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ORIGINAL ARTICLE

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The growth defect of *lrt1*, a maize mutant lacking lateral roots, can be complemented by symbiotic fungi or high phosphate nutrition

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Abstract The growth of three maize (*Zea mays* L.) mutants, each impaired in the formation of one individual element of its root system, was compared under "natural" limiting phosphate conditions (0.1 mM). Mutant plants exhibiting a reduction in root hairs (*rth3-1*) or a depletion of crown and brace roots (*rtcs*) grew as well as the corresponding wild-type plants. However, mutant plants lacking lateral roots (*lrt1*) showed a strong reduction in plant growth. The growth defect of *lrt1* was overcome when it was grown in association with an arbuscular mycorrhizal fungus, *Glomus mosseae*. Establishment of symbiosis was associated with the occurrence of a new type of lateral root. These new lateral roots were stunted and highly branched, giving rise to a bush-like structure. Supply of high phosphate (1 mM) ameliorated the growth of *lrt1* plants too, but less efficiently than the symbiosis did. Hence, arbuscular mycorrhizal fungi as well as phosphate functionally complemented the *lrt1* mutation.

Keywords Arbuscular mycorrhizal symbiosis · *Glomus* · Mutant (maize) · Phosphate nutrition · Root morphology · *Zea* (*lrt1* mutant)

Abbreviations AM: arbuscular mycorrhizal · AMF: arbuscular mycorrhizal fungi · Gm: *Glomusmosseae* · wpi: weeks post infection

Introduction

The root system of maize consists of two types of root, embryogenic and post-embryogenic. Embryogenic roots comprise the primary and the seminal lateral roots (called seminal roots throughout this manuscript). All other roots, namely the crown, brace and lateral roots, are formed later in development and are therefore termed post-embryogenic. The primary root emerges first from the embryogenic tissue, followed by the seminal roots arising from the scutellar node; subsequently, laterals form on these early roots. The root system of the seedling consists of these primary and seminal roots and their laterals. In many maize lines these seedling roots decay and are replaced by the permanent roots (Feldman 1994). Building the permanent root system starts with the formation below ground of crown roots at the coleoptilar node and progresses to the early nodes of the shoot. Finally, brace roots arise from aerial nodes. On the crown, and on soil-covered parts of the brace roots, lateral roots develop. Crown and brace roots play a major role in the acquisition of mineral nutrients and water, and they are also of crucial importance for the lodging resistance of adult maize plants (McCully and Canny 1988; Hetz et al. 1996).

Root hairs, another basic element of plant root systems, develop on all types of root and are thought to be of major importance for enhanced nutrient absorption as they increase the soil volume for nutrient acquisition (Clarkson 1985, 1996; Hofer 1996).

Most plant roots perform their main function to take up mineral nutrients and water not only directly, but also in association with mycorrhizal fungi. Symbiotic arbuscular mycorrhizal fungi (AMF) associate with the majority of terrestrial plants. Maize too, is efficiently and homogeneously colonized by AMF despite the fact that breeding for optimal plant performance has largely ignored traits associated with mycorrhiza-mediated nutrient uptake. These symbiotic fungi appear to be particularly important for their hosts with respect to uptake of inorganic phosphate: they take up phosphate through their extended hyphal network in the soil and transfer it to the plant, presumably by way of their arbuscules, i.e. branched haustoria formed inside the root cortex cells (reviewed in Harrison 1999).

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In the present work, we studied the impact of individual root traits in conjunction with arbuscular mycorrhizal (AM) symbiosis on the performance of maize plants under limiting (0.1 mM KH_2PO_4) phosphate conditions. We chose three different monogenic maize mutants that had been phenotypically characterized as affected in their root architecture, each of them having specific root elements eliminated. These mutants should enable us to identify individual components of the root system essential for phosphate acquisition in the presence or the absence of AMF.

The mutant *rth3-1* is not able to elongate its root hair primordia, and thus does not form root hairs (Wen and Schnable 1994). Mutant *lrt1* has normal root hairs but is impaired in the formation of lateral roots on embryogenic primary and seminal roots. The lack of lateral roots is, however, temporary and subsequent crown roots develop laterals comparable to those of wild-type plants (Hochholdinger and Feix 1998). Mutant *rtcs* is affected in the formation of seminal crown roots and brace roots, resulting in a root system consisting of only the primary root, supported by normal laterals and root hairs (Hetz et al. 1996).

The correlation between the degree of complexity of root systems, plant performance and the dependence on AMF has so far been investigated only by comparing different plant species or genetically distant cultivars (Baylis 1975; St. John 1980; Azcon and Ocampo 1981). It is, however, problematic to draw conclusions from analyses based on employing genetically diverse material since responses to other inherent factors like, for example, the demand for phosphate or the differences in growth rates are critical determinants of the mycotrophy of a given plant species or cultivar (Koide 1991; Smith and Read 1997). We provide here for the first time an analysis based on well-defined isogenic plant lines, and we show that the AM symbiosis can functionally complement the *lrt1* mutation.

Materials and methods

Plant material

The maize (*Zea mays* L.) mutants *rth3-1* (Wen and Schnable 1994), *lrt1* (Hochholdinger and Feix 1998) and *rtcs* (Hetz et al. 1996) and their isogenic wild-type lines were provided by the respective laboratories. The root hair mutant *rth3-1* (Wen and Schnable 1994) had been isolated from selfed *Mutator* families with complex genetic backgrounds. The isogenic wild type derived from backcrossing to a series of different lines (for details, see Wen and Schnable 1994). Mutant *lrt1* (Hochholdinger and Feix 1998) had been identified in an ethylmethane sulfonate (EMS16)-mutagenized B73 background and was backcrossed to A632. The mutant *rtcs* (Hetz et al. 1996) was obtained from selfed *En* families and had also been backcrossed to A632.

Mutant and corresponding wild-type kernels were surface-sterilized in 3.5% sodium hypochlorite for 10 min, followed by five cycles of washing in double-distilled H_2O. Kernels were pre-germinated at room temperature on moist filter paper for 4 days.

In order to provide a low-fertility soil substrate, and at the same time to facilitate the assessment of the root systems, germinating seedlings were transferred into a sand mixture containing sterilized coarse sand, fine quartz sand and loam (8:1:1, by weight, respectively) in 1-l pots (Schellenbaum et al. 1999). The phosphate content of the sand mixture was 39.25 mg P_2O_5/kg sand (for comparison: commercially available standard soil had a value of 183.95 mg P_2O_5/kg soil) following the standard protocol of the Deutsche Bodenkundliche Gesellschaft (Oldenburg, Germany).

Plants were grown for 8 or 15 weeks in the greenhouse at an average day temperature of 25 °C with artificial light supplement (Entladungslampen MT 400DL/BH, 400 W; RDW, Bern, Switzerland; 12 h light and 12 h dark). Once per week plants were watered with Hoagland solution, containing either full phosphate (1 mM KH_2PO_4) or reduced phosphate (0.1 mM KH_2PO_4; Fink 1979). This reduced phosphate supply has been shown before not to be limiting for wild-type tobacco plants but to allow high colonization of their roots by mycorrhizal fungi (Schellenbaum et al. 1999).

For inoculation with *Glomus mosseae*, 3 g of stock inoculum (see below) was added to the soil upon planting the 4-day-old germinating seedling at 2 cm depth.

Plant growth of all lines was documented by photography after 8 weeks and for *lrt1* additionally after 15 weeks. For the estimation of biomass, *lrt1* plants were harvested at 15 weeks and shoots were separated from roots before incubation at 80 °C for 3 days. Observations described within this manuscript have been consistently made on two independent experiments. Data shown are from one representative experiment.

Glomus mosseae inoculum

Inoculum of the fungus *Glomus mosseae* (Isolate number 12, European Bank of *Glomales*, http://www.bio.ukc.ac.uk/beg/) was produced on *Tagetes tenuifolia*, grown in a mixture of loam and fine quartz sand (1:1, w/w) for 3 months. For maximal colonization, plants were wilted for an additional 3 weeks to promote production of fungal spores. The resulting inoculum consists of fungal spores, hyphae and colonized root pieces. The exact repetition of this procedure ensured equal inoculum density in independent inoculum production cycles. The dry sand/loam mixture (stock inoculum) was kept at 4 °C prior to inoculation.

Microscopic analysis

The degree of mycorrhizal colonization was determined after trypan blue staining of lateral and crown root samples from 15 week-old plants. We followed the protocol of Brundrett at al. (1984), counting the number of intraradical fungal structures using the gridline-intersect procedure described by Giovanetti and Mosse (1980).

Results

Performance of root mutants at limiting phosphate supply

Growth of root mutants and of the isogenic wild-type plants was first assessed without mycorrhiza at limiting phosphate supply. Comparison of *rth3-1* and *rtcs* with the respective wild-type plants revealed no obvious difference in plant performance after 8 weeks: development had proceeded synchronously for mutant and wild-type plants (Fig. 1a, b). After approximately 3 weeks, *rtcs* plants had to be supported by a stick as they lacked lodging resistance due to the absence of crown and brace roots (Fig. 1b). In contrast, *lrt1* plants appeared smaller and more fragile than wild-type plants and were

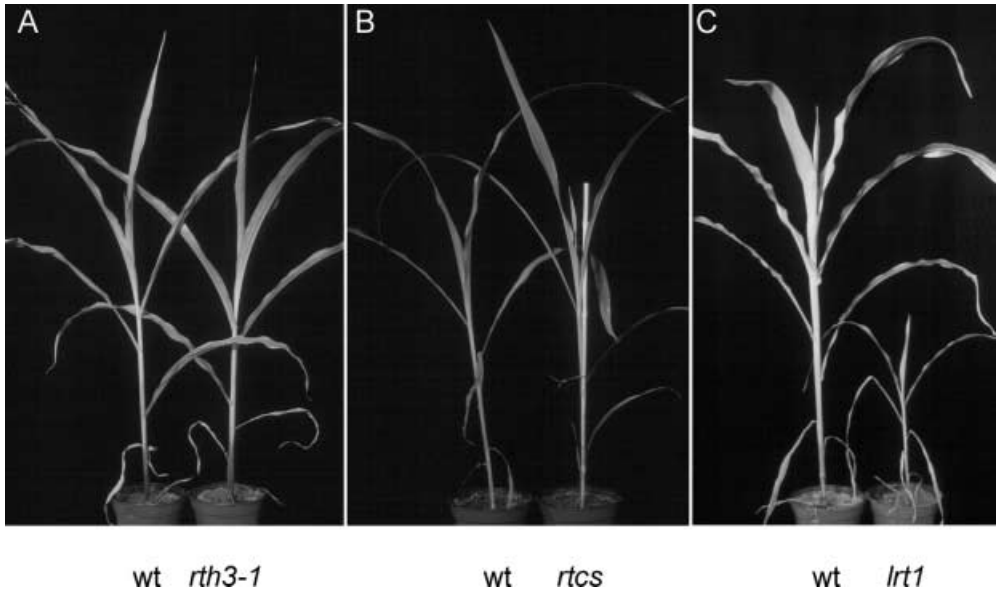

Fig. 1a–c Phenotypes of maize (*Zea mays*) root-architecture mutants and their isogenic wild type grown under low-phosphate application. Representative plants of *rth3-1* (**a**), *rtcs* (**b**) and *lrt1*(**c**) and the isogenic wild-type (*wt*) are shown after 8 weeks of growth at a reduced level of phosphate (0.1 mM KH_2PO_4). The experiment was repeated twice with three plants for each line and treatment

retarded in growth compared to the wild-type plants (Fig. 1c). Since *rth3-1* and *rtcs* plants did not show any altered growth phenotype relative to the wild type, we focussed our further investigations on the *lrt1* mutant.

Effect of the AM symbiosis on performance of *lrt1* plants

To investigate whether AMF had a beneficial effect on the growth of *lrt1* plants, half of the mutant and wild-type plants were inoculated with *G. mosseae* upon planting. At 8 wpi (weeks post infection) non-inoculated wild-type plants grew as well as inoculated plants (Fig. 2a) and at 15 wpi all wild-type plants had grown to maturity (data not shown), although non-mycorrhizal wild-type plants were weaker than the corresponding mycorrhizal wild-type plants, as reflected by the shoot dry-weight values (Table 1).

In contrast, as in the previous experiment, after 8 wpi the non-mycorrhizal *lrt1* plants were strongly retarded in development. Their growth appeared to be terminated at an early stage without reaching the reproductive adult stage at 15 wpi (Fig. 2b). Remarkably, when the *lrt1* plants were grown in the presence of *G. mosseae*, they no longer exhibited the growth retardation but instead displayed vigorous growth comparable to that of the wild type (Fig. 2a, b). The mycorrhizal *lrt1* plants developed as much as 20 times more biomass than the non-mycorrhizal counterparts, and they performed similarly to non-mycorrhizal wild-type plants (Table 1).

We further investigated whether the observed growth restoration could be correlated with changes in root morphology or, alternatively, whether it was simply due to the contribution of the fungal mycelia to plant nutrition. Inspection of the wild-type root system revealed no obvious differences in root morphology between non-mycorrhizal and mycorrhizal plants: elongated

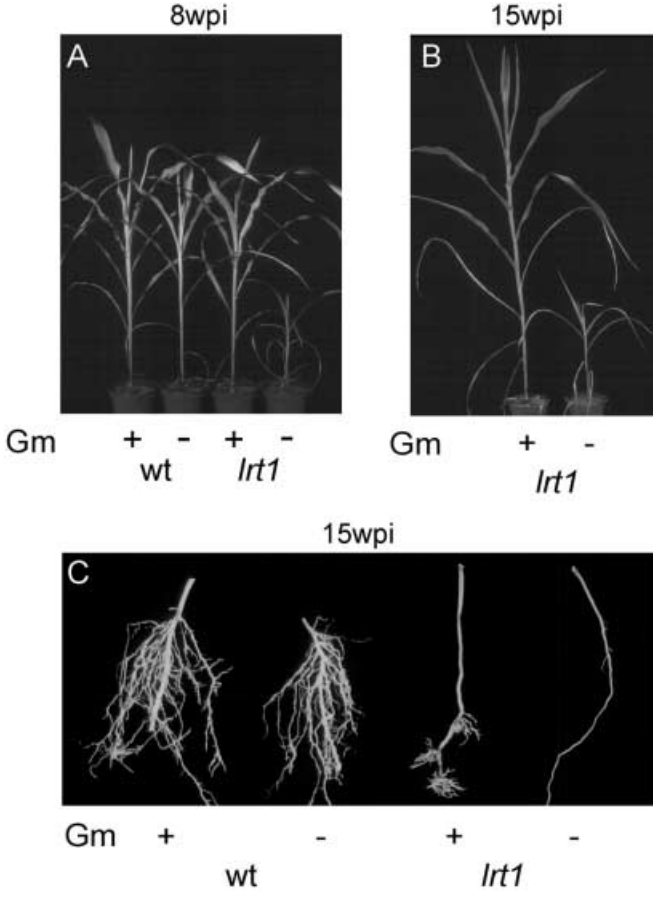

Fig. 2a–c Phenotypes of *lrt1* maize plants and the corresponding wild type (*wt*) after 8 and 15 weeks of growth under low-phosphate conditions in the presence and absence of *Glomus mosseae* (*Gm*). **a** Representative plants of *lrt1* and the isogenic wild type in the presence or absence of *G. mosseae* after 8 weeks of growth. **b** Representative *lrt1* plants in the presence or absence of *G. mosseae* after 15 weeks of growth. **c** Representative samples of brace and lateral roots of *lrt1* and wild-type plants after 15 weeks. The experiment was repeated twice with three plants for each line and treatment

Table 1 Biomass of wild-type (*wt*) and *lrt1 Zea mays* plants after 15 weeks of growth in the presence and absence of *Glomus mosseae* (*Gm*). Independent determinations of shoot and root dry weight (*DW*) values of plants grown in the presence or absence of *G. mosseae* at 0.1 mM or 1 mM KH_2PO_4. Values (means ± SD) originate from one experiment in which three plants for each line and treatment had been included. Numbers marked with the same letter indicate non-significant differences at $P < 0.05$; $^{a-e}$ shoot values, $^{a*-c*}$ root values

Plant system	Plants grown at 0.1 mM KH_2PO_4		Plants grown at 1 mM KH_2PO_4	
	Shoot DW (g)	Root DW (g)	Shoot DW (g)	Root DW (g)
wt, –Gm	11.4 ± 3.7^{a}	$2.5 \pm 0.3^{a*}$	15.2 ± 2.0^{a}	$4.2 \pm 0.3^{b*}$
wt, +Gm	20.2 ± 7.0^{b}	$5.1 \pm 1.0^{b*}$	27.0 ± 5.2^{d}	$4.0 \pm 0.9^{b*}$
lrt1, –Gm	0.6 ± 0.25^{c}	$0.25 \pm 0.09^{c*}$	$6.2 \pm 1.1e^{e}$	$1.3 \pm 0.25^{a*}$
lrt1, +Gm	12.4 ± 1.6^{a}	$2.9 \pm 0.4^{a*}$	7.6 ± 0.7^{e}	$2.1 \pm 0.2^{a*}$

laterals of first, second and third order had been uniformly developed on all nodal roots of colonized and non-colonized plants (Fig. 2c). However, roots of the mycorrhizal wild type seemed to be thicker than those of the non-colonized plants, and they had twice as much dry weight (Table 1).

Examination of the root system of *lrt1* mutant plants revealed a substantially altered morphology in the presence of the fungus relative to non-mycorrhizal control roots. Non-colonized *lrt1* plants had developed crown and occasionally brace roots on which, infrequently, first- and second-order lateral roots had formed (Fig. 2c). The mutant plants colonized by *G. mosseae* had similar, albeit somewhat thicker, crown and brace roots, but on the "late" crown roots and the subsequently emerging brace roots, highly branched laterals had regularly formed, displaying "bush-like" structures (Fig. 2c). These lateral "bushes" consisted of rather coarse and stunted roots of first, second, third and fourth order; rarely, laterals up to the fifth order were observed. Occasionally, thin laterals of first and second order were also monitored on early crown roots.

Comparison of the root biomasses of non-colonized and colonized mutant plants demonstrated once more the drastic alteration that had taken place. While the non-mycorrhizal root system had a dry weight of 0.25 ± 0.09 g (mean ± SD) the mycorrhizal one reached a value of 2.9 ± 0.4 g (Table 1).

Fungal colonization in crown and lateral roots was equally high in the mutant and the wild-type background, reaching $91 \pm 3\%$ (mean ± SE) in the wild type and $92 \pm 2\%$ in mutant roots.

Effect of increased phosphate supply on performance of *lrt1* plants

To investigate whether the appearance of bush-like laterals was associated with improved phosphate nutrition, we studied the direct effect of increased phosphate supply on the performances of wild-type and *lrt1* plants. For this purpose, the phosphate supplement was increased 10-fold to match the standard Hoagland concentration of 1 mM.

At 15 wpi, inoculated and non-inoculated wild-type plants showed no visible difference in growth; all wild-type plants had grown to maturity (data not shown). As in the previous experiment, mycorrhizal wild-type plants appeared stronger than non-mycorrhizal plants and displayed higher shoot biomass values (Table 1).

When grown in the high-phosphate regime, the *lrt1* mutant plants were found to develop to maturity even in the absence of AMF (Fig. 3a). Thus, high phosphate supply complemented the growth-retardation effect of the *lrt1* mutation in a way similar to the symbiosis with AMF.

Under the high-phosphate regime, *lrt1* plants grew equally well with and without inoculation with AMF, exhibiting almost identical shoot dry weight values, and remained smaller than the wild type independently of the mycorrhizal status (Fig. 3a, Table 1). Interestingly, in the presence of AMF, the *lrt1* mutant plants grown at reduced phosphate were more robust and produced more shoot biomass than those kept at high phosphate (Figs. 2b, 3a; Table 1).

The root morphology of the wild-type plants was unchanged in the presence or absence of *G. mosseae*, as had been observed for the plants grown at reduced phosphate (Fig. 3b). However, while at low phosphate supply mycorrhizal wild-type plants had increased root dry weight relative to the non-mycorrhizal plants, there was no difference in root biomass at high phosphate supply (Table 1).

Inspection of the root systems of *lrt1* plants grown at high phosphate without AMF showed that a more extensive lateral root formation had occurred than on *lrt1* plants grown with low phosphate nutrition. However, these laterals did not resemble wild-type laterals, as they were noticeably shorter (Fig. 3b).

Interestingly, on late crown and brace roots of the mycorrhizal root system of *lrt1* plants, the formation of lateral root bushes was again observed (Fig. 3b). These bush-like structures were comparable to those monitored for *lrt1* plants grown at low phosphate, built from thick and short laterals of first, second, third and fourth order. Under elevated phosphate nutrition, the root biomass of mycorrhizal relative to non-mycorrhizal *lrt1* plants was slightly higher (2.1 ± 0.2 g versus 1.3 ± 0.25 g, respectively; mean ± SD); however, the dramatic

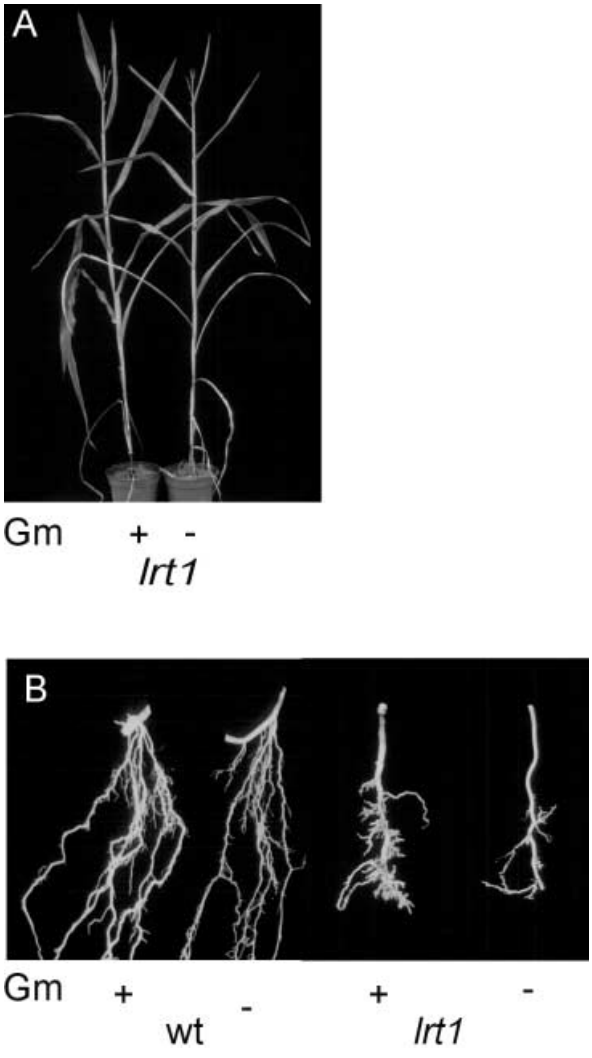

Fig. 3a, b Phenotype of maize *lrt1* plants and the corresponding wild type (*wt*) after 15 weeks of growth under high-phosphate conditions in the presence and absence of *G. mosseae* (*Gm*). **a** Representative *lrt1* plants in the presence or absence of *G. mosseae*. **b** Representative samples of brace and lateral roots of *lrt1* and wild-type plants after 15 weeks. The experiment was repeated twice with three plants for each line and treatment

increase documented for plants grown at lower phosphate was absent (Table 1).

Fungal colonization had similar high values for both genotypes. Colonization reached 88 ± 2% (mean ± SE) in the wild type and 86 ± 3% in the mutant background. These values were in the range of those of the first experiment at reduced phosphate.

Discussion

We have examined the growth of three maize mutants affected in single elements of their root system under low-phosphate conditions, and we found that a reduction in the root hair system (mutant *rth3-1*) or a lack of seminal, crown and brace roots (mutant *rtcs*) did not influence plant performance. This finding is particularly surprising for the root hair mutant *rth3-1* since root hairs have been thought to play a major role in nutrient acquisition (Clarkson 1996). However, Wen and Schnable (1994) already have reported that this mutant develops well under field conditions, and they have suggested that root hairs under some environmental conditions may be less important in nutrient acquisition than previously assumed (Hofer 1996; Clarkson 1996). With regard to *rtcs*, the main effect of the mutation is a loss of anchorage in the soil, but it could have been predicted to display reduced vigour as well, since it lacks all nodal roots, which are supposed to have a major function in water and nutrient uptake (McCully and Canny 1988; Hetz et al. 1996). The fact that this mutant grows normally under the low-phosphate regime used here indicates that the primary root, together with its laterals and root hairs, provides sufficient phosphate uptake to accomplish normal plant development, and can compensate for the absence of the nodal roots.

In contrast, the absence of lateral roots in the *lrt1* mutant resulted in small plants that were retarded in growth and terminated their development before reaching maturity. Previously, it has been reported that *lrt1* plants develop to mature fertile plants when grown in soil-containing pots under controlled conditions in phytochambers, but that they show reduced growth under field conditions (Hochholdinger and Feix 1998), indicating that the mutant depends on appropriate nutritional conditions to reach the adult stage.

Remarkably, when *lrt1* plants entered AM symbiosis, the above-ground growth performance was fully restored in comparison with the wild type. Development of the mutant proceeded synchronously with that of the wild type. Hence, under the conditions used here, *lrt1* plants depend on their symbiotic partner for normal development. A simple explanation for this finding could be the contribution of the fungal mycelia to nutrient acquisition. However, the observed rescue was also accompanied by a clear morphological change, namely by the induction of highly branched lateral root bushes on late crown and brace roots of *lrt1* plants. There were no lateral root bushes on early crown roots. Crown roots start to emerge from consecutive early nodes at approximately 10 days post germination (Hetz et al. 1996), and since it takes several weeks for the symbiosis to become established, laterals of the first (early) crown roots might have developed before the symbiosis is fully set up.

The increased growth performance of mycorrhizal *lrt1* plants might be due to combined nutrient absorption mediated by fungal hyphae plus lateral root bushes. However, the plant lateral root bushes have a rather limited soil volume to explore due to their shortness and thickness. It is more likely that the fungal mycelium functionally extends the plant's nutrient absorption capacity. Its hyphae are expected not only to extend into soil areas further distant from the roots but also to penetrate into smaller soil pores and to mobilize

adsorbed phosphate otherwise not accessible to the plant (Smith and Read 1997).

This enhanced, AMF-mediated nutrient uptake has received particular attention regarding the evolution of land plants. Since the occurrence of the AM symbiosis matches the colonization of land by plants (Simon et al. 1993) it has been hypothesized that AM fungi may have been instrumental in this invasion. Furthermore, fossil records showed that roots of the early land plants contained fungal structures of the Glomalean type (Remy et al. 1994). Taking into consideration that these ancient plants lacked true roots and possessed instead rather primitive protostelic rhizomes, the capability for sufficient exploration of the soil environment has likely been mediated by the hyphal mycelium of the intimately associated symbiotic fungi (reviewed in Smith and Read 1997). The results of our experiments further foster this model, suggesting that mycorrhizae specifically have worked in place of lateral roots.

The wild-type plants, too, exhibited an increased root biomass under low-phosphate conditions when infected with mycorrhizal fungi. However, this was rather due to thicker roots than to the production of additional roots. The bushes of lateral roots occurred only on mycorrhizal plants of mutant background; the reason for this is not clear.

Importantly, elevation of the phosphate addition rescued the mutant phenotype as well. Non-mycorrhizal and mycorrhizal *lrt1* plants developed equally well, indicating that the beneficial effect of the symbiosis had vanished. Interestingly, mycorrhizal mutant plants grown under higher phosphate remained noticeably smaller than mycorrhizal *lrt1* plants grown under low-phosphate conditions and also smaller than the wild type. A reduction in size of mature *lrt1* plants relative to the wild type was also monitored by Hochholdinger and Feix (1998). The reduced potential of mycorrhiza formation to rescue the mutant *lrt1* in the presence of high phosphate levels might be explained by a reduced functionality of mycorrhizae under these conditions (Smith and Read 1997).

It is interesting that the presence of a mycorrhiza induces *lrt1* plants to form lateral root bushes both under conditions of low and high phosphate. It is well known that induced proliferation of laterals can occur as part of the developmental root plasticity, leading to efficient exploration of nutrient-rich (e.g. phosphate-rich) soil pockets (Drew 1975; Schiefelbein and Benfey 1991; Fitter 1994; Robinson 1994). Colonization by AMF appears to have a similar effect on the root system of *lrt1* mutant plants, independently of the phosphate supply, indicating that the fungal symbiont has the capacity to influence the plant's developmental root plasticity in a way similar to uneven nutrient distribution.

Changes in root morphology of mycorrhizal versus control plants have been described previously. Whereas in the cotton root system, branch initiation was shown to be reduced in the presence of a mycorrhiza (Price et al. 1989), colonization of leek roots by *Glomus* strains promoted the formation of first- and higher-order lateral roots which were short and stunted (Berta et al. 1990, 1991).

Possibly, the alterations to host root morphology are due to changes in phytohormone levels induced by the fungus. It has been reported previously that axenically germinated spores of *G. mosseae* produce gibberellin- and cytokinin-like compounds (Barea and Ascon-Aguilar 1982), and that mycorrhizal alfalfa roots contain elevated levels of cytokinin (van Rhijn et al. 1997).

We conclude that for maize, normal formation of lateral roots at the seedling stage is essential for growth and development under low-phosphate conditions, and that the lack of these lateral roots in the mutant *lrt1* can be complemented by the AM symbiosis, accompanied by the mycorrhiza-specific induction of additional laterals displaying a bush-like structure. In our study, the maize mutant *lrt1* has been shown to be obligatorily dependent on mycorrhiza formation to reach maturity under low phosphate supply. This opens up the interesting possibility that even wild-type maize plants may prove to be obligatorily dependent on mycorrhizae under appropriately limiting nutrient conditions.

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