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

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Abstract

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

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

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

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

Keywords *Chenopodium quinoa* · *Chenopodium hircinum* · *Chenopodium pallidicaule* · Ecotypes · Rhizotron · Root traits · Root system topology

Introduction

Root system architecture considers the spatial structure, the geometric features and the branching complexity of the roots of whole plants (Fitter 1987). It has profound implications for plant growth and species distribution, enabling individual plants to cope with changing environmental conditions and plant species to thrive in different ecological niches (Lynch 2005; White et al. 2013). Differences in root system architecture are associated with differences in soil resource acquisition, not only between contrasting functional types (Paula and Pausas 2011; Roumet et al. 2006; Taub and Goldberg 1996), but also among genera and species of the same growth form originating from contrasted ecological habitats (Leva et al. 2009). *Chenopodium* is one of these genera that thrive under strikingly contrasted environments, notably in South America where strong ecological

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gradients develop from Amazonian or Southern Pacific lowlands of humid climate and nutrient-rich soil up to the Andean highlands of dry and cold climate and nutrient-poor soil (Troll 1968; Di Castri and Hajek 1976). In these highly contrasted habitats, annual chenopods have diversified, some of them as spontaneous chenopods (e.g. *C. hircinum* Schrad., *C. petiolare* Kunth, *C. carnosolum* Moq.), others as cultivated species like quinoa (*C. quinoa* Willd.) and cañahua (*C. pallidicaule* Aellen) with many ecotypes (Kühn et al. 1993; Vargas et al. 2011). None of these chenopods show the morphophysiological adaptations typical to dry or saline habitats environments, such as Kranz anatomy, C4 photosynthetic pathway, or succulence (Fuentes-Bazan et al. 2012). For surviving, these plants thus rely on common plant and life-history traits that control the balance between resource capture and resource use, for which root system architecture plays a key role (Singh et al. 2010).

Examining the various patterns of root system branching or topology, theoretical and experimental works suggest that a root system consisting of only a main axis and primary laterals (herringbone topology) would favour nutrient acquisition in low-resource habitats because it minimizes intraplant root competition (Fitter et al. 1991; Taub and Goldberg 1996). Conversely, a dichotomous topology associated with shorter root links (the segments of root between two nodes, or between a node and a root tip) and greater link number, would favour nutrient capture in high-resource habitats (Fitter et al. 1991; Taub and Goldberg 1996). Most chenopods show a herringbone root system (Fitter 1987), but detailed descriptions are lacking to appreciate differences among species or among ecotypes of contrasted habitats. Regarding plant species adapted to cold and high altitude habitats, they might develop a growth syndrome that includes short plant height and high root mass fraction (Poorter et al. 2011). Growing at elevations up to 4,600 m, the small-sized *C. pallidicaule* is renowned as the hardest Andean chenopods (Gade 1970) and yet the adaptive value of its morphophysiological traits remains unknown.

In a context of increasing scarcity of agricultural water and nutrients, improved root system functioning could enhance crop productivity while decreasing crop input requirements (De Dorlodot et al. 2007; Lynch and Brown 2012; White et al. 2013). Cultivated chenopod species such as *Ch. quinoa* and *Ch. pallidicaule* are promising candidates for exploring plant ideotypes suited to low-input agriculture (Rojas et al. 2009). In fact, for

centuries, Andean farmers have selected tens of local chenopod varieties for their hardiness under harsh climate and poor soil conditions (Bonifacio 2003). As it happened in other crop species (Hammer et al. 2009; Palta et al. 2011; Wasson et al. 2012), unconscious selection for improved rooting capacity is likely to have occurred in these Andean chenopod crops. Exploring the morphological variation in root architecture, and particularly the contrast between wild and cultivated species, would help testing this hypothesis of unconscious selection as well as defining root system ideotypes that optimize soil resource uptake.

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

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

Materials and methods

Study site and plant populations

The study was conducted outdoor under a transparent rain shelter at the CEFÉ-CNRS experimental field (Montpellier, France, 43°38'19"N, 3°51'46"E), from the 11th of March to the 22th of April 2011. Four *Chenopodium* population samples from contrasting

habitats were compared: *C. hircinum* and *C. pallidicaule* both from semi-arid highlands with nutrient-poor soils, *C. quinoa* from temperate lowlands with nutrient-rich soils (wet habitat), *C. quinoa* from arid and cold highlands with nutrient-poor soils (dry habitat) (Table 1). *C. hircinum* is a wild tetraploid species, *C. pallidicaule* is a domesticated diploid, and *C. quinoa* is a domesticated tetraploid. The wet-habitat *C. quinoa* pertains to the coastal quinoa ecotype of Chile while the dry-habitat *C. quinoa* is representative of the Salar quinoa ecotype of Bolivia. The seeds of *C. quinoa* and *C. pallidicaule* were from local landraces without pedigree. They were collected directly at the specified sites, as were the seeds of *C. hircinum*. In the four studied populations, seeds were selected for their size homogeneity and sterilized with sodium hypochlorite (1 %) for 10 min before sowing in rhizotrons at 3 cm depth.

Rhizotrons

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

Soil substrate and growth conditions

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 8.08, CEC Metson 9.02 cmol⁺/kg, and C/N 11.2. Prior to the experiment, the substrate was dried and

sterilized to 120 °C for 48 h. Then, it was humidified using a nutritive solution (N: 16 %, P: 10 %, K: 24 %, MgO: 3 %, micro-elements: 2.5 g/L). When the experiment started, rhizotrons were at field capacity (0.12 cm³/cm³) and no more water was applied until the end of the study. Over the course of the experiment, air temperature at 150 cm 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 and 35.2 °C (mean=14.9 °C±0.05), and air relative humidity varied between 30 and 89 % (mean=61 %±0.5). These conditions of temperature and soil humidity grossly satisfied the optimal growth requirements of the studied populations and no sign of plant physiological stress (e.g. leaf wilting, slow plant growth) was detected. Apart from being a convenient substrate in a comparative study under controlled conditions, the sandy substrate fitted the soil conditions commonly experienced by *C. pallidicaule* and the dry-habitat *C. quinoa* in their native highlands. As regards *C. hircinum* and the wet-habitat *C. quinoa*, their natural environments show a range of soil conditions, including sandy ones. The overall satisfactory growth of these plants in the present experiment indicates that they did not suffer any physical or nutritional limitation due to the soil substrate.

Plant sampling and measurements

Three days after emergence, plants were thinned to one seedling per rhizotron, and five replicate plants per population were followed weekly from 7 to 42 days after sowing (DAS) for non-destructive growth measurements. Root growth of each replicate plant was recorded weekly by tracing on a transparent acetate sheet the root axes visible through the windowpane of the rhizotron. The root system images were then

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

SOM soil organic matter

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

scanned at a resolution of 400 dpi (Acer Scan 300F, 6684 03A) (Fig. 1) and analyzed with the morphological and architectural procedures of the WinRHIZO Pro2009 software (Regent Instruments Inc., Quebec, Canada). The following root traits were calculated: total tip number (TTN), total link number (TLN), total root length (TRL, m) and total root length per link type (see Fig. 2a for a definition of root link types). The number of new

lateral roots appearing on the taproot in successive soil layers was also counted each week.

Following Glimskär (2000), two root topological indices were calculated. The topological quotient index (TQI) for individual plants at 42 DAS was calculated as the ratio $\log(\alpha)/\log(\mu)$, with α representing the altitude of the root system (i.e. the number of links of the longest path from the root collar to an external tip) and μ its

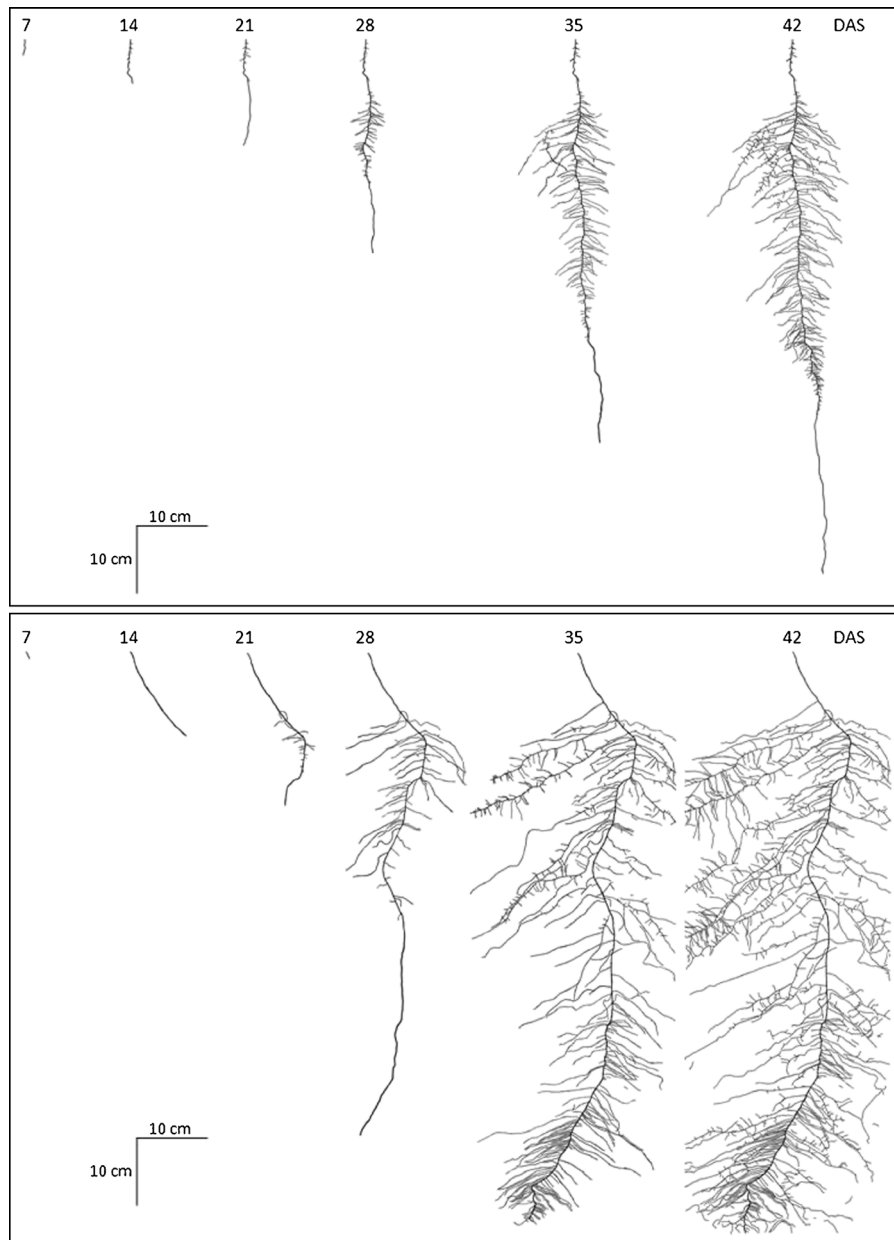
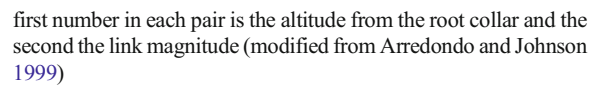


Fig. 1 Time course of the root system growth of two typical plants of *Chenopodium hircinum* (above) and *Chenopodium quinoa* from dry habitat (below) as observed in the rhizotron (DAS: days after sowing)



Seedlings of dry-habitat *C. quinoa* showed the most vigorous growth, resulting in higher plant height and deeper root system during the course of the experiment, and higher leaf area, root collar diameter and biomass

production at 42 DAS (Table 2). At that time, *C. pallidicaule*, the least vigorous of the studied populations, was only 6.5 % 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 terms of total root length. *C. hircinum* and wet-habitat *C. quinoa* showed intermediate values, with the wild *C. hircinum* always less productive than the cultivated *C. quinoa*, essentially due to lower aboveground growth. These differences in seedling growth among the studied populations were in relation with their respective mean seed mass (SM, Table 2). Despite contrasted growth capacities, *C. pallidicaule* and dry-habitat *C. quinoa* showed similar biomass allocation patterns with R:S ratios of 0.31 and 0.28 respectively, significantly lower than those observed in wet-habitat *C. quinoa* (0.45) and *C. hircinum* (0.39).

Root system profile and branching dynamics

After 6 weeks of plant growth (42 DAS), the vertical distribution of the root system showed significant differences among populations and among soil layers (Fig. 3). In each soil layer, the number of root tips was

highly correlated to the root length ($r=0.97$, $P<0.001$, $n=24$) and both traits showed similar vertical distributions. *C. quinoa* from dry and wet habitats had similar root profiles down to 65 cm depth, with maximum root development 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 soil). Beyond a 65 cm depth, dry-habitat *C. quinoa* showed significantly higher root colonization than the wet-habitat ecotype (ca. 4 m of root against 0.5 m respectively). Compared to *C. quinoa*, *C. hircinum* and *C. pallidicaule* showed significantly less root development, although the former still colonized deep soil while the latter was almost exclusively limited to the 35–50 cm layer (Fig. 3).

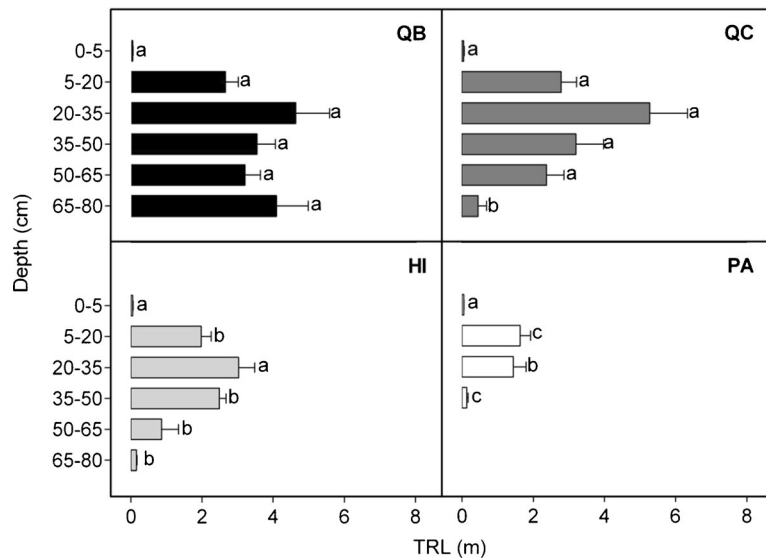
These patterns of vertical root distribution at 42 DAS resulted from the progressive proliferation of the root system through the soil profile (Fig. 1). The sequential analysis of the number of new lateral branches appearing on the taproot during the experiment revealed contrasted dynamics among the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

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

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

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

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 between populations at a given depth, $P<0.05$)



these two populations was in a more extended period of root proliferation in wet-habitat *C. quinoa*, starting 1 week earlier than in *C. hircinum*. By contrast, in dry-habitat *C. quinoa*, root branching was maximum at 75 cm as soon as 35 DAS, when none of the other populations had yet reached that depth. In *C. pallidicaule*, root branching occurred over the same period of time as in the other populations but at a much lower rate, and it hardly passed the 30 cm soil depth.

Root segment and root system morphology

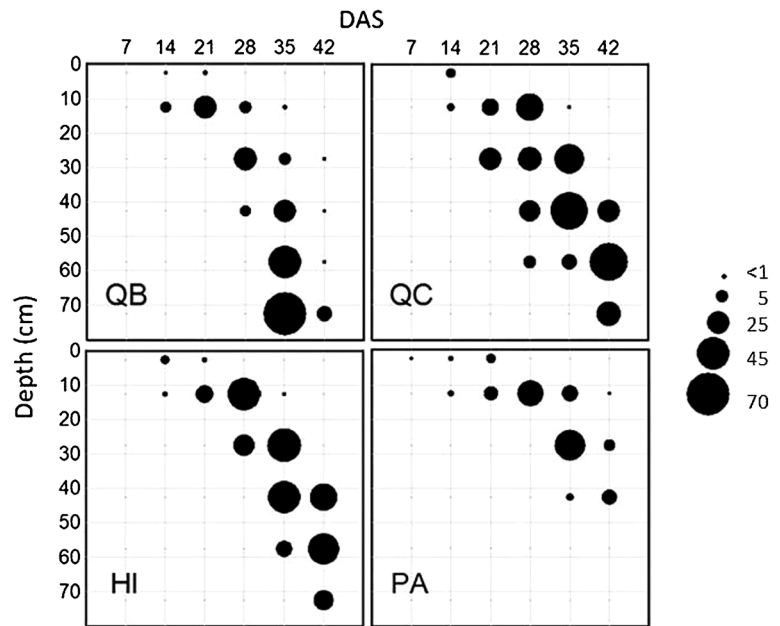
The morphology of individual root segments varied greatly among the studied populations, with SRL in *C. pallidicaule* showing roots three-fold finer on average than those of dry-habitat *C. quinoa*, the other two populations having intermediate values (Table 2). With regard to the shape of the root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

Root system architecture

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

A thorough analysis of the different kinds of root links reveals contrasted dynamics of root branching among the studied populations (Figs. 6, 7 and 8). Except in the first 3 weeks when the root system was essentially limited to the taproot (see Fig. 1), EI links concentrated most of the total root length in the four populations (Fig. 6). Considering the cumulated root length per link type, the highest increase was observed between 28 and 35 DAS in dry-habitat *C. quinoa*, particularly in EI links which, by the end of the experiment, totalled 8 m per plant on average (53 % of the total root length) (Fig. 6). In comparison, EI links in *C. pallidicaule* at the same stage totalled only 2 m per plant on average, though they amounted to a similar proportion of the total root length. Decomposing the total root length in its two components (namely: the mean number and the mean length of the different links, Figs. 7 and 8), it appeared that temporal changes in total root length reflected mostly the changes in link number ($r=0.84$, $P<0.001$, $n=65$) and not those in mean link length ($r=0.02$, $P>0.1$, $n=65$). The number of EI and EE links increased progressively from 14 DAS on, with EI links always in a

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)



higher proportion than EE links in all populations (Fig. 7). The appearance of new links reached its highest rate by the end of the experiment with wet-habitat *C. quinoa* showing the highest rate of root branching.

Regarding the mean length of the different types of links, considerable variation was shown with maximal values of nearly 7 cm observed in the young taproot of the dry-habitat *C. quinoa*, while the taproot of the other populations was limited to about 2 cm at that early developmental stage (Fig. 8). From 14 DAS on, the mean length of II links decreased rapidly as a consequence of the emergence of new lateral roots. While mean link length did not show much time variations

from 28 DAS on, it varied significantly among populations, with constantly longer II and EI links in dry-habitat *C. quinoa* than in the other three populations (Fig. 8 and Table 2). This trait compensated for lower or equal link numbers in this ecotype compared to that from wet habitat (Fig. 7 and Table 2), resulting in higher TRL in the dry-habitat *C. quinoa*, with a non-significant trend when considering the whole plant root system (Table 2, $P=0.12$) but a highly significant difference as regards the cumulated EI segments (Fig. 6, $P<0.001$) which formed the major part of the entire root system.

Discussion

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

This study found significant variation in initial seedling size (TPM or PH, Table 2) among three Andean *Chenopodium* species, with *C. quinoa* producing two to five-fold more biomass than *C. hircinum* and up to 15-fold more than *C. pallidicaule*. Among the two *C. quinoa* ecotypes, the one from the dry habitat showed the most vigorous growth, which should give it a decisive advantage since initial seedling size strongly determines early plant survival in arid environments (León et al. 2011). As observed in other wild and cultivated species (Coomes and Grubb 2003; Bertholdsson and

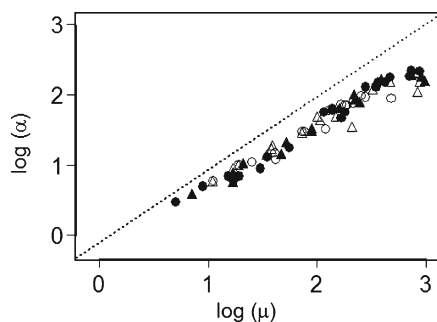


Fig. 5 Logarithmic regression of altitude (α) on magnitude (μ) of the root system observed during the experiment in dry-habitat *C. quinoa* (white triangle), wet-habitat *C. quinoa* (black triangle), *C. hircinum* (black circle) and *C. pallidicaule* (white circle) ($y=0.81x+0.08$, $r^2=0.96$, $n=80$; the dotted line corresponds to a maximally herringbone topology; see Material and methods for definitions of altitude and magnitude)

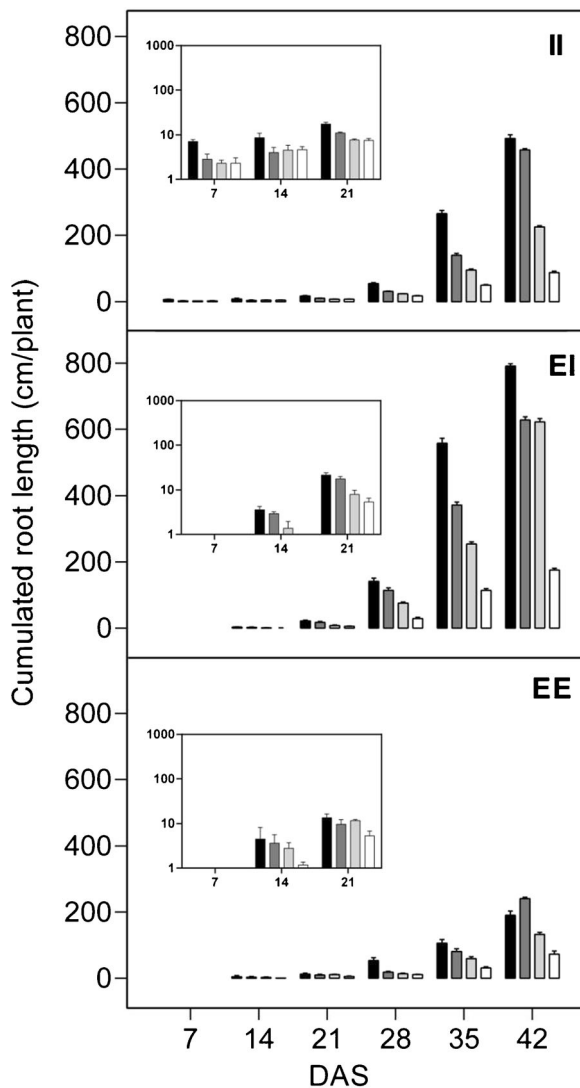


Fig. 6 Mean cumulative length of the internal-internal (II), external-internal (EI) and external-external (EE) root links per plant in the four studied *Chenopodium* populations (dry-habitat *C. quinoa*: black, wet-habitat *C. quinoa*: dark grey, *C. hircinum*: light grey, *C. pallidicaule*: white) ($n=5$, 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)

Kolodinska Brantestam 2009), the ranking in plant vigor among the studied populations was related to the differences in individual seed mass. This contrast between species did not affect the overall shape of the root system: all showed similar root topological indices (Table 2) with values characteristic of herringbone root systems, a feature commonly observed in chenopod species (Fitter 1987). Such similar topological indices

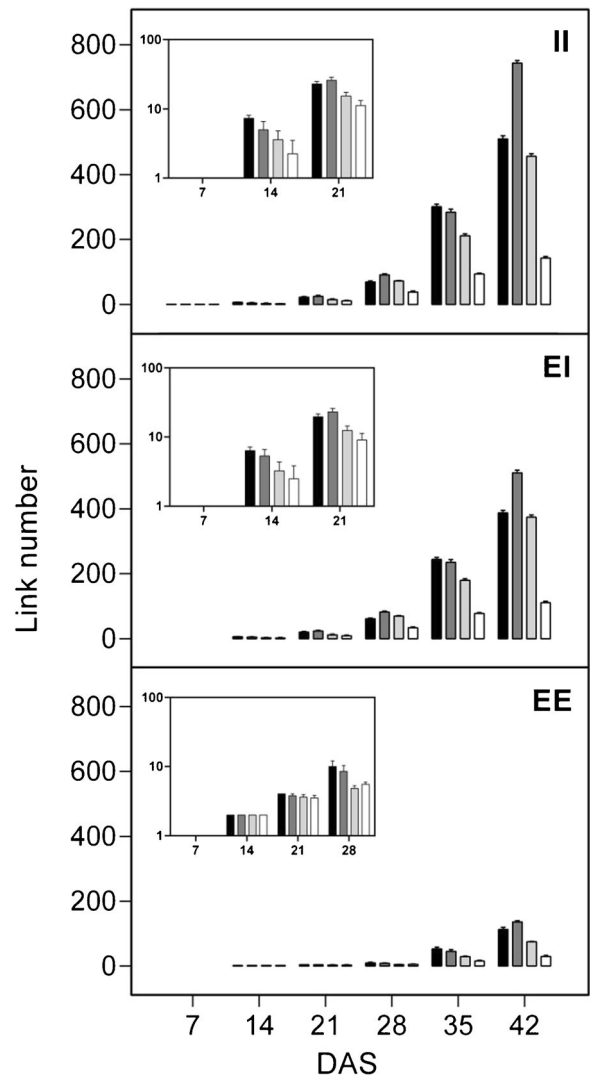


Fig. 7 Mean number of internal-internal (II), external-internal (EI) and external-external (EE) root links per plant in four *Chenopodium* populations (same color chart as in Fig. 6) ($n=5$, vertical bars show standard errors, insets show link number on a log scale for a better appreciation of changes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

could reflect the phylogenetic closeness of the studied species. In fact, *C. quinoa* was probably domesticated from *C. hircinum*, this latter being also a wild relative of *C. pallidicaule* (Gandarillas 1984). An alternative explanation to this topological similarity arises when comparing our results to those of Glimskär (2000). In his study on forbs and grasses grown at different nitrogen levels, a quite general relationship emerges between altitude (α) and magnitude (μ) with a curvature in the $\log(\alpha) / \log(\mu)$ relation suggesting a general size effect.

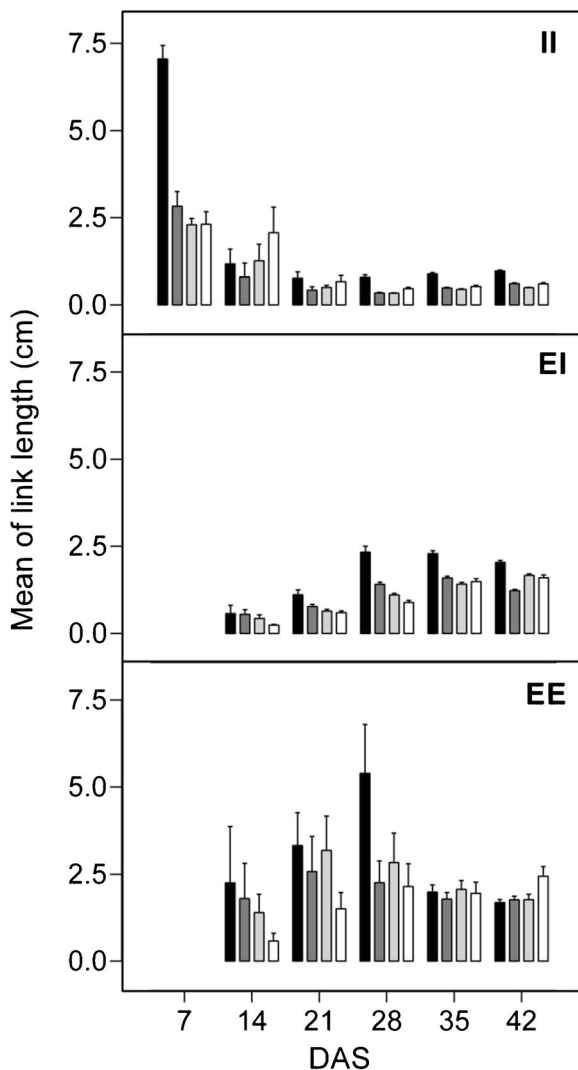


Fig. 8 Mean length of the internal-internal (II), external-internal (EI) and external-external (EE) root links in the four studied *Chenopodium* populations (same color chart as in Fig. 6) ($n=5$, vertical bars show standard errors, see Fig. 2 for the definition of II, EI and EE links)

Interestingly, the curvature in Glimskär's data appears at $\log(\mu)$ near 3, with $\log(\alpha)$ leveling near 2.4, both values which are quite close to our own data for three chenopod species (Fig. 5). The leveling in the altitude / magnitude relationship as plants grow could have an ontogenetic explanation related to the continued branching of a not strictly herringbone root system. After an initial period of seedling growth dominated by the elongation and branching of the main root, lateral roots begin to emerge from internal links, thus forming

new external links (EI) which directly increase the root system magnitude without necessarily increasing its altitude. In our study, such new lateral roots of second and higher orders emerged in great number from 21 DAS on (Figs. 4 and 7). The generality of the altitude / magnitude relation observed in forbs and grasses under different growth conditions (Arredondo and Johnson 1999; Fitter 1991; Glimskär 2000; Paula and Pausas 2011; Roumet et al. 2006; this study), suggests a general ontogenetic shift in the root topology of annual plant species, with lateral roots emerging in ever greater numbers (increasing magnitude) as soon as $\log(\alpha)$ exceeds a value of 2 approximately.

Due to this ontogenetic effect, the curvature in the altitude / magnitude relation points to a limitation of the topological slope index (TSI) as proposed by Fitter and Stickland (1991). Assuming a linear relation over a large size range, TSI overemphasizes small deviations from linearity (Glimskär 2000), which makes it a poorly suited index to discriminate root branching patterns in growing seedlings (Paula and Pausas 2011). As an alternative index, Glimskär (2000) proposed the TQI quotient calculated on individual plants, with a range of values from 0.69 to 0.79 for five different species. Our chenopod species fall within this range with an estimate of 0.77 (Table 2). Considering our results together with those of Glimskär, we suggest a general ontogenetic shift as a possible component of this size effect. Therefore, when evaluating species differences in root topology, we would recommend comparing not only plants belonging to a narrow size interval (Glimskär 2000), but also plants of similar developmental stages.

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

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

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

Among the *C. quinoa* populations, the one from the dry habitat had statistically fewer root tips and marginally fewer root links (Table 2) but consistently greater II and EI link lengths (Table 2, Fig. 8), resulting in marginally higher TRL values. Such compensation between link number and link length bears a general ecological significance as shown by Nicotra et al. (2002) who found, comparing 11 phylogenetically independent contrasts, that species originating from dry environments usually have fewer root links but with greater link length than species from wetter environments. From a functional point of view, greater root link length reduces the overlap between depletion zones of neighbouring branches and, thus, improves the root foraging efficiency particularly for mobile resources like nitrate or water (Arredondo and Johnson 2011; Fitter et al. 1991; Pagès 2011). In arid habitats where soil water recharge occurs during the wet season and where deeper soil layers maintain higher soil moisture, a fast elongation of the root system at depth seems more adapted to drought than multiplying root branches in the upper soil layers (Bauerle et al. 2008; Padilla and Pugnaire 2007; Reader et al. 1993). The vertical root growth allows the plants to access water resources at depth, while dense root colonization in the upper soil would rapidly lead to root competition and complete water depletion in the absence of new rainfall events. For the plant mineral nutrition, however, a dense root system in the superficial

layers, where soil nutrients generally accumulate, seems more favorable. In fact, most part of the root system in the three studied species was concentrated between 5 and 50 cm depth, with a maximum in the 20–35 cm soil layer (Fig. 3). But in the filtrating sandy soils typical of many arid and semi-arid areas, such a mobile element as nitrate moves easily to depth (Austin et al. 2004). In this case, a dense and fast root growth beyond 50 cm depth would be useful to better capture water as well as nitrate before they move beyond the root zone (Richards et al. 2007). This feature was indeed observed in the dry-habitat *C. quinoa* which produced abundant lateral roots at 75 cm depth as early as the fifth week of growth, when none of the other populations had reached that depth yet (Figs. 1b and 4). These observations substantiate those made in an independent experiment conducted on the same species, where dry-habitat *C. quinoa* reached 1 m taproot length between 42 and 49 DAS, 1 to 2 weeks earlier than wet-habitat *C. quinoa* and *C. hircinum*, while *C. pallidicaule* remained limited to the first 40 cm soil layer (Alvarez-Flores et al. 2014).

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

Specific root length is another trait of importance for root foraging capacity, as it influences the capacity of the root system to proliferate through the soil, with thick

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

Conclusion and perspectives

The present study brings the first detailed report of root system architecture and growth dynamics in three little-known Andean species of *Chenopodium*, including two cultivated ecotypes of *C. quinoa*. As a whole, the fast root elongation, with thicker roots allowing deep soil penetration, and abundant and long external links conferring an efficient soil exploration, make a suite of root traits that significantly improve the root foraging capacity of *C. quinoa* compared to *C. hircinum* and *C. pallidicaule*. This should be particularly true for the dry-habitat *C. quinoa*, which showed the highest ranking in these root foraging traits, and which actually thrives in a region of poor but frequently deep sandy soils under extremely dry and cold climate. As for *C. pallidicaule*, it exhibited a particular plant growth syndrome adapted to shallow soils at very high altitude. In both situations, specific suites of architectural root traits are expressed from very early developmental stages to support initial seedling growth and establishment which are crucial for field performance. These contrasted rooting syndromes

agree with two differential foraging strategies in dry environments described by several authors, namely: shallow root systems exploring topsoil layers to benefit from seasonal rainfalls, versus deep root systems with thick roots feeding from water stored at depth (Bauerle et al. 2008; Paula and Pausas 2011).

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

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

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