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REVIEW

Microgravity and ionizing radiation on plant development in space

Microgravidade e radiação ionizante no desenvolvimento de plantas no espaço

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ABSTRACT

The decision of various countries to build permanent human bases on the Moon, Mars, or other celestial bodies has sparked growing interest in understanding how plants develop in extraterrestrial environments, particularly because of microgravity and cosmic radiation. This study aimed to describe the state of the art in research on the effects of microgravity and ionizing radiation on plant growth under space conditions. Initially, it highlights the fundamental role of plant cultivation in life support systems, including food production, oxygen recycling for long-duration missions, and more. Subsequently, the review covers studies conducted aboard space platforms such as the International Space Station (ISS), describing how the absence of gravity can alter plant developmental processes. Experimental results demonstrate that microgravity alters cell structure development, hormonal signaling, and nutrient absorption capacity, while space radiation, particularly ionizing radiation, can induce genetic mutations and cause DNA damage in plant cells, affecting plant growth and long-term viability. Reviewing this topic is essential for understanding current knowledge and advancing new research toward the use of plants in efficient and self-sustaining agricultural systems for future interplanetary missions.

Index terms: Space farming; plant physiology; mutation.

RESUMO

A decisão de diversos países em construir bases permanentes na Lua, Marte ou outros corpos celestes gerou interesse em como plantas se desenvolvem fora da Terra, devido à microgravidade e à radiação cósmica. Este trabalho descreve o estado da arte das pesquisas sobre os efeitos da microgravidade e da radiação ionizante no crescimento de plantas em condições espaciais. Cultivar plantas é essencial para sistemas de suporte de vida, produção de alimentos e reciclagem de oxigênio em missões longas. Estudos realizados na Estação Espacial Internacional (ISS) mostram que a microgravidade altera o desenvolvimento celular, a sinalização hormonal e a absorção de nutrientes. Já a radiação ionizante pode causar mutações genéticas e danos ao DNA, afetando o crescimento e a viabilidade das plantas a longo prazo. A revisão desse tema é crucial para avançar em sistemas agrícolas eficientes e autossustentáveis, essenciais para missões interplanetárias futuras.

Termos para indexação: Agricultura espacial; fisiologia vegetal; mutação.

Review

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Introduction

In recent decades, the world's leading economic powers have increased investments in space research, aiming not only to study the effects of space environments but also to establish permanent bases beyond Earth (Galvão, 2023). The United States, China, Russia, ESA (European Space Agency) member countries, Japan, and others share several objectives in this renewed human presence in space, one of the primary goals being the creation of life support structures. The Artemis Program, launched by the United States government in 2017 and coordinated by NASA (National Aeronautics and Space Administration), seeks to achieve not only the return of humans to the Moon but also the eventual exploration of Mars. This is an international cooperation program currently involving 48 signatory countries.

China also pursues ambitious goals to establish a permanent human presence on the Moon, Mars, and other celestial bodies. Regardless of the specific national or international program, cultivating plants within closed and bioregenerative life support systems is indispensable, as sustainability during long-duration missions or the establishment of permanent extraterrestrial bases depends fundamentally on it (Carillo et al., 2020). Moreover, it is vital to leverage the technological spillover from space research, such as the development of innovative cultivation techniques and the identification of stress-tolerant plant species. These advances not only support space exploration but also have significant potential to improve terrestrial agriculture under extreme environmental conditions, offering sustainable strategies to mitigate the adverse effects of climate change (Massa et al., 2008).

In addition to government space agencies, private companies such as SpaceX, Blue Origin, and Interstellar Lab have also been investing in the space sector, driven not only by economic interests but also by a desire to lead the emerging space industry (Reddy, 2018). This movement reflects a transition from space as a purely scientific frontier to an arena for economic exploration, with implications for resource mining, technological development, and, fundamentally, plant cultivation in space conditions. In this new era of commercial space exploration, known as New Space, private companies play a critical role in reaching and establishing a presence on celestial bodies. Currently, NASA lists 14 commercial companies offering payload delivery services to the Moon, referred to as CLPS (Commercial Lunar Payload Services) (National Aeronautics and Space Administration -NASA, 2020; NASA, 2023a). These various forms of collaboration highlight the complexity and importance of the subject, which can be influenced by economic, political, and technological factors.

When plant cultivation in space becomes a priority research area for sustaining long-term human presence, it requires an integrated study of Biology and Astronomy, known as Bioastronomy or Bioastronautics (Young & Sutton, 2021). Alongside the consolidation of Bioastronomy, the concept of space agriculture has also taken root. According to Wheeler (2017), space agriculture involves the development of controlled agricultural systems that minimize energy consumption and maximize resource cycling, aiming to support human life in extraterrestrial environments.

The cultivation of plants in space has a history rooted in the 20th century, with initial attempts made during the Cold War as part of the space race between the United States and the Soviet Union (Kiss, 2014). These early experiments marked the beginning of an ongoing effort to understand how plants respond to the unique conditions of space, particularly the effects of microgravity and cosmic radiation on their growth and development.

Building on this foundation, advancing the field of space agriculture requires a comprehensive understanding of current research on plant cultivation in extraterrestrial environments. This review synthesizes recent key discoveries, addresses existing challenges, and explores future opportunities in the development of bioregenerative life support systems, which are essential for sustaining life during long-duration space missions and for the establishment of permanent human bases beyond Earth. It is important to clarify that this work is a narrative review, based on an extensive survey of primary research articles and technical reports. Through this approach, the authors aim to provide a broad overview of the field, identify critical knowledge gaps, and highlight promising directions for future research.

This review aims to compile and critically analyze current knowledge on the effects of microgravity and ionizing radiation on plant development in space environments. It will present key experimental findings, explore the physiological and molecular responses of plants to these unique stressors, and identify significant gaps in the existing literature. Furthermore, the review will discuss the implications of these factors for the design of effective bioregenerative life support systems, essential for future long-duration space missions and the establishment of sustainable extraterrestrial agriculture. By integrating insights from diverse studies, this work seeks to provide a comprehensive framework to guide future research and technological innovation in space plant biology.

Recent advances in plant research in space environments

Space exploration has recently regained prominence on a global scale. The conquest of deep space has become an increasing priority for major geopolitical powers such as the United States, China, Japan, European countries, and Russia. Barreiros and Grass (2022) highlight that the U.S., through NASA, seeks to maintain its international hegemony, while China and Russia compete for a similar position in space. Additionally, the European Space Agency (ESA) has established itself as a key player in space-related research and innovation, collaborating on various exploration and scientific projects. Since its creation in 1958, NASA has led space exploration, including in the field of plant biology in extraterrestrial environments.

United States of America

Beginning in the 1950s and 1960s, both NASA and the Soviet space agency (Roscosmos) initiated experiments with plants in space, aiming to understand how factors such as microgravity and cosmic radiation affect plant organisms (Kiss, 2014). Two key milestones have marked the progress of these studies: the development of the International Space Station (ISS), which features an orbital laboratory for biological research, and future ambitions to explore the Moon and Mars, which require a deeper understanding of food cultivation beyond Earth. The ISS has been routinely used for microgravity environment studies, where continuous plant experiments have been conducted (Jules et al., 2004). This unique setting is crucial for evaluating how organisms behave and adapt to space conditions, a prerequisite for long-duration missions.

Among the most notable advances in space plant cultivation is the Veggie system, developed by ORBITEC and installed on the ISS. Designed to produce fresh food for astronauts and to investigate the effects of space variables on plants, the system employs a low-mass, low-power design to minimize crew intervention (Massa et al., 2017). Tests with lights of different spectra have provided valuable data on the development of various plant species, including lettuce and other cruciferous crops. These experiments serve as a foundation for future modifications and technological adaptations aimed at creating more efficient life-support systems.

In addition to Veggie, the U.S. has also installed a plant growth chamber called the Advanced Plant Habitat (APH), a closed cultivation environment equipped with advanced sensors that monitor variables such as temperature and humidity in real time. These features are fundamental for understanding the physiological needs of plants in space conditions (NASA, 2017). The APH system includes red, blue, and green LED lights, as well as full-spectrum white light. It is also equipped with over 180 sensors that transmit real-time data on temperature, oxygen content, and humidity levels (in the air, soil near the plant roots, and at the stem and leaf levels), among other variables. The APH was first used for experiments on the International Space Station in 2018, growing *Arabidopsis thaliana* L. and dwarf wheat (NASA, 2023b).

The United States' efforts in space exploration have expanded beyond governmental programs to include significant contributions from private companies, marking a new era of space commercialization. Among these enterprises, Interstellar Lab, founded in 2018, stands out for its focus on developing advanced technologies aimed at supporting human habitation in extraterrestrial environments such as the Moon and Mars. The company specializes in creating self-sustaining biofactories and designing safe, functional habitats through simulation technologies for astronauts (Interstellar Lab, 2024). Furthermore, Interstellar Lab is an active participant in Mission 1, led by Astrolab in collaboration with SpaceX. Scheduled for 2027, the Little Prince mission aims to transport the FLEX rover to the lunar surface and deploy vegetation capsules to investigate the effects of the lunar environment on plant phenotype and genotype (Astrolab, 2023; SpaceX, 2023). This collaboration exemplifies the growing synergy between public and private sectors in advancing space biology and sustainable extraterrestrial agriculture.

China

Like the United States, China has made significant strides, particularly in recent decades, with notable advancements in biological research in space environments (Sheehan, 2007). In 1993, the People's Republic of China significantly expanded its space capabilities with the establishment of the China National Space Administration (CNSA). During the 1990s, the country initiated its manned space program through Project 921, later known as the Shenzhou Program, which culminated in China's first manned launch in 2003. Since then, China has become the second-largest investor in the space sector. Between 2000 and 2016, its investments in spacecraft research grew from $22.6 million to $386.6 million (ChinaPower, 2020).

A key highlight of China's space campaign was the launch of the carbon-monitoring satellite, Goumang. This satellite can identify and measure plant biomass, atmospheric aerosols, and chlorophyll fluorescence. Additionally, it collects data on carbon absorption by forests through remote sensing. This initiative aims to support the country's efforts to meet its allowable carbon dioxide emissions targets by 2030 and achieve carbon neutrality by 2060 (European Space Agency, 2023).

Another milestone in China's space campaign was the development of the Tiangong space station, one of its goals being to study the behavior of living organisms in space. Tiangong consists of three main modules: the core module, Tianhe, responsible for management and control, and two experimental modules, Wentian and Mengtian. The latter two provide an environment conducive to biological research, particularly on plant organisms. Wentian, which was docked with the station in 2022, is equipped with laboratories and growth chambers that enable studies on plant growth, aging, and genetic characteristics in space. These studies provide critical data to understand how microgravity and radiation affect plant biology (Yang, 2018).

Another notable achievement is the construction of China's first lunar bioregenerative ecosystem, Chang'e 4. The Chang'e 4 lunar module, which landed on the Moon in 2019, carried the BEP (Biological Experiment Payload), a capsule weighing 2.608 kg with dimensions of 198 mm in height and 173 mm in diameter. It provided a total internal space of 0.82L, with 0.42L designated as bioactive space. The payload contained seeds of cotton, potato, *Arabidopsis thaliana* L., and rapeseed, along with fruit fly eggs and the yeast *Saccharomyces fermentati*, supplemented with 18 ml of water.

The BEP was designed to simulate a self-sustaining microecosystem, capable of providing controlled temperature and lighting conditions for the plants. Although the seeds germinated, further development was halted due to the Moon's extreme environmental conditions, such as intense radiation. This experiment demonstrated the initial feasibility of germination in lunar soil, although significant challenges remain (Xie et al., 2024).

Europe

Europe, through the European Space Agency (ESA), has made significant contributions to research on life support systems in space. The ESA currently comprises 22 member states, including Germany, Denmark, Spain, France, Greece, Italy, Portugal, the United Kingdom, Sweden, and Switzerland, among others, with Canada participating as a Cooperating State. One notable project is GreenCube, developed by Sapienza University of Rome in collaboration with other Italian institutions. GreenCube is an unmanned nanosatellite designed to study the growth of microgreens in space, selected for their adaptability to the orbital environment and high nutritional value. This project aims to demonstrate the feasibility of an autonomous cultivation system suitable for long-duration missions, such as those planned for the Moon and Mars.

Another prominent European project is MELiSSA (Micro-Ecological Life Support System Alternative), led by ESA. This initiative focuses on developing bioregenerative life support systems (BLSS) for prolonged space missions. MELiSSA is structured into biological compartments, each responsible for a specific function within the life cycle, from waste recycling to oxygen and food production. The project is a pioneer in creating a self-sustaining environment in space, aiming to reduce reliance on terrestrial resources and enhance the autonomy of crewed missions (Frossard et al., 2024).

Russia

Russia, with its longstanding tradition in space exploration dating back to the Soviet era, remains a key player in the field, conducting plant-related space experiments since the 1950s (Kiss, 2014). One of the earliest milestones was the "Oasis 1" Space Garden, installed aboard the Salyut 1 station in 1971 by Roscosmos. This experiment was the first to test plant cultivation in space, laying the groundwork for over 20 subsequent space gardens and greenhouses that continue to be used for plant biology studies (Nguyen et al., 2023).

The "Lada" space greenhouse, installed in the Zvezda Module of the ISS, has been one of the main laboratories for ongoing plant growth research. Operational since 2002, it comprises five main modules: two for vegetation, two for water storage, and one for control. The first cultivation experiment involved mizuna, a variety of *Brassica rapa* L., with astronauts managing the irrigation and harvesting of the plants. This experiment demonstrated the feasibility of successfully cultivating plants in microgravity, though challenges such as water and nutrient management still require optimization (Bingham et al., 2003).

Among these challenges, the absence of gravity prevents the uniform distribution of water, leading to overly wet or dry zones, which directly affect root hydration. Additionally, dissolved nutrients in the solution do not move efficiently, limiting their availability to all parts of the root system. To mitigate these issues, automated systems equipped with moisture sensors have been employed to monitor and adjust irrigation in real-time. Porous substrates and the use of slow-release fertilizers are also effective strategies to ensure even distribution of water and nutrients, creating a more stable and efficient cultivation environment under adverse conditions (Bingham et al., 2003).

Roscosmos, in collaboration with the ESA, also developed the BIOMEX (Biology and Mars Experiment), which aimed to study lichens, archaebacteria, bacteria, cyanobacteria, algae, fungi, and bryophytes. Conducted in the Zvezda module aboard the International Space Station (ISS) during the EXPOSE-R2 mission, the experiment exposed these organisms to a simulated Martian environment using analog regolith, subzero temperatures, water stress, and high UV radiation. The experiment evaluated survival rates, physiological activity, and growth potential across all organisms. Viability significantly decreased, particularly in multicellular organisms such as the fungus *Cryomyces antarcticus* and the lichens *Buellia frigida* and *Circinaria gyrosa*. The stability and degradation of exposed bio-signatures, including pigments, secondary metabolites, and cell surfaces, were also assessed. Some proved resilient after the experiment and upon return to Earth, though degradation of DNA molecules, alteration of cell membranes, and inhibition of byproduct synthesis were observed (De Vera et al., 2019). Conversely, bryophytes such as the alpine species *Grimmia* survived exposure to UV radiation (200–400 nm) and extreme temperatures (−25°C to 60°C) (Huwe et al., 2019).

Other contributions

Although Brazil's initiatives in this field remain modest, the country has contributed to research on plant organisms in space environments. Notably, Brazilian astronaut Marcos Pontes participated in the Soyuz TMA-8 mission to the ISS in 2006. Alongside Pavel Vinogradov and Jeffrey Williams, Pontes conducted and analyzed experiments on the behavior of organisms under microgravity. One of the mission's most recognized experiments was the study of seed germination in gonçalo-alves (*Astronium fraxinifolium* Schott), a threatened Brazilian tree species, and beans. The primary goal was to evaluate how microgravity influenced the germination process and early plant development (Embrapa Recursos Genéticos e Biotecnologia, 2006).

More recently, following the establishment of the Australian Space Agency, Australia has embarked on a series of investments in the space sector. Biddington (2021) highlights that contemporary advancements have been primarily driven by two factors: Australia's strategic geography and national security concerns shaped by political alliances.

One notable Australian contribution is the ARC Centre of Excellence - Plants for Space, an international consortium that includes organizations such as NASA, the Australian Space Agency, and several universities. This initiative develops innovative solutions for long-term space habitation and sustainability on Earth, bringing together researchers from various fields. Guided by its overarching mission, Plants for Space focuses on creating systems that enable human survival and prosperity in space while promoting plant sustainability in both extraterrestrial and terrestrial environments (Australian Research Council, 2022).

Food safety and space-driven innovations

While there are reports of plant consumption in space, such as red romaine lettuce (Massa, 2016), food safety for astronauts is paramount. Tests to ensure microbial and chemical safety, including analyses of antioxidants, anthocyanins, and phenolic compounds, are conducted to guarantee that space-grown food is safe for consumption. However, there are few studies on potential concerns related to the long- or short-term consumption of space-grown foods.

Kim and Rhee (2020) emphasize that ensuring food safety during spaceflights poses significant challenges for crew health, particularly due to the risk of bacterial contamination and foodborne infections, which can have severe consequences in confined environments like spacecraft or space stations. Despite stringent efforts to control microbial quality and optimize recycling systems during missions, microorganisms inevitably accompany crewed habitats. These microorganisms can spread through various means, including food, surfaces, water systems, and even between crew members. Moreover, studies indicate that the space environment can increase stress resistance and virulence of pathogenic bacteria, amplifying the risks associated with food safety and crew health (Ilyin, 2005).

The challenges faced by nations engaged in space exploration are immense. Space presents an extremely hostile environment for life, characterized by intense radiation and extreme temperature fluctuations that severely impact plant development. Nonetheless, the study of plant growth under these conditions has emerged as a multidisciplinary field, progressing in response to scientific, economic, and geopolitical priorities.

Advancing cultivation technologies for extraterrestrial environments serves a dual purpose. It not only supports long-term space exploration by addressing the sustainability of life beyond Earth but also drives innovation with transformative applications on our planet. For instance, space research has already inspired over 2,000 spin-offs, impacting diverse fields such as Computational Technology (e.g., OpenStack, NASTRAN structural analysis software), Industrial Production (e.g., PS300 lubricant, Anthropometric Source Book), Health and Medicine (e.g., ventricular assist devices, LASIK, cochlear implants), and Transportation (e.g., anti-icing technology, runway/road surface grooving) (NASA Spinoff, n.d.).

Agriculture stands to benefit greatly from such advancements. Spin-offs like GPS correction technology for tractors and agricultural machinery, along with sophisticated water purification systems, exemplify how space-driven innovations can enhance farming efficiency and sustainability on Earth. As the exploration of plant cultivation in space continues, it holds the promise of addressing global challenges while paving the way for humanity's future beyond our planet.

Microgravity and its effects

Microgravity, often defined as a condition in which the force of gravity is significantly weaker than on Earth, typically about one-millionth (10^{-6}) of Earth's gravitational pull, is one of the most critical factors affecting plant growth and development in space environments. Unlike terrestrial conditions, where a constant gravitational vector governs key physiological processes such as water and nutrient transport, cell orientation, and growth direction, microgravity removes these gravitational cues, forcing biological systems to adapt to an altered environment. This absence of a consistent gravitational stimulus profoundly influences plant morphology, physiology, and metabolism, often resulting in altered cell structure, nutrient uptake, and growth patterns (Wolverton & Kiss, 2009; Herranz et al., 2013). Understanding plant responses to microgravity is therefore essential not only for advancing fundamental biological science but also for the development of agricultural technologies capable of sustaining human life during extended space missions.

Experiments conducted both on space stations and in terrestrial simulations have yielded significant insights into the effects of microgravity on plants. These studies also indicate that the space environment encompasses more than just microgravity, often including factors like cosmic radiation that are difficult to isolate. This challenging environment induces changes in cellular and molecular processes that alter plant growth. Thus, a holistic approach is necessary to fully understand the conditions plants face in space. The interaction of these environmental factors can result in unforeseen changes in plant development, directly influencing their viability for use in bioregenerative systems (Shymanovich & Kiss, 2022).

In short-term microgravity exposure, such as during parabolic flights or sounding rocket missions, plants respond with cellular signaling, including calcium and lipid signaling. In longer-term exposures, conducted in laboratories or space stations, the extended evaluation period allows for the study of metabolic adaptation, oxidative stress responses, and tropic reactions in plants (Zheng, Han, & Le, 2015).

Preliminary studies have shown that microgravity simulation equipment, such as clinostats, random positioning machines (RPM), and magnetic levitation devices, can be effectively used under laboratory conditions to study plant responses to altered gravity. These devices function by creating a balance between centripetal and centrifugal forces, thereby nullifying the perceptible gravitational effect on biological samples (Kiss, 2014; Kiss et al., 2019). For instance, Grudzińska et al. (2024) investigated simulated microgravity using an RPM on plants from the *Fabaceae* family and observed a reduction in shoot biomass alongside increased germination rates in white clover. Similarly, Pourhabibian et al. (2021) reported that *Hyoscyamus niger* L., a medicinal plant, produced higher levels of tropane alkaloids under clinostat-simulated microgravity conditions, highlighting potential applications for pharmaceutical production during extended space missions. Despite their usefulness, these simulation methods are still limited in fully replicating the complex and continuous microgravity conditions experienced in space. Consequently, experiments conducted aboard space stations remain the most reliable means of validating plant responses, as they allow direct observation of how microgravity influences cellular and physiological processes (Zheng, Han, & Le, 2015).

It is known that microgravity can alter various physiological processes in plants. The process of guttation and the growth of rice seedlings were found to differ aboard the Chinese space laboratory TG-2 compared to similar experiments on Earth. Guttation was significantly higher under microgravity, particularly under long-day photoperiods, suggesting that this condition promotes water exudation through the leaves, potentially influencing nutrient absorption and distribution (Wang, Han, & Zheng, 2018). Zaitialia et al. (2023) studied the effects of microgravity on pepper (*Capsicum annuum* L.) seeds and observed changes in capsaicin content and plant growth. While germination rates were similar between space-grown and Earth-grown plants, a slight reduction in capsaicin in space-grown plants suggests that microgravity may influence the production of secondary compounds. This knowledge is vital for selecting crops optimized for producing food and medicine in space environments.

Microgravity not only affects the physiological development of plants but also their responses to environmental stresses and interactions with pathogens (Ryba-White et al., 2001). For instance, soybean (*Glycine max* (L.) Merr.) seeds sent aboard the Space Shuttle Columbia showed increased susceptibility to the pathogen *Phytophthora sojae* and elevated ethylene levels in plants grown under microgravity, indicating that the absence of gravity can alter plant defense mechanisms.

Morphological differences have also been observed in experiments conducted in the absence of gravity. Baranova et al. (2019) studied "Super-Dwarf" wheat (*Triticum aestivum* L.) and found no significant visual differences between space-grown and Earth-grown grains. However, microscopic analysis revealed cellular distinctions associated with microgravity. Increased grain weight in space conditions suggests that microgravity may positively influence biomass accumulation, possibly due to changes in the cytoskeleton and cell wall. Sweet potato plants grown in space showed faster growth, with a higher number and length of adventitious roots compared to terrestrial controls. There was also a more random distribution of amyloplasts and increased concentrations of soluble sugars and starch. Thus, the interaction between microgravity and resource availability, such as carbon dioxide and oxygen, influenced plant metabolism (Mortley et al., 2008).

Minimal meiotic variations were observed in peas (*Pisum sativum* L.) and wheat (*Triticum compactum* (Binkel)) grown under microgravity. However, chromosome structure showed no differences between space-grown and Earth-grown plants, suggesting that the changes are more functional than structural (Samatadze et al., 2018).

In long-term experiments conducted with crops such as maize, wheat, barley, and rice, plants were observed to complete their life cycles and produce viable seedlings in space environments, even after extended periods. Chandler et al. (2020) noted that despite adverse conditions, plants adapt well, making them viable for the development of indoor cultivation technologies in space to support future deep-space missions.

In summary, understanding the effects of microgravity on plant growth is not only relevant for biological studies but also critical for future space missions and efforts to establish permanent human bases in deep space. The interaction between microgravity, radiation, and water availability demands a comprehensive approach capable of predicting and mitigating the challenges plants will face in extraterrestrial environments. Results from experiments such as Mortley et al. (2008) and Samatadze et al. (2018) suggest that understanding the impacts of microgravity on cellular processes will be crucial for ensuring the genetic health of plants during long-duration space missions. While microgravity may promote germination in some species, it can also hinder overall growth, underscoring the need to develop adaptive strategies for cultivation in space environments to ensure a reliable food supply for astronauts.

Ionizing radiation and its effects

Cosmic ionizing radiation poses another significant challenge to the adaptation and use of plants in long-duration space missions. Unlike Earth, where the atmosphere and magnetic field offer effective protection against most cosmic radiation, space environments expose plants to a range of ionizing radiation sources, including high-energy particles from solar winds, galactic cosmic rays (GCR), and solar particle events (SPE). These radiation types, when combined with the absence of gravity, create a uniquely hostile environment that can induce both direct and indirect effects on plant growth, development, genome stability, and physiological processes (Vandenbrink & Kiss, 2016; Prasad et al., 2021).

Studies indicate that while plants are more tolerant to radiation than animals, the effects of cosmic radiation on plant functions are not yet fully understood (Mohanta et al., 2021). Radiation can induce genetic variability by causing mutations in seeds, meristems, and reproductive cells, resulting in new genotypes and phenotypes. While this can be beneficial as a new technology for plant breeding on Earth, it is undesirable for cultivating plants in space. In space, direct damage to mature plant tissues can occur, affecting their morpho-anatomy and metabolism and compromising essential physiological processes like photosynthesis and reproduction (Arena et al., 2014).

The technology of sending seeds into space, exposing them to microgravity and ionizing radiation, has been a valuable tool for genetic improvement programs, particularly in China. Since the 1980s, new plant varieties have been developed from space-induced mutations in that country. A notable example is the indica-japonica rice variety developed in 1987, which has a high grain filling rate (Ma et al., 2021). Experiments conducted in space and in terrestrial laboratories simulating space radiation conditions have provided critical data on how different plants respond to varying radiation doses.

With the entry of private companies into the space economy, the use of space environments for experiments has expanded considerably. The number of scientific studies investigating the effects of ionizing radiation on higher plants has increased, particularly with economically important plants, aiming to compare space and terrestrial environments (De Micco et al., 2022). For example, rice (*Oryza sativa* L. cv. Nipponbare) seeds sent into space for 13 and 20 months showed a sharp decline in germination rates, with 48% germination after 13 months and only 8% after 20 months, compared to 96% and 76% in terrestrial conditions. Significant changes in gene expression were also observed, including an increase in glycolysis-related genes and a reduction in long-term mRNA expression (Sugimoto et al., 2016).

Pagliarello et al. (2023) reported that tomato (*Solanum lycopersicum* L.) plants exposed to doses of 0.5 Gy and 5 Gy still produced viable seeds, but higher doses, such as 30 Gy, severely affected molecular and physiological functions, significantly reducing the number of flowers and fruits. In the "Rocket Science" project, arugula (*Eruca sativa* L.) seeds stored aboard the International Space Station for six months exhibited delayed seedling development and accelerated seed aging upon return. Chandler et al. (2020) noted that space radiation induced the expression of DNA repair and thermal stress response genes, compromising plant vigor.

In another study, Luo et al. (2007) investigated genomic polymorphisms in rice plants derived from seeds exposed to space aboard the Shenzhou-3 spacecraft. They observed genetic variations in 30.2% of the plants compared to terrestrial controls. Seeds exposed to HZE (High atomic number and Energy) particles exhibited phenotypic changes, such as variations in plant height and grain size, with more stable mutations observed in subsequent generations.

Zhang et al. (2022) exposed mizuna mustard (*Brassica rapa* L. var. japonica) seeds to GCR2 radiation, used to simulate space radiation effects. Irradiated plants showed high germination rates but exhibited leaf deformities, especially after exposure to doses of 40 cGy and 80 cGy. Additionally, a 17% reduction in average root length was observed compared to the control group.

In conclusion, research on the effects of ionizing radiation remains essential for understanding how plants can become tolerant to grow in enclosed and extraterrestrial environments. Developing resilient crops for these extreme conditions will enable advancements in long-duration space missions and the eventual colonization of other planets. With the increasing involvement of various countries and public and private companies in the space sector, new opportunities are emerging for conducting experiments and developing novel plants. Understanding the molecular mechanisms that confer radiation tolerance is crucial for creating efficient crops capable of sustaining human bases beyond Earth (De Micco et al., 2022).

Conclusions

Space exploration demands resilient crops to sustain human life beyond Earth. This review showed that microgravity disrupts root orientation and cell structure, while ionizing radiation causes genetic damage, together impairing plant development. Future research must integrate emerging technologies into breeding programs to create cultivars adapted to extraterrestrial conditions. Interdisciplinary collaboration is crucial to scale innovations. Importantly, advances in space agriculture can also benefit terrestrial farming, especially in regions facing resource scarcity and climate change.

Author contribution

Conceptual idea: Arantes, J.H.B.; Fávero, A.P.; Methodology design: Arantes, J.H.B.; Lopes, M.A.; Fávero, A.P.; Data collection: Arantes, J.H.B.; Fávero, A.P.; Data analysis and interpretation: Arantes, J.H.B.; Lopes, M.A.; Fávero, A.P.; and Writing and editing: Arantes, J.H.B.; Lopes, M.A.; Fávero, A.P.

Data Availability Statement

Data available upon request to authors.

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