Effect of free air carbon dioxide enrichment combined with two nitrogen levels on growth, yield and yield quality of sugar beet: Evidence for a sink limitation of beet growth under elevated CO_2

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ABSTRACT

The increase in atmospheric CO_2 concentration [CO_2] has been demonstrated to stimulate the growth of C_3 crops. However, little information exists about the effect of elevated [CO_2] on biomass production of sugar beet, and data from field experiments are lacking. In this study, sugar beet was grown within a crop rotation over two rotation cycles (2001, 2004) at present and elevated [CO_2] (375 $\mu l\,l^{-1}$ and 550 $\mu l\,l^{-1}$) in a free air CO_2 enrichment (FACE) system and at two levels of nitrogen supply [high (N2), and 50% of high (N1)], in Braunschweig, Germany. The objective of the present study was to determine the CO_2 effect on seasonal changes of leaf growth and on final biomass and sugar yield. Shading treatment was included to test whether sugar beet growth is sink limited under elevated [CO_2]. CO_2 elevation did not affect leaf number but increased individual leaf size in early summer resulting in a faster row closure under both N levels. In late summer CO_2 enrichment increased the fraction of senescent leaves under high but not low N supply, which contributed to a negative CO_2 effect on leaf area index and canopy chlorophyll content under high N at final harvest. Petioles contained up to 40% water-soluble carbohydrates, which were hardly affected by CO_2 but increased by N supply. More N increased biomass production by 21% and 12% in 2001 and 2004, respectively, while beet and sugar yield was not influenced. Concentration of α-amino N in the beet fresh weight was increased under low N and decreased under high N by CO_2 enrichment. The CO_2 response of total biomass, beet yield and white sugar yield was unaffected by N supply. Averaged over both N levels elevated [CO_2] increased total biomass by 7% and 12% in 2001 and 2004, respectively, and white sugar yield by 12% and 13%. The shading treatment in 2004 prevented the decrease in leaf area index under elevated [CO_2] and high N in September. Moreover, the CO_2 effect on total biomass (24%) and white sugar yield (28%) was doubled as compared to the unshaded conditions. It is concluded that the growth of the storage root of sugar beet is not source but sink limited under elevated [CO_2], which minimizes the potential CO_2 effect on photosynthesis and beet yield.

1. Introduction

Sugar beet is grown on about 4 million hectares in Europe which represents almost 70% of the agricultural area used worldwide for this crop (FAOSTAT, 2007). Moreover, beet sugar accounts for approximately 20% of the world's sugar production. 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). Based on the A1B IPCC scenario the atmo-spheric CO_2 concentration [CO_2], which has already risen from 280 $\mu l\,l^{-1}$ in the pre-industrial period to ca. 385 $\mu l\,l^{-1}$ today, is predicted to reach 550 $\mu l\,l^{-1}$ in the middle of this century (Meehl et al., 2007). It has been noted in the last IPCC report that there is still a lack of knowledge about CO_2 and climate response of root crops (Easterling et al., 2007). In the present study the direct effects of elevated [CO_2] were determined for sugar beet. The direct effects of elevated [CO_2] on sugar beet photosynthesis, leaf area expansion dynamics and final and intermediate storage of assimilates are considered as most important with respect to sugar beet yield formation under elevated [CO_2].

Elevated [CO_2] increases photosynthesis in leaves of C_3 plants and, given the positive interaction of CO_2 and temperature on photosynthesis (Long, 1991), it can be assumed that among the C_3 crop

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species cultivated in the middle of Europe sugar beet should benefit most from the increase in [CO_2], since the period of maximum growth is during the warmest months of the year (e.g. Kenter et al., 2006). Several studies with sugar beet demonstrated an increase of net photosynthesis to elevated [CO_2] in the short-term (e.g. Ford and Thorne, 1967; Bunce, 1992). Whether in the longer term this increase continues or is reduced by downregulation of photosynthetic capacity has been addressed in several studies (Bunce, 1992; Ziska et al., 1995; Demmers-Derks et al., 1996) and this question is still under debate. Downregulation of photosynthesis under elevated [CO_2] can result from the limited ability to generate new sinks for carbon storage and utilization (Ainsworth and Long, 2005). According to Thomas (1999) there is no limitation in the growth of the sugar beet storage root and root yield during the season is only source-limited. Consequently this species should show a strong growth response to elevated [CO_2]. However, Demmers-Derks et al. (1998) failed to demonstrate a positive interaction of temperature and [CO_2] on sugar beet growth. It was found that the growth of the storage root was not always source-limited and it was concluded that sugar beet has a determinate ontogeny with a phase of slower taproot growth at the end of the season.

Increase in photosynthesis under elevated [CO_2] should result in stimulation of leaf growth of sugar beet, which would promote crop growth by increasing light absorption especially early in the season. Indeed, several experiments (Ford and Thorne, 1967; Wyse, 1980a; Ziska et al., 1995; Romanova et al., 2002) revealed a stimulation of leaf growth under elevated [CO_2] and leaves were found to be larger, while leaf number was not influenced (Ford and Thorne, 1967; Romanova et al., 2002). However, in the study of Demmers-Derks et al. (1998) elevated [CO_2] combined with two levels of nitrogen supply and temperature had no effect on leaf area. Biomass of storage roots increased in plants subjected to elevate [CO_2] (Ford and Thorne, 1967; Wyse, 1980a,b; Ziska et al., 1995; Demmers-Derks et al., 1998; Wolf, 1998; Romanova et al., 2002) and the effect was less strong under low nitrogen (Demmers-Derks et al., 1998; Wolf, 1998) and under cool temperatures (Ziska et al., 1995). Dry matter partitioning to the storage roots was mostly found to be enhanced resulting in an increase in the beet weight fraction (Ford and Thorne, 1967; Ziska et al., 1995; Wyse, 1980b; Demmers-Derks et al., 1998). Only Wyse (1980a) observed the root/shoot ratio to be unaffected by CO_2 fumigation.

In sugar beet, assimilates can accumulate along the translocation pathway from the leaves to the storage roots when the supply exceeds the demand by the growing tissue (Geiger et al., 1969). Thus, accumulation of water-soluble carbohydrates in the petioles may play a function similar to the stem reserves in cereals, which are known to be increased by CO_2 enrichment and even more by reducing nitrogen supply (Schnyder, 1993; Manderscheid et al., 2009). Ziska et al. (1995) found an increase of the soluble carbohydrate concentration in petioles of sugar beet grown with elevated CO_2 levels during summer under warm conditions. The combined effect of different nitrogen and CO_2 supply has not yet been studied.

Sugar yield depends on the sucrose concentration of the beet and the concentration of other soluble constituents, namely, potassium, sodium and α-amino-nitrogen, which impair white sugar recovery (Buchholz et al., 1995; Kenter and Hoffmann, 2006). In previous studies, the sucrose concentration of the taproot was found to be unaffected (Demmers-Derks et al., 1998; Ziska et al., 1995) or enhanced by CO_2 enrichment (Ford and Thorne, 1967; Wyse, 1980a; Ziska et al., 1995). Moreover, Demmers-Derks et al. (1998) observed a negative CO_2 effect on the concentration of α-amino-nitrogen in plants grown with deficient or abundant nitrogen supply.

All these previous studies on the growth response of sugar beet to elevated [CO_2] have been done in some type of enclosure, i.e. controlled environment (Ford and Thorne, 1967; Romanova et al., 2002; Wyse, 1980b; Ziska et al., 1995) or in the greenhouse (Demmers-Derks et al., 1996; Wolf, 1998). In the only field experiment (Wyse, 1980a) CO_2 fumigation started not until the middle of the growth period. Moreover, only in few studies CO_2 fumigation lasted over the whole growing period of the crop (Demmers-Derks et al., 1998; Wolf, 1998). No full-season field studies with elevated [CO_2] under real agricultural management conditions have been carried out yet. The variability in the experimental approaches chosen for studying the effect of elevated [CO_2] on sugar beet growth may account for the inconsistencies of the results presented so far. Thus, there still exists a large uncertainty with respect to the effect of future [CO_2] on sugar beet growth and yield.

In order to determine the effect of elevated [CO_2] on sugar beet under field conditions, sugar beet was regularly grown in the field and the plants were exposed season-long to elevated [CO_2] using the free air carbon dioxide enrichment technique (Lewin et al., 1992). The main objective of the present study was to quantify the effect of elevated [CO_2] combined with high and low nitrogen supply on the growth and yield of sugar beet. Temporal changes of leaf growth were analysed at the leaf and canopy level to determine whether green leaf area is enhanced under CO_2 enrichment over the season contributing to the CO_2 effect on crop growth. We also tested whether the sink limitation of growth observed under CO_2 enrichment in the greenhouse (Demmers-Derks et al., 1998) does also occur under field conditions by including a shading treatment. In addition, the effect of elevated [CO_2], nitrogen supply and shading on the content of water-soluble carbohydrates in the petioles was examined.

2. Materials and methods

2.1. Experimental site and FACE system

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 drained upper (0.01 MPa soil water tension) and lower limits (1.5 MPa) of plant available volumetric soil water content were 23% and 5%, respectively. The lower layers are almost pure sand. Overall, the soil is of low to intermediate fertility and provides a comparatively shallow rooting zone. A detailed description of the edaphic conditions of the experimental site has been given previously (Manderscheid et al., 2009).

Fumigation treatments included two FACE rings engineered by Brookhaven National Laboratory (Lewin et al., 1992) enriched with CO_2 (set to 550 µl l^{-1}) and two control rings with ambient air (about 375 µl l^{-1}), each 20 m of diameter. CO_2 fumigation operated during daylight hours and was stopped at wind speeds (>6 m s^{-1}). The FACE system and experimental design has already been described in detail (Manderscheid et al., 2009). In short, the rings were divided in two semicircles (Fig. 1), which were fertilised with nitrogen according to normal agricultural practice (N2) and with 50% of the normal mineral nitrogen (N1), respectively, while supply of other nutrients was identical in both nitrogen treatments.

The FACE experiment with sugar beet (*Beta vulgaris* 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 sugar beet (2001 and 2004). In 2001 the cultivar "Wiebke" was used, which was affected by rhizomania in August that year. Therefore, in 2004 another cultivar was grown ("Impuls"), which is resistant against this disease. Both cul-
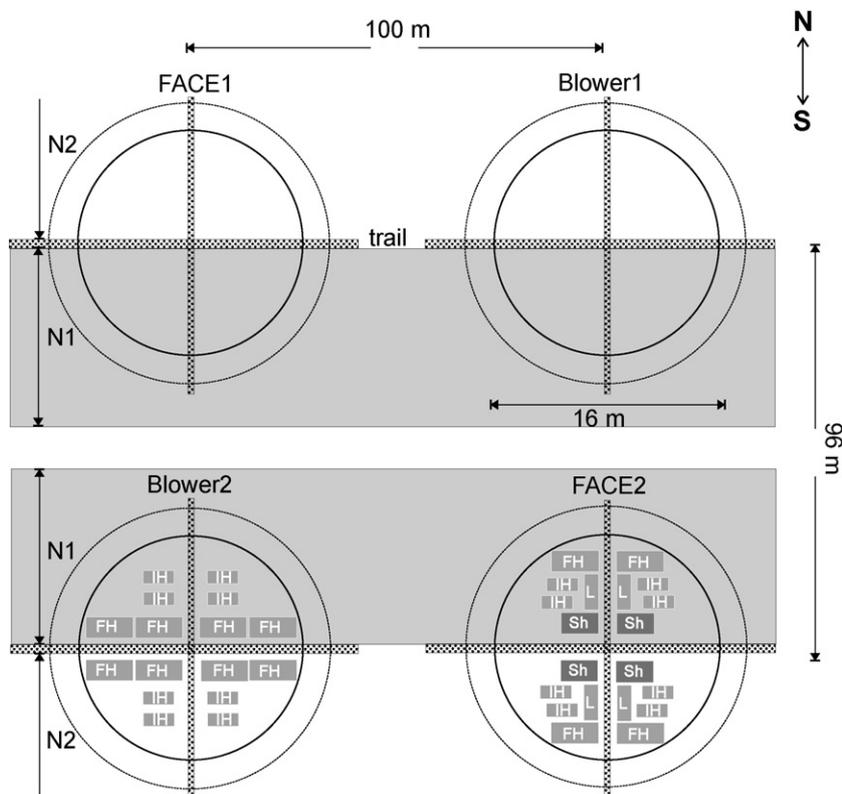
Fig. 1. Spatial arrangement of the two rings with ambient CO_2 (Blower 1 and 2) and elevated CO_2 concentration (FACE 1 and 2) and of the two levels of nitrogen supply. Plant material was harvested from an internal ring area of 16-m diameter. Distribution of the research activity zones within the ring in 2001 and 2004 is shown in Blower 2 and FACE 2, respectively. FH: final harvest areas; IH: areas for intermediate harvests; L: area for leaf growth analysis; Sh: area with shading net.

tivars were registered in Germany in 1998 and have similar sugar yield potential. Agricultural management measures were carried out according to local farm practices. At the end of winter the field was fertilised with macronutrients (K, Mg, P, S) based on soil nutrient analysis and subsequently ploughed and worked with a cultivator. Soil mineral nitrogen contents at springtime amounted to ca. 30 kg ha^{-1} in 0–60 cm depth. Sugar beet was sown in east-west rows spaced 0.45 m with a seeding density of 11 plants m^{-2}. Nitrogen fertilizer was added twice as ammonium nitrate-urea solution (Table 1). Moreover, in early spring of 2004 the total field was supplied with diammonium phosphate at a rate of 54 kg N ha^{-1}. Total mineral nitrogen added to the respective experimental area (N2/N1) amounted to 126/63 kg N ha^{-1} and to 156/78 kg N ha^{-1} in 2001 and 2004, respectively. Table 1 lists the major management measures for the two growing seasons.

The field was irrigated with a linear irrigation system to avoid water limitations and resulting interactions with the CO_2 treat-

ments by keeping the soil water content above 50% of maximum plant available soil water content as has been described for the previous barley crop (Manderscheid et al., 2009). The field was irrigated five times in 2001 (from 25th of June until 22nd of August) and four times in 2004 (from 1st of July until 15th of September) totally with 107 mm and 84 mm, respectively. Soil water content was monitored by four (1st year) or six (2nd year) TDR probes installed at 25 and 45 cm depth, respectively, in each of the four semicircles with normal fertilization. Volumetric soil water content was recorded approximately twice per week.

Climate data (air temperature, global radiation and precipitation) measured at 2 m height nearby the experimental field site (<500 m) were provided by the German Weather Service. Canopy air temperature was measured in the two half circles of one FACE and one blower ring in both years.

2.2. Shading treatment

In 2004, a shading treatment was included to test whether the growth of sugar beet is sink limited under elevated [CO_2]. The sink size of the storage root of sugar beet depends on the number of cambial rings most of which are developed until July (Milford, 1973). A portion of the plant area was shaded from mid July to decrease source activity without changes in sink activity as compared to the unshaded areas. Thus, restrictions to photosynthesis resulting from insufficient growth activity should rather be absent under these conditions. Shading was done by installation of nets (1.5 m × 2.5 m) in each quarter section of the four experimental rings, which reduced incident radiation to 51% of the unshaded area from 15 July until the final harvest. In order to control a possible shading effect on canopy climatic conditions, canopy air temperature was also measured in the shaded plots.

Table 1

Timetable of significant crop culture events in the first (2001) and second vegetation period (2004).

Event	1st growing season	2nd growing season
Sowing	10 April	14 April
1st nitrogen fertilization	23 April	19 April
Emergence	30 April	26 April
Start of CO_2 enrichment	14 May	14 May
1st application of herbicides	14 May	3 May
2nd application of herbicides	21 May	19 May
3rd application of herbicides	30 May	
2nd nitrogen fertilization	6 June	16 June
1st application of fungicides	9 August	27 July
2nd application of fungicides		2 September
End of CO_2 enrichment	25 September	30 September
Final harvest	27 September	30 September

2.3. Leaf growth analysis

Leaf number per plant was measured approximately weekly on twelve (2001) and eight (2004) representative plants per half circle. Coloured wire rings were placed around the petioles of the 10th and 20th leaves, as they appeared, and used as markers. Leaves were counted when they were 1–2 cm long. For analysis of leaf area expansion eight to twelve plants were selected within each half ring and on each plant rings of coloured wire were placed around the petioles of the 11th, 16th, 26th and 31st leaf as they appeared. The length (l) and breadth (b) of each leaf was measured with a ruler during its expansion period and leaf area was estimated from the product l × b using a correction factor of 0.75 (Milford et al., 1985b).

Percentage of canopy closure was determined by counting the number of neighbouring plants between two rows, which have contact with their leaves. In each half circle 40 pairs of plants were assessed.

2.4. Crop growth analysis

Three destructive harvests (shortly after canopy closure, in August and at the end of September) were carried out and samples were taken from each quarter per ring. The size of the sampling area per quarter amounted to $2\,m^2$ except for the final harvest, when sampling area was increased to $3\,m^2$ and $5\,m^2$ for the shaded and unshaded plots, respectively (Fig. 1). The major fraction (70–80%) of the total above ground biomass was dried in 2001 and the dry weight was determined. In 2004, fresh weight of the total green leaf fraction was measured and subsequently homogenized with a cutter. Sub-samples were used for the determination of the dry weight fresh weight ratio and of the chlorophyll content as described below. A smaller fraction (20–30%) of the harvested plant material was used for estimation of the dry weights of storage roots, petioles, dead and green leaves, and for determination of the numbers of green and non-green leaves per plant. The areas of the green leaves were measured with a leaf area meter (LI-3100, LICOR, Nebraska) and used to calculate green leaf area index. Dry weights of leaves, stems and roots were determined after drying at $105\,°C$.

2.5. Analysis of chlorophyll content of the total canopy

Chlorophyll measurements were only done in 2004. For analysis of the chlorophyll content of the total canopy 10 g fresh weight of the homogenized green leaf fraction from the destructive harvests were transferred to a volumetric flask filled with $CaCO_3$-saturated dimethysulfoxide up to a total volume of 200 ml and extracted at $5\,°C$ overnight and under darkness. Subsequently, the absorbance of the extract was measured at 665 and 648 nm against a $CaCO_3$ saturated dimethysulfoxide blank. The concentration of chlorophyll a and b in the extract was calculated using the equations given by Barnes et al. (1992). The amount of chlorophyll (a + b) per m^2 ground area was obtained by accounting for the volume and the green leaf fresh weight of the extract and the total green leaf fresh weight per ground area.

2.6. Analysis of water-soluble carbohydrate content in petioles and quality parameters of the beet

The petiole fraction of the destructive harvests was used for the analysis of water-soluble carbohydrates (WSC). The dried petioles were 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 in a water bath at $80\,°C$. After filtration the concentration of carbohydrates in the aqueous solution was determined colourimetrically by the anthrone method as described previously (Manderscheid et al., 2009). The WSC concentration of the petioles was mul-tiplied with the petiole dry weight per ground area to obtain the petiole reserves, i.e. the amount of WSC in petioles per m^2 ground area. Beets samples from final harvest were delivered to the Institute of Sugar Beet Research, Göttingen, Germany, and quality parameters (concentration of sucrose, potassium, sodium and α-amino-nitrogen) were determined as described elsewhere (Kenter and Hoffmann, 2006). White sugar yield was calculated according to Buchholz et al. (1995).

2.7. Statistical analysis

The two samplings taken in each semicircle for crop growth analysis per measurement date were averaged and used in the statistical analysis. Data were analysed as a completely randomised design with ambient CO_2 ($n = 2$) and elevated CO_2 ($n = 2$) treatments each split for N ($n = 8$) with the R statistical software package (Version 2.8.0, R Development Core Team, 2004). Variables connected to phenological development of the plant during the vegetation period (above ground biomass, LAI, chlorophyll content in the total canopy, carbohydrate content in petioles) were separately analysed as described above for each year on the basis of individual sampling dates. In several statistical analyses of sugar beet leaf growth leaf age class (young and old) or leaf number (11, 16, 26 and 31) were included as additional treatment factors in the analysis.

For the shading treatments in 2004 additional treatment sub-plots were established in each quarter of the ring halves (Fig. 1) and were included in the statistical analysis as additional splitting factor. In August 2001 an infection of the plants by rhizomania was observed in one blower and one FACE-ring, respectively. The data of the two rings were excluded from the analysis and data presented for August and September 2001 were derived from only one replicate ring and statistical analysis was not possible for these measurement dates. Final harvest data of 2001 represent means of four subsamples taken in one blower or one FACE ring for each of the two nitrogen levels (Fig. 1).

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 2% and 1% for the years 2001 and 2004, respectively. Main reasons for cut-off times in 2001 were high wind speeds and exceedance of target CO_2 concentration, while in 2004 mainly low temperatures and high wind speeds accounted for system cut-off times. During operation the FACE system worked satisfactorily with 98% of total fumigation time with 1 min average values within a tolerable concentration range of ±10 of the target concentration ($550\,\mu l\,l^{-1}$) in 2001, and 99% in 2004. Simultaneous average atmospheric CO_2 concentrations in the ambient rings during CO_2 fumigation times were $370\,\mu l\,l^{-1}$ and $377\,\mu l\,l^{-1}$ in the years 2001 and 2004, respectively.

The weather conditions during the two seasons are presented in Fig. 2. Seasonal changes in temperatures were within the range of normal variation. Late summer was quite sunny particularly in the 2nd season, when monthly averages of global radiation were more than 20% above the long-term mean for August and September. The FACE treatment hardly influenced canopy air temperature and the shading treatment resulted in a negligible decrease of this parameter (Table 2). At early June when the crop was still small, soil water content showed a higher value for the ambient than the FACE plots. In July and August the conditions changed gradually and FACE plots showed a higher soil water content than the ambient plots. However, these differences were not significant. The soil water contents
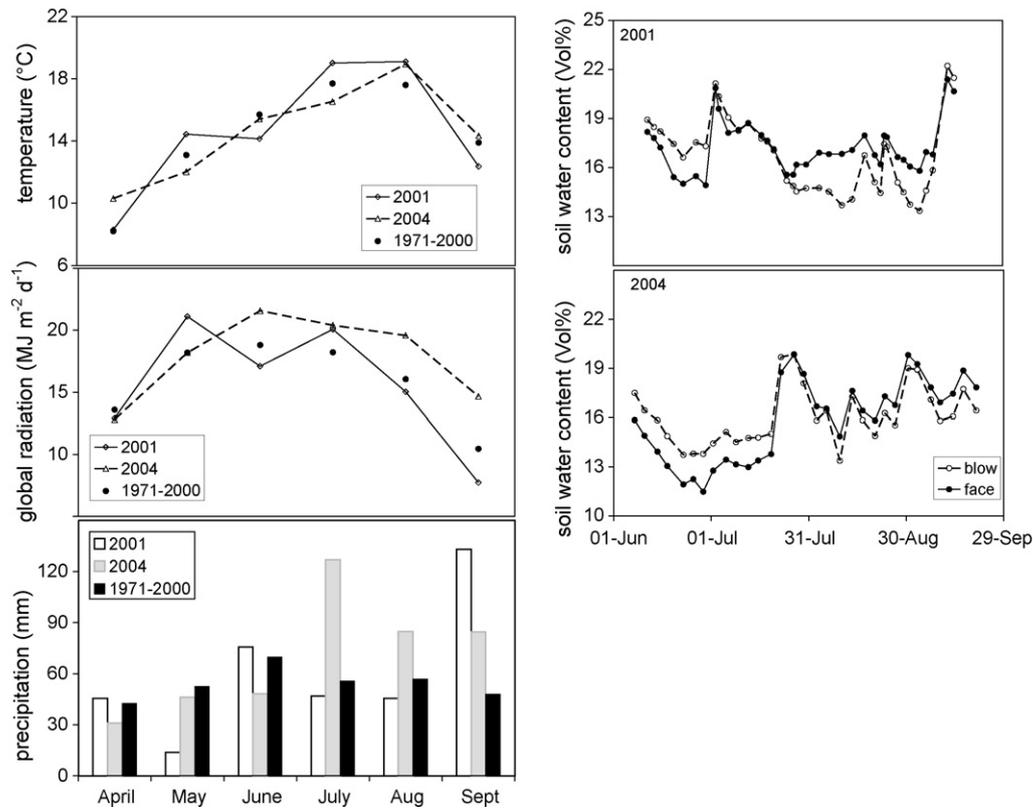
Fig. 2. Seasonal changes in climatic conditions in the 1st and 2nd vegetation period as compared to the long-term means, and temporal courses of volumetric soil water content in 2001 and 2004. Values represent averages of soil water content measured at two depths (25 and 45 cm) and in four rings (two blower rings (open circles) and two rings with CO_2 enrichment (filled circles)).

in Fig. 2 were generally above a level of 14 vol.% which is 50% of the capacity of plant available water at the study site, indicating the absence of water stress conditions. Only in 2004 the FACE study sites were slightly below this level in early summer.

3.2. Leaf growth

Plants developed some 40 leaves until the final harvest in both years. Leaf number per plant was not significantly influenced by CO_2 fumigation. More nitrogen supply significantly increased leaf number in the 1st year before the incidence of rhizomania in early August (data not shown)

The expansion of the 11th, 16th, 26th and 31st leaf is shown in Fig. 3. More nitrogen increased the expansion rate of leaves analysed and the final leaf area was significantly greater in the high as compared to the low N treatment (Table 3). CO_2 elevation significantly advanced growth of the 11th leaf also resulting in larger leaf area, but the effect decreased for subsequent leaves. ANOVA

Table 2
24 h averages of air temperature (°C) for the period July until August measured by a nearby Agrometeorological Research Station at 2 m height and within the canopies of sugar beet grown over two years (2001, 2004) under different nitrogen levels (low N1, high N2), atmospheric CO_2 concentrations (ambient and FACE) and light conditions (unshaded or shaded since July, in 2004 only).

Measuring site	N level	CO_2 level	2001	2004	
			Unshaded	Unshaded	Shaded
2 m height			19.1	17.7	
Canopy	N1	Ambient	17.8	16.9	16.8
	N2	Ambient	17.8	16.9	16.7
	N1	FACE	18.2	17.0	16.8
	N2	FACE	18.0	16.7	16.8

on final leaf area of all four leaves revealed a significant interaction between [CO_2] and leaf number (Table 3). This CO_2 effect was independent of the nitrogen supply.

The findings from several destructive harvests demonstrated that more nitrogen increased total biomass of green leaves and individual leaf size throughout the season (Table 4). There was no consistent CO_2 effect but rather diverse effects over the season. The areas and the weights of individual leaves were significantly increased in early summer but not later on in the season. In August, there was a significant $CO_2 \times N$ interaction on the number of dead leaves and CO_2 enrichment raised the number under high but not low nitrogen. In late September, total biomass of green leaves was decreased by CO_2 elevation under high nitrogen but not under low nitrogen as indicated by the significant $CO_2 \times N$ interaction. How-
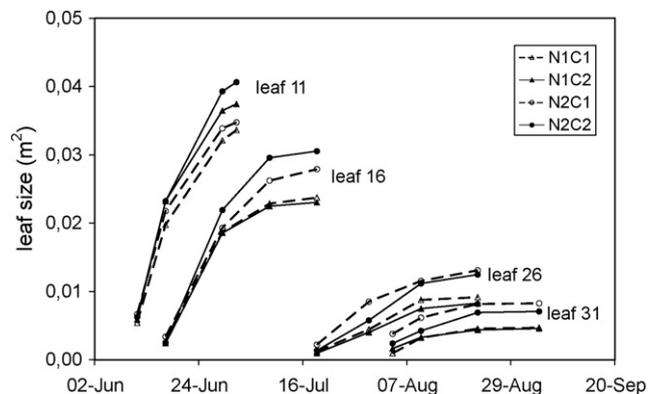

Fig. 3. Expansion in area of the 11th, 16th, 26th and 31st leaf of sugar beet grown in 2004 under two levels of nitrogen (N1, low; N2, high) and of atmospheric CO_2 concentrations (C1: ambient; C2: FACE).

Table 3

ANOVA results of the effects of two levels of nitrogen (low N1, high N2) and CO_2 supply (ambient and FACE) on the leaf area of different leaves of sugar beet (leaf number 11, 16, 26 and 31) on four measurement dates (M1–M4) shown in Fig. 2.

LN[a]	Factor[b]	M1[c]	M2	M3	M4
11	CO_2	n.s.	n.s.	(*)	(*)
	N	n.s.	n.s.	n.s.	n.s.
16	CO_2	n.s.	n.s.	n.s.	n.s.
	N	n.s.	n.s.	(*)	(*)
26	CO_2	n.s.	n.s.	n.s.	n.s.
	N	n.s.	n.s.	*	**
31	CO_2	n.s.	n.s.	n.s.	n.s.
	N	n.s.	(*)	*	*
11–31	CO_2				n.s.
	N				***
	LN				***
	$CO_2 \times LN$				**
	$N \times LN$				n.s.
	$CO_2 \times N \times LN$				n.s.

(*) $p < 0.10$.
[a] LN = leaf number.
[b] The $CO_2 \times N$ interaction was always n.s.
[c] Measuring date.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

ever, this interaction was not observed under shading. Moreover, the shading treatment resulted in a significant increase ($p = 0.09$) of the individual area of green leaves as compared to the unshaded plants.

Early canopy growth as measured by percentage canopy closure was only recorded in 2004. There was a significant positive effect
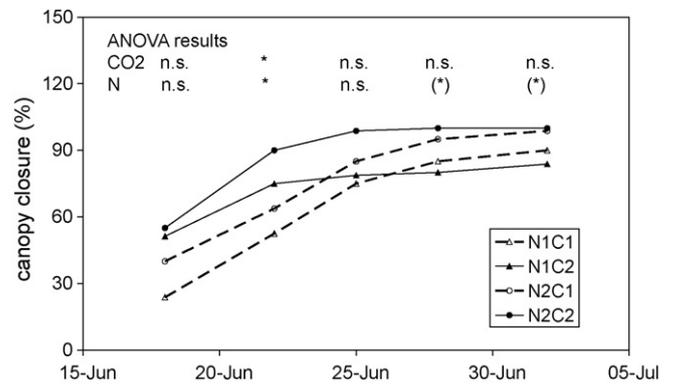

Fig. 4. Temporal changes in percentage of canopy closure of sugar beet grown in 2004 under two levels of nitrogen (N1, low; N2, high) and of atmospheric CO_2 concentrations (C1: ambient; C2: FACE).

of both nitrogen and CO_2 supply at the 20th of June on percentage canopy closure (Fig. 4). Thus, CO_2 enrichment accelerated early canopy growth under both nitrogen levels.

3.3. Seasonal course of green leaf area index and chlorophyll content of the whole canopy

As from July canopy of plants grown under FACE had lighter green colour than under ambient $[CO_2]$ as visible by eye in both years. The shading treatment in 2004, which was started in mid July, did not show this effect.

Green leaf area index had a maximum in July and declined thereafter (Fig. 5). More nitrogen increased LAI throughout the season. Under FACE the decrease of LAI late in the season was

Table 4

Leaf growth variables of sugar beet plants grown in 2001 and 2004 under different nitrogen (low, N1; high, N2) and CO_2 levels (ambient, C1; FACE, C2). Variables were measured at one (2001) or three (2004) destructive harvests (H1: end of June or beginning of July, H2: August, H3: late September). In 2004 an additional shading treatment was applied.

Date	Variable	N1		N2		ANOVA results		
		C1	C2	C1	C2	CO_2	N	$C \times N$
2001								
H1	Green leaves d.w.[a] ($g\,m^{-2}$)	150	170	211	229	n.s.	*	n.s.
	Individual area (cm^2)[b]	143	161	183	199	(*)	**	n.s.
	Individual d.w. (mg)[b]	843	983	1265	1296	n.s.	*	n.s.
	Number of dead leaves	3.5	3.6	3.2	3.2	n.s.	*	n.s.
2004								
H1	Green leaves d.w. ($g\,m^{-2}$)	194	225	235	259	n.s.	n.s.	n.s.
	Individual area (cm^2)	154	159	187	201	n.s.	(*)	n.s.
	Individual d.w. (mg)	875	999	962	1096	*	n.s.	n.s.
	Number of dead leaves	1.6	1.7	1.4	1.6	n.s.	n.s.	n.s.
H2	Green leaves d.w. ($g\,m^{-2}$)	160	183	257	257	n.s.	*	n.s.
	Individual area (cm^2)	98	87	130	134	n.s.	n.s.	n.s.
	Individual d.w. (mg)	554	539	719	786	n.s.	(*)	n.s.
	Number of dead leaves	6.7	5.7	4.4	5.8	n.s.	**	**
H3	Green leaves d.w. ($g\,m^{-2}$)	105	112	206	158	n.s.	***	**
	Individual area (cm^2)	41	33	80	67	n.s.	**	n.s.
	Individual d.w. (mg)	283	229	532	445	n.s.	**	n.s.
	Number of dead leaves	9.7	11.2	8.0	9.3	n.s.	**	n.s.
Shaded in 2004								
H3	Green leaves d.w. ($g\,m^{-2}$)	123	106	186	194	n.s.	(*)	n.s.
	Individual area (cm^2)	59	37	95	78	n.s.	(*)	n.s.
	Individual d.w. (mg)	348	226	531	484	n.s.	(*)	n.s.
	Number of dead leaves	11.3	9.9	6.0	6.7	n.s.	n.s.	n.s.

(*) $p < 0.10$.
[a] Dry weight.
[b] Of green leaves only.
* $p < 0.05$.
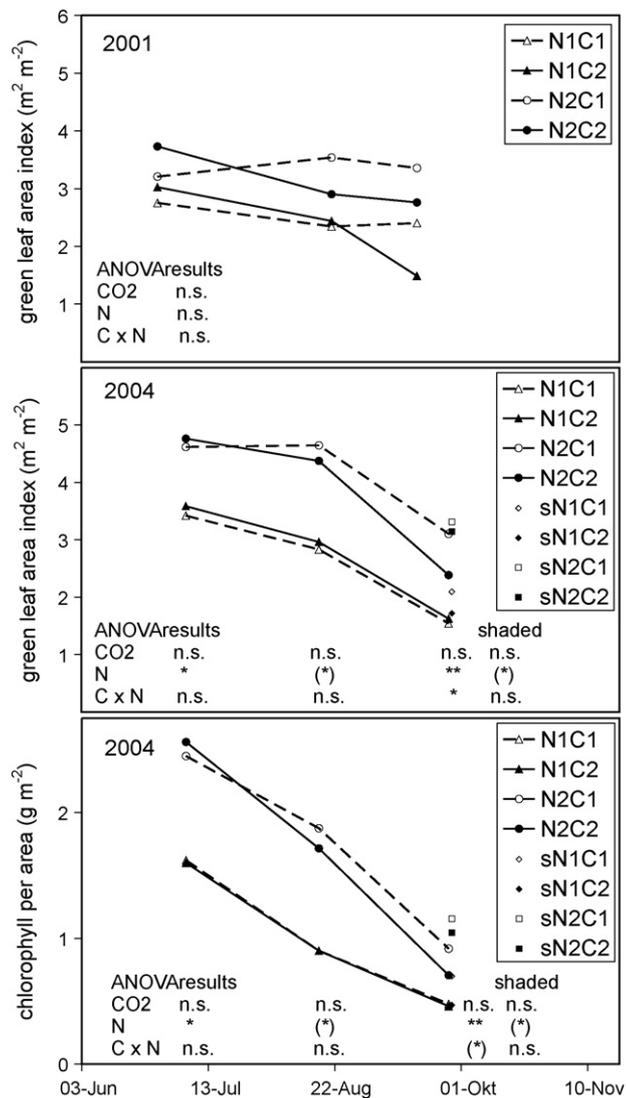** $p < 0.01$.
*** $p > 0.001$.

Fig. 5. Seasonal changes in green leaf area index of sugar beet grown in 2001 and 2004 under two levels of nitrogen (N1, low; N2, high) and of atmospheric CO_2 concentrations (C1: ambient; C2: FACE), and seasonal changes of chlorophyll content of the canopy per ground area measured in 2004 and at final harvest under two light conditions (normal light conditions, shaded (=s)).

accelerated especially under high nitrogen. In 2004 a significant $CO_2 \times N$ interaction was observed in September, since LAI varied +5% and −23% by FACE as compared to ambient conditions under low and high nitrogen, respectively. This is confirmed by the results on green leaf biomass measured at the final harvest (Table 4). Similar effects were found for the chlorophyll content per ground area (Fig. 5), which was increased by nitrogen supply all over the season but decreased by CO_2 enrichment in the high nitrogen treatment at the final harvest as supported by a significant $CO_2 \times N$ interaction. In 2004, LAI, green leaf biomass and chlorophyll content per ground area were also measured at final harvest in the shaded plots. There the crop received only 51% of incident radiation during summer and no significant interaction of nitrogen and CO_2 on LAI and chlorophyll content, and no negative CO_2 effect on the green canopy area could be observed. Moreover, under high nitrogen shading resulted in a significant increase ($p = 0.02$) of chlorophyll content per ground area (+35%) averaged over both CO_2 levels as compared to the unshaded plots.

3.4. Dry weights of leaves, petioles and storage roots

There was a quite consistent nitrogen effect over season and years on total leaf and petiole biomass (Table 5), which were roughly 20–40% larger in the high nitrogen as compared to the low nitrogen treatment. The nitrogen effect on the biomass of the storage root was considerably smaller, which was in the range of +10%. CO_2 elevation did not significantly influence biomass of leaves or petioles except for a transient stimulation of petiole biomass in early summer under low nitrogen. However, CO_2 enrichment had a significant effect on storage root at final harvest in 2004. Dry weight of storage roots was increased under FACE in both years by 8–10% and 14–17% under high and low nitrogen supply, respectively. The shading of the canopy from mid of July in 2004 did not significantly influence total leaf or petiole biomass at final harvest, but decreased storage root biomass significantly ($p = 0.003$). Although there was no significant interaction of $[CO_2]$ and radiation on storage root biomass, the CO_2 effect under shading in the high (+18%) and low (+36%) N treatment was doubled as compared to the findings under unshaded conditions.

3.5. Temporal changes of the content of water-soluble carbohydrates in the petioles

The concentration of WSC in the petioles of the sugar beet varied from 6% to 41% across all measuring dates and treatments (Fig. 6). In the 1st year, when global radiation in August and September was substantially lower than in 2004, the concentration of WSC was about half the value observed in the second year. The effect of nitrogen fertilization on the concentration of WSC changed over the season. In early summer, plants grown under high nitrogen had less WSC, however this effect was on the borderline of significance (2001: $p = 0.13$; 2004: $p = 0.15$). In late summer and autumn, plants grown under high nitrogen had significantly more WSC than those grown under low nitrogen as found in 2004. This positive N response was even greater for the petiole reserves when the amount of petiole dry weight was also taken into account. Plants grown under high nitrogen contained up to 190 g WSC per m^2 ground area, nearly twice the value of plants grown under low nitrogen. In early summer 2001, CO_2 elevation significantly increased WSC concentration. In 2004, plants from FACE plots had higher WSC concentrations than plants from blower plots; however, the CO_2 effect was not significant. At final harvest high nitrogen and non-shading as compared to shading increased WSC concentration by 13% and 6%, respectively, however, only the effect of nitrogen was significant ($p = 0.04$) and no significant interaction could be detected.

3.6. Beet yield and composition

Under normal light conditions in 2004 elevated CO_2 increased beet fresh weight significantly at final harvest, while nitrogen supply had no significant effect (Table 6). The CO_2 response of beet fresh yield ranged from 7% to 16% among the two nitrogen treatments, which corresponds to the findings in 2001. Both, CO_2 and nitrogen supply did not significantly affect the content of sucrose, potassium and sodium in the beet fresh weight. Low nitrogen supply reduced α-amino-nitrogen content significantly compared to the high nitrogen treatment. However, the decrease was stronger under ambient than elevated CO_2 as indicated by the slightly significant interaction of $CO_2 \times N$ ($p = 0.09$). Elevated CO_2 increased white sugar yield significantly in 2004 by 10–15% in the two nitrogen treatments, which is similar to the results obtained in 2001 (11–13%).

Table 5
Biomass of leaves, petioles and storage roots of sugar beet grown in 2001 and 2004 under two nitrogen (low, N1; high, N2) and CO_2 levels (ambient, C1; FACE, C2). Variables were measured at one (2001) or three (2004) destructive harvests (H1: end of June or beginning of July, H2: August, H3: late September). In 2004 an additional shading treatment was applied.

Date	Variable	N1		N2		ANOVA results		
		C1	C2	C1	C2	CO_2	N	C × N
2001								
H1	Leaf d.w.[a] (g m^{-2})	162	184	221	240	n.s.	*	n.s.
	Petiole d.w. (g m^{-2})	118	139	156	154	n.s.	*	n.s.
	Storage root d.w. (g m^{-2})	150	173	159	131	n.s.	n.s.	n.s.
	Total d.w. (g m^{-2})	430	496	536	525	n.s.	n.s.	n.s.
H3	Leaf d.w. (g m^{-2})	256	243	364	336	[b]		
	Petiole d.w. (g m^{-2})	339	287	438	509			
	Storage root d.w. (g m^{-2})	1323	1506	1493	1637			
	Total d.w. (g m^{-2})	1919	2036	2294	2481			
2004								
H1	Leaf d.w. (g m^{-2})	200	233	241	266	n.s.	n.s.	n.s.
	Petiole d.w. (g m^{-2})	146	187	212	223	n.s.	**	(*)
	Storage root d.w. (g m^{-2})	258	297	320	313	n.s.	n.s.	n.s.
	Total d.w. (g m^{-2})	604	717	773	803	n.s.	*	n.s.
H2	Leaf d.w. (g m^{-2})	220	250	305	323	n.s.	*	n.s.
	Petiole d.w. (g m^{-2})	260	280	443	457	n.s.	*	n.s.
	Storage root d.w. (g m^{-2})	1053	1144	1109	1158	n.s.	n.s.	n.s.
	Total d.w. (g m^{-2})	1532	1673	1852	1938	n.s.	(*)	n.s.
H3	Leaf d.w. (g m^{-2})	206	272	283	273	n.s.	n.s.	n.s.
	Petiole d.w. (g m^{-2})	347	459	523	566	n.s.	(*)	n.s.
	Storage root d.w. (g m^{-2})	1417	1658	1565	1689	**	n.s.	n.s.
	Total d.w. (g m^{-2})	1971	2318	2372	2528	*	(*)	n.s.
Shaded in 2004								
H3	Leaf d.w. (g m^{-2})	208	249	260	299	n.s.	n.s.	n.s.
	Petiole d.w. (g m^{-2})	380	454	493	610	n.s.	(*)	n.s.
	Storage root d.w. (g m^{-2})	1060	1438	1132	1339	(*)	n.s.	n.s.
	Total d.w. (g m^{-2})	1656	2142	1885	2248	n.s.	n.s.	n.s.

(*) $p < 0.10$.
[a] Dry weight.
[b] Statistical analysis was not possible, since data were obtained from one replicate ring only.
* $p < 0.05$.
** $p < 0.01$.

Shading significantly decreased beet fresh weight ($p = 0.003$), sucrose content ($p = 0.08$) and increased content of sodium ($p = 0.01$) and α-amino-nitrogen (0.004) compared to the unshaded treatments. Elevated CO_2 also enhanced beet fresh weight and white sugar yield significantly under shaded conditions. Although there was no significant CO_2 × radiation interaction, the CO_2 response of beet and white sugar yield under shading was nearly twice the number detected under normal light conditions.
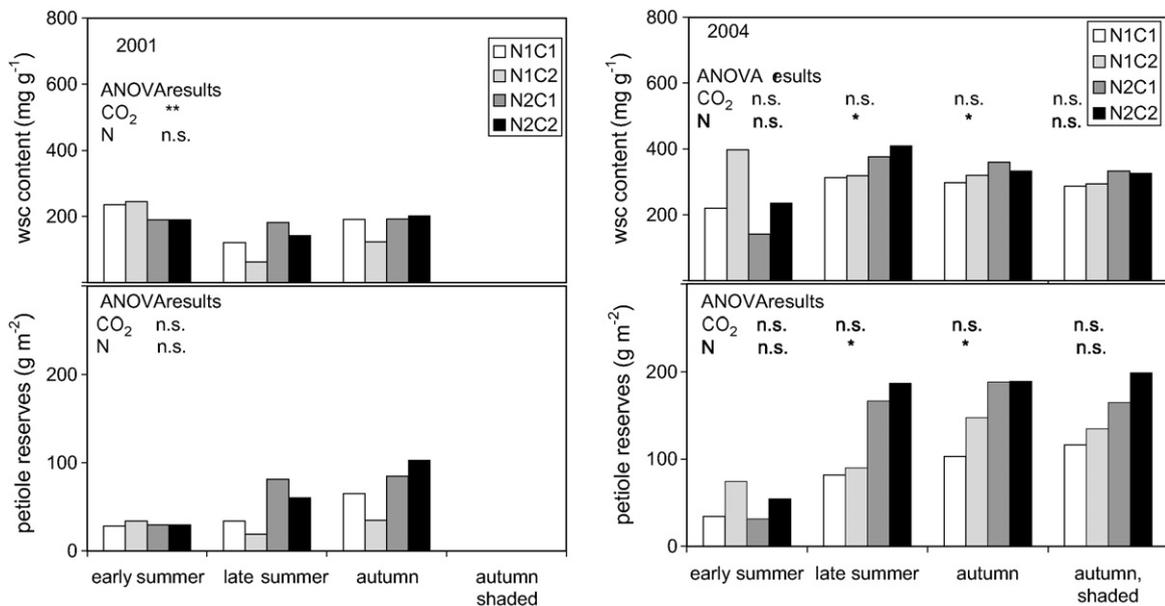

Fig. 6. Seasonal changes in water-soluble carbohydrate concentration of petioles and in amount of carbohydrates of petioles per ground area of sugar beet grown in 2001 and 2004 under two levels of nitrogen (N1, low; N2, high) and of atmospheric CO_2 concentrations (C1: ambient; C2: FACE). At final harvest in 2004 samples were also taken from two light regimes (normal light conditions, shaded).

Table 6
Effect of different nitrogen (low, N1; high, N2) and CO_2 levels (ambient, C1; FACE, C2) on beet weight and composition of sugar beet grown in 2001 and 2004. In 2004 an additional shading treatment was applied (2004S).

Year	N1			N2			ANOVA		
	C1	C2	%[a]	C1	C2	%[a]	CO_2	N	C × N
Beet fresh weight (t ha^{-1})									
2001	61.1 (1.2)	66.2 (1.1)	8	68.1 (0.5)	73.4 (1.7)	8	[b]		
2004	64.2	74.5	16	71.7	76.8	7	**	n.s.	n.s.
2004S	50.4	65.1	29	53.2	61.7	16	*	n.s.	n.s.
Sucrose content (g kg^{-1} fresh weight)									
2001	165(1)	172(2)	5	163(0)	167(1)	2	[b]		
2004	168	168	0	165	169	2	n.s.	n.s.	n.s.
2004S	157	168	7	160	163	2	n.s.	n.s.	n.s.
K (mmol kg^{-1} fresh weight)									
2001	34.8 (1.5)	38.4 (0.4)	10	36.9 (0.3)	37.4 (0.3)	1	[b]		
2004	34.0	35.9	6	37.4	35.7	−5	n.s.	n.s.	n.s.
2004S	33.4	36.4	9	36.8	36.9	0	n.s.	*	*
Na (mmol kg^{-1} fresh weight)									
2001	3.28 (0.1)	2.60 (0.1)	−21	3.51 (0.2)	2.68 (0.1)	−24	[b]		
2004	2.21	2.19	−1	2.65	2.34	−12	n.s.	n.s.	n.s.
2004S	3.61	2.60	−28	3.40	3.18	−7	n.s.	n.s.	n.s.
α-amino-nitrogen (mmol kg^{-1} fresh weight)									
2001	6.81 (0.4)	7.57 (0.1)	11	9.76 (0.5)	9.15 (0.2)	−6	[b]		
2004	4.83	5.92	23	8.08	7.61	−6	n.s.	*	(*)
2004S	6.10	7.62	25	10.9	11.1	1	n.s.	**	n.s.
White sugar content (g kg^{-1} fresh weight)									
2001	148(1)	154(2)	5	145(1)	149(1)	3	[b]		
2004	152	151	−1	148	152	3	n.s.	n.s.	n.s.
2004S	141	151	7	142	145	3	n.s.	n.s.	n.s.
White sugar yield (t ha^{-1})									
2001	9.02 (0.2)	10.2 (0.1)	13	9.86 (0.1)	10.9 (0.2)	11	[b]		
2004[c]	9.74	11.2	15	10.6	11.6	10	**	n.s.	n.s.
2004S[d]	7.17	9.81	37	7.52	8.95	19	(*)	n.s.	n.s.

(*) $p < 0.10$.

[a] Percentage CO_2 effect.

[b] There was only one FACE and control ring in 2001 not impaired by disease; number in parenthesis indicates standard error of subsamples ($n = 4$) taken within one ring.

[c] The individual replicates for the two N levels (N1/N2) are: Ambient, 9.72/10.59, 9.76/10.57; FACE, 10.76/11.98, 11.71/11.29.

[d] The individual replicates for the two N levels (N1/N2) are: Ambient, 8.86/7.00, 5.48/8.05; FACE, 9.65/8.52; 9.96/9.38.

* $p < 0.05$.

** $p < 0.01$.

4. Discussion

The objective of the present study, which is the first free air CO_2 enrichment experiment with sugar beet, was to determine the effect of [CO_2] and nitrogen supply on canopy growth and beet production under field conditions over two years without limitation by water supply. Overall, crop growth and final biomass production was quite similar in both years. During most of the season soil water contents were higher than 14% (level of 50% plant available water) indicating the absence of drought stress and no effect of plant water availability on the results. The similar change over both years towards higher soil water content in the FACE than blower ring as from July suggests a reduction in canopy water flux under FACE as has been found with canopy chambers (Weigel et al., 2006).

As the experimental field was expected to have low risk of rhizomania infection a non-resistant cultivar was grown in the first experimental year 2001. Half of the experimental area could not be considered for data analysis for this year due to a highly improbable rhizomania infection. In the second sugar beet growth period a rhizomania resistant cultivar was chosen. However, the good agreement of the sugar beet yields in both years show the high similarity of both cultivars with respect to CO_2 response and yield formation. The differences between both cultivars in both experimental years can be mainly attributed to the strong difference in weather conditions between the two growing seasons. So, despite the shortcomings in the experimental data set, the results presented can be considered as consistent and valid.

4.1. Effects of CO_2 and nitrogen on leaf growth

The higher response of canopy growth than beet growth to nitrogen supply as observed in this study is well known for sugar beet (Märländer, 1990; Malnou et al., 2008). Moreover, the positive N effect on leaf area index could be ascribed in detail to changes in leaf number, individual leaf size and leaf life span as demonstrated by others (Milford et al., 1985a,b).

We expected a positive CO_2 effect on leaf growth especially in summer when temperatures are high and stimulation of photosynthesis by CO_2 elevation is assumed to be strong (Long, 1991) which in fact was shown by canopy CO_2 exchange measurements (Burkart et al., 2009). However, in the present FACE study the response of leaf growth to elevated [CO_2] was not simple being characterized by different time patterns. Leaf number per plant was unaffected by CO_2 enrichment which corresponds to results of previous CO_2 fumigation studies (Ford and Thorne, 1967; Demmers-Derks et al., 1998; Romanova et al., 2002). Individual leaf size as a further major determinant of LAI is known to increase approximately up to the 11th leaf and successive leaves achieve progressively smaller final sizes (Milford et al., 1985b), which was also observed in this study in 2004. In the FACE experiment CO_2 elevation increased individual leaf size by enhancing the leaf expansion rate in early summer as detected for the 11th leaf and for the average individual leaf size and weight measured in early July. Moreover, the findings indicated that final leaf size of late leaves was smaller under elevated than under ambient [CO_2]. Increases in leaf size under CO_2 enrichment

have also been reported in several chamber studies with sugar beet (Ford and Thorne, 1967; Ziska et al., 1995; Romanova et al., 2002) and with other plant species (Pritchard et al., 1999). Increases in leaf sizes contributed to the accelerated canopy closure detected in 2004 under elevated [CO_2]. On the other hand, the decreasing CO_2 effect on leaf size of sugar beet later on in the season may account for the lack of an effect on maximum LAI. In addition, leaf life span turned out to be influenced by elevated [CO_2] under high nitrogen supply. More CO_2 increased the number of dead leaves in August and decreased the chlorophyll content of older leaves during September. These changes contributed to the accelerated LAI loss under elevated [CO_2] at the end of the vegetation period. A decrease in chlorophyll content and an acceleration of canopy senescence towards the end of the vegetation period was also found in several CO_2 fumigation studies with potato (Miglietta et al., 1998; Schapendonk et al., 2000; Hacour et al., 2002). A brightening of the sugar beet canopy under FACE was already observed in the 1st year in the ring without rhizomania infection. Total chlorophyll content of the canopy was closely related to LAI values over the season and the CO_2 response under high nitrogen at final harvest corresponded to findings for LAI. This is in contrast to a greenhouse study, in which elevated CO_2 had no effect on green leaf area over the season (Demmers-Derks et al., 1998).

4.2. Possible mechanisms responsible for the decrease of LAI under CO_2 enrichment and high nitrogen

The loss in LAI and in canopy chlorophyll content of 23% under FACE and high nitrogen at final harvest implies that the crop absorbed approximately 10% less radiation as compared to the plants grown under ambient [CO_2] (Azam-Ali et al., 1994), which could point to a decrease in crop growth under elevated [CO_2]. N shortage for leaf growth could have contributed to the decline in LAI under CO_2 enrichment e.g. due to reduced N uptake (McDonald et al., 2002) or increased demand by other organs (Miglietta et al., 1998). However, these hypotheses can not explain the interaction of CO_2 and nitrogen supply on LAI observed in the FACE study with sugar beet. As a different explanatory approach, it can be hypothesized that the CO_2-related accelerated loss of LAI under high nitrogen resulted from sink limitation of crop growth. This hypothesis is supported by the results of the shading experiment. The shading treatment resulted in both a higher CO_2 effect on total biomass production with no effect on LAI under high nitrogen. However, the reason for the interaction of CO_2 and nitrogen supply on LAI remains to be elucidated.

In late summer ca. 90% of assimilates enter the storage root (Milford and Watson, 1971). During August and September storage root dry weight was only slightly greater ($\leq 10\%$) under high than low nitrogen supply in the blower rings, the difference was even smaller in the FACE rings. In August, this was in agreement to the difference in canopy radiation absorption of ca. 10% estimated from LAI values. However, in September the green canopy of sugar beet plants grown with high nitrogen supply absorbed ca. 20% more light than that grown with low nitrogen. This indicates an imbalance in source-sink relations and is supported by the findings for WSC reserves in the two nitrogen treatments.

4.3. Effects of CO_2 and nitrogen on the content of water-soluble carbohydrates in the petioles

It was surprising that during summer and autumn in 2004 WSC content was higher under adequate nitrogen supply and not under low nitrogen supply as known for WSC content in stems of cereals (Schnyder, 1993). This nitrogen effect was even greater for the amount of WSC, i.e. the product of WSC content and total petiole biomass. There was a huge amount of WSC up to 190 g m^{-2} ground

area in the petioles under high nitrogen, when LAI was reduced by elevated [CO_2]. Under low nitrogen the amount of WSC was only 100 g m^{-2}. This is in contrast with findings for cereals, which had a higher amount of stem reserves under low nitrogen due to less vigorous growth (Schnyder, 1993). We supposed that treatments with direct effects on assimilation rate, i.e. variation in [CO_2] and in incident radiation, would mostly influence the amount of WSC stored in the petiole fraction. However, in our field experiment CO_2 enrichment increased WSC content only in early summer as has been reported by Ziska et al. (1995) in another study. It turned out that nitrogen supply was the most important factor influencing WSC storage in the petiole.

4.4. Effects of CO_2 and nitrogen on total biomass and storage root biomass

CO_2 elevation stimulated total biomass of sugar beet by ca. 7% in the 1st year in both nitrogen treatments and also in the 2nd year under high nitrogen. This is a lower CO_2-response than found for the preceding winter barley of the crop rotation experiment (Manderscheid et al., 2009). The small CO_2 effect on growth of sugar beet is in contradiction to expectation that photosynthesis should be increased especially during warm summer months (Long, 1991) and that growth of storage root is source-limited (Thomas, 1999). Rather the CO_2 response observed in the experiment points to a strong sink limitation of crop growth as has been shown by Demmers-Derks et al. (1998) in a greenhouse study.

The growth of the storage root proceeds by import of sucrose in the vacuoles of parenchyma cells produced by cambial rings (Thomas, 1999). These rings are initiated early in the season and most of them are developed until July (Milford, 1973). Since shading started in the middle of July it can be assumed that the potential sink size was similar for the plants grown with and without shading. Thus, the doubling of the CO_2 effect observed under shading as compared to normal light conditions on storage root biomass indicates that even under field conditions the growth is not source but sink limited as found by Demmers-Derks et al. (1998) for potted plants in the greenhouse.

There was no interaction of nitrogen and CO_2 supply on production of total biomass and storage root biomass in the field study, which contrasts with the results obtained in the pot study by Demmers-Derks et al. (1998). Under high nitrogen supply CO_2 enrichment increased storage root biomass by 10% and 8% in the two years, but by 18% in the 2nd year under shading. In previous CO_2 fumigation studies with sugar beet [CO_2] was elevated by 300–400 µl l^{-1}. Assuming a linear CO_2 response, these studies showed a mean increase in storage root dry weight of 14% (Wyse, 1980a) to 16% (Demmers-Derks et al., 1998; Wolf, 1998) for a CO_2 elevation of 175 µl l^{-1} as observed in our FACE experiment. The increase in beet yield detected in our FACE study was clearly lower and adds to the recent conclusion that crops grown under FACE show a lower CO_2 response than grown in enclosures (Long et al., 2005).

4.5. Does the dependency of the beet growth rate on temperature provide an explanation for the low CO_2 response?

The mechanism responsible for the sink limitation of the growth of sugar beet is still unclear. Demmers-Derks et al. (1998) suggested that sugar beet has a determinate ontogeny with a phase of slower taproot growth at the end of the season. This is confirmed by the findings that the canopy CO_2 exchange rate (Burkart et al., 2009) and the daily growth rate of the storage root of sugar beet (Manderscheid et al., 2007) decreased in late summer, although climate conditions, i.e. temperature and global radiation, did not

change substantially. However, if there is only a sink limitation due to a decrease in taproot growth towards the end of the season we should have seen a clear CO_2-response of beet growth in early and mid summer, which was not detected. Potato plants, which also have been assumed to be only source-limited due to their large carbon sink in the tubers, showed a higher percentage increase by CO_2 in a temperate than a warm year (Schapendonk et al., 2000). According to Kenter et al. (2006) the daily growth rate of the tap-root of sugar beet increased up to an optimum temperature of 18 °C. Higher temperature occurring in July and August decreased final taproot yield (Kenter et al., 2006). During the FACE experiments in 2001 and 2004 mean daily air temperature was higher than 18 °C on 34 and 26 days, respectively. Thus, the potential stimulation of canopy assimilation by elevated $[CO_2]$ under high temperature during summer probably outbalanced the assimilate demand of the storage root, since its growth rate does not increase but decrease above 18 °C.

4.6. Effects of CO_2 and nitrogen on the composition of the storage root

The absence of a significant CO_2 effect on sucrose concentration per unit root fresh weight in our FACE study corresponds to the findings of the long-term CO_2-study done by Demmers-Derks et al. (1998) in a greenhouse. However, they also observed a decrease in α-amino-nitrogen concentration in the beet under elevated $[CO_2]$ independent of nitrogen supply, which we found only under high but not under low nitrogen supply. Moreover, other soluble constituents of the beet, which affect sugar recovery, have been measured under elevated $[CO_2]$ for the first time in the Braunschweiger FACE experiment. According to these results concentrations of potassium and sodium were not affected by $[CO_2]$. Thus, the CO_2 response of white sugar yield among years and nitrogen levels, which ranged from 10% to 15%, was similar to that of beet yield. It is interesting to see that the carbohydrate reserves available in the petioles at final harvest in 2004, which ranged from 100 to 190 g m^{-2} ground area among the different nitrogen and CO_2 levels, would increase white sugar yield by 11–18% if transferred to the storage root.

5. Conclusions

The present FACE study with sugar beet showed that the atmospheric CO_2 concentration predicted by the A1B IPCC scenario for the middle of this century could increase beet yield by 7–16% and white sugar yield by 10–15%. The CO_2 response of beet growth measured under FACE was lower than expected from previous enclosure experiments and from theory. LAI was increased in early and decreased in late summer under elevated $[CO_2]$ and high nitrogen. Shading prevented the negative CO_2 effect on LAI in September and resulted in a higher CO_2 response of beet growth. Thus, the accelerated loss of LAI by elevated $[CO_2]$ under high nitrogen is assumed to be an adjustment of the carbon acquisition system at the canopy level to sink strength, which is primary determined by growth of the storage root. It is speculated that differences in the temperature dependence of the assimilation rate and of the beet growth rate have contributed to imbalances in source-sink relations under elevated $[CO_2]$. In order to exploit the beneficial effect of increasing $[CO_2]$ it seems necessary to increase the beet growth rate.

Acknowledgements

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