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Effects of nutrient (NPK) supply on faba bean 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 for maximal growth. 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 for faba bean, pot experiments have been carried out in two glass houses at ambient and doubled CO_2 concentration. Bean plants were grown at different supplies of N, P or K.

Doubling of atmospheric CO_2 resulted in a strong increase (+100%) in total yield. This CO_2 effect disappeared rapidly with increasing nitrogen, phosphorus or potassium shortage. Doubling of atmospheric CO_2 resulted in no change in minimum nitrogen concentration and a nil to slight decrease in minimum phosphorus concentration in crop residues. Nutrient requirements to attain a certain yield level might change with a future increase in atmospheric CO_2. However, such conclusions cannot yet be drawn because nutrient concentrations in seeds were not available.

Keywords: CO_2 enrichment, faba bean, K use efficiency, N use efficiency, P use efficiency

Introduction

Increasing concentrations of atmospheric CO_2 generally increase the rate of photosynthesis and suppress photorespiration of most (i.e. C3) plants (Acock, 1990; Goudriaan & Unsworth, 1990). This generally stimulates crop growth and leads to a much higher level of plant production (Cure, 1985; Cure & Acock, 1986; Kimball, 1983; Strain & Cure, 1994). Simultaneously dry matter allocation may change at increasing CO_2 (Stulen & Den Hertog, 1993) which may affect the amount of harvestable crop parts.

Growth of natural vegetations and of arable crops in large parts of the world is mainly limited by the availability of nutrients. In such situations 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 (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. Further dilution of the limiting nutrient below the minimum concentration level appears to be impossible. If this minimum concentration level and hence the maximum yield-nutrient uptake ratio of crops changes with an increase in atmospheric CO_2, this could affect crop growth and the attainable level of production (Van Keulen & Van Heemst, 1982), soil organic matter decomposition and nutrient cycling (Kuikman & Gorissen, 1993; Van de Geijn & Van Veen, 1993; Zak *et al.*, 1993).

The effects of atmospheric CO_2 on crop growth and dry matter allocation may be different, if severe nutrient shortage occurs than when nutrient supply is optimal (Idso & Idso, 1994). To study these effects of increased atmospheric CO_2 on crop growth and their interaction with 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 faba bean the results are reported here. Results for the other crops are reported separately (Wolf, 1996).

Materials and methods

Design of the experiment

The plants were grown in two similar glass houses, differing only in CO_2 concentration (315 and 695 ppmv). In each glass house all plant species 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 a sound statistical analysis of the CO_2 effect more glass houses would be required to assess the variability between the glass houses. In this experiment the variability between the CO_2 plus nutrient treatments was used to determine the significance of the CO_2 effect. This may have influenced the significance of differences. 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 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.

Soil and nutrient treatments

The plants were grown on coarse sand with a low water holding capacity and an almost nil organic matter content 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 in the glass house with artificial light was set at 16 hours. The total amount of added radiation (during 16 day hours) was determined to be 3.1 MJ m^{-2} d^{-1} (± 0.5 MJ m^{-2} d^{-1} for $P<0.05$). The temperature was set at 20 °C during the days and 15 °C during the 8 hours of night time, 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 doubled CO_2 glass house was on average 695 ppmv (± 60 ppmv for $P<0.05$). 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 for $P<0.05$). CO_2 enrichment began on 8 November when the plants were distributed over the two glass houses.

Plant material and methods

For these experiments with faba bean (*Vicia Faba* L.) the variety Minica was used. In each pot one plant was grown. Dates of sowing, emergence, start of flowering and harvest were respectively 12 October, 19 October, 20 November and 25 January. At harvest the fresh and dry weights (after 24 hours in an oven at 70 °C) were determined for roots, leaves, stems, pods and seeds. To determine the root weights, the roots were separated from the sand by carefully washing above a fine mesh. Leaf area of the harvested plants was measured. At three intermediate dates leaf area was also determined non-destructively.

Subsamples of dried plant tissue from the different plant organs were analysed for N, P and K concentration. 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 in the control treatment without nutrient limitation (NPK) and was very significant. The ratio between the yield at doubled and that at ambient CO_2 (i.e. ratio $2^*CO_2/1^*CO_2$) was 2.0 (Figure 1a; Table 1). In the 0.3N and 0.3K treatments where growth was reduced only to a limited extent by nutrient shortage, the ratio $2^*CO_2/1^*CO_2$ was 1.8 (significant effect) and 1.6 (non-significant because of large yield variation) respectively. In the other nutrient treatments the CO_2 effect on yield was nil.

The CO_2 effect on the total above-ground yield was also highest in the NPK treatment with a ratio $2^*CO_2/1^*CO_2$ of 2.0 (Table 1; Figure 1b). In the 0.3N and 0.3K treatments the ratio $2^*CO_2/1^*CO_2$ was 1.8 and in the other treatments the CO_2 effect was nil.

Table 1. The ratio between average dry matter yield at doubled atmospheric CO_2 and that at ambient CO_2 for faba bean 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 $2^*CO_2/1^*CO_2$	1.97	0.91	1.82	1.00	0.90	1.08	1.64
Level of significance							
– of CO_2 effect[2]	**	–	*	–	–	–	–
– of nutrient effect[3]	–	** n	* n	** n	** n	** n	** n
Total above-ground dry matter							
Ratio $2^*CO_2/1^*CO_2$	2.01	0.98	1.79	0.88	1.00	1.02	1.83
Level of significance							
– of CO_2 effect[2]	**	–	*	–	–	–	–
– of nutrient effect[3]	–	** n	* n	** n	** n	** n	** n

[1] for information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

[2] the level of significance is indicated by * for $P<0.05$, ** for $P<0.01$ 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.

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

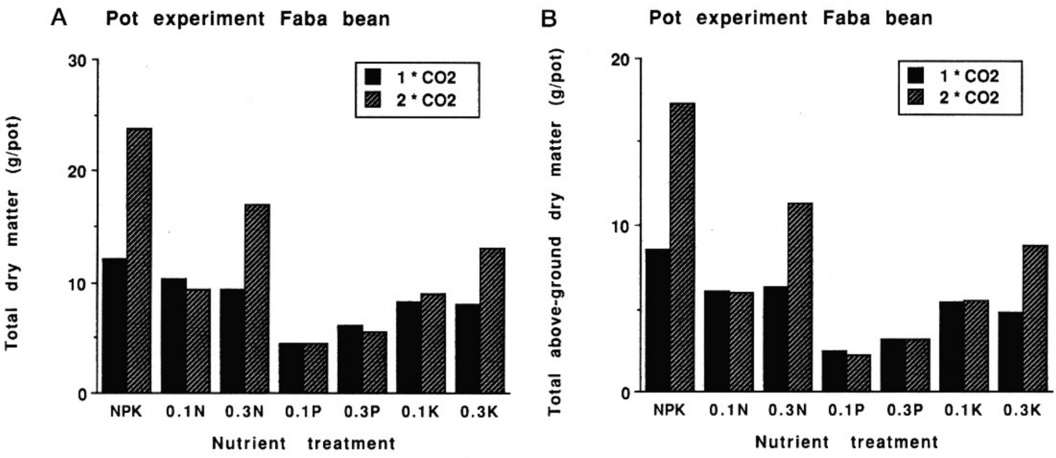

Figure 1. Average values for total dry matter (A) and total above-ground dry matter (B) (g/pot) of faba bean plants grown in pots at different nutrient treatments (with three replicates) at ambient (closed) and doubled (striped) atmospheric CO_2 concentrations. For information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

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

Dry matter partitioning

In the NPK and 0.3N treatments with nil or slight nutrient limitation, the root/shoot ratio did not change with CO_2 doubling (Figure 2). In the other treatments root/shoot ratios increased or decreased with CO_2 doubling, but these changes did not show a clear relation with the limiting nutrient. Root/shoot ratio clearly changed as a result of limited nutrient supply (Table 2). In comparison to the NPK treatment, both P limited and K limited treatments and also the 0.1N treatment caused a significant increase in root/shoot ratio. P deficiency resulted in the highest root/shoot ratio (Figure 2).

Seed yields were very low and variable. Hence, the CO_2 effect on seed yield and seed fraction could not be analysed.

Nutrient concentrations

The concentrations of N, P and K were determined in plant tissue from the different plant organs at final harvest. In the treatment with strongly limiting N supply (0.1N) the N concentration decreased with CO_2 doubling by 7% in roots and 3% in leaves, and increased by 11% in stems. These CO_2 effects were not significant (Table 3). This resulted in an increase in N concentration in straw with CO_2 doubling (Figure

Table 2. The ratio between root-shoot ratio at doubled atmospheric CO_2 and that at ambient CO_2 for faba bean plants grown in pots at different nutrient treatments (with three replicates) and the level of significance of CO_2 and nutrient effect on root-shoot ratio for each nutrient treatment.

	Nutrient treatment[1]						
	NPK	0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Ratio $2*CO_2/1*CO_2$	0.95	0.84	1.06	1.30	0.81	1.20	0.77
Level of significance							
– of CO_2 effect[2]	–	–	–	*	–	–	–
– of nutrient effect[3]	–	**	–	**	**	*	**

[1] for information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

[2] the level of significance is indicated by * for $P<0.05$, ** for $P<0.01$ 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.

[3] p indicates a positive nutrient effect on root-shoot ratio in comparison to NPK treatment and n indicates a negative effect.

3a). In the NPK and 0.3N treatments where N supply was respectively not and slightly limiting for crop growth, the N concentrations decreased with CO_2 doubling in straw, to a less extent in roots and nil in seeds (Figure 3a; Table 3). In these treatments N concentrations mainly decreased 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.

In the 0.1P treatment the P concentration decreased with CO_2 doubling by 6% in roots and 23% in leaves and increased by 11% in stems (Table 3), but these changes were not significant. This resulted in a small decrease in P concentration in straw with CO_2 doubling (Figure 4a). In the NPK and 0.3P treatments where P was respectively not and considerably limiting for crop growth, the P concentrations were only

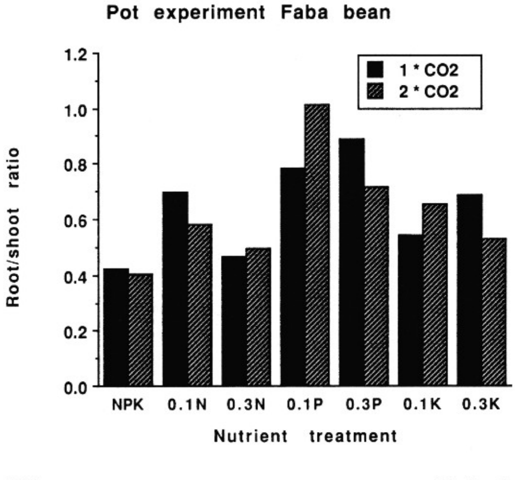

Figure 2. Average values for root/shoot ratio of faba bean plants grown in pots at different nutrient treatments (with three replicates) at ambient (closed) and doubled (striped) atmospheric CO_2 concentrations. For information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

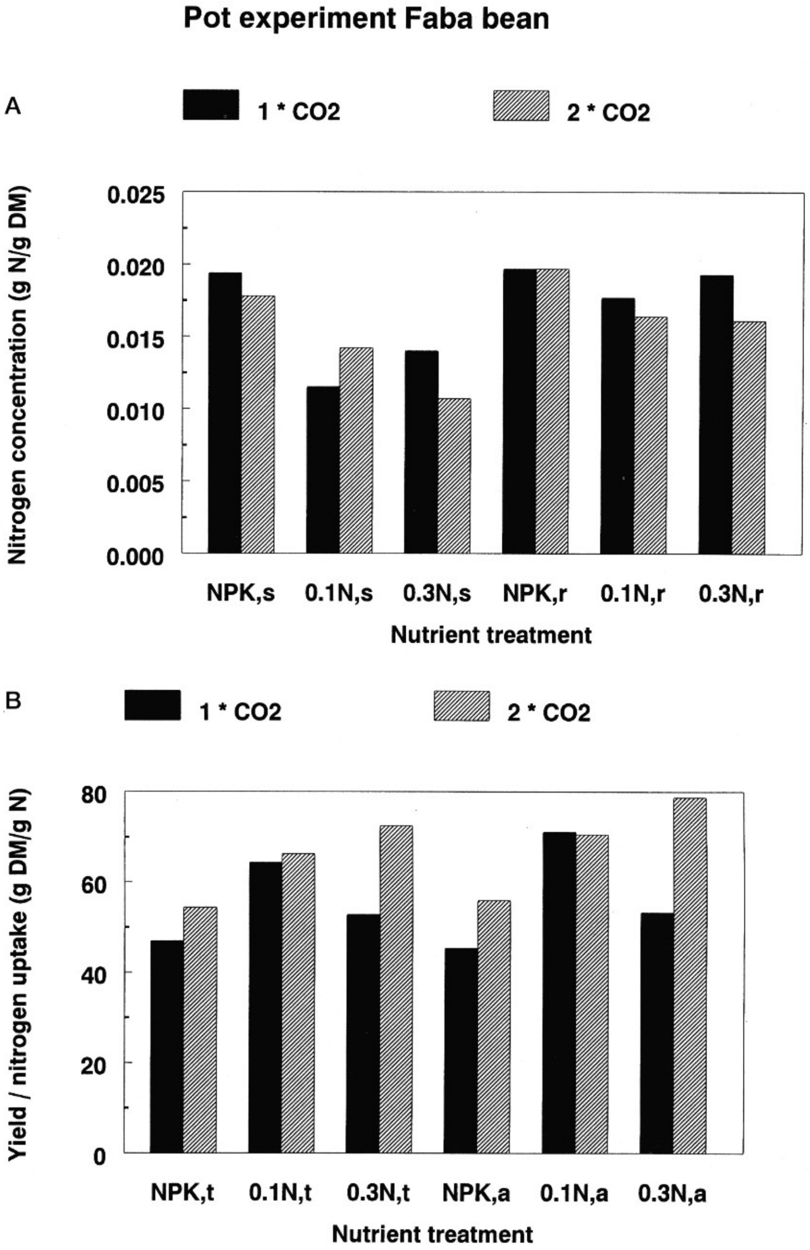

Figure 3. Average values for (A) N concentrations in straw (NPK,s etc.) and roots (NPK,r etc.) and for (B) total yield – N uptake (in total plant material) ratio (NPK,t etc.) and total above-ground yield – N uptake (in total above-ground plant material) ratio (NPK,a etc.) of faba bean plants grown in pots at different nutrient treatments (with three replicates) at ambient (closed) and doubled (striped) atmospheric CO_2 concentrations. For information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

Table 3. The ratio between average nutrient concentration (N, P or K) at doubled atmospheric CO_2 and that at ambient CO_2 for faba bean 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 $2*CO_2/1*CO_2$	1.00	1.22	0.66	0.93	0.83	0.94	1.04	1.40	1.49
Significance of CO_2 effect[2]	–	–	*	–	–	–	–	–	–
Leaves									
Ratio $2*CO_2/1*CO_2$	0.89	1.04	0.58	0.97	0.66	0.77	1.13	0.87	0.62
Significance of CO_2 effect[2]	–	–	*	–	–	–	–	–	*
Stems									
Ratio $2*CO_2/1*CO_2$	0.91	1.41	0.74	1.11	0.72	1.11	1.03	0.92	0.68
Significance of CO_2 effect[2]	–	*	*	–	–	–	–	–	*
Pods									
Ratio $2*CO_2/1*CO_2$	1.21	1.46	1.17	–	0.90	–	–	0.81	–
Significance of CO_2 effect[3]									
Seeds									
Ratio $2*CO_2/1*CO_2$	0.96	0.62	0.92	–	1.01	–	–	1.13	–
Significance of CO_2 effect[3]									

[1] for information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

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

[3] no statistical analysis because of lack of data.

slightly higher than those in the 0.1P treatment. P concentrations moderately increased with CO_2 doubling in the NPK treatment and almost did not change in the 0,3P treatment (Table 3).

In the 0.1K treatment the K concentration increased with CO_2 doubling by 40% and 13% in roots and seeds respectively and decreased by 13%, 8% and 19% in leaves, stems and pods respectively (Table 3). This resulted in a small decrease in K concentration in straw (Figure 5a). In the NPK and 0.3K treatments where K supply was respectively not and moderately limiting for crop growth, the K concentration in straw was clearly higher than that in the 0.1K treatment and decreased significantly with CO_2 doubling (Table 3; Figure 5a), mainly because of dilution of K in the larger amount of biomass.

Yield-nutrient uptake ratios

The ratio between total yield and N uptake (in total plant material) and the ratio between total above-ground yield and N uptake (in total above-ground plant material)

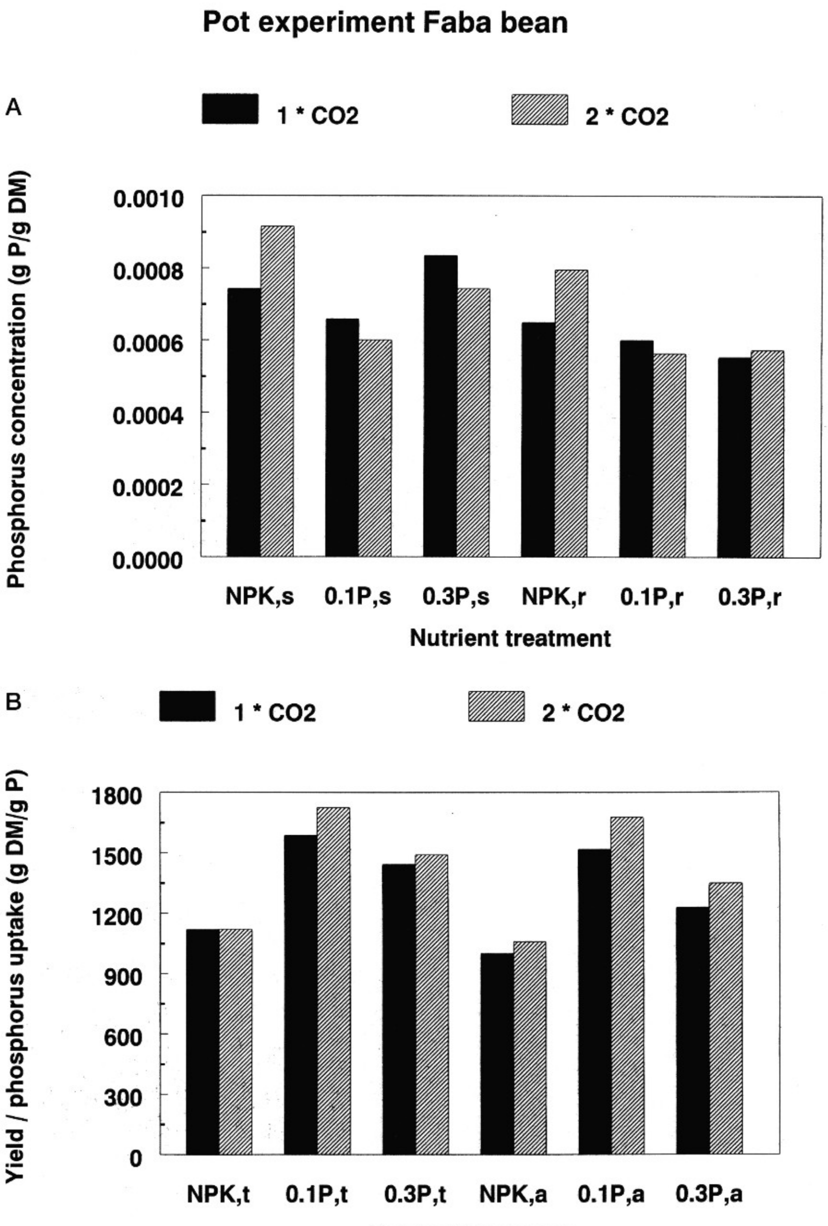

Figure 4. Average values for (A) P concentrations in straw (NPK,s etc.) and roots (NPK,r etc.) and for (B) total yield – P uptake (in total plant material) ratio (NPK,t etc.) and total above-ground yield – P uptake (in total above-ground plant material) ratio (NPK,a etc.) of faba bean plants grown in pots at different nutrient treatments (with three replicates) at ambient (closed) and doubled (striped) atmospheric CO_2 concentrations. For information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

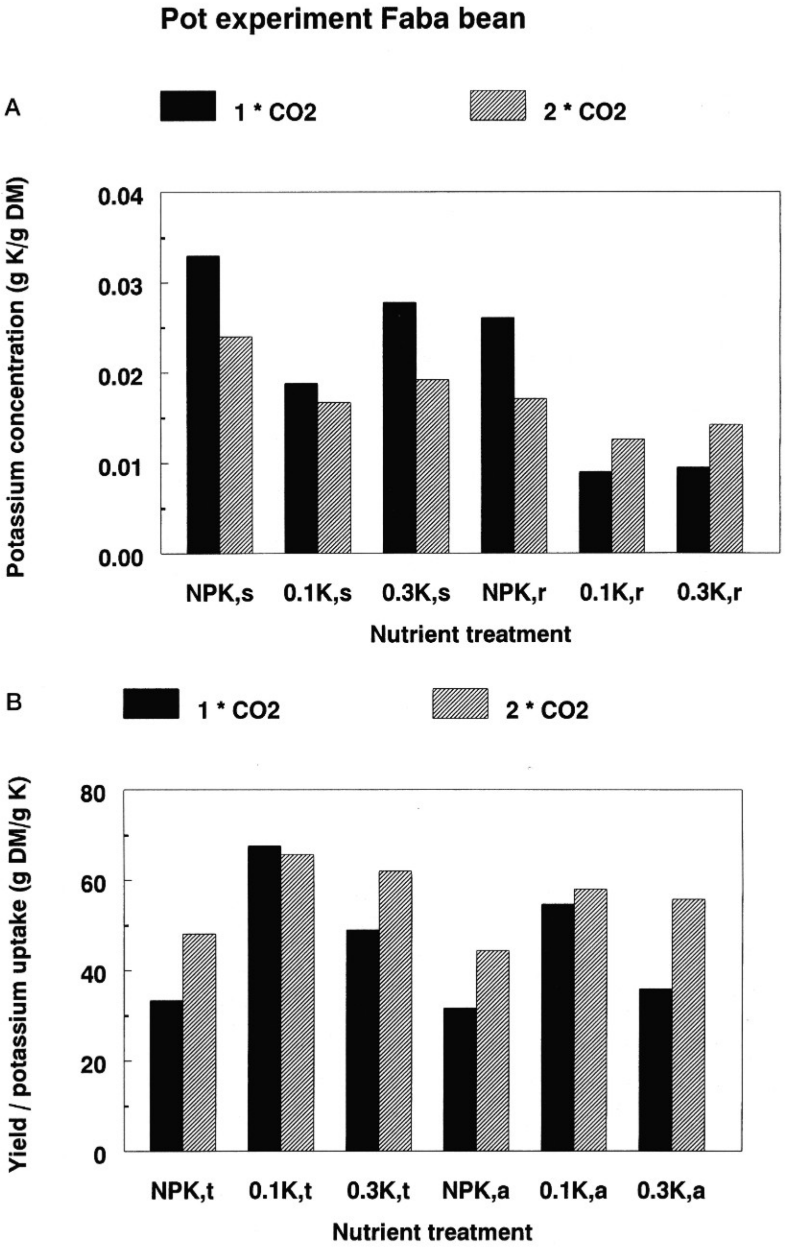

Figure 5. Average values for (A) K concentrations in straw (NPK,s etc.) and roots (NPK,r etc.) and for (B) total yield – K uptake (in total plant material) ratio (NPK,t etc.) and total above-ground yield – K uptake (in total above-ground plant material) ratio (NPK,a etc.) of faba bean plants grown in pots at different nutrient treatments (with three replicates) at ambient (closed) and doubled (striped) atmospheric CO_2 concentrations. For information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

Table 4. The ratio between average yield – nutrient (N, P or K) uptake ratio at doubled atmospheric CO_2 and that at ambient CO_2 for faba bean plants grown in pots at different nutrient treatments (with three replicates) and the level of significance of CO_2 effect on yield – nutrient uptake ratio 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
Total yield / nutrient uptake ratio A[2]									
Ratio 2*CO_2/1*CO_2	1.16	1.00	1.44	1.03	1.37	1.09	1.03	0.97	1.27
Significance of CO_2 effect[3]	*	–	–	–	**	–	–	–	–
Total yield / nutrient uptake ratio B[2]									
Ratio 2*CO_2/1*CO_2	1.20	1.05	1.37	0.92	1.51	1.24	1.00	1.13	1.39
Significance of CO_2 effect[3]	–	–	–	–	**	*	–	–	*
Total above-ground yield / nutrient uptake ratio A[2]									
Ratio 2*CO_2/1*CO_2	1.18	1.01	1.47	1.11	1.35	0.97	1.13	0.91	1.42
Significance of CO_2 effect[3]	–	–	–	–	**	–	–	–	–
Total above-ground yield / nutrient uptake ratio B[2]									
Ratio 2*CO_2/1*CO_2	1.23	1.06	1.40	0.99	1.48	1.10	1.10	1.06	1.55
Significance of CO_2 effect[3]	–	–	–	–	**	–	–	–	*

[1] for information on the different nutrient treatments the reader is referred to section 'Design of the experiment'.

[2] A : ratio calculated for nutrient uptake in total plant material; B : ratio calculated for nutrient uptake in total above-ground plant material.

[3] the level of significance is indicated by * for $P<0.05$, ** for $P<0.01$ and – for not significant. Significance of CO_2 effect is based on inter-pot variance.

did not change with CO_2 doubling if N supply was strongly limiting (0.1N) (Figure 3b; Table 4). In the NPK and 0.3N treatments the ratio between yield and N uptake was lower than the ratio in the 0.1N treatment (Figure 3b) and increased significantly with CO_2 doubling (Table 4).

The ratio between total yield and P uptake (in total plant material) and the ratio between total above-ground yield and P uptake (in total above-ground plant material) moderately increased (+10%) with CO_2 doubling if P supply was strongly limiting (0.1P) (Figure 4b; Table 4). In the NPK and 0.3P treatments the ratio between yield and P uptake was lower than the ratio in the 0.1P treatment and nil to slightly increased with CO_2 doubling (Figure 4b).

The ratio between total yield and K uptake (in total plant material) and the ratio between total above-ground yield and K uptake (in total above-ground plant material) did almost not change with CO_2 doubling if K supply was strongly limiting (0.1K) (Figure 5b; Table 4). In the NPK and 0.3K treatments the ratio between yield and K uptake was lower than the ratio in the 0.1K treatment and considerably increased with CO_2 doubling (Figure 5b).

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 2.0. In the 0.3N and 0.3K treatments where nutrient shortage reduced growth to a limited extent, the ratio $2^*CO_2/1^*CO_2$ was 1.6 to 1.8. In the other nutrient treatments growth was moderately or strongly limited by nutrient supply and the ratio $2^*CO_2/1^*CO_2$ was about 1.0. For total above-ground yield the ratios $2^*CO_2/1^*CO_2$ were identical. These results do not correspond with results from the experiment with faba bean by Goudriaan & De Ruiter (1983). In the NPK treatment they measured a ratio $2^*CO_2/1^*CO_2$ of 1.52 but in the low N and low P treatments the ratio was still high, i.e. 1.25 and 1.67 respectively. Possibly the difference can be explained from a relatively larger P supply in the experiment by Goudriaan & De Ruiter and from an increase in recovery fraction of applied P with CO_2 doubling.

The ratio $2^*CO_2/1^*CO_2$ for total yield in the NPK treatment was high, but typical for experiments in pots. In such pot experiments plants do not shadow each other. Hence, an increased rate of CO_2 assimilation at doubled atmospheric CO_2 results in more assimilates, more leaves, more light interception, even more CO_2 assimilation, etc. In another experiment where faba bean plants were grown in pots at two levels of water supply, total dry matter yields increased by a factor of two with CO_2 doubling (Goudriaan & Bijlsma, 1987). In a dense crop canopy however, a larger leaf area caused by CO_2 doubling results in a slightly higher light interception and a relatively smaller yield increase. For example, in crop enclosures under normal agricultural practice and plant density and with optimum nutrient supply, the ratio $2^*CO_2/1^*CO_2$ for total yield was 1.58 for faba bean (Dijkstra *et al.*, 1993). In that experiment the ratio $2^*CO_2/1^*CO_2$ for total yield of faba bean was 17% higher than that for spring wheat and that was also found for the control treatment of this pot experiment reported here and by Wolf (1996).

In the treatments with nil or slight nutrient limitation (NPK, 0.3N, 0.3K) CO_2 doubling resulted in identical or lower root/shoot ratios. In the other treatments with stronger nutrient limitation root/shoot ratios both increased and decreased with CO_2 doubling. However, there was no clear relation with the limiting element and probably these results only indicated the large variability in root/shoot ratios. According to a survey of experimental information on the direct effect of increasing atmospheric 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 crop species (no data for faba bean). The decreases and increases were generally found in situations with respectively optimum and limiting nutrient supply. This corresponds reasonably well with results found here for situations with nil or slight nutrient limitation. In the other treatments with stronger nutrient limitation CO_2 doubling did not result in a yield increase (Figure 1) and hence, in an increase in nutrient deficiency. In such situation root/shoot ratio probably does not change with CO_2 doubling, but the variability in results does not allow to draw such a conclusion. Apart from the CO_2 effect, nitrogen and potassium deficiency resulted in higher values and phosphorus deficiency in much higher values for the root/shoot ratio. This corresponds well with the functional equilibrium approach by Brouwer (1983).

In situations where nutrient supply is limiting for 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 faba bean crop the minimum concentrations are as follows: 0.0300 g N/g dry matter in seeds, 0.0080 g N/g dry matter in crop residues (above-ground), 0.0026 g P/g dry matter in seeds, 0.0008 g P/g dry matter in crop residues (above-ground), 0.0080 g K/g dry matter in seeds, 0.0100 g K/g dry matter in crop residues (above-ground) (Van Diepen *et al.*, 1988).

These minimum nutrient concentrations might change with CO_2 doubling. 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) and root/shoot ratios may change as described above. 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).

The concentrations of N, P and K were determined in plant tissue at the final harvest. When N supply was limiting for crop growth (0.1N treatment), average N concentration was 0.0115 g N/g dry matter in crop residues (without roots) and 0.0322 g N/g dry matter in seeds at ambient CO_2 and 0.0130 g N/g in crop residues (without roots) at doubled CO_2. For doubled CO_2 treatment no seeds could be harvested. These concentrations are a little above the minimum concentration levels. The increase in N concentration in crop residues is mainly the result of increased leaf fraction at doubled CO_2. Hence, minimum N concentration in crop residues does almost not change with CO_2 doubling. This results in a ratio between total above-ground yield and N uptake in above-ground yield that does not change with CO_2 doubling. In the 0.1N treatment a limited number of nodules was found on the roots. The resulting biological nitrogen fixation may have influenced these results, but as shown by the nil yield increase with CO_2 doubling (Figure 1), its influence was very small.

When P was strongly limiting for crop growth (0.1P treatment), average P concentration was 0.00063 g P/g dry matter in crop residues (without roots) at ambient CO_2 and 0.00060 g P/g at doubled CO_2. In this treatment no seeds could be harvested. These concentrations are at the minimum level. The decrease in P concentration in crop residues with CO_2 doubling is mainly the result of a decrease in leaf and pod fraction. Hence, minimum P concentration in crop residues remains identical or slightly decreases with CO_2 doubling. This results in a nil to slight increase in the ratio between total above-ground yield and P uptake.

When K was limiting for crop growth (0.1K treatment), average K concentration was 0.0188 g K/g dry matter in crop residues (without roots) and 0.0176 g K/g dry matter in seeds at ambient CO_2 and respectively 0.0167 g K/g and 0.0198 g K/g at doubled CO_2. These concentrations are rather high compared to the minimum concentration levels. Apparently, K was not completely diluted in plant tissue and hence, the decrease in K concentration with CO_2 doubling by 11% in crop residues and the increase by 13% in seeds do not indicate the change in minimum K concentration with CO_2 doubling.

Literature data indicate that with CO_2 enrichment minimum nutrient concentration in plant tissue may decrease, in particular for N and K and only slightly or not at all for P (Cure *et al.*, 1988a; Cure *et al.*, 1988b; Goudriaan & De Ruiter, 1983; Overdieck, 1993). This does not correspond well with the results found here. CO_2 doubling resulted in almost no change in minimum N concentration and a nil to slight decrease in minimum P concentration in crop residues. These results also contrast with those from the same pot experiments with spring wheat (Wolf, 1996). In that crop minimum N concentration in crop residues decreased with CO_2 doubling.

If for example minimum nutrient concentrations in plant tissue decrease with a doubling of atmospheric CO_2, this would result in lower fertilizer nutrient requirements to attain a certain yield level and in higher yields in situations where nutrients are mainly limiting for crop growth and no fertilizer nutrients are applied. As nutrient concentrations in seed yields were not available, such conclusions cannot yet be drawn.

The main conclusions from this study are:

1) Doubling of atmospheric CO_2 results in a strong increase (+100%) in total dry matter yield if the nutrient supply is optimum. This increase in yield is larger than that for spring wheat.
2) The CO_2 effect on total dry matter yield disappears rapidly with increasing limitation of both N, P or K supply for crop growth.
3) Doubling of atmospheric CO_2 results in no change in minimum N concentration and a nil to slight decrease in minimum P concentration in crop residues.
4) Nitrogen and potassium deficiency results in a higher root/shoot ratio and phosphorus deficiency in a much higher root/shoot ratio.

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