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SPACE BOTANY IN LITHUANIA. I. ROOT GRAVISENSING SYSTEM FORMATION DURING SATELLITE "BION-10" FLIGHT

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Abstract

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The paper deals with the results of space experiment, which was carried out on an original automatically operating centrifuge „Neris-5" on board of the satellite „Bion-10" in 1993. The peculiarities of gravisensing system formation in roots of garden cress (*Lepidium sativum* L.) seedlings grown in microgravity under simulated and natural gravity of 1*g* in space and on the ground, respectively, are presented. Quantitative study on the growth of root columella cells (statocytes), the state of their intracellular components, and the location of amyloplasts was performed by light and electron microscopy.
The growth of statocytes in microgravity and under 1*g* in space did not differ significantly though the location of amyloplasts experienced significant changes: it depended on the gravity and cell position in columella. Instead of the concentration of amyloplasts at the distal cell region of roots grown under 1*g*, most plastids in microgravity-grown roots were accumulated at the centre of statocytes. The obtained data on the formation and state of intercellular plastids confirm the supposition that the environment of microgravity alters the metabolism of plant cells; however, its alterations are not fateful for the formation of gravisensing cells and for the growth of the whole root.

Keywords: garden cress, root, statocyte, amyloplast, microgravity, morphogenesis.

INTRODUCTION

Plant growth patterns are affected by a variety of stimuli. The responses to stimuli such as gravity have been explored and documented for over a century. The starch-statolith hypothesis explaining how plants sense the gravity has remained virtually unchanged and continued to gain support from a number of molecular and cell biological studies (Baldwin et al., 2013; Hashiguchi et al., 2013). However, until today the role of gravity in the formation and morphogenesis of cells in gravity sensing systems remains only partly understood. Experiments carried out in space and on Earth revealed that the gravity may be considered as only one of the many components that actively participate in the formation and differentiation of root cap columella cells (Driss-Ecole et al., 2008; Laurinavičius et al., 2001; Yoder et al., 2001).

Amyloplasts need to be movable in the cytoplasm in order to convert the gravitational potential energy into sensor-activating kinetic energy and trigger subsequent intracellular signalling processes. It is suggested that gravitropic response correlates with the development of the columella cells and the amyloplasts or both (Fitzelle & Kiss, 2001; Kordyum & Guikema, 2001; Saiki & Sato, 2004). Starch grains increase the weight of amyloplasts what is important for fulfilling of their function as gravisensors. On the other hand, the amyloplasts with too much

starch weakens rather than promotes the response to gravity alterations (Vitha et al., 2007). As reported, spaceflight plants exhibited progressive vacuolization in the columella cells of roots (Kordyum, 1997; Klymchuk et al., 2003).

To evaluate the impact of microgravity alone, the effect of other spaceflight factors must be elaborated, which include the uplift and launch accelerations, vibration, space radiation, spacecraft inner environment and landing conditions (Porterfield, 2002). Comparison of morphological and structural features of cells formed in real microgravity and under the action of 1*g* centrifugal force during spaceflight, including ground control, may contribute to solve the above mentioned problem. Our experience for the detection of spaceflight effects caused by factors other than the lack of gravity action was obtained already in 1978–1982 by using originally developed in-flight centrifuges „Biogravistat-1, -1M“ on Russian orbital station „Salyut-7“ (Merkys et al., 1981, 1983, 1985). In order to detail the effects of microgravity environment on the state of plant gravisensing systems, the experiment with garden cress seedlings was performed during the Bion-10 satellite flight on an original automatically operating centrifuge. The objective of the present study was to study and compare the formation and structural patterns of gravity sensing cells in roots grown in microgravity, under 1*g* in space and on the ground.

MATERIALS AND METHODS

Garden cress (*Lepidium sativum* L., Crysant, Bonn, Germany) seedlings were used as test material. The experiment was carried out during the Russian unmanned biosatellite „Bion-10“ flight in December 1993 on the automatically operating space centrifuge „Neris-5“. This original device (height – 100 mm, diameter – 140 mm, total weight – 1200 g) was designed and produced by researchers from the Institute of Botany in cooperation with the engineers from the Experimental Scientific Research Institute of Machine Construction. The experiment in space was carried out in accordance with the agreement between the Institute of Botany (Lithuania) and the Space Research Institute of Russian Academy of Sciences. „Neris-5“ consisted of a stationary unit for the growth under microgravity conditions, a centrifuge for the generation of 1*g* centrifugal force at the seed level, an electronic control system 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 timeline of experiment; activation supply of water to dry seeds and a fixative to seedlings; control and registration of centrifuge rotor dynamic parameters; registration of temperature.

Fig. 1. View of „Neris-5“ device. A – external view, B – internal view

Sixteen special bio-containers (height – 25 mm, diameter – 23 mm) allowed moistening of dry seeds and their germination, the growth and chemical fixation of seedlings during spaceflight. Containers of cylindrical shape were made from titanium and consisted of three hermetic sections: a water reservoir of 0.3 ml, a fixative reservoir of 2.2 ml and a growth chamber of 4.5 ml. It contained a seed holder and separate systems for automatic water as well as a fixative feed (Fig. 2).

Before the launch of satellite, the device „Neris-5“ was constructed at the Sector of Gravitational Physiology (Laboratory of Plant Physiology, Institute of Botany). For each bio-container, a total of four 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 roots could grow and orient freely on the plane of humid filter paper surface. The fixative reservoir was filled with 4%

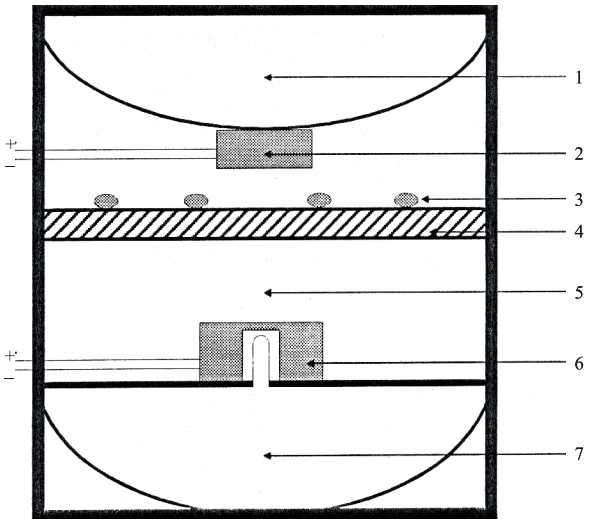

Fig. 2. Sketch of bio-container for seedling growth. 1 – water reservoir, 2 – mechanism for water reservoir opening, 3 – dry seeds, 4 – plate for seed fastening, 5 – seedling growth chamber, 6 – system for fixative reservoir opening, 7 – fixative reservoir

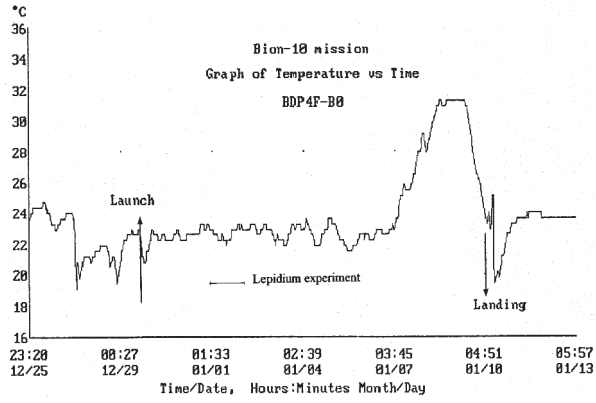

Fig. 3. Time-course of temperature during the mission of satellite „Bion-10"

(v/v) glutaraldehyde in 0.1M sodium phosphate buffer (pH 7.2), water reservoir – with distil water. After assembling of component parts, the bio-containers were closed hermetically and fixed to the device, which was sealed finally and transported to the launch place of the satellite. The experiment was carried out in accordance with the agreement between the Institute of Botany (Lithuania) and the Space Research Institute of the Russian Academy of Sciences. The automated experiment was started according to the forward timeline by the hydration of seeds and switch on the rotation of centrifuge (Fig. 3). The seedlings germinated and grew for 27 h and then were fixed without spinning off the centrifuge. Ground control seedlings were grown and fixed on the ground under the same cultivation conditions. During the experiment, the average temperature on the board of satellite was about 22°C, but after the fixation of the material it rose up to 31°C for a short time (Fig. 3).

After the satellite landing, the unopened device was retrieved to the laboratory. There the picked off holders with seedlings were washed 4 times for 15 min each with 0.1M sodium phosphate buffer (pH 7.2) 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 embedded in epoxy resin using routine methods for electron microscopy. Semi-thin and ultra-thin median longitudinal sections of root apices were prepared using an Ultramicrotome III8800LKB. Ultra-thin sections stained with uranyl acetate and lead citrate. Micrographs of these sections were taken for 8–9 roots of each test variant using an electron microscope (EM) JEM – 100S (JEOL, Japan) under magnification of ×5600 for measurement of cells and location of amyloplasts, and ×13500 – for the analysis of cell organelles. Cytomorphological analysis of root columella was performed on semi-thin median sections using a light microscope (SMP 03, Zeiss) under total magnification of ×875 after staining with 1% Toluidin-blue in 0.1% $Na_2B_4O_7$ (w/v). The enlarged drawings from EM negatives were analysed with a digitizer of IBAS 1 system (Kontron) under total magnification of ×7000. As a rule, 2–3 median sections were analysed of 4–6 root caps for each test variant. Statistical evaluation of the data was accomplished by MS EXCEL 7.

RESULTS

Growth and orientation of roots

After 27 h of growth, the roots of the ground and space control and microgravity grown seedlings were of comparable length (Table 1). In space, microgravity environment and the direction of centrifugal force acting as a reference signal for the root gravity sensing system remained unchanged. All seeds were planted so that the roots of developing seedlings could grow on the plane of humid paper surface in any direction. Two different modes of root growth direction were observed under all test conditions. As seen from Fig. 4, most roots grew straight, while the

others curved their apices slightly. To measure the absolute curvature of roots, the longitudinal axis of embryonic root was used as a reference line. A comparably small curvature of roots was determined under 1*g* on the ground and space centrifuge (Table 1). In microgravity environment, the roots showed statistically significant larger deviation from the reference line due to a primary divergence during protruding.

Table 1. Root growth and orientation

Test variant	Root length (mm)	Absolute curvature of roots (degrees)
1*g*-ground	11.6 ± 0.3	6.0 ± 1.2
1*g*-space	11.8 ±0.6	8.8 ± 2.3
Microgravity	11.3 ± 0.2	23.4 ± 6.1

In summary, these results suggest that linear growth of seedling roots proceeds almost equally as under the action of Earth gravity or equivalent centrifugal force as well as in the absence of the gravity, too. However, the orientation of growing roots in microgravity differed significantly from that under both ground and space control conditions.

Growth of root columella cells

Essential changes in anatomical structure of most root caps under all tested gravitational conditions were not observed. Six regular storeys of columella cells at various differentiation stages were obtained in median longitudinal sections of root caps (Fig. 5). Despite this, the roots of both space variants showed

Fig. 4. View of seedlings on bio-container holders after growth under 1*g* on the ground (CIGG) and space centrifuge (CIGS), and in microgravity (CMG)

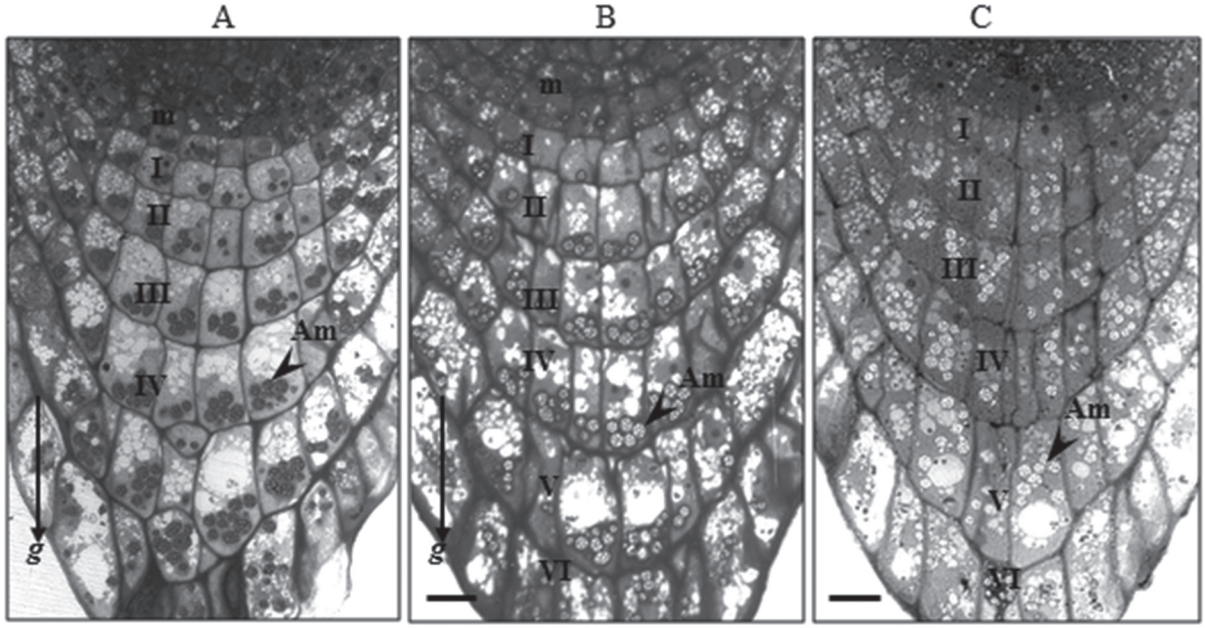

Fig. 5. Morphology of root caps formed under 1*g* on the ground (A) and on space centrifuge (B), and in microgravity (C). I–VI – gravity sensing cell rows, Am –amyloplasts. Bar – 15 μm

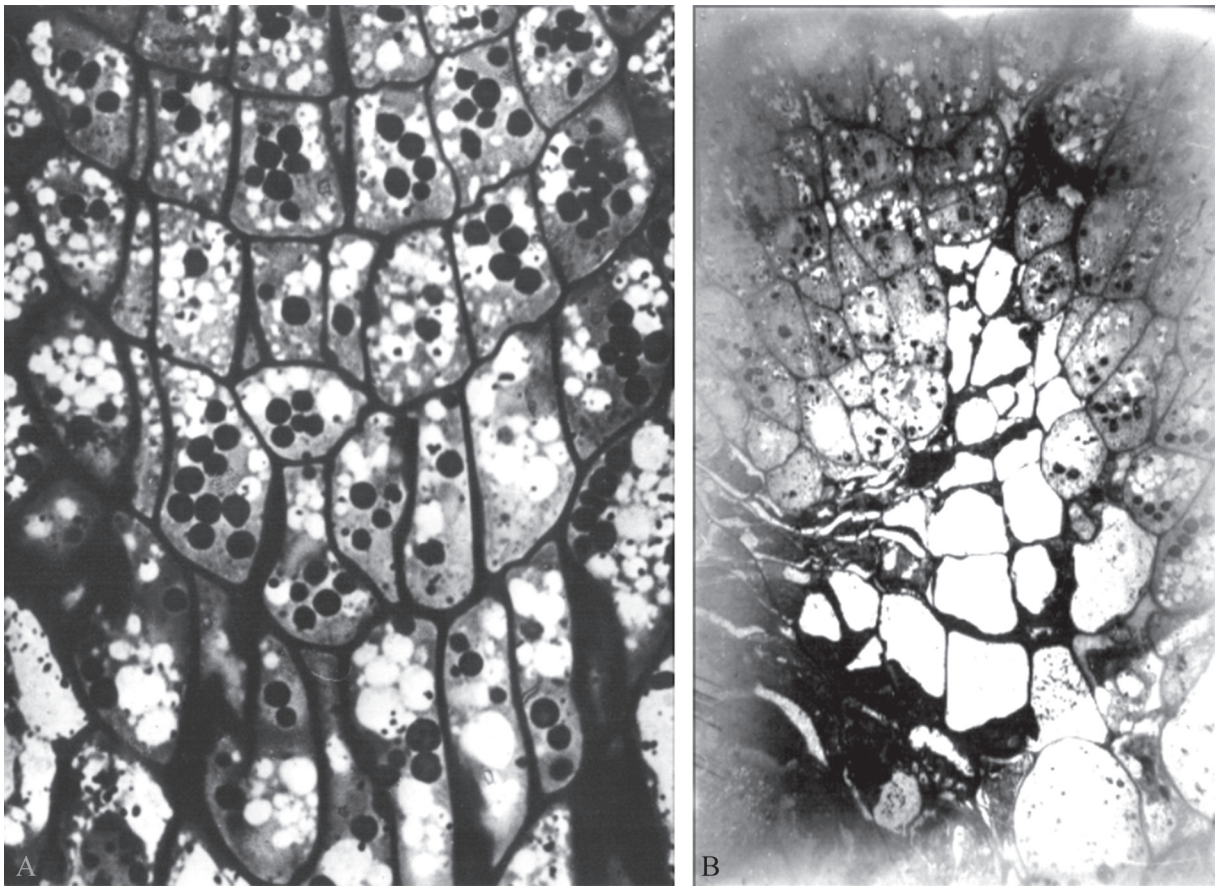

Fig. 6. Morphological disorders of root caps formed in microgravity environment

evident discrepancy in quality of embedding and staining of root tissues as well as in feature of the key gravisensing cell components – amyloplasts, displaying a distinct filling by starch grains. Morphologically disordered root caps were obtained in few microgravity grown roots (Fig. 6).

Analysis of root cap morphometrical parameters revealed the tendency of shorter and wider cap formation in microgravity than under the action of 1*g* on space centrifuge or on the ground (Table 2). Comparative analysis of columella cell dimensions, which developed in different gravitational environment, revealed the linear dependence of their length on the position in the columella. Fig. 7 shows the mean length of cells plotted against their location. One can see that the values are fitted correctly to the linear model (R-squared values from 0.93 to 0.98 for all variants). Coefficients *a* and *b* of regression lines ($y = a + bx$, where y – cell length, x – columella row): 7.67 ± 0.86 and 7.41 ± 0.98 for 1*g*-ground variant; 7.69 ± 0.86 and 6.60 ± 0.21 for 1*g*-space variant; 8.81 ± 0.98 and 6.07 ± 0.23 for microgravity grown roots, respectively. The presence of linear dependence between the position and the length of columella cells indicates a normal cell growth process, which goes on independently on the gravity presence. On the other hand, the cells of the 4–6 columella rows were significantly shorter ($p \leq 0.05$) in both space variant roots than in the ground variant ones (Fig. 7). Besides, the width of cells was slightly, but significantly increased in space (16.1 ± 0.2 μm under 1*g* and 15.2 ± 0.3 μm in microgravity) compared to that on the ground (14.8 ± 0.2 μm).

Table 2. Linear parameters of root caps formed under different gravitational conditions

Test variant	Length (μm)	Width (μm)
1*g*-ground	212.3 ± 3.3	221.3 ± 3.3
1*g*-space	199.2 ± 6.3	226.0 ±1.8
Microgravity	188.3 ± 3.5	230.3 ± 1.8

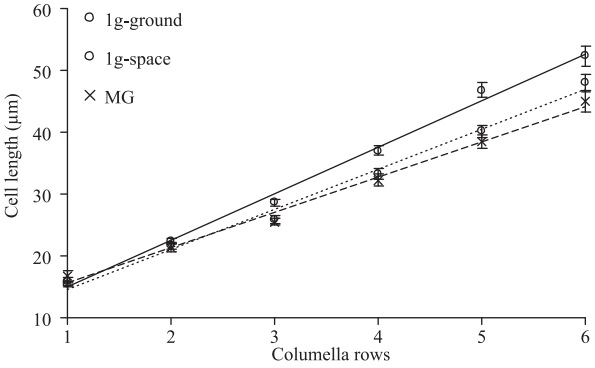

Fig. 7. Cell length in root columella rows under 1*g* on the ground (1*g*-ground)) and on space centrifuge (1*g*-space), and in microgravity (MG)

Thus, the effect of microgravity on the linear and radial growth of columella cells was negligible as compared to that of simulated gravity. In the Earth gravity environment, the linear growth of cells proceeded more intensively, but their radial growth was slower. Taken as a whole, the obtained data suggest that the growth of tested cells was affected by other spaceflight factors in addition to microgravity.

Structure properties of gravity sensing cells

The key components of columella cells are amyloplasts responding to alteration of the gravity force. For fulfilling that function, at least moderate levels of starch must be accumulated. How the decrease of gravity to microgravity level affects the formation of amyloplasts and the state of other intracellular components?

Table 3 shows summarized data, which characterize the properties of intracellular organelles in functioning statocytes formed in spaceflight and ground environment. As seen, the force of 1*g* had no significant effect on the number of amyloplasts per cell as in space as well as on the ground, either. While comparing the morphometric parameters of measured organelles, significant differences between the ground and both space variants are evident. The amyloplasts and starch grains inside them, nucleuses and mitochondria were larger under 1*g* on the ground than under 1*g* in space by 16%, 30%, 30% and 13%, respectively. Contrary, the number of starch grains in amyloplasts and lipid droplets per cell was smaller on the ground compared to analogous organelles parameters in space by 15% and 62%, respectively. Summarizing the obtained differences, it can be supposed that the other factors of spaceflight apart the absence of the gravity force could affect the number and state of amyloplasts in root gravisensing cells.

Comparison of the data on the organelles in the cells of both space variants revealed no significant difference in the number and average size of amyloplasts, and in that of lipid droplets per cell. However, in microgravity, starch grains and nuclei, and mitochondria were larger by 7%, 18% and 10% compared to those in 1*g* on the space centrifuge. The effect of microgravity on the formation of vacuoles was opposite. The vacuoles were smaller by 30% in microgravity grown root cells than in cells of roots grown on the centrifuge. In summary, the microgravity environment affected significantly the state of nucleus, vacuoles and mitochondria, and altered the content of starch in amyloplasts.

Root columella cells are the only cells in roots, which assume a structural polarity during differentiation to functioning statocytes. The position of amyloplasts in root columella cells is defined by the morphology of the statocyte and the row in which a separate amyloplast occurs (Fig. 5). Under 1*g* on the ground or space centrifuge, the amyloplasts were

Table 3. Effects of gravity alterations on the parameters of intracellular components of *Lepidium* root columella cells

Morphometric parameter	1*g*-ground	1*g*-space	Microgravity (MG)
Amyloplast number per cell	4.4 ± 0.1	4.6 ± 0.1	4.7 ± 0.1
Amyloplast area in relative sq. units	4.17 ± 0.09	3.47 ± 0.06*	3.46 ± 0.08*
Starch grain number per amyloplast	8.6 ± 0.2	9.9 ± 0.2*	9.3 ±0.1*^
Starch grain area, relative sq. units	0.349 ± 0.005	0.246 ± 0.003*	0.263 ± 0.004*^
Nucleus area, relative sq. units	18.0 ± 0.9	12.5 ± 0.6*	14.8 ± 0.6*
Mitochondria number per cell	69.7 ± 3.0	77.8 ± 6.3	70.0 ± 4.2
Mitochondria area, relative sq. units	0.132 ± 0.002	0.155 ± 0.001*	0.127 ± 0.001*
Vacuole area, relative sq. units	55.5 ± 2.1	54.1 ± 1.6	38.0 ± 1.2*^
Lipid droplet number per cell sq. unit	12.5 ± 2.1	33.4 ± 2.7*	34.3 ± 3.3*

* – differences from 1*g*-ground variant and ^ – from 1*g*-space variant are significant at $p \leq 0.05$

located mostly near the distal cell wall in the statocytes from the 1st to 6th columella rows in a similar manner. In microgravity, the plastids could be found at the different distance from the distal statocyte wall (Fig. 5C). Morphometric analysis of MG root statocytes showed that most statoliths concentrated around the cell centre and the mean distance from distal wall approached approximately the half length of appropriate statocyte in the each columella row (Figs 7, 8). Thus, the data on the position of amyloplast in the cells of separate columella rows show that it depends on the action direction and magnitude of the acting gravity, too.

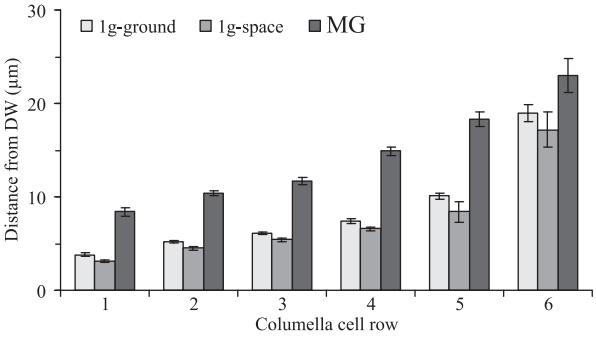

Fig. 8. The distance of amyloplasts from the distal cell wall (DW) in different columella rows under 1*g* on the ground (1g-ground) and in space (1g-space), and in microgravity (MG)

DISCUSSION

The investigation focusing on the morphogenesis of gravisensing cells – statocytes of garden cress primary roots under altered gravity conditions was performed on board the Bion-10 satellite. The experiment was carried out using automatically operating centrifuge, which generated the centrifugal force of 1*g* and in microgravity environment, when the centrifuge did not rotate. The opportunity of carrying out this experimental approach in near weightlessness (microgravity) allowed us to evaluate the morphogenetic and structural responses of root gravity sensing cells to the action and elimination of gravity force under the same cultivation and fixation conditions.

Gravity is the main factor influencing the direction of growth of plant organs on Earth. When the amplitude of simulated gravity (centrifugal force) was reduced from 1*g* to microgravity level during spaceflight, most roots remained straight growth direction, which corresponded to their primary location in embryo or the action direction of the force (Fig. 4). Our results are quite in agreement with the conclusions of our earlier space experiments (Merkys et al., 1981, 1983, 1985). The fact of distinct orientation of some roots in microgravity (Fig. 4, Table 1) may be an evidence of possibility to influence the growth direction by other spaceflight factors of physical nature (mass accelerations generated during manoeuvres of the satellite). So, our data confirm that the direction of protruding root growth is determined by an automorphogenetic mechanism (Merkys & Laurinavičius, 1990) and later on is corrected by the gravitational force.

Growth and development of gravisensing tissues ensure the ability of plants to sense and accept gravitational signals. It was possible to expect some growth reactions of these tissues to alterations of gravitational force from 1*g* to weightlessness. Essential changes in anatomical structure of columella of most tested roots in microgravity as well as under 1*g* on space centrifuge or on Earth were not observed (Fig. 5). Six regular storeys of cells at various differentiation stages were determined in root cap sections. On the other hand, a few roots grown in microgravity had the columella of disordered morphological structure (Fig. 6). A similar phenomenon was registered in garden cress roots grown on horizontal clinostat (Hensel & Sievers, 1980) or wheat roots grown in space (Cowles et al., 1984) and attributed to a consequence of the action of unknown nature spaceflight factors. Morphometrical analysis of caps revealed the tendency of shorter and wider cap formation in microgravity environment than under the action of 1*g* in space or on the ground (Table 2). However, the linear growth of statocytes proceeded almost at similar rate in roots growing in microgravity or under simulated gravity (Fig. 7). Thus, our test as well as other space experiments with different plants (Driss-Ecole et al., 2008; Kiss, 2000; Laurinavičius et al., 2001) revealed no reliable effects of microgravity on morphogenesis of roots statocytes. The absence of gravity exerted the effect on root columella growth rather than on its formation.

It is supposed that the number, size, shape as well as density of amyloplasts determine the functional properties of gravisensing cells. Our data demonstrate that the number of these organelles is geneti-

cally determined, because it remained unchanged under all test gravitational conditions (Table 3). The physical properties of amyloplasts as statoliths and first of all their specific weight or buoyant mass depend on the way how fully and compactly the plastids are filled with starch grains. The amyloplasts were found to be smaller in both space variants; however, they had more starch grains of smaller size (Table 3). Comparing of both space variants revealed statistically confirmed negative impact of microgravity on the number of starch grains per amyloplast though the grains were larger than under the action of simulated 1-*g* gravity. Our results correspond with the data presented by other researchers (Kordyum & Guikema, 2001; Merkys & Laurinavičius, 1990) on reduced starch content in space grown plant roots. This finding could be mentioned as a raising problem not only of the inhibition of its synthesis, but also as an enhancement of carbohydrate utilization during spaceflight, possibly, due to higher respiration rates (Moore et al., 1987; Porterfield, 2002).

The nucleus occupies a significant part of statocyte volume and loses the possibility to proliferate during columella cell differentiation to functioning statocyte. In spaceflight root functioning statocytes, the nuclei were found to be significantly smaller than in ground control ones (Table 3). It may be noticed a positive correlation between the size of statocytes and nuclei: the cells and nuclei of 1-*g* ground variant were larger compared to those of 1-*g* space variant. Our data on the minimal impact of microgravity on nucleus size are consistent with similar conclusions made from the space experiments on maize (Moore et al., 1987) and barley (Laurinavičius & Raklevičienė, 1995).

Mitochondria were measured in the statocytes of 4th columella row. Significant differences in the number of mitochondria per statocyte in roots grown under tested gravitational conditions were not determined (Table 3). On the other hand, the number of significantly larger mitochondria increased slightly in 1-*g* space root cells compared to that in the statocytes of roots grown on the ground or in microgravity.

The process of statocyte vacuolization is important for amyloplast mobility during gravisensing from physical view point. Taking into account the data on the vacuole size (Table 3), it is evident that the formation of vacuoles proceeded slower in microgravity compared to that under 1*g* as in space as well as on ground, too. This fact may be considered as the impact of microgravity on cell metabolism including the formation of tonoplast. The base for such suppositions could be the theoretical consideration of gravity interactions with the biological membranes (Laurinavičius, 1991).

According to our data, spaceflight conditions promoted approximately 2.5-fold higher formation of lipid bodies in root statocytes (Table 3). Moore et al. (1987) found an over 6-fold increase of the number and size of lipid droplets in the statocytes of maize roots grown in microgravity than in those grown on the ground. The reasons of such spaceflight impact have not been explained yet. To our opinion, the one may be the response of plant cells to the stress provoked by the sum of spaceflight factors acting on the board of space vehicle. This would be the case if any significant difference between the formations of lipid droplets in both space variants were obtained. However, comparing the whole populations of lipid droplets by size we found a more numerous number of small droplets in the statocytes of microgravity-grown roots than in that of 1*g* roots grown in space or on ground (data not shown). Thus, the above-discussed data on the organelle morphometry allow the supposition that the environment of microgravity affects the formation and state of tested plastids through the changes in the cell metabolism, which are not fateful for the formation of gravisensing cells or for the growth of the whole roots.

The key susceptors of gravity action in gravisensing cells are amyloplasts. When cress roots grew under 1-*g* gravitational force acting in root-tip direction on space centrifuge or on ground, the statoliths were concentrated near the distal cell wall in the statocytes of all columella rows (Figs 5, 8). In microgravity grown roots, the amyloplasts accumulated at the centre of statocytes. This fact is important for the understanding of the function of statocyte as a gravisensor, because a supposition exists about earlier and stronger gravitropic response of roots with centrally-located statoliths compared to distally-located ones (Laurinavičius et al., 2001; Driss-Ecole et al., 2008). As seen in Fig. 8, the location of amyloplasts also depends on the phase of statocyte differentiation, i.e. on its length or the columella row. This is important from the methodical point of view because of the re-

striction to combine and compare the data from different statocyte storeys. The problem can be solved by means of calculation of the amyloplast position as the distance from distal cell wall expressed in % from the total statocyte length. That parameter is almost independent on the cell row, therefore, it can be considered as a mean for the whole population of the functional statocytes of a definite variant.

The data of the present research provided a ground basis for further experiments and investigations on gravisensing process in garden cress roots during spaceflight of the satellite „Bion-11".

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KOSMINĖ BOTANIKA LIETUVOJE. I. GRAVITACIJĄ JUNTANČIŲ ŠAKNŲ LĄSTELIŲ FORMAVIMASIS PALYDOVO „BION-10“ SKRYDŽIO METU

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Santrauka

Straipsnyje pateikiami kosminiame „Bion-10“ palydove 1993 metais vykdyto eksperimento, panaudojus originalią, autonominę centrifugą „Neris-5“, rezultatai. Gravitaciją juntančių šaknų ląstelių formavimosi ypatumų mikrogravitacijos sąlygomis įvertinimui sėjamosios pipirnės (*Lepidium sativum* L.) daigai buvo išauginti mikrogravitacijos sąlygomis bei 1*g* gravitacinėje aplinkoje, centrifugos pagalba imituotoje kosmose, ir veikiant natūraliai gravitacijai Žemėje. Šaknų kolumelės ląstelių (statocitų) augimo įvertinimas, amiloplastų viduląstelinio išsidėstymo ir kitų organoidų būklės morfometrinė analizė atlikta šviesinės ir elektroninės mikroskopijos metodais.

Nenustatyta esminių skirtumų tarp statocitų formavimosi ir augimo mikrogravitacijos sąlygomis ar veikiant imituotai gravitacinei jėgai skrydžio metu. Amiloplastų išsidėstymas statocituose priklausė tiek nuo gravitacijos, tiek ir nuo statocito padėties kolumelėje. Statocitų plastidžių formavimosi ir būklės tyrimo rezultatai patvirtina prielaidą apie mikrogravitacijos sąlygų poveikį augalo ląstelių metabolizmui, tačiau gravitaciją juntančių ląstelių formavimuisi ir šaknų augimui šie pokyčiai nėra esminiai.