

Plant growth in response to CO₂ enrichment, at two levels of nitrogen and phosphorus supply. 1. Dry matter, leaf area and development

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Received 20 September 1982; accepted 17 January 1983

Key-words: CO₂ enrichment, nutrient shortage, growth, dry matter, yield, assimilate partitioning

Summary

The effect of doubling the normal aerial CO₂ content on plant growth was studied in lucerne, faba bean, perennial ryegrass, wheat, maize, poplar and potato. Because nutrients are often limiting growth, the effect of CO₂ under nitrogen or phosphorus shortage was also studied. CO₂ doubling had the largest effect on dry matter yield under good nutrient supply, but under nitrogen shortage part of the CO₂ effect was retained, even in the non leguminous species. Except for faba bean, no CO₂ effect existed under phosphorus shortage. Maize showed a small positive CO₂ reaction under good nutrient supply, but a negative one under nutrient shortage. Potato showed a small negative reaction to CO₂ enrichment.

Introduction

It is a classic observation that aerial CO₂ is necessary for plant growth, and that enrichment beyond the natural concentration usually has a stimulatory effect (Strain & Sionit, 1982; Wittwer & Robb, 1964). The two major mechanisms of this stimulation are a decreased diffusion limitation, and a suppressed photorespiration.

In horticulture, CO₂ addition in greenhouses has found widespread application, although probably more important for prevention of CO₂ depletion than for true enrichment (Briejer, 1959; Enoch et al., 1970; van Berkel, 1964, 1977). All terrestrial vegetation is subject to a steadily increasing atmospheric concentration of CO₂ (annual increase ca. 1.5 cm³/m³; present concentration 340 cm³/m³) due to release of CO₂ by combustion of fossil fuel. The rate of increase of atmospheric CO₂ corresponds to only about 60 % of the CO₂ produced by combustion of fossil fuel. Much of the remaining 40 % is absorbed by the ocean. The biosphere exchanges much carbon with the atmosphere but it is not clear if it is a net absorber or producer of CO₂ (Bolin et al., 1979; Pearman, 1980).

In most natural ecosystems severe shortage exists of nutrients or of water. The

question has arisen whether under such circumstances CO_2 will have a stimulatory effect (Lemon, 1976; Goudriaan & Ajtay, 1979). Because of partial stomatal closure under increased CO_2 , CO_2 enrichment improves the water use efficiency (Louwse, 1980; Rosenberg, 1981) so that the waterstress-free period is extended and production of organic matter is prolonged. Once waterstress had developed, CO_2 still promoted production in wheat (Gifford, 1979) apparently because the net CO_2 uptake was diffusion-limited.

There is much less evidence about the interaction of a high CO_2 concentration and shortage of nutrients. Wong (1979) studied the CO_2 reaction of cotton and maize under shortage of nitrogen (N). He reported a clear CO_2 effect in the C_3 plant cotton under N shortage but none in the C_4 plant maize. Sionit et al. (1981b) grew wheat on nutrient solutions of different strengths, obtained by dilution with demineralized water. He reported stimulation of growth by CO_2 at all nutrient levels.

The purpose of our experiment is to further investigate the interaction of CO_2 enrichment and nutrient shortage, not only of N but also of P. These two elements, N and P, form the major nutritional constraints in natural ecosystems, and also in extensive agriculture. The studied plant species were wheat, maize, lucerne, faba bean, perennial ryegrass, potato and poplar; to include important grain crops, C_3 plants as well as a C_4 plant, 2 leguminous species, one woody species and an important grassland species.

Materials and methods

Design of the experiment

The plants were grown in a greenhouse in two similar compartments presumably only differing in CO_2 concentration (350 ± 50 and $700 \pm 50 \text{ cm}^3/\text{m}^3$). For a sound statistical analysis many more compartments would have been required to assess the intercompartment variability. In this experiment only intracompartament variability could be determined by harvesting a number of pots. This variability was used in the statistical analysis, so that significance of differences may be biased. In each greenhouse compartment all species were subject to three nutritional treatments (+N+P (control), -N+P, +N-P). The positioning of the plants in the two CO_2 compartments was identical. Inevitably, nutrient treatments were subject to slightly different light conditions due to location. The plants were grown on sand in pots and received nutrient solution and additional tapwater. The nutritional control counted 10 pots, the -N and -P of each 6 pots. The first four weeks after germination or planting (at about 23 April 1981) all plants received the same treatment ($330 \text{ cm}^3/\text{m}^3$, nutritional control) and after that the six treatments were imposed for the remaining growing season. This procedure gave all plants an equal start at a reasonable size and nutrient content.

Treatment

Soil conditions. The plants were grown in black plastic pots with sand of a very low

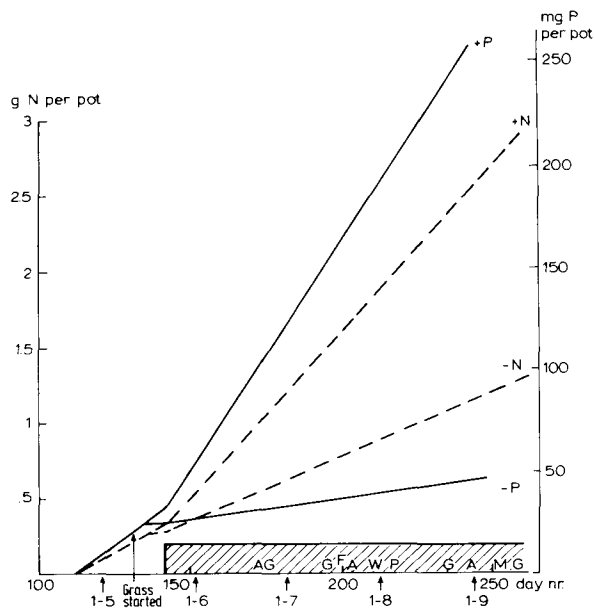


Fig. 1. Time course of nitrogen applied (dashed line) and phosphorus applied per pot. Hatched region indicates CO₂ treatment. Capitals indicate moments of harvest of lucerne (A), perennial ryegrass (G), faba bean (F), wheat (W), poplar (P) and maize (M).

organic matter content. The sand had been washed and brought down in pH from 8.5 to 6 with the use of HNO₃. Twice a week the pots received 250 cm³ of nutrient solution before 21 May, and 500 cm³ after 21 May. Concentration of components in the solution (in mmol/l) was for K⁺ 3; ½Ca²⁺ 5, ½Mg²⁺ 2, NO₃⁻ 11.1, ½SO₄²⁻ 2 and H₂PO₄⁻ 0.5 (control, treatment C). After 15 May the nutrient treatments started by replacing either 60 % of the NO₃⁻ (treatment -N) or 90 % of the H₂PO₄⁻ (treatment -P) by Cl⁻, so that the plants were not entirely deprived of their nutrient supply. The resulting cumulative gift of N and P per pot is drawn in Fig. 1 (grass started later). The nutrient solution also contained the necessary microelements and was acidified to pH 4 with HNO₃ to facilitate iron uptake. The effect of this additional N dose is included in Fig. 1.

The nutrient solution was given on Tuesday and Friday. After 30 June the pots received an additional 500 cm³ of tapwater on Wednesday whereas the nutrient solution supply of Tuesday was shifted to Monday. Nevertheless, waterstress sometimes visibly developed in lucerne and in poplar.

The pots had holes in the bottom so that excess water or nutrient solution could drain from the pots into the flat container carrying all pots of one species; the excess liquid remained available to them. All pots were covered with white plastic grains to prevent surface evaporation and crust formation. The pots with dry soil weighed about 5 kg. They were 17 cm high and 21 cm in diameter, and placed in a density of about 16 pots m⁻².

Potatoes were grown in containers of 0.7 m × 0.9 m with sand and a stock of fertilizer. They only received tapwater, and were not subject to nutrient-poor treatments.

Air conditions. CO₂ enrichment started at 21 May (Fig. 1) to prevent a differential nutrient uptake mediated by CO₂, before the nutrient treatments started. CO₂ was monitored with an IRGA and sampled once every 288 s under control of a Honeywell recorder. Whenever the CO₂ concentration was less than a pre-set value, pure CO₂ was automatically injected into the compartment.

This procedure gave a sawtooth-shaped time-course of CO₂ with a typical amplitude of ca. 100 cm³/m³, a mean at 700 cm³/m³ and a period of about 10 minutes. The glasshouse compartments were not completely air-tight and had still some ventilation at a typical rate of once per hour. Since no CO₂ could be removed, the CO₂ concentration in the low compartment sometimes rose considerably. In early mornings with still, inversion-like weather both compartments might reach 700 cm³/m³. A few hours later photosynthetic activity and increased ventilation had restored the normal situation.

Day/night temperatures were set at 21 °C (12 hours)/13 °C (12 hours). Occasionally, under high irradiation the temperature rose to 25 °C. Relative humidity fluctuated between 65 % in daytime to 95 % at night.

Plant material

In Table 1 some data on variety, sowing or planting dates and harvesting dates are given. Grass was planted as tillers detached from mother plants (11 May), and poplar as cuttings of ca. 20 cm length (31 March).

Table 1. Some characteristics of the plant material.

Crop	Cultivar	Sown	Planted	Number of plants per pot	Flowering (700 cm ³ /m ³)	Harvested
Wheat (<i>Triticum aestivum</i> L.)	Arkas	23 Apr		5	12 June	29 July
Maize (<i>Zea mays</i> L.)	LG 11	23 Apr		1	1 July	9 Sep
Perennial ryegrass (<i>Lolium perenne</i> L.)	368 ¹		11 May	8	—	25 June, 14 July, 21 Aug, 15 Sep
Lucerne (<i>Medicago sativa</i> L.)	Europe	23 Apr		1	15 June	22 June, 24 July, 1 Sep
Faba bean (<i>Vicia faba</i> L.)	Minica	23 Apr		1	25 May	20 July
Poplar (<i>Populus euramericana</i> (Dode))	Robusta		31 Mar	1	—	6 Aug
Potato (<i>Solanum tuberosum</i> L.)	Alpha		16 Apr			4 Aug

¹ Selected by the Foundation for Plant Breeding (SVP) Wageningen. See also Baan Hofman & Ennik (1980).

Methods

At the end of the experiment fresh and dry weight were determined of leaves, stems, grains or kernels, chaff or pod walls and of roots. Leaf area was measured in lucerne, faba bean and poplar. The roots were separated from the sand by carefully washing above a fine mesh.

Lucerne was harvested three times and perennial ryegrass four times. A stubble of about 5 cm high was left in the pots to resprout. In the last harvest also stubble and root were measured.

Results

Some non-destructive observations

The dates of flowering are given in Table 1. Poplar and perennial ryegrass remained vegetative. In some species (faba bean, wheat and lucerne) flowering dates were 2 or 3 days ahead in the high CO₂ environment. This effect did not occur in maize. Sionit et al. (1981c) mentioned some acceleration of flowering in wheat.

Both poplar and faba bean showed a practically constant rate of leaf appearance of about 0.5 per day. In contrast to Imazu et al. (1967), who found no effect of CO₂ on leaf appearance, the rate was higher by about 5–10 % with a high concentration of CO₂. Nutrient shortage had a small, but not significant, delaying effect on the rate of leaf appearance.

The effect of CO₂ on leaf length and width varied from absent (wheat) to moderately positive (poplar, faba bean). Internode length was invariably increased under high CO₂.

Nutrient shortage had a sizeable negative effect on leaf length and width. In poplar on 8 July the leaf lengths were reduced from 17.5 to 15.5 cm (–N) and to 12.5 cm (–P). In maize (16 June) the length of the largest leaf was reduced from 80 to 61 cm (–N) and to 72 cm (–P). Again wheat had quite stable leaf dimensions.

Potato plants were grown at only one nutrient level. Its leaves showed considerable damage symptoms under high CO₂.

Harvest data (Fig. 2)

Total dry matter. Before passing to details, first the overall reaction to CO₂ is shown (Table 2). Regression analysis indicated that the dry matter with doubled CO₂ was 20 % higher than with normal concentration ($Y(700) = 1.2 \times Y(350)$; $r^2 = 0.86$).

The CO₂ effect was greatest with good nutrient supply. With N deficiency, some reaction was still present, even in the non-leguminous species. No CO₂ response occurred with P shortage with the exception of faba beans. Maize had a small positive response to CO₂ with good nutrient supply, but a slightly negative one with nutrient deficiency. The negative response of potato was related to leaf damage.

Leaf area, specific leaf weight and dry matter content (Table 3). Leaf area was meas-

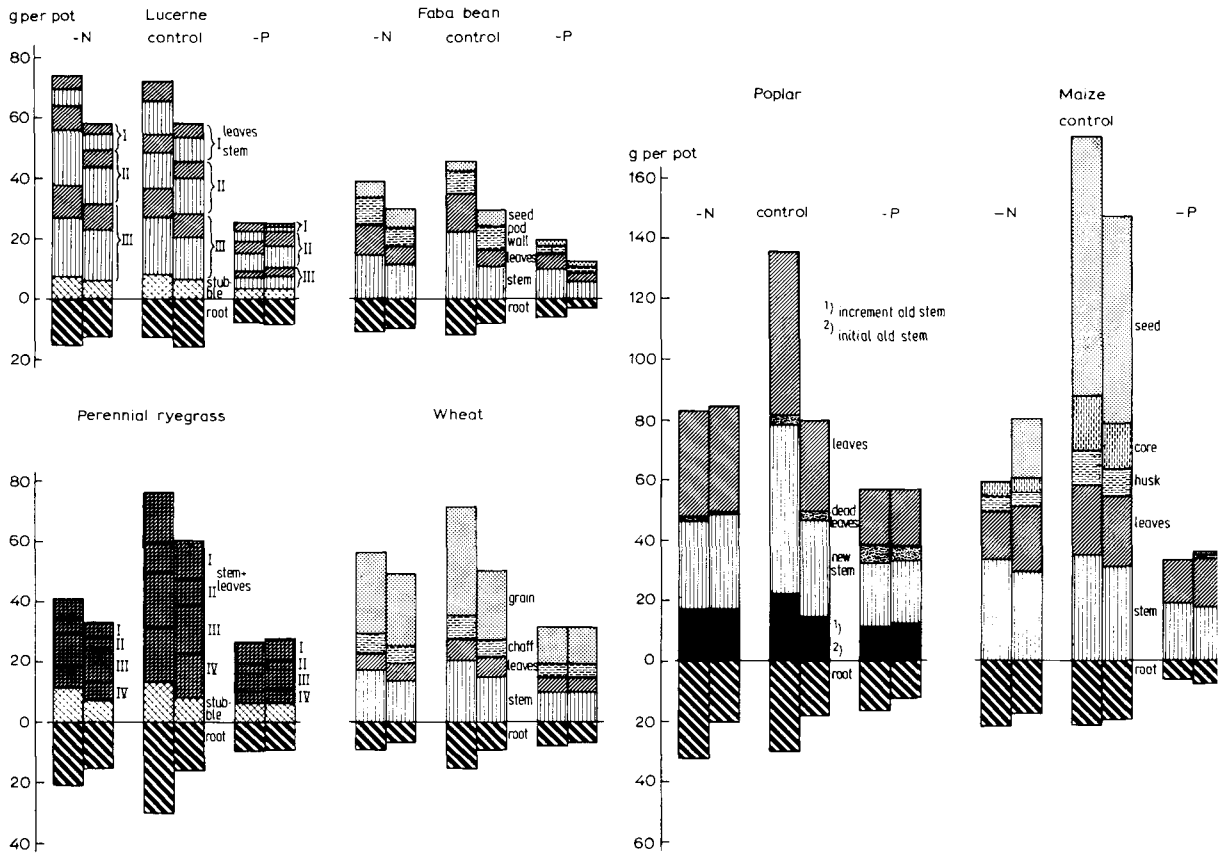


Fig. 2. Harvest data of dry matter per organ (in g per pot). In each pair the left column stands for 700 cm³/m³ CO₂, the right column for 350 cm³/m³ CO₂. In lucerne and ryegrass the data of the subsequent harvests are given from top to bottom.

ured in lucerne, field bean and poplar. A regression on these measurements showed an average of 15 % increase of leaf area under high CO₂ ($A(700) = 1.15 \times A(350)$; $r^2 = 0.83$). In faba bean CO₂ increased leaf area in all treatments. In poplar CO₂ increased leaf area in the nutrient control but decreased it in the nutrient-poor treatments. In lucerne no significant effect occurred.

In faba bean a minor part of the increase in leaf area is due to a greater number of leaves on the mainstem. Most of it is accomplished by a larger area of the individual leaves and in the control also by an increased tillering. In poplar leaf abscission was stronger under high CO₂ in the nutrient-poor treatments, presumably because a stronger root growth left less of the limited nutrient supply to the leaves. In the control treatment the larger leaf area was accomplished both by a larger number of leaves and a larger individual area.

At all nutrient levels specific leaf weight (SLW) increases under high CO₂ in lu-

Table 2. The ratios of the dry matter production under doubled CO₂ and normal CO₂. The level of significance, based on inter-pot variance, for the ratio being different from 1 is indicated by * P < 0.05 or ** P < 0.01.

	-N	Control	-P
Lucerne	1.26	1.14	1.01
Faba bean	1.25	1.52	1.67**
Perennial ryegrass	1.28**	1.39**	0.97
Wheat	1.17*	1.45*	1.03
Poplar	1.10*	1.73**	1.08
Maize	0.82	1.16*	0.9
Potato	—	0.94	—

Table 3. Some harvest data. Leaf area in cm²/pot, specific leaf weight (SLW) in mg/cm² and percentage dry matter (% DM) out of the fresh weight.

	-N		Control		-P	
	700 cm ³ /m ³	350 cm ³ /m ³	700 cm ³ /m ³	350 cm ³ /m ³	700 cm ³ /m ³	350 cm ³ /m ³
<i>Lucerne</i>						
I 23 June						
Leaf area	790	780	1270	1310	500	340
SLW	5.57**	4.12	5.46*	3.65	6.59*	4.44
Leaf % DM	28.1*	23.8	29.9**	21.9	29.2*	23.2
II 23 July						
Leaf area	2210	1710	1470	1940	720	980
SLW	3.70	3.24	4.17**	2.95	5.51	4.83
Leaf % DM	23.6	22.9	24.2	20.4	27.8	26.9
<i>Perennial ryegrass</i>						
% DM first cut	27.6**	22.8	23.7**	19.4	27.9*	25.1
% DM second cut	20.8	19.8	18.6*	16.6	21.4	21.4
% DM third cut	25.8	26.7	29.6*	26.9	33.3**	29.7
% DM fourth cut	24.3**	20.0	23.1**	19.1	24.5*	22.0
<i>Faba bean</i>						
Leaf area	2042	1734	2321*	1332	1130	670
SLW	4.81*	3.73	5.28	4.24	4.64	4.14
Leaf % DM	19.5*	16.7	19.5	17.0	18.2	16.1
<i>Poplar</i>						
Leaf area	3466**	4090	6596**	4547	2202*	2540
SLW	10.09**	8.53	8.28**	6.64	8.41**	7.53
Leaf % DM	42.3**	38.9	35.8**	30.3	32.8**	31.7

* P < 0.05; ** P < 0.01.

cerne, faba bean and poplar. The regression of these data shows a slope of unity, but an increment of 1.3 mg cm² (SLW (700) = SLW (350) + 1.3; r² = 0.93). Probably most of this increase is attributed by starch. The difference is equivalent to the total net photosynthetic production of the same leaf area of a few days only.

The content of dry matter (DM) in leaves always increases under high CO₂, but relatively less than the specific leaf weight does. The regression equation for these data is % DM (700) = 0.992 % DM (350) + 3.2; r² = 0.88. Typically about half of the increase in SLW can be ascribed to an increase in percentage dry matter. The percentage dry matter in the other organs was not significantly affected by CO₂, and has not been given in the tables.

Seed setting. Wheat is the only species that showed good setting and development in all circumstances.

Faba bean suffered from an insufficient pollination. Therefore the sink strength of the seeds developed too slow and vegetative growth continued too long, so that the plants had to be prematurely harvested to prevent lodging.

Maize only accomplished good seed setting under the normal nutrient supply. Shortage of phosphorus prevented any cob development, and shortage of nitrogen suppressed seed setting, especially under high CO₂.

In maize and wheat CO₂ increased the harvest index under good nutrient supply.

Yield components. In wheat (Table 4) no CO₂ effect was noticeable in the -P treatment, but in the control and in the -N treatment a clear growth stimulus occurred.

All yield components (number of ears/pot, number of kernels/ear and average kernel weight) were increased by CO₂ in the control, but in the -N treatment both kernel weight and the number of kernels per ear were suppressed under high CO₂. This anomalous effect can be explained by an excessive CO₂ reaction of the number of ears per pot. Increased CO₂ so much stimulated tillering or tiller survival that later the available sinks could not be filled.

In faba bean the number of seeds per pod was too low, compared to a good field

Table 4. Yield components in wheat.

	-N		Control		-P	
	700 cm ³ /m ³	350 cm ³ /m ³	700 cm ³ /m ³	350 cm ³ /m ³	700 cm ³ /m ³	350 cm ³ /m ³
Number of ears/pot	33.2**	21.3	25.2*	22.6	18.2	16.7
Number of kernels/ear	24.4	32.6	36.2**	27.8	23.9	25.8
Average kernel weight (mg DM) ¹	31.4	34.1	39.2*	36.1	27.5	27.2
Harvest index (grain/(straw + grain))	0.468	0.481	0.501**	0.450	0.385	0.376

¹ Divide by 0.84 (16 % moisture) to find agronomic kernel weight.

* P < 0.05; ** P < 0.01.

crop (2 in contrast to 4). At the harvest the seeds were not filled yet. With high CO₂ total plant dry weight is higher, but without any benefit for the yield components.

Roots. CO₂ has two counteractive effects on the shoot/root ratio. Growth of roots can be promoted by high CO₂ when there is an assimilate shortage in the roots. This effect dominates the majority of the results. In perennial ryegrass the root weight fraction even reached 0.33 under the (-N,700) treatment.

In lucerne and also in maize the opposite happened: root growth was suppressed under high CO₂. This effect is possibly caused by a reduction of transpiration through CO₂ induced stomatal closure and a consequently higher relative water content in plant and soil.

The partitioning of assimilates is influenced by the water status of the plants. When the water status is better, a smaller fraction of the assimilates flow to the roots and root growth is reduced. Therefore CO₂ can also suppress root growth. Which of the two opposing effects predominates is dependent on species and environment.

In the leguminous species heavy nodulation occurred in the -N treatment, but stronger with high than with normal CO₂. Nodulation was absent in the control at both CO₂ levels. Surprisingly, faba bean showed some nodulation in the (-P,700) treatment.

Leaf damage in potato. This species was not subjected to the -N and -P treatments and was grown in large containers with sufficient nutrients added. Four containers were placed in each compartment of the greenhouse on 25 May and the crop was harvested on 4 August.

Harvest data are given in Table 5. Almost all tubers were formed and filled during the period of CO₂ enrichment. Potatoes showed an unusual negative response to CO₂. Its leaves developed a brownish fringe as if diseased or suffering from potassium deficiency. Microscopic observations showed a very high content of starch. The growing starch grains probably have physically damaged the chloroplasts. Marked but unharmed accumulation of starch with CO₂ enrichment was recorded in tomato by Madsen (1968), in subterranean clover by Cave et al. (1981) and in cotton by Wong (1980).

Table 5. Harvest data of potato in g per container.

	700 cm ³ /m ³	350 cm ³ /m ³
Leaf DM	119	131
Stem DM	56**	97.5
Root DM	19**	30
Tuber DM	980	1135
Total DM	1174	1394
Tuber fresh weight	3619	4099

** P < 0.01.

Discussion and conclusions

Biometrical adaptation to increased CO₂

Closed leaf cover typically occurs at a leaf area index of 3, which corresponds to 120 g m⁻² of leaf dry matter at a specific leaf weight of 4 mg cm⁻². Since the pot density was about 16 pots m⁻² the transition from exponential to linear growth roughly takes place at a leaf area per pot of about 1900 cm² or a dry weight of about 7.5 g. In perennial ryegrass, lucerne and wheat the leaf area was at about this size at harvest, in the tall-growing poplar, maize and faba bean a couple of times larger. Therefore a major portion of growth must have taken place in the exponential phase of incomplete cover. The duration of this phase is about 30 days, which at a relative growth rate of 0.15 per day leads to a 90-fold multiplication. A conservative estimate of the effect of CO₂ doubling on the leaf assimilation rate as derived from leaf chamber measurements is an increase by 30 %. Without internal compensation the relative growth rate should rise to 0.2 per day so that the same 90-fold multiplication is reached after 22.5 days. At the time the control crop has only reached 30-fold multiplication so that the CO₂ effect after the exponential phase should be expected to be as high as a factor 3. Such high values are never found. The major reason is a considerable biometrical adaptation, such as increased specific leaf weight and leaf weight ratio. The mechanism of this adaptation is probably a limitation of the demand for products of photosynthesis by growth. Carbohydrate reserves like starch accumulate in cells with the high CO₂ treatment, and so a higher specific leaf weight results.

As a result of this adaptation the relative increase of total dry matter due to CO₂ doubling is not much larger in the exponential growth phase than it is in the linear phase after canopy closure.

As soon as all light is intercepted it is only the light utilization that matters. In this stage of growth the effect on net assimilation rate is no longer magnified by positive feedback through leaf area growth, so that partitioning has lost its influence on total dry matter accumulation.

Quantification of the CO₂ effect

The data of Table 2 suggest that on the average under good nutrient supply about 1.5 times as much dry matter is accumulated under double CO₂. With nitrogen deficiency this ratio drops to an average of 1.2, and with phosphorus deficiency even to just 1.0 except for faba bean.

To represent the overall effect of CO₂ induced growth in models for the global carbon cycle, the concept of the biotic growth factor β is used (Gifford, 1980). It modifies growth rate as follows

$$G = G_0(1 + \beta \ln(C/C_0))$$

where G is net growth, C is the CO₂ concentration and β is called the biotic growth

factor. The subscript 0 is assigned to a reference level, usually at the present CO₂ concentration. This equation has no physiological basis, but it is the simplest one-parameter equation that also shows diminishing returns with increasing CO₂.

The data just discussed suggest a value of the biotic growth factor of about 0.7 under good nutrient supply, dropping down to somewhere half this value with nitrogen shortage and to even zero with phosphorus deficiency.

C₃ versus C₄ response

Maize, as a C₄ plant, shows a much smaller response than the other species which is in agreement with a series of investigations by Imai & Murata (1976-1979) on C₃ versus C₄ response.

Some major reasons for the small growth reaction to CO₂ in C₄ plants are:

- a) a stomatal behaviour that tends to stabilize the internal CO₂ concentration (Goudriaan & van Laar, 1978). In C₃ plants this stabilization is less effective and so the CO₂ response of assimilation is larger;
- b) photorespiration is absent. In C₃ plants photorespiratory losses can be suppressed by higher CO₂.

In maize the remaining small positive effect under good nutrient supply is probably due to suppression of transpiration and a subsequent decrease of some water-stress, just before watering. Transpiration is also reduced in C₃ plants but to a lesser extent (Sionit et al., 1981a; Gifford, 1979; Wong, 1980; Rosenberg, 1981). Because photosynthesis is increased, water use efficiency appears to rise just as strongly in C₃ as in C₄ plants.

Interaction with nutrient deficiency

The remaining growth response to CO₂ under nitrogen shortage may be due to:

- a) improved uptake of nitrogen
- b) increased nitrogen use efficiency, which is equivalent to a lowered minimum nitrogen content.

Probably both effects occurred. For green leaves Wong (1979) found a decreased RuDP carboxylase content, which constitutes about half of leaf protein, with high CO₂. Although the mechanism is not clear, this reaction can be understood as an adaptation to a lowered demand for RuDP carboxylase with high CO₂. At the same time he found an increased mesophyll resistance in cotton as a result of a previous CO₂ treatment. This result is at variance with observations of Imai & Murata (1978c) who also recorded decreased assimilation as an after effect, but found increased stomatal resistance to be responsible.

Under P shortage no CO₂ effect was found. The interaction of CO₂ with shortage of phosphorus appears fully governed by the law of limiting factors. Apparently the biochemical role of phosphorus cannot be reduced with increased CO₂.

Acknowledgements

Our thanks are due to Drs K. B. A. Bodlaender and Ing. J. Marinus for their cooperation in the potato experiment, to Mr J. van Cleef for the construction of the CO₂ control system, to Mr G. C. Beekhof for the drawings and to Ms H. F. Helder and Mr B. H. J. van Amersfoort for typing the manuscript.

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