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Functioning of Plantago major and Urtica dioica exposed to elevated CO2

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Summary

The atmospheric CO_2 concentration has risen from 280 $\mu l\ l^{-1}$ at the start of the industrial revolution, around 1880, to over 350 $\mu l\ l^{-1}$ at present. This rise is expected to increase far into the next century, even if the release of CO_2 to the atmosphere would stabilise at the present level. The often predicted increase in the mean global temperature, the so-called 'greenhouse effect', is the most conspicuous consequence of this rise in CO_2 concentration. Although the eight o'clock news sometimes refers to CO_2 as an air-polluting gas, its presence is a prerequisite for plant growth and agricultural production. CO_2 is a substrate for photosynthesis, and is often in short supply and thereby it limits plant growth. An increase in the concentration of CO_2 may cause a rise in the rate of photosynthesis and an increase in the production of individual plants, crops and natural vegetation. Indeed, since the early sixties, in the dutch greenhouse vegetable production 'CO_2-fertilisation' is a common practice to increase yield.

In most plants from temperate climate zones grown under favourable conditions, in the short term, a rise in CO_2 concentration causes an increase in the rate of photosynthesis through an increased substrate supply as well as a suppression of photorespiration. The rate of growth closely follows this short-term effect on photosynthesis. Within a day the relative growth rate (RGR) is increased in plants grown at elevated CO_2 as compared to plants grown at ambient CO_2 levels. A plant's long term response to elevated CO_2 is more uncertain. In various plant species a continued stimulation of the rate of photosynthesis as well as a return of this rate to the level observed in control plants has been found.

For dutch agriculture an elevated CO_2 concentration may contribute to a rise in yield, since growth conditions approach optimal water and nutrient supply in many years. However, in regions with more extreme climates or poor soils, conditions of water and nutrient supply are often less favourable for plant growth and a rising atmospheric CO_2 concentration may not lead to the stimulation of agricultural production. The same applies to natural vegetation, which in many cases grows in marginal areas with respect to climatic and soil conditions. Under these circumstances, an elevation of the CO_2 concentration will interact with e.g. plant nutrition and water supply in determining the rate of photosynthesis and the growth pattern of the plant.

Over the last decades many reports have dealt with effects of elevated CO_2 on agricultural production. Since the early eighties wild plant species, natural vegetations and ecosystems begun to attract scientific attention. If plant species differ in their response to variations in the atmospheric CO_2 level, this would imply possible shifts in the interaction between species in their natural environment. In

addition, other growth conditions interfere with the plant's reaction to elevated CO_2 and even more changes in natural ecosystems could occur as a result of an increase in atmospheric CO_2 concentration.

This study focusses on the functioning of whole plants under conditions of elevated (700 μl l^{-1}) as compared to the ambient level of CO_2 (350 μl l^{-1}). The species used are *Plantago major* ssp. *pleiosperma* (great plantain) and *Urtica dioica* (stinging nettle), two species that grow in many (semi-)natural vegetations in Europe. All experiments were carried out in growth rooms, in nutrient solution, in order to have optimal control over environmental conditions.

The aim of the study was (i) to describe the growth response of plants, in the vegetative growth period, to this doubling of the atmospheric CO_2 concentration and (ii) to identify physiological and morphological traits that are sensitive to changes in the CO_2 level. The second aim was to relate the observed growth response to the nitrogen (N) metabolism of the plant, since nitrogen is quantitatively an important nutrient, that often limits plant growth under natural conditions. These two aims were a prerequisite for the following step, which was to analyse the response of *P. major* to elevated CO_2 under conditions of limiting N supply. Finally, the results of this study were used to evaluate if generalisations could be made of functional types of plant species, that respond either significantly or marginally to an increased atmospheric CO_2 concentration.

Both in *P. major* and in *U. dioica* the RGR was transiently stimulated by an elevation of the atmospheric CO_2 concentration (chapters 2 and 3). The higher RGR was accounted for by an increase of the rate of photosynthesis at elevated CO_2, but the stimulating effect on photosynthesis was counteracted by decreases in the Specific Leaf Area (SLA, chapters 2 and 3). Accumulation of nonstructural carbohydrates could partly explain this effect on the SLA. In addition, differences in plant size, due to the CO_2 treatment and a coupling between leaf morphology and plant size, accounted for the observed decrease of the SLA at elevated CO_2 (chapter 3). In some experiments the increase in the rate of photosynthesis was accompanied by increases in the rate of shoot and root respiration as well (chapters 2 and 6), but the latter responses were rather variable and the stimulation of the rate of respiration seemed to be restricted to the phase of growth stimulation by elevated CO_2 (chapter 6).

U. dioica showed a longer-lasting stimulation of the RGR at elevated CO_2 than *P. major*. After a doubling of the CO_2 concentration, the former species, accumulated nonstructural carbohydrates, starch and soluble sugars in the leaves to a lesser extent than the latter (chapter 3), which led to relatively smaller effects of elevated CO_2 on SLA and the % dry matter in the leaves of *U. dioica* as well. The observed decreases in the concentration of total nitrogen and those of different nitrogen pools in plants grown in elevated CO_2 were largely due to this accumulation of

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carbohydrates. The difference in response between the two species was explained as a consequence of the species-dependent RGR, which was higher in *U. dioica*, and the growth form. *P. major* forms rosettes of leaves and has a limited number of small secondary shoots, whereas *U. dioica* forms a widely branched shoot, in a so-called more indeterminate growth pattern. Those characteristics seem to enable *U. dioica* to allocate more of the extra carbon gained at elevated CO_2 to new branches, in comparison with that in *P. major.*

The interaction of an elevated CO_2 concentration and a limited supply of nitrogen was studied in *P. major* (chapter 4). Nitrate in the nutrient solution was supplied at various exponential rates, instead of different concentrations. An advantage of the exponential nutrient supply is, that growth is limited right from the start of the experiment, whereas in an experiment at different nutrient concentrations, an initial phase of nonlimiting nitrate supply is immediately followed by a complete exhaustion of the nutrient solution. The latter procedure creates a variable nutrient regime, and, consequently the plant is exposed to a continuously changing nitrate supply. Furthermore, if the RGR is stimulated, as is the case at elevated CO_2, the nutrient solution is exhausted more rapidly and the plant thus experiences a more severe nitrogen limitation than under control conditions. With exponential nitrogen supply the level of nutrient stress can be maintained at a constant and equal level for both CO_2 treatments.

Growth of *P. major* plants was compared between the two CO_2 treatments and at various rates of nitrogen supply, in the period after the transient stimulation of the RGR upon elevation of the CO_2 concentration. At this relatively long term, the differences in response to a growth-limiting N supply between the two CO_2 treatments was restricted to a large accumulation of nonstructural carbohydrates in the leaves at elevated CO_2 at all levels of nitrogen supply. No other shifts upon a doubling of the CO_2 concentration in the allocation of carbon were observed. The extra carbon gained per leaf area was invested in carbohydrates, which did not contribute to the synthesis of new leaf area. Although CO_2 kept entering the leaves and was fixed at a higher rate in plants grown at elevated CO_2, the extra CO_2 did neither lead to growth of new photosynthetic tissue nor to the formation of extra roots or storage organs. An investment of the extra carbon in roots has often been suggested as a way in which plants could benefit from elevated CO_2 even under nutrient-limited conditions. Apparently, however, this did not happen in *P. major* when grown at a constant exponential nitrate supply.

The data from chapter 4 were used to simulate, if the outcome of experiments with nutrient-limited growth at a constant nutrient concentration, which often includes a relatively larger root weight at elevated CO_2, could be explained by the scenario of those experiments. In chapter 5 a model was constructed, which mimicked the growth of *P. major* as described in chapter 4. Subsequently different nutrient regimes were modelled, which represented growth of plants at different concentrations of nitrate in a nutrient solution, with regular replenishment of the solution, such as occurs in the classical nutrient-limitation studies. The simulation indicated, that, indeed, the ratio of the root to total plant weight (root weight ratio, RWR) was increased in the period between free access to nitrate and severe nitrate limitation, when the RGR drops to almost zero. This study did not answer the question, which scenario for the availability of nitrate under natural field conditions is most likely. However, it did indicate that an increased supply of carbon in plants grown at elevated CO_2 did not lead to a relative increase in root size at a given level of nutrient stress.

In future studies concerned with elevated CO_2, which are designed to gain insight in the functioning of natural ecosystems, what responses can be expected in various plant species and what characteristics determine the responsiveness of a species to changes in the CO_2 concentration? The observed responses of *P. major* and *U. dioica* indicate, that differences in growth form and specific RGR are traits that may be indicative for the magnitude and duration of the growth response to be expected. Additionally, species with large non-photosynthetic organs, that only consume carbon, seem to possess a flexible so-called 'sink' that can use the extra carbon provided by growth at elevated CO_2. The degree to which a plant can respond to elevated CO_2 with an increase in RGR seems to be indicated by the balance between the production of structural and nonstructural carbohydrates; if the extra carbon can be invested in new structural dry matter, the accumulation of nonstructural dry matter is limited, and, alternatively, when the plant is not able to invest in more structural growth, the extra carbon ends up as nonstructural carbohydrates, mainly starch, in the leaves.

In ecological studies species are divided into functional groups, that are described in terms of a coherent set of traits, a life-history strategy. Plants with a high potential RGR often occur in highly productive, ruderal and disturbed habitats. Growth of those species is likely to be responsive to elevated CO_2. If species within such a community have a large sink, i.e. a tuber or stolon, or when they have an indeterminate growth pattern, they are expected to respond to an elevation of the atmospheric CO_2 concentration with a significant and prolonged increase in growth rate.

Samenvattin

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