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Direct Microscopic Demonstration of the Statolith Sedimentation in Endodermal Cells of Leaf Petioles after Gravistimulation; Evidence for the Crucial Role of Actin Filaments

By

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With 4 Figures

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Summary

PSARAS G. K. 2004. Direct microscopic demonstration of the statolith sedimentation in endodermal cells of leaf petioles after gravistimulation; evidence for the crucial role of actin filaments. – *Phyton* (Horn Austria) 44 (2): 191–201, 4 figures. – English with German summary.

Leaf petioles of *Calla palustris* (Araceae) show negative gravitropism. 12 h after they have been horizontally placed, they retain again a vertical position, bending upwards. The anatomical study of the petioles revealed that the bundle sheath (endodermis) of each vascular bundle consists of cylindrical cells possessing the features of statocytes. They contain 5–15 distinct amyloplasts, which after gravistimulation move towards the physically lower cell wall. The nuclei of endodermal cells are anchored in the upper part of the cells and they stay there even after the tissue sample has been inverted, showing, thus, a polarity similar to that of root statocytes. The movement of amyloplasts (statoliths) after gravistimulation, i.e. after inversion of the tissue section, from one end of the statocyte to the other can be continuously observed in vivo under a horizontally placed microscope. The amyloplasts–statoliths sediment individually through the parietal cytoplasm or through transvacuolar strands and the movement lasts about 30–40 min. After the application of the actin network modulator cytochalasin B, the statoliths, after gravistimulation, move

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downwards in clusters and the sedimentation lasts only 5–10 min. The results provide further evidence for the crucial role of the actin network in statolith movement, supporting the starch-statolith model for gravity perception.

Zusammenfassung

PSARAS G. K. 2004. Mikroskopische Darstellung der Statholithensedimentation in Blattstiellendodermiszellen nach Gravistimulation. – *Phyton* (Horn, Austria) 44 (2): 191–201, 4 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Blattstiele von *Calla palustris* (Araceae) zeigen negativen Gravitropismus. Zwölf Stunden nachdem sie horizontal exponiert wurden, nehmen sie neuerlich eine vertikale Position ein, indem sie sich aufwärts biegen. Anatomische Studien der Blattstiele ergaben, dass die Bündelscheide (Endodermis) von jedem Gefäßbündel aus zylindrischen Zellen besteht welche die Kennzeichen von Statocyten aufweisen. Sie besitzen 5 bis 15 deutliche Amyloplasten, welche sich nach Gravistimulation gegen die physikalisch untere Zellwand bewegen. Die Kerne der Endodermiszellen sind im oberen Teil der Zelle lokalisiert und sie verbleiben dort sogar noch dann, wenn das Gewebe umgedreht wurde. Sie zeigen so eine ähnliche Polarität wie die Wurzelstatocyten. Die Bewegung der Amyloplasten (Statolithen) nach der Gravistimulation, d.h. nach der Umkehrung des Gewebsbezirkes von einem Ende der Statocyte zum anderen kann kontinuierlich in vivo mit einem horizontal gestellten Mikroskop beobachtet werden. Die Amyloplasten-Statolithen sedimentieren entweder durch das parietale Cytoplasma oder durch Stränge, die die Vakuole durchziehen, wobei die Bewegung ungefähr 30 bis 40 Minuten dauert. Nach Zugabe des actinwirksamen Cytochalasin B bewegen sich die Statolithen nach Gravistimulation in Gruppen abwärts, wobei die Sedimentation nur 5 bis 10 Minuten dauert. Diese Ergebnisse beweisen neuerlich die entscheidende Rolle des Actinnetzwerkes bei der Statolithenbewegung und unterstützen das Stärke-Statolithenmodell für die Gravi-perception.

Introduction

Gravity is one of the most important external stimuli for living organisms. As far as it concerns the plants, gravity plays a significant role in the regulation of plant movement and development. Roots of higher plants exhibit positive gravitropism, whereas the shoots show negative gravitropism, i.e. when they are placed horizontally they bend upward, growing in opposite direction of the gravity vector. The gravitropic bending takes place via the chain reaction of perception, transduction and response. The two major hypotheses for graviperception are the protoplast-pressure, which seems to need further support (BLANCAFLOR 2002) and the starch-statolith model (reviewed by KISS 2000). According to the latter, the perception of gravity in plant organs after they are re-oriented is considered to take place by amyloplast sedimentation (VOLKMANN & SIEVERS 1979, SACK 1991). Among aerial plant organs coleoptiles, hypocotyls, young shoots and grass nodes have been known as sites of gravity perception many years ago (VOLKMANN & SIEVERS 1979 and literature therein). The

amyloplast sedimentation after gravistimulation was continuously followed with a horizontally placed microscope in the starch sheath cells of *Alocasia odora* leaf petioles by SCHEUERLEIN & PSARAS 1994. Perception of the change of gravity direction ascribed to amyloplast movement was reported more recently in the endodermis of *Arabidopsis* shoots (FUKAKI & al. 1998, TASAKA & al. 1999) and in snapdragon (*Antirrhinum majus* L.) flowering shoots (PHILOSOPH-HADAS & al. 1995, 2001).

The starch sheath (or endodermis) cells are believed to be the statocytes, that is, the gravity perceiving cells in the shoots (TASAKA & al. 1999, KATO & al. 2002). The endodermal cells are differentiated cells possessing large and central vacuoles and their amyloplasts are thought to play the role of statoliths. Other aerial plant organs showing negative gravitropism, i.e. hypocotyls and coleoptiles have also vacuolated cells with sedimenting amyloplasts. By contrast, the vacuoles in the root columella cells are small, thus not influencing the movement of amyloplasts. According to CLIFFORD & al. 1989, most of the amyloplasts sediment in the peripheral cytoplasm but some of them move through already existing or new transvacuolar strands. The fluidity of the tonoplast membrane seems to play a role for the statolith sedimentation in shoot statocytes (CLIFFORD & al. 1989, KATO & al. 2002).

The gravitropic response is also related to the cytoskeleton networks. It has been suggested that amyloplasts interact with the components of the cytoskeleton (SIEVERS & al. 1991, BALUŠKA & HASENSTEIN 1997, FRIEDMAN & al. 2003). Apart from cell growth control (Nick 1999) actin filaments are involved in the movement of organelles (HAWES & SATIAT-JEUNEMAITRE 2001). The disruption of actin network by modulators like cytochalasin causes sinking of statoliths, which suggests that statoliths are held by the acto-myosin complex (SIEVERS & al. 1991). Thus, actin filament network is an important factor participating in graviperception.

Usually amyloplast sedimentation is reported from end-point determinations, i.e. the new arrangement is observed some time after re-orienting the organ, but little is known about the process of the sedimentation. With this work a new system is introduced in the research of gravity perception. The mature leaf petioles of *Calla palustris* L. (*Araceae*) are easy to handle and they possess endodermal cells with abundant and large amyloplasts. The sedimentation of these amyloplasts-statoliths after gravistimulation can be continuously followed and recorded in vivo. The role of the actin network of the cytoskeleton in the amyloplast displacement has been also investigated applying the actin-modulator cytochalasin B.

Materials and Methods

Calla palustris L. (*Araceae*) is widely used as an ornamental plant. Thus, plant material was collected from outside growing plants. For the re-orientation experi-

ments whole plants were transplanted in pots. After a period of acclimation and after preliminary experiments several pots were placed horizontally in a dark room overnight and the resulting bending was visually followed every 2 h and finally recorded after 12 h, i.e. next morning.

Fixed plant material was used for the anatomical study of the petiole. For this purpose, samples of leaf petiole carefully cut in the field were fixed in 5% glutaraldehyde in 0.025 M phosphate buffer at pH 7 at room temperature for 2 h. Tissue was then post-fixed in 1% OsO₄ at 4°C, dehydrated in an acetone series and embedded in Durcupan ACM (Fluka Chemie GmbH, Switzerland and Germany). Semi-thin sections (1–2 µm) of plastic-embedded tissue were made on a Reichert Om-U2 (Austria) microtome using glass knives and stained with Toluidine Blue O. Sections were examined and photographed using a Zeiss Axioplan (Zeiss, Oberkochen, Germany) microscope.

For the observation of the sedimenting amyloplasts fresh cut whole leaves with their long (30–50 cm) petioles were transferred in the lab, held vertically in a glass with some water and immediately used for the experiments. Free hand longitudinal sections of the petioles were transferred on a water drop on a slide and mounted under a cover-slip with dental wax. Sections were observed under a horizontally placed microscope, having, thus, the stage vertically oriented. For gravistimulation, the slide with the petiole section was turned up side down.

For the experiments with the cytoskeleton modulator cytochalasin B (CB) the same procedure was followed but, instead of water, sections were transferred in a drop of 42 µM solution (FRIEDMAN & al. 2003) of CB (Sigma, Germany).

Results

In order to check the response of the plant after re-orientation, plants like that shown in Fig. 1a were placed horizontally and their response was visually followed every 2 h. After 12 h all petioles showed an upward bending, i.e. a typical negative gravitropic response. Some of them reached the vertical orientation (Fig. 1b).

The petiole anatomy was studied in cross sections (Fig. 2a,b). To the inside of the one cell-layered epidermis there are groups of sclerenchyma cells interrupting the chlorenchyma, which surrounds the extensive aerenchyma tissue (Fig. 2a). Vascular bundles constituting a more or less typical atactostele are scattered throughout aerenchyma. Each vascular bundle is surrounded by the endodermis, or starch sheath, a layer of cells without intercellular spaces. In some starch sheath cells, several amyloplasts can be seen (Fig. 2a,b). As seen in longitudinal sections, starch sheath cells are cylindrical with slightly oblique end walls, their nuclei occupy the upper part of the cell (Fig. 2c) and they contain a group (5–15) of large amyloplasts. When the petioles are vertically oriented, the amyloplasts are settled on the bottom of the starch sheath cells and this is shown in the free hand section of Fig. 2c. Due to the aggregation of the amyloplast near the lower cell wall, in cross-sectioned petioles several sheath cells seem to lack amyloplasts (Fig. 2a,b). In living plant material, although the

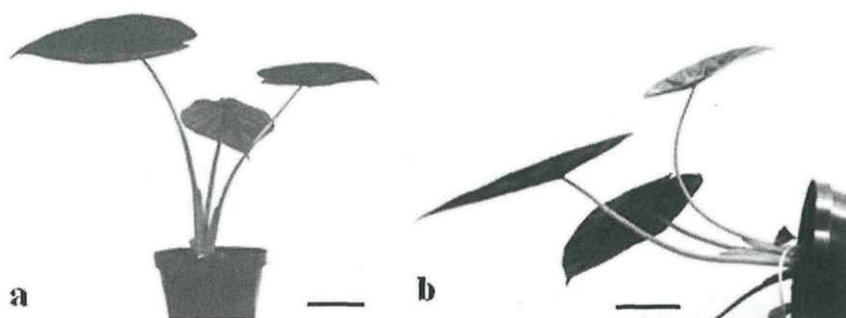


Fig. 1. A *Calla palustris* individual before and after gravistimulation. a. A plant in its normal position. b. A plant 12 h after it has been horizontally placed, showing a negative gravitropic bending. Scale bar = 10 cm.

amyloplasts are aggregated in the lower part of the cells, they continuously show a slight movement, which can be seen under the microscope. Longitudinal sections along a petiole revealed that statocytes occur throughout the whole petiole.

If the slide with the longitudinal section of the petiole is inverted, after 30-40 min practically all amyloplasts are settled on the lower end of the cell. The movement of the amyloplasts from the one to the other end of the

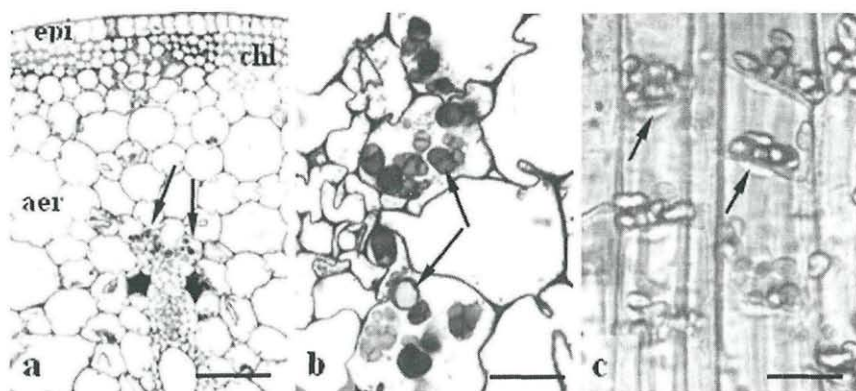


Fig. 2. The statocytes of *Calla palustris* petiole. a. Cross-sectioned petiole. The vascular bundles surrounded by endodermis (arrows) are embedded in the aerenchyma (aer) which is found to the inside the chlorenchyma (chl) and the one cell layered epidermis (epi). Stained with Toluidine Blue O. Scale bar = 100 μ m. b. Endodermal cells in cross-sectioned petiole with several amyloplasts (arrows) in detail. Stained with Toluidine Blue O. Scale bar = 20 μ m. c. Free hand longitudinal section of the petiole. Statocytes are cylindrical with their nucleus occupying the upper side of the cell (arrows) and the amyloplasts-statoliths aggregated near the lower cell wall. Unstained. Scale bar = 20 μ m.

starch sheath cells was continuously followed and photographed in vivo under a horizontally placed microscope. A few seconds after the inversion of the slide, the amyloplasts begin to move downwards. Representative pictures from a series of micrographs taken at 5 min intervals after the sample has been inverted are shown in Fig. 3a–f. Most of the amyloplasts sediment individually (Fig. 3c–e, arrows), but some of them form clusters, moving downwards through the parietal cytoplasm (Fig. 3b, arrowhead). The amyloplasts of Fig. 3c–e seem to be “in the vacuole”, either they move along the side cell wall and they are projected in the middle of the cell, or they move through transvacuolar strands. The experiment with the same section, which remains alive for 1–2 h, may be repeated 3–4 times by re-orienting the slide.

Amyloplast sedimentation was similarly followed after the application of the cytoskeleton modulator cytochalasin B (CB). The results of a representative experiment are shown in the series of micrographs a–f of Fig. 4. The amyloplasts move from the upper side to the bottom of the starch sheath cells within 8–10 min and practically they sediment in clusters (see arrows in Fig. 4b,c). Micrographs of Fig. 4 are representative snapshots from a series of micrographs taken at 1 min intervals after the specimen has been inverted. The experiment can be also repeated by re-orienting the slide.

Discussion

Root cap columella cells and shoot endodermal (or starch sheath) cells are believed to constitute the sites of gravity perception. In both cell types, the sedimentation of amyloplasts is considered to be the trigger for gravity perception (SACK 1991, KISS 2000, KATO & al. 2002). Root gravitropism and root statocytes have been the subject of extensive work (reviewed by VOLKMANN & SIEVERS 1979, SACK 1991, BOONSIRIHAI & al. 2002). Since it is difficult to observe and analyze living cells inside shoots we had little direct evidence concerning the gravity perception in above ground tissues. Some reports have been appeared on starch grain displacement in young negatively gravitropic organs such as grass nodes (LAWTON & al. 1986) and hypocotyls (FIRN & DIGBY 1977, VOLKMANN & al. 1993), but recently shoot gravitropism received increasing attention. The involvement of shoot endodermis in gravity perception has been also documented in shoots near to maturity. CLIFFORD & al. 1989, working with *Taraxacum officinale*, FUKAKI & al. 1998, FUKAKI & TASAKA 1999, TASAKA & al. 1999, KATO & al. 2002, working with *Arabidopsis* inflorescence shoots and FRIEDMAN & al. 1998 and PHILOSOPF-HADAS & al. 2001 working with *Antirrhinum majus* flowering shoots reported amyloplast sedimentation in shoot endodermis after gravistimulation. All these studies have been conducted using sections of fixed plant material. Leaf petioles of the monocotyledon *Calla palustris*

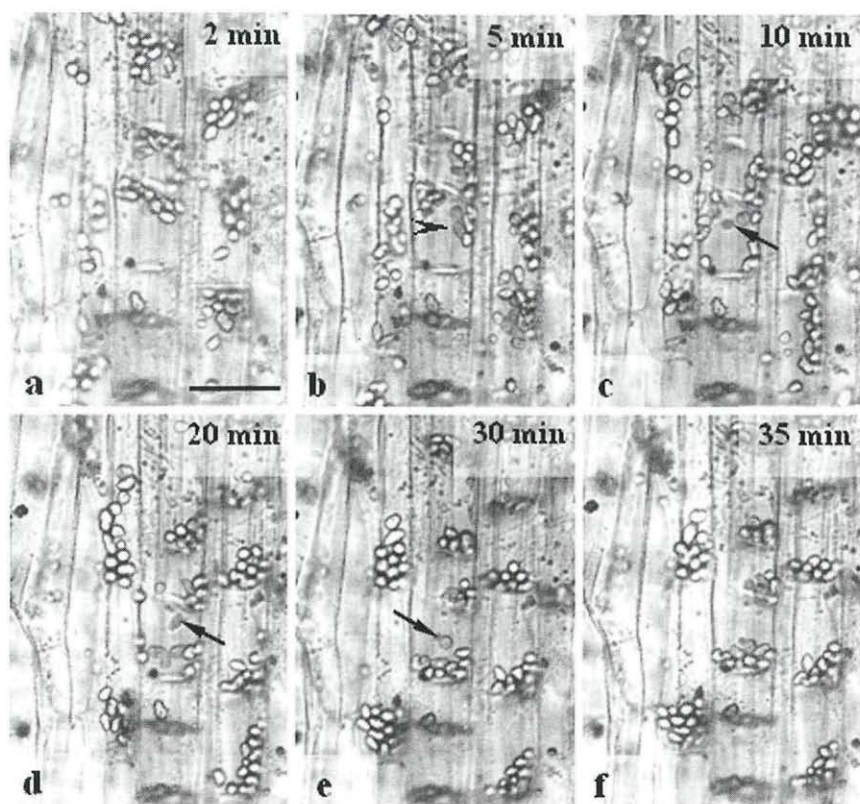


Fig. 3. The sedimentation of statoliths as seen in a free hand longitudinally sectioned *Calla palustris* petiole. a-f. Representative snapshots from a series of micrographs of the statocytes taken at 5 min intervals after the tissue has been inverted. The arrow-head in b shows a small cluster of amyloplasts. Arrows in c, d and e show amyloplasts which sediment individually. The time indicated in each micrograph denotes the time after the sample has been inverted. Scale bar = 20 μ m.

studied here are actually mature shoots and in their endodermis cells amyloplast sedimentation can be directly and continuously observed in vivo after gravistimulation.

TASAKA & al. 1999 reported a distribution of statocytes throughout the elongation zone of *Arabidopsis* shoots, but *C. palustris* petioles present several advantages. They are long (30–50 cm), easy to handle, with statocytes along the entire petiole. The presence of aerenchyma in *C. palustris* petioles makes the tissue optically transparent, which permits the microscopic observation of relatively thick sections containing non-sectioned, intact cells. The study of living endodermal cells of *C. palustris* revealed that they possess all characteristics of shoot statocytes. Apart from the

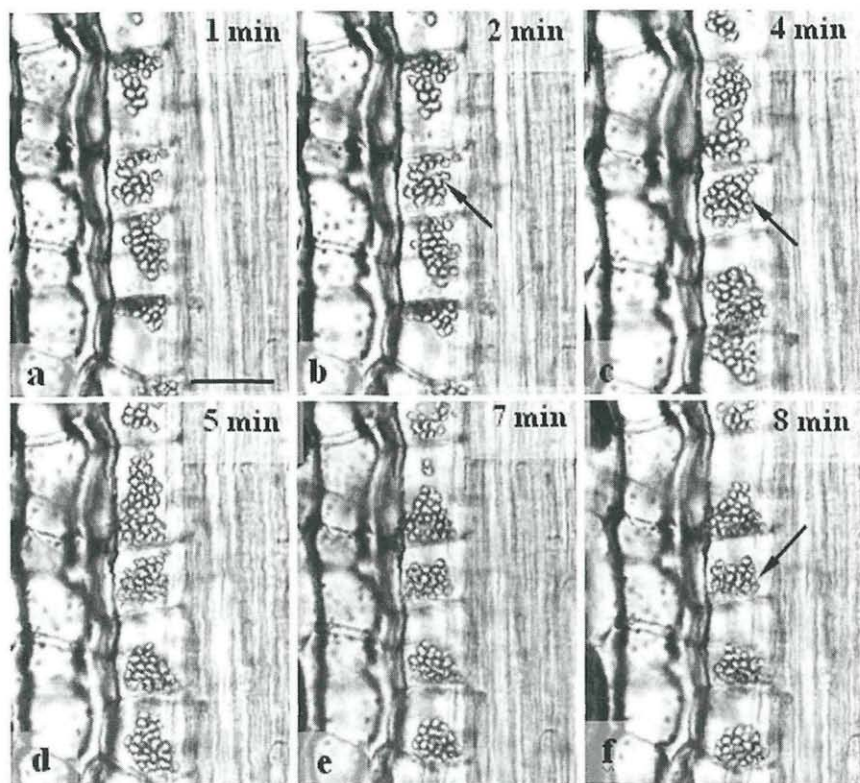


Fig. 4. Statolith sedimentation in a sample treated with cytochalasin B. a-f. Representative snapshots of the statocytes from a series of micrographs taken at 1 min intervals after the tissue has been inverted (the time indicated in each micrograph denotes the time after the sample has been inverted). Note that amyloplasts sediment practically in clusters (arrows in b, c, f). Scale bar = 20 μm .

presence of amyloplasts which sediment under gravity, they are vacuolated (see also CLIFFORD & al. 1989, KATO & al. 2002). *C. palustris* statocytes exhibit also a structural polarity like that of root statocytes (SIEVERS & al. 1976, VOLKMANN & SIEVERS 1979). The structural polarity of statocytes has been confirmed also in *Trifolium repens* roots, after a three-dimensional reconstruction of root columella cells (SMITH & al. 1997). The nucleus occupies always the upper part of the cell, "squeezed" between upper cell wall and vacuole (Fig. 2c). In shoots, this part of the cell is the distal one whereas in roots the site occupied by nucleus is the proximal, but in both, shoots and roots this is always the upper part of the statocyte. This is a worthy to note feature, since the cellular organization of the statocytes is considered to be crucial for their function (RANJEVA & al. 1999). The in vivo

microscopic observation of the endodermal cells revealed that the amyloplasts though settled on the lower part of the cell show a permanent slight movement. This has been shown again by SCHEUERLEIN & PSARAS 1994 in *Alocasia odora* (Araceae) endodermal statocytes using time-lapse photography. A similar permanent motion of the amyloplasts has been reported for the statocytes of root caps (VOLKMANN & al. 1999).

CLIFFORD & al. 1989 and KATO & al. 2002 argued that the vacuole of the endodermal cells is significantly involved in the distribution and sedimentation of amyloplasts. According to the micrographs of moving amyloplasts in intact statocytes shown here, most of the amyloplasts sediment individually through the parietal cytoplasm or through existing or created transvacuolar strands. In all cases, vacuoles seem to be involved in the amyloplast sedimentation. These data confirm the schematic representation of the amyloplast sedimentation proposed by CLIFFORD & al. 1989. On the contrary, in CB treated statocytes, amyloplasts fall in clusters and aggregate on the bottom of the statocyte very fast (within 5–10 min) after the inversion of the sample. These data further confirm that amyloplast movement is closely related to the actin filaments network of cytoskeleton (VOLKMANN & al. 1999, VOLKMANN & BALUŠKA 1999, BLANCAFLOR 2002, FRIEDMAN & al. 2003, yet, they further support that the vacuole participates in the early events of gravitropism (CLIFFORD & al. 1989, KATO & al. 2002, MORITA & al. 2002). The amyloplast grouping in CB-treated samples shown here is very similar to that observed under microgravity conditions which has been interpreted as a possible mechanism by which plants regulate their sensitivity to gravity (SMITH & al. 1997). Further experimental work with this new plant material might greatly add to our knowledge concerning the gravity perception mechanism.

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