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Root architecture of *Arabidopsis* is affected by competition with neighbouring plants

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Abstract How roots detect and respond to the presence of neighbors is relevant to understand plant belowground interactions. The aim of the present work was to evaluate the effect of the presence of neighboring plants and the limited availability of phosphorus on root architecture. A target plant of *Arabidopsis thaliana* (Ler or Col) was surrounded by combinations of two individuals (Ler and Col), and subjected to different growth conditions (levels of activated charcoal (AC) and phosphorus). Both accessions consistently concentrated their roots towards the competition zone shared with a neighbor of the same accession, avoiding the side shared with the other accession. All these competition strategies disappeared when plants were limited by phosphorus or when activated charcoal was added to the growth media. Plants produced consistently fewer but longer lateral roots when activated charcoal was added to the growth media irrespective of the neighbors. Our results indicate a direct role of secondary metabolites present in the root exudates and phosphorus availability in the response of presence and identity of neighboring roots.

Keywords *Arabidopsis thaliana* · Root architecture · Root exudates · Root competition

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Introduction

To understand plant belowground competition, it is important to know how the roots detect and respond to the presence of their neighbors. A classical view indicates that root competition is mainly regulated by their intrinsic competition for nutrients and water (Nord et al. 2011). Other views suggest that belowground competition is mainly mediated by the active detection of the presence of neighbors and the discrimination between self- and non-self roots (Callaway 2002).

Competition for both belowground and aboveground resources occurs when plants grow near other plants either from the same species or from different species (Aphalo and Ballaré 1995; Aerts 1999). Belowground competition takes place when the depletion volumes of neighboring roots overlap, and thus these roots compete for the resources located at that particular volume of soil (Schenk et al. 1999; Ge et al. 2000; Rubio et al. 2001). Because the radius of the depletion volume varies among the different plant nutrients, roots can compete for some nutrients but not for others at a particular time and space. The notion of root overlapping fits better for diffusion-mobile nutrients such as phosphate rather than for mass flow-mobile nutrients like nitrate. Uptake of diffusion-mobile nutrients creates a concentration gradient at the root surface that progressively depletes nutrient concentration in the rhizosphere and drives diffusive flux of nutrients to the root (Schenk et al. 1999; Ge et al. 2000; Rubio et al. 2001).

Most of the published studies on root competition are based on the evaluation of biomass accumulation and/or allocation traits (Brisson and Reynolds 1994; Casper and Jackson 1997; Nord et al. 2011) rather than on root architecture (Maina et al. 2002; Semchenko et al. 2007b; Nord et al. 2011). Root architecture is defined as the spatial configuration of the root system and determines the soil domains explored by the plant in search of below-ground resources (Fitter 1991; Lynch 1995). Recently, a direct role of secondary metabolites present in the root exudates has been observed in the development of root architecture (Caffaro et al. 2011) and in self/non-self root recognition mechanisms (Semchenko et al. 2007a).

Three patterns of root architectural responses based on the presence of neighbors have been proposed (Brisson and Reynolds 1994; Semchenko et al. 2007a): (1) non-compensatory response, (2) compensatory response, and (3) overlapping-type response. In the non-compensatory response, root elongation is discontinued when neighboring roots are detected. As a result, absorption of water and nutrients in this zone is restricted and finally plant growth is affected. In the compensatory response, root growth is also inhibited in the overlapping zone with the neighboring root but the plant increases root growth far from the competition area (Nord et al. 2011). Finally, in the overlapping-type response, root systems have about the same structure than plants grown in isolation. Unfortunately, there are few examples in the literature addressing these three types of root responses probably because of the inherent difficulty to observe and evaluate root architecture in the obscure and three dimensional space of the soil.

To fully understand plant belowground interactions, it is relevant to know how the roots detect and respond to the presence of their neighbors. The aim of the present work was to evaluate (1) the effect of the presence of neighboring plants on root architecture, and (2) the role of root exudates and phosphorus (P) availability in the recognition of neighboring roots and subsequent development of root architecture. We selected two accessions of *Arabidopsis thaliana* to perform neighboring combinations. We reasoned that the selection of *Arabidopsis* as a test plant to answer these questions will provide a model for subsequent determination of the genetics involved in root recognition of neighbors.

Materials and methods

Plant material and growth conditions

Arabidopsis thaliana seeds Landsberg erecta (Ler) and Columbia (Col) accessions were surface-sterilized using a sodium hypochlorite solution (5 % v/v) for 15 min. Then, the seeds were washed briefly in 70 % (v/v) ethanol, rinsed five times with sterile distilled water, and placed in 5 cm wide Petri dishes containing 0.8 % agar. The Petri dishes containing the seeds were subjected to a two-day cold treatment (4 °C) followed by a red light treatment for 2 h and then placed in the dark for two days. When seedlings were five days old, they were transferred to 15 cm wide Petri dishes filled with 1.6 % agar and 100 ml of *A. thaliana* solution (Williamson et al. 2001) (Fig. 1a). Three plants in each Petri dish were placed 2.5 cm apart from each other and grown in a growth room at 25 ± 2 °C with continuous light (approximately 65 μmol m^{-2} s^{-1} photosynthetically active radiation). The distance between plants was chosen after running preliminary tests in order to minimize aboveground shading to avoid competition for light. The upper section of the agar in the Petri dish (1.5 cm from the top) was removed to provide a ledge to sit the seedling on it (Fig. 1a). Petri dishes were sealed with Parafilm®, arranged in a vertical position and separated from each other by pieces of cardboard to prevent access of light to the rooting zone.

Competition between two accessions of *A. thaliana*

A 2 × 3 × 3 factorial experiment was conducted to determine the degree of recognition among neighboring roots and to evaluate the changes in root architecture as affected by the presence of a neighboring plant. Each treatment consisted in a combination of three plants of Ler and Col. The target plant was the one placed at the center of two flanking plants (Fig. 1c). The factors analyzed were accession (E), growth conditions (GC), and neighbor (N). The factor E had 2 levels: Ler and Col. The factor GC had 3 levels: (1) control treatment with a standard P dose of 2,500 μM KH_2PO_4; (2) activated charcoal (AC) treatment in which 5 g/l were added to the growth media; and (3) low P treatment (10 μM KH_2PO_4). Finally, the factor N had the following combinations from the perspective of the central focal plant: two plants of the same accession (LLL or CCC, see Fig. 1c); one plant of each accession (LLC or CCL); and two plants of different accessions (CLC or LCL). In the low P treatment, KCl 2.5 mM was added to maintain a constant potassium concentration. AC was incorporated into the AC treatments under the assumption that it adsorbs carbon-containing compounds present in the root exudates and therefore, creates a medium free of some phytochemicals released by roots (e.g. Mahall and Callaway 1992; Lau et al. 2008; Weißhuhn and Prati 2009; Caffaro et al. 2011).

Measurements

After 20 days of the beginning of the treatments, the root trajectories of the target plants on the agar media were traced to a transparent plastic sheet. The drawings were scanned and the images analyzed with the public domain software Image J (http://rsbweb.nih.gov/ij/). The following root architecture measurements were taken: primary root length, number and length of lateral roots, average lateral

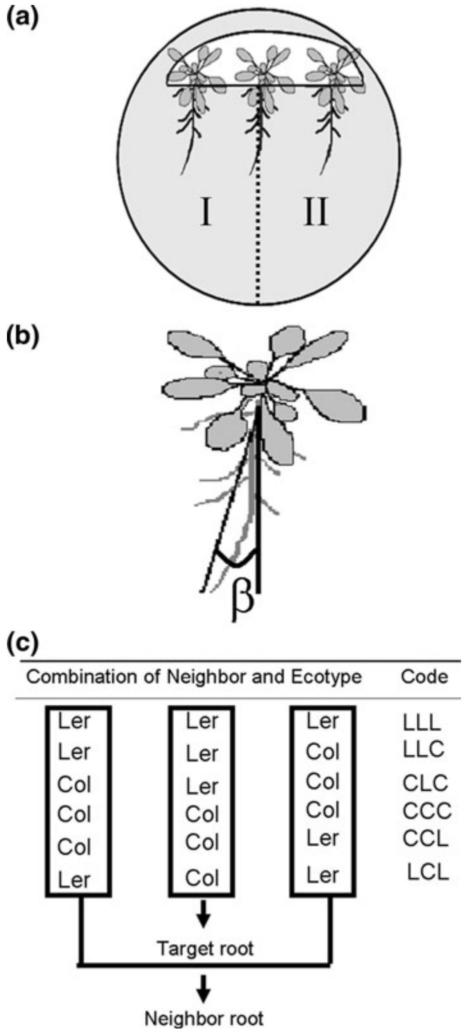

Fig. 1 Description of the experimental approach, measurements and treatments. **a** Experimental approach scheme with three plants per Petri dish. The two interaction zones were defined by creating an imaginary line at the center of the Petri dish (*dashed line* that defines zones I and II). The *upper* section of the agar in the Petri dish (1.5 cm from the top) was removed to provide a ledge to sit the seedling on it. **b** The diagram shows the calculation of primary root angle β of the target plant. **c** Combinations of the factors neighbor and accession. The target root is the one in the center (as in *panel* **a**) and is surrounded by two neighbor roots. A total of six neighbor and accession combinations were compared: neighbors and target plant from the same accession (Ler Ler Ler–LLL-; Col Col Col–CCC-). each neighbor from different accession (Ler Col Col-LCC-; Ler Ler Col-LLC); and both neighbors from the opposite accession, (Col Ler Col–CLC-; Ler Col Ler–LCL-)

root length, total root length (length of primary and lateral roots) and angle of the primary root. The angle (β, Fig. 1b) of the primary root growth was defined as the angle formed from the neck of the root to the tip. A positive or a negative sign was arbitrary assigned in case the root tip was orientated towards the right or the left side, respectively (Fig. 1b). Then the target plants were harvested, dried at 60 °C for 48 h and weighed. Total below- and aboveground biomasses were recorded.

Statistical analyses

Experimental units were arranged in a randomized complete block design. The number of replicates was 8. ANOVA and mean separation tests (LSD) were performed. Homogeneity of variances was tested using Bartlett's procedure. In case of rejection ($p < 0.01$), data were transformed. Due to the complexity of the experiment, specific contrasts were done to evaluate root architecture changes at every side of the competition zones. The contrasts were analyzed by Scheffé's test.

Results

Biomass accumulation and root architecture

ANOVA indicated that the GC factor strongly regulated biomass accumulation and root architecture of the target plant (Table 1). The other factors (E and N) did not exert significant effects on the target plant (Table 1). ANOVA also revealed that there were few significant interactions among the main factors. Only 1 (GC*N for total biomass) out of the 24 interactions was statistically significant (Table 1).

Total biomass of Ler and Col was not affected by the addition of AC but diminished 20 % under low P (Fig. 2a, b). In the low P treatment, biomass accumulation of the target plants that grew with a different neighbor at each side (LLC or CCL) decreased 10 % in comparison with plants that grew with neighbors of the same accession (LLL or CCC). In contrast, when plants grew with two different accessions (CLC or LCL) under low P conditions their biomass was increased 35 % in Ler and 51 % in Col (Table 1; Fig. 2a, b). In the control and AC treatments, we did not observe differences in plant growth based on the identity of the neighbor.

Compared to control plants, primary root length was reduced 25 % by the addition of AC to the growth media but was not affected by the low P treatment (Table 1; Fig. 3a, b). Total lateral root length was not affected by growth conditions (Table 1; Fig. 3c, d). However, average lateral root length was not affected by P, but adding AC resulted in a 21 % increase.

Root growth in the interaction zone

In the control treatment, the target plants of both accessions consistently showed an orientation of the primary root towards the left side of the Petri dish with an average angle of 6 degrees. When the growth conditions were changed

Table 1 *p*- values of ANOVA for the plant growth and root architecture traits of the target plant

	Total biomass	Root length			Lateral root number	Root angle
		Primary	Lateral (total)	Lateral (average)		
E	0.43	0.79	0.14	0.95	0.22	0.7
GC	<0.01	<0.01	0.10	<0.01	<0.01	<0.01
N	0.2	0.8	0.42	0.2	0.08	0.71
E*GC	0.45	0.24	0.11	0.18	0.16	0.75
E*N	0.2	0.17	0.13	0.63	0.09	0.43
GC*N	0.01	0.23	0.08	0.89	0.15	0.81
E*GC*N	0.17	0.37	0.13	0.48	0.14	0.92

Main factors were: growth conditions (GC, at three levels: control, low P, with AC); accession (E, at two levels: Ler and Col); neighbor [N, at three levels: two plant of the same accession (LLL, CCC); one plant of each accession (LLC, CCL) and two plants of different accessions (CLC, LCL)]. For accession and neighbor codes see Fig. 1c

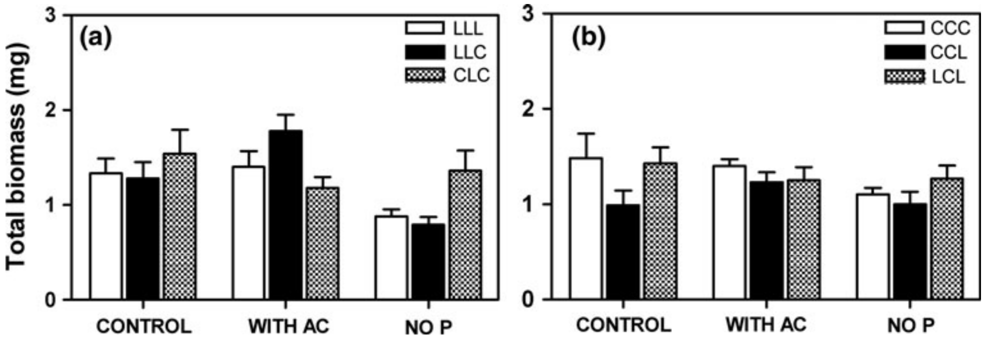

Fig. 2 Effect of phosphorus, neighbor and addition of 5 g/l of AC on plant growth of *A. thaliana* accession Ler (**a**) and Col (**b**). Main factors were: growth conditions (at three levels: control, with AC, no P); accession (at two levels: Ler and Col); Neighbor [at three levels: neighbors and target plant from the same accession (LLL, CCC); each neighbor from different accession (LLC, CCL); and both neighbors from the opposite accession, (CLC, LCL)]. For accession and neighbor codes see Fig. 1

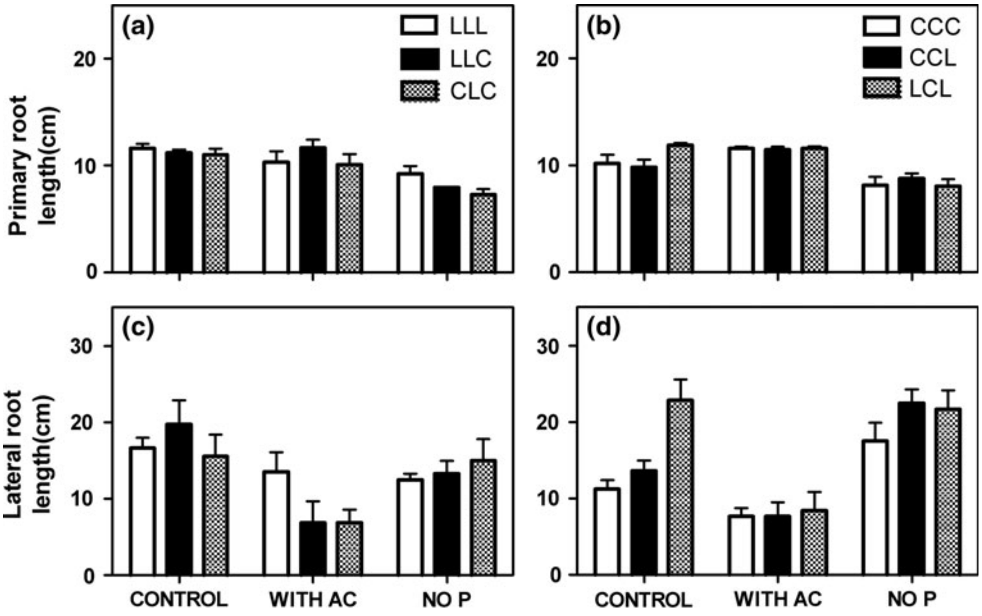

Fig. 3 Effect of treatments on primary root length (**a**, **b**) and total lateral root length (**c**, **d**) (see Fig. 1 for details). Two *A. thaliana* accessions were analyzed: Ler (**a**, **c**) and Col (**b**, **c**). Main factors were: growth conditions (at three levels: control, with AC, no P); accession (at two levels: Ler and Col); Neighbor [at three levels: neighbors and target plant from the same accession (LLL, CCC); each neighbor from different accession (LLC, CCL); and both neighbors from the opposite accession, (CLC, LCL)]. For accession and neighbor codes see Fig. 1 *Bars* represent the average of 8 plants ± SE

(either by adding AC or subtracting P from the growing media) the trend towards the left orientation of the primary root was less evident (Fig. 4a, b). The identity of the neighbor did not show clear effects on this parameter (Fig. 4a, b), and the interactions among treatments were not significant (Table 1).

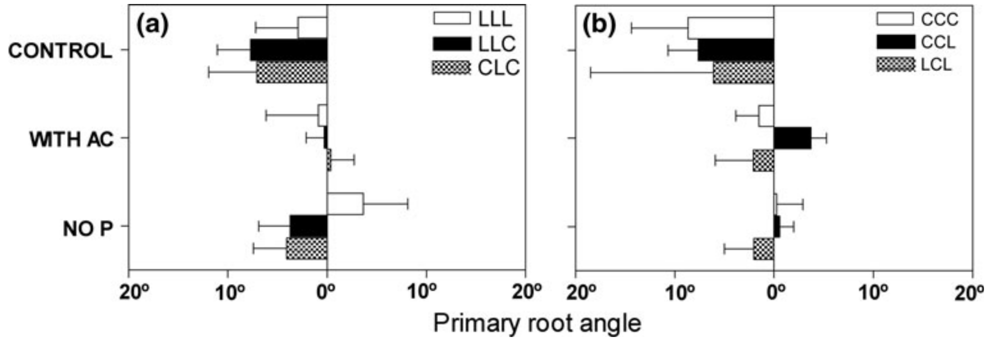

Fig. 4 Effect of treatments on the angle of the primary root (see Fig. 1 for details). Main factors were: growth conditions (at three levels: control, with AC, no P); accession (at two levels: Ler and Col); Neighbor [at three levels: neighbors and target plant from the same accession (LLL, CCC); each neighbor from different accession (LLC, CCL); and both neighbors from the opposite accession, (CLC, LCL)]. For accession and neighbor codes see Fig. 1 *Bars* represent the average of 8 plants ± SE

Interestingly, the only statistically significant effect of the orientation of the total root length of the target plant was towards a neighbor of the same accession only when a neighbor of the other accession was present on the other side in the control treatment (LLC or CCL) (Fig. 5a, d). The total root length of Ler plants that competed with another Ler (on the left side) and a Col plant (on the right) was 22 % higher towards the left in an effort to avoid competition with Col ($p < 0.01$, Fig 5a). Furthermore, Col plants of the control treatment concentrated also 22 % more root length in the space occupied by other Col compared to the space occupied by a Ler plant ($p < 0.01$, Fig. 5d). All these competition strategies disappeared when plants were limited by P or when AC was added to the growth media (Fig. 5b, c, e, f).

Discussion

Recent studies suggest that the ability of roots to recognize their neighbors may involve signaling events mediated by secondary metabolites exuded by the roots (Hess and de Kroon 2007; Semchenko et al. 2007a, b; Caffaro et al. 2011). The biological effect of root exudates is usually assessed by the comparison of treatments with and without the addition of AC to the growth media (e.g., Mahall and Callaway 1992; Falik et al. 2005; Semchenko et al. 2007a; Goldwasser et al. 2008; Lau et al. 2008; Weißhuhn and Prati 2009; Caffaro et al. 2011). The underlying assumption behind this comparison is that AC has a large number of small pores that adsorbs carbon-containing compounds present in the root secretions and thus neutralizes their

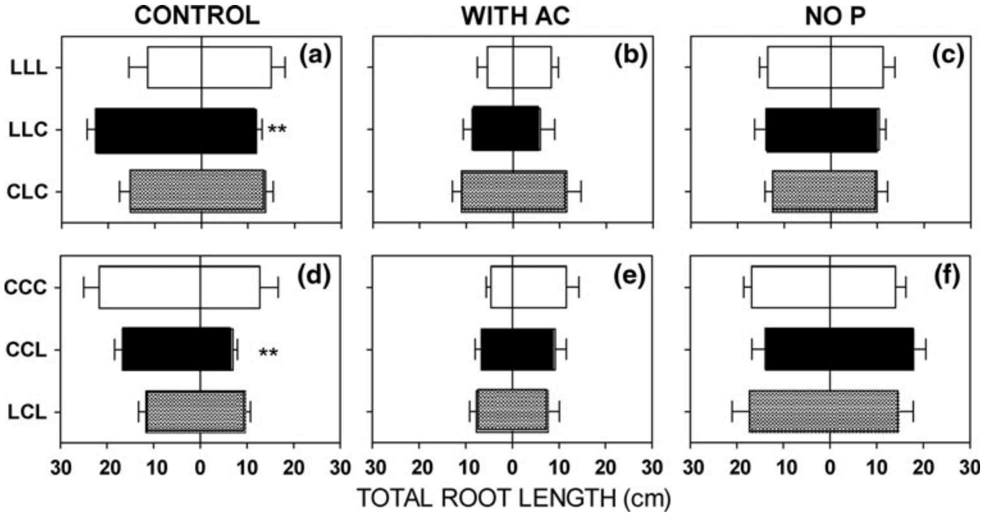

Fig. 5 Effect of phosphorus and addition of 5 g/L of AC into cultured media on total root length (primary and lateral) in both sides of the interaction zone of *A. thaliana* accessions Ler and Col. Main factors were: growth conditions (at three levels: control, with AC, no P); accession (at two levels: Ler and Col); Neighbor [at three levels: two same accession, (LLL, CCC); each accession (LLC, CCL) and two different accession, (CLC, LCL)]. The empty *bars* correspond to LLL or CCC treatment, *black bars* to LLC or CCL treatment and the *squared bars* to CLC or LCL treatment. Each *bar* represents the average of 8 plants ± SE for every treatment. * and ** correspond to significant differences between *left side* and *right side* realized by Scheffé's test ($p < 0.05$ and $p < 0.01$, respectively)

activity in the rhizosphere. In line with this, we recently found that the addition of AC drastically reduced (more than 90 %) the concentration of secondary metabolites in the root exudates of *A. thaliana* (Caffaro et al. 2011). In those experiments and in the ones reported here, AC did not affect the total biomass accumulation of *Arabidopsis*. Lau et al. (2008) and Weißhuhn and Prati (2009) observed that AC increased biomass accumulation of certain species such as *Festuca campestris*, *Festuca rubra* and *Artemisia vulgaris*. They attributed this effect to the modification of soil pH and changes in nutrient availability. In our preliminary studies, we observed that the promotion of plant growth by AC disappeared if AC is washed to remove chemicals adsorbed to it.

We observed that plants produced consistently fewer but longer lateral roots when AC was added to the growth media irrespective of the neighbor identity. Because both effects compensated each other, the effect of AC on the total length of lateral roots was not statistically significant. These observations are consistent with reports that demonstrated that root exudates play an important role in regulating traits related to root architecture (Basu et al. 2007) and lateral root emergence (Malamy 2005; Caffaro et al. 2011). Moreover, our results suggest that the final expression of root architecture is re-programmed if root exudates are absent or modified.

The lateral roots but not the primary roots were the ones directly affected by root exudates, supporting previous evidence (Caffaro et al. 2011). The other factors studied here, P availability and the identity of neighbors, did not affect neither the number and length of lateral roots nor the primary root length. In contrast, other studies have found that plants growing with neighbors of different genetic identity (i.e. different species or genotypes) increased the number of lateral roots (Endlweber and Scheu 2006) and total root length (Nord et al. 2011) in comparison with neighbors of the same genetic identity. In our study, it was observed that plants did not modify the lateral root number in any neighbor combination. We did not observe a greater development of the root system in response to P shortage in comparison to P-sufficient plants as reported elsewhere (Bates and Lynch 1996; Linkohr et al. 2002; López-Bucio et al. 2002).

Although several studies have highlighted the response of root systems to the presence of neighbors (e.g., Gersani et al. 2001; Falik et al. 2003; Gruntman and Novoplansky 2004; Weinig et al. 2006; Semchenko et al. 2007a, b), most of the published literature have not focused on whether root trajectories are modified when a neighbor root is present. In such sense, we developed an experimental approach that allows the observation and measurement of the spatial distribution of root systems of plants growing in competition.

Our principal finding was that plants growing in "normal" conditions (i.e. without P shortages or AC addition) and competing with one neighbor of the same accession at one side and other neighbor of a different accession at the other side, avoided the exploration of those spaces occupied by neighbor plants from different accesions. In contrast, their roots invaded the exploration zone of the neighbor plants of the same accesions. Interestingly, this root behavior was consistent for both Col and Ler. This would indicate a recognition signal of the neighbor identity, causing a change in the spatial distribution of the root system. When the competing plants were identical (i.e. LCL or CLC treatments), the target root did not modify its spatial distribution. This indicates that when the target root received similar signals from both left and right side neighbors, it had no possibility to escape towards any of the sides of the dish. Therefore, the plant would have adopted a no-response-type root architecture (Maina et al. 2002). Notably, this evidence of root recognition disappeared when AC was added to the growth media. This fact would indicate: (1) the existence of a recognition signal of the neighbor mediated by root exudates and operated at the level of recognizing plants of different accessions of the same species; (2) the absence of root exudates in the growth media (that were retained by the AC) determined that the root followed similar trajectories as if they were isolated; or (3) the response to the presence of neighbors is to avoid territories occupied by other accessions plants.

When plants were grown in a low P medium, the recognition appeared to be not operating, as shown in Fig. 5a, d. Several alternative hypotheses can explain these results. First, P stress could alter the composition of the root exudates by diminishing the secretion of those compounds responsible for the recognition process. It has been shown that P availability affect the secretion of strigolactones involved in attracting mycorrhizae as well as the exudation of organic acids that facilitate the absorption of phosphates (Calderón-Vázquez et al. 2011; Yoneyama et al. 2012). Second, P stress did not alter the composition of the root exudates but the process of avoiding neighbor roots would be regulated by P availability. If this hypothesis is valid, plants still sense the presence of neighbors but the need to find P sources in the growth media will drive plants to increase the explored soil volume. This hypothesis suggests that the response to P starvation will have a higher hierarchy than neighbor recognition in the regulation of the root exploration zones.

The study of natural genetic variation is a promising area to explore if we wish to understand the genetic mechanisms operating in the distribution of roots in the soil (Weigel 2012). Interestingly, Fitz Gerald et al. (2006) found natural variation for root system size and formation of lateral root primordia when Ler and Col accessions were grown under mild osmotic conditions. Besides, some studies found that Ler displays a lower osmotic sensitivity than Col (Fitz Gerald et al. 2006; Vallejo et al. 2010). These evidences suggest that Arabidopsis is a great platform to perform QTL mapping studies with recombinant inbred lines. This experimental strategy could allow us to explore the genetic architecture of recognition processes when roots grow under competition in the soil.

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References

Aerts R (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. J Exp Bot 50:29–37

Aphalo PJ, Ballaré CL (1995) On the importance of information-acquiring systems in plant–plant interactions. Funct Ecol 9:5–14

Basu P, Zhang YJ, Lynch JP, Brown KM (2007) Ethylene modulates genetic, positional, and nutritional regulation of root plagiogravitropism. Funct Plant Biol 34:41–51

Bates TR, Lynch JP (1996) Stimulation of root hair elongation in *Arabidopsis thaliana* by low phosphorus availability. Plant Cell Environ 19:529–538

Brisson J, Reynolds JF (1994) The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. Ecol 75:1693–1702

Caffaro MM, Vivanco JM, Gutierrez Boem FH, Rubio G (2011) The effect of root exudates on root architecture in *Arabidopsis thaliana*. Plant Growth Regul 64:241–249

Calderón-Vázquez CS, Ruairidh JH, Herrera-Estrella L (2011) Phosphate deprivation in maize: genetics and genomics. Plant Phys 156:1067–1077

Callaway RM (2002) The detection of neighbors by plants. Trend Ecol Evol 17:104–105

Casper BB, Jackson RB (1997) Plant competition underground. Ann Rev Ecol Syst 28:545–570

Endlweber K, Scheu S (2006) Effects of Collembola on root properties of two competing ruderal plant species. Soil Biol Biochem 38:2025–2031

Falik O, Reides P, Gersani M, Novoplansky A (2003) Self/non-self discrimination in roots. J Ecol 91:525–531

Falik O, Reides P, Gersani M, Novoplansky A (2005) Root navigation by self-inhibition. Plant Cell Environ 28:561–569

Fitter A (1991) The ecological significance of root system architecture. In: Atkinson D (ed) Plant root growth. An ecological perspective. Blackwell Scientific Publications, Oxford, pp 229–246

Fitz Gerald JN, Lehti-Shiu MD, Ingram PA, Deak KI, Biesiada T, Malamy JE (2006) Identification of quantitative trait loci that regulate *Arabidopsis* root system size and plasticity. Genetics 172:485–498

Ge Z, Rubio G, Lynch JP (2000) The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: results from a geometric simulation model. Plant Soil 218:159–171

Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z (2001) Tragedy of the commons as a result of root competition. J Ecol 89:660–669

Goldwasser Y, Yoneyama K, Xie X (2008) Production of stringolactones by *Arabidopsis thaliana* responsible for *Orobanche aegyptiaca* seed germination. Plant Growth Regul 55:21–28

Gruntman M, Novoplansky A (2004) Physiologically mediated self-non-self discrimination in roots. PNAS 101:3863–3867

Hess L, de Kroon H (2007) Effects of rooting volume and nutrient availability as an alternative explanation for root self/non-self discrimination. J Ecol 95:241–251

Lau JA, Puliafico KP, Kopshever JA, Steltzer H, Jarvis EP, Schwarzländer M, Strauss SY, Hufbauer RA (2008) Inference of allelopathy is complicated by effects of activated carbon on plant growth. New Phytol 178:412–423

Linkohr BI, Williamson LC, Fitter AH, Leyser HMO (2002) Nitrate and phosphate availability and distribution have different effects on root system architecture of *Arabidopsis*. Plant J 29:751–760

López-Bucio J, Hernández-Abreu E, Sánchez-Calderón L, Nieto-Jacobo MF, Simpson J, Herrera-Estrella L (2002) Phosphate availability alters architecture and causes changes in hormone sensitivity in the *Arabidopsis* root system. Plant Phys 129:244–256

Lynch JP (1995) Root architecture and plant productivity. Plant Physiol 109:7–13

Mahall BE, Callaway RM (1992) Root communication mechanisms and intracommunity distributions of two Mojave desert shrubs. Ecol 73:2145–2151

Maina GG, Brown JS, Gersani M (2002) Intra-plant versus inter-plant root competition in beans avoidance, resource matching or tragedy of the commons. Plant Ecol 160:235–247

Malamy JE (2005) Intrinsic and environmental response pathways that regulate root system architecture. Plant Cell Environ 28:67–77

Nord EA, Zhang C, Lynch JP (2011) Root responses to neighbouring plants in common bean are mediated by nutrient concentration rather than self/non-self recognition. Funct Plant Biol 38:941–952

Rubio G, Walk T, Ge Z, Yan X, Liao H, Lynch JP (2001) Root gravitropism and belowground competition among neighboring plants: a modeling approach. Ann Bot 88:929–940

Schenk HJ, Callaway RM, Mahall BE (1999) Spatial root segregation: are plant territorial? Adv Ecol Res 28:145–180

Semchenko M, Hutchings MJ, John EA (2007a) Challenging the tragedy of the commons in root competition: confounding effect of neighbour presence and substrate volume. J Eco 95:252–260

Semchenko M, John EA, Hutchings MJ (2007b) Effects of physical connection and genetic identity of neighbouring ramets on root-placement patterns in two clonal species. New Phytol 176:644–654

Vallejo AJ, Yanovsky MJ, Botto JF (2010) Germination variation in *Arabidopsis thaliana* accessions under moderate osmotic and salt stresses. Ann Bot 106:833–842

Weigel D (2012) Natural variation in *Arabidopsis*: from molecular genetics to ecological genomics. Plant Phys 158:2–22

Weinig C, Johnston J, German ZM, Demink LM (2006) Local and global costs of adaptive plasticity to density in *Arabidopsis thaliana*. Am Nat 167:826–836

Weißhuhn K, Prati D (2009) Activated carbon may have undesired side effects for testing allelopathy in invasive plants. Basic App Ecol 10:500–507

Williamson LC, Ribrioux SPCP, Fitter AH, Leyser HMO (2001) Phosphate availability regulates root system architecture in *Arabidopsis*. Plant Physiol 126:875–882

Yoneyama K, Xie X, Kim HI, Kisugi T, Nomura T, Sekimoto H, Yokota T, Yoneyama K (2012) How do nitrogen and phosphorus deficiencies affect strigolactone production and exudation? Planta 235:1197–1207