Abiotic stress tolerance of wheat under different atmospheric CO, concentrations

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Introduction

The quality and quantity of cereal yields depend on the joint effects of numerous factors. One of the most important of these is the yield potential, which is manifested to different extents under various growing conditions, depending on the adaptability of the variety to unfavourable climatic conditions and to differing geographical conditions. Under the continental climate of the Carpathian Basin, unfavourable environmental conditions generally consist of low or high temperature and a deficiency or excess of water.

The practical importance of stress tolerance was clearly demonstrated in the 2002/2003 vegetation season, when the extreme weather conditions were a severe test of the adaptability of winter cereals. A long, hard winter was followed almost immediately by a very hot, dry summer, which meant that all the unfavourable climatic factors characteristic of the region were experienced for long periods in a single season. The consequence was the lowest yield average for the last ten years.

There is still much debate not only on whether the climate is really changing or whether the Earth is simply going through a cyclic period of warming, but also on the extent to which change has been caused by human activities. Opinions also differ on whether we should wait until more evidence accumulates, or whether we should start preparing for the unfavourable effects that climate change is likely to involve.

The atmospheric concentration of CO_2 has been steadily increasing since the beginning of the industrial aera. Climate anomalies arising due to climate change, such as deficient or excessive rainfall, a higher frequency of heat days, drought, and winter or early spring frosts, are al-

ready causing problems for crop production each year.

These all appear to be clear warning signals that the climate is indeed changing substantially. If this is so, the main task facing mankind is to reduce emissions of the gases responsible for global warming, which means that every country in the world should adhere to the Kyoto Protocol. At the same time, preparations must be made to counteract the unfavourable effects of climate change. Scientists must prepare accurate predictions of likely changes, determine what effect these will have, and respond to the challenges involved, which for agricultural experts means increasing the adaptability of varieties to cope with these changes and preserving soil moisture.

Increased CO_2 levels during the growth of cereals result in higher rates of biomass accumulation, higher yields and better resistance to frost (VEISZ 1997, HARNOS et al. 1998). 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), but the effects of heat stress can be reduced by elevated CO_2 (TAUB et al. 2000, BENCZE et al. 2004).

High temperature may have negative effects on flour quality. BLUMENTHAL et al. (1995) reported that, despite the higher protein content, there was a decrease in the glutenin-gliadin ratio and in the percentage of very large glutenin polymers following heat stress.

It is a well-known fact that at higher CO₂ levels there is a reduction in stomatal conductance and an improvement in water use efficiency, due partly to a substantial decline in transpiration and partly to a simultaneous rise in the net photosynthesis level (TUBA et al. 1994). The net photosynthesis and water use effi-

ciency of C_3 plants were usually better at elevated CO_2 in water-limited environments, too (TUBA et al. 1996). In durum wheat KADDOUR and FULLER (2004) reported that water-deficient plants produced surplus yields at increased atmospheric CO_2 concentrations compared with those raised at normal CO_2 levels.

The present paper discusses the effect of doubled CO_2 level on the resistance of wheat varieties to frost, heat stress and drought, based on the results of phytotron tests.

Materials and methods

Cold stress

A freezing test was carried out to examine the frost resistance of Triticum aestivum genotypes (Alba, Apollo, Bánkúti 1201, Bezostaya 1 and Martonvásári 15). Germinated wheat seeds were sown in boxes, in 9 rows with 20 seeds to a row, in a random design with four replications. The plants were grown for six weeks on the M29 climatic programme (TISCHNER et al. 1997), either at ambient (375 imol*mol⁻¹) CO₂ level or at double this rate (750 imol*mol⁻¹). Other growth conditions (temperature, light intensity, duration of illumination, water supplies, etc.) were the same in all the chambers. Freezing was carried out in the frost resistance testing chamber. where the temperature was gradually reduced to -15°C, which was maintained for 24 hours. The plants were then grown for a further three weeks, after which plants that had survived freezing and had started to develop could be clearly distinguished from those that had died.

In order to evaluate the frost resistance of different varieties, the number of plants that had survived freezing was counted, and expressed as a percentage of the plant number prior to freezing.

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Heat stress

Three winter wheat (T. aestivum L.) varieties commonly cultivated in Hungary: Mv Martina, Mv Emma and Mv Mezõföld, all of which had different agronomic characteristics, were chosen for the tests. The experiment was carried out under controlled environmental conditions in Conviron PGV/36 growth chambers in the phytotron. Vernalised seedlings were planted four to a pot (21×21×17 cm) in a 4:1 mixture of garden soil and sand (corresponding to 3.82 kg dry weight) containing 0.1561 % total nitrogen (NH₄-N: 6.36; NO₂-N: 75.6 mg kg⁻¹ soil dry weight). The pots were placed randomly in the growth chambers and rearranged regularly. The plants were watered daily with tap water and provided with macro- and microelements weekly in 150 ml nutrient solution (for details see BENCZE et al. 2005) from the 4th until the 10th week with the exception of nitrogen. The plants received either no nitrogen (0N treatment) or a total of 400 mg N active agents per kg soil dry weight (400 N) in the form of ammonium nitrate dissolved in tap water, in ten instalments from tillering till heading. The atmospheric CO₂ level in the growth chambers was either ambient (375 ìmol*mol⁻¹) or doubled (750 ìmol*mol⁻¹). The temperature regime changed weekly, beginning with a min/ max/mean of 10/12/10.7°C during the first week and increasing until it reached 20/24/22.7°C in the 11th week. In the control and after the heat stress treatment it remained at this level till the end of the experiment. Heat stress began 12 days after the average heading date of each group (Zadoks 59). In the heat stress treatment the temperature was 20/35/ 25.2°C, the maximum temperature being maintained for 8 hours a day for 15 days. There were 28 plants in each treatment. After harvest the aboveground biomass (g), grain number per plant, thousand kernel weight (TKW, g) and grain weight per plant (g) were determined. The protein content of the wholemeal (per g dry weight) was measured using a Kjeltec 1035 Analyzer, applying a factor of 5.7 (ICC105/2), and the gluten quality parameters of the flour were characterized with a Glutomatic 2200 instrument (ICC 137/1, ICC 155).

Drought stress

Two winter wheat varieties, Alba, cultivated in Poland, and Martonvásári 15 (Mv 15), bred in Hungary, were used in the tests. All the growing conditions (including the CO_2 levels) were set as in the control treatment in the heat stress experiment, with the exception of the soil water content, which was adjusted to 65% of total soil water capacity in the control treatment, with two levels of water stress: 45% and 25% soil water capacity, in the other two treatments.

The plants were grown at a near-optimum nutrient supply level.

The statistical analyses in all the experiments were carried out on the collected data using two-way ANOVA to study the effects of the treatments on the varieties, one factor being the treatment and the other the variety.

Results and discussion

Cold tolerance and elevated CO, level

In all but one variety high CO_2 level increased the survival rate of cereals, to an extent depending on the variety (*Figure 1*). This effect was more pronounced in frost-sensitive genotypes, where the increase ranged from 47-240%. In Bezostaya 1, a variety with high frost resistance, there was no increase in the survival rate due to high CO_2 , while Marton-vásári 15, though being as tolerant as Bezostaya 1, had an even better survival rate at the doubled CO_2 level.

Heat stress and elevated CO, level

Heat stress had severe effects, decreasing biomass accumulation and grain size and resulting in a yield loss of up to 27% in the 0N treatment and 37% at 400N (Table 1). Plants grown at the doubled CO₂ level had higher aboveground biomass and number of grains per plant in Mv Martina and My Emma, leading to a significantly higher yield (20-22 % at 400N). In My Mezőföld there was also a slight, 12%, increase, but this was due to larger grain size. When grown at high CO₂, the plants often had better tolerance of high temperature during grain filling, depending on the combination of variety and nitrogen supply, as the thousand kernel weight and the grain yield were significantly higher at doubled CO₂ than at the ambient level, though the values were still lower compared to the control. The grain number responded the least to CO₂ elevation under heat stress. At the normal (400N) nitrogen level, however, CO₂ enrichment was able to counteract the yield-reducing affect of heat stress in two genotypes. In Mv Mezõföld, elevated CO₂ level was unable to compensate for the negative effects of heat stress on the yield due to the low value of thousand kernel weight, although the biomass and grain number were similar to the control values, as in the other varieties.

Despite the higher protein and gluten contents, yield quality deteriorated to a significant or lesser extent due to high temperature, as can be seen from most

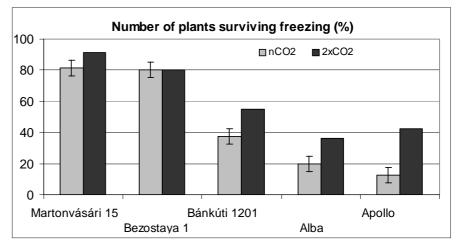


Figure 1: Effect of elevated CO_2 level on the survival of winter wheat varieties during freezing

Table 1: Effect of heat stress and elevated CO, leve
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		Mv Martina		Mv Emma		Mv Mezőföld		
Ν	Temperature	n CO ₂	2XCO ₂	n CO ₂	2XCO ₂	n CO ₂	2XCO ₂	LSD _{5%}
Above	eground biomass ((g)						
0	Normal	9.5	10.3	10.5	11.2	8.1	9.5	1.4
400	Normal	9.9	12.8	10.5	12.8	10.2	10.9	
0	Heat stress	8.1	10.4	8.5	9.7	8.1	7.7	
400	Heat stress	8.0	10.0	8.9	10.5	8.1	9.8	
Grain	weight per plant (g)						
0	Normal	3.70	3.84	3.63	4.31	3.27	3.80	0.54
400	Normal	3.79	4.54	3.60	4.40	3.49	3.91	
0	Heat stress	2.70	3.54	2.73	3.15	2.81	2.76	
400	Heat stress	2.40	3.27	2.28	3.10	2.27	2.61	
Grain	number per plant							
0	Normal	102.8	108.0	109.4	121.3	101.2	112.1	17.0
400	Normal	113.6	132.5	107.5	129.7	116.4	114.2	
0	Heat stress	102.5	121.9	95.1	111.6	113.3	99.8	
400	Heat stress	105.0	117.6	101.6	112.1	104.3	119.7	
TKW ((g)							
0	Normal	36.02	35.85	33.43	35.42	32.58	34.24	2.48
400	Normal	33.62	34.79	33.35	34.17	30.15	34.37	
0	Heat stress	26.74	29.24	28.92	28.63	24.71	28.22	
400	Heat stress	23.12	28.22	22.82	27.84	21.99	22.24	
Protei	n content % (d.w.)						
0	Normal	16.26	16.15	17.18	16.20	16.52	16.16	0.54
400	Normal	17.16	17.57	16.72	16.99	17.59	17.71	
0	Heat stress	17.36	16.90	18.79	18.38	18.23	17.34	
400	Heat stress	20.35	19.13	19.31	19.19	22.53	19.18	
Wet g	luten content %							
0	Normal	29.80	30.50	38.45	37.50	40.45	39.90	1.95
400	Normal	33.20	32.85	38.70	37.35	44.15	41.95	
0	Heat stress	35.70	32.55	40.85	38.60	46.30	41.40	
400	Heat stress	36.80	33.40	45.40	43.35	48.20	49.95	
Gluter	n index							
0	Normal	96.8	91.9	99.0	99.2	76.0	78.5	7.0
400	Normal	96.8	97.1	99.1	99.9	74.2	81.0	
0	Heat stress	86.0	87.0	94.4	95.1	61.4	72.2	
400	Heat stress	95.1	91.3	88.5	86.5	56.6	62.5	

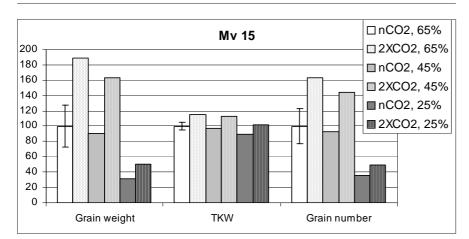


Figure 2: Effect of elevated CO_2 level on the yield of the varieties Mv 15 and Alba under water stress

of the gluten index values at both nitrogen levels (*Table 1*), indicating that protein traits determining spatial structure were negatively affected, leading to less elastic dough.

Elevated CO₂ had very little effect on the protein and gluten contents in any of the

varieties, a decrease in these values only being observed in one case. The gluten index was not changed significantly by the high CO_2 level.

The increase in the protein and gluten contents as the result of heat stress was generally counteracted to some extent by doubled CO₂. In most cases the poorest quality was recorded in this treatment.

Drought stress and elevated CO, level

Drought stress affected the plants dramatically, reducing the number of grains and the grain weight (TKW) and resulting in yield losses of 33% and 64% in Alba and 10% and 69% in Mv 15 at soil water levels of 45% and 25%, respectively (Figure 2, Figure 3). Doubled CO₂ level, however, affected the plants positively. While the thousand kernel weight did not change in Alba, the grains were larger in Mv 15 compared to the values at the ambient CO₂ level, and the number of grains increased in both varieties. These effects led to a yield increase of 58-89% in Mv 15 and 33-77% in Alba, depending on the treatment (though the increase was not significant in the 25 % soil moisture treatment).

As shown above, higher levels of atmospheric CO_2 could play an important role in reducing the deleterious effects of climate anomalies in a possible future environment. The existing differences between wheat genotypes enable breeders to produce new varieties more tolerant to environmental stresses and responding more positively to higher levels of CO_2 .

The reductions in grain yield in the experimental varieties exhibited significant differences for various types of stress (*Figure 4*). Heat stress alone caused the least loss of yield, while drought stress caused higher losses, and the greatest reduction in grain yield was observed when both stress factors were applied together. Substantial differences were observed between the varieties to different types of stress, indicating the possibility of selection for genotypes with better resistance to stress.

Summary

Climate change, a global environmental problem particularly affecting agriculture and the natural environment, is now seen to be associated with an increase in the frequency and intensity of climate anomalies. Weather extremes in Hungary have included droughts in the 1980s, hot, dry summers in 2001-2003, and excessive rainfall in 2004 and 2005.

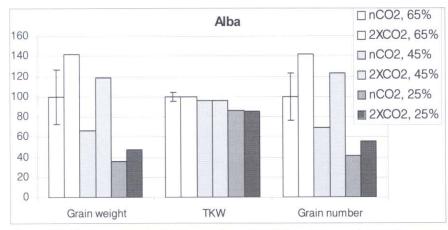


Figure 3: Effect of elevated CO_2 level on the yield of the variety Alba under water stress

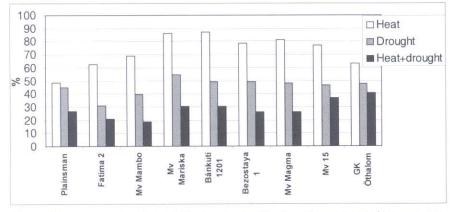


Figure 4: Decrease in grain yield as the result of various stress factors, as a percentage of the control

Research has been done in the phytotron of the Agricultural Research Institute in Martonvásár on the effect of climate extremes on the biomass, yield and abiotic stress tolerance of wheat. Studies were made on the frost resistance, heat tolerance and drought tolerance of wheat varieties with various genetic backgrounds when grown under normal and increased atmospheric CO₂ concentrations and at various nutrient supply levels. The following conclusions were drawn from the results:

- The frost resistance of wheat grown and cold-hardened at double the current level of atmospheric CO₂ concentration improved to various extents; this effect was more pronounced in frost-sensitive genotypes.
- Heat stress had severe effects: it decreased biomass accumulation and the thousand kernel weight, resulting in a yield loss of between 27% and 37%. Increased CO₂ concentration was able to counteract the deleterious effects of heat stress.
- When plants were exposed to heat stress, the yield loss was lower at low nitrogen levels.
- Yield quality deteriorated in heatstressed plants at doubled CO₂ concentration, to various extents depending on the genotype.
- The doubled CO₂ concentration was able to reduce the deleterious effects of drought stress on yield components. It can be seen from the results that genetic differences between winter wheat

varieties allow breeders to select genotypes with better adaptability, enabling them to be grown reliably even under altered environmental conditions.

Acknowledgements

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