Field Crops Research 110 (2009) 185–196

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Effects of free air carbon dioxide enrichment and nitrogen supply on growth and yield of winter barley cultivated in a crop rotation

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ARTICLE INFO

Article history:
Received 3 April 2008
Received in revised form 5 August 2008
Accepted 6 August 2008

Keywords:
Elevated CO_2
FACE
Green area index
Grain growth
Harvest index
Hordeum vulgare
Nitrogen supply
Radiation use efficiency
Yield

ABSTRACT

The increase in atmospheric CO_2 concentration [CO_2] has been demonstrated to stimulate growth of C_3 crops. Although barley is one of the important cereals of the world, little information exists about the effect of elevated [CO_2] on grain yield of this crop, and realistic data from field experiments are lacking. Therefore, winter barley was grown within a crop rotation over two rotation cycles (2000 and 2003) at present and elevated [CO_2](375 ppm and 550 ppm) and at two levels of nitrogen supply (adequate (N2): 262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year) and 50% of adequate (N1)). The experiments were carried out in a free air CO_2 enrichment (FACE) system in Braunschweig, Germany. The reduction in nitrogen supply decreased seasonal radiation absorption of the green canopy under ambient [CO_2] by 23%, while CO_2 enrichment had a positive effect under low nitrogen (+8%). Radiation use efficiency was increased by CO_2 elevation under both N levels (+12%). The CO_2 effect on final above ground biomass was similar for both nitrogen treatments (N1: +16%; N2: +13%). CO_2 enrichment did not affect leaf biomass, but increased ear and stem biomass. In addition, final stem dry weight was higher under low (+27%) than under high nitrogen (+13%). Similar findings were obtained for the amount of stem reserves available during grain filling. Relative CO_2 response of grain yield was independent of nitrogen supply (N1: +13%; N2: +12%). The positive CO_2 effect on grain yield was primarily due to a higher grain number, while changes of individual grain weight were small. This corresponds to the findings that under low nitrogen grain growth was unaffected by CO_2 and that under adequate nitrogen the positive effect on grain filling rate was counterbalanced by shortening of grain filling duration.

1. Introduction

Concern about the predicted changes in climate and the rapid rise in the concentration of atmospheric CO_2 has prompted strong interest in the response of agricultural food production to these changes (Easterling et al., 2007). Atmospheric CO_2 concentration [CO_2], which particularly affects photosynthesis of C_3 plants, has already risen from 280 ppm to 375 ppm in the past and based on the A1B IPCC scenario is predicted to double at the middle of this century (Meehl et al., 2007). Plant photosynthetic processes and consequently plant growth are known to be directly affected by elevated [CO_2] (Kimball et al., 2002; Long et al., 2005). Climate change alters the seasonal precipitation pattern and increases average temperatures, which have negative effects on agricultural food production (Meehl et al., 2007). Barley occupies about 30% and 9% of the cereal acreage of Germany and the whole world, respectively (FAO, 2006) being the fourth most important cereal in terms of world production. Thus, there is an urgent need to assess the effects of drought, warming and increasing [CO_2] on growth and yield of this crop. In the present study only the direct effects of elevated [CO_2] were determined.

Up to now, the CO_2 response of barley has only been investigated in few experimental studies using different types of enclosures for CO_2 fumigation, e.g. growth chambers (Bunce, 1998; Frank and Apel, 1987), greenhouses (Ford and Thorne, 1967; Kleemola et al., 1994; Thompson and Woodward, 1994; Van Kraalingen, 1990) and open-top chambers (Fangmeier et al., 1996; Pettersson et al., 1992; Saebo and Mortensen, 1996; Weigel et al., 1994). However, there are no data available how barley might respond to elevated [CO_2] under undisturbed agricultural field conditions.

Crop yield depends on three basic processes: (1) absorption of incident radiation (AR), (2) conversion efficiency of absorbed radiation into plant dry matter, which is usually called radiation

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0378-4290/$ – see front matter © 2008 Published by Elsevier B.V.
doi:10.1016/j.fcr.2008.08.002

use efficiency (RUE), and (3) partitioning of dry matter between grains and the total plant biomass, which is given by the harvest index (HI). Seasonal radiation absorption is determined by the duration and size of the green area of leaves, stems and ears. Crop yield (Y) can be expressed as product of these processes:

$$Y = AR \times RUE \times HI \quad (1)$$

Final grain yield is the product of grain number and individual grain weight. The latter depends on the rate and duration of grain filling. Variations in grain yield due to different growth conditions are primarily based on changes in grain number (Gallagher et al., 1975) and the contribution of individual grain weight is still under debate (Frederick and Bauer, 1999). Assimilates for grain growth are not only provided by photosynthesis but also by remobilization of stored carbohydrates in the stem (Schnyder, 1993), which are responsible for the relative stability of individual grain weight (Gallagher et al., 1975). Stem reserves can contribute significantly to final grain yield especially under unfavourable growth conditions and this storage buffer was found to be affected by nitrogen (Schnyder, 1993) and CO_2 supply (Gruters, 1999).

The investigation of yield formation consisting of the three components AR, RUE and HI is in the focus of many studies on the effect of elevated [CO_2] on yield of cereals (Jamieson et al., 2000; Long et al., 2005). In addition, grain number, grain filling duration, and grain weight should be determined for a proper analysis of yield composition.

Photosynthetic rate of single leaves of barley was found to increase with increasing [CO_2] (Ford and Thorne, 1967; Pettersson et al., 1992) while in other studies the stimulation of photosynthesis was only transient (Hibberd et al., 1996; Sicher and Bunce, 1997). Barley leaf growth showed variable response to CO_2 enrichment including a positive effect (Ford and Thorne, 1967), and no response (Bunce, 2004) while stem height was enhanced under CO_2 elevation (Saebo and Mortensen, 1996; Weigel et al., 1994). Two studies reported about an increase in harvest index under CO_2 elevation (Kleemola et al., 1994; Pettersson et al., 1992). However, in several other experiments no change or a decrease was detected (Weigel et al., 1994).

For cereals in general, all recent CO_2 fumigation experiments, in which [CO_2] was doubled as compared to the ambient value, showed a positive CO_2 effect on grain yield, which varied between ca. 20% and 90% (Kleemola et al., 1994; Thompson and Woodward, 1994; Fangmeier et al., 1996, 2000; Saebo and Mortensen, 1996; Weigel et al., 1994). This effect was modified by the influence of nitrogen supply (Fangmeier et al., 2000, Kleemola et al., 1994; Thompson and Woodward, 1994; Van Kraalingen, 1990) and temperatures (Saebo and Mortensen, 1996; Fangmeier et al., 2000; Weigel et al., 1994).

Previous CO_2 enrichment studies have shown that changes in grain yield were mainly due to stimulation of grain number (Kleemola et al., 1994; Pettersson et al., 1992; Thompson and Woodward, 1994; Saebo and Mortensen, 1996; Weigel et al., 1994). It has been hypothesized that elevated [CO_2] will increase the rate or duration of grain filling of wheat (Frederick and Bauer, 1999). Since higher temperatures reduce the grain filling duration (Frederick and Bauer, 1999), global warming associated with increasing CO_2 will tend to reduce the duration of grain filling in all determinant crops. Findings of a recent free air CO_2 enrichment experiment showed an increase in grain growth, while CO_2 effects on grain filling duration were inconclusive because of the confounding effect of blower-induced temperature changes (Li et al., 2000). To our knowledge, detailed studies on grain growth of barley under CO_2 enrichment have not yet been done.

To some extent inconsistency and variability of the data presented can be attributed to the experimental approaches chosen for simulating future [CO_2]. In previous experiments barley was normally grown in pots (Ford and Thorne, 1967; Fangmeier et al., 2000; Frank and Apel, 1987; Kleemola et al., 1994; Van Kraalingen, 1990; Weigel et al., 1994), which restricted root growth and thereby water and nutrient supply as compared to the situation in the field. The aerial microclimate in enclosures is darker, warmer and drier than in the field which can alter the magnitude of the CO_2 response (Long et al., 2005). Moreover, samples were mostly taken from small isolated areas, in which edge effects can interact with the CO_2 treatment and modify the CO_2 effect on grain yield.

In order to obtain realistic data on winter barley yield formation under elevated [CO_2], the present study was undertaken with the free air carbon dioxide enrichment technique (Lewin et al., 1992). The objectives were (1) to quantify the effect of elevated [CO_2] combined with adequate and restricted nitrogen supply on grain yield, (2) to analyze the treatment effects on the three processes influencing yield, i.e. seasonal radiation absorption, radiation use efficiency and biomass partitioning, and (3) to investigate the effects on yield formation, i.e. stem reserves and individual grain growth.

2. Materials and methods

2.1. Experimental site and experimental design

The experimental plots were set-up in a 22-ha field located at the Federal Agricultural Research Centre (FAL) in Braunschweig, south-east Lower Saxony, Germany (52°18′ N, 10°26′ E, 79 m a.s.l.). The soil is a luvisol of a loamy sand texture (69% sand, 24% silt, 7% clay) in the plough horizon. The profile has a depth of about 60 cm (–30 cm Ap, –15 cm Al, –15 cm Bt, >60–70 cm CII). The lower layers, in particular >70 cm, are characterized by a coarser soil texture (almost pure sand) and are structured by the succession of thin silt/clay layers. The plough layer has a pH of 6.5 and a mean organic matter content of 1.4%. The drained upper (0.01 MPa soil water tension) and lower limits (1.5 MPa water tension) of plant available volumetric soil water content were 23% and 5%, respectively. Thus, the soil has a volumetric plant available water content of ca. 18% in the plough layer, which decreases slightly with increasing soil depth. Overall, the soil is of low to intermediate fertility and provides a comparatively shallow rooting zone.

Fumigation treatments included two FACE circular experimental areas (rings) enriched with CO_2 (set to 550 ppm) and two control rings with ambient air (about 375 ppm), each 20 m of diameter. The rings were 100 m apart from each other and arranged in two rows (100 m distance) with FACE and ambient treatment, respectively. The rings were divided in two semicircles fertilized with low (N1, 50% of adequate) and adequate (N2) level of mineral nitrogen, respectively.

For monitoring of soil water content in the upper 40 cm of the soil profile, six TDR probes were installed at 10 cm and 30 cm depth, respectively, in the adequately fertilized halves of the experimental rings resulting in a total number of 48 TDR probes (28 P2Z sensors from IMKO, Ettlingen, Germany; 20 probes from EASY TEST, Lublin, Poland). Volumetric soil water content was recorded approximately twice per week.

For crop analysis each half of a ring was divided into two quarters and crop samples were taken. Mean values were calculated for each ring half for statistical analysis.

2.2. The FACE system

A FACE system engineered by Brookhaven National Laboratory (Lewin et al., 1992) was operated as described previously by

Weigel et al. (2005). The target [CO_2] in the enriched rings was set to 550 ppm during daylight hours. Fumigation was stopped when wind speeds were >6 m/s or air temperatures <5 °C. This low temperature threshold value was used because crop growth is low and the reaction of photosynthesis to increased [CO_2] is negligible below 5 °C (Long et al., 2005). Each experimental ring was fumigated with air containing normal or elevated [CO_2] through 32 butterfly valve controlled vertical vent pipes (blowers). CO_2 was released from the vent pipes at the height of the crop canopy layer. In general, 12 valves from direction of the actual wind direction were opened for CO_2 fumigation; in case of low wind speed (<0.5 m s^{-1}) every second vent pipe was activated. This allowed for the exclusive fumigation of the area inside the experimental rings. The target [CO_2] was controlled by continually modifying the amount of CO_2 added to the air blown into the rings. The control algorithms were implemented in PC controlled software and employed actual [CO_2], wind speed and wind direction as input values.

2.3. Crop management

The FACE experiment with barley (*Hordeum vulgare* L.) was carried out as part of a typical North German crop rotation consisting of winter barley, ryegrass as a cover crop, sugar beet and winter wheat. The rotation cycle was repeated twice, resulting in two growing seasons with winter barley (1999/2000 and 2002/2003). Agricultural management measures were carried out according to local farm practices. The six-rowed winter barley cultivar ''Theresa'' was used, which was registered in 1994 and is still one of the most frequently cultivated winter barley varieties in Germany. After ploughing and preparation of the field with a cultivator, winter barley was sown in east-west rows spaced 0.12 m with a seeding density of approximately 275 plants m^{-2}. At the beginning of September in 1999, organic manure was applied to the field, and total nitrogen added amounted to about 110 kg ha^{-1} and 30 kg ha^{-1} for the N2 and N1 plots, respectively. Total mineral nitrogen added to the respective experimental area (N2/N1) amounted to 152/77 kg N ha^{-1} and to 179/105 kg N ha^{-1} in 2000 and 2003, respectively. Total organic and inorganic N applied in the 1st year was 262 kg ha^{-1}. Two thirds of total nitrogen fertilizer were added until stem elongation (Table 1) as ammonium nitrate–urea solution or as ammonium sulphate at a rate of 20–60 kg ha^{-1}. The reminder was applied before anthesis as calcium ammonium nitrate. For both experiments, mineral nutrients were added according to local fertilizing practices and based on analysis of soil nutrient contents (K, Mg, N, P, S) determined in early springtime. Table 1 lists the major management measures for the two growing seasons.

In order to avoid interacting effects of elevated [CO_2] and drought stress, the field was irrigated using a linear irrigation system to keep the soil water content above 50% of maximum plant available soil water content. This was achieved by modelling soil water budget with the AMBAV model (Kersebaum et al., 2005), which was done by the Agrometeorological Research Station of the German Weather Service at Braunschweig. The model runs were continually controlled and re-parameterized by regularly measuring the soil water content by soil coring and with TDR probes. Based on these data, the field was irrigated three times in 2000 (from 5th of May until 5th of June) and five times in 2003 (from 23rd of April until 4th of June) and the total water added amounted to 72 mm and 77 mm, respectively.

2.4. Crop growth analysis

Six (1st experiment) or five (2nd experiment) destructive harvests were carried out from stem elongation until grain maturity and samples were taken from each quarter per ring. For the intermediate harvests, the size of the sampling area amounted to 0.4 m^2 and 0.5 m^2 in 2000 and 2003, respectively, and at grain maturity the sampling area represented 2.0 m^2 and 1.0 m^2. The major fraction (70–90%) of the total above ground biomass was dried and the dry weight was determined. The remaining subsample was used for estimation of green areas and biomass partitioning. The projected areas of green plant parts (leaves, stems and ears) were measured with a leaf area meter (Model LI-3100 from LICOR) and used to calculate green area index (GAI) of leaves, stems, ears and of all green parts. Dry weights of leaves, stems and ears were determined after drying at 105 °C. At maturity yield components (ear number, grain number, mean grain weight and grain yield) were measured.

Canopy height was recorded by measuring the height of a styrofoam disc (0.01 m × 0.5 m × 0.5 m) placed on the top of the canopy. Four measurements were taken per ring quarter and averaged. Fraction of photosynthetic active radiation absorbed by the green canopy (f_{ar}) was measured at noon (±2 h) on sunny days approximately once per week from stem elongation until canopy senescence. The measurements were carried out with a line quantum sensor (in the 1st year with Transmission Meter EMS 7 from PP Systems, Herts, UK; in the 2nd year with the SUNSCAN system from Delta-T-Devices, Cambridge, UK) and included the radiation incident on the canopy (J_0), reflected by the canopy (J_r), and the radiation at the lower limit of the green canopy (J_c), which was estimated by eye. J_r and J_c were measured four times and averaged per ring quarter, f_{ar} was calculated using the following equation:

$$f_{ar} = \frac{(J_0 - J_r - J_c)}{J_0} \quad (2)$$

Table 1
Timetable of significant crop culture events in the first (1999–2000) and second vegetation period (2002–2003)

Event	1st growing season	2nd growing season
Sowing	24 September	27 September
Emergence	1 October	4 October
Start of CO_2 Enrichment	4 October	10 October
Application of herbicides	13 October	1 November
Application of nutrients (Ca, Mg, Mn, N, S) in springtime	22 March, 11 April	17 March, 3 and 25 April, 5 May
First node stage	3 April	25 April
Application of growth regulator	11 and 27 April	–
1st application of fungicides	11 April	12 May
Nitrogen fertilization before anthesis	5 May	15 May
Anthesis	9 May	26 May
2nd application of fungicides	16 May	2 June
End of CO_2 enrichment	19 June	23 June
Grain maturity	26 June	25 June

Accumulated radiation absorbed over the whole vegetation period was estimated as the sum of the daily values, which represent the product of incident global radiation measured and f_{ar}. Data from intervening days were obtained by linear interpolation of the f_{ar} readings.

Radiation use efficiency of above ground biomass production was calculated as the slope of the regression of above ground biomass on cumulative global radiation absorbed by the green canopy starting after the first destructive harvest.

2.5. Grain growth analysis

During the second vegetation period, in 2003, every 4–7 days from anthesis until maturity 10 spikes per ring quarter were harvested. Final grain size along the ear varies and there are also large differences in grain weight between the central and lateral florets (Cottrell and Dale, 1984). Therefore, from each spike three spikelets were collected from mid-spike nodes. The central and the two lateral grains were separated and the awns were detached resulting in samples of 30 central and 60 lateral grains per quadrant. Dry weight of samples was measured after drying to constant weight at 105 °C and used to calculate average grain weight.

Grain filling duration (GFD) and grain filling rate (GFR) were calculated with a logistic model (Robert et al., 1999):

$$y = \frac{a}{1 + e^{-(x-c/b)}} \quad (3)$$

where y: grain weight (mg); a: final grain weight; x: accumulated growing degree days from anthesis, c and b: empirical values related to GFD and GFR.

Elevated CO_2 reduces stomatal conductance (Bunce, 2004; Weigel et al., 2005), which can result in a warmer canopy microclimate and thus should be considered for the calculation of grain filling duration. Air temperature of the canopy was measured in one FACE and one blower ring in both years. Mean daily canopy air temperature during the grain filling period was slightly higher (+0.1 °C) in 2000 and slightly lower in 2003 (−0.2 °C) in the FACE than the blower ring. Since we did not find a warming of the canopy microclimate due to CO_2 enrichment, we used the air temperature (2 m above ground level) recorded by the Agrometeorological Research Station of the German Weather Service at Braunschweig and a base temperature of 0 °C for calculation to growing degree days. The coefficients of determination (r^2) of the model fits were always higher than 0.96. GFD was calculated when 95% of the final grain weight was achieved, and GFR was estimated as the mean filling rate from 5% to 95% of maximum grain weight.

2.6. Analysis of water soluble carbohydrate content

The stem fraction of the intermediate harvests was used for the analysis of water soluble carbohydrates (WSC). The dried stem material including leaf sheath was milled to a fine powder (1 mm). A sub-sample of 100 mg dry weight was shaken in 10 ml hot water for 30 min at 80 °C in a water bath. After filtration the concentration of carbohydrates in the aqueous solution was determined colourimetrically by the anthrone method (Laws and Oldenburg, 1993). The WSC concentration of the stem was multiplied with the stem dry weight per ground area to obtain the stem reserves, i.e. the amount of WSC in stems per m^2 ground area. The contribution of stem reserves to grain yield was calculated from the maximum values at grain filling and the value at grain maturity assuming an efficiency of mobilized WSC conversion into grain mass of 0.9 reported for wheat (Gebbing et al., 1999).

2.7. Statistical analysis

Data were analyzed with the R statistical software package (Version 2.0.0, R Development Core Team, 2004). The experiment was designed as a split–split-plot. The [CO_2] was the split-plot treatment, and N was the split–split-plot treatment. Average values of the variables calculated for each ring half were used in the statistical analysis. In general, experimental year was treated as a fixed effect. Variables connected to phenological development of the plant during the vegetation period (above ground biomass, GAI, carbohydrate content and stem reserves) were separately analyzed for each year on the basis of individual sampling dates.

For the analysis of the grain filling data obtained in the year 2003 the factor grain position was included in the statistical model.

The three parameters of the logistic model for the grain filling process were estimated by fitting the curve to experimental data with the Sigma-Plot statistical package.

3. Results

3.1. Performance of the FACE system and environmental conditions over the two seasons

Cut off times for CO_2 fumigation as compared to potential maximum fumigation times (daylight hours) were 33% in 2000 and 38% in 2003, almost exclusively due to low temperatures (<5 °C). At temperatures <5 °C plants were considered as physiologically inactive without response to changes of [CO_2]. During fumigation times, the seasonal mean of the daytime [CO_2] was 373 ppm and 378 ppm for ambient CO_2 rings in 2000 and 2003, respectively. In the enriched rings, the [CO_2] were 551 ppm and 547 ppm. [CO_2] in the FACE rings (1 min average values) in the times with active fumigation varied 98.0% and 97.5% of total fumigation time within a range of $<\pm 10\%$ of the target concentration in the years 2000 and 2003, respectively.

The meteorological conditions during the two seasons for winter barley (1999/2000 and 2002/2003) are shown in Fig. 1. Seasonal changes in air temperatures were within the range of normal variation. Winter and early spring were slightly warmer in 2000 than in 2003 which allowed an earlier canopy growth in the 1st than the 2nd growing period (Table 1). From February until May in 2003, monthly means of precipitation were extremely low and global radiation was rather high (Fig. 1). This caused an unusual early beginning of soil drying in 2003 (Fig. 1) and a slight drought stress occurred in springtime of the 2nd growing period. Although the FACE rings mostly showed higher mean water content in 0–40 cm soil depth than the ambient rings, these differences were not statistically significant in the 1st year. In the 2nd year, a statistically significant CO_2 effect on soil water content was observed at the 5th of May ($p = 0.03$), and at the end of May, a statistically significant interaction of CO_2 and measuring depth ($p < 0.001$) was found. At both dates volumetric soil moisture in 10 cm depth was 2–3% higher under FACE than under ambient (data not shown).

3.2. Seasonal course of crop biomass and green area indices

Above ground biomass production was considerably higher in the first compared to the second year (Fig. 2) which was associated with great differences in the seasonal dynamics of green area index (Fig. 3). Both variables were strongly affected by nitrogen supply. In the 1st year, CO_2 enrichment increased total above ground biomass beginning at anthesis, while green area index was unaffected over the whole measuring period by the CO_2 treatment. In the 2nd year, CO_2 enrichment increased above ground biomass

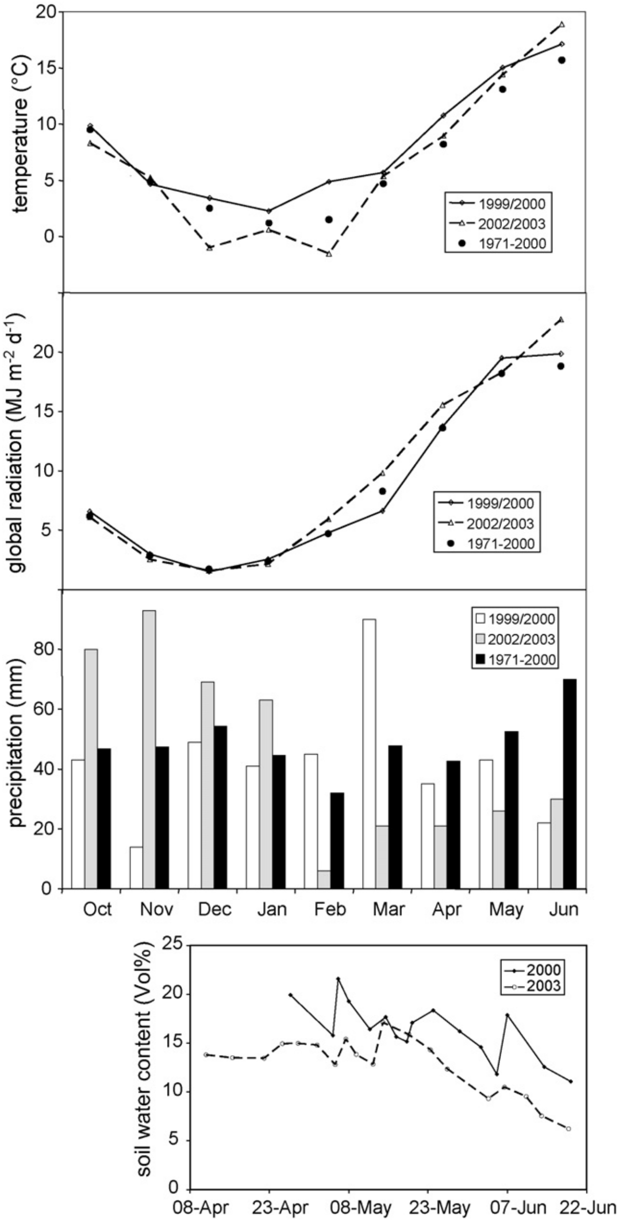

Fig. 1. Seasonal changes in climatic conditions in the 1st and 2nd vegetation period as compared to the long-term mean, and temporal courses of volumetric soil water content in 2000 and 2003. Values represent averages of soil water content measured at two depths (10 cm and 30 cm) and in four rings (two blower rings and two rings with CO_2 enrichment).

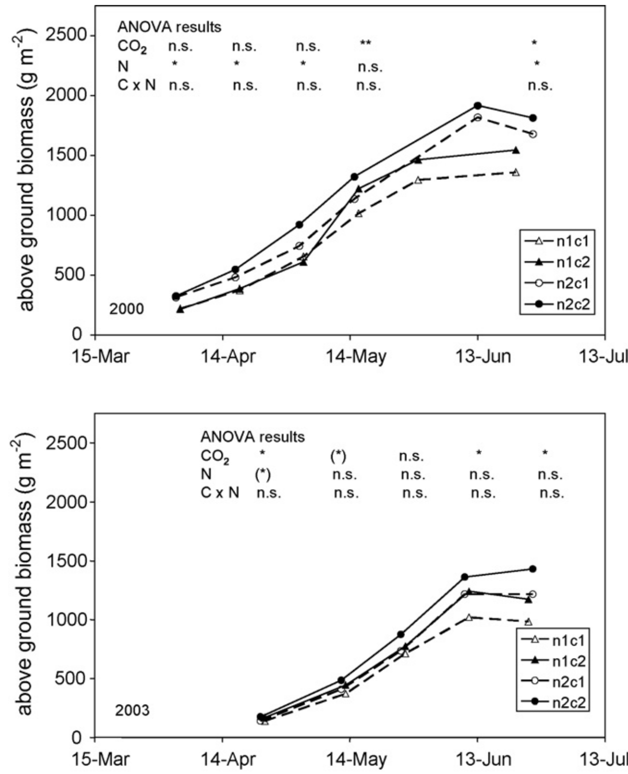

Fig. 2. Seasonal changes in above ground dry weight of winter barley in 2000 and 2003 grown under two levels of nitrogen [N2: adequate N supply (262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year), N1: ca. 50% of N2] and of atmospheric CO_2 concentrations (ambient (C1) and enriched (C2)).

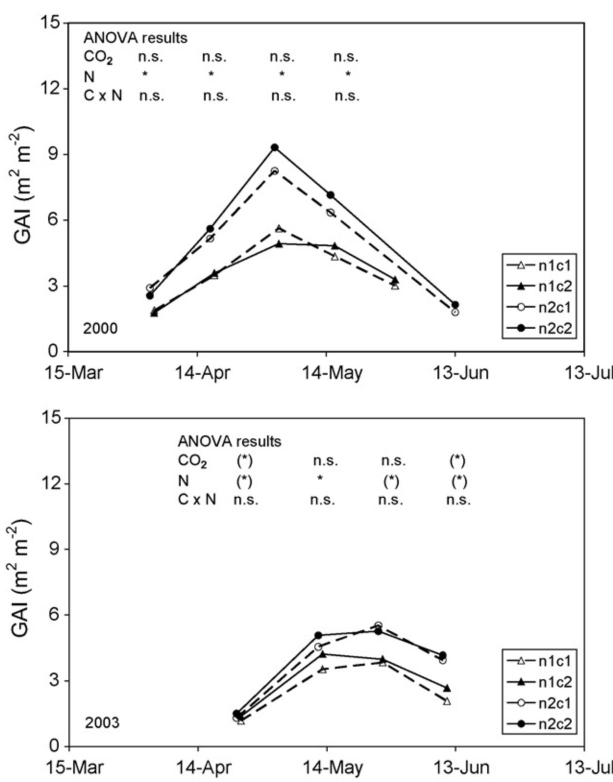

Fig. 3. Seasonal changes in total green area index (GAI) of winter barley in 2000 and 2003 grown under two levels of nitrogen [N2: adequate N supply (262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year), N1: ca. 50% of N2] and of atmospheric CO_2 concentrations (ambient (C1) and enriched (C2)).

already at stem elongation and also green area index at this stage and during grain filling. The CO_2 related stimulation in total biomass in April 2003 was based on statistically significant CO_2 effects on stem ($p = 0.051$) and leaf dry weights ($p = 0.008$). During subsequent harvests in 2003 and on all dates in 2000 leaf dry weight was not found to be affected by CO_2 elevation (Tables 2 and 4) and increases in above ground biomass resulted from CO_2 effects on stem and ear growth. This corresponds to the absence of a CO_2 effect on green leaf area index. At anthesis, green area index of ears was only measured in 2003 and showed higher values under FACE than ambient CO_2 (Table 2). There were statistically significant CO_2 effects on stem height and green stem area index, and the latter was increased by over 20% averaged over years and nitrogen treatments (Table 2).

Table 2
Effect of different nitrogen supply [N2: adequate N supply (262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year), N1: 50% of N2] and atmospheric CO_2 concentrations (ambient and FACE) on growth variables of winter barley at anthesis in 2000 and 2003

Year	CO_2	Leaf biomass (g m^{-2})		Stem biomass (g m^{-2})		Ear biomass (g m^{-2})		Green leaf area index (m^2 m^{-2})	
		N1	N2	N1	N2	N1	N2	N1	N2
2000	Ambient	230	271	580	647	208	220	3.42	4.77
	FACE	248	293	730	776	244	254	3.57	5.17
	%[a]	7.8	8.1	25.9	19.9	17.3	15.5	4.4	8.4
2003	Ambient	131	164	441	442	139	129	2.20	3.53
	FACE	126	145	491	555	156	171	2.15	3.03
	%	−3.8	−11.6	11.3	25.6	12.2	32.6	−2.3	−14.2
ANOVA results									
CO_2		n.s.		*		n.s.		n.s.	
C × year		n.s.		n.s.		n.s.		n.s.	
N		**		n.s.		n.s.		***	
C × N		n.s.		n.s.		n.s.		n.s.	
N × year		n.s.		n.s.		n.s.		n.s.	
C × N × Y		n.s.		n.s.		n.s.		n.s.	

Year	CO_2	Green stem area index (m^2 m^{-2})		Stem height (m)		Green ear area index (g m^{-2})	
		N1	N2	N1	N2	N1	N2
2000	Ambient	0.93	1.58	0.751	0.946	n.d.[b]	n.d.
	FACE	1.26	1.98	0.802	0.985	n.d.	n.d.
	%	35.5	25.3	6.8	4.1		
2003	Ambient	1.15	1.40	1.00	1.06	0.487	0.589
	FACE	1.28	1.58	1.03	1.13	0.556	0.659
	%	11.3	12.9	3.0	6.6	14.2	11.9
ANOVA results							
CO_2		(*)		(*)			
C × year		n.s.		n.s.			
N		***		***			
C × N		n.s.		n.s.			
N × year		*		*			
C × N × Y		n.s.		n.s.			

(*), $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.
[a] % Represents the percentage difference between FACE and Ambient.
[b] Green ear area index was not determined in 2000.

3.3. Seasonal radiation absorption and radiation use efficiency

The accumulated seasonal radiation absorbed by the green canopy from stem elongation until canopy senescence (AR) ranged from 675 MJ m^{-2} to 1230 MJ m^{-2} (Table 3). In the 1st experiment the green canopy absorbed approximately 40% more radiation than in the 2nd experiment. Low N supply decreased AR by more than 20% in the ambient treatment. There was a statistically significant CO_2 effect on AR, which could be attributed to an increase in AR under low nitrogen but not under adequate nitrogen although the $CO_2 \times N$ interaction was not statistically significant ($p = 0.18$). RUE of above ground biomass production was unaffected by nitrogen supply but significantly increased by CO_2 elevation (Table 3). Averaged over the two nitrogen levels, CO_2 enrichment caused an increase in RUE of 10% and 13% in the 1st and 2nd season, respectively.

3.4. Final biomass and grain yield

At grain maturity, plants grown under low nitrogen supply had approximately 20% less stem, grain and total biomass than those grown under adequate nitrogen (Table 4). CO_2 enrichment significantly increased dry weights of stems and grains. The mean CO_2 response of stem biomass over both seasons was higher under

Table 3
Effect of different nitrogen supply [N2: adequate N supply (262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year), N1: 50% of N2] and atmospheric CO_2 concentrations (ambient and FACE) on accumulated seasonal radiation absorbed by the green canopy (AR, MJ m^{-2}) and radiation use efficiency of above ground biomass production (RUE, g dry weight per MJ absorbed global radiation) of winter barley in two vegetation periods

Year	CO_2	AR		RUE	
		N1	N2	N1	N2
2000	Ambient	936	1230	1.29	1.23
	FACE	992	1210	1.48	1.30
	% Change[a]	6.0	−1.6	14.1	6.4
2003	Ambient	675	858	1.26	1.33
	FACE	738	862	1.43	1.51
	% Change	9.3	0.5	12.8	13.5
ANOVA results					
CO_2		*		**	
C × year		n.s.		n.s.	
N		***		n.s.	
C × N		n.s.		n.s.	
N × year		(*)		n.s.	
C × N × Y		n.s.		n.s.	

(*), $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.
[a] % Represents the percentage difference between FACE and Ambient.

Table 4
Effect of different nitrogen supply [N2: adequate N supply (262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year), N1: 50% of N2] and atmospheric CO_2 concentrations (ambient and FACE) on growth and yield variables of winter barley at grain maturity in 2000 and 2003

Year	CO_2	Leaf biomass (g m^{-2})		Stem biomass (g m^{-2})		Stem weight ratio (g/g)		Grain yield[a] (g m^{-2})		Total biomass (g m^{-2})	
		N1	N2	N1	N2	N1	N2	N1	N2	N1	N2
2000	Ambient	126	142	394	522	0.291	0.311	784	952	1360	1679
	FACE	129	154	499	564	0.323	0.311	850	1023	1546	1815
	%[b]	2.2	8.3	26.5	8.1	11.2	0.2	8.5	7.5	13.7	8.1
2003	Ambient	60	90	318	394	0.324	0.325	474	590	983	1216
	FACE	59	104	408	469	0.349	0.328	558	687	1173	1430
	%	−0.8	15.7	28.2	18.8	7.6	0.9	17.6	16.5	19.3	17.6
ANOVA results											
CO_2		n.s.		***		*		**		***	
C × year		n.s.		n.s.		n.s.		n.s.		n.s.	
N		*		*		n.s.		**		**	
C × N		n.s.		n.s.		*		n.s.		n.s.	
N × year		n.s.		n.s.		n.s.		n.s.		n.s.	
C × N × Y		n.s.		n.s.		n.s.		n.s.		n.s.	

Year	CO_2	Ear number (m^{-2})		Grain number (m^{-2})		Thousand grain weight (g)		Harvest index	
		N1	N2	N1	N2	N1	N2	N1	N2
2000	Ambient	452	543	17613	22512	44.4	42.3	0.509	0.502
	FACE	482	563	18592	23746	45.8	43.2	0.487	0.499
	%	6.7	3.6	5.6	5.5	3.2	2.0	−4.3	−0.6
2003	Ambient	529	612	12345	16594	38.3	35.6	0.482	0.484
	FACE	544	635	14176	18359	39.3	37.5	0.475	0.480
	%	2.9	3.6	14.8	10.6	2.7	5.5	−1.5	−0.7
ANOVA results									
CO_2		(*)		*		(*)		n.s.	
C × year		n.s.		n.s.		n.s.		n.s.	
N		**		***		n.s.		n.s.	
C × N		n.s.		n.s.		n.s.		n.s.	
N × year		n.s.		n.s.		n.s.		n.s.	
C × N × Y		n.s.		n.s.		n.s.		n.s.	

(*), $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.
[a] The individual replicate values for the two N levels (N1/N2) are for 2000: Ambient, 833/941, 734/962; FACE, 860/1046, 840/1000; and for 2003: Ambient, 533/546, 415/634; FACE, 556/697, 559/677.
[b] % Represents the percentage difference between FACE and Ambient.

low (+27%) than adequate nitrogen supply (+13%) and for the stem weight ratio a statistically significant interaction of CO_2 and nitrogen supply could be detected.

Reduction in nitrogen supply decreased grain yield by reducing ear number and grain number. Thousand grain weight was slightly increased, though not significantly ($p = 0.16$).

Averaged over both nitrogen levels, plants grown under high CO_2 had 8% and 17% higher grain yield in the 1st and 2nd year, respectively. The greatest part of this positive CO_2 effect on yield resulted from a statistically significant stimulation in ear and grain number. Furthermore, slight changes in mean grain weight also contributed to the increase in grain yield. There was no statistically significant interaction of CO_2 and nitrogen supply on any yield component. However, in the 2nd year the CO_2 effect on thousand grain weight was higher under adequate than under low nitrogen supply. Harvest index was slightly decreased by CO_2 elevation; however, this effect was not statistically significant.

3.5. Stem reserves

The concentration of WSC in the stem was highest around anthesis and then declined until grain maturity (Fig. 4). There were great differences between years, and the maximum carbohydrate percentage in the stem reached up to 30% and 20% in the 1st and 2nd season, respectively. Reduction in nitrogen supply mostly resulted in a statistically significant increase of WSC concentration. Except of the statistically significant CO_2 effect observed in 2003 before anthesis for both nitrogen treatments, CO_2 enrichment enhanced WSC preferentially under low nitrogen. This is supported by the statistically significant interaction of CO_2 and nitrogen supply at grain maturity and during grain filling in the 1st and 2nd year, respectively.

The stem reserves, i.e. the amount of WSC in stems per m^2 ground area, were roughly two times higher in the 1st compared to the 2nd year (Fig. 4) and also in the reduced as compared to the adequate nitrogen fertilization level. Before anthesis CO_2 enrichment increased stem reserves in both nitrogen treatments. Thereafter, the CO_2 effect was greater for the low nitrogen level. During grain filling in 2003 a statistically significant interaction of CO_2 and nitrogen supply on this variable was observed.

Thus, plants under low nitrogen had a higher amount of stem reserves than those with normal nitrogen nutrition, and CO_2 enrichment amplified the difference between the two nitrogen levels. Under ample nitrogen the contribution of stem reserves to grain yield amounted to 6% and was quite stable among years and CO_2 treatments (Table 5). With low nitrogen the respective number increased to 13% in 2000 and was up to 18% under high CO_2 in the 2nd year.

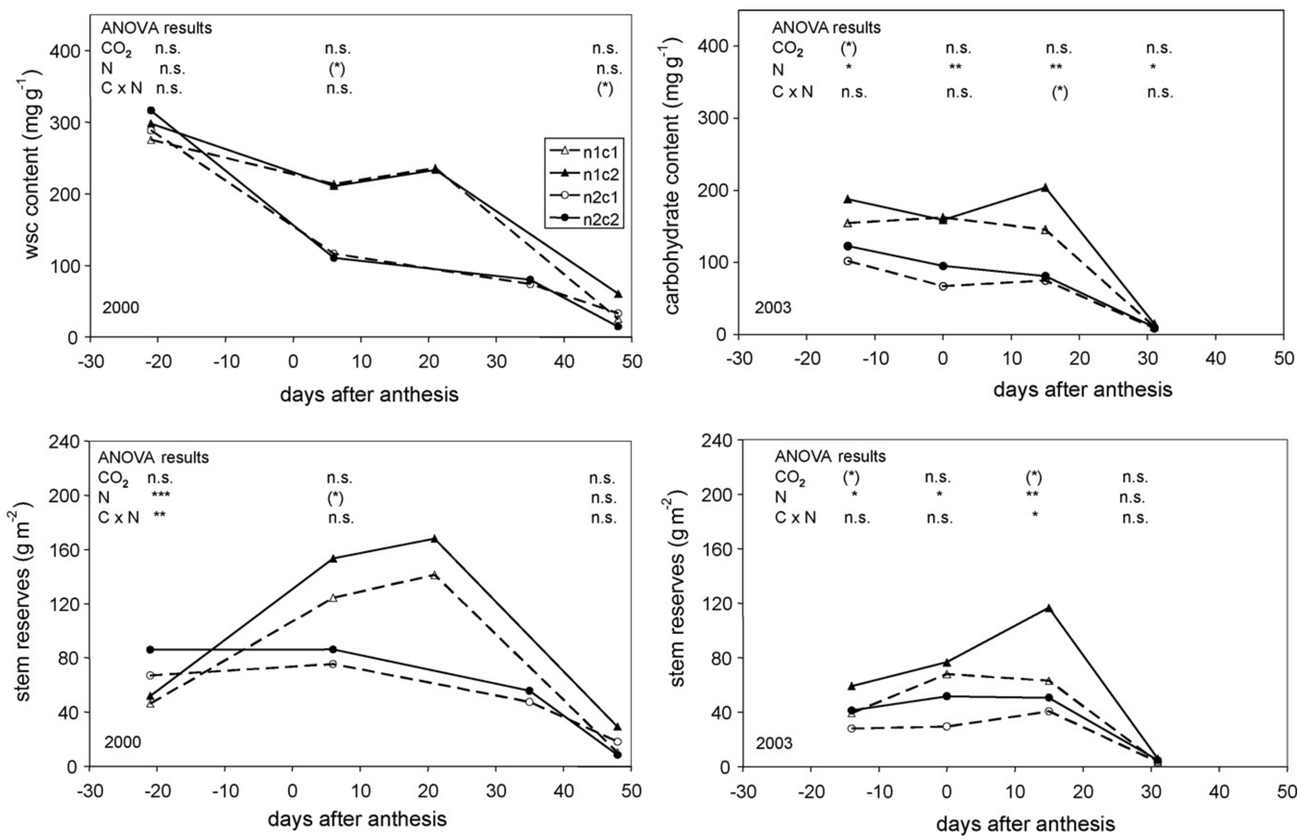

Fig. 4. Temporal changes in stem water soluble carbohydrate concentration and in stem reserves per ground area of winter barley grown in 2000 and 2003 under two levels of nitrogen [N2: adequate N supply (262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year), N1: ca. 50% of N2] and of atmospheric CO_2 concentrations (ambient (C1) and enriched (C2)).

3.6. Grain growth

A detailed grain growth analysis was carried out only in 2003. Fig. 5 shows the increase in grain weight during the grain filling period for the adequate (Fig. 5a) and reduced nitrogen treatment (Fig. 5b), respectively. Statistical analysis indicated significant differences in weight between central and lateral grains during grain filling in both nitrogen treatments. Under low nitrogen, grain weights were highest and unaffected by CO_2 enrichment except for a transient interaction of CO_2 and grain position at the 5th grain harvest. This is in contrast to the results obtained under high nitrogen supply. Grain weight was significantly stimulated by CO_2 enrichment at midway of the grain filling period. However, this CO_2 effect levelled off towards grain maturity.

Calculated final grain weight as fitted model parameter was not significantly increased by CO_2 enrichment and unaffected by nitrogen supply, but it depended strongly on grain position.

GFR was influenced by grain position and nitrogen supply (Table 6). Central grains had a higher growth rate than lateral grains and a decreased nitrogen supply increased GFR. CO_2 enrichment treatments showed a different response with no decrease in GFR with increasing nitrogen supply. This is confirmed by the statistically significant interaction of CO_2 and nitrogen supply detected for this parameter.

Table 5
Effect of different nitrogen supply [N2: adequate N supply (262 kg ha^{-1} in 1st year and 179 kg ha^{-1} in 2nd year), N1: 50% of N2] and atmospheric CO_2 concentrations (ambient and FACE) on stem reserves at grain filling and maturity, and on the percentage contribution to grain yield

	N-level	2000			2003		
		Ambient	FACE	% Change[a]	Ambient	FACE	% Change
Stem reserves at grain filling (g m^{-2})	N1	124	153	23	63	117	86
	N2	75	86	15	41	51	24
Stem reserves at maturity (g m^{-2})	N1	10	29	190	3	6	100
	N2	18	8	−56	3	5	67
Stem reserves lost (g m^{-2})	N1	114	124	9	60	111	85
	N2	57	78	37	37	46	24
Contribution of stem reserves to grain yield (%)	N1	13.1	13.1	–	11.3	17.8	–
	N2	5.4	6.8	–	5.7	6.0	–

[a] % Represents the percentage difference between FACE and Ambient.

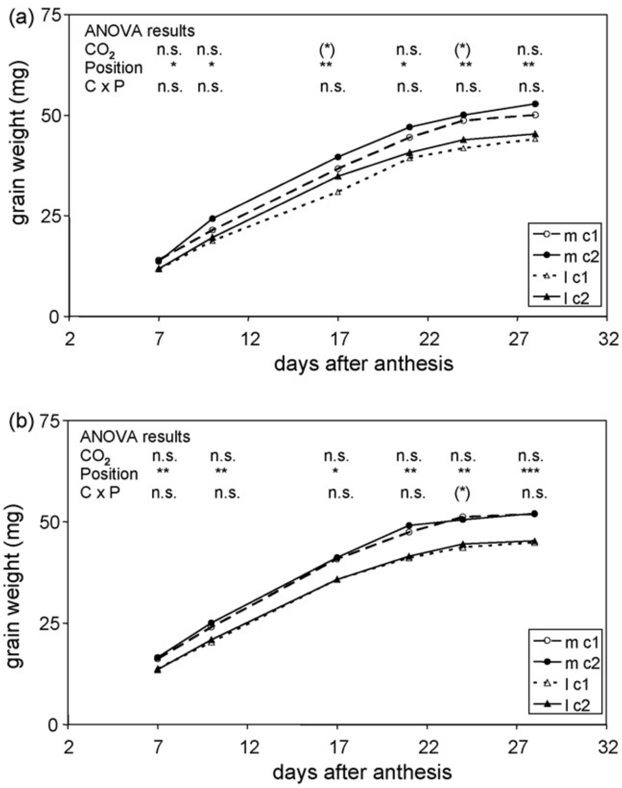

Fig. 5. Temporal changes in individual weight of central (m) and lateral (l) grains of winter barley in 2003 grown under ambient (C1) and enriched (C2) atmospheric CO_2 concentrations and two levels of nitrogen [(a) adequate N supply (179 kg ha^{-1} year) and (b) ca. 50% of adequate N supply].

GFD was independent of the grain position, but was longer with increasing nitrogen supply (Table 6). CO_2 enrichment resulted in a different nitrogen response of this parameter also by preventing the elongation of GFD with increasing nitrogen supply found under ambient CO_2 which was supported by the statistically significant interaction of CO_2 and N on this variable. Consequently, the positive CO_2 effect on GFR under adequate nitrogen is almost counterbalanced by a negative effect on GFD. This phenomenon was proven for both grain positions and there was no statistically significant interaction between CO_2 and grain position.

Table 6
Effect of different nitrogen supply [N2: adequate N supply (179 kg ha^{-1}), N1: 50% of N2], atmospheric CO_2 concentrations (ambient and FACE) and grain position (P, central and lateral) on grain filling rate (GFR, μg $^{\circ}$C^{-1} d^{-1}) and grain filling duration (GFD, $^{\circ}$C $\times$ d) of grains harvest in 2003

Position	CO_2	GFR (μg $^{\circ}$C^{-1} d^{-1})		GFD ($^{\circ}$C $\times$ d)	
		N1	N2	N1	N2
Central	Ambient	80.5	76.5	541	607
	FACE	82.3	81.3	519	547
	% Change[a]	2.3	6.2	−4.0	−9.9
Lateral	Ambient	71.6	63.7	525	629
	FACE	72.0	74.1	526	530
	% Change	0.5	16.3	0.2	−15.8
ANOVA results					
CO_2		n.s.		n.s.	
N		(*)		*	
Position		***		n.s.	
C × N		*		(*)	
C × P		n.s.		n.s.	
N × P		n.s.		n.s.	
C × N × P		n.s.		n.s.	

(*), $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.
[a] % Represents the percentage difference between FACE and Ambient.

4. Discussion

The objective of the present study was to investigate the effect of [CO_2] and nitrogen supply on barley growth in 2 years as parts of a triennial crop rotation repeated for two times. In the 1st year, total above ground biomass production was not affected by CO_2 enrichment until the first node stage, which might be explained by the low temperature, at which stimulation of photosynthesis by CO_2 enrichment is negligible (Long et al., 2005). However, at later growth stages with warmer temperatures, CO_2 elevation increased total biomass in both years due to a stimulation of stem and ear growth. This is in contrast to the CO_2 response detected early in the season of the 2nd year, when total biomass was already enhanced at the beginning of stem elongation particularly due to an increase in leaf biomass. In late wintertime and spring of the 2nd growing period the weather was exceptionally sunny and dry. This resulted in soil drying, which could not be prevented by the irrigation systems since it was not yet set-up at this early time of the vegetation period. Soil water content dropped down to ca. 50% of plant available water, at which leaf expansion is impaired (Sadras and Milroy, 1996). CO_2 enrichment is known to mitigate drought stress effects on plant growth by increasing stomatal resistance (Bunce, 2004; Weigel et al., 2005) and by increasing the exploitation of soil water via a stimulation of root growth (Burkart et al., 2004). Consequently, it can be assumed that the positive CO_2 effect on leaf growth observed in springtime of the 2nd year resulted from an interaction of CO_2 enrichment and restriction in water availability.

The absence of a CO_2 effect on leaf growth in the present FACE study with barley corresponds to findings from open-top chamber studies (Bunce, 2004; Kleemola et al., 1994; Weigel et al., 1994). CO_2 enrichment affects mainly stem and ear growth as observed in the present experiment and in previous studies (Fangmeier et al., 1996; Pettersson et al., 1992). Moreover, in our FACE experiment the stimulation in stem growth was connected with an increase in stem height which was also reported by other chamber studies (Saebo and Mortensen, 1996; Weigel et al., 1994). It has been shown that the CO_2 effect on total biomass of barley decreased if the nitrogen availability is reduced (Fangmeier et al., 1996, 2000; Thompson and Woodward, 1994). However, under FACE conditions the percentage CO_2 effect on total biomass was similar among the nitrogen treatments and the effect on stem biomass was even higher under low than under adequate nutrient supply in both years. In addition, the stem weight fraction was increased under CO_2 in the low nitrogen treatment indicating that CO_2 enrichment affected assimilate partitioning under these conditions. Similar findings have been obtained by Van Kraalingen (1990) who demonstrated that under low nitrogen supply plants responded with increased growth to CO_2 enrichment through changes in dry matter partitioning towards organs with low minimum nitrogen concentrations.

Variation in nitrogen and CO_2 supply affected radiation absorption and radiation use efficiency, which both determine crop production in different ways. As shown here, nitrogen supply influenced plant growth mainly by variation in seasonal course of total green leaf area index and the accumulated radiation absorbed over the season. Total green area index was not affected by CO_2 enrichment as has also been found for barley in a recent field study with open-top chambers (Bunce, 2004). Nevertheless, we detected a stimulation of green area index of stems combined with an increase in canopy height. In this respect, these findings for barley are not consistent with results of previous FACE experiments with other C_3 crops (Kimball et al., 2002), which showed that green area response to elevated CO_2 was much smaller at low nitrogen than at ample nitrogen supply. On the contrary, our results of the accumulated radiation absorption rather indicated that CO_2 enrichment had a positive effect at low but not at adequate nitrogen supply. This could be explained by greater CO_2 effects on stem growth and root growth at low compared to high nitrogen (Weigel et al., 2005), and the latter effect could have mitigated the nitrogen shortage by increasing the exploitation of soil nitrogen.

As the effects on GAI and radiation absorption were rather small, the positive CO_2 effect on growth of winter barley was mainly based on an increase of radiation use efficiency of ca. 12%, which is in the range of previous findings for wheat (Rudorff et al., 1996; Mulholland et al., 1998) but slightly lower than the number used in some wheat growth models for predicting the impact of global climate change on food production (Jamieson et al., 2000).

With low nitrogen supply, elevated CO_2 effects on yield of barley (Fangmeier et al., 1996, 2000; Thompson and Woodward, 1994; Van Kraalingen, 1990) and other cereals (Amthor, 2001) are usually small. This has been confirmed in FACE studies with wheat but only in one of two years (Amthor, 2001) and with rice over three years (Kim et al., 2003). The range in nitrogen supply and the decrease in grain yield due to nitrogen shortage, which amounted to ca. 20%, were similar to the conditions in our FACE study. However, the percentage grain yield response of winter barley to CO_2 enrichment was similar among the nitrogen levels, but higher in the 2nd (+17%) than the 1st year (+8%), which also applies to final biomass with 18% and 11%, respectively. Although there was no statistically significant $CO_2 \times$ year interaction on these growth variables, the interannual differences were striking. The CO_2 effect on plant growth is known to be modified by water availability (e.g. Amthor, 2001) and temperature (Bunce, 1998; Long et al., 2005), which both strongly varied between years. The average air temperature for the period from 1st node stage until anthesis, when grain number is determined (Frederick and Bauer, 1999), was higher in 2003 (13.7 °C) than in 2000 (12.3 °C). Differing soil moisture conditions in both experimental periods probably had an even stronger effect. In the 2nd year there was an unintended decline in soil moisture in early springtime, and during April plant available water content remained at the threshold level, at which leaf expansion is affected (Sadras and Milroy, 1996). Thus, the lower soil water content and the later anthesis date and accordingly the higher temperature in 2003 as compared to 2000 may account for the higher CO_2 effect on biomass production in 2003. In previous field studies with enclosures barley was always grown in pots (Fangmeier et al., 1996, 2000; Kleemola et al., 1994; Pettersson et al., 1992; Saebo and Mortensen, 1996; Thompson and Woodward, 1994; Weigel et al., 1994) and the CO_2 concentration was elevated by approximately 300 ppm. Assuming a linear CO_2 response, these studies showed a mean increase in grain yield of 28.4% for a CO_2 elevation of 175 ppm as observed in our FACE experiment. Thus, the 8% and 17% increase in barley yield detected in our FACE study are clearly lower and support the recent conclusion that FACE data show a lower crop yield response than those obtained from enclosure experiments (Long et al., 2005).

CO_2 related increase in grain yield of winter barely was primarily due to an increase in grain number as found by others (e.g. Saebo and Mortensen, 1996; Thompson and Woodward, 1994). In addition, individual grain weight of winter barley, which was increased under nitrogen shortage, responded slightly to CO_2 elevation as also observed in chamber studies with spring barley (e.g. Frank and Apel, 1987; Pettersson et al., 1992). Harvest index was marginally decreased by CO_2 enrichment under low nitrogen which agrees with other findings for barley (Fangmeier et al., 1996; Van Kraalingen, 1990) and FACE experiments with rice (Kim et al., 2003). The reason for the change of harvest index in the present experiment was obviously the preferred partitioning of dry matter to stem growth.

Decreasing nitrogen supply and increasing CO_2 supply both stimulated the amount of stem reserves in barley as has already been demonstrated (Gebbing et al., 1999; Gruters, 1999; Schnyder, 1993), and the effects were greatest during grain filling. It may be speculated that the higher amount of stem reserves under low nitrogen is due to less vigorous vegetative and reproductive growth (Schnyder, 1993) and that this response is intensified by CO_2 enrichment. In fact, in the present case a great part of variation in stem reserves results from changes in tissue carbohydrate concentration, which was particularly modified by nitrogen supply. CO_2 influenced stem reserves mainly via changes in stem biomass, and effects on tissue carbohydrate concentration were small. In addition, there was a higher carbohydrate concentration in the 1st than the 2nd year, which can be ascribed to differences in temperature (Schnyder, 1993). It is notable that under adequate nitrogen the contribution of stem reserves to grain yield remains constant among years and at a quite low level (Schnyder, 1993).

Final grain size varies among the position along the spike with greatest weights in the middle sector and in six-rowed cultivars grains from central positions were heavier than those from lateral position (Cottrell and Dale, 1984; Voltas et al., 1998). In the present study kinetics of dry matter accumulation was measured for grains with high and small final size, respectively. It was found that an increase in nitrogen supply, which raised grain number, produced a decrease in individual grain weight, which corresponds to the results obtained for mean grain weight and findings of another study for spring barley (Grashoff and dAntuono, 1997). GFD was stable among treatments and grain positions, but was elongated under ambient CO_2 by increasing nitrogen supply, which might represent a compensation of the reduced assimilate availability per single grain (Bauer et al., 1985). Conversely, the absence of a nitrogen effect on GFD under high CO_2 can be attributed to the high photosynthetic rate under these conditions, which were probably sufficient for grain growth although the grain number was higher as compared to ambient conditions. Variation in GFR accounted for the differences in final grain weight between central and lateral position as reported by Voltas et al. (1998). The higher GFR under low as compared to high nitrogen supply contradicts the findings from some crop models (Jamieson et al., 2000), but corresponds to results obtained with a grain growth model (Wang and Gifford, 1995). The lack of a CO_2 effect on GFR under low nitrogen indicates that grain growth was limited by sink activity. This is further supported by the large stem reserves found under low nitrogen and the observation that this storage pool, which depends on excess assimilates not needed for ear growth (Schnyder, 1993), was still filled up when grain growth has already started. Our study clearly showed that under normal nitrogen supply CO_2 enrichment increased GFR. Moreover, the relative size of the CO_2 effect was greater for lateral than central grains, which corresponds to the different degree of source limitation of these grain positions (Voltas et al., 1998). Similarly, Li et al. (2000) observed in a FACE study with wheat that CO_2 advanced GFR at those spike positions where individual grain weight was low. However, in our FACE study with barley the positive CO_2 effect on GFR was levelled out to a great extent by a concomitant decrease in GFD. Consequently, the net effect on mean grain weight determined at maturity was small.

5. Conclusions

The present FACE study with winter barley showed that the atmospheric CO_2 concentration predicted by the A1B IPCC scenario for the middle of this century could increase grain yield by approximately 8% if there is no restriction of water supply. This stimulation in crop growth mainly resulted from an increase in radiation use efficiency. If nitrogen supply was about half of the optimum level the reduction in radiation absorption by the green canopy was slightly mitigated by CO_2 due to an increase in green area of stems and ears. Moreover, under reduced nitrogen supply CO_2 elevation increased the fraction of stem biomass. The grain yield response to CO_2 was similar between the two nitrogen treatments. Our investigations also suggest that individual grain growth was strongly sink limited under elevated CO_2. One mechanism to counteract sink limitation of grain growth and to increase yield of barley under future higher CO_2 levels might be the prolongation of the time period between stem elongation and anthesis as has recently been suggested for wheat (Miralles and Slafer, 2007). This would cause an increase in grain number and individual grain weight (Cottrell and Dale, 1984).

Acknowledgements

Technical assistance by the FAL experimental farm and by the staff of the Institute of Agroecology is gratefully acknowledged. We thank Dr. H. Sourell and H.-H. Thoermann from the Institute of Production Engineering and Building Research of the FAL and F.-J. Loepmeier from the Agrometeorological Research Station of the German Weather Service at Braunschweig for assistance in field irrigation and providing meteorological data. We are also grateful to George Hendrey, Keith Lewin and John Nagy (Brookhaven National Laboratory, Upton, New York, USA) for their help in establishing and operating the FACE system. We would like to thank the Federal Ministry of Food, Agriculture and Consumer Protection for financial support.

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