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Role of Endodermal Cell Vacuoles in Shoot Gravitropism

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Abstract

In higher plants, shoots and roots show negative and positive gravitropism, respectively. Data from surgical ablation experiments and analysis of starch deficient mutants have led to the suggestion that columella cells in the root cap function as gravity perception cells. On the other hand, endodermal cells are believed to be the statocytes (that is, gravity perceiving cells) of shoots. Statocytes in shoots and roots commonly contain amyloplasts which sediment under gravity. Through genetic research with *Arabidopsis* shoot gravitropism mutants, *sgr1/scr* and *sgr7/shr,* it was determined that endodermal cells are essential for shoot gravitropism. Moreover, some starch biosynthesis genes and *EAL1* are important for the formation and maturation of amyloplasts in shoot endodermis. Thus, amyloplasts in the shoot endodermis would function as statoliths, just as in roots.

The study of the *sgr2* and *zig/sgr4* mutants provides new insights into the early steps of shoot gravitropism, which still remains unclear. *SGR2* and *ZIG/SGR4* genes encode a phospholipase-like and a v-SNARE protein, respectively. Moreover, these genes are involved in vacuolar formation or function. Thus, the vacuole must play an important role in amyloplast sedimentation because the *sgr2* and *zig/sgr4* mutants display abnormal amyloplast sedimentation.

Key words: Shoot gravitropism; Endodermis; Amyloplast; Vacuole; Mutant; *Arabidopsis thaliana*

Introduction

Higher plants must adapt to particular environmental conditions to achieve optimal growth. Tropisms are important directed growth responses to environmental conditions. When shoots are reoriented, they bend upward to grow away from gravity, whereas roots grow down towards gravity. The gravitropic response enables leaves to efficiently acquire light and roots to acquire water and various nutrients.

The physiology and cytology of the gravitropic response have been studied in various organs of different plants. Studies indicate that several organelles and molecules play important roles in this response (Kaufman and others 1995; Sack 1991). The gravitropic response can be divided into at least four temporal steps: gravity perception, signal formation, signal transduction, and asymmetric cell elongation to induce bending (Tasaka and others 1999). There are two major hypotheses regarding plant gravitropism: the "starch-statolith hypothesis" states that amyloplast sedimentation in gravity sensing cells is a trigger event in the gravitropic reaction (Kiss 2000; Sack 1991, 1997). In addition the "Cholodny-Went Theory" states that auxin is

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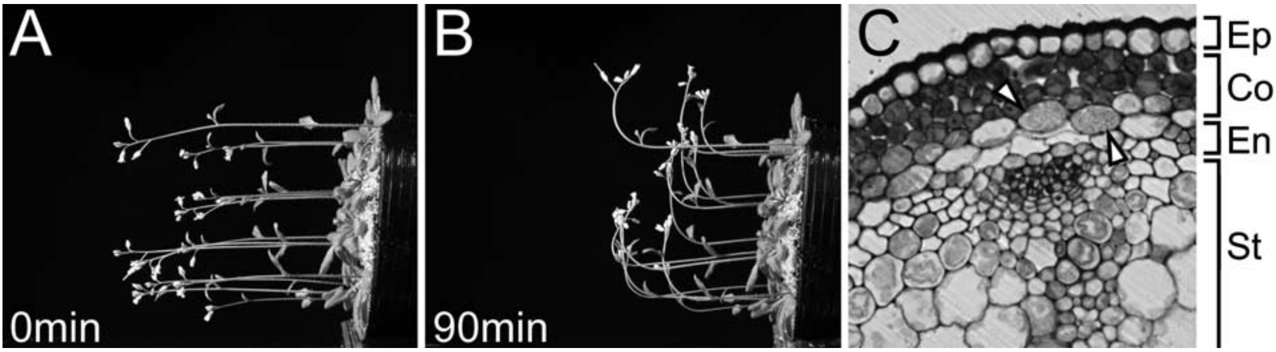

Figure 1. Shoot gravitropism in *Arabidopsis thaliana.* After inflorescence stems are placed horizontally (**A**), the stems begin to bend upward within 30 minutes, and the curvature reaches approximately 90 degrees in 90 minutes (**B**). (**C**) A part of transverse section of an inflorescence stem in *Arabidopsis* showing a radial symmetrical pattern. A potential graviperceptive endodermal cell contains amyloplasts (arrowheads). Ep, epidermis; Co, cortex; En, endodermis; St, stele.

involved in differential cell elongation in gravitropism (Firn and others 2000).

Many *Arabidopsis* mutants with aberrant shoot and/or root gravitropism have been isolated, and the mutated genes have recently been cloned (see recent reviews on this subject by Chen and others 1999; Firn and others 2000; Rosen and others 1999; Tasaka and others 1999, 2001). In this paper, we concentrate on describing the mechanism of gravity perception in shoots.

Endodermal Cells Function as Gravity Perception Cells in Shoots

After vegetative growth of six to seven rosette leaves, *Arabidopsis* inflorescence stems bolt and elongate in a straight, upward direction. When inflorescence stems are placed horizontally (Figure 1A), they begin to bend within 30 minutes, and the curvature reaches approximately 90 degrees in 90 minutes (Figure 1B) (Fukaki and others 1996a). Hypocotyls also exhibit negative gravitropism. Etiolated hypocotyls elongate upward and bend negatively when they are reoriented (Fukaki and others 1996a).

Many mutants with abnormal shoot gravitropism have been isolated in *Arabidopsis*, including a series of *shoot gravitropism* (*sgr*) mutants. Seven independent loci have been identified by genetic analysis to relate to shoot gravitropism (Fukaki and others 1996b, 1998; Yamauchi and others 1997). Interestingly, all of these mutants show normal root gravitropism, indicating that shoot gravitropism is genetically distinct from root gravitropism. The *sgr* mutants can be categorized into two groups; one group, including *sgr3, 5* and *6,* shows abnormal gravitropism only in inflorescence stems, the other, including *sgr1, 2, 4* and *7,* shows abnormality both in inflorescence stems and hypocotyls. This indicates that the genetic regulation of gravitropism can be slightly different in inflorescence stems and hypocotyls, even though the tissue and cellular structures involved in gravitropism are similar (Tasaka and others 1999, 2001).

Although dicot inflorescence stems curve in a short zone after gravistimulation, the region of gravity perception and response is broad in the elongation zone of shoots. This is shown by the fact that every short fragment of an inflorescence stem responded to gravity in physiological experiments (Fukaki and others 1996a; Tasaka and others 1999; Weise and others 2000). Moreover, the region of gravity perception and response in hypocotyls also is broad in the elongation zone.

The tissue structure of monocot shoots is somewhat different from that of dicots. The stems of grasses such as maize and oat also show negative gravitropism, but they curve only at a defined location called the pulvinus which is located just at the base of the leaf and shows differential growth in response to gravity stimulation. However, interestingly, the pulvinus does not elongate during development of the stem (Collings and others 1998; Kaufmann and others 1987, 1995). The coleoptile, an embryonic organ of grass plants, is a sheath-shaped organ and the top part is more sensitive to gravity orientation, although the region responsible for orientation covers the entire organ (Sack 1991).

Root tissues are easy to study microscopically via microsurgical operations. Surgical ablation, or disruption of the root cap (by inserting a toxic gene under the control of the root cap specific promoter), has indicated that the root cap is important for root gravitropism (Juniper and others 1966; Tsugeki and Fedoroff 1999). Additionally, laser ablation of columella cells has clearly demonstrated that columella cells are essential for root gravitropism (Blancaflor and others 1998). However, since it is difficult to observe and analyze living cells inside of shoots, we had little direct evidence indicating where gravity perception occurs in shoot tissue.

Dicot shoots generally grow in a simple radial pattern. In *Arabidopsis,* the inflorescence stem consists of one epidermal layer, two to three cortical layers, one endodermal cell layer, and a stele containing vascuolar systems. Each layer arises cylindrically from the apex to the base of the shoot. The first three layers are arranged from outside to inside in a radial symmetrical manner; (Figure 1C). The hypocotyl has almost the same tissue pattern. Both inflorescence stems and hypocotyls of *sgr1* and *sgr7* mutants have no endodermal cells and show no gravitropic response, indicating that endodermal cells are essential for gravitropism in both organs (Fukaki and others 1998). The *sgr1* and *sgr7* mutants are allelic to *scarecrow* (*scr*) and *short-root* (*shr*), respectively, which were isolated as mutants lacking root endodermal cells (Fukaki and others 1998; Scheres and others 1995). Since both mutants show normal root gravitropism, endodermal cells must not be important for root gravitropism. The *SCR* and *SHR* genes encode putative transcription factors and seem to regulate the formation and differentiation of endodermal cells, which are essential for shoot gravitropism (Di Laurenzio and others 1996; Helariutta and others 2000).

Amyloplasts in Endodermal Cells Are Important for Gravity Perception

Both columella cells of the root cap and endodermal cells of the shoot contain specific amyloplasts that settle to the bottom of these cells. Amyloplasts are plastids that contain large starch granules and are differentiated from proplastids. The amyloplasts in root columella and shoot endodermal cells are somewhat larger than other cells and sediment towards gravity. It is hypothesized that the amyloplast functions as a statolith during gravity perception (Kiss and others 2000; Sack 1991).

The Arabidopsis *endodermal-amyloplast less1* (*eal1*) mutant shows abnormal gravitropism in inflorescence stems and hypocotyls. The *eal1* mutant has no amyloplasts in the endodermal cells of either organ. However, the roots, which have columella cells with normal amyloplasts, exhibit normal gravitropism. Thus, these observations suggest that the amyloplasts in the endodermis of shoots and hypocotyls are essential for shoot gravitropism (Fujihira and others 2000).

Starch-deficient mutants that store fewer or no starch granules in amyloplasts, have been isolated. The starchless mutants show abnormal gravitropic response in shoots, hypocotyls, and roots. The plastids in these mutants do not sediment towards gravity in shoots, and the reduced-starch mutants also show reduced gravitropism. The response of each mutant roughly corresponds to the amount of accumulated starch granules in three organs (Kiss and others 1996, 1997; Kiss 2000; Weise and Kiss 1999).

Interestingly, hypocotyls of the starchless mutants show an almost normal gravitropic response when they are placed in hypergravity (5*g*). Moreover, the amyloplasts in hypocotyl endodermal cells do not sediment under normal conditions (1*g*) but sediment fully under hypergravity. When wild-type plants are placed under hypergravity, they show an even more rapid gravitropic response, and the amyloplasts sediment to a greater degree. These results suggested that the normal distribution and movement of amyloplasts is important for the full response to a change in the orientation of gravity (Fitzelle and Kiss 2001).

Additionally, the starch-deficient tobacco NS458 mutant contains small amyloplasts that do not sediment in the endodermis of etiolated hypocotyls, and these plants exhibit abnormal gravitropism (Kiss and Sack 1990). However, when NS458 is grown under light conditions, the amyloplasts increase in volume and sediment again, resulting in recovery of gravitropism (Vitha and others 1998).

Analyses of starch-deficient mutants strongly suggest that amyloplasts functions as statoliths and that the movement or positioning of amyloplasts may be a key factor in gravity perception. The movement of amyloplasts in columella cells has been described in detail (Yoder and others 2001). In maize coleoptiles, the sedimentation of amyloplasts also has been extensively studied. Statistically, most amyloplasts sediment to the new distal position of a cell within 30 seconds, which is faster than the gravitropism presentation time (that is, a measure of gravisensitivity) of 40 seconds (Sack and others 1984). Additionally, most amyloplasts are grouped and sediment together, but some independent amyloplasts seem to be able to pass through the transvacuolar strand or the peripheral cytoplasm (Sack and Leopold 1985).

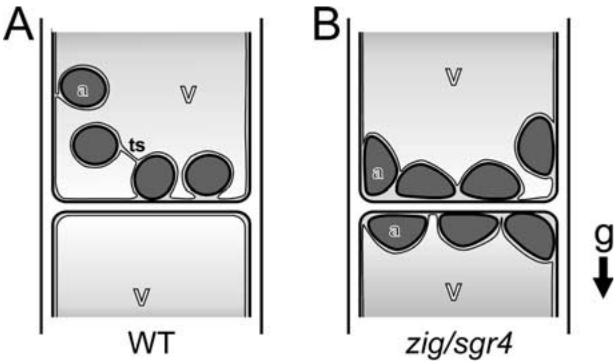

Figure 2. The existent manner of amyloplasts in shoot endodermis. (**A**) In wild-type shoot endodermis, the amyloplasts are localized at the bottom of the cell and surrounded by cytoplasm and the vacuolar membrane. (**B**) In *zig/sgr4* shoot endodermis, the amyloplasts are localized not only at the bottom but also at the top of the cell. All of the amyloplasts seem to be appressed to the plasma membrane and not surrounded by cytoplasm and vacuolar membrane. g, gravity; V, vacuole; a, amyloplast; ts, transvacuolar strand.

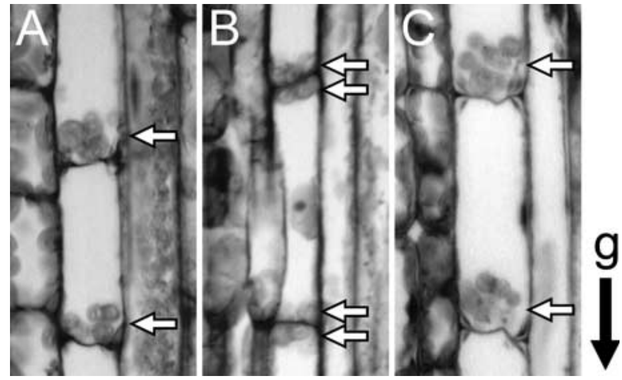

Figure 3. Localization of amyloplasts (arrows) in shoot endodermal cells. Orientation of stems toward gravity (g) was maintained during fixation. (**A**) Longitudinal section of the wild-type inflorescence stem. Most amyloplasts sediment in the endodermis. (**B**) In *sgr2* mutants, some amyloplasts are localized in the upper side of the endodermis. **(C)** Transgenic *sgr2* expressing SGR2 specifically in the endodermal cell rescues abnormal amyloplast sedimentation.

Endodermal Vacuoles Involved in Shoot Gravitropism

To investigate the molecular mechanism of shoot gravitropism, we analyzed the *Arabidopsis* shoot gravitropic mutants, *sgr2* and *sgr4*. Both mutants show normal tropic responses to light and form endodermal cell layers in their shoot, indicating that *SGR2* and *SGR4* are involved in the steps from gravity perception to transduction (Fukaki and others 1996; Yamauchi and others 1997). The *sgr4* mutant, which was renamed *zigzag* (*zig*) due to its zigzag phenotype of inflorescence stems, shows almost no gravitropism in inflorescence stems (Yamauchi and others 1997). *ZIG/SGR4* encodes the AtVTI11 (initially called AtVTI1a) protein which is homologous to yeast VTI1 (Vps ten interacting 1) (Kato and others 2002). This protein is a v-SNARE, which is localized on the transport vesicle and provides specific recognition between the vesicle and target membrane. The subcellular localization of ZIG/AtVTI11 in root cells, analyzed by immunoelectron microscopy, was shown to be in the *trans*-Golgi network and the prevacuolar compartment (Zheng and others 1999). In addition, serious abnormalities were observed in endodermal cells of *zig/sgr4* shoot. In wild-type inflorescence stems, the endodermal cells contained one large vacuole. The amyloplasts, present at the bottom of these cells, are surrounded by cytoplasm and the vacuolar membrane, while others are distributed in transvacuolar strands (Figure 2A and 3A). In the endodermal cell of *zig/sgr4* shoots, one large vacuole was detected, as well as some aberrant vacuolar/vesicular structures. Fragmentation of the vacuolar membrane or disappearance of trans-vacuolar strands was also observed. Moreover, the amyloplasts were located both at the bottom and top of the shoot endodermis but were also occasionally dispersed peripherally.

All of the amyloplasts seem to be appressed to the plasma membrane and not surrounded by cytoplasm and vacuolar membrane (Figure 2B) (Morita and others 2002). Interestingly, transgenic *zig/sgr4* plants that express the *ZIG/SGR4* gene specifically in endodermis controlled by the *SCARECRAW* promoter recovered in terms of amyloplast sedimentation and gravitropism. However, the morphological phenotype, such as the zigzag-shaped inflorescence stems and wrinkled leaves, was not completely recovered, indicating that vesicle transport in the endodermis, mediated by *ZIG/SGR4*, is essential for shoot gravitropism. Taken together, we propose that the *ZIG/SGR4* functions as a SNARE protein in membrane trafficking to form a normal central vacuole which regulates the positioning and movement of amyloplasts (Figure 4) (Morita and others 2002).

The *sgr2* mutant also exhibits abnormal gravitropism in inflorescence stems and hypocotyls. The inflorescence stems of *sgr2* wind slightly and the lateral shoots bend downward (Kato and others 2002; Fukaki and others 1996b). Anomalies of vacuolar structure, such as small-vacuole mem-

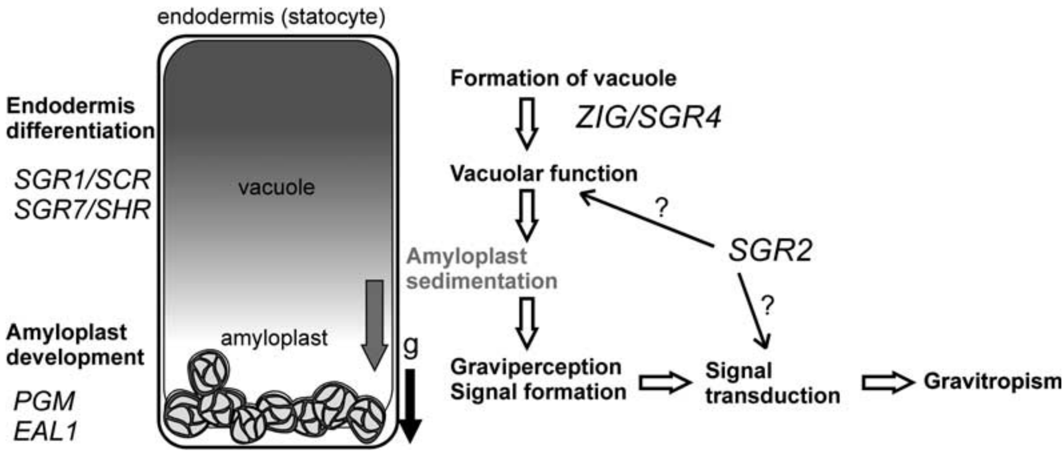

Figure 4. A model to explain how vacuoles in the endodermis are involved in shoot gravitropism in *Arabidopsis thaliana*. In inflorescence stems, the endodermal cell is filled with a large central vacuole. The vacuolar membrane surrounds the amyloplasts, which are sedimenting toward gravity (g). Through the amyloplast sedimentation, gravity stimulation would be perceived, and signals would be created in endodermal cells. *SGR1/SCR* and *SGR7/SHR* are essential for the formation and differentiation of endodermal cells. *PGM (PHOSPHOGLUCOMUTASE),* which encodes a starch biosynthesis enzyme, and *EAL1,* not cloned, are involved in the development and differentiation of the amyloplast in shoot endodermis. *ZIG/SGR4,* which encodes a v-SNARE, may be related to intact vacuolar formation. *SGR2* is a phospholipase-like gene and may function at the vacuolar membrane to change membrane fluidity or signal formation. Moreover, *ZIG/SGR4* and *SGR2* affect amyloplast sedimentation.

brane structures, and accumulation of cytoplasm at both the top and bottom of endodermal cells, were occasionally observed. Moreover, abnormal amyloplast distribution, which is similar to that in *zig/sgr4,* is observed in the *sgr2* endodermis (Figure 3B) (Morita and others 2002). The *SGR2 gene* encodes a protein with homology to a phospholipase A1 that displays specificity towards phosphatidic acid and possesses one putative transmembrane domain. Functional SGR2, fused to Green Fluorescent Protein (GFP), localizes in the vacuolar membrane and putative small vesicles. The SGR2 protein, driven by the *SCR* promoter, rescues shoot gravitropism and amyloplast sedimentation of the *sgr2* mutant, indicating that SGR2 in shoot endodermis is essential for shoot gravitropism (Figure 3C). The SGR2 presence in the vacuole membrane may change the lipid composition and/or fluidity of a vacuolar membrane, which may affect the sedimentation of amyloplasts (Kato and others 2002; Morita and others 2002). Of course, there remains a possibility that the products of SGR2 act as signal molecules after gravity perception. If so, there is no doubt that the vacuole would still play an important role in gravity perception or signal transduction (Figure 4).

Taken together, the vacuole in endodermal cells is involved in shoot gravitropism and seems to contribute significantly to the distribution and sedimentation of amyloplasts (Figure 4).

Different Gravity Perception Mechanisms in Shoots and Roots

The endodermal cells in shoots and the columella cells in root caps function in gravity perception, respectively. In both types of cells, the presence and/or movement of amyloplasts seem to be the important trigger of gravity perception (Kiss 2000; Sack 1991). With respect to subcellular structure, however, there are some differences between the two organs.

The columella cells are polarized cells, with the nucleus on the proximal side and the endoplasmic reticulum (ER) on the peripheral side (Sack 1991). A specialized form of the ER, termed ''nodal ER'', in the peripheral region of tobacco columella cells, was detected recently using high-pressure freezing/freeze-substitution techniques (Zheng and Staehelin 2001). It has been suggested that the ER perceives gravity and produces signals (Hensel and Sievers 1981). In addition, a tensegrity-model, stating that ER domains shield the local plasma membrane where the stretch-sensitive receptors are localized, has also been proposed (Yoder and others 2001).

In contrast, the endodermal cells of shoots contain a large central vacuole. Analysis of the *SGR2* and *ZIG/SGR4* genes has led to the suggestion that a large central vacuole influences the sedimentation or movement of amyloplasts in the endodermis

(Morita and others 2002). Although it has been reported that the ER is localized in the peripheral region of endodermal cells of pea epicotyl, it is not yet clear that the ER plays a role in graviperception in endodermal cells (Sack 1987).

The vacuole has a very different role in graviperception in roots compared with shoots. The vacuoles in root columella are relatively small and do not influence amyloplast movement, consistent with *sgr2* and *zig/sgr4* roots showing normal gravitropism (Fukaki and others 1996b; Sack 1991; Yamauchi and others 1997). Interestingly, the other aerial organs, which show negative gravitropism, such as the hypocotyl and coleoptile, also have vacuolated cells with sedimenting amyloplasts (Sack and Leopold 1985; Sack 1991). Thus, vacuoles may function as a common factor for gravity perception in aerial organs showing gravitropism.

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