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Terrestrial planetary plants: Essential preparations for interstellar migration

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ABSTRACT

Interstellar migration offers great potential for expanding human habitable space. As a powerful entropy-reducing system, plants convert simple, disordered chemical elements into complex, ordered organic macromolecules. They are expected to grow successfully on some planets and meet the essential nutritional and medical requirements for future interstellar migration. Taking Mars as a model planet, we analyze the basic physical, chemical and biological laws of plant growth on the terrestrial planet and propose terrestrial planetary plants (TPPs) for future terrestrial planetary agriculture (TPA). Biotechnological improvement of 25 TPPs candidates screened from 450,000 plants would reduce the dependence of interstellar migrants on farmland, poultry, livestock and hospitals, thus achieving self-sufficiency in food and medicine on Mars and other terrestrial planets. The TPPs are expected to break the 10 % rule in traditional food chains and provide new insights into enhancing agricultural production and food security on the earth.

1. Introduction

A wide range of cosmic catastrophes, including epidemic outbreaks, resource scarcity, climate catastrophe, solar expansion, and planetary impact events, may pose a critical threat to Earth-humanity's only homeland [1]. Thus, the establishment of additional homelands in the universe in order to guarantee the sustainable continuation of humanity is a shared goal. Majority of the universe is uninhabitable, and only a limited number of places could serve as oases for human life. To date, more than 1000 habitable terrestrial planets have been discovered [2,3], all of which are rocky planets formed by the Big Bang, with the similar chemical elements to Earth. They orbit around a star similar to the sun at a suitable distance, and have Earth-like necessary conditions for survival (e.g., light, heat, water, air, and nutrients) [4,5]. Nevertheless, these planets exist in a relatively closed and isolated state of increasing entropy, and no life forms have yet been detected.

Plants are the most efficient, robust, and powerful entropy-reduction system in the universe. Given the right amount of light, heat, water, air, and inorganic elements, plants are capable of photosynthesis to initiate chemical and biological reactions, thereby producing abundant and diverse organic matter to support human survival [6]. From desert steppes to polar seabeds and volcanic craters, Earth harbors numerous plants that adapt to various extreme environments, providing ample plant germplasm resources for the terraforming of terrestrial planets. Earth and other terrestrial planets obey the same physical and chemical laws, which implies that plants originating from Earth may be applied to other terrestrial planets in order to overcome the isolated and closed state of the latter, thereby transitioning from increasing to decreasing entropy [5,7].

Since the mid-20th century, humans have successfully cultivated certain plants on the International Space Station, on the far side of the moon, and in simulated controlled space environmental conditions [8–10], suggesting that plants can play a key role in providing the substances required for human prosperity in extraterrestrial environments. Furthermore, scientists have (i) uncovered a large number of functional genes related to plant growth, resistance, and nutrition, (ii) elucidated various molecular mechanisms underlying the balance between plant growth and stress responses, (iii) obtained numerous high-quality germplasm resources, iv) analyzed the protein components of animal-derived foods (e.g., meat, eggs, and milk) and related genes,

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(v) identified biosynthetic pathways for the production of natural drug molecules that are effective against space diseases. Taken together, these achievements have provided fundamental support for the screening and modification of terrestrial planetary plants (TPPs), which are Earth-originated plant species that have been adapted to survive in extreme space conditions, including intense radiation, microgravity, and extreme temperature fluctuations. These plants exhibit optimized growth characteristics such as rapid maturation, high yield efficiency, and complete edibility, making them essential for sustaining long-duration extraterrestrial missions by ensuring both food supply reliability and ecosystem stability. For example, the CRISPR-Cas9 gene editing technology was employed to introduce three mutations (*sp*, *sp5g,* and *sler*) in tomatoes to produce a compact, early-maturing germplasm in which the yield remains unaffected [11]. Such "condensed" crops can increase the production of interstellar colonies in controlled environments. Molecular farming technology enables the biosynthesis of animal proteins and natural drug molecules within plants, providing a basis for overcoming the 10 % rule inherent to food chains in nature, which means average only 10 percent of energy available at one trophic level is passed on to the next [12,13]. This, therefore, lays the foundation for plants to use extraterrestrial resources to produce oxygen, drugs, food, and other materials *in situ*.

Mars is one of the most frequently explored and well-understood terrestrial planets [14]. Space agencies in many countries have focused on formulating and implementing missions to Mars in the hopes of establishing semi-permanent or permanent colonies. In this paper, we regarded Mars as a model candidate for interstellar colonization to screen for potential TPPs. Based on these results, we discuss the establishment of an integrated, self-sufficient interplanetary agricultural system that can provide oxygen, drugs, and food (especially animal protein) independent of farmland, livestock, or hospitals.

2. Screening TPPs based on physical and chemical laws

Mars and Earth share the same origin, with both maintaining similar rotational periods and axial tilt and exhibiting similar day-night and seasonal cycles [4]. They are comparable in geological structures, with rocky crusts on the surface containing mineral elements essential to life [15,16]. Furthermore, both planets have atmospheres containing basic elements necessary for biological life, despite differences in their composition and density [17–19]. Thus, by "introducing" plants to Mars to "build a bridge" between Mars and the sun, it may be possible to drive the transition of Mars from increasing entropy to decreasing entropy. However, the extreme environmental conditions on the surface of Mars, including the low ambient temperature, extreme dryness, low atmospheric pressure, low oxygen level, barren regolith, thin atmosphere, and weak magnetic field, are all formidable barriers to plant growth [20]. Therefore, in the initial stages of human landings on Mars, it will be necessary to construct shelters for humans and plants. Compared to transporting materials from Earth or building new enclosed spaces using resources on the surface of Mars, it is more economical and feasible to find places that can provide shelter *in situ*. Studies have shown that there is a large amount of water hidden under the soil in Valles Marineris (a vast canyon near the Martian equator) to a depth of about 1 m, and numerous lava tubes have been discovered around Tharsis Montes near Valles Marineris [21–24]. Hence, these lava tubes can serve as initial shelters for colonists and plants.

3. Screening TPPs based on biological laws

The entropy reduction process based on plants, essentially, a process of energy and matter transformation. A highly conserved protein kinase, the target of rapamycin (TOR), regulates plant cell growth, development, and metabolism by detecting and integrating various chemical elements, energy, and signals in the environment, thereby controlling the process of plant-based entropy reduction [25,26]. For example, under favorable conditions, plants can activate TOR to accelerate the cell cycle and promote growth [27–29] (Fig. 1). During growth and development, plants will inevitably encounter unfavorable conditions. To cope with stressful conditions, plants have evolved efficient stress sensing and signal transduction systems, the most important of which is the abscisic acid (ABA) phytohormone signaling system [30]. Under environmental stress, plants first exhibit an increase in ABA concentration, which activates the ABA signaling pathway [31,32]. ABA signaling not only induces cell cycle arrest but also triggers the transcriptional expression of numerous ABA-responsive genes [33] (Fig. 1). Studies have demonstrated that a close association between TOR and ABA signaling mechanisms that act synergistically to balance plant growth and development in responses to stresses [34–36].

Under favorable conditions, TOR can inhibit stress-mediated ABA signaling (Fig. 1). On the other hand, under stressful conditions, ABA signaling can inhibit the activity of TOR complex, thereby sacrificing growth in favor of survival [35,36] (Fig. 1). A recent study has revealed another link between TOR and ABA [34]. At low ABA concentrations in plants, the TOR negative regulator SnRK2 is inhibited, permitting TOR activation and promoting plant growth. When ABA concentrations in plants increases sharply, the ABA core signaling pathway activates SnRK2, which in turn suppresses the activity of TOR, thereby blocking plant growth. TOR and ABA are analogous to opposing Yin and Yang forces that mediate the intricate balance of plant growth and development in response to stress.

During the initial stages of Mars landings, plants will be exposed to completely different growing conditions from those on the earth. Despite being grown in controlled environments, they experience enclosed environments, low gravity (~0.38 g), and various adverse conditions such as water scarcity and nutritional deficiencies. This implies that TPPs must not only be able to grow rapidly under ideal environmental conditions but must also be able to respond and adapt quickly under stress. Furthermore, given that TPPs are expected to transition from closed to semi-closed and eventually open environments, they should also be capable of readily coping with the manifold challenges of extreme stress on the surface of Mars. The TOR complex is the core regulatory protein involved in plant growth, and ABA is the most important stress hormone in plants. The ability to rapidly alter TOR activity in response to stimulation by external environmental factors is an important requirement for candidate TPPs. In addition, due to ABA signaling is involved in the adaptation of extremophile plants to adversity conditions [37], it is necessary to determine whether candidate TPPs carry duplicated ABA signaling-related genes in their genomes and whether they are equipped with adaptive traits to extreme environments. Notably, Mars can be regarded as a microcosm of all terrestrial planets and the results from the related studies could be applied to other terrestrial planets.

4. TPPs for subsistence

With respect to TPPs specifically for food production, it is necessary to consider other factors such as reproductive mode, harvest index, and production in addition to TOR- and ABA-mediated plant growth and stress response (Table 1). Some crops reproduce asexually and only undergo mitosis throughout their life cycle. Others undergo mitosis during vegetative growth and meiosis during reproductive growth. The harsh environment on Mars can pose a significant risk to crops required sexual reproduction, whereas crops with asexual reproduction can conserve the resources required for gamete production during meiosis, allowing plants to pass on their entire genome to offspring, and ensuring active and persistent reproduction over time and space [38]. Due to constraints in space and energy, TPPs must provide a high yield per unit of time/space, while minimizing energy consumption. Restricted by cultivation space, TPPs for subsistence must have the characteristics of high harvest index (i.e., proportion of edible biomass), high production efficiency (i.e., yield per unit of time and space), and high

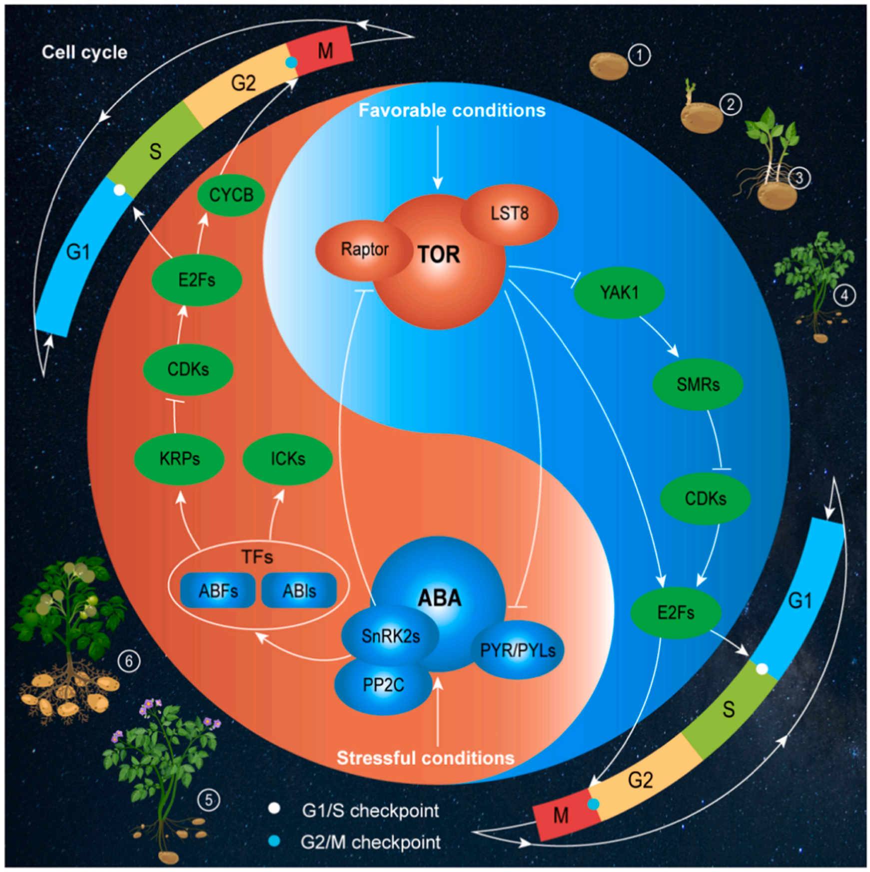

Fig. 1. A Yin-Yang model depicts the co-mediation of the cell cycle by TOR kinase and ABA signaling to maintain the balance between plant growth and stress response. Under normal circumstances, TOR exerts a regulatory effect on the G1/S phase by directly phosphorylating E2Fs, while inhibiting the activity of the downstream signaling element, YAK1 kinase to suppress the expression of SIAMESE-RELATED (SMR) cyclin-dependent kinase inhibitors, thereby activating CDKs and promoting the transition from the G1/2 and G to the M phase. On the other hand, TOR can phosphorylate ABA receptors, PYLs, disrupting the link between PYLs with ABA and the phosphatase effector PP2C which results in the inactivation of SnRK2 kinases. This prevents stress-responsive signaling and promotes plant growth. Under stressful conditions, the ABA signaling pathway activates CDK inhibitors (e.g., ICKs or KRPs), leading to cell cycle arrest. Furthermore, activated SnRK2s can phosphorylate a component of the TOR complex, Raptor, triggering dissociation and inhibition of the TOR complexes. This causes plants to divert energy and resources from promoting plant growth to stress response. ①-⑥ represent stages in the growth and development of potatoes.

photosynthetic efficiency to ensure the establishment of low-waste, space-optimized farming [39].

Based on the screening criteria, principal TPPs for subsistence should focus on crops with whole-plant consumable such as potatoes and sweet potatoes (Table 1 and Fig. 2). The edible parts of these plants proliferate via amitosis, and their mode of reproduction is predominantly asexual. Furthermore, both crops are widely cultivated in different regions on the earth, have high biomass and stress tolerance and hence are highly eurytopic. Aside from their edible tuberous root, the aboveground parts of sweet potatoes are widely used as vegetable in China. Even though potatoes are not wholly consumable (stems/leaves are toxic with solanine), with the deciphering of key genes related to solanine biosynthesis, it will be possible to create whole-plant edible and elite potatoes, fulfilling its criteria as a candidate TPP [40]. Rapeseed and peas are also the great candidates due to their high lipid/protein in addition to edible young plants, high harvest indices, as well as excellent adaptability to stresses such as low temperature and low air pressure [41,42]. Fruits and vegetables provide lipids, and proteins, vitamins, minerals, and dietary fiber necessary for human health. Lettuce has always been favored by astronauts owing to its rapid growth rate, high harvest index, and small footprint, which denotes that lettuce occupies minimal space during its growth, making it suitable for efficient resource utilization in cultivation within confined environments such as space stations [43]. The recent whole-genome resequencing of 445 germplasm worldwide provides a wealth of digital resources for in-depth exploration of key genes contributing to agronomic and biological traits of lettuce and the creation of ideal space lettuce [44]. The plant statures, harvest indices, and growth cycles of radish, carrot, beet, and cabbage also meet the requirements of efficient agriculture, and possess the prerequisites for candidate TPPs (Table 1). Tomatoes have considerable yields and are rich in vitamins. Combining these with its compact and biofortified germplasm, tomato provides additional TPPs options for subsistence [11]. Quinoa has been recognized by the Food and Agricultural Organization (FAO) of the United Nations as a single crop species that can satisfy all of the nutritional needs of human beings. Furthermore, due to its strong stress resistance and comprehensive nutritional value, quinoa has also been listed by NASA as an ideal "space food" for future space colonization [45]. The quinoa genome has now been profiled. Through the construction of the quinoa "5 G" (Genome; Germplasm; Gene function; Genomic breeding; Gene editing) breeding platform, quinoa germplasm with the characteristics of dwarfing, high yield, low consumption, and no anti-nutritional factors has been obtained, providing more options for TPPs [46].

Although water has been discovered on Mars, most of it exists in the form of hydrates or is hidden under the surface and hence humans cannot directly access or consume it. Given that 99 % of urine excreted by the human body is composed of water, recycling the water in urine should support the long-term survival of colonists. Plants can promote the circulation and purification of water on Mars and from urine through transpiration and internal water treatment systems, providing water for

Table 1
Twenty-five of representative TPPs for subsistence, health, and ecological transformation.

Parameters / Species		Reproductive Mode	Harvest Index/ Yield (kg/mu)	Whole Edible	Stature	Growth Cycles (d)	Fresh Food	Stress Resistance	Genetic Transformation
TPPs for Subsistence	Lettuce	Seed	> 0.7	Yes	Dwarf	30–130	Yes	Moderate	Easy
	Pea	Seed	0.37–0.46	Yes	Dwarf	60–100	No	Moderate	Easy
	Tomato	Seed	10,000–14,000	No	Dwarf	60–170	Yes	Moderate	Easy
	Quinoa	Seed	250–300	No	Tall	90–160	No	Strong	Difficult
	Onion	Tuber	3000–4000	Yes	Dwarf	90–120	Yes	Moderate	Difficult
	Radish	Seed	600–1000	Yes	Dwarf	20–35	Yes	Moderate	Very Difficult
	Sweet Potato	Tuber	2500–4000	Yes	Dwarf	100–200	Yes	Moderate	Very Difficult
	Potato	Tuber/Seed	0.60–0.75	No	Dwarf	60–150	Part (Fruit Potato)	Moderate	Easy
	Carrot	Seed	2750–3750	Yes	Dwarf	60–140	Yes	Moderate	Difficult
	Beet	Seed	> 4300	Yes	Dwarf	90–180	Yes	Moderate	Difficult
	Cabbage	Seed	3500–4000	Yes	Dwarf	80–120	Yes	Moderate	Difficult
	Peanut	Seed	300–500	Yes	Dwarf	90–180	Yes	Moderate	Difficult
	Rapeseed	Seed	600–1000	Yes	Tall	80–120	No	Moderate	Difficult
TPPs for Health	Honeysuckle	Seed/Cuttage	750–1000	Yes	Tall	2–3 Y	Yes	Strong	Very Difficult
	Rugosarose	Cuttage	150–400	No	Tall	2–3 Y	Yes	Strong	Very Difficult
	Rhodiola rosea	Seed/ Cuttage/ Rhizome Propagation	1500–3000	No	Dwarf	2–5 Y	Yes	Strong	Very Difficult
	Chuanxiong Rhizoma	Tuber/Cuttage	300–400	Yes	Dwarf	280–290	No	Moderate	Difficult
TPPs for Ecological Transformation	*Crucihimalaya Himalaica*	Seed	-	-	Dwarf	1–2 Y	-	Strong	-
	Selaginella	Spore Propagation	-	-	Dwarf	180	-	Strong	Very Difficult
	Lichen	Spore/Vegetative Propagation	-	-	Dwarf	3–5 Y	-	Strong	Very Difficult
	Bryophytes	Spore Propagation	-	-	Dwarf	180–360	-	Strong	Easy
	Sea-Buckthom	Seed/Cuttage	-	-	Tall	3–4 Y	-	Strong	Difficult
	Dandelion	Seed	-	Yes	Dwarf	50–80	Yes	Strong	Easy
	Tumbleweed	Seed	-	-	Dwarf	1 Y	-	Strong	-
	Camelthorn	Root Propagation/ Seed	-	-	Dwarf	2–3 Y	-	Strong	Easy

Note: Because of their long survival time, the growth cycle of TPPs for health and ecological transformation refers to the period from spore/seed germination to the new spore/seed formation. Y: year.

direct consumption of interstellar colonists.

Animal proteins are complete sources of amino acids in quantities and ratios close to human needs. Compared with plant proteins, animal proteins have higher nutritional value and are the optimal sources of essential amino acids for human body. Adequate intake of animal proteins can improve physical fitness and enhance disease resistance. However, it is a major challenge to establish an agricultural system on other terrestrial planets, let alone establishing animal husbandry for the acquisition of animal proteins. An alternative approach is to employ synthetic biology techniques to express high-quality protein genes from meat, eggs, and milk which can be achieved through TPPs by genetically modifying plants with animal protein genes, therefore meeting the urgent need for animal proteins without livestock after Mars colonization (Fig. 3).

Inducible expression systems enable target gene expression at specific times and in specific quantities by adding appropriate concentrations of inducers at appropriate time points. It is the ideal method by which to express exogenous proteins in chassis organisms. The ABA signaling pathway in plants is a natural inducible expression system [47–49]. During the rapid growth stage of plants, ABA-responsive genes are not expressed due to low ABA concentrations. Upon reaching maturation, ABA is synthesized, the ABA core signaling pathway is initiated, and the associated transcription factors (e.g., ABF4) are activated and target the promoter regions of ABA-responsive genes, thereby inducing their transcriptional expression. By incorporating biosynthetic genes of specific animal protein into the promoter regions of various ABA-responsive genes, the corresponding animal proteins genes can be expressed with increasing ABA concentrations (Fig. 2). This inducible expression system will not increase the burden on the chassis caused by constitutive expression of exogenous genes and will also enable the simultaneous acquisitions of animal proteins and other nutrients when TPPs are harvested.

5. TPPs for health

Space radiation and microgravity are two major factors that can have detrimental effects on interstellar colonists [50]. Ionizing radiation can induce the excessive production of free radicals in the body, resulting in oxidative stress. Antioxidants that are widely found in nature scavenge or bind competitively to free radicals, thereby preventing the biological damage caused by excessive exposure to ionizing radiation and improving cellular responses. Astaxanthin, hailed as the "king of antioxidants," is an effective free radical scavenger that can protect cells from oxidative damage [51,52]. In addition, various vitamins and other substances are believed to have protective effects against ionizing radiation. In fact, some studies have incorporated astaxanthin and vitamin biosynthetic genes into tomatoes, potatoes, and lettuce to confer health-protective functions [53,54]. It is feasible to increase the intake of antioxidants by the consumption of such plants in order to cope with oxidative stress. Ionizing radiation can also cause DNA damage, while defective DNA repair can lead to cell death, mutations, chromosomal rearrangements, and even carcinogenesis [55]. Studies of tardigrades exhibiting extreme tolerance to radiation have found that these organisms carry a variety of unique damage-suppressing proteins able to prevent DNA damage caused by long-term exposure to space radiation [56,57]. By applying molecular farming techniques, such as compartmentalized localized transformation and posttranslational modification, it is possible to express these damage-suppressing proteins in TPPs and hence preventing radiation-induced DNA damage by the consumption of genetically modified TPPs or their derived tissues. Another crucial

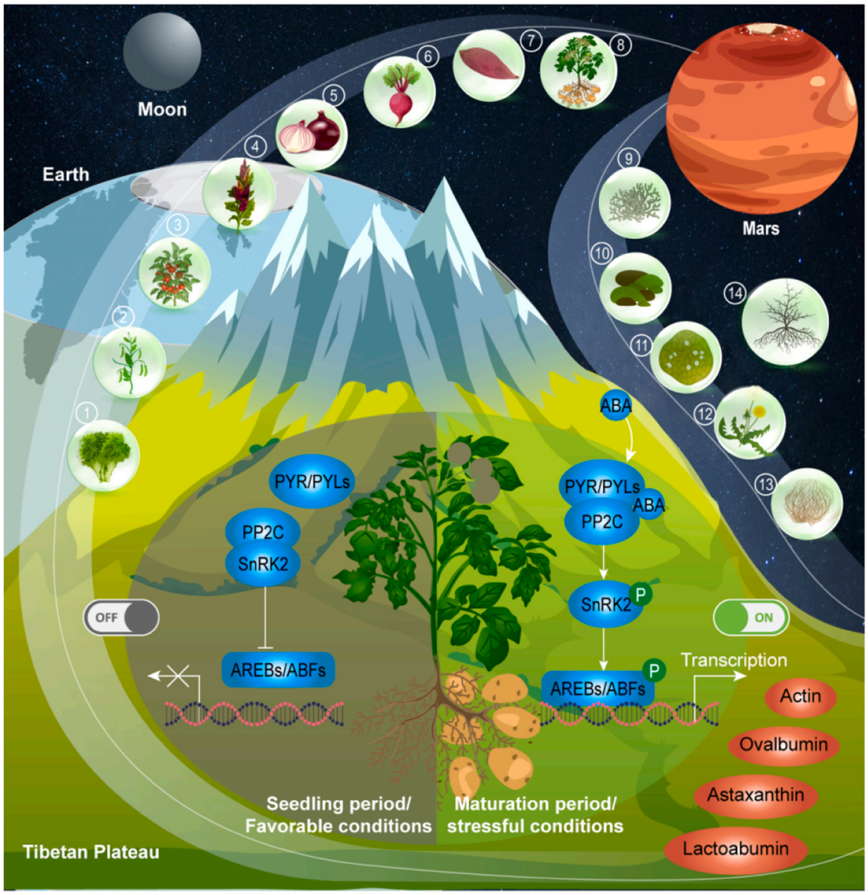

Fig. 2. TPPs biomanufacturing of animal proteins and drugs, and enhanced TPPs extremotolerance based on ABA signal transduction. At the seedling stage or under favorable growing conditions, lower ABA concentrations, allow the negative regulator PP2C to bind to the phosphokinase SnRK2 and inhibit its activity, causing insufficient AREB/ABF transcriptional activity and hence preventing the expression of exogenous genes. Upon maturation or under stressful conditions, plants rapidly increase ABA concentrations. This causes the binding of PYR/PYLs to ABA, which in turn enhances its affinity to the negative regulator PP2C, leading to the recruitment of PP2Cs to form PYR/PYLs-ABA-PP2C ternary complexes. Once released from PP2Cs, SnRK2s undergo autophosphorylation, which activates downstream transcription factors AREBs/ABFs. Transcriptionally active AREBs/ABFs can induce the transcription of target genes, such as the actin, ovalbumin, lactalbumin, and astaxanthin biosynthetic genes. Plants in the left panel are representative TPPs for subsistence that can be used as chassis plants for the production of animal proteins and drugs. ①: lettuce; ②: pea; ③: tomato; ④: quinoa; ⑤: onion; ⑥: radish; ⑦: sweet potato; ⑧: potato. Plants in the right panel are TPPs for ecological transformation. The endogenous ABA-inducible expression system can be employed for the biological enhancement of TPPs for ecological transformation with the aim of improving extreme tolerance. ⑨: lichen; ⑩: bryophytes; ⑪: cushion plants; ⑫: dandelion; ⑬: tumbleweed; ⑭: camelthorn.

physiological change that occurs in humans living in extraterrestrial environments such as oxidative stress in terrestrial planets is mitochondrial dysregulation. Many natural compounds synthesized in plants can counteract mitochondrial oxidative stress and mitigate or suppress the resulting pathological changes. Plant secondary metabolites, such as salidroside (SAL), withaferin A, curcumin, and quercetin, significantly alleviate mitochondrial stress [58–60]. As the biosynthetic pathways of these functionally active molecules continue to be elucidated, the creation of TPPs for the integrated supply of drugs and food will eventually become a viable solution for ameliorating mitochondrial dysregulation (Fig. 3).

Alterations in human physiology caused by the Martian environment can have severe impacts on the cerebrovascular and cardiovascular systems [50]. Evidence suggests that circulating microRNAs (miRNAs) can serve as potential biomarkers for space related cerebrovascular and cardiovascular health risks [61]. For example, miR-125, miR-16, and let-7a regulate vascular damage induced by ionizing radiation [62]. Using antagonists to inhibit the expression of corresponding miRNAs can rescue radiation-induced vascular damage [62,63]. Thus, biosynthesis of these antagonists in chassis TPPs (e.g., lettuce) and consumption of the bioengineered crops containing miRNA antagonists may help to prevent microvascular damages caused by ionizing radiation (Fig. 3). Additionally, based on the possibility of viral infections following Martian colonization, using TPPs (e.g., lettuce) as a chassis to synthesize edible vaccines presents a promising strategy for disease prevention and control [64]. Given that the proposed consumption of peptides/proteins or miRNA antagonists is biologically implausible due to digestion in the human gut, it is necessary to use the protective effect of special delivery systems, such as nanocarriers [65–67]. Damage to the human central nervous system is also recognized as a main space disease [50]. γ-aminobutyric acid (GABA) can cause the hyperpolarization of neuronal membranes by binding to the corresponding ion channel receptors, thereby preventing neuronal hyperactivity, while also improving sleep, relieving stress, and inhibiting neural aging and neurodegeneration [68–70]. The positive effects of GABA can help prevent the occurrence of neurodegenerative diseases in humans living on Mars and other extraterrestrial planets. In fact, a number of studies have successfully increased GABA accumulation in tomato fruits by overexpressing or editing the glutamate decarboxylase gene and/or silencing the GABA transaminase gene [71]. Furthermore, colonists on Mars will undoubtedly experience psychological stress, such as anxiety, when exposed to unfamiliar space environments, and plants can provide psychological benefits similar to horticultural therapy. The cultivation of highly tolerant plants with medicinal and nutritional value (e.g., honeysuckle,

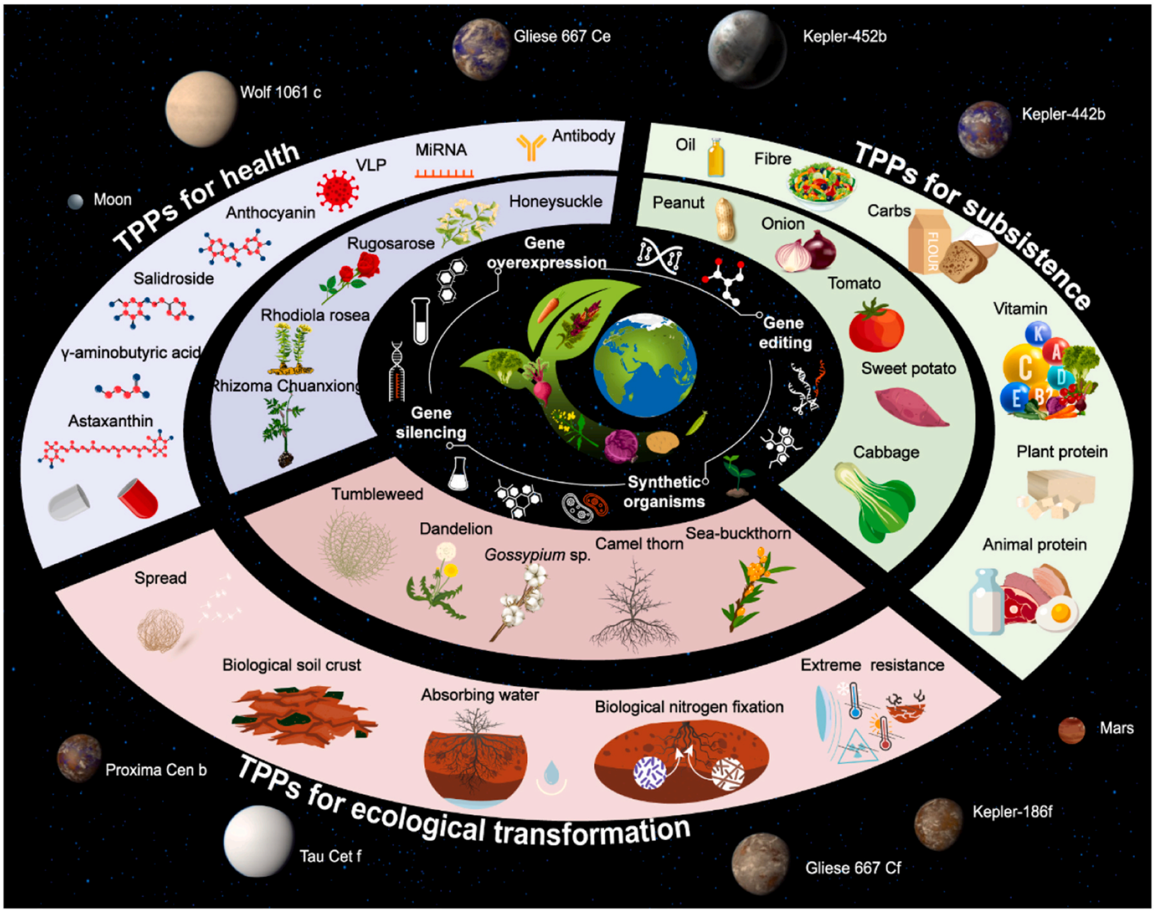

Fig. 3. TPPs can meet the survival, health, and ecological needs of interstellar colonists. The planets listed above are some of the terrestrial planets reported to date. The outer circle represents the substances or functions that need to be provided by the three group of TPPs. The middle circle shows representative TPPs that satisfy the preliminary screening criteria listed in the outer circle. The inner circle depicts the modification of several core TPPs by modern techniques, such as gene editing, to achieve self-sufficiency in the materials required for interstellar colonization, thereby laying the foundation for establishing a second human home on other terrestrial planets.

rugosarose, Rhodiola rosea [51], Chuanxiong Rhizoma [72]) can relieve stress and improve the physical and mental health of interstellar colonists.

To summarize, we propose that TPPs should be created to improve general health issues likely to affect Martian colonists, employing endogenous inducible expression systems (e.g., the ABA signal transduction mechanism) to promote the biosynthesis of functionally active substances or drugs for the prevention or treatment of diseases (Figs. 2 and 3). Advances in astrobiology, space nutrition, synthetic biology, and other disciplines promise to develop, treatments and preventions of diseases that could affect human colonists

6. TPPs for ecological transformation

Extremophile plants on Earth provide a basis for developing plant species that can adapt to the harsh conditions on Mars and other terrestrial planets. The high-altitude regions on Earth, especially the Tibetan Plateau, are environments characterized by low pressure, low oxygen, low temperature, low rainfall, drought, frequent winds, strong radiation, large day-night temperature differences, and barren soil. These regions are most similar to the low-altitude plains on Mars (Table 1, Figs. 2 and 3) [73]. Lower plants growing in such habitats, including bryophytes and lichen, are not only able to tolerate harsh ecological conditions but can also secrete unique substances to dissolve and corrode rocky surfaces and drive pedogenesis, thereby creating conditions for the growth of other higher plants. Resurrection plants, such as *Crucihimalaya himalaica* and *Selaginella*, enter a dormant state in extreme environments, and "resurrecte" (i.e., revive under favorable conditions. "Migratory" plants represented by tumbleweeds can capitalize *in situ* resource on Mars such as wind force for distant dispersal, facilitating the spread of populations. The root system of some plants, such as *Ceratoides* and camelthorn, can grow over tens of meters in arid soil and adapt to the specific water distribution on Mars, which would enable the utilization of deep water resources and promote the water cycling in the soil.

Perchlorate at concentrations of 0.4–0.6 % has been detected in the Martian regolith [74], and this powerful oxidant is harmful to both humans and plants. However, there is a class of dissimilatory perchlorate-reducing bacteria on Earth with highly conserved perchlorate reductase (PcrABC) capable to reduce perchlorate to chlorite, which is further decomposed into molecular oxygen and chloride under the catalysis of chlorite dismutase (Cld) [75]. Introducing this series of perchlorate detoxification mechanisms into candidate TPPs for ecological transformation not only protects against perchlorate toxicity but also enhances the oxygen generation capacity. Furthermore, the modification of candidate TPPs for ecological transformation by combining the perchlorate detoxification system with nitrogen fixation systems will permit the establishment of an agricultural system based on the Martian regolith [76]. The intensity of sunlight on Mars is substantially lower than on Earth. The low atmospheric pressure and lack of an ozone layer on Mars lead to higher ultraviolet fluxes. Thus, redesigning the light-harvesting antenna and reaction center complexes and expanding the spectral region for photosynthesis, especially the spectral coverage of the ultraviolet and/or infrared regions, will serve as effective means by which to enhance the utilization efficiency of solar energy by plants [77,78].

The Martian surface environment has other extreme conditions that are not conducive to plant growth. Therefore, it is necessary to further strengthen the stress resistance mechanisms of plants and enhance the performance of TPPs for ecological transformation across a range of factors, which would facilitate adaptive processes to the harsh habitats [79–82]. Growing TPPs for ecological transformation on the Martian surface will lead to subtle changes in the compositions of the atmosphere and soil over time, which may promote the establishment of Martian ecosystems and hence create suitable conditions for long-term survival from the closed space to the open one (Fig. 4).

7. Conclusion

Humans rely on livestock for animal proteins. However, humans and livestock need to consume oxygen, potable water, and plant-based food, which can lead to serious competition for resources. Therefore, it is difficult to obtain animal proteins through animal husbandry during the process of interstellar colonization. In this paper, we propose an interplanetary agricultural system involving the direct production of animal proteins using bioengineered TPPs. This system not only effectively resolves the conflict between interstellar colonists and livestock and provides a solution to the acquisition of animal proteins but also shortens the traditional food supply chain (i.e., from plants to livestock and poultry and finally to humans), which may resolve prominent issues on Earth caused by insufficient arable land.

According to the general rule of energy efficiency in food reduction, it is only 10 % of energy conversion from plants to livestock and various parts of livestock (e.g., hair, bone, organs, brain, and limbs) are generally not consumed by humans, leading to only ~5 % of energy efficiency for meat production (13). In addition, animal fat contains large amounts of saturated fatty acids, cholesterol, and other substances that are harmful to human health, whereas animal proteins taken by humans only account for near 16 % (measured according to average nitrogen content) of mean composition.

Based on these estimates, the energy conversion efficiency of animal proteins provided by plants via livestock is only 0.5 %. With reference to the content of heterologous proteins expressed in plants, the energy conversion efficiency of animal proteins produced directly by TPPs is about 5 % [83], suggesting that animal protein production by a TPA system is advantageous over traditional agricultural methods. TPA system refers to the establishment of sustainable agricultural production systems in space or extraterrestrial environments, leveraging advanced biotechnology and engineering methods with TPPs as the foundational chassis. This approach aims to address food supply and ecological cycle challenges in deep-space exploration missions. The innovative concept of TPPs can also serve as a reference for building a cost-effective, easy-to-storage, and easy-to-transport animal protein production platform. In addition, it has been reported that traditional agriculture requires 15,415 kg of water to produce 1 kg of beef, 3300 kg of water to produce 1 kg of chicken, and 1020 kg of water to produce 1 liter of milk [84,85]. The TPA system can significantly reduce the amount of water used for production and greatly enhance the utilization efficiency of water resources, which is of crucial significance for both arid Mars and the increasingly water-scarce Earth. Other disadvantages of animal husbandry include excessive carbon emissions and an elevated epidemic risk of major zoonotic disease (e.g., avian influenza, SARS, and

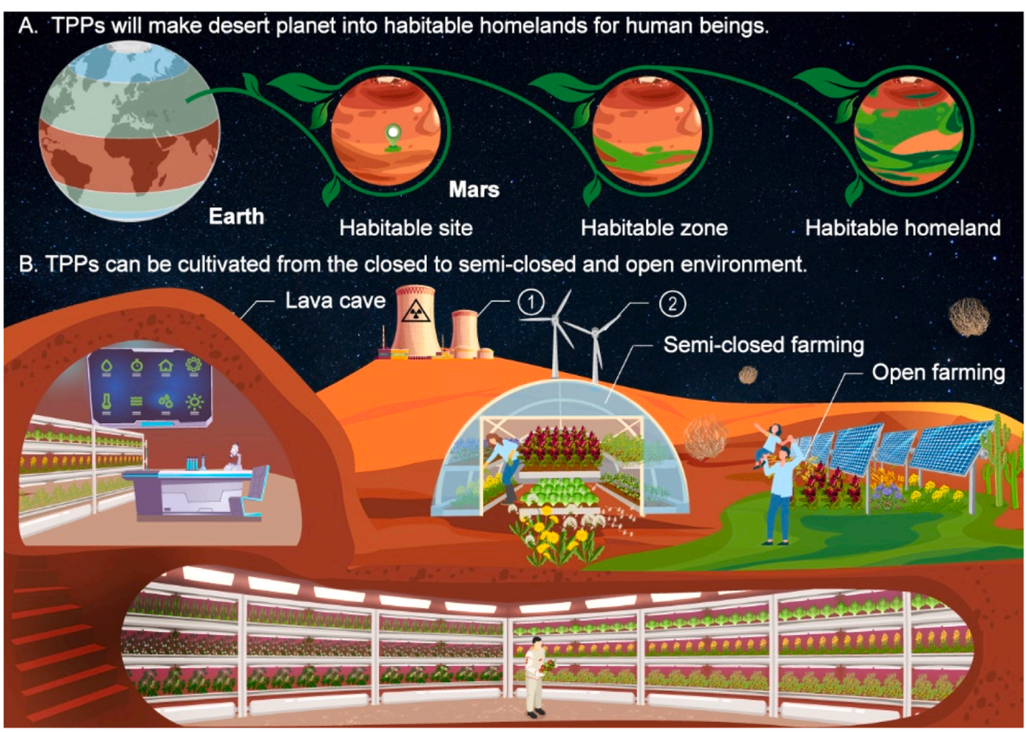

Fig. 4. The terraforming of Mars from point to line to a plane and the cultivation of pioneering TPPs from closed to semi-closed to open farming. (A) TPPs originating from Earth are introduced to Valles Marineris and gradually spread to regions near the Martian equator, eventually forming preliminary "oases" in the habitable zone. (B) Lava tubes can serve as initial refuge for TPPs. A controlled-environment agricultural system is established in the lava tubes. Various plant growth parameters (e.g., nutrition, light, and temperature) are dynamically deployed and optimized by artificial intelligence and soilless cultivation techniques aimed at the sustainable production of food and drugs. As the ecological transformation of Mars continues to progress, TPPs will gradually adapt to some extreme environments on the surface of the planet and transition from living in underground to aboveground spaces, where they can survive and grow in semi-closed greenhouses. Finally, TPPs will fully overcome the environmental obstacles on Mars and transition from semi-closed to open farming, thus transforming Mars into an extraterrestrial homeland. ①: nuclear reactor;②: wind turbine.

COVID-19), which can have an immense impact on ecosystem of the earth and public health security. From this perspective, constructing a TPA system without livestock will help to accelerate the achievement of carbon neutrality with significant ecological and health benefits. With respect to potential diseases on extraterrestrial planets, TPPs can be used to produce targeted drugs for prevention and treatment, thus reducing dependence on hospitals and medical facilities. This has great significance for safeguarding the health of interstellar colonists, while also serving as a valuable reference for the convenient and rapid acquisition of drugs on Earth. Finally, nearly one-quarter of the total land area on Earth is occupied by desertified land. As the area of desertification continues to expand on Earth due to natural factors or the impact of human activities, the application of a TPA system based on TPPs may also contribute to improvements in ecological conditions. In summary, the prominent advantages of a TPA system, including its high efficiency, greenness, environmental conservation, and safety, are not only able to facilitate the survival of interstellar colonists but also are of great significance to maintaining the healthy development of the earth.

Although the vision of building TPPs into core systems for off-world Bioregenerative Life Support Systems (BLSS) [86] may not be achievable in the short term, continuous interdisciplinary advances make this goal increasingly attainable in the future. The TPP screening and bioengineering strategies discussed in this study hold immediate value for urban agriculture development, as establishing high-efficiency agricultural systems in controlled environments represents a shared objective for both space farming and urban vertical farming. Furthermore, research on TPPs modification and application will advance functional gene mining in extremophile organisms, accelerate plant-based pharmaceutical development, and contribute to global desertification control initiatives.

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CRediT authorship contribution statement

Xiumei Luo and Ying Wang: Funding Acquisition, Conceptualization, Investigation, Writing – original draft; **Jiasui Zhan:** Writing – review and editing; **Maozhi Ren:** Funding Acquisition, Supervision, Validation, Writing – review and editing. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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