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BIOREGENERATIVE LIFE SUPPORT SYSTEMS IN SPACE (BLSS): THE EFFECTS OF RADIATION ON PLANTS

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ABSTRACT

The growth of plants in Space is a fundamental issue for Space exploration. Plants play an important role in the Bioregenerative Life Support Systems (BLSS) needed to sustain human permanence in extraterrestrial environments. From this perspective, plants are basic elements for oxygen and fresh food production, air regeneration as well as providing psychological support to the crew. The potential of plant survival and reproduction in space is limited by the same factors that act on Earth (e.g. light, temperature and relative humidity) and by additional factors such as altered gravity and ionizing radiation.

This paper analyzes plant response to space radiation, which is recognized as a powerful mutagen for photosynthetic organisms thus being responsible for morpho-structural, physiological and genetic alterations. Until now, many studies have shown evidence as to how the response to ionizing radiation is influenced by several factors associated both with plant characteristics (e.g. cultivar, species, developmental stage, tissue structure) and/or radiation features (e.g. dose, quality and exposure time). The photosynthetic machinery is particularly sensitive to ionizing radiation. The severity of the damage induced by ionizing radiation on plant cell and tissues may depend on *the capability of plants to adopt protective mechanisms and/or repair strategies. In this paper, a selection of results from studies on the effects of ionizing radiation on plants at the anatomical and eco-physiological level is reported and some aspects related to radioresistance are explored.*

Keywords: *Bioregerative Life Support System (BLSS), higher plants, ionizing radiation, photosynthesis, radioresistance*

SISTEM ZA BIOREGENERATIVNO PODPORO ŽIVLJENJU (BLSS): VPLIVI SEVANJA NA RASTLINE

IZVLEČEK

Rastlinska rast v vesolju je temeljno vprašanje na področju raziskovanja vesolja. Rastline igrajo pomembno vlogo v sistemih za bioregenerativno podporo življenju (»Bioregenerative Life Support Systems« ali BLSS), ki so potrebni za ohranjanje človeškega bivanja v nezemeljskih okoljih. S tega vidika so rastline osnovni elementi za nastajanje kisika in sveže hrane, obnavljanje zraka, prav tako pa nudijo psihološko podporo posadki. Možnosti preživetja rastlin in razmnoževanja v vesolju so omejene z enakimi dejavniki, ki so prisotni na zemlji (npr. svetloba, temperatura in relativna vlažnost), ter še z dodatnimi dejavniki, kot sta spremenjena gravitacija in ionizirajoče sevanje.

V tem prispevku analiziramo odzive rastlin na sevanje v vesolju, ki pa se smatra kot močan mutagen za fotosintezne organizme ter je tako odgovorno za morfološko strukturne, psihološke in genetske spremembe. Do danes so rezultati mnogih študij pokazali, kako mnogi dejavniki, ki so povezani tako z značilnostmi rastlin (npr. kultivar, vrsta, razvojna faza, struktura tkiv) in/ali z značilnostmi sevanja (npr. količina, kakovost in čas izpostavljenosti), vplivajo na odzivnost na ionizirajoče sevanje. Fotosintezni mehanizem je še posebej občutljiv za ionizirajoče sevanje. Stopnja škode, ki jo ionizirajoče sevanje povzroči na rastlinskih celicah in tkivih, je lahko odvisna od zmožnosti rastlin, da vzpostavijo zaščitne mehanizme in/ali strategije odprave škode. V tem prispevku je opisan izbor rezultatov študij o učinkih ionizirajočega sevanja na rastline na anatomski in eko-fiziološki stopnji, prav tako so predstavljeni tudi nekateri vidiki, povezani z odpornostjo na sevanje.

Ključne besede: *sistem za bioregenerativno podporo življenju (BLSS), višje rastline, ionizirajoče sevanje, fotosinteza, odpornost na sevanje*

INTRODUCTION

The possibility of growing plants in Space is an important topic within plans for space exploration from the point of view of future long-duration manned missions. All scenarios for the long-term habitation of space platforms and planetary stations involve plants as a fundamental part of Bioregenerative Life Support Systems (BLSS) to support the crew (Salisbury, 1999; Salisbury et al., 2002; Drysdale et al., 2003). Indeed, humans and plants are ideal space traveling companions: plants consume carbon dioxide, purify water and release oxygen, humans consume oxygen and release carbon dioxide; moreover humans can use the edible parts of plants for nourishment, while human waste and inedible plant matter can provide nutrients for plant growth after the digestion processes mediated by microbes in bioreactors (Wheeler, 2003). The sole input needed to keep such a system going is light energy. The most important characteristics of a BLSS is "self-sufficiency" since it can be considered a "miniature ecosystem" where each element supports and is supported by each of the others. In terrestrial ecosystems, most energy entering the biosphere comes in via photosynthesis by plants (producers) and is transferred along the many steps in a food chain to the consumers (herbivores, carnivores). This process is responsible for most of the organic carbon in the biological world. At the death of living organisms, detritivores and decomposers (bacteria and fungi) collectively account for the use of all such "waste" and, through the processes called decomposition and mineralization, allow the recycling of the organic matter and the return of nutrient to plants. In Figure 1 the analogies between a natural ecosystem and a BLSS are shown.

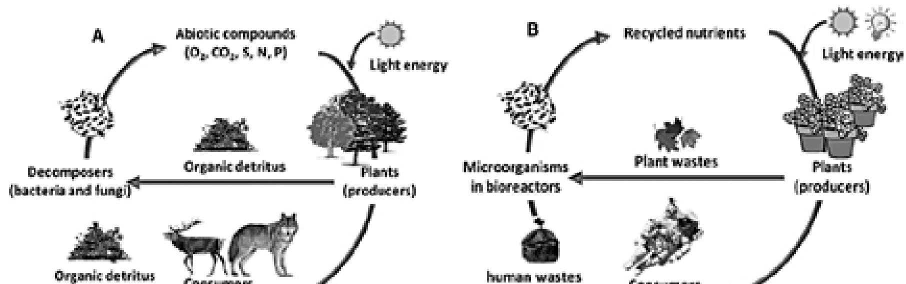

Figure 1: The analogies between a natural ecosystem (A) and a Biological Life Support System, BLSS, (B).

Another important aspect of plant cultivation in space is related to the human psychological implications of having plants present in a confined living space: there is evidence to support the benefits of working with plants and consuming fresh foods (as opposed to stored foods) on long-duration missions (Flagler & Poincelot, 1994; Waters et al., 2002).

In the long term, to reduce the need for resupplying life support materials for extended missions, it is interesting to evaluate the potential of plant survival and reproduction in extraterrestrial environments. Actually, the presence of plants on Earth is the result of an evolution process which started millions of years ago and can be considered the consequence of the continuous process of plant adaptation to specific ecological factors such as light, temperature, water and nutrient availability. The complexity of these factors and their synergistic effects have determined the characteristics of the higher plants now living on the Earth and their success in the colonization of such an environment. Similarly, the cultivation in space is strictly dependent on the scientific knowledge of the effects of space factors on plant growth processes. In space, plant growth can be altered not only by factors like those on Earth but also by the action of new environmental factors such as microgravity and ionizing radiation. On Earth, radiation has influenced the colonization of lands by early higher plants which evolved a number of adaptations such as the synthesis of pigments and antioxidants as well as gene-repair mechanisms (Hessen, 2008). It has to be expected that in space where radiations of different qualities and levels of intensity (Rozema et al., 1997) occur, plant life might be severely constrained by this factor.

THE EFFECTS OF IONIZING RADIATION ON PLANTS

The effect of radiation on plants has been the object of extensive research in the past, with different aims concerning several fields of research. From the beginning of the nineteen-sixties until now, low doses of low- and high-LET (Linear Energy Transfer) ionizing radiation have been widely used for agricultural interests such as the development of new decontamination methods (alternative to heating and chemical sterilization) (Farkas, 1988), or in breeding programs for the selection of new cultivars, especially cereals, legumes and vegetables with improved yields in crops (Maity et al., 2005; Yu, 2005), enhanced resistance to diseases and semi-dwarf growth (Mei et al., 1994; Li et al., 2007).

A second area of application is radioecology, namely the study of the effects of radiation pollutants in ecosystems. This topic was widely considered after the Chernobyl accident (Real et al., 2004; Fesenko et al., 2006) and has sparked renewed interest after the recent Fukushima disaster. As a result of the Chernobyl accident, tens of thousands of hectares of forests experienced massive radioactive contamination, offering a unique opportunity to study in situ the effects of acute and chronic exposure of plants to ionizing radiation. These studies were mainly concerning conifers (Scotch pine), but also herbaceous plants and grasses (Sidorov, 1994; Real et al., 2004).

The third area of interest on radiation concerns space-oriented experiments focused on the cultivation of plants under space conditions, being plants an essential component of Bioregenerative Life Support Systems (BLSSs). These studies explore the response of seeds, higher plants and photosynthetic microorganisms to low-LET (γ- and X-rays) and high-LET (heavy ions) ionizing radiation. Generally, ionizing radiation may have different effects on plant metabolism, growth and reproduction depending on the dose: positive effects at very low doses, detrimental consequences at intermediate levels and pronounced damage at high doses are expected (Figure 2). Besides the dose, it is widely documented that the severity of the effects is dependent upon other factors such as species, cultivars, plant developmental stage, physiological and morphological traits as well as genetic characteristics (Holst & Nagel, 1997; De Micco et al., 2011). At the same dose, high-LET are more dangerous than low-LET radiation because heavy ions have been shown to cause a higher induction of mutation in the genome (Shikazono et al., 2002; Wei et al., 2006).

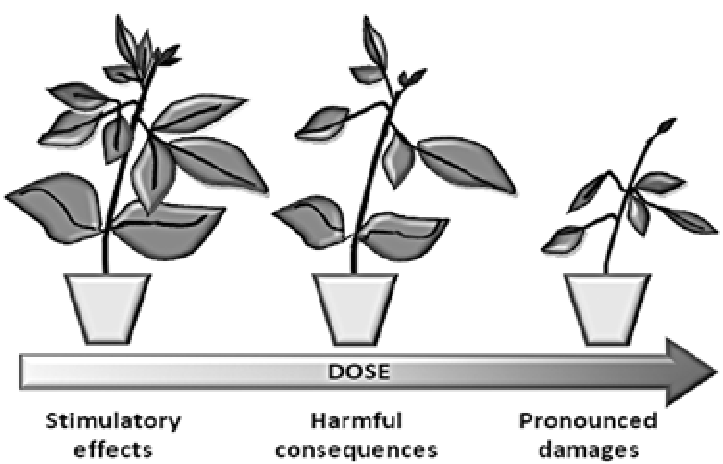

Figure 2: The effects of ionizing radiation on plants depend on dose: generally the effects are positive at very low doses, detrimental at intermediate doses and pronounced at high doses.

Consequences for plant growth

Ionizing radiation may have several impacts on different plant organs and tissues. Generally, more complex tissue architecture is less sensitive to damage. The alteration in morphological traits can be positive or negative depending not only on the species but also on the dose. Generally the exposure to ionizing radiation increases embryo lethality, induces dwarf architecture and modification of floral elements (Mei et al., 1998; Shikazono et al., 2002). However, radiation has also been reported to increase growth (e.g. taller plants), yields, reproductive success (e.g. formed seeds) and increase the ability to endure water shortage (Zaka et al., 2002; Maity et al. 2005; Yu et al., 2007).

At the anatomical and cytological level, there is evidence that irradiation with cosmic- and γ-rays affects cell wall traits (Bayonove et al., 1984; Kovàcs et al., 1997). Irradiation increases the activity of enzymes responsible for the degradation of pectins, the dissolution of middle lamellae and the separation of cells. Irradiation would also stimulate the autolysis of polysaccharides, also determining the dissolution of matrix material which results in alterations during the arrangement of cellulose microfibrils with a loss in firmness (Kovàcs et al., 1997).

Implications for photosynthetic machinery

The growth and reproduction of an individual plant and ultimately, the survival of the species, depend upon photosynthesis, the key process for the conversion of solar radiation into stored biomass energy. The photosynthesis of higher plants is considered one of the most critical biological processes of plant-based BLSSs (Wheeler et al., 2003). Light energy harvested by photosystems drives all the subsequent reactions leading to the production of ATP and NADPH utilized for the reduction of CO_2 in the carbon reduction cycle. Many studies have been performed on photosynthetic microorganisms and higher plants in order to elucidate the consequences of radiation exposure (De Micco et al., 2011). It is clear that the photosynthetic process may be altered at any step by ionizing radiation: electron transport carriers, light-harvesting pigment-protein complexes and enzymes of the carbon reduction cycle (Figure 3).

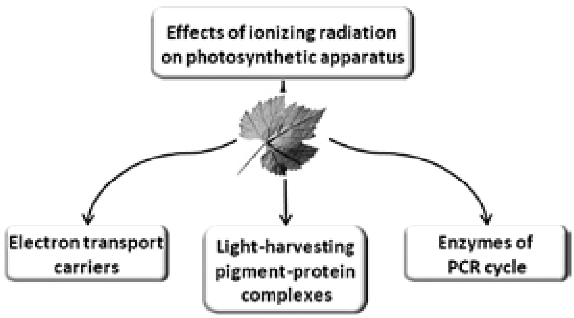

Figure 3: Ionizing radiation affects several steps of the photosynthetic apparatus: carriers of the photosynthetic electron transport chain, light-harvesting complexes, enzymes of photosynthetic reduction cycle (PCR).

The carriers of photosynthetic electron transport chain (i.e photosystems and cytochromes) seem to be specific targets of the damaging effect of γ- radiation. Experiments conducted on cyanobacteria by means of stratospheric balloons and spaceflights have shown evidence that photosystem II (PSII), one of the pigment–protein complex in the chloroplast, is particularly sensitive (Angelini et al., 2001; Rea et al., 2008). The damage on PSII is mainly localized at the D1 protein level where the electron transfer between the primary electron donor and the secondary plastoquinone acceptor happens. The degree of PSII damage is influenced by the level of light, being more pronounced at high light conditions which favour the photoinhibition of the photosynthetic apparatus (Giardi et al., 1997; Esposito et al., 2006).

The components of the photosynthetic electron transport are vulnerable also in higher plants where the exposure to both acute and chronic doses of γ-radiation induces the oxidative damage by the over-production of reactive oxygen species (ROS) (Zaka et al., 2002). The increase of ROS affects not only the photosynthetic apparatus but also the whole cell, being responsible for membrane lipid peroxidation and protein modifications (Foyer & Mullineaux, 1994).

The light harvesting complexes are also injured by low- and high-LET ionizing radiation. Irradiation of plants with γ- and heavy ions may determine the dilation between thylakoid membranes and the incidence of defective chloroplasts with chlorophyll mutations (Cheng & Chandlle, 1999; Abe et al., 2002). The consequence of chlorophyll depletion is a reduced absorbance spectrum pattern and a loss of functionality of the whole antenna complexes (Palamine et al., 2005).

Radioresistance

An interesting issue related to plant exposure to ionizing radiation is the induction of radioresistance. The occurrence of radioresistance has been observed mainly in plants growing in the radioactively contaminated areas of Chernobyl and neighboring regions (Zaka et al., 2002). After the Chernobyl accident, due to the impossibility of leaving the polluted zone, plants experienced both acute and chronic doses of radiation. It has been observed that radioresistance depends on the species (Real et al., 2004). Generally herbaceous species are less sensitive to irradiation than woody species because the latter experience cumulative detrimental effects of radiation (Holst & Nagel, 1997).

The ability to develop protection mechanisms and the capability of repairing damage are the basis for the radioresistance of a given species. However, it is clear that long-term exposure to γ-radiation generates the potential for irreversible consequences due to the accumulation of unrepaired damages. The acquisition of radioresistance may be ascribed to both biochemical and molecular mechanisms (Esnault et al., 2010). It is ascertained that the exposure of plants to ionizing radiation triggers an overproduction of ROS. However, even if ROS production is deleterious to the photosynthetic machinery, it has to be remarked that the rise of radicals in the plant cell can act as a signal for the activation of protective response and defense pathways (Foyer & Noctor, 2005). In this context, the overproduction of scavenger enzymes as well as the over-activation of poly(ADPR)polymerases enzymes (PARPs), represent essential mechanisms to counteract the cell oxidative damage and enhance stress tolerance in plants (Alscher et al., 1997; Doucet-Chabeaud et al., 2001; Esnault et al., 2010). More specifically, PARPs recognize the damaged DNA acting as a stress signal; the PARP over-activation produces the formation of PAR polymers that work as effectors recruiting on damaged DNA site the enzymatic machinery for the repair (Amor et al., 1998).

The acquisition of radioresistance may be considered an adaptive response of plants to the changing environment and may represent a valuable benefit in the sight of the plant growth in BLSSs.

AN IDEAL CANDIDATE PLANT FOR BLSSs

One of the main concerns of plant space biology is which species should be considered an ideal plant candidate for life support in Space. Until now, many research groups have been involved in the identification of the most suitable plant species for BLSSs (Mitchell et al., 1996; Salisbury & Clark, 1996; Tibbitts & Henninger, 1997). The criteria for the selection of such species include high photosynthetic rates, nutritional value and the ratio edible dry mass/total dry mass, as well as dwarf growth that is a desirable property in reduced volumes (Hoff et al., 1982; Salisbury, 1997; Tibbitts & Henninger, 1997). The high photosynthetic yield is essential because despite the crop harvest, a fraction of the biomass should always remain photosynthetically active in order to provide continuous O_2 production, CO_2 removal and water recycling (Stutte et al., 1999). In addition, the suitable crops should respond to specific dietary requirements (i.e. carbohydrate, protein and fat content), providing also vitamins and minerals, while being free from anti-nutritional compounds. Apart from resistance to diseases, another important aspect for an ideal candidate plant for BLSS is radioresistance, useful to mitigate the higher level of ionizing radiation in space. Studies from both ground-based and space-oriented experiments have demonstrated that radioresistance is an important characteristic that makes species less sensitive to the detrimental effects of radiation (Doucet-Chabeaud et al., 2001).

In light of these considerations, it is clear that identifying a species having all the desirable characteristics is very difficult. The needs of space crews (including the complete diet requirements) might be fulfilled more efficiently through a combined cultivation of various species (Hoff et al., 1982; Wheeler et al., 1996).

CONCLUSIONS

Future human exploration of space will be centered on biological life support systems which utilize compartments supported by plants and microorganisms. However, the use of plants as the basis for biological life support systems presents limitations due not only to the lack of knowledge about the impact of new environmental factors on plant growth but also to challenges in technology. Many experiments, both space-oriented and ground-based, have identified several deleterious factors of spaceflight in restraining plant physiological performance, in particular microgravity and ionizing radiation. With regards to radiation, results are often contrasting and not easily comparable because plant response depends on many factors including type and dose of radiation, plant species and plant developmental stage. Generally the damage increases with increasing doses. Furthermore, at same dose, high-LET radiations are more dangerous than low-LET ones in inducing genetic mutations (Shikazono et al., 2002). Even if plant response to ionizing radiation is not yet fully understood, it is clear that some species exhibit an intrinsic radioresistance due to molecular and biochemical mechanisms (Esnault et al., 2010).

At present, although many experiments have been performed, a comprehensive understanding of plant response to irradiation in space is still far off and its achievement is further complicated by other source of perturbations such as microgravity. Within this scenario, further experimentation is needed before the efficient cultivation of higher plants in ecologically closed support systems for life in Space can become a reality.

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