Compensatory growth of lateral roots responding to excision of seminal root tip in rice

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Abstract: Development of lateral roots (LRs) is promoted when parental root elongation is suppressed. Promotion of LR growth compensates for parental root growth, which contributes to the maintenance of total root length. However, the developmental processes underlying the compensatory growth of LRs are still unclear. In this study, we induced LR compensatory growth in rice by surgical excision of a parent (seminal) root tip, and analyzed the morphological and anatomical changes in LRs. Our analysis revealed that seminal root-tip excision increased the diameter of first-order LRs by increasing in the number of ground-tissue layers and the stele diameter and also promoted elongation, with higher order LRs emerging in the remaining proximal portions. We also found that LR primordia in early developmental stages increased in diameter markedly and then produced higher order LRs pronouncedly in response to seminal-root cutting. Furthermore, the degree of change in LR morphology differed depending on the distance from the cut site, with changes in morphologies weakening further from the cut site. Taken together, the morphological and anatomical changes of LRs that are induced by the root-tip excision of the parent vary continuously, and are dependent on both the developmental stage of LR primordia at the site of root-cutting and the distance from the cut site.

Keywords: compensatory growth, lateral root, lateral root primordia, rice (*Oryza sativa* L.), root tip excision

Abbreviations: CRs, crown roots; LR, lateral root; LRP, lateral root primordia; SR, seminal root

Introduction

The root systems of rice are composed of several different types of roots. A seminal root is produced embryonically, whereas crown roots develop post-embryonically from the stem. Seminal and crown roots (parent roots) produce lateral roots (LRs), which are classified into S-types and L-types according to distinct morphological and anatomical characteristics (Kawata and Shibayama 1965, Kono et al. 1972, Yamauchi et al. 1987); S-type LRs are short and thin, and never produce higher order LRs, whereas L-type LRs are long and thick, and often produce higher order LRs. L-type LRs are more similar anatomically to parent roots—for example in developed vascular structure, and the presence of sclerenchyma and multiple cortex layers—than are S-types. These two different types of LRs vary in developmental characteristics and genetic control of their development (Kawata and Shibayama 1965, Sasaki et al. 1984, Wang et al. 2006, Niones et al. 2015). In addition, production of L-type LRs is important for expanding the root system because of their ability to produce higher order LRs.

Development of LRs is promoted when elongation of the parent root is inhibited; one such factor inhibiting parent root elongation is soil compaction, as compact soils, which are heterogeneously distributed, causes mechanical impedance of parent root growth. This mechanical impedance of the parent root triggers LR development in various plant species (Goss 1977, Shierlaw and Alston 1984, Atwell 1990, Montagu et al. 2001). Even in compact soil, LRs can elongate into the narrow pore spaces and cracks in the soil (Bingham and Bengough 2003, White and

Kirkegaard 2010, Haling et al. 2011). Compensatory growth of LRs facilitates the uptake of water and nutrients by maintaining sufficient total root length, which in turn contributes to shoot growth maintenance (Montagu et al. 2001). However, the developmental processes underlying compensatory LR growth remain largely unknown.

Compensatory growth of LRs can be also induced by surgical excision of the root tip, which disrupts parent root elongation and stimulates the development of L-type LRs in the remaining proximal portions of the root (Sasaki et al. 1984). The ability of a plant to produce higher order LRs in response to the root-tip excision is defined by the developmental stage of the lateral root primordia (LRP); however, morphological and anatomical changes induced by the root-tip excision and their relation with the developmental stage of LRP have yet to be determined.

Here, we examined the morphological and anatomical changes in LRs induced by seminal-root cutting, focusing on the developmental stage of LRP at the location of the root cut and the LR position relative to the cut site. Morphological changes in LRs induced by seminal-root cutting varied continuously according to the developmental stage of LRP at the root-cutting site and the LR position relative to the cut site. We also found that the anatomical characteristics of LRs were different depending on the developmental stage of LRP at the root-cutting site. Moreover, analyses of the relationships between several LR characteristics revealed that larger diameter LRs grow longer and produce second-order LRs more frequently than do smaller diameter LRs.

Materials and Methods

Plant growth conditions and root-cutting treatment

Seedlings of rice (*Oryza sativa* L. var. Taichung 65) were used in all experiments. Rice seeds were sterilized by soaking in a Benlate solution dissolved in tap water (2.5 g L⁻¹) at 28°C for 3 d, then rinsed three times with tap water and transferred onto plastic nets floating on nutrient-free filtered water in a black plastic box. The water was aerated with a pump (OX-30, Tetra-Japan, Japan) beginning 2 d after seedling transference and kept at a constant level through the addition of filtered water. Seedlings were grown in a growth chamber (MLR-351, Sanyo, Japan) at 28°C under continuous light. Seminal root length and the distance from the base to the LR emergence site, where the youngest LR appears from the outer surface of the seminal root, were measured 4 d after transference (Fig. 1A).

Seedlings having more than 10 mm distance from the base to the LR emergence site as like Fig. 3A were used for the following experiments. The seminal roots were cut into various root-cutting ratios using a cutting knife (Fig. 2A). Root-cutting ratio (%) was calculated as:

$$\frac{\text{Distance behind root tip (mm)}}{\text{Distance from root tip to LR emergence site (mm)}} \times 100$$

After root cutting, seedlings were put back onto the floating nets and allowed to continue to grow.

Morphological and anatomical characterization

Measurement of emerged LR characteristics: Seminal roots were sampled and fixed in FAA (5% formaldehyde, 5% acetic acid, 63% ethanol [v v⁻¹]) 10 d following root cutting (14 d after transplanting). Diameters of first-order LRs were measured at the basal region using a microscope (IX71, Olympus, Japan) and a micrometer. For the measurement of LR length, LRs, along with the seminal root, were fully extended on an agar plate, and images were taken with a digital camera (D90, Nikon, Japan) at 300 dpi. Length of the first-order LR was measured using image-analysis software (LIA for Win32, <https://www.agr.nagoya-u.ac.jp/~shinkan/LIA32>). For evaluating the effect of root cutting in the different root-cutting ratios, morphology of the LRs that emerged in the region between the excision site and a 10% higher ratio were analyzed (Fig. 3A). For analyzing the relationship between morphological changes in LR induced by the root-tip excision and distance from the cut site to each LR, morphology of the LRs that emerged in the 10% root-cutting ratio were analyzed every 5 mm up to a distance of 25 mm from the cut site (Fig. 5A).

Observation of LRP by rapid transparency method: Seminal roots of 4-d-old seedlings were fixed and cleared with TOMEI-I (Hasegawa et al. 2016). Images of LRP in the cleared seminal roots were captured using a differential interference microscope (BX60, Olympus, Japan), and distance from root tip to the LR emergence site and distance from root tip to the LRP were measured. LRP position was defined as relative distance from root tip, which is distance from root tip to LRP based on distance from root tip to the LR emergence site as 100% (Fig. 1A). Width of the meristem region, excluding the ‘Tasche’ (which originates from the endodermis of the parent root; Kawata and Shibayama, 1965) and distance from the base to the tip were measured as LRP diameter and length using imaging software (LIA for Win32), respectively (Fig. 1B).

Histological analysis of LRs: The thickest LR among the LRs that emerged 4 d following 10%, 50%, 60%, 80% and 100% root-cutting in each plant were sampled. The sampled LRs were placed in FAA solution, and de-aerated with a vacuum for 30 min. The FAA solution was then renewed and samples were kept for 24 h at 4°C. Fixed samples were dehydrated in a graded ethanol series and embedded in Technovit 7100 (Heraeus Kulzer, Germany); embedded samples were then sectioned into 6- μ m-thick slices using a rotary microtome (RM2125 RTS, Leica, Germany) and observed under a microscope (IX71, Olympus, Japan). Stele diameters and thicknesses of the ground tissues (exodermis, sclerenchyma, cortex, and endodermis) were measured using imaging software (LIA for Win32), and the number of ground-tissue layers were counted (Fig. 4A).

Data analysis

The morphological and anatomical characteristics of the LRs of the different groups were compared using ANOVA and a multiple comparison Tukey's test in R commander ver. 2.3-1 (Fox 2005). The relationships between relative distance from root tip and LRP size

was analyzed using regression analysis, and correlation coefficients were calculated in Microsoft Excel 2016.

Results

Relationship between developmental stage of LRP and responsiveness to root-tip excision

For determining the relationship between LRP developmental stage and responsiveness to the root-tip excision, we first analyzed the LRP developmental stage in the intact seminal roots of 4-d-old seedlings. As a result, positive correlations were detected between LRP size (diameter or length) and relative distance from root tip, which were stronger than the correlations between LRP size (diameter or length) and the distance from root tip to LRP ($r = 0.68$ and 0.64 respectively; data not shown), suggesting that LRP located at the same relative distance from root tip within root tip to the LR emergence site are at the same developmental stages in the seminal roots of 4-d-old seedlings (Fig. 1A–D; see Materials and Methods).

Based on the revealed relationship between LRP developmental stage and relative distance from root

Fig. 1. Relationship between position and size of LRP on intact seminal roots. (A) Schematic diagram of a 4-d-old seminal root. LRP position was defined as the relative distance from root tip based on distance from root tip to the LR emergence site, where the youngest LR appears from the outer surface of the seminal root, as 100%. (B) Schematic diagram of LRP in a seminal root; LRP diameter and length were defined as the width of the meristem region (a) and the distance from the base to tip (b), respectively. (C, D) Relationships between relative distance from root tip to primordia within root tip to the LR emergence site and diameter (C) or length (D) of LRP in seminal roots. Asterisk indicates a significant correlation between relative distance from root tip and LRP diameter or length ($P < 0.01$, $n = 44$ primordia from 5 plants).

tip, seminal roots were cut into various root-cutting ratios for determining the relationship between LRP developmental stage and responsiveness to the root-tip excision (Fig. 2A; see Materials and Methods). No LRs with higher order LRs emerged from intact seminal roots. For root-cutting ratios of less than 60%, maximum diameter of first-order LR (hereinafter diameter of first-order LR is referred to simply as LR diameter), which is a diameter of the thickest LR among the LRs that emerged after root cutting, was greater than 160 μm (control with intact roots: $104.0 \pm 4.6 \mu\text{m}$, $n = 30$ plants), and almost all of the thickest LRs produced second-order LRs (Fig. 2B). For root-cutting ratios of more than 60%, increases in the maximum LR diameter gradually slowed along with increasing root-cutting ratio, and few LRs produced second-order LRs.

For a more quantitative evaluation of the relationship between LRP developmental stage and responsiveness to the root-tip excision, seminal roots were cut into 10%, 50%, 60%, 80%, and 100% root-cutting ratios, and morphology of the LRs emerged after root cutting were analyzed (Fig. 3A; see Materials and Methods). Maximum LR diameters were virtually identical in the 10% and 50% root-cutting ratios, and LRs with second-order

LRs emerged equally in both (Fig. 3B, C, G, H). In the 60% root-cutting ratio, the increase in the maximum LR diameter induced by root cutting was smaller than those of the 10% and 50% root-cutting ratios, and few LRs with second-order LRs emerged (Fig. 3D, G, H). The maximum diameter of LRs was slightly higher in the 80% root-cutting ratio than that of control (Fig. 3E, G). Notably, some LRs with second-order LRs that sometimes emerged in the 80% root-cutting ratio had a much smaller diameter (about 120 μm) than those that emerged in the 10% and 50% root-cutting ratios. In the 100% root-cutting ratio, LR diameter was unaffected by root cutting, and no LRs produced higher order LRs (Fig. 3F, G, H). The diameter of LRs that emerged in the region between the excision site and a 10% higher ratio was distributed successively in the 10%, 50%, 60%, and 80% root-cutting ratios (Fig. 3I), and LRs with second-order LRs were more often of a larger diameter in each root-cutting ratio.

Anatomical changes of LR induced by seminal-root cutting in the different developmental stages of LRP

We analyzed the anatomical characteristics of LRs of various diameters emerged in the different root-

Fig. 2. Relationship between root-cutting ratio and LR morphology. (A) Schematic diagram showing the definition of the root-cutting ratio. (B) Seminal roots were cut into various root-cutting ratios. Diameter of the thickest LR among the LRs that emerged after root cutting in each plant and whether second-order LRs were produced are shown ($n = 44$ plants).

Fig. 3. Morphological characteristics of LR that emerged in the different root-cutting ratios. Seminal roots were cut into 10%, 50%, 60%, 80%, and 100% root-cutting ratios, and the morphology of the LR that emerged in the region between excision site and a 10% higher ratio were analyzed. Morphologies of LR emerged in the regions corresponding to those of root cuttings in intact seminal roots were analyzed for the control (- cut). (A) Image of a seminal root before the root cutting (bar = 5 mm). Arrow heads indicate the cut site of each root-cutting ratio. Squares indicate the regions where morphological characteristics of emerged LR were measured for each root-cutting ratio. SR, Seminal root; CRs, Crown roots. (B-F) Images of seminal and LR near the cut site 10 d after root cutting (bars = 5 mm). (G, H) Maximum LR diameter (G) and the number of LR with second-order LR (H). Different letters indicate significant differences between groups ($P < 0.05$); values represent means $\pm$ SDs ($n = 10$ plants for each root-cutting ratio). (I) Distributions of LR diameters with or without second-order LR.

cutting ratios (Fig. 4A; see Materials and Methods). Anatomical characteristics were virtually identical in the 10% and 50% root-cutting ratios (Fig. 4B–D). In the 60% root-cutting ratios, stele diameter, ground-tissue thickness and the number of ground-tissue layers were smaller than those of the 10% and 50% root-cutting ratios, but still significantly larger than those of LR emerged in intact seminal roots. In the 80% root-cutting ratio, stele diameter of LRs was significantly larger than that of control, whereas ground-tissue thickness and the number of ground-tissue layers were not.

Relationship between morphological changes in LR induced by root-tip excision and distance from cut site to each LR

We examined how far the effects of the root-tip excision extended in the remaining proximal portions of the 10% root-cutting ratio by analyzing LR morphology through the 10–60% ratios from

root tip, in which LRP had the same potential to respond to the root-tip excision as shown in Fig. 2B (Fig. 5A; see Materials and Methods). Maximum LR diameter increased in distances up to 15–20 mm from the cut site (Fig. 5B), whereas significant increases in the maximum length of the first-order LR and emergence of LRs with second-order LRs were limited to distances of 0–5 mm from the cut site (Fig. 5C, D). The degree of change weakened with distance from the cut site for all LR morphological characteristics (Fig. 5B–D). We next analyzed the relationships between LR morphological characteristics using the three individuals having different distributions of LR diameters and lengths of first-order LRs (Fig. 5E). In the region where both diameter and length of first-order LRs were increased to some extent (0–10 mm from the cut site; Fig. 5B, C), larger diameter LRs tended to become longer and produced second-order LRs more frequently regardless of distance from the cut site to the LRP in all individuals.

Fig. 4. Relationship between developmental stage of LRP and anatomical changes of LR induced by seminal-root cutting. The thickest LR among the LRs emerged in each root-cutting ratio were cross-sectioned and their anatomy analyzed. Anatomical characteristics of LRs emerged in the regions corresponding to those of root cuttings in intact seminal roots were analyzed for the control (– cut). (A) Image of a cross-section of LR indicating stele (a) and ground tissue (b) (bar = 100 μm). (B–D) Stele diameter (B), thickness of ground tissue (C), and the number of ground-tissue layers (D) of LRs emerged in different root-cutting ratios. Different letters indicate significant differences between groups ($P < 0.05$); values represent means $\pm$ SDs ($n = 5$ plants for each root-cutting ratio).

Fig. 5. Relationship between distance from the cut site and LR morphology. LRs in the 10% root-cutting ratio were analyzed every 5 mm up to a distance of 25 mm from the cut site. Morphologies of LRs emerged in the regions corresponding to those of the root cutting in intact seminal roots were analyzed for the control (– cut). (A) Schematic diagram showing the region analyzed. (B–D) Means of maximum LR diameter (B), maximum length of first-order LR (C), and the number of LRs with second-order LR (D) of each region. Different letters indicate significant differences between groups ($P < 0.05$); values represent means $\pm$ SDs ($n = 10$ plants). (E) Relationships between LR diameter, length of first-order LR, and production of second-order LR at distances of 0–5 mm and 5–10 mm from the cut site. Data from three different individuals, which have different distributions of LR diameters and lengths of first-order LR, were shown.

Discussion

The morphology of LR that emerged following the root-tip excision varied continuously depending on the LRP developmental stage at the site of root cutting (Fig. 6A). Relationship between LRP developmental stage and relative distance from root tip to LRP was revealed (Fig. 1C, D), which is consistent with observations for crown roots (Sasaki et al. 1984), and enabled us to examine the relationship between LRP developmental stage and responsiveness to seminal-root cutting by using the various root-cutting ratios. In less than 60% root-cutting ratio, LR diameter increased to over 160 μm , with the thick LR producing second-order LR (Fig. 2B, Fig. 3B, C, G, H, Fig. 6A). The LRP at the 60% ratio from root tip had a diameter of 80 μm and a length of 70 μm (Fig. 1C, D), demonstrating that the diameters of LRP at early developmental stages increase markedly and produce second-order LR in response to the root-tip excision. Moreover, increases in LR diameter gradually declined with increasing root-cutting ratio, and few LR produced second-order LR in more than 60% root-cutting ratio (Fig. 2B, Fig. 3D–H, Fig. 6A). In addition, small increases in LR diameters were also induced in LRP at later developmental stages. We found that there was a relationship between LRP developmental stage and emergence of LR with higher order LR in seminal roots, which is consistent with observation for crown roots (Sasaki et al. 1984), and furthermore, that the diameter of LR that emerged after the root-tip excision varies continuously depending on the LRP developmental stage at the site of the root cutting.

Seminal-root cutting induces the anatomical changes in LR and the anatomical characteristics of LR are different depending on the developmental stage of LRP at the root-cutting site. LRP at early developmental stage markedly increased both the number of ground-tissue layers (and hence increase in thickness of ground tissue) and stele diameter responding to seminal-root cutting (Fig. 4B–D). The increase in the number of ground-tissue layers was driven by the activation of periclinal division of the initial cells in the LRP (Kawata and Shibayama 1965); it may be that seminal-root cutting activates periclinal division of the initial cell in LRP. In later LRP developmental stage, the increase in ground-tissue layers decreased as proceeding of LRP development, however, stele diameter was still increased to some extent even in LRP at 80% ratio from root tip (Fig. 4B, D). Few LR produced second-order LR for root-cutting ratios of more than 60%, but LR with comparatively small

diameters at times produced second-order LR in the 80% root-cutting ratio (Fig. 3I). Thus, the increase in LR diameter induced by the increase in the number of ground-tissue layers is not necessary for production of second-order LR, but developed stele may play an important role in the production of higher order LR. This hypothesis is supported by the finding that thicker roots with second-order LR tend to have larger stele with thicker late metaxylem, and greater abundances of proto-xylem and proto-phloem (Sasaki et al. 1981).

The degree of change in LR morphology induced by the root-tip excision is dependent on the distance from the cut site (Fig. 6B). Maximum diameter and length of first-order LR were relatively larger, and LR with second-order LR emerged more frequently the closer to the cut site (Fig. 5B–D, Fig. 6B). The region where increase in LR diameter occurred was further distant from the cut site than those of increase in length of first-order LR and production of second-order LR.

Relative LR diameter among the LR that emerged in the region where both diameter and length of first-order LR were increased to some extent by the root-tip excision determines the length of the first-order LR and whether or not the LR produces second-order LR (Fig. 6B). Relatively large diameter LR were longer than smaller-diameter LR and produced second-order LR in the 10% root-cutting ratio regardless of distance from the cut site (Fig. 5E, Fig. 6B), indicating that relative LR diameter among the LR that emerged from the same parent root after the root-tip excision might determine the length of the first-order LR and whether the LR produces second-order LR. Root apical diameter was positively correlated with root elongation rate (Cahn et al. 1989, Pages 1995, Lecompte and Pages 2006, Wu et al. 2016), and is regarded as an indicator of the sink strength of a root (Thaler and Pages 1999). Thus, increased assimilate supply to first-order LR of larger diameter and sink strength as a result of excision of a seminal root tip induces preferential elongation and production of second-order LR. Based on these findings, we are now planning to undertake several experiments to further our understanding of the molecular mechanisms underlying compensatory LR growth.

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Fig. 6. (A) Schematic model illustrating the relationship between the morphological changes in LRs induced by the root-tip excision and LRP developmental stage. (Left) Prior to root cutting, the LRP developmental stage proceeded along the seminal root, which positively correlated with relative distance from root tip within root tip to the LR emergence site. (Middle) LRP and LR diameters increased as a result of root cutting, with the degree of change in diameter depending on the LRP developmental stage at the site of the root cutting. For root-cutting ratios of less than 60%, diameters increased by more than 160 μm , but gradually declined for root-cutting ratios of more than 60%. (Right) Large-diameter LRs often produced second-order LRs in the region for root-cutting ratios of less than 60%, but second-order LRs rarely emerged from first-order LRs for root-cutting ratios of more than 60%. (B) Schematic model showing the relationship between morphological changes in LR and distance from the cut site. The region where increase in LR diameter occurred was further distant from the cut site than those of increases in length of first-order LR and production of second-order LRs. Thicker LRs grew longer and produced second-order LRs at a greater frequency regardless of distance from root tip.

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