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RESEARCH ARTICLE

Physiological processes in *Phalaenopsis pulcherrima* cultivated in hermetically sealed vessels

Nataliya Zaimenko, Nataliya Didyk *, Iryna Kharytonova, Arsen Viter

M.M. Gryshko National Botanical Garden, National Academy of Sciences of Ukraine, Sadovo-Botanichna str. 1, 01014 Kyiv, Ukraine;
* nataliya_didyk@ukr.net

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Abstract

The hermetic condition is the least studied factor associated with the spaceflights. *Phalaenopsis pulcherrima* is promising for space farming as it can be cultivated in small substrate blocks, and its photosynthetic apparatus is well adapted to elevated CO_2 concentrations and temperatures.

Three-year-old meristematic *P. pulcherrima* plants were planted into plastic (acrylic) vessels filled with fibrous substrate. In control, vessels had an open top. The hermetic conditions were reached by sealing the vessels' covers with a parafilm. Both control and hermetic vessels were placed in a plant growth chamber where test plants were cultivated under controlled conditions of air temperature, illumination, air humidity, and soil moisture. After 6 and 24 months of cultivation, the CO_2 concentration in the hermetic and control vessels was measured, and the physiological characteristics of each test plant, such as the content of macro- and micronutrients, photosynthetic pigments, free amino acids, and content of labile carbohydrates (%) in the leaves of the test-plants were determined.

It was revealed that cultivation of *P. pulcherrima* in hermetic conditions affected its basic physiological processes such as photosynthesis, mineral nutrition, carbohydrates, and amino acid metabolisms. The effect size of this stress factor depended on the duration of exposition period. Long-term cultivation of *P. pulcherrima* under hermetic conditions promoted the accumulation of nonenzymatic antioxidants (viz. chlorophyll *b*, carotenoids, and amino acids), which contributed to the adaptation of this orchid species to oxidative stress caused by hermetic environment.

Keywords: *Phalaenopsis pulcherrima*, hermetic conditions, photosynthetic pigments, assimilates allocation, mineral nutrients, amino acids

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Introduction

Higher plants are irreplaceable components of the bioregenerative life support system (BLSS) required for long-term exploration missions (Brykov et al., 2018). They can provide the astronauts with oxygen and food, reduce CO_2 concentration, contribute to waste recycling and water management, and improve the crew's psychological health. Since the 1960s, there has been a consistent effort to estimate the adaptive potential of various higher plant taxa to spaceflight conditions (Kiss et al., 2019; Nguyen et al., 2023). It has been proved by many experimental studies that higher plants can grow and reproduce in the space environment due to their ability to adapt to space conditions (Zabel et al., 2016; Nguyen et al., 2023). The spaceflight conditions could have long-term physiological effects over multiple generations of the tested plants. The most pronounced influence on higher plants physiology is attributed to altered gravity, space radiation, magnetic fields, and hermetic conditions (Manzano et al., 2022). It was proved that microgravity alters the transport and exchange of gases and liquids between the plant and its surroundings, leading to changes in photosynthesis, uptake and transport of water and mineral nutrients, and allocation of assimilates in the tissues of higher plants (Wolff et al., 2013; Zaimenko et al., 2021). Providing the plant growth facilities with the convectional movement of the atmosphere and moderate light levels helps to restore regular gas exchange, metabolism, and photosynthesis under microgravity and hermetic conditions (Wolff et al., 2013). Experimental simulating shielding from the Earth's magnetic field altered plant gas exchange and metabolism (Wolff et al., 2013).

In space research, the vital state of crops has been evaluated as a rule in terms of their growth, development, productivity, and nutritional value (Oluwafemi & Olubiyi, 2019; Khodadad et al., 2020). However, the continuous cultivation of plants in closed artificial ecosystems requires long-term monitoring of their functional state, the stability of their associations, and their adaptive capacity to the spaceflight environment (Zabel et al., 2016).

Despite a significant amount of studies devoted to adaptive reactions of higher plants to spaceflight conditions, which cover different levels of organization from the molecular to the ecosystem level, a sufficient understanding of the physiological mechanisms of these processes has not yet been achieved (Manzano et al., 2022). Among all the above-mentioned stress factors associated with space, hermetic condition is the less studied factor. Most of the available information on growing plants in hermetic vessels considers the combined effect of hermetic conditions and microgravity. Research publications on the physiological reactions of higher plants to hermetic conditions alone are rather scarce. It is well established that plants perceive the combined effect of microgravity and hermetic environment as a stress factor, which triggers a series of nonspecific as well as specifically targeted adaptive reactions (Manzano et al., 2022). Some of these reactions maintain cell integrity, plant metabolism, photosynthesis, and respiration, while others are similar to the ones triggered by oxidative stress (Zaimenko et al., 2021; Manzano et al., 2022).

Understanding the specific and nonspecific mechanisms of plant adaptation to stress factors related to space travel will make it possible to adjust controlled environmental factors (e.g., light, temperature, CO_2 concentration, humidity, fertilization with mineral nutrients) to reduce the harmful effects of uncontrollable factors (e.g., microgravity, hermetic conditions, limited volume, etc.) of the spacecraft's growth facilities (Brykov et al., 2018). The experimental studies proved that regulating the light intensity could reduce the negative effects of elevated high CO_2 concentrations on wheat seedlings' antioxidant capacity and photosynthetic characteristics under hermetic conditions (Yi et al., 2020). The application of red lamps could induce the adaptation response of plants to microgravity (Manzano et al., 2022).

Another approach implies the selection of the resilient genotypes of higher plants to the space flight environment. To date, only a limited number of plant species, mainly vegetables and grain crops, have been tested for their sensitivity to microgravity and other stress factors caused by spaceflight (Zaimenko, 1999; Brykov et al., 2018; Manzano et al., 2022). The transcriptomic studies carried out on various species of higher plants cultivated in growth chambers on satellites and space stations as well as in ground-based microgravity simulators showed that despite differences in experimental conditions, there have been quite a few processes responsible for adaptation to space flight environment. Among the latter are cell wall remodeling, the ability to cope with oxidative stress, and photosynthesis (Manzano et al., 2022). From this perspective, plant species capable to grow and reproduce in a limited substrate volume, having the ability to maintain a high photosynthetic rate under specific conditions of a spaceflight, and strong antioxidant defense systems are among promising candidates for space farming.

Phalaenopsis pulcherrima (Lindl.) J.J. Sm., is an epiphytic orchid, which could be cultivated in small substrate blocks. Due to crassulacean acid metabolism (CAM) its photosynthetic apparatus is well adapted to elevated CO_2 concentrations and temperatures (Song et al., 2019). Therefore, we suggested the possible good adaptive potential of this species for the spaceflight environment. Our study aimed to analyze the effect of hermetic conditions on physiological processes such as photosynthesis, mineral nutrition, carbohydrates, and amino acid accumulation in leaves of *P. pulcherrima*.

Material and methods

The experiments were conducted at the Department of Allelopathy of the M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine (Kyiv, Ukraine). Three-years-old meristematic *P. pulcherrima* plants were planted into plastic (acrylic) vessels filled with fibrous substrate, consisting of a mixture of basalt and polyacrylonitrile fibers in a ratio of 1:1. In control, vessels had an open top part. While hermetic conditions were reached by sealing the vessel's cover with a parafilm. There were ten vessels with open tops and 20 hermetically sealed vessels. Both control and hermetic vessels were placed in a plant growth chamber. Test plants were cultivated under controlled conditions of air temperature (22–24° C), illumination (1700 lux), air humidity (80–83%), and soil moisture of 70–75% of the soil field capacity. The duration of the experiment was 24 months, from January 2020 to January 2022. After six months of cultivation, ten out of 20 hermetically sealed vessels were opened, and the first sampling was made. At the end of the experiment (after 24 months of cultivation), the remaining ten hermetically sealed vessels were opened, and the second (last) sampling was made. The sampling procedure included measurement of CO_2 concentration inside the vessels and the physiological characteristics of each test plant, such as the content of macro- and micronutrients, photosynthetic pigments, free amino acids, and the content of labile carbohydrates (%) in the leaves of the test-plants.

The CO_2 contents in the hermetically-sealed vessels were measured using S157-P (Qubit Systems, Canada, 2019) CO_2-analyzer with gas pump (0–2000 ppm) and temperature control.

Photosynthetic pigments (chlorophylls *a* and *b*, and carotenoids) were extracted from the leaves (fully expanded, exposed) of the tested plants with dimethylsulfoxide (DMSO) following Hiscox & Israelstam (1979). The optical density was measured with a SPECORD 200 (Analytik Jena, Germany, 2003) at 665 nm for chlorophyll *a*, 649 nm for chlorophyll *b*, and 480 nm for carotenoids.

The macro- and micronutrients in the leaves were determined using an inductively coupled plasma spectrometer iCAP 6300 DUO (Thermo Fisher Scientific, USA, 2006).

The qualitative and quantitative content of free amino acids was determined using an amino acid analyzer Hitachi 835 (Japan) following Ovchinnikov (1974).

The carbohydrates were extracted from the freshly collected leaves with hot distilled water. The extracts were purified from proteins and pigments. The sucrose was hydrolyzed during heating in the presence of hydrochloric acid to glucose and fructose. Afterward, the quantitative amount of carbohydrates was determined spectrophotometrically using a color reaction with Fehling's reagent (Serdyuk et al., 2020).

The data was subjected to the one-way analysis of variance (ANOVA) applied after testing the homogeneity of error variances using Levene's mean-based F-test procedure with modifications outlined by Sharma & Golam Kibria (2013). The statistical analysis was performed using Statistica 10.0 software (Stat Soft. Inc., Tulsa, USA, 2011). P-values of less than 0.05 were considered statistically significant.

Results

Measurement of CO_2 concentrations showed that in the room outside vessels, the CO_2 level was 420–430 ppmV. In the open-top vessels, it ranged from 405 to 413 ppmV. In the hermetically-sealed vessels, CO_2 concentration reached 275–280 ppmV at the first sampling procedure (after six months of exposition) and 312–318 ppmV at the second sampling procedure (after 24 months of exposition).

Despite drastic difference in CO_2 concentrations between open-top and hermetically sealed vessels, after six months of cultivation, the content of photosynthetic pigments (chlorophylls *a* and *b*, and carotenoids) in the leaves of the exposed and control test plants displayed no significant differences. However, after 24 months of cultivation, the concentrations of the mentioned photosynthetic pigments in the leaves of the test plants cultivated under hermetic conditions were 1.8- and 2.0-fold as much as in control (Table 1).

After a six-month exposition of test plants to hermetic conditions, the content of monosaccharides and disaccharides decreased insignificantly, while starch content increased by 10 %. More prolonged cultivation of plants in hermetic conditions revealed a sharper fluctuation of these indices: a 1.5–1.8-fold decrease in the concentration of mono- and disugars and a 2.3-fold increase in starch content (Table 2).

The obtained dependence can be explained by changes in the activity of phosphorylation reactions in the test plant tissues, which occur against the background of a higher content of chlorophylls *a* and *b* in leaves after 24 months of cultivation under hermetic conditions.

An increase in nitrogen, potassium, and manganese content in the foliar tissues of *P. pulcherrima* under hermetic conditions was observed compared to the control (Table 3). The effect size positively correlated with the duration of the exposition period.

Noticeable changes in amino acid composition were observed in the leaves *P. pulcherrima* cultivated under hermetic conditions: the amount of aspartic, glutamic acids, and alanine reduced drastically, while the content of histidine, arginine, tyrosine, and phenylalanine increased (Table 4). As a rule, the size of the effect positively correlated with the duration of the exposition period.

Table 1. The effect of hermetic conditions on the content of photosynthetic pigments (mg / 100 g of fresh weight) in the leaves of *Phalaenopsis pulcherrima*.

Exposition time	Treatment	Chlorophyll				Carotenoids	Chlorophylls $(a+b)$ / carotenoids
		a	*b*	$a+b$	a/b		
6 months	control	22.1±1.7	9.9±0.5	31.9	3.3	12.0±0.9	2.66
	hermetic conditions	22.7±1.8	10.2±0.6	32.9	2.2	12.5±0.8	2.63
24 months	control	10.3±0.7	3.5±0.2	13.8	2.9	5.7±0.3	2.42
	hermetic conditions	19.2±1.3	7.1±0.5	26.3	2.7	10.5±0.9	2.51

Table 2. The effect of hermetic conditions on carbohydrates content (%) in the leaves of *Phalaenopsis pulcherrima* after 6 and 24 months of cultivation.

Exposition time	Treatment	Chlorophyll				Carotenoids	Chlorophylls $(a+b)$ / carotenoids
		a	*b*	$a+b$	a/b		
6 months	control	22.1±1.7	9.9±0.5	31.9	3.3	12.0±0.9	2.66
	hermetic conditions	22.7±1.8	10.2±0.6	32.9	2.2	12.5±0.8	2.63
24 months	control	10.3±0.7	3.5±0.2	13.8	2.9	5.7±0.3	2.42
	hermetic conditions	19.2±1.3	7.1±0.5	26.3	2.7	10.5±0.9	2.51

Discussion

Hermetic conditions exclude gas exchange and air movement inside vessels, which, in turn, affect temperature and air humidity conditions and create prerequisites for developing unfavorable microflora in the rhizosphere and phylloplane. Unfortunately, most studies in space biology are devoted to the combined effect of the two factors, viz. hermetic conditions and clinorotating, considering the last factor as the main acting factor. In our opinion, hermetic condition is no less important for the physiological processes in test plants than microgravity. Measuring the level of carbon dioxide inside sealed and open vessels showed that in the latter, it was 47 % higher than in the former after six months of exposure and only 30 % higher after 24 months of exposure. This indicates the formation of a complementary microbiocenosis, which consumes the oxygen produced by plants and restores the reserves of carbon dioxide necessary for the normal course of photosynthesis in the test plants.

The results of the analysis of the content of photosynthetic pigments in the leaves confirm this conclusion. Thus, in experimental plants, after six months of cultivation under hermetic conditions, the content of photosynthetic pigments

Table 3. The effect of hermetic conditions on the content of macro- (%) and micronutrients (mg / L) in the leaves of *Phalaenopsis pulcherrima*.

Nutrient	Exposition time			
	6 months		24 months	
	control	hermetic conditions	control	hermetic conditions
N, %	3.2 ± 0.33	3.44 ± 0.07	3.0 ± 0.06	3.84 ± 0.48
P, %	0.59 ± 0.08	0.47 ± 0.04	0.54 ± 0.09	0.42 ± 0.01
K, %	2.73 ± 0.15	4.4 ± 0.55	2.3 ± 0.12	4.9 ± 0.68
Ca, %	1.19 ± 0.12	0.94 ± 0.05	1.10 ± 0.24	0.87 ± 0.01
Mg, %	0.30 ± 0.07	0.26 ± 0.02	0.27 ± 0.04	0.21 ± 0.01
Fe, mg / L	121.72 ± 3.57	105.4 ± 5.47	108.4 ± 4.36	93.9 ± 3.68
Mn, mg / L	49.8 ± 2.29	55.3 ± 2.23	53.8 ± 2.43	68.7 ± 2.85
Cu, mg / L	19.2 ± 1.06	15.1 ± 1.54	18.6 ± 1.37	14.3 ± 1.13
Zn, mg / L	39.4 ± 4.15	33.6 ± 2.22	39.5 ± 1.12	32.7 ± 2.12

Table 4. The effect of hermetic conditions on amino acid composition (μg / 100 g of fresh weight) in the leaves of *Phalaenopsis pulcherrima*.

Amino acid	Exposition time			
	6 months		24 months	
	control	hermetic conditions	control	hermetic conditions
Aspartic acid	1.39 ± 0.03	0.15 ± 0.01	0.21 ± 0.01	0
Glutamic acid	5.27 ± 0.24	1.84 ± 0.44	1.87 ± 0.02	0.33 ± 0.01
Alanine	1.16 ± 0.18	0.12 ± 0.01	0.12 ± 0.01	0
Histidine	0.27 ± 0.02	0.44 ± 0.01	0.08 ± 0.01	0.39 ± 0.01
Arginine	9.15 ± 0.23	13.27 ± 1.14	8.64 ± 0.22	13.04 ± 0.01
Tyrosine	0.44 ± 0.01	0.68 ± 0.01	0.09 ± 0.01	0.51 ± 0.01
Phenylalanine	0.97 ± 0.01	1.03 ± 0.04	0.21 ± 0.01	0.74 ± 0.01

remained practically unchanged, but after 24 months, their concentration increased sharply (see Table 1).

The increase in the intensity of photosynthesis was positively correlated with the increase in biosynthetic processes, particularly starch biosynthesis and the activation of nitrogen metabolism. This was evidenced by the increase in the amount of amino acids (histidine, arginine, tyrosine, and phenylalanine) in the leaves of *P. pulcherrima*. On the other hand, the accumulation of arginine, histidine, and phenylalanine in the leaves of the test plants may indicate a disorder of growth processes and suppression of oxidative phosphorylation.

It should also be noted that a sharp increase in the content of carotenoids and chlorophyll *b* during long-term (for 24 months) cultivation of test plants in sealed conditions, while the ratio of chlorophyll $a+b$ / carotenoids, which is considered a marker of stress in higher plants, did not reveal statistically significant changes. Carotenoids and chlorophyll *b* are efficient antioxidant scavengers essential in protecting photosynthetic systems against photooxidative processes (McElroy & Kopsell, 2009). Thus, the observed increase in chlorophylls and carotenoids contents and stable chlorophylls / carotenoids ratio in the leaves of *P. pulcherrima* exposed to prolong hermetic conditions indicate activation of antioxidant defense systems as a part of nonspecific adaptive responses to unfavorable environmental factors.

Prolonged cultivation of higher plants in hermetic conditions is known to cause oxidative stress, which could lead to the inhibition of basic physiological processes such as mineral nutrition, metabolism of amino acids, protein biosynthesis, and photosynthesis (Zaimenko et al., 2021). Our previous studies revealed increases in the contents of phosphorus, calcium, potassium, and manganese in the vegetative organs of terrestrial orchids after three months of clinorotation in hermetically sealed vessels (Zaimenko, 1999). At the same time, the concentration of magnesium in the tissues of all tested plants decreased, while the iron content remained unchanged. Exposition to hermetic conditions in combination with clinorotation (for six and 12 months) resulted in a sharp decrease in the levels of macronutrients in the leaves and aerial roots of treated plants (Cherevchenko et al., 2000). However, prolonging clinorotation to 24 months could induce some adaptations of mineral nutrition processes, resulting in stimulation of specific macro- and micronutrients (i.e., K, N, Fe, Mn, and Zn) accumulation.

In the present study, it was also established that hermetic conditions alone (without clinorotation) could result in noticeable changes in the accumulation of some macro- and micronutrients in *P. pulcherrima* leaves, which depended on the exposition period. In particular, the nitrogen, potassium, and manganese content in the leaves increased under hermetic conditions, suggesting intensifying photosynthetic and growth functions. The increase in the content of protective antioxidants (chlorophyll *b*, carotenoids, and certain amino acids) indicated the activation of protective mechanisms preventing the adverse effects of oxidative stress caused by a hermetic environment.

Conclusions

To sum up, this research revealed a significant influence of the hermetic conditions on the basic physiological processes in *P. pulcherrima*. In particular, cultivation for 24 months in a hermetic vessels contributed to an increase in the content of photosynthetic pigments (chlorophylls *a* and *b*, and carotenoids), the accumulation of starch in leaves, and the content of some amino acids (histidine, arginine, tyrosine, and phenylalanine) and macro- and microelements (nitrogen, potassium, and manganese). The intensification of photosynthesis and biosynthetic processes indicates the improvement of growth and productivity of *P. pulcherrima* after long-term cultivation under hermetic conditions. The increase in the content of protective antioxidants (chlorophyll *b*, carotenoids, and certain amino acids) indicates the activation of protective mechanisms that prevent the manifestation of the negative effects of oxidative stress.

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Фізіологічні процеси *Phalaenopsis pulcherrima* за умов вирощування у гермооб'ємі

Наталія Заіменко, Наталія Дідик *, Ірина Харитонова, Арсен Вітер

Національний ботанічний сад ім. М.М. Гришка Національної академії наук України, вул. Садово-Ботанічна, 1, 01014 Київ, Україна; * nataliya_didyk@ukr.net

Замкнене герметичне середовище є найменш дослідженим фактором серед тих, що пов'язані з космічними польотами. *Phalaenopsis pulcherrima* є перспективним для космічного рослинництва, оскільки цю рослину можна культивувати в невеликих блоках субстрату, а її фотосинтетичний апарат добре пристосований до підвищених концентрацій CO_2 і температур.

Трирічні меристематичні рослини *P. pulcherrima* висаджували у пластикові (акрилові) посудини, наповнені волокнистим субстратом. У контрольних посудинах верхню частину лишали відкритою. У гермооб'ємах посудини закривали кришками, які заклеювали парафільмом. Контрольні та герметичні посудини поміщали в камеру для росту рослин, де дослідні рослини культивували за контрольованих умов температури повітря, освітлення, вологості повітря та ґрунту. Через 6 і 24 місяці культивування вимірювали концентрацію CO_2 в герметичних і контрольних посудинах і визначали фізіологічні характеристики для кожної дослідної рослини, такі як вміст макро- і мікроелементів, фотосинтетичних пігментів, вільних амінокислот і вміст лабільних вуглеводів (%) у листках дослідних рослин.

Виявлено, що культивування P. pulcherrima в гермооб'ємах впливає на основні фізіологічні процеси, такі як фотосинтез, мінеральне живлення, вуглеводний та амінокислотний обміни. Величина впливу цього стрес-фактора залежала від тривалості експозиційного періоду. Тривале культивування *P. pulcherrima* за герметичних умов сприяло накопиченню неферментативних антиоксидантів (а саме хлорофілу *b*, каротиноїдів та амінокислот), що сприяло адаптації цього виду орхідей до окислювального стресу, спричиненого герметичним середовищем.

Ключові слова: *Phalaenopsis pulcherrima*, герметичні умови, фотосинтетичні пігменти, розподіл асимілятів, мінеральні поживні речовини, амінокислоти