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The effect of cadmium on several photosynthetic parameters of pea (*Pisum sativum* L.) at two growth stages

Irena JANUŠKAITIENĖ

Vytautas Magnus University

K. Donelaičio 58, Kaunas, Lithuania

E-mail: I.Januskaitiene@gmf.vdu.lt

Abstract

Plant growth stage is an important factor in plant response to stress. The paper investigates the impact of cadmium (Cd) on pea (*Pisum sativum* L.) photosynthetic parameters and development at different growth stages. The peas were sown in pots with a peat substrate of neutral acidity. Ten (leaf development BBCH 14–16 stage) and seventeen (formation of lateral shoots BBCH 21–23 stage) days after germination, the pea plants were exposed to 1 and 6 mM CdSO₄ solution concentrations. The photosynthetic response of pea leaves at BBCH 14–16 stage to cadmium stress was slightly different from that at BBCH 21–23 stage: intercellular CO₂ concentration (C_i) of peas at BBCH 14–16 stage decreased by 27.4% and 32.8% under 1 and 6 mM Cd impact respectively; by contrast, C_i of peas at BBCH 21–23 stage increased by 28.5% and 22.1% under the mentioned impact ($p < 0.05$) compared to the age adequate control. Also, 6 mM Cd induced a stomatal closure in pea leaves at BBCH 14–16 stage and reduced the transpiration rate more than photosynthesis, which resulted in an increase in water use efficiency by 119.4% of the mentioned peas. On the contrary, 6 mM Cd increased the transpiration rate (T_n) and decreased water use efficiency (WUE) of peas at BBCH 21–23 stage. A lower 1 mM Cd treatment had a very low and mostly insignificant impact on the biomass accumulation and photosynthetic parameters of peas. A higher 6 mM Cd treatment provoked an almost three-fold higher decrease in dry biomass of peas at BBCH 14–16 stage (56.1%) than at BBCH 21–23 stage (21.9%), as compared with the age adequate control. Also chlorophyll content decreases were higher in pea leaves at BBCH 14–16 stage than at BBCH 21–23 stage.

Key words: development stages, cadmium, photosynthesis, intercellular CO₂ concentration, water use efficiency, pigments, biomass, *Pisum sativum*.

Introduction

Plants have to regulate the protection of their photosynthetic active tissue when exogenous factors or other conditions change in the environment (Reifenrath, Muller, 2007). The metabolic responses of plants vary according to the type of stress. These responses can be rather specific since the metabolic pool of plant defense is composed of a variety of constitutive and induced metabolites (Jahangir et al., 2009). Even within an individual plant, the quality and quantity of metabolites may differ between young and old leaves (Reifenrath, Muller, 2007). Stress induced responses take a lot of energy which might otherwise be used for the growth and development of the plant. Plants at more advanced growth stages have a larger amount of biomass and also higher energy resources (Larcher, 2003). Thus, environmental stresses are most harmful to plants at early growth stages until the formation of generative parts. This stage might last long or be late, or might not appear at all, when environmental conditions are unfavourable (Duchovskis, 1998).

Highly polluted soils containing over 100 mg kg⁻¹ Cd are reported in China, France and some other countries (Goncalves et al., 2009). The concentrations of cadmium in Lithuanian soils are not as high, but there exists another problem: in the fields close to the highways, the previous main risk factor lead has now been replaced by cadmium (Antanaitis et al., 2007). Cadmium is easily taken up by

plant roots and can be loaded into the xylem for its transport into leaves. A large number of studies have demonstrated the toxic effect of cadmium on plant metabolism, such as a decrease in the uptake of nutrient elements and changes in nitrogen metabolism (Sandalio et al., 2001). This heavy metal can exert a negative effect on basic processes of plant growth, development and physiology. The responses to cadmium can be different and sometimes opposite according to the species. For instance, in leaves of *Brassica napus*, cadmium leads to a reduction of mesophyll cell size, while leaf thickness and cell size increases are observed in *Pisum sativum* as exposed to the heavy metal (Sandalio et al., 2001). The photosynthetic apparatus appears to be especially sensitive to cadmium negative effect. The primary targets of cadmium impact are PSII and the enzymatic phase of photosynthesis, particularly ribulose-1, 5-bisphosphate carboxylase/oxygenase (Krantev et al., 2008; Popova et al., 2008). Whereas in other research no direct cadmium effects on the photosystem have been found in either *Brassica juncea* (Haag-Kerwer et al., 1999) or *Arabidopsis thaliana* (Perfus-Barbeoch et al., 2002), it has been demonstrated that Cd²⁺ induces changes in the antioxidant status in plants (Balestrasse et al., 2006). Moreover, in pea plants, a long-term exposure to Cd²⁺ produces oxidative stress in roots as a result of disturbances in enzymatic and no

enzymatic antioxidant defenses, bringing about an increase in reactive oxygen species (ROS) accumulation (Rodríguez-Serrano et al., 2006). Recently, Garnier et al. (2006) have demonstrated that cadmium induces a transient increase in cytosolic Ca^{2+} concentration that appears to regulate the extracellular NADPH-oxidase depending generation of H_2O_2 (Smiri et al., 2010) too.

There have been many reports on the photochemical (Haag-Kerwer et al., 1999; Sandalio et al., 2001; Perfus-Barbeoch et al., 2002; Smiri et al., 2010), biochemical (Krantev et al., 2008; Popova et al., 2008) or morphological (Burzynski, Zurek, 2007; Lopez-Millan et al., 2009) events occurring in plants during the impact of cadmium and among them a few (Skorzynska-Polit, Baszynski, 1997) are about the relationship between the time of cadmium action and its application to the growth substrate or the growth stage of the plants. Thus, the aim of this work is to investigate the impact of 1 and 6 mM Cd concentrations on gas exchange, chlorophyll content and development of pea (*Pisum sativum* L.) at different growth stages.

Materials and methods

Pea (*Pisum sativum* L., cv. 'Ilgiai') was chosen for investigation. The experiments were conducted in a vegetation room with a controlled environment: with a photoperiod of 14 h, average temperature of night and day of 20 and 25°C, relative air humidity of 60%. "Philips Master Green Power CG T" 600W lamps (the Netherlands), light intensity at the level of plants 14000 Lx, provided light. The experiments were carried out at the Department of Environmental Sciences of Vytautas Magnus University in 2009–2010.

Peas (20 plants per pot) were sown in a neutral (pH 6.0–6.5) peat substrate in 5 l pots (21 cm in diameter). Each treatment was replicated three times; overall there were 15 pots and 300 pea plants. The seeds were germinated and grown for nine days. Ten days after germination, pea plants were divided into five groups (3 pots in each group): 1) reference treatment group watered with distilled water, 2) growth substrate of peas watered with 1 mM Cd (CdSO_4) concentration solution at leaf development BBCH 14–16 stage (Growth stages..., 2001), 3) growth substrate of peas watered with 6 mM Cd at BBCH 14–16 stage, 4) growth substrate of peas watered with 1 mM Cd one week later, i.e. at the stage of lateral shoots BBCH 21–23 (Growth stages..., 2001), 5) growth substrate of peas watered with 6 mM Cd at BBCH 21–23 stage.

Each pot of peat substrate received 1 l of solution. According to the previous experiments conducted at the Department of Environmental Sciences of Vytautas Magnus University, very weak 1 mM and medium 6 mM Cd solution treatments were chosen (Januškaitienė et al., 2008). The duration of cadmium treatment was five days.

Gas exchange was measured with a portable photosynthesis system LI-6400 (LI-COR, USA) at the end of each experiment. Photosynthetic rate (Pn) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), transpiration rate (Tn) ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), intercellular CO_2 concentration (Ci) ($\mu\text{mol CO}_2 \text{ mol air}^{-1}$) of the second pair of fully expanded leaves were registered every 30 seconds for 40 minutes. The measurements were performed for one randomly selected seedling per pot. From these data, a daily mean of measured indices was calculated. Water use efficiency (WUE) ($\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$) was calculated by dividing photosynthetic rate by transpiration rate. The environmental conditions

during the experiments were as follows: air flow rate – 400 $\mu\text{mol s}^{-1}$, block and leaf temperature – 25°C, CO_2 concentration in sample cell – 300–400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, relative humidity in sample cell – 30%, lightness in quant – 180 $\mu\text{mol m}^{-2} \text{ s}^{-1}$.

The second pair of fully expanded leaves was harvested for the photosynthetic pigment determination at the end of the experiment. The photosynthetic pigments were analyzed using a spectrophotometer "Genesys 6" ("ThermoSpectronic", USA) and 100% acetone extracts were prepared according to Wettstein's method (Wettstein, 1957). Photosynthetic pigments were expressed in mg g^{-1} of fresh weight.

At the end of the experiment, the plants were harvested. Fresh weight reading for shoots was taken immediately after harvesting. Then the shoots were dried in an oven at 60°C until a constant dry biomass weight. The shoot biomass was expressed in mg plant^{-1} .

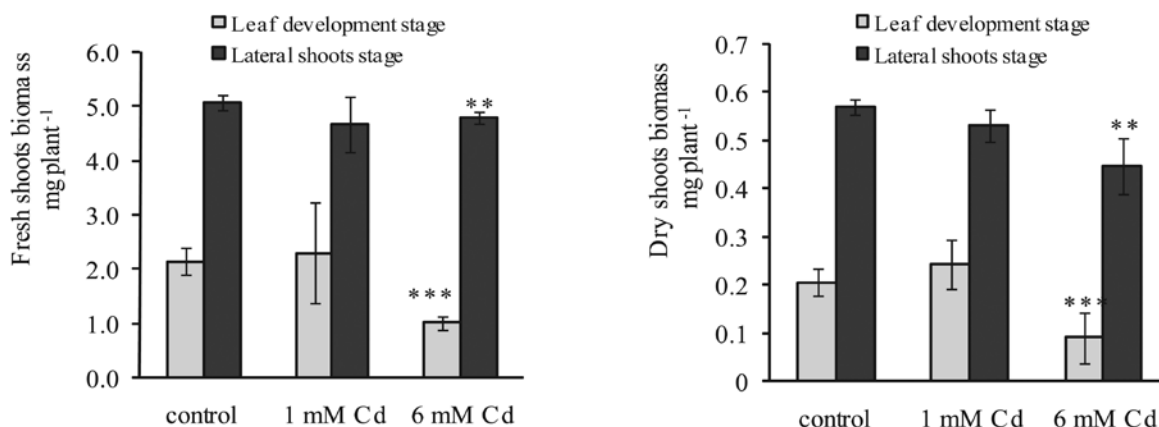
ANOVA was used to determine the effects of cadmium pollution and the growth stage. For independent variables comparison, *Student's t* (for parametric) and *U* test (for nonparametric) were used. All the analyses were performed by *Statistica* and the results were expressed as mean values and their confidence intervals (CI) ($p < 0.05$).

Results and discussion

Fresh and dry shoot biomass of all treated plants varied according to the same tendency. Dry shoot biomass of peas at leaf development BBCH 14–16 stage increased by 17% ($p > 0.05$) after treating it with 1 mM Cd solution (Fig. 1). The most marked reduction of growth of pea plants at leaf development stage was observed after 6 mM Cd solution treatment. As compared with the reference treatment, almost a two-fold decrease can be seen (Fig. 1). A higher concentration of cadmium also decreased dry biomass of peas at lateral shoots BBCH 21–23 stage, as dry shoot biomass showed approximately 6.7% and 21.9% reduction in 1 and 6 mM Cd solution treated plants respectively.

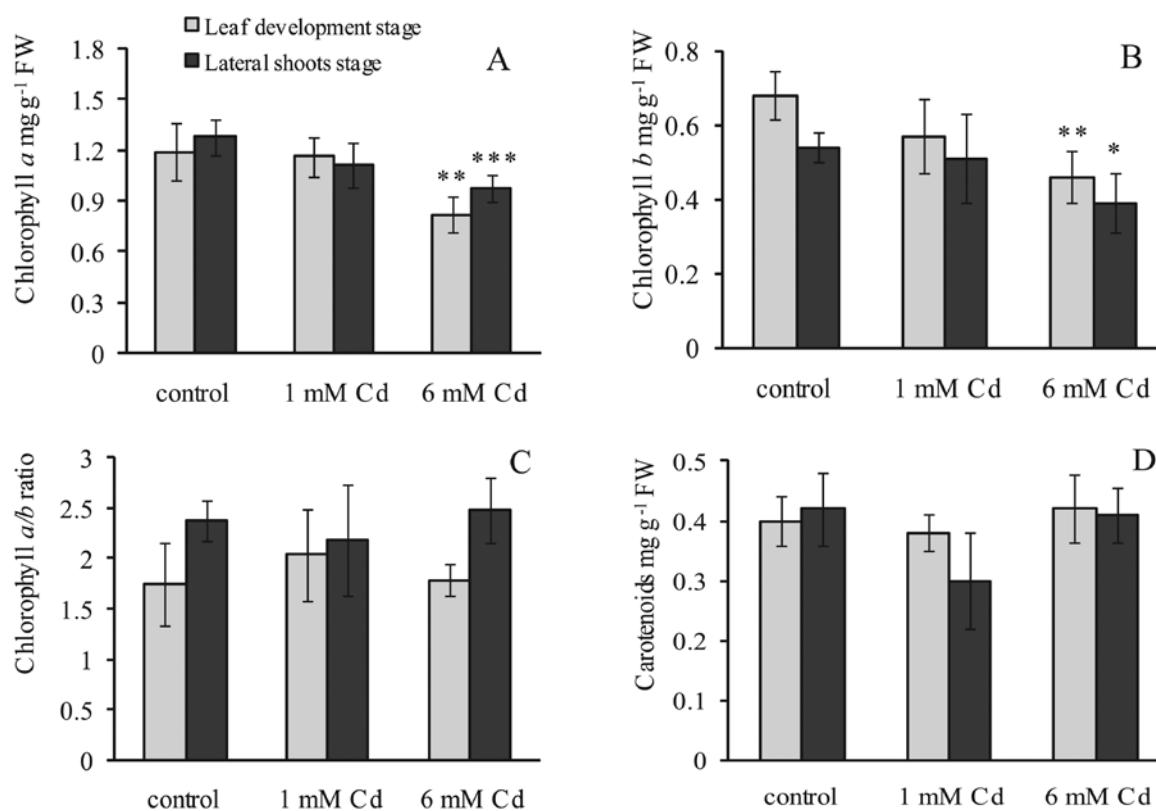
Cadmium treatment decreased chlorophyll *a* content in pea leaves at both development stages, but statistically significant parameters were only observed under the higher impact (Fig. 2). Under a 6 mM Cd exposure, chlorophyll *a* content of peas at leaf development BBCH 14–16 stage decreased by 31.0% ($p < 0.05$), and the same impact on peas at lateral shoots BBCH 21–23 stage decreased it by 24.2% ($p < 0.05$). Chlorophyll *b* was also more sensitive to a 6 mM Cd concentration exposure and its content decreases were higher in pea leaves at leaf development stage than in pea leaves at lateral shoots stage (32.3% of BBCH 14–16 stage and 27.8% of BBCH 21–23 stage). Chlorophyll *a/b* ratio changes under Cadmium impact in pea leaves at both investigated growth stages were statistically insignificant. Investigated Cadmium exposure effect on the content of carotenoids was very low and statistically insignificant too.

Photosynthetic rate (Pn) decreased in pea plants at both growth stages after they had been treated with cadmium (Fig. 3 A). 1 mM Cd concentration had no statistically significant impact on the Pn. Yet a 6 mM Cd exposure resulted in high and statistically significant decreases of Pn, i.e. 79.9% in peas at BBCH 14–16 and 56.0% at BBCH 21–23 stage compared to the reference treatment.



Notes. The values are means \pm CI_{0.05}; asterisks indicate a statistically significant difference from the age-adequate control (** – $p < 0.01$, *** – $p < 0.001$).

Figure 1. Changes in fresh and dry shoot biomass of pea plants treated with 1 mM and 6 mM Cd at different growth stages



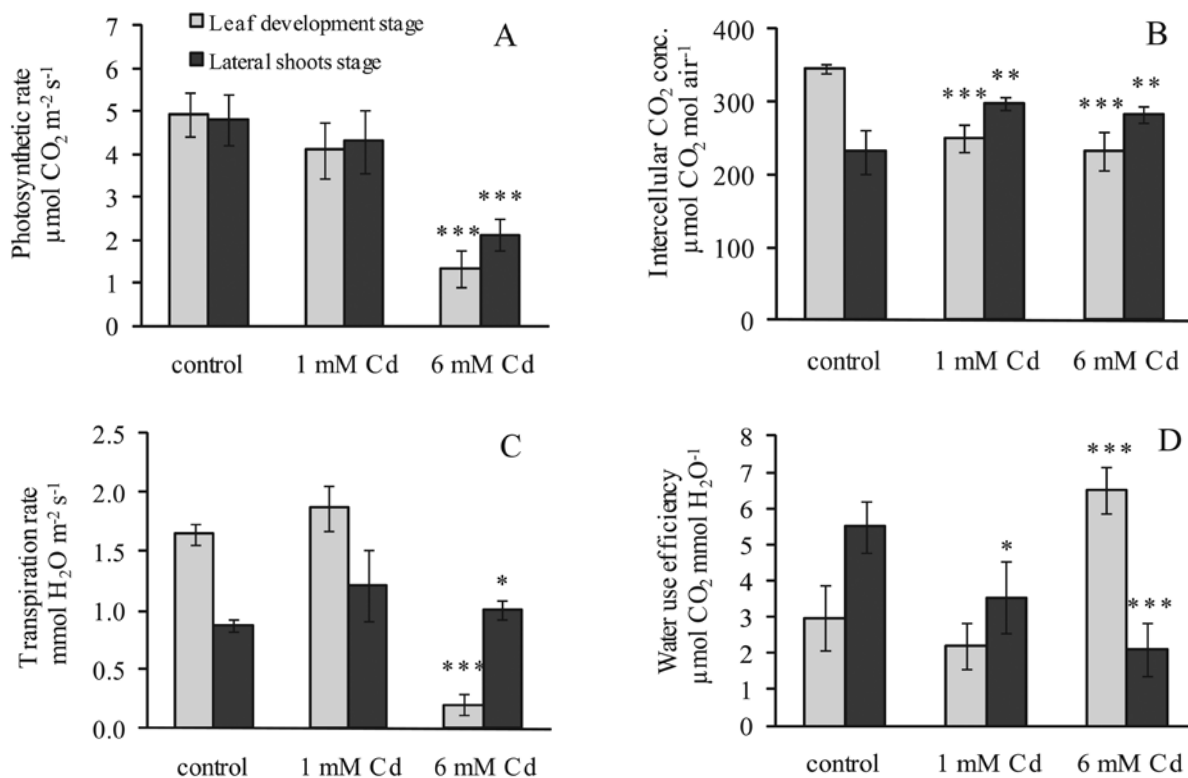
Notes. The values are means \pm CI_{0.05}; asterisks indicate statistically significant difference from the age-adequate control (* – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$); FW – fresh weight.

Figure 2. Changes in the content of chlorophyll a (A), chlorophyll b (B), chlorophyll a/b ratio (C) and carotenoids (D) in the leaves of pea plants treated with 1 mM and 6 mM Cd at different growth stages

Intercellular CO₂ concentration (Ci) in peas at leaf development stage decreased by 27.4% and 32.8% under 1 and 6 mM Cd impact respectively (Fig. 3 B); by contrast, Ci of peas at lateral shoots stage increased by 28.5% and 22.1% under the mentioned impact, compared to the reference treatment.

The transpiration rate (Tn) of peas at leaf development (BBCH 14–16) and lateral shoots (BBCH

21–23) stages, after treatment with 1 mM Cd solution, increased by 13.3% ($p > 0.05$) and 38.1% ($p > 0.05$), respectively (Fig. 3 C). A higher 6 mM Cd exposure decreased the Tn in peas at BBCH 14–16 stage by 87.9% ($p < 0.05$), however, it increased Tn by 15.3% ($p < 0.05$) in the ones at BBCH 21–23 stage, as compared to the reference treatment.



Notes. The values are means \pm CI_{0.05}; asterisks indicate statistically significant difference from the age-adequate control (* – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$).

Figure 3. Changes in gas exchange parameters (A – photosynthetic rate, Pn; B – intercellular CO₂ concentration, Ci; C – transpiration rate, Tn; D – water use efficiency, WUE) of pea plants treated with 1 mM and 6 mM Cd at different growth stages

Under the impact of 1 mM Cd, WUE of peas at leaf development and lateral shoots stages decreased by 26.5% ($p > 0.05$) and 35.4% ($p > 0.05$), respectively (Fig. 3 D). Yet, a 6 mM Cd exposure affected WUE of peas at the investigated growth stages differently, i.e. WUE of peas at leaf development stage increased by 119.4% ($p < 0.05$) and WUE of peas at lateral shoots stage decreased by 61.8% ($p < 0.05$).

Among the many reports on the influence of cadmium on plants, an important problem has emerged, which concerns the relationship between the time of cadmium action, its application to the nutrient solution and age/development stage of plants. Heavy metals disturb the uptake and the distribution of essential nutrients including the uptake and transport of Fe to leaves (Krupa et al., 2002), which is necessary for normal functioning of all the processes associated with CO₂ assimilation. Consequently, a contact of plants with Cd leads to the reduction of the total photosynthetic area and plant biomass (Burzynski, Zurek, 2007; Lopez-Millan et al., 2009). In the current research, dry shoot biomass decreased in almost all plants treated with cadmium, except for the peas at leaf development stage exposed to 1 mM Cd (Fig. 1). Under a higher (6 mM) Cd impact, dry biomass diminished to 56.1% ($p < 0.05$) and 21.9% ($p < 0.05$) for plants at BBCH 14–16 and BBCH 21–23 stages respectively, when compared with the reference treatment plants. A 6 mM Cd solution treatment led to an almost three-fold higher decrease of biomass (as compared with the reference treatment) in the peas at leaf development stage as compared to the ones at the lateral shoots stage

(Fig. 1). This supports the findings of Skorzynska-Polit and Baszynski (1997), who also reported that younger Cd-treated plants had bigger changes in growth parameters than older ones.

In roots and leaves of pea plants cadmium produces a significant inhibition of growth as well as a reduction in the transpiration and photosynthesis rate, chlorophyll content of leaves (Sandalio et al., 2001; Smiri et al., 2010). Cadmium treatments not only led to decreases in net CO₂ uptake (Pn), but also induced decreases in chlorophyll concentration in leaves. In addition, the negative effect was more marked in the 6 mM Cd solution treatment than in the 1 mM one (Figs 2–3). The level of chlorophyll and carotenoids was postulated as a simple and reliable indicator of heavy metal negative impact on higher plants (Goncalves et al., 2009). However, the effects of cadmium on the photosynthetic activities are controversial. Some investigations have provided evidence that cadmium is a potent inhibitor of the photochemical activity of the chloroplasts (Mobin, Khan, 2007; Singh et al., 2008); other studies have concluded that the photochemical activity is not sensitive to cadmium. In this study, the contents of chlorophyll *a* and *b* decreased significantly only in the 6 mM Cd solution treatment (Fig. 2 A, B), while no significant differences were observed in a lower cadmium treatment. Chlorophyll content decreases were higher in pea leaves at leaf development stage than at lateral shoots stage. Also, chlorophyll bleaching effect of cadmium on leaf tissues was more intensive at pea leaf development stage. This might be attributed to a number of effects such as the inhibition of chlorophyll biosynthe-

sis, chlorophyll degradation, hastened senescence and the disorganization of chloroplasts, a decreased number of photosynthetic membranes, and oxidative stress (Rascio et al., 2008; Goncalves et al., 2009). However, older peas (at lateral shoots stage) had stronger antioxidant system, which was sufficiently efficient to reverse the stress burst (Goncalves et al., 2009).

Cadmium can negatively affect different steps of the photosynthetic process, i.e. efficiency of photosystem 2 (PSII), photochemistry and photosynthetic electron transport chain (Pagliano et al., 2006). In this study, photosynthetic rate was one of the most evidently Cd-affected parameters. A photosynthetic response of pea leaves at leaf development (BBCH 14–16) stage was slightly different from that of peas at lateral shoots (BBCH 21–23) stage. Ci in peas at BBCH 14–16 stage decreased under 1 and 6 mM Cd impact (Fig. 3 B), whereas Ci in peas at BBCH 21–23 stage increased under the mentioned impact, compared to the reference treatment ($p < 0.05$). A Ci decrease in pea leaves at BBCH 14–16 stage shows that despite the decrease in the Pn by 16.7% ($p > 0.05$) and 79.9% ($p < 0.05$) (under 1 mM and 6 mM Cd impact respectively), the CO₂ reduction processes in pea leaves were intensive. Ci and Pn reduction of (6 mM) Cd-treated peas at leaf development stage could also cause the closure of stomata (Musyimi et al., 2007; Shi, Cai, 2008; Wang et al., 2009), because, as it is presented in Figure 3 C, the Tn of 6 mM Cd-treated peas decreased by as much as 87.9% ($p < 0.05$), compared to the reference treatment. Cadmium induced a stomatal closure in leaves and reduced the Tn more than Pn; it also caused a high increase in WUE in 6 mM Cd-treated peas at BBCH 14–16 stage. Conversely, 6 mM Cd exposure increased a Tn in peas at BBCH 21–23 stage by 15.3% ($p < 0.05$), compared to the reference treatment. Other authors reported similar results as well – cadmium may increase transpiration rate and/or stomatal conductivity. Thus an increase in Ci in pea leaves at lateral shoots stage indicates that cadmium reduced Pn mostly by reducing CO₂ fixation by Rubisco (Wahid et al., 2007). Cadmium stress also produces disturbances in water balance and thus a reduction in WUE was observed with cadmium treatments in other (Popova et al., 2008; Rascio et al., 2008) as well as our (Fig. 3 D) research. This might be due to the inhibition of absorption and translocation of water, as previously observed by Poschenrieder and Barcelo (1999).

Thus, the peas at leaf development (BBCH 14–16) stage were more sensitive to cadmium treatment than at lateral shoots (BBCH 21–23) stage, and cadmium application to the growth substrate at different growth stages of pea influenced its response to the stress.

Conclusions

1. The obtained results showed that the lower 1 mM cadmium (Cd) solution treatment had a very low and mostly insignificant impact on biomass accumulation as well as on photosynthetic and transpiration rates. The higher 6 mM Cd solution treatment led to an almost three-fold higher decrease in dry biomass (as compared with the age adequate control) in peas at leaf development stage in comparison with those at lateral shoots stage. Chlorophyll content decreases were also higher in pea leaves at leaf development stage than at lateral shoots, and the bleaching effect of cadmium on leaf tissues at leaf development stage of peas was more intensive too.

2. The photosynthetic rate of peas at leaf development stage (ten days after germination) was more sensitive to cadmium treatment. One week older plants, i.e. peas at lateral shoots stage, reacted to cadmium stress slightly differently. Intercellular CO₂ concentration (Ci) in peas at leaf development stage decreased, whereas, Ci in peas at lateral shoots stage increased, compared to the reference treatment ($p < 0.05$). Cadmium induced a stomatal closure in leaves and reduced transpiration rate (Tn) more than photosynthesis, and this caused a high increase in water use efficiency (WUE) in 6 mM Cd-treated peas at leaf development stage. Conversely, 6 mM Cd increased Tn and decreased WUE of peas at lateral shoots stage.

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Kadmio poveikis dviejų vystymosi tarpsnių sėjamojo žirnio (*Pisum sativum* L.) fotosintezės rodikliams

I. Januškaitienė

Vytauto Didžiojo universitetas

Santrauka

Tyrimų tikslas – ištirti 1 ir 6 mM CdSO₄ poveikį dviejų vystymosi tarpsnių sėjamojo žirnio (*Pisum sativum* L.) fotosintezei ir augimui. Žirniai buvo pasėti į vegetacinius indus su paruoštu neutralaus rūgštumo durpių substratu, o praėjus 10 ir 17 dienų po sudygimo, t. y. lapų vystymosi (BBCH 14–16) ir šoninių ūglių formavimosi (BBCH 21–23) tarpsnių, palaistyti 1 ir 6 mM Cd tirpalu. Tirtų kadmio koncentracijų poveikis BBCH 14–16 ir BBCH 21–23 tarpsnių žirnių viduląsteliniam CO₂ kiekiui, transpiracijai ir vandens naudojimo efektyvumui buvo skirtingas. Lapų vystymosi tarpsnio žirnių viduląstelinis CO₂ kiekis, esant 1 ir 6 mM Cd poveikiui, sumažėjo 27,4 ir 32,8 %, o šoninių ūglių formavimosi tarpsnio žirnių padidėjo atitinkamai 28,5 ir 22,1 % ($p < 0,05$), palyginti su šių tarpsnių kontroliniais augalais. Stipresnis 6 mM Cd poveikis sąlygojo BBCH 14–16 tarpsnio žirnių žiotelių užsivėrimą ir transpiracijos intensyvumą sumažino labiau nei fotosintezės, o tai lėmė šių žirnių vandens naudojimo efektyvumą padidėjimą net 119,4 %. Priešingai, BBCH 21–23 tarpsnio žirnių 6 mM Cd poveikis transpiracijos intensyvumą padidino, o vandens naudojimo efektyvumą sumažino. 1 mM Cd koncentracijos poveikis žirnių fotosintezei bei biomasės kaupimui buvo labai silpnas ir dažniausiai neesminis. Po palaistymo praėjus penkioms dienoms, stipresnis 6 mM Cd poveikis BBCH 14–16 tarpsnio žirnių biomasę sumažino 56,1 %, o BBCH 21–23 tarpsnio – tik 21,9 %, palyginti su atitinkamo vystymosi tarpsnio kontroliniais augalais. Chlorofilų kiekio nuostoliai taip pat buvo didesni BBCH 14–16 nei BBCH 21–23 tarpsnio žirnių lapuose.

Reikšminiai žodžiai: vystymosi tarpsnis, kadmio, fotosintezės intensyvumas, viduląstelinis CO₂ kiekis, vandens naudojimo efektyvumas, pigmentai, biomasė, *Pisum sativum*.