Seed and Vegetative Propagation of Plants in Microgravity

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Abstract：A short review of the available data on plant development, seed-to-seed, and next generations, and formation of generative and vegetative organs in real and simulated microgravity is presented. It is emphasized the timeliness of the emergence of plant space reproductive biology and its importance for progress in space agriculture that is necessary for future human exploration of space.

Keywords：seed；tuber；stem；propagation；storage tissue；endosperm microgravity；reproductive biology

Highlights：

- Approaches are proposed for solving the problems of food production by agricultural crops in BLSS.
- Foods (seeds, fruits, tubers, edible roots etc) should provide a nutritional value in composition (carbohydrates, proteins, fats) and taste to astronauts in deep space exploration.

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Introduction

Postulate of the present: future long manned space-flights, building of lunar bases and human long-term residence on the moon, martian expeditions require a large amount of metabolic resources, i.e water, food, oxygen, too heavy for existing rockets. Outer space is hostile to all living things, usually astronauts live and work in pressurized, controlled environment. Physico-chemical systems provide the regeneration of air and water and recycle waste, but they must be supplemented by bio-regenerative life support systems (BLSS) for long-term space missions. Higher plants and other photosynthetic organisms have been identified as essential components of BLSS and advanced moon habitats for production of edible biomass, oxygen and recycling water[1-6]. Plants can serve as biofilters for improving the atmosphere in a closed space environment, where the risk of microbial infections and trace contaminant build-up can be a concern. In addition, “phytodesign” created by a combination of ornamental plants and colored soil substitutes could support psychological health of astronauts in long-term space missions. During the 1980s, orchids in blooming state were delivered in the MALACHITE greenhouse on board the orbital station Salyut-7 and bloomed for a long time admiring astronauts (see Fig. 1).

Since the late 1960s to the present time a significant number of space experiments with algae (5 species), mosses (3 species), ferns (1 species), gymnosperms (2 species) and angiosperms (22 species) *in vivo* and *in vitro* (cultures of organs, tissues, cells and protoplasts) have been performed aboard biosatellites, spacecraft, and orbital stations. The experiments had different tasks and duration—from 2 days to months and more, and different technical capabilities. Long-term studies of plant growth and development in the conditions of real microgravity in space flight and simulated microgravity in ground experiments allowed baselines studies of plants at the organism, cellular and molecular levels[8-15]. The main

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conclusion is that microgravity, which is unusual for terrestrial organisms, let the plants to adapt on the principle of self-regulating systems in the range of a physiological response, i.e. in the framework of genetically determined program of ontogenesis. It is proved that flowering plants successfully grow in orbit under more or less optimal conditions in space greenhouses, above all temperature, humidity, CO_2 content, light intensity and directivity, and substrate aeration. It should be noted that high-quality seeds germinate completely, which has been convincingly shown in space experiments with *Brassica rapa*.

Fig. 1　French astronaut Jean-Loup Chrétien with orchids *Dendrobium phalaenopsis* on board the orbital station Salyut-7[7]

1　Seed Reproduction

To date, plants of *Arabidopsis thaliana* (L.) Heynh.[16–19], *Brassica rapa* L.[20–26] *Triticum aestivum* L.[26-28], *Pisum sativum* L.[29] have been grown from seeds in orbit, flowered and fruited in space flight. Two generations of *A. thaliana, B. rapa* (Astroplants), and *T. aestivum* (dwarf cv. Apogee) and four generations of dwarf *P. sativum* have been obtained. However, numerous aspects of plant fertility in the conditions of microgravity, that is, complete adaptation of the seed reproduction to the space environment are not yet fully understood. Morphological and embryological studies of these species grown in space flight revealed certain differences might negatively influence crop yields and food quality. For example, there were changes in *A. thaliana* plants grown on board the ISS in a size of protein bodies in the cotyledons, which were 55% smaller in comparison with controls, although protein content decreased by only 9%. Morphologically, *Arabidopsis* plants in space flight differed from those in ground controls by the nearly perpendicular position of the secondary inflorescence branches and siliques to the inflorescence stems[18].

The differences in starch, protein and lipid accumulation in seeds of spaceflight and ground control *B. rapa* plants have also been described. At 15 day post pollination of *B. rapa* plants (Fig. 2), plastids in cotyledon cells contained only single starch grains and large protein bodies in cotyledon cells of ground controls, while in developing seeds in orbit (cv. Astroplants, space shuttle Columbia, STS-87), plastids were filled with starch grains, and the protein bodies were absent (Fig. 3). Multiple lipid drops, which often aggregated in homogenous complexes, were observed in embryo cotyledons of spaceflight plants. In ground controls, lipid drops were present more freely widely dispersed in embryo cells[22, 24, 30]. Starch was also retained in cotyledons in mature seeds of *B. rapa* grown on board the orbital station Mir, whereas protein and lipid were already present in cotyledon cells in ground controls as storage reserves. Protein bodies in mature *B. rapa* cotyledons in space flight were 44% smaller than those in the ground controls. Also, cotyledon cell numbers

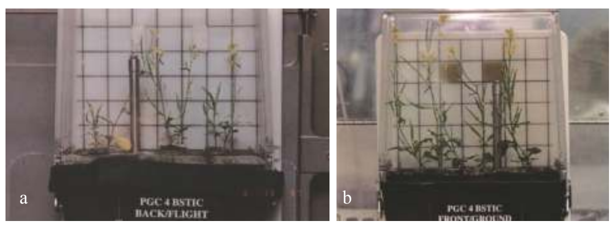

Fig. 2　*Brassica rapa* (cv. Astroplants) with siliques after 15 days post pollination: a-in orbit (STS-87), b-ground control[15]

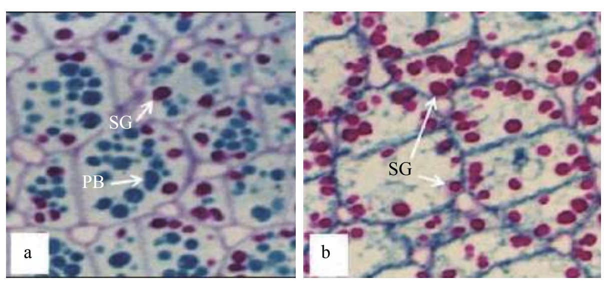

Fig. 3　Cells of embryo roots from *Brassica rapa* (cv. Astroplants) premature seeds developed in the ground control (a) and in orbit (b). SG-starch grain, PB-protein body (original photos from A.F. Popova)

decreased by 20% in comparison with ground controls[23]. The described changes in the quality and quantity of storage reserves in cotyledon and radicle cells in microgravity may underlie the formation of seeds of smaller size, weight, and viability and accordingly smaller siliques.

A delay in growth and development of embryos 15 d after pollination in *B. rapa* was noted in orbit compared to ground controls. Most embryos at the premature stage have elongated radicles, but high packing of radicles in folding cotyledons is characteristic of premature embryos at 1 g[31]. These data were supported with clinorotation experiments that showed variations in cotyledon and radicle arrangement when grown on clinostats[32] (Fig. 4). Deviations in late embryogenesis may be considered as developmental anomalies, as cell division and differentiation occur normally in space flight.

Fig. 4 *Brassica rapa* (cv. Astroplants) embryos developed in the stationary control (a) and under clinorotation (b, c) (original photos from A.F. Popova)

Caryopses formed on wheat plants of a cv. Apogee on board the orbital station Mir had a smaller size and their mass was less than in ground controls. Spaceflight plants showed weaker development of the vascular bundle in an embryo scutellum and greater elongation. The suspensor's cells had a large sizes and increased vacuoles in comparison with ground controls. Sinuous walls of suspensor's cells were often observed[27]. In related studies, four generations of dwarf pea plants grown on board the ISS and showed little difference from the ground controls[29]. Unfortunately, data on the accumulation of storage reserves in pea seeds in orbit were not measured.

After analyzing the available data on growth, development and seed propagation of plants in space flight and under clinorotation, we agree with the opinion expressed in the literature that gravity is not absolutely required for the vegetative phase in the plant life cycle, but its absence may adversely affect the fruiting phase, i.e. seed quality can be "compromised" by development in microgravity[18, 23, 32].

2 Vegetative Reproduction

The ability of angiosperm plants to reproduce vegetatively is very important for space planting, since specialized reproductive structures (such as rhizome, tuber, corm, or bulb) contain reserve starch and proteins-major foodstuffs for astronauts in long-term space flights.

Today, the possibility of successful vegetative propagation in space flight has been demonstrated in three spaceflight experiments, two with *Solanum tuberosum* L.[33–38] and one with *Ipomoea batatas* (L.) Lam.[39]. In the first experiment with potato (cv. Zarevo) on board the orbital station Mir, small stem segments with one leaf and its axillary bud grew 9 days (18 to 26 May 1991) in the hardware "BIOCONTAINER" with no light and temperature control, so specimens were exposed to the temperature of the space vehicle cabin. In microgravity and in the ground control, minitubers had a shape and an epidermis color, which were typical for this cultivar. They were spherical and 2.0-3.5 mm in diameter with no statistically significant differences in the frequency of formation or the size (Fig. 5). The ultrastructure of well-developed storage parenchyma in minitubers in microgravity was quite similar to that in control. Some differences were found in the ultrastructure of amyloplasts and mitochondria as well as the appearance of amyloplasts having a dumb-bell shape in spaceflight cells; each half of such amyloplast contained one starch grain (Fig. 6). A decrease in starch grain size in amyloplasts was also noted, with flight starch grains being 3.10 ± 0.16 μm in diameter, and ground control being 4.20 ± 0.22 μm in diameter[33-34]. In the second experiment with potato (cv. Norland) on the space shuttle Columbia (STS-73), small stem segments with a leaf and axillary bud grew 16 days (20 October to 5 November 1995) in the ASTROCULTURE (TM) flight package, which provided a controlled environment for plant growth. As in the first experiment, space-grown and control tubers were similar in size and shape, the structure of tuber tissues, and size range of starch grains. An increase in the percentage of small starch grains in tubers formed in space flight in comparison with ground control was also noted[36-37].

Spaceflight experiment with vegetative stem cuttings of sweet potatoes (cv. Whatley/Loretan), which grew 5 days on space shuttle Columbia, demonstrated that such explants should be a viable means for propagating sweet potato plants in microgravity. Space-grown stem cuttings with three to four nodes regenerated adventitious roots as in ground control but the total root length was significantly (≈12%) greater for roots developed in microgravity. Simultaneously, a substantial increase in the concentration of soluble sugars, glucose, fructose, sucrose and total starch in space-grown stems in comparison with those in ground control was determined. There were minimal differences in cell development between space flight and ground-based samples[39].

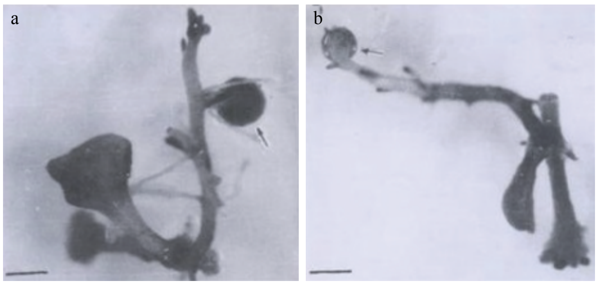

Fig. 5　Formation of minitubers of potato in orbit (a) and in the ground control (b). Arrows show the minitubers. Bar = 2.5 mm[34]

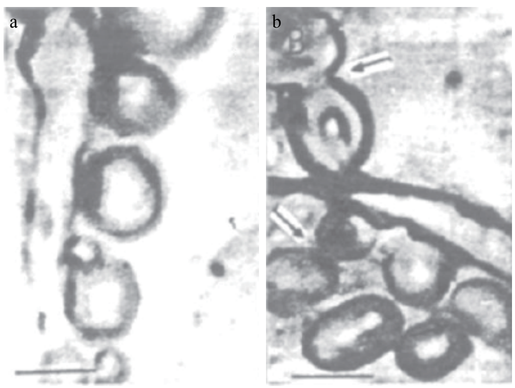

Fig. 6　Amyloplasts in the storage parenchyma cells of minitubers formed in the ground (a) and in orbit (b). Arrows show dumb-bell amyloplasts. Bar = 3 μm[34]

The significant changes in carbohydrate metabolism were revealed in potato tubers (cv. Adreta and Svitanok Kievskii) formed and grown under long-term (30 and 45 days) slow horizontal clinorotation in comparison with upright controls[40]. The content of mono- and disaccharides decreased under 45 days of clinorotation to 12 ± 0.7 mg/g fresh mass (FM), as compared to 15.8 ± 0.5 mg/g FM in controls, and the starch content increased to 261 ± 8 mg/g FM, as compared to 198 ± 5.5 mg/g FM in controls. Since the amylose content in starch in clinorotated tubers decreased 4.5 times in comparison with control, and the content of amylopectin increased, a ratio of amylose/amylopectin in starch changed from 1:3 in control samples as compared to 1:16 under clinorotation. As a consequence, starch in clinostat-grown potato tubers differed in physical properties, namely solubility in hot water and the swelling force that decreased 6–8 times in comparison with control samples. Our findings were consistent with literary data[41] on the association of amylose reduction with starch solubility inhibition in water. It was found that these parameters of starch state correlated with the amount of amylose in starch. It is known that the taste qualities of starch depend on its solubility in hot water and its swelling in water[42]. During long-term clinorotation, a number of minitubers increased more 18% in comparison with controls, and their size enlarged also due to the increased number of storage parenchyma layers. The expanded tubers had the more total starch content (mg/g FM). The appearance of giant amyloplasts of ovoid shape and size of 45.90 ± 4.81×9.79 ± 2.80 μm was noted in clinorotated tubes along with the rounded and oval amyloplasts in size similar to those in the control cells. Intriguing are the differences in the accumulation of starch in the tubers, which were formed in the short-term spaceflight experiments and under long-term clinorotation, as potato could become a major source of food for future flight in deep space and building lunar bases[3]. But the precise mechanisms of real and simulated microgravity effects on starch accumulation and properties are still unclear and requires future detail research.

3　Concluding Remarks and Prospects

To date, there is a broad bank of data on real and simulated microgravity effects on plants at the organism, cellular and molecular levels, which includes fundamental studies of vegetative plant organs, mainly leaves and roots. On the other hand, there are limited reports on the effects of space flight on the development of plant regenerative organs, especially fruits and seeds. We can state that plants adapt to the absence of gravity, because accomplishment of the ‘reproductive imperative’ of plants, i.e. seed production, is the major indicator in plant adaptation to new conditions. However, a delay and some disturbances in seed development in orbit make it impossible to say that we fully understand the adaptation of plants to microgravity. In connection with tasks to produce by plants, such as cereal crops and grain legumes, in the BLSS much of the needed food for humans in space exploration, one must think that the time has come to talk about the development of space reproductive biology of plants in the very near future. Reproductive biology of plants is one of the longest standing areas of biology that includes a comprehensive study of seed, from the initiation of generative organs to the ripening of seeds and their germination, and vegetative propagation processes at all levels of their organization using a whole arsenal of modern methodical approaches of cell and molecular biology, biochemistry, bioinformatics and statistics. In the light of the available data on seed development in space flight, it might be more effective to focus future research on the processes determining the productivity of plants, namely the fertility of pollen grains and embryo sacks, pollination, and critical stages in embryo and endosperm development. In order to understand events that cause deviations in seed formation and quality, of particular interest will be studying the processes of synthesis and accumulation of storage nutrients in embryos and endosperm at the molecular and biochemical levels, including genomic imprinting for endosperm.

At present time, gene expression and protein synthesis have been established to change under real microgravity in space and parabolic flights and simulated microgravity under ground-based experiments[43-48]. An increase or a decrease in the expression level due to microgravity action is characteristic of a large number of the genes involved in a wide range of cellular processes, including protein synthesis, carbohydrate and lipid metabolism, responses to stress, lipid and Ca^{2+} signaling, cell membrane biosynthesis, and more. However, these data were obtained from studies of vegetative organs. Similar research of generative organs are needed. Meanwhile, novel specific data of fundamental and applied character can be expected in studies of the transcriptome, proteome, carbohydrate and lipid metabolism in generative organs, especially seeds and fruits and their components-embryo, endosperm, pericarp, and testa, as well as in the same studies of storage tissues of vegetative organs-tubers, bulbs, and storage roots. Such an opinion is based on the discovery of organospecific plant responses at the molecular level based on the broad investigations of the proteome and transcriptome of vegetative organs in microgravity[49]. Authors emphasized that further studying proteomics and transcriptomics will help discover differentiated responses of different cell types inside organs to the spaceflight factors[50].

Of special interest are studies of biochemical and cellular events of storage protein deposition, including specific transport ways, selective accumulation and packaging of proteins into vacuoles, i.e. formation of protein bodies[51-53]in microgravity, for example in endosperm of cereals and in cotyledons of grain legumes. Endosperm of cereals, including wheat and rice, which are in the list of species recommended for growing in BLSS[54], represents the most important source of food, that requires a great attention to the regulatory systems of their development. It consists mainly of natural polymers-starch and proteins, which total content, for example in wheat grain, is about 85% per dry matter. In the developing seed, endosperm is the most plastic, responsive to environmental factors and especially to various pollination methods[55-56]. Morphophysiological studies of the endosperm in connection with various conditions of its occurrence (distant hybridization, pseudogamy, various pollination methods or its absence) showed the versatility of endosperm functions in the process of seed and fruit formation.

It seems remarkable that genomic imprinting, which refers to the epigenetic modification of alleles inherited by the maternal or paternal line, i.e., maternal and paternal genomes are not functionally equivalent[57-58] is now reliably known, primarily for endosperm. It was shown that imprinted genes differentially expressed after double fertilization in the zygote and early nuclear endosperm *Arabidopsis thaliana, Zea mays* and *Oryza sativa*[59] as a result of differences in transcriptional activity of genetically identical alleles. In general, expediently to focus attention on epigenetic systems for the control of gene expression and inheritance of genome functional changes in plant adaptation to microgravity as a new insight into plant developmental biology in space flight.

Except cereals and grain legumes, a list of plants recommended for space agriculture includes a sufficiently wide range of vegetable crops[3,54] eaten in the form of leaves or storage roots. Using such crops in long-term space missions poses the challenges of obtaining many their generations, the implementation of which will be ensured by research in the field of space reproductive biology. Therefore, further understanding of plant reproductive biology in microgravity in space flight, as well as in the conditions of gravity on moon (1/6 of Earth's gravity) and on Mars (1/3 of Earth's gravity) will be crucial for progress in space agriculture to assure high yields of crops for astronauts in the extraordinary conditions of long-term missions in deep space. Also, negative changes in seed formation in orbit compel us to return to an idea that was widely discussed in the 1970s and 1980s: the need to carry out corresponding plant genetic and breeding work for obtaining cereals and vegetables that would be most useful for growing in space greenhouses and human requirements.

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植物在微重力下的种子繁殖和营养繁殖

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摘　要：简要回顾了在真实和模拟微重力下植物发育、种子到种子、后代、生殖和营养器官形成的现有数据。强调了植物空间生殖生物学的出现及其对空间农业发展的重要性，这是人类未来探索空间所必需的。

关键词：种子；块茎；茎；繁殖；贮藏组织；胚乳微重力；生殖生物学

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