

Chapter

Perspective Chapter: Seed Priming – A Novel Approach to Combat Microgravity Associated Stress Management in Plants

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Abstract

The colonization of space presents a significant challenge due to the difficulty of cultivating crops in microgravity environments. For long-term space exploration and extraterrestrial settlements to become viable, establishing reliable methods of food production beyond Earth is critical. However, the effects of spatial factors on plant physiology—and their subsequent impact on crop yield—remain incompletely understood. Gravity is a fundamental regulator of plant development, influencing essential cellular processes such as cell division and growth. Alterations in gravitational conditions can profoundly affect both developmental pathways and physiological behaviors in plants. Notably, plant hormones exhibit differential responses to microgravity. For instance, cytokinin displays a distinct distribution pattern in microgravity, contrasting with auxin, which orchestrates directional root growth through a gravity-dependent signaling network. Emerging research has identified significant changes in gene expression under microgravity conditions, particularly in genes associated with the tricarboxylic acid (TCA) cycle, oxidative stress, carbohydrate metabolism, plant defense mechanisms, and DNA methylation (especially at the 5-position of cytosine). Short-term spaceflight experiments in low-Earth orbit have demonstrated disruptions in plant redox balance, stress-related protein expression, energy and amino acid metabolism, hormonal activity, and transcriptional regulation. Intriguingly, seeds primed prior to microgravity exposure exhibit enhanced resilience to space-induced stress, suggesting a promising strategy to improve plant adaptability in extraterrestrial environments. These findings underscore the need for further research to optimize agricultural systems for space colonization.

Keywords: plant growth in space, microgravity, seeds priming, stress response, gene expression

1. Introduction

Fresh sources of water, minerals, and human habitation can be found in space [1–3]. To sustain space travel and colonization, the ability to generate food in extraterrestrial settings is critical. Plants evolved on Earth with the help of gravity,

photoperiod, barometric pressure, and other signals, and plants that live on space stations or other planets would face stressors that have never been seen before [1–4]. Plants are essential components of life support systems that are required to keep humans alive during prolonged space travel and on exoplanets. Plants thrive in space stations and have potential as food and energy sources. These plants may yield low quality or quantity of food under microgravity stress conditions [5–7]. The primary model organisms for investigating space life science over the last few decades have been rice, *Arabidopsis*, corn, fruit flies, and mice [8, 9]. Vegetables could be used by humans as a dependable food source on long-duration space missions. Previous research has shown that plants may modify their metabolic networks to adapt to space flight. The phytochemical components of fresh vegetables that contribute to the reduction of risks are essential for such applications [9, 10]. You need to be knowledgeable about how plants grow and develop in low gravity for space farming to be successful. Because gravity is one of the key factors that distinguish the environment on Earth from that in space or on exoplanets, it is also crucial for plant space biology [10].

Plants have not evolved mechanisms to cope with changes in gravity. To gain insight into how they respond to spaceflight conditions, researchers have investigated the biological pathways and processes that plants engage in while in orbit. Most studies exploring the effects of microgravity on plant growth have concentrated on specific responses, like gravitropism and gravimorphogenesis. In contrast, relatively few investigations have attempted to confirm whether plants can successfully complete a full seed-to-seed life cycle in space. Additionally, studies that have explored seed production in microgravity often pursued different objectives, such as evaluating seed quality or identifying the factors responsible for reproductive issues [11–13]. Due to the rising incidence of climate variability and extreme weather events, plants are more likely to experience multiple abiotic stresses throughout their lives rather than a single stress occurrence [14, 15]. To survive and adapt under such harsh conditions, plants need to develop effective mechanisms to cope with repeated stress exposures. Studies have shown that subjecting plants to mild biotic or abiotic stress beforehand can help them better endure more intense stress later, as demonstrated by Ramírez et al. [16] and Walter et al. [17]. This phenomenon, referred to as “plant priming,” is linked to “plant stress memory” and has been found to enhance stress tolerance [15, 18]. While the term “plant priming” is commonly applied in cases involving biotic stress and chemical inducers, the same adaptive response is often called “hardening” or “acclimation” when related to abiotic stress [19–23]. This review explores recent insights into how priming influences plant development, both under Earth conditions and in microgravity.

1.1 Microgravity and plants

Studies on plants in space have a long history [14, 15, 18, 19]. Plants are regarded as essential tools for identifying gravity-related biological processes because of the link between plant architecture and gravity [19]. The completion of the plant cycle has additional space restrictions because of factors such as microgravity. The course of the cell cycle, mitotic index, and phase length were significantly altered in groundbreaking space and terrestrial research on lentil seedlings. There was variation in cell proliferation and growth rates between the Earth-grown and space-grown *Arabidopsis* seedlings [12, 13, 20–23]. In addition to plant-level priming, stress memory, and cross-stress resistance, seed priming plays a vital role in helping plants cope with adverse conditions. The process of imbibition marks the beginning of cell

division and expansion and includes three phases of seed development: rapid water absorption, stabilization of water content, and continued water uptake [24].

1.2 Effect of microgravity on seed germination

The combined impact of multiple stressors is likely responsible for the diminished efficiency of various biological processes and the lower quality of plant structures formed in space. Among the primary challenges to plant development in space environments are the use of imbalanced nutrient solutions and lighting conditions that are suboptimal in both quality and intensity. These unfavorable environmental factors can impair plant growth directly and also heighten plant sensitivity to microgravity [25]. Research focusing on nutrient uptake in plants has revealed that absorption rates may increase, decrease, or remain unaffected, depending on factors such as the specific nutrient involved and the plant species [25–27].

In a recent review, Wolff et al. [27] concluded that although there are indications that plant nutrition is affected by the space environment, available information is limited and inconclusive [28, 29]. Merkys and Laurinavicius [30] used *Arabidopsis thaliana* in their first successful seed-to-seed experiment conducted in microgravity [22, 31]. Some viable seeds were observed, but the majority of seeds had nonviable embryos. *Brassica rapa* was the subject of a second successful experiment in space [32, 33]. Brassica seeds were found to have abnormal starch grain deposition, reduced protein, and fewer cotyledon cells, while being healthy and viable.

The challenging conditions of microgravity are more likely to account for the outcomes observed in both studies. Several researchers have reported changes in starch accumulation in a variety of plants grown in space—*Arabidopsis*, *Lepidium* roots, pepper plants, and maize root columellae [34–38]. A recurring issue in space-based plant research is the elevated production of ethylene, which can negatively impact plant growth. Experiments using clinostats [39] and those conducted in space have shown increased ethylene synthesis in plants [40]. Notably, Kuang et al. [41] reported exceptionally high ethylene concentrations (800–1200 ppb) aboard the Mir space station during a Brassica experiment. Remarkably, Brassica plants managed to produce seeds under these conditions, whereas wheat plants grown in the same environment failed to do so [42]. However, when seeds are bioprimered with plant growth-promoting *rhizobacteria* (PGPRs), the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) is efficiently broken down by ACC deaminase, helping to regulate ethylene synthesis [43]. The researchers emphasize that achieving reproductive success in space requires not only a robust mother plant capable of supporting an energy-intensive process but also the successful completion of every stage of reproduction [25, 26].

The harsh conditions associated with microgravity—rather than the mere absence of gravity—are increasingly recognized as key contributors to the reduced efficiency of biological processes and the impaired quality of plant structures grown in space. Factors such as imbalanced nutrient media, suboptimal lighting, and heightened ethylene production present major stressors that compromise plant development and reproductive success in extraterrestrial environments [25, 34–38]. These stressors, individually and in combination, can drastically increase plant sensitivity to microgravity [25], challenging their ability to survive and complete their life cycle.

Ensuring strong initial growth—from dormant seed to viable seedling—is thus a critical step for completing the plant reproductive cycle in such resource-limited and stress-intensive environments [25, 44, 45]. While dry seeds are naturally resilient to adverse conditions, their resistance wanes quickly during germination, making the

early seedling stage highly vulnerable to the types of physical and chemical stresses commonly encountered in space [25, 26]. Seedling survival under these challenging conditions hinges on three key attributes: rapid establishment in the substrate, the capacity to develop morpho-functional adaptations to cope with stress (including drought and biotic interactions), and a fast progression through early developmental stages. These traits, which are genetically determined, are heavily influenced by environmental stressors, such as those present in microgravity settings [26].

To counteract these effects, seed priming emerges as a vital strategy to support normal germination and seedling establishment under stress conditions, including those encountered in space. Research has demonstrated that hydropriming significantly improves germination rates and early seedling growth in maize (*Zea mays L.*) during drought stress [46], while hydroprimed cotton seeds (*Gossypium hirsutum L.*) exhibit enhanced growth and yield under limited water availability [47]. Under similar stress conditions, melatonin-primed rapeseeds show improved germination and early development. These findings highlight the potential of seed priming not only for terrestrial agriculture but also as a key tool to enhance plant performance in the extreme conditions of space.

1.3 Microgravity stress and breeding approaches

The microgravity environment in space disrupts several physiological and developmental processes in plants, presenting a unique stress condition not encountered on Earth. These disturbances include altered cell division, disrupted hormonal signaling, reduced nutrient uptake, and compromised reproductive development. Such stress not only affects plant morphology but also impairs yield and seed viability, crucial parameters for sustainable space farming [25, 38, 48].

To counteract these negative effects, plant breeding and biotechnological approaches are emerging as powerful tools. Traditional breeding, molecular breeding, and modern genome-editing techniques like CRISPR/Cas9 can be harnessed to develop stress-resilient genotypes capable of thriving under microgravity and other extraterrestrial stressors. These approaches focus on identifying and integrating traits that enhance germination, growth, and reproduction under space-relevant stress conditions. For example, identifying quantitative trait loci (QTLs) linked with traits such as efficient nutrient use, ethylene regulation, and enhanced antioxidant production could support the development of elite cultivars adapted for space. Similarly, marker-assisted selection (MAS) enables the rapid introgression of desirable traits, including enhanced stress memory and efficient hormonal responses, into target cultivars. Emerging omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, have revealed stress-responsive gene networks and metabolic pathways triggered during spaceflight. These insights can guide the selection and engineering of crops with enhanced gravitropic insensitivity, stress hormone balance, and improved reproductive resilience [12, 13, 33, 43]. Furthermore, leveraging plant-microbe interactions through inoculation with beneficial microorganisms such as plant growth-promoting rhizobacteria (PGPRs) offers a promising avenue for improving plant performance in space. These microbes can mitigate the accumulation of ethylene by metabolizing its precursor ACC, enhancing root architecture and nutrient uptake under stress [43]. Combined with priming strategies, this represents a holistic approach to increasing plant robustness in extreme conditions.

Therefore, integrating breeding approaches with physiological priming and microbial inoculation can enable the design of multi-stress-tolerant plants, capable

of completing their full life cycle and producing viable seeds in microgravity. This integrative strategy is essential for the success of bioregenerative life support systems on long-term space missions and planetary colonization efforts.

1.4 Jasmonic acid signaling and microgravity stress

Researchers at the University of Zurich have discovered that a specific plant hormone may be crucial for enabling plant growth in environments with limited nutrients and gravity, potentially paving the way for future extraterrestrial agriculture. The hormone strigolactone plays a key role in promoting symbiosis between plant roots and beneficial fungi, a relationship that enhances plant development and may prove effective even under extreme conditions, such as those found on the Moon. Secreted by plant roots, strigolactone supports mycorrhization, thereby boosting growth even in nutrient-poor soils. Unlike auxin, cytokinin, another plant hormone, exhibits distinct distribution patterns in microgravity compared to Earth. While auxin is known for its role in gravity sensing within root zones, cytokinins often act as regulatory counterparts to auxin [49, 50].

Hormonal priming has shown promise in improving plant performance under stress. For instance, treatments with auxin significantly enhanced wheat growth and led to greater grain yield compared to untreated plants [49–53]. Additional studies revealed that tomato seedlings treated with copper- and zinc-based elicitors experienced gene expression changes associated with the jasmonic acid (JA) signaling pathway, which is linked to stress responses such as pathogen attacks, hormone signaling, and mechanical injury. Notably, the *Solyc12g009220.2* gene was upregulated in these treated plants [54]. Moreover, transcript levels of various auxin transporter genes, including *Solyc01g007010.3*, a RING-type E3 ubiquitin ligase, were significantly altered. Genes involved in the abscisic acid (ABA) signaling pathway were also found to be upregulated in primed seedlings, indicating the critical role of hormonal regulation in stress adaptation and development [54].

Genes associated with jasmonic acid-mediated signaling pathways play a crucial role in regulating plant defense mechanisms and responses to various stress factors (**Figure 1**). Specifically, genes involved in wound response and the regulation of stimulus response are modulated by jasmonic acid (**Figure 1**). These findings have potential implications for developing drought-resistant crop varieties. Enhancing plant resilience through stress-preconditioning treatments promotes healthy growth and may serve as a foundation for future research on plant priming and stress memory, particularly for enabling seed production under microgravity conditions.

1.5 Effect of microgravity on the citric acid cycle

Spaceflight alters the mitochondrial activity [30, 48] in plants. TCA flux is dramatically altered by numerous abiotic stressors [55]. In *Arabidopsis*, changes in TCA cycle-related genes have been validated using transcriptome analysis [24]. Because the adaptation of plants to abiotic stress is regulated by TCA, it is regarded as a crucial physiological response. Amino acids, fatty acids, and secondary metabolites can be synthesized from TCA cycle intermediates [25, 55]. According to our research, some of the acid content of organic acids include aconitic acid, alpha-ketoglutarate, aconitic acid, maleate, succinate, fumaric, fumuvic, pyruvic, citrate, and isocitric acid. Hell and Stephan [56] noted that numerous physiological and biochemical events rely on the presence of citric acid, which is an essential organic acid [26]. Citric acid has been

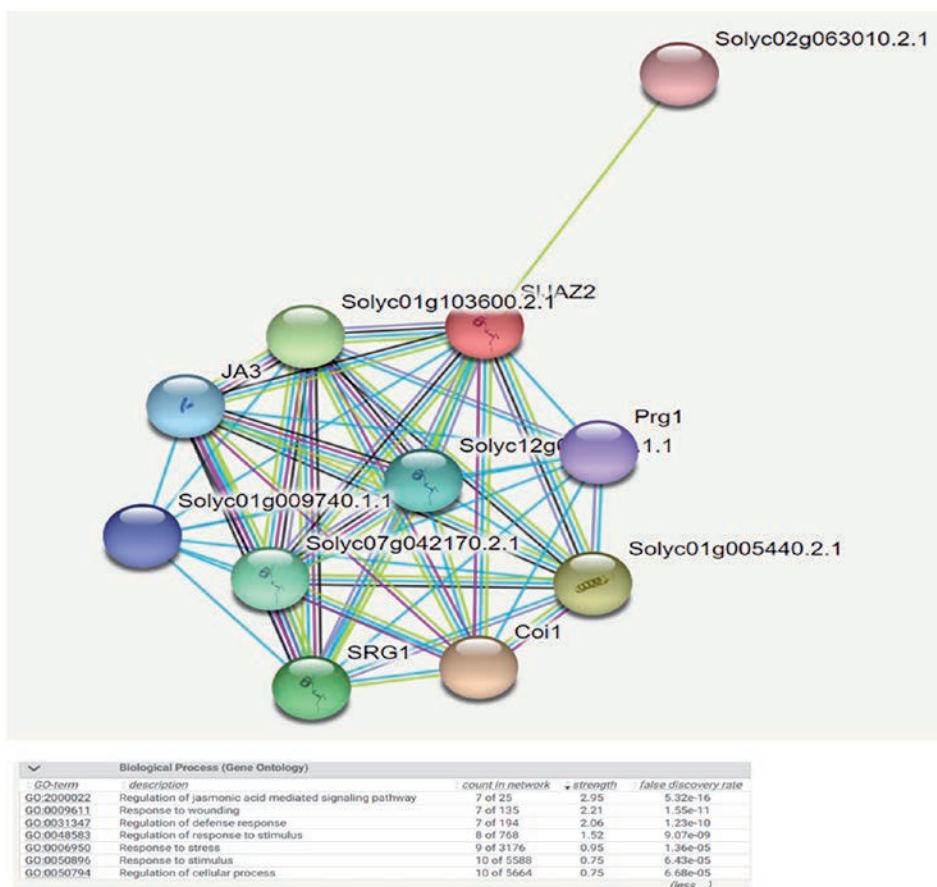


Figure 1. String map of the JA3 (Jasmonic acid) with other pathways in Tomato. Where JA3 is Jasmonic acid linked to seven pathways for the regulation of various genes in response to stress or defense.

linked to aluminum poisoning, iron stress, heavy metal stress tolerance, and salt stress [27]. Citric acid level is a good indicator of the ability of rice cultivars to withstand spaceflight at different ages [48]. A comparable response has been observed in primed Arabidopsis seeds, where elevated levels of carboxylic acids have been shown to strengthen defense mechanisms through intricate signaling networks. Elevated levels of tricarboxylic acid (TCA) are related to an increase in plant resistance stimulated by inducers [57]. Similarly, Copper- and zinc-based elicitors have been shown to induce carboxylic acids in okra seeds [58].

1.6 Genes related to oxidative stress-related genes

Antioxidants and ROS-scavenging/detoxifying enzymes must maintain flexible redox states to mitigate oxidative damage [59–64]. During spaceflight, plants tend to express more ROS- and redox-associated genes compared to those grown under Earth's gravity. This upregulation reflects an adaptive response to the novel and potentially stressful environment of microgravity [32, 64–66]. Reactive oxygen species (ROS), produced in various subcellular compartments, elicit a wide range of physiological, biochemical, and molecular responses in plants [51, 61–64, 67–70]. To

cope with the oxidative stress induced by microgravity, plants may engage multiple ROS-response mechanisms. This environmental unfamiliarity prompts plants, being sessile organisms, to deploy sensitive and adaptive strategies for metabolic regulation. Soluble sugars play a critical role in plant metabolism and structural integrity. In microgravity, sugar signaling interacts closely with ROS signaling to modulate the plant's redox state [71, 72]. While some aspects of sugar metabolism may adapt to spaceflight conditions—evident in crops like rice—the precise mechanisms can differ from terrestrial systems.

As nutrient and metabolite signaling molecules, soluble sugars can influence hormone signaling pathways, thereby affecting gene expression and protein abundance. Our previous study identified several significantly expressed genes involved in ROS scavenging under metal treatment, including prephenate/arogenate dehydrogenase (Solyc09g011870.2), Fe2OG dioxygenase (Solyc12g006370.2), and L-ascorbate oxidase (Solyc04g054690.3). These findings highlight the modulation of oxidative stress responses in tomato seedlings subjected to Cu and Zn treatments, which could offer insights into similar mechanisms under spaceflight-induced stress. In seeds, ROS act not only as damaging agents but also as signaling molecules during germination [73]. Oxidative modifications of storage proteins serve as triggers for reserve mobilization. For instance, eggplant seeds exhibited an increase in ROS levels after 24 hours of hydropriming, followed by a gradual decline [74]. Interestingly, ROS levels post-dry-back were even lower than in dry seeds, suggesting an effective antioxidant response and potential memory of oxidative stress, which could be relevant for seedling establishment in microgravity conditions [75].

1.7 Differential gene expression in plants in microgravity

Experiments conducted aboard the International Space Station (ISS) have demonstrated that spaceflight significantly alters gene expression patterns in plants. Although the full extent of these transcriptomic changes is still being unraveled, research indicates that DNA methylation at the fifth cytosine position, a critical epigenetic modification, plays an essential role in helping plants adapt to both terrestrial and extraterrestrial stress conditions. These findings suggest that exposure to spaceflight activates complex regulatory systems that could be leveraged to enhance plant resilience and performance beyond Earth. As more transcriptomic and proteomic data emerge from ISS-based plant studies, consistent trends are becoming evident. Genes that are differentially expressed during spaceflight influence a range of biological pathways, including redox regulation, stress response, energy and hormone metabolism, amino acid biosynthesis, and transcriptional control [9, 50, 65, 76–81]. While the ISS can support relatively normal plant development in orbit, this is only possible due to extensive metabolic and structural reprogramming induced by microgravity.

For instance, in *Arabidopsis thaliana*, microgravity-induced oxidative stress has been found to activate molecular chaperones, which protect cellular integrity [82]. Seeds of *Eruca sativa* that were exposed to 6 months of microgravity exhibited delayed growth and heightened sensitivity to senescence, along with reduced expression of genes linked to transcription and translation [83]. Similarly, seedlings of pea, maize, oat, mung bean, and sunflower grown in space showed impaired cell division, altered mitotic activity, and disrupted auxin transport in root regions. These observations confirm that spaceflight acts as a severe abiotic stressor, leading to broad genomic reprogramming that influences plant growth, development, and yield, as well as cellular structures like cell wall composition, as seen in *Arabidopsis*

[26, 84–86]. Parallel responses have also been documented in metal ion-primed tomato seedlings, where oxidative bursts triggered by copper and zinc-based elicitors resulted in the upregulation of WRKY transcription factors, including WRKY81. This particular transcription factor modulates jasmonic acid signaling and regulates genes involved in stress adaptation and biosynthesis (**Figure 2**).

These insights offer valuable direction for space agriculture breeding strategies. By identifying gene variants and regulatory sequences associated with traits such as improved oxidative stress resistance, optimized hormone signaling, and stable cell division, scientists can develop cultivars better suited for growth in microgravity. Moreover, integrating epigenetic and transcriptomic data into breeding pipelines—using tools like CRISPR-Cas9 and marker-assisted selection—could accelerate the creation of space-adapted crop varieties. Ultimately, the molecular insights gained from spaceflight experiments not only deepen our understanding of plant stress physiology but also provide a foundation for next-generation breeding aimed at supporting life beyond Earth.

Early gene expression studies indicated that the metabolic adaptation of plants to spaceflight relied on changes in calcium signaling, but they could not identify a single

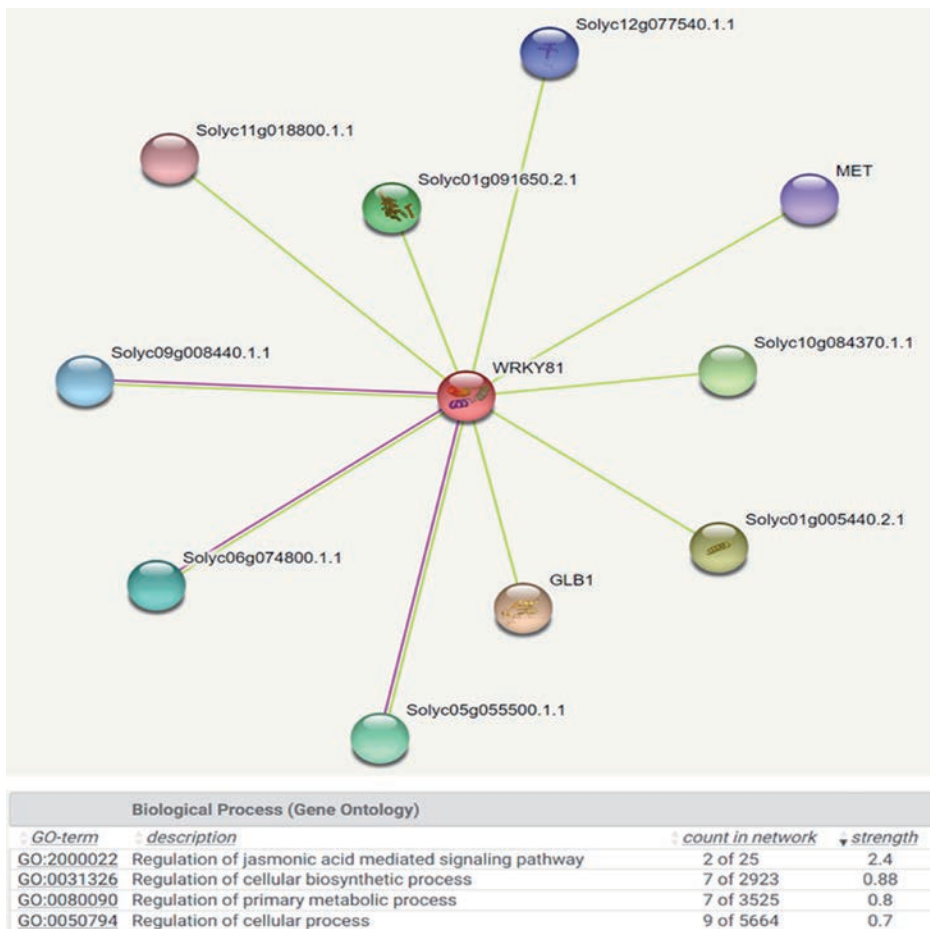


Figure 2. The WRKY related with other pathways in Tomato. Where, WRKY81 is transcription factor regulating the Jasmonic acid-mediated signaling pathway.

or specific environmental stress that characterized spaceflight [37–40, 42, 43]. In addition to the well-documented changes in gene expression, plants aboard the ISS also exhibit notable shifts in DNA methylation patterns. This supports the idea that plant adaptation to spaceflight involves epigenetic regulation, aligning with findings that gene regulatory networks are influenced by environmental stressors and ecological factors on Earth [87–96]. Numerous studies have demonstrated the central role of epigenetic modifications in regulating gene activity [97, 98] with DNA methylation emerging as a key mechanism by which organisms adjust to environmental stimuli through stable, heritable changes in gene expression. These modifications can become embedded in the genome and may be transmitted across generations [99–101]. Despite mounting evidence that DNA methylation is responsive to terrestrial environmental changes, few studies have explored this process in space. However, some research has examined plants grown on Earth from seeds previously exposed to spaceflight, as well as seedlings that experienced 60 hours of spaceflight aboard a satellite. These studies contribute to the growing body of work on spaceflight-associated epigenomic responses in plants [102]. Thanks to advancements in space-based research, well-replicated transcriptomic studies can now be performed aboard the ISS, offering deeper insights into the global transcriptional landscape of *Arabidopsis thaliana*. Transcriptomic data now span multiple cultivars, cell types, and growth conditions [103], revealing a substantial number of differentially expressed genes in space-grown plants. Interestingly, many of these genes encode proteins whose functions are still not fully understood, highlighting the need for further investigation [104].

2. Roots development in spaceflights and auxins

Beyond the well-established alterations in gene expression, plants grown aboard the ISS also demonstrate significant changes in DNA methylation patterns. This observation reinforces the idea that epigenetic regulation plays a key role in how plants adapt to spaceflight, consistent with the understanding that gene regulatory systems are influenced by environmental stressors and ecological conditions on Earth [105–107]. Extensive research has confirmed the importance of epigenetic mechanisms, particularly DNA methylation, in modulating gene expression [100–103]. DNA methylation enables organisms to respond to environmental cues by introducing stable and potentially heritable genetic modifications, which may be retained across generations [102–104]. Although there is substantial evidence supporting DNA methylation as a response to environmental factors on Earth, only a limited number of studies have examined this process in space conditions. Some of these studies include analyses of plants cultivated on Earth from spaceflight-exposed seeds, as well as seedlings subjected to 60 hours of microgravity during satellite missions. These findings are gradually expanding the field of space-related epigenomic research in plants [105].

With recent advancements in space-based research infrastructure, comprehensive and reproducible transcriptome analyses are now feasible aboard the ISS. These studies provide valuable insights into the transcriptional dynamics of *Arabidopsis thaliana* under spaceflight conditions. A growing body of transcriptomic data covers various plant cultivars, cell types, and environmental conditions [106], revealing numerous differentially expressed genes in space-grown plants. Notably, a significant portion of these genes encode proteins with yet-to-be-determined functions, indicating a promising area for future exploration [107].

IAA5 and IAA1 have been linked to several key developmental processes, including pollen maturation, lateral root initiation, auxin-mediated signaling, root branching, and gravitropic responses (**Figure 3**). Plant organ systems, shoot system development, and postembryonic development are also associated with IAA. The most

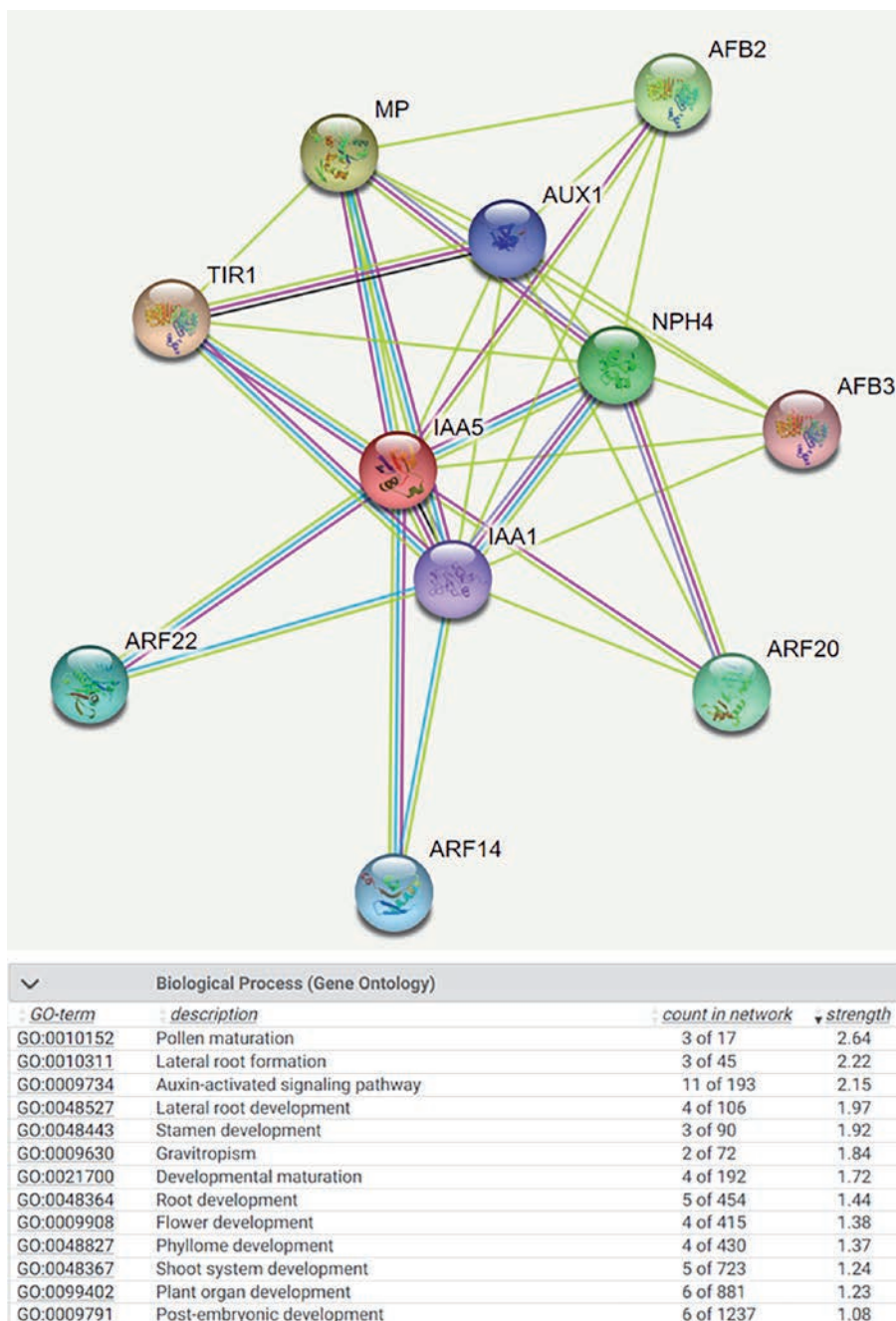


Figure 3. The IAA5 and IAA1 interaction with other pathways in primed seedlings in Tomato.

important pathways regulated by IAA were root and lateral root development (**Figure 3**). Auxins induce root formation in seedlings [108–111]. Primed plants have an induced auxin level to form root systems. Earlier studies have shown that copper and zinc treatments led to significant alterations in the transcript levels of several auxin transporter-related genes, such as *Solyc01g007010.3*, which encodes a RING-type E3 ubiquitin ligase. Copper and Zinc treatment of seeds induces auxin levels in seedlings and helps root formation in a microgravity environment [54]. Other hormones related to root development were also upregulated by priming tomato seedlings. Cu and Zn induce a priming mechanism in the seed to make the seeds more sustainable under microgravity environmental stress during growth and development.

2.1 Engineering the future of cosmic cultivation: Advanced breeding paradigms for space agriculture

The formidable challenge of establishing sustainable agriculture in space demands revolutionary breeding strategies that transcend terrestrial limitations. Microgravity, ionizing radiation, and resource scarcity necessitate a fundamental reimagining of crop development protocols through synergistic integration of cutting-edge biotechnologies and classical breeding wisdom.

At the molecular frontier, CRISPR-Cas9 systems enable surgical precision in editing stress-responsive genetic networks. Targeting key regulators of redox homeostasis (APX, CAT), phytohormone crosstalk (ARF, DELLA), and epigenetic memory (ROS1, DME) allows creation of plants with engineered resilience [49, 50, 111–113]. This genome-editing revolution is amplified by high-throughput phenotyping platforms that screen mutant libraries under simulated space conditions.

Marker-assisted selection has evolved into ultra-precise genomic prediction models incorporating machine learning algorithms. By analyzing millions of single-nucleotide polymorphism (SNP) markers associated with radiation tolerance (RAD51, DMC1) and microgravity adaptation (LAZY1, ARG1), breeders can accelerate development of space-optimized cultivars [105–111]. The integration of multi-omics pipelines reveals previously hidden adaptation mechanisms—from stress-induced metabolite fluctuations to alternative splicing variants that enhance extraterrestrial survival.

A groundbreaking approach combines primed epigenomes with fixed genetic improvements. Chemically or environmentally primed seeds exhibit transgenerational stress memory through DNA methylation patterns (NRPD1, CMT3) and histone modifications (HDA6, SUVH4), while CRISPR-edited loci provide permanent trait enhancements [111–114]. This dual strategy creates crops capable of both immediate adaptation and long-term evolutionary success in space environments.

The next phase involves developing autonomous breeding systems utilizing AI-driven genomic selection and robotic phenotyping under artificial gravity gradients. Such closed-loop systems will be essential for establishing self-sustaining agricultural ecosystems on Mars and beyond, ensuring food security for a multiplanetary civilization.

3. Conclusion

As human exploration extends beyond Earth for prolonged periods, reliable and sustainable Advanced Life Support (ALS) systems will become essential. Plants form the cornerstone of these systems, providing food, oxygen, and waste recycling. To

thrive in extraterrestrial environments, especially under microgravity conditions, it is vital to enhance plant resilience from the earliest stages of growth. Seed priming with metal ions such as copper (Cu) and zinc (Zn) has shown promising results in inducing stress memory and activating signaling pathways related to germination, root architecture, hormone balance, and defense responses. These priming strategies promote the development of gravity-resistant seedlings and can significantly improve germination rates, root establishment, and overall plant vigor in space environments. Integrating such approaches with molecular breeding techniques offers a robust path toward developing cultivars tailored for space farming, ultimately supporting human life beyond Earth.

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