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Cadmium exposure of heavy metal-tolerant *Mesembryanthemum crystallinum* L. (the common ice plant) stimulates gas exchange

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Abstract: When exposed to high cadmium concentrations applied to the soil, the abiotic stress-tolerant, semi-halophytic C₃/CAM (Crassulacean Acid Metabolism) photosynthetic intermediate plant *Mesembryanthemum crystallinum* L. demonstrates negligible poisoning symptoms with well-protected photochemical activity. Gas exchange analysis of the soil-grown plants exposed to Cd concentrations ranging from 0.01 to 10.0 mM revealed stimulation of net photosynthesis in the C₃ metabolic state, and this observation coincided with an increase in the transpiration level. The obtained results suggest that the initial action of Cd after the administration of this heavy metal is the stimulation of stomata opening.

Introduction

Several heavy metals (HMs) are elements known to be necessary for proper plant development, provided they occur at appropriately low concentrations. Some other, however, including Cd, are biologically non-essential and can act as severely toxic agents even at very low levels, eliciting poisoning symptoms in plants (Ali et al. 2013, Chibuike and Obiora 2014, Śliwa-Cebula et al. 2020). We know many plants capable of removing HMs from the soils (Gawroński et al. 2022). Numerous deleterious effects on plants were observed due to the action of various HMs and, among them, also cadmium contamination (Gallego et al. 2012). Well-known symptoms include changes in shoot and root functioning, as well as a reduction in biomass. In particular, exposure of the photosynthetic apparatus to Cd can considerably inhibit the net photosynthesis rate, photochemical activity, stomatal conductance and transpiration (Gallego et al. 2012, Moradi and Ehsanzadeh 2015). Plants are equipped with a variety of defense mechanisms that can be triggered in response to cadmium exposure. Among the proposed mechanisms are the immobilization of Cd ions sequestered in vacuoles, increased uptake of nitrogen and sulfur accompanied by the accumulation of manganese and zinc, enhanced synthesis of metallothioneins, phytochelatins and stress proteins, as well as increased activity of antioxidant enzymes (Małachowska-Jutysz and Gnida 2015, Carvalho et al. 2019).

The common ice plant, *Mesembryanthemum crystallinum* L., originates from environments where harmful ions are abundant. This semi-halophyte plant is capable of shifting its photosynthetic metabolism from C₃ to CAM (Crassulacean Acid Metabolism) and has become a frequent model in physiological and molecular studies (Cushman and Borland 2002). Its unusual properties (Adams et al. 1998), especially high resistance to stress as well as heavy metal tolerance, have led to a suggestion for the environmental use of *M. crystallinum* as a promising and efficient phytoremediator (Kholodova et al. 2005, Amari et al. 2014, Nosek et al. 2019, Śliwa-Cebula et al. 2020, 2023). In the case of cadmium, it has been shown that *M. crystallinum* can accumulate and deposit this metal in plant organs at relatively high levels without showing any overt signs of damage (Nosek et al. 2019, 2020, Śliwa-Cebula et al. 2020). However, the effect of the Cd ion presence on the transpiration process and photosynthetic rate in the common ice plant has not been investigated, yet.

It is well known that, when analyzing plant sensitivity/tolerance to different stresses, photosynthetic activity plays a crucial role. In considering the mechanisms of the stress response, a key question arises whether they depend on the plant's carboxylation potential (involving RubisCO, ribulose-1,5-bisphosphate carboxylase/oxygenase or PEPC, phosphoenolpyruvate carboxylase), or on photochemical activities connected with PSI and PSII function, along with the chloroplastic electron transport chain. Thus, it is important

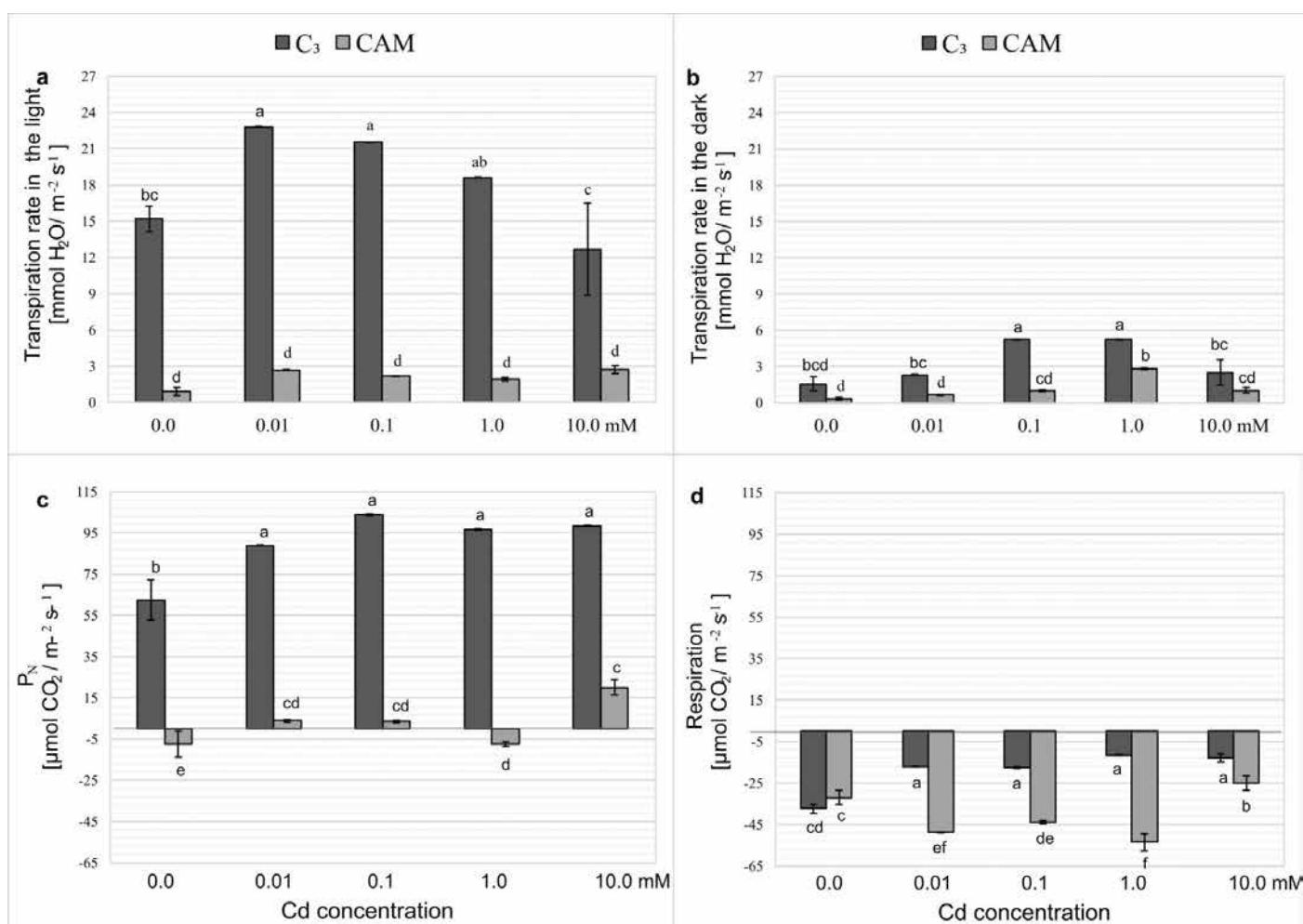


Figure 1. The rate of transpiration measured (a) in the light and (b) in the dark; (c) net photosynthesis; (d) intensity of respiration in C₃- and CAM-performing *Mesembryanthemum crystallinum* exposed to 0 (control), 0.01, 0.1, 1.0, and 10.0 mM Cd concentrations for 8 days. The mean values with standard deviations are shown as bars. Different letters represent statistically significant differences at $p \leq 0.05$ ($n = 4$).

to distinguish between photosynthetic and photochemical activities. As both activities do not occur parallel in time in CAM-performing plants (day/night), a comparison of C₃ and CAM metabolisms can help address this question. Studying *M. crystallinum* provides a unique opportunity to compare the C₃ and CAM photosynthetic states using a single plant model with one genome. A characteristic feature of plants that carry out CAM photosynthesis is that they keep their stomata closed throughout the day, while the CO₂ assimilation process primarily occurs at night. In C₃-performing plants, CO₂ can only be fixed during the day when stomata remain open.

In this study we have made an attempt to explain how the exposure of *M. crystallinum* to cadmium affects the photosynthesis and respiration of either C₃- or CAM-performing plants. In addition, we aimed to identify whether the observed changes in gas exchange and photochemical activity of plants subjected to Cd are primary or secondary effects.

Material and methods

Plant growth and treatment with cadmium

The *M. crystallinum* seeds were obtained from the Technische Universität in Darmstadt, Germany. They were sown in pots

containing a mixture of garden soil ("Athena" Bio-Products, Golczewo, Poland; density, $d = 0.24 \text{ kg dm}^{-3}$; pH of 6.75) and sand, mixed at the 4:1 (v/v) ratio. After two weeks, the seedlings were transferred to 9 x 9 x 10 cm containers. The cultivation followed the instructions outlined in Nosek et al. (2020), under the following conditions: a photoperiod of 16/8 h (day/night; 25°C/17°C), white light intensity of 300–350 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR (Photosynthetically Active Radiation), and relative humidity of 65–70%. Six-week-old plants were divided into two groups: one set was irrigated with a 0.4 M NaCl solution to stimulate the CAM photosynthesis, and a second group of C₃-performing plants was watered with tap water. The induction of CAM was verified after 14 days by measuring the diurnal Δ -malate (the difference between malate concentrations in the leaf cell sap recorded at the beginning and end of the light phase) according to Gawronska and Niewiadomska (2015). In the next step, eight-week-old plants of each metabolic group (C₃ or CAM) were separated into 5 experimental variants. The first variant included plants irrigated with water and served as a control, while the other four variants were the plants exposed for eight days to cadmium. Cadmium was applied as CdCl₂ (Sigma-Aldrich, Poznań, Poland) solutions in water (for C₃ plants) and in 0.4 M NaCl (for CAM). Each day, 10 mL volumes of water

(control) and 0.01, 0.1, 1.0, and 10 mM CdCl₂ solutions were applied to the tested pots. No leakage from pots was detected during Cd application. Such treatment led to the final Cd doses of 0 (control), 0.8, 8.0, 80 and 800 µmol per pot, respectively, calculated as 0.82, 8.2, 82 and 818 mg per kg of soil d.w.

Gas exchange assessment

Gas exchange measurements were conducted using an LCpro-SD apparatus (ADC Bioscientific Ltd., UK) equipped with a 6.24 cm² cuvette outfitted with a head with a mixed red/blue LED light source. The measurements were performed at a high CO₂ level of 400 µmol · mol⁻¹, airflow of 300 µmol s⁻¹, relative humidity of 50 to 55 %, leaf temperature of 28 °C, and a red-light intensity of 130 µmol m⁻² · s⁻¹. Net photosynthesis was calculated by subtracting the values of the rate of carbon dioxide lost during respiration in the dark from the rate of carbon fixation during exposure to light over the same time period (Tokarz et al. 2019).

Chlorophyll a fluorescence

Photosystem II (PSII) efficiency was calculated based on the measurement of the rate of fluorescence quenching at room temperature using a Handy-PEA fluorimeter (Hansatech Instruments, UK) with saturation light at 3500 µmol m⁻² · s⁻¹. The analyses were conducted the day after the last application of CdCl₂ at a given concentration. Plants were subjected to dark adaptation for 20 min., and then a pulsed light emission was used to initiate fluorescence. Chlorophyll *a* fluorescence was characterized by assessing the following parameters: maximum PSII quantum yield (Fv/Fm), performance index based on energy absorption (PI_{ABS}), maximum efficiency of the water-splitting complex on the donor side of PSII (Fv/Fo), retained photons flow (reducing Q_A) in PSII per reaction center (RC), and electron transport via carriers in the electron transport chain after Q_A per RC.

Statistical analysis

The obtained results were evaluated with Statistica 13.3 (StatSoft, USA) software. Individual treatment effects were determined using one-way ANOVA and post-hoc Duncan's test at $P \leq 0.05$.

Results

Gas exchange in *M. crystallinum* plants performing either C₃ or CAM photosynthesis upon Cd treatment

We observed an increase in transpiration in C₃ plants under light conditions in the presence of Cd at concentrations of 0.01 and 0.1 mM (Fig. 1a). In the case of CAM plants examined under light conditions, no evidence of transpiration modification by Cd treatment was noted. When measured in the dark, the transpiration of C₃ plants treated with 0.1 and 1.0 mM Cd increased (Fig. 1a). None of the tested Cd concentrations significantly affected dark transpiration of the CAM-performing plants with the only exception noted for 1.0 mM Cd (Fig. 1b).

Taken the data together, the transpiration rate was considerably higher in C₃-performing plants compared to those carrying out CAM photosynthesis. In addition, based on statistical evaluation, for both tested plant groups (C₃ as

well as CAM) there was an increase in P_N parameter upon Cd treatment (Fig. 1c). However, this effect was much more pronounced in C₃ plants, since the individual P_N values are relatively high. Respiration intensity decreased in C₃ plants treated with Cd (higher values compared to the control group, Fig. 1d), which correlated with an increase of P_N (Fig. 1c). In CAM plants exposed to Cd, an increase in the respiration process was observed (lower absolute values), except for Cd concentration of 10.0 mM (Fig. 1d).

Photochemical activity in C₃ and CAM-performing *M. crystallinum* exposed to Cd

The Fv/Fm levels, representing a potential activity of PSII of both C₃- and CAM-performing plants, did not show any significant changes due to exposure to Cd (Fig. 2a). Moreover, no differences were observed between plants treated with variant CdCl₂ concentrations and the respective controls. Cadmium treatment, except for the C₃ case treated with the concentration of 0.01 mM, did not affect the PI_{ABS} parameter in any metabolic group. Similar values were obtained for controls and Cd treated plants in both C₃- and CAM- plants (Fig. 2b). The Fv/Fo values remained unchanged for all tested Cd levels in both plant groups (Fig. 2c). However, this parameter was slightly lower in CAM-performing plants compared to the C₃ plants. In plants revealing the C₃ metabolic state, Cd treatment resulted in an increasing tendency in energy dissipation calculated per active reaction center (DI₀/RC), whereas in CAM plants a visible decrease in this parameter level was observed (Fig. 2d). Comparing C₃ and CAM plants with the control, no significant differences in ET₀/RC values were found (Fig. 2e). In addition, C₃-performing plants showed approximately 1.5-fold higher values compared to CAM ones. All applied Cd concentrations had no significant effect on TR₀/RC in the C₃ plant group (Fig. 2f). However, in the CAM state, Cd at 0.01 and 0.1 mM led to a decrease of these values. As in the previous case, a 1.5-fold higher values of TR₀/RC were noted for C₃ compared to CAM plants.

Discussion

According to Moradi and Ehsanzadeh (2015), cadmium exposure affects plant primary metabolism in several ways, including changes in lipoprotein-chlorophyll system, an increase in lipid peroxidation and decrease of chlorophyll synthesis. Gas exchange and chlorophyll *a* fluorescence are two key parameters that offer a fast and simple means of directly assessing the influence of heavy metals on plants (Dias et al. 2013). Previous research has demonstrated that treatment with 25.0 µM Cd altered gas exchange intensity, leading to a decrease in the transpiration rate in *Brassica juncea* (Haag-Kerwer et al. 1999, Prasad et al. 2001). In turn, a decrease in P_N and transpiration was reported to impede growth of *Triticum aestivum* treated with 100 µM Cd for 28 days (Arshad et al. 2015).

On the contrary, it has been shown that Cd at lower concentrations stimulates net photosynthesis in *Lonicera japonica*, a plant classified as a hyperaccumulator (Jia et al. 2015). Plants exposed to the so-called 'minor metal stress' may experience heightened respiration intensity (Lösch et al. 1999). Such a dependence has been observed in instances

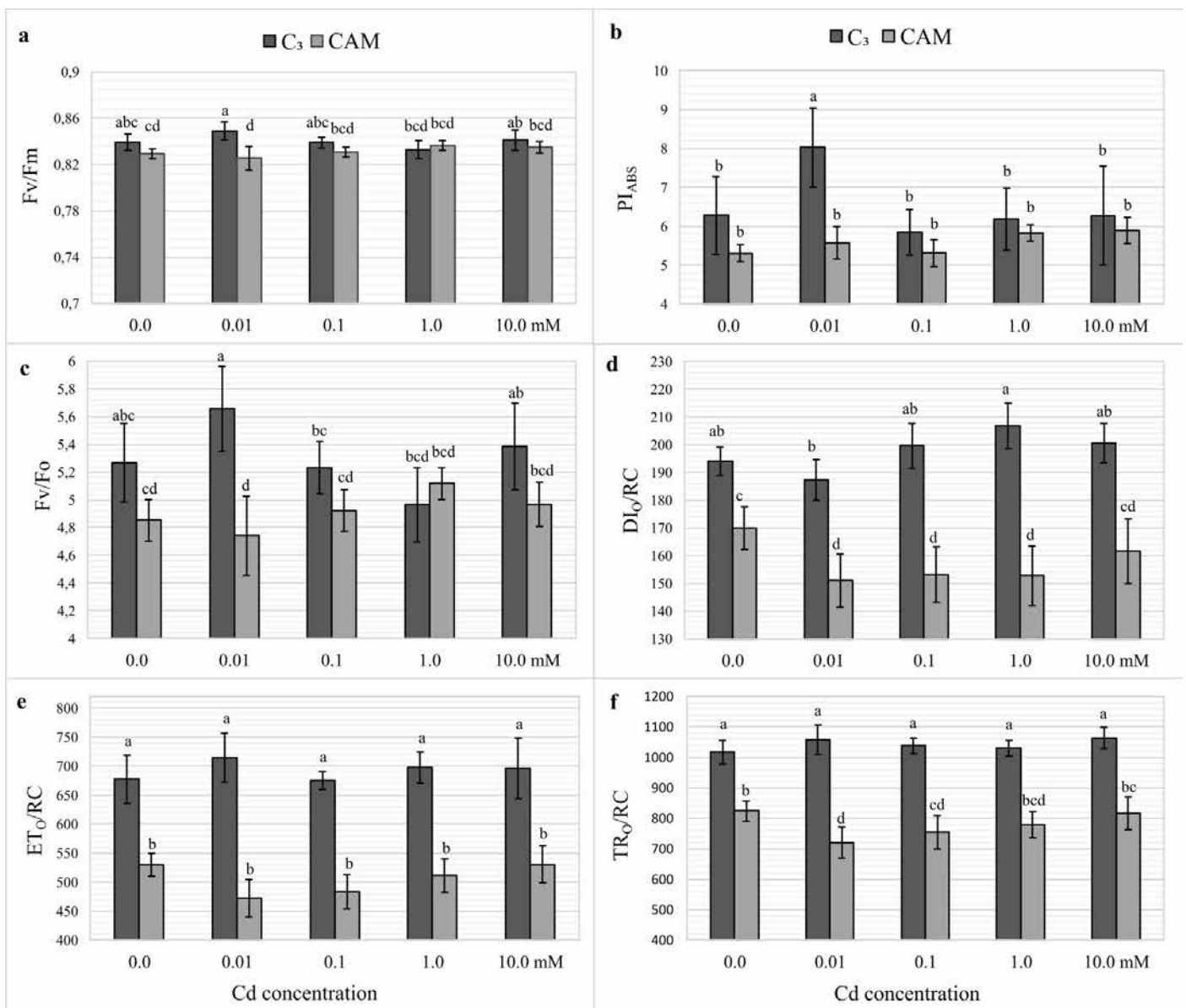


Figure 2. Photochemical parameters of C₃- and CAM-performing *M. crystallinum* exposed to 0 (control), 0.01, 0.1, 1.0, and 10.0 mM Cd concentrations for 8 days. (a) maximum quantum yield of PSII; (b) performance index assessed according to an energy absorption; (c) maximum efficiency of the water splitting system on the PSII side; (d) nonphotochemical quenching estimated per one reaction center; (e) electron transport via carriers located in the electron transport chain after QA per reaction center (RC); (f) flux of retained photons in PSII per RC. The mean values with standard deviations are shown as bars. Different letters represent statistically significant differences at $p \leq 0.05$ ($n = 12$).

such as *Lemna trisulca* treated with 5.0 mM Cd, where the stress induced by Cd is proposed to intensify plant metabolism, thus leading to higher respiration rate (Prasad et al. 2001). Authors suggest that this phenomenon, known as hormesis, refers to the stimulatory effect of relatively low HM doses, including Cd. Hormesis has been extensively studied in plants recently (Adamakis et al. 2020, Moustakas et al. 2022) and is considered an evolutionary adaptation mechanism enabling plants to respond to environmental stressors.

As previously reported, our investigation into a model plant *M. crystallinum* treated with high cadmium concentrations did not reveal any adverse reactions to the applied Cd ions (Nosek et al. 2019). In this study, we investigated how Cd might influence gas exchange in the common ice plant exhibiting either C₃ or CAM metabolism, under both light and dark

conditions. Our goal was to elucidate the primary effects of Cd exposure on the tested plant material. Based on the data shown in Figs. 1a and 1c, we speculate that P_N stimulation coincides with enhanced transpiration within the Cd concentration range of 0.1–1.0 mM. Since a similar result was observed in the dark (Fig. 2b), it suggests that the initial effect is stomata aperture stimulation. The stimulatory impact of Cd was not detected for CAM plants, as their stomata are typically closed during the day. It is noteworthy that Cd increased respiration only in CAM-performing plants at night, while the opposite process occurred in the C₃ phase. Photochemical activity data demonstrate no damage within the photosynthetic system upon the Cd treatment (Fig. 1). The low transpiration intensity observed is directly related to stomatal closure throughout the day in CAM plants. The P_N level under this metabolic state

is significantly lower compared to C_3 due to photosynthesis. Considering P_N values, Cd may stimulate the CO_2 fixation rate at lower concentrations, thereby improving photosynthesis. The relatively low respiration, as observed in our measurements, could be attributed to the accumulated Cd fraction, as earlier demonstrated by Nosek et al. (2019).

Given that the plants were treated with $CdCl_2$ solutions, it is essential to consider the potential effect of Cl^- ions, which were applied together with Cd^{++} . Halophytic plants are usually not sensitive to high concentrations of Cl^- and may even require this compound for proper functioning. As shown in the literature (Liang et al. 2017), the level of Cl^- anions in soils for halophytes in most cases exceeds 100 mM. In our study, the highest concentration of $CdCl_2$ used for treatment was 10 mM, and therefore the Cl^- presence was not expected to have any significant impact on *M. crystallinum* photosynthesis parameters (Nosek et al. 2019).

The Fv/Fm parameter can serve as a convenient stress indicator when evaluating plant responses to various stress conditions. Typically, a decrease in Fv/Fm values is indicative of oxidative stress, and thus, we focused special attention on this parameter in our study. As reported in numerous studies, the presence of heavy metals is most often associated with increased production of reactive oxygen species (ROS) resulting in oxidative stress. In our investigation, we considered additional fluorescence parameters related to more specific changes in the electron transport chain of both PSII and PSI. Fv/Fm values exceeding 0.75 suggest a high potential performance of PSII, indicating that it remains unaffected (Björkman and Demmig 1987). Our results revealed that plants were resistant to Cd and exhibited no signs of oxidative damage. In addition, no significant changes in Fv/Fo and PI_{ABS} values were found for either metabolic state. Cadmium was demonstrated to limit electron transport within PSII while increasing non-photochemical quenching (Larsson et al. 1998). However, in our study, no negative Cd influence on electron transport (ET_o/RC) was observed. At the same time, differences between C_3 - and CAM-performing plants were most probably caused by the presence of osmotic stress, particularly pronounced in CAM plants. This group is expected to have lower PSII activity in the overall photosynthesis process. These findings support the hypothesis that osmotic stress-induced CAM photosynthesis occurs due to a decrease in the efficiency of the photosynthetic apparatus (Nosek et al. 2022). No observable changes in both C_3 and CAM plants, even at the maximum applied cadmium, could result from the presence of some additional system or mechanism that protects plants from the toxicity of this heavy metal.

To conclude, the variations in transpiration intensity caused by plant exposure to Cd appear to be linked to stomatal aperture, which results in changes in photosynthetic intensity, particularly noticeable in C_3 -performing plants. The administered Cd dosages show no effect on Fv/Fm, suggesting that oxidative stress is not a contributing factor. The increased P_N values are also associated with lower energy dissipation (determined as DI_o/RC). Because of differences in the metabolic performance, no similar changes are found in CAM plants. The relatively high tolerance to Cd applied even at the highest (10.0 mM) concentration suggests the presence of other, as yet unknown mechanisms, that may protect the

photosynthetic machinery. For the above reasons, while considering the enhanced resistance of the common ice plant to Cd toxicity, *M. crystallinum* may prove efficient in cadmium phytoextraction or phytostabilization of Cd-contaminated soils.

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Ekspozycja na kadm rośliny tolerującej metale ciężkie *Mesembryanthemum crystallinum* L. (Przypołudnik kryształkowy) stymuluje wymianę gazową

Streszczenie: Przypołudnik kryształkowy (*Mesembryanthemum crystallinum* L.) to semihalofit o metabolizmie przejściowym C₃/CAM, cechujący się dużą odpornością na stres abiotyczny, w tym na obecność wysokich stężeń kadmu w podłożu. W przeprowadzonych eksperymentach, przy stężeniach 0.01, 0.1, 1.0 oraz 10.0 mM soli kadmu aplikowanej do gleby stwierdzono znikome uszkodzenia tkanek liściowych zarówno u roślin realizujących fotosyntezę typu C₃, jak i CAM. U roślin typu C₃ po ekspozycji na kadm zaobserwowano stymulację fotosyntezy netto (P_N), który to proces zachodził równolegle ze zwiększeniem intensywności transpiracji. Zaobserwowany wzrost intensywności transpiracji w ciemności wskazuje na stymulację otwarcia aparatów szparkowych pod wpływem działania Cd. Udokumentowano brak istotnych zmian w aktywności fotochemicznej u obu grup roślin w odpowiedzi na traktowanie roztworem kadmu, co wskazuje na obecność dodatkowych mechanizmów chroniących aparat fotochemiczny, a uruchamianych w celu zapobiegania pojawianiu się toksycznych efektów tego metalu.