

Expanding frontiers: harnessing plant biology for space exploration and planetary sustainability

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Summary (200 words max)

Plants are critical for sustaining human life and planetary health. However, their potential to enable humans to survive and thrive beyond Earth remains unrealized. This Viewpoint presents a collective vision outlining priorities associated with plant science to support a new frontier of human existence. These priorities are drawn from the International Space Life Sciences Working Group (ISLSWG) *Plants for Space Exploration and Earth Applications* workshop, held at the European Low Gravity Research Association (ELGRA) conference in September 2024. We highlight transformative advances gained from using the ‘*laboratory of space*’ in understanding how plants respond to gravity and stress and introduce a new crop bioregenerative life support systems (BLiSS) readiness level (BRL) framework—extending the existing crop readiness level (CRL)—to assist in overcoming challenges in establishing resilient, sustainable crop production. Realizing the vision of plants as essential enablers of space exploration will require innovative approaches, including predictive modeling, synthetic biology, robust Earth-based analog systems, and reliable space-based instruments to monitor biological processes. Success relies upon a unified international community to promote sharing of resources, facilities, expertise, and data to accelerate progress. Ultimately, this work will both advance human space exploration and provide solutions to enhance sustainable plant production on Earth.

Key words (5-8): Plant Space Biology; Space Crop Production; BLiSS; Controlled Environment Agriculture; Synthetic Biology; Sustainability; Space Exploration

Introduction

Humankind faces formidable challenges as it transitions from Low Earth Orbit (LEO) to destinations beyond LEO (BLEO) such as the Moon and Mars. Foremost among these is developing space habitats that can reliably sustain human life. Ensuring adequate nutrition in such environments has been identified as a critical “red risk” that need to be mitigated to enable long-duration missions (>1 year) far from Earth (Patel et al., 2020).

Plants, foundational to life on Earth, are becoming widely recognized as essential components of Bioregenerative Life Support Systems (BLISS) in space. Plants are lightweight and easy to store in their dormant form (seeds), provide a renewable source of fresh food and oxygen, remove carbon dioxide, purify water, and recycle waste. Moreover, they can produce high-value products on demand, helping meet unforeseen needs for materials and medicines (McNulty et al., 2021). Plants are also known to promote psychological well-being on Earth, with anecdotal evidence suggesting similar benefits for astronauts on long-duration missions (De Micco et al., 2023a,b).

International space agencies have invested in plant research for decades, leading to technological advances that are transforming aspects of terrestrial agriculture—vertical farming, the use of light-emitting diodes (LEDs) in controlled environment agriculture (CEA), hydroponic and aeroponic systems, closed-loop nutrient recycling, and precision plant monitoring via remote sensing and automation. These innovations have optimized resource use, reduced inputs, and supported sustainable food production in challenging Earth environments (Wheeler, 2023). Yet, to continue reaping these benefits—and to enable long-term human habitation beyond Earth—persistent challenges must be addressed, including the scarcity of terrestrial space analogs, the high cost of spaceflight experiments, limited funding, and the technical hurdles inherent in biological research in space.

With the ambitious goals of returning humans to the Moon before the end of the decade and preparing for crewed missions to Mars, there is an urgent need to streamline BLISS development. Critical questions about the sustainability and suitability of current

strategies for conducting plant research in space were central to discussions at the 3rd International Space Life Sciences Working Group (ISLSWG) *Plants for Space Exploration and Earth Applications* workshop, held in Liverpool (UK) from 3–6 September 2024. Here, scientists from around the world reviewed current advances in plant gravitational and space biology, identified critical plant science needs to address the challenges of space exploration, and prioritized future research directions to accelerate the translation of fundamental discoveries into applications for BLiSS and space food systems. The workshop was organized into four scientific sessions: plant gravitational biology and space genomics; plant adaptation to space environmental stresses; plants for environmental control and life support systems; and enabling technologies for space crop production.

In this Viewpoint, we also revisit open questions and recommendations from the 2nd ISLSWG *Plant Biology in Space* workshop, held in Freiburg (Germany) in 2012 (Ruyters and Braun, 2014). The 2024 Liverpool workshop provided opportunities to assess progress since Freiburg, revealing that while notable advances have been achieved, many questions remain unanswered—and new ones have emerged. Here, we present a collective vision that calls for a robust global research community, united behind a bold, tangible goal with plants at the heart of space exploration, while maintaining strong investment in fundamental research. Central to this vision is the need to minimize barriers to collaboration by promoting open sharing of resources, data, experimental protocols, and facilities across the international *Plants for Space* community.

Advances in plant space biology enabled by fundamental research

The Liverpool workshop revealed that traditional fields in plant gravitational and space biology, such as gravitropism, have seen the most significant advances since Freiburg. Over the past decade, however, research has shifted more toward understanding plant responses and adaptation to spaceflight stressors—with the exception of ionizing radiation, many of the space stressors covered in Liverpool were new (Figure 1). The expanding battery of 'omics and modern biological tools have not

only helped shed light on fundamental plant research in space but also provide ideas for more efficient sharing of resources.

Plant tropisms

Tropism refers to the growth of plant organs toward or away from an environmental stimulus. *Gravitropism*, the process by which plant organs redirect growth in response to the gravity vector, has received the most attention and was covered extensively in Freiberg (Ruyters and Braun, 2014). The microgravity environment of space—and gravity's reimposition through centrifuges, e.g. on the Kibō module of the International Space Station (ISS) or in previous work with the European Modular Cultivation System (EMCS) (Millar et al., 2010)—provides a unique laboratory to understand how organisms sense and respond to gravity. Interest in gravitropism in the context of plant space biology is driven by the desire to understand root interactions with the growth substrate to help guide crop cultivation in the micro- and partial-gravity environments of space and the Moon/Mars surface, respectively (Maffei et. al., 2024). Furthermore, gravitropism has implications for crop productivity on Earth because the angles by which plant organs grow influence the efficiency of resource acquisition.

Gravitropism is understood to involve gravity perception, signal transduction, and differential growth (Chin and Blancaflor, 2022). A key focus at Freiburg was how gravity perception—believed to rely on the sedimentation of starch-filled amyloplasts (statoliths) in gravity-sensing cells (Kiss, 2025)—is linked to growth responses, potentially via the cytoskeleton, cytoplasmic calcium, and the endomembrane system (Ruyters and Braun, 2014). Traditionally, statoliths were viewed as force sensors, transmitting gravitational information through contact with the cell periphery. However, findings presented in Liverpool challenged this view, proposing that statoliths behave more like a fluid, which may explain how plants can detect very slight inclinations (Berut et al., 2018).

The transport and redistribution of auxin, as first articulated by the Cholodny–Went theory in the 1920s, remains central to explaining gravitropism. The discovery of the PIN-formed (PIN) protein family revolutionized understanding of auxin-mediated regulation of

gravitropism and broader plant development (Del Bianco et al., 2023). While PINs were a primary focus at Freiburg, attention in Liverpool shifted to the LAZY proteins following growing evidence that their localization in the amyloplasts of root cap columella cells forms a mechanistic link between gravity perception and PIN-mediated auxin redistribution (Nishimura et al., 2023). Although most LAZY research has focused on primary roots, new results presented in Liverpool suggest a role in controlling gravitropic set-point angle (GSA) in lateral roots, with implications for overall root system architecture (Roychoudhry and Kepinski, 2024).

Research on *hydrotropism* (root growth toward water) has progressed through studies of the MIZU-KUSSE 1 (MIZ1) protein, revealing that MIZ1's localization in the root cortex, rather than the root cap, is essential for hydrotropic responses, implying a distinct mechanism from gravitropism (Dietrich et al., 2017). Discussions also covered *electrotropism* (galvanotropism), the growth of roots toward or away from electric fields. Like hydrotropism, electrotropism was found to be independent of the root cap and dependent on cytokinin, rather than auxin, to initiate curvature (Salvalaio et al., 2022).

An emerging concept presented in Liverpool was *proprioception*—a plant's ability to sense its own shape (Moullia et al., 2021). Proprioception involves sensing organ curvature and initiating active de-curving (*autotropism*) that, together with gravitropism and gravity perception, forms a complex feedback system governing plant posture and architecture. The workshop underscored the potential of mathematical modeling and advanced phenotyping to disentangle these interactions (Hartmann et al. 2024), with applications for understanding how plant growth adapts in space environments where proprioception may play a dominant role.

The rapid progress in understanding PIN and LAZY function was largely driven by advances in live-cell imaging using fluorescent protein markers (Roychoudhry et al., 2023). These imaging approaches have expanded to a wide array of cellular components, including the cytoskeleton, organelles, membranes, hormones, and signaling molecules (Colin et al., 2022). Despite calls in Freiburg to implement fluorescence microscopy in spaceflight experiments (Ruyters and Braun, 2014), progress has been limited. However,

new imaging systems designed for space, such as FLUMIAS and COSMIC could finally enable high-resolution live imaging in microgravity. These platforms would allow researchers to exploit a growing toolbox of genetically encoded biosensors in LEO and BLEO. For example, the CaMPARI calcium reporter, combined with 96-well plate imaging hardware, opens the door to high-throughput, replicated bioimaging studies in model plants (Hammer et al., 2022). Such tools will increase *in situ* analytical capacity, reducing reliance on sample return.

For terrestrial applications of tropism research, the *LAZY* and *MIZ1* genes were proposed as targets for improving root system architecture. For example, a mutation in a gene belonging to the same family as *LAZY* produced deeper roots and exhibited enhanced drought resistance in rice (Uga et al., 2013). Similarly, understanding electrotropism could inform root directionality in hydroponic systems.

The Liverpool workshop reaffirmed that the removal of gravity provides a unique laboratory to unveil new information about less dominant plant tropisms and provide fundamental insights into plant–environment interactions, evolution, cell–cell communication, and hormone signaling (Chin and Blancaflor, 2022), with applications for both space and Earth agriculture. Looking forward, integrating emerging fields like synthetic gene circuits and digital agriculture with plant space biology offers exciting opportunities to deepen fundamental knowledge and customize plants for specific applications (Lloyd et al., 2022).

Stress responses

Outside the safety of Earth's geostationary magnetic field (GMF), which protects against harmful solar and cosmic radiation, BLEO presents a challenging environment for biological organisms. Even on the ISS in LEO, GMF protection is diminished, and exposure to radiation increases further by regular passage through the inner Van Allen belt. Understanding how plants respond to such extreme environments is critical for developing sustainable crop production systems (De Micco et al., 2023). Workshop discussions in Liverpool highlighted how the absence of GMF can delay flowering, reduce

photosynthesis, and alter photoreceptor activity (Vigani et al., 2021). Other space stressors discussed included ionizing radiation, regolith, low magnetic fields, hypoxia, and phytopathogens (Maffei et al., 2024) (Figure 1). Among these, low magnetic fields remain understudied, and whether they represent a limiting stress for crop cultivation in space remains an open question.

Discussions on the impacts of space radiation, a feature at Freiburg (De Micco et al., 2014), continued in Liverpool. Radiation is known to alter plant morphology, physiology, and biochemistry, with specific effects depending on species, developmental stage, radiation type, and dose (Maffei et al., 2024). While concerns persist about radiation's potential to reduce plant productivity in BLISS, observations that radiation can stimulate antioxidant biosynthesis raise intriguing possibilities for enhancing crop nutritional value. Developing crop shielding strategies that balance protection against radiation damage with induction of beneficial stress responses will require more comprehensive studies across diverse plant species, using radiation types and doses that mimic space conditions (De Micco et al., 2022).

A new and rather controversial topic covered in Liverpool was *regolith*, the fragmented rock material that covers the lunar and martian surface. A recent study on *Arabidopsis thaliana* grown in lunar regolith collected during the Apollo missions generated renewed interest in its potential as a growth substrate in future planetary bases. However, the severe developmental defects and stress-related gene expression observed in seedlings (Paul et al., 2022) highlighted concerns about the diminished fecundity of regolith-grown plants, while regolith's detrimental effects on human health and equipment prompted critical discussions about its practicality. Nonetheless, experiments using lunar regolith simulants suggest that antioxidant supplementation could improve plant growth (Barcenilla et al., 2024), and further research into plant–regolith interactions could inform strategies for bioremediation and terraforming marginal environments on Earth. Advancing this research will require increased access to authentic lunar regolith. Despite differing opinions, a key outcome was the shared recognition of the need to shift from a laboratory-based to a crop production mindset that acknowledges the operational complexities of space travel.

Another key topic was water delivery in microgravity. The absence of gravity-driven percolation can lead to water deficits or excess water in root zones, and transcriptomic studies of space-grown plants consistently reveal gene expression patterns indicative of hypoxic stress. An example presented in Liverpool demonstrated how transcriptomics and mutant analysis in model plants identified the vacuolar cation exchanger 2 (CAX2) as a potential target for engineering flooding-resistant crops (Bakshi et al., 2023), with potential applications for both space and terrestrial agriculture.

Although much of the discussion focused on abiotic stress, attention also turned to biotic challenges. While the 2012 workshop did not cover microbial pathogens, evidence has since emerged of their impact on plants in space. For example, *Fusarium oxysporum* infected *Zinnia hybrida* plants in the ISS *Vegetable Production System (Veggie)* system (Schuerger et al., 2021), prompting investigations into whether microgravity influences plant–pathogen interactions. Preliminary transcriptomic data on tomatoes from the ISS *Advanced Plant Habitat (APH)* revealed differential gene expression linked to salicylic acid–mediated immunity, suggesting space-induced modulation of defense responses. These findings mirror the growth–defense trade-offs observed in terrestrial plants (He et al., 2022). Upcoming ISS experiments will explore additional pathogens, such as powdery mildew, offering opportunities to assess whether these trade-offs are conserved across different plant–pathogen systems in space.

The session on plant adaptation to spaceflight stressors underscored multiple factors that may constrain crop productivity. However, participants noted that gene expression patterns observed in model plants under spaceflight conditions do not always correlate with the growth and development of crops cultivated in ISS growth chambers (Hasenstein et al., 2023). The need for standardized experimental conditions—first raised in Freiburg (Ruyters and Braun, 2014)—resurfaced. For example, integrating considerations of the plant circadian clock into experimental design and interpretation was recommended, including documentation of the apparent time of day during sample collection. Similarly, employing RNA spike-ins in RNA-seq experiments was proposed as a strategy to improve normalization and more reliably identify spaceflight-induced gene expression changes (Laosuntisuk et al., 2024).

'Omics: Defining expectations

The Freiburg workshop sparked enthusiasm around the potential of *'omics technologies*—transcriptomics, proteomics, and metabolomics—to advance plant space biology (Ruyters and Braun, 2014), prompting collection of a substantial volume of *'omics* data from plant experiments conducted in LEO, including suborbital flights, and ground-based microgravity analogs (Meyers and Wyatt, 2022). Much of this data is accessible through NASA's Open Science Data Repository (OSDR) via the GeneLab portal (Berrios et al., 2021). Since its launch, OSDR has broadened its scope through the formation of international Analysis Working Groups, which collaboratively reanalyze raw *'omics* datasets and extract new insights into how spaceflight affects plant biology (Barker et al., 2023). Parallel efforts to develop similar repositories are underway at the European Space Agency (ESA). The growing need for mechanisms to consolidate these large-scale data across space agencies, and to maximize the utility of these rare and costly resources by standardizing experimental and data processing protocols, were key topics of discussion in Liverpool.

To date, *'omics* in space has had greatest impact in the realm of medicine, where it is poised to offer powerful tools for mitigating human health risks associated with spaceflight (Coppens et al., 2025). Translating plant *'omics* data into practical applications—even on Earth—has proven more challenging (Purugganan and Jackson, 2021), but still holds significant promise (Overbey et al. 2021). Looking ahead, the application of emerging single-cell *'omics* technologies in space presents an exciting frontier (Rutter et al., 2024). To maximize the impact of plant space *'omics* research, it will be essential to clearly define its objectives—particularly in terms of translating discoveries into tangible benefits for BLiSS and space food production. Central to achieving these goals is a strong commitment to open science and data sharing. Platforms like NASA's OSDR and emerging ESA repositories exemplify how global collaboration and transparent access to high-quality data can accelerate discovery, reduce redundancy, and foster innovation. As space exploration becomes increasingly international and interdisciplinary, open science must remain a cornerstone for building the knowledge base to support sustainable life beyond Earth.

The path from basic plant space biology to functional space crop production

The central rationale for studying plants in space is to convert scientific insights into practical solutions that support space food systems and, ultimately, a fully operational BLiSS (Figure 1). This rationale has remained consistent since the early missions that sent plants to LEO and continues to be reinforced (De Micco et. al., 2023a,b, Maffei et al., 2024). Its significance is further underscored by the NASA Biological and Physical Sciences Division's *2023–2032 Decadal Survey*, published by the US National Academies of Sciences, Engineering, and Medicine (NASEM), along with white papers from ESA member states that highlight key scientific priorities to accelerate development of BLiSS technologies. However, despite decades of foundational research, a fully integrated space food system remains an unrealized goal.

Food provision for crew members is considered one of the highest risks within NASA's Human Research Program. Long-duration BLEO missions will require reliable access to safe, nutritious food that meets both dietary requirements and crew preferences. Plants will play an important role, as demonstrated by a NASA Human Exploration Research Analog (HERA) study that showed that a diet including fruits and vegetables led to measurable health and performance benefits (Douglas et al., 2022). In the near term, missions will primarily depend on physico-chemical regenerative Environmental Control and Life Support Systems (ECLSS) and pre-packaged food supplemented with fresh produce to enhance nutritional value with bioavailable, whole-food sources. This approach serves as a critical stepping stone toward the eventual integration of crop production into BLiSS.

However, integrating crop production into the space food system presents significant challenges, particularly due to the associated mass and volume requirements (Figure 2). Success will require advancing the technology readiness levels (TRLs) of crop production systems and developing supporting infrastructure to protect a consistent, safe food supply. These challenges underscore the need to revisit and refine fundamental research priorities aimed at accelerating the realization of space-based crop cultivation (Figure 1).

Space crop production challenges

While many of the challenges faced in space controlled environment agriculture (SpaCEA) parallel those encountered in terrestrial vertical farming and CEA (Wright et al., 2023) (Figure 2), several key challenges unique to space remain. Microgravity alters fluid dynamics, complicating delivery of water and nutrients to plant roots while also making it difficult to maintain proper aeration. Additionally, the absence of natural convective air movement in microgravity affects both heat transfer and air circulation around plants, which can disrupt transpiration, impair water and nutrient uptake, and cause water to accumulate on plant surfaces. A notable result of not addressing these challenges was the observed *Fusarium* infection on zinnia plants in the ISS *Veggie* system, attributed to high water stress resulting from inadequate ventilation (Schuerger et al., 2021).

Atmospheric differences also exist. Carbon dioxide (CO₂) levels typically range from 2,500–3,000 parts per million (ppm) aboard the ISS—significantly higher than the ~420 ppm in Earth’s atmosphere. The full impact of these differences on crop growth is not yet fully understood, but research presented in Liverpool indicated that ISS-level CO₂ can influence plant physiology, including the uptake of different nitrogen forms. Resources for plant cultivation, such as growth volume, power, and crew time, are exceedingly limited in space, placing stringent constraints on crop selection and growth systems. Food safety is another key concern, especially given that astronauts grow crops in the same enclosed environment where they live and work, raising the stakes for contamination control and sanitation.

Looking ahead, new challenges will also emerge when extending plant cultivation to the lunar surface. These include uncertainties around crop performance and system functionality under reduced gravity, increased radiation, and lower atmospheric pressure. Crew time is expected to be even more constrained during early lunar missions, where scientific exploration will be prioritized over food production. As missions move to destinations such as the Moon and Mars, ensuring a reliable supply of essential

resources—water, nutrients, and growth substrates—will be crucial, especially as regular resupply becomes increasingly impractical.

Crop production technology for space

For the past decade, SpaCEA systems such as NASA's *Veggie* and *APH* have enabled significant advances in crop production aboard the ISS. *Veggie* has supported the successful cultivation of crops like lettuce, kale, and tomatoes, while *APH* has enabled more complex experiments with radishes and chile peppers. The introduction of NASA's Crop Readiness Level (CRL) (Romeyn et al., 2019) has established a standard for preparing crop species for SpaCEA (Figure 3), considering key requirements for successful growth and acceptability in space; several crops have reached CRL9, i.e. grown and consumed in space. ISS-grown crops have been shown to be safe, nutritious, and well-accepted by astronauts, with positive effects on crew well-being (Bunchek et al., 2024; Khodadad et al., 2020). These findings are now guiding development of *OHALO III*, a next-generation testbed for operational space crop production, slated for launch to the ISS in 2026. The development of several other platforms was announced in Liverpool, notably through funding from the Japanese (JAXA) and UK–Australian (UKSA, ASA) Space Agencies for ISS and commercial platforms, respectively.

Plants as core components of Bioregenerative Life Support Systems (BLiSS)

The integration of plants in BLiSS has many advantages. Most hardware-based life support systems developed to date are single-function and difficult to repair or resupply; plants, however, are self-replicating and adaptable. Including plants in BLiSS should reduce reliance on expendable supplies from Earth, particularly when paired with regenerative systems for recycling waste and atmospheric by-products. Plants alone are not a solution but rely on the right hardware control systems for temperature, humidity, lighting, and irrigation to safeguard reliable, low-input production in controlled environments. This mirrors vertical farming requirements on Earth and is especially promising for lunar or martian habitats, where gravity and airflow are more stable than in orbit. However, the criteria for making plants a truly viable component of a life support

system are still poorly defined. Key questions emerging from Liverpool focused on the energy, mass, and volume requirements for plants to be a net-positive element of such a system; and which current systems could be downsized or made redundant through plant integration.

Another benefit of integrating plants in BLiSS is their ability to recycle waste and by-products, such as human waste, food scraps, atmospheric gases, and excess biomass. Access to important nutrients in waste streams is a notable gap that must be addressed to allow closure of nutrient loops while providing whole-food nutrition to maintain crew performance. Moreover, current fertilizer formulations do not reflect nutritional requirements of specific plants in the space environment, nor nutrients available through waste streams. Promising solutions for waste management and nutrient recovery discussed in Liverpool included ESA's Micro-Ecological Life Support System Alternative (MELiSSA) loop for urine processing, the German Aerospace Center (DLR)'s Combined Regenerative Organic food Production (C.R.O.P.[®]) air filter, and insect-based recycling systems. These technologies show potential in isolation but will need to be integrated into a closed-loop, systems-based approach to be viable. Ground-based analogs and future lunar testbeds will be critical for validating such integration.

Once technical challenges are overcome, the plants themselves will need to be selected and tailored for BLiSS applications. To accelerate crop development, we propose a set of 9 BLiSS Readiness Levels (BRLs) (Figure 3) that builds directly on the existing CRL scale and establishes a framework to develop and prepare high-CRL crops for BLiSS (Figure 4). These additional steps will characterize crop contributions to BLiSS, including CO₂ scrubbing, O₂ production, water purification, and edible biomass production compared to crop and system requirements in both optimal (BRL1) and spaceflight (BRL2) environments. We also introduce the concept of crop modification to fully leverage developments in molecular breeding approaches and gene editing not previously considered in the CRL scale (Rodríguez-Leal et al., 2017). Modified crops identified in BRL1 may be required to pass through some, or all, CRL levels before progressing to BRL2. The identification of processing, storage, and shelf-life requirements of edible biomass (BRL3) will characterize the crop's suitability for sustained cultivation, and

determination of waste management strategies (by the crop and from inedible plant material) will help close the nutrient loop (BRL4) to support fertigation for the next crop cycle (BRL5). Plant ability to support BLiSS should be tested in flight hardware (BRL6) followed by integration of crop cultivation with resource recovery, atmospheric management, and water purification subsystems in high-fidelity Ground Test Demonstrators (BRL7). Verification of a crop's capability to provide BLiSS functions in a lunar and/or martian setting (BRL8) is the final step before a crop is considered an 'operational' component of BLiSS (BRL9).

While still anecdotal, plants are reported to contribute to psychological well-being in space. Astronauts consistently report that caring for and consuming plants boosts morale and provides a comforting connection to Earth, though robust metrics will be required for rigorous assessment. Researchers have recently identified a promising new frontier: the sensory experience of food in space. Microgravity can significantly alter human sensory perception (Viejo et al., 2024a,b), particularly by diminishing retronasal aroma while enhancing mouthfeel. These changes suggest that flavor perception fundamentally differs in space, opening exciting new directions for food design in extraterrestrial settings.

One innovative concept is the development of "pick-and-eat" leafy greens optimized for space conditions, as astronauts tend to prefer leafy greens more in microgravity than on Earth, showing a greater appreciation for enhanced aroma and texture (Viejo et al., 2024a,b). Researchers are now leveraging machine learning to model the complex interactions between plant physiology—such as transpiration and stomatal conductance—and human sensory feedback. These efforts aim to create "digital twins": real-time, sensor-driven simulations that use technologies like electronic noses and near-infrared spectroscopy to optimize plant growth and food quality. This integrated approach holds the potential to not only improve the sensory appeal of space-grown food but also strengthen the overall health and morale of future crews.

Future BLiSS platforms

The importance of developing BLiSS has led many space agencies (NASA, DLR, JAXA, Canadian (CSA) and Chinese National (CNSA) Space Agencies) to integrate plants in ground demonstrators (e.g. EDEN-ISS, NASA's Crew Health And Performance Exploration Analog (CHAPEA), Yuegong-1), and future high-fidelity analogs outlined in Liverpool (e.g. EDEN-LUNA, LAM-GTD, BIOBASE). Performance in such analogs is vital to inform what future systems in space may include (Figure 4). The continued development of SpaCEA hardware will ensure space crop production efforts progress as we transition from ISS to Commercial LEO Destinations (CLDs). Plans for CLD SpaCEA capabilities are still not clear but workshop participants agreed that plant growth capabilities must continue to be available to support future BLEO missions. Options include transitioning legacy hardware such as *Veggie* and *APH* to CLD destinations (Figure 4), and/or commercial partners developing new SpaCEA hardware that extends current systems. New hardware, such as *OHALO III* that focuses specifically on crop production, is another possibility for transition to CLDs as well as BLEO destinations such as the Lunar Gateway and an eventual Mars transit vehicle (Figure 4).

High-fidelity ground test demonstrators (GTD) are essential to support the development of BLiSS hardware capabilities and extend the role of plants in space beyond simple food production. Some GTD projects, such as NASA's CHAPEA, are already generating useful data on the effect of crop production/ consumption on crew health and performance in long-term exploration missions. The joint DLR/ESA EDEN LUNA project, currently under development, will focus more on BLiSS considerations for SpaCEA. The next phase of GTDs, including Lunar Agricultural Modules (LAM) and Martian Agricultural Modules (MAM), was also discussed by CSA, ESA, and DLR alongside continued research in microgravity environments (Figure 4). Application of these technologies and growth strategies in highly constrained, resource-limited space environments will, in turn, feed back to improve the sustainability of terrestrial CEA efforts (Mortimer and Gilliam, 2022; Wright et al., 2023).

Frontier biotechnology for space and Earth

Another opportunity to emerge since the 2012 Freiburg workshop is the application of plant synthetic biology both for engineering ‘designer’ plants for specific end-uses, and for biomanufacturing. The rapid pace of synthetic biology technological advances shifts the paradigm for both farming and biopharming in any environment, sidestepping the CRL framework and instead allowing us to engineer plants ideally suited to specific constraints. Projected to become a multi-trillion dollar global industry by 2030, we anticipate near-term tailoring of plants for faster growth rates, optimized architecture, and enhanced stress resilience for vertical and broad-acre farming; and for on-demand production of high-value products such as fuels, plastics, and medicines. Rapid progress in microbial synthetic biology—enabled by modular cloning, DNA synthesis and sequencing, and high-throughput phenotyping—offers a blueprint for what may also be achievable in plants (Morgan et al. 2024). Advances in plant genetic transformation, including artificial chromosome insertion, further accelerate potential deployment. Leveraging plants as natural producers of many valuable biomolecules remains underdeveloped, even though angiosperms, due to their more complex metabolism, may be an ideal biofactory. Increasing global investment in these areas will also inform key questions for space-based plant and biomolecule production.

Ethical, cultural, and legal considerations in plant space research

As humanity returns to the Moon and sets its sights on Mars, it is important to consider the human dimensions of space exploration beyond engineering and biology. In 2023, NASA held a workshop on the societal implications of the Artemis missions, which identified key concerns regarding sustainability, anticipatory governance, and the importance of addressing cultural sensitivities regarding lunar activities. Importantly, the report emphasized the need to integrate expertise in the social sciences, ethics, and law into technical and scientific endeavors (Pirtle et al. 2023). The Moon holds deep cultural and spiritual significance for many societies, and respecting this diversity must be a consideration in planning future missions. In the context of plant-based life support and food production, cultural differences also influence dietary and food preparation needs

and preferences. These considerations were discussed in Liverpool and are particularly relevant to planning long-duration missions to support physical health and psychological well-being.

Further complexity arises from divergent international views on technologies like genetic modification. While some countries embrace these tools for food security and sustainability, others maintain strict regulatory or cultural opposition, raising critical questions: Should mission design adapt to these differences or should a new, globally agreed-upon ethical and legal framework specific to deep space exploration be established? How much influence should cultural values have on guiding mission objectives?

Fostering international collaboration to accelerate progress

The cost, logistics, and difficulties associated with research that underpins space exploration necessitates that countries share the load—and benefits. As of May 2025, 55 countries have signed up to the Artemis Accords. We suggest that these Accords be a unifying narrative to align international resources and deliver synergistic benefits while avoiding unnecessary duplication. The formation of multi-lateral funding schemes between space agencies, or at least aligned funding between bi-lateral partners, would be a sensible way forward to leverage and maintain the significant resources and skillsets dedicated to progressing BLiSS. Of course, two space nations with significant heritage in space plant sciences are absent from the Artemis Accords. Instead, Russia and China lead the International Lunar Research Station initiative (involving 10 countries), with many of the same aims and technological needs as Artemis. The prospects of combining these groups, however, is currently remote—a missed opportunity for the planet and humanity.

Smaller scale collaborations have started, including from the UK and Australia through the UK–Australia Space Bridge, a partnership that facilitates government-to-government collaboration on space technology and programs, knowledge-sharing, research, and education. With funding from the UKSA and ASA, an international project between universities in both countries, the UK startup Vertical Future, and Axiom Space

(US) will focus on characterizing the design requirements for ‘*a fully autonomous agriculture system that can be monitored and operated remotely or through the use of artificial intelligence and will be used to support space exploration including future Moon-to-Mars Artemis missions*’. This specific project was enabled through a pre-existing large-scale collaboration that has grown since 2019—Plants for Space (P4S) (Box 1)—that was also instrumental in facilitating connections in the Lunar Effects on Agricultural Flora (LEAF) project, scheduled to grow and bring back the first plants from the Moon with Artemis III in 2027. These projects have been built through leveraging large Australian investment as in kind or cash support to attract funding into partners' own jurisdictions.

However, to fully take advantage of international collaboration, incentives need to be introduced and significant legislative barriers removed, e.g. the amount of paperwork required to establish collaborative agreements and funding, particularly constraints on agencies funding only projects carried out in their home country. Another barrier is that much research is hidden behind a paywall and/or firewall and, while it is important for data to be protected, lack of access to the necessary data, literature, and tools to tackle the big questions without duplication is a barrier to progress.

The path forward

While the Liverpool meeting raised as many questions as answers, it has allowed us to nominate priorities for plant and space research and development communities in upcoming years. Here, we list 12 priorities to allow for accelerated progress (Figure 5). We welcome continued dialog on these matters and look forward to these priorities stimulating new plant-based technologies for both space and Earth applications.

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Figures

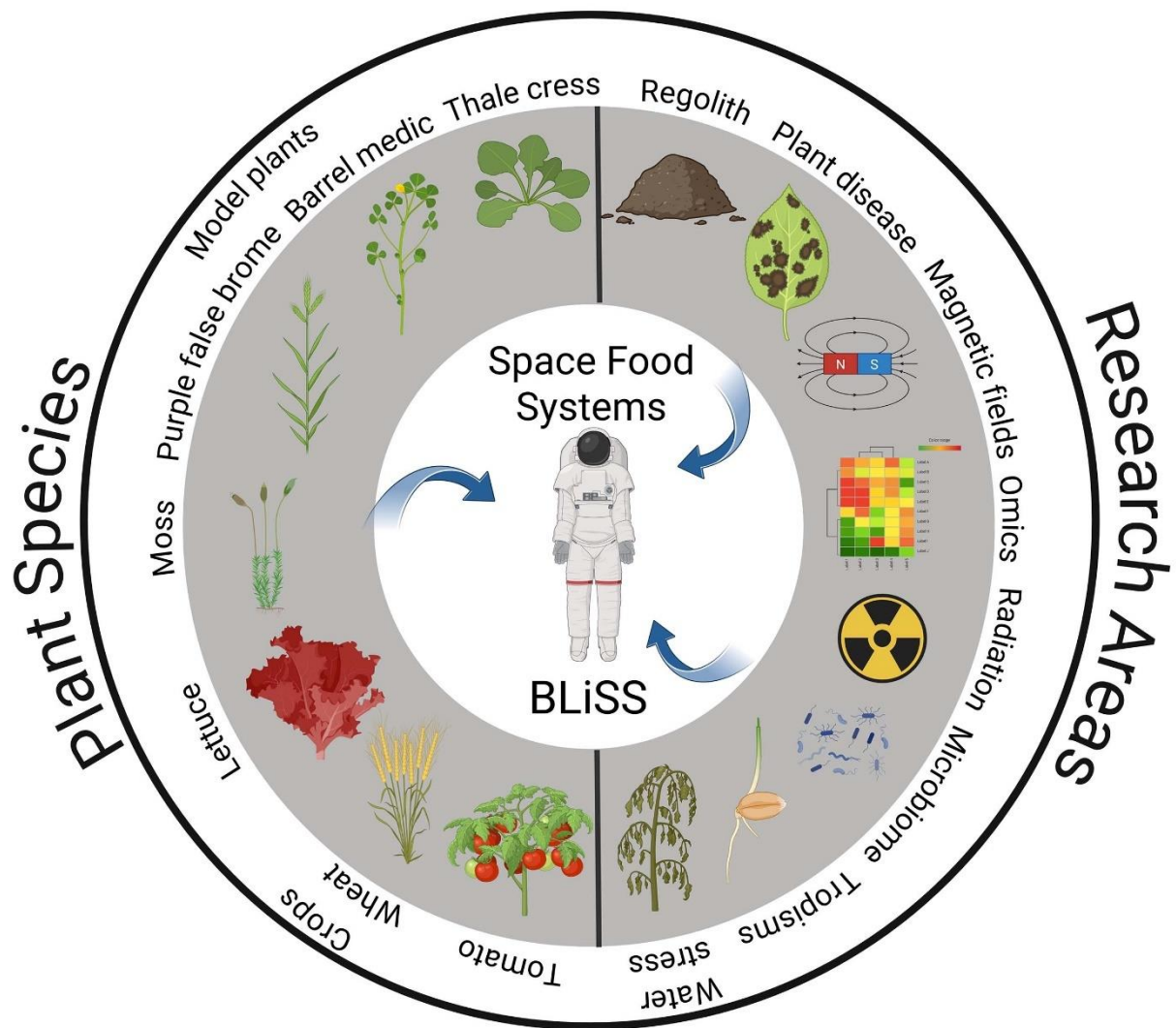


Figure 1: Representative model plant and crop species studied in space, and research topics discussed at the Liverpool workshop. Translating fundamental and applied plant research into tangible products that can be integrated into sustainable space food systems and a fully operational BLISS should be a priority moving forward.

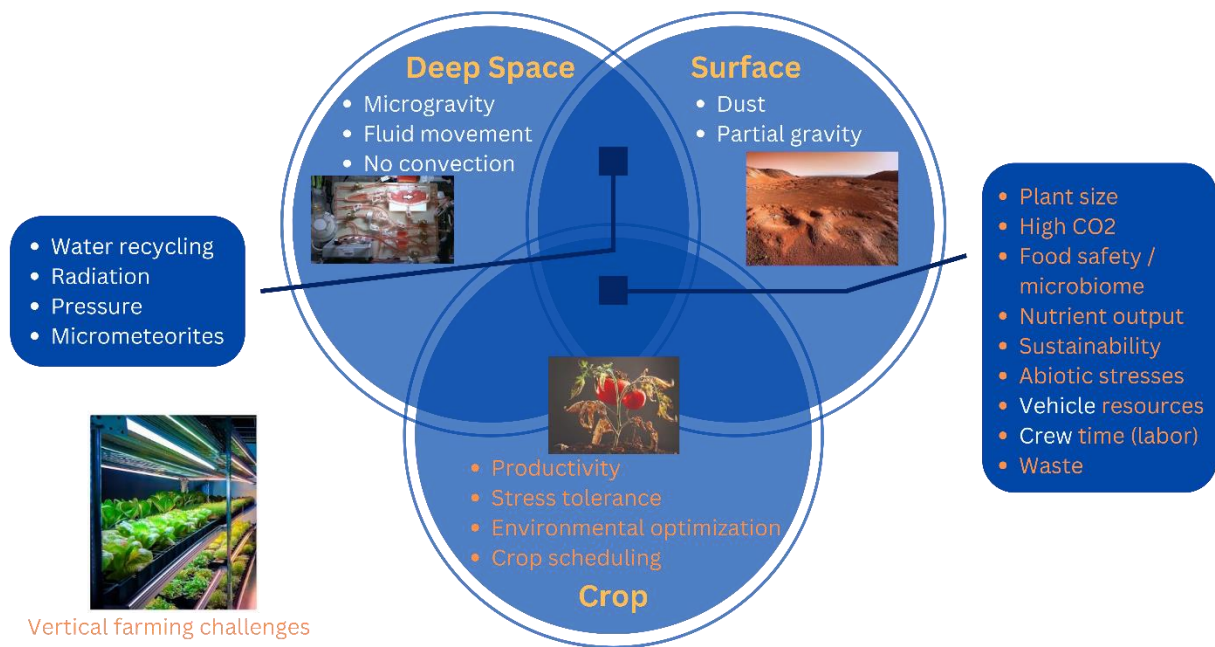


Figure 2: Summary of challenges faced in space crop production in deep space (microgravity) and surface (partial gravity) environments. Challenges also relevant to terrestrial CEA and vertical farming are highlighted in orange.

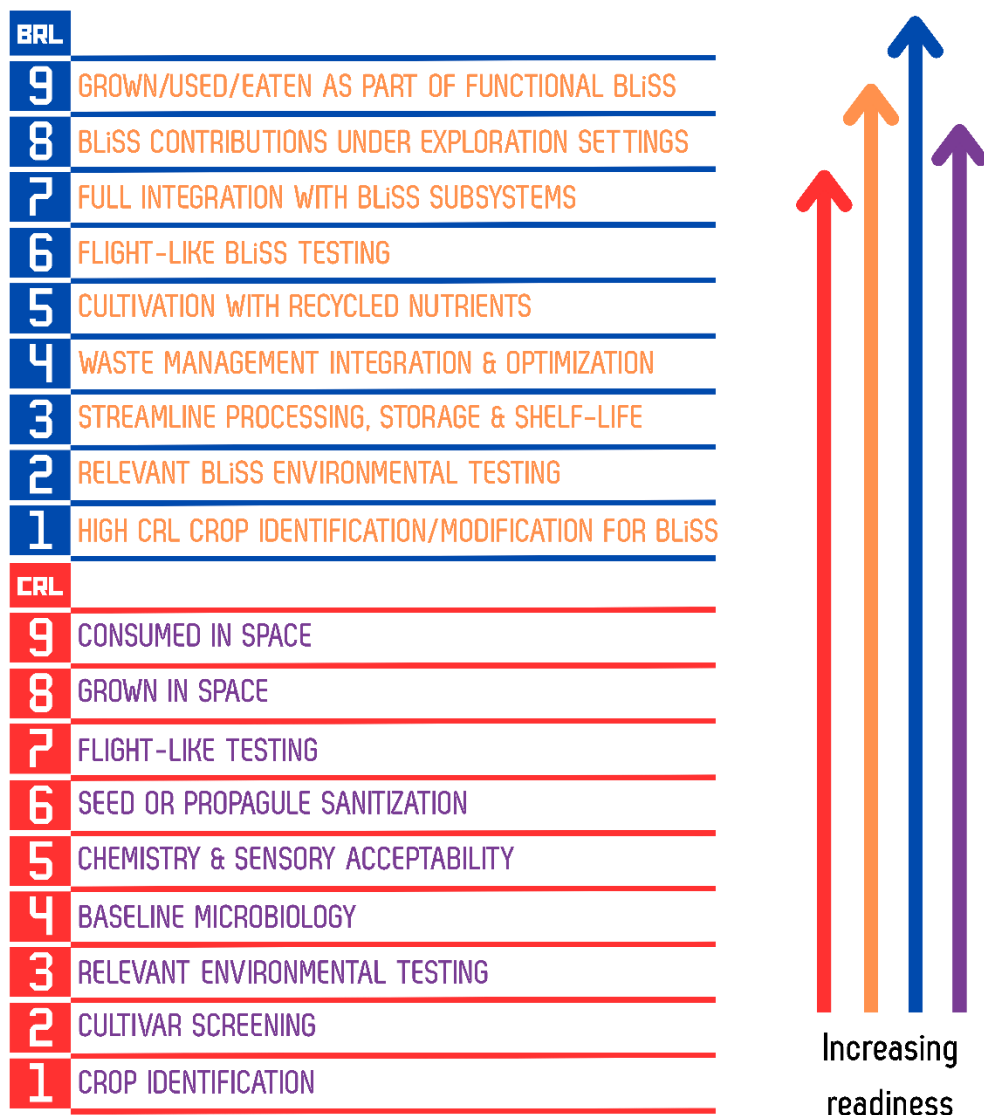


Figure 3: Crop Readiness Level (CRL) scale to develop crops suitable for supporting long-term human exploration missions, adapted from Romeyn et al. (2019); and proposed BLiSS Readiness Level (BRL) scale for preparing crops for lunar and martian surface BLiSS.

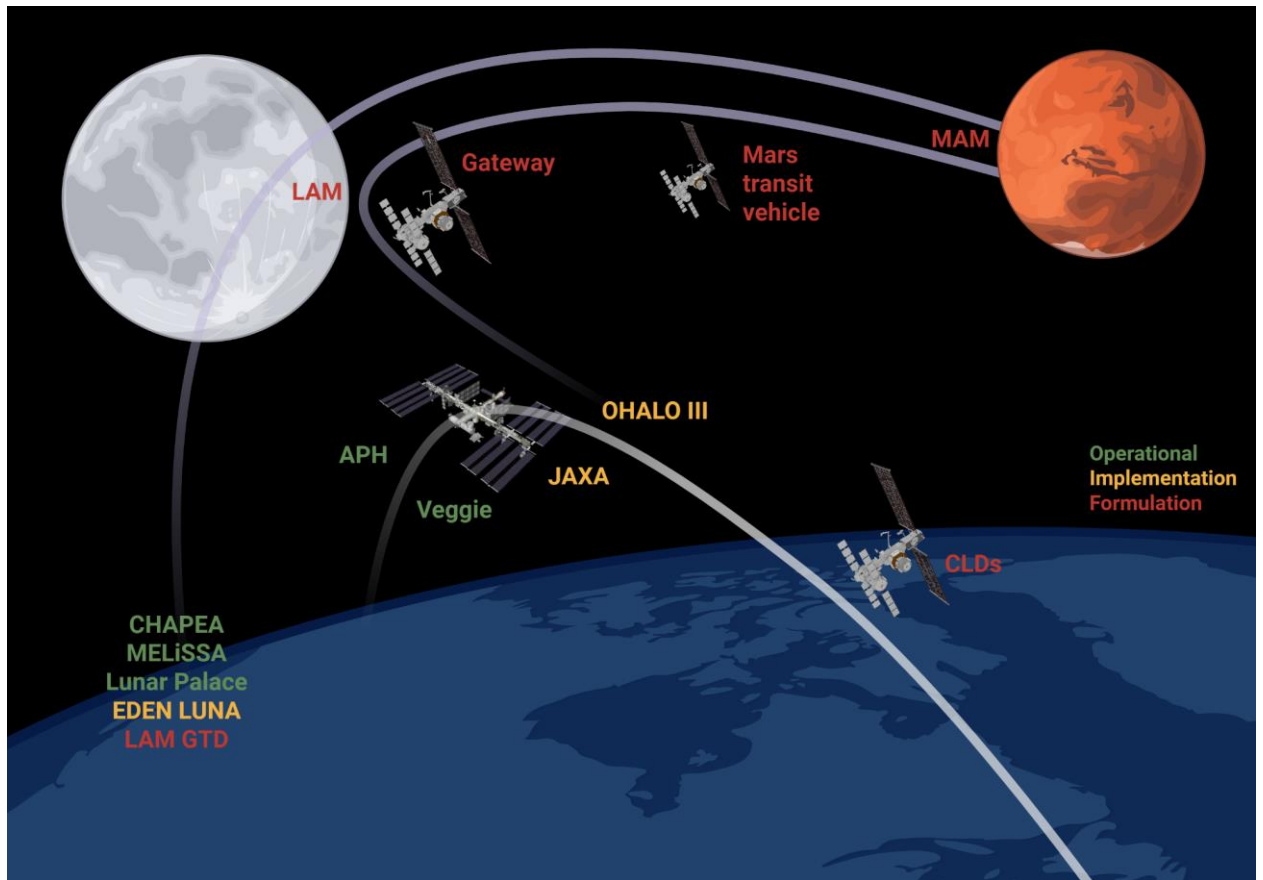


Figure 4: Current, planned, and potential future space crop production platforms for development of SpaCEA and BLiSS to support long-term human space exploration.

Figure 5: Priorities for accelerated progress towards BLiSS, drawn from the presentations and discussions of the ISLSWG workshop in Liverpool (2024).

Priorities for accelerated progress towards BLiSS

- 1 Collaborate with CLD providers**
Collaborate with future providers of commercial LEO research platforms to ensure facilities are in place to perform high-quality research.
- 2 Establish high-fidelity Earth-based analogs**
Develop high-fidelity analogs for Lunar and Martian agriculture and make available for the international research community.
- 3 Determine plant responses to partial gravity environments**
Develop an in-depth understanding of how partial gravity on the Moon and Mars affects plant growth and development.
- 4 Increase number of CRL9 crops**
Expand the range of crops suitable for CEA and SpaCEA systems through all available tools, raising their crop readiness level (CRL).
- 5 Determine energy & resource tradeoffs for crop inclusion in BLiSS**
Develop models to establish the energy and resource tradeoffs to enable crop production as part of BLiSS.
- 6 Consider and raise crop BLiSS Readiness Level (BRL)**
Refine and implement crop BLiSS Readiness Level (BRL), taking into consideration their growth requirements, potential life support contributions to the system, and factors such as processing, storage, shelf-life, waste management, and integration with other life support subsystems.
- 7 Advance development of autonomous SpaCEA systems**
Advance development of autonomous growth systems, integrating monitoring and control of plant growth, nutrients, pathogens, and stress, along with automated harvesting and resource recovery from inedible plant material and waste streams.
- 8 Develop plants as on-demand biofactories**
Develop plants and other biological systems as on demand synthetic biofactories for a range of useful compounds, flavors, materials, fuels, and medicines.
- 9 Promote increased sharing of knowledge and resources**
Further develop an international collaborative research and communications platform to realize synergies and streamline progress towards functional BLiSS.
- 10 Promote international collaboration, funding, and open science**
Remove barriers to, and increase incentives for, international collaborative funding and open science for the development of BLiSS.
- 11 Consider legal and ethical factors**
Develop legal and ethical frameworks to acknowledge the cultural significance of space and differences in diet, and opposing views on the use of genetically modified organisms.
- 12 Plan future SpaCEA/BLiSS systems while ensuring flow through for Earth impact**
Based on all the above considerations, plan the footprint of Lunar and Martian plant growth systems, and ensure that technologies developed during this research flow through for on Earth impact.

Box 1. The Plants For Space initiative: A case study

In 2022, the Australian Research Council announced the seven-year, multi-million dollar Centre of Excellence in Plants for Space (P4S; www.plants4space.com). This multidisciplinary initiative comprising plant and food scientists, engineers, modelers, psychologists, and lawyers, brings together over 30 international organizations including universities, space agencies, technology providers, defence organizations, primary industries, controlled environment agriculture specialists, and food companies—and it continues to grow.

The shared mission of P4S is to develop technologies that support long-term human space exploration while advancing sustainability on Earth through the redesign of plant and food systems. The Centre's research is structured around four key missions:

1. Optimized zero-waste CEA plants
2. Complete nutrition plant-based foods
3. On-demand plant biomanufacturing
4. A future-ready workforce and society

These missions were developed through consultation with space and plant research communities to identify critical technological gaps that must be addressed for successful implementation. The capacity and capability of this large international consortium has been leveraged by partner institutions around the world to attract additional funding for research projects and fellowships in their own jurisdictions, including from research councils and government agencies. Ensuring alignment and complementarity with existing international efforts—avoiding duplication while seeking synergies—was a priority in establishing P4S. For example, the Center for the Utilization of Biological Engineering in Space (CUBES), a NASA-funded initiative involving five US universities, focuses on biomanufacturing and shares several collaborative projects and partner investigators with P4S.

Similarly, the ESA-aligned MELiSSA Foundation (established in 1989) has assembled 14–40 primarily European partners working on BLiSS from an engineering perspective. Opportunities for synergy between MELiSSA, P4S, and other initiatives are emerging but still under active development. In addition to these major efforts, space plant and food research centers and networks have recently been launched in Japan (Space Food Sphere, Chiba- and Tsukuba-led initiatives), South Korea, and Brazil. While there is growing interest in connecting these global

initiatives through shared projects, doing so will require considerable coordination—and importantly, dedicated resources.

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