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REVIEW ARTICLE

PLANT GROWTH AND DEVELOPMENT IN SPACE: CHALLENGES AND OPPORTUNITIES

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Abstract: The growth of plants in outer space has elicited much scientific interest. Plants are expected to be essential for sustaining human life during extended space missions, likely starting soon with a journey to Mars. Given their ability to endure harsh conditions on Earth and evidence that model plants can complete their life cycle in microgravity, plants are well-suited for space-based life support systems. Their role goes beyond biology—successfully cultivating plants in space also reflects our technological ability to (re)create supportive living environments in microgravity. This knowledge also benefits humanity on Earth: by understanding how to grow plants in harsh conditions in space, we could apply that knowledge to growing agriculturally important crops in challenging conditions on Earth. Decades of research have revealed many challenges of growing plants in microgravity, space and on other celestial bodies, but our understanding of this endeavor has improved significantly. As space exploration moves forward, we can be increasingly confident in our capability to cultivate plants aboard spacecraft, on the Moon and beyond. Although plants will need specially designed environments to thrive in microgravity, we already possess the knowledge and tools to create such systems on a small scale.

Keywords: Space biology, Gravitational biology, Microgravity, Plant development, Spaceflight

INTRODUCTION

The term "plants in space" refers to cultivating plants beyond the Earth's atmosphere, specifically in outer space, which begins at the Kármán line—roughly 200 to 450 kilometers above sea level. This altitude range includes the typical orbits of the Space Shuttle and the International Space Station (ISS), where the majority of human spaceflight and associated scientific research has occurred (Darrin, 2009). Outer space presents a hostile environment for living organisms due to extreme temperature fluctuations, the vacuum of space, exposure to electromagnetic and particle radiation and magnetic anomalies. To ensure the survival of both humans and plants in such conditions, it is essential to understand how biological systems respond to spaceflight and to develop countermeasures to mitigate harmful effects. Furthermore, the high financial cost of launching any payload into space makes efficiency a critical consideration. In this environment, plants are grown under microgravity—often referred to as weightlessness—within specialized, controlled growth chambers designed for space.

The field of plant space biology is intrinsically linked with human space exploration, as plants are envisioned as key components of biologically-based life support systems. Successfully growing crops in space is critical for long-duration missions because it contributes to air purification, food supply and water recycling (Stankovic, 2002; Musgrave, 2007; Wolff *et al.*, 2014; Wheeler, 2017; Brown *et al.*, 2008). Missions to distant destinations impose strict limitations on the amount and weight of supplies that can be transported. In this context, higher plants are indispensable for in situ resource utilization, offering sustainable sources of food, breathable air and potable water.

Conducting plant research in space, however, comes with numerous logistical and operational challenges. Constraints include limited space, energy availability, astronaut time, cold storage capacity and restricted data transmission. Additional complications arise from the need for custom hardware, rigorous safety protocols and the differing priorities between engineering objectives and scientific inquiry within space programs. There is, quite literally, little room to grow plants in space. Scientific publication of spaceflight plant studies is also hindered by small sample sizes, lack of suitable experimental controls, difficulty in reproducing results and the indirect effects introduced by the unique environment of space.

Ultimately, the goal of cultivating plants in space is not only about enabling them to grow under microgravity, but also about nurturing a mutually beneficial relationship between plants and astronauts.

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Plants serve vital functions in the spacecraft environment, enhancing air quality by regulating humidity and converting exhaled carbon dioxide into breathable oxygen. The cornerstone of regenerative life support systems is the ability of photosynthetic organisms, under artificial lighting, to produce both oxygen and nourishment continuously. In addition to their physical benefits, plants may also provide psychological support to astronauts, serving as a form of stress relief and improving cognitive well-being through positive human-plant interactions (Odeh and Guy, 2017).

History

Human exploration of space began in the 20th century, starting with high-altitude balloon missions and progressing to rocket launches. From the outset of the space age, plants were included in experimental missions. The earliest plant-related space experiments involved "specially developed strains of seeds" sent into suborbital space to an altitude of 134 km on July 9, 1946, via a U.S. V-2 rocket. However, these early samples were not recovered. Just weeks later, on July 30, 1946, "ordinary corn seeds" became the first successfully retrieved seeds following a spaceflight. A chronological account of these early experiments can be found in Beischer and Fregly (1962). These initial, short-duration studies focused largely on examining the biological effects of space radiation on plant tissues, especially seeds.

A more extended exposure of plant material to the space environment occurred in 1960 when seeds of wheat, pea, maize and onion were flown aboard Sputnik 4, introducing these organisms to microgravity for longer durations (reviewed in Stankovic, 2001). A significant milestone in plant space biology came when *Arabidopsis thaliana* first completed its full life cycle aboard Salyut-7. However, while some viable seeds were produced, many had nonviable embryos, with evident developmental alterations (Merkys and Laurinavicius, 1983).

The launch of orbital research stations, especially the International Space Station (ISS), greatly expanded the opportunities for conducting plant experiments in microgravity. These advancements enabled researchers to utilize purpose-built plant growth chambers specifically designed for the space environment. These facilities, as described by Link *et al.* (2003), provided optimal conditions for plant development in orbit and demonstrated that plants could complete their full life cycle—germination to seed production—on the ISS in a manner similar to Earth-based controls.

In a notable achievement during experiments on the ISS in 2000–2001, *Arabidopsis thaliana* was grown in space for two successive generations (seed-to-seed-to-seed), confirming the possibility of multi-generational cultivation in microgravity (Link *et al.*, 2014). With the advent of advanced, well-regulated plant growth systems aboard the ISS, many of the limitations that plagued earlier space-based experiments were resolved. It became evident that gravity is not a strict requirement for completing a plant's life cycle, although it does influence plant morphology and may affect how seeds store nutrients (Link *et al.*, 2014).

While plant cultivation in space has provided many insights, it has also prompted new questions for further investigation. The impacts of microgravity on plants are occurred at phenotypic, cellular and molecular levels. Comprehensive reviews of plant space biology have detailed how gravity affects plant development at both cellular and molecular levels, influencing processes such as the cell cycle, embryogenesis, seed development, photosynthesis, gas exchange, gravitropism, phototropism, cell wall formation and gene expression (Halstead and Dutcher, 1987; Wolverton and Kiss, 2009; Chebli *et al.*, 2011; Morrow, 2014). More sophisticated experiments conducted during the Space Shuttle and ISS eras have deepened our understanding of the molecular and cellular responses of plants to microgravity, revealing important findings related to plant tropisms, stress responses and overall biological adaptation to spaceflight (Paul *et al.*, 2012; Paul *et al.*, 2013; Vandenbrink and Kiss, 2016; Kordyum and Chapman, 2017).

Plant Growth and Development in Space

The earliest space experiments involving higher plants aimed to determine whether plants could grow outside Earth's environment and to identify any differences between those cultivated in space and their Earth-grown counterparts. As plant cultivation hardware evolved to suit the demands of space missions, more complex and controlled experiments became possible. This allowed researchers to begin distinguishing between the direct effects of microgravity and those caused by physical confinement. Earth orbit effectively became a laboratory where plants could be observed and studied in the absence of Earth's gravitational pull.

Gravity exerts a wide range of physiological effects on plants, influencing not only gravitropism but also numerous molecular and cellular processes. Many early plant experiments in spaceflight revealed various structural and functional abnormalities. These included chromosomal damage (Krikorian and O'Connor, 1984), failure to produce seeds (Mashinsky *et al.*, 1994), nonviable or malformed embryos (Merkys and Laurinavicius, 1983), modifications in cell wall structure and composition (Hoson *et al.*, 2003), increased degradation of xyloglucans (Soga and Wakabayashi, 2002), altered auxin transport patterns (Ueda *et al.*, 2000) and other visible abnormalities in morphology (Link and Cosgrove, 2000). It has become clear that spaceflight induces significant molecular and cellular restructuring in plants. This includes the emergence of genomic and epigenomic mutations triggered by the space environment (Shi and Sun, 2014). Without gravity, plants depend on alternative environmental cues to initiate essential developmental changes, driven by organ-specific gene expression (Link *et al*., 2014; Paul *et al*., 2012; Paul *et al*., 2013), followed by changes in the proteome as a result of microgravity exposure (Rea *et al*., 2016).

Various technological platforms have been used to simulate and study microgravity effects. A recent overview of these platforms explores the plant responses to altered gravity for advancing space agriculture and also summarizes the advances in understanding plant gravitropism, including critical steps such as gravity sensing, signal transduction and curvature response. Phenotypic plant responses include random root growth, larger branching angles, delayed flowering and smaller seeds. Cellular plant responses include amyloplast dispersion, increased cell proliferation and thinner cell walls. Molecular plant responses include shifts in gene networks tied to cell walls, stress responses, ROS signaling and epigenetics (Nie *et al*., 2025).

Reflecting on past experiments, we now understand that many of the early anomalies were due more to the challenges of the microgravity environment itself than simply to the lack of gravity. For example, altered starch levels have been observed in various species grown in space, such as pepper (Johnson and Tibbitts, 1968), Lepidium (Volkmann *et al*., 1986), maize (Moore *et al*., 1987) and Arabidopsis (Brown *et al*., 1996). However, studies later revealed that improving air circulation during flight could eliminate differences in carbohydrate accumulation (Musgrave *et al*., 1998). Ethylene—a plant hormone associated with stress—is another factor complicating plant growth in space. Its production tends to increase under microgravity conditions (Klymchuk *et al*., 2003) and elevated concentrations (1100–1600 ppb on the Shuttle) have been linked to abnormal Arabidopsis seedling growth, though graviresponsiveness remained unaffected (Kiss *et al*., 1999). Similar issues arose aboard the Mir space station, where ethylene levels (800–1200 ppb) allowed Brassica to produce seeds but inhibited seed production in wheat (Kuang *et al*., 2000; Campbell *et al*., 2001). To address this, newer plant growth systems on spacecraft incorporate ethylene scrubbers to reduce hormone buildup (Link *et al*., 2003; Link *et al*., 2014).

Another key constraint in microgravity is the lack of natural convection, which can lead to oxygen deprivation (hypoxia) in plants (Porterfield, 2002). This oxygen deficit can cause severe developmental issues in seeds, including undersized protein bodies, incomplete filling, floating lipid droplets, abnormally vacuolated cells and even partial embryo degeneration. A full-life-cycle experiment involving Brassica revealed that protein bodies were 44% smaller, starch was irregularly distributed and cotyledon cell counts were reduced by 80% (Kuang *et al*., 2000). These abnormalities were linked to disruptions in oxygen and ethylene concentrations inside developing siliques. Although the Svet greenhouses aboard Mir employed fans to circulate air, the flow rate—below 0.5 m/s—was inadequate to prevent hypoxia (Porterfield, 2002). Overall, maintaining a stable and well-regulated gaseous environment is critical for successful plant reproduction in space (Musgrave *et al*., 1997).

Plant as Components of Bio-Regenerative Life Support Systems

Sustaining human life on extended space missions requires a comprehensive life support system capable of regenerating essential resources. On the International Space Station (ISS), current systems generate oxygen through water electrolysis, manage carbon dioxide removal, filter harmful emissions (e.g., ammonia, acetone) and recycle water. However, these systems rely heavily on physical and chemical processes.

Bio-regenerative life support systems (BLSS), on the other hand, harness the power of photosynthetic organisms and controlled lighting to produce oxygen and food. Mastering the cultivation of plants in space is therefore central to ensuring sustainable long-term missions, as plants aid in producing breathable air, nourishing food and recycled water (Stankovic, 2001; Sager and Drysdale, 1996). In addition to yielding scientific insights into plant responses to microgravity and environmental stress, plant-based systems lay the foundation for BLSS that integrate oxygen generation, nutrition and nutrient cycling (Zabel *et al*., 2016).

Higher plants play a pivotal role in these systems, contributing to the closure of critical life support loops. These include oxygen production, carbon dioxide absorption, food cultivation, water reuse and waste recycling—thereby simulating Earth-like conditions. Moreover, consuming fresh produce may help improve astronaut psychological well-being during missions. Indeed, the integration of plant-based bioregenerative life support systems is a central objective in NASA's Moon to Mars strategy. As humanity prepares for sustained off-world habitation, the development of regolith-based agriculture (RBA) is essential for achieving self-sufficiency in space crop production. In that context, the physiological and gene expression responses of *Arabidopsis thaliana* grown in two off-world regolith simulants (*i*) LHS-2 (lunar highlands) and (*ii*) MGS-1 (Martian global) have been studied. Plants exposed to these substrates exhibited significant reductions in root elongation, biomass and chlorophyll content, along with elevated anthocyanin levels and transcriptional upregulation of stress-related genes including IRT1, PCS1, SOD1 and JAZ1. Evidence of jasmonic acid pathway activation and auxin signaling suppression suggests metal-induced hormonal misregulation (Buckner *et al*., 2025). In addition, some research groups are specifically developing plants for off-world agriculture. For example, a stress-adaptive, anthocyanin-rich tomato variant of a dwarf tomato ('Inkspot') was recently engineered for growth in lunar soil simulant (Lang *et al*., 2025).

As technology has evolved, various flight experiments have incorporated different growth system designs. Ongoing refinement of subsystems and expanding knowledge of plant behavior in space have led to the development of advanced plant growth facilities like NASA's Veggie system (NASA Vegetable Production System [Internet], 2017; Stutte *et al*., 2011) and the Advanced Plant Habitat (NASA Advanced Plant Habitat [Internet], 2017). While plants are already known to withstand extreme environmental conditions on Earth, model species have successfully completed full life cycles in microgravity. For sustained cultivation in space, it is critical to maintain robust environmental controls, including forced air circulation, trace gas regulation and efficient systems for water and nutrient delivery (Wolff *et al*., 2014; De Micco *et al*., 2009).

To contextualize this need, consider that early crewed Mars missions—expected to last around 500 days—will rely on efficient water recycling, air regeneration and food storage. Given the limited launch and return windows (either 30 days or over two years apart, depending on planetary alignment), such missions will necessitate regenerative systems. It is estimated that, to meet 80–90% of the crew's oxygen and food requirements, each astronaut will need access to approximately 40–50 m² of cultivated plant area (De Micco *et al*., 2009). This underscores the importance of developing permanent space-based greenhouses or modular agricultural systems.

Plant for Food in Space

One of the most pressing challenges in space exploration is ensuring a reliable, cost-effective food supply. The evolution of space food began in 1961 when cosmonaut German Titov became the first person to eat in orbit. Early space meals were highly processed and packed to meet the stringent requirements of spacecraft. Yet, both the Apollo and Space Shuttle missions revealed that astronauts often failed to meet their nutritional needs, partly due to unappealing food forms. Research has shown that providing familiar, appetizing food is essential for adequate nutrition (Perchonok and Bourland, 2002).

Since then, space cuisine has made significant progress. Today's astronauts aboard the ISS can choose from a variety of meal types, including individually packaged, thermostabilized, irradiated, moisture-controlled and natural foods (Perchonok and Bourland, 2002). However, the long-term objective is to achieve continuous food production in orbit, on the Moon, or on other planets. This would require self-sustaining agricultural systems.

The primary obstacles to space farming include delivering nutrients, ensuring proper lighting and maintaining adequate gas exchange. While space-adapted plant chambers enable growth comparable to that on Earth, morphological differences persist. To date, only small-scale plant growth experiments have been conducted in orbit, which provide limited data on yield potential under space conditions (Poulet *et al*., 2016). Microgravity has been shown to impair cell expansion, modify gene and protein expression and alter overall plant morphology—all of which affect productivity. Additionally, seeds grown in space may differ in composition, potentially impacting both nutrition and flavor, which is especially concerning for crews that depend heavily on plant-based diets (Poulet *et al*., 2016).

Efforts in space agriculture have mutually benefited and drawn insights from terrestrial controlled environment agriculture. Historical reviews—such as Wheeler (2017)—document the evolution of these systems, from mid-20th-century algal production experiments in the USA and USSR, to NASA's Controlled Ecological Life Support Systems (CELSS), Japan's CEEF, ESA's MELiSSA program and China's Lunar Palace 1 plant factory (Wheeler, 2017; Dong *et al*., 2015).

These advancements have led to transformative technologies for both space and Earth. Innovations include the use of LED lighting for crop cultivation, vertical farming systems and hydroponics for root vegetables, which have enabled record-breaking yields and the monitoring of volatile organic compound emissions from entire crops. Other breakthroughs involve novel methods for regulating water and converting waste into plant nutrients (Wheeler, 2017). Space conditions have even been proposed as a unique environment for crop breeding and mutagenesis (Shi *et al*., 2014).

Recent research has also explored the viability of growing plants on the Moon and Mars (Karoliussen *et al*., 2013; Wamelink *et al*., 2014). Experiments suggest that crops can grow in lunar and Martian soil simulants, without added nutrients. The Mars soil simulant, sourced from a volcanic cone in Hawaii, chemically resembles the soil analyzed by Viking 1. The Moon simulant, collected near Flagstaff, Arizona, comes from local volcanic ash. Trials involving 14 plant species in these simulants suggest that future colonists might cultivate crops using native soil (Wamelink *et al*., 2014). However, further research is needed to understand better the water retention properties and other physical attributes of extraterrestrial soils, including nitrogen availability and other nutrient levels. Research must also explore how extraterrestrial gravity, lighting and environmental conditions affect growth (Wamelink *et al*., 2014). Progress will require advanced modelling to unravel and predict the complex biological, chemical and physical dynamics involved in extraterrestrial plant cultivation.

Psychological Benefits of Plants in Space

Beyond their nutritional and life-support functions, plants in space offer significant psychological benefits. They serve as emotional anchors, providing what is often referred to as horticultural therapy. For astronauts confined to isolated environments, the presence of plants can help alleviate psychological stress. Humans have a natural affinity for nature and the presence of greenery has been shown to generate a wide range of positive effects, including improved mental well-being, a sense of control over the environment, social engagement, health support, relief from monotony, reduced mental fatigue and recovery from stress (Lewis, 1995; Ulrich *et al.*, 1991). Studies on the psychological effects of prolonged isolation—common in space missions—indicate that humans are less stressed and function more effectively when surrounded by natural elements, including plants (Lewis, 1995; Ulrich *et al.*, 1991).

evidence continues to mount for plants having positive psychological effects on humans living in closed environments (Williams, 2002; Zimmermann, 2003) but much of this evidence is anecdotal, e.g. reports from cosmonauts on the Mir Space station and the use of hydroponic systems for Antarctic habitats.

Spaceflight environments subject astronauts to numerous physiological, biomedical and environmental stressors. Long-duration missions have been associated with psychological challenges such as hypochondria, low motivation, reduced cognitive performance, withdrawal, impulsiveness, hallucinations, mood swings, depression, helplessness and anger (Morphew, 2001). These issues have led to the development of dedicated subfields in behavioral science, such as space psychology, space human factors, habitability, performance and space sociology (Morphew, 2001). Within this context, plants are increasingly recognized as valuable tools for mitigating the psychological toll of extreme and isolated environments, including deep space (Bates *et al.*, 2009). A symbiotic relationship between astronauts and plants—perhaps even a garden for "Major Tom"—could play a vital role in supporting human mental health during space travel.

Case Study: Growth and Development of *Arabidopsis thaliana* on the International Space Station

As part of the early assembly of the International Space Station (ISS), we developed a novel, advanced plant growth chamber specifically designed for microgravity experiments: the Advanced Astroculture (ADVASC) system (NASA Advanced Astroculture™ (ADVASC) fact sheet [Internet], 2001). This chamber, the first of its kind flown aboard the ISS, was used to grow Arabidopsis thaliana from seed through two complete generations entirely in microgravity (Zhou *et al.*, 2002). Plants germinated, matured and were harvested on the ISS and their seeds were used to produce a second generation of Arabidopsis under the same conditions (Link *et al.*, 2003; Link *et al.*, 2014).

ADVASC offered precise control over environmental conditions such as temperature, humidity, lighting, nutrient and water delivery, CO_2 levels and ethylene concentrations. Automated software systems allowed for finely tuned adjustments, enabling a variety of plant species to be cultivated in space. Energy-efficient technologies reduced power needs during launch and re-entry and fault-tolerant systems improved performance. The inclusion of tele-science features allowed ground-based scientists to monitor plant growth and send remote commands via live video and telemetry.

The first experiment using ADVASC aboard STS-100 (ISS-6A) lasted approximately 70 days and completed a full Arabidopsis life cycle. The experiment functioned autonomously and included all growth stages—germination, development, flowering, seed formation and seed maturation. Post-mission results showed that 90% of seeds germinated successfully, comparable to Earth controls. About 70% of plants matured and produced siliques, each yielding an average of 36 seeds (Link *et al.*, 2003). The plants thrived overall, although deviations in root orientation and inflorescence branch angles were observed, demonstrating clear morphological effects of microgravity.

While general development was similar to Earth-grown controls, space-grown Arabidopsis exhibited noticeable differences in plant architecture. Secondary inflorescence branches and siliques grew almost perpendicular to the primary stem, showing that gravity plays a dominant role in determining branch and pod angles. The light source influenced the direction of the main shoot, but had little effect on the lateral branches (Link *et al.*, 2003; Link *et al.*, 2014). Although protein bodies in space-grown seeds were 55% smaller, overall protein content was only modestly reduced (by 9%) and germination rates remained high at 92%. These findings support the idea that gravity is not required for full plant reproduction, but it does affect form and seed reserves. The plants displayed automorphogenesis—development shaped by internal cues—rather than the gravity-influenced gravimorphogenesis observed on Earth (Hoson, 2014).

Biochemical and cellular analysis of the returned plants confirmed that aerial parts were not oxygen-starved. This was attributed to high airflow rates (2–3 m/s) and ethylene removal, which created improved growth conditions compared to earlier studies (Merkys and Laurinavicius, 1983; Musgrave *et al.*, 1997; Musgrave *et al.*, 1998). However, hypoxia in the root zone likely contributed to the reduced seed protein content. ADVASC relied on passive air circulation through a porous arcillite substrate—a widely used rooting medium in space plant experiments (Porterfield *et al.*, 2000). Although arcillite helps improve gas exchange, its effectiveness can be limited when saturated with roots or water, restricting oxygen diffusion to the root system.

Most roots formed a dense mat within the top 13 mm of the root tray, unlike Earth-grown controls, which extended more deeply. Water delivery averaged 110 mL/day, which proved insufficient to meet root oxygen demands (Stout *et al*., 2001). Without real-time moisture sensors, it was impossible to measure hydration levels in the root zone. The resulting anoxic conditions mimic waterlogged soil on Earth, limiting nitrogen uptake and reducing seed protein levels. Although liquid fertilizer was applied four times during the experiment to compensate for the artificial substrate's lack of nutrients, the final seed protein content reached only 82% of normal (Link *et al*., 2003; Link *et al*., 2014).

The distinct growth angles and reduced branch curvature of siliques observed in this study represent new phenotypes triggered by microgravity. The phenotype persisted across the second experiment, suggesting it is a consistent developmental trait under spaceflight conditions (Link *et al*., 2003; Link *et al*., 2014). While the main axis of the plant consistently grew toward the light source, confirming light's role in axial orientation, side branches did not respond similarly. This suggests that gravity plays a primary role in controlling branch and silique orientation, while light plays a supporting or negligible role (Weise and Kiss, 1999). Microgravity induces organ-specific remodeling at the cellular level, driven by differential gene expression (Paul *et al*., 2013).

We also conducted the first transcriptional profiling of higher plants grown entirely in microgravity (Link *et al*., 2014). Although the gene expression data pointed to an abiotic stress response, interpretation was cautious. Some patterns might have resulted from technical problems, such as delayed chamber stabilization and possible hypoxic conditions in the root zone during the second seed-to-seed experiment (Link *et al*., 2014).

Overall, the ADVASC system enabled healthy plant growth and full reproductive cycles under microgravity conditions, revealing key insights into plant adaptation in space. The results highlight the importance of improving root zone aeration in future systems such as Veggie (Stutte *et al*., 2011) and the Advanced Plant Habitat (NASA Advanced Plant Habitat [Internet], 2017). Further studies are needed to validate these findings across different plant species and refine the conditions for sustainable space-based agriculture.

Prospects

This is a very exciting time for space science, as the search for extraterrestrial life is one of the great intellectual enterprises of our species. At the same time, better understanding of the profound biodiversity and adaptability of life on Earth is part of the same continuum. Results from the performed space experiments were previously plagues by inconclusiveness due to the small number of experiments, small number of replicates, use of diverse flight hardware, growth conditions, limited possibilities for tissue preservation and subsequent analysis, etc. Our evolving understanding of this field suggests that future space experiments should therefore have standardized conditions for plant growth (Wolff *et al*., 2014; Ruyters and Braun, 2014). Plus, it is the one area of space science in which you get to eat your experiment.

The theme of agriculture for space has contributed to and benefited from, terrestrial, controlled environment agriculture; it will continue to do so into the future. The ISS provided an opportunity for direct comparison of microgravity vs. 1 *g* (in on-board centrifuge) conditions and for on-the-spot modification to the experiment conditions, which created unprecedented advantages for plant space biology investigators. This is particularly helpful when investigators are surprised after taking a well-understood experiment on Earth and attempting to reproduce it in microgravity conditions.

Understanding gene and protein expression is the key to unlocking the mechanisms behind microgravity-induced problems and to finding effective countermeasures to spaceflight-induced phenotype alterations. Even though large-scale tests on growing crops for food production in microgravity are lacking, the body of acquired knowledge that there is little impediment to growing plants in microgravity, in outer space and on other planets; even if the plants do experience some level of genotoxic stress and anatomic changes (Karoliussen *et al*., 2013). As human space exploration continues to advance, we should feel confident about our ability to grow plants on the Moon, on other planets and on-board spacecraft during long-term space missions. We still need to thoroughly investigate how plants deal long-term with cosmic radiation and with the soils of other planets. We do, however, know that plants require specialized environments for growth and development in microgravity, including efficient watering and nutrient-delivery systems, precise environmental controls for temperature, humidity and air composition and low-energy lighting. We already known how to produce such specialized growth chambers and greenhouses; we could design light absorption systems that take advantage of sunlight on the surface of planets and moons, to help us more efficiently grow plants in them.

Finally, it is not far beyond the realms of possibility that selected plant species can be genetically engineered and remotely controlled to provide food, clean air and potable water, while at the same time acting as a source of raw materials and as small pharmaceutical factories, many miles away from Earth. Such "programmable plants" could uniquely support human missions in space by receiving and responding to remote signals for the synthesis of compounds needed yet unavailable off-the-shelf in deep space (Brown *et al*., 2008). Synthetic biology could thus become a powerful booster for future multiplanetary agriculture and in a variety of ways, for example by engineering microbes (e.g., cyanobacteria) to produce vitamins and biomolecules in space, by enhancing plant robustness under low pressure and by optimizing photosynthesis, water reclamation, nutrient recycling (Llorente *et al*., 2018; Wang *et al*., 2022).

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REFERENCES

Bates, S., Gushin, V., Bingham, G, Vinokhodova, A, Marquit, J. and Sychev, V. A. (2009) Review of the literature and application to habitation systems for humans living in isolated or extreme environments. *Habitation,* **12**: 33-40.
Google Scholar

Beischer, D.E. and Fregly, A.R. (1962) Animals and man in space. A chronology and annotated bibliography through the year 1960. US Naval School of Aviation Medicine. Pensacola, FL. ONR REPORT ACR-64 (AD272581).
Google Scholar

Brown, C.S., Tipathy, B.C. and Stutte, G.W. (1996) Photosynthesis and carbohydrate metabolism in microgravity. In: Plants in Space Biology (eds. H. Suge and H. Takahashi). Tohoku University Press, Sendai, Japan, pp. 127-134.
Google Scholar

Brown, C.S., Winter-Sederoff, H., Davies, E. and Stankovic, B. (2008) Plan(t)s for space exploration. In: Simon Gilroy and Patrick H Masson, editors. Wiley-Blackwell Publishing; p 183-195.
Google Scholar

Buckner, A., Lang, S. and Loureiro, R. (2025) Physiological and transcriptional responses of *Arabidopsis thaliana* to simulated lunar and Martian regolith substrates. *arXiv*:2505.13583 [q-bio.QM].
Google Scholar

Campbell, W.F., Salisbury, F.B., Bugbee, B., Klassen, S., Naegle, E., Strickland, D.T., Bingham, G.E., Levinskikh, M., Iljina, G.M., Veselova, T.D., Sytchev, V.N., Podolsky, G., McManus, W.R., Bubenheim, D.L., Stieber, J. and Jahns, G. (2001) Comparative floral development of Mir-grown and ethylene-treated, earth-grown Super Dwarf wheat. *Journal of Plant Physiology,* **158**: 1051-1060.
Google Scholar

Chebli, Y. and Geitmann, A. (2011) Gravity research on plants: use of single-cell experimental models. *Frontiers in Plant Science,* **2**(56): 1-10.
Google Scholar

Darrin, A. and O'Leary, B.L. (2009) Handbook of Space Engineering, Archaeology and Heritage. Boca Raton: CRC Press; 1035 p.
Google Scholar

De Micco, V., Aronne, G., Colla, G., Fortezza, R. and De Pascale, S. (2009) Agro-biology for bioregenerative life support systems in long-term space missions: general constraints and the Italian efforts. *Journal of Plant Interactions,* **4**: 241-252.
Google Scholar

Dong, C., Shao, L., Fu, Y., Wang, M., Xie, B., Yu, J. and Liu, H. (2015) Evaluation of wheat growth, morphological characteristics, biomass yield and quality in Lunar Palace-1, plant factory, green house and field systems. *Acta Astronautica,* **111**: 102-109.
Google Scholar

Halstead, T.W. and Dutcher, F.R. (1987) Plants in space. *Annual Review of Plant Physiology,* **38**: 317-345.
Google Scholar

Hoson, T., Soga, K., Wakabayahis, K., Kamisaka, S. and Tanimoto, E. (2003) Growth and cell wall changes in rice roots during spaceflight. *Plant and Soil,* **255**: 19-26.
Google Scholar

Hoson, T. (2014) Plant growth and morphogenesis under different gravity conditions: relevance to plant life in space. *Life,* **4**: 205-216.
Google Scholar

Johnson, S.P. and Tibbitts, T.W. (1968) The liminal angle of a plagiogeotropic organ under weightlessness. *Bioscience,* **18**: 655-661.
Google Scholar

Karoliussen, I., Brinckmann, E. and Kittang, A-I. (2013) Will plants grow on Moon or Mars? *Current Biotechnology,* **2**: 235-243.
Google Scholar

Kiss, J., Edelmann RE and Wood PC. (1999) Gravitropism of hypocotyls of wild-type and starch-deficient Arabidopsis seedlings in spaceflight studies. *Planta,* **209**: 96-103.
Google Scholar

Klymchuk, D.O., Vorobyova, T.V., Chapman, D.K. and Brown, C.S. (2003) Changes in vacuolation in the root apex cells of soybean seedlings in microgravity. *Advances in Space Research,* **31**: 2283-2288.
Google Scholar

Kordyum, E.L. and Chapman, D.K. (2017) Plants and microgravity: patterns of microgravity effects at

the cellular and molecular levels. *Cytology and Genetics*, **51**(2): 108-116.
Google Scholar

Krikorian, A.D. and O'Connor, S.A. (1984) Karyological observations. *Annals of Botany*, **54**: 49-63.
Google Scholar

Kuang, A., Xiao, Y., McClure, G. and Musgrave, M.E. (2000) Influence of microgravity on ultrastructure and storage reserves in seeds of *Brassica rapa* L. *Annals of Botany*, **85**: 851-859.
Google Scholar

Lang, S., Buckner, A., Jones, S., Erwin, G., Lee, S. and Loureiro, R. (2025) Inkspot: A stress-resilient, anthocyanin rich, dwarf tomato variant for off-world cultivation. *arXiv*:2505.16890 [q-bio.OT].
Google Scholar

Lewis, C.A. (1995) Human health and well-being: the psychological, physiological and sociological effects of plants on people. *Acta Horticulturae*, **391**: 31-39.
Google Scholar

Link, B.M. and Cosgrove, D.J. (2000) Analysis of peg formation in cucumber seedlings grown on clinostats and in a microgravity (space) environment. *Journal of Plant Research*, **112**: 507-516.
Google Scholar

Link, B.M., Durst, S.J., Zhou, W. and Stankovic, B. (2003) Seed-to-seed growth of *Arabidopsis thaliana* on the International Space Station. *Advances in Space Research*, **31**: 2237-2243.
Google Scholar

Link, B.M., Busse, J.S. and Stankovic, B. (2014) Seed-to-seed-to-seed growth and development of *Arabidopsis* in microgravity. *Astrobiology*, **14**: 866-875.
Google Scholar

Llorente, B., Williams, T.C. and Goold, H.D. (2018) The Multiplanetary Future of Plant Synthetic Biology. *Genes*, **10**; 9(7):348.
Google Scholar

Mashinsky, A., Ivanova, I., Derendyaeva, T., Nechitailo, G. and Salisbury, F. (1994) "From seed-to-seed" experiment with wheat plants under space-flight conditions. *Advances in Space Research*, **14**: 13-19.
Google Scholar

Merkys, A.L. and Laurinavicius, R.S. (1983) Complete cycle of individual development of Arabidopsis thaliana (L.) Heynh. Plants on board the Salyut-7 orbital Station. *Doklady Akademii Nauk SSSR*, **271**: 509-512.
Google Scholar

Moore, R., McClelen, C.E., Fondren, W.M. and Wang, C.L. (1987) Influence of microgravity on root-cap regeneration and the structure of columella cells in *Zea mays*. *American Journal of Botany*, **74**: 218-223.
Google Scholar

Morphew, M.E. (2001) Psychological and Human Factors in Long Duration Spaceflight. *McGill Journal of Medicine*, **6**: 74-80.
Google Scholar

Morrow, R. (2014) A brief history of growing plants in space. Engineering and Technology for Sustainable World. *American Society of Agricultural and Biological Engineers*, **3**: 17-19.
Google Scholar

Musgrave, M.E., Kuang, A. and Matthews, S.W. (1997) Plant reproduction during spaceflight: importance of the gaseous environment. *Planta*, **203**: S177-S184.
Google Scholar

Musgrave, M.E., Kuang, A., Brown, C.S. and Mathews, S.W. (1998) Changes in Arabidopsis leaf ultrastructure, chlorophyll and carbohydrate content during spaceflight depend on ventilation. *Annals of Botany*, **81**: 503-512.
Google Scholar

Musgrave, M. (2007) Growing plants in space. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, **2**(065), 9.
Google Scholar

NASA Vegetable Production System (Veggie) [Internet] (2017) Available from: https://www.nasa.gov/mission_pages/station/research/experiments/383.html [Accessed 2017-11-15].
Google Scholar

NASA Advanced Astroculture™ (ADVASC) Fact Sheet [Internet] (2001) Available from: http://www.nasa.gov/centers/marshall/news/background/facts/advasc.html [Accessed 2017-11-15]
Google Scholar

NASA Advanced Plant Habitat [Internet] (2017) Available from: https://www.nasa.gov/mission_pages/station/research/experiments/2302.html [Accessed 2017-11-15].
Google Scholar

Nie, H., Zhou, W., Zheng, Z., Deng, Y., Zhang, W., Zhang, M., Jiang, Z., Zheng, H., Yuan, L., Yang, J. and Wang, H. (2025) Exploring plant responses to altered gravity for advancing space agriculture. *Plant Communications*, **6**: 101370.
Google Scholar

Odeh, R. and Guy, C. (2017) Gardening for therapeutic people-plant interactions during long-duration space missions. *Open Agriculture*, **2**: 1-13.
Google Scholar

Paul, A-L., Zupanska A.K., Ostrow, D.T., Zhang, Y., Sun, Y., Li, J-L., Shanker, S., Farmerie, W.G., Amalfitano, C.E. and Ferl, R.J. (2012) Spaceflight transcriptomes: unique responses to a novel environment. *Astrobiology*, **12**: 40-56.
Google Scholar

Paul, A-L., Zupanska, A.K., Schultz, E.R. and Ferl, R.J. (2013) Organ-specific remodeling of the Arabidopsis transcriptome in response to spaceflight. *BMC Plant Biology*, **13**: 112.
Google Scholar

Perchonok, M. and Bourland, C. (2002) NASA food systems: past, present and future. *Nutrition*, **18**: 913-920.
Google Scholar

Porterfield, D.M., Matthews, S.W., Daugherty, C.J. and Musgrave, M.E. (1997) Spaceflight exposure effects on transcription, activity and localization of alcohol dehydrogenase in the roots of *Arabidopsis thaliana*. *Plant Physiology*, **113**: 685-693.
Google Scholar

Porterfield D.M., Dreschel, T.W. and Musgrave, M.E. (2000) A ground-based comparison of nutrient delivery technologies originally developed for growing plants in the spaceflight environment. *Horticulture Technology*, **10**: 179-185.
Google Scholar

Porterfield, D.M. (2002) The biophysical limitations in physiological transport and exchange in plants grown in microgravity. *Journal of Plant Growth Regulation*, **21**: 177-190.
Google Scholar

Poulet, L., Fontaine, J.-P. and Dussap, C.-G. (2016) Plant's response to space environment: a comprehensive review including mechanistic modelling for future space gardeners. *Botany Letters*, **163**: 337-347.
Google Scholar

Rea, G., Cristofaro, F., Pani, G., Pascucci, B., Ghuge, S.A., Corsetto, P.A., Imbriani, M., Visai, L. and Rizzo, A. (2016) Microgravity-driven remodeling of the proteome reveals insights into molecular mechanisms and signal networks involved in response to the space flight environment. *Journal of Proteomics*, **137**: 3-18.
Google Scholar

Ruyters, G. and Braun, M. (2014) Plant biology in space: recent accomplishments and recommendations for future research. *Plant Biology*, **16**: 4–11.
Google Scholar

Sager, J.C. and Drysdale, A.E. (1996) Concepts, components and controls for a CELSS. In: *Plant Production in Closed Ecosystems: the International Symposium on Plant Production in Closed Ecosystems* (eds E. Goto, K. Kurata, M. Hayashi and S. Sase) Kluwer Academic, Dordrecht, The Netherlands; pp. 205-223.
Google Scholar

Shi, J., Lu, W. and Sun, Y. (2014) Comparison of space flight and heavy ion radiation induced genomic/epigenomic mutations in rice (*Oryza sativa*). *Life Sciences in Space Research*, **1**: 74-79.
Google Scholar

Soga, K. and Wakabayashi, K. (2002) Stimulation of elongation growth and xyloglucan breakdown in Arabidopsis hypocotyls under microgravity conditions in space. *Planta*, **215**: 1040-1046.
Google Scholar

Stankovic, B. (2001) 2001: A plant space odyssey. *Trends in Plant Science*, **6**: 591-593.
Google Scholar

Stout, S.C., Porterfield, D.M., Briarty, L.G, Kuang, A. and Musgrave, M.E (2001) Evidence of root zone hypoxia in *Brassica rapa* L. grown in microgravity. *International Journal of Plant Science*, **162**: 249–255.
Google Scholar

Stutte, G., Wheeler, R., Morrow, R. and Newsham, G. (2011) Operational evaluation of VEGGIE food production system in the habitat demonstration unit. *Proceedings of the 41st International Conference on Environmental Systems*, Portland, Oregon; 3357.
Google Scholar

Ueda, J., Miyamoto, K., Yuda, T., Hoshino, T., Sato, K., Fujii, S., Kamigaichi, S., Izumi, R., Isioka, N., Aizawa, S., Yoshizaki, I., Shimazu, T. and Fukui, K. (2000) STS-95 space experiment for plant growth and development and auxin polar transport. *Biological Sciences in Space*, **14**: 47-57.
Google Scholar

Ulrich, R.S., Simons, R.F., Losito, B.D., Fiorito, E., Miles, M.A. and Zelson, M. (1991) Stress recovery during exposure to natural and urban environments. *Journal of Environmental Psychology*, **11**: 201-230.
Google Scholar

Vandenbrink, J.P. and Kiss, J. (2016) Space, the final frontier: a critical review of recent experiments performed in microgravity. *Plant Science*, **243**: 115-119.
Google Scholar

Volkmann, D., Behrens, H.M. and Sievers, A. (1986) Development and gravity sensing of cress roots under microgravity. *Naturwissenschaften*, **73**: 438-441.
Google Scholar

Wamelink, G.W.W., Frissel, J.Y., Krijnen, W.H.J., Verwoert, M.R. and Goedhart, P.W. (2014) Can plants grow on Mars and the Moon: a growth experiment on Mars and Moon soil simulants. *PLOS ONE*, **9**(8): e103138.
Google Scholar

Wang, L., Zang, X. and Zhou, J. (2022) Synthetic biology: A powerful booster for future agriculture. *Advanced Agrochem.*, **1**: 7-11.
Google Scholar

Weise, S.E. and Kiss, J.Z. (1999) Gravitropism of inflorescence stems in starch-deficient mutants of Arabidopsis. *International Journal of Plant Science*, **160**: 521-527.
Google Scholar

Wheeler, R.M. (2017) Agriculture for space: people and places paving the way. *Open Agriculture*, **2**: 14-32.
Google Scholar

Williams, D.R. (2002) Isolation and integrated testing: An introduction to the Lunar-Mars life support test project. In: Isolation NASA experiments in closed-environment living, science and technology series, Edited by: Lane, HW, Sauer, RL and Feeback, DL., Vol. **104**, 1 – 6. San Diego: Univelt Incorporated.

Google Scholar

Wolff SA, Coelho L H, Karoliussen I, Jost A-IK. (2014) Effects of the extraterrestrial environment on plants: recommendations for future space experiments for the MELiSSA higher plant compartment. *Life*, **4**: 189-204.

Google Scholar

Wolverton, C and Kiss, J. (2009) An update on plant space biology. *Gravitational Space Biology*, **22**: 13-20.

Google Scholar

Zabel, P., Bamsey, M., Schubert, D. and Tajmar, M. (2016) Review and analysis of over 40 years of space plant growth systems. *Life Sciences in Space Research*, **10**: 1-16.

Google Scholar

Zhou, W., Durst, S.J., De Mars, M., Stankovic, B., Link, B.M., Tellez, G., Meyers, R.A., Sandstrom, P.W. and Abba, J.R. (2002) Performance of the Advanced ASTROCULTURE plant growth unit during ISS-6A /7A mission. *SAE Technical Paper* 2002-01-2280.

Google Scholar