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SPACE BOTANY IN LITHUANIA. II. STUDY ON ROOT GRAVITY SENSING DURING SATELLITE "BION-11" FLIGHT

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Abstract

Švegždienė D., 2016: Space botany in Lithuania. II. Study on root gravity sensing during satellite "Bion-11" flight [Kosminė botanika Lietuvoje. II. Šaknų gravitacijos jutimo tyrimas palydovo „Bion-11" skrydžio metu]. – Bot. Lith., 22(2): 145–152.

This paper addresses the space experiments performed on board of the unmanned satellite "Bion-11" in 1997. To detail root gravity sensing in stimulus-free microgravity environment, researchers from the Institute of Botany developed an automatically operating centrifuge "Neris-8" to grow garden cress seedlings and to chemically fix them at the end of the experiments. There was examined behaviour of gravity sensors – amyloplasts within cap cells of roots responding to stimulation by artificial fractional gravity. The static of amyloplasts was determined in roots after continuous growth for 25 h in microgravity, 0.005, 0.02, 0.1 and 1-*g* environment. The movement kinetics of amyloplasts was studied in roots during the exposition to microgravity after 24-h growth in 1-*g* environment or conversely. Quantitative study on the patterns of positioning and movement of plastids was performed by light microscopy. The results obtained led us to detail a mode of gravity sensing by roots in which the interactions between moving amyloplasts, cytoplasm and cytoskeleton were discussed.

Keywords: amyloplast, garden cress, gravity sensing, microgravity, root, statocyte.

INTRODUCTION

To produce gravitropic response, a plant must first be able to perceive gravity and convert a received physical signal into chemical ones. In roots, gravisensing occurs primarily in the gravity sensing cells – statocytes, which are the columella cells in root caps. The statocytes are characterized by the presence of large, starch-filled and mobile amyloplasts, which fulfil the function of statoliths. These plastids are denser than the surrounding cytoplasm and sediment towards the direction of acting mechanical force of gravity within minutes of gravitropic stimulation (Leitz et al., 2009; Laurinavičius et al., 1998). This movement has been hypothesized to be translated into some type of biochemical signal that elicits the directional growth response of root.

During the last decade, studies combining genetic approach and novel microscopy techniques have been devoted to structural state of cytoskeleton components – actin filaments and motor protein-myosin, their possible contacts with amyloplasts and role in gravisensing (Driss-Ecole et al., 2008; Morita, 2010; Baldwin et al., 2013; Hashiguchi et al., 2013). However, it is still unclear what is the role of these cytoskeleton elements in the positioning and movement of amyloplasts in roots responding to the change in direction and/or magnitude of gravity force.

Because the direction and the magnitude of gravity are almost constant on the Earth, space experiments provide a unique opportunity to study the gravity sensing mechanisms in plants without the complications considering unacceptable Earth gravity effects. The data of our earlier studies during spaceflight of the satellite "Bion-10" (Švegždienė et al., 2013) provided a ground basis for planning of further experi-

ments. Therefore, the goal of the present study was to verify some of the obtained results and examine the behaviour of amyloplasts in statocytes of roots, which respond to the artificial gravity of different magnitude in stimulus-free microgravity environment. We studied: 1) the growth of gravisensing cells in microgravity; 2) location of amyloplasts under continuously acting gravity of different magnitude; 3) motion of amyloplasts in roots transferred from 1-*g* environment to microgravity; 4) sedimentation of amyloplasts in roots transferred from microgravity to 1-*g* environment.

MATERIALS AND METHODS

Garden cress (*Lepidium sativum* L., Crysant, Bonn, Germany) seedlings were used as a test material. The experiments were carried out on the automatically operating space centrifuge "Neris-8" during the flight of Russian unmanned biosatellite "Bion-11" from 24 December 1996 to 7 January 1997. This original device (height – 100 mm, diameter – 140 mm, total weight – 1200 g) was designed and produced by the researchers from the Institute of Botany in cooperation with the engineers from the Experimental Scientific Research Institute of Metal Cutting Machines (Vilnius, Lithuania). The experiments in space were carried out in accordance with the agreement between the Institute of Botany (Lithuania) and the Space Research Institute of the Russian Academy of Sciences. "Neris-8" consisted of two plate rotors for the generation of centrifugal force with the electronic control system, units for the registration of centrifuge rotation rate, temperature and humidity, and an autonomous power supply unit (Fig. 1). The electronic control system accomplished the following operations: switch on/off of the centrifuge according to the programme and timeline of each experiment; activation of the supply of water to dry seeds and a fixative to seedlings; maintenance control of rotor rotation at appropriate rate. Sixteen special cylindrical containers allowed moistening of dry seeds, their germination, the growth and chemical fixation of seedlings during spaceflight (Švegždienė et al., 2013). In dependence on the rotor rotation rate, the gravitational environment of 0.005, 0.02, 0.1 and 1 *g* was produced at the level of growing seedlings. If the centrifuge did not rotate or it was switched off, the seedlings grew in microgravity (MG) or were exposed to these conditions, respectively.

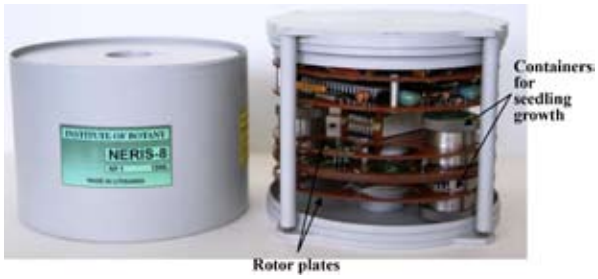

Fig. 1. External and internal view of the space centrifuge "Neris-8"

Before the launch of the satellite, the device "Neris-8" was prepared for planned experiments. For each container, a total of six dry seeds were fastened with 1% agar-agar solution on circle-shaped filter paper covered by cotton material. After drying, they were fastened by lignin with cotton material strips and covered by seed fastening plate. The seeds were placed so that the growing roots could slide freely on the surface of the paper. The fixative reservoir was filled with 4% (v/v) glutaraldehyde in 0.1 M sodium phosphate buffer (pH 7.2), water reservoir – with distil water. After assembling of the component parts, the containers were fixed to device rotor plates. The device was sealed finally and transported to the launch place of the satellite. A set of 16 containers were prepared for the series of experiments in space.

The experiments were started automatically according to the forward programme of experimental procedures for each container by the hydration of seeds, switch on/off the device and supply of fixative. The programme included five experiments for continuous growth in MG (centrifuge did not rotate), 0.005, 0.02, 0.1 and 1-*g* environment, and two experiments – for short stimulation procedures, which were devoted to study the intracellular motion of statoliths in response to alteration of gravity magnitude from 1 *g* to microgravity level (Fig. 2). During the experiments, the temperature inside the space centrifuge remained comparatively stable and equalled approximately to +22°C.

After landing of the satellite, the unopened device was retrieved to the laboratory. The picked off holders with seedlings were washed four times for 15 min each with 0.1 M sodium phosphate buffer (pH 7.2)

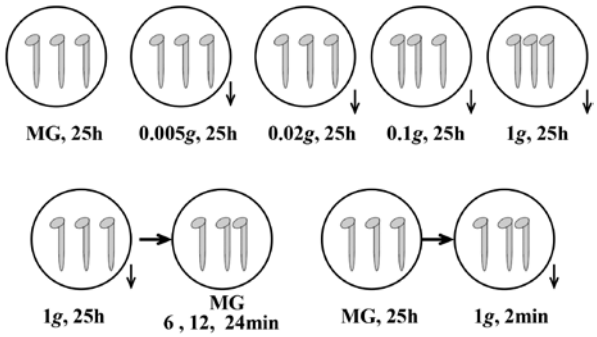

Fig. 2. Scheme of the experiments with garden cress seedlings on the satellite "Bion-11". MG – microgravity environment. Arrows show the direction of artificial gravity

and photographed. Then the seedlings were removed from the holders and post fixed in 1% OsO_4 in the same phosphate buffer for 2 hours at 4°C. Root apices of seedlings were embedded in epoxy resin using routine methods for electron microscopy.

Amyloplast positioning and movement in root statocytes were measured on micrographs of median longitudinal sections of root caps. Semi-thin sections of root apices were prepared using an Ultra microtome III8800LKB (Sweden). The sections were stained with 1% Toluidin-blue in 0.1% $Na_2B_4O_7$ (w/v) or 1% basic fuxin, and photographed using a PENTAX*ist digital camera attached to an SMP 03 light microscope (Opton, Germany). The micrographs were analyzed using the Sigma ScanPro 5 (Jandel Scientific Software). As a rule, 2–3 median sections were analyzed of 3–6 root caps for each test variant. Statistical evaluation of the data was accomplished by MS EXCEL 7.

RESULTS

Growth of gravisensing cells in microgravity. In order to verify the results of our earlier space experiment, the linear growth and orientation of roots, and formation of root gravity sensing tissue under extremely different gravitational loads, usual 1-*g* gravity and microgravity, were compared. It was found that the roots were of comparable length after 25 h of growth under both gravitational loads (Table 1). The roots displayed minor deviation from straight-line growth direction under the action of 1 *g* and showed statistically insignificant bilateral curving in microgravity.

Table 1. Root growth and orientation in space centrifuge "Neris-8" on board of the satellite "Bion-11"

Test variant	Root length (mm)	Absolute curvature of roots (degrees)
1-*g* space	5.4 ± 0.2	0.8 ± 1.5
Microgravity	4.9 ± 0.1	4.6 ± 4.3

The quantitative evaluation of gravity effects on the growth of root columella cells and location of amyloplasts is summarized in Table 2. Comparison of the lengths of statocytes from the 1st to 6th columella layer revealed no significant difference between the linear cell growth in microgravity and artificial 1-*g* gravity environment. Despite the normal statocyte formation, the intracellular location of statoliths has changed considerably in microgravity. At 1 *g*, the amyloplasts sedimented towards the gravity force and their distance from the distal cell wall depended on its length or columella layer, i.e. on the phase of statocyte differentiation (Table 2). This fact is important from methodical point of view because of the restriction to combine and compare the data from the statocytes of different layers.

Table 2. Impact of gravity loads on the length of statocytes and intracellular location of amyloplasts

Columella cell row	Statocyte length (μm)	Amyloplast distance from the distal statocyte wall (μm)	Relative distance of amyloplasts from the distal statocyte wall (in % from cell length)
1-*g* space			
1	15.4 ± 0.8	3.1 ± 0.2	19.9 ± 1.1
2	22.7 ± 0.5	4.5 ± 0.2	21.0 ± 0.7
3	26.3 ± 0.7	5.4 ± 0.2	20.9 ± 0.6
4	33.2 ± 0.8	6.6 ± 0.2	19.9 ± 0.6
5	40.2 ± 1.4	8.4 ± 0.3	20.8 ± 0.7
6	48.2 ± 0.9	17.7 ± 1.0	51.9 ± 2.3
Microgravity			
1	16.8 ± 0.6	8.4 ± 0.3	50.2 ± 1.8
2	20.3 ± 0.4	10.4 ± 0.3	50.0 ± 1.4
3	24.5 ± 0.6	11.7 ± 0.3	46.4 ± 1.2
4	32.2 ± 0.5	14.9 ± 0.4	47.4 ± 1.3
5	38.4 ± 0.8	18.3 ± 0.6	48.7 ± 1.5
6	51.9 ± 1.2	22.7 ± 0.8	60.8 ± 1.4

To solve this problem, the real distance of each amyloplast from the distal cell wall was recalculated and expressed in % from the length of test cell. As a

result, the values of relative distance varied in very narrow intervals for the statocytes of the 1st to 5th columella storeys of both test variant roots (Table 2). In microgravity, the relative distance of these plastids reached approximately the half of statocyte length (about 50%). At 1 *g*, it amounted to about 20% of cell length in the 1st to 5th columella storey. Despite distinct gravitational loads, the amyloplasts showed a substantial change in location in the cells of the 6th storey as compared to that in the youngest cells. The cells of the first columella storey were considerably smaller than those of the other storeys, because they were elongating and undergoing the differentiation. Therefore, later on, the patterns of statics and kinetics of amyloplasts were analysed in the fully differentiated statocytes of the 2nd to 5th columella row.

Thus, the data obtained from two independent experiments on the satellites "Bion-10" and "Bion-11" confirmed the fact of similarity between the growth and orientation of garden cress roots in microgravity and under artificial gravity of 1 *g*.

Amyloplast location under fractional gravity. To characterize the relationship between the magnitude of gravity and intracellular positioning of amyloplasts, the seedlings were grown continuously under microgravity and artificial gravity of 0.005, 0.02, 0.1 or 1 *g*. Despite the decrease of gravity to 0.005 *g* and microgravity level, only a few roots showed visible curvature from the straight growth direction (Fig. 3). Most roots grew straight-line towards the direction of the gravity of 0.1 and 0.02 *g*.

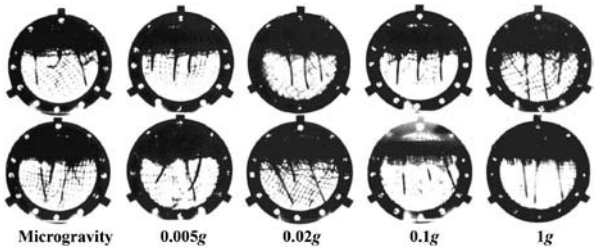

Fig. 3. Overall view of roots of garden cress seedlings on seed fastening plates after growth under fractional gravity on board of the satellite "Bion-11"

Morphological analysis of the statocytes in the 2nd to 5th columella layers revealed the polynomial relationship between the magnitude of applied gravity force and the positioning of statoliths (Fig. 4). Under permanent action of the 1-*g* force, the amyloplast sediment nears the distal cell wall. According to diminishing of the force magnitude, a gradual displacement of these plastids towards the centre of cells was determined. This lift up was essential in the statocytes of roots grown under the action of tenfold weaker gravity. The diminishing of gravity to 0.02-*g* level provoked a significant lift up of amyloplasts from the location which was obtained at 0.1 *g*. If the roots grew under 0.005 *g* and in microgravity, the distance of amyloplasts from the distal cell wall did not differ statistically and varied slightly from the 48% of total cell length. Thus, the effect of continuous action of 0.005-*g* gravity force and microgravity on the positioning of statoliths in root statocytes was similar.

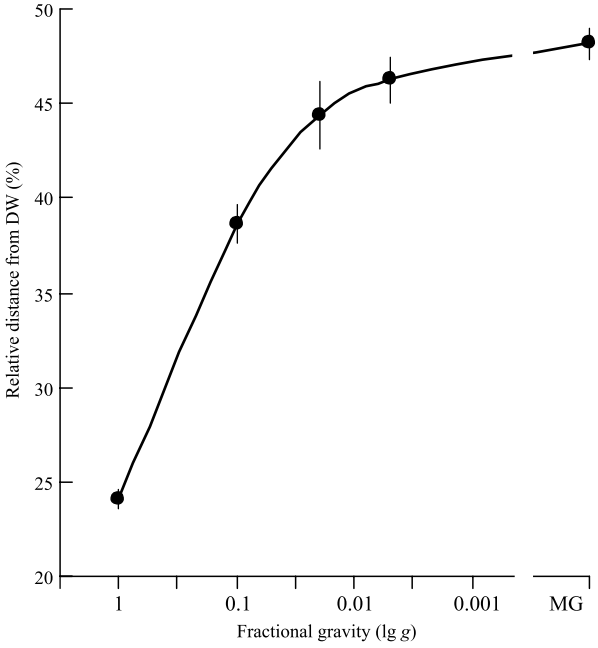

Fig. 4. The distance of amyloplasts from the distal cell wall (DW) in root statocytes after continuous growth under fractional gravity of different magnitude. MG – microgravity

Movement of amyloplasts in roots transferred from 1-g environment to microgravity. The behaviour of statoliths in response to the change of 1-*g* environment to microgravity ones was studied in roots grown for 25 h on space centrifuge at 1 *g* and then exposed to microgravity for 6, 12 and 24 min (Fig. 2). As seen from Fig. 5, the plastids lifted up immediately towards the centre of statocytes, i.e. in an opposite direction than previously applied the 1-*g* gravity force.

A statistically confirmed displacement of amyloplasts in the cells of all tested columella storeys was determined after the first 6 min after switching off the centrifuge (Figs 5B, 6A). It must be noticed that the measured and exact value of this displacement must be considered with some reserve. Really, the zero time in microgravity was defined at the stop of centrifuge rotation, but not at switching off the centrifuge itself. Therefore, the motion of amyloplasts may begin during the rotation braking period, which equalled to about 200 s. In the subsequent 6-min period, the statoliths continued to displace away from the distal cell wall and after 24 min their relative distance reached 38.4% of cell length (Fig. 6A). It must be noticed that the location of plastids after 24- min period of 1-*g* roots exposition to microgravity remained statistically smaller than that of 48% in the statocytes of roots grown continuously in microgravity (Fig. 4). On the base of polynomial equation approximating satisfactorily the obtained data (R^2 = 0.99), the amyloplasts will reach the distance characteristic of that in microgravity after 55 min.

To characterize the course of proximal movement of amyloplasts, the velocity values of statolith displacement in average statocyte of the 2nd to 5th columella storeys within 0–6, 6–12 and 12–24 min of MG-exposure were calculated (Fig. 6B). Thus, within the first 6 min of MG-exposure, the velocity was 0.31 μm/min and within the subsequent intervals – 0.19 and 0.12 μm/min, respectively. Extrapolation of the logarithmic curve approximating the obtained data to the time of about 60 min gives a very low (0.009 μm/min) velocity. This fact indicates that the amyloplasts are reaching the stable location near the cell centre.

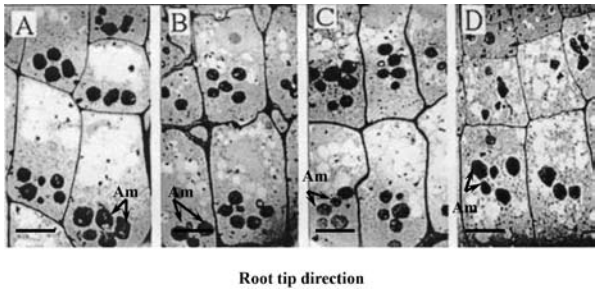

Fig. 5. Micrographs of statocytes in roots after growth at 1 *g* (A) and then exposed to microgravity for 6 min (B) and 24 min (C), and after continuous growth in microgravity (D). Am – amyloplasts

Movement of amyloplasts in roots transferred from microgravity to 1-*g* environment. To follow the patterns of statoliths movement from the central part of statocytes, the roots were stimulated by the 1-*g* gravity in root tip or root base direction after growth in microgravity (Fig. 2). As shown earlier, morphometric analysis of statocytes of microgravity grown roots showed that most amyloplasts concentrated around the cell centre (Table 2, Fig. 4). Fig-

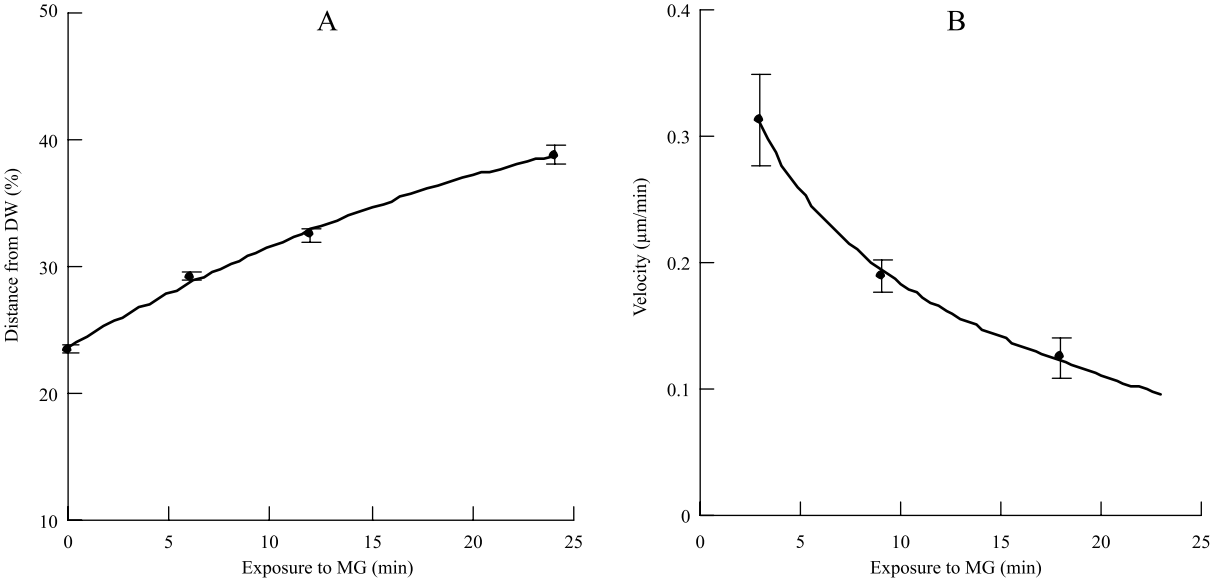

Fig. 6. Relative distance (A) and velocity (B) of amyloplast movement from the distal statocyte wall (DW) in roots grown at 1 *g* and then exposed to microgravity

ure 7 represents the obtained data on statoliths displacement in real units after the 1-*g* stimulation for 2 min in separate columella cell rows of such roots. As seen, an essential displacement of amyloplasts from the initial location towards the stimuli direction was obtained in the functional statocytes of the 2nd to 5th columella rows. Interestingly, the greatest and comparable change of plastid location (about 3μm) in both directions was determined in the statocytes of the 2nd columella row. In the cells of another rows, the statoliths displacement proceeded by approximately similar but lower extent.

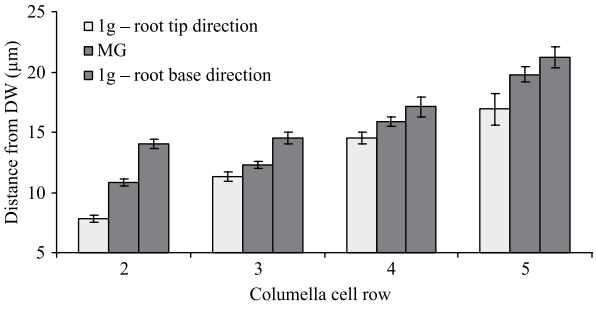

Fig. 7. Amyloplast location in statocytes of roots grown in microgravity (MG) and then exposed to artificial gravity of 1 *g* in root tip or root base direction for 2 min. DW – distal cell wall

To characterize the course of movement of amyloplasts from the location at the cell centre, the velocity values of their displacement were calculated for average statocyte of the 2nd to 5th columella rows. It equalled approximately to 1.0 μm/min regardless of the opposite direction of acting the 1-*g* gravity. In summary, this finding shows that the amyloplasts could easily sediment towards either pole of the cell during the 2-min period of stimulation.

DISCUSSION

To obtain additional information about the mechanism of plant root gravisensing, the experiments were performed on board of the satellite "Bion-11" using the in-flight centrifuge "Neris-8". The development of this hardware allowed firstly studying the behaviour of amyloplasts in response to the continuous and short-term application or the removal of artificial gravity of different magnitude. Thus, in comparison with our earlier experiment on board of the satellite "Bion-10" (Švegždienė et al., 2013), the possibility to study the interaction of amyloplasts with the gravity during gravity sensing was considerably extended by means of changing its magnitude.

The data obtained from two independent experiments on unmanned satellites "Bion-10" and "Bion- 11" confirmed the fact of similarity between the growth and orientation of garden cress roots under the gravity of usual 1-*g* magnitude and in microgravity despite an essential change of amyloplast location in statocytes (Table 1). The displacement of plastids from their usual position at the distal pole of the statocyte did not disturb noticeably the morphogenesis of root cap, because the length of columella cells remained at the same level under both gravitational conditions (Table 2). Thus, both our tests revealed no reliable effects of microgravity on the formation of root statocytes, but showed a slight negative impact on root columella cell growth.

Under the action of 1-*g* gravity in root tip direction, the amyloplasts in root statocytes were grouped close to the distal cell wall. Therefore, the longitudinal polarization of cell structure is obvious. Thus, the location of amyloplasts is largely impacted by the 1-*g* gravity force, which balance the intracellular forces (buoyant, drag, the elastic forces generated by cytoskeleton elements, etc.) as a whole (Yoder et al., 2001). In microgravity, amyloplasts were grouped in the central part of statocytes and their distance from the morphological cell bottom in relative units was about 48% of cell length (Table 2). Thus, it can be assumed that when cress seedlings grow without gravity, amyloplast location, although different, depends upon the activity of the above-mentioned intracellular forces. When the ratio of these forces changes due to reducing the magnitude of the artificial gravity on a spaceflight centrifuge (Fig. 4) or transferring the roots from the 1-*g* environment to microgravity (Laurinavičius et al., 1997; Driss-Ecole et al., 2000), the statoliths move away from the distal cell wall possibly under the action of elastic forces generated by cytoskeleton. Thus, there may be the interplay between the magnitude of gravity acting in the longitudinal direction, the elastic forces generated by the cytoskeleton, and statolith location.

The study on the relationship between intracellular distribution of statoliths upon the artificial gravity of 0.005, 0.02, 0.1 and 1 *g* continuously acting the seedlings in the root tip direction, revealed that

this dependence is satisfactorily described by the logarithmic function (Fig. 5). As mentioned above, 1-*g* gravity keeps the statoliths at the distal statocyte wall. What magnitude of the gravity will be insufficient for compensation of the opposite-directional intracellular forces? According to our data, statistically significant lift up of plastids in root statocytes proceeded under the action of tenfold lower than 1-*g* force (Fig. 5). This fact suggests that in root statocytes the statoliths will be shifted up by the force, the magnitude of which is reduced from 1 *g* to 0.1 *g*. It must be noticed that the gravity of 0.02 *g* essentially affecting the location of amyloplasts is approximately tenfold higher than the *g*-threshold for lateral gravitropic stimulation of garden cress roots (Laurinavičius et al., 2001).

When the action of 1-*g* artificial gravity was eliminated by switching off the centrifuge, the statoliths moved away from the distal cell region within the first 6 min in microgravity (Figs 5A, 6A) at an average velocity of 0.31 μm/min (Fig. 6B). This displacement might be driven by elastic forces involving the cytoskeleton, which actively transport the statoliths from its distal position. When the statoliths were approaching the central cell region, the proximal displacement of them slowed gradually due to the impact of the same elastic forces. Thus, over the 24-min period in microgravity, the relative distance of statoliths changed from 24.0% to 38.4% in respect to the distal cell wall and the motion velocity slowed down to 0.12 μm/min (Fig. 6). It is worth noting that the position of the statoliths after 24 min in microgravity remained smaller than in the statocytes of roots grown continuously in MG (48.1 ± 0.8%). This fact indicates that a stable position has not been reached yet.

Our data on statolith movement velocity in microgravity were appended by the data from the later space experiment with lentil roots, which were grown at 1 *g* and then exposed to MG. It was determined that within the 29-min MG-exposure, the statoliths moved in the proximal direction of the statocytes at the velocity of 0.154 μm/min, which decreased during the following 93 min (Driss-Ecole et al., 2000). Interestingly, the 122-min period in microgravity was insufficient to reach the statolith location close to the stable state characteristic of roots grown continuously in microgravity.

To compare the properties of statolith movement from the central region of the statocyte, the roots grown in microgravity environment were stimulated by the 1-*g* gravity in root-tip and root-base directions for 2 min. It was determined that within 2 min of both treatments the statoliths were moving from the initial position towards the gravity by a similar extent (Fig. 7) and at a similar velocity of 1.0 μm/ min. Thus, they can easily move towards either pole of the cell under the impact of gravity and possibly of cytoskeleton components. This finding shows the cytoplasm of the central region of the statocytes to be almost homogeneous.

In summary, our data demonstrated, although indirectly, the effect of cytoskeleton network on the longitudinal distribution and movement of amyloplasts in plant root statocytes. Based on the experimental strategy of space experiments on the satellites "Bion-10" and "Bion-11", a further research on plant gravity sensing was successfully extended at the Institute of Botany by using original hardware – a centrifuge-clinostat for the simulation of fractional gravity.

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KOSMINĖ BOTANIKA LIETUVOJE. II. ŠAKNŲ GRAVITACIJOS JUTIMO TYRIMAS PALYDOVO „BION-11" SKRYDŽIO METU

Danguolė Švegždienė

Santrauka

Straipsnis skirtas kosminiams eksperimentams, atliktiems 1997 metais nepilotuojamame palydove „Bion-11". Šaknų gravitacijos jutimo tyrimui nesvarumo (mikrogravitacijos) sąlygomis Botanikos instituto mokslininkai sukūrė ir panaudojo autonominę centrifugą „Neris-8" sėjamosios pipirnės sėklų sudrėkinimui, daigų auginimui ir cheminei fiksacijai skrydžio metu. Atlikta kiekybinė gravitacijos jutiklių – amiloplastų elgsenos analizė šaknų, reaguojančių į dirginimą skirtingo dydžio imituota gravitacija, kolumelės ląstelėse (statocituose) šviesinės mikroskopijos metodu. Amiloplastų statika vertinta 25 val. mikrogravitacijos ir 0,005 *g*, 0,02 *g*, 0,01 *g* ir 1 *g* sąlygomis augusių šaknų statocituose. Amiloplastų judėjimo kinetika analizuota šaknyse, kurios 24 val. augo 1 *g* aplinkoje ir buvo perkeltos į mikrogravitacijos sąlygas arba priešingai. Gauti duomenys apie amiloplastų statiką ir kinetiką sėjamosios pipirnės šaknų statocituose, veikiant skirtingo dydžio dirbtinei gravitacijai kosminio skrydžio sąlygomis, suteikė pagrindą šaknų gravitacijos jutimo hipotezės detalizavimui.