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Response of different agricultural plants to elevated CO_2 and air temperature

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Abstract

The aim of this study was to estimate the response of different agricultural plants to elevated CO_2 and temperature and to check a hypothesis that current ambient CO_2 concentration is a limiting factor for growth of most agricultural species. Experiments were conducted in the chambers with a controlled climate. Seven most common agricultural crops and one weed species fat hen (*Chenopodium album* L.) were selected for the investigation. Dry over-ground biomass, concentration of chlorophylls and carotenoids were evaluated at the end of the experiments. The over-ground biomass of all investigated species significantly increased along with an increase in CO_2 concentrations and for most species the greatest biomass accumulation was observed at 700–1500 ppm. Response of fat hen biomass accumulation to elevated CO_2 concentration was comparatively small and statistically insignificant, indicating that for this species current CO_2 concentration is not a limiting factor. Analysis of the results on integrated impact of elevated CO_2 (700 ppm) and temperature (+4ºC) on the growth of investigated plants showed that the plant response is highly species specific. Tomato and soybean, which are considered the greatest warmth-loving plants under local climate conditions, produced the highest amount of biomass at elevated both CO_2 and temperature. For other investigated species, no positive interaction between CO_2 and temperature was detected and differences in biomass formation under elevated CO_2 alone and elevated both CO_2 and temperature ere not statistically significant.

Key words: climate change, carbon dioxide, plant response, temperature, agricultural species, weeds, biomass, photosynthetic pigments.

Introduction

Global average temperature has increased by 0.6 ± 0.2ºC over the past century and according to the most reliable global climate change scenario, the concentration of greenhouse gases is predicted to double and to reach approximately 700 ppm within the 21st century, while an increase in the mean earth surface temperature is expected to rise by 1.4–5.8ºC (IPCC, 2007; Le Treut et al., 2007). The impact of global climate warming on ecosystems has become increasingly apparent during the last decades and can essentially affect the growth and development of vegetation (Morison, Lawlor, 1999; Amthor, 2001; Fuhrer, 2003; Lee, 2011).

An impact of elevated CO_2 concentrations on photosynthesis, biomass and yield of agricultural crops has been the subject of different studies. Since elevated CO_2 reduces an oxygenase component of Rubisco (RuBP carboxylase/oxygenase), and Rubisco being not saturated with current CO_2 concentrations, theoretically an increase in photosynthesis intensity and biomass production can be expected up to 1000 or even 2000 ppm of CO_2 (Kirschbaum, 2004). However, plant response to elevated CO_2 differs greatly for different species and is affected by different external factors, such as temperature, nutrients, etc. (Wolfe et al., 1998; Ziska, 2001).

An increase in photosynthesis by 25–75% has been detected in many experimental studies on the impact of doubled CO_2 concentration on C_3 crops (Urban, 2003; Kirschbaum, 2004). An extensive review of the results obtained in the experiments on CO_2 effects on wheat yield has shown an average 30% increase at doubled CO_2 concentration (Amthor, 2001; Pritchard, Amthor, 2005). However, the majority of wild species (trees and grasses) have been found to experience none or very small CO_2 stimulation of net photosynthesis and growth (Ro et al., 2001; Gaucher et al., 2003; Ramo, 2006). The biochemical basis for the elevated atmospheric CO_2 stimulation of C_3 photosynthesis is that high CO_2 around Rubisco accelerates the carboxylation reaction while suppressing the competing oxygenation reaction and subsequently reducing the CO_2 loss and energy costs associated with photorespiration (Long et al., 2004; Leakey et al., 2009). In C_4 species, however, photosynthesis is likely to be CO_2-saturated at low concentrations due to the mechanism for concentrating CO_2 around Rubisco and, therefore, C_4 crops would not benefit much from increases in atmospheric CO_2 levels (Ainsworth, Rogers, 2007). C_3 grasses are also more responsive to elevated CO_2 than are C_4 grasses. As found by Wand et al. (1999), in C_3 grasses, aboveground biomass and nonstructural carbohydrates increased 38% and 37%, respectively, while in C_4 grasses they increased only 12% and 11%. However, a number of researchers have reported enhanced photosynthesis and biomass production in some C_4 species (De Souza et al., 2008; Vu, Allen, 2009).

An impact of elevated CO_2 on photosynthesis and growth depends on the temperature, thus the cumulative effects of the warmed climate (elevated CO_2 and elevated temperature) are of great importance (Morison, Lawlor, 1999; Kirschbaum, 2004; Norby, Luo, 2004). Because of specific Rubisco kinetic properties and a shift of its activity toward carboxylation at higher temperature, carbon dioxide should stimulate net photosynthesis more effectively at elevated temperature (Ziska, 2000).

Experimental studies in most cases have confirmed these theoretical presumptions, and it has been established that not only the plant growth response to elevated CO_2 is usually much more pronounced at higher temperatures but the temperature optimum increases with the increasing CO_2 concentration as well (Sage et al., 1995; Kirschbaum, 2004).

The main aim of this study was to estimate the response of different agricultural plants to elevated CO_2 and temperature and to check a hypothesis that current ambient CO_2 concentration is a limiting factor for growth of most agricultural plants.

Materials and methods

Experiments were conducted during 2004–2008 in four controlled environment chambers located at the Lithuanian Institute of Horticulture. Seven most common agricultural crops: barley (*Hordeum vulgare* L. cv. 'Aura'), pea (*Pisum sativum* L. cv. 'Ilgiai'), red clover (*Trifolium pratense* L. cv. 'Liepsna'), timothy (*Phleum* pratense L. cv. 'Gintaras'), tomato (*Lycopersicon esculentum* Mill. cv. 'Svara'), radish (*Raphanus sativus* L. cv. 'Zara'), soybean (*Glycine max* Merr. cv. 'Progress') and weed – fat hen (*Chenopodium album* L.) were selected for the investigation.

The plants were sown and grown in 5 L pots with neutral (pH 6.0–6.5) peat substrate, 25 plants per pot. All treatments were run in three replicates. Until germination and one week after, the plants were grown in a greenhouse at an average temperature of 20–25ºC under natural solar radiation. Then the plants were transferred to the chambers with a photoperiod of 14 h and 21ºC-day/14ºC-night temperature. High-pressure sodium lamps "SON-T Agro" ("Philips", Germany) were used for illumination. After two days of adaptation, different 10–14 days duration treatments were started.

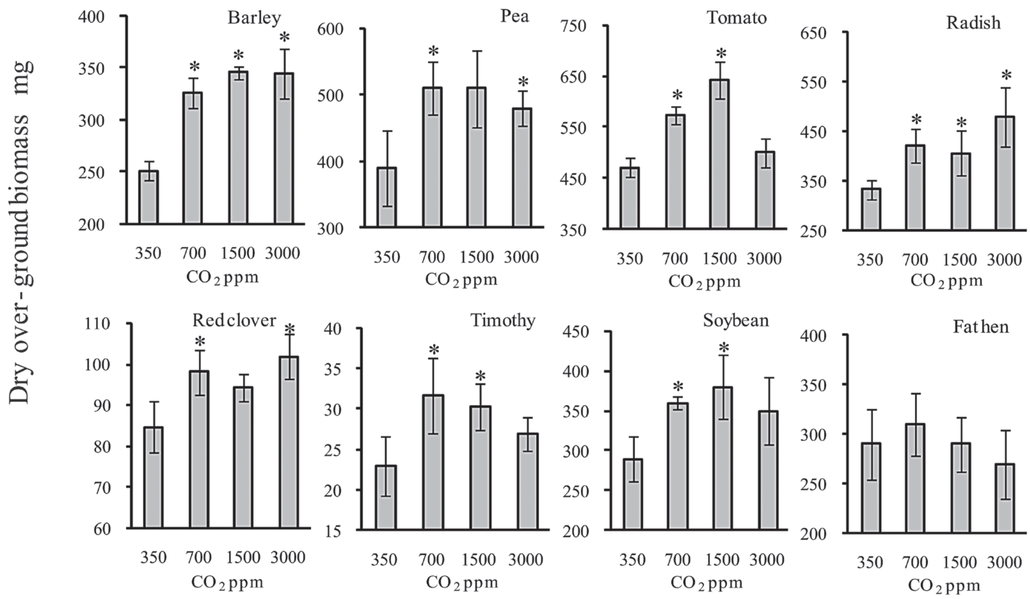
Tolerance of the investigated species to different CO_2 concentrations (350, 700, 1500 and 3000 ppm) was primarily investigated. CO_2 concentration was maintained by an automatic gas system in a phytotron chamber and monitored by a CO_2 controller ("Regin", Sweden). An integrated impact of elevated both CO_2 and temperature on the investigated plant species was analyzed according to four variants of treatment: reference treatment, i.e. current temperature and CO_2 concentration (21ºC-day/14ºC-night, 350 ppm); current temperature and elevated CO_2 (21ºC-day/14ºC-night, 700 ppm); elevated temperature and current CO_2 concentration (25ºC-day/18ºC-night, 350 ppm); elevated both – temperature and CO_2 (25ºC-day/18ºC-night, 700 ppm).

Dry over-ground biomass and concentration of photosynthetic pigments *a* and *b* chlorophylls and carotenoids were evaluated at the end of each treatment on the 21st day after germination. For determination of dry weight, shoots were dried in an electric oven at 70ºC for 24 hours. Samples of the investigated plants for pigment extraction were taken from fully expanded canopy leaves. Photosynthetic pigments were analyzed by a spectrophotometer Genesys 6 ("ThermoSpectronic", USA) in 100% acetone extracts prepared according to the method of Wettstein (1957).

The independent-samples *t*-test was applied to estimate the difference between reference and treatment values. The levels of significance for differences between the over-ground biomass and the concentration of photosynthetic pigments were analyzed using one-way *Anova*. All analyses were performed by *Statistica* and the results were expressed as mean values and their standard errors (SE).

Results

Tolerance of plans to different CO_2 concentrations. The over-ground biomass of all investigated species significantly increased along with an increase in CO_2 concentration and for most species (barley, pea, tomato, timothy, soybean and fat hen) the greatest biomass accumulation was observed at 700–1500 ppm (Fig. 1). In the case of doubled CO_2 (700 ppm) an increase in dry biomass for most investigated species was found to be in the range of 20–30% as compared to the plants grown under the reference conditions (350 ppm). The highest investigated concentration of CO_2 (3000 ppm) stimulated biomass formation only for radish and red clover, while in all other investigated species reduction in biomass accumulation was found at that concentration, as compared to 1500 ppm (Fig. 1).



Note. Asterisks indicates statistically significant ($p < 0.05$) difference from the reference (350 ppm).

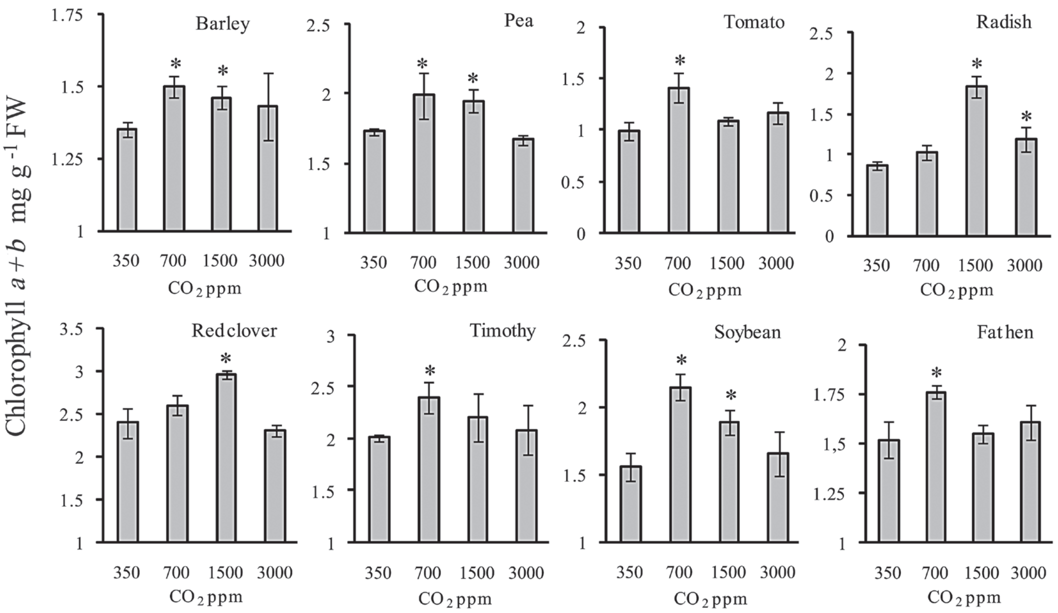
Figure 1. Dry over-ground biomass of agricultural plants at different CO_2 concentrations

Dependence of fat hen (*Chenopodium album* L.) biomass accumulation on CO_2 concentration was not so much pronounced as in agricultural species and the changes in the dry over-ground biomass along with an increase in carbon dioxide were comparatively small (6.8%) and statistically insignificant (Fig. 1).

The concentration of chlorophylls (*a* + *b*) varied much less along with an increase in CO_2 concentration compared with the biomass accumulation; however, a general pattern was quite similar and the concentration of chlorophylls was found to be the highest at 700–1500 ppm for the majority of investigated species except for radish and fat hen (Fig. 2). The most pronounced differences in the total chlorophyll at different CO_2 concentrations was observed for radish and almost a twofold increase in the chlorophyll concentration was registered at 1500 ppm as compared to reference plants. In the majority of other investigated species the chlorophyll concentration at elevated CO_2 concentrations did not exceed the reference treatment (350 ppm) more than 10–20% (Fig. 2).

The ratio of *a/b* chlorophyll tended to decrease slightly along with an increase in CO_2 concentration, and these changes, though in the most cases statistically insignificant ($p > 0.05$), being in the range of 3–15% for different investigated species. The most pronounced and statistically significant changes in a chlorophyll structure were observed for radish and soybean, and a chlorophyll a/b ratio decreased by 12.3% and 15.2%, respectively, at 3000 ppm as compared to reference treatment. Less distinct (about 10%), though statistically significant decrease of *a/b* chlorophyll ratio was registered in the case of red clover at 700 and 1500 ppm of CO_2.

Elevated CO_2 almost did not affect the concentration of carotenoids in the leaves of the most investigated species (barley, tomato, timothy, fat hen), and only in the leaves of red clover almost a double increase in the concentration of that photosynthetic pigment was noticed at 700 and 1500 ppm of CO_2. Less marked, however statistically significant increase in the concentration of carotenoids was registered in the case of pea and radish at 1500 ppm, and in the case of soybean at 700 ppm of CO_2.



Notes. Asterisks indicates statistically significant ($p < 0.05$) difference from the reference (350 ppm). FW – fresh weight.

Figure 2. Concentration of chlorophyll $a + b$ in the leaves of agricultural plants at different CO_2 concentrations

Table 1. Chlorophyll a/b ratio (±SE) in the leaves of agricultural plants at different CO_2 concentrations

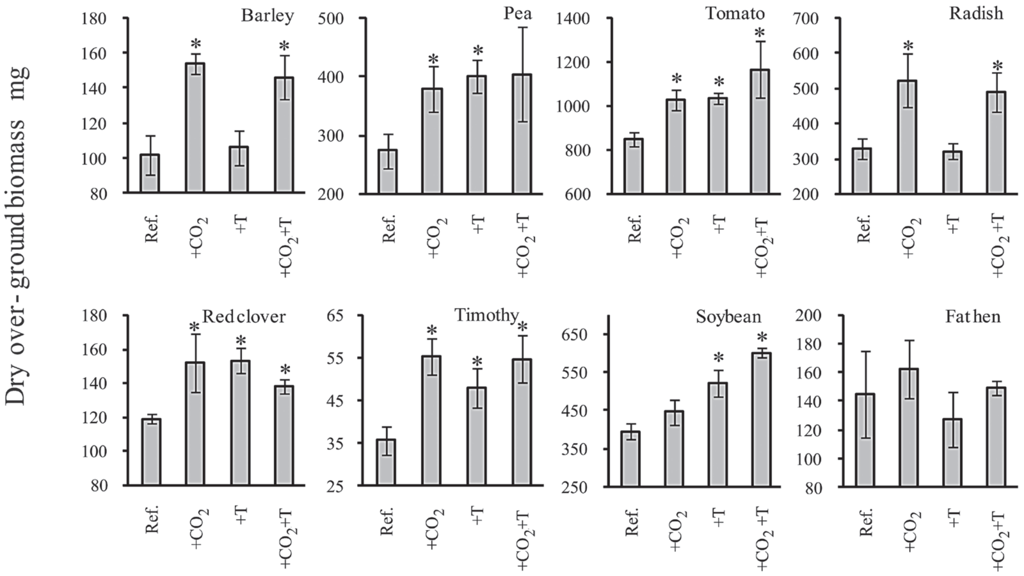
Plants	CO_2 concentration ppm			
	350	700	1500	3000
Barley	3.38 ± 0.051	3.21 ± 0.017	3.18 ± 0.073	3.22 ± 0.055
Pea	3.05 ± 0.062	2.85 ± 0.043	2.77 ± 0.037	2.90 ± 0.026
Tomato	3.22 ± 0.088	2.71* ± 0.047	2.95 ± 0.097	2.95 ± 0.007
Radish	3.60 ± 0.146	3.08 ± 0.043	2.72 ± 0.060	3.16* ± 0.045
Red clover	3.46 ± 0.030	3.14* ± 0.092	3.12* ± 0.044	3.19 ± 0.058
Timothy	3.11 ± 0.115	3.00 ± 0.154	2.93 ± 0.040	3.09 ± 0.087
Soybean	3.46 ± 0.030	3.45 ± 0.077	3.25 ± 0.091	2.90* ± 0.026
Fat hen	3.72 ± 0.107	3.21 ± 0.045	3.32 ± 0.045	3.22 ± 0.022

Note. Asterisks indicates statistically significant ($p < 0.05$) difference from the reference (350 ppm).

Table 2. Concentration of carotenoids (mg g^{-1} FW ± SE) in the leaves of agricultural plants at different CO_2 concentrations

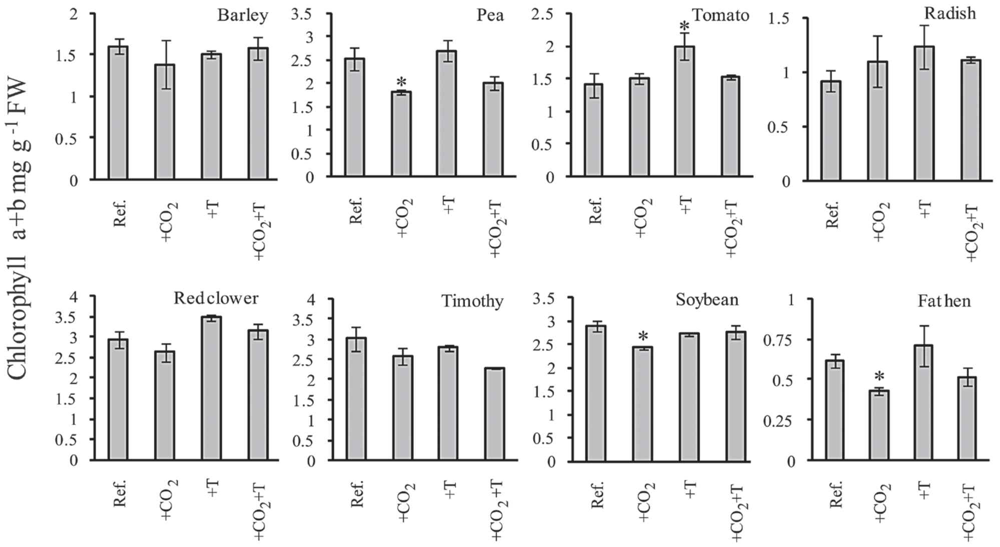
Plants	CO_2 concentration ppm			
	350	700	1500	3000
Barley	0.36 ± 0.006	0.32 ± 0.008	0.37 ± 0.013	0.36 ± 0.027
Pea	0.45 ± 0.012	0.48 ± 0.033	0.50* ± 0.014	0.47 ± 0.007
Tomato	0.32 ± 0.028	0.37 ± 0.030	0.35 ± 0.017	0.34 ± 0.012
Radish	0.24 ± 0.009	0.23 ± 0.036	0.44* ± 0.029	0.30 ± 0.032
Red clover	0.42 ± 0.055	0.70* ± 0.043	0.75* ± 0.032	0.61 ± 0.011
Timothy	0.50 ± 0.003	0.48 ± 0.027	0.50 ± 0.050	0.51 ± 0.043
Soybean	0.50 ± 0.033	0.63* ± 0.030	0.49 ± 0.035	0.47 ± 0.045
Fat hen	0.42 ± 0.023	0.42 ± 0.007	0.39 ± 0.019	0.41 ± 0.024

Notes. Asterisks indicates statistically significant ($p < 0.05$) difference from the reference (350 ppm). FW – fresh weight.



Notes. Ref. (reference treatment) – current temperature and CO_2 (21ºC-day/14ºC-night, 350 ppm); +CO_2 – elevated CO_2 (700 ppm) and current temperature, +T – elevated temperature (25ºC-day/18ºC-night) and current CO_2; +CO_2 + T – elevated both, CO_2 and temperature (25ºC-day/18ºC-night, 700 ppm).

Figure 3. Dry over-ground biomass of agricultural plants under different treatments



Notes. Ref. (reference treatment) – current temperature and CO_2 (21ºC-day/14ºC-night, 350 ppm); +CO_2 – elevated CO_2 (700 ppm) and current temperature, +T – elevated temperature (25ºC-day/18ºC-night) and current CO_2; +CO_2 + T – elevated both, CO_2 and temperature (25ºC-day/18ºC-night, 700 ppm). FW – fresh weight.

Figure 4. Concentration of chlorophylls *a* + *b* in the leaves of agricultural plants under different treatments

Response of plants to elevated CO_2 and temperature. Analysis of the results of single and integrated impacts of elevated CO_2 (700 ppm) and temperature (+4ºC as compared to current day and night temperature) on the growth of investigated plants showed that the plant response was highly species dependent (Fig. 3).

Only in the case of tomato and soybean, which are considered the greatest warmth-loving plants under local climate conditions, the biggest increase in biomass was achieved at elevated both CO_2 and temperature (37.7% and 52.1%, respectively). For the other investigated species, no positive interaction between CO_2 and temperature was detected and the differences in biomass formation under elevated CO_2 alone and elevated both CO_2 and temperature were not statistically significant.

For investigated weed (fat hen), no statistically significant differences between investigated treatments were detected and similar biomass is characteristic of current and warmed (elevated both CO_2 and temperature) climate conditions.

Differences in the total chlorophyll concentration in various treatments were much less pronounced than those in dry biomass, and in the most cases statistically insignificant. For the majority of species (pea, tomato, red clover, radish and fat hen) the highest values of chlorophyll were detected at elevated temperature and current CO_2 (Fig. 4).

Discussion

Theoretically, a current level of ambient CO_2 limits the photosynthesis rate of C_3 plants and along with an increase in the CO_2 concentration up to 1000 ppm or even to 2000 ppm an increase in photosynthesis intensity could be expected (Amthor, 2001; Fuhrer, 2003; Kirschbaum, 2004), however, response of plants to direct effect of elevated CO_2 is still not fully understood (Urban, 2003; Gaucher et al., 2003; Ramo, 2006). The results of the present study indicated the increased over-ground biomass at elevated CO_2 of all investigated cultivars and for most of them the greatest biomass accumulation was observed at 700–1500 ppm. However, no significant changes were observed in the biomass accumulation of wild plant – fat hen (*Chenopodium album* L.) at elevated CO_2 (Fig. 1).

As some authors have emphasized, the response at the whole plant level does not always correspond to theoretical presumptions made on the molecular or cellular levels and the source-sink interaction is critical to the whole plant growth response to elevated CO_2. Lack in sink capacity leads to a negative feedback and down-regulation of the photosynthetic rate and growth (Wolfe et al., 1998; Urban, 2003; Burkart et al., 2009). The homeostatic mechanisms of such self-regulation are not fully understood; however, these plant responses are often associated with the increased accumulation of saccharides in leaves. In the case of limited sinks, high concentrations of mono and disaccharides are accumulated in cytosol repressing the expression of genes transcribing for key photosynthetic enzymes and cause feedback inhibition of the photosynthesis (Jang, Sheen, 1994; Urban, 2003).

Despite down-regulation of the photosynthetic rate at elevated CO_2, the doubled CO_2 concentration stimulates growth and production of most agricultural crops (Amthor, 2001; Kirschbaum, 2004; Long et al., 2004). However, in some studies an impact of elevated CO_2 on agricultural crops was reported to be negligible (Morison, Lawlor, 1999; Wurr et al., 2000) and it was considered that plant response could be modified by other limiting factors, such as nutrient and water deficiency, low temperature, etc. (Daepp et al., 2000; Fuhrer, 2003; Kirschbaum, 2004).

In general, plant response to elevated CO_2 is species dependent (Fig. 1) and usually in most wild species it is much less expressed, non-existent or even negative. Experiments with woody plants have shown that seedlings of sugar maple do not respond to elevated CO_2 and their assimilation rate and Rubisco activity have not been stimulated by doubled CO_2 concentration (Gaucher et al., 2003). The growth of apple-tree seedlings was suppressed by elevated carbon dioxide (Ro et al., 2001). Pine and birch seedlings, exposed to elevated CO_2, initially showed high net assimilation rates, which declined to a reference level in a day, and doubled CO_2 had no effect on their growth. Experiments with native grasslands also did not show any marked response to elevated CO_2 (Shaw et al., 2002; Ramo, 2006). According to our investigation, fat hen as a wild species almost did not respond to elevated CO_2.

On the basis of this and other studies a conclusion can be drawn that for agricultural cultivars, bred to reach higher productivity, current ambient CO_2 concentration is usually a limiting factor and they are able to develop additional sinks for the allocation of increased assimilates and enhance biomass formation under elevated carbon dioxide. Conversely, for wild species, that are evolutionary well adapted to the ambient CO_2 level, current concentration of CO_2 is not a limiting factor and their response to elevated CO_2 is usually much less pronounced or non-existent.

According to our investigations, photosynthetic pigments responded to elevated CO_2 less obviously as compared to over-ground biomass of investigated plants. In the case of doubled CO_2, an increase in dry biomass for most investigated species was found to be in the range of 20–30% as compared to the plants grown under the reference conditions (Fig. 1). However, chlorophyll ($a + b$) concentration at doubled CO_2 concentrations did not exceed the reference treatment more than 10–20% (Fig. 2).

The ratio of *a/b* chlorophylls tended to decrease along with an increase in CO_2 concentration. Though in most cases these changes were statistically insignificant ($p > 0.05$), decrease of *a/b* chlorophylls ratio by 3–15% was registered at elevated CO_2 for investigated species. Our earlier investigations (Dukhovskis et al., 2003) have proved that chlorophyll *a* is more sensitive to the impact of external stressors than chlorophyll *b*.

In the case of an integrated impact of elevated CO_2 and temperature, the changes in the concentration of chlorophylls were much less expressed than the changes in above-ground biomass as well (Fig. 3 and 4), and only in rare cases differences from reference treatment were statistically significant.

Plant response to an integrated impact of elevated CO_2 and temperature does not always support theoretical presumptions that CO_2 stimulation of net assimilation and growth is more intensive at higher temperatures. As demonstrated in some studies, the whole plant response to the combination of these factors may vary in different species and different growth conditions, and the magnitude or even the direction of plant response to elevated CO_2 is dependent on the relationship between the current and optimal temperatures (Morison, Lawlor, 1999; Ziska, 2000).

Results of other investigators have shown that growth and yield of plants should be most responsive to CO_2 when temperature is optimal (Norby, Luo, 2004). However, our investigations did not support these findings. As seen from the data presented in Figure 3, the most pronounced stimulation of growth at elevated CO_2 and elevated temperature is observed in warmth-loving species i.e. tomato and soybean, the local ambient temperature being lower to them than optimal. Apparently CO_2 growth stimulation at the elevated temperature can be greater than at the current temperature mostly in the situation when current ambient temperature is lower than optimal.

If this problem is dealt with from the view of homeostatic mechanisms and assimilates source-sink interaction, it is obvious that the possibilities for faster growth and development of additional sinks are reduced not only at lower but also at higher than the optimal temperature.

Conclusions

1. For agricultural cultivars, bred for higher productivity, current ambient CO_2 concentration is usually a limiting factor for growth and they are able to enhance biomass formation under elevated carbon dioxide. For wild species, that are evolutionary well adapted to the ambient CO_2 level, current concentration of CO_2 is not a limiting factor and their growth at elevated CO_2 is usually much less pronounced or non-existent.

2. Response of agricultural plants to combined impact of elevated CO_2 and temperature is highly species specific. Only in the case of tomato and soybean, which are considered the most warmth-loving plants under local climate conditions, the biggest increase in biomass was achieved at elevated both CO_2 and temperature. For other investigated cultivars, no positive interaction between CO_2 and temperature was detected, and the differences in biomass formation under elevated CO_2 alone and elevated both CO_2 and temperature were not statistically significant. Evidently, CO_2 growth stimulation at the elevated temperature can be greater than at current temperature mostly for the species and cultivars for which current local temperature is lower than optimal.

3. For the investigated weed (fat hen), no statistically significant differences between investigated treatments were detected and similar biomass is characteristic of current and warmed (elevated both – CO_2 and temperature) climate conditions.

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Įvairių žemės ūkio augalų atsakas į padidėjusius CO_2 kiekį ir oro temperatūrą

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Santrauka

Tyrimų tikslas – įvertinti įvairių žemės ūkio augalų atsaką į padidėjusius CO_2 kiekį bei temperatūrą ir patikrinti hipotezę, kad atmosferoje esantis CO_2 kiekis yra daugelio žemės ūkio augalų augimą ribojantis veiksnys. Tyrimai atlikti fitotrone kontroliuojamo klimato sąlygomis. Tyrimams pasirinkta septyni žemės ūkio augalai ir piktžolė baltoji balanda (*Chenopodium album* L.). Tyrimų pabaigoje išmatuota augalų antžeminės dalies sausa biomasė ir nustatyta fotosintetinių pigmentų koncentracija lapuose. Didėjant CO_2 kiekiui, iš esmės didėjo ir visų tirtų veislių augalų sausa biomasė, intensyviausias didėjimas nustatytas CO_2 esant 700–1500 ppm. Baltosios balandos biomasės pokyčiai buvo maži ir neesminiai, o tai rodo, jog CO_2 kiekis atmosferoje nėra šios rūšies augalų augimą ribojantis veiksnys. Kompleksinis CO_2 (700 ppm) ir temperatūros (keturiais laipsniais aukštesnė nei dabartinė) poveikis tirtiems augalams skyrėsi priklausomai nuo jų rūšies. Pomidorai bei sojos, kurie esamo klimato sąlygomis yra labiausiai šilumą mėgstantys augalai, padidėjus CO_2 kiekiui ir pakėlus temperatūrą, sukaupė ir didesnę biomasę. Kitiems tirtiems augalams vien padidėjusio CO_2 ir didesnis kompleksinis abiejų veiksnių – CO_2 bei temperatūros – poveikis iš esmės nesiskyrė.

Reikšminiai žodžiai: klimato pokyčiai, anglies dioksidas, augalų atsakas, temperatūra, žemės ūkio augalai, piktžolės.