

Conquering Space with Crops That Produce Ample Oxygen and Antioxidants

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Abstract: Sustainable long-term space missions require regenerative life support from plants. Traditional crop plants lack some features desirable for use in space environments. The aquatic plant family Lemnaceae (duckweeds) has enormous potential as a space crop, featuring (i) fast growth, with very high rates of O₂ production and CO₂ sequestration, (ii) an exceptional nutritional quality (with respect to radiation-fighting antioxidants and high-quality protein), (iii) easy propagation and high productivity in small spaces, and (iv) resilience to the stresses (radiation, microgravity, and elevated CO₂) of the human-inhabited space environment. These traits of Lemnaceae are placed into the context of their unique adaptations to the aquatic environment. Furthermore, an overview is provided of the challenges of galactic cosmic radiation to plant and human physiology and the mechanisms involved in oxidative injury and the prevention/mitigation of such effects by antioxidant micronutrients. A focus is placed on the carotenoid zeaxanthin accumulated by Lemnaceae in unusually high amounts and its role in counteracting system-wide inflammation, cognitive dysfunction, and other oxidative injuries in humans.

Keywords: carotenoids; duckweed; homeostasis; Lemnaceae; reactive oxygen species; zeaxanthin



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1. Introduction

1.1. Molecular Oxygen Plays Unique and Essential Roles for Life

Molecular oxygen (O₂) is necessary for much of life on Earth to function. Most of the oxygen in the atmosphere has been produced over the last two billion years by photosynthetic organisms, which supported the evolution of multicellular organisms that depend on aerobic respiration [1,2]. This dependency applies to both heterotrophs and autotrophs, such as plants that can be killed when roots have diminished access to oxygen because of insufficient aerobic respiration in water-logged soils [3] (except for specialist plants with unique adaptations facilitating oxygen diffusion to the roots [4]).

For space travel and habitation, enough molecular oxygen must be transported or continuously generated for long missions to sustain a human crew. Currently, molecular oxygen is produced on the International Space Station through electrolysis or the splitting of water [5]. For long human-crewed space missions, plants can serve as a regenerative life support system that continuously produces O₂ and removes CO₂ [6,7] and provides additional essential services (highlighted below).

1.2. Reactive Oxygen Can Kill

While essential for much of life on earth, oxygen is a double-edged sword. The first mass species extinction event was likely caused by the rise in atmospheric O₂ levels, deemed the Great Oxidation Event [8,9]. Today, aerobic organisms carefully maintain internal redox homeostasis, i.e., the balance between oxidants and antioxidants [10]. Notably, primary

energy metabolism in the organellar powerhouses that interact with O_2 (chloroplasts and mitochondria) continuously creates reactive oxygen species (ROS; [10,11]). ROS are essential in small doses, but excess ROS can cause a host of adverse effects (see below). The life-supporting quality of oxygen is thus inextricably linked to its potential dangers.

In small quantities, ROS act as universal regulators of master control genes that orchestrate growth, development, aging, and various metabolic defenses of humans, plants, and many microorganisms [12,13]. For example, ROS can stimulate the cell cycle as well as trigger programmed cell death [14,15], both of which can be enhanced in spaceflight environments [16] (for details, see the next section). One example of an ROS is superoxide (superoxide anion radical; $O_2^{\bullet-}$), which various organisms actively produce to kill pathogens [17] and other unwanted cells. However, excess superoxide can cause cell damage unless redox homeostasis is maintained by keeping ROS in check with antioxidants. A lasting departure from redox homeostasis can cause continuous low-grade activation of the human immune system with system-wide inflammation and a host of resulting diseases, disorders, and dysfunctions (see below). In large quantities, ROS can be lethal. In viral diseases (such as HIV-AIDS and, evidently, COVID-19), snowballing production of ROS and other inflammation-promoting messengers (the cytokine storm) can lead to massive organ damage (i.e., “cellular suicide” rather than direct “virological murder”; [18]).

Superoxide can be detoxified by antioxidant enzymes like superoxide dismutase that converts two $O_2^{\bullet-}$ to one uncharged O_2 and one doubly reduced O_2^{2-} corresponding to hydrogen peroxide (H_2O_2). H_2O_2 can, in turn, be converted to harmless water by enzymes like catalase [19] or ascorbate peroxidase with the cofactor ascorbate (vitamin C, an antioxidant metabolite) as the source of electrons [20]. While plants can produce all necessary antioxidant metabolites *de novo*, humans must consume many of these antioxidants with their diet to maintain internal redox homeostasis. Space crops with superior antioxidant levels are needed to protect the plant and the human consumer from radiation damage in space (see, e.g., [21]). For the future of space travel, astronaut diets will need to strike the right balance to prevent the negative effects of excess ROS without dampening the positive effects of small amounts of ROS.

2. The Challenges of Space Environments

A major challenge for human utilization of space is exposure to galactic cosmic radiation (GCR, consisting of heavy ions/high-density charged particles [16,22]) that generates dangerous amounts of ROS through radiolysis of water in all hydrated cells. This ROS can lead to DNA mutations, and GCR can also produce direct DNA breaks (Figure 1; [23]). The effects of GCR-induced ROS on gene regulation are complex and include induction of some protective (e.g., antioxidant) effects as well as negative snowballing effects that further exacerbate ROS production and DNA damage. For example, a feed-forward cycle in space environments involves ROS stimulation of the human ROS-producing enzyme NADPH oxidase [24,25] via genetic programs that normally potentiate superoxide production during a pathogen attack. Specifically, an initial wave of ROS production triggers consecutive waves of ROS production to activate and recruit other immune cells (as may be warranted under pathogen attack [15]). Excess ROS production and DNA damage can thus lead to signaling cascades that produce more and more ROS (Figure 1).

ROS and Chronic Inflammation in Astronauts

In humans, continuous exposure to excess ROS triggers immune-system dysfunction with chronic, non-resolving inflammation [26]. Astronauts return from space missions with elevated levels of inflammation markers and evidence of inflammation-related cognitive dysfunction [27], cellular aging [28], and other adverse conditions [29]. Humans must consume essential ROS-balancing antioxidant micronutrients in their diet to counter such oxidative stress. Identification of space crops that produce high levels of essential dietary antioxidants will thus be essential to oppose radiation damage and chronic inflammation in human-inhabited space environments.

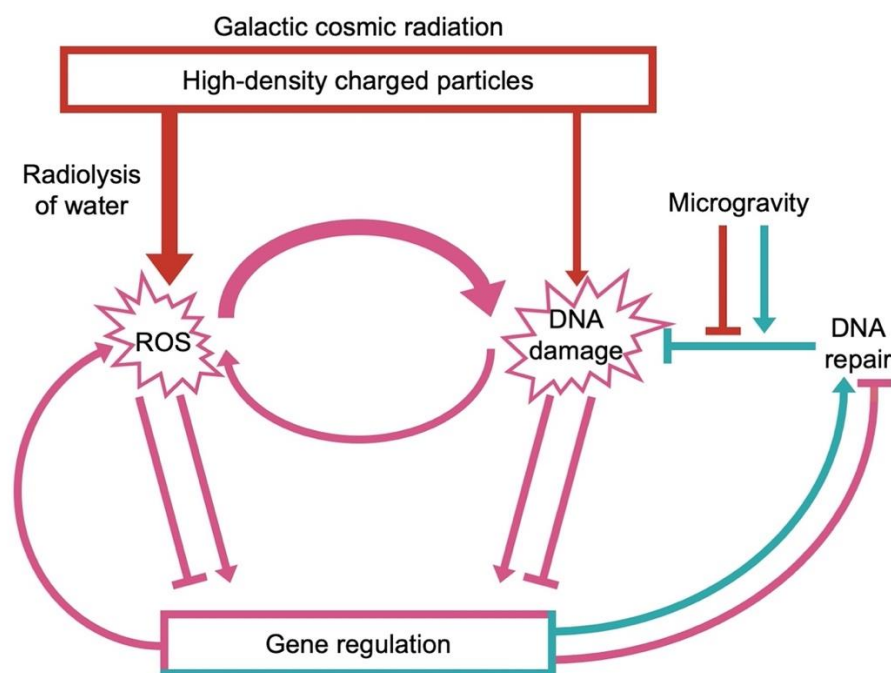


Figure 1. A schematic flowchart of how galactic cosmic radiation can lead to the production of ROS and DNA damage. Both ROS and DNA damage can either encourage (pink arrows) or prevent (pink T-shaped lines) multiple gene regulation events, including those that support (blue arrow) or prevent (pink T-shaped line) DNA repair.

3. The Multi-Hit Hypothesis: Interaction among Different Stresses in a Space Environment

This section addresses additional factors present in space environments that can exacerbate the effects of GCR in plants or humans. This phenomenon and associated inquiry have been described as the multi-hit hypothesis [30]. These additional stressors include microgravity and elevated CO₂ in a cabin environment. Microgravity can interfere with DNA repair in humans [31] and exacerbate DNA damage, which leads to “genomic instability” [32]. For example, the end portions of chromosomes (telomeres) that are determinants of cellular aging and human lifespan increase in average length in space environments and then rearrange within 48 h upon astronauts returning to earth, thereby revealing a much shorter average telomere length post-space exposure [33,34]. This behavior is like the increase of average telomere length observed on Earth under exposure to ionizing radiation [23]. Telomere length has been found to respond directly to ROS level [16].

Inhibition of DNA repair by microgravity in the presence of GCR can, furthermore, trigger programmed cell death [35] and inflammatory responses [36]. As shown in Figure 1, both inhibitory and stimulatory effects of microgravity on DNA repair are principally possible. For example, an unusual radiation-resistant bacterium, *Deinococcus radiodurans*, exhibited an increase in DNA repair and other defenses in the presence of microgravity [37,38]. More studies in spaceflight environments are needed to understand the synergistic effects of radiation and microgravity in humans [39].

3.1. Specific Plant Responses

In land plants, microgravity can interfere with plant responses to radiation by inhibiting directional signal translocation between shoots and roots [40]. More research is needed into the effect of microgravity in space environments as different species can respond in different ways [41]. Elevated CO₂ in a confined environment is also a concern. Plants growing under elevated atmospheric CO₂ levels can produce excessive levels of ROS (Figure 2), which can lead to an imbalance in redox homeostasis [42]. Specifically, elevated CO₂ can enhance ROS production via carbohydrate backup as photosynthesis utilizes the

greater level of available CO₂ to produce more sugars and starch. The resulting backup of electrons in photosynthetic electron transport leads to the transfer of electrons and/or excitation to oxygen, forming ROS [42]. Land plants tend to respond to prolonged exposure to elevated CO₂ with photosynthetic downregulation and growth inhibition, and accelerated senescence in some but not all species (Figure 2; [42]). In particular, elevated CO₂ can exacerbate growth penalties imposed by other environmental factors [43–46]. In other words, ROS production is additively increased by various environmental stressors that offset the source-sink balance between carbohydrate production in leaves (sugar source) relative to carbohydrate consumption in all the plant's sugar sinks [42].

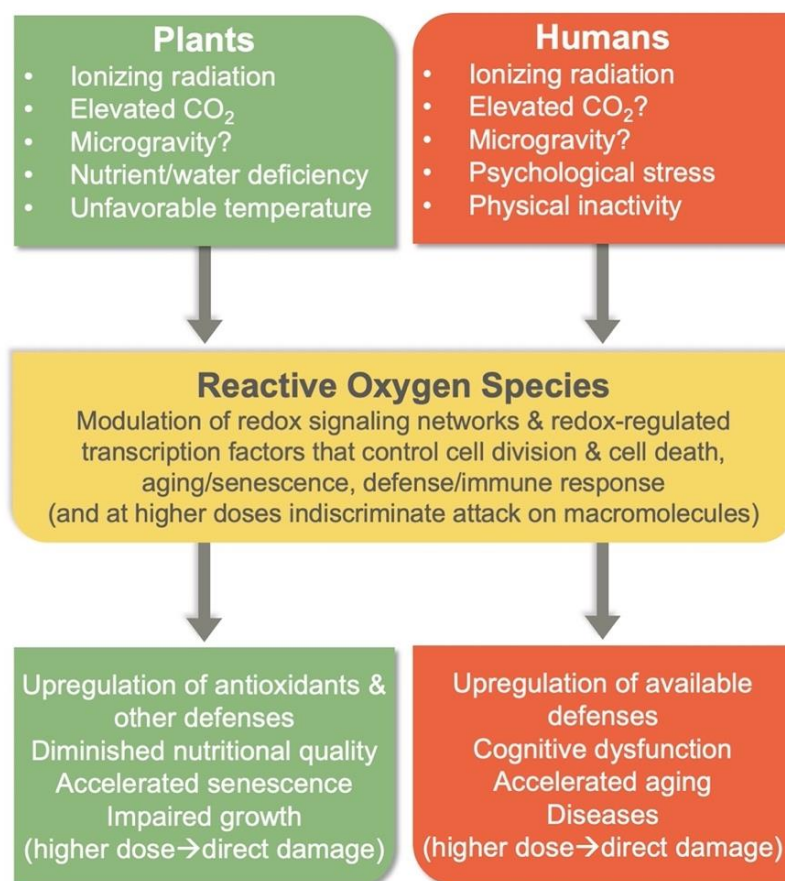


Figure 2. Flowchart depicting the causes (top boxes) and effects (bottom boxes) of reactive oxygen species (middle box) in plants (green; left) and humans (red; right).

Various additional environmental conditions can further unbalance the plant source-sink ratio and enhance ROS production [47,48]. For example, excess light supply adds to carbohydrate production and unfavorable nutrients/temperatures (Figure 2) slow growth and the consumption of carbohydrates in plant sinks [49]. Whereas increased ROS production generally triggers upregulation of ROS-detoxifying processes (see above), chlorophyll-associated carotenoids exhibit a different response. One effect of excess ROS under source-sink imbalance is downregulation of photosynthesis (as the sugar source) via repression of photosynthetic proteins, including chlorophyll-binding proteins [50]. In plants grown under elevated CO₂ levels, lower chlorophyll levels were, furthermore, accompanied by lower levels of the carotenoids that protect chlorophyll [51]. A lowering of plant antioxidant metabolite content in space environments with elevated CO₂ levels in the habitable enclosure would be problematic. However, an intriguing possibility is that the combination of elevated CO₂ (lowering antioxidant production) and GCR (that may increase antioxidant levels) could potentially offset each other to some extent in plants (that are able to upregulate antioxidant metabolites).

3.2. Human Physiology

To mitigate the risks associated with spaceflight, it is important to consider multiple lifestyle factors for humans [52]. Diet, physical activity, and psychological stress (Figure 2) all provide inputs into cellular redox homeostasis and thus affect health outcomes [53,54] (see [55] for specific effects on telomere length). For example, the combination of physical inactivity and chronic psychological stress can constitute additional “hits” in a space environment. Specifically, chronic stress fatigues the immune-suppressive stress response, resulting in chronic (non-resolving) inflammation associated with excess ROS production [56]. In addition, whereas physical activity triggers the synthesis of endogenous antioxidant enzymes to combat ROS production during exercise, physical inactivity fails to induce antioxidant enzymes [57] and thus to counter ROS production (Figure 2).

In addition to high levels of radiation and microgravity, the elevated levels of CO₂ typical of a spacecraft cabin environment also have the potential to induce adverse physiological changes in humans, including vascular leakage, edema, and interference with the draining of cerebrospinal fluid [30,58,59].

4. Redox-Based Orchestration of Growth, Development, and Defenses

4.1. Early-Warning Systems for Oxidative Stress

A hallmark of metabolically active cells is to allow for moderate amounts of ROS to play fundamental roles in cellular metabolism and other biological processes [60,61] while avoiding unwanted effects of excess ROS. To support this redox homeostasis, macromolecules—particularly sensitive to oxidation—serve as sentinels for rising internal ROS production. For example, oxidation products of highly oxidation-prone polyunsaturated fatty acids (PUFAs) of membrane lipids serve as gene regulators [62,63]. These regulators target antioxidant production and other protective responses [64,65] as well as multiple other processes that are redox-modulated (see above). In humans, immunostimulatory regulators are mainly derived from omega-6 PUFAs and inflammation-resolving regulators mainly from omega-3 PUFAs [66]. In addition, easily oxidized thiol-containing proteins are also linked to redox-based gene-regulation [67–69].

4.2. Gene Regulation by Derivatives of Lipid Peroxidation and the Need for Dietary Antioxidant Metabolites

Just like ROS and their various products, antioxidant systems are potent modulators of redox-modulated signaling networks and genes [70]. Dietary membrane-embedded antioxidants keep the formation of PUFA-derived regulators in check and thus control and resolve acute inflammation in humans [71]. Furthermore, a balanced dietary ratio of omega-3 to omega-6 fatty acids is critical to support immunity and avoid non-resolving inflammation.

The human brain is particularly susceptible to non-resolving inflammation due to its large complement of biological membranes, with a high proportion of PUFAs and a high level of oxygenation that increases the propensity for PUFA oxidation [72–74]. Resulting non-resolving neuroinflammation leads to low mental function in otherwise healthy individuals as well as to mental and learning disorders and neurodegenerative diseases [54,75]. Antioxidation is needed to prevent neuroinflammation [54,76].

Whereas a whole suite of diet-derived antioxidant metabolites can operate in aqueous environments, only a few are able to dissolve in biological membranes. These latter lipophilic antioxidant metabolites include the antioxidant vitamin E (tocopherol) and carotenoids [54,77,78]. The structure of these molecules determines their orientation in the membrane, and two carotenoids can integrate into biological membranes in a way that can provide stabilization [79] and oppose PUFA oxidation [54,80,81]. These two are the xanthophyll (oxygen-containing) carotenoids zeaxanthin and lutein [54,80] (see also [82]).

Zeaxanthin is the more potent antioxidant of the two [83], exhibiting a particularly stabilizing orientation in biological membranes [84] (see also [26] for a recent review). Zeaxanthin and/or lutein can reduce neuroinflammation [54,85,86]. Specifically, sup-

plementation with zeaxanthin and lutein lowered markers of inflammation [87,88] (see also [89,90]) and enhanced cognitive function [54,91–94] (see also [95–97]).

The dietary supply of zeaxanthin and lutein is thus highly relevant for humans living and working in space environments. Healthy astronauts exposed to elevated levels of GCR for even a few weeks developed significant cognitive dysfunction, even when signs of accelerated cellular aging and increased chronic disease were mild. Commercial airline pilots are also at an elevated risk of exposure to GCR; pilots who consumed greater levels of zeaxanthin exhibited significantly reduced levels of inflammation and decreased cumulative DNA damage [98]. Future research should test the attractive hypothesis that astronauts will benefit from zeaxanthin and/or lutein supplementation in conjunction with (i) additional dietary antioxidant metabolites capable of recycling oxidized carotenoids (see below) and (ii) sufficient intake of omega-3 PUFAs such as docosahexaenoic acid (DHA). Supplementation with a combination of xanthophylls and DHA (i) enhanced memory as well as the rate and efficiency of learning [96] and (ii) resulted in positive outcomes in patients with Alzheimer’s disease [97].

4.3. Zeaxanthin and Lutein Protect Photosynthesis

Unlike humans, plants synthesize zeaxanthin and lutein *de novo* for specific roles in the prevention of radiation damage. Whereas lutein is constitutively present in leafy crops, zeaxanthin is formed only under bright light and quickly removed again when light levels drop in these photosynthetic systems [99]. Only leafy greens harvested and eaten shortly after exposure to bright light thus deliver significant levels of zeaxanthin. In contrast, leafy green produce purchased at a grocery store provides lutein but little to no zeaxanthin. Moreover, typical edible crops are fast-growing annual plants that accumulate much less zeaxanthin than the inedible leaves of slow-growing evergreens [99] (see next paragraph for details). Food other than leaves can provide high levels of zeaxanthin and lutein on earth, including orange peppers, corn, and eggs (Figure 3; [100–103]). Zeaxanthin was named after the yellow color of an ear of corn (genus *Zea*, with “xanthos” the Greek word for golden/yellow). While being unable to synthesize carotenoids *de novo*, most animals do accumulate carotenoids when they have access to carotenoid-containing food [104]. For example, chickens raised with alfalfa-based feed, corn, or other sources of zeaxanthin and lutein transfer considerable amounts of these carotenoids into their eggs [105,106]. However, egg production is not feasible on a spaceship, and the growth of peppers or ears of corn is much less volume-efficient than a crop like duckweed that is 100% edible.



Figure 3. Images of whole food sources that contain high levels of zeaxanthin and lutein including, duckweed (see below), eggs (see above), orange peppers (see below), and corn (see above).

The above-mentioned general tradeoff between fast growth and accumulation of high levels of zeaxanthin in photosynthetic plant organs occurs because zeaxanthin diverts light away from photochemical pathways and into alternative nonphotochemical pathways [99]. Such removal of absorbed light energy is desirable only when more light is absorbed than can be utilized in photosynthesis. Under exposure to full sunlight, fast-growing crops with high maximal photosynthesis rates experience much less excess absorbed light than slow-growing evergreens with low maximal photosynthesis rates. Consequently, leaves of

slow-growing plants accumulate more zeaxanthin than those of fast-growing plants [99]. Due to this inverse relationship between photosynthesis/growth rate and zeaxanthin accumulation, fast-growing, rapidly photosynthesizing crops produce high oxygen levels and consume large quantities of CO₂ but accumulate little zeaxanthin.

On the other hand, slow-growing plants produce less oxygen, consume less CO₂, and accumulate more zeaxanthin [99]. Bacteria growing on a radioactive site in Japan had an exceptionally high zeaxanthin content suggesting an additional role of zeaxanthin in protection against ionizing radiation [107]. In contrast to zeaxanthin, lutein is a constitutive component of the photosynthetic apparatus in plants growing naturally across a wide range of light environments, from deep shade to full sunlight [108] (see also [99]).

To extend the lifetime of xanthophylls in membranes, their oxidation products must be recycled (by re-reduction) to prevent them from becoming harmful oxidants themselves (Figure 4; [109,110]). The recycling of zeaxanthin radicals by membrane-soluble vitamin E and/or water-soluble vitamin C (and other water-soluble antioxidants), neither of which can be synthesized by humans, has been studied extensively in lipid bilayers [78]. It is thus desirable to provide a balanced mix of antioxidant metabolites in the human diet, preferably through the consumption of whole foods rich in essential micronutrients [111], because high-dose antioxidant supplementation can have negative effects [112]. Specifically, excess dietary consumption of antioxidants from high-dose supplements can lower ROS levels to the extent that essential ROS signals fail to be produced and, e.g., the synthesis of endogenous antioxidant enzymes is suppressed [57]. Due to the benefits of whole food as well as the finite lifetime of vitamin supplements, nutritious crops will be critical to extended space missions.

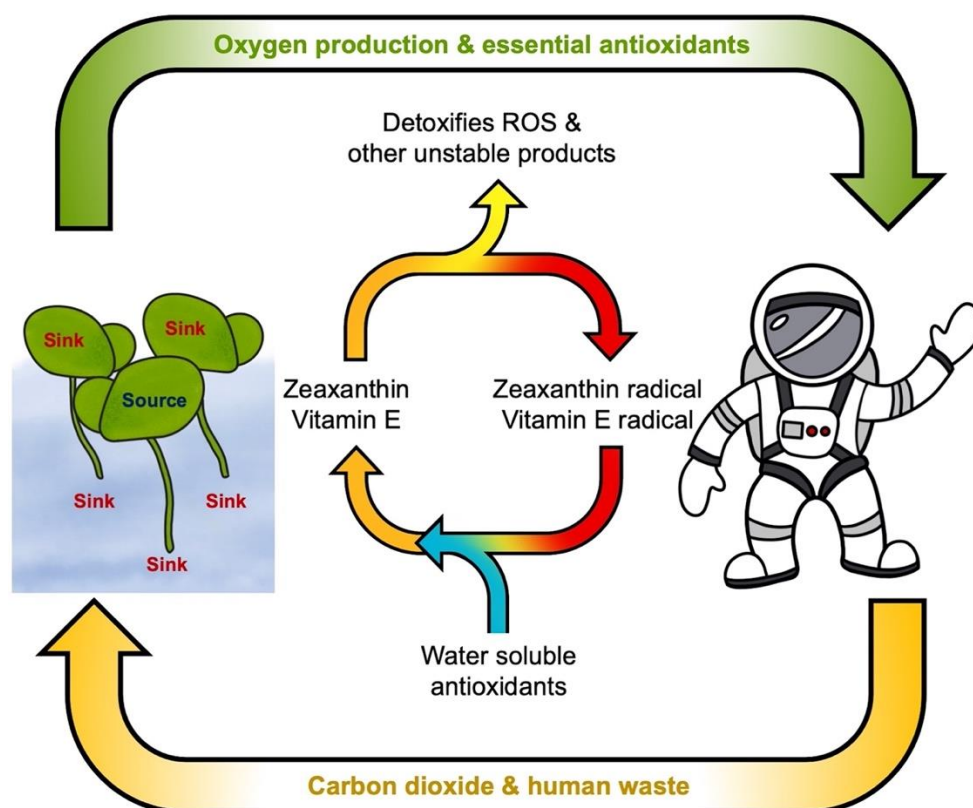


Figure 4. A schematic depiction of the interconnectedness of duckweed (left) and astronauts (right). In the center is a schematic depiction of the intertwined cycle of detoxification of ROS and the recycling of vitamin E and zeaxanthin by water-soluble antioxidants. A mother frond (leaf-like structure) is the initial source for photosynthetically produced sugars and its daughter fronds and rootlets are sinks for the sugars until the synthesis of sugars by daughter fronds exceeds the import of sugars and they, in turn, become source tissues.

5. The Case for Lemnaceae as Space Crops

5.1. An Unusual Combination of Multiple Attractive Traits

Successful long-term space missions will likely require regenerative life-support from plants that provide oxygen, recycle waste and CO₂, and produce high-quality food, including micronutrients that mitigate radiation damage (Figure 4). In addition, a space crop must be resilient under the stresses of the space environment. The first step in identifying suitable food crops and cultivation conditions for long-duration missions is understanding the effect of the space environment on crop physiology, especially growth, propagation, and nutritional quality.

Traditional model plants lack some features desirable for space crops. The enormous potential of the aquatic plant family Lemnaceae (duckweeds) as both model species (for, e.g., radiobiology and genomic studies) and edible space crops has been recognized since the beginning of the space program (Figure 5). Lemnaceae were the very first plants studied for photosynthesis in space, grew well under these conditions [113], and have been recommended as a good candidate for bioregenerative life support systems [114–117]. Additional flight experiments, including NASA STS-4 Getaway Special (1982), Russian satellite Bion 8 (1987), Russian satellite Bion 10 (1992), NASA STS-60 Getaway Special (1994), and STS-67 (1995), indicated the tolerance of Lemnaceae to GCR and microgravity of space.

Lemnaceae – pre-adapted for space?	
Tolerant of space conditions	Exceptional nutritional quality
Insensitive to microgravity Relatively insensitive to eCO ₂ in cabin Radiation-fighting antioxidants	High antioxidant (& zeaxanthin) levels High-quality protein Beneficial fat composition
Exceptional productivity	Easy to propagate
Doubles area in 1-3 days Majority photosynthetic tissue for maximal O ₂ production & CO ₂ removal	Can be stored and propagated vegetatively No germination or flowering required
Wastewater recycling	Small size
Efficient uptake of nitrogen from human waste & conversion to protein	High yield per volume and can grow on a film of water

Figure 5. Summary of Lemnaceae features suitable for spaceflight environments (light orange text boxes) and brief explanations (white text boxes) below each point. See text for additional details.

Lemnaceae are consumed around the globe and hailed as a new superfood (e.g., [118]). Lemnaceae have multiple features that make them particularly attractive candidates for space crops (Figure 5). In addition to fast growth, which entails very high rates of O₂ production and CO₂ sequestration, Lemnaceae have an exceptional nutritional quality (especially radiation-fighting antioxidants and high-quality protein with all essential amino acids for humans; see next section for further details), is highly volume-efficient (with particularly small size and the complete or near-complete absence of non-photosynthetic parts), and easy to propagate, allowing for rapid multi-generational studies [119]. Additionally, Lemnaceae have a higher edible protein content than any known terrestrial plant as they accumulate storage protein throughout the whole plant.

5.2. Can the Aquatic Lifestyle Be Seen as a Pre-Adaptation for Spaceflight Environments

The attractive traits of Lemnaceae for spaceflight environments listed in Figure 5 can be traced back to apparent selective pressures acting on plants in aquatic environments [46]. In other words, evolution may have led to a group of plants with traits that can be viewed as pre-adaptations for spaceflight environments.

To design a plant suitable as a regenerative life support system for a space environment (Figure 4), one would want the plant to consist mainly, or only, of leaves—that produce O_2 and take in CO_2 —with little to no tissue allocated to stems, roots, or any other parts that consume O_2 and release CO_2 . Aquatic plants like the Lemnaceae naturally consist mostly or entirely of photosynthetic tissue. Duckweed’s almost total (or total in some species) absence of non-photosynthetic tissue makes it such that all photosynthetically produced sugar can be reinvested in more photosynthetic tissue that supports more O_2 production and sequesters more CO_2 . By re-investing most, or all, photosynthetically produced sugars into additional photosynthetic tissue, aquatic plants can also sustain much higher growth rates than land plants that must invest substantial resources in non-photosynthetic tissues (see Figure 5; [51]).

Land plants must invest resources into substantial structures to hold themselves in place and display their photosynthetic organs for efficient light capture, mine for water and nutrients in the soil, and transport the latter from roots to shoots. Their upright shoots and downward-growing roots also make land plants susceptible to disruption of the necessary directional communication between these organs by microgravity [41,120]. In contrast, aquatic plants consisting of fronds with minimal or no roots, stems, and branches are apparently impervious to the lack of gravity; in fact, Lemnaceae exhibited growth stimulation rather than inhibition under microgravity (Figure 5; [115]). Moreover, unlike most land plants, Lemnaceae can be propagated indefinitely without requiring the processes, such as flowering, pollination, seed development, or seed germination, which can be susceptible to disruption by microgravity (see Figure 5; [40,121]).

Each green leaf-like structure of Lemnaceae is, in fact, a plant that divides and forms clonal colonies vegetatively. When conditions are not conducive to growth, Lemnaceae produce vegetative storage forms that can quickly resume growth when conditions permit [119]. Due to their diminutive size and aquatic nature, Lemnaceae can be grown on thin films of water that adhere to shallow growth trays, making them independent of gravity and allowing stacking of multiple layers for an exceptionally high volumetric yield (Figure 5; [122]).

A good space crop should also recycle human nitrogenous waste (Figure 5). Unlike land plants that typically prefer to take up nitrogen from the soil as nitrate, aquatic plants have an exceptional genetic capacity to take up ammonium from animal waste [123], efficiently convert it to amino acids [124,125], and accumulate large amounts of protein. This protein is accumulated throughout the whole plant (rather than mainly in seeds like land plants), which helps avoid the ammonium toxicity seen in most land plants [126] (see also below). The protein accumulated in Lemnaceae contains all essential amino acids needed by humans [127]. The combination of duckweed’s small size and high capacity to store vegetative protein throughout the plant results in 20 times greater edible protein production per plant-cultivating area compared to soybean [128].

A combination of several classes of essential antioxidant micronutrients that act in tandem to protect the human consumer against GCR-induced ROS production and its multiple adverse effects (Figure 1; for more details, see next section) is also desirable in a space crop. These antioxidants are needed in the plant to remove excess ROS under the influence of GCR (Figure 5). Such antioxidant protection will likely be instrumental in allowing space crops to render their life-supporting services.

5.3. Exceptional Antioxidant Content

Duckweeds are an exception to the general trend that fast-growing plants do not accumulate large amounts of zeaxanthin in their leaves. Two *Lemna* species showed similarly high levels of zeaxanthin accumulation as sun-grown slow-growing land plants when the duckweeds were grown either under full natural sunlight or in continuous low light in growth chambers [129,130]. Moreover, *Lemna* exhibited uniquely high levels of zeaxanthin when grown under continuous high light in a growth chamber [129,130], where zeaxanthin levels reached 0.4 mg/g plant dry weight (based on [129]), which corresponds to

3.4 mg/100 g plant fresh weight (assuming 8.5% dry weight; [127]). Therewith, duckweed's zeaxanthin levels fall within the range reported for orange peppers as a superb zeaxanthin source. Typical values for orange pepper range from 1.4 mg/100 g fresh weight [131] and 1.7 mg/100 g fresh weight [132] to 6.2 mg/100 g fresh weight [133] (see also [134,135]).

Duckweed is thus the only known plant that accumulates high levels of zeaxanthin in its photosynthetic organs while also growing very rapidly [51]. Duckweed may also be unique among dietary zeaxanthin sources in providing a particularly well-rounded cocktail of dietary factors that interact synergistically with zeaxanthin in opposing inflammation. Duckweed also has a high content of vitamin E [130,136] and phenolic antioxidants [137,138]. In addition, duckweed has a high ratio of inflammation-resolving omega-3 PUFAs to immunostimulatory omega-6 PUFAs (Figure 5; [128]).

Overall, duckweed has a unique pigment composition with an emphasis on carotenoids that prevent radiation damage [129,130]. The architecture of Lemnaceae is consistent with the exceptionally high antioxidant production in this group of plants [129,130]. Specifically, the relatively thin fronds and absence of a fixed tiered canopy maximize light receipt as well as exposure to excess light in high-light environments. The high antioxidant levels support the plant's ability to avoid radiation damage and could thus provide its life-sustaining services to a crew in space environments. The essential human antioxidant metabolites accumulated by duckweed counter chronic inflammation and associated mental dysfunction as well as other adverse health outcomes experienced by astronauts.

5.4. Performance under Elevated CO₂

Growth under the elevated CO₂ levels typical of a space cabin environment was unimpaired in Lemnaceae even under continuous very high light levels that lead to carbohydrate build-up [51]. In contrast, the other candidates of leafy vegetable species considered for use on the International Space Station, such as Chinese cabbage (*Brassica rapa* cv. Tokyo Bekana), exhibited decreases in growth, leaf number and leaf area, and shoot dry biomass under elevated CO₂ concentrations [139]. The robustness of Lemnaceae may be related to (i) a relaxation of the controls on growth rate acting in land plants [140] and (ii) preferential use of ammonium over nitrate. It is the use of nitrate as a nitrogen source that can enhance ROS production under elevated CO₂ [47]. The combination of high nitrate levels and elevated CO₂ can trigger premature senescence in land plants [43,45,141]. In terms of environmental controls on growth, most land plants quickly curb growth when water or nutrients begin to become limiting, which is accompanied by carbohydrate build-up that causes feedback downregulation of photosynthesis (see above) and speeds up the completion of the plant life cycle [142]. In contrast, Lemnaceae floating on water and with large nitrogen stores (in the form of storage protein) exhibited unabated growth across a wide range of environmental conditions irrespective of carbohydrate build-up under earth-ambient CO₂ levels [129,130].

On the other hand, exposure to elevated CO₂ did cause some of the same regulatory adjustments in the photosynthetic apparatus in *Lemna* as commonly seen in C₃ land plants, with a lowered content of protein and chlorophyll [129,130]. Furthermore, the lower chlorophyll level was associated with lower levels of the antioxidants that protect chloroplasts from radiation damage [51]. In theory, elevated CO₂ could thus make plants, including Lemnaceae, more vulnerable to damaging effects by GCR because of lowered plant antioxidant levels. However, there is an intriguing possibility that GCR may offer some protection against the loss of nutritional quality under elevated CO₂, especially for zeaxanthin. The enzyme zeaxanthin epoxidase (ZEP) removes zeaxanthin when plants exposed to high light are returned to low light levels and operates concurrently with the zeaxanthin-forming enzyme violaxanthin de-epoxidase [143,144] in high light. There are several reports that ZEP is downregulated under conditions of oxidative stress [145–147]. Such inhibition of zeaxanthin removal can be expected to enhance zeaxanthin levels across a range of light levels.

6. Conclusions

Here we identify the importance as well as the dangers of oxygen and the formation of ROS. Organisms need to maintain a delicate balance between antioxidants and oxidants to support cellular redox homeostasis and cell signaling in support of growth, development, and stress protection. Space environments expose plants and astronauts to additional stresses. Identification of plant species with superior rates of production of oxygen and essential human micronutrients as well as the removal of CO₂ and recycling of human waste, are essential to the success of future long-term space missions (Figure 4). Plants of the family Lemnaceae have multiple traits that may help minimize the negative impacts of the combination of stressors encountered in space environments. Unlike land plants, Lemnaceae showed a stimulation, rather than inhibition, of growth under microgravity and exhibited relatively low sensitivity to elevated CO₂. Lemnaceae's exceptional antioxidant content may also reduce its sensitivity to GCR. These attractive genetic traits of Lemnaceae for space environments are features of the plants adapted to the unique aquatic environment.

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