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The physiology of plants in the context of space exploration

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The stress that the space environment can induce on plant physiology is of both abiotic and biotic nature. The abiotic space environment is characterized by ionizing radiation and altered gravity, geomagnetic field (GMF), pressure, and light conditions. Biotic interactions include both pathogenic and beneficial interactions. Here, we provide an overall picture of the effects of abiotic and biotic space-related factors on plant physiology. The knowledge required for the success of future space missions will lead to a better understanding of fundamental aspects of plant physiological responses, thus providing useful tools for plant breeding and agricultural practices on Earth.

International space agencies are developing human space exploration capabilities required to venture beyond low-Earth orbit. The Artemis Lunar Exploration Program[1] will allow testing of these systems and operations on the Moon, in preparation for future manned missions to Mars. During long-term missions to the Moon and Mars, the crew will not be able to rely on constant resupply from Earth for water, food, and breathable air. Solving this problem will require the creation of Biological Life Support Systems (BLSS)[2], where resources are produced and recycled thanks to organisms with bioregenerative functions[3]. Plants are a fundamental component of BLSS, as they generate O_2, assimilate CO_2, purify water, and produce fresh food[4]. Exploration will move from a scenario where plants are supplements to the diet to one where in situ crop production will cover almost if not all, the nutritional requirements of the crew. To allow for sustainable and reliable plant production, plant physiologists are studying plant growth and physiology in space. It should be noted, however, that the environmental stressors and constraints that will characterize orbiting stations or bases on the surface of other celestial bodies will differ[5]. Indeed, while objects on orbiting stations and transit vehicles will experience microgravity conditions, partial gravity will be present on the surface of the Moon (1.62 m/s^2) and Mars (3.71 m/s^2). Radiation exposure will increase, and the environmental magnetic field will decrease, as exploration moves away from the protection of the geomagnetic field (GMF). Moreover, spacecraft and planetary bases differ in their constraints in terms of mass, energy, and available in situ resources. All these environmental differences not only affect plant development to different degrees but also determine the requirements and constraints.

Here we describe the developmental and physiological responses of plants to the space environment by considering both abiotic and biotic (Fig. 1) interactions. Among abiotic stress conditions, altered gravity, the presence of ionizing radiation, the absence or reduction of the GMF, altered pressure and light conditions are the most important factors that can impact on plant growth and productivity. Biotic aspects include plant interactions with pathogenic or beneficial microorganisms.

The abiotic environment in space

Altered gravity affects the physiology of plants at both organ and cellular level

Gravity is a major environmental factor in plant evolution, deeply affecting all aspects of plant biology. The effects of altered gravity on plant development and reproduction have been extensively studied[6], but our understanding of the genetic/molecular pathways mediating this response remains incomplete.

Plants perceive gravity through specialized cells, called statocytes, located in the root columella and in the shoot endodermis. Within the statocytes, dense, starch-filled organelles (statoliths) reposition themselves according to the gravitational vector, thus providing information for the developmental response of the plant shoot[7] and root[8] (Fig. 1). Statolith repositioning triggers a complex biochemical cascade that is translated in a transverse auxin gradient across shoots[9] and roots[10]. This, in turn, regulates cell expansion, causing asymmetric organ growth, and, consequently, changes in the whole plant developmental program, deeply influencing plant architecture and shape[11,12]. Recently, the gravity-dependent root growth

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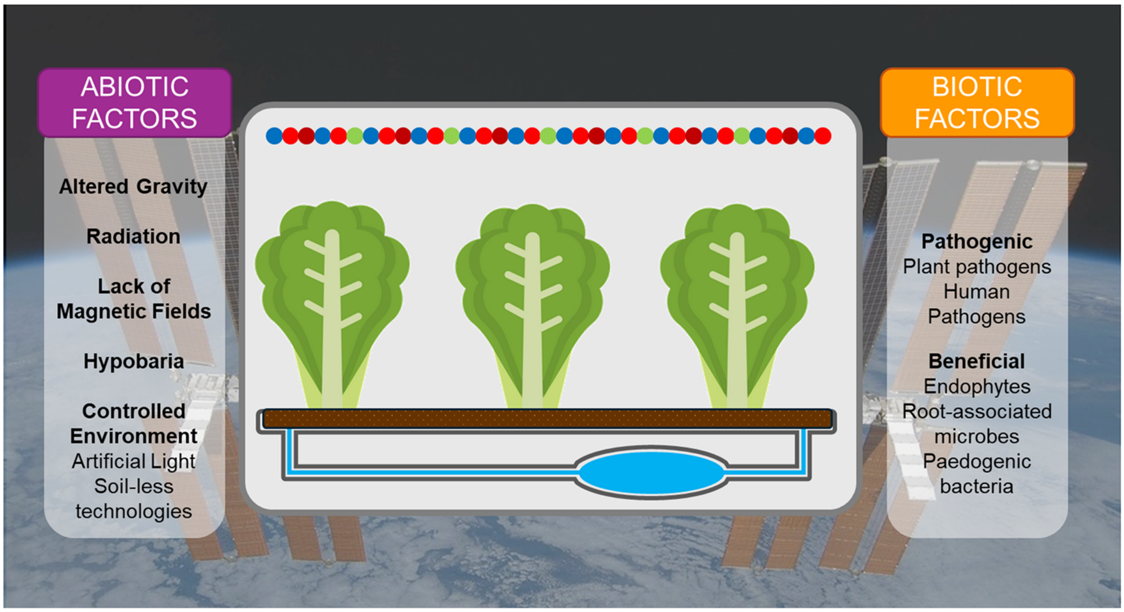

Fig. 1 | Abiotic and biotic factors interfering with plants in the space environment. Abiotic factors include elements that are features of the space environment, like altered gravity, radiations, and the lack of a magnetic field, but also characteristics of the artificial environment that can be created in space, like hypobaria, and the controlled environment for plant growth (artificial light, soil-less technologies). Biotic factors relevant for plant production in space can be both pathogenic (plant and human pathogens) and beneficial (endophytes, root-associated microbes, and paedogenic bacteria) in nature.

mechanism has been described[13]. In gravity-sensing columella cells, the protein MPK3 phosphorylates the proteins LAZY3 and LAZY4, which results in the increased association of LAZY proteins with the TOC proteins on the surface of amyloplasts. Upon amyloplast sedimentation, LAZY3 and LAZY4 are released from the amyloplast and move to the plasma membrane, where they recruit the auxin efflux proteins PIN3 and PIN7, by means of interaction with RLD family proteins. The activity of PIN proteins allows the movement of auxin out of the cells and the formation of an asymmetrical gradient of the hormone, that causes the inhibition of cell elongation on the lower side of the root, thereby causing the gravitropic root growth[14,15]. Other plant growth regulators play a role in gravitropism, including brassinosteroids[16], ethylene[17], gibberellic acid[18], jasmonic acid[19], and Ca^{2+} signaling[20]. While the lack of a gravitropic input, whether real (spaceflight) or simulated (e.g., clinostats or Random Positioning Machines), can be compensated by other tropisms[21], it is important to understand how altered gravity can affect non-vertical growth angles and, therefore, plant architecture for long-term space exploration objectives. The threshold for the onset of a gravitropic response has been estimated to be around 10^{-3} g, above which the magnitude of the graviresponse is only dependent on the inclination[22]. This suggests that altered gravity would be problematic, from a gravitropic point of view, only in orbiting stations and transit vehicles.

Gravisensitivity, i.e., the metabolic and structural adaptation to altered gravity conditions, is common to all cells, whether specialized or not specialized for gravity perception[23]. Reduced gravity induces changes in the content of lignin, cellulose, callose, and hemicelluloses of the plant cell wall[24]. Within the cell, altered gravity can cause alteration of the structural and functional organization of organelles and of the subcellular structures of mitochondria[25], chloroplasts[26], cortical microtubules[27], and ER bodies[28]. While the molecular mechanism mediating these effects is still largely unknown, it has been shown that reduced gravity induces changes in the activity of peroxidases, pectinases, and cellulases and in the calcium balance in the cytoplasm and apoplast[23]. Other microgravity-induced alterations include a higher production of reactive oxygen species[29] and of heat shock proteins[30], alterations of the cell cycle and nucleolar[31], and meristematic activity[32]. In this context, gravity alterations can significantly influence plant reproduction, as they modulate the growth of and traffic in the pollen tube[33], affect the development of male and female reproductive organs, and impact seed germination[34]. Interestingly, studies on cell proliferation in partial gravity conducted using a modified RPM system have shown that the response is more complex than expected. Indeed, in plants grown in Moon gravity the effects on cell proliferation and cell growth were worse than in simulated microgravity. Interestingly, in the simulated Mars *g*-level, cell proliferation was similar to the 1 *g* control, suggesting, again, that some environmental conditions might not be challenging for plant growth on Mars[35].

In view of the utilization of plants, as life-supporting systems in human long-term space travel, it is imperative that the effects of gravity on such crucial plant processes as development and reproduction are approached at a basic level. While we are starting to decipher the last missing details of the graviresponse[13], very little is still known regarding gravisensitivity at cellular and organism levels. Moreover, phytohormones are hardly mentioned in plant-based studies in space due to technical constraints, like sample storage. In addition to the crop species, the use of plant model systems, for which numerous genetic/molecular resources and tools are available, is facilitating the study of these basic mechanisms and subsequent translational research. The knowledge gained on the control of key traits affecting plant adaptation, survival, and productivity will provide powerful tools for space-targeted precision breeding.

The impact of ionizing radiations on plants

Deep space radiation environment beyond low-earth orbits (LEO), i.e., outside Earth's protective GMF, is characterized by a flux of ionizing radiation. Space radiation is mostly composed of protons and heavier nuclei stripped of their orbital electrons, but also includes a minority of electrons and positrons, corresponding mainly to high-energy heavy-ion (HZE), charged particles of galactic cosmic rays (GCRs) and solar energetic particles (SEPs)[36]. In addition, as a result of space radiation interacting with matter, e.g., the surface of planetary bodies or spacecraft structures, secondary radiation, which is constituted by neutrons of different energies, is generated[37]. Plants can be affected by ionizing radiations at both genetic and epigenetic levels. Genetic effects are mainly due to the occurrence of DNA double-strand breaks (DSBs), which can lead to chromosomal aberrations, structural variation, or point mutations. These are mainly the result of inaccurate repair processes such as those caused by the non-homologous end joining repair pathway, which has been shown to be prevalent in plants[38]. Another peculiar feature of angiosperms is that most species studied so far, including most crops, carry very active transposable elements (TEs). It is believed that TE activation has frequently caused massive amplification, which led to profound genome reorganization and extensive structural variation in intergenic regions[39]. Many TEs appear to be activated by different types of environmental stress, including radiation exposure[40]. The availability of a vast range of technologies that exploit the power of next-generation sequencing allows us today to analyze all these phenomena at the whole genome level.

The effects of ionizing radiations have been investigated only on a small proportion of plant species, and increasing inquiries on a wider number of plants will improve our understanding of the biological effects of radiation[41]. Plant cells show higher radiation resistance compared with their animal counterparts. Different studies, performed in space and with simulated space-like levels of radiation on the ground, have assessed the structures and mechanisms conferring radioresistance to plant cells[42]. Densely ionizing radiations are more efficient in inducing damage, in comparison with sparsely ionizing radiations[43]. For this reason, there is significant literature concerning the effects of acute high-dose-rate exposures on plant genetics, growth, and development. Much less is known regarding the effects of chronic, low-dose radiations, especially those related to the impacts of the high-energy protons and heavy ions that are encountered in the space environment[44]. Under chronic irradiation conditions, pollen and seed viability are reduced, growth rates are slower, and the frequency of developmental abnormalities is increased, although there is considerable variation among taxa. In addition, it has been shown that the response elicited by radiation exposure has complex interactions with other environmental stressors (e.g., temperature, drought, heavy metals)[44], suggesting that the other risks associated with the space environment could play important roles in determining susceptibility to radiation-induced stress.

The reactions induced by primary radiation include the formation of various forms of reactive oxygen species (ROS) and are the cause of the observed changes in the functional activity of plants[45]. It is, therefore, expected that plants react to radiation by altering their redox status. X-ray exposure of *Brassica rapa* to doses up to 30 Gy does not induce detrimental effects on growth, while it stimulates the production of antioxidants, improving plant defence and, concurrently, nutritional value[46]. In *Beta vulgaris*, ionizing radiation (10 Gy) and specific light quality regimes interact in a complex manner to regulate photosynthesis and the accumulation of bioactive compounds in leaf edible tissues. In particular, while under a white light regime, gas exchanges of irradiated plants strongly declined compared to control, irradiation with titanium high-energy ions under red-blue light improved the water use efficiency and increased pigments, carbohydrates, and antioxidant content[47]. It should be noted that the exposure of seeds to these conditions negatively affected the germination rate; however, these results introduce the idea of exploiting space growth conditions to produce plant species with increased antioxidants as a supplemental functional food[46,48].

Work should be done to elucidate the effects and the molecular mechanisms of response to ionizing radiation exposure, in both model and crop plants. Moreover, while considerable information is available on the effects of ionizing radiation at the genetic level, much less is known on whether it can also lead to inheritable epigenetic changes, which could determine changes in DNA methylation or histone modification and chromatin conformation changes[41,49]. Unfortunately, most of the current studies on plants derive from experiments conducted with different radiation types and doses[50]. Moreover, it is hard to reproduce the complexity of the full space radiation spectrum, which is composed of solar electromagnetic particles and high-energy protons and heavy ions from outside our solar system. A standardization of methods and protocols for irradiation experiments is necessary to validate the current knowledge of space-relevant radiation.

Magnetic field requirement for plant life in space

The GMF is a natural component of our planet. The GMF is a three-dimensional vector field, which is generated in the outer core of our planet and surrounds the circum-terrestrial environment, shielding it from energetic solar wind and harmful cosmic rays. In addition, plants, like all other living organisms, have evolved in the presence of the GMF. While phototropism, gravitropism, hydrotropism, and thigmotropism have been thoroughly studied, the plant response to magnetic field (MF) variations is not yet well understood. However, plants responses to MF have been extensively documented[51–54]. Concerning the current theories of magnetoperception, the mechanism involving radical pairs (i.e., magnetically sensitive chemical intermediates that are formed by photoexcitation of cryptochrome[55]) has been demonstrated both in animals[56,57] and in plants[58]; moreover, the interaction between cryptochrome (Cry)[59] and iron-sulphur complex assembly[60], define a magnetosensing protein complex named MagR[61] (see below) that is present in several living organisms[62–64], apparently as a response to the GMF. However, the mechanisms of plant magnetoreception and adaptation to different MF remain to be elucidated[65]. Such information will be important to forecast the behavior of plants, and other organisms, in environments where the MF will be different, such as the Moon Space Gateway (SG), the Moon's surface, Mars and other planets that lack a MF. On the other hand, some moons of the gas giants Jupiter and Saturn, like Europa and Enceladus, are of great astrobiological interest and are subject to the strong MFs of their planets[66].

Several lines of evidence have shown that plants are able to perceive MF variations, both below and above the GMF, and respond with physiological, metabolic, and anatomical changes[51,54,67]. For instance, experiments performed with a triaxial Helmholtz coil system could clearly demonstrate that plants react to changes in GMF inclination[68] and intensity[69], with genes responding specifically to MF variations as a typical stress response. GMF variations were found to alter the plant redox status[70], which in turn affects the photosynthetic activity[71] and the cryptochrome biological activity[58]. Indeed, there is a partial association between the MF-induced changes in gene expression and an alteration in Cry activation[72]. A mechanism for magnetoreception has been proposed in the fruit fly (*Drosophila melanogaster*) and involves a magnetosensor (Drosophila CG8198, MagR) complex constituted by iron-sulphur cluster assembly (ISCA) and Cry[61]. In the fruit fly magnetic receptor, a linear polymerization of magnetoreceptors containing Fe–S cluster leads to the formation of a rod-like biocompass center, surrounded by photoreceptive cryptochromes[61]. Interestingly, four plant proteins were found to be highly similar to MagR: IscA-like 3 (*At2g36260*), IscA-like 1 (*At2g16710*), IscA-like 2 (*At5g03905*) and cpIscA (*At1g10500*)[60]. *Arabidopsis thaliana* plants grown under single or combined Fe- and S-deficient conditions and in hypomagnetic field (HMF), show alteration in Fe and S uptake and homeostasis[73,74]. This variation may lead to reduced Fe-S availability for ISCA formation, which in turn would reduce MF sensing in plants exposed to HMF[70]. In plants, the flowering time and fruit set are important for plant productivity and are regulated by the circadian clock. The amplitude of the oscillating genes that are part of the plant's internal clock is significantly different under varying MF conditions, regardless of the lighting conditions, implying that, unlike animals, plants can respond to changes in MF in the dark[72,75].

The proximity to gas giants, like Jupiter and Saturn, implies the presence of strong MFs. The magnetic field effect (MFE) depends on the strength of a MF that can be classified as weak (<1 milliTesla-mT), moderate (1 mT to 1 T), strong (1 T to 5 T), and ultra-strong (>5 T). Weak MFs, as the GMF, can be perceived by animals and plants as described above. Moderate-intensity static MFs (SMFs) influence those biological systems where function depends on the properties of excitable membranes[76]. Strong and ultra-strong fields affect living organisms by altering the preferred orientation of a variety of diamagnetic anisotropic organic molecules[54]. It has been shown that strong MFs can induce alterations of the cleavage plane during cell division[77] and other cellular disorders[78]. In Arabidopsis, strong MFs may compromise some aspects of the transcriptional machinery, by perturbing the delicate conformational dynamics involved in gene regulation, resulting in differential gene expression and, in extreme cases, the halt of transcription[79]. MFs can be perceived by plants through their amyloplasts, which can be displaced by a sufficiently intense, high-gradient MF. By displacing amyloplasts with MFs, it is possible to induce curvature in roots, triggering the developmental response that is normally activated during graviresponse downstream of amyloplast sedimentation. This effect is defined as magnetotropism, although it seems that the cause of the growth response is a ponderomotive force and not the MF[80].

Variations in MF intensity influence many plant biological processes. Unlike an electric field, an MF is not attenuated by living tissues and penetrates through the whole plant body. Reduction of the GMF, a condition typical of the deep space environment, alters the plant morphology and redox status by delaying flowering[81] and altering the plant defence to pathogens[82,83]. The study of the plant response to strong MFs could also guide future research designed to explore the possibility of life on moons of planets with high MFs, such as the solar system gas giants. Plants show both light-dependent and light-independent magnetoperception and recent data have suggested that different organs may perceive MFs in a differential way, with a typical hormetic behavior[69]. The recent discovery that plant ISCA may play a role in magnetoreception[60,71] could help understand the plant signaling cascade triggered by MF variations, which contributes to the plant responses in space. Indeed, the reduction of the GMF to HMF was shown to significantly alter the gene expression of the fruit fly homolog MagR in important crop plants such as bean[71] and maize[84], suggesting an important role of plant MagR homologs in plant magnetoperception. Unlike migratory birds, plants presumably have no use for a magnetic compass and may derive some other evolutionary benefit from the presence of the GMF. Optimization of growth, for example, seems more likely than the development of a new sensory modality[85].

Plants respond to atmospheric variations in pressure and composition

The development of greenhouses on Mars, on the Moon, and in Earth orbit considers the use of low atmospheric pressures (hypobaria) to address systems and engineering limitations[86]. It is reasonable to expect that reduced-pressure atmospheres will be used to decrease the lift costs of structural components and consumables for future transit vehicles and surface missions. In fact, mass reduction increases the space mission length and launched payloads[87]. However, alterations in atmospheric pressure are known to have effects on the physiology and development of plants[88]. Clarifying the mechanisms behind the physiological adaptation of plants to hypobaria is therefore very relevant to space exploration in the effort to expand food production in orbital and extra-terrestrial controlled agriculture. Growing plants under reduced pressure affects their growth and, depending on the species, may lead to either positive or negative effects. These effects are also correlated to atmospheric O_2 and CO_2 concentrations[89]. Low atmospheric pressure also affects water movement: transpiration rates increase as atmospheric pressure is reduced, even at high relative humidity, influencing stomatal aperture independently of relative humidity[90]. In general, plants show adaptation not only to hypobaria but also to gradients of atmospheric pressure, which induces the activation of genes that code for metabolic processes involved in the hypoxia stress response[88]. Crucially, under microgravity conditions free air convection is restricted, limit heat and gas distribution, causing unfavorable conditions close to the leaf. Long-term experiments conducted onboard the ISS have shown that the precise control of environmental parameters, including air circulation, normal evapotranspiration, and net photosynthetic rates, can be achieved by the plant, even in microgravity conditions[91].

The reduced partial pressure of O_2 (hypoxia) is widely used in plant experiments aimed at the partial mimicking of hypobaria. Recent work aimed at uncoupling the effects of hypoxia and hypobaria has shown that the latter causes phenotypic changes in development and metabolism, and in the expression of related genes, both in roots and shoots[89,92]. Early experiments with peas (*Pisum sativum*) and bean (*Phaseolus aureus*) showed that plants respond to hypobaria and hypoxia with alteration in the basic metabolism, including the Krebs cycle, mitochondrial respiration, and photosynthesis[93,94]. Evaluation of the *A. thaliana* differentially expressed genes (DEGs) showed that, in shoots exposed to hypobaria and/or hypoxia, adaptation to hypobaria included metabolic pathways well beyond those activated for the adaptation to hypoxia[87]. It was also demonstrated that the Arabidopsis net photosynthetic rate increased in hypobaria when CO_2 partial pressure was a limiting factor and did not change at normal or increased CO_2 partial pressure[95]. This indicates that CO_2 concentrations can be kept elevated in hypobaric plant growth modules without affecting photosynthesis. In lettuce (*Lactuca sativa*), growth under hypobaria conditions has adverse effects on plant growth, gas exchange, and resistance to hypoxic conditions[96,97]. In this important crop, hypobaric conditions induce a higher production, compared to sole hypoxia, of the plant growth-inhibiting phytohormone ethylene[98–100]. While uptake of NH_4^+ and NO_3^- were improved by 30 kPa hypobaria under the same O_2 partial pressure[101], low oxygen stress induces the production of lettuce protective phytochemicals and the free radical scavenging potential[102]. In another important crop, wheat (*Triticum aestivum*), average rates of photosynthesis and transpiration increased in hypobaria (50 kPa) and also increased when oxygen partial pressure was reduced further; however, lower oxygen partial pressure (2.5 kPa) was unsuitable for reproductive growth of wheat[103]. In radish (*Raphanus sativus*), growth can be enhanced and transpiration reduced in hypobaria by enriching the atmosphere with CO_2, although at high CO_2 levels leaf damage may occur[104]. In this crop, hypobaric conditions perturbed the shoot nitrogen-related metabolism.

Ongoing research has demonstrated that, in plants, there is a clear separation between the effects of hypoxia and water stress, and hypobaria. Root and shoot DEGs of plants exposed to hypobaric conditions display a more complex regulatory pattern than simple hypoxia, a condition that cannot be recovered by increasing the O_2 partial pressure[89]. This important result underlines the importance of evaluating the biological consequences of hypobaric environments for the exploration of life-support habitats. Our overall understanding of how atmospheric pressure influences plants and, hence, directly plant-driven bioregenerative fluxes is still very limited, and studies of the underlying genetic/molecular mechanisms are much needed[89]. Other environmental factors, such as humidity and atmospheric temperature and composition (including volatile organic compounds, or VOCs, airborne contaminants, and dust), which could crosstalk with the hypobaria response, are also very important and could affect plant growth in planetary greenhouses.

Light requirements for plant growth in the space context

Light is a critical environmental factor that has an influence on plant growth, from seed germination to flowering and fruiting. Light conditions, including photoperiod, intensity, and spectral quality, are among the most relevant external factors affecting plant growth and development[105]. Light spectral composition and intensity influence morphology, physiology, and development by impacting processes ranging from photosynthesis to secondary metabolism[106,107]. Genomic studies reported that light induces extensive reprogramming of gene expression patterns, and the effect of light (mainly red light) can help in restoring meristematic competence under microgravity conditions[108]. Furthermore, different photoperiods can modify the expression of genes regulated by the circadian clock, affecting flowering time[109]. Importantly for space applications, in the presence of light, roots remain negatively phototropic in microgravity[110]. In Arabidopsis, both WS and Col-0 ecotypes remained negatively phototropic in microgravity, although with differences in wave and skew directions[111].

BLSS involving photoautotrophic organisms is needed to sustain long-duration crewed missions beyond LEO. Sunlight for plant growth is an unreliable source that depends on local conditions, while electric lighting (or hybrid electric-solar) systems are more suitable for growing plants in space[108]. Experiments have been conducted to verify plant growth using fluorescent lamps in the Lada plant chamber housed in the Russian module onboard the International Space Station (ISS)[112]. However, currently, Light-emitting diodes (LEDs) are considered the best option for BLSS growth facilities due to the limited space present onboard future orbiting and planetary stations. Moreover, LEDs are highly energy efficient, difficult to damage with physical shocks, and more resistant to extreme temperature changes than fluorescent lamps[105]. LEDs can also be used to modulate spectral composition in time and, therefore, tune plant productivity and yield[110,113,114]. Onboard the ISS, LEDs are currently used in the VEGGIE system, which includes red (630 nm), blue (455 nm), and green (530 nm) LEDs[115].

The development of the so-called "light recipes" could help increase the efficiency of plant growth and modulate nutritional qualities. Experiments on wheat and Arabidopsis, conducted in the advanced plant habitat (APH) facility onboard the ISS, have already successfully tested optimized light spectra composed of blue, green, and red LED illumination at diverse light levels (e.g., 150 $\mu mol\ m^{-2}\ s^{-1}$ for Arabidopsis and 600 $\mu mol\ m^{-2}\ s^{-1}$ for wheat/Arabidopsis)[116]. Interestingly, it has been suggested that the red-light phototropic response can compensate for the stress induced by microgravity at the cellular level[117]. Moreover, in the plant, the light spectrum can regulate the production of secondary metabolites, like phenolic compounds, anthocyanins, and ascorbic acid, that are often beneficial for human health[118]. It is therefore paramount to further understand how light affects plant physiology, in an exploration context, to design adaptive growth regimes[119,120].

The biotic challenges of growing plants in space

On Earth, plant growth, health and productivity are deeply influenced by a multitude of microorganisms, collectively known as the plant microbiota, that thrive on the outer surfaces as well as in internal tissues[121,122]. Some of these microbes are beneficial while other are commensal or pathogenic. The nature of the relationship established with the host plant depends on the partners involved, but the functional roles can also vary in response to environmental factors[123,124].

Beneficial microbes, especially endophytes, significantly increase host fitness through improved nutrition and protection from biotic and abiotic stress[122,125]. Photosynthetic microorganisms may contribute to plant growth with their potential biostimulant effects for life in closed environments, as recently reviewed[126]. On the other hand, plant-microbe associations can contribute to supporting plants survival, growth, and health under harsh environmental conditions such as those of space missions. Microbes can promote plant growth through more efficient and sustainable use of nutrients—e.g., nitrogen provided by nitrogen-fixing rhizobia[127] and phosphorus provided by mycorrhizal fungi[128]—as well as through the emission of volatile organic compounds[129,130], which can even more efficiently accumulate in close environments. In addition, plant-associated microbes can provide higher tolerance to abiotic stresses (water shortage, high/low temperature, etc.) and to phytopathogens, which can be accidentally introduced in space environments, through the activation of plant immune responses[131,132].

Plant pathogens: a threat also for space farming

Plant disease control in enclosed environments, especially in microgravity conditions, is regarded as a serious issue for precision farming. Prevention and control of plant pathogens in space are particularly critical because plants are known to be more susceptible to fungal pathogen infection in microgravity condition[133,134]. The choice in plant species, management practice, and growth conditions can dictate the presence and abundance of microbial pathogens. Moreover, spacecrafts and space habitats supporting human exploration, which harbor diverse microbial populations, can act as a reservoir of potential pathogens[135]. Beside good sanitation procedure, a better understanding of phytopathogen interactions is of relevance to guarantee food security and safety in space. New strategies involve the optimization of growth conditions to stir plant development towards tolerance to pathogens, *e.g.*, inducing the production of specialized metabolites with a role in defence (including VOCs), and the use of beneficial plant-associated microbes that can lead to a priming status[129].

Plant pathogens can affect the success of a mission by destroying plants serving as food sources or in as recycling systems[136,137]. The formation of the plant structural barriers and the activation of plant defence responses has been shown to be impaired in spaceflight conditions, while altered gravity can stimulate pathogens growth and reproduction, increasing their pathogenicity[134]. Interestingly, after five/seven years in space, tomato seeds did not show a relevant decrease in germination or performance, but enhanced resistance to pathogens[138]. However, pathogens in enclosed habitats, including seed-borne ones, can lead to extensive plant damage[136]. The first instance of plant pathogens in space was related to *Neotyphodium chilense*, a fungal plant pathogen fungus, that was found to be the underlying disease agent of wheat seedlings inside the Plant Growth Unit[139]. An experiment dedicated to verifying the effect of microgravity on plant-phytopathogen interaction was performed on the Shuttle STS-87 flight. Soybean roots were inoculated with oospores of the *Phytophthora sojae*, which is a common root-rotting pathogen in this plant species[140]. The disease symptoms, the extent of the infection, and the number of new oospores were significantly higher in space-flown plants compared to ground controls. The Vegetable Production System (Veggie), a facility onboard the ISS to produce fresh vegetables,[115,141] uses the ISS cabin air for dehumidification and temperature control. When this air happened to be contaminated with infective propagules of the plant pathogen *Fusarium oxysporum*, it led to severe disease in *Zinnia hybrida* plants that were being grown in the Veggie module[142]. The development of symptoms in microgravity conditions was correlated to a reduced airflow that led to an increase in the water enveloping the leaves and stems. Generally speaking, the increase in disease severity in microgravity, reported in all the above-mentioned cases, was correlated to low-light levels, elevated relative humidity, and the environment in the spacecraft[136,142,143]. It has been suggested that challenges related to microbial and insect pests that occur in field, greenhouse, or vertical-farming, are also valid for future BLSS-supported missions. Specific protocols based on an Integrated Pest Management approach should therefore be developed, taking into account all aspects of plant production, to avoid the spreading of potential pathogens[136].

Beneficial interactions between plants and microbes can sustain plant production for space applications

Beneficial components of the plant microbiota can significantly increase plant fitness through the modulation of regulatory networks involved in nutrient acquisition, development, and immune responses[122,144–146]. Special attention has been given to bacterial and fungal endophytes that, by colonizing plant tissues, establish a more intimate association with plants[124,125,147]. Well-known examples are symbiotic, nitrogen-fixing rhizobia[148] and plant growth-promoting rhizobacteria (PGPR) such as *Bacillus subtilis*[149]. Beneficial fungal endophytes include the shoot grass *Epichloë* spp.[150], the plant-growth-promoting and biocontrol agent *Trichoderma* spp.[151], and the well-known mycorrhizal fungi, which are characterized by specialized plant-fungal interfaces for mutualistic resource exchanges[128,152]. Root-associated microbes activate the so-called induced systemic resistance (ISR) that can accelerate defense-related gene expression in the host, thus priming the plant immune system and improving tolerance to a broad range of pathogens and insect herbivores[132].

Current knowledge about the potential of plant-associated microorganisms to support plant life in spaceflight and extra-terrestrial environments is limited[153,154]. There is evidence that rhizobia can improve soil fertility and plant growth in Martian regolith simulant[155]. However, it has been shown that microgravity can have a negative impact on the formation of nodules[156]. Similarly, mycorrhization and phosphate uptake were reduced in the model plant *Petunia hybrida* under simulated microgravity[157]. This effect, likely due to an inhibition of hyphal elongation and branching, could be reduced with an increase in root exudate of strigolactones, plant rhizospheric signals able to promote arbuscular mycorrhizal colonization[157]. This suggests the possibility of manipulating plant-fungal chemical communication for the successful establishment of mycorrhizas under challenging conditions. Careful consideration of the plant microbiota should, therefore, be included in the development of crops with improved performance and better adaptability to space conditions[153,158].

Other mutualistic symbiotic systems of interest for astrobiotechnological applications are lichens, where unicellular green algae and/or cyanobacteria associate with fungi. Lichens represent ideal meta-organisms for investigating the survival and adaptability of living organisms to harsh environments as they can show tolerance to extreme space-like conditions, e.g., dehydration, extremely low temperatures, and oxygen depletion[134]. In addition, some lichens were shown to produce, under specific conditions, a high amount of molecular hydrogen (H_2)[159], which is considered one of the most promising fuels in the future.

Abiotic and biotic interactions converge in the definition of plant substrates for space farming

On Earth, plant growth is sustained by soil, a complex mixture of organic matter, minerals, gases, liquids, and organisms, that is not found on any other known planetary body. However, the transport of soil to future space settlements is not logistically feasible. While establishing an in situ paedogenic process starting from lunar and Martian regolith is a possibility in the long term, space farming will rely on the modern cultivation practices of the soilless system for the foreseeable future. Soilless growth practices require less water and nutrient application and are, overall, more sustainable to produce plants in a controlled environment. Depending on the exploration objective, plants could be grown with hydroponics (classical or nutrient film technique, NFT), aeroponics, on various solid substrates, or amended regolith and technosols. Onboard the ISS, plant growth in the Veggie is sustained by clay-based "pillows" filled with fertilizer. The pillows have been designed to help distribute water and air in an optimal way, considering fluid behavior in space[160]. Generally speaking, the use of soilless growth systems allows to counteract the altered behavior of fluids in microgravity and actively supplies the roots with the nutrient solution.

The properties of different growth substrates can affect water, oxygen, and nutrient availability for the plant. Localized deficiency or oversupply of nutrients and gasses can induce morphological, physiological, and biochemical adaptations[161]. For instance, it has been shown that plants grown in a hydroponic system differ from their solid substrate-grown counterparts in the number of leaves, stomatal density, and content of pigments, sugars, and ions[162]. Moreover, it has been shown that while natural fiber substrates tend to promote yield and production turnover, this is accompanied by a reduction in phytochemical content in microgreens[163]. It is therefore important to understand how plants adapt to different substrates, in the context of all different applications of plants in space exploration (food production, biomining, and bioremediation). Issues could arise with pH, nutrient availability, air and fluid movement, the presence of potentially toxic elements, and altered root microbiota.

Indigenous regoliths are being considered as potential substrates for plant growth[164]. In addition to being available in situ, regoliths could represent a solid substrate and a source of inorganic nutrients. The growth of many species of plant has been tested using Moon and Mars regolith simulants, with various degrees of success[165]. When present, the effects of regolith simulants ranged from stunted growth to reduced seed quality and viability[165–167]. Recently, it was shown that the use of actual lunar regolith brought back from Apollo 11, 12, and 17 missions[168], slows plant development and induces severe stress-related morphologies. Plants grown in lunar soils differentially expressed genes related to ionic stresses, similar to plant reactions to salt, metal, and reactive oxygen species. These data indicate that, although in situ lunar regoliths can be useful for plant production in lunar habitats, they are not ideal substrates for plant growth[168]. The amendment with compost percolates and bioweathering has already been shown to improve the fitness of plant growth regolith simulants[166], so subjecting lunar and Martian regolith to a paedogenic process could make them suitable for plant space farming for future applications[169,170].

The growth substrate is a critical element for space farming applications. It must fulfill specific characteristics, such as guaranteeing the respiration of roots and the absorption of nutrients. This can be achieved by the geometry, distribution and size of the pores, and the type of material used[171]. An emerging technology capable of providing this improvement in current space agriculture systems is 3D printing, also called "Additive Manufacturing" (AM). AM can be used to create complex and hierarchical structures by using different printing techniques and different materials, that could also be, in the future, recycled[172,173]. AM is a rapidly developing technology, for which new materials and technologies capable of building increasingly complex and tailored structures are constantly developed.

Figure 1 summarizes abiotic and biotic factors that characterize the space environment.

Ionizing radiations can affect plants at both the genetic and epigenetic levels. Gravity alterations can significantly influence plant reproduction and affect the development of male and female reproductive organs. Understanding plant response to magnetic fields will be important to forecast the behavior of plants in extreme environments where the magnetic fields will be different (Lunar Gateway, Moon, Mars). Understanding the plant responses to atmospheric pressure variations, like hypobaria, is very relevant to space exploration in the effort to expand food production in orbital and extra-terrestrial controlled agriculture. Light influences plant growth, from seed germination to flowering and fruiting. The effect of light quality and quantity can help restore meristematic competence under microgravity conditions, and light-emitting diodes (LEDs) are currently used in space farming to modulate spectral composition for optimal plant growth. Plant-microbe associations can contribute to support plants survival, growth and health under harsh environmental conditions such as those of space missions. Nutrient assimilation in plants can be improved by nitrogen-fixing rhizobia and mycorrhizal fungi. Pathogens can affect plant productivity and pose a risk to food safety, both on Earth and in space.

Conclusions

To achieve the current human exploration goals, future space outposts must be designed as self-sufficient, closed ecosystems that require minimum expenditure of energy and in which resources, like air, water, and food, are regenerated. Plants are a fundamental component of BLSS as they supply O_2, sequester CO_2, purify water, and produce fresh food. Additional research on the fundamental mechanisms underlying the interaction between plants and their adaptation to the space environment is essential to guide future applied research and guarantee the success of long-term goals (Fig. 2). Despite the wealth of knowledge produced in the past few decades, a lot of work still needs to be done to understand the synergy between different stressors and their possible impact on crop growth and productivity. Importantly, it has been shown that in the multifactorial stress combination, even if the level of each individual stressor is below the response threshold, plant growth and survival will decline dramatically with the number and complexity of stressors involved[174]. This is partially due to technical difficulties and the many constraints of performing biological research in space[175,176]. Genetic engineering (biotechnologies), guided by fundamental molecular research and applied to plant breeding, has the potential to accelerate the production of optimal crops for space applications[177]. Advances in these fields could have positive impacts on Earth, by creating novel, highly efficient agricultural technologies suited to meet the "From Farm to Fork" strategy objectives and innovative concepts for sustainability.

The knowledge of the plant responses on Earth and the available technologies (substrates, light, etc.) for precision farming, represent the starting point to understand how plant physiology is affected by space conditions. Future trends in plant biotic interactions include optimization of space-oriented plant-microorganism interactions, whereas the abiotic conditions require a deep knowledge of the multi-omics responses and of the mechanisms adopted by plants to tolerate and adapt to the space environment.

There are different genetic engineering technologies that can result in plants that contain different types of ameliorative modifications. On Earth,

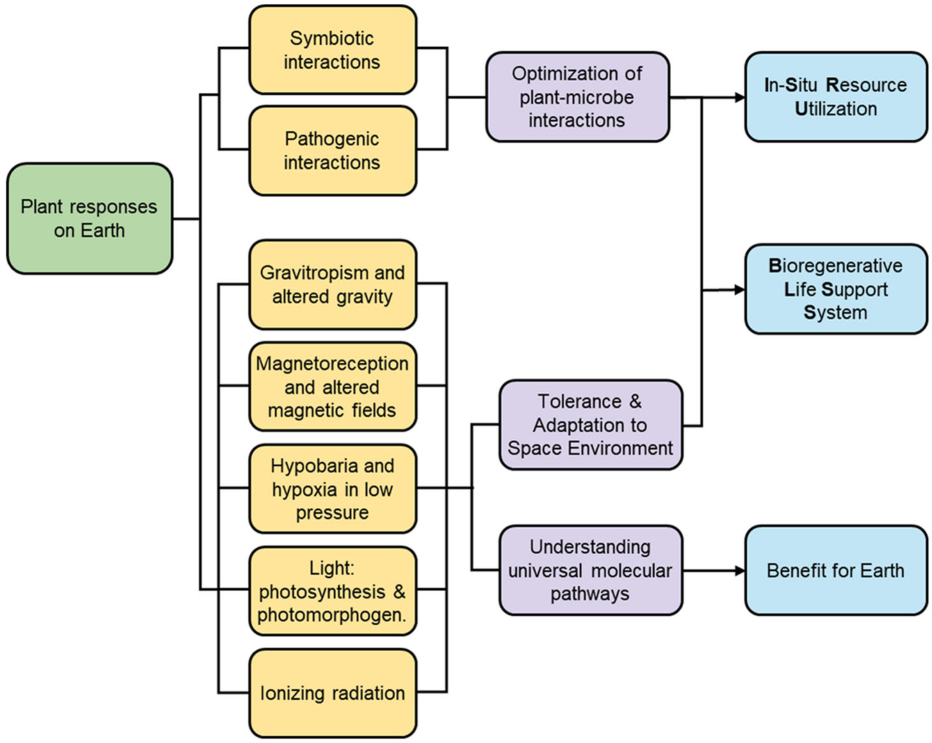

Fig. 2 | General scheme that encompasses plant biotic and abiotic interactions in the space environment. Investigations regarding plant responses and adaptation to the space environment are built on the previous work done to understand fundamental mechanisms of plant physiology, but also contribute to the understanding of universal molecular pathways and the development of tools that will benefit life on Earth. The optimization the plant adaptation to the space environment and the plant-microbe interactions will allow the design of reliable and sustainable Bioregenerative Life Support Systems (BLSS) and the obtainment of In-Situ Resource Utilization (ISRU).

current legislation concerning the growth and human consumption of biotechnological products is often country- and technology-specific. Some countries, like the US and Canada, have more relaxed rules for genetically modified organisms (GMOs) and allow growth and consumption. Being especially concerned by the environmental risks posed by GMO cultivation, the EU has only recently ruled to relax the legislation on Category-1-NGT (New Genomic Techniques) plants, i.e., plants that have been produced using targeted mutagenesis technologies, like CRISPR/Cas, and contain only genetic material that is present in the gene pool of the species used for breeding. Naturally, to ensure food security for space consumption and exclude any risk to human health, all crops would need to be severely evaluated, at least to the same standards used on Earth. Moreover, while contamination of space and celestial bodies should be avoided, as also stated in the Space Law Treaties of the United Nations Office for Outer Space Affairs, GMO products in space should not cause the same environmental concerns as on Earth, since they are equally contaminants to space than any other terrestrial biological material. As the more long-term objectives of human space exploration become closer, there is a need to start discussing the use of GMO and gene-edited organisms, beyond research purposes, for food production and human consumption.

In 2015, astronauts onboard the ISS consumed the first lettuce produced in space[143]. However, we are still far from achieving a reliable and sustainable plant food production system in space that can meet the dietary needs of a crew. A pragmatic approach that focuses on technological advances and applied research is needed to meet the requirements of already planned missions and stimulate the involvement of the private sector.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

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