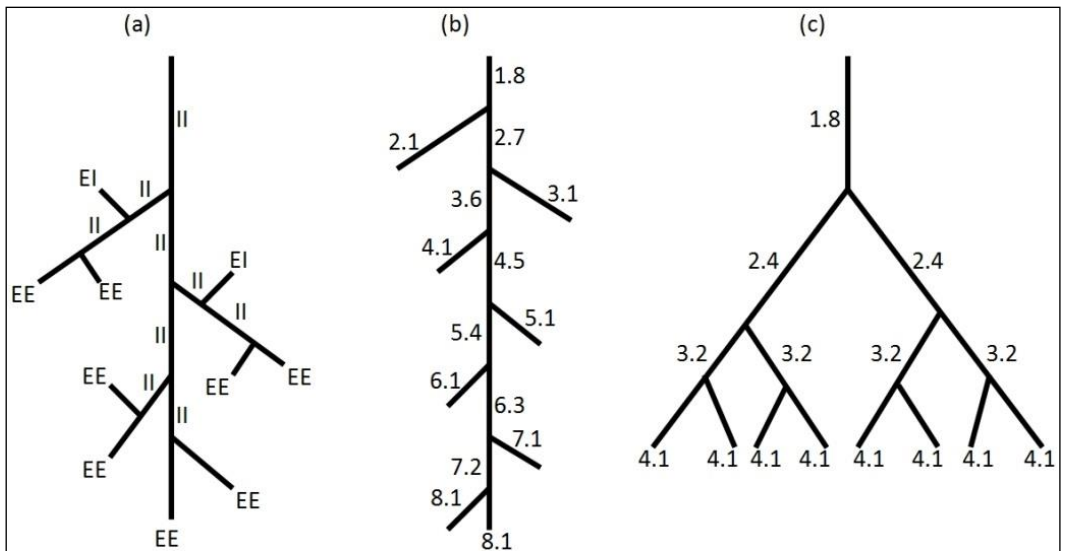
525 **Fig. 6** Mean cumulative length of the internal-internal (II), external-internal (EI) and external-external (EE) root
526 links per plant in the four studied *Chenopodium* populations (dry-habitat *C. quinoa*: black, wet-habitat *C. quinoa*
527 from wet habitat: dark grey, *C. hircinum*: light grey, *C. pallidicaule*: white) (n = 5, vertical bars show standard
528 errors, insets show root length on a log scale for a better appreciation of changes at early stages, see Fig. 2 for the
529 definition of II, EI and EE links).

530 **Fig. 7** Mean number of internal-internal (II), external-internal (EI) and external-external (EE) root links per plant
531 in four *Chenopodium* populations (same color chart as in Fig. 6) (n = 5, vertical bars show standard errors, insets
532 show link number on a log scale for a better appreciation of changes at early stages, see Fig. 2 for the definition
533 of II, EI and EE links).

534 **Fig. 8** Mean length of the internal-internal (II), external-internal (EI) and external-external (EE) root links in the
535 four studied *Chenopodium* populations (same color chart as in Fig. 7) (n = 5, vertical bars show standard errors,
536 see Fig. 2 for the definition of II, EI and EE links).

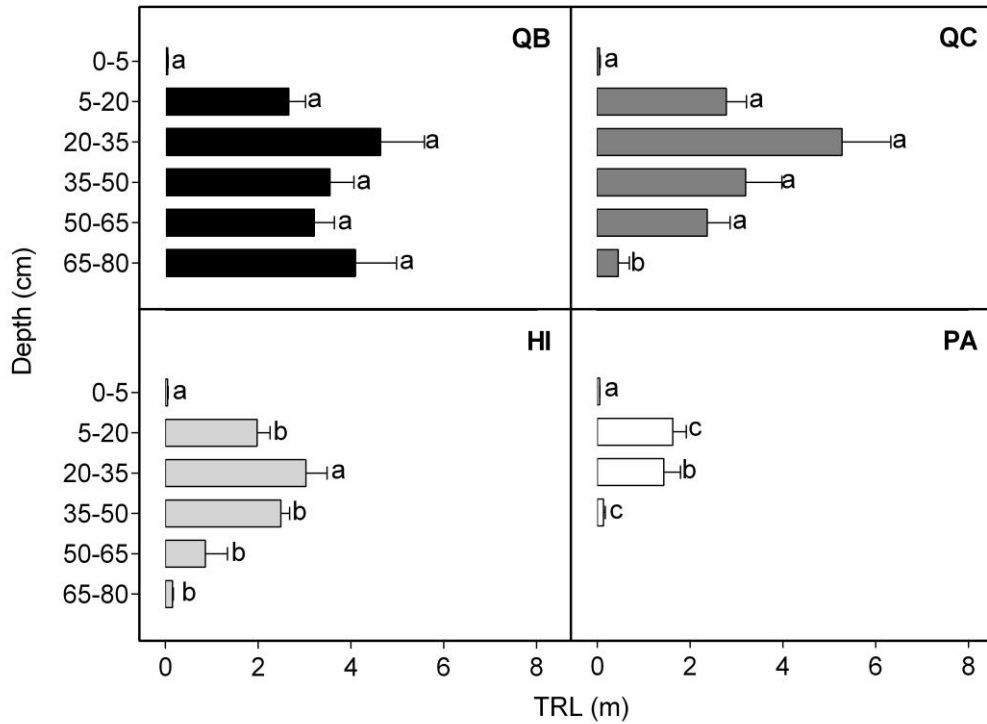


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541 habitat *Chenopodium quinoa* (below) as observed in the rhizotron (DAS: days after sowing).



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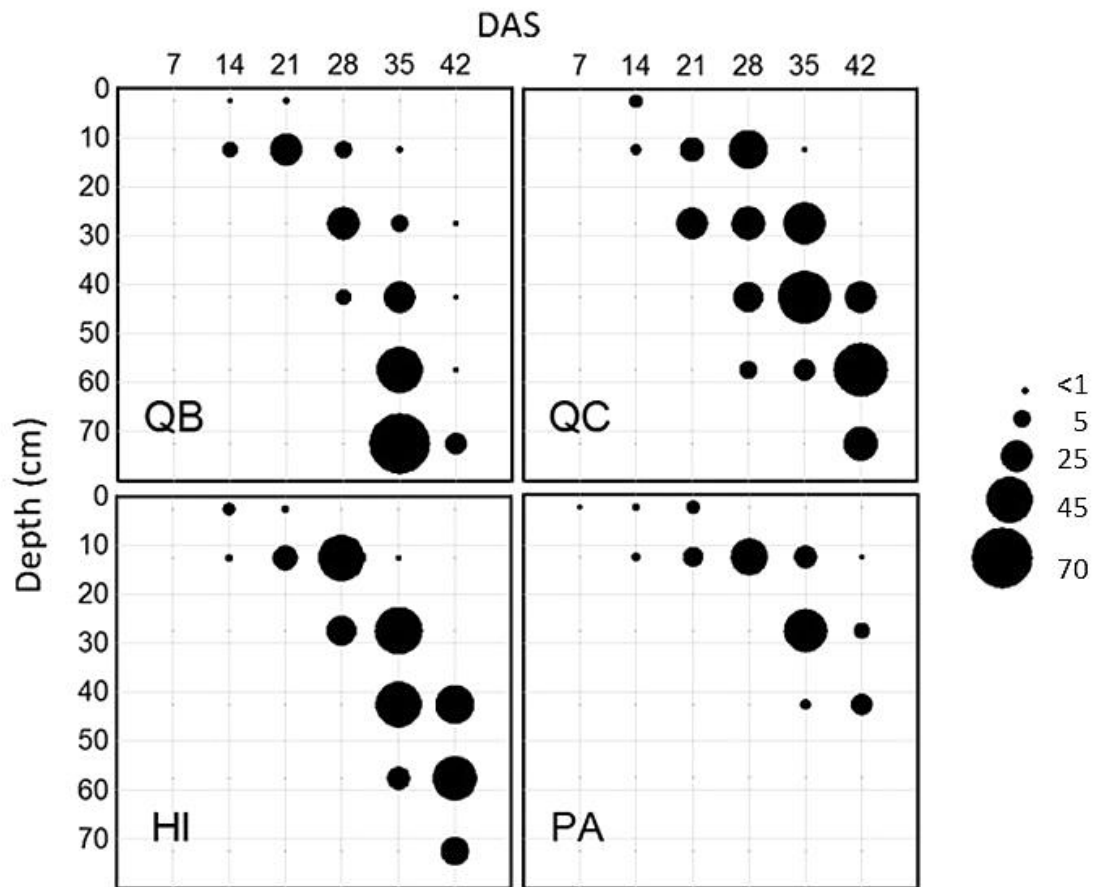
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Fig. 3 Total root length distribution in the soil profile at 42 DAS in dry-habitat *C. quinoa* (QB), wet-habitat *C. quinoa* (QC), *C. hircinum* (HI) and *C. pallidicaule* (PA) (mean \pm standard error, n = 5, letters show statistical differences among populations at a given depth, P < 0.05).

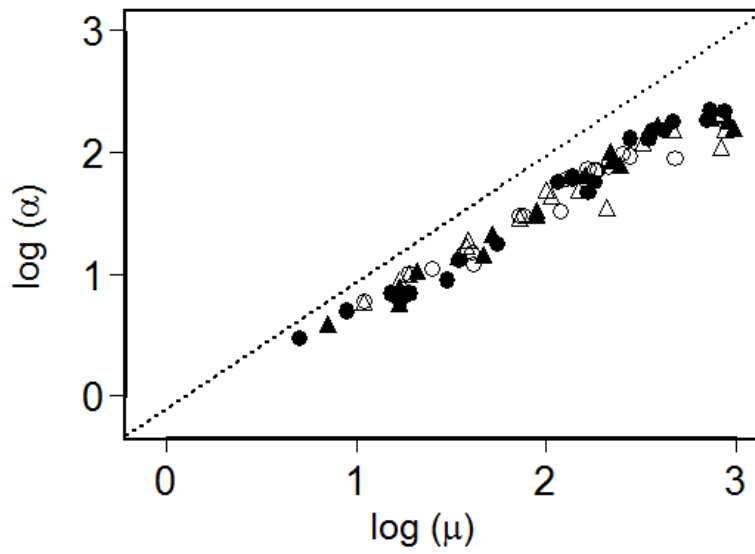
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Fig. 4 Vertical distribution of the mean number of new lateral roots appearing on the taproot during the experiment in dry-habitat *C. quinoa* (QB), wet-habitat *C. quinoa* (QC), *C. hircinum* (HI) and *C. pallidicaule* (PA) (each point is the mean of n = 5 plants).

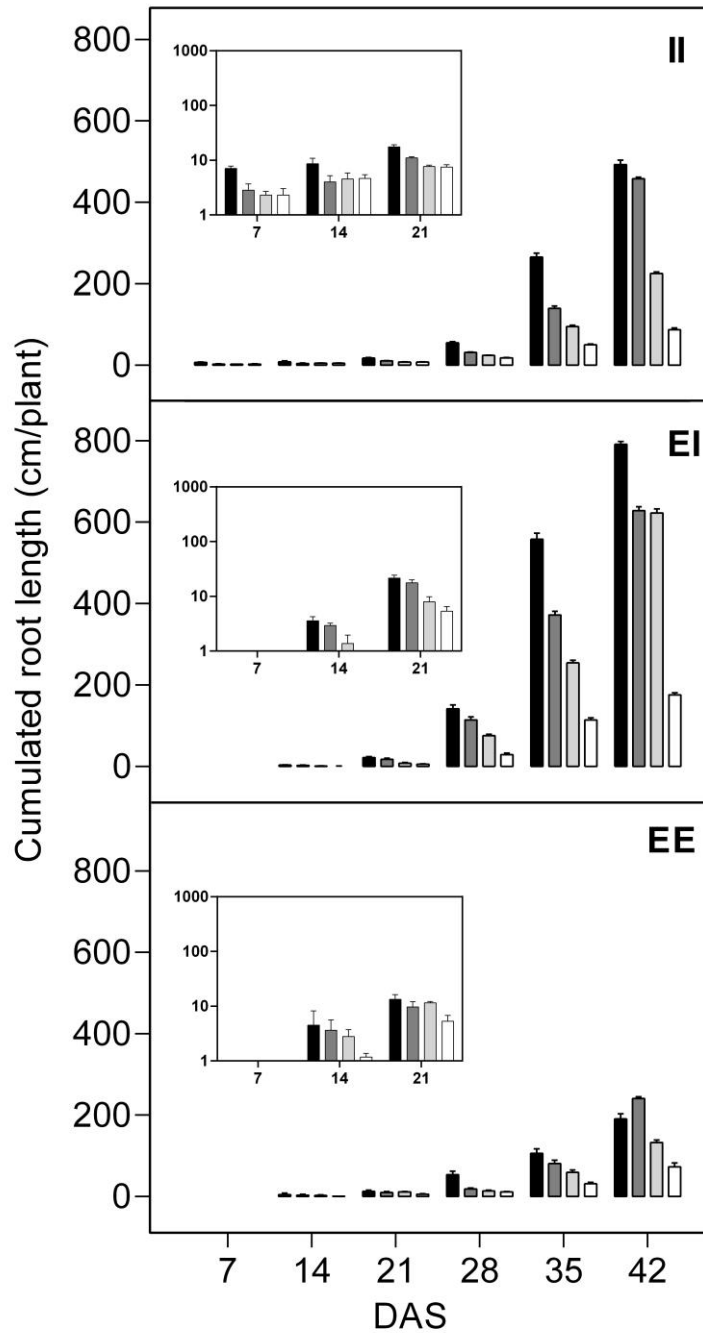
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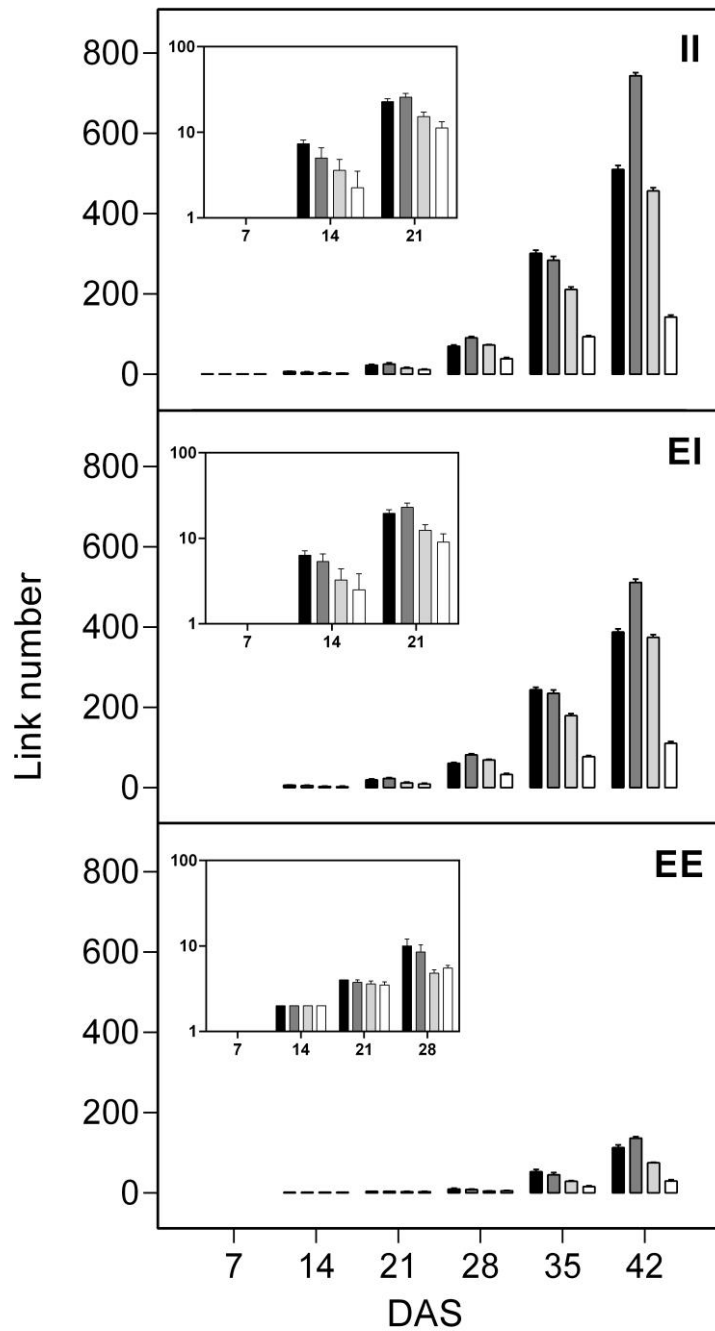
565 **Fig. 5** Logarithmic regression of altitude (α) on magnitude (μ) of the root system observed during the experiment
566 in dry-habitat *C. quinoa* (Δ), wet-habitat *C. quinoa* (\blacktriangle), *C. hircinum* (\bullet) and *C. pallidicaule* (\circ) ($y = 0.81x +$
567 $0.08, r^2 = 0.96, n = 80$; the dotted line corresponds to a maximally herringbone topology; see Material and Methods
568 for definitions of altitude and magnitude).

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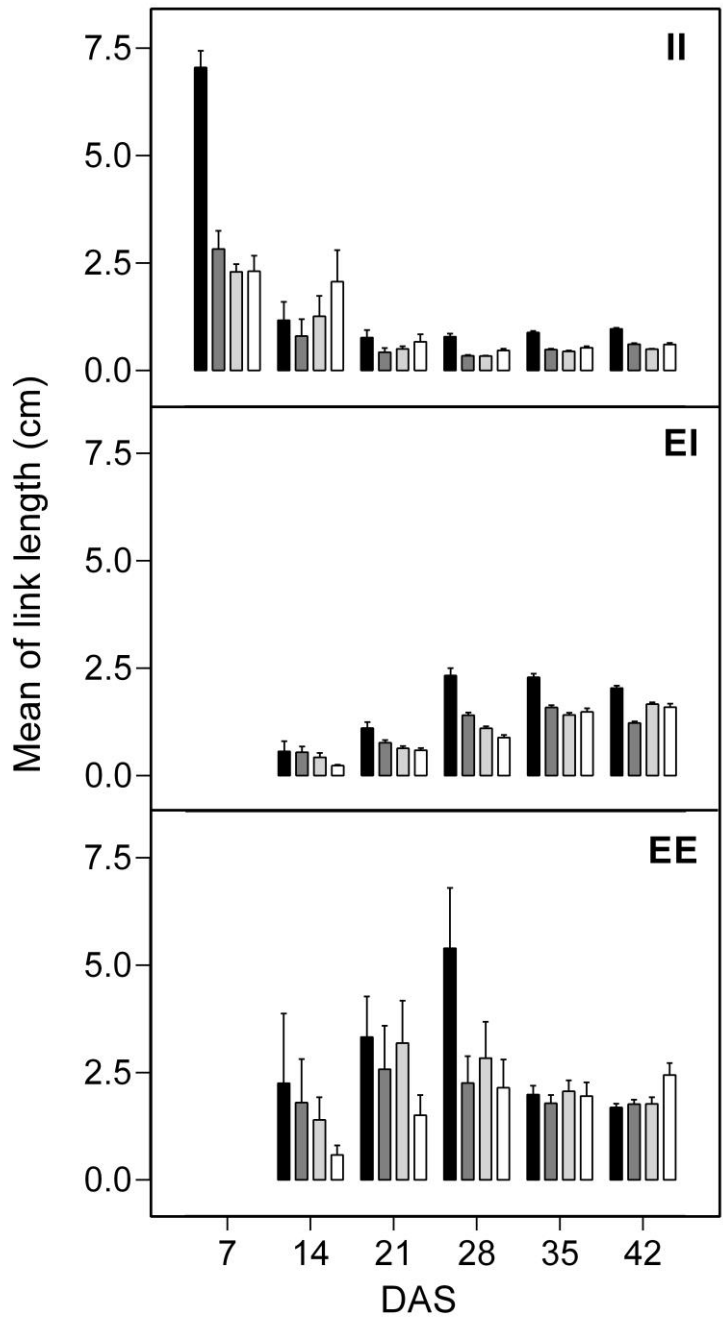


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Fig. 6 Mean cumulative length of the internal-internal (II), external-internal (EI) and external-external (EE) root links per plant in the four studied *Chenopodium* populations (dry-habitat *C. quinoa*: black, wet-habitat *C. quinoa*: dark grey, *C. hircinum*: light grey, *C. pallidicaule*: white) (n = 5, vertical bars show standard errors, insets show root length on a log scale for a better appreciation of changes at early stages, see Fig. 2 for the definition of II, EI and EE links).



577
 578 **Fig. 7** Mean number of internal-internal (II), external-internal (EI) and external-external (EE) root links per plant
 579 in four *Chenopodium* populations (same color chart as in Fig. 6) (n = 5, vertical bars show standard errors, insets
 580 show link number on a log scale for a better appreciation of changes at early stages, see Fig. 2 for the definition of
 581 II, EI and EE links).
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583
 584 **Fig. 8** Mean length of the internal-internal (II), external-internal (EI) and external-external (EE) root links in the
 585 four studied *Chenopodium* populations (same color chart as in Fig. 6) (n = 5, vertical bars show standard errors,
 586 see Fig. 2 for the definition of II, EI and EE links).
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