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Root system architecture determines fitness in an *Arabidopsis* mutant in competition for immobile phosphate ions but not for nitrate ions

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Plant root systems often have complex branching patterns. Models indicate that a complex architecture is only required for the acquisition of immobile resources, such as phosphate; mobile ions, notably nitrate, can be effectively taken up by very restricted root systems. We have tested this prediction using the *axr4* mutation of *Arabidopsis thaliana*, the principal phenotypic effect of which is to reduce the number of lateral roots. *Arabidopsis thaliana* is not a host for mycorrhizal fungi and so acquires all its nutrients through the root system. In both a pot experiment and a field experiment conducted under natural conditions for *A. thaliana*, we found that only phosphate, and not nitrate, affected the fitness of the mutant relative to the isogenic wild-type line, Columbia. These results confirm model predictions and have implications both for the evolution of complex root systems and for the design of efficient root systems for crops.

Keywords: *Arabidopsis thaliana*; Columbia; *axr4*; phosphate; nitrate; root branching

1. INTRODUCTION

The root systems of plants vary greatly in their architecture, from unbranched to highly complex branching patterns. Extremes include wholly unbranched axes, found in many Liliaceae and Orchidaceae, to adventitious root systems with many orders of branching; total lengths of root can vary by several orders of magnitude for similar-sized plants (Fitter 1996). This variation is assumed to be adaptive and to relate to the efficiency of soil exploration and nutrient acquisition, although other root functions such as anchorage (Ennos 1995) could also be involved.

However, in many root systems with repeated branching, daughter roots extend only a short distance from the parent. The depletion zone that surrounds the parent root for mobile resources (e.g. nitrate ions or water) may be nearly as wide as, or even wider than, the extent of these daughter roots, which therefore do not contribute to uptake. Indeed, most root systems are apparently over-engineered for the uptake of mobile resources such as water or nitrate ions (Robinson 1996), since a small length of root can absorb nitrate from a large volume of soil. Because nitrate ions are very soluble (even in soils), the diffusion coefficient for NO_3^- in soil is *ca.* 10^{-10} m^2 s^{-1}, giving an effective mobility of *ca.* 3 mm d^{-1}. Since median lifespans for fine roots are rarely less than 10 days (Bloomfield *et al.* 1991; Fitter 1999), this mobility will allow a single root to exploit *ca.* 30 cm^3 soil cm^{-1} root for nitrate. By contrast, phosphate ions adsorb strongly to surfaces dominated by Ca^{2+}, Al^{3+} and Fe^{3+}, which are the principal cations in most soils. Consequently, they are very poorly mobile ($D_{soil} < 10^{-12}$ m^2 s^{-1}), leading to an effective diffusion distance in one day of *ca.* 0.03–0.3 mm (Baldwin *et al.* 1973; Jungk 1996; Tinker & Nye 2000) and an exploitation volume of less than 0.3 cm^3 cm^{-1} root.

These differences imply that complex architectures would only be required for the uptake of less mobile ions such as phosphate, and Robinson (1996) questioned why plants exhibited responses such as the proliferation of lateral roots in nitrogen-rich patches in soil. However, Robinson *et al.* (1999) and Hodge *et al.* (1999) resolved this paradox by showing that when plants were in competition for ions, even mobile ions, they acquired them in proportion to the total amount of root each produced. In other words, in the absence of competition, the supply of ions can be viewed as invariant, whereas in competition it is time dependent. This explanation is based on a uniform distribution of roots in the soil. In practice, since competition occurs in defined spatial domains, the spatial and temporal placement of roots in the soil, determined by the architecture of the root system will determine the effectiveness of individual roots in the acquisition of mobile and immobile resources by competing root systems.

Beyond architecture, membrane transport systems, exudates and symbiotic microbes all affect the ability of a root to acquire nutrient ions from soil. Models (Baldwin 1975; Barber & Cushman 1981) predict that the movement of ions through the soil to the root surfaces should be the limiting step for the uptake of phosphate. Therefore, architecture, symbionts and exudates should be more important than transport; by contrast, nitrate moves rapidly through the soil and the inherent competence of the root system in uptake will be more important in its uptake. However, there are no experimental data that unequivocally demonstrate the role of root system architecture in the uptake of mobile, as well as immobile, ions, since comparative studies (Fitter & Stickland 1991; Taub & Goldberg 1996) have used different plant species or cultivars that therefore differ in a wide range of characteristics.

We have exploited the phenotype of the *axr4* mutant of *Arabidopsis thaliana*, which differs from the wild-type (Columbia ecotype) principally in having fewer lateral roots. Other root phenotypes of this mutant include weak auxin resistance and a slightly reduced rate of root gravi-

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tropism, but there are no differences in root hair number or morphology (Hobbie & Estelle 1995). The shoot phenotype is scarcely distinguishable from the wild-type, although the leaves have a slight tendency to curl. Thus, the *axr4* mutant is one of the least pleiotropic of all root-branching mutants. The root systems of Columbia and *axr4* also respond similarly to a variation in nutrient supply. When grown with a deficient supply of phosphorus (P) both genotypes have shorter internodes (distance between laterals), longer laterals and a shorter root tip; with deficient nitrogen (N), both genotypes have longer internodes and laterals, but in neither case are there any significant differences in total lateral or axis length (Williamson *et al.* 2001; Linkohr *et al.* 2002). We proposed that the competitive ability of *axr4* and Columbia would be a simple function of root system size when the mobile nitrate ion was limiting growth, because architectural differences would not affect their ability to capture nitrate. By contrast, when phosphate was limiting, we expected Columbia to be competitively superior because its greater lateral root development would allow it to expand the effective radius of the depletion zone around the main axis, without the depletion zones of elements of its root system overlapping.

2. MATERIAL AND METHODS

(a) *Characterization of* axr4

The growth of root systems on agar was measured after 14 days on ATS (*A. thaliana* salts; Wilson *et al.* 1990) agar without added sucrose. Four plants of either Columbia or *axr4* were placed on each plate. Plates were kept in a controlled environment room at 22 °C (continuous) with 16 h of fluorescent lighting per day (65 μmol m^{-2} s^{-1}). Twelve plants of each genotype were measured. To measure root characteristics in soil media, plants were grown in thin layers between two glass plates (31 cm × 29 cm), a 3 mm space between them being maintained by Perspex spacers. The growth medium was a 6.5 cm layer of a uniform mix of 200 g of dried silica sand (Hepworth Minerals and Chemicals) and 4 g of garden soil, above 23 cm of pure sand. Two plants of either Columbia or *axr4-2* were planted in each of six plates and placed in a Conviron growth cabinet (16 h at 25 °C by day, 8 h at 15 °C by night; 80% relative humidity) for 35 days.

(b) *Pot experiment*

We grew Columbia and *axr4-2* in competition both in a pot experiment in a glasshouse and in the field. The pot experiment comprised 144 7.5 cm diameter pots, which were arranged in three blocks in a lit, heated glasshouse (16 h day with 98 μmol m^{-2} s^{-1} supplementary lighting; mean temperature of 20 °C, range of 16–28 °C). The pots were filled with a mixture of 10% autoclaved garden soil and 90% Leighton Buzzard sand. Plants were sown in both monocultures and in equal mixtures at two densities, two and eight seeds per pot; seeds were pre-imbibed for 48 h in the dark and at 5 °C, and each seed was planted into a minute amount of sterilized garden soil, to aid establishment. There were four nutrient treatments: (i) full strength ATS solution (Wilson *et al.* 1990), which contained 9 mM of N and 2.5 mM of P; (ii) low P, which had the potassium phosphate replaced by KCl; (iii) low N which had 1.8 mN of N and the remainder of the Ca (NO_3) replaced by $CaCl_2$; and (iv) low N and P which had 1.8 mM of N and no P. These treatments (three combinations, two densities, two N concentrations and two P concentrations) were combined in a full factorial design with six replicates. For logistical reasons, pots were set out in randomized trays, each containing a complete set of the three combinations at a given density and nutrient supply rate; this enabled the accurate addition of nutrient solution, which comprised an initial 50 ml per pot, followed by three additions of 25 ml at 3, 4 and 4.5 weeks. The experiment ran for 35 days. For each pot, plants were harvested in two halves and these were kept separate. In mixtures, plants were separated into genotypes, in monocultures, simply into equal numbers of plants. Shoot dry weights were determined, but it was not feasible to recover the very fine and much-branched roots of *A. thaliana* from the pots. We calculated the relative crowding coefficient (de Wit 1960) following Harper (1977, pp. 258–259):

$$k_{ij} = (\mathrm{mix}_i/\mathrm{mono}_i)/(\mathrm{mix}_i/\mathrm{mono}_j),$$

where 'mix' is the biomass in the mixture and 'mono' is the biomass in the monoculture of the two genotypes (*i*, *axr4*; *j*, Columbia). If k_{ij} has a value less than 1, then *axr4* is competitively inferior to Columbia. The experiment was analysed as a full factorial with five factors, namely density, nitrate, phosphate, genotype of target plants and genotype of competitors; weight data were ln-transformed. All interaction terms were examined. Evidence of competition for a specific nutrient would be (i) a significant effect in ANOVA of that nutrient on values of *k*, or (ii) interactions between nutrients and genotypes for values of shoot biomass.

(c) *Field experiment*

To test the theory under realistic field conditions, we sowed an equal mixture of Columbia and *axr4* at a rate of 9000 seeds per square metre onto a grid of plots representing a 3 × 3 factorial combination of N and P supply rates. The plots were laid out on an area of gravel path with a flora of winter and summer annuals, including *Poa annua, Capsella bursa-pastoris* and *Cardamine hirsuta*. A large population of *A. thaliana* occurred nearby, but not in the area selected. A moss carpet (*Bryum capillare*) covered the ground surface and this was raked and treated with glyphosate before the experiment to provide a suitable seedbed. Four plots were marked out in a line, each 1 m × 1 m and separated by 0.5 m, and sub-divided into nine sub-plots in a 3 × 3 grid. Sub-plots were 0.33 m × 0.33 m but samples were only taken from the central area of 0.25 m × 0.25 m. The nine sub-plots were each assigned to one treatment, within a 3 × 3 factorial of N and P applications. The application rate for N was 0.0, 0.5 and 2.5 g m^{-2} applied as $NaNO_3$; P application rate was 0.0, 0.16 and 1.6 g m^{-2} applied as NaH_2PO_4. Nutrients were added before planting and twice weekly for six weeks. For ease of application, N and P treatments were applied as strips of three plots and the locations of the three strips were randomized among the plots. Twenty milligrams of an equal mixture of Columbia and *axr4* seed of *A. thaliana* (*ca.* 500 seeds of each) was sown on 6 May 1998 onto each sub-plot, and plants were grown for 79 days, until seed-set. On 24 July, all seed produced from the central 0.25 m × 0.25 m of each sub-plot was collected. A sample of *ca.* 4 mg (*ca.* 150–200 seeds) was taken from each sub-plot and tested for auxin resistance by germination on ATS agar containing 50 nM of 2,4-D, an auxin analogue. Columbia roots have very stunted growth under these conditions, but *axr4* develop more normally.

Table 1. Mean shoot dry weight of *Arabidopsis thaliana* in response to planting density, nutrient supply and genotype.
(Data are means for each factor or combination of factors, averaged across all other factors, and represent mean shoot dry weight per plant. Analysis of variance was performed on ln-transformed data. All *F*-tests have 1,254 d.f. Target genotype is the genotype for which data were analysed; competitor genotype is that comprising the other half of plants in each pot. Col, Columbia.)

factors			factor states		*F*	*p*
			low	high		
1 density			162	52	2070	< 0.001
2 nitrate			66	148	1122	< 0.001
3 phosphate			107	107	0.00	0.969
			Col	*axr4*		
4 target genotype			115	99	28.5	< 0.001
5 competitor genotype			104	110	6.54	0.011
interactions						
6 phosphate × target		low P	118	96	6.50	0.011
		high P	111	103		
7 phosphate × competitor		low P	99	114	7.19	0.008
		high P	108	106		
8 phosphate × competitor × density	low P	low density	149	175	4.07	0.045
		high density	50	54		
	high P	low density	166	157		
		high density	50	56		

3. RESULTS

When grown on agar for 14 days on full-strength ATS medium, Columbia produced an average of 25 (s.e. of 2) laterals, whereas *axr4* produced only 14 (s.e. of 1). We grew both genotypes in thin soil slices between glass plates. After 35 days of growth, wild-type plants had a mean lateral root number of 88 (s.e. of 12) while *axr4* mutant plants had a mean of only 43 (s.e. of 10). However, total root length did not differ significantly between genotypes once differences in plant size (shoot dry weight) were taken into account.

In the pot competition experiment, plant growth was principally determined by plant density and nitrogen (table 1, lines 1 and 2; figure 1); overall, phosphate had no effect on growth (table 1, line 3), but this was because of interactions between the phosphate supply and other factors. The two genotypes also differed overall in growth, with Columbia plants being, on average, 16% heavier (shoot weight only) than *axr4* plants (table 1, line 4). They also differed in their impact as competitor: the mean weight of plants irrespective of genotype when Columbia was the competitor was 5% less than when *axr4* was the competitor (table 1, line 5). Only four out of the 26 possible interaction terms were significant: that between density and nitrogen is not shown, but those between phosphate and genotype as either target or competitor are shown in table 1. Columbia showed no growth response to added P: it was actually 6% smaller at high than at low P, whereas *axr4* increased its biomass at high P by a similar amount (table 1, line 6). When responses of the two genotypes to N and P were examined in detail (figure 1), Columbia growth exceeded that of *axr4* only at low P supply and in a mixture (figure 1*c*,*d*), except for the single case of growth in high N and high P at high density (figure 1*c*). This is presumably because of a superior ability of Columbia to exploit high N in these extreme conditions. Otherwise, at high P there was no difference in the competitive impact of the two genotypes, whereas at low P Columbia had a much greater impact as a competitor than *axr4* (table 1, line 7); this interaction is again apparent by comparing monoculture (figure 1*a*,*b*) and mixture (figure 1*c*,*d*) results.

The relative crowding coefficient (k) of *axr4* with respect to Columbia was only affected by P supply, with a value of 0.79 ± 0.10 (95% confidence limit) at low P and 1.09 ± 0.91 at high P. The difference between the two values was significant ($F_{1,38} = 7.4$, $p = 0.010$), but only the low P value was significantly different from 1.

In the field experiment, mean mass per seed did not differ between the treatments (data not shown) but both N and P increased total seed production. At high P, the highest N supply doubled seed production relative to the lowest N treatment, but at high N, the response to P was only 30% (figure 2). The fraction of *axr4* seed recovered was unaffected by N, and averaged 39%, showing that there was selection against the mutant. Increasing P supply, however, increased the *axr4* fraction overall from 37% to 41% (figure 3); at high N the effect was more marked, ranging from 34% *axr4* at low P to 44% at high P. Although figure 3 appears to show an interaction between N and P supply, this was not significant, nor was the main effect of N, whereas the main effect of P was (see figure 3 caption).

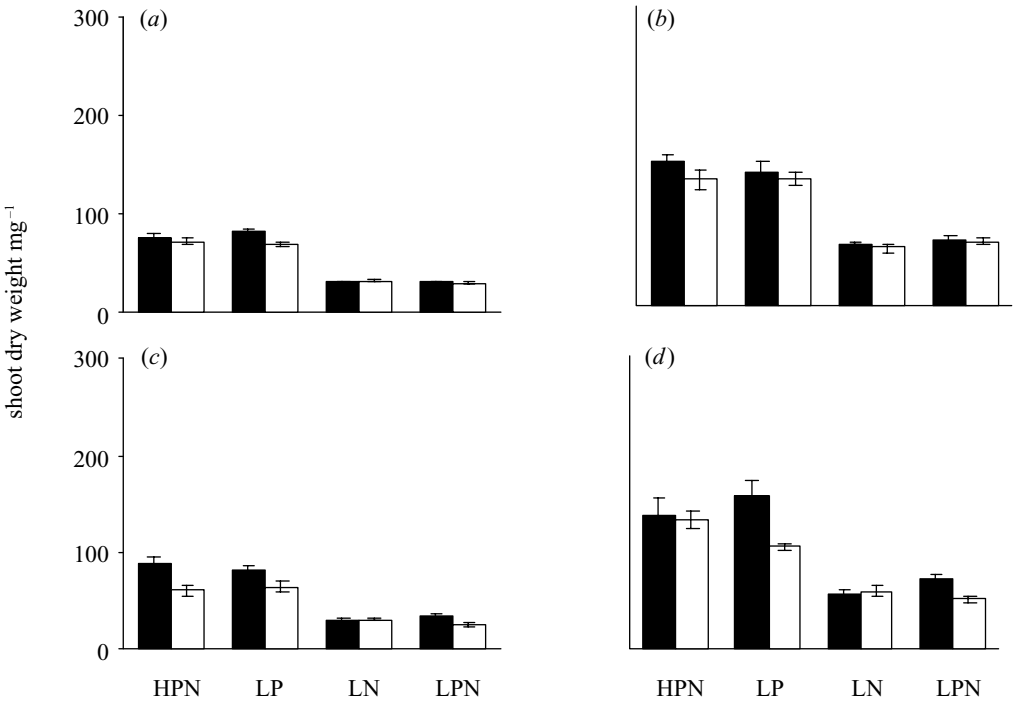

Figure 1. The mean shoot dry weights of plants of each genotype, *axr4* (open bars) or wild-type Columbia (filled bars), grown in monoculture (*a*,*b*) or as mixtures (*c*,*d*), and at high density (*a*,*c*) or low density (*b*,*d*). Bars represent one standard error. For a full statistical analysis see table 1. HPN, high P and N; LP, low P and high N; LN, low N and high P; LPN, low P and N.

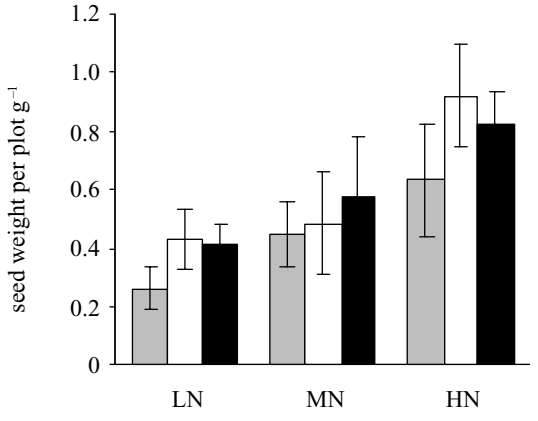

Figure 2. Weight of seed produced by an equal mixture of Columbia and *axr4* plants, when grown in the field at three levels of N and P supply. LN, low (zero) N; MN, medium N; HN, high N addition rate; LP (grey bars), low (zero) P; MP (open bars), medium P; HP (black bars), high P supply rate. Bars represent one standard error. The effect of N ($F_{2,24} = 20.28$, $p < 0.001$) and P ($F_{2,24} = 3.70$, $p = 0.040$) are both significant. The mean mass of each seed was not affected by nutrient treatment (data not shown).

4. DISCUSSION

In both pot and field experiments, we have shown that the competitive ability of the *axr4* mutant is strongly affected by phosphate, but scarcely at all by nitrate, even though overall growth of both the mutant and the wild-type was much more responsive to nitrate than to phosphate. In the pot experiment, only *axr4* responded to phosphate, and then only because of its inability to compete with Columbia. However, we have found that growing these same genotypes in the same medium but with 5% rather than 10% soil does induce responsiveness to phosphate in both (E. C. Williamson, unpublished data). Whereas *axr4* was much less competitive (as measured by the growth of plants grown with it) than Columbia at low P, it was equally competitive at high P, as shown by the relative crowding coefficient. Neither of these effects was observed with nitrate, confirming our prediction that the two genotypes would only differ in relation to the immobile phosphate ion and not to nitrate. However, competitive ability in a pot experiment may not be a good indicator of selective advantage in a field situation.

In an annual such as *A. thaliana*, seed production is a good measure of fitness (Carey *et al.* 1995). The data from the field experiment do not allow a complete measurement of fitness, since they exclude the performance of F_1 seedlings. Nevertheless, they demonstrate a powerful effect of the immobile phosphate ions, but not the mobile nitrate, on the fecundity of a genotype with fewer lateral roots. This confirms both the results of the pot experiment and theoretical predictions from simulation models (Baldwin 1975). The results have implications for the evolution of root system architecture. Niklas (1999) has developed models to parameterize the morphospace through which early land-plant shoot systems could have evolved. He identified four 'biological tasks' that can be used to estimate selective forces determining the pathways that evolution followed, namely maximizing light interception, mechanical stability and reproductive success, and minimizing surface area. He shows that the best match to the known fossil record is achieved by assuming that the initial selective forces acted on surface area, and that light interception emerged as a major focus for selection later. Unfortunately, the fossil record for root systems is minimal, although it is known that the earliest land plants had

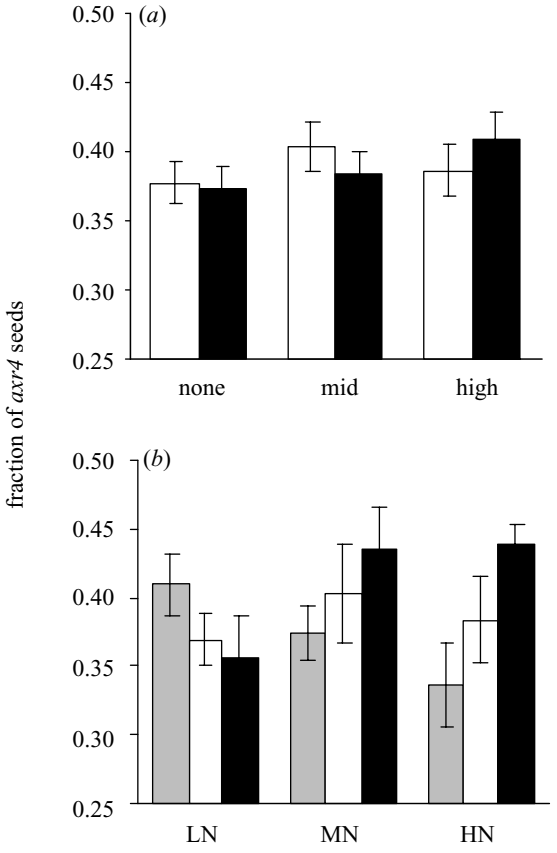

Figure 3. (*a*) The fraction of *axr4* seed after one generation from a field-grown population originally containing 50% *axr4* and 50% Columbia, as a function of N (open bars) and P (black bars) addition. In analysis of variance, the effect of P is significant ($F_{2,27} = 4.06$, $p = 0.029$); the apparent interaction between N and P shown in (*b*) is not significant ($F_{4,27} = 1.85$, $p = 0.15$). Bars represent one standard error. See figure 2 for definition of bars in (*b*).

little-branched root systems and were almost certainly obligatorily mycorrhizal as an essential requirement for the acquisition of immobile phosphate ions (Pirozynski & Malloch 1975; Remy *et al.* 1994). Our data confirm that even relatively simple root systems would have been adequate for the acquisition of nitrate and other mobile ions, and that the evolution of complex branching architecture has probably, therefore, occurred in response to phosphate deficiency. Consequently, there has been an evolutionary trend towards reduced dependence on mycorrhiza, with non-mycorrhizal species such as *A. thaliana* being habitat specialists (Peat & Fitter 1993) and having apparently arisen on several occasions, and comparatively recently (Fitter & Moyersoen 1996; Cairney 2000). Even though mycorrhizal plants have that alternative mechanism for P capture, the data in this paper show that increased complexity of branching would still have offered a competitive advantage.

Other possible explanations for complex root system architecture include anchorage and the insurance against damage achieved by having multiple growing points. Anchorage is almost wholly achieved by the major root branches nearest the stem base (Fitter & Ennos 1989; Ennos 1995) and so does not explain the need for more complex architectures. It is possible that the possession of many growing points is an insurance against damage by grazing animals or pathogens, but this also seems improbable since most plants have an enormous capacity to regenerate vegetative meristems.

The demonstration that root system architecture determines root function has important implications for the design of efficient root systems for crop plants. Some plants display pronounced proliferation responses to locally applied nutrients, including nitrate (Drew 1975; Zhang & Forde 1998), but because of the mobility of nitrate ions in soil, this proliferation response only increases nitrogen acquisition by a plant when it is in competition with neighbours (Robinson *et al.* 1999). In monoculture, the normal situation in agriculture, proliferation will therefore not increase crop N uptake. Our data imply that even plants with very restricted root system architecture may be highly efficient at acquiring mobile resources. However, acquisition of phosphate and other immobile ions requires a more complex root system architecture. In most plants, such nutrients are obtained via mycorrhizal symbionts, it may therefore be possible to develop plant varieties with reduced root system development, sufficient for the acquisition of mobile resources, but reliant on mycorrhizal symbionts to acquire immobile ions. Such varieties would have reduced investment in root growth. However, this strategy will require both crop breeders and agronomists to give attention to conditions that encourage the formation of the symbiosis.

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