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Greenhouse-based pot experiments on spring wheat, faba bean and sugar beet.
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4.5 Greenhouse-based pot experiments on spring wheat, faba bean and sugar beet

4.5.1 Background

Increasing concentrations of atmospheric CO_2 appear to increase the rate of photosynthesis and to suppress photorespiration of most (i.e. C_3) plants (Goudriaan and Unsworth, 1990). This generally stimulates crop growth and leads to a much higher level of plant production (Cure, 1985; Cure and Acock, 1986; Kimball, 1983). Simultaneously dry matter allocation within the plant may change with increasing CO_2 (Stulen and Hertog, 1993) which may affect the amount of harvestable crop parts. Another effect of increasing CO_2 is an increased closure of stomata in the epidermis of leaves. This causes a higher exchange resistance between leaf and ambient air to gases such as CO_2 and water vapour which results in lower water losses by crop transpiration and in a much higher water use efficiency (Goudriaan and Bijlsma, 1987; Morison, 1993).

Growth of natural vegetation and of arable crops is mainly limited by the availability of nutrients in large parts of the world. If the nutrient use efficiency in crops at increased atmospheric CO_2 changes, this may affect crop growth and the attainable level of production (van Keulen and van Heemst, 1982), soil organic matter decomposition and nutrient cycling (Kuikman and Gorissen, 1993; van de Geijn and van Veen, 1993; Zak *et al.*, 1993). The effects of atmospheric CO_2 on crop growth, dry matter allocation and crop transpiration may be different if severe nutrient shortage occurs. To study the effects of increased atmospheric CO_2 on crop growth and their interaction with nutrient shortage pot experiments have been carried out. These experiments have been conducted with spring wheat, sugar beet and faba bean for a limited supply of nitrogen (N), phosphorus (P) and potassium (K), respectively. The results for spring wheat are reported in this section. Results for the other crop species and more detailed information on the spring wheat experiment are reported in Wolf (1995).

4.5.2 Experimental approach

4.5.2.1 *Design of the experiment*

The plants were grown in two similar glasshouses, presumed to differ only in CO_2 concentration (315 and 695 ppmv). In each glasshouse all plant species were subject to seven nutritional treatments: a control without nutrient limitation (NPK), 10% (0.1N) and 30% (0.3N) of optimum nitrogen supply, 10% (0.1P) and 30% (0.3P) of optimum phosphorus supply, and 10% (0.1K) and 30% (0.3K) of optimum potassium supply with the other elements sufficiently supplied. For a sound statistical analysis of the CO_2 effect more glasshouses would be required in order to assess the variability between the glasshouses. In this experiment the variability between the CO_2 plus nutrient treatments is used to determine the significance of the CO_2 effect. This may have influenced the significance of differences. For the NPK and the 0.1N treatments there were six replicates of which half were used for an intermediate harvest. For the other treatments there were three replicates, all used in the final harvest.

The plants were grown on coarse sand. They 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 glasshouse, identical nutrient supply). On 8 November the plants were distributed between the two glasshouses (having different CO_2 concentrations) and from that date the pots received different nutrient solutions. In each glasshouse 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 wind direction in the glasshouse. For each replicate of each plant species seven pots with different nutritional treatments and two pots for the intermediate harvest were distributed at random within one row. The pots were standing apart.

4.5.2.2 *Soil and nutrient treatments*

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 10 l (spring wheat, faba bean) and 20 l (sugar beet). The pots received nutrient solution weekly. For the control (NPK) a Hoogland solution was used, which consisted of 5 mmol/l KNO_3, 2 mmol/l $MgSO_4.7H_2O$, 5 mmol/l $Ca(NO_3)_2.4H_2O$ and 1 mmol/l KH_2PO_4. For the 0.1 N 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 0.1 K 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.

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. Water stress was prevented by regularly adding tap water. In each glasshouse, pots without plants but with the soil covered by plastic grains, were weighed to allow a correction for surface evaporation.

4.5.2.3 *Air/light conditions*

Plants were grown almost completely under artificial light from sodium high-pressure agro-lamps, as during the main period of crop growth (November until February) the amount of natural light was almost nil. To attain sufficient light for plant growth the daylength in the glasshouses was set at 16 hours. The total amount of radiation (during 16 day hours) was determined to be 3.64 and 2.60 $MJm^{-2}d^{-1}$ in the glasshouse with present CO_2 and doubled CO_2, respectively, if the amount of natural light was nil. The temperature was set at 20°C during the day and 15°C during the 8 hours of night time, resulting in an average daily temperature over the whole growth period of 18.5°C. The relative humidity was set at 70% in both glasshouses, but turned out to be 60%, on average, during the growth period in the glasshouse with present CO_2 and 75% in that with doubled CO_2. The large differences in relative humidity and in amount of radiation may have resulted in different growing conditions and water use efficiency of plants between glasshouses.

The CO_2 concentration in the doubled CO_2 glasshouse was on average 695 ppmv (± 60 ppmv for $P < 0.05$). The concentration was maintained by monitoring the CO_2 concentration with an IRGA and by injecting pure CO_2 into the glasshouse, whenever the CO_2 concentration was less than a pre-set value. In the other glasshouse CO_2 concentration was not controlled and was on average 315 ppmv (± 30 ppmv for $P < 0.05$). CO_2 enrichment started in the doubled CO_2 glasshouse at the date that the plants were distributed over the two glasshouses (8 November).

4.5.2.4 *Plant material and methods*

Table 4.5.1 shows data on plant variety, dates of sowing, intermediate and final harvest, and number of plants per pot. At intermediate and final harvests the fresh and dry weights (after 24 hours in an oven at 70°C) were determined of leaves, stems and roots, plus chaff and grains for spring wheat, beets for sugar beet and pods and seeds for faba bean. To determine the root weights roots were separated from the sand by washing carefully above a fine mesh. Leaf area of the harvested plants was measured. At four intermediate dates leaf area was also determined in a non-destructive way. For spring wheat the number of ears and grains was counted.

By weighing the pots and adding sufficient tap water to bring them back to their initial weights, the total amount of water used by the plants during their growth periods was determined. Identical pots without plants were weighed to make a correction for surface evaporation. Subsamples of dried plant tissue from the different plant organs were analysed for their nitrogen, phosphorus and potassium concentration. The nitrogen concentrations were determined using the Dumas method, the phosphorus concentrations colorimetrically and the potassium concentrations with atomic absorption.

Table 4.5.1 Some characteristics of the plant material.

Crop	**Cultivar, Number of plants per pot**	**Sowing date**	**Emergence date**	**Flowering date**	**Intermediate harvest date**	**Final harvest date (1x/2xCO_2)**	**Ripe-ning date**
Faba bean (*Vicia Faba* L.)	Minica, 1	12 Oct.	19 Oct.	from 20 Nov.	6 Jan.	25/26 Jan.	-
Spring wheat (*Triticum aestivum* L.)	Minaret, 3	12 Oct.	17 Oct.	20-30 Dec.	6 Jan.	8/22 Feb.	5/12Feb.
Sugar beet (*Beta vulgaris* L.)	Univers, 1	12 Oct.	21 Oct.	-	6 Jan.	14/15 Feb.	-

4.5.3 Results

4.5.3.1 Phenological development

Dates of emergence, flowering and ripening were recorded for the three crops (Table 4.5.1). For spring wheat the date of flowering appeared to be some days later in the doubled CO_2 glasshouse. The date of ripening for spring wheat was also later in the doubled CO_2 glasshouse, about 7 days for pots with NPK treatment but about nil for pots with strongly limited N and P supply. This is in contrast with results from Goudriaan and de Ruiter (1983) and Sionit *et al.* (1981a) who found an acceleration of flowering for wheat at increased CO_2. As there were not only differences in the CO_2 concentration but also in the amount of radiation and relative humidity between the glasshouses, these may have caused the unexpected changes in rate of phenological development.

4.5.3.2 *Yields*

The CO_2 effect on total above-ground dry matter yield was greatest in the control treatment without nutrient limitation (NPK) and was highly significant, and the ratio between the yield at doubled CO_2 and that at present CO_2 (i.e. ratio $2xCO_2/1xCO_2$) was 1.7 (Figure 4.5.1a; Table 4.5.2). In the K limited treatments (0.1K, 0.3K) where growth reduction only occurred to a limited degree, the CO_2 effect was also highly significant and the yield ratio $2xCO_2/1xCO_2$ was about 1.4. In the 0.1N treatment the CO_2 effect was significant and the yield-ratio $2xCO_2/1xCO_2$ was about 1.3 . In the 0.1P treatment, P supply limited growth to such extent that the CO_2 effect on yield became nil. In the 0.3P treatment the CO_2 effect was highly significant, but it was probably overestimated as a result of the very low yield level at present CO_2.

The CO_2 effect on grain yield was also highest in the NPK control treatment with a grain yield-ratio $2xCO_2/1xCO_2$ of 2.1 (Table 4.5.2; Figure 4.5.1b). In the 0.3N, 0.3P, 0.1K and 0.3K treatments the CO_2 effect was also highly significant but the ratio $2xCO_2/1xCO_2$ decreased to about 1.4 to 1.6 because of increasing nutrient limitation. For the same reason as mentioned in the previous paragraph the CO_2 effect in the 0.3P treatment was probably overestimated. In the 0.1N treatment the ratio $2xCO_2/1xCO_2$ was about 1.3 but was not significant, and in the 0.1P treatment the CO_2 effect on grain yield was very small and not significant.

For both present and doubled atmospheric CO_2 concentration the average effect of a limited nutrient supply on yield was determined. In comparison to the NPK treatment, a limited

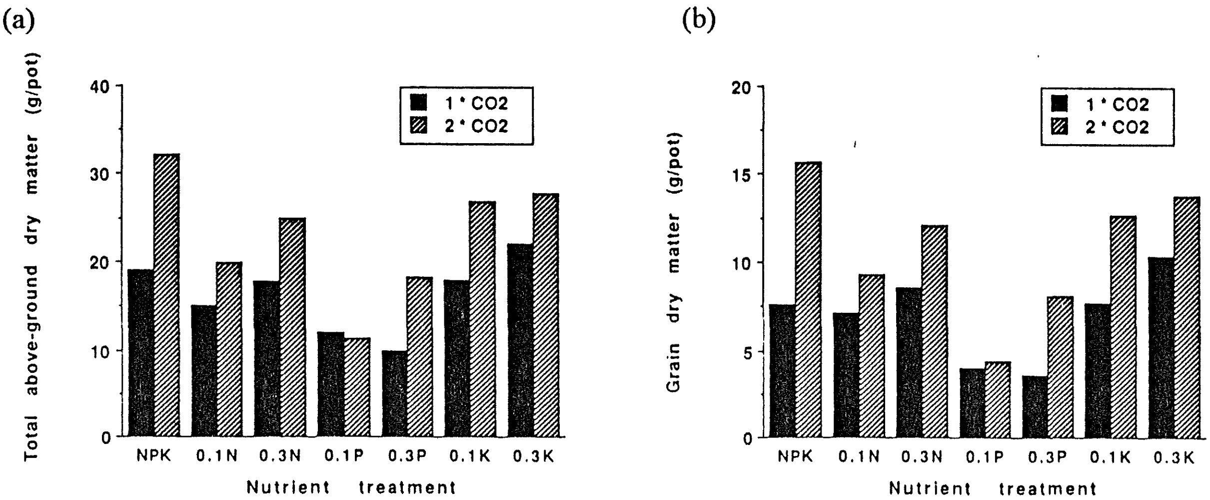

Figure 4.5.1 Average values for (a) total above-ground dry matter and (b) grain dry matter (g/pot) of spring wheat plants grown in pots at different nutrient treatments (with three replicates) at present and doubled atmospheric CO_2 concentrations.

Table 4.5.2 The ratio between average dry matter yields at doubled atmospheric CO_2 and those at present CO_2 for spring wheat 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						
	NPK	0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Total above ground dry matter							
Ratio $2xCO_2/1xCO_2$	1.69	1.33	1.40	1.07	1.84	1.49	1.26
Level of significance							
- of CO_2 effect[1]	**	*	**	-	**	**	**
- of nutrient effect[2]	-	** n	** n	** n	** n	* n	-
Grain dry matter							
Ratio $2xCO_2/1xCO_2$	2.07	1.31	1.41	1.10	2.25	1.64	1.34
Level of significance							
- of CO_2 effect[1]	**	-	**	-	**	**	**
- of nutrient effect[2]	-	** n	-	** n	** n	-	-

[1] 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 significance of nutrient effect is determined in comparison to NPK treatment.

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

supply of nitrogen and phosphorus generally resulted in a highly significant decrease in total above-ground dry matter yield (Table 4.5.2). Compared to the NPK treatment the grain dry matter yield was significantly lower in the 0.1P, 0.3P and 0.1N treatments. In the other treatments the nutrient effect on grain yield was not significant.

4.5.3.3 *Dry matter partitioning*

In the NPK treatment the root/shoot ratio at doubled CO_2 was about 0.8 of the ratio at present CO_2 (Figure 4.5.2a; Table 4.5.3). In the 0.1P, 0.3P and 0.1K treatments identical decreases in root/shoot ratio by CO_2 doubling were found. The inter-pot variance, however, was such that

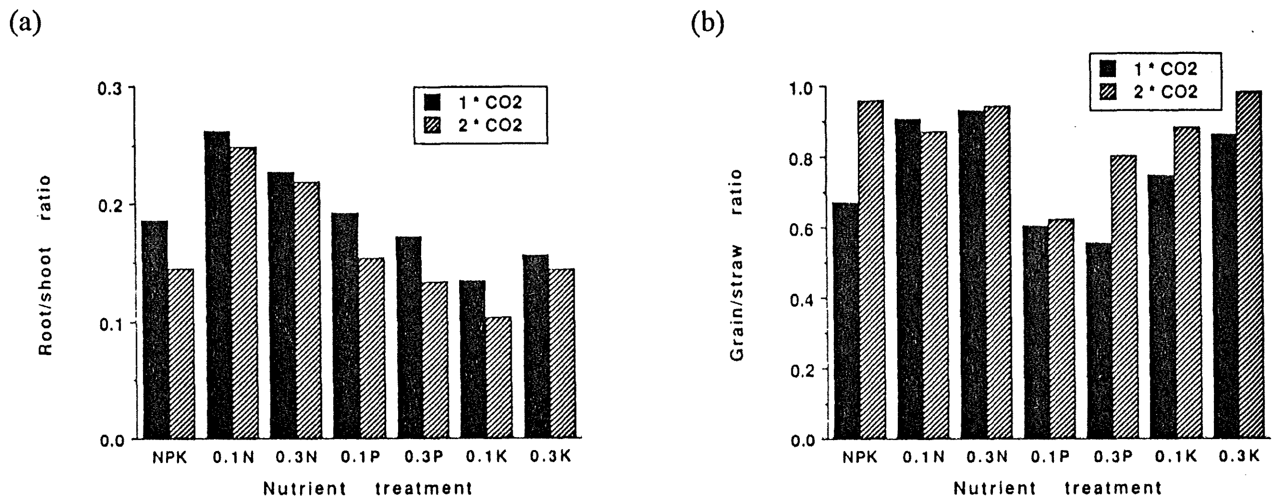

Figure 4.5.2 Average values for (a) root/shoot ratio and (b) grain/straw ratio of spring wheat plants grown in pots at different nutrient treatments (with three replicates) at present and doubled atmospheric CO_2 concentrations.

these CO_2 effects were not significant. In the other nutrient treatments the root/shoot ratio also decreased by CO_2 doubling but to a very limited and non-significant extent. Root/shoot ratio also changed as a result of limited nutrient supply. In comparison to the NPK treatment, the 0.1N and 0.3N treatments caused highly significant increased in root/shoot ratio and the 0.1K treatment a very significant decrease.

In the NPK and 0.3P treatments the grain/straw ratio at doubled CO_2 was significantly higher than in the ratio at present CO_2 (Figure 4.5.2b; Table 4.5.3). As these ratios at $1xCO_2$ were relatively low, this CO_2 effect was uncertain. In the other nutrient treatments the CO_2 effect on the grain/straw ratio was nil to small (0 to 15% increase) and not significant. Limited P supply caused a significant decrease in grain/straw ratio.

4.5.3.4 *Transpiration*

From the date that the plants were distributed over the two glasshouses and CO_2 and nutrient treatments were started, until the date of final harvest the water use by the plants was determined. Crop transpiration was calculated based on total water use corrected for surface evaporation. The transpiration coefficient, calculated as total transpiration per total above-ground dry matter yield, was about 260 g/g at present atmospheric CO_2 for the NPK treatment and slightly but not significantly higher for the N and K limited treatments (Figure 4.5.3a; Table 4.5.4). Limited P supply resulted in significantly higher transpiration coefficients.

By doubling atmospheric CO_2 the transpiration coefficient decreased to about 160 g/g in the NPK

Table 4.5.3 The ratio between average dry matter distribution at doubled atmospheric CO_2 and that at present CO_2 for spring wheat 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						
	NPK	0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Root/shoot ratio							
Ratio $2xCO_2/1xCO_2$	0.78	0.95	0.96	0.80	0.77	0.77	0.92
Level of significance							
- of CO_2 effect[1]	-	-	-	-	-	-	-
- of nutrient effect[2]	-	** p	** p	-	-	** n	-
Grain/straw ratio							
Ratio $2xCO_2/1xCO_2$	1.43	0.96	1.01	1.04	1.44	1.18	1.14
Level of significance							
- of CO_2 effect[1]	**	-	-	-	**	-	-
- of nutrient effect[2]	-	-	* p	** n	* n	-	-

[1] 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 significance of nutrient effect is determined in comparison to NPK treatment.

[2] p indicates a positive nutrient effect on root/shoot and grain/straw ratios in comparison to NPK treatment and n indicates a negative effect.

treatment (Figure 4.5.3a). In the nutrient limited treatments again slightly higher values were found. For the 0.1P treatment a significantly higher value was determined which corresponded with a relatively high total leaf fraction. The ratio between the transpiration coefficient at doubled CO_2 and that at present CO_2 was about 0.6 for both the NPK and the nutrient-limited treatments (Figure 4.5.3b). This ratio was determined by the difference in CO_2 concentration between both glasshouses and the difference in relative humidity and level of radiation (see section 4.5.2.3). For these reasons the significance of the CO_2 effect cannot be determined and a statistical analysis of the nutrient effect on transpiration coefficients has been conducted separately for each CO_2 treatment (Table 4.5.4).

Transpiration rates have been calculated for the conditions in each glasshouse using the Penman formula (Frère & Popov, 1979). The ratio between transpiration rates has been used to make a correction for the difference in glasshouse conditions (except CO_2 concentration level). The direct effect of CO_2 doubling on the transpiration coefficient (Table 4.5.4: ratio $2xCO_2/1xCO_2$ with Penman correction) was a 10% lower transpiration coefficient at optimum or almost optimum nutrient supply (NPK, 0.3N and 0.3K treatments); a 5 to 7% lower coefficient for 0.1N and 0.1K treatments; and a 2% lower coefficient for the 0.1P treatment. The result for the 0.3P treatment differed strongly from the other treatments because of the high transpiration coefficient at present CO_2.

To overcome the problem of the different conditions in the glasshouses and to allow a statistical analysis of the significance of the CO_2 effect for each nutrient treatment, the transpiration coefficients have been standardised. This was done by dividing transpiration coefficients for each treatment by the average transpiration coefficient for the NPK treatment and the same CO_2 treatment. The ratio $2xCO_2/1xCO_2$ of these relative transpiration coefficients indicates the extent to which the decrease in transpiration coefficient at optimum nutrient supply as a result of CO_2 doubling was also found at limited nutrient supply. For the 0.3N and 0.3K treatments the decrease in transpiration coefficient was almost identical to that for NPK treatment and for the 0.1N and 0.1K treatments the decrease was smaller. Only for the 0.1P treatment was the CO_2 effect significant, resulting in about a 10% smaller decrease compared to the NPK treatment. This means that the transpiration coefficient in the 0.1P treatment almost did not change with CO_2 doubling.

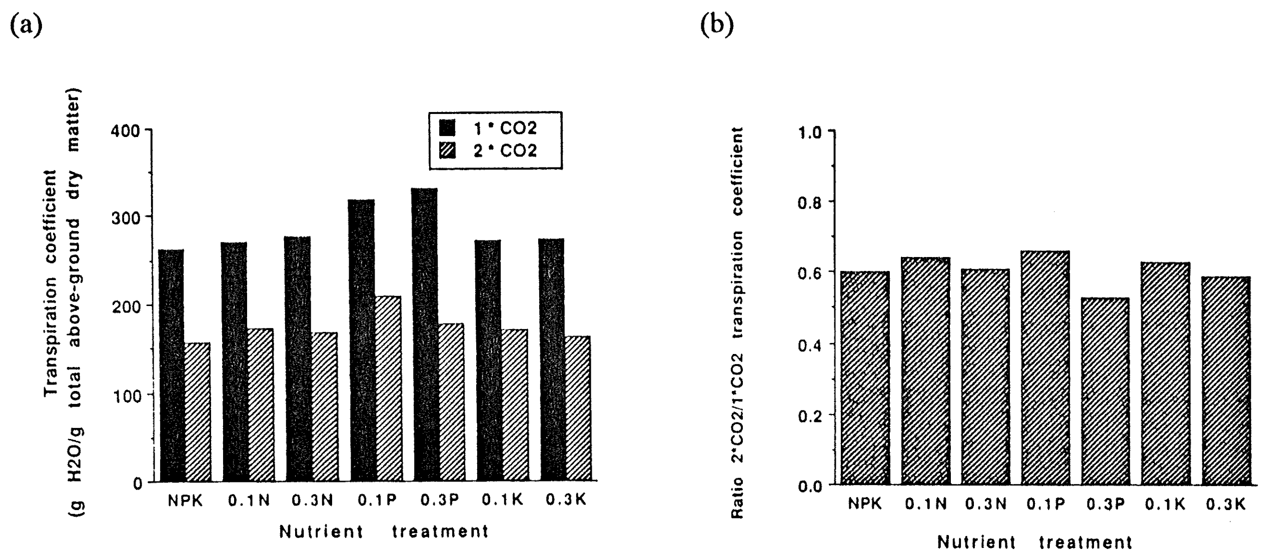

Figure 4.5.3 Average values for (a) transpiration coefficient (i.e. total transpiration divided by total above-ground dry matter yield (g/g)) at present and doubled atmospheric CO_2 concentrations and (b) the ratio of the transpiration coefficient at doubled to that at present atmospheric CO_2 concentration of spring wheat plants grown in pots at different nutrient treatments (with three replicates).

Table 4.5.4 Average values (AVG) of transpiration coefficients of spring wheat plants grown in pots at different nutrient treatments (with three replicates) and at present ($1xCO_2$) and doubled ($2xCO_2$) atmospheric CO_2 concentrations, the ratio between average transpiration coefficients at doubled CO_2 and those at present CO_2, and the level of significance of nutrient effect on transpiration coefficients.

	Nutrient treatment						
	NPK	0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Transpiration coefficient (per total[1], g/g)							
AVG ($1xCO_2$)	263	271	277	319	331	272	274
Level of significance - of nutrient effect ($1xCO_2$)[2]	-	-	-	**	**	-	-
AVG ($2xCO_2$)	157	173	168	210	177	171	163
Level of significance - of nutrient effect ($2xCO_2$)[2]	-	*	-	**	*	-	-
Ratio $2xCO_2/1xCO_2$	0.60	0.64	0.61	0.66	0.53	0.63	0.59
AVG ($2xCO_2$) with Penman correction[3]	233	258	250	313	263	254	243
Ratio $2xCO_2/1xCO_2$ with Penman correction[3]	0.89	0.95	0.90	0.98	0.79	0.93	0.89

[1] Total transpiration during the growth period divided by total dry matter (above ground) yield.
[2] The level of significance is indicated by * for $P < 0.05$, ** for $P < 0.01$ and - for not significant. It indicates the difference in transpiration coefficient from that of the NPK treatment.
[3] To allow comparison of transpiration coefficients at the two CO_2 treatments, total transpiration at doubled CO_2 has been multiplied with the ratio between the transpiration rate in the glasshouse at present CO_2 and that in the glasshouse at doubled CO_2, both calculated with the Penman formula for the climate conditions in the glasshouses.

4.5.3.5 *Nutrient concentrations and nutrient use efficiency*

The concentrations of N, P and K in plant tissue from the different plant organs were determined at final harvest. In the treatment with strongly limited N supply (0.1N) the N concentration decreased with CO_2 doubling by 11% in roots, about 30% in leaves and chaff, and 25% in grains, but these CO_2 effects were not significant (Table 4.5.5). In the stems the N concentration increased with CO_2 doubling, contrary to expectations. This resulted in a very small decrease in N concentration in straw with CO_2 doubling, differing from the considerable decrease in N concentration in the grains (Figure 4.5.4a). In the NPK and the 0.3N treatments where N supply was not or slightly limiting, the N concentrations decreased in all plant organs with CO_2 doubling except for the roots (Table 4.5.5). In these treatments N concentrations were higher than those in the 0.1N treatment and decreased considerably with CO_2 doubling (Figure 4.5.4a), probably because of dilution of N in the larger amount of biomass produced at doubled CO_2.

In the 0.1P treatment the P concentration decreased with CO_2 doubling by 5% in chaff and grains and increased by 6% and 30% in roots and leaves, respectively and much more strongly and significantly in stems (Table 4.5.5). This resulted in a small increase in P concentration in straw with CO_2 doubling (Figure 4.5.5a), as opposed to the small decrease in P concentrations in grains. In the NPK and 0.3P treatments where P was not or slightly limiting, the P concentrations decreased slightly in roots and decreased considerably in chaff and grains, slightly increased in leaves or were strongly variable in stems (Table 4.5.5). In these treatments the P concentrations were higher than in the 0.1P treatment and decreased considerably with CO_2 doubling (Figure 4.5.5a), probably because of dilution of P in the larger amount of biomass.

In the 0.1K treatment the K concentration decreased significantly with CO_2 doubling in leaves and stems (by about 30%) and in chaff and grains (by about 20%) (Table 4.5.5). This resulted in a considerable decrease in K concentration in straw which was stronger than that in grains (Figure 4.5.6a). In the NPK and 0.3K treatments the K concentrations decreased considerably in leaves, stems, chaff and grains (Table 4.5.5). In these treatments the K concentrations in straw were higher than in the 0.1K treatment and decreased considerably with CO_2 doubling (Figure 4.5.6a), probably because of dilution of K in the larger amount of biomass. In the grains the K concentrations were almost the same for the different treatments and almost did not change with CO_2 doubling.

The ratio between total above ground yield and nitrogen uptake was highest, and significantly increased (28%), with CO_2 doubling if nitrogen supply was strongly limiting (0.1 N), both for nitrogen uptake in total plant material and in total above ground plant material (Figure 4.5.4b; Table 4.5.6). This probably indicates a decrease in the minimum N concentrations with CO_2 doubling.

Table 4.5.5 The ratio between average concentrations of nitrogen (N), phosphorus (P) and potassium (K) in different plant organs at doubled atmospheric CO_2 and those at present CO_2 for spring wheat 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								
	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 $2xCO_2/1xCO_2$	1.17	1.00	1.37	0.89	3.47	1.06	0.91	0.33	0.53
Significance of CO_2 effect[1]	-	-	-	-	*	-	-	-	-
Leaves									
Ratio $2xCO_2/1xCO_2$	0.72	1.09	0.82	0.65	0.78	1.30	1.04	0.68	0.84
Significance of CO_2 effect[1]	*	-	*	-	-	-	-	*	-
Stems									
Ratio $2xCO_2/1xCO_2$	0.45	1.10	0.95	1.35	0.62	2.34	0.73	0.74	0.85
Significance of CO_2 effect[1]	-	-	-	-	-	*	*	*	-
Chaff									
Ratio $2xCO_2/1xCO_2$	0.39	0.67	0.89	0.71	0.77	0.94	0.72	0.78	0.86
Significance of CO_2 effect[1]	*	*	*	-	-	-	-	**	*
Grains									
Ratio $2xCO_2/1xCO_2$	0.83	0.90	0.80	0.75	0.94	0.96	0.81	0.84	0.91
Significance of CO_2 effect[1]	-	-	**	-	-	-	*	**	-

1 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.

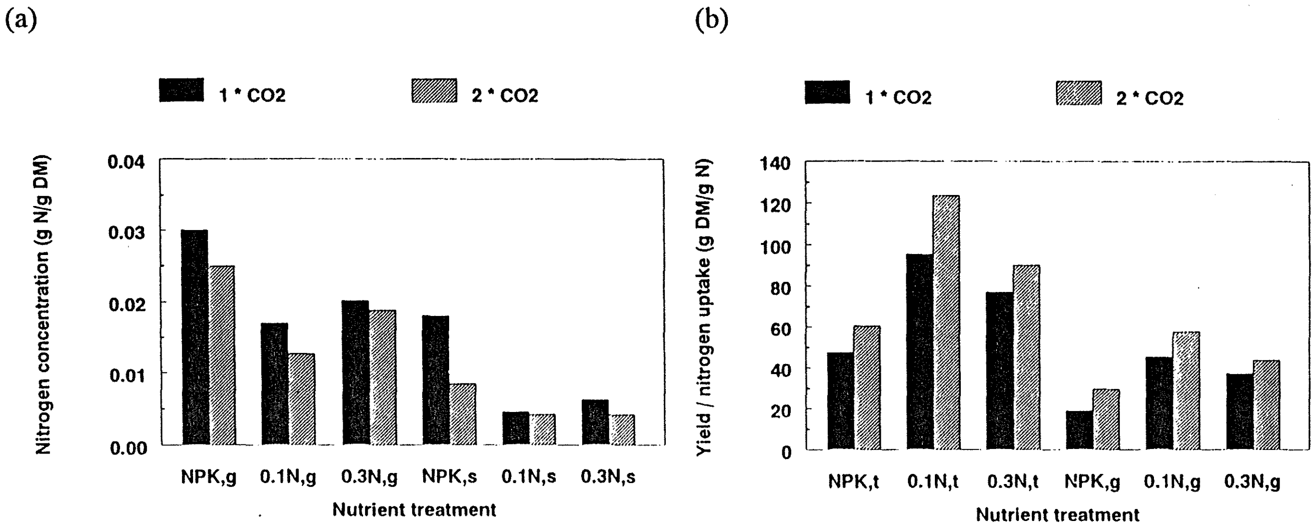

Figure 4.5.4 Average values for (a) nitrogen concentrations in grains (NPK,g etc.) and straw (NPK,s etc.) and for (b) total above ground yield to nitrogen uptake (NPK,t etc.) and grain yield to nitrogen uptake ratios (NPK,g etc.) of spring wheat plants grown in pots at different nutrient treatments (with three replicates) at present and doubled atmospheric CO_2 concentrations (nitrogen uptake in ratios applies to total above ground plant material).

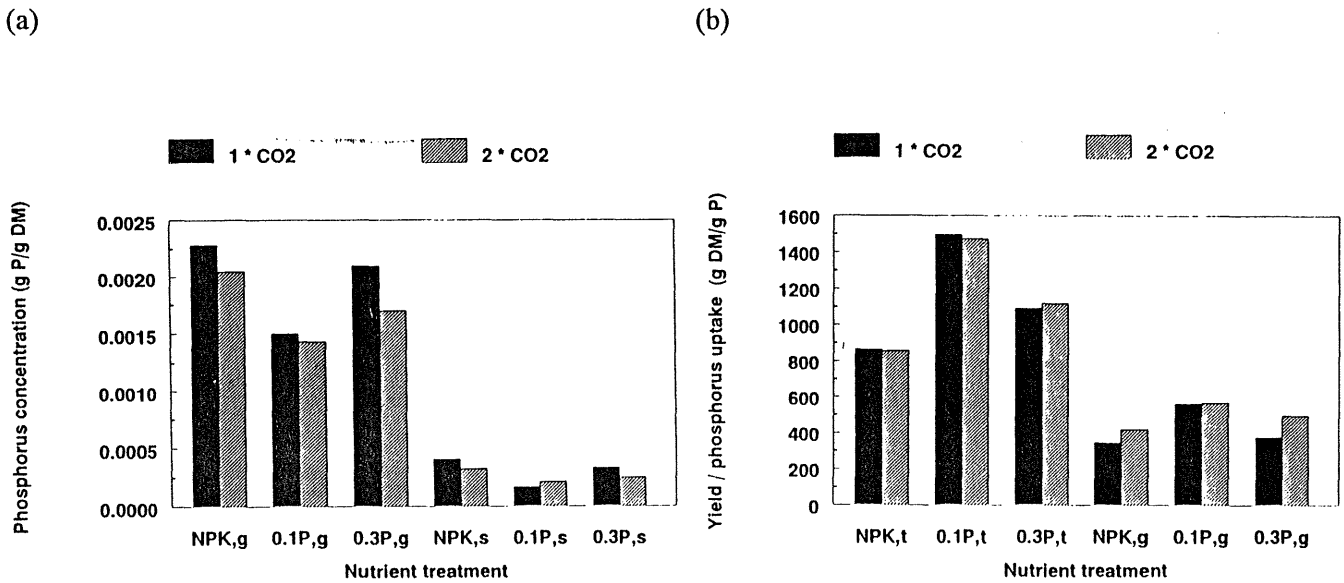

Figure 4.5.5 Average values for (a) phosphorus concentrations in grains (NPK,g etc.) and straw (NPK,s etc.) and (b) total above ground yield to phosphorus uptake (NPK,t etc.) and grain yield to phosphorus uptake ratios (NPK,g etc.) of spring wheat plants grown in pots at different nutrient treatments (with three replicates) at present and doubled atmospheric CO_2 concentrations (phosphorus uptake in ratios applies to total above ground plant material).

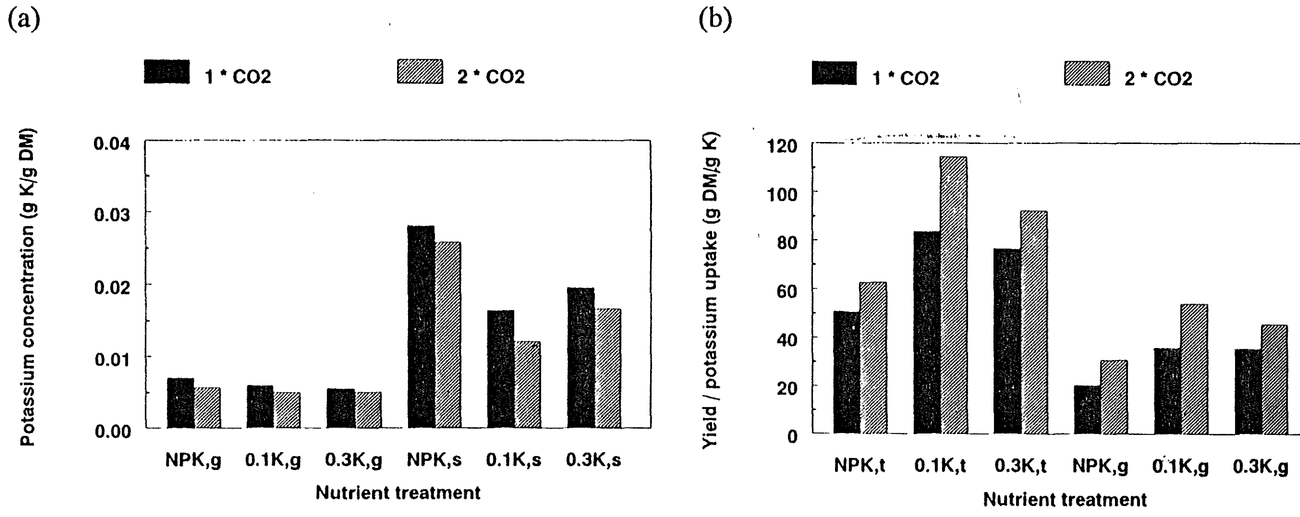

Figure 4.5.6 Average values for (a) potasssium concentrations in grains (NPK,g etc.) and straw (NPK,s etc.) and (b) total above ground yield to potassium uptake (NPK,t etc.) and grain yield to potassium uptake ratios (NPK,g etc.) of spring wheat plants grown in pots at different nutrient treatments (with three replicates) at present and doubled atmospheric CO_2 concentrations (potassium uptake in ratios applies to total above ground plant material).

Table 4.5.6 The ratio between average yield to nutrient (N, P or K) uptake at doubled atmospheric CO_2 and present CO_2 for spring wheat plants grown in pots at different nutrient treatments (with three replicates) and the level of significance of CO_2 effect on yield to nutrient uptake ratio for each nutrient treatment.

	Nutrient treatment								
	NPK			**0.1N**	**0.3N**	**0.1P**	**0.3P**	**0.1K**	**0.3K**
Nutrient	**N**	**P**	**K**	**N**	**N**	**P**	**P**	**K**	**K**
Total above ground yield / nutrient uptake ratio A[1]									
Ratio $2xCO_2/1xCO_2$	1.27	1.01	1.23	1.28	1.01	1.00	1.05	1.38	1.22
Significance of CO_2 effect[2]	-	-	-	*	-	-	-	**	*
Total above ground yield / nutrient uptake ratio B[1]									
Ratio $2xCO_2/1xCO_2$	1.27	0.99	1.23	1.29	1.17	0.98	1.02	1.37	1.20
Significance of CO_2 effect[2]	-	-	-	*	-	-	-	**	*
Grain yield / nutrient uptake ratio A[1]									
Ratio $2xCO_2/1xCO_2$	1.56	1.23	1.50	1.26	1.02	1.02	1.34	1.51	1.30
Significance of CO_2 effect[2]	-	-	*	-	-	-	*	**	*
Grain yield / nutrient uptake ratio B[1]									
Ratio $2xCO_2/1xCO_2$	1.57	1.21	1.50	1.27	1.17	1.01	1.32	1.50	1.28
Significance of CO_2 effect[2]	*	-	*	*	-	-	*	**	*

[1] A : ratio calculated for nutrient uptake in total plant material with roots included; B : ratio calculated for nutrient uptake in total above ground plant material.

[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.

In the 0.3N and NPK treatments the ratio between total above ground yield and nitrogen uptake was much lower (i.e. higher N concentration) than that in the 0.1N treatment (Figure 4.5.4b) and increased slightly and moderately respectively with CO_2 doubling (Table 4.5.6). This can probably be explained from the dilution of N in the larger amount of biomass produced at doubled CO_2. In the 0.1N and 0.3N treatments the change in ratio between grain yield and nitrogen uptake with CO_2 doubling was identical to that between total above ground yield and nitrogen uptake (Table 4.5.6). In the NPK treatment, however, the change in ratio between grain yield and nitrogen uptake with CO_2 doubling was higher than that between total above ground yield and nitrogen uptake, which was a result of the increase in harvest index with CO_2 doubling.

The ratio between total above ground yield and phosphorus uptake did not change with CO_2 doubling (Table 4.5.6; Figure 4.5.5b) both if phosphorus was strongly limiting (0.1P) and if phosphorus was slightly or not limiting (0.3P, NPK). This constant ratio for the 0.3P and NPK treatments was caused by both a decrease in P concentration and an increase in harvest index with CO_2 doubling. Results from the 0.1P treatment probably indicate that minimum phosphorus concentrations do not change with CO_2 doubling. The ratio between grain yield and phosphorus uptake did not change with CO_2 doubling in the phosphorus limited treatment (0.1P) and increased in the other treatments (0.3P, NPK). This increase was a result of the increase in harvest index with CO_2 doubling.

The ratio between total above ground yield and potassium uptake increased very significantly with CO_2 doubling (Table 4.5.6; Figure 4.5.6b) if potassium supply was strongly limiting (0.1K). This probably indicates a decrease in the minimum potassium concentrations with CO_2 doubling. In the treatments (0.3K, NPK) where K supply was slightly or not limiting for crop growth, the ratio between total above ground yield and potassium uptake was lower (i.e. higher K concentration) than the ratio in the 0.1K treatment (Figure 4.5.6b) and increased considerably with CO_2 doubling (Table 4.5.6). This can be explained from dilution of K in the larger amount of biomass produced at doubled CO_2. The change in ratio between grain yield and potassium uptake with CO_2 doubling was larger than that between total above ground material and potassium uptake (Table 4.5.6) both for the 0.1K treatment and the other treatments (0.3K, NPK). This was a result of the increase in harvest index with CO_2 doubling.

The recovery fraction of applied N changed little with CO_2 doubling if nitrogen supply was strongly limiting crop growth (0.1N treatment; Table 4.5.7). The recovery fractions of applied P and K also did not change with CO_2 doubling in the 0.1P, 0.1K and 0.3K treatments. In the treatments with larger N supply (0.3N, NPK) the recovery fraction of applied N was higher at doubled CO_2 which was a result of the increased biomass production with CO_2 doubling. In the treatments with larger P and K supply the recovery fractions of applied P and K were significantly higher at doubled CO_2 which also was a result of the increased biomass production.

For both applied N, P and K the recovery fraction became higher, if its supply became more limited (Table 4.5.7). The recovery fraction of applied P was much lower than for applied N and K because a large part of the applied amount of this element became less available by absorption and precipitation. The very high recovery fraction in the 0.3N treatment at doubled CO_2 cannot be explained. If the K supply was clearly limiting (0.1K treatment) the recovery fraction of applied K was higher than 1, indicating that some potassium was also supplied by the sandy soil.

4.5.4 Implications for modelling

The positive effect of CO_2 enrichment on the rate of CO_2 assimilation becomes smaller when crops are grown under severe nutrient stress. Models should incorporate this interaction between nutrient limitation and CO_2 enrichment. Increased CO_2 results in larger biomass production and, thus, in more dilution of available nutrients in plant tissue when nutrient supply is limiting. If the assimilation rate decreases with decreasing nutrient concentrations in the leaves, CO_2 enrichment and nutrient stress interactions, such as those used in the NWHEAT model (Groot, 1987), can be incorporated into models.

Table 4.5.7 Average recovery fractions (g/g) of applied nutrients (N, P and K) for spring wheat plants grown in pots at different nutrient treatments (with three replicates) and at present and doubled atmospheric CO_2 concentrations, the ratio between average recovery fraction at doubled CO_2 and that at present CO_2, and the level of significance of CO_2 effect on the recovery fraction for each nutrient treatment.

	Nutrient treatment								
	NPK			0.1N	0.3N	0.1P	0.3P	0.1K	0.3K
Nutrient	N	P	K	N	N	P	P	K	K
Recovery fr., 1 x CO_2	0.65	0.23	0.49	0.93	0.87	0.29	0.23	1.09	0.92
Recovery fr., 2 x CO_2	0.81	0.39	0.67	0.99	1.30	0.31	0.41	1.18	0.96
Ratio 2xCO_2/1x CO_2	1.25	1.70	1.37	1.06	1.49	1.07	1.78	1.08	1.04
Significance of CO_2 effect[1]	-	**	*	-	*	-	**	-	-

[1] 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.

Increased CO_2 results in lower transpiration coefficients but the effect becomes smaller if nutrient shortage occurs. The decrease in transpiration coefficient with increased CO_2 is mainly determined by the larger biomass production while the transpiration roughly remains the same. If models are able to calculate biomass production under the interacting effects of CO_2 enrichment and nutrient stress as described above, they may also simulate the smaller decrease in transpiration coefficient under nutrient stress. In simpler models fixed values for transpiration coefficients are often used to calculate crop production in a water-limited situation. Such values should be corrected for both increased CO_2 and nutrient supply.

To calculate crop yields on unfertilized soils or the fertilizer requirements for attaining a specified yield level, elaborate models use plant-specific nutrient concentrations and simpler models (Janssen *et al.*, 1990) use yield-nutrient uptake ratios. Increased CO_2 concentrations result in lower nutrient concentrations (with the exception of P), so higher yield to nutrient uptake ratios should be incorporated into models for application in situations with increased CO_2.

Baking quality of wheat grains is determined by variety, growing conditions and the rate and timing of nitrogen application. To attain a high protein content in the grains, which is a requirement for good baking quality, the wheat crop should be able to accumulate large amounts of nitrogen during its growth (van Keulen and Seligman, 1987). Conversely, Darwinkel (1987) showed that baking quality was mainly variety-specific and although protein content in the grains increased with the rate of nitrogen application, baking quality improved little with increasing protein content. Elevated CO_2 concentrations resulted in lower nutrient concentrations in the grains in this experiment. This may reduce baking quality. Simulation models can be used to calculate recommendations for fertilizer rates and timing in a changed climate with increased CO_2, to prevent a reduction in yield quality.

4.5.5 Discussion

In the control (NPK) treatment without nutrient limitation the ratio between total yield at doubled CO_2 and that at present CO_2 (i.e. ratio $2xCO_2/1xCO_2$) was 1.7. In the K limited treatment which reduced growth to a limited extent, the ratio $2xCO_2/1xCO_2$ was 1.4. In the 0.1N and 0.1P treatments where growth was strongly limited by nutrient supply, the ratio was 1.3 and 1.1, respectively. For the grain yield the CO_2 effect was also highest in the control treatment. This corresponds well with results from other experiments with wheat under nutrient limitation. For example, Sionit *et al.* (1981b) found a decrease in the ratio $2xCO_2/1xCO_2$ for total yield if the nutrient solution was diluted and Goudriaan and de Ruiter (1983) measured a ratio $2xCO_2/1xCO_2$ for total yield of 1.4 at optimum nutrient supply, 1.2 at severe N shortage and 1.0 at severe P shortage.

The ratio $2xCO_2/1xCO_2$ for total yield in the NPK treatment was much higher than the values that are generally found. In this experiment the pots were placed apart and shading did not occur. In such conditions a higher rate of CO_2 assimilation at doubled atmospheric CO_2 results in more assimilates, more leaves, more light interception, even more CO_2 assimilation and so on. In two other experiments where spring wheat was grown in pots that were placed apart, the ratio $2xCO_2/1xCO_2$ for total yield was also high, i.e. 1.93 and 1.83 respectively (Sionit *et al.*, 1981a; Morrison and Gifford, 1984). In a dense crop canopy a larger leaf area caused by CO_2 doubling results in a slightly higher light interception and a much smaller yield increase. For example, in crop enclosures under normal agricultural practice and plant density and with optimum nutrient supply the ratio $2xCO_2/1xCO_2$ for total yield was 1.35 for spring wheat (Dijkstra *et al.*, 1993) and in a pot experiment at an almost identical plant density the ratio was 1.15 for winter wheat (Mitchell *et al.*, 1993).

In the NPK treatment root/shoot ratio decreased with CO_2 doubling but this effect was not significant. In the P and K limited treatments the root/shoot ratio decreased to approximately the same extent, but in the N limited treatments the decrease in root/shoot ratio with CO_2 doubling was negligible. 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 and den Hertog, 1993), increasing CO_2 may cause either an increase or a decrease in the root/shoot ratio of a wheat crop. The increases are generally found in situations with a limiting nutrient supply. This corresponds well with results found in this experiment for the N limited treatments but not with those for the P limited treatments.

Grain/straw ratio did not increase with CO_2 doubling if nitrogen or phosphorus were strongly limiting and slightly increased in the other treatments. Slight increases which become nil with the nutrient limitation, were also found in a survey of experimental information for wheat by Cure (1985). Compared to the control, P limited treatments resulted in significantly lower grain/straw ratios.

The ratio between the transpiration coefficient at doubled and present CO_2 was about 0.6, both in the control and the nutrient limited treatments. This corresponds well with an increase in water use efficiency of 80% with CO_2 doubling which was determined for single wheat plants growing in pots (Morison, 1985). This high value only applies to single plants. If wheat plants are grown in stands, water use efficiency increases by only 25 to 35% (Morison, 1993). This difference can be explained from the micro-meteorological feedback in the crop canopy (Goudriaan and Unsworth, 1990). If a correction for the difference in glasshouse conditions (except CO_2 concentration level) is taken into account, the ratio $2xCO_2/1xCO_2$ became 0.89 for the control. This decrease in transpiration coefficient is very small compared to literature data, particularly because pots in this experiment were standing apart.

In nutrient limited conditions the decrease in transpiration coefficient with CO_2 doubling was smaller than that in the control and close to zero if the supply of nutrients, in particular the supply of P, was severely limiting. This can be explained mainly by the fact that CO_2 enrichment did not lead to increases in yield with severe P shortage. This was also found for seedlings of *Pinus radiata* (Conroy *et al.*, 1988). However, the literature survey of Cure and Acock (1986) indicates for corn, soybean and cotton that the reduction in transpiration by CO_2 doubling is almost identical in both non-limited and nutrient limited conditions.

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. Such levels will only be attained if all required nutrients are supplied sufficiently and only one nutrient strongly limits crop growth. Further dilution appears to be impossible. It is feasible that minimum concentrations may change with CO_2 doubling. In general, experiments with doubled CO_2 have been carried out with diluted nutrient solutions which cause a limited supply of more than one nutrient (e.g. Sionit *et al.*, 1981b). This means that complete dilution of nutrients down to the minimum concentration will not occur (Janssen *et al.*, 1990) and minimum concentration levels cannot be established.

For a large number of fertilizer experiments van Keulen and 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 wheat crop the minimum concentrations are as follows: 0.0110 g N/g dry matter in grains, 0.0030 g N/g dry mattter in crop residues (above-ground), 0.0016 g P/g dry matter in grains, 0.0004 g P/g dry matter in crop residues (above-ground), 0.0030 g K/g dry matter in grains, 0.0070 g K/g dry mater in crop residues (above-ground) (van Diepen *et al.*, 1988).

The concentrations of nitrogen, phosphorus and potassium in plant tissue were determined in the present experiment at final harvest. This was done for different organs of the wheat crop. When nitrogen was strongly limiting for crop growth (0.1N treatment), the average N concentration was 0.0046 g N/g dry matter in crop residues (without roots) and 0.0170 g N/g dry matter in grains at present CO_2 and 0.0042 g N/g and 0.0127 g N/g, respectively at doubled CO_2. These concentration levels are slightly higher than the minimum concentration levels reported and probably indicate that CO_2 doubling causes a decrease in minimum N concentration by 9% in crop residues and by 10 to 25% in grains (dependent on the assumed degree of dilution by increased biomass production with CO_2 doubling). This resulted in an increase in the ratio between total above-ground yield and N uptake in above-ground yield by 10 to 30% (lower value applies if the dilution effect is removed).

When phosphorus was strongly limiting for crop growth (0.1P treatment), the average P concentration was 0.00017 g P/g dry matter in crop residues (without roots) and 0.00150 g P/g dry matter in grains at present CO_2 and 0.00021 g P/g and 0.00143 g P/g, respectively at doubled CO_2. These concentrations are at the minimum level and, hence, indicate that CO_2 doubling causes a decrease in minimum P concentration by 5% in grains and an increase by 24% in crop residues. This resulted in a decrease in the ratio between total above-ground yield and P uptake in above-ground yield by 2%, which indicates that minimum P concentrations remain almost constant with CO_2 doubling.

When potassium was limiting for crop growth (0.1K treatment), the average K concentration was 0.0164 g K/g dry matter in crop residues (without roots) and 0.0060 g K/g dry matter in grains at present CO_2 and 0.0121 g K/g and 0.0050 g K/g, respectively at doubled CO_2. These concentrations are rather high compared with the minimum concentration levels (van Diepen *et al.*, 1988) and, hence, potassium was not completely diluted in plant tissue. The decrease in K concentration with CO_2 doubling by 26% in crop residues and by 17% in grains only indicates the degree of dilution by increased biomass production as a result of CO_2 doubling and not the change in minimum K concentration.

Literature data indicate that with CO_2 enrichment nutrient concentrations in plant tissues may decrease, in particular for nitrogen, somewhat less for potassium and only slightly or not at all for phosphorus (Cure *et al.*, 1988a, 1988b; Goudriaan and de Ruiter, 1983; Overdieck, 1993). This corresponds well with results in this experiment for nitrogen and phosphorus.

4.5.6 Conclusions

A broad survey of the effects of doubling atmospheric CO_2 as determined in this study, are given in Table 4.5.8. Doubling of atmospheric CO_2 resulted in a strong increase in total dry matter and grain yield for spring wheat if the nutrient supply was optimal. In the 0.1N and 0.1K treatments the CO_2 effect was approximately halved and in the 0.1P treatment it became negligible.

Table 4.5.8 Summary table of the effects of doubling atmospheric CO_2 for yield, transpiration coefficient, nutrient concentrations and nutrient use efficiency of spring wheat plants grown in pots at different nutrient treatments and for the recovery fraction of applied nutrients.

	Nutrient treatment			
	NPK	**0.1N**	**0.1P**	**0.1K**
Total above-ground dry matter	+	+	0	+
Grain dry matter	+	+	0	+
Root/shoot ratio	-	0	-	-
Grain/straw ratio	+	0	0	+
Transpiration coeficient	-	-	0	-
Nutrient concentration straw	- - -[1]	-	0	-
Nutrient concentration grains	- - -[1]	-	0	-
Total biomass/nutrient uptake	+ 0 +[2]	+	0	+
Grain yield/nutrient uptake	+ + +[2]	+	0	+
Recovery fraction	+ + +[3]	0	0	0

[1] Change in N, P and K concentration respectively.
[2] Ratio between yield and N uptake, P uptake and K uptake respectively.
[3] Recovery fraction of applied N, P and K respectively.

Doubling of atmospheric CO_2 resulted in a decrease in the transpiration coefficient for spring wheat by 11% if the nutrient supply was optimal. In the 0.1N and 0.1K treatment this decrease was approximately halved and in the 0.1P treatment it became negligible. Doubling of atmospheric CO_2 resulted in an approximately 10% lower minimum N concentration and no change in the minimum P concentration. The supply of potassium appeared to be too high to derive a change in minimum concentration level.

With increasing limitation of nutrient supply for crop growth, in particular severe P deficiency, the effects of CO_2 enrichment on yield and transpiration coefficient disappeared in most cases. The change in minimum N concentration in plant tissue with CO_2 doubling should be incorporated in wheat models and evaluation systems of soil fertility. This will result in lower fertilizer N requirements for a given yield level at doubled CO_2.

For other varieties of wheat which might have other nutrient concentration levels and for other crop species the change in minimum concentration levels of macro-nutrients with CO_2 doubling should be determined. Such information is practically not available and is required to adjust fertilizer recommendations to future conditions with a higher atmospheric CO_2 concentration. This is of interest from both an economic and an environmental point of view.

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