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Changes in the sensitivity of agricultural plants to the impact of ozone and UV-B radiation in simulated warmer climate conditions

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The sensitivity of agricultural crops and weed to the impact of ozone and UV-B radiation was evaluated according to changes in their dry biomass and concentration of photosynthetic pigments. Pisum sativum L., Raphanus sativus L. and Phleum pretense L. were most sensitive to the impact of ozone in current climatic conditions (350 ppm of CO2 and 21 °C day/14 °C night temperatures). The sensitivity of all test crops to the impact of ozone decreased significantly under warmer climatic conditions – 700 ppm of CO2 and 25 °C day/19 °C night temperatures. Pisum sativum L. and Chenopodium album L. appeared to be most sensitive to the impact of UV-B radiation under current climatic conditions. Changes in the sensitivity of plants to the impact of UV-B radiation under warmer climatic conditions were not as pronounced as those for ozone, and were highly species-dependent. Sensitivity to the impact of UV-B radiation under warmer climatic conditions decreased for Lycopersicon esculentum Mill. and Chenopodium album L. and increased for Raphanus sativus L. and Phleum pretense L.

Key words: climate warming, carbon dioxide, tropospheric ozone, UV-B radiation, plant sensitivity

INTRODUCTION

Increased anthropogenic emissions of carbon dioxide and other greenhouse gases into the atmosphere cause global climatic changes which can essentially affect the growth and development of vegetation (Fuhrer, 2003; Norby, Luo, 2004). According to the most reliable scenario of global climatic change, the concentration of greenhouse gases is predicted to double in the 21st century, while the mean ground surface temperature is expected to increase by 2–4.5 °C (IPCC, 2007).

Along with climate warming, other important environmental changes, such as an increase in the concentration of tropospheric ozone and UV-B radiation, are usually considered as the most significant anthropogenic factors on both regional and global scales, so the prediction and evaluation of the response of plants to multiple climatic and environmental stresses are highly important (Morgan et al., 2003).

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Investigation of the interaction between ozone and CO_2 has shown that in most cases elevated CO_2 mitigates the adverse impact of ozone (Lutz et al., 2000; Donnelly et al., 2001). The reduction in leaf conductance under elevated CO_2 and reduced ozone uptake are the main explanations for this phenomenon (Fuhrer, 2003; Morgan et al., 2003). Other possible mechanisms such as an increase in Rubisco content and activity, increased carbon and energy through a more intensive net assimilation, and an increase in the activity of antioxidant enzymes are also used to explain the protective effects of elevated CO_2 (Donnelly et al., 2001; Gaucher et al., 2003). However, data on the ameliorative effects of elevated CO_2 are rather controversial because experiments with wild plants in most cases failed to reveal the ameliorative effects of CO_2, or the effect was much less pronounced when compared to that associated with agricultural crops (Karnosky et al., 2005; Ramo, 2006).

Plants have developed various defense mechanisms to protect themselves against UV-B radiation and can adapt to low levels of UV-B radiation; however, elevated UV-B doses have a detrimental impact on the photosynthetic apparatus and growth of plants and cause DNA damage, changes in gene expression, and affect the content of protective pigments and the morphology of leaves (Qaderi et al., 2007).

The susceptibility of plants to UV-B radiation can be influenced by ambient conditions, including elevated CO_2 and temperature (Shi et al., 2004). Theoretically, it could be argued that due to an increased content of secondary metabolites under elevated CO_2, the amount of UV-B absorbing compounds should increase and the negative impact of increased UV-B doses would be reduced. However, only a limited number of investigations have confirmed these predictions (Koti et al., 2007).

Considering that most studies have only taken into account the impact of elevated CO_2 on the sensitivity of plants to increased concentrations of tropospheric ozone and UV-B radiation, the aim of the present study was to evaluate changes in the sensitivity of agricultural plants to the impact of ozone and UV-B radiation under conditions of elevated CO_2 and temperature.

MATERIALS AND METHODS

Experiments were conducted in chambers of a controlled environment, located at the Institute of Horticulture (Lithuania, Babtai). Four chambers (24 m^2 each) were used for the study. Seven of the most widespread agricultural crops were selected for the investigation: barley (*Hordeum vulgare* L. cv 'Aura'), pea (*Pisum sativum* L. cv 'Ilgiai'), red clover (*Trifolium pretense* L. cv 'Liepsna'), timothy (*Phleum pretense* L. cv 'Gintaras'), tomato (*Lycopersicon esculentum* Mill. cv 'Svara'), radish (*Raphanus sativus* L. cv 'Zara') and soybean (*Glycine max* Merr. cv 'Progres'). The weed known as fat hen (*Chenopodium album* L.) was also included.

Plants (25 per pot) were sown and grown in a neutral peat substrate in 5-l pots (21 cm in diameter). In every treatment, there were three pots of replication. The plants were grown in a greenhouse at an average temperature of 20–25 °C under natural solar radiation until germination and then for a further week. The plants were then transferred to chambers with a photoperiod of 14 h and a 21 °C-day / 14 °C-night temperature. High-pressure sodium lamps (SON-T Agro, PHILIPS) were used for illumination. After two days of acclimation, different treatments were started. The duration of a treatment was 9 days.

To compare the sensitivity of plants to the impact of ozone and UV-B radiation, the plants were grown under current (21 °C-day / 14 °C-night, 350 ppm) and elevated temperature and CO_2 (25 °C-day / 19 °C-night, 700 ppm) conditions. The response of plant species to the impact of different ozone concentrations (20, 40 and 80 ppb) and UV-B daily doses (0, 2 and 4 kJ/m^2) were investigated in both current and warmed (elevated temperature and CO_2) climatic conditions.

Ozone concentrations were maintained with a OSR-8 ozone generator (Ozone Solutions, Inc.) 7 hours a day, 5 days a week. The level of ozone was monitored using the portable ozone sensor OMC-1108 (Ozone Solutions, Inc.). The UV-B radiation was supplied by special lamps (TL 40W / 12RS UV-B Medical, Philips). The daily UV-B doses were regulated by the duration of exposure.

Dry over-ground biomass and the concentration of photosynthetic pigments (a, b chlorophylls and carotenoids) were determined at the end of each treatment. Photosynthetic pigments were analysed using a spectrophotometer (Genesys 6, ThermoSpectronic, USA) and 100% acetone extracts prepared according to Wettstein's method (Wettstein, 1957; Гавриленко, 1975). Photosynthetic pigments were expressed in mg/g of fresh weight. The samples were dried in an oven at 60 °C until a constant dry overground biomass was obtained. The overground biomass was expressed in mg $plant^{-1}$.

The independent-samples *t*-test was applied to estimate the difference between reference and treatment values. The levels of significance for differences between the overground biomass and the concentration of photosynthetic pigments were analysed using one-way ANOVA. All analyses were performed employing STATISTICA software (version 6.0), and the results were expressed as mean values and their standard errors (S. E.).

RESULTS

The overground biomass of reference plants (ozone concentration 20 ppb) in both current and warmed climates was considered as the 100% level, and the biomass of plants under elevated concentrations of ozone (40 and 80 ppb) was expressed as a percentage relative to the reference treatment for a more obvious comparison of the response of plants to ozone impact in different climatic conditions (Fig. 1).

An essentially lower sensitivity of plant species to elevated ozone concentrations was detected in warmed climatic conditions (Fig. 1), and plants accumulated a higher biomass relative to current climatic conditions under the same ozone concentrations. These differences were statistically significant ($p < 0.05$), with the exception of fat hen. Another important feature of the response under elevated climatic conditions to the impact of ozone was characteristic and involved the accumulation of the highest biomass by the majority of examined species under an elevated ozone (40 ppb) concentration, with a decrease in biomass starting only under 80 ppb.

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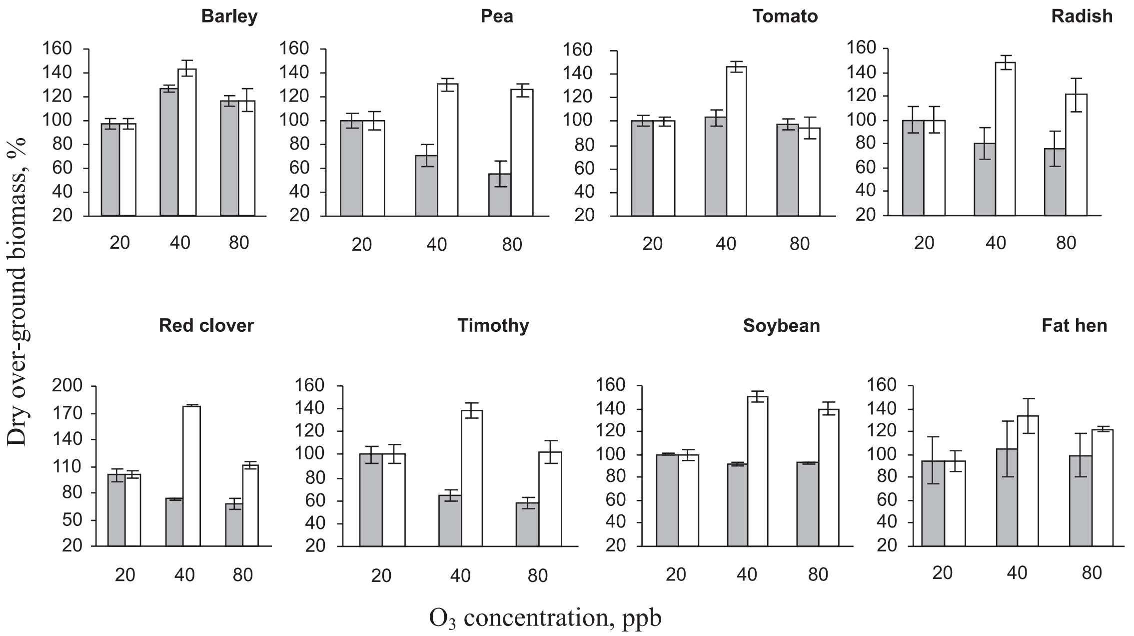

Fig. 1. The impact of elevated ozone concentrations on dry overground biomass (mean ± SE; n = 25) of agricultural plants under current (grey boxes) and simulated warmed (white boxes) climatic conditions. The value of the dry overground biomass (mg plant^{-1}) for the reference treatment (20 ppb) was considered the 100% level

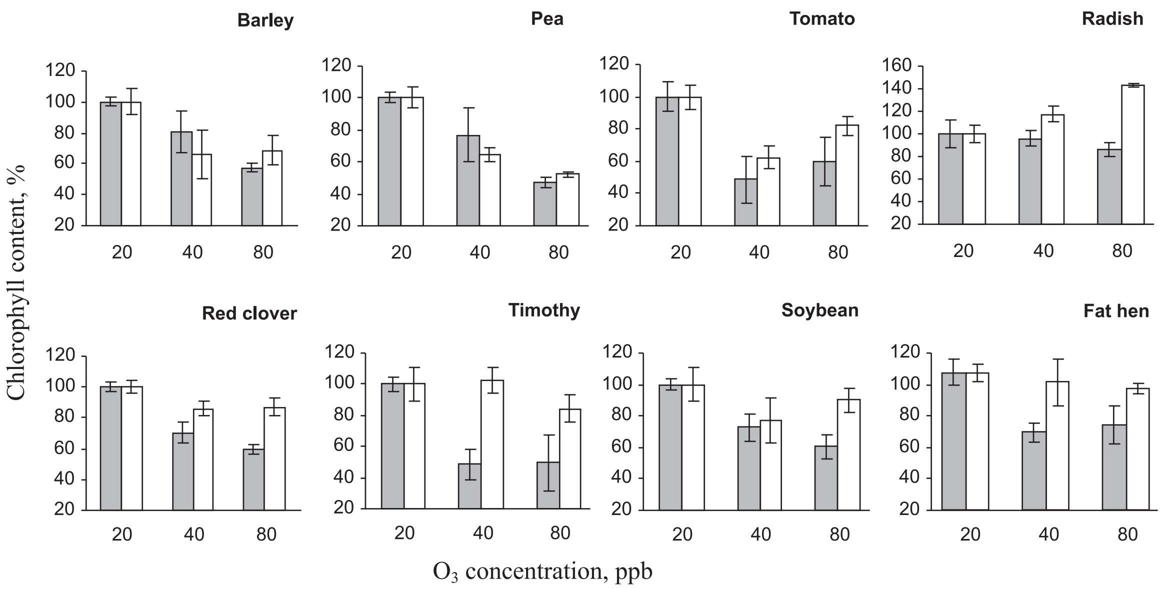

Fig. 2. The impact of elevated ozone concentrations on total chlorophyll content (mean ± SE; n = 3) in leaves of agricultural plants under current (grey boxes) and simulated warmed (white boxes) climatic conditions. The value of chlorophyll (a + b) content (mg/g of fresh weight) for the reference treatment (20 ppb) was considered as 100%

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Data on the total content of chlorophyll (a + b) in the leaves of species under different ozone concentrations in current and elevated climatic conditions (Fig. 2) are presented in the same manner as the biomass data in Fig. 1. In current climatic conditions, a gradual decrease in the content of total chlorophyll (a + b) following an increase in ozone concentrations is characteristic of barley, pea, radish, red clover, timothy and soybean. This trend is the most pronounced for pea and timothy, the content of chlorophyll in the weight of fresh leaves of these plants under an ozone concentration of 80 ppb being 46% and 49%, respectively, versus the reference treatment.

The negative impact of ozone on the content of chlorophyll (a + b) in the warmed climate was much less pronounced relative to that of the current climate. An exception was the radish, in which an increase in chlorophyll content was detected follow-

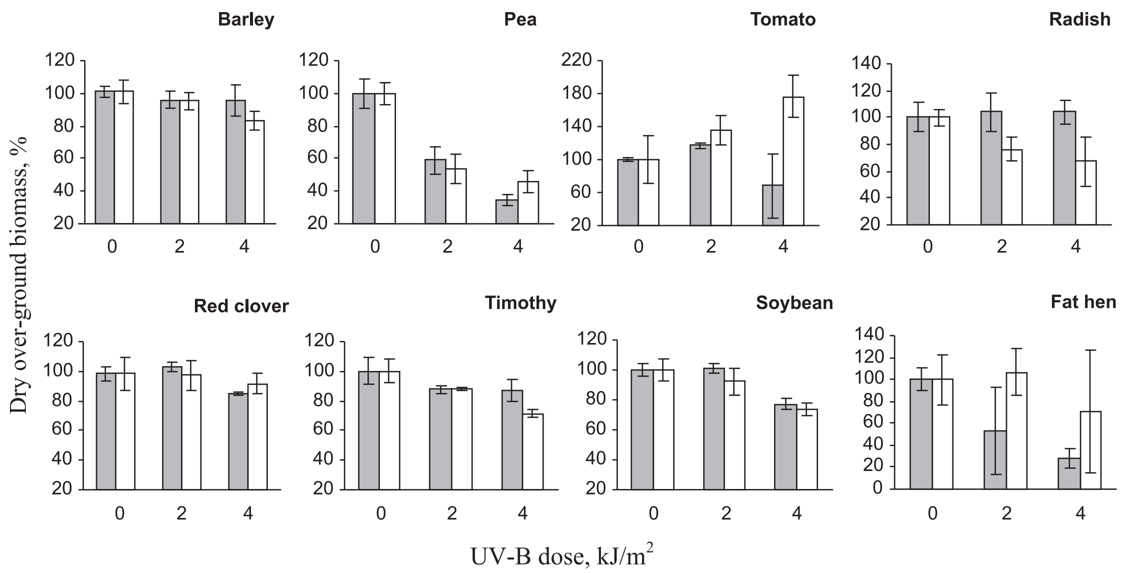

Fig. 3. The impact of different daily UV-B doses on dry over-ground biomass (mean ± SE; n = 25) of agricultural plants under current (grey boxes) and simulated warmed (white boxes) climatic conditions. The value of dry overground biomass (mg plant^{-1}) for the reference treatment (zero UV-B dose) was considered as 100%

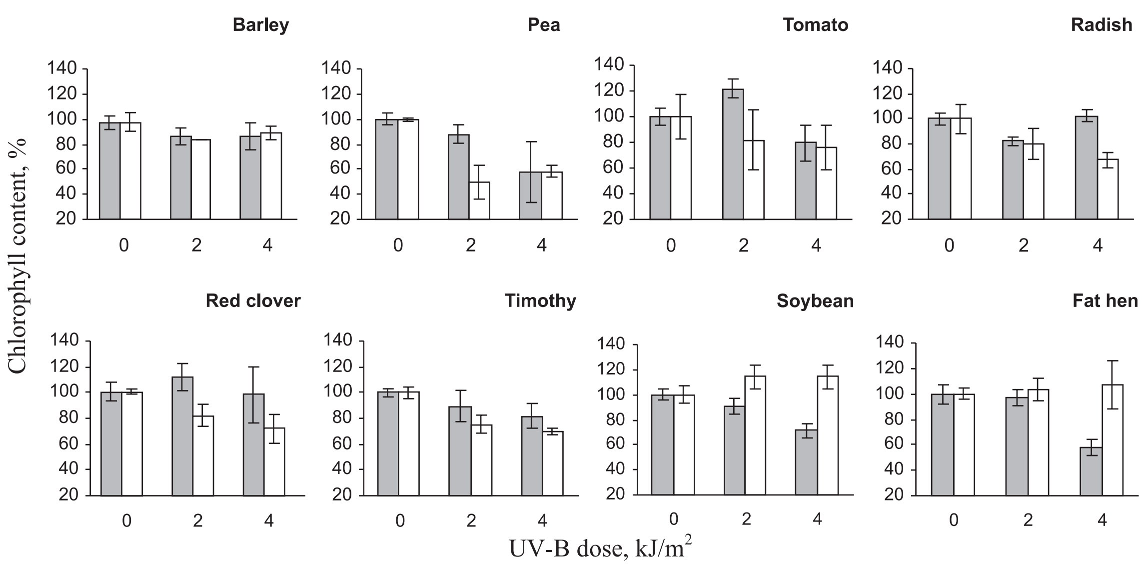

Fig. 4. The impact of different daily UV-B doses on total chlorophyll content (mean ± SE; n = 3) in leaves of agricultural plants under current (grey boxes) and simulated warmed (white boxes) climatic conditions. The value of chlorophyll content (mg/g fresh weight) for the reference treatment (zero UV-B dose) was considered as 100%

ing an increase in ozone concentration under elevated climatic conditions (Fig. 2).

Data on the impact of different daily UV-B doses on plants in current and warmed climatic conditions are presented in the same way as for ozone, i. e. values for reference treatments (zero UV-B dose) in current and simulated warmed climates were taken as the 100% levels, and measurements made under different UV-B (2 and 4 kJ/m^2) doses are expressed as a percentage relative to the values of the reference treatment.

Under current climatic conditions, pea and fat hen appeared to be most sensitive to the impact of UV-B radiation (Fig. 3). Dry overground biomass following daily exposures of 2 kJ/m^2 was reduced by 41% for pea and 46% for fat hen, while a UV-B dose of 4 kJ/m^2 reduced the biomass by 65% and 74%, respectively. The negative impact of UV-B radiation on the other species was less pronounced. However, the lowest UV-B dose (2 kJ/m^2) tended to stimulate the accumulation of biomass in radish, red clover and soybean, and this stimulation was statistically significant for tomato ($p < 0.05$) (Fig. 3).

Changes in the sensitivity of plants to the impact of UV-B radiation in the warmed climate were not as pronounced or consistent as in the case of ozone (Fig. 1) and were highly species-dependent. No statistically significant differences in the impact of UV-B dose on biomass were determined for barley or red clover under the different climatic conditions (Fig. 3). The sensitivity of tomato and fat hen to the impact of UV-B radiation decreased in elevated climatic conditions relative to that of current climatic conditions. Tomato accumulated the greatest biomass under the highest daily UV-B dose (4 kJ/m^2), while fat hen showed the greatest accumulation under the medium dose

(2 kJ/m^2). In contrast, the sensitivity of radish and timothy to the impact of UV-B increased, and these species accumulated a lower biomass under simulated warmed climatic conditions as compared to that measured for the same UV-B radiation dose under current climatic conditions.

The total content of chlorophyll (a + b) under current climatic conditions decreased following increased UV-B doses for most of the study species (Fig. 4). However, an about 10% increase in chlorophyll content was detected with UV-B doses of 2 kJ/m^2 in tomato and red clover leaves. The maximum (over 40%) reduction in the content of chlorophyll under a UV-B dose of 4 kJ/m^2 was detected in pea and fat hen leaves.

A depression in chlorophyll synthesis due to UV-B radiation was more pronounced under warmed climatic conditions for most of the study species. Differences between total chlorophyll content and the reference treatment for tomato, radish, red clover and timothy ranged from 20.0 to 33.8%. A statistically insignificant ($p > 0.05$) increase in chlorophyll content was detected following an increase in UV-B radiation under warmed climatic conditions for soybean and fat hen (Fig. 4).

DISCUSSION

Our investigations have shown a significantly increased resistance of agricultural crops to the impact of ozone in the warmed climate, whereas relative differences between the accumulated biomass under the same ozone concentrations in current and elevated climatic conditions for weed (*Chenopodium album* L.) were statistically insignificant (Fig. 1). Other experiments with wild plants (trees and grasses) also failed to show the ameliorative effect of CO_2 on the impact of ozone in most cases, or this effect was much less pronounced than that recorded for agricultural crops (Karnosky et al., 2005; Ramo, 2006). Taking into account the positive response of wild species to elevated CO_2 and the less pronounced response of agricultural crops (Gaucher et al., 2003; Ramo, 2006), it seems that elevated CO_2 usually does not ameliorate the impact of increased ozone concentrations.

Considering the impact of ozone on the growth and yield of agricultural plants, it should be noted that low concentrations of ozone may stimulate the growth of some plant species (Morgan et al., 2003; Bender et al., 2006). Our study revealed an increase in biomass accumulation under an ozone concentration of 40 ppb for barley, tomato and fat hen, but the difference from the reference treatment (20 ppb) was significant only for barley in current climatic conditions. In the simulated warmed climate (elevated CO_2 and temperature), the greatest biomass of most species was accumulated under an increased concentration (40 ppb), and that of barley under a concentration of 80 ppb, the differences from the reference treatment (20 ppb) being statistically significant.

The results of our investigations have shown that pea and fat hen are most sensitive to the impact of UV-B radiation in the current climate. At the same time, the lowest daily UV-B dose (2 kJ/m^2), which corresponds to the average summer ambient UV-B radiation level in our latitudes, tended to stimulate biomass accumulation in tomato, radish, red clover and soybean (Fig. 3). Although no mechanisms concerning the positive impact of ambient UV-B level have been determined, several experiments by other authors have also indicated a positive impact of ambient UV-B levels on the photosynthetic accumulation and growth of species (Shi et al., 2004). Our results and those of other studies might suggest that some species are well adapted to the current ambient level of UV-B radiation.

Data on the possible changes in the sensitivity of plants to UV-B radiation under warmed climatic conditions are very contradictory and species-dependent (Caldwell et al., 2003). According to our investigations, changes in the sensitivity of plants to UV-B radiation in warmed climate are not as pronounced or consistent as those caused by ozone. Statistically significant differences between current and simulated warmed climate treatments for the impact of UV-B doses on biomass accumulation were observed for barley, pea, red clover and soybean. In elevated climatic conditions, the sensitivity of tomato and fat hen to UV-B radiation decreased. In contrast, the sensitivity of radish and timothy increased in the warmed climate (Fig. 3).

CONCLUSIONS

A comparison of changes in the sensitivity of plant species to ozone and UV-B radiation in the warmed climate showed that these changes differ greatly. The sensitivity of agricultural crops to the impact of ozone was essentially reduced, while changes in sensitivity to UV-B were less pronounced and varied from negative to positive depending on the species.

A partial stomatal closure under elevated CO_2 and reduced ozone uptake is usually regarded as the main reason for a decreased plant sensitivity to ozone. More general mechanisms are also presumed to explain this phenomenon, such as an increase in Rubisco content and activity, an increased activity of enzymes, and increased carbon and energy through augmented net assimilation.

If these presumptions regarding the role of general mechanisms (increased activity of enzymes, increased energy, etc.) in reducing plant sensitivity to the impact of ozone were valid, plants under elevated CO_2 should be more resistant not only to ozone, but also to the impact of other stressors, including UV-B. Since the results of the present study and other investigations fail to support these expectations, further investigations concerning the protective mechanisms of elevated CO_2 are needed.

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KULTŪRINIŲ AUGALŲ JAUTRUMO OZONUI, UV-B SPINDULIUOTEI IR DIRBTINAI SUKURTO ŠILTESNIO KLIMATO SĄLYGOMS POKYČIAI

S a n t r a u k a

Tirti septyni žemės ūkio augalai (*Hordeum vulgare* L., *Pisum sativum* L., *Trifolium pretense* L., *Phleum pretense* L., *Lycopersicon esculentum* Mill., *Raphanus sativus* L. ir *Glycine max* Merr.) bei piktžolė – *Chenopodium album* L. Augalų jautrumas ozonui ir UV-B spinduliuotei buvo vertinamas pagal sausos biomasės ir chlorofilų kiekio pokyčius. Esamo klimato sąlygomis (350 ppm CO_2 ir 21°C dienų / 14°C naktį) ozonui jautriausi buvo *Pisum sativum* L., *Raphanus sativus* L. ir *Phleum pretense* L. Mažiau jautrūs ozonui *Hordeum vulgare* L., *Lycopersicon esculentum* Mill. ir *Chenopodium album* L. buvo silpniau pažeisti, o praėjus 3–4 dienoms po poveikio nustatytas spartus regeneracijos procesas. Šiltesnio klimato sąlygomis (700 ppm CO_2 ir 25°C dieną / 19°C naktį) visų tirtų žemės ūkio augalų jautrumas ozono poveikiui sumažėjo statistiškai patikimai. Esamo klimato sąlygomis UV-B spinduliuotės poveikiui jautriausi yra *Pisum sativum* L. ir *Chenopodium album* L., tuo tarpu mažiausia tirta 2 kJ/m^2 UV-B spinduliuotės dozė stimuliavo *Lycopersicon esculentum* Mill., *Raphanus sativus* L., *Glycine max* Merr. ir *Trifolium pretense* L. augimą. Augalų jautrumo pokyčiai šiltesnio klimato sąlygomis buvo išreikšti mažiau, nei ozono poveikio atveju, ir daugiausia priklausė nuo augalo rūšies. Veikiant UV-B spinduliuotei statistiškai patikimų esamo ir šiltesnio klimato sąlygų skirtumų nenustatyta *Hordeum vulgare* L., *Pisum sativum* L., *Trifolium pretense* L. ir *Glycine max* Merr. jautrumui, tuo tarpu *Lycopersicon esculentum* Mill. ir *Chenopodium album* L. jautrumas UV-B šiltesnio klimato sąlygomis sumažėjo, o *Raphanus sativus* L. ir *Phleum pretense* L. padidėjo.

Raktažodžiai: klimato atšilimas, anglies dvideginis, troposferinis ozonas, UV-B spinduliuotė, augalų jautrumas