

Effect of elevated atmospheric CO₂ level on the abiotic and biotic stress tolerance of cereals

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Abstract

Effect of elevated CO₂ level (EC) was studied on the tolerance of cereals to elevated temperature and drought and on the resistance of wheat to fungal diseases. In general, elevated growth temperature did not affect final grain size, thus having less harmful effects than heat stress or drought during grain-filling. The plants subjected to low water supply levels or elevated temperature had higher biomass and grain yield at EC than at the ambient level. Susceptible wheat varieties were, however, usually more prone to diseases when grown at EC, while resistant varieties remained resistant even at EC.

Keywords

Barley, disease resistance, drought, durum, global warming, high temperature, oat, triticale, wheat

Introduction

The CO₂ concentration of the atmosphere has been steadily increasing since the beginning of the industrial era, reaching a value 40% higher nowadays than the last stable level. The greenhouse effect is considered as one of the main driving forces of global warming of the Earth's surface causing a change in climate which results in considerable uncertainty in crop production due to e.g. lack of precipitation or excessive rainfall, a higher frequency of heat days or early spring frosts.

Elevated atmospheric CO₂ levels also have direct impacts on plants: CO₂ assimilation and transpiration is positively affected and as a result of water use efficiency and rate of organic matter accumulation is increased (TUBA et al. 1994). Crop yield is affected not only in quantitative but also in qualitative terms, as elevated CO₂ may change the nutrient demand and uptake of plants, and cause a dilution of various elements in plant tissues. The change in the composition of plant parts, together with a higher level of protective compounds produced in response to elevated CO₂ also affect infection severity of plant pathogens, while the reduced stomatal opening and lower humidity on the plant surface may hinder the penetration of certain pathogens (HIBBERD et al. 1996, McELRONE et al. 2005, CHAKRABORTY et al. 2008, EASTBURN et al. 2011).

Increased CO₂ levels during the growth of cereals result in better resistance to frost (VEISZ 1997, HARNOS et al. 1998). The rate of net photosynthesis and water use efficiency (WUE) of C₃ plants are higher at elevated CO₂ also in

water-limited environments (TUBA et al. 1996). Although high temperature during anthesis and grain filling causes reductions in kernel number and size, kernels per spikelet, grain yield and harvest index (BLUMENTHAL et al. 1995), the effects of heat stress can be reduced by elevated CO₂ (TAUB et al. 2000, BENCZE et al. 2004, KADDOUR and FULLER 2004). High temperatures may, however, have negative effects on flour quality (BLUMENTHAL et al. 1995).

Realizing the importance of interactions between elevated CO₂ and other environmental factors in cereal production, the staff of the Agricultural Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, began research on the impacts of elevated CO₂ on a wide basis including nutrient supply, elevated growth temperature, drought and heat stress during grain filling, and some fungal pathogens as biotic stress factors. The present paper discusses the effect of elevated CO₂ level on the resistance of a variety of small grain cereal species to biotic and abiotic stresses, based on results of experiments carried out in the Martonvásár phytotron.

Materials and methods

A series of experiments was conducted under controlled environmental conditions in Conviron PGV-36 growth chambers in the phytotron of the Agricultural Institute, Centre for Agricultural Research, HAS, Martonvásár, Hungary. Varieties of small grain cereal species were chosen for the tests. Four seedlings in the one-leaf stage were planted directly (spring varieties) or after vernalization (4°C, 42 d) (winter varieties) in 2.8 l pots. There were at least 8 pots per genotype and treatment. The pots were placed randomly in the growth chambers and rearranged regularly.

The plants were watered daily and supplied with nutrients in tap-water (0.33 g·l⁻¹ Volldünger Linz solution, Austria, 3 dl·pot⁻¹) two times per week until the beginning of the first stress treatment (for the experiment on low nitrogen (N) supply the information given below applies). Growth conditions in the chambers were the same, except for atmospheric CO₂ level, which was either ambient *i.e.* normal (NC, 390 µmol·mol⁻¹) or elevated (EC, 750 µmol·mol⁻¹). Temperature was changed weekly increasing from 10/12/10.7°C (min/max/mean) at the beginning 20/24/22.7°C at maturity (TISCHNER et al. 1997). The maximum photosynthetic photon flux density increased from 280 to 400 µmol·m⁻²·s⁻¹.

The following treatments were applied as abiotic environmental factors: (i) low N supply with no added N above that provided in the soil, compared to 400 mg N·kg⁻¹ soil

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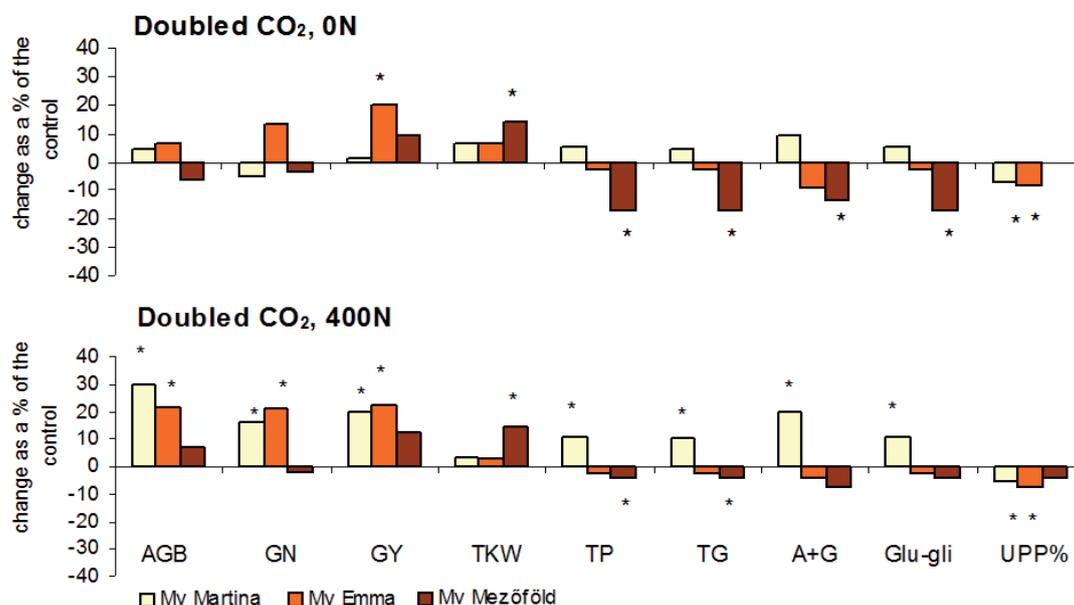


Figure 1. Impact of nitrogen supply on the development and grain quality of winter wheat grown at elevated CO₂ (*significant at $P < 0.05$ compared to the control: 400 mg·kg⁻¹ soil N, ambient CO₂). AGB, aboveground biomass; GN, grain number; GY, grain yield per plant; TKW, thousand kernel weight; TP, total protein content; TG, total gluten content; A+G, albumins and globulins; Glu-gli, glutenin to gliadin ratio; UPP%, unextractable polymeric protein content (determined with HPLC according to BATEY et al. (1991) and GUPTA and MACRITCHIE (1994)).

dry weight (in the form of NH₄NO₃ in ten applications until heading); (ii) heat stress during grain filling (35°C max. temperature for 15 d, 8 h daily, starting 12 d after heading); (iii) elevated growth temperature (+2°C from seedling stage, compared to ambient levels); (iv) drought (7 d water withdrawal, beginning 10 d after heading).

To study the impact of elevated CO₂ on disease severity, artificial inoculations with uredospore suspensions of leaf rust (LR, *Puccinia triticina*) and stem rust (SR, *Puccinia graminis*), and conidia of Fusarium head blight (FHB, *Fusarium culmorum*) were applied on plants of three winter wheat varieties differing in resistance levels (for details see BENCZE et al. 2013). The disease severity of spontaneously occurring powdery mildew (PM, *Blumeria graminis*) was evaluated twice, using a 0-9 scale (SAARI and PRESCOTT 1975). The disease progress of LR, SR and FHB was monitored till early maturity. The results were evaluated with Mann-Whitney Test (SPSS 16.0).

Results and discussion

Effect of nitrogen on winter wheat grown at elevated CO₂

Elevated CO₂ has been reported to lead to more intense biomass accumulation (KIMBALL et al. 1995, HARNOS et al. 1998). However, the stimulating effect of elevated CO₂, as was found here, is dependent on the nutrient supply, and especially on the availability of N (Figure 1). At low N, EC had no significant effect on biomass production while one variety still had higher grain yield. At optimal N supply, however, significant increases in biomass, grain number and grain yield per plant were recorded in two varieties in response to EC. One variety had increased thousand kernel

weight (TKW) at both N levels due to elevated CO₂, but at low N it had lower protein and gluten contents and glutenin to gliadin ratio in the grain. The decline in the unextractable polymeric protein content in two varieties suggested a possible weakening of dough due to elevated CO₂.

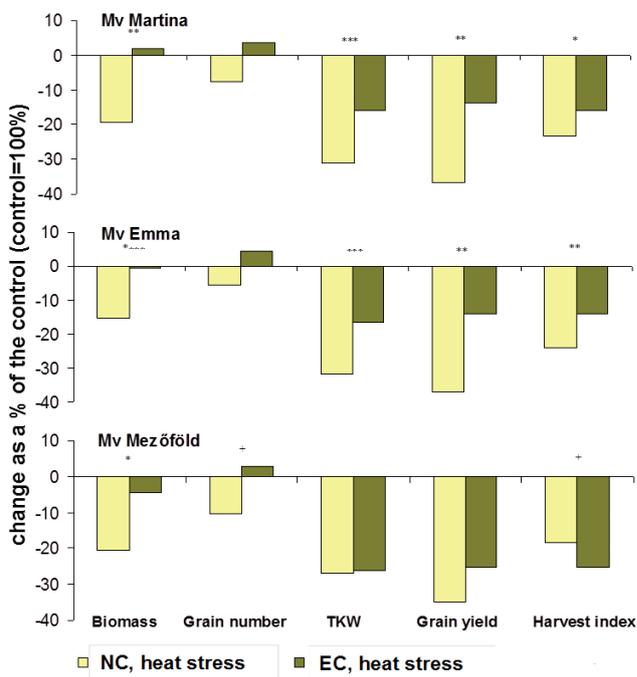


Figure 2. Effect of elevated CO₂ level and heat stress on yield and yield components of winter wheat (Control = ambient temperature and CO₂; NC, normal CO₂ level; EC, elevated CO₂ level; significance levels are indicated for the difference between NC and EC)

Effect of elevated CO₂ on heat stress tolerance of wheat

EC resulted in more intense biomass accumulation also in heat stressed plants, which had similar biomass values to unstressed plants grown at NC (Figure 2). Heat stress caused a 16-24% decrease in TKW in all the varieties at ambient CO₂ level, resulting in a 19-35% loss in grain yield (significant in two varieties). This was similar to results of BLUMENTHAL et al. 1995. When grown at high CO₂, two varieties tolerated heat stress better as both TKW and grain yield were significantly higher at doubled CO₂ than at the ambient level, though the values were still lower than the control. In the third variety, EC resulted in a higher grain number causing a slight increase in grain yield. Heat stress caused a significant increase in grain protein content but the decrease in gluten index indicated deterioration of gluten quality in two varieties (Figure 3). EC had, however, counteracting effects on protein content.

Effect of elevated CO₂ and growth temperature on cereals

Elevated growth temperature, 2°C higher than the ambient level, resulted in a decrease in biomass accumulation, grain number and yield per plant and in reduced harvest index (Figure 4). This was due to a faster phenological development; as heading and maturation took place on average 4 and 6 days earlier, respectively, than at the ambient temperature. However, TKW and grain protein content did not change in response to elevated growth temperature, suggesting a more harmonious development of the plants than in the case of heat stress. When the plants were grown at EC, the loss of grain yield due to elevated temperature was fully compensated by increased grain number and TKW.

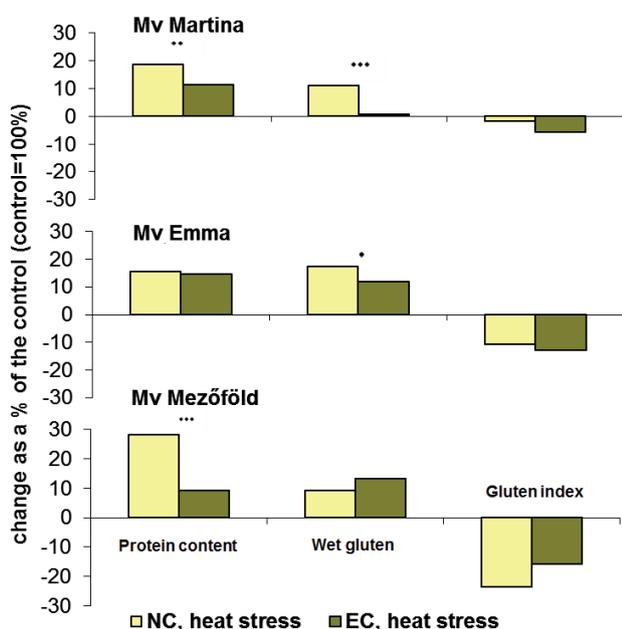


Figure 3. Effect of elevated CO₂ level and heat stress on quality traits of winter wheat (Control = ambient temperature and CO₂; NC, normal CO₂ level; EC, elevated CO₂ levels; significance levels indicate the difference between NC and EC)

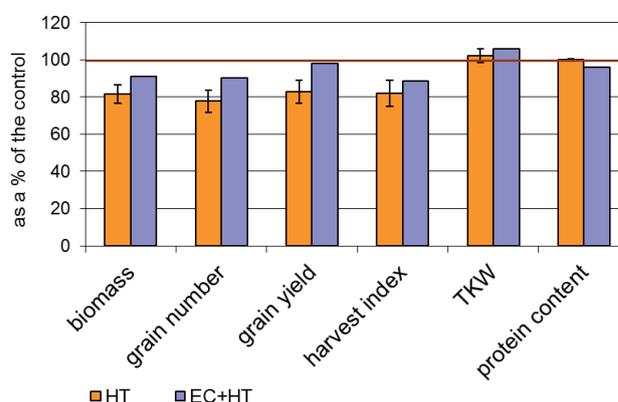


Figure 4. Effect of elevated growth temperature on mean performance of cereals at ambient and elevated CO₂ levels (Control = ambient temperature and CO₂ level; ET, elevated temperature; EC, elevated CO₂ level; investigated varieties: 'Petra' (winter barley), 'Bezostaja 1', 'Apache', 'Libellula', 'Mv Regiment', 'Mv Béres', 'Mv Emma' (winter wheat), 'Kitaro' (winter triticale), 'Jubilant' (spring barley), 'Mv Pehely', 'Kwant' (spring oat))

Effect of elevated CO₂ and drought on cereals

Drought stress had a severe effect, very similar to heat stress, on grain yield per plant; mainly due to decreased TKW (Figure 5). There was also a slight decrease in grain number per plant, which was eliminated when the plants were grown at EC. Although there was some increase of TKW in response to EC also under drought, CO₂ enrichment probably had more influence in the period preceding heat stress than during or after it. Grain protein content was increased by drought as a result of a decrease in starch accumulation.

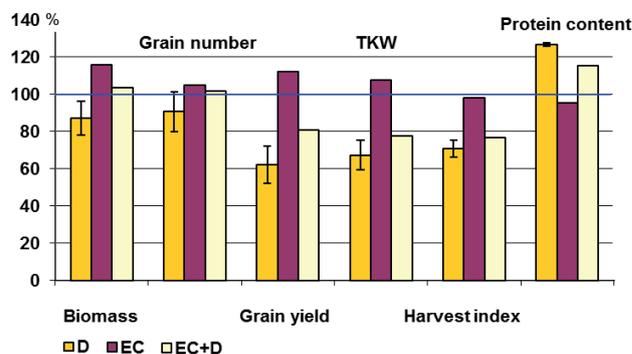


Figure 5. Effect of elevated CO₂ on mean performance of cereals under drought (Control = ambient temperature and CO₂ level; D, drought stress; EC, elevated CO₂ level; investigated varieties: 'Petra' (winter barley), 'Libellula', 'Mv Regiment', 'Mv Mambó' (winter wheat), 'Mv Makaróni' (winter durum), 'Lona' (spring wheat), 'Mv Pehely' (spring oat))

Effect of elevated CO₂ on wheat diseases

EC had also a considerable impact on the diseases severity of wheat. Susceptible varieties exhibited rarely similar but usually more severe symptoms of PM, SR and LR at EC than at the ambient level (Table 1). There was only one exception recorded for increased resistance to LR; in the highly susceptible variety at seedling stage. Resistant varieties, however, remained resistant even at EC. When the whole spikes were inoculated with a suspension of FHB conidia,

Table 1. Change in disease severity of wheat varieties in response to elevated CO₂ (LR, leaf rust; SR, stem rust; PM, powdery mildew; FHB, Fusarium head blight; –, not tested; NS, no significant change; ↑, more severe; ↓, less severe; +, *, **, ***, significantly at $P < 0.1, 0.05, 0.01$ and 0.001 , respectively; NS, not significant; R, resistant)

Variety	LR seedling stage	LR adult plant	SR	PM	FHB single floret inoculation	FHB whole spike inoculation
Alcedo	↓ ***	-	-	-	-	-
Mv Regiment	↑ +	↑ ***	NS	R	↓ *	NS
Mv Emma	-	↑ ***	↑ **	↑ ***	↑ +	↑ *
Mv Mambó	-	R	R	↑ ***	NS	↑ *

two varieties exhibited increased susceptibility while there was no change in the third variety. In the case of single floret inoculation with FHB, this latter variety showed increased resistance at high CO₂, while there was no change or FHB was more severe in the other two varieties.

The above results suggest that EC had very favourable effects on plants under high temperature stress or drought, as it could decrease or eliminate their negative effects on yield parameters. In the case of diseases, however, more severe symptoms were found on plants of the susceptible varieties at high CO₂, but resistant varieties remained unaffected, exhibiting no visible symptoms even when grown at EC.

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