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Effect of potassium bicarbonate on photosynthetic parameters of *Setaria viridis* under drought conditions

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Abstract

The current study set out to investigate the effects of drought stress and potassium bicarbonate (KHCO_3) on green foxtail (*Setaria viridis* (L.) Beauv.) photosystem II (PSII) photochemistry under a moderate and severe drought. The plants at phenological stage 13 (according to BBCH scale) were divided into three groups and sprayed with water or with 10, 20 and 30 mg l⁻¹ KHCO_3 . The plants of the first group (well-watered) were hand-watered every second day. The plants of the second (moderately stressed) and third (severely stressed) groups were used for drought stress treatment by withholding water. The results indicated that drought conditions resulted in a decrease in maximum quantum yield and effective quantum yield most likely due to the expected photoinhibition of photosystem II. Decreased gas exchange parameters revealed that the reduction in photosynthesis of green foxtail under drought stress was caused by the stomatal factors. A significant increase in the maximum quantum yield, effective quantum yield and gas exchange parameters in KHCO_3 treated plants showed that KHCO_3 protects photosystem II of green foxtail from drought, and may have potential benefit for other C₄ plants.

Key words: drought stress, green foxtail, KHCO_3 , photosystem II.

Introduction

Among different abiotic stresses, such as low and high temperature, salinity, pollutants, etc., drought is considered as a major abiotic factor that limits plant growth and development (Reddy et al., 2004). Earl and Davis (2003) have suggested that three main mechanisms decrease crop yield under drought stress: reduced absorption of photosynthetically active radiation, decreased radiation-use efficiency and reduced harvest index. Drought-induced stomatal limitation is generally accepted as the main factor which determines reduction in photosynthesis (Farooq et al., 2009). Moreover, restricted availability of carbon dioxide resulted in increased sensitivity to photo-damage (Reddy et al., 2004; Pinheiro, Chaves, 2011). Besides, inhibition of CO₂ assimilation results in accelerated production of active oxygen via the chloroplast Mehler reaction because of the excessive light energy that cannot be converted to biochemical energy (Foyer, Noctor, 2005).

Ghannoum (2009) assumed that C₄ plants make a significant contribution to the global carbon budget, and C₄ crops, including maize, sugarcane, sorghum, millets, giant miscanthus and switchgrass, are determinant to current and future food security around the world. *Setaria viridis* (L.) Beauv. (green foxtail) is a member of the *Panicoideae* subfamily and is a close

relative of several major forage and bioenergy grasses. Due to its C₄ carbon fixation pathway, diploid nature, short life cycle and relatively small genome (~510 Mb), green foxtail has been rapidly adopted as a model for investigations the genetic of the biofuel crop switchgrass and for C₄ photosynthesis (Doust et al., 2009; Brutnell et al., 2010; Li, Brutnell, 2011; Layton, Kellogg, 2014). Ghannoum (2009) has indicated that C₄ plants may be similarly or even more sensitive in comparison with C₃ plants but the response of C₄ plants to drought stress has not been so well studied as response of C₃ plants and it is important to understand how drought stress influences the photosynthesis in C₄ plants.

Potassium is one of the essential macro elements in plant nutrition and energy metabolism such as accumulation of carbohydrates, photosynthesis, and maintenance of normal water regime (Wang et al., 2013). In plant cells, potassium is found in various salts, including potassium bicarbonate (KHCO_3). Because KHCO_3 is harmless for the environment, it can be used in ecological farms (European Commission, 2014). It has been reported that KHCO_3 can be used to reduce plant stress under low amounts of CO₂ (Li, Hao, 2013), as an effective fungicide against mildew (Wenneker, Kanne, 2010) and apple scab (Marku et al., 2014). It was shown that spraying with

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KHCO_3 resulted in increased photosynthesis in rice and soybean (Yao et al., 2009; Li, Hao, 2013). However, no information is available in the literature on the influence of potassium bicarbonate on the photosynthesis in C_4 plants. Therefore, the aim of this study is to evaluate the effect of potassium bicarbonate (KHCO_3) on photosystem II (PSII) photochemistry in green foxtail (as a model C_4 plant) under drought conditions.

Materials and methods

Research was carried out in Institute of Biology and Plant Biotechnology of Aleksandras Stulginskis University and Laboratory of Agrobiotechnology of Joint Research Centre in 2015.

Plant cultivation and drought treatment. The plants of green foxtail (*Setaria viridis* (L.) Beauv.) were grown in plastic pots 12 cm in diameter and 10 cm in height, 50 plants per pot, in a growth chamber MLR-351 (Sanyo Electric Co., Ltd). The pots were filled with substrate which was composed of peat and sand at 3:1 volume ratio. Environmental conditions in the growth chamber were as follows: light intensity – $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, photoperiod – 16/8 h (day/night), temperature – $25/18^\circ\text{C}$, relative air humidity – $65 \pm 5\%$. The plants were hand-watered every second day to maintain $65 \pm 5\%$ substrate humidity. After four weeks, the plants (at phenological stage 13 according to BBCH scale) were divided into three groups and sprayed with water or with 10, 20 and 30 mg l^{-1} potassium bicarbonate (KHCO_3). The plants of the first group (well-watered) were hand-watered every second day. The plants of the second (moderately stressed) and third (severely stressed) groups were used for drought stress treatment by withholding water. Substrate water content (SWC) was determined by taking daily samples with a cylindrical borer (1.4 cm diameter and 10 cm length) and gravimetrically measuring by weighting the samples shortly after sampling and after drying them to a constant weight. Substrate water content (%) was calculated as $\text{SWC} = \text{wet weight} - \text{dry weight} / \text{wet weight} \times 100$. Experiments were set up in a complete randomized design with three replicates per treatment and 150 plants per each replicate. At the end of experiment, when substrate humidity was $65 \pm 5\%$ for well-watered, $45 \pm 5\%$ for moderately stressed and $25 \pm 5\%$ for severely stressed plants, chlorophyll fluorescence and gas exchange parameters were measured.

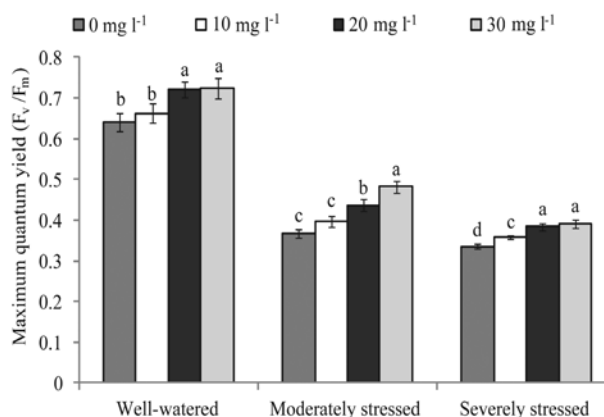
Measurement of chlorophyll fluorescence. Chlorophyll fluorescence was measured at room temperature in dark-adapted for 20 minutes green foxtail leaves with a portable fluorometer IMAGING-PAM M-Series (Walz, Germany). The experimental protocol of Genty et al. (1989) was followed. The minimal (F_0) and maximal (F_m) fluorescence levels were measured in the middle region of the second pair of fully expanded leaves after 20 minutes dark adaptation. All measurements were performed on 3 plants of each replication. Maximum quantum yield (F_v/F_m) of effective quantum yield (Φ_{PSII}) of PSII photochemistry and non-photochemical quenching (NPQ) were calculated according to the following equations: $F_v/F_m = (F_m - F_0) / F_m$, $\Phi_{\text{PSII}} = (F_m - F_s) / F_m$ and $\text{NPQ} = (F_m - F_m') / F_m'$ (Genty et al., 1989).

Measurement of gas exchange. Gas exchange was measured with a portable fluorescence system GFC-3000 (Walz, Germany). Stomatal conductance (g_s) ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), transpiration rate (E) ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) and net photosynthetic rate (P_N) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of a second pair of fully expanded leaves were registered every 30 seconds for 40 minutes; from these data there were calculated. All measurements were performed on 3 plants of each replication. 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 a sample cell – $300\text{--}400 \mu\text{mol CO}_2 \text{mol}^{-1}$, relative humidity in a sample cell – 30% and lightness in quant – $180 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Statistical analysis. The least significant differences of the results were calculated using the software *STAT 1.55* from *SELEKCIJA* and *IRRISTAT* (Tarakanovas, Raudonius, 2003). The mean value and standard error (SE) for each treatment were calculated based on the number of independent replications.

Results and discussion

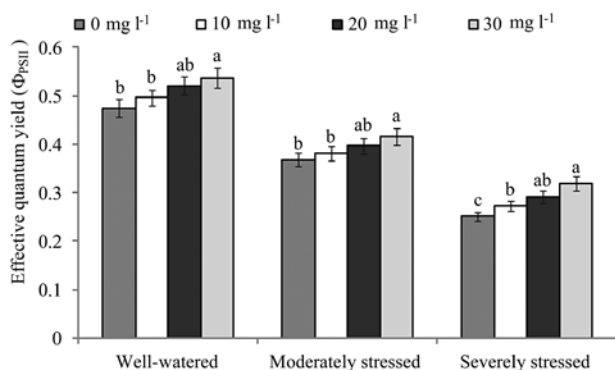
The effect of KHCO_3 on the stability of PSII under drought stress was investigated. The responses of the maximum quantum yield (F_v/F_m) of PSII photochemistry to KHCO_3 treatment are shown in Figure 1. Decreased F_v/F_m under drought stress indicates damage to the PSII reaction centre (Nar et al., 2009; Oukarroum et al., 2012). In this study, the decrease of the F_v/F_m in the KHCO_3 untreated plants under drought stress was more pronounced in comparison with KHCO_3 treated plants. Under KHCO_3 treatment, F_v/F_m value was 1.1–1.3-fold higher (in moderately stressed plants) and 1.1–1.2-fold higher (in severely stressed plants) as compared to KHCO_3 untreated plants. Lower decrease in F_v/F_m values in KHCO_3 treated plants indicates that KHCO_3 might have a protective role in PSII under drought stress.



Note. Means not sharing a common letter (a, b) are significantly different ($P < 0.05$).

Figure 1. Effect of potassium bicarbonate (KHCO_3) on the maximum quantum yield (F_v/F_m) of green foxtail plants under different ($65 \pm 5\%$ for well-watered, $45 \pm 5\%$ for moderately stressed and $25 \pm 5\%$ for severely stressed plants) substrate humidity

Decrease of effective quantum yield (Φ_{PSII}) of PSII photochemistry is related to down-regulation of electron transport and increase in excitation energy quenching in the PSII antennae (Ghannoum, 2009; Saglam et al., 2014). The Φ_{PSII} of the KHCO_3 untreated plants under drought stress was decreased by 0.107 in moderately stressed plants and by 0.224 in severely stressed plants in comparison with well-watered plants (Fig. 2).



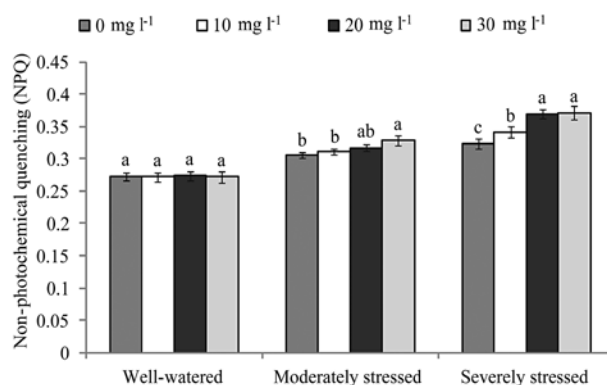
Note. Means not sharing a common letter (a, b) are significantly different ($P < 0.05$).

Figure 2. Effect of potassium bicarbonate (KHCO_3) on the effective quantum yield (Φ_{PSII}) of green foxtail plants under different ($65 \pm 5\%$ for well-watered, $45 \pm 5\%$ for moderately stressed and $25 \pm 5\%$ for severely stressed plants) substrate humidity

Under drought conditions, Φ_{PSII} of the green foxtail treated with 20 and 30 mg l⁻¹ KHCO_3 increased significantly in comparison with KHCO_3 untreated plants. The obtained changes in the Φ_{PSII} parameter also supported the protective role of KHCO_3 in the photosynthetic system of green foxtail under drought stress.

Increase in non-photochemical quenching (NPQ) resulting from drought stress has been previously reported by several research groups (de Souza et al., 2013; Huang et al., 2013). The NPQ of KHCO_3 untreated plants under drought stress was increased by 0.033 in moderately stressed plants and by 0.05 in severely stressed plants in comparison with well-watered plants (Fig. 3). NPQ of the well-watered green foxtail plants was not affected by the KHCO_3 treatment, while under drought stress a statistically significant increase of NPQ in comparison with the KHCO_3 untreated plants was obtained under 20 and 30 mg l⁻¹ KHCO_3 treatment. In the present study, NPQ increase under the highest KHCO_3 treatment indicated the thermal dissipation of energy load on the leaves, perhaps preventing photo damage. The increases in NPQ in foxtail leaves under KHCO_3 indicated thermal dissipation of excess energy in our study and protective role of KHCO_3 in the photosynthetic system.

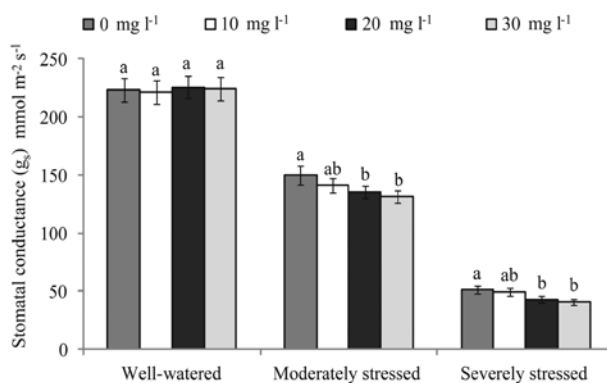
Drought stress usually resulted in stomatal closure which resulted in decreased CO_2 fixation (Chaves et al., 2009). Photosynthesis inhibition can disturb the balance between reactive oxygen species (ROS) and antioxidant production, which can result in ROS accumulation. At high concentration ROS become very injurious to



Note. Means not sharing a common letter (a, b) are significantly different ($P < 0.05$).

Figure 3. Effect of potassium bicarbonate (KHCO_3) on the non-photochemical quenching (NPQ) of green foxtail plants under different ($65 \pm 5\%$ for well-watered, $45 \pm 5\%$ for moderately stressed and $25 \pm 5\%$ for severely stressed plants) substrate humidity

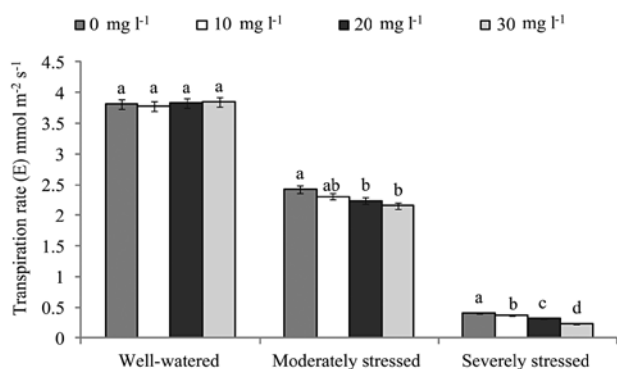
various cell components (Farooq et al., 2009). It has been reported that drought stress can decrease potassium content in the chloroplast which may result in inhibited of photosynthesis and induce further ROS formation (Cakmak, 2005). Under drought conditions, the values of stomatal conductance (g_s) of KHCO_3 untreated green foxtail plants in the present study decreased by 73.9 mmol m⁻² s⁻¹ in moderately stressed plants and by 172.3 mmol m⁻² s⁻¹ in severely stressed plants in comparison with well-watered plants (Fig. 4).



Note. Means not sharing a common letter (a, b) are significantly different ($P < 0.05$).

Figure 4. Effect of potassium bicarbonate (KHCO_3) on the stomatal conductance (g_s) of green foxtail plants under different ($65 \pm 5\%$ for well-watered, $45 \pm 5\%$ for moderately stressed and $25 \pm 5\%$ for severely stressed plants) substrate humidity

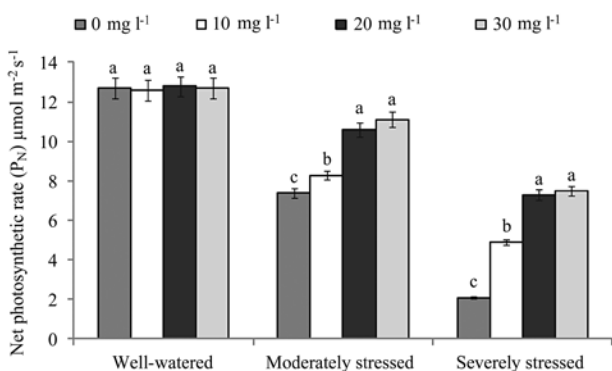
As a result, the transpiration rate (E) also decreased (Fig. 5). Stomatal conductance (g_s) and transpiration rate (E) of the well-watered green foxtail plants were not affected by the KHCO_3 treatment, while under drought stress a statistically significant decrease of both parameters in comparison with the KHCO_3 untreated plants was obtained under 20 and 30 mg l⁻¹ KHCO_3 treatment (Figs. 4 and 5).



Note. Means not sharing a common letter (a, b) are significantly different ($P < 0.05$).

Figure 5. Effect of potassium bicarbonate (KHCO_3) on the transpiration rate (E) of green foxtail plants under different ($65 \pm 5\%$ for well-watered, $45 \pm 5\%$ for moderately stressed and $25 \pm 5\%$ for severely stressed plants) substrate humidity

Net photosynthetic rate (P_N) of green foxtail plants was considerably affected by drought stress (Fig. 6). Under drought conditions, P_N values of KHCO_3 untreated plants decreased by $5.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in moderately stressed plants and by $11.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in severely stressed plants in comparison with well-watered plants. The decrease of P_N in KHCO_3 treated plants was significantly lower as compared with untreated plants.



Note. Means not sharing a common letter (a, b) are significantly different ($P < 0.05$).

Figure 6. Effect of potassium bicarbonate (KHCO_3) on the net photosynthetic rate (P_N) of green foxtail plants under different ($65 \pm 5\%$ for well-watered, $45 \pm 5\%$ for moderately stressed and $25 \pm 5\%$ for severely stressed plants) substrate humidity

Stomatal and non-stomatal factors cause reduction in photosynthesis (Farooq et al., 2009). Decreased g_s , E and P_N in the present study indicated that reduction in photosynthesis of green foxtail under drought stress was caused by the stomatal factors. Under drought conditions, K concentration in plant cells decreases which can depress the plant resistance to drought stress (Wang et al., 2013). Stomatal closure and internal moisture retention are requisite for control plant water loss via transpiration during drought stress. It has been reported that potassium deficiency under drought increases the

production of ethylene which could inhibit the action of abscisic acid on stomata, suspend stomatal closure and increase transpiration rate (Benlloch-Gonzalez et al., 2010). According to Farooq et al. (2009), drought induced stomatal closure resulted in parallel decline in net photosynthesis. In the present study, decreasing of net photosynthetic rate in KHCO_3 treated plants under drought conditions was significantly lower in comparison with untreated plants. A significant increase in all gas exchange parameters in KHCO_3 treated plants showed that KHCO_3 may minimize photosynthetic losses under drought conditions and possibly could be useful for other C_4 plants. Similar positive effect of potassium supply on g_s , E and P_N was obtained for *Hibiscus rosa-sinensis* (Egilla et al., 2005) and *Gossypium hirsutum* (Pervez et al., 2004).

Conclusions

1. Drought conditions resulted in a significant increase in photoinhibition of photosystem II (PSII) in the plants of green foxtail. Decreased gas exchange parameters revealed that reduction in photosynthesis of green foxtail under drought stress was caused by stomatal factors.

2. Exogenous application of potassium bicarbonate (KHCO_3) increased the tolerance of green foxtail to the drought stress through increasing thermal dissipation of excess energy.

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Kalio hidrokarbonato poveikis *Setaria viridis* fotosintezės parametrams sausros sąlygomis

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Santrauka

Tirtas sausros streso ir kalio hidrokarbonato (KHCO_3) poveikis žaliosios šerytės (*Setaria viridis* (L.) Beauv.) II fotosistemai (PSII) vidutinės ir stiprios sausros sąlygomis. Augalai, esantys 13 fenologinėje fazėje (pagal BBCH skalę), buvo suskirstyti į tris grupes ir nupurkšti vandeniu arba 10, 20 ir 30 mg^{-1} koncentracijų KHCO_3 tirpalais. Pirmosios grupės augalai (įprastos drėgmės sąlygos) buvo laistomi kas antrą dieną. Antrosios (vidutinės sausros sąlygos) ir trečiosios (stiprios sausros sąlygos) grupių augalai buvo nelaistomi sudarant sausros sąlygas. Nustatyta, kad sausros sąlygos mažino maksimalų ir efektyvų kvantų našumą, veikiausiai dėl II fotosistemos slopinimo. Sumažėję dujų apytakos parametrai parodo, kad žaliosios šerytės fotosintezės intensyvumo sumažėjimas sausros sąlygomis nulemiamas žiotelių laidumo. Reikšmingas maksimalaus ir efektyvaus kvantų našumų ir dujų apytakos parametru padidėjimas paveikus KHCO_3 įrodo, kad kalio hidrokarbonatas apsaugo žaliosios šerytės augalų II fotosistemą nuo sausros pažeidimų ir gali būti veiksmingas kitiems C_4 fotosintezės tipo augalams.

Reikšminiai žodžiai: II fotosistema, KHCO_3 , sausros stresas, žalioji šerytė.