PHYSIOLOGIA PLANTARUM 108: 61–70. 2000
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ISSN 0031-9317

Effects of elevated carbon dioxide, ozone and water availability on spring wheat growth and yield

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Received 20 May 1999; revised 9 September 1999

Spring wheat (*Triticum aestivum* L. cv. Dragon) was exposed to elevated carbon dioxide (CO_2), alone (1995) or in combination with two levels of increased ozone (O_3) (1994) or increased irrigation (1996) during three successive growing seasons as part of the EU ESPACE-wheat programme and conducted in open-top chambers (OTCs) and ambient air (AA) plots at Östad, 50 km north-east of Göteborg, Sweden. Doubling the CO_2 concentration had a positive effect on grain yield in all 3 years (+21, +7 and +11%, respectively), although only statistically significant in 1994. That year was characterised by a warm and dry summer in comparison with 1995 and 1996, in which the summers were more humid and typical for south-west Sweden. In 1994, the CO_2-induced increase in grain yield was associated with an increase in the duration of the green leaf area, a positive effect on straw yield and on the number of ears per square metre and a negative effect (−13%) on grain protein concentration. Harvest index was unaffected by the elevated CO_2 concentration. The only statistically significant effect of elevated CO_2 in 1995 was a decrease in the grain protein concentration (−11% in both CO_2 concentrations), and in 1996 an increase (+21%) in the straw yield. In 1996 the soil water potential was less negative in elevated CO_2, which is likely to reflect a lower water consumption of these plants. Addition of extra O_3 significantly affected the grain yield (−6 and −10%, respectively) and the 1000-grain weight negatively (−3 and −6%). Statistically significant interactions between CO_2 and O_3 were obtained for the number of ears per unit area and for the 1000-grain weight. The 1000-grain weight was negatively affected by O_3 in low CO_2, but remained unaffected in the high CO_2 treatment. There was a significant decrease (−6%) in the grain protein concentration induced by elevated irrigation. The chambers, compared with AA plots, had a positive effect on plant development and on grain yield in all 3 years.

Introduction

The atmospheric environment of the earth is changing. From an ecophysiological perspective, two important changes are the increasing concentrations of carbon dioxide (CO_2) and tropospheric ozone (O_3). The continuing increase of the CO_2 concentration is mainly caused by the extensive use of fossil fuels for combustion, and partly by altered land use. Tropospheric O_3 is formed in sunlight by reactions involving nitrogen oxides and volatile organic compounds. The problem of phytotoxic O_3 concentrations is well established in Europe (Jäger et al. 1992) and North America (Heck et al. 1988) and, in recent years, also in other parts of the world, such as in Pakistan (Wahid et al. 1995).

CO_2 is the substrate for photosynthesis and it has been estimated that, due to decreases in photorespiration and in the substrate inhibition of Rubisco, net photosynthesis may increase between 25 and 75% in the short term when the CO_2 level is doubled (Stitt 1991). Additional CO_2 usually increases the growth of C_3 plants, in which a doubling of the CO_2 level has been shown to increase vegetative growth with an average of 41% (data on 156 species, Poorter 1993) and 47% (data on 250 species, Poorter et al. 1996). The growth response varied considerably, both between and within species. For example, in wheat the increase in vegetative growth varied between 7 and 97% (Poorter 1993). Other important

Abbreviations – AOT40, accumulated exposure over a threshold concentration of 40 nmol mol^{-1}; GPC, grain protein concentration; OTC, open-top chamber; PAR, photosynthetically active radiation; VPD, vapour pressure deficit.

ecophysiological effects of CO_2 are also known. Increased intercellular concentrations of CO_2 in the leaves can reduce stomatal conductance (Cure and Acock 1986) and consequently improve water use efficiency. In an annual crop like wheat (*Triticum aestivum* L.), water economy is crucial for the duration of green leaf area and thus for yield, especially under dry conditions.

A lower stomatal conductance due to elevated CO_2 is important in the present context not only because of the possibility of an improved water use efficiency, but also another significant aspect is that a lower conductance will reduce the uptake of O_3 and other pollutants which are taken up through stomata (Allen 1990). This effect of CO_2 has been observed in some studies (e.g. McKee et al. 1997b).

One important indirect effect of elevated CO_2 concentrations in the atmosphere, apart from higher temperatures, is that the amount of rainfall may change. In some areas, the rainfall is predicted to decrease, while in other, such as Scandinavia, some models have suggested an increased precipitation (Boer et al. 1990). Increased precipitation is not necessarily beneficial for a field crop, since flooding of the roots may cause oxygen deficiency, yet it may enhance plant growth under other circumstances.

Unlike some other O_3 sensitive species, such as tobacco (*Nicotiana tabacum* L.) and clover (*Trifolium* spp.) (Heggestad 1991, Pihl Karlsson et al. 1995), wheat does not seem to develop characteristic and specific visible injury in response to moderately elevated O_3 concentrations. Instead, the main effect of O_3 on wheat seems to be a shortening of the life span of the leaves and early senescence (Grandjean and Fuhrer 1989, Ojanperä et al. 1992, Pleijel et al. 1997). The period of grain filling is strongly linked to (flag) leaf duration. The leaf area duration has been shown to be of crucial importance for the final grain yield of wheat (Evans 1993). The O_3-induced yield loss has been found to be correlated with a reduction in flag leaf duration (e.g. Pleijel et al. 1998).

In 1994 the EU-funded ESPACE-wheat (European Stress Physiology and Climate Experiment – Project 1: Wheat) research programme was started and then continued for three growing seasons. The aim of this research programme was to determine the sensitivity of wheat growth, development and productivity to the combined effects of changes in CO_2 concentration, climatic variables and physiological stresses. The Swedish part of the ESPACE-wheat programme consisted of four different experiments, three of which are reported in the present paper. All three experiments contained an approximately doubled CO_2 concentration, the first year in combination with two elevated O_3 concentrations, the second year included an intermediate CO_2 concentration between ambient and doubled, and the third year in combination with increased irrigation and thereby an elevated water availability.

Materials and methods

Experimental site

The experiment was conducted in a spring wheat field at Östad, 50 km north-east of Göteborg, Sweden (N57°54′, E12°24′). The field was situated 60 m above the sea level and the soil was a loamy sand. No major air pollution sources are located in the vicinity of the investigation area.

Open-top chambers

The open-top chambers (OTCs) were 1.24 m in diameter and 1.6 m high including the frustum. In 1995 and 1996, a roof was attached 0.25 m above the upper part of the frustum in order to control the water availability of the plants completely by irrigation. Air was blown day and night through a circular perforated annulus situated 0.1 m above the canopy at a rate corresponding to approximately 10 m^3 min^{-1}.

Cultural practices

The spring wheat cultivar *Triticum aestivum* L. cv. Dragon was sown (240 kg seeds ha^{-1}) with 0.125 m row spacing. The fertiliser application rate was 120 kg N ha^{-1}, 24 kg P ha^{-1} and 48 kg K ha^{-1}. Further details of the cultural practices of the three experiments are given in Table 1. Irrigation was made with 10 mm water every second day in all treatments except the treatments with elevated water availability in 1996, which received 20 mm every second day.

Experimental design

The experimental design, the treatments and the number of replicates used in the three experiments are presented in Table 2. The treatments were distributed in a completely randomised design in all experiments. In all experiments non-filtered air chambers with ambient CO_2 concentrations were used as controls. In the high CO_2 treatments CO_2 was added day and night. To retain the normal diurnal variation with low O_3 concentrations during the night-time, the additional O_3 was added each day between 08.00 and 20.00, local time. O_3 was generated using pure oxygen and electrical discharge and distributed to the chambers via Teflon tubes. Ambient air (AA) plots were used in all years to check the chamber effect on plant growth and development. One replicate chamber was excluded from analysis in 1994 due to abnormal growth pattern. In 1995 and 1996, 3 and 4

Table 1. Timetable of events (day of year) during the Swedish ESPACE-wheat experiments. –: Not used.

Event	1994	1995	1996
Sowing	118	123	134
N fertilisation	140	123	134
PK fertilisation	146	123	134
Installation of chambers	153–154	144	165–166
Start of irrigation	169	144	165
Start of CO_2 fumigation	164	149	169
Start of O_3 exposure	165	–	–
Installation of tensiometers	–	–	172, 176
Herbicide, MCPA	140	167	172
Insecticide, Pirimor	–	209	201, 229
Fungicide, Tilt Top	–	–	194, 206, 220
Removal of chambers and harvest	235	242	267

Table 2. The experimental design used in the three experiments. AA: ambient air plots without chamber; 350, 520 and 680: chamber plots with ambient, 1.5 × ambient and 2.0 × ambient CO_2 concentrations, respectively; NF: non-filtered chamber air; 350+ and 680+: 1.5 × NF O_3 concentration; 350++ and 680++: 2.0 × NF O_3 concentration; 350 H_2O and 680 H_2O: chamber plots with increased irrigation; n: number of replicates per treatment.

Year	Treatment	CO_2	O_3	H_2O	n
1994	AA	Ambient	Ambient	Normal	3
	350	Ambient	NF	Normal	2
	350+	Ambient	1.5 × NF	Normal	3
	350++	Ambient	2.0 × NF	Normal	3
	680	2 × ambient	NF	Normal	3
	680+	2 × ambient	1.5 × NF	Normal	3
	680++	2 × ambient	2.0 × NF	Normal	3
1995	AA	Ambient	Ambient	Normal	4
	350	Ambient	NF	Normal	5
	520	1.5 × ambient	NF	Normal	3
	680	2 × ambient	NF	Normal	5
1996	AA	Ambient	Ambient	Normal	5
	350	Ambient	NF	Normal	6
	350 H_2O	Ambient	NF	High	6
	680	2 × ambient	NF	Normal	4
	680 H_2O	2 × ambient	NF	High	5

replicate plots, respectively, were excluded due to weeds or aphids.

Pollutant monitoring

Air samples were drawn through 50 m long Teflon (PTFE) tubes (6 mm diameter), which were continuously ventilated and connected to a time-share sampling system with PTFE solenoid valves. Gas concentrations were measured twice per hour in every measurement point. O_3 concentrations were monitored using Thermo Environmental 49 UV absorption analysers and the O_3 analysers were calibrated monthly, using a portable O_3 generator (Monitor Labs 8500). The CO_2 concentrations were monitored using a CIRAS-1 (1994) and FRGA (WMA-1) (1995–1996), both delivered by PP-system, Hitchin, UK. Data were collected with a Campbell Scientific CR10 data logger. In 1994, O_3 concentrations were monitored in all chamber treatments except in the 350 treatment and CO_2 concentrations were measured in all treatments with elevated CO_2. In 1995, O_3 and CO_2 concentrations were monitored in all chamber treatments, and in 1996 CO_2 was monitored in all chambers. In addition to chamber measurements, O_3 and CO_2 concentrations were also measured in the AA at 1 m above the ground (AA 1 m) and in a meteorological mast at 9 m above the ground (AA 9 m).

Climate monitoring

Air temperature and relative humidity were monitored using Rotronic YA-100 hygrometer/thermometers at 0.1 m above the crop in one chamber and at one ambient plot. The photosynthetically active radiation (PAR) was measured using a Li-Cor LI 190SA Quantum sensor in the AA. Water vapour pressure deficit (VPD) was calculated according to Jones (1983). All three climatic parameters were measured continuously (time resolution 1 min) and stored as 30-min averages using a Campbell Scientific CR10 data logger. These values were used to calculate the seasonal mean daytime (08.00–20.00) and night-time (20.00–08.00) values for the whole exposure period. In 1996, the soil water potential was measured at two depths (0.15 and 0.50 m) in 10 of the chambers and in two AA plots, using tensiometers (Soilmoisture Equipment Corp. Santa Barbara, CA, USA) equipped with electronic pressure transducer probes. Water potential data were stored as 30-min averages using a Campbell Scientific CR10 data logger.

Harvests

To facilitate the harvest, each circular plot was marked by a plastic strip with a diameter of 1.10 m and a height of 0.06 m. The circular plot was divided into 2 equally sized parts. The southern part was kept untouched throughout the experiment and was used for the final harvest while the northern half was used for sampling for determination of leaf area and other parameters not discussed in the present paper. All the above-ground plant material in the southern part was harvested at the final harvest. The ears were separated from the straw and the number of ears was counted. The grains from each plot were carefully threshed by hand and weighed. The water content of the grains, as well as of the straw, was determined by drying three subsamples at 70°C to constant weight and used to calculate the total dry weights of grains and straw respectively. The rest of the grains were sent to an authorised agricultural laboratory (AnalyCen, Lidköping, Sweden) for determination of the crude protein concentration (Kjeldahl nitrogen multiplied by 6.25) and the 1000-grain weight. The harvest index was calculated as the proportion of the above-ground biomass which is found in the grains at harvest.

Plant development

The date of emergence (growth stage 10) and mid-anthesis (growth stage 65) was determined according to the decimal code (Tottman and Broad 1987). The end of grain filling (the date when there was no further dry weight increase of

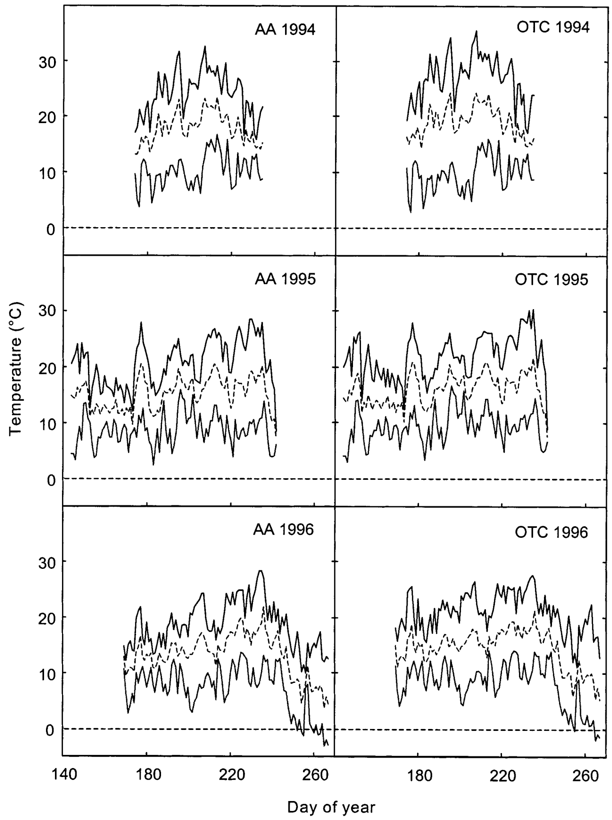

Fig. 1. Temperature (°C) in the ambient air (AA) plots and in the open-top chambers (OTCs) in 1994, 1995 and 1996. 24-h mean temperature (broken line); maximum and minimum 1-h mean temperatures (upper and lower curve, respectively).

the grains) was determined in 1995 and 1996 only. In 1995, the end of grain filling was determined by measuring the dry weight and water content of sampled ears; while in 1996, the sampled ears were threshed and the dry weight per grain was measured.

Leaf area

In 1994, the green leaf area was measured using an area meter (Delta-T instruments). The delimitation of what should be considered as yellow areas, and thus excluded from the green area, on each leaf was estimated visually. On each sampling occasion three plants were harvested at random from the northern part of the chamber. Green leaf area was studied also in 1995 and 1996. No treatment effects were observed in 1995 and 1996 and therefore these data will not be considered further.

Statistical analysis

For the statistical analysis, analysis of variance (ANOVA) was used. For the data set of 1995, one-way ANOVA was performed; for 1994 and 1996, two-way ANOVA was used.

Results

Climate

The weather in 1994 was characterised by a cold spring, but later by an unusual warm and dry period starting in July and lasting approximately 6 weeks (Fig. 1). In both 1995 and 1996, the summer weather was cooler and wetter, rather typical for southwest Swedish conditions (Fig. 1). Due to the unusually cold and prolonged winter of 1996, spring was late in that year and consequently sowing was delayed 16 days and harvest 32 days compared with 1994 (Table 1).

In Table 3, the daytime and night-time temperatures, water vapour pressure deficit (VPD) and photosynthetically active radiation (PAR) inside and outside the chambers during the experiments are presented as mean daytime (08.00–20.00) and night-time (20.00–08.00) values. The maximum daytime chamber effect on temperature, +2.6°C, was obtained in 1994. This was related to the sunny weather, which was also reflected in the higher daytime PAR values. Also on absolute terms, 1994 was the warmest year of the three with average daytime temperatures above 20°C, and the driest year with rather high VPD values for south Swedish conditions, especially inside the OTCs. The lowest temperature value (16.5°C, daytime average) was reported in 1996, while the VPD differed slightly between 1995 and 1996. During the night, the chamber effect on temperature was around 1°C or lower in all years. VPD values for the nights were generally low, but the positive chamber effect on VPD in 1994 was relatively large also during the night.

CO_2 and O_3 concentrations

The measured CO_2 concentrations are presented as daytime (08.00–20.00) mean values in Table 4. The values in the treatments with elevated CO_2 were relatively close to the

Table 3. Seasonal mean temperature (°C), vapour pressure deficits, VPD (kPa) and photosynthetically active radiation, PAR (μmol m^{-2} s^{-1}) during daytime (08.00–20.00) and night-time (20.00–08.00) in the ambient air (AA) and inside the open-top chambers (OTCs) during the 3 years of experimentation. NMV: no measured value. Seasons (day of year): 1994, 174–235; 1995, 144–242; 1996, 169–267.

Year	Treatment	Temperature		VPD		PAR	
		08–20	20–08	08–20	20–08	08–20	20–08
1994	AA	21.6	12.8	11.4	1.4	816	96
	OTC	24.2	13.8	16.0	3.1	NMV	NMV
1995	AA	18.7	11.8	6.9	1.3	742	48
	OTC	19.6	12.4	6.2	1.7	NMV	NMV
1996	AA	16.5	10.0	6.7	1.1	655	36
	OTC	18.1	10.8	5.9	1.4	NMV	NMV

Table 4. Carbon dioxide concentrations (μmol mol^{-1}) expressed as 12-h means (08.00–20.00, local time) during the 3 years of experimentation; NMV: no measured value. Seasons (day of year): 1994, 162–235; 1995, 144–242; 1996, 166–267. For abbreviations, see Table 2. AA 1 m, ambient air in the field; AA 9 m, ambient air 9 m above ground; –, not used.

Treatment	1994	1995	1996
AA 1 m	NMV	349	362
AA 9 m	355	353	360
350	NMV	347	355
350+	NMV	–	–
350++	NMV	–	–
350 H_2O	–	–	358
520	–	515	–
680	660	667	675
680+	646	–	–
680++	663	–	–
680 H_2O	–	–	696

target values, 520 and 680 μmol mol^{-1}, respectively. O_3 exposures are reported in Table 5. O_3 treatments formed part of the experimental design only in 1994, but are nevertheless reported whenever measured in 1995 and 1996. Average concentrations of the elevated O_3 treatments in 1994 were very similar at high and low CO_2 concentrations while the AOT40 (accumulated exposure over a threshold concentration of 40 nmol mol^{-1}) values varied somewhat more. The exposure index AOT40 is sensitive to small changes in the average O_3 concentration in the concentration range typical for the experimental site, where the exceedance of 40 nmol mol^{-1} was rather small. The AOT40 values ranged from slightly above 2000 nmol mol^{-1} h in the treatments with ambient O_3 concentrations to around 12000 nmol mol^{-1} h in the treatments with the highest O_3 level.

Plant development

In Table 6, the dates for emergence (growth stage 10), mid-anthesis (growth stage 65) and the end of grain filling are shown. The late spring in 1996 was reflected in later emergence date compared with 1994 and 1995. Grain filling ended 5 days earlier in 680 μmol mol^{-1} CO_2 in 1995, but 3 days later in the 680 H_2O treatment in 1996 compared with other treatments. In 1994, the end of grain filling was not determined.

Table 5. Ozone concentrations (nmol mol^{-1}) expressed as 12-h means (08.00–20.00) and as accumulated exposure over a threshold concentration of 40 nmol mol^{-1} (nmol mol^{-1} h AOT40). NMV: no measured value. Seasons (day of year): 1994, 162–235; 1995, 144–242; 1996, 166–267. For abbreviations, see Table 2. AA 1 m, ambient air in the field; AA 9 m, ambient air 9 m above ground; –, not used.

Treatment	12-h mean			AOT40		
	1994	1995	1996	1994	1995	1996
AA 1 m	NMV	34	29	NMV	2 455	1 148
AA 9 m	42	37	34	6 403	4 622	3 039
350	NMV	26	NMV	NMV	789	NMV
350+	39	–	–	7 162	–	–
350++	46	–	–	12 052	–	–
520	–	27	–	–	900	–
680	33	28	NMV	2 271	959	NMV
680+	39	–	–	5 648	–	–
680++	47	–	–	11 870	–	–

Table 6. Julian days for emergence (GS 10), mid-anthesis (GS 65) and end of grain filling (EOG) in the different experiments. Growth stages (GS) are according to Tottman and Broad (1987). NMV: no measured value. For abbreviations, see Table 2.

Year	Treatment	Julian day		
		GS 10	GS 65	EOG
1994	AA	129	190	NMV
	350	129	190	NMV
1995	AA	132	198	228
	350	132	195	228
	520	132	195	228
	680	132	195	223
1996	AA	145	211	243
	350	145	208	243
	350 H_2O	145	207	243
	680	145	206	243
	680 H_2O	145	207	246

Soil water potential

Table 7 summarises the measurements of the soil water potential during 1996. The integrated soil water potentials over the treatment period (MPa h) were relatively similar at 0.15 and 0.50 m depth. Increased irrigation resulted in statistically significantly higher soil water potentials at 0.50 m depth, yet the soil water potentials were higher also at 0.15 m depth. The CO_2 treatments also influenced the water potentials to a considerable extent, although not statistically significant. The soil in the low CO_2 treatments had lower water potentials than in the high CO_2 treatments.

Yield, yield components and grain protein

The yield data from 1994 are presented in Fig. 2. Elevation of the CO_2 concentration had a statistically significant effect on the grain and straw yields, the grain protein concentration and the number of ears per unit area. The effect of elevated CO_2 on grain protein concentration was negative by approximately 12%, while the effects on grain and straw yield were positive by 21 and 29%, respectively. The harvest index and the 1000-grain weight were not significantly affected by CO_2. The number of grains per ear was calculated using data on grain yield, 1000-grain weight and the number of ears per

Table 7. Soil water potential in the different treatments expressed as the integrated value over the exposure period in 1996 at 0.15 and 0.50 m soil depth (MPa × h). SE denotes standard error, n: number of replicates. Season (day of year): 178–267. For abbreviations, see Table 2.

Treatment	n	0.15 m depth		0.50 m depth	
		Mean	SE	Mean	SE
AA	2	−15.4	8.1	−19.3	0.2
350	4	−61.4	17.8	−54.7	8.5
350 H_2O	2	−24.4	1.2	−25.7	2.7
680	2	−30.4	6.3	−32.1	4.6
680 H_2O	2	−20.2	1.8	−18.3	1.1

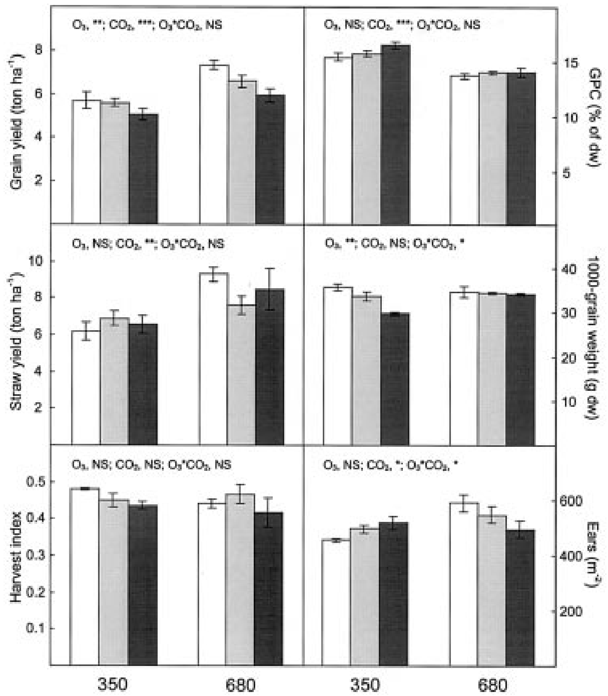

Fig. 2. Grain yield (ton ha^{-1}), grain protein concentration (GPC, %), straw yield (ton ha^{-1}), 1000-grain weight (g dry weight), harvest index and number of ears per square metre in the 1994 experiment. 350: 350 µmol CO_2 mol^{-1}; 680: 680 µmol CO_2 mol^{-1}; white bars: NF; light grey bars: NF+; dark bars: NF++; treatments as in Table 2. Error bars show SE and the levels of significance are the results of a two-way ANOVA; NS: no significant treatment effect; significance levels: * $P = 0.05$; ** $P = 0.01$; *** $P = 0.001$.

square metre and was statistically significantly higher (+5%) in elevated CO_2 compared with ambient CO_2. Increasing the O_3 level affected grain yield and 1 000-grain weight negatively. A significant interaction between elevated CO_2 and O_3 was observed in the number of ears per unit area and in the 1 000-grain weight. In low CO_2, the effect of O_3 on the number of ears per square metre was positive (+9 and +14% in 350+ and 350++, respectively, compared with 350), while the 1 000-grain weight was negatively affected (−6 and −17%, respectively). In high CO_2, on the other hand, the effect of O_3 on the number of ears per unit area was negative and the 1 000-grain weight was unaffected.

The effects of elevated CO_2 concentration on yield parameters were much smaller in 1995 compared with 1994, as evident from Fig. 3. The grain yield was only 7% larger in 680 µmol CO_2 mol^{-1} compared with ambient CO_2, and this effect was not statistically significant. The only parameter that was significantly influenced by CO_2 in 1995 was the grain protein concentration, which decreased by 11% in both 520 and 680 compared with 350 µmol mol^{-1} CO_2.

Also in 1996, treatment effects were generally small and significant only in a few cases (Fig. 4). Overall there was a tendency towards stimulation of grain as well as straw yield by both elevated CO_2 concentration and increased water availability. However, the only significant effect among these was the higher straw yield by elevated CO_2 concentration. The protein concentration of the grain was negatively influenced by both elevated CO_2 and water availability, but only the latter effect was statistically significant. The number of grains per ear was 12% higher in elevated compared with ambient CO_2 (data not shown). No significant interaction effects by CO_2 concentration and water availability were obtained.

Green leaf area

In 1994, substantial treatment effects on the green leaf area duration were obtained. The changes in the green leaf area with time for the four youngest leaves are presented in Fig. 5. Elevated CO_2 resulted in a statistically significant larger flag leaf area at day 213 and thus a longer green leaf area duration. O_3 had a statistically significant negative effect on green leaf area of the fourth leaf at anthesis.

Chamber effects

In Table 8, the chamber effect on the different yield parameters for the 3 years of experimentation is expressed as the ratio (%) between the 350 treatment and the AA treatment. In 1994, there were no statistically significant effects of chamber enclosure, except a positive effect on the calculated number of grains per ear, although a non-significant increase in grain yield. There was however a statistically significant chamber effect on grain yield and the number of ears per square metre in 1995, on grain protein concentration in 1996 and on 1000-grain weight and harvest index in both 1995 and 1996.

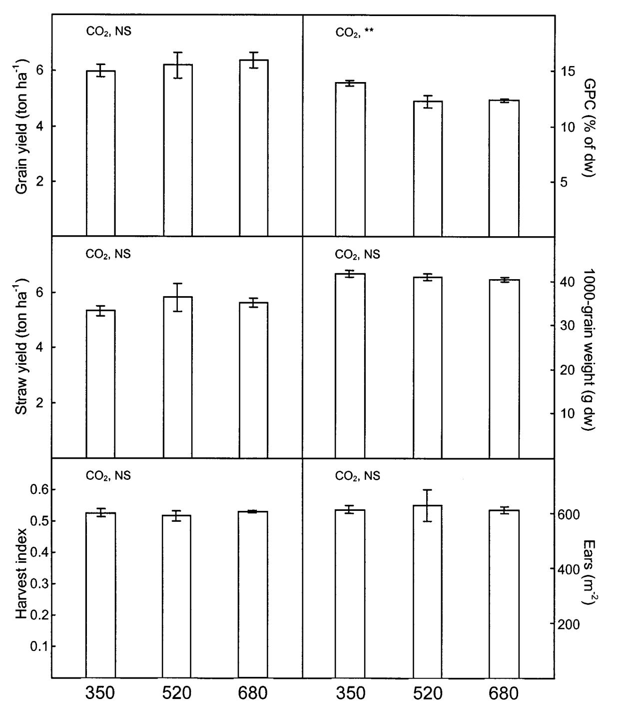

Fig. 3. Grain yield (ton ha^{-1}), grain protein concentration (GPC, %), straw yield (ton ha^{-1}), 1000-grain weight (g dry weight), harvest index and number of ears per square metre in the 1995 experiment. 350: 350 µmol CO_2 mol^{-1}; 520: 520 µmol CO_2 mol^{-1}; 680: 680 µmol CO_2 mol^{-1}. Error bars show SE and the levels of significance are the results of a two-way ANOVA; NS: no significant treatment effect; significance level: ** $P = 0.01$.

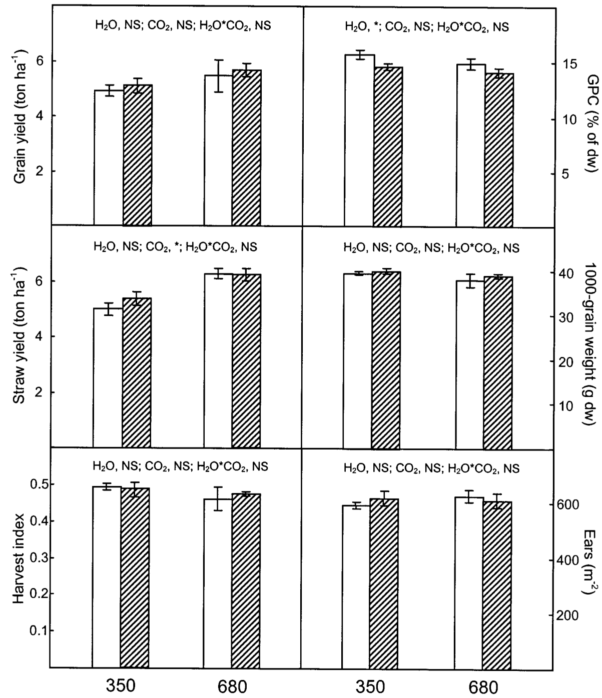

Fig. 4. Grain yield (ton ha^{-1}), grain protein concentration (GPC, %), straw yield (ton ha^{-1}), 1000-grain weight (g dry weight), harvest index and number of ears per square metre in the 1996 experiment. 350: 350 µmol CO_2 mol^{-1}; 680: 680 µmol CO_2 mol^{-1}; white bars: normal irrigation; hatched bars: increased irrigation. Error bars show SE and the levels of significance are the results of a two-way ANOVA; NS: no significant treatment effect; significance levels: * $P = 0.05$.

In 1996, there was a negative chamber effect on straw yield. In 1995 and 1996, there was also a positive chamber effect on the date for anthesis (Table 6).

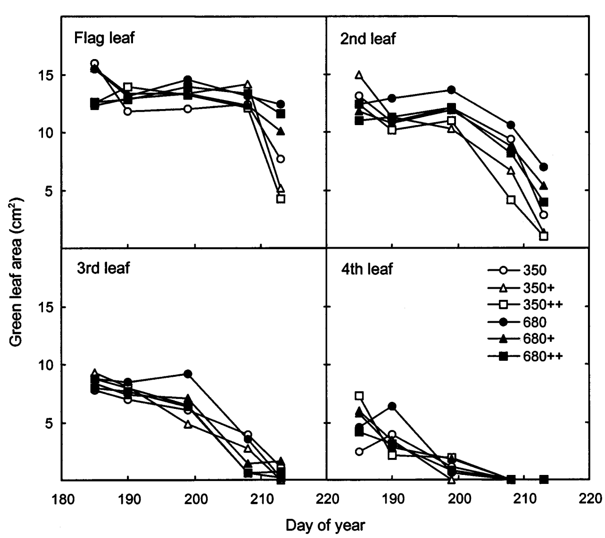

Fig. 5. Development of green leaf area per plant (cm^2) for the youngest four leaves around and after anthesis in the different treatments in 1994. Mid-anthesis was at Julian day 190.

Table 8. The chamber effects expressed as the value for the 350 treatment in percent of the AA treatment. GY: grain yield (ton ha^{-1}); GPC: grain protein concentration (% of dry weight); SY: straw yield (ton ha^{-1}); 1000-g w: 1000-grain weight; HI: harvest index; Ears: number of ears per unit area.

Year	GY	GPC	SY	1 000-g w	HI	Ears
1994	124	91	119	93	102	102
1995	126	105	100	116	112	109
1996	108	113	85	105	114	101

Discussion

Yield responses to elevated CO_2

The core parameter of the ESPACE-wheat programme has been the elevation of the CO_2 concentration of the air. An approximately doubled CO_2 concentration was used during all 3 years of experimentation in the Swedish part of the programme. This treatment resulted in a growth stimulation, which however varied to a considerable extent between the years. There was a large and statistically significant positive effect of doubled CO_2 on both grain and straw yield only in 1994, but the stimulation by doubled CO_2 on straw yield was statistically significant also in 1996.

The grain yield increase due to doubled CO_2 concentration in the present study (21% in 1994, 7% in 1995 and 11% in 1996) is small compared with results of many earlier studies. Kimball (1983) compiled a large number of studies and found the average stimulation of grain yield in wheat by doubled CO_2 concentration to be 37%. In a similar study, Cure and Acock (1986) found a corresponding figure of 35%. More recent experiments have found that doubled CO_2 concentration increased wheat grain yield by 20–50% (Manderscheid and Weigel 1997), 29% (McKee et al. 1997a), 33% (Mulholland et al. 1997) and 12–65% (Batts et al. 1998). Only the 21% higher grain yield found in 1994 was of the same magnitude as yield responses reported in the literature.

Leaf area duration

Not only straw and grain yield were positively affected by elevated CO_2 in 1994. Another important trait that was influenced to a considerable degree was the duration of the green leaf area, especially of the flag leaf. Since green leaf area duration is of great importance for final grain yield in wheat (e.g. Lawlor 1995), it seems reasonable to link the CO_2 stimulation effect on the green leaf area duration to the stimulation on grain yield. Since a reduction of stomatal conductance in elevated CO_2 will improve the water use efficiency of the plant, drought effects may be less severe at high CO_2. Drought is an important trigger of leaf and plant senescence (e.g. Larcher 1995), and the improved water use efficiency may thus retard plant development and improve the green leaf area duration. On the other hand, the reduced transpiration associated with lower stomatal conductance will tend to increase leaf temperature and this may increase the rate of plant development and thus shorten the growth duration (Baker and Allen 1994). Thus, the net result of elevated CO_2 on development is a delicate balance between these factors depending on the conditions prevailing in the particular situation. Therefore, CO_2 can have a variable effect on plant development, which is also consistent with what has been presented earlier in the literature (Conroy et al. 1994).

In the present study, the beneficial effect of reduced drought stress dominated in 1994, resulting in a delayed senescence of plants grown in elevated CO_2. In 1995, however, the plants grown in doubled CO_2 concentration senesced earlier, as seen from the date of end of grain filling and also from leaf chlorophyll and carbohydrate measurements (Sild et al. 1999). In 1996, the effect was smaller, with a delay in the end of grain filling in the 680 H_2O treatment, but no effect on that in the other treatments. An explanation for this difference is likely to be found in the much drier and warmer conditions (Table 3) prevailing in 1994, which made an improved water use efficiency by elevated CO_2 more important in 1994 compared with 1995 and 1996. That the stimulation of grain yield due to elevated CO_2 concentration is higher in warmer conditions has also been found in other experiments (Rawson 1995, Blumenthal et al. 1996). Idso and Idso (1994) concluded that the relative growth stimulation due to CO_2 enrichment rises with increasing air temperature, since photorespiration increases with increasing temperature and elevated CO_2 concentration decreases photorespiration. Differences in temperature and humidity between locations and years may also explain the differences in the grain yield responses reported in the literature.

The less negative soil water potential in elevated CO_2 in 1996 suggests that an elevation of the CO_2 concentration reduced the water consumption of the plants. This is in line with the rather general observation that CO_2 decreases stomatal conductance (Morison 1987). Van Vuren et al. (1997) studied directly the water consumption of wheat plants grown at 350 and 700 μmol mol^{-1} CO_2. They found that the water use per plant was 25% higher at 350 μmol mol^{-1} compared with 700 μmol mol^{-1}, which is consistent with our observation. The soil water potential was remarkably lower in ambient CO_2, and more positively affected by elevated CO_2 in low irrigation. It has often been observed that the effect of CO_2 is higher in low water availability (e.g. Gifford 1979). Nevertheless, the water use per plant in water limiting conditions does not necessarily decrease in high CO_2, despite an improved WUE, since the leaf area or tiller number may be increased (Morison and Gifford 1984, Samarakoon et al. 1995).

Yield parameters and grain protein

CO_2 had a positive effect on grain yield in 1994 but no influence on the 1000-grain weight. The higher grain yield in elevated CO_2 was instead associated with a higher number of ears per square metre, which is in agreement with other studies (Mulholland et al. 1998). The higher CO_2 concentration seems to have stimulated the development and/or survival of productive tillers. An abundance of assimilates produced in elevated CO_2 could enhance the survival of tillers and grain primordia (Lawlor and Mitchell 1991), which might explain the higher number of grains per ear in elevated CO_2 in 1994 and 1996. Water deficit leads to a reduction of tillering in grasses (Jones 1983). An increase in water use efficiency, and hence a decrease in water deficit, could thus provide another explanation to the increased number of ears per square metre. However, there was no significant effect of elevated CO_2 or increased irrigation on the number of ears per square metre in 1996.

The protein concentration and hence the quality of the grain were negatively affected by elevated CO_2. This effect was significant in 1994 and 1995, yet more pronounced in 1994 compared with 1995. This pattern, i.e. that an increase in grain yield is associated with a decrease in the grain protein concentration, has been observed in a number of studies (e.g. Manderscheid et al. 1995, Fangmeier et al. 1997) and seems to be rather general (Pleijel et al. 1999). If carbon accumulation is stimulated at a certain level of nitrogen availability, the nitrogen will become diluted within the plant (Mooney and Koch 1994).

Yield responses to increased water availability

The only parameter that responded to the water treatment was the grain protein concentration, which was significantly lower in the high water regime. This probably reflects the same kind of growth dilution effect as discussed above in relation to CO_2, although the effect on grain yield of increased irrigation was not significant. Although both grain and straw yield responded slightly positively to elevated irrigation, none of these effects were significant, despite the rather large difference in water added between the two levels of irrigation. Therefore, we conclude that an increased water availability, as predicted by some circulation models for the Nordic countries, will not necessarily result in improved yield of spring wheat in the climate prevailing in that region, except for years with drought.

Yield responses to O_3

O_3 exposure had a negative effect on grain yield in both ambient and elevated CO_2. In the low CO_2, O_3 induced grain yield reduction as a result of a lower 1000-grain weight. O_3-induced reduction in grain weight has been reported in many experiments (e.g. Pleijel et al. 1998). In the high CO_2, O_3 induced grain yield reduction as a result of a lower number of ears per square metre. The leaf area duration data of 1994 and the soil water potential measurements of 1996 indicate a lower stomatal conductance, and hence probably a lower O_3 uptake in the higher CO_2 concentration. The actual O_3 dose (the O_3 taken up by the plant) might thus be lowered in high CO_2, which may explain the different effects of O_3 on 1000-grain weight in low and high CO_2. Under high CO_2 conditions, O_3 exposure had no impact on the 1000-grain weight. The different effect of O_3 on 1000-grain weight may also be associated with a CO_2 stimulation effect on green leaf area duration. It may also be associated with an O_3-induced decrease in ear number per square metre in high CO_2, which may have a positive effect on the 1000-grain weight of the remaining ears. CO_2 enrichment had a positive effect on the number of ears per unit area in low and medium O_3 concentration (680 and 680+ as compared with 350 and 350+), but a negative effect in the high O_3 concentration (680++ compared with 350++). It is possible that the positive effect of elevated CO_2 on tillering was accompanied by higher tiller mortality and/or a lower proportion of ear bearing tillers in the 680++ treatment. The grain yield of all elevated CO_2 treatments (680, 680+ and 680++) was higher than the grain yield of the 350 treatment, indicating that the positive effect of elevated CO_2 could compensate for the yield losses due to O_3. The grain yield was, however, negatively affected by O_3 in both CO_2 concentrations.

Conclusions

Based on the experience from the present 3-year study, the effect of elevated CO_2 on the yield of spring wheat can be expected to vary from year to year. In years when the beneficial effect of the CO_2-induced improved water use efficiency on leaf area duration is expressed, i.e. warm and dry years, the yield is likely to be significantly increased. Under wetter and cooler conditions, typical for southwest Sweden in many summers, the yield increase will be smaller.

O_3 decreased the grain yield in both ambient and elevated CO_2. However, the grain yield in elevated CO_2, regardless of O_3 concentration, was higher than the grain yield in any of the O_3 concentrations with ambient CO_2. Thus, in climatic conditions that allow the CO_2 effect to be expressed to a significant extent, elevated CO_2 will probably compensate for the yield losses due to O_3.

Increasing the water availability did not affect the grain yield, in neither ambient nor in elevated CO_2. Occasionally, spring wheat yield in the Nordic countries is suppressed by drought stress. An overall increased water availability, as predicted by some models as a consequence of global greenhouse warming, will decrease the occurrence of drought. In normal years, increased water availability is likely to have small effects on spring wheat yield.

Acknowledgements – The present study formed part of the EU Environment ESPACE-wheat programme (Contract No. EV5V-CT93-0301). It was funded by the Swedish Environmental Protection Agency, the Swedish Council for Forestry and Agricultural Research and Göteborg University. Thanks are expressed to Patrik Alströmer, Östad Säteri for making available the investigation area and to Christina Westberg for technical assistance.

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Edited by C. H. Foyer