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ORIGINAL ARTICLE

Comparison Study of Gravity-Dependent Displacement of Amyloplasts in Statocytes of Cress Roots and Hypocotyls

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Abstract In this study, the kinetics of gravity-dependent movement of amyloplasts (statoliths) along root statocytes and hypocotyls (endodermis cells) has been analyzed and compared in order to testify cytoskeleton involvement in the displacement of statoliths in cress (*Lepidium sativum* L.) seedling statocytes. After 32 h of growth at 1 g or under a fast clinorotation (50 rpm), the seedlings were treated for 24 min as follows: exposition to clinorotation or 180° inversion and the action of gravitational force in root tip or hypocotyl tip direction. Statolith displacement was studied by light microscopy on semi-thin longitudinal sections of hypocotyls and root caps, measuring the distance between the centre of plastids and morphological cell bottom. Considerable temporal differences have been determined between the kinetics of the longitudinal motion of amyloplasts in root and hypocotyl statocytes of 1-g seedlings upon exposition to fast clinorotation and inversion. In statocytes of both organs of seedlings grown under fast clinorotation, the gravity provoked displacement of statoliths in the direction of its action; however, the displacement was much faster in hypocotyl than in root statocytes. It has been assumed that the gravity-determined longitudinal transport of amyloplasts, both in hypocotyl endodermic cells and root statocytes of cress seedlings, is modulated by the cytoskeleton.

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Introduction

Gravity (1 g), a constant and prevailing force throughout life evolution on the Earth, exerts an intricate influence on the development and growth of plants. Although gravity acts equally on all plant cells, gravity perception occurs in specialized cells (statocytes) which are localized in root tip columella and shoot endodermis. Most studies to date support the starch–statolith hypothesis of gravity perception associated with the movement of amyloplasts acting as statoliths (Laurinavičius et al. 2001; Kato et al. 2002; Driss-Ecole et al. 2003; Vitha et al. 2007; Kumar et al. 2008). The cytoskeleton system is supposed to be implicated in gravity signal perception in roots through the positioning of statoliths and modulation of their movement (Sievers et al. 1991; Baluška and Hasenstein 1997; Volkmann and Baluška 2000; Palmieri et al. 2007).

In vertically growing root caps, the gravitational and opposite endocellular cytoskeleton forces have been suggested to determine the equilibrium position of statoliths in the distal region of statocytes (Björkman 1988; Todd 1994). There are some reports to indicate that after reducing the magnitude of gravity from 1 g to microgravity in space or simulated by clinorotation on the Earth, the latter forces pull the amyloplasts towards the cell centre (Volkmann et al. 1991; Driss-Ecole et al. 2000; Laurinavičius et al. 1997, 2001; Yoder et al. 2001; Gaina et al. 2003). In endodermal cells of hypocotyls, the actual relationship between movable amyloplasts and cytoskeleton is not clearly understood, and data

of experiments with gravitropic mutants (Kumar et al. 2008), actomyosin system disrupting drugs (Palmieri and Kiss 2005; Palmieri et al. 2007) as well as employing lateral gravitropic stimulation (Švegždienė et al. 2007; Kumar et al. 2008) are often contradictory. Therefore, comparison of amyloplast motion along root and hypocotyl statocytes of the same seedling in response to alterations of the magnitude and action direction of gravitational force during periods shorter than a reliable latent reaction time could help to clarify the role of the cytoskeleton in the early phases of graviperception in above-ground organs. We analysed the kinetics of statolith motion in root and hypocotyl statocytes of seedlings: (1) grown under 1 g and then exposed to fast clinorotation or 180° inverted; (2) grown under fast clinorotation and then stimulated in root-tip or hypocotyl-tip direction by the gravitational force.

Materials and Methods

Investigations were carried out with seedlings of garden cress (*Lepidium sativum* L.) on a centrifuge-clinostat (Laurinavičius et al. 2001). It is designed as a device with two orthogonal axes (Fig. 1a) allowing independent or simultaneous rotation around four horizontal (clinostat) and one vertical (centrifuge) axes (Fig. 1a). The rotation rate of the clinostat was controlled by software commands and equalled to 50 rpm. The rotation stability of the low-vibration electric drives was no less than 2%. To sustain an appropriate position and orientation of growing seedlings during experimental manipulations, closed biocontainers with a special inside equipment (Fig. 1b) were used.

A total of twenty moistened seeds were planted in open 10 μl thin glass funnels to retain their respective orientation during germination, stimulation and fixation. The biocontainers with five packed funnels were attached to horizontal axes of the centrifuge-clinostat or placed vertically at 1 g. For gravistimulation, the seedlings grown for 32 h in both gravitational conditions were stimulated for 24 min according to the scheme presented in Fig. 2. The experiments were carried out at 23°C ± 1°C. After stimulation procedures, the seedlings were fixed for 45 min in 4% (v/v) glutaraldehyde in 0.1 M sodium phosphate buffer (pH 7.2), preserving the same gravitational conditions as in the period of stimulation. After transferring into a fresh portion of glutaraldehyde solution for 2 h at 4°C, the samples were post-fixed in 1% (w/v) OsO_4, dehydrated and embedded in Epon by standard procedures.

The morphometrical analysis of gravisensing cells was performed employing light microscopy on semithin (1 μm) median longitudinal sections of hypocotyls and root apices. Toluidine-blue [1% (w/v) in 0.1% (w/v) $Na_2B_4O_7$] stained sections were photographed with a PENTAX*ist D digital camera attached to an SMP 03 microscope photometer (Opton, Germany). The images were analysed using the SigmaScanPro 5 (Jandel Scientific Software).

To characterize the dependence between the positioning of amyloplasts and the parameters of the acting force, the distance of each plastid centre from the morphological cell bottom was measured and expressed in percent of the length of test statocytes. In hypocotyls, the length of the analyzed endodermic cells varied

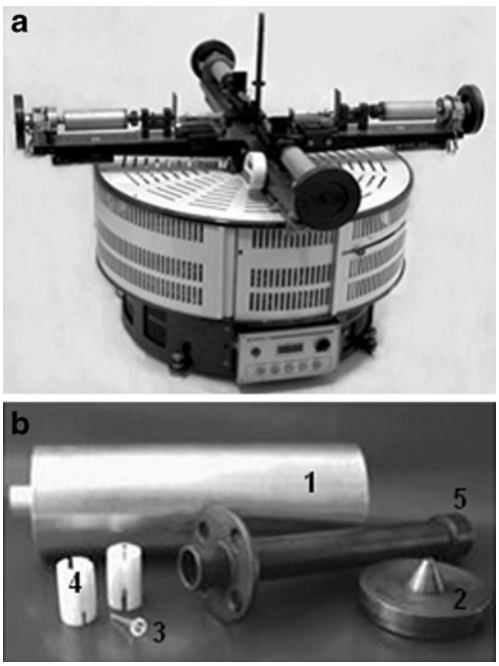

Fig. 1 Centrifuge-clinostat with two orthogonal axes (**a**) and equipment for seedling growth (**b**: *1* biocontainer; *2* cap of bio container; *3* glass funnel for seed planting, *4* fluoroplastic holders for glass funnels, *5* cylindrical holder for centering of fluoroplastic holders with funnels in biocontainer)

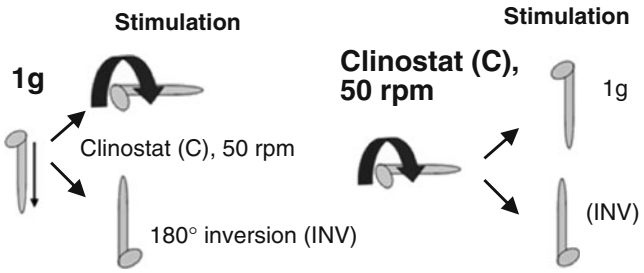

Fig. 2 Scheme of experimental procedures with cress seedlings grown vertically at 1 g and under clinorotation

from 75 to 130 μm. In roots, cells of the third to fifth columella storey of root caps were analyzed. As a rule, 2–3 sections of three hypocotyls or roots were examined for each test variant. Statistical analysis was carried out using the standard MS EXCEL 7 package. Values are represented as the mean ± standard error (SE). Statistical significance was determined using Student's test.

Results

Statolith Displacement Along Statocytes of 1-g Seedlings Exposed to Fast Clinorotation and After 180° Inversion

The displacement of amyloplasts was evaluated in statocytes of roots and hypocotyls of cress seedlings grown vertically at 1 g and then exposed to fast clinorotation, and fixed after 1, 2, 4, 6, 12 and 24 min. For comparison, the sedimentation of statoliths was studied in 1-g seedlings after a 180° inversion for analogous periods. Before gravistimulation the amyloplasts had been grouped at the distal pole of cells of the third to fifth columella storeys (Fig. 3a) and at the basal pole of endodermal cells of hypocotyls (Fig. 4a). Thus, the statoliths were located near the morphological bottom of both cell types.

On transferring to the clinostat, they moved from the initial location towards the morphological top of statocytes both in roots (Fig. 3b) and in hypocotyls (Fig. 4b). However, the velocities of plastid motion differed significantly. Within 6 min the majority of statoliths reached the central region of root statocytes (Fig. 3c). In endodermic cells, the lengthwise displacement of plastids was slight in this period (Fig. 4b), but it proceeded until the 24th minute of clinorotation (Fig. 4c).

Upon 180° inversion of 1-g seedlings, amyloplasts sedimented along the gravitational force in root statocytes (Fig. 3d, e) more rapidly than in hypocotyl ones (Fig. 4d, e). Besides, the mode of this redislocation was different. Within the period of 6 min, a bulk of amyloplasts travelled to the central part of root statocytes. During the same period, several plastids slid into the top part of endodermic cells of inverted hypocotyls. The other amyloplasts continued sliding until the 24th minute.

In addition to the qualitative observations described above, quantitative measurements of plastid positions with respect to the morphological bottom of statocytes were made. Figure 5 shows the displacement of statolith along root and hypocotyl statocytes of 1-g seedlings in response to both stimulation treatments. Before stimulation, the average distance of statoliths from the morphological cell bottom was found to equal 26.2% of the whole length of root cap cells tested versus 8.3% from the whole length of the test endodermic cells. In root statocytes, a statistically confirmed longwise displacement of amyloplasts was determined as soon

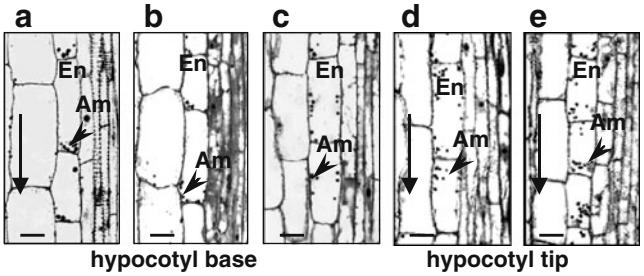

Fig. 4 Light micrographs of statocytes of cress hypocotyls after growth at 1 g (**a**) and exposed to fast clinorotation for 6 min (**b**), 24 min (**c**) or 180° inverted for 6 min (**d**) and 24 min (**e**). *En* endodermis, *Am* amyloplasts. *Bars* 12 μm. *Arrowheads* indicate the action direction of gravity

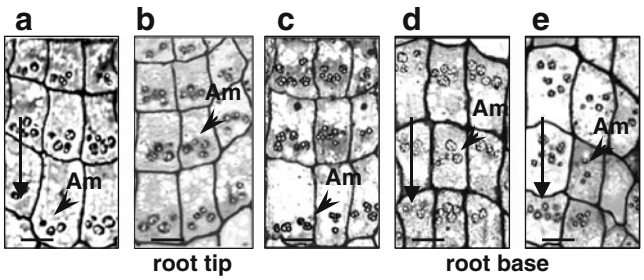

Fig. 3 Light micrographs of cress root statocytes after growth at 1 g (**a**) and exposed to fast clinorotation for 2 min (**b**), 6 min (**c**) or 180° inverted for 2 min (**d**) and 6 min (**e**). *Am* Amyloplasts. *Bars* 10 μm. *Arrowheads* indicate the direction of gravity

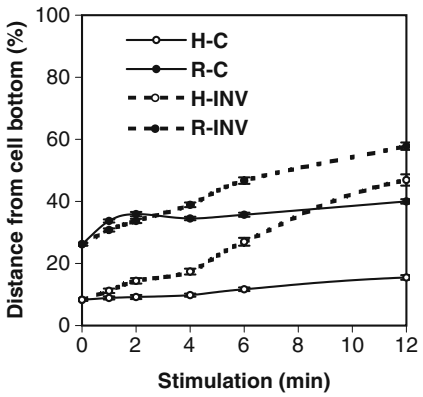

Fig. 5 Displacement of amyloplasts from the morphological bottom of statocytes in roots (*R*) and hypocotyls (*H*) of cress seedlings exposed to clinorotation (*C*) or inverted (*INV*) after growth at 1 g

as after the first and second minutes of clinorotation and inversion. Later on, this statolith movement became significantly slower under clinorotation; however, it proceeded at a constant velocity during inversion.

In hypocotyl statocytes, a significant shift of amyloplasts in longitudinal direction was found only after the 6-min period of clinorotation and as soon as after the first minute of inversion (Fig. 5). A comparatively slow sliding of plastids continued until the 24th minute of clinorotation, and the mean distance of plastids from the bottom of hypocotyl statocytes increased up to 18.0 ± 0.9% of the whole cell length. Under inversion, plastid sedimentation increased even more, and over the 24-min period the final distance of statoliths from the bottom cell wall equalled 58.6 ± 1.7% of the total length of endodermic cells.

For comparison of real velocities of statolith displacement, the evaluated relative measurements were evaluated in real values of the mean length of test cells of 1-g seedlings, which equalled to 22.9 ± 0.6 μm for root statocytes and to 95.0 ± 2.1 μm for endodermic cells of hypocotyls. Thus, during the first and second minute of clinorotation and inversion, the amyloplasts moved in longitudinal direction with the velocity of approximately 1 μm/min in roots. In hypocotyls, these plastids moved from the initial positions with the velocity of about 0.5μm/min within the first 2 min of clinorotation, retained the comparable speed until the 12th minute and continued this sliding with the velocity of 0.2μm/min. Under inversion, the amyloplasts sediment towards the cell top at the rate of about 3.0μm/min as soon as during the first 2 min, and the displacement proceeds until the 12th minute.

These results suggest that both modes of applied stimulation (elimination of the unidirectional action of the gravitational force and its action in an unusual direction) provoke similar effects on the longitudinal motion of amyloplasts in root statocytes and endodermal cells of cress seedlings after vertical growth at 1 g.

Gravity-Induced Statolith Sedimentation Along Statocytes of Clinorotated Seedlings

In order to compare the features of statolith displacement along the different regions of root and hypocotyl statocytes, cress seedlings grown under fast clinorotation were stimulated by the gravitational force in root-tip or hypocotyl-tip directions and fixed after 1, 2, 4, 6, 12 and 24 min. Figures 6a and 7a show the positioning of amyloplasts before the stimulation in root and hypocotyls statocytes, respectively. One can see, that the plastids are grouped in the central region of root statocytes but dispersed mostly throughout the entire periphery of endodermal cells.

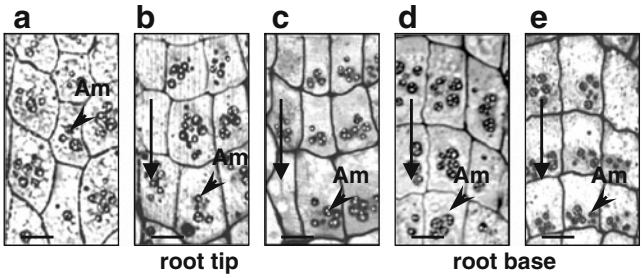

Fig. 6 Light micrographs of root statocytes of cress seedlings grown under clinorotation (**a**) and stimulated by gravity in root-tip direction for 1 min (**b**), 6 min (**c**) or in hypocotyl-tip direction for 2 min (**d**) and 6 min (**e**). *Am* Amyloplasts. *Bars* 10 μm. *Arrowheads* indicate the action direction of gravity

Despite the distinct mode of statolith distribution along these cells, plastid sedimentation was noted as soon as after the first 2 min and later towards the direction of the acting gravitational force both in roots (Fig. 6) and in hypocotyls (Fig. 7). The results of quantitative analysis of statolith displacement in response to both stimulations are presented in Fig. 8. They show that the mean values of plastid distance from the morphological cell bottom evaluated for root and hypocotyls statocytes before stimulation were very close. In root statocytes, amyloplasts sedimented intensively in the direction of gravity action to a comparable extent even during the first minutes of treatments. However, after the fourth minute, plastid displacement became more active towards the cell top in comparison to that towards the cell bottom.

In endodermic cells, during the first minute of stimulation, the longitudinal sliding of amyloplasts was more pronounced downwards under the action of gravity in root-tip direction than upwards under the inversion of

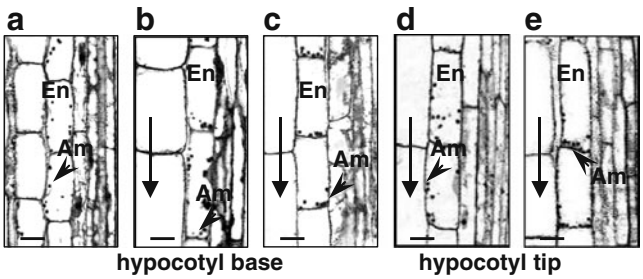

Fig. 7 Light micrographs of hypocotyl statocytes of cress seedlings grown under clinorotation (**a**) and stimulated by gravity in root-tip direction for 1 min (**b**), 24 min (**c**) or in hypocotyl-tip direction for 2 min (**d**) and 24 min (**e**). *En* Endodermis, *Am* amyloplasts. *Bars* 12 μm. *Arrowheads* indicate the action direction of gravity

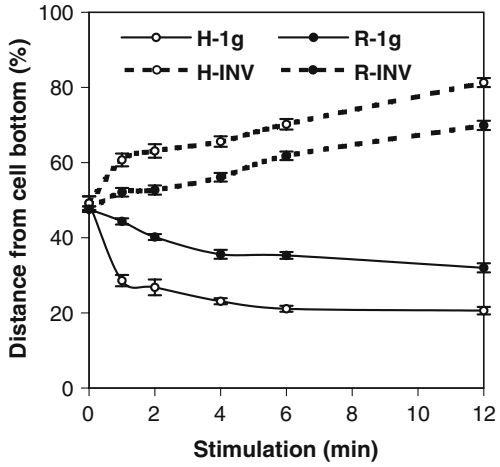

Fig. 8 Displacement of amyloplasts along statocytes in roots (*R*) and hypocotyls (*H*) during 1-g stimulation in root-tip (1 g) and hypocotyl-tip (*INV*) directions after growth under clinorotation

seedlings. Later on, the plastid displacement slowed down in both directions. Within 6–12 min, the mean distance of amyloplasts from the bottom of hypocotyl statocytes remained almost unchanged under the action of gravity in root-tip direction but increased essentially under inversion. Finally, after the 24-min period, it reduced to 13.0 ± 0.6% of the total cell length under the first mode of stimulation and increased up to 82.8 ± 1.2% under the second ones.

The mean length of the statocytes was found to be 23.9 ± 0.7 μm in roots and 93.8 ± 2.4 μm in hypocotyls of cress seedlings grown under clinorotation. Based on these values, the average velocities of statolith movement during the first minute of both 1-g stimulations were calculated. In root statocytes, the displacement of amyloplasts proceeded towards both gravity directions at an approximate rate of 1.0 μm/min. In endodermic cells of hypocotyls, the statoliths travelled by at a velocity of about 19.1 μm/min towards the cell bottom and 10.3 μm/min towards the cell top with respect to the direction of gravity.

Thus, the direction of amyloplasts movement along the statocytes of roots and hypocotyls of cress seedlings after growth on a fast clinostat depended on the direction of the stimulating gravitational force. The maximal longitudinal shift of amyloplasts from their initial location was determined within the first minute of stimulation both in root-tip and hypocotyl-tip directions.

Discussion

Although in most cell types gravity does not affect the position or movement of organelles, gravity-sensing statocytes of higher plants allow their amyloplasts-statoliths to sediment along the gravity vector or to settle in response to reducing its magnitude. There is no doubt about the role of actomyosin-driven transport of amyloplasts during early stages of gravisensing in roots (Volkmann and Baluška 2000; Laurinavičius et al. 2001; Gaina et al. 2003; Driss-Ecole et al. 2003); however, experimental studies in shoot gravisensing give often a contradictory results (Volkmann et al. 1993; Palmieri et al. 2007; Hou et al. 2003; Kumar et al. 2008; Švegždienė et al. 2007). In this study, involvement of elastic forces from the cytoskeleton in the longitudinal motion of amyloplasts in the statocytes of roots and endodermic cells of hypocotyls of the same seedling was analysed using one of the indirect methods to investigate the lifting of plastids, caused by changes in the magnitude and action direction of gravitational force.

When cress seedlings grew vertically under 1 g, the amyloplasts sedimented closer to the morphological statocyte bottoms in hypocotyls (Fig. 4a) than in roots (Fig. 3a). Following elimination of the unidirectional effect of gravity or the inversion of seedlings, the plastids moved towards cell centre in the statocytes of both organs (Figs. 3 and 4). After withdrawing 1-g stimulation by in-flight centrifuges in space or by clinostating on the ground, these intracellular forces from the cytoskeleton provoke the longitudinal sliding of statoliths towards the centre of root statocytes (Volkmann et al. 1991; Driss-Ecole et al. 2000; Laurinavičius et al. 1997, 2001). Data of the present study on the kinetics of amyloplast displacement in the statocytes of both seedling organs allow adjusting the above-mentioned process to the endodermic cells of 1-g hypocotyls because statolith motion preferentially correlated with the direction and magnitude of the stimulating gravitational force (Fig. 5).

On the other hand, there are some differences between the behaviour of statoliths in root and hypocotyl statocytes under applied stimulations. In root statocytes, comparable lengthwise shifts of statoliths during the first 2 min of both stimulation modes were determined. The possible reasons for this process in the statocytes of the youngest cress roots were discussed in detail in our earlier paper (Gaina et al. 2003). In hypocotyl statocytes, plastid movement towards the cell centre proceeded significantly slower under clinorotation than after the 180° inversion. This finding show that gravity is much stronger compared with the cytoskeleton elastic forces which could pull the statoliths in the same direction. However, endodermic cells of aerial organs possess very large central vacuoles (Volkmann et al. 1993; Kiss 2000; Kato et al. 2002) and

cytoplasm streaming which is driven by the actomyosin system (Grolig and Pierson 2000). In statocytes of cress hypocotyls, amyloplasts are localized and travelling mostly along the cell periphery in all of the test gravitational situations (Figs. 4 and 7). These two findings imply that the action of intracellular forces could be modulated by central vacuoles and therefore exert only a limited impact on the lengthwise sliding of statoliths in 1-g hypocotyls exposed to clinorotation.

It should be noted that there is a considerable difference in the displacement time-scale and real values of the sliding path of amyloplasts in gravisensing cells of roots and hypocotyls. In 1-g roots, the remarkable longwise shift of statoliths proceeded within the first 2 min of clinoration or inversion (Fig. 5) at the rate of about 1 μm/min, evaluated in real mean length of the test cells. Similar data were obtained in inversion experiments with cress roots, in which the rate of 1.1 μm/min (Iversen et al. 1968) and 1.2 μm/min (Volkmann et al. 1991) during 6 min was determined. In 1-g hypocotyls, a significant plastid displacement was detected after 6 min of clinorotation, but it occurred much earlier—after the first minute—in the case of inversion (Fig. 5). Our study showed that relatively real velocities of statolith displacement in hypocotyl statocytes during the 6-min exposure to clinorotation might be about 0.5 μm/min. According to data of space experiments, the velocity of 0.3 μm/min was evaluated during 6 min of microgravity in statocytes of cress roots grown on an in-flight centrifuge (Gaina et al. 2003) and 0.15 μm/min during 29 min of microgravity in lentil roots (Driss-Ecole et al. 2000). Thus, despite ultrastructural disparities, the sliding of amyloplasts towards the cell centre might proceed at a comparable velocity in statocytes of both roots and hypocotyls during the whole 6-min period of clinorotation. Furthermore, it can be suggested that under the 1-min upward effect of gravity on seedlings, the displacement of statoliths from the morphological bottom towards the centre of statocytes was approximately tree times greater in hypocotyls than in roots (at the velocities of 3.0 and 1.0 μm/min, respectively). In contrast, under clinorotation it was more vigorous in root than in hypocotyl statocytes.

In cress seedlings grown under fast clinorotation, the mode of amyloplast distribution along root and hypocotyl statocytes differed essentially (Figs. 6a and 7a). Under longitudinal stimulation by gravity, the statoliths showed remarkable shifts within the first minute in the statocytes of both organs in the direction of gravity (Fig. 7). Thus, plastids can easily move towards any of the cell poles under the impact of gravity and possibly of actin filaments. This finding shows the cytoplasm of the central part of statocytes of both types to be almost homogenous. Later on, in hypocotyl endodermis, the sedimentation of statoliths slowed down towards the cell bottom but proceeded at the comparable velocity until the 12th minute towards the cell top. In root statocytes, similar changes of plastid sedimentation proceeded later—from the fourth minute. Consequently, conditions for the longitudinal movement of statoliths are different closer to the opposite poles of statocytes both in roots and hypocotyls.

Although the displacement of amyloplasts towards the bottom of hypocotyl statocytes slowed down under the action of gravitational force in root-tip direction, the obtained drag effect might be caused by the elastic properties of the cytoskeleton interacting with the statoliths. A comparable character of amyloplast displacement from the central cell region was observed in root statocytes where it proceeded to a much lesser extent within the 6 min of stimulation (Fig. 8). Considering that the mean length of the statocytes in roots was approximately fivefold smaller than in hypocotyls, we can suppose that the intracellular forces of the cytoskeleton affect the amyloplast motion induced by gravity in the statocytes of hypocotyls in a similar manner. Thus, the obtained data allow a supposition that the gravity-determined transporting of amyloplasts along statocytes of cress roots and hypocotyls is modulated by the cytoskeleton.

References

Baluška, F., Hasenstein, K.H.: Root cytoskeleton: its role in perception of response to gravity. Planta **203**, 69–78 (1997)

Björkman, T.: Perception of gravity by plants. Adv. Bot. Res. **15**, 1–41 (1988)

Driss-Ecole, D., Jeune, B., Prouteau, M., Julianus, P., Perbal, G.: Lentil root statoliths reach a stable state in microgravity. Planta **211**, 396–405 (2000)

Driss-Ecole, D., Lefranc, A., Perbal, G.: A polarized cell: the root statocyte. Physiol. Plant. **118**, 305–312 (2003)

Gaina, V., Švegždienė, D., Raklevičienė, D., Koryznienė, D., Stanevičienė, R., Laurinavičius, R.: Kinetics of amyloplasts movement in cress root statocytes under different gravitational loads. Adv. Space Res. **31**, 2275–2281 (2003)

Grolig, F., Pierson, E.S.: Cytoplasmic streaming: from flow to track. In: Staiger, C.J., Baluška, F., Volkmann, D. (eds.) Actin: A Dynamic Framework for Multiple Cell Functions, pp. 557–571. Kluwer, Norwell (2000)

Hou, G., Mohamalawari, D.R., Blancaflor, E.B.: Enhanced gravitropism of roots with disrupted cap actin cytoskeleton. Plant Physiol. **131**, 1360–1373 (2003)

Iversen, T.H., Pedersen, K., Larsen, P.: Movement of amyloplasts in the root cap cells of geotropically sensitive roots. Physiol. Plant. **21**, 811–819 (1968)

Kato, T., Morita, M.T., Tasaka, M.: Role of endodermal cell vacuoles in shoot gravitropism. J. Plant Growth Regul. **21**, 113–119 (2002)

Kiss, J.Z.: Mechanisms of early phases of plant gravitropism. Crit. Rev. Plant Sci. **19**, 551–573 (2000)

Kumar, N.S., Stevens, M.H.H., Kiss, Z.J.: Plastid movement in statocytes of the ARG1 (altered response to gravity) mutant. Am. J. Bot. **95**(2), 177–184 (2008)

Laurinavičius, R., Švegždienė, D., Gaina, V.: Force sensitivity of plant gravisensing. Adv. Space Res. **27**(5), 899–906 (2001)

Laurinavičius, R., Švegždienė, D., Sievers, A., Buchen, B., Tairbekov, M.: Statics and kinetics of statolith positioning in cress root statocytes (Bion-11 Mission). Gravit. Space Biol. Bull. **11**(1), 50 (1997)

Palmieri, M., Kiss, Z.J.: Disruption of the F-actin cytoskeleton limits statolith movement in *Arabidopsis* hypocotyls. J. Exp. Bot. **56**(419), 2539–2550 (2005)

Palmieri, M.M., Schwind, M.A., Stevens, R.E., Edelmann, R.E., Kiss, Z.J.: Effects of the myosin ATPase inhibitor 2, 3-butanedione monoxime (BMD) on amyloplast kinetics and gravitropism of *Arabidopsis* hypocotyls. Physiol. Plant. **130**, 613–626 (2007)

Sievers, A., Buchen, B., Volkmann, D., Hejnowicz, Z.: Role of the cytoskeleton in gravity perception. In: Lloyd, C.W. (ed.) The Cytoskeletal Basis of Plant Growth and Form, pp. 169–182. Academic, London (1991)

Švegždienė, D., Raklevičienė, D., Koryznienė, D.: Gravisensing in hypocotyls and roots of garden cress seedlings. Biologija (Vilnius) **53**(2), 63–66 (2007)

Todd, P.: Mechanical analysis of statolith action in roots and rhizoids. Adv. Space Res. **14**(8), 121–124 (1994)

Vitha, S., Yang, M., Sack, F.D., Kiss, J.Z.: Gravitropism in the starch excess mutant of *Arabidopsis thaliana*. Am. J. Bot. **94**(4), 590–598 (2007)

Volkmann, D., Baluška, F.: Actin cytoskeleton related to gravisensing in higher plants. In: Staiger, C.J., Baluška, F., Volkmann, D. (eds.) Actin: A Dynamic Framework for Multiple Cell Functions, pp. 557–571. Kluwer, Norwell (2000)

Volkmann, D., Buchen, B., Hejnowicz, Z., Tewinkel, M., Sievers, A.: Oriented movement of statoliths studied in a reduced gravitational field during parabolic flights of rockets. Planta **185**, 153–161 (1991)

Volkmann, D., Winn-Borner, U., Waberzeck, K.: Graviresponsiveness of cress seedlings and structural status of presumptive statocytes from hypocotyls. Plant Physiol. **142**, 710–716 (1993)

Yoder, T.L., Zheng, H.Q., Todd, P., Staehelin, L.A.: Amiloplast sedimentation dynamics in maize columella cells support a new model for the gravity—sensing apparatus of roots. Plant Physiol. **125**, 1045–1060 (2001)