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PHOTOSYSTEM II OF *KALANHOE DAIGREMONTIANA* SHELTERED BY BACTERIAL CONSORTIUM UNDER MARS-LIKE CONDITIONS

The maximum quantum yield of the photosystem II (F_v/F_m) and other parameters were measured in situ fluorometrically in Kalanhoe daigremontiana under simulated martian-like conditions (low atmospheric pressure, high CO_2 concentration, and UV irradiation of near-martian surface spectrum) in a Mars simulation chamber. We found no differences in F_v/F_m at hypobaria (10 mbar) and ambient pressure, as well as between treated with bacteria and control plants. However, a difference was seen between variants of kalanchoe exposed to CO_2 of a high concentration (95 %). The maximum quantum yield was higher in presence of bacteria, although F_v/F_m decreased in both variants (inoculated and noninoculated) under a high CO_2 concentration in the atmosphere, in contrast to low-pressure conditions. The F_v/F_m values for kalanchoe plants grown in martian regolith simulant or in earth soil under simulated martian conditions were lower than in the case of normal earth conditions. The positive effect of bacterial inoculation on plant accommodation to adverse simulated martian conditions was more pronounced for the kalanchoe plants grown in martian regolith simulant and depended on bacterial species, especially, under rigorous conditions of the joint action of low pressure, high content of CO_2, and UV irradiation. For K. daigremontiana plants treated with Klebsiella oxytoca, Methylobacterium sp., the photochemical quenching coefficient qP and Stern-Volmer non-photochemical quenching coefficient NPQ were lower during diurnal and nocturnal periods as compared to the nontreated plants. This revealed some protection for PSII. The majority of bacterial strains and their consortium demonstrated protective effect in K. daigremontiana under abiotic stressors and after the impact of stressors, as distinct from arbuscular mycorrhiza fungi.

INTRODUCTION

Efficient plant growth in extraterrestrial greenhouses under low availability of nutrients and permanent resistance to stressful conditions (changed gravity and atmosphere composition, irradiation, etc) will be a vital problem in outposts. The ability of microorganisms, including resident endophytes, to confer stress tolerance to plants may provide a novel low cost strategy for mitigating the impacts of the environmental conditions outside the Earth in consistence with the concept of using microbial technology for plant growing/protosoil formation for lunar/martian greenhouses [13, 14, 19, 28].

Numerous studies on plant growth under low gravity led the to conclusion that plants tolerate low atmospheric pressure [6, 22, 25]. However, the response to hypobaria results in considerable changes in a gene expression pattern, including in genes involved in tolerance to dessication, indicating combating stress [22]. A water-deficit stress may inhibit plant growth under hypobaria. It is well known that CAM (Crassulation Acid Metabolism) plants normaly found in arid and semi-arid habitats possess a high water-use efficiency to adapt to water stress [26]. CAM-photosynthesis provides strong protection from photoinhibition during periods of high irradiance at midday by establishing a high internal CO_2 concentration as a result of organic acid decarboxylation in the leaves that can be used for further photochemical work [27]. CAM species show an average increase in biomass productivity

of 35 % in response to a doubled atmospheric CO_2 concentration. Increases in net daily CO_2 uptake by CAM plants under elevated atmospheric CO_2 concentrations reflect increases in both Rubisco-mediated daytime CO_2 uptake and phosphoenolpyruvate carboxylase mediated night-time CO_2 uptake, the latter resulting in increased nocturnal malate accumulation [9]. The performance of the CAM can be estimated measuring photosystem II (PSII) fluorescence with instruments.

The relationship between chlorophyll fluorescence and the overall process of photosynthesis are rather complicated, but it should be noted that the registration process of chlorophyll fluorescence of green leaf plants can be used for analysis of plants under the influence of stress in laboratory or field [17]. Chlorophyll fluorescence has proven to be a useful, non-invasive tool for the study of different aspects of photosynthesis, and for the quantification of any stress impact in plants [16]. Because a single leaf spot may not be representative for the whole leaf, two-dimensional chlorophyll fluorescence imaging instruments have been developed [4, 5]. Measuring the chlorophyll fluorescence emission with a pulse amplitude-modulated fluorometer showed that the plant growth-promoting soil bacterium *Bacillus subtilis* GB03 augments photosynthetic capacity by increasing photosynthetic efficiency and chlorophyll content in arabidopsis [29].

The main objectives of this study were:

(1) to evaluate photosynthetic activity (F_v/F_m) and other parameters measured *in situ* in kalanchoe leaves when exposed to martian-like conditions;

(2) to find out protective effect of rationally selected bacterial species and arbuscular mycorrhiza fungi on the kalanchoe plant grown in martian regolith simulant under near-Mars simulated conditions.

MATERIALS AND METHODS

The Experimental Mars simulation chamber (MSC) HUMULAB (DLR Berlin) was used for short-term experiments on *in situ* measurement of PA and other photochemical parameters with help of the MINI-PAM fiberoptical mounted in MSC. Technical parameters of MSC and a gas-mixing system, including mass flow controllers, are described well in [7].

Plant material and growth conditions. Five-month-old plants *Kalanchoe daigramontiana* Hamet & Perr (possessing 3-4 pairs of leaves) were grown in commercially available soil in plastic pots ($V = 200$ cm^3) under controlled conditions (air temperature 25 °C, light irradiance 57.0 μmol quanta $m^{-2}s^{-1}$ of the photosynthetically active radiation (PAR), humidity 70 %) with a 14/7 h day/night period. Martian regolith simulant (MRS) was purchased from Naturkundemuseum (Berlin). One-week before exposure to simulated martian conditions in MSC at the HUMULAB kalanchoe plants were inoculated, when needed, with either consortium of all bacterial strains or with any bacterial culture, separately. For this roots of individual plants were drown into diluted (with a sterile water) overnight bacterial cultures at titre of 10^6 colony-forming units per ml within 30 min. One month before planting in MRS kalanchoe plants grew in soil inoculated with arbuscular mycorrhizal fungi, when needed.

Inoculated plants were grown in the commercial soil, and three days before exposure to stressors the plants replanted in MRS, when needed. Plant samples were placed on a tiny stand within MSC. Plants were irradiated with LED light in an intensity of about 131.67 μmol quanta $m^{-2}s^{-1}$ of PAR or subjected to irradiation of UV Xenon lamp with an optical collimation 10–150 W (DLR Berlin). 100 % atmospheric humidity and temperature 25 °C within a night-day period (8/16 h) were inside MSC.

Microbial species and culturing. Klebsiella oxytoca was grown in LB [21], *Paenibacillus* sp. in MZ [15], *Pseudomonas fluorescens.* in King's B [12], *Methylobacterium* sp. in M9 medium [21] with 1 % methanol during 18—24 hours at 28 °C. Arbuscular mycorrhizal (AM) fungi *Glomus intraradices* GV (kindly provided by H. Bothe, Cologne University) were accumulated in *Tagetes patula* L. roots, and the propagules were used in the experimental soils (10 %/v). Internal root colonization in kalanchoe was tested with standard lactophenol method [20].

Chlorophyll fluorescence analyses. Photosynthetic activity and other parameters of the PSII under simulated martian conditions were measured with the use of the pulse amplitude-modulated fluorometer MINI-PAM (Heinz WALZ GmbH, Effeltrich, Germany). To reach maximal fluorescence yield under modeled conditions, a light was switched off inside the MSC for 1 h within simulated "martian" day. The

ratio F_v/F_m ($F_v = F_m - F_0$) was used to estimate the potential quantum yield of PSII photochemistry of *K. daigremontiana* plants at night period in MSC. F_0 is minimal level of fluorescence measured on dark-adapted leaves (in the dark-adapted state at night-time in MSC). The maximal level of fluorescence in the dark-adapted state (F_m) was measured by a 1-s pulse of saturating light. The parameter Φ_{PSII} represents the actual quantum yield of PSII photochemistry for light-acclimated samples under illumination and was calculated $\Phi_{PSII} = (F_m' - F)/F_m'$ where F is the level of fluorescence just before the pulse of saturating light and F_m' is maximal light-adapted fluorescence was applied. The following parameters were calculated: coefficient of photochemical quenching $qP = (F_m' - F)/(F_m' - F_0')$; and quantum efficiency of non-photochemical dissipation in PSII complexes NPQ = $(F_m - F_m')/ F_m'$. Outside the model Mars-like chamber we used chlorophyll fluorometer IMAGING-PAM, M-series (Heinz WALZ GmbH, Effeltrich, Germany) for measurement of PA (F_v/F_m) in leaves before and after exposure to simulated martian conditions. Before and after exposure to MSC under martian simulated conditions plants were adapted in a dark chamber within 1 h to gain maximal yield with the IMAGING-PAM instrument.

Statistical tests. Statistical tests of the significance of differences between means from two-three experiments were based on Student's *t*-test ($p < 0.05$).

RESULTS AND DISCUSSION

Photosynthetic activity of K. daigremontiana plantlets under model Mars-like conditions. Photosynthetic activity is an indicator of functionality of photosystem under simulated Mars-like parameters [8]. We studied the effect of simulated martian conditions on the PS II of *K. daigremontiana* five-month-old plants, as well as the potency of microorganisms to alleviate stress in plants. Earlier we showed that two defined bacterial strains promoting plant growth protected plants after acute irradiation with γ-quanta (^{60}Co) [2]. Actually, the reduction of F_v/F_m is based on damage of the PS II as a result of stress [23], and priming plants with microbes could rise effectivity of defensive system to withstand stresses or may lead either to direct interaction with the photosystem II, or change its regulation indirectly.

In initial experiments five days before exposure to Mars-like conditions the plants were inoculated with the bacterial consortium composed with *K. oxytoca* and *Paenibacillus* sp. and grew in local soil. Directly before experiment samples received 1 ml water and were fixed in MSC under fiberoptics of MINI-PAM fluorometer. The levels of F_v/F_m under impact of independent stress factors or their combination were measured with this device. The first experiment involved the simulation of low pressures reached step-by-step 10 mbar (near-martian pressure) during 24 hs, beginning from 1013 mbar (earth pressure) (Fig. 1a). There was no significant effect of a pressure drop from normal to the martian surface conditions on the photosynthetic activity of kalanchoe plants. These results are in agreement with recent data of Tang et al. [25] on photosynthetic rate calculated for lettuce grown under low pressure. F_v/F_m of other photosynthesizing organism — lichen — demonstrated the same tendency under low atmospheric pressure [7]. The plant treated by bacteria had higher activity of the PS II at daytime then in the night.

Next experiments involved step-by-step increasing CO_2 from 0.03 % (earth conditions) to 95 % CO_2 (near-martian surface conditions) (Fig. 1b) and combination of low preassure and CO_2 concentration at 45 % or 95 % under LED light (Fig. 1c). At high CO_2 concentration quantum yield of the *K. daigremontiana* PS II decreased sharply to 0.1 e.u. in noninoculated plantlets and to 0.25 in treated ones. The same tendency observed in F_v/F_m value of lichens in experiments conducted in MSC by de Vera and coauthors [7]. The application of high CO_2 concentration resulted in protection of PS II by the bacterial consortium. Under cooperative action of both stressors F_v/F_m was approximately 0.65; this value was a 6-fold higher than when only high CO_2 concentration applied and comparable with yield under low pressure. We can assume that the negative impact of high content of CO_2 in atmosphere balanced with low atmospheric pressure. Under these conditions, when PSII was not impaired heavily, protective effect given by bacteria was not so pronounced during a daytime, as compared separate action of CO_2 and low pressure. Our results have proven data of Paul and others [22] that hypoxia and hypobaria to be different stressors, effecting different plant systems. Bacterial impact on plant defensive system appeared to be

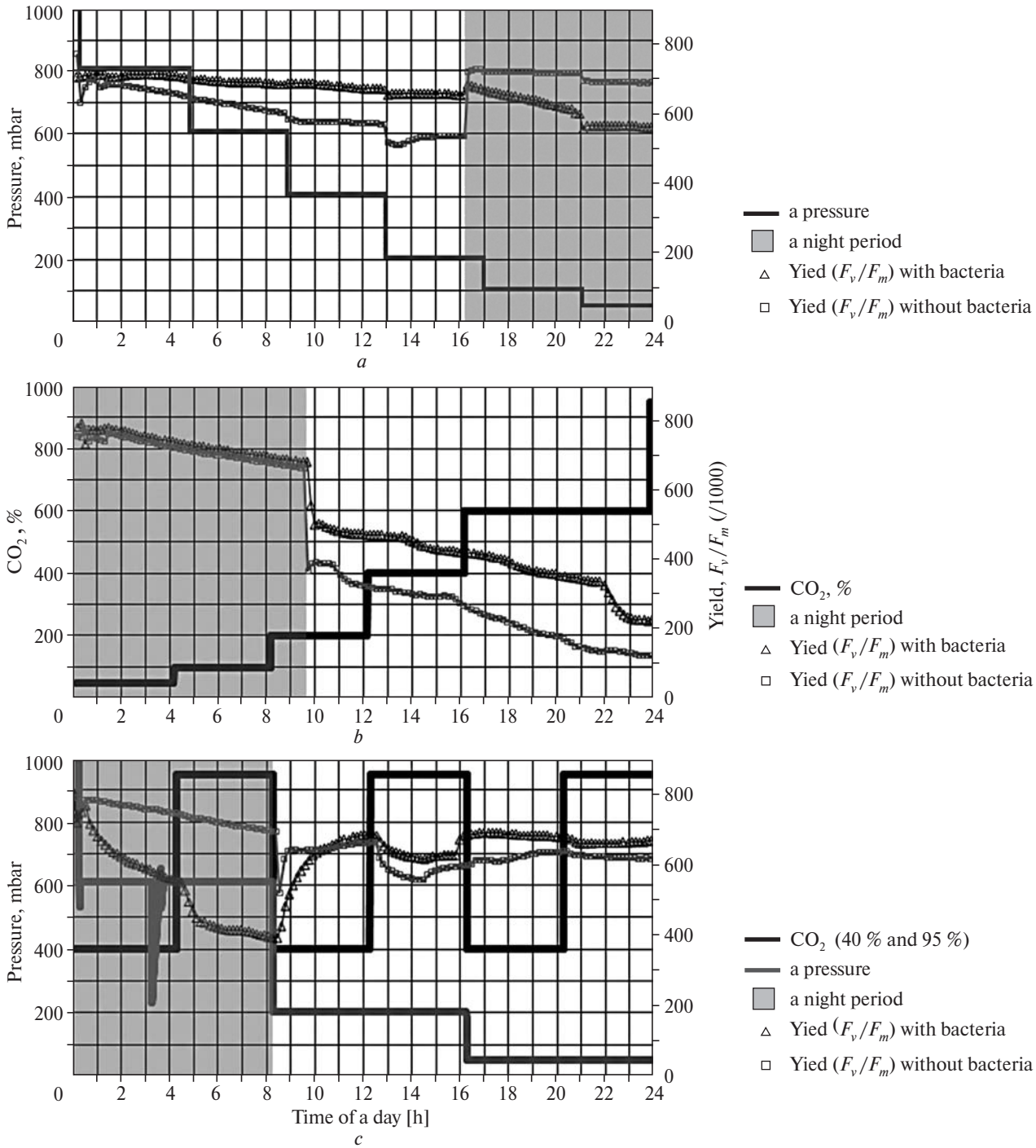

Fig. 1. Photosynthetic activity (F_v/F_m) of the *Kalanchoe daigremontiana* plants grown in the earth soil under low pressure (*a*) or high CO_2 concentration (*b*), as well as in combination of low pressure and high CO_2 concentration (*c*). Kalanchoe plants inoculated with a dual bacterial consortium of *Paenibacillus* sp. and *Klebsiella oxytoca,* when needed

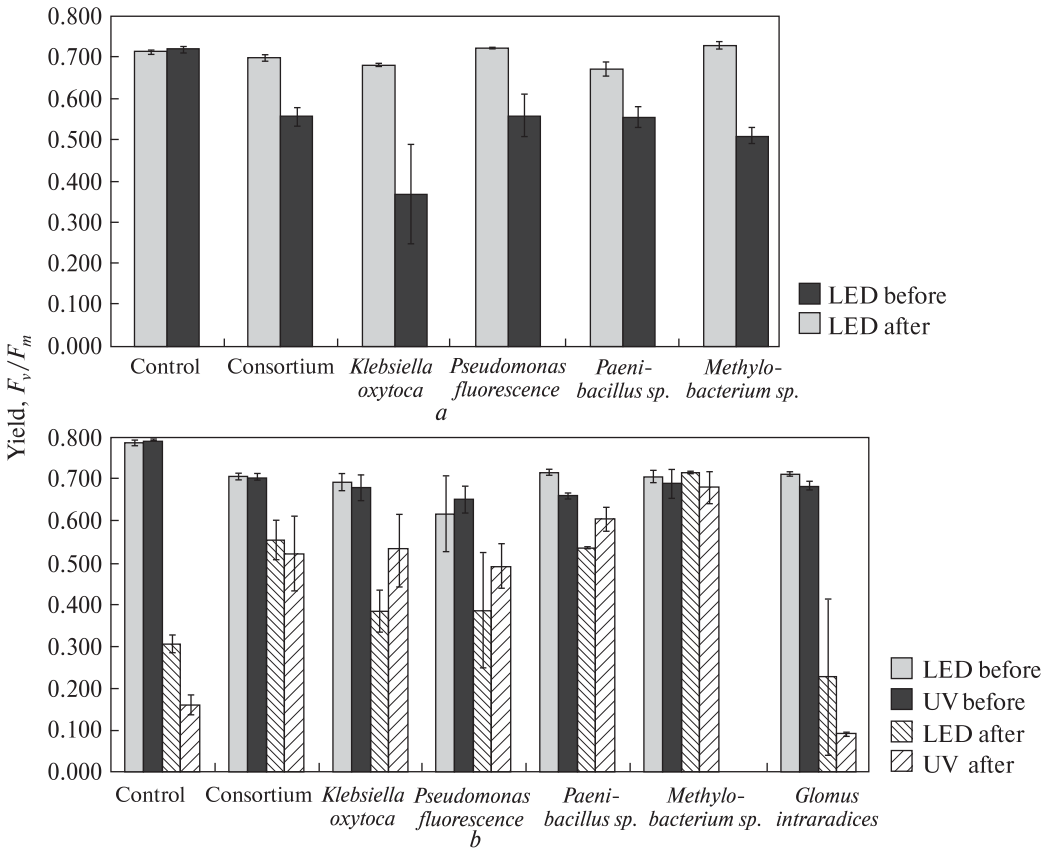

Fig. 2. Photosynthetic activity (F_v/F_m) before and after martian conditions of the *Kalanchoe daigremontiana* plants grown in the earth soil (*a*) and Mars-simulated soil (*b*). *Error bars* indicate the SD of the means ($n = 2$ for *a* and $n = 3$ for *b*). Kalanchoe plants treated with various bacterial strains. Plants lighted with LED (PAR) and UV irradiated during a day-night period inside Mars simulation chamber

different under these stressors, and there was a trend to decreasing the maximum quantum yield in the night in inoculated kalanchoe variants where low pressure was simulated (Fig. 1a, c).

Contribution of individual bacterial strains in protection of kalanchoe (LED). It is well known that bacteria capable to influence plant physiology under normal conditions; for example, *B. subtilis* enhances photosynthetic activity in arabidopsis plants [29]. Our objective was to find out what model bacterial species makes a positive contribution to the protection of kalanchoe under/after abiotic stresses in order to know more about mechanisms of plant protection mediated by microbes. The maximum yield in dark-adapted plants grown in the fertile soil recorded with the IMAGING-PAM instrument before exposition to martian-like conditions and after 24 hours. On Fig. 2a protective effects of *Paenibacillus* sp., *Pseudomonas fluorescens, Methylobacterium* sp. and *K. oxytoca,* as well as consortium of all bacterial strains used are seen under a partialy simulated martian conditions, but not of AM-fungi. The latter was surprising, because it was expected that AM had a potency to improve a water supply in the plant and to alleviate so far a water-deficit stress in kalanchoe under low atmospheric pressure. In the low-pressure environment water is pulled out through the leaves very quickly, and so extra water is needed to replenish it. Probably, kalanchoe does not loose water so quickly due to CAM-type of photosynthesis, and a role of AM fungi in such a case (a short-term experiment) was overestimated.

Contribution of individual bacterial strains in protection of kalanchoe (UV). In next experiments kalanch-

oe plants were exposed to more rigorous conditions: UV irradiation of near-Mars spectrum and growth in mineral soil stimulant (MRS) of low bioavailability were added to low pressure and high concentration of CO_2. Before exposure to MSC *K. daigremontiana* plants were inoculated with different bacterial species, when needed, or used kalanchoe specimens colonized with AM fungi for independent measurements. Both treated with microbes and control plants were grown during three days under low availability of plant-essential nutrients. In MSC one half samples were exposed to LED light and others were under UV irradiation: both sets of specimens mounted inside the chamber during a day-night period. The F_v/F_m value in kalanchoe plants exposed to mentioned conditions declined approximately five-times as compared to normal conditions, and under UV it was 2-time lower then under LED (Fig. 2b). Inoculation of kalanchoe plants with *K. oxytoca, Paenibacillus* sp., *P. fluorescens,* and *Methylobacterium* sp. resulted in improving F_v/F_m value after simulated martian conditions. The yield in kalanchoe plants inoculated with *Methylobacterium* sp. practically did not change after exposure to low pressure, high concentration of CO_2, UV and deficit of nutrients. AM fungi had no effect on kalanchoe F_v/F_m under stressful conditions.

Maximum quantum efficiency of PSII photochemistry and other parameters of kalanchoe under stress. Using the MINI-PAM fiberoptical mounted in the Mars-like camera we were able to measure maximal quantum yield of PS II and other parameters such as photochemical quenching coefficient (*qP*), Stern–Volmer non-photochemical quenching (*NPQ*) in kalanchoe plants grown in MRS under simulated Mars-like conditions. Published results demonstrate that with the increase of light intensity the quantum yield of the PS II decreases and the *NPQ*-value was higher at diurnal than at nocturnal period [11] indicating photoinhibition effect [18]. F_v/F_m reflects the maximum efficiency at which light absorbed by light-harvesting antennae of PSII is converted to chemical energy and decrease the values indicating in particular the phenomenon of inhibition when the plant has been exposed to stress, and in water-stressed *K. daigremontiana* leaves F_v'/F_m' decreased, and *NPQ* increased [10]. High value-*NPQ* may represent a mechanism of dissipating excess of excitation energy and down-regulate photosynthetic electron transport so that production of ATP and NADPH would match the decreased CO_2 assimilation. Increase of *qP* indicated a better production of ATP and NADPH and incorporation of the latter in antioxidant and CO_2-fixing systems of plant [3].

In situ chlorophyll fluorescence measurement under stressful low pressure and high concentration of CO_2 in the experimental camera showed positive impact of *Methylobacterium* sp. treatment on kalanchoe plants expressed in higher F_v/F_m value at a day-time (Fig. 3a). In contrast, treatment plants with *K. oxytoca* led to decrease of F_v/F_m value under the same conditions. However, treatment with *K. oxytoca* resulted in significantly higher the maximum quantum yield in kalanchoe leaves compared to untreated plants under high concentration of CO_2 in atmosphere and normal pressure at a day-time. In both cases effect of bacteria was associated with influence on the photosynthetic reactions associated with PSII.

To get detailed information of participation of endophytes in photorespiratory process in kalanchoe under stresses, some parameters of PSII were measured within the experimental facility *in situ*. The photochemical quenching coefficient (*qP*) in untreated plants outside of the facility was the highest, especially in lighted with LED plants (Fig. 3 b). This supposes the intense flow of electrons through the electron transport chain of PSII and synthesis of ATP and NADPH. These processes consume relatively less ATP than does photosynthesis.

On the other side, increase of *qP* indicates a better production of ATP and NADPH and incorporation of the latter in antioxidant and CO_2-fixing systems of the plant. In MSC the treated with *Methylobacterium* sp. and *K. oxytoca* specimens had lower *qP* within both diurnal and nocturnal periods then in untreated plants. These values approached to control's ones under normal conditions (Fig. 3 b). In normal conditions the beet plants inoculated with endophytes exhibited higher value of *qP* than noninoculated plants [24]. In case of untreated kalanchoe sharp increase of *qP* was a reaction of the kalanchoe PSII on the stress and a loss of effective energy needed for a defensive reaction. Given that the light in the chamber was identical and constant flux quanta was constant (there was no photoinhibition effect of light) under

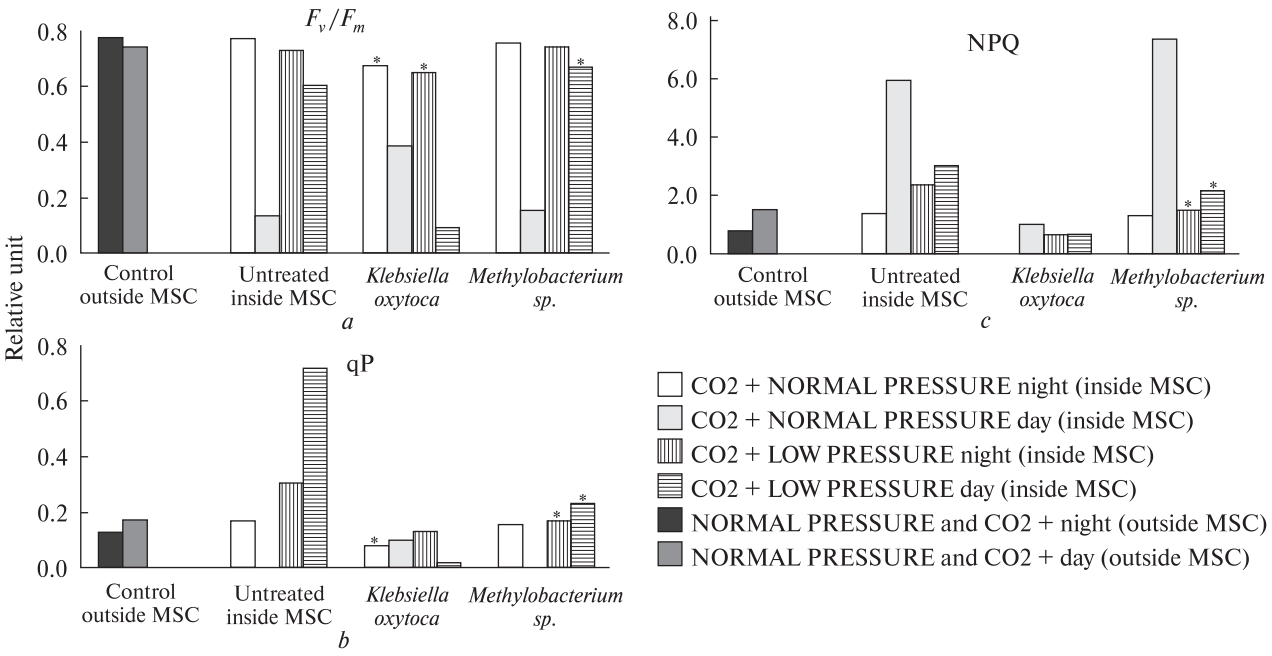

Fig. 3. The maximum quantum yield (F_v/F_m) at nocturnal period and effective quantum yield Φ_{PSII} at daytime period (*a*), photochemical quenching coefficient (*qP*) (*b*), Stern-Volmer non-photochemical quenching (*NPQ*) (*c*) under simulated martian conditions (low atmosphere pressure or ambient pressure, high concentration 95 % of CO_2, low availability of nutrients in the susbstrate). Kalanchoe plants were treated with *Klebsiella oxytoca* or *Methylobacterium* sp. or left untreated under ambient conditions and inside of Mars simulation clamber. Plants lighted with LED (PAR) only during a day under Mars-like simulations. Chlorophyll fluorescence was measured inside Mars-like facilty with the MINI-PAM fluorometer. In column average significance of 6 measurements (every 30 min) over the past three hours of a day-night period is represented. Asterisks indicate significant difference between the treatments and corresponding control (untreated) inside Mars simulation chamber by Student's *t*-test (* indicate $P < 0.05$). Error bars was 0.0 in most cases

high concentration of CO_2, it can be assumed that the photochemical quenching was enhanced in untreated plants by the intensive use of recovered molecules of ATP and NADPH under abiotic stress.

Endophyte-inoculated beet plants exhibited higher value of *qP* than noninoculated plants [24]. In case of untreated kalanchoe sharp increase of *qP* was a reaction of the *Kalanchoe* PSII on the stress and a loss of effective energy needed for a defensive reaction.

It was earlier reported that the coefficient *NPQ* was higher at diurnal than at nocturnal period in stressed kalanchoe plants [10, 11]. *In situ* chlorophyll fluorescence measurement in kalanchoe leaves under both stressors in the facility showed a growing *NPQ,* in contrast to control plants outside of MSC. High value-*NPQ* may represent a mechanism of dissipating excess of excitation energy and of down-regulation of a photosynthetic electron transport in such a way that production of ATP and NADPH would match the decreased CO_2 assimilation. *NPQ* transforms into heat the excess of light energy that cannot be used in photosynthesis and which could lead to ROS (Reactive Oxygen Species) formation. The pH- and xanthophyll-dependent conformational change and the PsbS protein are necessary for *NPQ*, but the actual biophysical mechanism of Chl de-excitation is still unknown. Both *qP* and *NPQ* could help to minimize production of singlet oxygen formed in PSII. In our experiments *K. daigremontiana* plants treated with *Methylobacterium* sp. had higher *NPQ* within both diurnal and nocturnal periods than control untreated plants within MSC (Fig. 3 c). The inhibition of both *NPQ* and *qP* during simulated martian day in *K. daigremontiana* plants treated with *K. oxytoca* may suggest that there is another mechanism of protective potency in this bacterium under multi-factor stress

(Fig. 3 b, c). In another study the quantum yield of non-photochemical dissipation in PSII complexes was reduced by *B. subtilis* GB03 volatiles [29], indicating improved electron transport downstream from PSII. Different modes of changes in photochemical and non-photochemical parameters in kalanchoe leaves in response to stressful conditions displayed different putative mechanisms of protection of PSII with bacteria.

In all phases of photosynthesis in the light period (Phases II to IV) CAM plants are subjected to oxidative stress and perform photorespiration. Vigorous photosynthetic CO_2 assimilation due to high internal CO_2 concentration behind closed stomata in Phase III also generates high internal O_2 concentrations. Chlorophyll triplets are known to readily react with oxygen to produce very reactive oxygen species. Photoinhibitory process leads to impairment of PSII electron transport, especially under stresses. The activation of plant ROS-detoxification system by bacteria, including resident endophytes, may be a way to protect plants from toxic effects of ROS. We may assume that the associated bacteria that have their own ROS-eliminating systems could complement the deficient antioxidative systems of the plant.

In summary, effect of bacteria was associated with a day-time phases of PSII activity and appear reflected increase in Rubisco-mediated daytime CO_2 uptake and was not relevant to PEPC-mediated night-time CO_2 uptake. It is possible to assume that the protective role of *Methylobacterium* sp. manifested by both improving photorespiration (the stimulation of ATP and NADPH molecules by *K. daigremontiana* under model stressful conditions) and in a priming of plant defense system. Protecting mechanism provided by *K. oxytoca* in kalanchoe plants grown under multifactor stress plus a poor supply of essential nutrients in the system may be explained with improved electron transport downstream from PSII, as well as a supply of the plant partner with biological nitrogen and growth stimulators, leading to general strengthening a plant-host. Probably, tested bacteria possess the mechanism of quick utilization of excessive light energy that causes photooxidative effect, for example, utilization of ATP and NADPH either directly or via endophytic endemics, assissting in decreasing Φ_{PSII} in kalanchoe leaves and preventing photooxidation of PSII. On the other hand, both species are able to activate antioxidative systems [13]. We can assume that due to these bacteria elimination of ROS that actively formed in leaf tissues in stressful conditions occurred more efficiently than in untreated plants, and this process may protect photosynthetic centers.

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ЗАХИСТ ФОТОСИСТЕМИ II *KALANHOE DAIGREMONTIANA* БАКТЕРІЙНИМ КОНСОРЦІУМОМ У МОДЕЛЬНИХ МАРСІАНСЬКИХ УМОВАХ

За допомогою флуорометра було виміряно *in situ* максимальний квантовий вихід ФС II (F_v/F_m) та інші параметри *Kalanhoe daigremontiana* в імітованих марсіанських умовах (низький атмосферний тиск, висока концентрація CO_2 і УФ, за спектром близький до марсіанського) у марс-симуляційній камері. В умовах зниженого (10 мбар) і звичайного тиску не виявлено відмінностей у максимальній ефективності ФС II рослин, у тому числі інокульованих бактеріями. Однак спостерігалася відмінність між варіантами каланхое в умовах високої концентрації CO_2 (95 %). Максимальний квантовий вихід був вищим у присутності бактерій, хоча при високій концентрації CO_2 в атмосфері він знижувався в обох варіантах (інокульованих і неінокульованих), на відміну від F_v/F_m при низькому тиску. Величина F_v/F_m рослин каланхое, вирощених у штучному марсіанському ґрунті (MRS) або земному ґрунті за штучно створених марсіанських умов, була нижчою, ніж у звичайних земних умовах. Позитивний вплив від інокуляції бактеріями на пристосування рослин до несприятливих модельних марсіанських умов був більш виражений у рослин каланхое, вирощених на MRS, і залежав від виду бактерій, особливо в жорстких умовах спільної дії низького тиску, високого вмісту CO_2 і УФ-опромінення. Рослини *K. daigremontiana*, оброблені *Klebsiella oxytoca* та *Methylobacterium* sp., мали нижчий коефіцієнт фотохімічного гасіння *qP* і коефіцієнт нефотохімічного гасіння Штерна — Фольмера NPQ в денний і нічний період порівняно з необробленими рослинами, виявивши протекторний механізм. Більшість бактеріальних штамів і їхній консорціум продемонстрували протекторний ефект на *K. daigremontiana* за дії абіотичних стресорів, на відміну від арбускулярних мікоризних грибів.