Viewpoint

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

Summary

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. First, we highlight transformative advances gained from using the 'laboratory of space' in understanding how plants respond to gravity and other stressors. Second, we introduce a new crop Bioregenerative Life Support System (BLSS) readiness level (BRL) framework – extending the existing Crop Readiness Level (CRL) – to assist in overcoming challenges to establish resilient, sustainable crop production. Materializing the vision of plants as enablers of space exploration will require innovative approaches, including predictive modeling, synthetic biology, robust Earth-based analogue 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.

Introduction

Humans face formidable challenges as they transition from low Earth orbit (LEO) to destinations beyond low Earth orbit (BLEO) such as the Moon and Mars. Foremost among these is developing space habitats that can reliably sustain human life. Ensuring adequate astronaut nutrition in such environments has been identified as a critical 'red risk' that needs to be mitigated to enable long-duration missions (>1 yr) far from Earth (Patel *et al.*, 2020).

Plants, foundational to life on Earth, are essential components of Bioregenerative Life Support Systems (BLSS) in space. Plants are lightweight and easy to store in their embryonic quiescent state (seeds) and can 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). There is evidence suggesting that plants also promote psychological well-being to astronauts on long-duration missions (De Micco *et al.*, 2023a, 2023b).

International space agencies have invested in plant research for decades, leading to technological advances that continue to transform terrestrial agriculture. For example, vertical farming, the use of light-emitting diodes in controlled environment agriculture (CEA), hydroponic and aeroponic systems, closed-loop nutrient recycling, and precision plant monitoring via remote sensing and automation (Mitchell, 2022). These innovations have optimized resource use efficiency, reduced inputs, and supported sustainable food production in challenging Earth environments (Wheeler, 2023). Yet, to continue leveraging these benefits, and to enable long-term human habitation beyond Earth, persistent challenges must be addressed, including the scarcity and poor fidelity of terrestrial space analogs, the high cost of spaceflight experiments and a lack of coordination among different plant space experiments, limited funding, and the technical hurdles inherent in biological research in space. These challenges have hindered our ability to acquire an in-depth understanding of plant responses to space-related stresses and mitigate the negative impact of these stresses on space agriculture.

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 BLSS development. Critical questions about the sustainability and suitability of current strategies for conducting plant research in space were central to discussions at the Third International Space Life Sciences Working Group (ISLSWG) *Plants for Space Exploration and Earth Applications* workshop, held in Liverpool (UK) from September 3–6, 2024. At the workshop, we reviewed current advances in plant 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 BLSS 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 present insights from these sessions and also revisit open questions and recommendations from the second ISLSWG *Plant Biology in Space* workshop, held in Freiburg (Germany) in 2012 (Ruyters & Braun, 2014). The 2024

Box 1 List of acronyms and corresponding definitions.

Acronym	Definition	Acronym	Definition
APH	Advanced Plant Habitat	GMF	Geo-Magnetic Field
ARC	Australian Research Council	GSA	Gravitropic Set-point Angle
ASA	Australian Space Agency	GTD	Ground Test Demonstrator
ASI	Agenzia Spaziale Italiana	HERA	Human Exploration Research Analogue
BLEO	Beyond Low Earth Orbit	ISLSWG	International Space Life Sciences Working Group
BLSS	Bioregenerative Life Support Systems	ISS	International Space Station
BRL	BLSS Readiness Level	JAXA	Japan Aerospace Exploration Agency
C.R.O.P.®	Combined Regenerative Organic food Production	LAM	Lunar Agricultural Module
CAX2	Vacuolar cation exchanger 2	LEAF	Lunar Effects on Agricultural Flora
CEA	Controlled Environment Agriculture	LED	Light-Emitting Diode
CHAPEA	Crew Health and Performance Exploration Analogue	LEO	Low Earth Orbit
CLD	Commercial LEO Destinations	MAM	Martian Agricultural Module
CNES	Centre National d'etudes Spatiales	MELiSSA	Micro-Ecological Life Support System Alternative
CNSA	Chinese National Space Agency	MIZ1	MIZU-KUSSE 1
COSMIC	Confocal Space Microscopy	NASA	National Aeronautics and Space Administration
CRL	Crop Readiness Level	OSDR	Open Science Data Repository
CSA	Canadian Space Agency	P4S	Plants For Space
DLR	German Aerospace Center	SIM	Structured Illumination Microscopy
ECLSS	Environmental Control and Life Support Systems	SpaCEA	Space Controlled Environment Agriculture
ELGRA	European Low Gravity Research Association	STFC	Science and Technologies Facilities Council
EMCS	European Modular Cultivation System	TRL	Technology Readiness Level
ESA	European Space Agency	UKSA	United Kingdom Space Agency
FLUMIAS	FLuorescence Microscopic Analysis in Space	Veggie	Vegetable Production System

Liverpool workshop provided opportunities to assess progress since the Freiburg meeting, 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. Space research and missions tend to generate many acronyms and abstract names. To orient readers, we have included Box 1 that lists all acronyms and their respective definitions.

Advances in plant space biology enabled by fundamental research

The Liverpool workshop revealed that traditional fields in plant space biology, such as gravitropism, have seen the most significant advances. However, over the past decade, research has shifted more toward understanding plant (both crops and model species) responses and adaptation to other spaceflight stressors. With the exception of ionizing radiation, many of the space stressors covered in Liverpool were new (Fig. 1). The expanding capabilities of 'omics' and modern biological tools help provide a means to shed light on these new challenges and provide an opportunity for more efficient sharing of data and 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 Freiburg (Ruyters & Braun, 2014). The microgravity environment of space_ and gravity's reimposition through centrifuges, for example, on the Kibō module of the International Space Station (ISS) or in 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 need to understand root interactions with the growth substrate to help guide crop cultivation in the microgravity 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 entire root system architecture and, as a consequence, the efficiency of resource acquisition (Morris *et al.*, 2017).

Gravitropism is understood to involve gravity perception, signal transduction, and differential growth (Chin & Blancaflor, 2022). A key focus in Freiburg was the relationship between gravity perception – believed to rely on the sedimentation of starch-filled amyloplasts (statoliths) in gravity-sensing cells (Kiss, 2025) – and growth responses – potentially via the cytoskeleton, cytoplasmic calcium, and the endomembrane system (Ruyters &

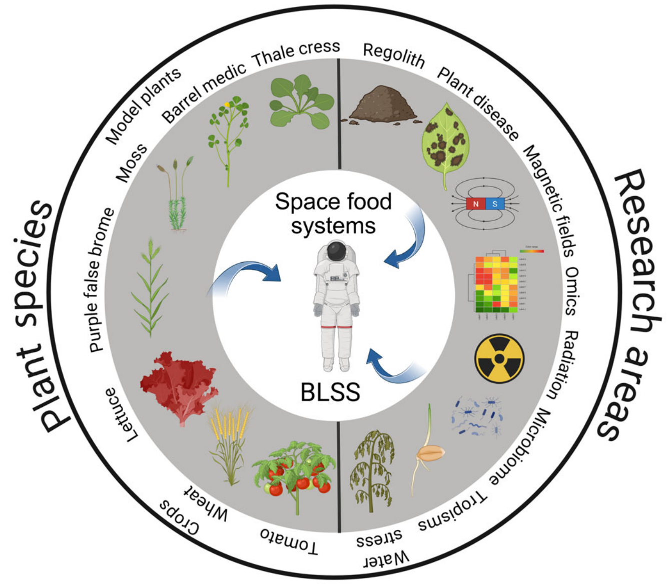

Fig. 1 Representative model plant and crop species studied in space, and research topics discussed at the Liverpool workshop. Translating fundamental and applied plant research into tangible products that can be integrated into sustainable space food systems and a fully operational Bioregenerative Life Support System (BLSS) should be a priority moving forward. This figure was created in BioRender (Gilliham, M. (2025) https://BioRender.com/r9wldfx).

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 (Bérut *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). The name PIN was derived from the bare, needle-like phenotype of flower stems of *pin1* mutants, which mirror plants treated with auxin transport inhibitors. 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). The name LAZY originated from early observations of *lazy* mutants that were deemed 'lazy' because of their prostate growth habit and inability to grow vertically. 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 & Kepinski, 2024).

Research on *hydrotropism* (root growth toward water) has also progressed through studies of the Endoplasmic Reticulum (ER)-localized MIZU-KUSSE 1 (MIZ1) protein (Yamazaki *et al.*, 2012). *MIZ1* was found to be a gene indispensable for root hydrotropism and is conserved in the genome of terrestrial plants (Kobayashi *et al.*, 2007). 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). Additionally, discussions covered *electrotropism* (galvanotropism), the growth of roots toward or away from electric charges. Previous research demonstrated that weak electric fields (1–3 V cm^{-1}) can guide root growth direction with responses functionally equivalent to gravitropism (Salvalaio *et al.*, 2022). The elimination of gravitropic competition in microgravity or partial gravity conditions may prevent the habituation effects observed in terrestrial electrotropism experiments (Salvalaio & Sena, 2024), making electric field-guided root control a potential strategy for sustainable food production in orbital, lunar, or Martian agricultural systems. 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). Tropisms, such as hydrotropism, electrotropism, and phototropism, are more prominent and better studied in microgravity as the overwhelming gravitational stimulus is removed (Millar *et al.*, 2010).

An emerging concept presented in Liverpool was *proprioception* – a plant's ability to sense its own shape (Moulia *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 & Braun, 2014), progress has been limited. The slow pace of implementing high-resolution microscopy in space stems from several challenges, such as image blurriness from crew activity vibrations and liquid handling in microgravity. Moreover, instruments face radiation, thermal fluctuations, and launch stress impacts on microscope optical paths. Experiments must also consider crew time, mass, power, and data bandwidth. The aforementioned problems prompted the development of specialized microscopes for space. The Fluorescence Microscopic Analysis in Space (FLUMIAS), for example, was developed by DLR to address these challenges (Corydon *et al.*, 2016). Recent plant experiments involved imaging *Arabidopsis thaliana* seedlings during parabolic flights and sounding rocket launches, focusing on calcium changes and plastid dynamics. Counterweight systems enhance z-axis focus stability, and microfluidic and solid media chips enable high-resolution imaging. A miniaturized FLUMIAS structured illumination microscope (SIM) prototype was successfully tested aboard the ISS in 2018 (Thiel *et al*., 2019). Currently, DLR is developing the full-sized FLUMIAS-ISS facility (Vinken *et al*., 2025), and ESA has selected the first plant experiment. This facility features a high-resolution SIM microscope on a centrifuge, enabling the imaging of a wide range of biological samples, from living cells to whole organisms, as well as nonbiological research samples, under varying gravity conditions. It will hold multiple experiment blocks in a powered magazine for automatic loading, enabling, for the first time, immediate visual observation of gravity effects, threshold detection, and essential 1-g control during or after experiments – all without crew involvement.

COSMIC (for Confocal Space Microscopy), on the other hand, was developed by JAXA and is currently housed in the Kibō module of the ISS. COSMIC is equipped with a spinning disk unit that will enable time-lapse imaging of live cells with minimal phototoxicity. COSMIC also has a triple-layered laser containment control system to ensure crew safety and a custom holder to secure samples on the stage.

These platforms would allow researchers to exploit a growing toolbox of genetically encoded biosensors in LEO and BLEO. For example, the CaMPARI calcium reporter, when combined with 96-well plate optogenetics 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 – and when integrated with in-orbit imaging hardware – reduce 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). Moreover, *MIZ1*-overexpressing lines of *Arabidopsis thaliana* display accelerated hydrotropism and are more tolerant of drought (Iwata *et al*., 2013).

The Liverpool workshop reaffirmed that the removal of gravity can provide a unique laboratory to unveil new information about less dominant plant tropisms and deliver fundamental insights into plant–environment interactions, evolution, cell–cell communication, and hormone signaling (Chin & Blancaflor, 2022), with applications for both space and Earth agriculture. Looking forward, the integration of 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).

Space stressors and cultivation factors

Outside the safety of Earth's geomagnetic field (GMF), which protects against harmful solar and cosmic radiation, space is a challenging environment for biological organisms. Even in LEO, GMF protection is diminished, and exposure to radiation increases further by regular passage through the inner Van Allen belt, making BLEO an even harsher environment. Understanding how plants respond to these extreme environments is critical for developing sustainable crop production systems (De Micco *et al*., 2023b). Discussions in Liverpool highlighted how the absence of GMF can delay flowering, reduce photosynthesis, and alter photoreceptor activity that is likely independent of radiation effects (Vigani *et al*., 2021). Other space stressors discussed included hypoxia, phytopathogens, and regolith (Maffei *et al*., 2024) (Fig. 1). Among these, the effects of magnetic fields on plants remain understudied. However, there is evidence that quantum effects, such as the radical pair mechanism, might be involved in plant responses to hypomagnetic fields (Maffei, 2025). Whether this represents a constraint for crop cultivation in space remains an open question.

Discussions on the impacts of ionizing radiation, a feature at Freiburg (De Micco *et al*., 2014), continued in Liverpool. Ionizing radiation is known to alter plant morphology, physiology, and biochemistry, with specific effects depending on species, developmental stage, radiation type, and dose (De Micco *et al*., 2011). While concerns persist about radiation's potential to reduce plant productivity in BLSS, observations that radiation can stimulate antioxidant biosynthesis raise intriguing possibilities for enhancing crop nutritional value. Understanding radiation damage, or the potential for some beneficial stress responses, is critical to designing crop shielding strategies and will require more comprehensive studies across diverse plant species over multiple generations, 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, as an *in-situ* available growth substrate. A recent study on *Arabidopsis thaliana* grown in lunar regolith collected during the Apollo missions generated renewed interest in its potential within the *in situ-resource-utilization* approach in future planetary bases (Paul *et al*., 2022). However, the severe developmental defects and stress-related gene expression observed in seedlings in this study highlighted concerns about the diminished fecundity of regolith-grown plants. Additionally, 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 (Caporale *et al*., 2023; Barcenilla *et al*., 2024), and further research into plant–regolith interactions could inform strategies for bioremediation of lunar/Martian regolith and marginal environments on Earth. Advancing this research will require increased access to authentic lunar (and 1 d Martian) regolith, anticipated to be obtained from future Artemis missions (Cockell *et al*., 2024). Despite differing opinions, a key outcome was the shared recognition of the need to build from the research on plant model organisms towards a crop production mindset that acknowledges the operational complexities of spaceflight.

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 Freiburg 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 responses to spaceflight stressors underscored multiple factors that may constrain crop productivity. However, participants noted that gene expression patterns and phenotypes observed in model plants under spaceflight conditions do not always correlate with the growth and development of crops cultivated in ISS growth chambers, nor are they consistent between subsequent space experiments (Hasenstein *et al.*, 2023). This lack of correlation is true even between the same plant species and argues for the need for replicated spaceflight experiments (Land *et al.*, 2024). The need for standardized experimental conditions – first raised in Freiburg (Ruyters & 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. On-board and on-ground 1 g controls should also be systematically used together with careful annotation of metadata in spaceflight-related databases, so cross-comparison between experiments is more likely to succeed. 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 & Braun, 2014), prompting the collection of a substantial volume of 'omics' data from plant experiments conducted in LEO, including suborbital flights, and ground-based microgravity analogs (Meyers & Wyatt, 2022). Many of these data are 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 and integrate the data into existing ones are underway at the European Space Agency (ESA). In this regard, three key topics were discussed in Liverpool. First, the need to consolidate these large-scale data infrastructures across space agencies to maximize the utility of these rare and costly resources. Second, the need to standardize both experimental and data-processing protocols. Third, the value of having multiple ground controls ideally done across the world would increase confidence that observed effects are due to spaceflight and not batch variation.

To date, 'omics' in space has had a significant impact in biomedical research and has offered tools to mitigate human health risks associated with spaceflight (Garrett-Bakelman *et al.*, 2019). Translating plant 'omics' data into practical applications – even on Earth – while challenging (Purugganan & Jackson, 2021), 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 BLSS 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 (Gebre *et al.*, 2024).

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

The central rationale for studying plants in space is to translate scientific insights into practical solutions that support space food systems and, ultimately, a fully operational BLSS (Fig. 1). This rationale has remained consistent since the early missions that sent plants to LEO and continues to be fundamental (De Micco *et al.*, 2023a, 2023b; 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, 2023), along with white papers from ESA member states that highlight key scientific priorities to accelerate the development of BLSS technologies. However, despite decades of foundational research, a fully integrated space food system, let alone a complete BLSS, 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 Analogue (HERA) study that showed 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

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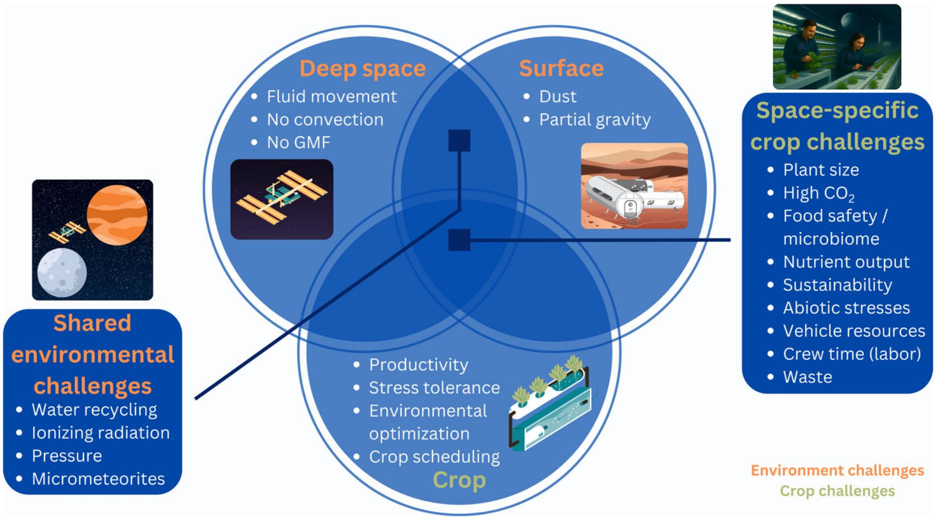

Fig. 2 Summary of environmental challenges in deep space (microgravity) and surface (partial gravity) environments (orange) and crop challenges (green) faced in space crop production. Crop challenges displayed in the lower circle are equally relevant to terrestrial controlled environment agriculture (CEA) and vertical farming, but many are space-specific and are highlighted in the right-hand box.

(ECLSS) and pre-packaged food supplemented with plant-derived 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 BLSS.

Integrating crop production into the space food system presents significant challenges, particularly due to the associated mass and volume requirements (Fig. 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 to accelerate the realization of space-based crop cultivation (Fig. 1).

Space crop production challenges

While many of the crop-focused challenges faced in space-controlled environment agriculture (SpaCEA) parallel those of terrestrial vertical farming and CEA (Wright *et al.*, 2023) (Fig. 2), there are several key challenges unique to space. 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 these challenges was the observed *Fusarium* infection on zinnia plants in the ISS *Veggie* system, attributed to high water stress resulting from a failure in the ventilation system (Schuerger *et al.*, 2021).

Atmospheric differences can also impact plant growth and development. For example, carbon dioxide (CO_2) levels typically range from 2500 to 3000 parts per million (ppm) aboard the ISS (Beard, 2020) – significantly higher than the *c.* 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 CO_2 can influence plant physiology, including the uptake of different nitrogen forms. These elevated CO_2 levels, along with constraints such as growth volume, power availability, and crew time, place stringent constraints on crop selection and cultivation systems in space. Food safety is another key concern, especially when 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 crop cultivation to the lunar and Martian surface. These include uncertainties around crop performance and system functionality under reduced gravity, increased radiation, reduced atmospheric pressure, and limitations in energy and mass budget being planned for future habitats. Crew time is anticipated to be even more limited during early lunar missions, with operational demands taking precedence over scientific investigations, including those aimed at advancing our understanding of plant biology to improve food production systems. As missions expand 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, systems such as NASA's *Veggie* and *APH* have enabled significant advances in crop production aboard the ISS. *Veggie* – with its semi-closed structure – has supported the cultivation of leafy greens and tomatoes, and *APH* – a more complex environmental control system – has enabled experiments with radishes and chili peppers. The introduction of NASA's Crop Readiness Level (CRL) metric (Romeyn *et al.*, 2019) has established a standard for preparing crop species for SpaCEA (Fig. 3), considering key requirements for successful growth and acceptability in space; several crops have reached CRL9, that is, been 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 (Khodadad *et al.*, 2020; Bunchek *et al.*, 2024). These findings are now guiding the

Fig. 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 Bioregenerative Life Support System (BLSS) Readiness Level (BRL) scale for preparing crops for lunar and Martian surface BLSS.

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 (BLSS)

The integration of plants in BLSS 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, adaptable, and seeds are lightweight, with the potential to contain a long-duration supply within a small volume. Including plants in BLSS 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 not fully 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.

Building from decades of research (Wheeler, 2009), we acknowledge that another benefit of integrating plants in BLSS is their ability to purify water and 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 the nutritional requirements of specific plants in the space environment, nor the 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.®) urine 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 (Cockell *et al.*, 2024). It will also be important to consider the trade-offs of relying on crops for food and other BLSS functions. Maintaining the health of crops will be critical, and additional approaches to water and waste recycling and recovery may be necessary, such as noncrop plants, microbial bioreactors, fungi, or insects. Ground-based analogs and future lunar testbeds will be critical for validating waste treatment approaches and conducting trade studies to determine the optimal role for plants in BLSS.

Once technical challenges are overcome, the plants themselves will need to be selected and tailored for BLSS applications. To accelerate crop development, we propose a set of 9 BLSS Readiness Levels (BRLs) (Fig. 3) that builds directly on the existing CRL metric (Romeyn *et al.*, 2019) and establishes a framework to develop and prepare high-CRL crops for BLSS. These additional steps will characterize crop contributions to BLSS, including CO_2 scrubbing, O_2 production, water purification, and edible biomass production compared to crop and system requirements in both optimal (BRL1) and spaceflight-relevant (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 such as improved harvest index and/or processing of inedible plant biomass into other feedstocks like cellular agriculture or edible mushroom feedstocks will help to close the nutrient loop (BRL4) to support fertigation for the next crop cycle (BRL5). Plant ability to support BLSS should be tested in ground analog hardware (BRL6) followed by integration of crop

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cultivation with resource recovery, atmospheric management, and water purification subsystems in high-fidelity ground test demonstrators (GTDs, BRL7). Verification of a crop's capability to provide BLSS functions in a lunar and/or Martian setting (BRL8) is the final step before a crop is considered an 'operational' component of BLSS (BRL9).

While still anecdotal in most cases, plants are reported to contribute to psychological well-being in space and terrestrial analogs. 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, 2024b), 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 (Bunchek *et al.*, 2024; Viejo *et al.*, 2024a, 2024b). 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 BLSS platforms

The importance of advancing BLSS has led many space agencies (ESA, NASA, DLR, JAXA, Canadian (CSA) and Chinese National (CNSA) Space Agencies) to integrate plants in current/past ground demonstrators (e.g. MELiSSA Pilot Plant, EDEN-ISS, NASA's Crew Health and Performance Exploration Analogue (CHAPEA), and Yuegong-1) (Fu *et al.*, 2025), and future high-fidelity analogs outlined in Liverpool (e.g. EDEN-LUNA, LAM-GTD, BIOBASE). Operations and performance in such analogs are vital to inform what future systems in space may include and to increase the readiness level of SpaCEA technologies (Fig. 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 (Fig. 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 (Fig. 4).

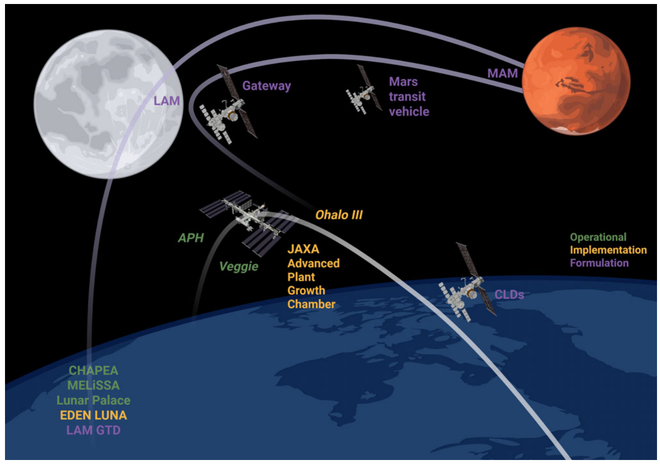

Fig. 4 Current, planned, and potential future space crop production platforms for the development of SpaCEA and Bioregenerative Life Support System (BLSS) to support long-term human space exploration. Advanced Plant Habitat (APH), Bioregenerative Life Support Systems (BLSS), Crew Health and Performance Exploration Analogue (CHAPEA), Commercial LEO Destinations (CLDs), Ground Test Demonstrator (GTD), Lunar Agricultural Module (LAM), Martian Agricultural Module (MAM), Micro-Ecological Life Support System Alternative (MELiSSA). This figure was created in BioRender (Gilliham, M. (2025) https://BioRender.com/jmd9013).

High-fidelity GTDs are essential to support the development of BLSS 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 BLSS 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 (Fig. 4). Application of these technologies and growth strategies in highly constrained, resource-limited space environments will, in turn, improve the sustainability of terrestrial CEA efforts (Mortimer & Gilliham, 2022; Wright *et al.*, 2023).

Frontier biotechnology for space and Earth

Another opportunity that has emerged since Freiburg is the application of plant synthetic biology both for engineering 'designer' plants for specific end-uses and for biomanufacturing (Lloyd *et al.*, 2025). The rapid pace of synthetic biology technological advances, projected to become a multi-trillion dollar global industry by 2030 (McKinsey Global Institute, 2020), shifts the paradigm for both farming and biopharming in Earth and space environments. Gill *et al.* (2025) detail opportunities for engineering plants so they are ideally suited to specific constraints instead of just selecting from existing germplasm; they 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 through genetic manipulation (Gill *et al*., 2025). 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 or manipulation (Wang *et al*., 2024; Sun *et al*., 2025), 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 (Morgan *et al*., 2024; Gill *et al*., 2025). 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 humans return to the Moon and set their sights on Mars, it is important to consider the cultural, ethical, and legal 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. 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. These positions raise questions about whether mission designs should adapt to these differences, or a new globally agreed-upon framework could be established.

These considerations were discussed in Liverpool and are particularly relevant to support our responsible research practice and to plan missions that support the physical health and psychological well-being of those involved.

Fostering international collaboration to accelerate progress

The cost, logistics, and difficulties associated with research that underpins space exploration necessitate that countries share the load – and benefits. As of May 2025, 55 countries have signed 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 multilateral research agreements and 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 skill sets dedicated to progressing BLSS. 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, are 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

Box 2 The Plants for space initiative: A case study

In 2022, the Australian Research Council announced the 7-yr, 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, defense organizations, primary industries, CEA 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 have 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 BLSS 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.

Fig. 5 Priorities for accelerated progress toward BLSS, drawn from the presentations and discussions of the International Space Life Sciences Working Group (ISLSWG) workshop in Liverpool (2024).

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 preexisting large-scale collaboration that has grown since 2019—Plants for Space (P4S) (Box 2)—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; for example, 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 significant 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

The Liverpool workshop has allowed us to look at what has been achieved by the community since Freiburg, and while it has 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 (Fig. 5). We welcome continued dialogue on these matters and look forward to these priorities stimulating new plant-based technologies for both space and Earth applications.

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None declared.

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