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An *Arabidopsis short root and dwarfism* Mutant Defines a Novel Locus That Mediates Both Cell Division and Elongation

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***Arabidopsis* leaf morphology is determined by the coordinated action of cell division and elongation. Of all the hormones that control leaf shape, the brassinosteroids (BRs) are active components in this process. BRs are a group of plant-originated steroidal compounds that induce growth along the long axes of organs. Here, we report the isolation and characterization of a novel mutant, *short root and dwarfism* (*srd*). Its dwarf phenotype includes round and curled leaves, reduced fertility, and short hypocotyls in the light and dark. Dwarfism in the aerial portions and a short-root morphology are not rescued by exogenous application of BRs, suggesting that *srd* is not impaired in BR metabolic pathways. Anatomical analysis revealed that *srd* roots are much shorter and thicker than the wild type due to additional layers of cortical cells. A lack of cell elongation but an increase in division results in these short but horizontally swollen roots. A double mutant *srd/bri1-5* also displays the short-root phenotype, implying that *srd* is epistatic to *bri1*. Cloning and further characterization of *SRD* should provide additional information about its role in the determination of leaf shape and root elongation.**

Keywords: brassinosteroids, cell division, cell elongation, dwarf, short root

Brassinosteroids (BRs) are the primary determinant of leaf shape. BR-deficient mutants usually display short-round shapes due to defects in cell elongation on the long axis. These poly-hydroxylated plant steroids are structurally similar to animal steroid hormones, such as ecdysones and progesterones (Choe, 2004). Their essential roles in plants include cell division and elongation, leaf development, pollen tube growth, xylem differentiation, acceleration of senescence, and photomorphogenesis (Choe, 2004). Accordingly, mutants defective in BR biosynthesis or signaling may have a dwarf phenotype, longer life span, irregular patterns in their vasculature, round and dark green leaves when grown in the light, and greatly reduced hypocotyl growth under darkness (Kwon and Choe, 2005). BR mutants have been recovered from *Arabidopsis*, rice, tomato, barley, and pea (Bishop, 2003).

Arabidopsis BR dwarf mutants are divided into two classes, based on their responses to exogenously-applied BRs (Choe, 2004). One class is impaired in its BR biosynthesis and can be rescued by exogenous applications. The BR biosynthetic pathway has become relatively well-understood through the molecular genetic characterization of *Arabidopsis* BR dwarf mutants (Choe, 2004). The second class resembles the biosynthetic mutants in morphology, but its functioning is not rescued by BR feeding. This class is predicted to be blocked in the perception or in essential downstream steps in the BR signal transduction pathways.

BR signals are detected at the cell surface by the plasma membrane with localized leucine rich repeat (LRR) receptor kinase *BRI1*. *BRI1* perceives these signals through its extracellular domain, and initiates a signal transduction cascade using cytoplasmic kinase activity (Li and Chory, 1997). *BRI1-ASSOCIATED RECEPTOR KINASE1* (*BAK1*) represents another component of the BR receptor complex. *BAK1* encodes an LRR-receptor-like kinase (RLK) but, unlike *BRI1*, it has only 5 LRRs and lacks the 70 amino acid island (Li et al., 2002). BR signals perceived by the BRI1-BAK1 heterocomplex are then conveyed to repress GSK3β-like kinase BIN2/DWF12 activity via a yet unknown mechanism (Choe et al., 2002; Li et al., 2001; Perez-Perez et al., 2002). Analogous to most SHAGGY/GSK3 kinases in animal systems, BIN2/DWF12 acts as a negative regulator in the BR signaling pathway. It

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phosphorylates *BRI1-EMS-SUPPRESSOR1* (*BES1*) (Yin et al., 2002), and *BRASSINAZOLE-RESISTANT1* (*BZR1*) (Wang et al., 2002). Phosphorylated BES1 and BZR1 are possibly degraded by the 26S proteasomes. BZR1 belongs to a novel class of plant-specific transcription factors that repress transcriptional expression of *CPD*, a BR biosynthetic gene (He et al., 2005). BES1 is another transcription factor that heterodimerizes with a group of bHLH-type transcriptional regulators to turn on many of the BR- and auxin-dependent genes (Yin et al., 2005).

Although BRs stimulate cell division, little is known about their signaling cascades in relation to the cell division process. Hu et al. (2000) have shown that BRs can substitute for cytokinin in an *Arabidopsis* callus and suspension culture system, and that BRs activate *CYCD3* transcription in cultured cell lines to stimulate division. In addition, mitotic activity increases when wheat roots are treated with BRs, an effect similar to cytokinin-mediated cell division (Sasse, 2003). Although BR mutants display dwarfism, their retarded growth is more attributable to reduced cell sizes than to any decrease in cell numbers (Kauschmann et al., 1996), suggesting that conventional BR dwarf mutants are not devoid of cell division. To understand this BR-induced cell division process, we have now screened populations available from the Arabidopsis Biological Resources Center for a mutant that possesses a short-round leaf morphology. Here, we describe a novel mutant, *short root and dwarfism* (*srd*), that exhibits semi-dwarfism due to reduced cell elongation in its aerial portions. Unlike other BR dwarfs, however, *srd* plants have shorter roots because of improper elongation.

MATERIALS AND METHODS

Plant Materials and Growth Conditions

A mutant *Arabidopsis* population containing *srd* was originally generated by Albert Kranz, using Enkheim-2 (En-2) as the ecotype background. Seed stocks for mutants that display BR dwarfism were ordered from the Arabidopsis Biological Resources Center (ABRC). Among them, a dwarf mutant, whose locus was not previously defined but which displays a phenotype similar to BR-related dwarf mutants, was isolated and named *srd*. This *srd* mutant was backcrossed to obtain a monogenic loss-of-function mutation. Two genes -- *bri1-5* (Noguchi et al., 1999) and *dwf7-1* (Choe et al., 1999b) -- were used for our morphological comparisons. Seeds of the wild type (En-2) and these three mutants were surfaced-sterilized as described (Choe et al., 1999b), then plated on 0.8% (w/v) agar-solidified medium containing 0.5x Murashige and Skoog salts plus 1% (w/v) sucrose. For growth under darkness, the cold-treated plates were exposed to the light for 5 h, then wrapped with aluminum foil for 5 d. For the feeding experiments, different concentrations of BRs were supplemented to the agar-solidified MS medium, and the seedlings were grown for 4-5 d after germination. In a separate set-up, En-2 and mutant seeds were also sown on soil (Sunshine Mix #5, SunGro, USA) that was pre-soaked with distilled water. The pots were covered with plastic wrap and cold-treated (4°C) for 3 d before being transferred to a growth chamber [16-h photoperiod from light of 240 μmol m^{-2} s^{-1}, at 23°C (day)/21°C (night), and 75% humidity]. The plastic wrap was removed 5 d after germination and the pots were sub-irrigated with distilled water as required.

Morphometric and Anatomical Analyses of *srd* Seedlings

At 5 weeks old, 20 potted seedlings that had been grown under long days were assessed for various traits (Table 1). Gross morphology of the En-2, *srd*, *bri1-5*, and *dwf7-1* seedlings was recorded with either a digital camera (Nikon, Japan) or under a stereomicroscope (SZX-ZB12; Olympus, Japan). For anatomical analysis, stem and root tissues were cut with razor blades, and immediately fixed in a solution containing 2% glutaraldehyde and 2% paraformaldehyde in 0.05 M phosphate buffer (pH 6.8) for 48 h at 4°C. The tissues were gradually dehydrated in an ethanol series, infiltrated, and embedded with a mounting medium (Technovit 7100, Kulzer, Germany). Sections (3 μm thick) were made with disposable tungsten knives (Leica, Germany) on an autocut rotary microtome (Leica RM 2165). They were then mounted on microscopic slides (Fisher Scientific, USA), and stained with periodic acid Schiff's reagent and 0.05% toluidine blue-O (Sigma, USA). Cross-sectional and longitudinal views were taken with a light microscope (Leica DMR).

Quantitative Analysis of Endogenous Levels of BRs and Sterols

Samples (60 g) of the aerial portions from 5-week-old plants were harvested and subjected to BR extraction and analysis for sterols and BR intermediates via GC (5890A-II; Hewlett-Packard, USA)-MS (JMS-AM150; JEOL, Japan), using procedures described

by Fujioka et al. (2002).

Genetic Crosses and Double Mutant Generation

srd was crossed with *bri1-5* to create a *bri1-5/srd1* double mutant. The resulting F1 seeds were allowed to self-fertilize for production of F2 seeds. Putative double-homozygote plants were first chosen among the segregating F2 populations based on their short-root phenotype. The double homozygote of *bri1-5/srd1* was then confirmed using molecular markers closely linked to *bri1-5* and *srd1,* because we have shown that *srd1* is closely linked to the bottom arm of Chromosome 1 (unpublished data).

RESULTS AND DISCUSSION

Isolation of the Novel Recessive *srd* Mutant

Major roles for plant steroid hormone BRs include directional elongation of newly divided cells. Once disrupted in the BR biosynthesis or signaling processes, mutants display characteristic phenotypes attributable to defects in this elongation. For example, the rosette leaves of BR dwarf mutants appear more round than oblong due to defective growth on the long axis (Choe, 2004; Kim et al., 1998). In addition, organs, such as pedicels, petioles, and inflorescences, are dramatically shorter because of this reduction in directional growth (Choe, 2004). These characteristic BR dwarf phenotypes are excellent keys for identifying mutants from populations that are defective either in biosynthesis or signaling cascades.

To obtain a novel locus involved in the BR response or biosynthetic pathways, mutant lines were screened for BR dwarf phenotypes. This screening resulted in novel alleles of BR-biosynthetic as well as BR-signaling genes reported previously (Choe et al., 1999a). We also identified a new mutant, "*short root and dwarfism* (*srd*)", with a conventional BR dwarf phenotype but which we have mapped to a new locus at Chromosome 1. Although *dwf5* is near *srd*, genetic complementation tests have revealed that they are not allelic (data not shown). Genetic analysis of the *srd* locus has shown that the mutant phenotypes are due to a recessive and monogenic loss-of-function mutation (data not shown).

Developmental Abnormalities of the *srd* Mutant

Because the overall gross morphology of *srd* plants resembles that of BR-related mutants, we examined the similarities between *srd* and other BR dwarfs (*bri1-5* and *dwf7-1*) and compared them with the wild type, En-2 (Fig. 1). Characteristic phenotypes of *srd* mutants include a short stature, reduced fertility, short internodes, and round leaves similar to those of the *bri1-5* and *dwf7-1* mutants (Fig. 1, Choe, 2004). For a more thorough comparison, key phenotypes of

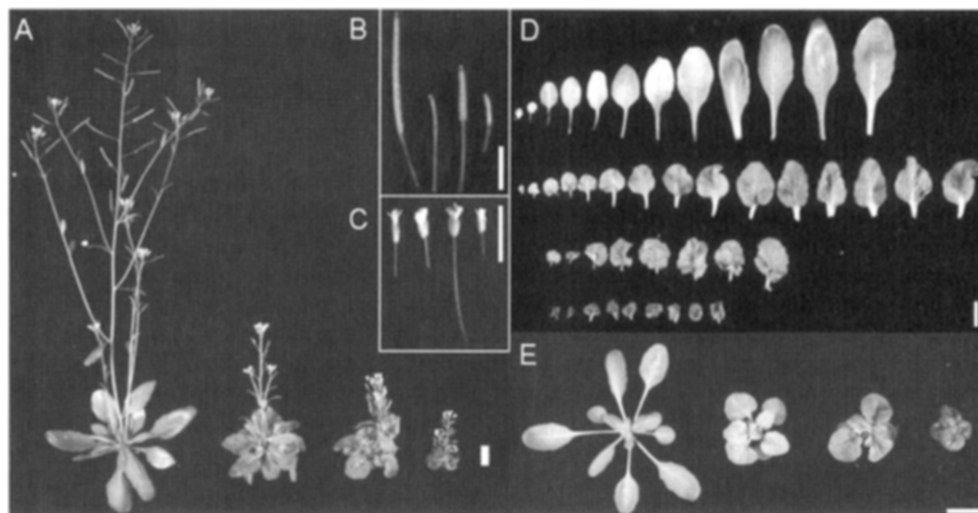

Figure 1. Morphological comparison of 6-week-old *srd* plants with wild-type En-2 seedlings and BR mutants. **(A)** *srd* seedling displays short stature, short internodes, and round leaves similar to other BR dwarf mutants, such as *bri1-5* and *dwf7-1* (left to right: En-2, *srd, bri1-5, dwf7-1*). **(B)** Siliques and **(C)** flowers with pedicel of En-2, *srd, bri1-5,* and *dwf7-1* (left to right). **(D)** Set of rosette leaves from En-2, *srd, bri1-5,* and *dwf7-1* (top to bottom). **(E)** Top views of 3-week-old En-2, *srd, bri1-5,* and *dwf7-1* (left to right). Scale bar = 1 cm (A, D, E) or 5 mm (B, C).

Table 1. Morphometric analysis of wild-type En-2, *srd*, *bri1-5*, and *dwf7-1* plants. Various organs were measured from 6-week-old seedlings. Each value represents the mean of 20 measurements.

	En-2	*srd*	*bri1-5*	*dwf7-1*
Inflorescence				
Height (mm)	316.58	103.75	62.5	22.67
Number (ea)	3.89	4.2	4	4
Rosette leaf (mm)				
Width*	17.11	15.18	20	9.33
Length*	36.66	18.07	20.5	9.33
Petiole length*	13.87	4.15	2.75	1.33
Number (ea)	14.74	17.8	18	15
Reproductive organ length (mm)				
Siliques	13.38	3.82	4.1	2.17
Pedicels	7.66	6.81	10.6	2.9

*, Measured from second leaf pair.

the plants (n = 20) were measured (Table 1). The gross height of the *srd* inflorescences was only 30% of that measured from En-2, but was greater than those of the *bri1-5* and *dwf7-1* plants, indicating that dwarfism in *srd* is relatively weak. The *srd* leaves were nearly half as long as the wild type, but leaf widths were not significantly different (Table 1, Fig. 1D). Ratios of leaf length to width were approximately 2 for En-2, but only 1 for *srd*, *bri1-5*, and *dwf7-1*, indicative of the typical round shape of BR dwarfs. Interestingly, *srd* pedicel sizes did not differ much from the wild type, but their petioles and siliques were dramatically shorter. Reflecting the latter difference, *srd* plants set seeds with decreased efficiency relative to the wild type and *bri1-5*. When seen from the top, the small, round-leaf morphology of *srd* was obviously similar to that of *bri1-5* (Fig. 1E).

Compared with the wild type, *srd* seedlings had shorter hypocotyls and roots, regardless of the light regime used in their growth. Dark-induced hypocotyl development in En-2 was about 3-fold greater than for those grown in the light (Fig. 2A). Similarly, dark-grown *srd* hypocotyls were approximately 4 times longer than those grown under the light, suggesting that *srd* can distinguish light from dark. However, root growth from those mutant seedlings was noticeably impaired, which, compared with canonical BR dwarfs, is an unusual phenotype. The root length of *srd* seedlings was merely 14% that of light-grown wild types (Fig. 2). Developmentally, it was more appropriate to compare the ratio of hypocotyl to root length rather than abso-

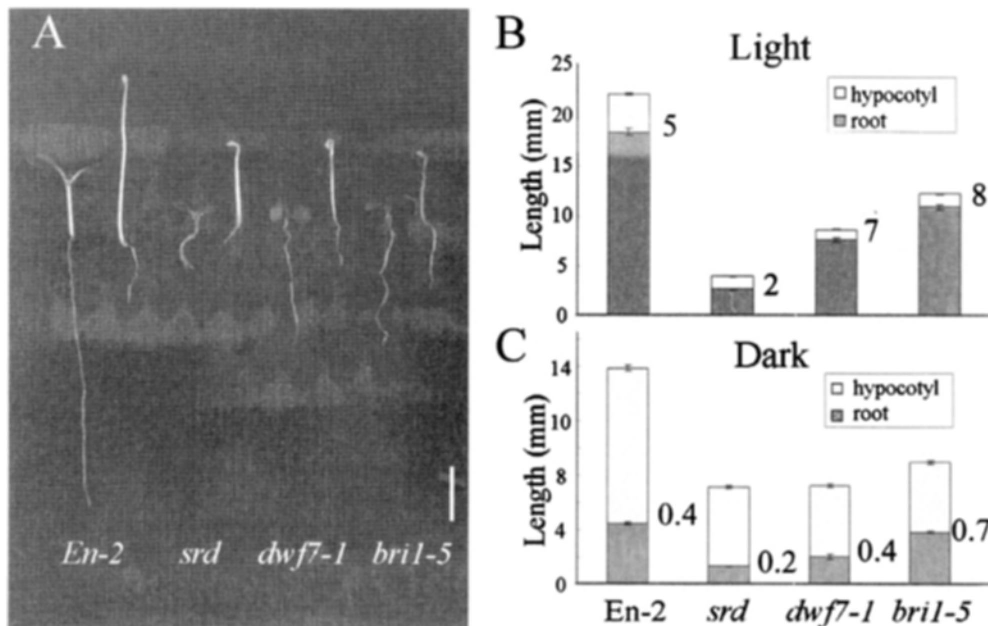

Figure 2. Light-and dark-grown seedling phenotypes of En-2, *srd*, *dwf7-1*, and *bri1-5*. Root growth of *srd* seedlings is noticeably impaired as its ratio of roots to hypocotyls is greatly decreased compared with wild type and canonical BR dwarfs, such as *dwf7-1* and *bri1-5*. **(A)** *srd* seedlings display short hypocotyls and roots regardless of light regime, relative to wild type. **(B)** and **(C)** Mean lengths of hypocotyls and roots. Each bar represents combined length of hypocotyls (top) and roots (bottom). Numbers next to each bar indicate ratios of roots to hypocotyls. From left: En-2, *srd*, *dwf7-1*, and *bri1-5*. Scale bar = 5 mm

Table 2. Endogenous levels of C-28 sterols and BRs in aerial portions of 5-week-old wild-type (En-2) and *srd* plants. Values indicate the detected amount (ng g^{-1} fresh wt) of each intermediate. Summed subtotals of C-28 sterols and BRs are in the two grayed rows.

	En-2	*srd*
Sterols		
24-Methylenecholesterol (24-MC)	3930	2780
Campesterol (CR)	34400	22300
Campestanol (CN)	558	213
6-Oxocampestanol (6-OxoCN)	27.6	9.29
C-28 sterol content	38915.6	25302.29
BRs		
6-Deoxocathasterone (6-DeoxoCT)	1.33	1.09
6-Deoxoteasterone (6-DeoxoTE)	0.05	0.06
6-Deoxo-3-dehydroteasterone (6-Deoxo3DT)	0.08	0.08
6-Deoxotyphasterol (6-DeoxoTY)	1.29	0.85
6-Deoxocastasterone (6-DeoxoCS)	1.63	1.13
Cathasterone (CT)	nd	nd
Teasterone (TE)	0.01	0.01
Typhasterol (TY)	0.13	0.09
Castasterone (CS)	0.22	0.26
Brassinolide (BL)	nd	nd
BR content	4.74	3.57

nd, not detect.

lute values for root or shoot lengths. In the light, the root:hypocotyl ratio for En-2 was 5 versus a ratio of 2 for *srd*. Under darkness, those ratios were 0.4 and 0.2 for En-2 and *srd*, respectively. Therefore, our comparisons of ratios clearly indicate that *srd* root lengths were greatly reduced, regardless of the light regime.

More interestingly, the response of *srd* roots to darkness differed from the wild type, with roots of the latter (En-2) decreasing in length to only 24% of the value measured from light-grown plants. In contrast, *srd* root lengths were reduced to only 51% of those for light-grown samples (Fig. 2A, 2B; Table 2), suggesting that the control mechanism for inhibiting dark-responsive root growth is also impaired in the *srd* mutant.

srd Plants Have Shorter Shoots and Roots

Previously we showed that *Arabidopsis* BR dwarf mutants are shorter and, hence, the length of their cells is proportionally reduced in the inflorescences. To examine cell sizes in *srd* shoots, we made cross and longitudinal sections, and compared their patterns with those of the wild type (Fig. 3). Differences were obvious among shoot diameters. For example, cross sections of the lower portions of the inflores-

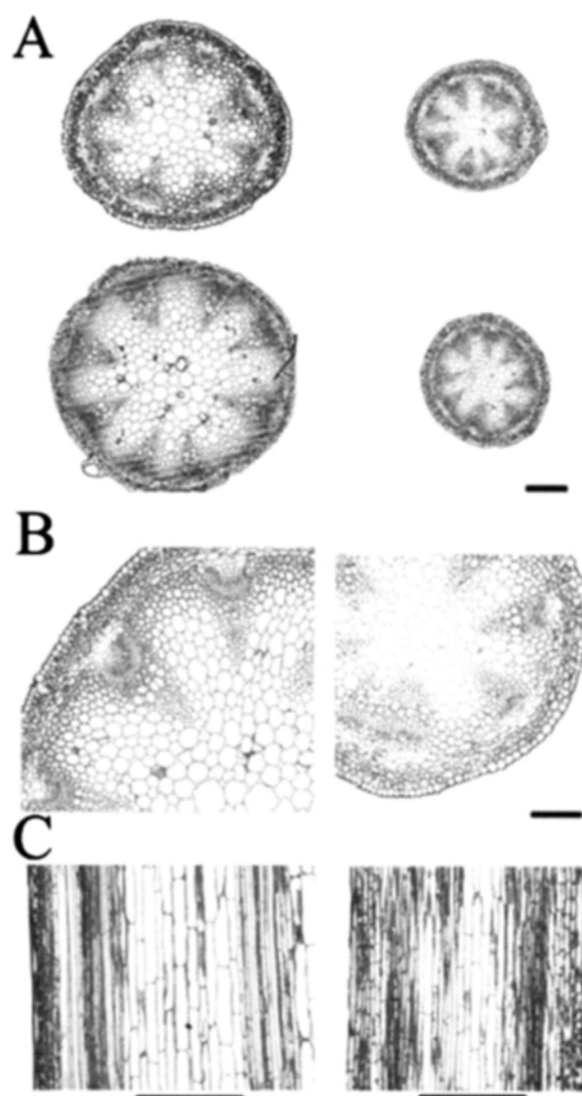

Figure 3. Anatomical analysis of wild-type and *srd* inflorescences. Diameter of *srd* shoot was approximately 60% that of wild type; this significant reduction is partially due to reduced cell width. **(A)** Cross-sectional views of middle (upper panel) and bottom (lower panel) portions from wild-type En-2 (left) and *srd* (right) inflorescences. **(B)** Magnified images of cross-sectional views of bottom portions of inflorescence from wild-type En-2 (left) and *srd* (right). **(C)** Longitudinal views of bottom portions of inflorescences from En-2 (left) and *srd* (right). Bar = 200 μm in A and C; 100 μm in B.

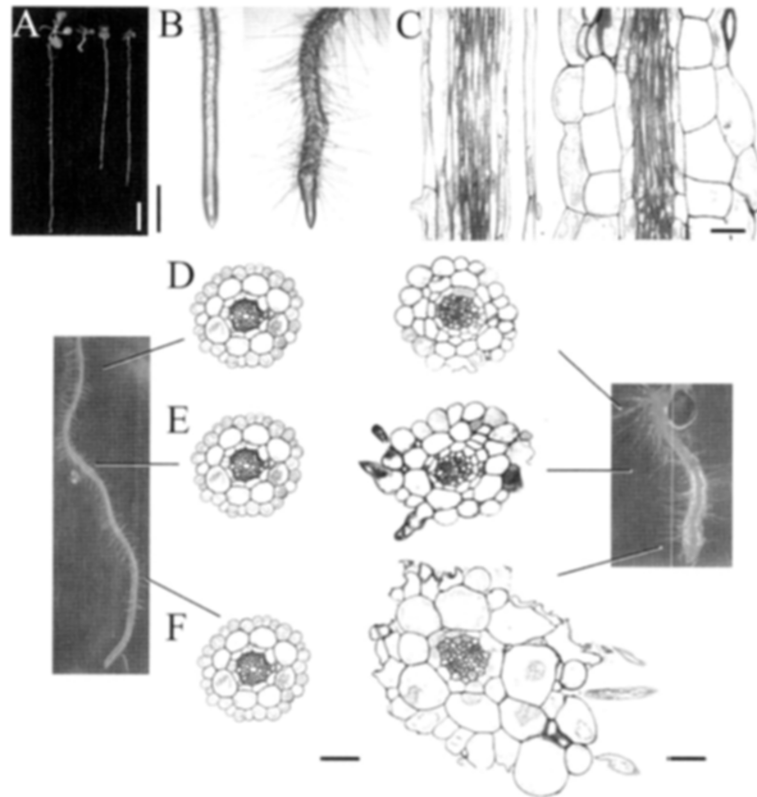

Figure 4. Anatomical characteristics of *srd* roots. Mutant has short, but abnormally thicker roots than those of wild-type En-2 and canonical BR dwarfs *dwf7-1* and *bri1-5*. **(A)** Seedlings of En-2, *srd*, *dwf7-1*, and *bri1-5* (left to right) grown for 10 d in light. *srd* displays significantly shorter roots. **(B)** Magnified views of root tip portions from *srd* (right) under stereomicroscopy, with unusually thicker root phenotypes, even greatly swollen in parts compared with wild type (left). **(C)** Longitudinal view of roots from wild-type En-2 (left) and *srd* (right). Increase in root thickness is attributable to increased cell widths in *srd*. **(D)** Cross-sectional views of roots from various locations in En-2 (left) and *srd* (right) demonstrate that mutant roots have additional layers of cortical or endodermal cells. Scale bars = 1 mm (A), 200 μm (B, C), or 50 μm (D, E and F).

cences showed that the diameter of an *srd* shoot was approximately 60% that of the wild type (Fig. 3A, 3B). To examine if this reduced thickness was due to narrowing of the cells, we also compared longitudinal sections. Within a 200-μm stretch of the pith region (black bar in Fig. 3C), cells counts for En-2 and *srd* were 10 and 14, respectively. This suggests that cell width was indeed reduced. During normal development, the diameter of wild-type inflorescences is greatest at the bottom, then gradually tapers upward to the shoot tip. For example, at 5 weeks old, the diameter of a wild-type inflorescence decreases by 10 to 15% from the lowest portion up to the middle section; diameter does not differ significantly between these two positions on an *srd* mutant inflorescence (Fig. 3A, 3B). This contrast can be interpreted in two ways – either a stem has only a small number of cells, or else expansion is limited for the cells of *srd* shoots. Here, in comparing the cross sections of the two genotypes, it is likely that both the cell number and possibility for cell expansion were decreased in the mutant inflorescences (Fig. 3).

srd Seedlings Have Abnormally Thickened Roots

The *srd* plants manifested unique phenotypes in their roots. Although the root hairs and subsequent elongation of those hairs appeared normal (Fig. 4A, 4B), their overall root lengths were much shorter than those of the wild type (Fig. 2A, 4A). Unlike conventional BR dwarfs, which possess greatly elongated roots, *srd* roots were dramatically shorter (Fig. 4A). Therefore, we examined the longitudinal growth of the root cells, and found that cortical cell lengths were reduced to approximately 30% of those measured from the wild type (Fig. 4C). Thus it is likely that

the shorter mutant roots could partly be attributed to the smaller size of individual cells.

Although the BR-dwarf roots were shorter than the En-2 roots, the *bri1-5* and *dwf7-1* roots were not any thicker than those of the wild type (Fig. 4A). In contrast, the *srd* roots displayed surprisingly thicker root phenotypes, and were even severely swollen in some portions (Fig. 4B). To examine if this phenotype was caused by increased cell numbers or by diagonally expanded cells, both wild-type and *srd* roots were longitudinally sectioned and observed by light microscopy. The mutant cells of the root epidermis, cortex, and endodermis all were thicker than the wild-type controls. When transversely sectioned, the *srd* roots showed additional layers of cortical or endodermal cells (Fig. 4D-F), which were more obvious in the swollen sections (Fig. 4E, 4F). Based on their morphology, the mutant cortical cells likely underwent extra rounds of cytokinesis; these divided cells continuously expanded further to the short axis of the root, and were eventually sheared off (Fig. 4E). Because of this uncontrolled cell division, the number of cortical cells increased to more than 10, compared with only 8 in the wild type (Fig. 4E). In addition, the extra cells in the cortical regions of *srd* roots originated from the endodermis. Although endodermal cells normally curtail their developmental process, these mutant cells seemed to divide continuously.

Endogenous Levels of BRs Are Slightly Lower Than Those of the Wild Type

BR mutants, such as *bri1*, *dwf12/bin2,* and *rot3*, have altered levels of endogenous BRs (Noguchi et al., 1999a; Choe et al., 2002; Kim et al., 2005). In determining whether this applies to *srd*, our quantitative analysis showed that endogenous levels of BRs and sterols were slightly lower in the mutant than in the wild-type plants (Table 2). However, the levels of 6-deoxo-BRs, e.g., 6-deoxotyphasterol and 6-deoxocastasterone, were not significantly lower than from the wild type, so we cannot conclude that these mutants are defective in a specific step in the BR biosynthetic pathways.

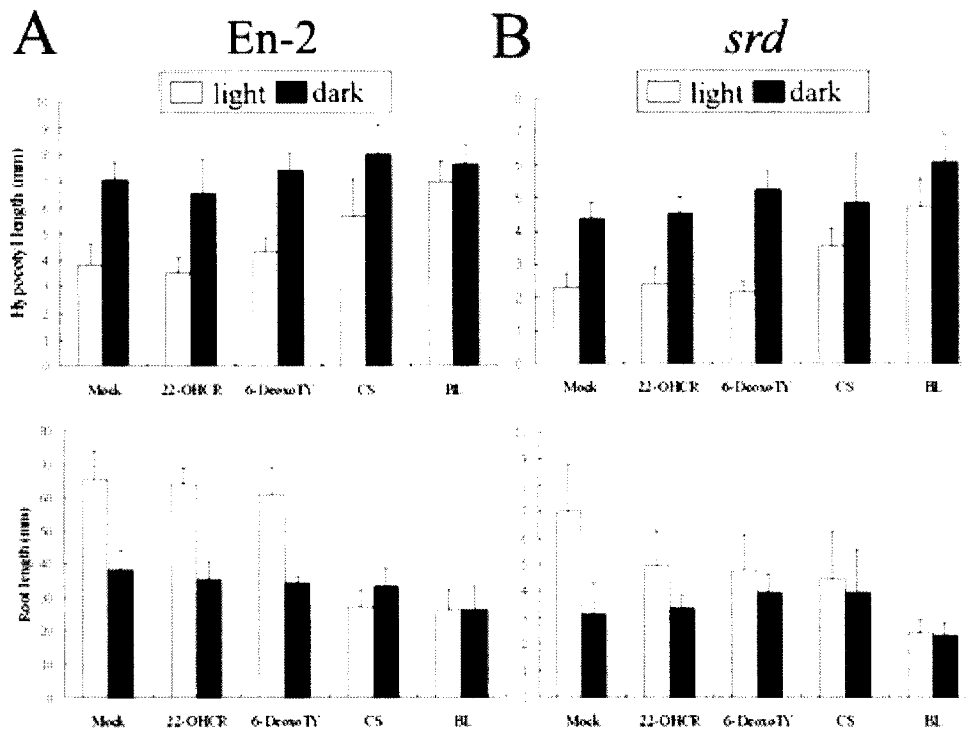

Figure 5. Response of hypocotyls and roots of wild-type En-2 **(A)** and *srd* mutant **(B)** to various BRs, such as 22-hydroxy campesterol (22-OHCR), 6-deoxotyphasterol (6-deoxoTY), castasterone (CS), and *epi*-brassinolide (BL), in the light or dark. **(A)** Hypocotyl length increases (top) whereas roots are shortened (bottom) upon BR treatments, both in light and dark. Roots of light-grown wild type are dramatically shortened when treated with active BRs while wild-type roots of dark-grown seedlings are relatively less sensitive to treatment. **(B)** Responses by hypocotyl (top) and root (bottom) of *srd* are similar to those of wild-type En-2 both in light and dark, but absolute length of root is much shorter than wild type; roots of light-grown *srd* seedlings also are significantly shortened. Data represent mean ± SE of 20 individual seedlings.

srd Can Respond to Exogenously Applied BRs

Wild-type and mutant *Arabidopsis* seedlings were treated with bioactive BRs, including 22-hydroxy campesterol (22-OHCR), 6-deoxotyphasterol (6-deoxoTY), castasterone (CS), and *epi*-brassinolide (BL). These are listed here in the order of the biosynthetic pathway, with their activities becoming stronger as the process approaches the end product BL. Light-grown En-2 roots were dramatically shorter when CS and BL were exogenously applied (Fig. 5A, bottom), but the already shorter and dark-grown wild-type roots were relatively less sensitive to BR treatment (Fig. 5A, bottom). Similar responses were observed with the *srd* roots. Although their absolute lengths were much shorter than the wild types, light-grown *srd* roots were significantly shorter (Fig. 5B, bottom). Those of the BL-treated *srd* seedlings were approximately 40% shorter than the untreated controls (Fig. 5B, bottom). Under darkness, root lengths did not change significantly.

Hypocotyls of the light-grown wild type lengthened in response to CS and BL treatments, while elongation was not significant for those of the dark-grown seedlings. This is a result of their saturated growth in the dark (Choe et al., 2001). Similar to the wild type, light-grown *srd* hypocotyls significantly increased in length, whereas the dark-grown hypocotyls did not show dramatic elongation. Hypocotyls grown in the light on media supplemented with BL were nearly twice as long as those from both the wild-type and the *srd* seedlings. Overall, BR treatments caused root growth to be inhibited to the point where those roots were only half the length of untreated controls from both the wild-type and the light-grown *srd* seedlings. In addition, light-grown hypocotyls (both En-2 and *srd*) responded to bioactive BRs and doubled in length compared with the controls.

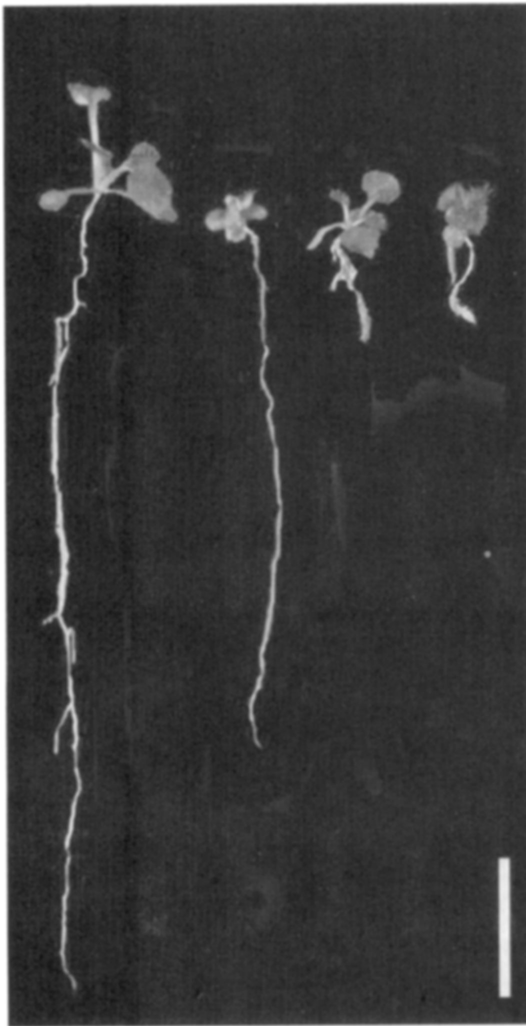

Figure 6. Genetic interaction between *srd* and *bri1-5*. Double mutant of *srd* and *bri1-5* displays short-root phenotype also found in *srd* but not in *bri1-5*. Shown are 10-day-old En-2, *bri1-5*, *srd*, and *srd/bri1-5* plants (left to right). Scale bar = 1 cm.

srd/ bri1-5 Displays a Short-Root Phenotype

Exogenously applied BRs inhibit root growth (Choe et al., 2001). Here, we made a double mutant between *srd* and *bri1-5*, and examined their epistatic relationship. This double mutant clearly displayed the short-root phenotype typical of *srd* seedlings but not occurring in *bri1-5,* indicating that the former is epistatic to the latter. The double mutant phenotype suggests that *SRD* defines a gene that is associated with cell division acting downstream of BRI1 in the BR signaling pathway. Nevertheless, we cannot exclude the possibility that *SRD* is a general regulatory factor involved not only in BR-specific events but also in processes controlled by other phytohormones, such as auxins and cytokinins.

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