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STATOLITHS DISPLACEMENT IN ROOT STATOCYTES IN REAL AND SIMULATED MICROGRAVITY

Despite the long-term employment of different types of clinostats in space and gravitational biology, the discussions about their reliability to mimic microgravity in space flight are still ongoing. In this paper, we present some data about the behaviour of amyloplasts-statoliths in root cap statocytes of higher plant seedlings growing during 3—5 days under slow and fast 2-D clinorotation and real microgravity in orbital flight. In addition, data on the displacement of amyloplasts in the statocytes of seedlings subjected to vibration and acceleration in the launch mode of a spacecraft are also given. A comparative analysis showed sharp differences in statolith responses to slow and fast clinorotation with a speed of 50 rpm. In the first case, the behaviour of amyloplasts was more or less similar to that in space flight, they did not touch the plasmalemma. In the second case, the contacts of statoliths with the plasmalemma or its invaginations (plasmalomasomes), like those under the action of vibration and acceleration, were clearly observed. Thus, slow 2-D clinostat is more suitable to study gravity sensing by root cap amyloplasts-statoliths and their responses to microgravity in the ground-based experiments.

***Keywords**: slow clinorotation, fast clinorotation, amyloplasts, gravity perception, plant root, simulated microgravity, microgravity.*

INTRODUCTION

To simulate biological effects of microgravity in space flight, various ground-based facilities — slow (1—10 rpm) and fast (50—120 rpm) 2-D clinostats, Random Positioning Machine, Free Fall Machine, Rotating Wall Vessels and magnetic levitation — are widely used [1—7] as experiments in "real μ*g* are scarce, costly and time-consuming" [8]. Capacities and limitations of various devices for accurate and reliable simulations of microgravity conditions comparable to real microgravity in space are constantly discussed [6, 9—16].

Recent comparative studies of the quality of microgravity simulation provided by different operational modes have shown the greatest suitability of fast 2-D clinorotation for investigating the gravi-perception mechanism in *Chara* rhizoids compared with slower 2-D and 3-D clinorotation and rotation of samples around two axes [8]. In the given paper, we compare the position of amyloplasts-statoliths in root cap statocytes of higher plants at 1 g, slow and fast 2-D clinorotation, real microgravity in space flight, vibration and acceleration in the spacecraft launch mode.

1*g* conditions

Root cap statocytes in angiosperm plants are highly specialized graviperceptive cells and characterized by the structural polarity shown by the position of a blade-shape nucleus in the proximal part of the cell and the endoplasmic reticulum (ER) complex in its distal part. Not all investigated species have a massive

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ER complex. Amyloplasts perform a statolithic function sediment in the distal part of the statocytes in the direction of the gravitational vector at some distance from the plasmalemma and thus not in contact with it [17—19]. This polar arrangement of organelles, which is genetically determined, is achieved and maintained by means of the cytoskeleton [20—23].

Results of our investigations of root cap statocytes in *Beta vulgaris, Brassica rapa,* and *Pisum sativum* 3—5-day old seedlings grown in stationary conditions using light and electron microscopy correspond to literary data on the whole. As a rule, round or oval amyloplasts on sections are in close contact with each other, often with the outgrowths of the outer membrane of the organelle envelope and sediment in the distal part of a statocyte (Fig. 1).

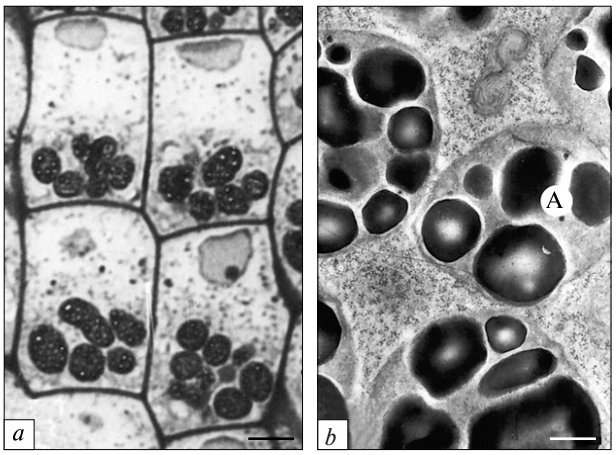

Fig. 1. *a* — Root cap statocytes of *Beta vulgaris* 3-day old seedling grown in the stationary conditions, *b* — amyloplasts. A — amyloplast. Bar: *a* — 5 μm, *b* — 0.5 μm

μg conditions

Histogenesis and cell differentiation in the embryonal root cap of investigated plants occurred normally in real microgravity in space flight [18, 19, 24—26]. In the cap columella, as in control, the following zones are distinguished: the meristem, the differentiating statocytes, the mature statocytes (central statenchyma), and the peripheral secretory cells. Cell quantity in the different zones varies among species. A continuous replacement of cells of all the cap zones occurs constantly in the root growth as a result of cap meristem proliferative activity and the removal of peripheral cells. Statocytes preserve structural polarity: a nucleus is situated in the proximal part of a cell and ER cisterns — in distal. Amyloplasts, which did not sediment in the distal part of statocytes in the absence of the gravitational vector, mainly grouped in the center of a statocyte, organelles could contact in this case, and more rarely throughout the cell without contacting the plasmalemma (Fig. 2). Increased vacuolization of the cytoplasm was observed.

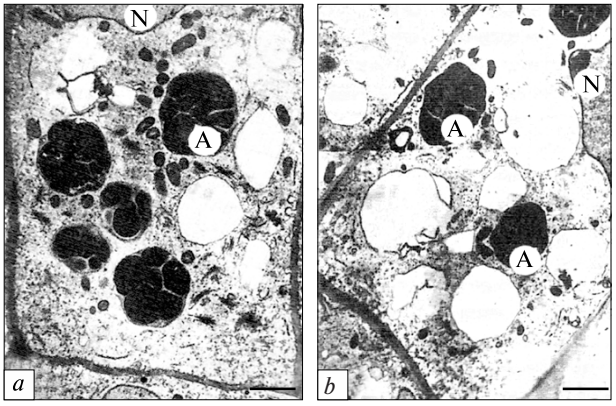

Fig. 2. *a* — Root cap statocytes of *Brassica rapa* 5-day old seedlings grown onboard space shuttle Columbia (STS-87). *a* — amyloplasts grouped in the cell center, *b* — amyloplasts distributed over the cell. N — nucleus, A — amyloplast. Bar: 1 μm

Slow 2-D clinorotation (2 rpm)

As in microgravity, amyloplasts, lacking the opportunity to perceive the gravitational stimulus, did not sediment in the distal part of statocytes [27—32]. Amyloplasts also tended to group closer to the center of a cell or near the nucleus but could be located in separate groups of 2–3 organelles without contacting the plasmalemma (Fig. 3). Organelles could be in contact with each other being at some distance from the plasmalemma. Progressive vacuolization of the cytoplasm also occurred.

Fast 2-D clinorotation (50 rpm)

Large amyloplasts in the root cap statocytes of pea 5-day old seedlings contained up to 15 starch grains per section, osmiophilic globules, and peripheral reticulum and varied in shape and size. Rounded plastids dominated. Unlike slow clinorotation, amyloplasts are distributed in different parts of root cap statocytes. Direct contacts of amyloplasts with the

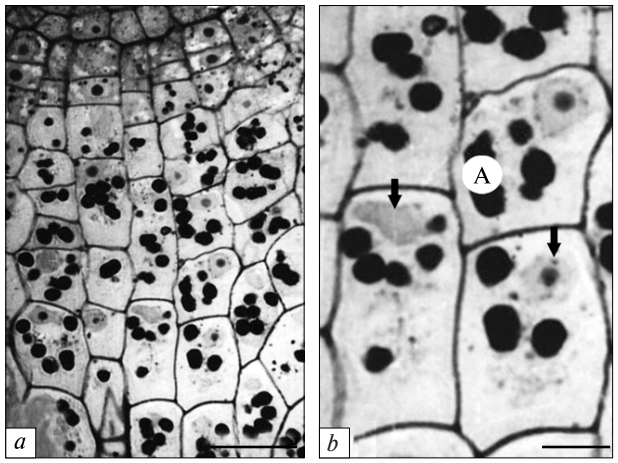

Fig. 3. *a* — Root cap central statenchyma of *Beta vulgaris* 3-day old seedling grown under slow clinorotation (2 rpm), *b* — statocytes. Arrows – nucleus, A — amyloplast. Bar: *a* — 20 μm, *b* — 5 μm

plasmalemma were one of the distinctive features of these organelles under fast clinorotation. Changes in organelle shape, size, stroma density, and volume of starch grains were the second distinctive feature. Plastids acquired an oval, pear-shaped or somewhat elongated or angular shape, often with a nose of the various thickness, which came in contact with the plasmalemma. The electron density of the stroma increased, and the number and size of starch grains significantly decreased. It is interesting to note that contacts of plastids with the plasmalemma were often observed at the sites of bends of the cell walls (Fig. 4).

Vibration and acceleration

To analyze the impact of vibration and acceleration in the spacecraft launch mode, 5-day old *P. sativum* seedlings were placed on the installation modeling dynamic factors of space flight in the N. I. Vavilov Institute of General Genetics of the Russian Academy of Sciences within 8 min. The maximum spectral density of vibration on the installation was reached in the frequency band 300–800 Hz. In so doing, acceleration with the total level of 7—10 g, as when spacecraft launching, was the attendant effect [33]. Samples were fixed directly after exposure.

Unlike control, amyloplasts were distributed throughout the cytoplasm, and tight approaching or close contacts of amyloplasts with the plasmalemma were observed. The distance between the outer membrane of the organelle envelope and the plasmalemma could vary from 2.5 to 18 nm. Amyloplasts came into contact with the plasmalemma papillae or invaginations (lomasomes) of various shapes. In sections, lomasomes could consist of the plasmalemma double invaginations or more and contained few small vesicles or thin fibrillar substances. Electron-dense lomasomes of a somewhat angular shape, in which the membranes were no longer distinguished, were also observed. On a number of sections, it was especially clearly seen that the places of contact of the plastids with the plasmalemma were located under the plasmodesmata. In some cases, the narrow protrusions of the plastid stroma were in contact with the plasmalemma. Such protrusions lacked starch grains or contained one or more small rounded starch grains. Contacts of amyloplasts with a nucleus and endoplasmatic reticulum were also characteristic of pea root statocytes after the impact of vibration and acceleration (Fig. 5). Such behaviour of plastids was more or less similar to that under fast 2-D clinorotation.

Short overview

We considered some examples of spatial responses of amyloplasts-statoliths in root cap statocytes of *B. vulgaris, Brassica rapa,* and *Pisum sativum* seedlings to slow and fast 2-D-clinorotation, vibration and acceleration in spacecraft launch mode. As well known, currently different types of clinostats are widely used in space and gravitational biology but the physical principles of slow and fast clinostats as well as a degree of reproducibility of real microgravity biological effects by these devices, in particular depending on the plane and speed of rotation, are also repeatedly described and debated (see for details [5—7]). The slow rotating clinostat enjoys a stable reputation as a reliable tool for reproducing a crucially important feature of microgravity, namely, the absence of a permanently orienting effect of a gravity vector [10, 18, 28, 31, 34—36]. The use of the fast clinostat is limited to small living objects, which are strictly on the axis of rotation; in this case, the centrifuge forces are immaterial. Organs and cells, which deflect the axis for some distance, will undergo centrifugal forces. A comparison of results from flight experiments

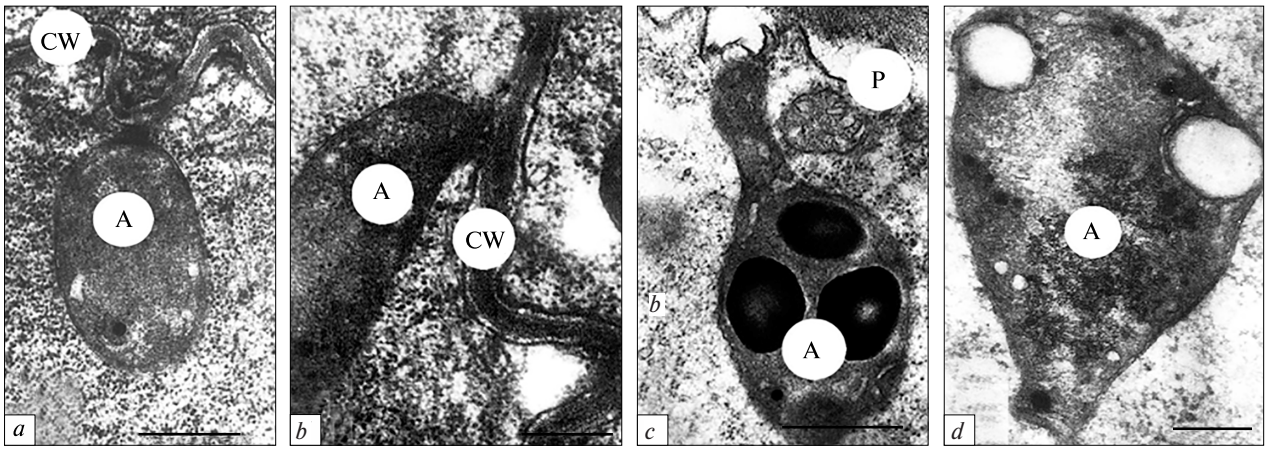

Fig. 4. Fragments of root statocytes of *Pisum sativum* 5-day old seedlings grown under fast clinorotation (50 rpm). Contacts of amyloplasts with the plasmalemma (*a*—*c*), amyloplast (*d*). A — amyloplast, CW — cell wall, P — plasmalemma. Bar: *a*—*c* — 0.5 μm, *d* — 0.2 μm

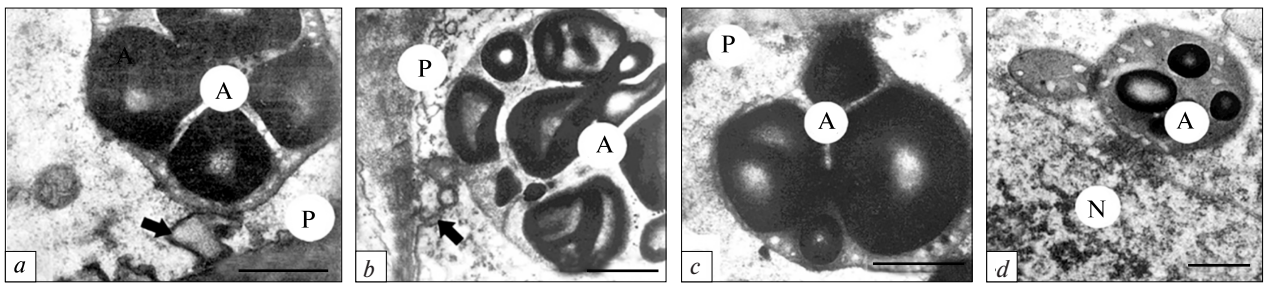

Fig. 5. Fragments of root statocytes of *Pisum sativum* 5-day old seedlings exposed to vibration and acceleration for 8 min. Contacts of amyloplasts with a simple (*a*) and double (*b*) lomasomes, plasmalemma (*c*), and a nuclear envelope (*d*). A — amyloplast, N — nucleus, P — plasmalemma, arrows — lomasome. Bar: *a*, *b*, *d* — 0.5 μm, *c* — 0.2 μm

and clinorotation with unicellular and multicellular organisms and tissue cultures showed that the fast clinostat is a valuable tool for evaluating an organism's sensitivity to altered gravity [8, 9, 37]. The absolute magnitude of the vector is incidentally preserved, consequently, the environmental properties are not changed. Clinorotation is unable to remove globally scalar effects of gravity such as hydrostatic pressure and surface tension. This naturally limits the simulation of microgravity by clinorotation to effects caused by the absence of a gravity vector. That is why currently, clinorotation is considered to reproduce only partially the biological effects of microgravity caused by the absence of the gravitational vector. Despite these restrictions, clinostats are widely used to investigate the effects of altered gravity because they make it possible to carry out experiments in the necessary time parameters and to use a great number of analytical methods that are equivalent to the tasks of experiments in comparison with spaceflight conditions. A comparison of the indices of linear growth and the gravitropic reaction of seedlings that depend on the magnitude of centrifugal forces in microgravity showed that there is no direct correlation between growth and morphogenesis with a gravisensory system determining the spatial orientation of plant organs [35]. The realization of plant growth and development in microgravity and under clinorotation makes it possible to analyze the nature of changes occurring under these conditions and to establish certain general patterns in their manifestation.

During the last two decades, 3-D clinostat and RPM successfully used to study the impact of simulated microgravity on plant proteome, transcriptome,

and metabolome [3, 4, 6, 7, 16]. For instance, the certain similarity of data on activation or inhibition of gene expression and protein synthesis associated with cell wall remodeling detected both in *A. thaliana* seedlings grown in real microgravity [38—40] and under 3-D clinorotation [41], as well as loosening and thinning of cell walls in microgravity and under clinostation can be explained in the light of biochemical data on quantitative and qualitative changes in the composition of poly- and monosaccharides [42, 43]. A fast-rotating 2-D clinostat is also considered to be an efficient tool for studying the plant responses to simulated microgravity [8, 15]. Changes in gene expression in roots of 5-day old *A. thaliana* seedlings as well as in the location of amyloplasts-statoliths in cap statocytes after 3 min and 6 min of fast 2-D clinirotation were described [15]. Basipetal transport of statoliths in *Chara globularis* rhizoids under 2-D clinorotation with speeds in the range of 60—85 rpm occurred the most closely with that in real microgravity of MAXUS-Sounding Rocket flights [8]. Authors emphasize that such positive results were provided by the perfect conformity of rhizoid cell tip to the rotation axis.

Roots of plant seedlings deviate from the clinostat rotation axis during their growth for 3—5 days and thus can undergo the acceleration of rotation. The distribution of amyloplasts in statocytes sharply differed under slow and fast 2-D clinorotation. The location of amyloplasts under slow clinorotation was more or less similar to that in real microgravity. Direct contacts of amyloplasts with the plasmalemma have never been observed. Decreasing the volume of starch grains in amyloplasts and progressive vacuolization of statocytes occurring under clinorotation are not destructive, as W. Hensel and A. Sievers noted in 1980 [27]. Later ground-based and space-flight experiments showed that such changes are usual traits of root statocytes of seedlings grown under slow clinorotation and in orbital flights. A decreased starch volume in statocytes indicates changes in carbohydrate metabolism, which is very sensitive to the impact of altered gravity. Direct contacts of amyloplasts with the plasmalemma, especially in the sites of cell wall bends, is the striking feature of the impact of fast 2-D clinorotation with a speed of 50 rpm on the root graviperceptive cells. A comparison of amyloplast position in statocytes under fast clinorotation and after the impact of acceleration and vibration during 8 min clearly showed that amyloplasts undergo these factors under fast 2-D clinorotation. It is suggested that amyloplasts act to sense vibration by changing their position rapidly inside plant cells in response to vibration [44]. Drastic changes in shape and the ultrastructure of amyloplasts, in particular alteration in the volume and position of starch grains, also indicate the adverse impact of clinorotation with a speed of 50 rpm and thus the unacceptability of fast clinorotation to simulate the microgravity conditions. We agree with the opinion of L. Krause at al. [8] that "higher rotational speeds, residual g-forces or even centrifugal forces with increasing distance from a fast rotating axis, induce shear forces and might cause stress symptoms in the organisms". That is why we considered a slow 2-D clinostat as the qualified tool to study the higher plant organ gravisensitivity, firstly sensing and the response of root graviperceptive cells to simulated microgravity.

REFERENCES

1. Dedolph R. R., Dipert M. H. (1971). The physical basis of gravity stimulus nullification by clinostat rotation. *Plant Physiol.,* **47**, 756—764.
2. Brown A. H., Chapman D. K., Johnsson A., Heathcote D. (1995). Gravitropic responses of the *Avena* coleoptile in space and on clinostats. I. Gravitropic response thresholds. *Physiol. plant.*, **95**, 27—33.
3. Kraft T., van Loon J., Kiss J. Z. (2000). Plastid position in *Arabidopsis* columella cells is similar in microgravity and on a random-positioning machine. *Planta*, **211**, 415—422.
4. van Loon J. (2007). Some history and use of the random positioning machine, RPM, in gravity related research. *Adv. Space Res.*, **39**, 1161—1165.
5. Beysens D., Carotenuto L., van Loon J., Zell M. (2011). *Laboratory Science with Space Data.* Berlin: Springer.
6. Herranz R., Anken R. Boonstra J., Braun J. M., Christianen P. C. M., de Geest M., Hauslage J., Hilbig R., Hill R. J. A., Lebert M., Medina F. J., Vagt N., Ullrich O., van Loon J. J. W. A., Hemmersbach R. (2013). Ground-based facilities for simulation of microgravity: organism-specific recommendations for their use, and recommended terminology. *Astrobiology*, **13**, 1—17.

7. Kiss J. Z., Wolverton C., Wyatt S. E., Hasenstein K. H., van Loon J. J. W. A. (2019). Comparison of microgravity analogs to spaceflight in studies of plant growth and development. *Front. Plant Sci*. doi.org/10.3389/fpls.2019.01577
8. Krause L. Braun M., Hauslage J., Hemmersbach R. (2018). Analysis of statolith displacement in *Chara* rhizoids for validating the microgravity-simulation quality of clinorotation modes. *Microgravity Sci. and Technol.,* **30**, 229—236.
9. Cogoli M. (1992). The fast rotating clinostat: a history of its use in gravitational biology and a comparison of ground-based and flight experiment results. *ASGSB Bull.,* **5**, 59—67.
10. Hilaire E., Paulsen A. Q., Brown C. S., Guikema J. A. (1995). Effects of clinorotation and micrograyity on sweet clover columella cells treated with cytochalasin D. *Physiol. plant.*, **95**, 267—273.
11. Hoson T., Kamisaka S., Masuda Y., Yamashita M., Buchen B. (1997). Evaluation of the three-dimensional clinostat as a simulator of weightlessness. *Planta*, **203**, suppl., 187—197.
12. Hoson T., Soga K., Mori R., Saiki M., Wakabayashi K., Kamisaka S. (1999). Plant growth and morphogenesis under different gravity conditions: relevance to plant life in space. *J. Plant Res.*, **112**, 477—486.
13. John S. P., Hasenstein K. H. (2011). Effects of mechanostimulation on gravitropism and signal persistence in flax roots. *Plant Signaling and Behaviour*, **6**, 1365—1370.
14. van Loon J. J. W. A. (2016). Centrifuges for microgravity simulation. The reduced gravity paradigm. *Frontiers in Astron. and Space Sci*. URL: https://doi.org/10.3389/fspas.2016.00021 (Last accessed 23.07.2020).
15. Wang H., Li X., Krause L., et al. (2016). Erratum to: 2-D clinostat for simulated microgravity experiments with *Arabidopsis* seedlings. *Microgravity Sci. and Technol.*, **28**, 307.
16. Chantseva V., Bilova T., Smolikova G., Frolov A., Medvedev S. (2019). 3-D clinirotation unduces specific alterations in metabolite profiles of germinating *Brassica napus* L. seeds. *Biol. Communications*, **54**, 55—68.
17. Volkman D., Sievers A. (1979). Graviperception in multicellular organs. *Encyclopedia of Plant Physiology. New Series*. **7**, 573—600.
18. Kiss J. (2000). Mechanisms of the early stages of plant gravitropism. *Critical Reviews in Plant Sci*., **19**, 551—573.
19. Perbal G. (2009). From ROOTS to GRAVI-1: twenty five years for understanding how plants sense gravity. *Microgravity Sci. and Technol.*, **21**, 3—10.
20. Hensel W. (1984). A role of microtubules in the polarity of statocytes from roots of *Lepidium sativum* L. *Planta*. **162**, 404—414.
21. Hensel W. (1988). Demonstration by heavy meromyosin of actin microfilaments in extracted cress (*Lepidium sativum* L.) root statocytes. *Planta*, **173**, 142—143.
22. Lorenzi G., Perbal G. (1990). Actin filaments responsible for the location of the nucleus in the lentil statocyte are sensitive to gravity. *Biol. Cell*, **68**, 259—263.
23. Sievers A., Buchen B., Volkmann D., Hejnowicz Z. (1991). *Role of the cytoskeleton in gravity perception*. The Cytoskeletal Basis of Plant Growth and Form. Lloyd C. W. (ed.). London: Acad. Press, 169—182.
24. Volkman D., Behrens H., Sievers A. (1986). Development and gravity sensing of cress roots under microgravity. *Naturwissenschaften*, **73**, 438—441.
25. Klymchuk D. O., Kordyum E. L., Chapman D. K., Brown C. S., Vorobyova T. V. (2003). Changes in vacuolization in the root apex cells of soybean seedlings in microgravity. *Adv. Space Res.*, **31**, 2283—2288.
26. Driss-Ecole D., Legue V., Carnero-Diaza E., Perbal G. (2008). Gravisensitivity and automorphogenesis of lentil seedling roots grown on board the International Space Station. *Physiol. plant.*, **134**, 191—201.
27. Hensel W., Sievers A. (1980). Effects of prolonged omnilateral gravistimulation on the ultrastructure of statosytes and on the graviresponse of roots. *Planta*, **150**, 338—346.
28. Sytnik K. M., Kordyum E. L., Nedukha E. M., Sidorenko P. G., Fomicheva V. M. (1984). *Plant Cell under Changes of Geophysical Factors*. Kyiv: Naukova Dumka.
29. Moore R. (1990). Comparative effectiveness of a clinostat and a slow-turning lateral vessel at mimicking the ultrastructural effects of microgravity in plant cells. *Ann. Bot.*, **66**, 541—549.
30. Smith J. D. Todd P., Staehelin L. A. (1997). Modulation of statolith mass and grouping in white clover (*Trifolium repens*) grown in 1 g, microgravity and on the clinostat. *Plant J.*, **12**, 1361—1373.
31. Kordyum E. L. (1993). Effects of microgravity and clinostating on plants. *Giornale Botanico Italiano,* **27**, 379—385.
32. Kordyum E. L., Martyn G. I., Ovcharenko Yu. V. (2008). Growth and differentiation of root cap columella cells and a root proper in stationary conditions and under clinorotation. *Cytology and Genetics*, **42**, 3—12.
33. Moskvitin E. V. (1974). *Effects of Space Flight and Dynamic Factors of Flight on Chlorella*: Thesis of Ph.D. Moscow.
34. Lyon C. J. (1970). Choice of rotation rate for the horizontal clinostat. *Plant Physiol.*, **46**, 355—358.
35. Merkys A. I. (1990). *Gravity in Growth Processes of Plants*. Moscow: Nauka.
36. Kordyum E. L. (1994). Effects of altered gravity on plant cell processes: Results of recent space and clinostatic experiments. *Adv.Space Res.*, **14**, 77—85.

37. Hemmersbach-Krause R., Briegleb W. (1994). Behavior of free-swimming cells under various accelerations. *J. Gravit. Physiol.*, **1**, 85—87.
38. Correll M. J., Pyle T. P., Millar K. D., Sun Y., Yao J., Edelmann R. E., Kiss J. Z. (2013). Transcriptome analyses of *Arabidopsis thaliana* seedlings grown in space: implications for gravity-responsive genes. *Planta*, **238**, 519—533.
39. Ferl R. J., Koh J., Denison F., Paul A. L. (2015). Spaceflight induces specific alterations in the proteomes of Arabidopsis. *Astrobiology*, **15**, 32—56.
40. Kwon T., Sparks J. A., Nakashima J., Allen S. N., Tang Y. Blancaflor E. B. (2015). Transcriptional response of Arabidopsis seedlings during space flight reveals peroxidase and cell wall remodelling genes associated with root hair development. *Amer. J. Bot.*, **102**, 21—35.
41. Soh H., Auh C., Soh W. Y., Han K., Kim D., Lee S., Rhee Y. (2011). Gene expression changes in Arabidopsis seedlings during short- to long-term exposure to 3-D clinorotation. *Planta*, **234**, 255—270.
42. Hoson T. (2014). Plant growth and morphogenesis under different gravity conditions: relevance to plant life in space. *Life*, **4**, 205—216.
43. Kordyum E. L. Chapman D. K. (2017). Plants and microgravity: Patterns of microgravity effects at the cellular and molecular levels. *Cytology and Genetics*, **51**, 108—116.
44. Uchida A., Yamamoto K. T. **(**2002). Effects of mechanical vibration on seed germination of *Arabidopsis thaliana* (L.) Heynh. *Plant Cell. Physiol.*, **43**, 647—651.

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РУХ СТАТОЛІТІВ У СТАТОЦИТАХ КОРЕНЕВОГО ЧОХЛИКА В УМОВАХ РЕАЛЬНОЇ ТА МОДЕЛЬОВАНОЇ МІКРОГРАВІТАЦІЇ

Незважаючи на тривале використання різних видів клиностатів у космічній і гравітаційній біології, дискусії про їхню спроможність відтворювати ефекти реальної мікрогравітації в космічному польоті тривають дотепер. В роботі представлено дані про поведінку амілопластів — статолітів у статоцитах кореневих чохликів вищих рослин, що зростали протягом 3—5 днів при повільному і швидкому 2D-клиностатуванні, а також — реальної мікрогравітації в орбітальному польоті. Крім того, наведено дані про переміщення амілопластів у статолітах в умовах вібрації і прискорення у стартовому режимі польоту космічного апарата. Порівняльний аналіз показав чіткі відмінності в реакції статолітів на повільне (2 об./хв) і швидке клиностатування (50 об./хв). У першому випадку поведінка амілопластів була схожа на їхню поведінку в космічному польоті, вони не торкалися плазмалеми, у другому — чітко спостерігалися контакти статолітів з плазмалемою або її інвагінаціями (ломосоми), що є характерним для явищем для вібрації і прискорення. Таким чином, повільне 2D-клиностатування є найбільш адекватним методом для вивчення гравітропічних процесів статоцитах кореневого чохлика, а також їхньої реакції на мікрогравітацію у модельних наземних експериментах.

Ключові слова: повільне клиностатування, швидке клиностатування, амілопласти, сприйняття гравітації, корінь рослин, модельована мікрогравітація, мікрогравітація.