PHYSIOLOGIA PLANTARUM 73: 553-559. Copenhagen 1988

The effect of an elevated atmospheric CO_2 concentration on growth, photosynthesis and respiration of *Plantago major*

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Poorter, H., Pot, C. S. and Lambers, H. 1988. The effect of an elevated atmospheric CO_2 concentration on growth, photosynthesis and respiration of *Plantago major*. Physiol. Plant. 73: 553-559.

The effect of an elevated atmospheric CO_2 concentration on growth, photosynthesis and root respiration of *Plantago major* L. ssp. *major* L. was investigated. Plants were grown in a nutrient solution in growth chambers at 350 and 700 µl l^{-1} CO_2 during 7 weeks. The total dry weight of the CO_2-enriched plants at the end of this period was 50% higher than that of control plants. However, the relative growth rate (RGR) was stimulated only during the first half of the growing period. The transient nature of the stimulation of the RGR was not likely to be due to end-product inhibition of photosynthesis. It is suggested that in *P. major,* a rosette plant, self-shading causes a decline in photosynthesis and results in an increase in the shoot:root ratio and a decrease in RGR. CO_2-enriched plants grow faster and consequently suffer more from self-shading. Corrected for this ontogenetic drift, high CO_2 concentrations stimulated the RGR of *P. major* throughout the entire experiment.

Key words - Biomass allocation, carbon dioxide enrichment, photosynthesis, *Plantago major,* relative growth rate, respiration, self-shading.

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Introduction

The growth-stimulating effect of an elevated atmospheric CO_2 concentration has been reported by many authors (for reviews see Carlson and Bazzaz 1980, Kramer 1981). Most experiments encompass only 1 harvest at the end of the growing period. On the average a stimulation in yield of 30-35% is found with a doubling of the CO_2 concentration (Kimball 1983).

Reports in which the time course of the effect of a high CO_2 concentration has been investigated are much scantier. Rogers et al. (1984) found an increase in relative growth rate (RGR) of *Glycine max* only during the first 2 weeks. Thereafter, high CO_2 concentrations no longer stimulated the RGR. Neales and Nicholls (1978) also found a strong interaction between time and the stimulation of the RGR of *Triticum aestivum* plants. During week 1 the RGR was increased by high CO_2 concentrations. However, during week 2 a negative correlation between RGR and the applied CO_2 concentration was found.

What may be the cause of the transient nature of this stimulation? Hicklenton and Jolliffe (1980) combined a growth analysis with measurements on photosynthesis. In a study of *Lycopersicon esculentum* plants grown in CO_2-enriched atmosphere, they found that photosynthesis was enhanced at an early stage of development but not at a later stage. This was correlated with a time-dependent stimulation of the RGR. The same correlation was observed in a study of growth and photosynthesis of *Desmodium paniculatum* (Wulff and Strain 1982). Electron micrographs of chloroplasts showed high starch accumulation and reduced grana formation in CO_2-enriched plants. High starch concentrations inhibit photosynthesis, as has been shown in a short-term experiment by Nafziger and Koller (1976). In a long-term experiment the reduction of photosynthesis of *Gossypium hirsutum* could be reversed within a few

Received 25 January, 1988; revised 10 May, 1988

days by transferring plants grown at 1000 µl l^{-1} CO_2 to 350 µl l^{-1} CO_2 (Sasek et al. 1985). The recovery of photosynthesis was correlated with a rapid depletion of the starch pool. Thus, a high CO_2 concentration enhances photosynthesis more than is needed to fulfill the demand of the sinks, resulting not only in a higher RGR, but also in accumulation of assimilates. This causes an end-product inhibition of photosynthesis (Azcón-Bieto 1983) and, consequently, a decrease in RGR.

Little attention is paid in the literature to other factors that may influence the RGR stimulation. Not only photosynthesis, but also respiration may be affected by CO_2 (Gifford et al. 1985, Hrubec et al. 1985), as well as the pattern of biomass allocation to shoots and roots (Sionit et al. 1981, Carter and Peterson 1983). All these factors may interact and cause the growth stimulation to be transient.

The present study was undertaken to investigate the effects of a high atmospheric CO_2 concentration on RGR and carbon economy of *Plantago major*. Special attention was given to a possible time dependence in the stimulation of the RGR and the importance of photosynthesis, respiration and the pattern of biomass allocation in explaining such a time dependence.

Abbreviations - AC, ambient CO_2 concentration (350 µl l^{-1}); HC, high CO_3 concentration (700 µl l^{-1}); NAR, net assimilation rate; RGR, relative growth rate; SLA, specific leaf area.

Materials and methods

Growth of the plants

Germination and growth occurred in two growth rooms. The CO_2 concentration in both growth rooms was controlled using two infrared gas analysers (Siemens, type ZFPCS and Hartman & Braun, type 2T). The CO_2 cylinders did not contain ethylene in detectable amounts (cf. Morison and Gifford 1984). Light was provided by Philips HPI-T lamps (400 W) and 40 W glowing bulbs in a 1:1 ratio. The photosynthetic photon flux density was 230-270 µmol m^{-2} s^{-1} during 12 h a day. The day temperature was 20 ± 0.5°C, the relative humidity ca 60%. At night these values were 18 ± 0.5°C and 90%, respectively.

An inbred line of Plantago major L. ssp. major L. (line G1 in Van Dijk and Van Delden 1981) was used in this experiment. The original genotype was collected along a roadside in a frequently mown lawn with a dense grass cover (Poorter and Lambers 1986). Seeds were germinated in sterilized vermiculite moistened with rain water at a CO_2 concentration of 350 ± 20 µl l^{-1}. After 18 days, the seedlings were transferred to a nutrient solution as described by Smakman and Hofstra (1982). Once a week this solution was renewed. To prevent growth limitation by nutrients or mutual shading, the number of plants in each container varied between 5 and 20, depending on their size.

Experimental design

Two experiments were carried out. In the first experiment half of the plants were placed in a growth room with a CO_2 concentration of 700 ± 20 µl l^{-1}, eighteen days after sowing. The control plants were kept at 350 µl l^{-1}. A destructive growth analysis was carried out. During 8 weeks 12 plants of each treatment were harvested every week. Leaf thickness, the number of leaves, total leaf area, projected leaf area and fresh and dry weight of leaf blades, petioles and roots were determined.

The destructive analysis was complemented by a non-destructive growth analysis, to avoid the problems with the interpretation that the former might cause (Poorter and Lewis 1986). The fresh weights of 14 individual plants of both treatments were determined each week. The results of such a non-destructive experiment might be influenced by the repeated handling of the plants. However, since no significant difference in weight was found between the non-destructively measured plants and the other ones at the end of the experiment, it was concluded that the handling did not cause any growth difference.

During the experiment some measurements of photosynthesis and root respiration were carried out.

In the second experiment attention was focussed on the CO_2 exchange. Again, half of the plants were transferred to a growth chamber with a CO_2 concentration of 700 µl l^{-1} after the period of germination. During 6 weeks photosynthesis, shoot respiration and root respiration were measured for both CO_2-enriched and control plants (n = 4). After the measurements plants were harvested and total leaf area, projected leaf area, and dry weight of leaf blades, petioles and roots were determined. For both treatments, leaf blade length and petiole length were measured throughout the experiment for each leaf of 8 individual plants.

Every week the plants and the CO_2 concentrations were switched between the two growth rooms, to avoid interaction of the growth room and the CO_2 treatment.

Measurements

Leaf area was measured with a leaf area meter (model 3100 LI-COR Inc., Lincoln, NE, USA). The projected leaf area was determined, using slides made with a camera placed perpendicularly to the horizontal plane. The slides were projected, the projected area was drawn on paper, and then the area was measured using a Hewlett Packard digitizer (model 9847a).

Dry weight of the different plant parts was measured after drying for at least 24 h at 80°C. In the non-destructive experiment, fresh weight was determined using the following procedure: Plants were removed from the nutrient solution and, with the roots hanging freely, exposed to the air for 2 min. Thereafter, the last drops of attached water were removed by gently blotting the roots with paper tissues, whereupon the plants were

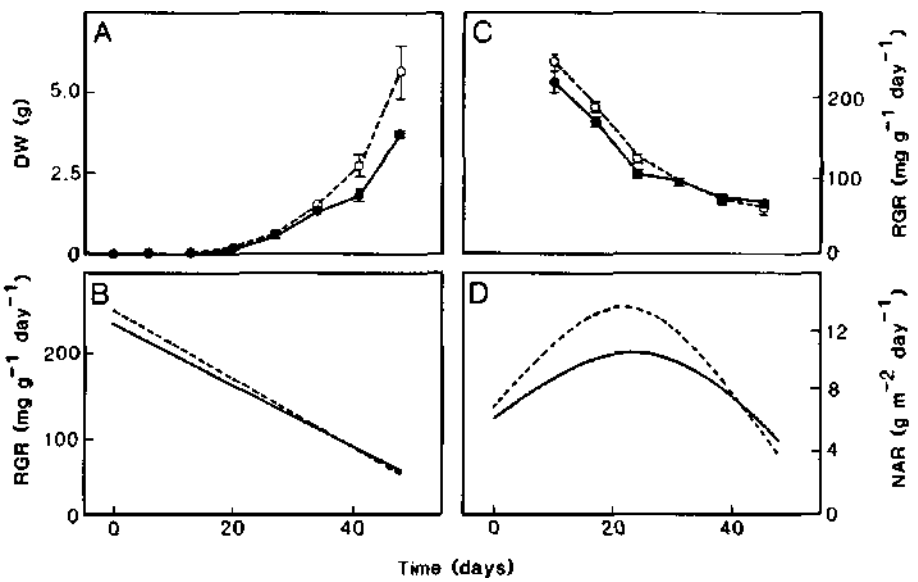

Fig. 1. A, Time course of total dry weight of *Plantago major* plants grown at 350 (● ——— ●) and 700 (○– – –○) µl l^{-1} CO_2; mean values ± SE (n = 10). B, Time course of the RGR (on dry weight basis) of plants grown at 350 (continuous line) and 700 (broken line) µl l^{-1} CO_2. RGR was calculated by curve fitting (Hunt 1982). C, RGR (total fresh weight basis) derived from the non-destructive growth experiment; mean values ± SE (n = 12). D, Net assimilation rates, calculated by curve fitting. Time is indicated as days after start of the treatment.

weighed, and subsequently transferred back to the nutrient solution.

Whole shoot photosynthesis and respiration of the shoot and the roots were measured by CO_2 exchange. Intact plants were placed in a cuvette with the shoot and roots in separate compartments. The photosynthetic photon flux density was the same as in the growth rooms. Plants grown at 700 µl l^{-1} CO_2 were measured at 700 µl l^{-1} CO_2, plants grown at 350 µl l^{-1} measured at 350 µl l^{-1}. CO_2 exchange was measured differentially with an infrared gas analyser (ADC, model 225 MK3, Hoddesdon, UK) in an open system. Errors in the measurements due to transpiration were minimized by leading the airstream trough a cooling device (Penning de Vries et al. 1984).

Chemical analyses

Soluble sugars were extracted with 80% (v/v) ethanol from dried and pulverized plant material. In the residue, starch was hydrolyzed by boiling in 3% (w/v) HC1. Both sugars and starch were determined colorimetrically after reaction with anthrone (Fales 1951).

Statistical analysis of the data

The Statistical Package for the Social Sciences, procedure MANOVA was used to analyse the data (Hull and Nie 1981). Analyses of variance were performed on the data with CO_2 and Time as independent variables. To minimize the effect of outlying observations, data were trimmed by excluding the plant with the highest and the plant with the lowest total dry weight in each cell from the analysis (Barnett and Lewis 1978). Differences in RGR are tested as Time × CO_2 interaction in an analysis of variance with ln-transformed plant weight as dependent variable (Poorter and Lewis 1986).

Results

Growth of the plants was increased by the CO_2 treatment (Fig. 1A). At the end of the experimental period the total dry weight of the CO_2-enriched plants in the destructive analysis was 50% higher than that of the

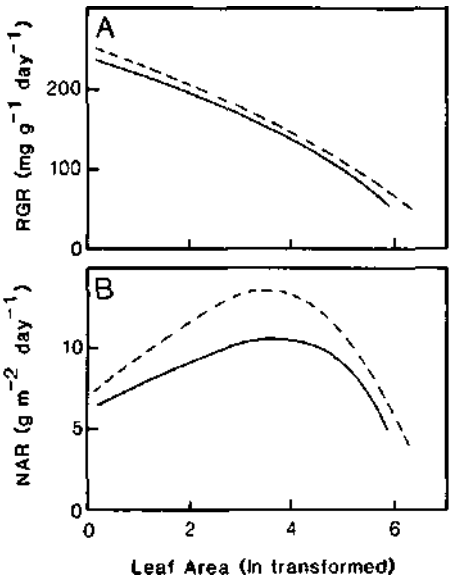

Fig. 2. Time courses of (A) the RGR (on total dry weight basis) and (B) the net assimilation rate plotted versus total leaf area (ln-transformed) of plants grown at 350 (continuous line) and 700 (broken line) µl l^{-1} CO_2.

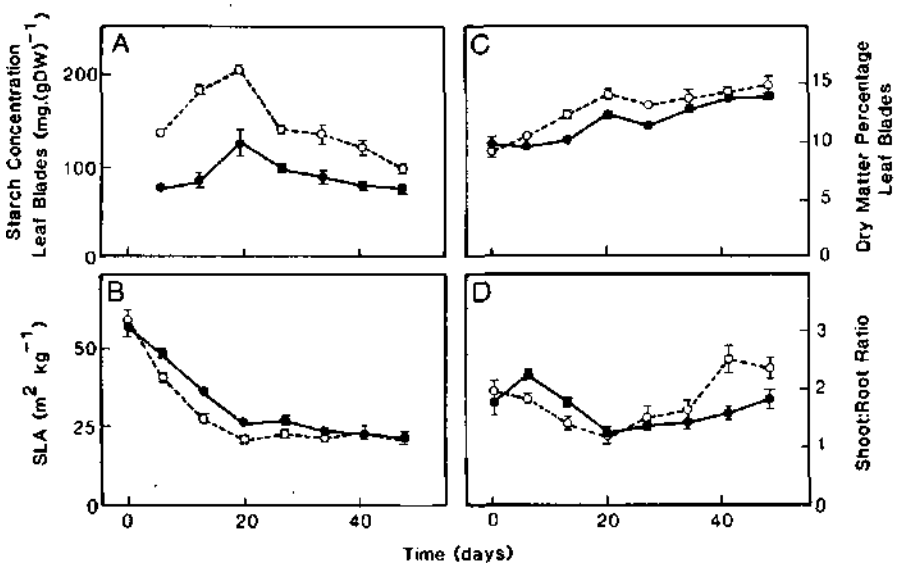

Fig. 3. Time courses of (A) starch concentration in the leaf blades, (B) specific leaf area, (C) dry matter percentage of the leaf blades, and (D) shoot to root ratio of plants grown at 350 (●——●) and 700 (○– – –○) µl l^{-1} CO_2;. All ratios were calculated on a dry weight basis. Mean values ± SE (n = 10), except for A, where 10 plants were pooled in 1 group (day 6) or 2 groups (day 13 and after) prior to the starch determination.

control plants. Figure 1B shows the RGR of these plants. The treatment had a significant effect on the RGR ($P \leq 0.05$). However, this stimulation was found only during the first 30 days of the experiment. Thereafter, the RGR of the enriched plants was the same as or even lower than that of the control plants. The results of the non-destructively measured plants (Fig. 1C) confirm those of the destructive growth analysis: a stimulation of the RGR by the CO_2 treatment at the beginning of the experiment (11%), but a reduction at the end (12%). On the average the RGR was stimulated by 7%.

The difference in RGR caused a marked difference in plant size during the experiment. Therefore, at the end of the experimental period, plants of different size, and possibly of different ontogenetic development, are compared. To correct for this, the RGR was plotted against a measure of plant size, i.e. leaf area (Fig. 2A). In contrast with Fig. 1B, the RGR of the CO_2-enriched plants, when plotted versus ln-transformed leaf area, remained stimulated, even at the highest leaf area.

NAR was stimulated by the CO_2 treatment at the beginning of the experiment, but, as for RGR, this stimulation disappeared in the last 3 weeks, when NAR was plotted against time (Fig. 1D). The NAR was stimulated throughout the whole experiment, when plotted against leaf area (Fig. 2B).

There was a marked difference in the starch concentration of the leaf blades (Fig. 3A), whereas no significant differences between treatments were found in the starch concentration of petioles and roots (data not shown). Similar results were obtained for soluble sugars, although quantitatively of less importance. The mean concentration of soluble sugars in the leaf blades was 37 mg g^{-1} for the HC plants and 26 mg g^{-1} for the AC plants (other data not shown). The difference in concentration of starch and soluble sugars was time dependent: large at the beginning of the experiment,

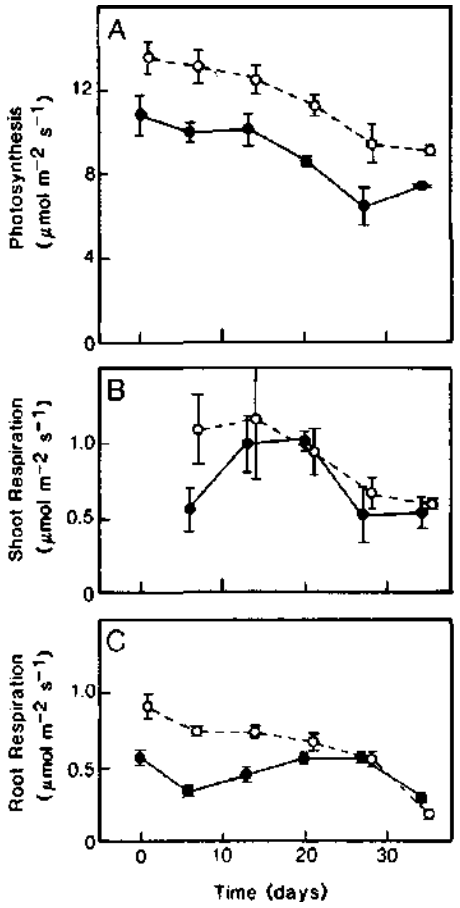

Fig. 4. A, Time course of (A) the net photosynthesis rate per leaf area, (B) shoot respiration, and (C) root respiration for slants grown at 350 (●——●) and 700 (○– – –○) µl l^{-1} CO_2. Photosynthesis was measured at the same CO_2 concentration and photosynthetic photon flux density as during growth. Mean values ± SE (n = 4).

smaller at the end. The same holds for the parameters related to starch accumulation: SLA (Fig. 3B) and the dry matter percentage of the leaf (Fig. 3C). Another parameter for which a time-dependent difference between treatments was found ($P \leq 0.001$) was the shoot: root ratio (Fig. 3D). This ratio was lower for the CO_2-enriched plants during the first phase of the experiment and higher at the end.

In the second experiment the energy metabolism of *P. major* was further studied. Net photosynthesis rate, expressed on a leaf area basis, declined with time ($P \leq 0.01$, Fig. 4A). A significant enhancement by the CO_2 treatment was found throughout the entire experiment. To obtain insight in the relative contribution of photosynthesis and respiration to the observed difference in NAR, both shoot and root respiration were expressed on a leaf area basis (Fig. 4B,C). Shoot respiration may have been slightly higher for HC plants in the beginning of the experiment, but thereafter no differences were found. The root respiration was affected for a longer time than respiration in the shoot. Expressed on both a leaf area and a root dry weight basis, root respiration was higher for HC than for AC plants during the first 4 weeks. The rate of leaf appearance was slightly enhanced, so that by week 6 HC plants had formed 16.9 leaves, the control plants 15.1 leaves. As long as leaves were alive they increased in length; both the leaf blades and the petioles elongated continuously (Fig. 5).

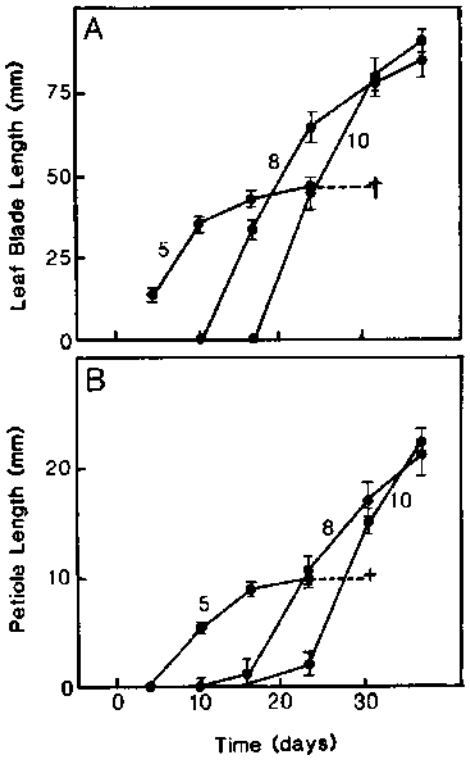

Fig. 5. Time course of the petiole length of different leaves of plants grown at 350 µl l^{-1} CO_2. Mean values ± SE (n = 8). The numbers refer to the sequence of appearance of the leaves. Plants grown at 700 µl l^{-1} CO_2 showed comparable time courses.

Discussion

Plant weight increased considerably due to CO_2 enrichment. Grown with ample supply of water and nutrients, but under relatively low light conditions, dry weight increased by 50%. This value is high compared to those reported by Kimball (1983) in his analysis of 430 observations on CO_2 enrichment.

Photosynthesis was stimulated during at least the first 6 weeks of the experiment. This is rather a long time compared to other experiments (Wulff and Strain 1982, Spencer and Bowes 1986). The long stimulation may be caused by a combination of a relatively low light intensity (ca 250 µmol m^{-2} s^{-1}), a short light period (12 h), and a rather high night temperature (18°C). In combination with the self-shading discussed later, these factors limit the production of carbohydrates in comparison with the demand in the sinks, thus preventing end-product inhibition (cf. Clough et al. 1981).

Shoot respiration was hardly affected by the CO_2 treatment. This is in apparent contrast with data of Hrubec et al. (1985), who measured the time course of dark respiration in individual soybean leaves. They found that the respiration was enhanced in young leaves, but not in mature ones. However, also in soybean the shoot respiration may have been similar in CO_2-enriched and control plants, when all leaves are taken into account. The root respiration in the present experiment was stimulated by CO_2 enrichment in young plants, but not in elder ones. This may have been a consequence of the faster growth of the roots of the HC plants at the beginning of the experiment (cf. Van der Werf et al. 1988). Data on root respiration of CO_2-enriched plants are scarce in literature. Gifford et al. (1985) describe some results for three species. In wheat, root respiration of enriched plants was sometimes reduced, in sunflower respiration was enhanced, and in mung bean no significant differences were found. However, as can be seen from Fig. 4C, it is rather premature to compare species if no systematic time trends are available.

The stimulation of the RGR was not constant. The increase in RGR was highest at the beginning of the experiment (Fig. 1B, C). After 4 weeks the difference in RGR had disappeared, and towards the end of the experiment the RGR of the AC plants was even higher than that of the HC plants. Such a disappearance of the stimulation of the RGR is in accordance with earlier observations (Neales and Nicholls 1978, Rogers et al. 1984).

Could the accumulation of starch in the chloroplasts and the following inhibition of photosynthesis explain the disappearance of the RGR stimulation in the present experiment? As there are no data on gas exchange

for the last 2 weeks, we cannot be conclusive about what happens in that time. The difference in NAR disappears during the last 2 weeks (Fig. 1D), indicating that photosynthesis of the HC plants is no longer stimulated. However, end-product inhibition is unlikely, as the difference in starch concentration of the leaves at the end of the experiment is less than in the beginning (Fig. 3A).

In our opinion the present results can best be explained by the shoot architecture of the plants. *P. major* is a rosette plant with, for the inbred line used in this experiment, prostrate leaves. The angle between the older leaves and the horizontal plane does not exceed 10°. Due to these properties, there is a considerable amount of self-shading as plants form more leaves. This is shown in Fig. 6, where the ratio between total leaf area and the projected leaf area is plotted, a leaf area index for individual plants. After 3 weeks leaves start to overlap each other. However, self-shading is partly avoided by a steady growth of blades and petioles of the older leaves (Fig. 5). The lower leaves are thus "pushed" beyond the new ones. This enables the old leaves to intercept, at least partly, as much as possible of the available photon flux. The importance of this extension becomes clear, when the relation between CO_2 assimilation and leaf area is examined. It appears that there is a negative correlation ($P \leq 0.001$) between total leaf area and whole plant photosynthesis, when the latter is expressed on a leaf area basis: A higher total leaf area does not result in a proportionally higher photosynthesis. However, such a negative relationship does not exist between projected leaf area and photosynthesis expressed per projected leaf area. Apparently, enlargement of the projected leaf area is more important in enhancing whole plant photosynthesis than an increase in total leaf area.

The above-mentioned events are reflected in both the pattern of biomass allocation to shoot and roots and in the starch accumulation in the leaf blades. When plants are transferred from low to high CO_2 conditions, the shoot:root ratio will adjust to the higher rate of photosynthesis, in accordance with the theory of the "functional equilibrium" (Brouwer 1963): The shoot to root ratio will decrease (Fig. 3D). In addition, an extra amount of starch and soluble sugars is accumulated. But as plants grow larger self-shading occurs and relatively more material has to be invested in the shoot to maintain the energy supply of the plant: The shoot to root ratio increases. At the end of the experiment the shoot to root ratio of the HC plants is even higher than that of the control plants. By that time, the difference in starch concentration in the leaf blades of the HC plants and the AC plants is reduced, and the differences in SLA and dry matter percentage of the leaf have disappeared. Self-shading, increasing with the size of the plants, is supposed to be one of the major causes of the clear ontogenetic drift in RGR in *P. major*. As HC plants show a higher RGR at the beginning of the experiment, their development will be accelarated. This implies an earlier constraint on the RGR due to size, compared to the control plants, a factor which may be confounded with the CO_2 treatment. If the RGR is corrected for this difference in size between plants of both treatments (Fig. 2A), the high CO_2 concentration appears to stimulate growth throughout the whole experiment. The same conclusion holds for the NAR (Fig. 2B).

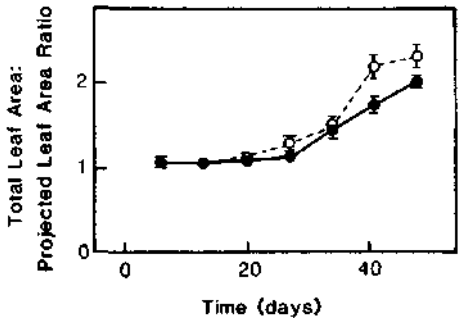

Fig. 6. Time course of the ratio between total leaf area and projected leaf area of plants grown at 350 (●—●) and 700 (○– – –○) µl l^{-1} CO_2. Mean values ± SE (n = 10).

Conclusions

Growth of *P. major* strongly reacts to a rise in the atmospheric CO_2 concentration due to an increased photosynthesis. The growth reaction is time dependent. This is unlikely to be due to end-product inhibition of photosynthesis, but is rather a consequence of the growth form of the species: CO_2-enriched plants are larger and larger plants have a lower RGR due to self-hading. Corrected for this ontogenetic drift, a high CO_2 concentration enhances the RGR during the whole experimental period.

Acknowledgements - We thank Adrie van der Werf, Paul Dijkstra, Thijs Pons and Katrien Jansen for stimulating discussions and critical reading of the manuscript. This investigation was supported by the Ministeries of Housing, Physical Planning and Environment and of Education and Science. Grassland Species Research Group Publ. no 122.

References

Azcón-Bieto, J. 1983. Inhibition of photosynthesis by carbohydrates in wheat leaves. - Plant Physiol. 73: 681-686.

Barnett, V. & Lewis, T. 1978. Outliers in Statistical Data. - John Wiley & Sons, Chichester. p. 48. ISBN 0-471-99599-1.

Brouwer, R. 1963. Some aspects of the equilibrium between overground and underground plant parts. - Meded. Inst. Biol. Scheik. Onderz. Landb. Gewas. 213: 31-39.

Carlson, R. W. & Bazzaz, F. A. 1980. The effects of elevated CO_2 concentrations on growth, photosynthesis, transpiration and water use efficiency of plants. - *In* Environmental and Climatic Impact of Coal Utulization (J. Singhjag and A. Depek, eds), pp. 609-623. Academic Press, New York. ISBN 0-12-646360-3.

Carter, D. R. & Peterson, K. M. 1983. Effects of a CO_2-enriched atmosphere on the growth and competitive interaction of a C_3 and a C_4 grass. - Oecologia 58: 188-193.
Clough, J. M., Peet, M. M. & Kramer, P. J. 1981. Effects of high atmospheric CO_2 and sink size on rates of photosynthesis of a soybean cultivar. - Plant Physiol. 67: 1007-1010.
Fales, F. W. 1951. The assimilation and degradation of carbohydrates by yeast cells. - J. Biol. Chem. 193: 113-124.
Gifford, R. M., Lambers, H. & Morison, J. I. L. 1985. Respiration of crop species under CO_2 enrichment. - Physiol. Plant. 63: 351-356.
Hicklenton, P. R. & Jolliffe, P. A. 1980. Alterations in the physiology of CO_2 exchange in tomato plants grown in CO_2 enriched atmospheres. - Can. J. Bot. 58: 2181-2189.
Hrubec, T. C., Robinson, J. M. & Donaldson, R. P. 1985. Effects of CO_2 enrichment and carbohydrate content on the dark respiration of soybeans. - Plant Physiol. 79: 684-689.
Hull, C. H. & Nie, N. H. 1981. SPSS update 7-9: New procedures and Facilities for Releases 7-9. - McGraw-Hill, New York. pp. 1-79. ISBN 0-07-046542-8.
Hunt, R. 1982. Plant Growth Curves. The Functional Approach to Plant Growth Analysis. - E. Arnold Publishers, London, pp. 14-120. ISBN 0-7131-2844-5.
Kimball, B. A. 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. - Agron. J. 75: 779-788.
Kramer, P. J. 1981. Carbon dioxide concentration, photosynthesis and dry matter production. - BioScience 31: 29-33,
Morison, J. I. L. & Gifford, R. M. 1984. Ethylene contamination of CO_2 cylinders. - Plant Physiol. 75: 275-277.
Nafziger, E. D. & Koller, H. R. 1976. Influence of leaf starch concentration on CO_2 assimilation in soybean. - Plant Physiol. 57: 560-563.
Neales, T. F. & Nicholls, A. O. 1978. Growth response of young wheat plants to a range of ambient CO_2 levels. - Plant Physiol. 57: 560-563.
Penning de Vries, F. W. T., Akkersdijk, J. W. J. & Oorschot, J. L. P. 1984. An error in measuring respiration and photosynthesis due to transpiration. - Photosynthetica 18: 146-149.
Poorter, H. & Lambers, H. 1986. Growth and competitive ability of a highly plastic and a marginally plastic genotype of *Plantago major* in a fluctuating environment. - Physiol. Plant. 67: 217-222.
– & Lewis, C. 1986. Testing differences in relative growth rate: A method avoiding curve fitting and pairing. - Physiol. Plant. 67: 223-226.
Rogers, H. H., Cure, J. D., Thomas, J. F. & Smith, J. M. 1984. Influence of elevated CO_2 on growth of soybean plants. - Crop Sci. 24: 361-366.
Sasek, T. W., DeLucia, E. H. & Strain, B. R. 1985. Reversibility of photosynthetic inhibition in cotton after long-term exposure to elevated CO_2 concentrations. - Plant Physiol. 78: 619-622.
Sionit, N., Mortensen, D. A., Strain, B. R. & Hellmers, H. 1981. Growth response of wheat to CO_2 enrichment and different level of mineral nutrition. - Agron. J. 73: 1023-1027.
Smakman, G. & Hofstra, R. 1982. Energy metabolism of *Plantago lanceolata* as affected by change in root temperature. - Physiol. Plant. 56: 33-37.
Spencer, W. & Bowes, G. 1986. Photosynthesis and growth of water hyacinth under CO_2 enrichment. - Plant Physiol. 82: 528-533.
Van der Werf, A., Kooijman, A., Welschen, R. & Lambers, H. 1988. Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis.* - Physiol. Plant. 72: 483-491.
Van Dijk, H. & Van Delden, W. 1981. Genetic variability in Plantago species in relation to their ecology. Part 1: Genetic analysis of the allozyme variation in *P. major* subspecies. - Theor. Appl. Gen. 60: 285-290.
Wulff, R. D. & Strain, B. R. 1982. Effects of CO_2 enrichment on growth and photosynthesis in *Desmodium paniculatum.* - Can. J. Bot. 60: 1084-1091.

Edited by A. Kylin