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Impact of warming climate on barley and tomato growth and photosynthetic pigments

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One of the major issues of global concern today is rapidly increasing levels of CO_2 in the atmosphere and its potential to change the world climate. It is important to understand how different agricultural cultivars will respond to different projected future levels of elevated CO_2 and its association with increasing temperatures. In this experiment, there were examined single and combined effects of different CO_2 levels (ambient 350 ppm, 700, 1500 and 3000 ppm) and elevated temperature (ambient +4 °C-day/5 °C-night) on barley (*Hordeum vulgare* L. cv. 'Aura') and tomato (*Lycopersicon esculentum* Mill. cv. 'Svara') growth characteristics. Experiments were conducted in the closed environment-controlled chambers. The results showed that the current ambient level of atmospheric CO_2 concentration was a growth limiting factor for the investigated agricultural species. Under single CO_2 effect the greatest biomass accumulation of both plants was observed at 1500 ppm concentration. However the highest investigated concentration of CO_2 (3000 ppm) significantly stimulated only biomass of barley. The highest biomass accumulation was detected under combined effect of elevated CO_2 and temperature, when the increases were 43.0 and 37.6% ($p < 0.05$) for barley and tomato respectively, compared to reference treatment. The factorial *Anova* analysis of all measured indices of investigated plants showed that the prior climate factor for barley was elevated CO_2 (700 ppm) while the effect of increased temperature (ambient +4 °C-day/5 °C-night) was much weaker. Whereas for tomato, which is considered as warmth-loving plant, substantial climate factor was elevated temperature, and the effect of 700 ppm CO_2 had a markedly weaker input.

Key words: elevated CO_2, elevated temperature, barley, tomato, biomass, pigments

INTRODUCTION

Levels of carbon dioxide concentration are undoubtedly rising in the world wide. Since late 1950s, the global atmospheric CO_2 concentration has increased by of 2 ppm per year and curently (~385 ppm) is about 38% higher than at a pre-industrial level (~280 ppm) (IPCC, 2007). Over the same period of time global average temperature has increased by ~0.8 °C (Hansen et al., 2006).

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Latest climate change scenario projections for Europe suggest that by 2100 in Central Europe temperature will increase to about 3 °C (Christensen et al., 2007), and CO_2 concentration will be in the range between 730 and 1 020 ppm (Meehl et al., 2007). However, according to Lunt et al. (2010), the earth's temperature might be as much as 30–50% more sensitive to atmospheric CO_2 concentration than previously anticipated. As changes in CO_2 and temperature are likely to occur concomitantly, it is of particular interest to quantify the interactions of these two climate variables.

Ambient atmospheric CO_2 limits photosynthesis of many plant species and the photosynthetic machinery of plants, particularly that of C_3 plants, is able to handle far higher than current CO_2 concentrations (Körner, 2006). Thus higher CO_2 could potentially improve productivity of important crops, among which C_3 species are likely to inherit such benefit most of all. According to Körner (2006), C_3 leaf photosynthesis saturates when CO_2 concentration approaches ~1 000 ppm. Experimental evidence almost univocally shows that the rate of photosynthesis in C_3 species leaves increases under exposure to elevated CO_2 (Amthor, 2001; Long et al., 2004; Nowak et al., 2004; Ainsworth, Long, 2005; Ainsworth, Rogers, 2007; Leakey et al., 2009). Growth and over-ground biomass production also generally increased with exposure to elevated CO_2. However, as revealed studies by Nowak et al. (2004), Ainsworth and Long (2005) and Weigel et al. (2008), growth responses of plants are often much weaker than those predicted by the photosynthetic responses. They also differ considerably between species and the magnitude of responses varies highly depending on the plant development, duration of exposure and growth conditions. As demonstrated by Kirschbaum (2004), there is no unique sensitivity of plant productivity to increasing CO_2 concentration, but that responses to doubling CO_2 can differ from close to zero to increases of up to 70% dependent on circumstances.

As both the specificity of Rubisco for CO_2 and the solubility of CO_2 relative to O_2 decline with temperature, it could be expected that increasing temperature would increase the affinity of Rubisco for CO_2, leading to an increase in the CO_2-stimulation of photosynthesis with temperature and thus lead to increased plant productivity (Long et al., 2004). A number of researchers working with a range of crops, including alfalfa plants, peanut and cotton, and even with C_3 annual weed have confirmed these theoretical presumptions and reported that CO_2 effects generally increase with increasing temperatures (Aranjuelo et al., 2005; Reddy et al., 2005; Vu, 2005; Yoon et al., 2009; Lee, 2011). Also 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 (Kirschbaum, 2004). However temperature optima differ between species and if the temperature is below optimum for photosynthesis, a slight increase in temperature may lead to increased plant growth and development, but if the temperature is close to maximum, a small increase in temperature can negatively affect crop growth and also decrease yield. Amthor (2001) found that warming by only a few degrees may offset the positive effect of elevated CO_2 on yield, and that the combination of doubled CO_2 and a warming of 1.6–4.0 °C have a negative effect on yield. Similarly Prasad et al. (2005) reported that elevated CO_2 can increase yields of grain legume crops (e. g. soybean, dry bean, peanut and cowpea), but this beneficial effect is offset by negative effects of the above-optimum temperature, which leads to decreased seed yield and quality. Heinemann et al. (2006) determinated too that for soybean aboveground biomass, an increase in the CO_2 level caused a more vigorous growth at lower temperatures and an increase in temperature also decreased seed weight. Thus analysis of the CO_2 effect and its interaction with increasing temperature is of great relevancy since the responsiveness of plants to enhanced both CO_2 and temperature has been shown to differ.

The objective of this study was to evaluate the single effect of different CO_2 levels (ambient, 350 ppm, *versus* 700, 1 500 and 3 000 ppm) and elevated temperature (ambient +4 °C-day/5 °C-night) on two different agriculture plants, i. e. barley and tomato growth and to examine how the interactive effect of doubled than ambient CO_2 concentration (700 ppm) and elevated temperature (ambient +4 °C-day/5 °C-night) might affect the growth characteristics of these important crops.

MATERIALS AND METHODS

Experiments were conducted in four controlled environment chambers located at the Lithuanian Institute of Horticulture during 2004–2008. Two different agricultural plants: barley (*Hordeum vulgare* L. cv. 'Aura') and tomato (*Lycopersicon esculentum* Mill. cv. 'Svara') were selected for the investigation. The plants were sown and grown in 5 L pots of neutral (pH 6.0–6.5) peat substrate (25 plants per pot). Both treatments were run in three replicates. Until germination and one week after, the plants were grown in a greenhouse at an average temperature of 20–25 °C under natural solar radiation. Then the plants were transferred to the chambers with a photoperiod of 14 h and 21 °C-day/14 °C-night temperature. High-pressure sodium lamps "SON-T Agro" ("Philips", Germany) were used for illumination. After two days of adaptation 10 days duration treatment was started.

Primarily the responsiveness of the investigated species to different CO_2 concentrations (ambient, 350, *versus* 700, 1 500 and 3 000 ppm) was evaluated. CO_2 concentration was maintained by an automatic gas system in a phytotron chamber and monitored by a CO_2 controller ("Regin", Sweden). The combined effect of CO_2 and temperature on the investigated plant species was analyzed according to four variants of treatment:

1. ambient CO_2 concentration and temperature (350 ppm, 21 °C-day/14 °C-night) (reference treatment);
2. double than ambient CO_2 concentration and ambient temperature (700 ppm, 21 °C-day/14 °C-night);
3. ambient CO_2 concentration and elevated temperature (350 ppm, 25 °C-day/19 °C-night);
4. elevated both CO_2 and temperature (700 ppm, 25 °C-day/19 °C-night).

As in the past century the daily minimum (or nighttime) temperature has increased faster than the daily maximum (daytime) temperature (Braganza et al., 2004), elevated nighttime temperature (ambient +5 °C) was maintained higher than elevated daytime temperature (ambient +4 °C).

At the end of experiments, on the 21st day after germination were evaluated both treatment dry over-ground biomass and concentration of photosynthetic pigments (a and b chlorophylls and carotenoids). For determination of dry weight, shoots were dried in an electric oven at 70 °C 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

The single effect of different CO_2 concentration on barley and tomato plants

The CO_2 treatment had significant effect on the growth of investigated agricultural plants. Increased CO_2 compared to ambient had significant effect on over-ground biomass accumulation of barley and tomato. However there was a difference among CO_2 levels and their impact on dry over-ground biomass of these different agricultural species. The greatest biomass accumulation of both species was observed at 1 500 ppm CO_2 concentration – 37.8 and 36.5% ($p < 0.05$) higher dry over-ground biomass of barley and tomato, respectively, as compared to the plants grown under the reference conditions (350 ppm CO_2) (Fig. 1). However the highest investigated concentration of CO_2 (3 000 ppm) significantly stimulated biomass only of barley, while the highest 3 000 ppm concentration of CO_2 reduced biomass accumulation of tomato, as compared to the lower elevated CO_2 concentrations (Fig. 1).

Effect of elevated CO_2 concentration on photosynthetic pigments in leaves of two agricultural plant species was much weaker (Fig. 2). Both investigated plant leaves produced similar total chlorophyll a + b content, as compared to reference plant leaves. The most pronounced and significant differences in the total chlorophyll

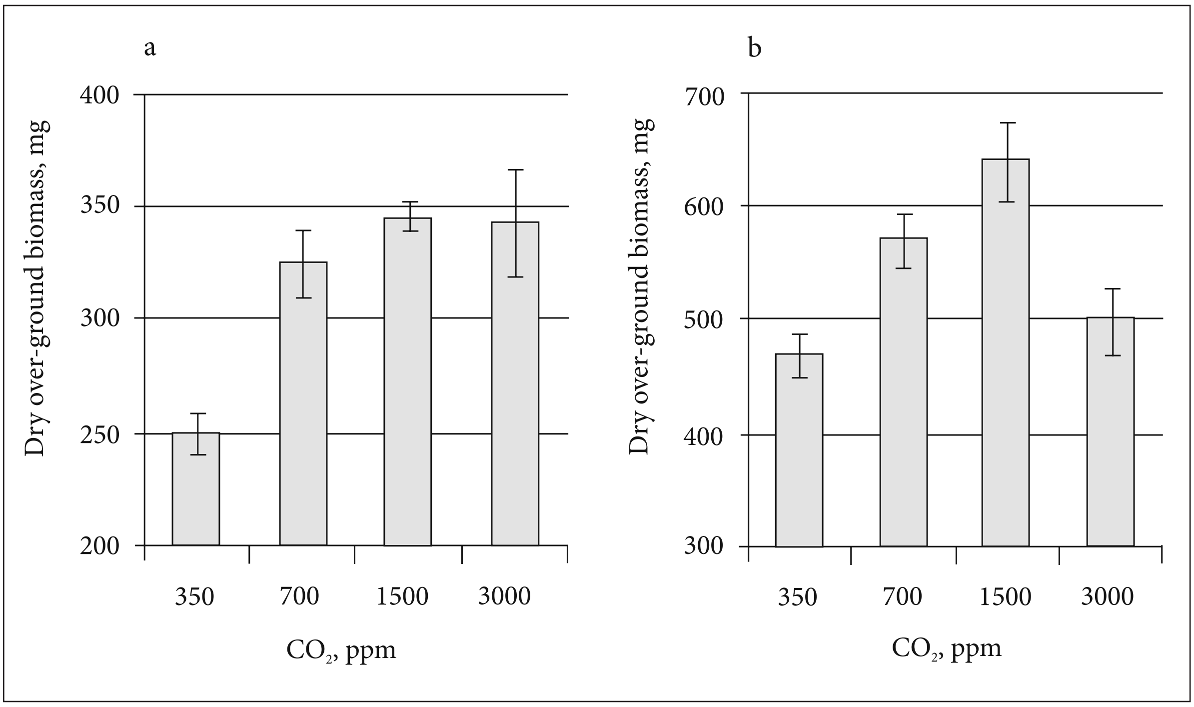

Fig. 1. Dry over-ground biomass (mg) of barley (a) and tomato (b) at different CO_2 concentrations

content at different CO_2 concentrations were observed in tomato plants only under the doubled CO_2 concentration (700 ppm), when more than 40% ($p < 0.05$) increase in the chlorophyll content was registered, as compared to reference plants (Fig. 2b).

However the ratio of chlorophyll a/b tended to decrease along with an increase in CO_2 concentration in leaves of both species (Fig. 2c, d). Differences in chlorophyll a/b ratio for barley among CO_2 levels were not significant, whereas for tomato in plants exposed to elevated CO_2 significant chlorophyll a/b ratio differences were observed, compared to reference treatment. The most pronounced changes in a chlorophyll structure of tomato leaves were observed at 700 ppm, when chlorophyll a/b ratio was almost 16% ($p < 0.05$) lower for plants exposed to the doubled CO_2 concentration, as compared with reference treatment plants (Fig. 2d). The effect of elevated CO_2 concentration on content of carotenoids of two plant species was not significant (Fig. 2e, f).

The combined effect of CO_2 and temperature on barley and tomato plants

Positive interaction between CO_2 and temperature on the growth of barley and tomato was detected. Both species accumulated the biggest biomass at elevated both CO_2 and temperature. Barley and tomato dry over-ground biomass increased by 43 and 37.6% ($p < 0.05$), respectively, as compared to the plants grown under the reference conditions (350 ppm, 21 °C-day/14 °C-night) (Fig. 3). However, in the case of single effects of these two climate factors, dry over-ground biomass of barley increased (29.9%; $p < 0.05$) significantly only under doubled CO_2 concentration, compared to reference treatment, while increase in temperature had no significant effect on the growth intensity (Fig. 3a). While tomato as warmth-loving plant accumulated higher dry over-ground biomass at elevated temperature (ambient +4 °C-day/5 °C-night) than under doubled CO_2 concentration (700 ppm) – 22.5 and 21.9% ($p < 0.05$) (temperature and CO_2), respectively, compared to reference treatment (Fig. 3b).

Differences in photosynthetic pigments content in both treatments have been much less pronounced than those in dry biomass. Single and integrated impacts of doubled than ambient CO_2 concentration and elevated temperature on total content of pigments of barley plants were insignificant (Fig. 4a, c). While in leaves of tomato plants warmed climate induced higher accumulation

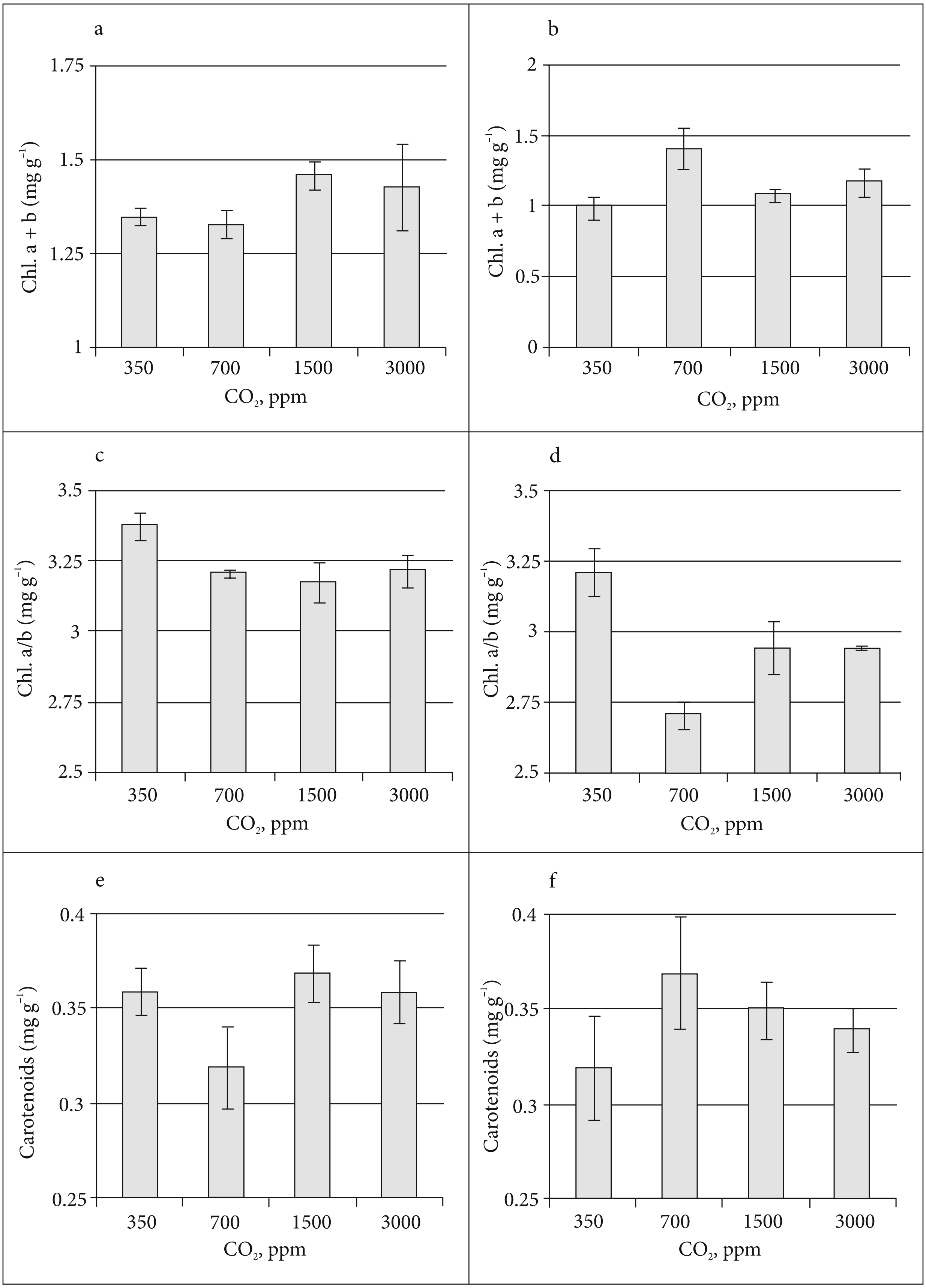

Fig. 2. Content of chlorophyll a + b (mg g^{-1}), the ratio of chlorophyll a/b and content of carotenoids (mg g^{-1}) in the leaves of barley (a, c, e – respectively) and tomato (b, d, f – respectively) at different CO_2 concentrations

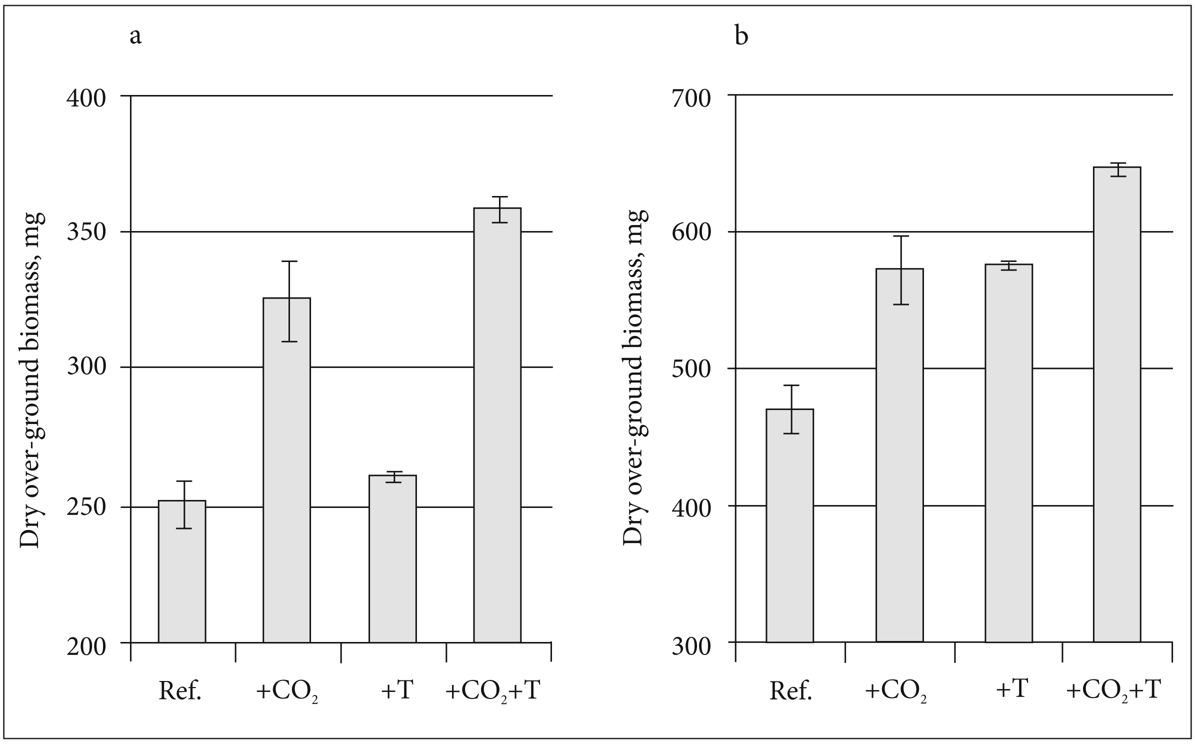

Fig. 3. Dry over-ground biomass (mg) of barley (a) and tomato (b) under different treatments: ref. (reference treatment) – ambient CO_2 and temperature (350 ppm, 21 °C-day/14 °C-night); +CO_2 – double than ambient CO_2 and ambient temperature (700 ppm, 21 °C-day/14 °C-night); +T – ambient CO_2 and elevated temperature (350 ppm, 25 °C-day/19 °C-night); +CO_2+T – elevated both CO_2 and temperature (700 ppm, 25 °C-day/19 °C-night)

of photosynthetic pigments, as compared to the plants grown under the reference conditions (Fig. 4b, d). Leaves of tomato plants exposed to only doubled CO_2 and only elevated temperature produced significantly higher total chlorophyll a + b content (42.4 and 41.4%, respectively), compared to reference plants (Fig. 4b).

The interaction of CO_2 and temperature had a significant effect on ratio of chlorophyll a/b of both investigated species. The chlorophyll a/b ratio was 15.4 and 22.7% higher for barley and tomato plants, respectively, grown at elevated both CO_2 and temperature (700 ppm, 25 °C-day/19 °C-night), compared to reference treatment (350 ppm, 21 °C-day/14 °C-night). While in the case of single effects of these two climate variables, for both species no significant differences concerning this ratio was observed (Fig. 4e, f).

DISCUSSION

The CO_2 treatment had a significant effect on the growth of investigated agricultural plants. Increased CO_2 compared to ambient had a significant effect on over-ground biomass accumulation of barley and tomato. From data of this experiment it is apparent that growth of both investigated agricultural species is limiting with the current ambient levels of atmospheric CO_2 concentration and the growth responses of both species are expected to show an increase in over-ground biomass accumulation in response to elevated CO_2 concentration. However there was a difference among CO_2 levels and their impact on dry over-ground biomass of barley and tomato plants (Fig. 1). As demonstrated Kimball et al. (2002), as atmospheric CO_2 is the sole source of carbon for plants, CO_2 enrichment will act as carbon fertiliser resulting in far reaching consequences for plant production. Now it is widely accepted that the current atmospheric CO_2 concentration is a limiting factor for maximum photosynthesis of plants with the C_3 photosynthetic pathway and, despite physiological adaptation of plants and down-regulation of the photosynthetic rate, an increase in the atmospheric CO_2

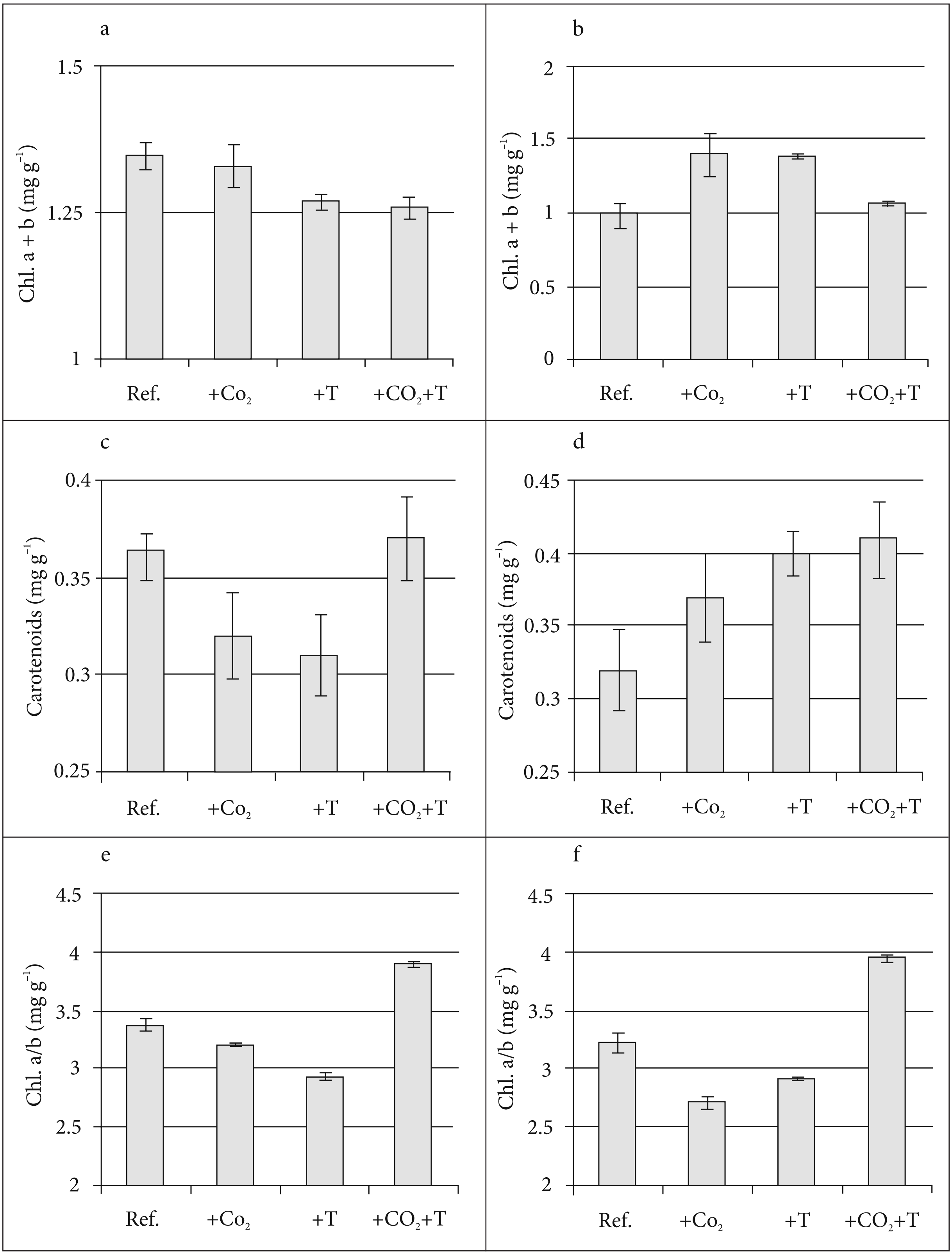

Fig. 4. Contents of chlorophyll a + b and carotenoids (mg g^{-1}) and the ratio of chlorophyll a/b in the leaves of barley (respectively a, c, e) and tomato (respectively b, d, f) under different treatments: ref. (reference treatment) – ambient CO_2 and temperature (350 ppm, 21 °C-day/14 °C-night); +CO_2 – double than ambient CO_2 and ambient temperature (700 ppm, 21 °C-day/14 °C-night); +T – ambient CO_2 and elevated temperature (350 ppm, 25 °C-day/19 °C-night); +CO_2+T – elevated both CO_2 and temperature (700 ppm, 25 °C-day/19 °C-night)

concentration has the potential to enhance the growth and yield of many agricultural crops of this group (Amthor, 2001; Kimball et al., 2002; Kirschbaum, 2004; Ainsworth, Long, 2005; Prasad et al., 2005; Burkart et al., 2009; Högy et al., 2009; Leakey et al., 2009; Manderscheid et al., 2010).

Elevated CO_2 conditions tend to alter the foliar chemistry of plants, i. e. photosynthetic pigment contents of leaves. Various responses of chlorophyll content can be found in literature. For barley and wheat plants grown under elevated CO_2 concentration decreased content of chlorophyll and carotenoids has been reported (Sicher et al., 1997). On the other hand, Nie et al. (1995) found no change in the amount of chlorophyll in wheat, which did show a faster development. Whereas treatment to elevated CO_2 concentration had a definite positive effect on total chlorophyll content of two different edible beans (*Vigna radiata* and *Vigna unguiculata*) (Hamid et al., 2009). In this experiment, elevated CO_2 concentration in most cases had insignificant effect on total content of pigments of barley and tomato plants. However the ratio of chlorophyll a/b tended to decrease along with an increase in CO_2 concentration in both investigated species leaves (Fig. 2). The results demonstrate that the whole range of chlorophyll response among individual species or in one family and even in one genus is possible with application of elevated CO_2. Moreover, growth response and chlorophyll response are not necessarily positively related. It has been stated that a positive growth response is related to a decrease in chlorophyll content due to an increased photosynthetic efficiency (Graham, Nobel, 1996).

Significant difference was found among the responses of barley and tomato plant to investigated single and combined effects of doubled than ambient CO_2 concentration (700 ppm) and elevated temperature (ambient +4 °C-day/5 °C-night) on their growth (Fig. 3). This was no surprise since the selected agricultural plants are different in terms of the temperature optimum for their growth – tomato are considered as more warmth-loving plants under local climate conditions. These results also confirm the factorial ANOVA analysis of the growth parameters of barley and tomato plants, which showed that the interaction of CO_2 × temperature was significantly positive for both species (Tables 1 and 2). The greatest effect for all measured physiological and morphological indices (contents of chlorophyll a + b and carotenoids, chlorophyll a/b ratio and accumulation of dry over-ground biomass) of barley and tomato was under elevated both CO_2 and temperature. These results indicate that 4/5 °C-day / night increased temperature under doubled concentration of ambient CO_2 was optimum for growth of both species. However ANOVA analysis revealed that for growth of barley plants considerably prior climate factor, which was crucial for their response intensity to combined effect of elevated CO_2 and temperature, was doubled than ambient carbon dioxide concentration, while the effect of increased temperature was much weaker (Table 1). Whereas for growth of tomato plants, which are considered warmth-loving plants, substantial climate factor, determined their response intensity to integrated

Table 1. Analysis of interaction for the effect of CO_2 and temperature on all investigated physiological and morphological indices of barley

Effect	Test	Value	F	p
CO_2	Wilks	0,021299	57,44	0,000228
Temp.	Wilks	0,183856	5,55	0,044067
CO_2 * Temp.	Wilks	0,013909	88,62	0,000079

Table 2. Analysis of interaction for the effect of CO_2 and temperature on all investigated physiological and morphological indices of tomato

Effect	Test	Value	F	p
CO_2	Wilks	0,151580	6,996	0,027919
Temp.	Wilks	0,061547	19,060	0,003145
CO_2 * Temp.	Wilks	0,010348	119,550	0,000038

impact of doubled CO_2 and elevated temperature, was 4/5 °C day / night increase in temperature, while the effect of 700 ppm CO_2 concentration had a markedly weaker input (Table 2). In the study of Reddy et al. (2005) with cotton, temperature also showed a higher impact on biomass than CO_2. Yoon et al. (2009) found that, within the optimum range of temperature for cotton, CO_2 will be beneficial for cotton production. Moreover, Lee (2011) showed that biomass production of C_3 annual weedy species *Chenopodium album* grown in warmer temperatures combined with elevated CO_2 was significantly increased when compared to plants subjected to ambient or elevated temperatures alone.

The interaction of CO_2 and temperature had a significant positive effect on ratio of chlorophyll a/b of both investigated species. While a significant impact on total chlorophyll content was noticed only under single effects of doubled than ambient CO_2 concentration and elevated temperature and only for tomato plants (Fig. 4). Contrariwise, Kim and You (2010) in the study with *Phytolacca insularis* and *Phytolacca americana* determined that the chlorophyll content of both species was reduced under elevated CO_2 and temperature, however, the photosynthetic rates were higher in the treatment, despite the observed decline in chlorophyll content. As stated by Hamid et al. (2009), chlorophyll is the central part of the energy manifestation of every green plant system and, therefore, any significant alteration in its levels is likely to cause a marked effect on the entire metabolism of plants.

CONCLUSIONS

The current ambient level of atmospheric CO_2 concentration was growth limiting factor for the investigated tomato and barley species. The highest biomass accumulation was detected under combined effect of elevated CO_2 and temperature, when the increases were 43.0 and 37.6% ($p < 0.05$) for barley and tomato, respectively, compared to reference treatment. The prior climate factor for barley was elevated CO_2 (700 ppm), while the effect of increased temperature (ambient +4 °C-day/5 °C-night) was much weaker. Whereas for tomato, which is considered a warmth-loving plant, substantial climate factor was elevated temperature, and the effect of 700 ppm CO_2 had a markedly weaker input.

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ŠYLANČIO KLIMATO POVEIKIS MIEŽIŲ IR POMIDORŲ AUGIMUI IR FOTOSINTEZĖS PIGMENTAMS

Santrauka

Sparčiai didėjantis CO_2 kiekis atmosferoje ir jo galimybė keisti pasaulio klimatą pastaruoju metu yra viena iš svarbiausių susirūpinimą pasaulyje keliančių problemų. Svarbu išsiaiškinti, kaip įvairios žemės ūkio kultūros reaguos į suprojektuotus skirtingus padidėjusio CO_2 lygius ateityje ir jo sąveiką su aukštesne temperatūra. Šiame eksperimente buvo tiriamas diferencijuotas ir kompleksinis skirtingos koncentracijos CO_2 (dabartinė – 350 ppm, 700, 1 500 ir 3 000 ppm) ir aukštesnės temperatūros (dabartinė +4 °C dieną / 5 °C naktį) poveikis miežių (*Hordeum vulgare* L. cv. 'Aura') ir pomidorų (*Lycopersicon esculentum* Mill. cv. 'Svara') augimo savybėms. Eksperimentas buvo vykdomas uždarose kontroliuojamos aplinkos kamerose. Rezultatai rodo, kad dabartinis atmosferos CO_2 lygis ribojo tirtų žemės ūkio rūšių augimą. Tiriant diferencijuotą CO_2 koncentracijos poveikį, didžiausia abiejų rūšių biomasė buvo nustatyta esant 1 500 ppm CO_2 koncentracijai, tačiau didžiausia tirta CO_2 koncentracija (3 000 ppm) buvo reikšminga tik miežių biomasės stimuliacijai. Didžiausia abiejų rūšių sukaupta biomasė buvo nustatyta esant kompleksiniam padidėjusios koncentracijos CO_2 ir aukštesnės temperatūros poveikiui, kai miežių ir pomidorų ji padidėjo atitinkamai 43,0 ir 37,6 % ($p < 0,05$), palyginti su kontroliniais augalais. Tirtų rūšių visų matuotų rodiklių faktorinė dispersinė analizė *Anova* rodo, kad miežiams svarbesnis klimato veiksnys buvo didesnė CO_2 koncentracija (700 ppm), o aukštesnės temperatūros (dabartinė +4 °C dieną / 5 °C naktį) poveikis buvo daug silpnesnis. Pomidorams, kaip šilumą mėgstantiems augalams, esminis klimato veiksnys buvo aukštesnė temperatūra, o 700 ppm CO_2 koncentracijos poveikis buvo kur kas mažesnis.

Raktažodžiai: didesnė CO_2 koncentracija, aukštesnė temperatūra, miežiai, pomidorai, biomasė, pigmentai