J Plant Growth Regul (2012) 31:165–172
DOI 10.1007/s00344-011-9228-6

Strigolactone Positively Controls Crown Root Elongation in Rice

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Received: 17 March 2011 / Accepted: 8 July 2011 / Published online: 17 August 2011

Abstract Strigolactones are recently identified plant hormones that inhibit shoot branching. Pleiotropic defects in strigolactone-deficient or -insensitive mutants indicate that strigolactones control various aspects of plant growth and development. However, our understanding of the hormonal function of strigolactones in plants is very limited. In this study we demonstrate that rice *dwarf* mutants that are strigolactone-deficient or -insensitive exhibit a short crown root phenotype. Exogenous application of GR24, a synthetic strigolactone analog, complemented the crown root defect in strigolactone-deficient mutants but not in strigolactone-insensitive mutants. These observations imply that strigolactones positively regulate the length of crown roots. Histological observations revealed that the meristematic zone is shorter in *dwarf* mutants than in wild type, suggesting that strigolactones may exert their effect on roots via the control of cell division. We also show that crown roots of wild type, but not *dwarf* mutants, become longer under phosphate starvation.

Keywords Cell division · *Oryza sativa* · Root development · Phosphate starvation · Strigolactone

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Introduction

Strigolactones (SLs) are a group of terpenoid lactones, consisting of a tricyclic lactone and a methylbutenolide coupled with an enol ether bond. SLs were initially identified in root exudates of various plants as a signal molecule that stimulates germination of the parasitic weeds witchweed (*Striga* spp.) and broomrape (*Orobanche* spp.) (Bouwmeester and others 2003). The reasons why plants exude SLs have been an enigma until it was found that they act as a rhizosphere signal that induces the hyphal branching of arbuscular mycorrhizal (AM) fungi (Akiyama and others 2005). Now, it is thought that plants release SLs to enhance uptake of inorganic nutrients by facilitating symbiosis with AM fungi. Moreover, SLs have been identified as new plant hormones that inhibit shoot branching (Gomez-Roldan and others 2008; Umehara and others 2008).

Several genes that are involved in the synthesis or signaling of SLs have been isolated from both monocot and eudicot species: *MORE AXILLARY GROWTH* (*MAX*) of *Arabidopsis*, *RAMOSUS* (*RMS*) of pea, and *DWARF* (*D*) of rice. Molecular cloning of these genes revealed that *MAX1*, *MAX3/RMS5/D17*, and *MAX4/RMS1/D10* encode a cytochrome P450 monooxygenase (CYP711A1), carotenoid cleavage deoxygenase (CCD) 7, and CCD8, respectively (reviewed by Beveridge and Kyozuka 2010). In the *max1*, *max3/rms5/d17*, and *max4/rms1/d10* mutants, the levels of SLs are decreased significantly and their mutant phenotype is rescued by exogenous application of SLs. This indicates that *MAX1*, *MAX3/RMS5/D17*, and *MAX4/RMS1/D10* are involved in the biosynthesis of SLs, consistent with the prediction from previous grafting experiments (reviewed by Beveridge and Kyozuka 2010). *D27* of rice, which encodes an iron-binding protein of unknown function, is

also involved in SL biosynthesis (Lin and others 2009). On the other hand, *MAX2/RMS4/D3*, which encodes an F-box leucine-rich repeat (LRR)-containing protein, is considered to be involved in the signaling of SLs (reviewed by Beveridge and Kyozuka 2010). *D14* of rice, which was also reported as *D88* and *HTD2*, encodes a protein of the alpha/beta-fold hydrolase superfamily (Arite and others 2009; Gao and others 2009; Liu and others 2009). Because *d14* is insensitive to exogenous SLs and shows an accumulation of a higher level of endogenous SLs, it was hypothesized that *D14* works downstream of SL synthesis (Arite and others 2009). Currently, it remains to be determined whether D14 acts as a SL signaling component or as an enzyme that catalyzes conversion of SLs to the bioactive form of the hormone.

Besides the well-documented excess branching phenotype, *max*, *rms*, and *d* mutants exhibit pleiotropic defects, including reduced plant height, a thinner stem, delayed leaf senescence, and elongation of the mesocotyl (Woo and others 2001; Stirnberg and others 2002; Yan and others 2007; Hu and others 2010). In *decreased apical dominance* (*dad*) *1-1* of petunia, a SL-deficient mutant, a reduction of root mass was reported, indicating that SLs may be involved in the control of root growth (Snowden and others 2005). Recent studies showed that endogenous and exogenous SLs affect root system architecture in tomato and *Arabidopsis*, and this effect would be mediated through the control of auxin efflux (Kapulnik and others 2010; Koltai and others 2010; Ruyter-Spira and others 2011). These various observations suggest that SLs play multiple roles in the control of plant growth and development; however, a comprehensive view of the role of SLs is still not sufficient.

To better understand the hormonal function of SLs, we analyzed root growth in *d* mutants. We found that *d* mutants exhibit a short crown root phenotype and that an exogenous application of SLs enhanced crown root elongation. We also showed that crown roots of WT, but not *d* mutants, become longer under phosphate starvation. These results indicate that SLs or their downstream metabolites regulate root development and act as an integrator of growth and phosphate starvation.

Material and Methods

Plant Materials

d3-1, *d10-1*, *d14-1*, *d17-1*, and *d27-1* Shiokari-background mutants were described previously (Ishikawa and others 2005). For the observation of root morphology, plants were grown in 1.2-l pots in a greenhouse under natural conditions.

Observation of Crown Roots from Coleoptilar Node

Seeds were surface-sterilized and germinated in sterile water in the dark for 2 days. The germinated seeds were transferred into 1/2 Murashige and Skoog media (0.8% agar, 3% sucrose) and incubated at 24°C under fluorescent light, with a 16-h light/8-h dark photoperiod. To evaluate the effect of phosphate (Pi) deficiency, the germinated seeds were transferred into the Pi-deficient media (phosphate-removed 1/2 Murashige and Skoog medium containing 0.8% agar and 3% sucrose) and incubated under the same conditions. After 14 days, the seedlings were sampled to measure their height, seminal root length, number of crown roots, and crown root length. For the complementation test and the application of high-concentration SLs, the germinated seeds were transferred into the medium containing GR24 at the final concentration of 0.01, 0.1, 1.0, and 10 μM. Seedlings were grown and measured under the above-mentioned conditions. To keep concentrations of GR24 constant in the medium for the duration of the experiment, the initial dose of GR24 diluted by water was absorbed into the medium every fourth day. For the mock treatment, 0.1% acetone was added into the medium.

Histological Observation

To observe cells in root tips, crown roots were excised from 4-day-old seedlings and soaked in 10 μM of propidium iodide for 5 min. After staining, roots were washed with distilled water three times and made transparent by soaking in chloral hydrate solution (chloral hydrate, 8 g; glycerol, 1 ml; water, 2 ml). Roots were then observed by laser-scanning confocal microscopy (Fluoview FV 1000, Olympus). The lengths of mature cells in the second layer of the cortex were measured in 54 cells of WT (Shiokari), 36 cells of *d10-1*, and 51 cells of *d14-1*. Cell numbers of the root meristem were determined by counting the cortical cells in files extending from the quiescent center to the first elongating cell. The length and cell number of the meristematic zone were measured in 7 seedlings of WT (Shiokari), 10 seedlings of *d10-1*, and 7 seedlings of *d14-1*.

Statistical Test

Homogeneity of variances was tested by the *F*-test and *P* values >0.05 were assumed to have equal variances. The significance of a difference between two means was tested by Student's *t*-test (equal variances) or Welch's *t*-test (unequal variances).

Results

Root Morphology in the *d* Mutants

Gross morphology 6 weeks after germination of *d10-1*, a SL-deficient mutant, and *d14-1*, a SL-insensitive mutant, is shown in Fig. 1a. As reported previously (Ishikawa and others 2005), *d10-1* and *d14-1* mutants exhibit shorter plant height and an increased number of tillers compared to WT (Table 1). *d10-1* and *d14-1* roots are clearly shorter (Fig. 1b) and their dry weight is slightly reduced compared to WT (Table 1).

Growth of Crown Roots is Affected in *d* Mutants

The rice root system consists of two types of roots, namely, the embryonic seminal root and the crown roots (Fig. 2a) (Hoshikawa 1989). Crown roots are post-embryonic shoot-borne roots that emerge from aboveground and underground stem nodes. In rice, the seminal root functions only during the early stages of plant development; accordingly, the crown roots constitute the backbone of the rice root system (Hoshikawa 1989). To identify which type of root is affected in the *d* mutants, we observed 14-day-old seedlings of *d3-1*, *d10-1*, *d14-1*, *d17-1*, *d27*, and WT. Under our growth conditions, 14-day-old rice seedlings usually contain a seminal root and five crown roots emerging from the node of a coleoptile (Fig. 2a, b). This growth pattern was essentially maintained in all *d* mutants (Fig. 2c). Although the length of the seminal root was slightly variable among *d* mutants, it was not significantly different from the WT (Fig. 2d). On the other hand, crown roots of all *d* mutants were shorter than those of WT (Fig. 2e). Neither the number of crown roots emerging from the coleoptilar node nor the total number of crown roots differed between WT and *d* mutants (data not shown).

We also analyzed the pattern of crown root growth. Crown roots first became visible 5 days after sowing in both WT and *d10-1*. Then WT elongated vigorously between 6 and 9 days after sowing and gradually stopped growing by 12 days after sowing (Fig. 2f). The pattern of crown root growth was not different for *d10-1* seedlings but they showed a reduced elongation rate that led to the formation of shorter crown roots (Fig. 2f).

Rescue of the Root Defects by SL

To determine whether the short crown root phenotype in *d* mutants is attributable to the deficiency/insensitivity of SLs, we asked if the defect is restored by exogenous application of SL. Exogenous application of GR24, a synthetic strigolactone analog, had no significant effect on crown root growth in WT seedlings, but it enhanced

Fig. 1 Phenotype of *d10-1* and *d14-1* mutants. **a** Overall structure of 6-week-old WT and *d10-1* and *d14-1* mutant plants. **b** Close-up of root stocks of WT, *d10-1*, and *d14-1*. *Scale bar* 10 cm

elongation of crown roots of *d10-1* seedlings in a concentration-dependent manner (Fig. 3a). However, the *d14-1* mutant was insensitive to exogenous GR24 (Fig. 3a).

Although it was not statistically significant, a slight increase in crown root length was observed by the application of 1 μM GR24 to WT seedlings. It was previously reported that high concentrations of GR24 inhibited outgrowth of tiller buds in WT (Minakuchi and others 2010). This suggests that high concentrations of GR24 may affect normal root growth of WT plants. An application of GR24 at 10 μM, which was sufficient to inhibit tiller bud outgrowth of WT plants, accelerated the elongation of crown roots in WT seedlings (Fig. 3b). In contrast, *d14-1* mutant seedlings did not respond to 10 μM GR24, indicating that the elongation of crown roots was a direct effect of SL function (Fig. 3b).

Table 1 Morphological characteristics of WT and *d10-1* and *d14-1* mutants

Character	Wild type	*d10-1*	*d14-1*
Plant height (mm)	552.0 ± 11.4	411.7 ± 14.7	425.7 ± 5.3
No. of tillers (/plant)	4.7 ± 0.5	11.7 ± 1.7	11.0 ± 1.6
Longest root length (mm)	226.7 ± 18.0	144.7 ± 11.0	130.0 ± 6.7
Total dry weight (g)	2.30 ± 0.21	1.74 ± 0.23	1.64 ± 0.30
Dry weight of roots (g)	0.42 ± 0.06	0.33 ± 0.02	0.28 ± 0.01

Each value represents the mean ± SD of three plants

Effect of Pi Deficiency on the Elongation of Crown Roots

The levels of SLs in roots and root exudates are increased under phosphate (Pi) starvation (Yoneyama and others 2007, 2008; López-Ráez and others 2008; Umehara and others 2008). We have demonstrated that exogenous application of SLs caused elongation of crown roots. These results raised the possibility that SL could mediate crown root elongation under Pi deficiency. Consistent with this prediction, growth of crown roots was enhanced when WT seedlings were grown on the Pi-deficient media (Fig. 4a, c). On the other hand, we observed that Pi-deficiency-induced root growth did not take place in *d10-1* or *d14-1* mutant seedlings (Fig. 4b, c).

Histological Observations of Root Cells in the *d* Mutants

A root is divided into zones along the distal–proximal axis according to the activity of cells (reviewed by Ishikawa and Evans 1995). During root development, cells generated by the root apical meristem undergo a certain number of cell divisions in the zone of the proximal meristem, and subsequently they elongate in the transition zone and differentiate into mature cells. After differentiation, the size of each mature cell is maintained relatively constant. Therefore, the rate of root elongation is determined by two factors: the frequency of cell division and the extent of cell elongation. We asked whether cell division or elongation is affected in crown roots of *d* mutants. To compare the size of cells, we analyzed the length of mature cells whose sizes are relatively uniform. The morphology and the arrangement of mature cells were not impaired in *d10-1* and *d14-1* (Fig. 5a–c). There was no significant difference in the sizes of mature cells between WT and mutants (Fig. 5d).

As shown in Fig. 5e–g, the meristematic zone, which contains small cells, seems to be shorter in *d10-1* and *d14-1*. For a more precise comparison, the length of the meristematic zone, which is expressed as the distance between the root tip and the first elongated cortex cell, was measured (Fig. 5h–j). This analysis clearly indicates that the meristematic zone was significantly shorter in *d10-1* and *d14-1* than in WT (*d10-1*, 584 ± 86 μm; *d14-1*, 542 ± 102 μm; WT, 799 ± 74 μm). Cell numbers of the meristematic zone were also determined by counting cortical cells in files extending from the quiescent center to the first elongating cell. Actually, cell numbers of the meristematic zone were clearly decreased in *d10-1* and *d14-1* mutants (Fig. 5k). Taken together, these results suggest that SL regulates the frequency of cell division in the meristematic zone rather than the rate of cell elongation in roots.

Discussion

In this study we showed that rice *d* mutants with impaired SL biosynthesis or signaling exhibit a shorter crown root phenotype. The phenotype in crown roots of *d10-1*, a SL-deficient mutant, but not *d14-1*, a SL-insensitive mutant, was complemented by exogenous application of GR24, a synthetic SL analog. Moreover, application of high concentrations of GR24 enhanced the elongation of crown roots in WT plants. Based on these results, we conclude that crown root elongation is positively regulated by SLs or their downstream metabolites in rice.

In rice seedlings, the vigor of shoot growth correlates well with the total length of roots. Crown roots from the coleoptilar node are important in rooting and subsequent plant development (Hoshikawa and Shoji 1990; Sasaki and Hoshikawa 1997). Therefore, we cannot rule out the possibility that the short crown root phenotype observed in this study is an indirect consequence of the decreased height of shoots or excessive shoot branching. However, this is unlikely because there were few differences in plant height and number of axillary shoots between *d* mutants and WT in 14-day-old seedlings that we investigated (data not shown). Moreover, no significant difference in seminal root length was detected, indicating that the effect is not a general consequence of retarded shoot development. In tomato and *Arabidopsis*, lateral root densities are increased in SL-insensitive and -deficient mutants, suggesting that SLs affect lateral root formation (Kapulnik and others 2010; Koltai and others 2010; Ruyter-Spira and others

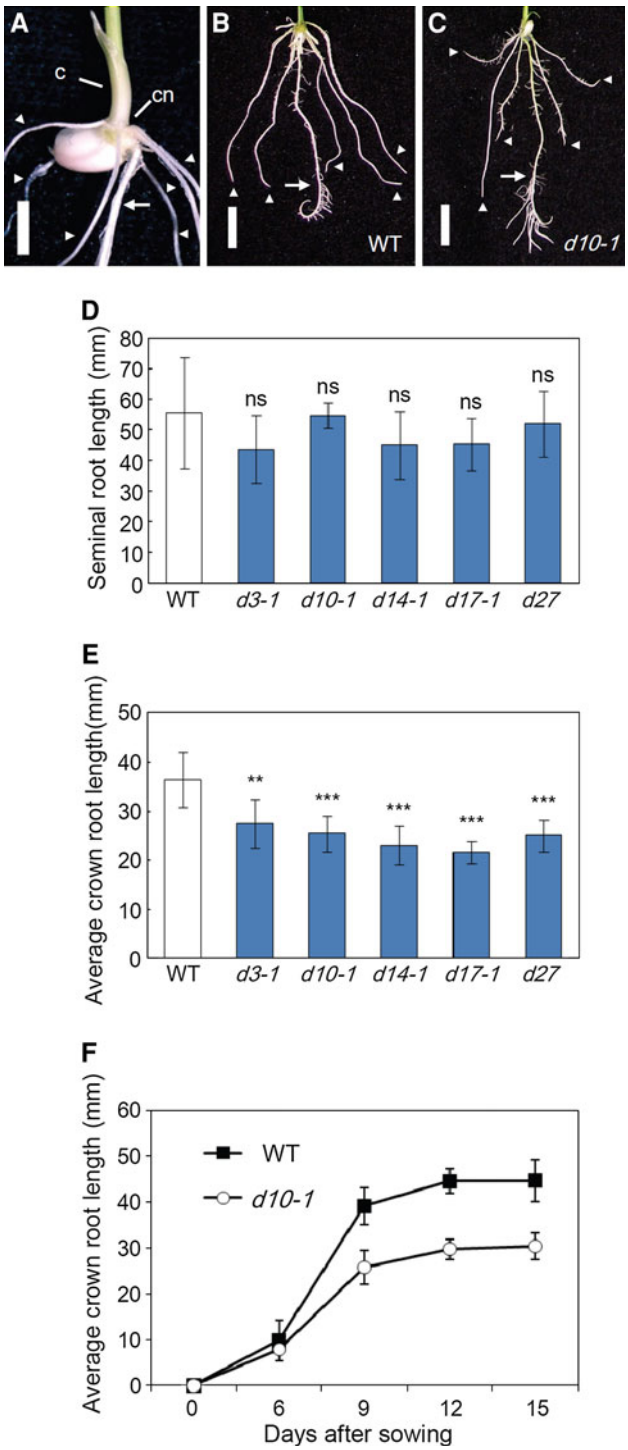

Fig. 2 Root morphology of *d* mutants. **a** Stem and crown roots from the coleoptilar node. *c* coleoptile, *cn* coleoptilar node. **b**, **c** Fourteen-day-old seedlings of WT and *d10-1* mutant. *White arrows* and *arrowheads* indicate the seminal root and crown roots. *Scale bar* 5 mm in **a**; *scale bar* 1 cm in **b** and **c**. **d**, **e** Length of the seminal root and crown roots in WT and *d* mutants. Each value represents the mean of ten seedlings. *Error bars* indicate standard deviation. *ns* not significant, * and ***significant at 5 and 0.1% levels from WT. **f** Time-dependent changes in average crown root length of WT and *d10-1* mutant. Each value represents the mean of every crown root length in six seedlings. *Bars* indicate standard deviation

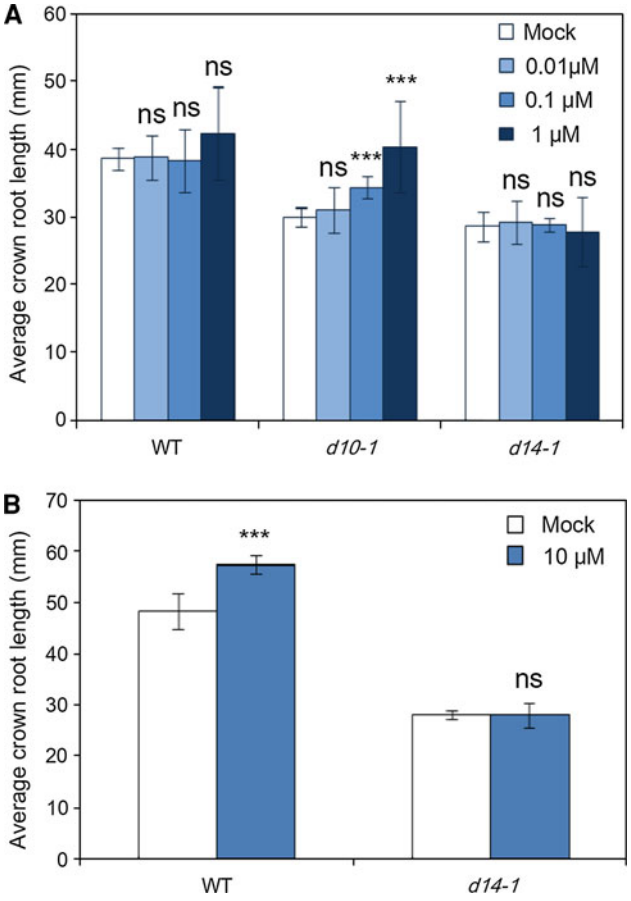

Fig. 3 Complementation test in WT and *d10-1* and *d14-1* mutants. **a** Average crown root lengths after application of 0.01, 0.1, and 1 μM GR24 and mock treatment (1% acetone). Each value represents the mean of every crown root length in eight seedlings. *Error bars* indicate standard deviation. *ns* not significant, ***significant difference at 0.1% level from the mock treatment. **b** Average crown root length after application of 10 μM GR24. Each value represents the mean of every crown root length in eight seedlings. *Error bars* indicate standard deviation. *ns* not significant, ***significant difference at 0.1% level from the mock treatment

2011). Unlike these studies, numbers of lateral roots in the seminal root were not different among WT, *d10-1*, and *d14* (data not shown). However, we cannot rule out the possibility that aberrant lateral root formation was stimulated in our experiments, because many lateral roots were observed especially in the root tip of seminal roots (Fig. 2b, c), which is less common in rice plants grown in soil. Further analysis is required to understand the effect of SLs on lateral root formation in rice.

We showed that the number of cells of the meristematic zone decreased in *d10-1* and *d14-1* mutants. Moreover, the length of the meristematic zone was shorter whereas the size of each mature cell was not affected in crown roots of *d* mutants. These results suggest that cell division might be repressed in *d* mutants; thus, SLs would positively regulate cell division in root meristems. Similarly, a reduction in the

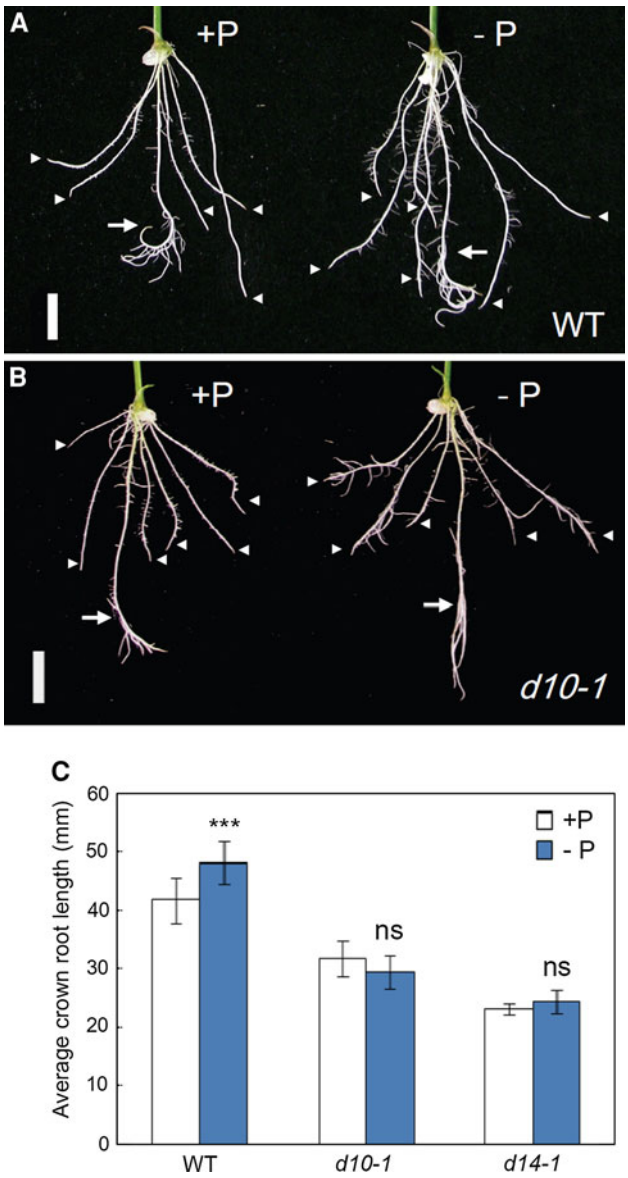

Fig. 4 Effect of Pi starvation on the elongation of crown roots. **a**, **b** Fourteen-day-old seedlings of WT and *d10-1* mutant grown on Pi-containing media (600 μM of Pi, *left*) and in the absence of Pi (*right*). *White arrows* and *arrowheads* indicate the seminal root and crown roots. *Scale bar* 1 cm. **c** Average crown root length of WT, *d10-1*, and *d14-1* seedlings grown on the Pi-containing media (+P) and in the absence of Pi (−P). Each value represents the mean of every crown root length in 18 seedlings. *Error bars* indicate standard deviation. *ns* not significant, ***significant difference at 0.1% levels from seedlings grown on Pi containing media

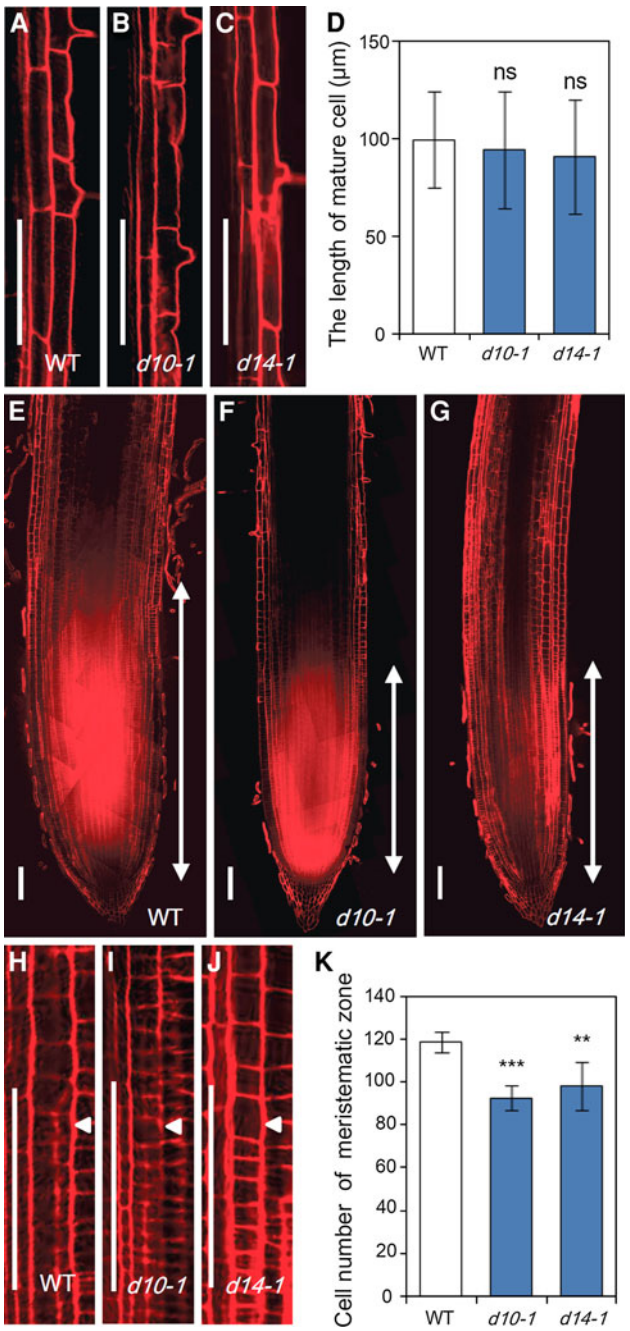

Fig. 5 Histological analysis of root cells. **a–c** Mature cells of WT, *d10-1*, and *d14-1*. *Scale bars* 100 μm. **d** Length of mature cells. Each value represents the mean of 36–54 cells. *Bars* indicate standard deviation. *ns* not significant difference from WT. **e–g** Vertical sections of root tip of WT, *d10-1*, and *d14-1*. The *white arrows* indicate the length of meristematic zone. *Scale bars* 100 μm. **h–j** Cells in the meristematic zone and elongation zone of WT, *d10-1*, and *d14-1*. *White arrowheads* indicate the boundary between the meristematic zone and the elongation zone. *Scale bars* 100 μm. **k** The cell number of the meristematic zone. The cell number was determined by counting cortical cells in files extending from the quiescent center to the first elongating cell. Each value represents the mean of seven to ten roots. *Error bars* indicate standard deviation. ** and ***significant at 1 and 0.1% levels from WT

number of meristem cells causes short primary roots in the SL-deficient and -insensitive *Arabidopsis* plants (Kapulnik and others 2010; Ruyter-Spira and others 2011). It was suggested that SL could modulate the local auxin level, which leads to the reduction in meristem cell number (Kapulnik and others 2010; Ruyter-Spira and others 2011). However, the detailed mechanisms of SL action may not be

fully understood. SLs are known to regulate shoot branching through suppression of axillary bud outgrowth (Gomez-Roldan and others 2008; Umehara and others 2008) and to suppress cell division in the mesocotyl under the dark conditions (Hu and others 2010). In both cases, SLs negatively regulate cell proliferation. The opposite action of SLs on cell division observed in this study suggests that SLs might control cell proliferation both positively and negatively depending upon the context. *d* mutants also exhibit extremely thin stems, which could reflect negative regulation of the proliferation of stem cambium cells by SLs. Further analyses of *d* mutants of rice as well as SL-related mutants in other species are required to better understand the function of SLs.

Phosphorus is essential for growth and development of plants. Generally, the bioavailability of phosphate (Pi) is extremely low due to mineralization and fixation processes in alkaline and acidic soils (Bar-Yosef 1991). To improve the efficiency of Pi uptake from the soil, plants have evolved a wide range of adaptive strategies (Raghothama 1999). Elevated SL biosynthesis upon Pi deficiency is considered to be one such adaptive strategy (Yoneyama and others 2007, 2008; Gomez-Roldan and others 2008; Umehara and others 2008, 2010). It has been proposed that SLs might play dual roles in helping plants to adapt to the Pi deficiency. First, SLs promote symbiosis with AM fungi by inducing hyphal branching so that plants are able to collect more Pi. Second, SLs optimize shoot architecture by suppressing bud outgrowth so that plants can utilize the limited Pi resource efficiently (Umehara and others 2008, 2010). In this study we showed that SLs enhance crown root elongation. Our findings raise the possibility that the positive regulation of root elongation by SLs is also a strategy of plants to adapt to Pi deficiency. Control of root architecture is an effective mechanism that enables plants to explore and exploit the insoluble Pi in the soil. In *Arabidopsis*, primary root elongation is reduced and proliferation of lateral roots is enhanced upon Pi starvation (Williamson and others 2001; Linkohr and others 2002; Ruyter-Spira and others 2011). Rice depends mostly on a well-developed root system for Pi uptake because infection by AM fungi is not very efficient (St. John 1980; Isobe and Tsuboki 1998). There are a number of agronomic reports describing the relationship between root development and Pi starvation in rice; however, the causality between root length and Pi starvation is still not clear. In this work, the direct relationship became evident partly because we used seedlings that depend upon the endosperm as a source for most of their nutrients.

It has been reported that auxin plays a critical role in modulating root architecture under Pi starvation (Pérez-Torres and others 2008). The distal auxin maximum correlates with root pattern formation and extension of cell division in the root meristem (Sabatini and others 1999). The application of low concentrations of exogenous auxin increases the density of lateral roots and root hairs. These observations indicate that auxin may play a role in the control of root architecture in response to Pi starvation (López-Bucio and others 2002, 2005). In addition to auxin, we also showed that SLs are involved in the regulation of root elongation. Recent studies using tomato and *Arabidopsis* suggested that the effect of SLs on root growth would be dependent on the auxin status of the plants (Kapulnik and others 2010; Koltai and others 2010; Ruyter-Spira and others 2011). Meanwhile, auxin and SLs regulate shoot branching by multiple independent and interacting pathways (Heyward and others 2009). Further studies are needed to understand the detailed relationship between auxin and SLs and how SLs affect crown root elongation in rice seedlings.

Acknowledgments We thank Tadao Asami (University of Tokyo) for providing GR24, and Miho Takemura and Kanji Ohyama (Ishikawa Prefectural University) for providing T. Arite with facilities for carrying out the experiments.

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