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3 Effect of CO₂ increase on the productivity of cereals and legumes; model exploration and experimental evaluation

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Summary

The effect of an increased atmospheric CO₂ concentration on the productivity of spring wheat and faba bean was explored with simulation models for crop growth. The simulations were carried out for the Netherlands growing seasons of 1975-1988, assuming adequate water supply, for each season with the ambient CO₂ concentration (350 ppm) and also with a concentration of 700 ppm. The results were compared with those of experiments with increased CO₂ concentration under semi-field conditions and adequate water supply, with spring wheat in 1991 and with faba bean in 1992.

For spring wheat, the simulations with a 700 ppm CO₂ concentration showed an increase of above-ground biomass of 35-50 % and the experiment showed an increase of 35 %. Faba bean showed a larger CO₂ response, both in the simulations (+ 47-56 %) and in the experiment (+ 58 %).

Model explorations further showed that the experimental difference in CO₂ response between spring wheat and faba bean may not be due to a fundamental physiological difference between the two crops, but can be explained by differences in daily air temperature between growing seasons.

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3.1 Introduction

The steady increase of the CO₂ concentration in the atmosphere and the associated probable rise of temperature may affect the functioning of crops and agro-ecosys-

tems in future. Various crop physiological processes are affected by climatic change. CO₂ increase stimulates photosynthesis and affects stomatal conductance (Lemon, 1983; Cure & Acock, 1986) and water use efficiency (Gifford, 1979; Sionit et al., 1980). Temperature rise may increase the developmental rate of crops, resulting in an adverse effect on production. Direct experimental evaluation of the combination of these contradictory effects is difficult. Crop growth simulation models may be used to this end, as the causal relations between rate variables and forcing variables are present in such models.

Simulation studies were carried out for several scenarios of climatic change for different crops including faba bean and spring wheat (Wolf, 1993; Grashoff et al., 1993; Nonhebel, 1993a; Adams et al., 1990; Jansen, 1990). The explorations showed that the positive effect of CO₂ increase on photosynthesis often compensates for the negative effect of temperature rise on crop longevity.

However, the large positive effect of CO₂ increase on crop growth assessed with model studies is a subject of discussion. It is argued that the models were constructed and validated based on the short-term effects of CO₂ increase. These were measured in greenhouses and climate chambers and often on individual plants (Kimball, 1983). Negative feed-back mechanisms, such as thicker leaves resulting in slower canopy closure, or leaves with decreasing photosynthetic rates after a prolonged exposure to a high CO₂ concentration, may reduce the positive effect (Wong, 1979; Rowland-Bamford et al., 1991). Differences in CO₂ response between species have been reported as well (Sage et al., 1989).

A further validation of model explorations with long-term experiments in the field was needed. Till recently, this validation was technically impossible but since 1991 the new Wageningen rhizolab (Van de Geijn et al., 1993) provides the facilities. In this study we investigate if former model explorations of the CO₂ response of spring wheat and faba bean (Nonhebel, 1993a; Grashoff et al., 1993) agree with the CO₂ response measured in recent long-term experiments. Crops were grown under high CO₂ concentration with radiation and temperature similar to the field situation. Moreover, we investigate if there are differences in CO₂ response between the two crops and, if yes, how these can be explained.

3.2 Materials and methods

Feasibility studies and experiments. In the simulations, growth and production of spring wheat and faba bean were calculated for the present CO₂ concentration of 350 ppm and for a concentration of 700 ppm. The model studies were carried out for 14 seasons, with daily solar radiation and temperature data from Wageningen during 1975-1988 as input. Additional simulations were conducted using weather data of 1991 and 1992.

The experiments were conducted in the Wageningen rhizolab (Van de Geijn et al., 1993). The crops were grown under a removable rain shelter with adequate irrigation and radiation and temperature were almost similar as in the undisturbed field situation. Transparent boxes were placed in the canopy to allow a constant CO₂ concentration of 350 ppm or 700 ppm, respectively. Measurements of photosynthesis and final biomass were carried out in the boxes. The experiment with spring

wheat was conducted in 1991 and the experiment with faba bean in 1992. Details about the experimental design are presented by Dijkstra et al. in a previous chapter.

3.3 Model description

Gross photosynthesis of a crop was calculated based on the photosynthesis/light response curve of individual leaves, characterized by the initial light use efficiency (EFF) and the maximum rate of leaf gross photosynthesis (AMAX) (Figure 3.1). Both values are affected by the CO₂ concentration. According to Goudriaan (1985), the value of AMAX is almost proportional to the CO₂ concentration but the value of EFF is less sensitive. At an average temperature of 20 °C, doubling the CO₂ concentration increases EFF by 15 % and AMAX by 100 % (Figure 3.1)(Goudriaan & Unsworth, 1990).

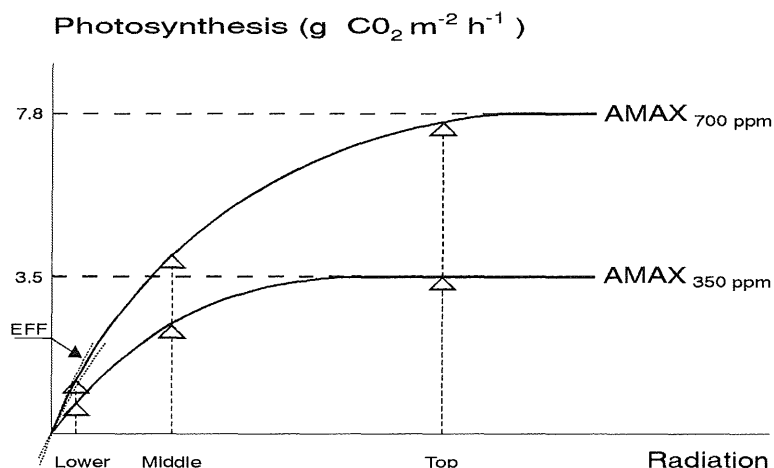


Figure 3.1. The photosynthesis/light response curve for individual leaves with a CO₂ concentration of 350 ppm and with a concentration of 700 ppm. EFF=initial light use efficiency; AMAX=maximum photosynthetic rate; L, M, T = maximum radiation levels at a clear day for leaves placed at a low level in the canopy (L); leaves in the middle (M); leaves at the top of the canopy (T).

In a canopy, the top leaves are shading the lower ones. In the middle of a clear day with high radiation, the lower leaves (level L in Figure 3.1) photosynthesize at a much lower rate than at light saturation. Leaves in the middle of the canopy (level M in Figure 3.1) photosynthesize somewhat below the rate at light saturation and only top leaves (level T) photosynthesize at their maximum rates. Figure 3.2 includes the effect of the daily course of radiation and shows that doubling the CO₂ concentration has a strong positive effect on the photosynthesis at the top of the canopy, but only a small effect at the lowest level. This implies that a doubling of the CO₂

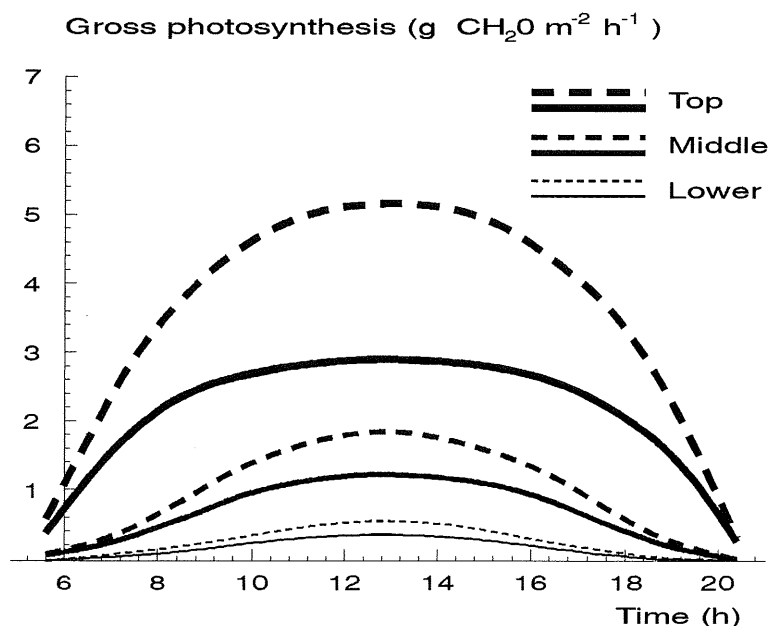


Figure 3.2. The theoretical course of photosynthesis of three levels in a closed canopy on a clear day under CO₂ concentrations of 350 ppm (—) and 700 ppm (---).

concentration results in much less than a doubling of the daily total photosynthesis. From the relations in Figure 3.1 and 3.2 it was calculated that, generally for C₃ plants, a doubling of the CO₂ concentration increases AMAX by 100 %, *maximum* rate of crop photosynthesis by 45-65 % (due to light extinction) and *total* daily crop photosynthesis by only 40 % (due to the diurnal course of the sun)(Goudriaan & Unsworth, 1990).

Each day the model calculates the gross photosynthesis as described above, using the actual values of radiation and temperature and the calculated value of the Leaf Area Index (LAI) of the previous day. Part of the produced photosynthate is used for the maintenance respiration of the standing crop (Figure 3.3)(Spitters et al., 1989; Penning de Vries et al., 1989). The remainder is allocated to the various organs and this process is controlled by the developmental stage of the crop (cf. van Heemst, 1986). Rate of development is controlled by air temperature. In the organs (roots, stems, seeds, leaves), the photosynthate is converted into structural dry matter, using an amount of energy ('growth respiration') which depends on the specific chemical composition of the organ type (Vertregt & Penning de Vries, 1987). The LAI is calculated from the dry matter growth of the leaves and their specific weight. The LAI is used for the calculation of the light interception of the next day, closing the simulation loop (Figure 3.3).

This part of the models for spring wheat and faba bean was derived from a general crop growth simulator (Spitters et al., 1989; Penning de Vries et al., 1989). The specific parameters and functions of spring wheat were mainly based on the spring wheat model of van Keulen & Seligman (1987). The characteristics of faba bean

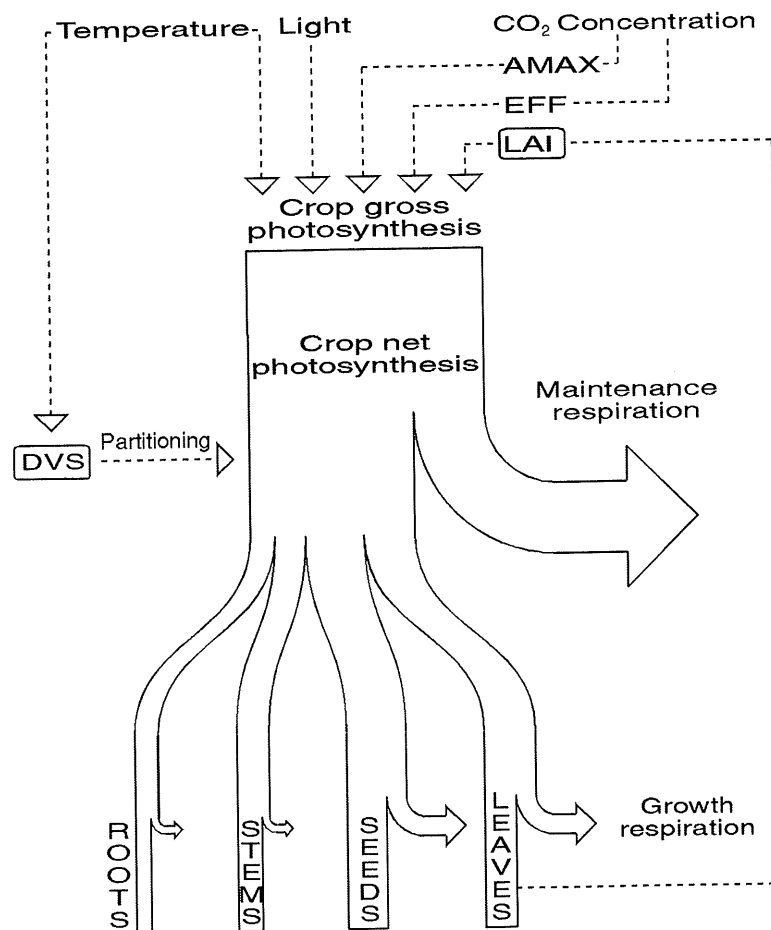


Figure 3.3. Schematic representation of crop growth. Dotted lines indicate information lines.

were derived from experiments with faba bean in the Netherlands (Grashoff, 1990a, 1990b).

3.3.1 Model validation

The reliability of the model for spring wheat was tested comparing data from experimental farms in Emmercompascuum and Wieringermeer (Nonhebel, 1993a). The results of the faba bean model proved to be reliable comparing measured yields of experiments of 14 years at Wageningen, the Netherlands, and of 2 years at 9 locations of the so-called 'EC-Joint Faba Bean Trials' in Denmark, France, Germany, the Netherlands, United Kingdom and Austria (Grashoff & Stokkers, 1992).

3.3.2 Input data for the simulation study for the effect of CO₂ increase

Input for the simulation models were daily measurements of solar radiation and maximum and minimum temperature data of Wageningen (Meteostation Haarweg of the Agricultural University of Wageningen) during 1975-1988 and 1991 and 1992. Additional input values, only used at the beginning of each simulation, were sowing date (in the spring wheat model) or emergence date (faba bean model) and values of crop dry matter and leaf area index at emergence.

3.4 Results

In the simulation studies for 1975-1988, a doubled CO₂ concentration resulted in a 40-60 % increase of above ground biomass and seed yield, calculated at crop maturity. This agreed very well with the measured increments for spring wheat in 1991 and faba bean in 1992 (Table 3.1). In the simulations, this result was due to a doubling of the maximum photosynthetic rate of *individual leaves* (AMAX). AMAX was not measured in the 1991 and 1992 experiments, but measurements of maximum rates of *crop* photosynthesis were available for a further comparison. The measured maximum rates of crop photosynthesis showed a CO₂ response of 45-65 % which agreed with the values calculated in the simulations (Figure 3.4). Moreover, the measured rates were not correlated with the age of the crop.

Table 3.1. Simulated and measured above-ground biomass (t ha⁻¹) and seed yields (t ha⁻¹) for spring wheat and faba bean, grown under CO₂ concentrations of 350 ppm (control) and 700 ppm (C700). The average CO₂ response (%-increase) and the response range over the individual years (increase range) is presented as a percentage (C700/Control - 1)* 100 %

	Above-ground biomass		Seed yield	
	Simulated	Measured	Simulated	Measured
Spring wheat	(1975-1988)	(1991)	(1975-1988)	(1991)
Control	18.5	13.0	7.7	4.4
C700	26.2	17.5	11.0	5.8
%-increase	41	35	42	34
increase range	35-50	--	40-50	--
Faba bean	(1975-1988)	(1992)	(1975-1988)	(1992)
Control	12.6	13.5	6.1	5.6
C700	19.1	21.3	9.0	8.5
%-increase	52	58	48	51
increase range	47-56	--	42-53	--

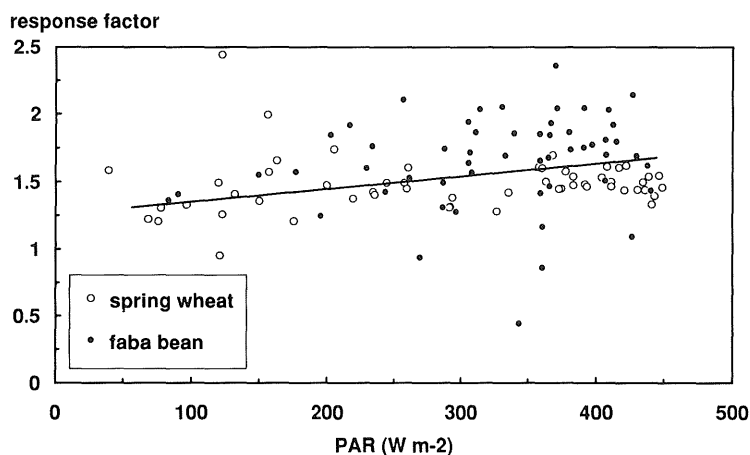


Figure 3.4. Measured (symbols) and simulated (line) values of the ratio between maximum rates of crop photosynthesis at 350 and 700 ppm CO₂ at various light intensities during the period of a closed canopy

Both in the simulation studies and in the experiments, spring wheat showed 10 % less response to CO₂ increase than faba bean (Table 3.1). In further model explorations it was analysed which factor may be responsible for this difference. These simulations showed that for both crops the effect of a doubled CO₂ concentration on final above-ground biomass increased with later emergence (Table 3.2). Due to a combination of sowing practices and germination properties, the actual average emergence date of faba bean (used in Table 3.1) is almost a month later than for the spring wheat crop. Part of the difference in CO₂ response between the crops may be due to the simple fact that early emergence coincides, in general, with lower temperatures and radiation. The effect of lower temperatures was illustrated for the experimental years 1991 and 1992. Incidentally, the sowing and emergence dates of the rhizolab experiment with spring wheat in 1991 were almost the same as these dates for faba bean in 1992. Radiation and temperature in the spring of 1991,

Table 3.2. Simulated biomass at a CO₂ concentration of 700 ppm and CO₂ response (%-increase) on above-ground biomass for spring wheat and faba bean (1975-1988) with early and late dates of emergence (Julian daynumber).

Emergence	Spring wheat		Faba bean	
	Biomass	%-increase	Biomass	%-increase
90 (normal for spring wheat)	18.5	41	20.9	46
120 (normal for faba bean)	14.2	52	19.1	52

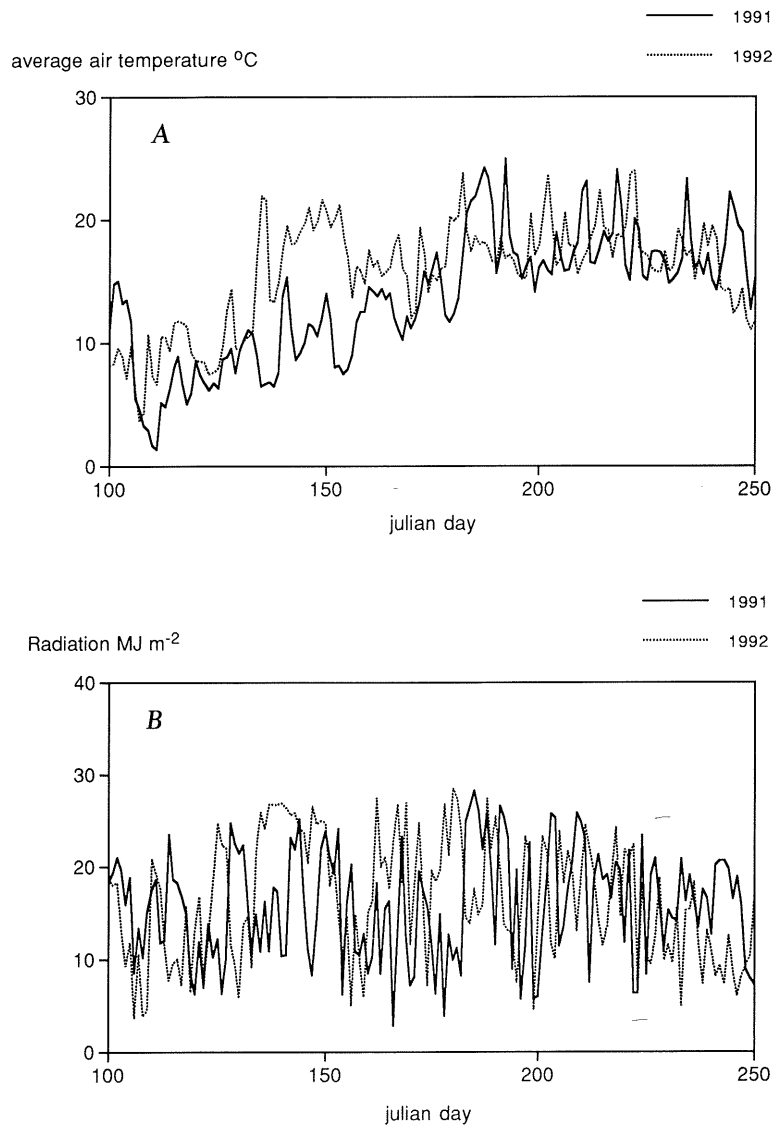


Figure 3.5. Daily weather data for 1991 and 1992. a: Average air temperature; b: Total radiation.

however, were much lower than in 1992 (Figures 3.5a and 3.5b). The simulations for both crops showed a smaller CO₂ response in 1991 than in 1992 (Table 3.3), although the effect for faba bean was smaller than for spring wheat. A last set of runs was made to separate the interaction between weather and CO₂ effect in temperature and radiation. Two weather data sets were compiled: one with the (lower) 1991 temperature data and the 1992 radiation data and one with

Table 3.3. Simulated above-ground biomass (t ha^{-1}) for spring wheat and faba bean, grown under CO_2 concentrations of 350 ppm (control) and 700 ppm (C700) in 1991 and 1992. The average CO_2 response (%-increase) is presented as a percentage $(\text{C700}/\text{Control} - 1) * 100 \%$

	Spring wheat		Faba bean	
	Simulated (1991)	Simulated (1992)	Simulated (1991)	Simulated (1992)
Control	16.5	13.6	12.8	12.7
C700	23.3	21.1	19.1	19.7
%-increase	41	55	49	55

the 1992 temperature data and the (lower) 1991 radiation data. Simulation runs were made with these 'new' weather files. The results are given in Table 3.4. Replacing the high radiation levels of 1992 by the low levels of 1991 (1992R'91) had hardly any effect on the magnitude of the CO_2 effect. When the high temperatures of 1992 were replaced by the lower ones from 1991 (1992T'91) a large reduction in CO_2 effect was observed. From this analysis it is concluded that the difference in CO_2 response was caused by differences in air temperature between the years and not by the differences in radiation.

Table 3.4. Simulated above-ground biomass (t ha^{-1}) under the present CO_2 concentration (Control) and for a CO_2 concentration of 700 ppm (C700) and the response to high CO_2 expressed as a percentage (%-increase) for: 1991, for 1992 with only the temperature data of 1991 (1992 T'91), for 1992 with only the radiation data of 1991 (1992 R'91), and for 1992.

	Control	C700	%-increase
Spring wheat			
1991	16.5	23.3	41
1992 T'91	18.5	26.1	41
1992 R'91	10.3	16.1	56
1992	13.6	21.1	55
Faba bean			
1991	12.8	19.1	49
1992 T'91	13.6	19.8	46
1992 R'91	11.2	17.7	58
1992	12.7	19.7	55

3.5 Discussion

The simulated 40-60 % increase of total above-ground biomass production due to a doubling of CO₂ concentration agrees with simulation results of Jansen (1990) with rice in Asia, Nonhebel (1993b) with wheat at various locations in Europe and Grashoff et al. (1993) with faba bean in the Netherlands, Israel and Syria. The CO₂ response predicted with these model studies, which was only validated by climate chamber and greenhouse results till recently, is now supported by the effects measured in a field-like crop, grown under a permanently doubled CO₂ concentration (Table 3.1). This shows that the simulation modeling approach for assessments of the effects of CO₂ increase on crop biomass in future is valid.

It is dangerous, however, to base this conclusion solely on the agreement between simulated and measured final yields, as this provides no physiological evidence. It is important to compare also the simulated and measured processes which lead to the final yields. The physiological basis for comparing simulations and measurements is the effect of CO₂ concentration on the photosynthesis/light response curve (Figure 3.1), especially on AMAX, but measurements were not carried out on this detailed level.

In this respect, the comparison of simulated and measured maximum crop photosynthesis provides more physiological information. In the presentation of the Figures 3.1 and 3.2 it has been said that, theoretically, a doubling of the CO₂ concentration increases AMAX by 100 %, but *maximum* rate of crop photosynthesis only by 45-65 %. The simulated increase of 45-65 % was based on this theory and the measured increase agreed with the simulations throughout the period of a closed canopy (Figure 3.4). As these measurements correspond theoretically and quantitatively with a 100 % increase in AMAX, this shows that the agreement between simulated and measured final biomass was actually based on a correspondence between simulated and measured physiological processes.

A doubling of AMAX associated with doubled CO₂ concentration, however, is not always found in literature. Cure & Acock (1986) estimated in their review that on average leaf photosynthesis is stimulated by 52 % shortly after doubling the CO₂ concentration. Pot experiments with wheat showed almost no increase of AMAX, due to CO₂ (A. Visser, University of Amsterdam, pers. comm.). The small increments recorded in some pot experiments may be due to other limitations, for instance nitrogen (Wong, 1979), which reduce the effect of CO₂ increase on AMAX. Faba bean, which is supplied with nitrogen through bacterial nitrogen fixation in its root nodules, may be less sensitive to nitrogen limitation in pots. It is interesting that for faba bean, a nearly doubling of AMAX was actually measured (Dijkstra, pers. comm.), like it was measured for soya bean (Clough et al., 1981). In our experiments, the 45-65 % increase in maximum daily canopy photosynthesis corresponded quantitatively with a doubling of AMAX in both spring wheat and faba bean (see previous paragraph). Our results obtained under long-term exposure to doubled CO₂ concentration in the field may be more representative for the actual CO₂ response of crops than the results from pot or greenhouse experiments.

Another question is the importance of processes which progressively reduce the effect of CO₂ increase on crop photosynthesis during the season, such as a reduction of AMAX after a prolonged period of exposure to a high CO₂ concentration. Baker

& Allen (1993) found no negative feed-back of a long-term CO₂ exposure in soya bean, but they found a decrease in rice due to a decrease in rubisco activity. Stitt (1991) attributed these negative feed-backs on crop photosynthesis to sink limitation. Our simulation models did not include such negative feed-backs. The agreement between simulated and measured maximum crop photosynthesis (Figure 3.4) persisted during the whole period of a closed canopy. This shows that such negative long-term effects did not occur in spring wheat and faba bean. It may not be important to include these negative feed-backs in further assessments of the effect of CO₂ increase in future, at least not for cereals and leguminous crops under optimum nutrient supply.

Our simulations showed that the difference in CO₂ response between spring wheat and faba bean is not likely based on a fundamental physiological difference. It was shown that the smaller CO₂ response of spring wheat was due to lower temperatures. In general, this was a result of early sowing (Table 3.2) or, specifically for the experiments in 1991 and 1992, a result of the lower temperatures in the spring of 1991, when the spring wheat experiment was carried out (Table 3.4).

The origin of this temperature effect during the season was further analysed. As measurements of intermittent harvests were not available, this was done with the aid of the simulation approach. In the faba bean explorations, the Specific Leaf Area (SLA) is not affected by CO₂ increase, which is confirmed by the experimental results (Dijkstra, pers comm.) and experiments with soya bean (Lieth et al., 1986). Theoretically, a doubled CO₂ concentration increases maximum daily photosynthesis by 45-65 % (due to the process of light extinction) and total daily photosynthesis by only 40 % (due to the diurnal course of the sun (Figures 3.1 and 3.2; Goudriaan & Unsworth, 1990). During the phase of exponential growth (before the canopy is closed) the 40 % increase of total daily photosynthesis has a positive feed-back on leaf area growth and thus on biomass increase. At the end of the exponential phase the simulated standing biomass can be up to a factor 2.8 higher due to a doubled CO₂ concentration, which means an increase of 180 % (Figure 3.6). After canopy closure, the difference in daily biomass *increase* is only 40 % and during this period the CO₂ effect on simulated *cumulative* biomass will steadily decrease, from 180 % to an 'asymptote' of 40 %. As lower temperatures (like in 1991) elongate the length of the growing period, it is clear that this decrease is continued longer and the value of 40 % is almost reached before the crop stops growing. In shorter seasons due to higher temperatures (1992), crops senescent earlier and the CO₂ response on cumulative biomass remained higher than 40 % (Figure 3.6a).

The results of this analysis also hold for spring wheat, although this crop shows an additional effect. In spring wheat, leaf area growth during the phase of exponential growth is determined by temperature itself (Spitters et al., 1989). This means that lower temperatures (1991) result in a later and lower peak of the relative CO₂ response curve (Figure 3.6b). This additional effect probably explains why the simulated differences in CO₂ response between 1991 and 1992 are 14 % for spring wheat and only 6 % for faba bean (compare Figure 3.6b with Figure 3.6a). It is interesting for a further analysis in another article. The temperature effect also explains the higher CO₂ response with later sowing (or emergence) dates within one season (Figure 3.7). With later emergence, the average temperatures are higher and the growing season is shorter. Figure 3.7 shows that with a shorter season, the curves of

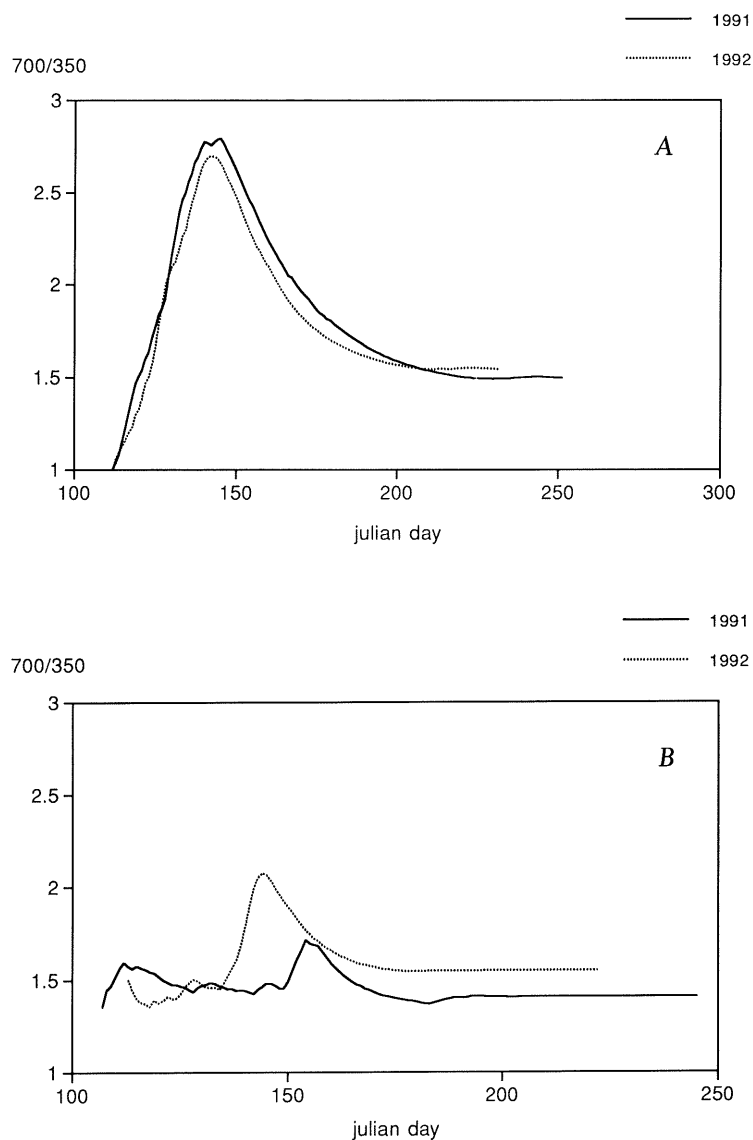


Figure 3.6. The relative CO₂ response of cumulative biomass (C700/C350) versus time for simulations in a season with low temperatures (1991) and a season with higher temperatures (1992). a: faba bean; b: spring wheat

the relative CO₂ response of cumulative biomass stop at higher values. The experimental confirmation of model explorations showed that simulation models, including a synthesis of the most important physiological processes of crop growth, are a reliable tool to explore the possible effects of environmental changes such as increase of CO₂ concentration on crop growth and yields. Moreover, it was

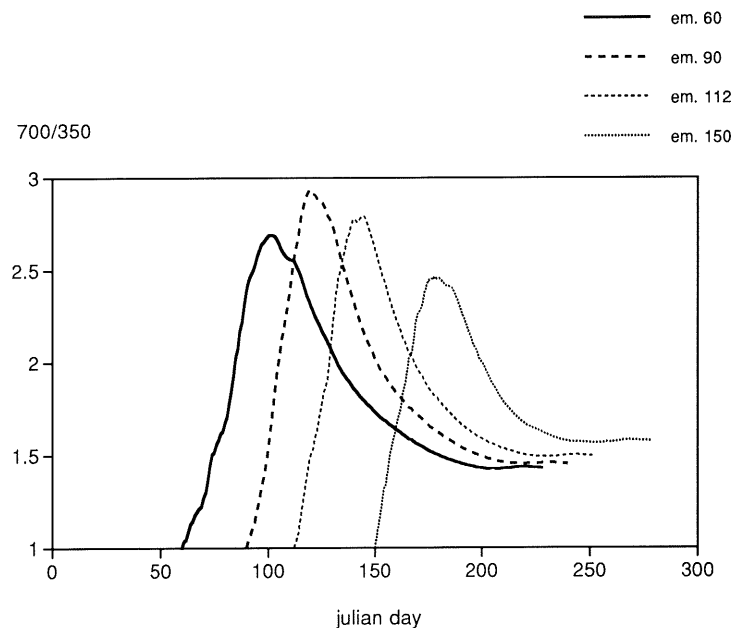


Figure 3.7. The relative CO₂ response of cumulative biomass (C700/C350) versus time for four faba bean simulations with increasing emergence dates in 1991.

demonstrated that models adequately analyse the causes of observed differences in experimental results and can help to distinguish the most promising hypotheses for new experimental work, thus contributing to an efficient use of labour and expenses.

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