Curiosity has driven humankind to explore and conquer space. However, today, space research is not a means to relieve this curiosity anymore, but instead has turned into a need. To support the crew in distant expeditions, supplies should either be delivered from the Earth, or prepared for short durations through physiochemical methods aboard the space station. Thus, research continues to devise reliable regenerative systems. Biological life support systems may be the only answer to human autonomy in outposts beyond Earth. For construction of an artificial extraterrestrial ecosystem, it is necessary to search for highly adaptable super-organisms capable of growth in harsh space environments. Indeed, a number of organisms have been proposed for cultivation in space. Meanwhile, some manipulations can be done to increase their photosynthetic potential and stress tolerance. Genetic manipulation and screening of plants, microalgae and cyanobacteria is currently a fascinating topic in space bioengineering. In this commentary, we will provide a viewpoint on the realities, limitations and promises in designing biological life support systems based on engineered and/or selected green organisms. Special focus will be devoted to the engineering of key photosynthetic enzymes in pioneer green organisms and their potential use in establishment of transgenic photobioreactors in space.

Introduction

Foundation of a multipurpose and reliable life support system (LSS) is a necessity in providing astronauts with essential requirements in long-term space missions. This is in line with NASA Strategic Plan to extend and sustain human activities across the solar system and to create the innovative new technologies for exploration, science and economic future. Based on a recent report from NASA Marshall Space Flight Center, each average individual human being will need 0.84 kg oxygen, 0.62 kg food solids and a total of 29.00 kg water every day and in return will produce a total of 30.60 kg waste (including carbon dioxide, respiration and perspiration water, food preparation, latent water, urine, urine flush water, feces water, sweat solids, urine solids, feces solids, hygiene water and clothes wash water). Autonomous biological LSS (BLSS) is believed to be the key to human long-term presence in space. Such a system will require a multispecies combination of higher plants, microorganisms, and physiochemical processes for revitalization of air and water, waste processing and definition of appropriate food webs. Designing probiotics with immunological benefits has also been proposed for replenishing the microbiome of astronauts, which may open a new chapter in designing future BLSS.

Green organisms are solar-powered and self-perpetuating, a fact which reduces the need for expensive re-supply missions. Plants are capable of supplying humans with food and oxygen and mitigating carbon dioxide. Nonetheless, not all plants can withstand the harsh conditions of space such as varying temperatures, drought, radiations, exposure to heavy metals, microgravity and high...
Carbon dioxide concentrations. Although many projects have been launched such as Herb Ward, BIOS project, Biosphere 2, Micro-Ecological Life Support System Alternative (MELISSA), Closed Ecology Experiment Facilities, Controlled Ecological Life Support Systems, BIOplex (never completed), Salad Machine and Advanced LSS (ALSS), majority of these projects have been conducted in small scale and in contained environments. Establishing large hydroponic or aeroponic greenhouses is difficult due to inadequacy of light, microgravity, irrigation and accommodation issues. Since most of these plants cannot tolerate real space exposure, search continues to find super-species from extreme environments around the globe. There are terrestrial examples of successful adaptation on Earth such as species tolerant to low atmospheric pressure (Alpine), low temperature (Arctic species, Araceae), drought (Tortula ruralis, Physcomitrella), and those tolerant to high radiation such as Deinococcus radiodurans. It is surmised that making an Earth-like analog in space will end up in a fiasco, unless lessons are learned from the evolution of life on Earth. Classical breeding, involving cross-breeding and screening of populations, is slow and hampered by labor-intensiveness. Thus, genetic manipulation toolkits hold promise in making sophisticated green organisms resistant to extreme conditions in a more realistic and foreseeable time frame. In this commentary, three strategies will be presented to enrich the genetic reservoir of plants and microalgae to increase their resistance and photosynthetic yields, (1) screening of resistant organism from extreme environments on the Earth, (2) adaptation of organisms to harsh conditions and (3) genetic manipulation. Our knowledge about the origin and evolution of photosynthesis can advance our understanding of the origin of life. Life on Earth probably dates back to 3.8 billion years ago. However, scientists have hypothesized that life may have existed earlier on other planets and was translated to Earth by a meteorite. Either way, today we know that the atmosphere has been produced by a phenomenon known as oxygenic photosynthesis, before which the Earth was anoxic. A great deal of atmospheric oxygen is produced not by plants, but by the photosynthetic cyanobacteria and microalgae in oceans, seas and lakes (Fig. 1). Establishment of an Earth-like atmosphere in short time will be feasible through construction of closed environments in space. The strategy to accelerate this process is screening candidate organisms and manipulating them to create super-species with higher photosynthetic efficiency and higher adaptability to grow in extraterrestrial environments. Apart from improving the photosynthetic efficiency, genetic manipulation of crops that are better suited to a spaceflight environment (e.g., dwarfed crops, or those that have high harvest indexes and grow well under artificial light, reduced atmospheric pressures or elevated carbon dioxide concentrations) remain promising research topics to explore. In this line, studying the evolution machinery in the Earth will help us reverse-genetic engineer green organisms to construct an artificial atmosphere as well as an autonomous food web in space. For instance, robust photosynthetic enzymes of ancient extremophile photosynthetic microorganism can be employed to enrich the genetic reservoir in candidate plants and microalgae.

Candidate Green Organisms for Integration in BLSS

Plants. Plants are generally regarded as essential elements of any successful BLSS. In recent centuries, advances in plant genetic breeding have brought about significant progress in increasing crop yields. Although many investigations have been done to genetically engineer plants for exploitation in BLSS. Thousands of cultivars of each major crop plants (each adapted to a unique habitat on our planet) as well as national germplasm collections provide us with the genetic diversity to explore and engineer. Lettuce, kale, turnip, Swiss chard, endive, dandelion, cabbage, cauliflower, radish, New Zealand spinach, tamarula and sweet potato were the first crops chosen for use in BLSS. According to Wright Patterson Air Force Base symposium, selection criteria included the ability of growth under low light intensity, compact size, high productivity, nutritional value and adaptability to the space condition need to be taken into consideration as well. Although a large number of studies have been conducted to investigate the effect of microgravity on plants, few
plants have been grown in space for revi-
talization of air and production of biomass
to sustain human life. In 1979, Sporoeleda
polyrhiza and later potato and wheat, were
used with the purpose of photosynthetic
gas exchange.10,11 Other successful stud-
ies reported the production of wheat and
potato biomass in space.12,13 Elevated
ethylene levels hindered the development
of wheat seeds in Russian Mir Space
Station.12,14 In the PESTO experiment
on successive plantings of wheat on the
International Space Station, elegant gas
exchange was noted.15

The plants have adapted with respect to
different environmental conditions on the
Earth.20 C3 plants have low photosyn-
thetic efficiency due to photorespiration.
However, they are resistant to extremely
cold situations.17 Wheat is among C3
plants and has been widely considered as
an attractive candidate for cultivation in
space. II. On the other hand, owing to the
higher density of mesophyll cells, C4 plants
such as maize have a higher photosyn-
thetic efficiency, since in such a compact
environment where little oxygen diffusion
happens, Rubisco enzyme will solely act as
carboxylation and oxygenation reactions
involved. The extensively investi-
gated Rubisco is currently considered as
one of the leading targets for genetic engi-
neering to improve the photosynthetic
efficiency of green organisms.18 Both
photosynthesis and oxygenation reactions
are catalyzed at the same active site on
Rubisco which makes carbon dioxide and
oxygen competitive substrates.19 There

is general consensus that reducing the
inhibitory effect of oxygen can enhance the
photosynthetic efficiency and, subse-
quently, the productivity of plants. It has
also been hypothesized that carbon diox-
ide enrichment can increase crop yield by
enhancing photosynthetic efficiency even
as a global scale.20 Although in the absence
of oxygen in space, Rubisco will function
only as a carboxylase, through construc-
tion of a closed ecosystem or air cabin,
oxygen diffusion to the space between
mesophyll cells will definitely affect the
activity of Rubisco. Furthermore, micro-
gravity will reduce the density of tissues
and will increase the intracellular space,
allowing more oxygen to come in contact
with the Rubisco and influence its func-
tion. Thus, studying Rubisco evolution
can provide us with the knowledge to
manipulate Rubisco in higher plants to
produce genetically modified plants har-
boring Rubisco enzymes with more car-
boxylase function than oxygenase.

Research can also focus on elucidat-
ing other green organisms embedded with
better Rubisco machineries. For example,
the red alga Galdieria partita has one of
the highest reported values for Rubisco
specificity factor, almost 3-times greater
than that of most crop plants.26 There
have been several attempts to select green
organisms with higher specificity factors
through maintaining them at above the
compensation point, in which the species
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| Green organism | Resistance to low temperatures | Resistance to high temperatures | Resistance to dryness | Photosynthetic efficiency | CO₂ removal/O₂ production |
|----------------|--------------------------------|---------------------------------|----------------------|--------------------------|--------------------------|
| C3 plants      | Resistant                     | Sensitive                       | Medium               | High                     | High                     |
| C4 plants      | Sensitive                     | Resistant                       | Medium resistant     | High                     | High                     |
| CAM plants     | Medium resistant              | Resistant                       | Low                  | Low                      | Low                      |
| Microalgae     | Resistant                     | Resistant                       | Medium resistant     | High                     | High                     |
oxygen. Rubisco can thus be isolated from archaic microorganisms and introduced into green candidates. Furthermore, engineering Rubisco activase, or increasing its stability holds promise for enhancing the adaptability of plants in stressful or extreme environments. However, researchers must have an eye on the hypothesis that "genetic engineering to improve Rubisco might lead to a productivity runaway that removes all atmospheric carbon dioxide." Carbonic anhydrase. Carbonic anhydrase is another key photosynthetic metalloenzyme which catalyzes the rapid interconversion of carbon dioxide to bicarbonate and is responsible for delivery of atmospheric carbon dioxide to Rubisco. In microgravity in which the cellular density in plant leaves is lower than that of Earth, the presence of a robust carbonic anhydrase can capture high amounts of carbon dioxide and enhance photosynthetic functionality. This enzyme is of utmost importance in CAM plants. However, naturally, carbonic anhydrase has low activity in C3 and C4 plants. The amount and robustness of carbonic anhydrase is higher in microalgae. Thus, these enzymes can be engrafted into plants to enhance their photosynthetic efficiency.

Pro and cons of plant in BLSS. From a more realistic point of view, there is little possibility that plants can establish a successful BLSS alone. A number of major drawbacks exist: First, it may not be practical to take large number of plants to off-planet stations and if so, a large surface area will be needed to accommodate them. For example, based on the best photosynthetic rates from studies on gas exchange of potato stands for continuous cultivation are required to remove the carbon dioxide and supply oxygen for one person. The oxygen need of one human can be provided by 11 m² of wheat grown at high light intensity. This is while 17 L of the microalgae Chlorella culture spread in a thin layer with light-receiving surface area of 8 m² is sufficient for gas exchange of an average human subject. Besides, super-elevation of the carbon dioxide concentration to 5000–10000 ppm which can occur in spacecraft, sometimes has negative and/or toxic effects on plant growth or seed yield in some species. Trimming, watering and taking care of these plants can turn into a daily chore for astronauts. Other problems such as lack of adequate light and difficulty of supplying water to plants in microgravity also exist. Besides, since the nutritional composition of a single crop is not adequate for a healthy diet, different species may need to be incorporated. Another inconsistency is that almost half of the plant biomass is inedible. There are also concerns about the damages that may be induced by freezing and UV-B radiation in space. Sewage-water recycling is a serious problem of any LSS and though plants have been proposed as means to recycle water, plants used in hydroponics are sensitive to pH changes and inorganic toxic elements. Taken altogether, it seems that other green organisms can be used along with higher plants to increase the functionality of BLSS (Table 1).

Microalgae as alternative green organisms. Microfossil records indicate that cyanobacteria and microalgae were the earliest residents of the Earth. Some of these organisms have the capability to grow in extreme environments on our planet (Fig. 1) and even in simulated conditions of Mars and Moon. They have been shown to survive in habitats with a wide range of salinity, pH, heavy metal, light intensity, UV radiation and extreme temperatures. Million years ago, photosynthetic microorganisms started to generate the atmospheric oxygen and can thus be integrated into BLSS as functional components in revitalization of air and supplying food. Microalgae are microscopic unicellular photoautotrophic organisms (Fig. 2) with various industrial, pharmaceutical and nutritional applications and have recently come into attention in molecular farming. Microalgae have also been incorporated in several BLSSs because of high growth rate and little growth requirements, simple cultivation and relatively easy collection. Among other microalgae, Spirulina platensis is the most commonly used organism in BLSS owing to its rich nutritional merit. Not only can microalgae function in nutrition and air revitalization but also in waste water treatment and producing biofuel. So far, in BLSS studies, microalgae have only been considered for revitalization of air and providing food, and the capability of microalgae in production of biofuels including bioglycerol has been ignored. This functional- ity can be regarded as an added benefit. Protein and biomass quality and biological value of various microalgae including Chlorella, Chlamydomonas, Spirulina and Euglena has been calculated in a study by Antonian et al. In this study, the high biological value of the algal biomass was demonstrated in animal experiments and
A new method is presented in Figure 3 for adaptation and genetic screening of microalgae (or other microorganisms) in order to select superior species or strains. Microalgae can be artificially selected to survive in the simulated stressful conditions of space. Unlike any previous experiments in which different stressors have been simultaneously imposed to select superior microalgae and cyanobacteria, in this method, stressors can be applied in a stepwise manner. In each stage, a new sublethal stressor can be applied to microalgae cell culture and a couple of cell in a population may survive the challenge, adapt to it and proliferate to enter the other stage while carrying the heritable variations (Fig. 3).

The environmental stressors in space or in other extreme situations include but are not limited to microgravity, temperature extremes, high carbon dioxide consumption can partly protect astronauts against radiations. Ability of microalgae to adapt to harsh environments. Crossing over and mutations are random phenomena during replication which contribute to adaptation of an organism to changing conditions, unusual and/or extreme environments by acquiring new genotypic and/or phenotypic traits. Unlike plants, microorganisms (including microalgae) are hypermutable and have high crossing over and mutation rate in response to new stressors. The higher rate of recombination partly gets back to the higher rate of reproduction in microorganisms in comparison with higher organisms. These characteristics render microorganisms highly adaptable to the environment. This may be the reason why microalgae are found in very diverse habitats on Earth from fresh water to saturated salt lakes and the Antarctic sea.39

The lack of its toxic or other adverse effects was confirmed. The authors concluded that the quantity and quality of proteins from the unicellular microalgae indicate their high nutritional value and applicability to BLSS.

Microalgae possess a set of vital enzymes which can be used in higher plants to increase the photosynthetic yield as well as resistance to space environment. Microalgal carbonic anhydrase is more robust than that of plants and can thus be cloned into other green organisms. Other important genes involved in carotenoid synthesis such as lycopene cyclase (lyc) and phytoene desaturase (pds) can be transferred to higher plants to confer resistance against high solar radiation and to protect chlorophyle molecules. On the other hand, these genes can be manipulated to increase the carotenoid content of the microalgal biomass which upon consumption can partly protect astronauts against radiations.

Figure 3. Rapid stepwise artificial Darwinian selection of super microorganisms for exploitation in BLSS and in terraforming of Mars.
concentration, heavy metals exposure and high UV illumination. All these stressors can be applied to a microalgal cell culture in a stepwise manner. If this process is carried out, a super-species may be selected which will be resistant to all tested stressors. Afterwards, these microalgae can be used in cultivation in BLSS and/or utilized for farming on Moon and Mars. In our opinion, rapid stepwise artificial Darwinian selection of superior microorganisms can open new and interesting avenues for further advances in designing BLSS.

Conclusions

Photosynthetic organisms are considered to be indispensable components of BLSS; however, no known plant may be capable of tolerating such harsh growth conditions. The Earth already possesses a diverse genetic reservoir for us to choose from. Among other green organisms, microalgae are highly tolerant of and adaptable to new stressors. Genetic engineering holds promise for production of superorganisms through introduction of robust enzymes into both photosynthetic machinery of pioneer green organisms. Furthermore, artificial selection can be considered as a tool in screening populations in search for tolerable and adaptable species. The engineered and selected green organisms can then be used in BLSS or employed in terraforming of Mars.

Disclosure of Potential Conflicts of interest

The authors declare there are no conflicts of interest.

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