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Effects of nutrient (NPK) supply on sugar beet response to elevated atmospheric CO_2

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Abstract

The effects of increased atmospheric CO_2 on crop growth and dry matter allocation may change if nutrient supply becomes insufficient. Increased atmospheric CO_2 may also cause changes in maximum dilution of nutrients in plant tissue and hence, in the minimum nutrient concentration levels and the maximum yield-nutrient uptake ratios of crops. To study these effects of increased CO_2 for sugar beet (*Beta vulgaris* L.), pot experiments have been carried out at ambient and doubled CO_2 concentration. Beet plants were grown for four monthes at different supplies of N, P or K.

Doubling of ambient CO_2 resulted in a moderate increase in total yield (+24%) and beet yield (+34%), however this CO_2 effect disappeared with increasing nutrient shortage (in particular nitrogen). CO_2 doubling did not result in significant changes in the minimum nutrient concentrations in leaves and beets.

Keywords: CO_2 enrichment, N use efficiency, P use efficiency, K use efficiency, sugar beet

Introduction

Increasing concentrations of atmospheric CO_2 generally increase the rate of photosynthesis and suppress photorespiration of most plants (Acock, 1990; Goudriaan & Unsworth, 1990). This stimulates plant growth and leads to considerably higher crop production and yields (Cure, 1985; Cure & Acock, 1986; Kimball, 1983; Strain & Cure, 1994) in situations with optimal nutrient supply. Simultaneously dry matter partitioning may change at increased CO_2 (Stulen & Den Hertog, 1993).

In nutrient-limited conditions, nutrient concentrations in plant tissue strongly decrease during the growth cycle and at harvest, nutrients appear to be diluted to a plant-specific minimum concentration level (Janssen *et al.*, 1990). Such levels will only be attained in situations where all required nutrients are supplied sufficiently and only one nutrient strongly limits crop growth (Van Keulen & Van Heemst, 1982). Further dilution of the limiting nutrient appears to be impossible. If this minimum concentration decreases and hence the maximum yield-nutrient uptake ratio of crops increases with an increase in atmospheric CO_2, this could result in an increase in crop growth and attainable level of production. For example, a large part of leaf N is incorporated in enzymes involved in the photosynthesis process. As the photosynthetic efficiency increases with an increase in atmospheric CO_2, the amount of enzymes (in particular Rubisco) and hence the N concentration in the leaves generally decreases. However, for the P concentration in plant tissue a decrease with increasing CO_2 was not found (Conroy, 1992; Hocking & Meyer, 1991; Goudriaan & De Ruiter, 1983; Wolf, 1996a).

The effects of atmospheric CO_2 on crop growth and dry matter allocation may be different under conditions of nutrient shortage compared to optimal nutrient supply (Idso & Idso, 1994). To study these effects of increased atmospheric CO_2 on crop growth at different degree of nutrient deficiency, and the effects of increased CO_2 on the plant-specific minimum nutrient concentration levels, pot experiments were carried out. These experiments were done with spring wheat, sugar beet and faba bean for a limited supply of N, P and K, respectively. For sugar beet the results are reported here. Results for the other crops are reported separately (Wolf, 1996a, b).

Growth of natural vegetations and arable crops in large parts of the world is mainly limited by the availability of nutrients. If the minimum nutrient concentrations do not change with an increase in atmospheric CO_2, this means that the positive effects on crop production and yield of an increase in atmospheric CO_2 as mentioned above for crop growth under optimal conditions, do not occur in the large areas with limiting nutrient supply. This has important consequences for the food production potential under future high CO_2 conditions. In the opposite situation (i.e. a decrease in minimum nutrient concentrations), a CO_2 increase may also result in higher yields under nutrient-limited conditions. In such case, however, the lower nutrient concentrations in crop residues remaining after harvest may result in a reduced soil organic matter decomposition and nutrient cycling (Kuikman & Gorissen, 1993; Van de Geijn & Van Veen, 1993; Zak *et al.*, 1993), which in the long term might give a lower nutrient supply and might nullify the positive effect of elevated CO_2.

Materials and methods

Design of the experiment

The beet plants (*Beta vulgaris* L.) were grown in two similar glass-houses, differing only in CO_2 concentration (315 and 695 ppmv). In each glass-house the plants were subject to seven nutritional treatments: a control without nutrient limitation (NPK), 10% (0.1N) and 30% (0.3N) of optimum N supply, 10% (0.1P) and 30% (0.3P) of optimum P supply, and 10% (0.1K) and 30% (0.3K) of optimum K supply with the other elements sufficiently supplied. For all treatments there were three replicates, all used for one final harvest.

The plants received nutrient solution and additional tap water. During the first four weeks after sowing (12 October 1993) all plants received the same treatment

(315 ppmv CO_2, same glass-house, identical nutrient supply). On 8 November the plants were distributed between the two glass-houses (having different CO_2 concentrations) and from that date on the pots received different nutrient solutions. In each glass-house there were three blocks (i.e. replicates). Each block consisted of three separate rows of sugar beet, faba bean and spring wheat, respectively. The rows were situated perpendicular to the main direction of air movement within the glass-house. For each replicate of each plant species seven pots with the different nutritional treatments were distributed at random within one row. The pots were placed apart to prevent shading.

For a sound statistical analysis of the CO_2 effect more glass-houses would be required to assess the variance of the glass-houses. In this experiment the variance of all (CO_2 * nutrient) treatments was used to determine the significance of the CO_2 effect. This may have influenced the significance of differences.

Soil and nutrient treatments

The plants were grown on coarse sand with a low water holding capacity and almost no organic matter in black plastic pots of about 20 L. Once a week the pots received nutrient solution. For the control (NPK) a Hoagland solution was used, consisting of 5 mM KNO_3, 2 mM $MgSO_4.7H_2O$, 5 mM $Ca(NO_3)_2.4H_2O$ and 1 mM KH_2PO_4. For the 0.1N and 0.3N treatments 90% and 70% of the NO_3^- in this solution was replaced by SO_4^{2-}, for the 0.1P and 0.3P treatments 90% and 70% of $H_2PO_4^-$ was replaced by SO_4^{2-}, and for the 0.1K and 0.3K treatments 90% and 70% of K^+ was replaced by Ca^{2+}. The nutrient solution also contained the necessary microelements and FeEDTA to allow sufficient iron uptake.

Water stress during crop growth was prevented by regularly weighing the pots and adding sufficient tap water to bring them back to their initial weights. The pots had holes in the bottom so that excess water could drain from the pots into a saucer but remained available for the plants. The soil surface in all pots was covered with white plastic grains to prevent surface evaporation and crust formation.

Air/light conditions

The plants grew almost completely under artificial light from sodium high-pressure agro-lamps, as during the main growth period (November until February) the amount of natural light was very low. To attain sufficient light for plant growth the day length was set at 16 hours. The total amount of added radiation (during 16 day hours) was 3.1 MJ m^{-2} d^{-1} ± 0.5 MJ m^{-2} d^{-1} ($P<0.05$). The temperature was set at 20°C during day and 15°C during night, resulting in an average day temperature over the whole growth period of 18.5°C. The relative humidity was set at 70% in both glass-houses.

The CO_2 concentration in the elevated CO_2 glass-house was on average 695 ppmv ± 60 ppmv ($P<0.05$). The CO_2 concentration was monitored with an IRGA and maintained by injecting pure CO_2 into the glass-house whenever the CO_2 concentration was less than a pre-set value. In the other glass-house, CO_2 concentration was not controlled and was on average 315 ppmv = 30 ppmv ($P<0.05$). CO_2 enrichment started on 8 November when the plants were distributed over the two glass-houses.

Plant material and methods

For these experiments with sugar beet (*Beta vulgaris* L.) the variety Univers was used. In each pot one plant was grown. Dates of sowing, emergence and harvest were respectively 12 October, 21 October and 14 February. At harvest the fresh and dry weights (after 24 hours drying at 70°C) were determined for roots, leaves and beets. To determine the root weights, the roots were separated from the sand by carefully washing above a fine mesh.

Subsamples of dried plant tissue from the different plant organs were analysed for N, P and K. N concentrations were determined with the Dumas method, P concentrations colorimetrically and K concentrations with atomic absorption.

Results

Yields

The CO_2 effect on the total dry matter yield was strongest (+24%) in the control treatment without nutrient limitation (NPK) and was significant (Figure 1a; Table 1). In the P and K limited treatments the CO_2 effect was smaller (except the 0.1P treatment) and not significant. In the N limited treatment N deficiency reduced growth considerably and the CO_2 effect on yield became nil.

The CO_2 effect on beet yield in the NPK treatment was considerable (+34%) but not significant (Table 1; Figure 1b). In the P and K limited treatments the CO_2 effect was rather variable, differing from strongly positive to negative, and it was not significant. In the N limited treatments the CO_2 effect was negative but not significant.

For both ambient and doubled atmospheric CO_2 concentration the average effect of a limited nutrient supply on yield has been determined. In comparison to the NPK treatment, limited supply of N, P and K (except 0.3K treatment) resulted in a significant decrease in both total dry matter and beet yield (Table 1).

Dry matter partitioning

In the NPK treatment the root fraction (i.e. root dry weight divided by total dry matter yield) at doubled CO_2 was about 0.8 times the root fraction at ambient CO_2 (Figure 2a). In the 0.1P treatment, an identical decrease in root fraction by CO_2 doubling was found and in the 0.3P treatment the root fraction did not change. In the N limited treatments slight to moderate increases in root fraction by CO_2 doubling occurred and in the K limited treatments moderate to strong increases. The inter-pot variance however (Table 2), was such that in all treatments (except 0.3K) CO_2 effects were not significant Root fraction may also change as a result of limited nutrient

Table 1. The ratio between average dry matter yield at doubled atmospheric CO_2 and that at ambient CO_2 for sugar beet plants grown in pots at different nutrient treatments (with three replicates) and the level of significance of CO_2 and nutrient effect on yield for each nutrient treatment.

	Nutrient treatment[1]						
	NPK	0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Total dry matter							
Ratio $2^*CO_2/1^*CO_2$	1.24	0.97	1.00	1.24	1.11	1.12	0.98
Level of significance							
of CO_2 effect[2]	*			-		-	
of nutrient effect[3]		** n	** n	** n	** n	** n	
Beet dry matter							
Ratio $2^*CO_2/1^*CO_2$	1.34	0.90	0.94	1.46	1.07	1.08	0.82
Level of significance							
of CO_2 effect[2]	-						-
of nutrient effect[3]		** n	** n	** n	* n	** n	-

[1] for information on the different nutrient treatments see section 'Design of the experiment'.

[2] the level of significance is indicated by * for $P<0.05$, ** for $P<0.01$ and – not significant. Significance of CO_2 effect is based on inter-pot variance and of nutrient effect is determined in comparison to NPK treatment.

[3] p indicates a positive nutrient effect on dry matter yield in comparison to NPK treatment and n indicates a negative effect.

supply. In comparison to the NPK treatment, only the 0.1K treatment resulted in a significantly higher root fraction.

The beet fraction (i.e. beet dry matter yield divided by total dry matter yield) at doubled CO_2 was higher than the beet fraction at ambient CO_2 in the NPK and the 0.1P treatment, similar in the 0.3P treatment, and lower in the N and K limited treatments (Figure 2b). The effect of doubled CO_2 on the beet fraction was not significant in all treatments except for 0.3K (Table 2). In comparison to the NPK treatment, the nutrient effect on beet fraction was not significant in all treatments.

Nutrient concentrations

In the treatment with strongly limited N supply (0.1N) the N concentration decreased with CO_2 doubling in roots, dead leaves and green leaves respectively (Table 3), and slightly increased in beets (i.e. from 0.0136 to 0.0117 g N/g dry matter in leaves (green + dead) and from 0.0049 to 0.0050 g N/g dry matter in beets (Figure 3a)). These changes in N concentration by CO_2 doubling were not significant. In the NPK and 0.3N treatments where N supply was respectively not and considerably limiting, the N concentrations were higher than those in the 0.1N treatment (Figure 3a). In these treatments (NPK, 0.3N) N concentrations decreased moderately with CO_2 doubling in most plant organs (Table 3). In the NPK treatment the N concentration decreased mainly because of dilution of N in the larger amount of biomass produced at doubled CO_2, and not by a change in minimum N concentration level.

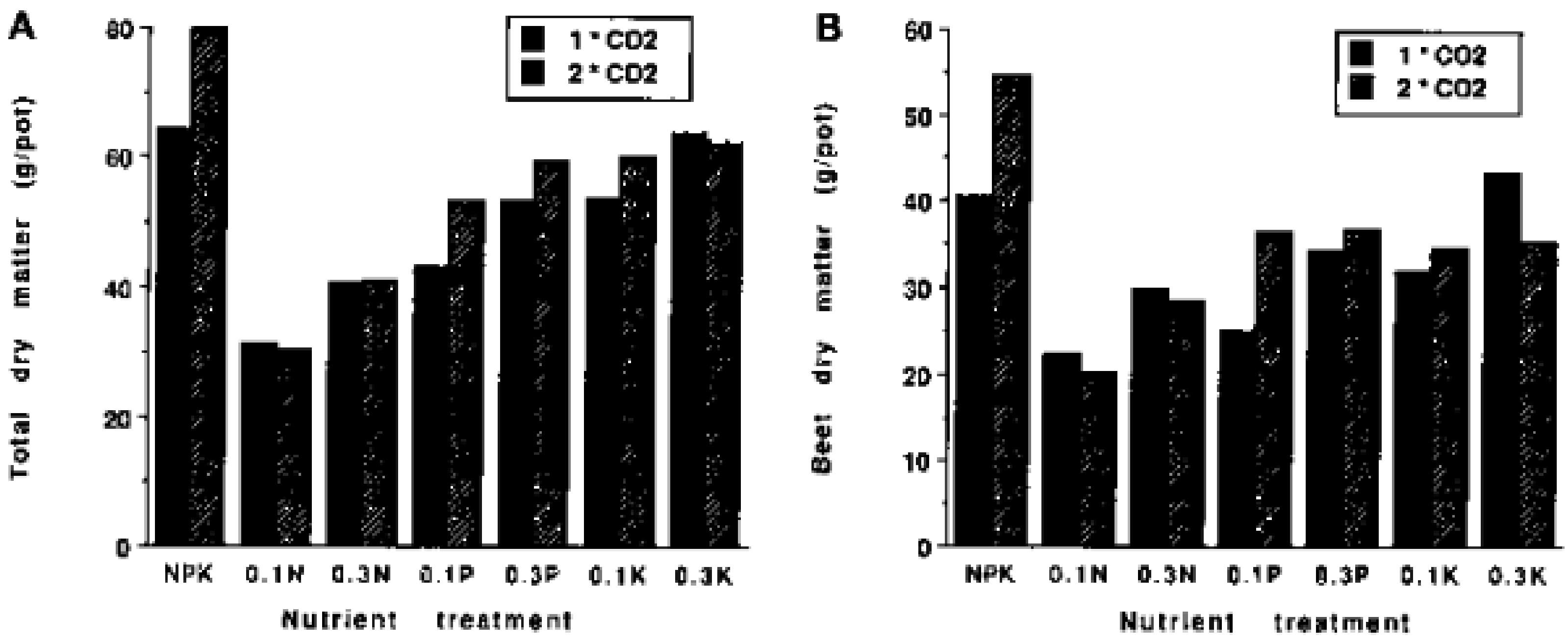

Figure 1. Average values for total dry matter (A) and beet dry matter (B) (g/pot) of sugar beet plants grown in pots at different nutrient treatments (with three replicates) at ambient (filled) and doubled (hatched) atmospheric CO_2 concentrations. For information on the different nutrient treatments see section 'Design of the experiment'.

In the 0.1P treatment the P concentration decreased with CO_2 doubling in roots, beets and green leaves, and slightly increased in dead leaves (Table 3) (i.e. from 0.00058 to 0.00063 g P/g dry matter in leaves (green +dead) and from 0.000373 to

Table 2. The ratio between average dry matter distribution (i.e. root fraction and beet fraction) at doubled atmospheric CO_2 and that at ambient CO_2 for sugar beet plants grown in pots at different nutrient treatments (with three replicates) and the level of significance of CO_2 and nutrient effect on distribution for each nutrient treatment.

	Nutrient treatment[1]						
	NPK	0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Root fraction[2]							
Ratio $2^*CO_2/1^*CO_2$	0.78	1.06	1.14	0.81	1.03	1.16	1.46
Level of significance							
of CO_2 effect[3]							*
of nutrient effect[4]						* p	
Beet fraction[2]							
Ratio $2^*CO_2/1^*CO_2$	1.12	0.92	0.93	1.17	0.99	0.96	0.83
Level of significance							
of CO_2 effect[3]							*
of nutrient effect[4]							

[1] for information on the different nutrient treatments see section 'Design of the experiment'.

[2] root fraction is dry matter in roots divided by total dry matter; beet fraction is dry matter in beets divided by total dry matter.

[3] the level of significance is indicated by * for $P<0.05$ and for not significant. Significance of CO_2 effect is based on inter-pot variance and of nutrient effect is determined in comparison to NPK treatment.

[4] p indicates a positive nutrient effect on root and beet fraction in comparison to NPK treatment and n indicates a negative effect.

Table 3. The ratio between average nutrient concentration (N, P or K) at doubled atmospheric CO_2 and that at ambient CO_2 for sugar beet plants grown in pots at different nutrient treatments (with three replicates) and the level of significance of CO_2 effect on nutrient concentration for each nutrient treatment.

	Nutrient treatment[1]								
	NPK			0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Nutrient	N	P	K	N	N	P	P	K	K
Roots									
Ratio $2*CO_2/1*CO_2$	1.08	1.15	1.15	0.95	0.85	0.89	0.83	0.85	0.81
Signif. of CO_2 effect[2]					–		–		
Beets									
Ratio $2*CO_2/1*CO_2$	0.89	0.98	0.94	1.03	1.08	0.92	1.03	0.99	1.04
Signif. of CO_2 effect[2]								–	
Leaves dead									
Ratio $2*CO_2/1*CO_2$	0.76	0.81	1.34	0.89	0.78	1.04	0.71	1.12	0.95
Signif. of CO_2 effect[2]		*					*		
Leaves green									
Ratio $2*CO_2/1*CO_2$	0.78	0.89	0.85	0.86	0.96	0.98	0.82	0.79	0.70
Signif. of CO_2 effect[2]								–	

[1] for information on the different nutrient treatments see section 'Design of the experiment'.

[2] the level of significance is indicated by * for $P<0.05$ and for not significant. Significance of CO_2 effect is based on inter-pot variance.

0.000345 g P/g dry matter in beets (Figure 4a)). These changes in P concentration by CO_2 doubling were not significant. In the NPK and 0.3P treatments where P was respectively not and moderately limiting, the P concentrations were higher than those in the 0.1P treatment (Figure 4a). In these treatments (NPK, 0.3P) P concentrations decreased moderately with CO_2 doubling in leaves, but in beets P concentrations remained unchanged. This decrease in P concentration in the leaves was largely the result of dilution of P in the larger amount of biomass produced at doubled CO_2.

In the 0.1K treatment the K concentration decreased with CO_2 doubling in roots, beets and green leaves and increased in dead leaves (Table 3) (i.e. from 0.00769 to 0.00642 g K/g dry matter in leaves (green + dead) and from 0.00426 to 0.00420 g K/g dry matter in beets (Figure 5a)). These changes in K concentration by CO_2 doubling were not significant. In the NPK and 0.3K treatments the K concentrations in beets were almost identical to those in the 0.1K treatment and almost did not change with CO_2 doubling (Figure 5a). K concentrations in leaves in the NPK and 0.3K treatments were much higher than those in the 0.1K treatment and moderately decreased with CO_2 doubling. In the NPK treatment this decrease in K concentration with CO_2 doubling was mainly caused by dilution of K in the larger amount of biomass.

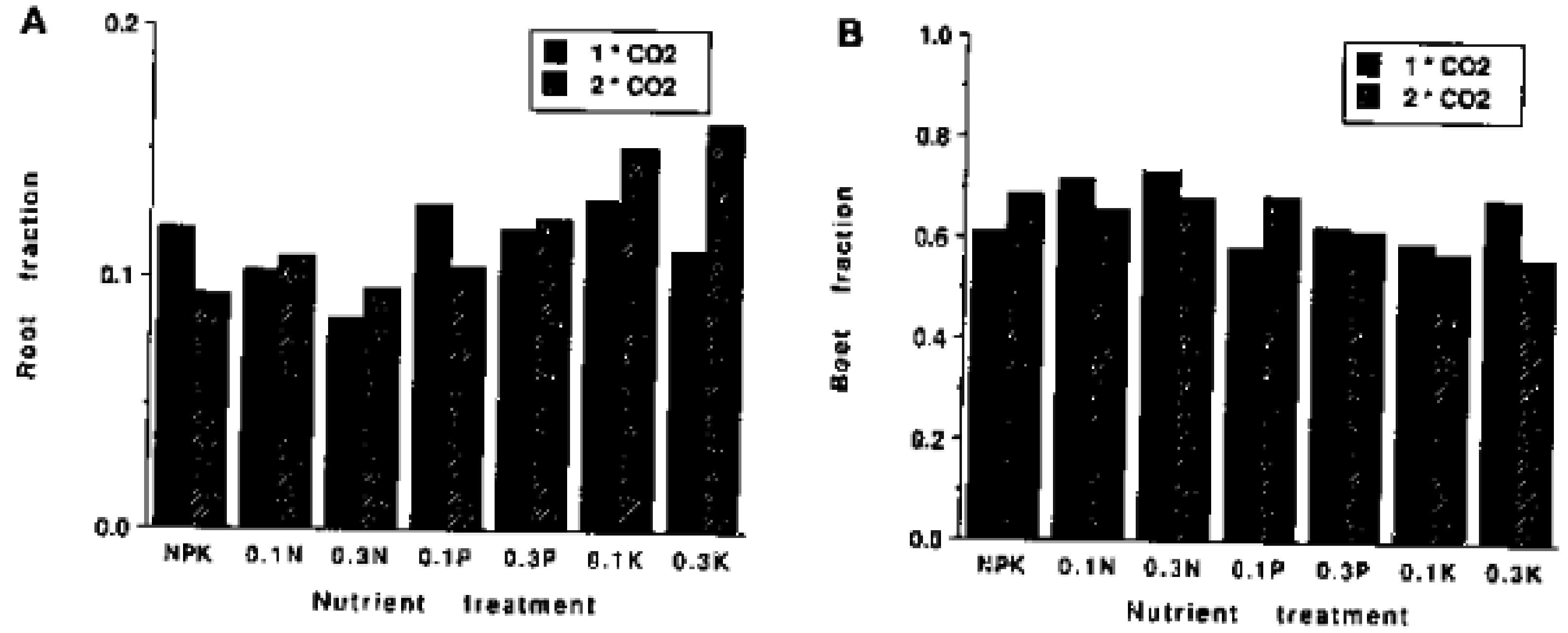

Figure 2. Average values for root fraction (A) and beet fraction (B) of sugar beet plants grown in pots at different nutrient treatments (with three replicates) at ambient (filled) and doubled (hatched) atmospheric CO_2 concentrations. For information on the different nutrient treatments see section 'Design of the experiment'.

Yield-nutrient uptake ratios

The ratio between total yield (without roots) and N uptake did not change with CO_2 doubling if N supply was strongly or moderately limiting (0.1N or 0.3N; Figure 3b). In the NPK treatment where N supply was not limiting for crop growth, the ratio between both total yield (without roots) and beet yield and the N uptake was relatively low and increased with CO_2 doubling. The change in ratio between beet yield and N uptake with CO_2 doubling for the 0.1N and 0.3N treatments was slightly negative, which can be explained from the decrease in beet fraction with CO_2 doubling (Table 2). These changes in yield-N uptake ratios by CO_2 doubling were not significant.

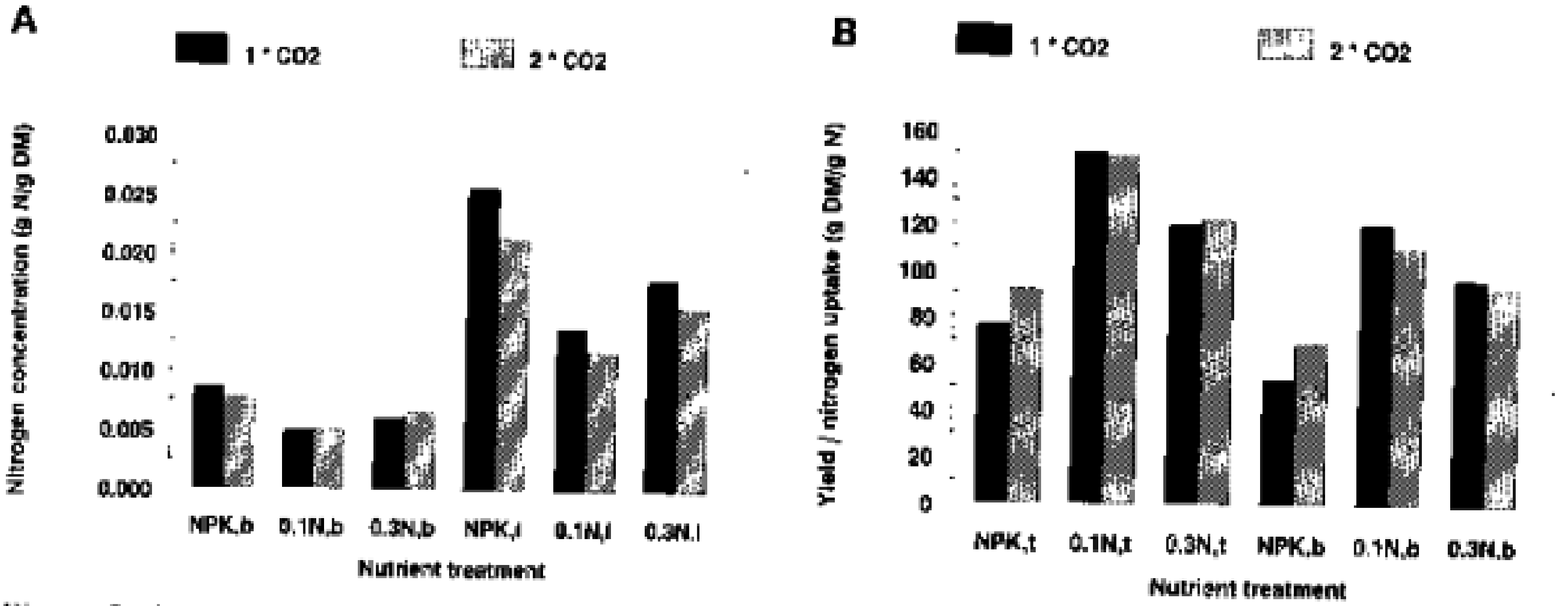

Figure 3. Average values for (A) N concentrations in beets (NPK,b etc.) and leaves (NPK,l etc.) and for (B) total yield (without roots) N uptake (NPK,t etc.) and beet yield N uptake ratios (NPK,b etc.) of sugar beet plants grown in pots at different nutrient treatments (with three replicates) at ambient (filled) and doubled (hatched) atmospheric CO_2 concentrations (N uptake in ratios applies to total plant material without roots). For information on the different nutrient treatments see section 'Design of the experiment'.

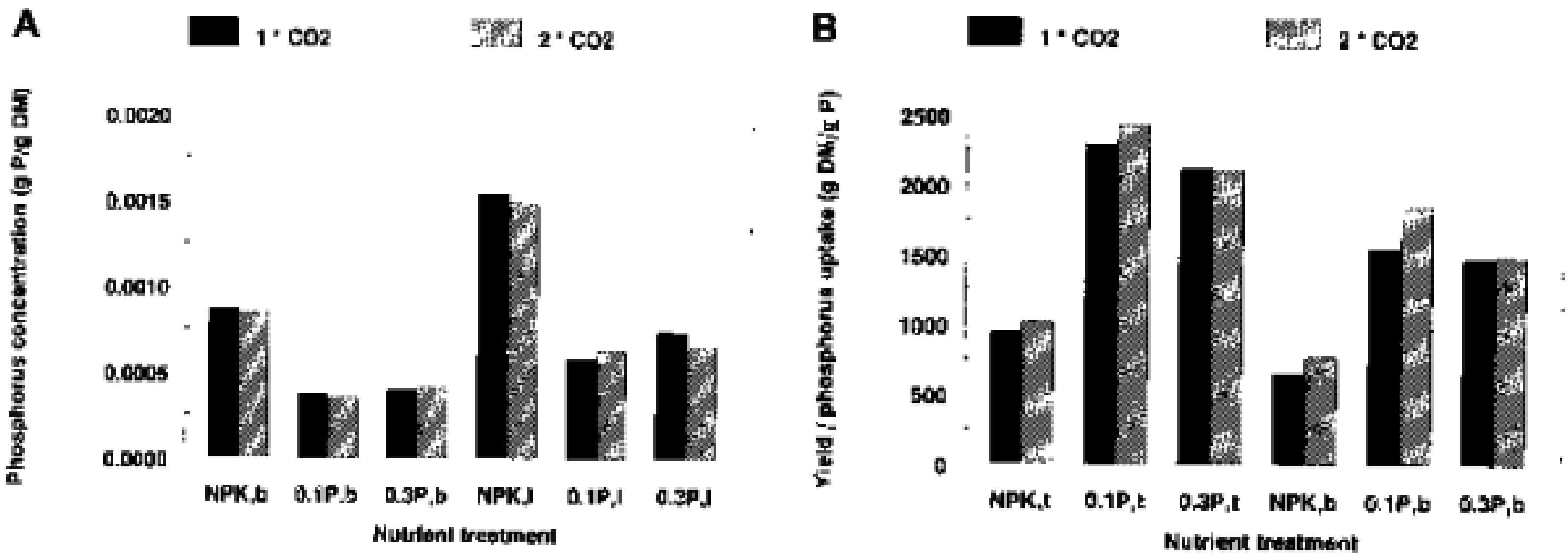

Figure 4. Average values for (A) P concentrations in beets (NPK,b etc.) and leaves (NPK,l etc.) and for (B) total yield (without roots) - P uptake (NPK,t etc.) and beet yield - P uptake ratios (NPK,b etc.) of sugar beet plants grown in pots at different nutrient treatments (with three replicates) at ambient (filled) and doubled (hatched) atmospheric CO_2 concentrations (P uptake in ratios applies to total plant material without roots). For information on the different nutrient treatments see section 'Design of the experiment'.

The ratio between total yield (without roots) and P uptake nil to slightly increased (up to 8%) with CO_2 doubling (Figure 4b), whether P was strongly (0.1P), slightly (0.3P) or not limiting (NPK). The change in ratio between beet yield and P uptake with CO_2 doubling for the 0.1P and NPK treatments was more positive than the change in ratio between total yield and P uptake. This can be explained from the increase in beet fraction with CO_2 doubling (Table 2). These changes in yield-P uptake ratios by CO_2 doubling were not significant.

The ratio between total yield without roots and K uptake slightly increased (+ 8%) with CO_2 doubling (Figure 5b) if K was limiting (0.1K). In the NPK treatment where K supply was not limiting for crop growth, the ratio between total above-ground yield and K uptake was lower than that in the 0.1K treatment and increased consider-

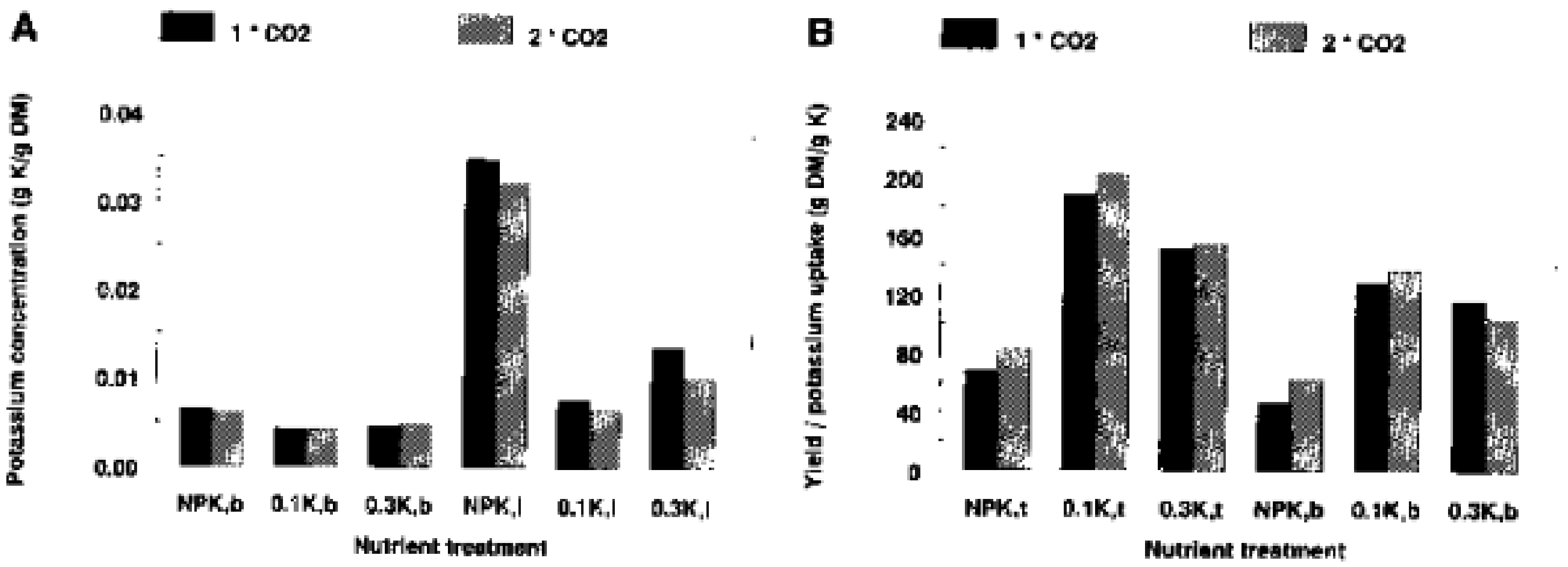

Figure 5. Average values for (A) K concentrations in beets (NPK,b etc.) and leaves (NPK,l etc.) and for (B) total yield (without roots) - K uptake (NPK,t etc.) and beet yield - K uptake ratios (NPK,b etc.) of sugar beet plants grown in pots at different nutrient treatments (with three replicates) at ambient (filled) and doubled (hatched) atmospheric CO_2 concentrations (K uptake in ratios applies to total plant material without roots). For information on the different nutrient treatments see section 'Design of the experiment'.

ably with CO_2 doubling. The changes in ratio between beet yield and K uptake with CO_2 doubling for the 0.1K, 0.3K and NPK treatments were slightly different from those between total yield and K uptake. This was caused by changes in beet fraction with CO_2 doubling (Table 2). These changes in yield-K uptake ratios by CO_2 doubling were not significant.

Discussion

In the control (NPK) treatment without nutrient limitation the ratio between the total yield at doubled CO_2 and that at ambient CO_2 (i.e. ratio $2*CO_2/1*CO_2$) was 1.24 . In the P and K limited treatment the CO_2 effect was smaller and not significant and in the N limited treatment the CO_2 effect was absent. For the beet yield the CO_2 effect was also highest in the control. For a low supply of the nutrient that most strongly limits crop growth, i.e. N for the growth of sugar beet, the CO_2 effect was absent. For spring wheat this was also found but then for a low supply of P (Wolf (1996a): 0.1P treatment). This might indicate a general rule that the CO_2 effect disappears with increasing shortage of the nutrient which is most limiting for crop growth.

In the control the CO_2 effect was rather small compared to that for spring wheat (Wolf (1996a): ratio $2*CO_2/1*CO_2 = 1.7$). This small CO_2 effect does not agree with results from pot experiments with sugar beet in growth chambers by Sionit *et al.* (1982) and Ford & Thorne (1967). They found CO_2 effects on total yield for sugar beet and grain crops such as barley and wheat to be approximately similar. Photosynthetic capacity of plants that are grown in small pots, may be reduced. This leads to a reduction of the CO_2 effect on crop growth, as shown by Arp (1991). Based on his data (mainly reduction of CO_2 effect in pots with volumes below 12 L) and the pot size used in this experiment, it can be assumed that the pot size has not limited the CO_2 effect.

In the NPK treatment the root fraction decreased with CO_2 doubling. In a situation with severe nutrient limitation (N limited treatments) however, the root fraction increased and in a situation with moderate nutrient limitation (P and K limited treatments) the root fractions both increased and slightly decreased. These results were not significant. According to a survey of experimental information on the direct effect of increasing CO_2 for crop growth and dry matter partitioning (Cure, 1985: Stulen & Den Hertog, 1993), increasing CO_2 may cause either an increase or a decrease in the root/shoot ratio of various crops (no data for sugar beet). The decreases and increases were generally found in situations with optimal and limiting nutrient supply, respectively. This corresponds well with results found here for the control and the N limited treatments. Such difference in change in root/shoot ratio between optimal and nutrient limited conditions can be explained as follows. If yields increase with CO_2 doubling, nutrient shortage becomes more severe in the nutrient limited treatments. This increasing limitation of the nutrient supply for crop growth generally results in a higher root/shoot ratio (Brouwer, 1983). In a situation with optimal nutrient supply, however, CO_2 doubling results mainly in a larger shoot and thus in a lower root/shoot ratio.

Beet fraction slightly increased with CO_2 doubling in the NPK treatment and nil to slightly decreased in the nutrient limited treatments. Slight increases that became nil in the nutrient limited treatments, were found for wheat, both in the survey of experimental information by Cure (1985) and in these pot experiments (Wolf, 1996a). For sugar beet no data are available from the literature. CO_2 doubling may result in a lower beet fraction if nutrient supply is strongly limiting and the larger amount of vegetative tissue produced at doubled CO_2 retains a larger amount of nutrients and results in less growth of storage organs (Van Kraalingen, 1990).

In situations where nutrient supply is limiting crop growth, nutrient concentrations in plant tissue may gradually decrease during the growth cycle and at harvest, nutrients appear to be diluted to a plant-specific minimum concentration level. For a large number of fertilizer experiments Van Keulen & Van Heemst (1982) and Van Keulen (1986) have analysed relations between yield and nutrient uptake. From these relations they have derived minimum concentration levels for a large number of crop species. For a sugar beet crop the minimum concentrations are as follows: 0.0060 g N/g dry matter in beets, 0.0180 g N/g dry matter in leaves, 0.0008 g P/g dry matter in beets, 0.0015 g P/g dry matter in leaves, 0.0060 g K/g dry matter in beets, 0.0180 g K/g dry matter in leaves (Van Diepen *et al.*, 1988).

These minimum concentrations might change with CO_2 doubling, as has been observed for a large number of crops (Goudriaan & De Ruiter, 1983; Overdieck, 1993; Wolf, 1996a, b). In the literature several explanations for such changes in nutrient concentration are given. First, elevated atmospheric CO_2 generally causes an increase in dry matter production which may result in dilution of nutrient concentrations in plant tissue (Overdieck, 1993). Second, elevated atmospheric CO_2 may give a higher efficiency of carboxylating enzymes. As a large fraction of leaf N is contained in these enzymes, CO_2 enrichment may result in lower enzyme and thus N concentrations in leaves (Owensby et al., 1993; Wong, 1979). Third, elevated CO_2 may result in a changed partitioning of assimilates to plant organs and a changed plant composition. This may be due to a changed degree of nutrient or water deficiency or temperature stress. For example, the harvest index of a wheat crop may decrease with CO_2 enrichment and a low N supply (Van Kraalingen, 1990). In this experiment, however, dry matter partitioning did not change significantly with CO_2 doubling. At last, elevated CO_2 may give a suppression of the photorespiratory cycle and this may result in a reduction of N requirements of leaves (Conroy, 1992).

When N supply was strongly limiting for crop growth (0.1N treatment), the N concentrations were at the minimum concentration level reported above. CO_2 doubling gave a decrease in minimum N concentration by 14% in leaves and almost no change in minimum N concentration in beets. This resulted in a decrease with CO_2 doubling in the ratio between respectively total above-ground yield and beet yield and the N uptake in above-ground yield of 0% and 8%, mainly as a result of the decreasing beet fraction.

When P was strongly limiting for crop growth (0.1P treatment), the P concentrations were at the minimum concentration level reported above. CO_2 doubling gave a decrease in minimum P concentration by 8% in beets and an increase by 9% in leaves (mainly caused by lower fraction of dead leaves at doubled CO_2). This resulted in an increase with CO_2 doubling in the ratio between both total above-ground and beet yield and P uptake in above-ground yield by about 5% (however, for beet yield the increase in this ratio would be much larger if the increase in beet fraction for the 0.1P treatment (Table 2) was taken into account).

When K was limiting for crop growth (0.1K treatment), the K concentrations were at the minimum concentration level as reported above. CO_2 doubling gave a decrease in minimum K concentration by about 16% in leaves and no change in beets. This resulted in an increase with CO_2 doubling in the ratio between both total above-ground and beet yield and K uptake in above-ground yield by about 8%.

Literature data indicate that with CO_2 enrichment minimum nutrient concentrations in plant tissue may decrease, in particular for N and K, and only slightly or not at all for P (Conroy, 1992; Cure *et al.*, 1988a, b; Goudriaan & De Ruiter, 1983; Overdieck, 1993). This corresponds well with results mentioned above for leaves. In beets CO_2 doubling gave different changes in nutrient concentration, such as a small decrease in minimum P concentration and almost no changes in minimum N and K concentration. From these changes in nutrient concentrations in beets and leaves it can be concluded that with CO_2 doubling (and assuming that the beet fraction remains constant) fertilizer nutrient requirements to attain a certain yield level slightly decreases and that beet yields in situations where the nutrient supply mainly limits crop growth, slightly increases.

The main conclusions from this study are:

1) Doubling of atmospheric CO_2 results in a moderate increase in total yield (+24%) and beet yield (+34%) if the nutrient supply is optimal. This increase in yield is small compared to that for spring wheat.
2) The CO_2 effect on total and beet yield disappears with increasing limitation of nutrient supply for crop growth, in particular severe N deficiency.
3) Doubling of atmospheric CO_2 did not result in significant changes in the minimum nutrient concentrations in leaves and beets.

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