Climate change; crops and terrestrial ecosystems

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Climate change; crops and terrestrial ecosystems

S.C. van de Geijn, J. Goudriaan &
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Abstract

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The publication consists of eight chapters dealing with the impact of climate change, i.e. elevated CO_2 levels and temperature, on physiological processes in crops and terrestrial ecosystems: Effects of CO_2 enrichment on photosynthesis and carbohydrate utilization: consequences for regrowth of *Lolium perenne*; Effects of elevated CO_2 on crop photosynthesis, carbon economy and productivity of wheat and faba beans; Effects of CO_2 increase on the productivity of cereals and legumes: model exploration and experimental evaluation; Influence of air pollution on carbon dioxide effects on plants; Effects of climate change on crop production and land use in the Rhine basin; Carbon fluxes and organic matter transformations in plant-soil-systems; Plant growth and nutrient cycling in nutrient-poor ecosystems; Carbon cycle and ecosystem productivity on a global scale.

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Preface

Expected changes in the world's climate due to the enhanced greenhouse effect caused by elevated CO_2 levels and other radiatively active trace gases have increasingly attracted the attention of the scientific community and policy makers over the last decade. The impact that climate change could have, very much depends on present local and regional weather conditions. However, climate projections of so-called GCMs (Global Circulation Models) at a regional scale are still very poor, and do not generate detailed information on changes of temperature, air humidity and precipitation, that are crucial for the dynamics of growth and development of crops and vegetations.

By far the best documented change is the steady rise in the CO_2 concentration of the atmosphere. Over the last decades this rise has been of the order of 0.5% per year (about 2 ppm rise per year at the actual level of 353 ppm). Notwithstanding abatement policies advocated by the IPCC (Intergovernmental Panel on Climate Change) and the World Climate Conference, the rise is expected to continue at the present pace for much of the next century. Although frequently publicised as being a pollutant, CO_2 is essential for plant growth and rising concentrations enhance plant productivity and reduce transpiration, provided that no other factors are limiting growth. Moreover, CO_2 has effects on the composition of the plant material.

Storage of carbon in the various pools on earth and fluxes between pools not only depend on abiotic but also on biotic processes like sequestration of carbon dioxide in the photosynthetic process, fixation in plant biomass, transfer to litter and decaying organic matter, and finally conversion into soil organic matter and humus, with very long residence times in the soil. Potential feed-back or feed-forward mechanisms, related to the "quality" of the organic material might be in operation, and complicate the extrapolation. The probably enhanced storage of carbon through fixation by the terrestrial ecosystems, sometimes referred to as the CO_2-fertilizing effect, might give at least a partial explanation for the so-called "missing carbon".

The contributions in this book give a birds eye view of the research at CABO-DLO in cooperation with TPE-WAU, IB-DLO and SC-DLO on effects of climate change. It comprises research from the process and crop level up to global cycles. The unifying aspect is the approach taken: combining a detailed analyses of systems and there internal structure, and quantifying the relationships in mechanistic and comprehensive models. The research has many links to international programmes (EC Environment; IGBP-GCTE), and is partly funded by the Dutch National Programme on Global Air Pollution and Climate Change (NOP-MLK) and EC sources.

For readers from various backgrounds the presented material with its inherent uncertainty, although limited to agriculture and natural ecosystems, will help to clarify why there are so many aspects to be clarified when discussing the need for policy measures regarding the world-wide abatement of emissions of greenhouse gases.

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1 Effects of CO_2 enrichment on photosynthesis and carbohydrate utilisation: consequences for regrowth of *Lolium perenne*

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Summary

*Because CO_2 is the primary substrate for photosynthesis, the present rise of the CO_2 concentration in the global atmosphere will affect crop productivity and terrestrial ecosystems. Here, we argue that focusing on photosynthesis alone is not enough to predict effects of elevated CO_2 concentration on plant growth. Instead, the whole process of carbon partitioning should be included. We suggest a model of carbon partitioning within a tissue, which includes photosynthesis, respiration, biosynthesis, carbon import and carbon export. Between connected model units, carbon translocation takes place. Although the partial processes of carbon partitioning are rather well understood, we hardly know how these processes are linked to each other. Farrar (1992) proposed a mechanistic hypothesis of carbon partitioning in which sucrose has a regulatory messenger function. In this paper, we explain the principles of Farrar's hypothesis about carbon partitioning. Effects of elevated CO_2 concentration on the partial processes of carbon partitioning are described and related to this hypothesis. Farrar's hypothesis is used as a starting-point in our present research about effects of CO_2 enrichment on regrowth of ryegrass (*Lolium perenne*) after defoliation. Regrowth after defoliation may be considered as a special case of carbon partitioning where the sinks (meristems) can draw on two carbon sources - current photosynthesis and remobilization of reserves - while in general there is only one carbon source, i.e. current photosynthesis.*

In: S.C. van de Geijn, J. Goudriaan & F. Berendse (eds), (1993), Climate change: crops and terrestrial ecosystems. Agrobiologische Thema's 9, CABO-DLO, Wageningen: 1 - 22.

1.1 Introduction

The present rise of the CO_2 concentration in the global atmosphere caused by human activities as fossil-fuel burning, deforestation and intensive land use, has recently become a major issue of political and scientific interest. Calculations of CO_2 rise predict a doubling of the present concentrations by the end of the next century (King *et al.*,1992 cited in Bowes,1993).

Expectations about global warming and other climatic changes by a more intense "greenhouse effect" have been reported many times. Another aspect is the impact of increased CO_2 concentration on crop and ecosystem productivity. Since growth is essentially the accretion of carbon metabolites (Farrar, 1992) and CO_2 is the main source of carbon in plants it is evident that elevated CO_2 will affect global plant growth.

Plant populations adapt to changing environmental conditions by genetic modifications as shown by evolution (Bowes, 1993). However, biological evolution is a slow process, likely too slow for adaptation to the present rapidly increasing CO_2 concentration in the atmosphere. For two reasons it is important to improve our knowledge of the mechanisms of CO_2 effects on plant growth, if we want to control future crop productivity and predict ecosystem behaviour. Firstly, the plasticity of the present genotypes with respect to their response to CO_2 is not known. Secondly, the physiological processes, i.e. enzymes that would need to be modified for adequate adaptation to high CO_2 concentration, are as yet unknown.

Still, much knowledge is available on metabolic processes affected by CO_2, e.g. photosynthesis and respiration. Even though most of the data only concern carbon metabolism, it is important to integrate the present information into a general model, as a tool in generating working hypotheses for future research. Although the primary action of CO_2 on plants may not be via pathways of carbon metabolism, it is appropriate to adopt the simplest model that summarizes our present knowledge, that is a model of plant carbon partitioning.

The objective of this paper is two-fold:

Firstly, we want to review known effects of CO_2 enrichment on partial processes of carbon partitioning of plants. We try to fit these findings in a recent mechanistic hypothesis on carbon partitioning proposed by Farrar (1992). As will be made clear in sections 1.2 and 1.3, relating CO_2 effects to changed photosynthesis rates alone is not enough to explain effects on plant growth.

Secondly, we use the considerations about the regulation of carbon partitioning in plants made in section 1.2 as a physiological framework for our own recently started experimental study about effects of CO_2 elevation on regrowth of ryegrass (*Lolium perenne*) after defoliation. An important part of the agricultural land-use in temperate regions consists of pastures in which ryegrasses provide the mainstay of production (Ryle *et al.*, 1992). Unlike most crop species, managed grassland is usually frequently defoliated during its growing season (e.g. by cattle grazing or by mowing). So far, CO_2 effects on growth of grass, including defoliation have hardly been studied. From an agronomic point of view, knowledge about CO_2-effects on (re)growth of ryegrass is wanted. Also, regrowth of ryegrass is a suitable model system to study carbon partitioning and in particular CO_2 effects on carbon partitioning in perennials. A study on this subject started recently at CABO-DLO, in collaboration with partners in the EC-CROPCHANGE project. In section 1.4 we summarize the present knowledge about changes in carbon partitioning during regrowth of grass and our experimental approach.

Apart from CO_2 effects on the carbon partitioning of plants, significant effects on water economy are to be expected. Normally stomata close to varying degrees in enhanced atmospheric CO_2 concentrations (Mansfield *et al.*, 1990). This results in a decreased stomatal conductance and with that in decreased transpiration rates. As a consequence, the water use efficiency (WUE), defined as the ratio of the weight of dry matter produced to the weight of water transpired (Eamus, 1991), is increased. Especially in areas with limited water availability this effect of CO_2 enrichment may be of major importance. In this paper, we focus on effects of CO_2 on carbon partitioning only and pay no attention to the effect of CO_2 enrichment on crop productivity via changed WUE. More information about this subject can be found in other chapters of this volume (e.g. Dijkstra *et al.*, 1993).

1.2 Carbon partitioning: partial processes and effects of CO_2 enrichment

1.2.1 Towards a model of carbon partitioning

Carbon partitioning has been used in various meanings. It may be defined as the whole of processes acting on carbon in the plant, or, alternatively, as the "final" result of these processes in terms of carbon weight of the various plant tissues and compartments. We prefer the former definition, because of its potential to incorporate biochemical and biophysical processes into a mechanistic model of carbon partitioning (Farrar, 1992). It must be clear that such a model is essential for an adequate approach of the problem of CO_2 effects on plant growth in general and the regrowth of ryegrass in particular.

Such a model should incorporate: major carbon pools, and main pathways of carbon transport and metabolism. Let us consider a simple unit of a source or a sink. Its carbon partitioning is described by five carbon fluxes within the tissue:

(1) carbon influx by fixation of CO_2 (photosynthesis);
(2) carbon influx by import of assimilate;
(3) carbon accumulation by biosynthesis or storage of organic compounds ('growth');
(4) carbon efflux by respiration of CO_2, determined by the cost of biosynthesis and maintenance processes;
(5) carbon efflux by export of assimilates.

Figure 1.1 presents a simple model of carbon partitioning summarizing the above views. It contains only one carbon compartment. This compartment acts like a source when there is net export of organic carbon, such as in photosynthesizing leaves and in storage organs at certain developmental stages. The compartment acts like a sink when there is net import of carbon, such as in growing meristems and fruits.

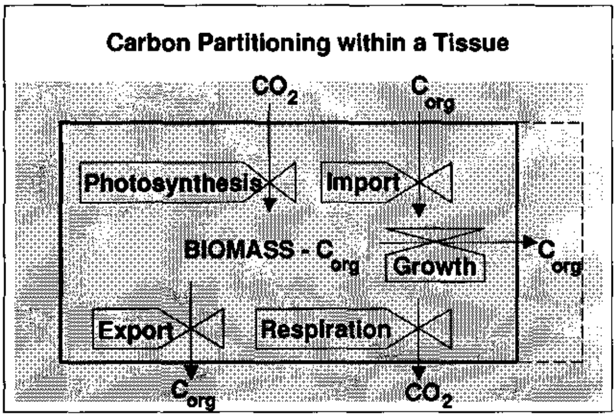

Figure 1.1 Model of carbon partitioning within a plant tissue. Carbon influx occurs via photosynthesis (CO_2) and/or import of organic compounds (Corg). Carbon efflux takes place by respiration as CO_2 or by export of organic compounds. Growth includes biosynthesis and storage. The tissue is called a sink when carbon import exceeds export, or a source when carbon export is greater than import (adapted from de Visser & Schnyder, in prep.).

A problem is the nature of the driving variable in the model. In many models (e.g. SUCROS87, Spitters *et al.* 1989) this is photosynthesis, which in the real world may only be so in the long-term. In the short-term, *in planta* it is more likely to be metabolic activity of the sink, which is genetically programmed. Exceptions are extreme conditions where other processes may dominate the regulation of photosynthesis.

The model may be extended by connecting several compartments as in Figure 1.1, as in plants with multiple sinks and/or sources (partitioning within a plant). In this way the process of translocation of carbon via the phloem becomes integrated in the model. The partitioning of carbon between the various sinks is probably determined by their individual metabolic sink activities and their distances to the source. By distinguishing multiple carbon pools, (1) a labile, cytoplasmic pool, (2) a storage pool and (3) a structural biomass pool, regulation of the diversion of carbon into the various metabolic pathways is also included.

The final outcome of CO_2 changes on the performance of whole plants will be the integrated result of the effects of CO_2 on partial processes of carbon partitioning. It is obvious that a quantitative and mechanistic model is essential as a tool for this integration.

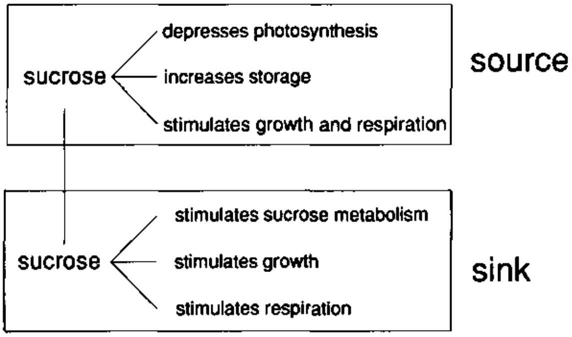

Figure 1.2 A hypothesis for the regulation of carbon partitioning between sink and source by sucrose. In both sink and source tissues, sucrose regulates key processes of carbon partitioning at the level of gene expression (adapted from Farrar, 1992).

1.2.2 The search for the mechanism(s) of carbon partitioning

Recently Farrar (1992) proposed a hypothesis which deals with carbon partitioning in a mechanistic way. This hypothesis, based on existing and accepted ideas on par tial processes of carbon partitioning, integrates these assumptions into one theory, which is capable to explain the various responses of carbon partitioning to perturbations, like CO_2 enrichment or defoliation. It will be briefly discussed here.
Sucrose is not only considered as the major product of the source, and the substrate of sink metabolism, but it is also proposed to regulate the expression of genes coding for pivotal enzymes involved in the carbon fluxes leading to growth. Sucrose is proposed to be a messenger between sources and sinks (Farrar, 1992). This messenger enables the plant to adjust its photosynthetic capacity to assimilate utilisation in sinks and to balance the realized sink growth with the availability of sucrose.
Cytosolic sucrose in a source leaf depresses photosynthesis and stimulates respiration and carbohydrate storage, while sucrose in a sink stimulates sucrose assimilation and with that growth and respiration (Figure 1.2).
The long term regulation by sucrose of fluxes involved in carbon partitioning takes place by coarse control, that is regulation of gene expression (Farrar, 1992). Fine control, in which sucrose acts on the existing machinery, and buffering by cytosolic, vacuolar and plastidic pools are important for short term regulation of carbon fluxes. These controls are characterized by their time scales, varying from days (coarse control) to hours (coarse control, buffering) to minutes and seconds (fine control; Farrar, 1992).

1.3 CO_2 effects on the partial processes of carbon partitioning.

1.3.1 *CO_2 effects on carbon translocation.*

Transport of carbon between sources and sinks is generally in the form of a non-reducing sugar via the phloem. It depends on export by the sources, and import by the sinks. The pressure-flow hypothesis, first proposed by Ernst Münch, is widely accepted as the most probable mechanism of phloem translocation (Taiz & Zeiger, 1991). Because the phloem may be considered as a continuous tube, without membrane boundaries, flow of water and solutes is driven by the pressure gradient rather than the water potential gradient.

The pressure gradient between source and sink is determined by the difference in osmotic potential in the apoplast, i.e. cell wall and intercellular space ($\Delta\pi_o$), the difference in osmotic potential of the phloem sap ($\Delta\pi_i$), and the difference in the turgor pressure in the cell wall (ΔP_o) (Lang & Thorpe, 1986; Figure 1.3):

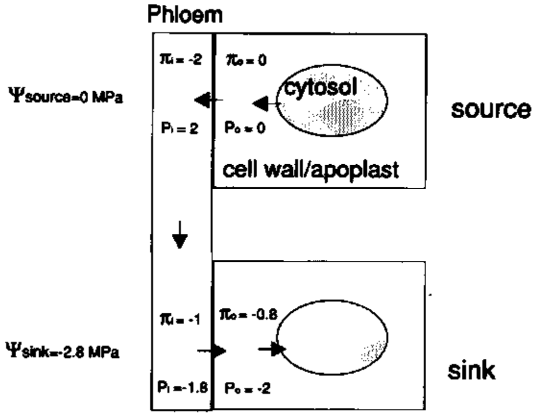

Figure 1.3 Schematic diagram showing the pressure-flow model (Münch hypothesis) describing the mechanism of assimilate, i.e. organic carbon, translocation in the phloem. In the source, sucrose is actively loaded into the phloem. Water enters the phloem osmotically, building up a high turgor pressure. At the sink, sucrose is actively unloaded from the phloem, and water leaves the phloem tube resulting in a lower pressure. Water and its dissolved solutes move by mass flow from the area of high pressure ion the source to the area of low pressure in the sink. Representative values, in MPa, of osmotic potential in apoplast (π_o) and inside the phloem (π_i), turgor pressure in apoplast (P_o) and phloem (P_i), and water potential (Ψ) are shown. The turgor pressure difference between the phloem in source and sink is the driving force of carbon translocation. The turgor pressures of the phloem in source and sink are calculated as: $P_i = \pi_o - \pi_i + P_o = 0 - -2 + 0 = 2$ MPa (in the source) and $P_i = \pi_o - \pi_i + P_o = -0.8 - -1 + -2 = -1.8$ MPa (in the sink). The turgor pressure difference $\Delta P_i = \Delta\pi_o - \Delta\pi_i + \Delta P_o = 3.8$ MPa (after Lang and Thorpe, 1986).

$$\Delta P_1 = \Delta\pi_o - \Delta\pi_i + \Delta P_o \qquad (1)$$

The flux of sucrose, $J_{sucrose}$ (mol s^{-1}), is calculated as the product of ΔP_1, the sucrose concentration of the phloem at the source side (C), and the conductivity of the transport pathway (k), which is in part determined by the distance between source and sink (Farrar, 1992):

$$J_{sucrose} = \Delta P_1.C.k \qquad (2)$$

The pressure gradient is established as a consequence of energy-driven phloem loading at the source and energy-driven phloem unloading at the sink. The long-distance transport of carbon in the sieve tubes may be regarded as a passive process. Therefore, control of carbon translocation takes place at the sites of phloem loading and unloading, i.e. export and import, respectively (cf. Figure 1.1).
At the source site sucrose is at a higher concentration in the sieve cells of the phloem than in the surrounding cells of the source organ. This indicates that sucrose is transported against its chemical potential gradient via active transport mechanisms, requiring metabolic energy. Also sucrose transport into sink tissues depends on active carriers in membranes of sink cells (Taiz & Zeiger, 1991). A direct control of phloem loading and unloading by cytosolic ATP is unlikely, but the rate of phloem loading and unloading may depend on metabolic activity of source and sink.
When the activity of source metabolism is high and cytosolic sucrose is not limiting, phloem loading generates a high turgor pressure in the sieve tubes of the source, a prerequisite for high translocation rates. When sucrose is unloaded at a lower rate, sucrose will accumulate in the sieve tubes at the sink site, causing an increase of the phloem turgor pressure in the sink and a decrease of translocation rate. Translocation rates will therefore be determined by sink metabolism. The opposite may also occur: when phloem loading takes place at lower rate than phloem unloading, source metabolism will determine translocation.
The few studies, which attempted to measure assimilate export from CO_2 enriched leaves, showed contradictory results. Both enhanced and unchanged rates of export were found after short-term or long-term exposure to high CO_2 concentrations. Such variability may be expected, given the dependence of phloem transport on both source and sink (Farrar & Williams, 1991). In most of the experimental studies cited by these authors, the responses of sinks to enhanced CO_2 were not studied. Characterisation of the metabolic activities of both source and sink is necessary to explain effects of elevated CO_2 concentration on carbon translocation.

1.3.2 CO_2 effects on photosynthesis

Perhaps the best understood process involved in the carbon economy of a plant is photosynthesis. It is the process in which light, CO_2 and water are converted to triose-phosphates and oxygen (Taiz & Zeiger, 1991; Figure 1.4).
Photosynthesis consists of two reactions. In the first one (the light reaction) light energy is harvested by pigments and used to synthesize O_2, ATP and $NADPH_2$. In the

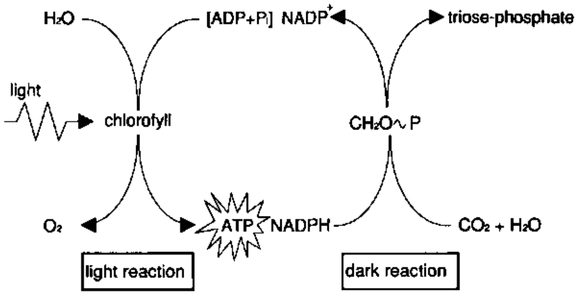

Figure 1.4 Photosynthesis as performed by algae and higher plants. Light is required to generate energy-rich intermediates: ATP and NADPH. The reduction of CO_2 to carbohydrate is not directly dependent on light, and is therefore referred to as the dark reaction (Taiz & Zeiger, 1991).

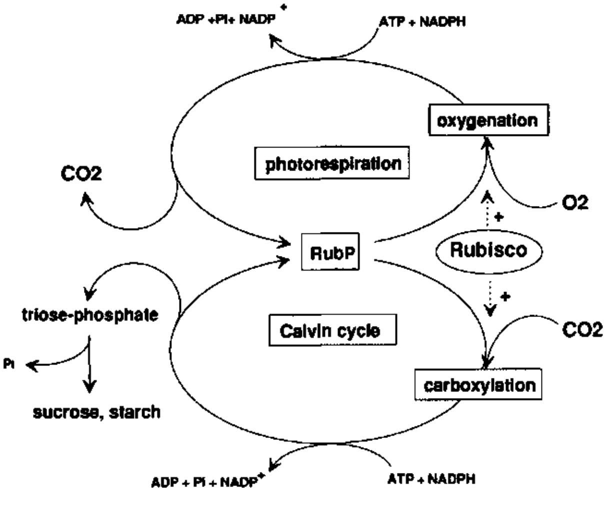

Figure 1.5 Schematic diagram of the biochemical pathways involved in the dark reaction of photosynthesis. Carboxylation of ribulose bis-phosphate (RuBP) by ribulose-bis-phosphate carboxylase/oxygenase (Rubisco) is the first reaction of the Calvin cycle. The first reaction of photo respiration is the oxygenation of RuBP by Rubisco. The energy-rich intermediates ATP and NADPH are produced in the light reaction of photosynthesis.

Table 1.1 Energetic consequences of carboxylation and oxygenation of RubP (after Taiz & Zeiger, 1991)

Net reaction of carboxylation	
$3CO_2 + 3H_2O + 9ATP + 6\ (NAD(P)H + H^+)\text{-->}$	$\text{triose-P} + 9ADP + 6\ NAD(P)^+ + 8P_i$
energy cost of fixing one CO_2 :	$3ATP + 2(NAD(P)H + H^+)$
net gain of carbohydrate	1/3 triose-phosphate
Net reaction of oxygenation:	
$RubP + O_2 + 2ATP + 2.5(NAD(P)H + H^{+)}\ \text{-->}$	$0.9RubP + 0.5CO_2 + ADP + 2.5NAD(P)^+ + 2P_i$
energy cost of fixing one O_2 :	$2ATP + 2.5(NAD(P)H + H^+)$
net loss of carbohydrate	0.1 RubP

second reaction (the dark reaction) the binding of CO_2 to ribulose-bis-phosphate (RubP) takes place. The enzyme catalysing the fixation of CO_2 is ribulose-bis-phosphate carboxylase oxygenase (Rubisco). Bound CO_2, ATP and $NADPH_2$ are assimilated in the Calvin cycle, to form triose-phosphate, the primary substrate for synthesis of sucrose and starch and RubP (Figure 1.4).

Rubisco actually catalyses two reactions (Figure 1.5). One involves the already mentioned binding of CO_2 to RubP (the carboxylation reaction), the other catalyses the binding of O_2 to RubP (the oxygenation reaction). In the biochemical pathways of the latter reaction CO_2 is released, which explains why oxygenation of Rubisco is usually indicated as photorespiration. In photorespiration, a large part of the energy harvested in the light reaction is lost, while there is no net production of carbohydrates (Table 1.1). Therefore, photorespiration can be considered as a wasteful process.

In the short-term, elevation of the CO_2 concentration stimulates photosynthesis for two reasons: Firstly, more CO_2 substrate is available for the carboxylation of RubP. Secondly, the competition of O_2 and CO_2 for binding at Rubisco is changed in favour of CO_2, and photorespiration is decreased.

The short-term stimulation of the photosynthesis rate by CO_2 enrichment depends on the activities of the partial processes of photosynthesis. The most important are (Stitt, 1991):

(a) Carboxylation of RubP by Rubisco:

The CO_2 response of the photosynthesis rate is determined by the amount and properties of active Rubisco in the chloroplast. Therefore, limitation of photosynthesis at relatively low CO_2 concentrations is called Rubisco limitation. Doubling the CO_2 concentration at Rubisco limitation stimulates photosynthesis rate by about 75 % at 25 °C.

(b) Regeneration of RubP:

After every carboxylation or oxygenation reaction, a RubP molecule needs to be regenerated. If carboxylation and oxygenation takes place faster than regeneration of RubP, the latter process will become limiting for photosynthesis rate. Regeneration of RubP is determined by the light harvesting process, activities of enzymes involved in synthesis of ATP or $NADPH_2$ and the activity of the Calvin cycle enzymes. A doubling of the CO_2 concentration still results in a stimulation of the photosynthesis rate by about 25 % at 25 °C, because photorespiration is depressed and as a result there is an increased availability of ATP, $NADPH_2$ and Calvin cycle activity for regeneration of RubP.

(c) P_i supply:

During synthesis of sucrose and starch from triose-phosphates, inorganic phosphate (P_i) is released from ATP utilisation. If sucrose and starch synthesis occur to slowly, phosphorylated intermediates accumulate and the pool of P_i in the cytosol of the cell and in the chloroplast will be depleted. Because P_i is required for ATP synthesis in the light reaction (and ATP is required for regeneration of RubP) photosynthesis becomes limited. If P_i availability is limiting photosynthesis, an increase in CO_2 concentration will have no effect on photosynthesis rate (0 % stimulation).

The characteristics of photosynthesis of a leaf are expressed by the relationship between photosynthesis rate (A) and the intercellular CO_2 concentration (C_i), which is the effective CO_2 concentration controlling photosynthesis rate and stomatal conductance. In this so-called A/C_i curve (Figure 1.6) the near-linear increase of photosynthesis with CO_2 concentration at low CO_2-concentrations marks Rubisco limitation. The following curvilinear region is the result of limitation by RubP regeneration and the plateau indicates P_i-limitation. At present ambient CO_2 conditions, photosynthesis rates are usually in the linear and the curvilinear part of the A/C_i curve, indicating co-limitation by Rubisco and RubP regeneration. P_i-limitation

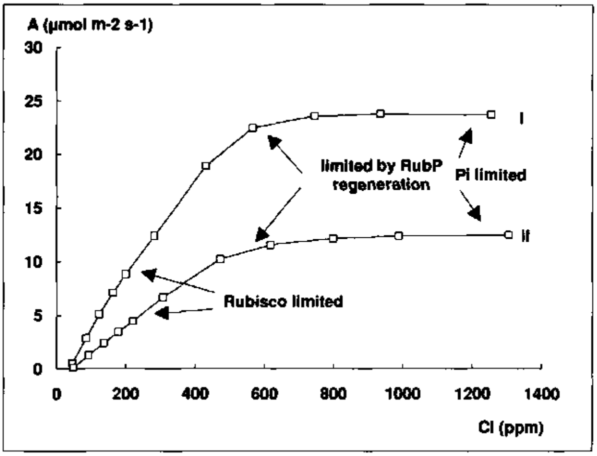

Figure 1.6 Response of net leaf photosynthesis (A) to intercellular CO_2 concentration (C_i) of Vicia faba, grown at 700 ppm CO_2 concentration (plants grown at 350 ppm show similar A/C_i curves). The various regions of the curve correspond with various processes limiting photosynthesis. **I**: Photosynthesis of young, sunlit leaves high in the canopy. **II**: Photosynthesis of fully expanded, shaded leaves low in the canopy (S. Pot, A.H.C.M. Schapendonk & P. Dijkstra, unpubl.).

is hardly ever found *in vivo* , even when the CO_2-concentration is doubled compared to the present ambient CO_2 concentration (Stitt 1991). A/C_i curves are affected by environmental factors, e.g. the initial slope and the plateau increase with increasing light intensities and developmental stage, e.g. young leaves usually have Rubisco limited photosynthesis, while photosynthesis of older leaves is usually limited by RubP regeneration at ambient CO_2 concentrations (Stitt, 1991). The A/C_i curves of canopies also depend on canopy characteristics: photosynthesis of shaded leaves may be limited by RubP regeneration while photosynthesis of sunlit leaves may be Rubisco-limited. Moreover, photosynthesis of leaves of different age within the canopy will differ in their response to CO_2 enrichment.

Apart from characterization of photosynthesis, A/C_i curves may be used for prediction of short-term responses to CO_2 enrichment. However, short-term responses have little relevance for predicting plant growth in a future high CO_2 world. The response of leaf and canopy photosynthesis at long-term exposure to high CO_2 concentrations could be markedly different from the short-term response: Averaged results of several studies on plants grown at 350 ppm and 700 ppm CO_2 (cited by Stitt, 1991) showed that the initial stimulation of net photosynthesis by 52 % decreased to 29 % after a few weeks. This decline of net photosynthesis rate after a long-term exposure to elevated CO_2 is referred to as "negative photosynthetic acclimation". Photosynthetic acclimation is defined as the ratio of the long-term photosynthesis response to the short-term response to elevated CO_2 (cf. Arp, 1991).

Several explanations for the occurrence of photosynthetic acclimation have been proposed:

Photosynthetic acclimation is unlikely to be an artefact. i.e. it is not the result of differences in developmental stage, leaf age or morphology, because of the large number of reports of photosynthetic acclimation measured on various species in different growth stages. Mechanical damage of the machinery of photosynthesis by starch bodies, which accumulate in the chloroplast at high photosynthesis rates, has often been proposed as a cause of photosynthetic acclimation (Stitt, 1991). Starch accumulation may also lead to reduced light transmission or reduced CO_2 diffusion in the chloroplast. However, these explanations don't seem sufficient since photosynthetic acclimation also occurs in *Lolium perenne* (Ryle & Powell, 1992),a species which accumulates fructans in the vacuole and little starch in the chloroplast.

Photosynthetic acclimation to elevated CO_2 concentrations can be explained by Farrar's hypothesis about the control of carbon partitioning (Farrar, 1992):

Let us assume that transfer from ambient to an elevated CO_2 concentration results in a short-term stimulation of the photosynthesis rate. This will increase levels of cytosolic sucrose in the leaf, which will increase the metabolic activity of the source leaf. This increases phloem loading and thereby turgor pressure in the phloem of the source. Because the turgor pressure difference between source and sink is enhanced, sucrose translocation to the sink increases. If unloading in the sink is not adjusted in a proportional way to an increased loading of sucrose, the turgor pressure in the phloem of the sink rises due to sucrose accumulation and, as a result, translocation rates decreases again. Because sucrose loading into the phloem is hindered, sucrose accumulates in the source leaves, causing inhibition of expression of genes coding for enzymes involved in photosynthesis and stimulation of expression of genes coding for enzymes involved in carbohydrate storage. Decreased photosynthesis rates and increased carbohydrate storage are the result. Indeed, photosynthetic acclimation to elevated CO_2 concentrations can often be related with altered activities of Rubisco and carbohydrate storage (Stitt, 1991). Photosynthetic acclimation will not occur if the activity of sink metabolism is adjusted proportionally to an increased activity of source metabolism. This explains why photosynthetic acclimation is not always found.

Comparison of A/C_i curves of different species, grown at ambient and high CO_2 concentrations, indicates that the occurrence of photosynthetic acclimation may be species specific. Photosynthetic acclimation becomes visible by a changed slope of the A/C_i curve, caused by altered activities of Rubisco and/or other Calvin-cycle enzymes. The slopes of the A/C_i curves of *Brassica oleracea*, *Chenopodium album* and *Solanum tuberosum*, grown at 950 ppm CO_2, indicated a 37 %, 10 % and 0 % decrease respectively, of Rubisco activity, relative to 300 ppm grown plants (Sage *et al.*, 1989). Thus, *Brassica oleracea* and to a lesser extent *Chenopodium album* showed photosynthetic acclimation after CO_2 elevation, whereas *Solanum tuberosum* did not.

According to Farrar's hypothesis on carbon partitioning, long-term response of photosynthesis to CO_2 enrichment should correlate with the long-term response of sink metabolism. Sage *et al.* (1989) did not include this aspect in their study.

Indications for sink metabolism being crucial for photosynthesis response to CO_2 elevation comes also from Arp (1991): in a review of several studies on effects of CO_2 enrichement on plant growth, he demonstrated a clear positive relationship between the size of the root medium and photosynthetic acclimation.

It was concluded that in pot grown plants, activity of the metabolism of a major sink (the roots) was restricted, due to physical limitations.

1.3.3 CO_2 effects on respiration and biosynthesis

Respiration is defined as the whole of processes in cytosol and mitochondria from which the net result is the formation of ATP, CO_2 and water from sucrose and O_2 (see Figure 1.7). Respired CO_2 is a major component of the plant's carbon balance: as much as 50 % of the fixed carbon may be lost in this process (Amthor, 1991). CO_2 production by a tissue is a net flux and should be referred to as 'apparent dark respiration', since other processes than respiration may also be involved, e.g. dark fixation of CO_2. Fine control of respiration rate takes place by ATP utilisation. Coarse control is proposed to occur by sucrose (Farrar, 1992).

In a review Poorter *et al.* (1992) analysed effects of CO_2 enrichment on apparent dark respiration rates of a wide range of C_3 species. On average, leaf respiration per unit leaf area was 16 % higher for plants grown at high CO_2, whereas a 14 % decrease was found when respiration was expressed on a leaf weight basis. These changes in apparent dark respiration rate were not significant. This may suggest that CO_2 enrichment has no effect on apparent dark respiration rate. However, Poorter *et al.* (1992) also showed that variability in reported values is considerable, values ranging form a 55 % inhibition to a 100 % stimulation. This indicates quantitatively important responses of apparent dark respiration rates to CO_2 enrichment in the individual studies, even though these responses are opposite due to different experimental conditions.

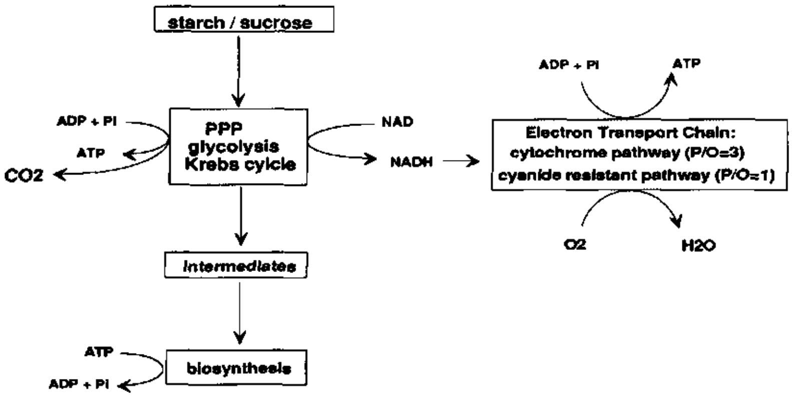

Figure1.7 Schematic representation of respiration and biosynthesis in higher plants. Starch is hydrolyzed to sucrose, which is oxidized in the pentose-phosphate pathway (PPP) and in glycolysis in the cytosol. The resulting carbon skeletons are further oxidized in the Krebs or Tri-Carboxylic Acid Cycle. During oxidation, ATP and CO_2 are formed, and NAD(P) is reduced. Oxidation of NAD(P)H via the cytochrome pathway of mitochondrial electron transport chain yields more than 90 % of the ATP produced in respiration: 3 ATP for every oxygen atom reduced. The cyanide-resistant pathway gives rise to only 1 ATP molecule for every O reduced. Intermediates of PPP, glycolysis and the Krebs cycle are substrates of the biosynthesis of organic compounds.

Changes in biomass composition are often reported after growth at elevated CO_2 concentrations (Amthor 1991): Plants grown in high CO_2 concentrations usually have relatively high C:N ratio's. Growth efficiency (g dry matter g^{-1} glucose) and carbon dioxide produced (g CO_2 g^{-1} glucose) depend on the chemical composition of the end product (Penning de Vries, 1975; Table 1.2). Because synthesis of carbohydrates requires less energy than synthesis of proteins, due to increased C:N composition of the biomass accompanies growth efficiencies are increased and respiration rates are decreased. However, changed respiration rates may be an artefact: high C:N ratios may only be the result of increased accumulation of carbohydrates, with synthesis of structural biomass not being affected. In this situation, respiration rate expressed on a total dry matter basis is lowered, whereas respiration expressed on a structural dry matter basis is not changed (Amthor, 1991).

Enhanced growth efficiencies and lowered dark respiration rates at high CO_2 may also be the result of reduced activity of the cyanide-resistant respiratory pathway (Gifford *et al.*, 1985). The cyanide-resistant or alternative respiratory pathway is a side-branch of the electron transport chain (see Figure 1.7) in which 2/3 of the energy in NADH is not used to synthesize ATP, but is lost as heat. When the activity of this alternative pathway is reduced at high CO_2, dark respiration rate is affected, but ATP production is not.

Table 1.2 Values characterizing the conversion of glucose into the main chemical fractions of plant dry matter in darkness (after Penning de Vries, 1975).

Chemical fraction	Growth efficiency (g struct.dry matter g^{-1} glucose)	Carbon dioxide produced (g CO2 g^{-1} glucose)
nitrogenous compounds (consisting of amino acids, proteins, nucleic acids)	0.616 (+NH_3) 0.404 (+NO_3^-)	0.256 0.673
carbohydrates	0.826	0.102
lipids	0.330	0.530
lignin	0.465	0.292
organic acids	1.104	-0.050

Recently, Reuveni *et al.* (1993) cited several studies in which apparent dark respiration rate was significantly inhibited, directly after exposure to high CO_2 concentration. This effect proved to be reversible; after decrease of the CO_2 concentration, apparent dark respiration rate increased again. This direct inhibitory effect of CO_2 enrichment on CO_2 efflux may also be important during long-term growth at high CO_2 concentrations. The mechanism of this may be increased dark fixation of CO_2 because decreased respiratory activity is unlikely in combination with increased growth rates.

Explanations for opposite responses of CO_2 enrichment on dark respiration may also be given. Increased dark respiration rates at elevated CO_2 concentrations may be caused by increased utilisation of ATP resulting from an increased activity of growth and maintenance processes (Amthor, 1991). This increased metabolic activity may be induced by increased cytosolic sucrose concentration. (cf. Farrar, 1992).

The net result of the counteracting CO_2 effects on CO_2 efflux depends on which processes are most affected by CO_2 enrichment. This is illustrated by measurements of apparent dark respiration rates and relative growth rates of several species grown at 350 ppm and 700 ppm CO_2 concentration by Bunce & Caulfield (1991): At high CO_2 concentrations, dark respiration rate of *Lolium perenne* was significantly lower, while relative growth rate was not significantly affected. Plants of *Dactylis glomerata* grown at 700 ppm CO_2 had a significantly increased relative growth rate, but there were no significant differences in dark respiration rate. This supports the idea of a relatively strong effect of CO_2 enrichment on biomass composition and/or dark fixation.

Bunce & Caulfield (1991) expressed apparent dark respiration rates and relative growth rates on a total dry matter basis. A shortcoming in their study is the omission of analyses of the chemical composition of the biomass. The importance of this was demonstrated by Baker *et al.* (1992). They measured dark respiration of rice plants grown at different CO_2 concentrations. A lower dark respiration rate at high CO_2 was found when it was expressed on a total dry matter basis, but there were no effects of CO_2 elevation if respiration rates were expressed on a nitrogen content basis. Thus, for a clear insight in the effects of elevation of the CO_2 concentration on the respiratory processes, respiration rates should be expressed on a structural dry matter or protein (-N) basis.

Changed dark respiration rates, expressed on a protein content basis would indicate an effect on enzymes involved in the respiratory pathways. Also effects on coarse control of respiration are possible. This may not be reflected by the protein content, but will certainly appear as changed protein and/or m-RNA composition.

1.3.4 Effects of CO_2 enrichment on photosynthesis and carbohydrate utilisation: concluding remarks

For understanding the effects of CO_2 enrichment on the growth of plants it is necessary to focus on all the partial processes of carbon partitioning. In our model (Figure 1.1) carbon partitioning within a tissue is described by five major processes: photosynthesis, organic carbon import, growth (biosynthesis and storage), respiration, and organic carbon export.

Translocation of carbon between sources or sinks which may be considered as a sixth partial process of carbon partitioning, although in itself a passive process. Its rate is determined by the metabolic activities of the tissues at both sides of the phloem tube. When two or more sinks compete for carbon, translocation is affected by their distance to the source (Farrar 1992; see section 1.3.1).

The way partial processes of carbon partitioning are regulated and interact is not clear. Farrar (1992) presented a hypothesis in which a pivotal role is played by sucrose, being the product of photosynthesis, the substance of carbon translocation and the substrate of growth and respiration. He suggests that the expression of genes coding for enzymes involved in photosynthesis, carbohydrate storage, biosynthesis and respiration are regulated by cytosolic sucrose concentration (coarse control; Figures 1.2, 1.8).

Because CO_2 is the substrate of photosynthesis, elevation of the CO_2 concentration will generally enhance gross photosynthesis rates of leaves in the short-term. The extent of stimulation depends on the regulatory state of the photosynthesis process: when photosynthesis rate is limited by Rubisco, a large stimulation is expected. When photosynthesis rate is limited by the concentration of inorganic phosphate in the chloroplast , there will be no stimulation. An intermediate stimulation is expected when photosynthesis is limited by RubP regeneration. The short-term response of canopy photosynthesis to CO_2 enrichment, is determined by the same processes, although leaf age and light distribution within the canopy should also be taken into account.

The long-term photosynthesis response of the source organ to CO_2 enrichment is also determined by the response of the sink organ: if sink metabolism is not adjusted proportionally to the increased activity of source metabolism, a change in the rate of photosynthesis, called photosynthetic acclimation, takes place by changed gene expression. This is a crucial point illustrating that apart from information on the short-term response of photosynthesis to CO_2 enrichment, knowledge of the sink response is necessary to explain long-term responses. Farrar's hypothesis about sucrose control of carbon partitioning, suggests a mechanism of photosynthetic acclimation (see Figure 1.8).

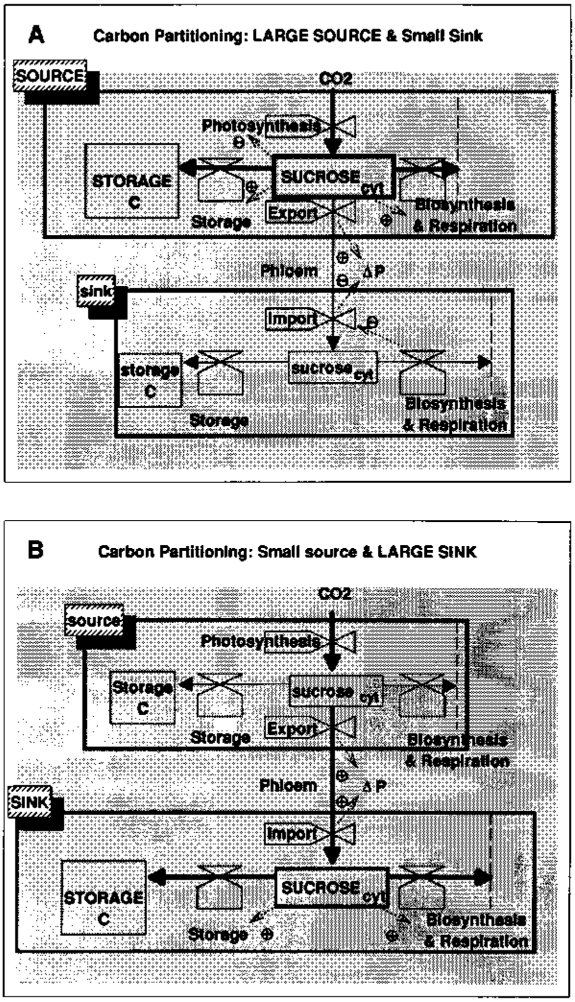

Figure 1.8 Model of carbon partitioning within and between a source and a sinkof a higher plant (see Figure 1.1.), as regulated by the cytosolic sucrose concentration (see Figure 1.2.). **A**: At a high source to sink ratio, low rates of sink-biosynthesis, storage and respiration limit sucroseimport by the sink, thereby lowering the turgor pressure difference in the phoem (ΔP). This hampers sucrose export by the source, leading to a build up of cytosolic sucrose in the source.The high sucrose concentration stimulates C-storage and/or biosynthesis in the source at the level of gene expression, and down-regulates photosynthesis. **B**: In the case of a low source to sink ratio, high metabolic activity in the large sink stimulates import (phloem unloading), thereby increasing the turgor pressure difference ΔP. This results in high rates of C translocation in the phloem. Sucrose levels in the source will remain low, preventing down-regulation of photosynthesis.

Effects of CO_2 enrichment on respiration are not clear: responses vary from a 55 % reduction of respiration rates to a 100 % stimulation (Poorter *et al.*, 1992).

Reduced respiration rates may be caused by a shift from biosynthesis of 'expensive' organic compounds, e.g. proteins, to biosynthesis of 'less expensive' compounds, such as (structural) carbohydrates. Storage of sucrose is not a part of biosynthesis, but contributes to carbon accumulation. When studying CO_2 effects on respiration rate, the basis of expression is important. Because increased storage of soluble carbohydrates is often found at high CO_2 concentrations, respiration rates should not be expressed on a total dry matter basis but on a structural dry matter or protein basis.

Decreased apparent respiration rates at high CO_2 concentrations may also be caused by enhanced CO_2 dark fixation. Increased respiration rates at high CO_2 concentration are caused by increased utilisation of ATP in growth and maintenance processes.

Effects of long-term exposure to elevated CO_2 concentrations vary with plant species and developmental stage, mainly due to varying ratio of source and sink activities. The sucrose-control-hypothesis proposed by Farrar (1992), may explain these different growth responses (see Figure 1.8). Although the theory needs further testing, it offers a physiological framework for explaining CO_2 effects on plant growth.

1.4 Regrowth of ryegrass (*Lolium perenne*) after defoliation

1.4.1 Regrowth of grass: a special case of carbon partitioning

Minchin and Thorpe (1992) have argued that perturbing a plant system in equilibrium gives rise to direct responses providing information on mechanisms currently at play. In terms of Farrar's (1992) classification of processes of carbon partitioning, there are three time scales of these responses, all of which are relevant to the process of regrowth of a grass plant. In the short-term (sec-min), activities of the present machinery will be affected (fine control, e.g. by allosteric control of enzymes). Later (h), assimilate pool sizes will change (buffering). In the long-term (h-day), gene expression will change to modify the metabolic pathways (coarse control). Thus, studying the kinetics of the processes of carbon partitioning (cf. Figure 1.1) after a perturbation, like defoliation or CO_2 enrichment, gives insight in the nature of the control mechanisms operating at different stages of the response. Farrar (1992) proposes a central role of sucrose in the coarse control of carbon partitioning, i.e. on the expression of genes controlling the fluxes of carbon in the plant. In the present case of regrowing grass, much of the responses will be programmed, since grass is a species specifically adapted to defoliation.

Some information on the kinetics of carbon partitioning processes in ryegrass after defoliation is available, i.e. on carbon fluxes within and between tissues due to import, export, accumulation (growth) and respiration. Most plants show a characteristic time pattern of the shoot to root (dry weight) ratio, which is under genetic and environmental control. Disturbing this system evokes a response of the plant tending to neutralize the effects. For example, defoliation of a plant results in a transient standstill of net root dry matter accumulation, while shoot growth continues till the original shoot to root ratio is re-established (Brouwer 1962). In ryegrass, the root to shoot ratio may decrease from higher than 3 to less than 1 just after defoliation, with complete recovery requiring two to three weeks (de Visser *et al.*, unpubl.). Due to photoinhibition, photosynthetic properties (Amax, quantum yield) of the remaining and new leaves are inferior to those of full-grown leaves (de Visser & de Kock, 1991), although approaching original values after about one week (de Visser 1990). Root respiration is temporarily (one week) decreased by approximately 25-60 %, depending on genotype and growth conditions (unpublished data). Thus, defoliation initiates large changes in carbon partitioning processes (fluxes), eventually restoring the balance between shoot and root size and activity. The kinetics of these changes (de Visser *et al.*, in prep.; Schnyder *et al.* in prep.) provides information on the mechanisms involved in the control of carbon partitioning. In particular, growth zones of leaves and young tillers are major carbon sinks. A longstanding question is, which carbon source supplies most of the carbon for regrowth: current photosynthesis or pre-defoliation carbon reserves. Such knowledge enables the selection of important processes in studying CO_2 effects on regrowth.

Regrowth of grasses after defoliation may be considered as a special case of carbon partitioning. Two separate carbon sources for sink growth may be distinguished: Apart from photosynthesis of remaining and regrowing leaves, there is ample evidence for remobilization of carbon reserves from the remaining shoot (and/or roots) to the growing apices of the shoot (Danckwerts & Gordon, 1987; Johansson, 1993; Schnyder *et al.*, 1993). Water soluble sugars are considered an important carbon source for remobilization (Davies, 1988). They are mainly accumulated in the sheaths, which are usually not removed during cutting. Gonzalez *et al.* (1989) found considerable decreases of soluble sugar content in the stubble just after cutting of *Lolium perenne* plants, indicating an increased utilisation.

After defoliation of a grass plant, shoots grow faster than roots, leading to recovery of the shoot to root ratio. However, roots remain active carbon sinks as shown by their activities. Root respiration rate is not affected by defoliation within 1.5 to 2.5 hours, suggesting buffering of carbon supply, root growth and ion uptake (no fine control of root activities by the shoot). Subsequently, root respiration declines within 24 hours to approximately 40-75 % of control values. Root tips resume growth within 2 days after defoliation (de Visser, unpubl. data). Since the amount of carbon in the root system remains constant during a week after defoliation, carbon import (from the shoot) must be significant to compensate for the carbon losses by respiration. Actual gross carbon import may even be higher, because roots export significant amounts of carbon in the form of organic nitrogen (de Visser, Vianden & Schnyder, in prep). Summarizing, roots constitute a sink rather than a source of carbon for shoot regrowth, in accordance with findings of Danckwerts and Gordon (1987). This points to carbon partitioning within the shoot as the main target for studying the processes supplying carbon to growing (shoot) tissues. The net carbon balance of regrowing grass tillers (Schnyder *et al.* 1993, de Visser *et al.* in prep) shows that 80-90 % of the carbon in a tiller shoot is in three tissues, i.e. the most rapidly expanding leaf, the old leaf sheaths, and the young (daughter-) tillers in the axils of these old sheaths. Old leaf sheaths show net export of carbon only during the first two days of regrowth, while carbon accumulation (growth) of leaves and young tillers is negative (the first day), just positive (second day), and increasing greatly thereafter. Combining carbon-balance data with $^{13}C/^{12}C$ ratios of the tissues (steady-state ^{13}C labelling from the day of defoliation; Schnyder 1992, Schnyder *et al.* 1993, de Visser *et al.* in prep) yields the fraction of currently accumulated carbon which originates from photosynthesis. This fraction is larger than 1 in the most rapidly growing leaf and in the young tillers, already on the second day after defoliation, indicating import of 100 % photosynthetic carbon and turnover of part of the tissue carbon.

In conclusion, reserve-carbon is the main substrate of respiration (and some biosynthesis) during the first day of shoot regrowth, while photosynthesis constitutes the primary carbon-source of shoot growth on the second day and thereafter (Schnyder *et al.* 1993; de Visser *et al.*, in prep).

The main question of our research is how CO_2 enrichment affects plant growth. Regrowth of a grass plant after defoliation is used as a paradigm system and Farrar's theory about carbon partitioning as a physiological framework. As put forward by Farrar (1992), the source:sink status of a plant is crucial for its response to CO_2 elevation. A combination of CO_2 elevation and defoliation, the latter strongly affecting the source:sink balance of a plant, might reveal interesting and unexpected aspects of control of carbon partitioning. This certainly concerns the initiation of remobilization of storage carbohydrates, of which the regulation is hardly known, but also a changed control of the other partial processes of carbon partitioning may be expected. In fact, carbon remobilization is a partial process which is not included in Farrar's theory on sucrose control of carbon partitioning (Farrar, 1992; Fig. 1.2).

1.4.2 Regrowth of grass after defoliation: expected effects of CO_2 enrichment

Starting from the hypothesis of Farrar, what effects of CO_2 elevation on regrowth of grass after defoliation might be expected? In particular, what might be expected about utilisation of carbon reserves in comparison with utilisation of assimilates from photosynthesis for growth and respiration?

Just after defoliation, source size (leaf area) is small compared to sink size (growing tissue) and photosynthetic acclimation is not expected to occur. Thus, maximal stimulation of photosynthesis by CO_2 enrichment might be expected. However, the matter is complicated because photosynthesis of young leaves is initially very low, due to photoinhibition (de Visser & de Kock, 1991), but is rapidly increasing during the first week after defoliation (de Visser, 1990). We do not know anything about effects of CO_2 enrichment on this change in the photosynthetic process.

Just after cutting, when there is little photosynthetic capacity, the effect of CO_2 elevation on respiration could be of much more importance than the effect on photosynthesis. CO_2 elevation may effect apparent respiration in various ways, as described in section 1.3.3., making predictions hard to make. If CO_2 efflux is decreased during growth at high CO_2 concentrations, regrowth rate may be enhanced.

CO_2 enrichment often increases levels of storage carbohydrates. Thus, more carbon reserves are available at the moment of defoliation. However, increased carbon substrate availability does not necessarily increase remobilization rate. In accordance with Farrar's theory, regulation of remobilization may take place by cytosolic sucrose concentrations.

Adjustment of sink and source metabolism by cytosolic sucrose as the regulatory factor is the essence of Farrar's hypothesis on the control of carbon partitioning. For testing this hypothesis by means of studying regrowth of *Lolium perenne*, we should concentrate on studying activities of photosynthesizing and remobilizing sources, sink activities (gene expression, biosynthesis and respiration), and cytosolic sucrose concentrations, as affected by perturbations like CO_2 enrichment and defoliation.

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2 Effects of CO_2 enrichment on canopy photosynthesis, carbon economy and productivity of wheat and faba bean under field conditions

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Summary

Spring wheat (1991) and faba bean (1992) were grown under field conditions in naturally lit climatized enclosures, with temperatures tracking outside conditions under ambient and elevated (750 µmol mol^{-1}*)* CO_2 *concentration. Measurements of carbon- and water-economy were made continuously throughout the growing season from sowing till harvest. At elevated* CO_2 *concentration, yield and above-ground biomass increased with 34 % resp. 35 % for spring wheat, and 51 % resp. 58 % for faba bean. Canopy photosynthesis was stimulated by* CO_2 *concentration with 51 % and 71 % for spring wheat and faba bean respectively. Relative increase of the dark respiration rate was greater than for canopy photosynthesis for both crops. Soil respiration rate of faba bean increased to the same extent as canopy dark respiration. No significant shifts in the response factor of canopy photosynthesis could be detected during the season, except for the period of senescence, where the response to CO2 increased. Transpiration rates were not affected much by* CO_2 *concentration, notwithstanding the greater biomass at harvest. It is concluded that water use efficiency is increased by doubling of* CO_2 *concentration, mainly due to the increased canopy* CO_2 *uptake.*

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2.1 Introduction

There is no doubt that human activity influences the earth's biosphere on a global scale. Evidence can be found, among others, in the rising atmospheric CO_2 concentration. Present-day knowledge about the earth's atmosphere strongly indicates that this rise, and that of other greenhouse gasses, will affect the global climate. With the growing awareness of the human factor, the responsibility of mankind for its own fate becomes evident. "The ability of human societies to amelioriate, adapt to, and benefit from these rapid changes requires fundamental knowledge of the responses of terrestrial ecosystems to the forces of global change" (Steffens *et al.*, 1992).

This ambitious goal calls for an intimate knowledge of the effects of CO_2 concentration and climate change on a (representative selection of) plant species, from simple to very complex plant communities, up to complete ecosystems under different environmental conditions. Knowledge about the effects of CO_2 concentration at the process and leaf level (Ammerlaan & De Visser, 1993) need to be incorporated in models with which consequences of different environmental and growth conditions for the response of vegetations to CO_2 concentration can be examined (Grashoff & Nonhebel, 1993).

Independent experimental validation of these models is required by growing plants under different CO_2 concentrations under field conditions. These field experiments are also needed for understanding the quantitative importance of the reported long-term adaptation responses at the leaf or single plant level (Ammerlaan & De Visser, 1993) for plants growing in vegetations. As a start, a very simple vegetation, a mono-specific short-duration crop stand of spring wheat and faba bean, is used to analyze the effects of CO_2 concentration on canopy carbon- and water-economy under field conditions. The limitation of field experiments lies in the naturally-occurring year-to-year weather fluctuations. The use of crop models to overcome this set-back may be rewarding (Grashoff & Nonhebel, 1993). Arp & Berendse (1993) study the more complex vegetations and their interactions with the abiotic environment under elevated CO_2 concentrations and temperature.

The number of studies where plants were exposed to elevated CO_2 concentrations *under field conditions* is rather limited. In their review, Lawlor & Mitchell (1991) report 43 publications of which 33 were Open Top Chamber experiments, 9 were enclosed chamber studies, and one was a FACE experiment. The number of independent experiments is even lower, as often more than one publication comes from a single experiment. In addition to this review, studies concerned with perennial rye-grass and white clover (Nijs *et al.*, 1988a, b, 1989a, b, 1992; Overdieck, 1993 (and references cited herein); Ryle *et al.*, 1992a, b), an estuarine marsh (Arp & Drake, 1991; Arp *et al.*, 1993; Curtis *et al.*, 1989a, b, 1990; Drake & Leadley, 1991; Ziska *et al.*, 1990) and tundra vegetation (Grulke *et al.*, 1990) are available. The latter two projects are concerned with complex natural plant communities.

Whole-season carbon balance of the above-ground canopies of soybean and rice was studied in great detail (Allen *et al.*, 1991; Baker *et al.*, 1989, 1990a, b, c, 1992a, b; Baker & Allen, 1993; Campbell *et al.*, 1988, 1990; Jones *et al.*, 1984, 1985a, b; Rowland-Bamford *et al.*, 1991; Valle *et al.*, 1985a, b). Similar observations on grass and clover (Nijs *et al.*, 1988a, b, 1989a, b) and a C_3-sedge (Arp & Drake, 1991; Drake & Leadley, 1991) were done at much lower frequencies.

In this paper we report the effects of CO_2 concentration on crop productivity, carbon- and water-balance of spring wheat (*Triticum aestivum* L.) and faba bean (*Vicia faba* L.)

2.2 Experimental set-up

Crops were grown at two CO_2 concentrations, ambient (350 µmol mol^{-1}) and elevated (750 µmol mol^{-1}), under normal agricultural practice from sowing till harvest in climatized sun-lit crop enclosures (Table 2.1). The crop enclosures were surrounded by border plants. The enclosures are part of the Wageningen Rhizolab Facility, a joint research facility of the CABO-DLO Institute and the Wageningen University (described in more detail by Van de Geijn *et al.* 1993, Van de Geijn *et al.* submitted).

Spring wheat cultivar Minaret was used. A 100 % self-pollinating inbredline of faba bean cultivar Minica was used to ascertain a good seed-set without insects. A short summary of the experimental details is given in Table 2.1. Plants received optimal water and nutrients, with the exception of faba bean, which did not receive nitrogen fertilizer, but were inoculated with a compatible strain of Rhizobium.

The crop enclosures (1.25 x 1.25 m^2) were made of 5 mm thick polycarbonate, and could be adjusted in height to accommodate plants up to harvest. The temperature in the enclosures followed the outside temperatures, as registered by the weather station linked to the Wageningen Rhizolab.

Air refreshment rate of the above-ground compartment was typically 50 m^3 per hour, with a recirculation rate of about 800 m^3 per hour. Temperature was controlled by air-conditioners, separately for each compartment. CO_2 concentration of the ingoing and chamber air, and air flow rates were monitored every 10 and 20 minutes respectively. On the basis of these measurements, CO_2 concentration of the

Table 2.1 Description of experiments in Wageningen Rhizolab in 1991 and 1992.

	1991	1992
Crop species	spring wheat	field bean
cultivar	Minaret	inbred line of Minica
Soil	sandy soil	sandy soil
Soil depth (cm)	100	100
pH-KCl	5.4	5.6
organic matter content (%)	4.1	4.1
Bulk density (cm^{-3})	1.3	1.4
Plant density (pl m^{-2})	250	20
Irrigation	optimal	optimal
Fertilizer	optimal	optimal (-N)
Temperature	tracking ambient	tracking ambient
Sowing dat	4-Apr-91	3-Apr-92
Flowering date	2-Jul-91	25-May-92
Harvest date	26-Aug-91	7-Sep-92

chambers was adjusted by computer controlled valves, and carbon dioxide exchange calculated. The system is essentially an open system. Additionally, part of the air was forced into the soil by a slight over-pressure and recovered in an air-drain, placed in the soil at 15 cm depth. This prevented air of the soil compartment from entering the canopy compartment, and at the same time, allowed for measurement of the soil-root CO_2 production. The soil-root respiration option was in operation for the 1992 season, while for 1991 only a limited data-set is available. For the water-balance, dew-point temperatures were measured of the ingoing and chamber air. In addition, the condensate of the air conditioner, as part of the total water-balance, was measured using a tipping-bucket rain gauge.

The complete data-set was converted into hourly means. In this paper, data are used from day 188 in 1991 and 1992, selected for their high light intensities in the middle of the growing season. Furthermore, CCER (Canopy CO_2 Exchange Rate) and CET (Canopy EvapoTranspiration rates) values at maximum light intensity were selected for each day. CDR (Canopy Dark Respiration rates) were averaged over the period from 24.00 to 4.00 hours, while RSR (Root-Soil Respiration rates) were averaged over the whole 24 h period. Only those days were selected when the enclosures were undisturbed for the full 24 h. Disturbances were caused by opening the enclosures for non-destructive observations, and agronomic measures, such as weeding and spraying against diseases and pests.

2.3 Results

2.3.1 *Biomass and yield*

CO_2 concentration increased grain yield for both crops with 34 % (spring wheat, 1991) and 51 % (faba bean, 1992, Table 2.2). A similar increase was found for total biomass. Harvest index was not affected. The yield increase of spring wheat was explained by a 16 % increase in the number of ear-bearing tillers, and a 14 % increase in the number of spikelets per ear. Seed weight was not affected much (+2 %). For faba bean the number of stems per plant increased with 19 %, while the number of pods per stem increased with 25 %. Seed weight (+ 4 %) and number of seeds per pods (-2 %) were hardly affected. Although very different responses of

Table 2.2 Response of yield (ton/ha^{-1}), total biomass (ton/ ha^{-1}) and harvest index to CO_2 concentration (ppm).

	spring wheat			faba beans		
concentration	350	750	750/350	350	750	750/350
seed (g)	4.38		1.34	5.68	8.60	1.51
biomass (g)	13.08	17.60		13.48	21.25	1.58
HI	0.33	0.33	1.00	0.42	0.41	0.96

Table 2.3 Monthly averaged daily mean temperature (°C) and light intensity (PAR, MJ m^{-2} d^{-1}) for the period 1961 - 1990 at De Bilt, The Netherlands (Anon, 1992) and 1991, 1992 at the Wageningen Rhizolab.

	Temperature			PAR		
	1961-1990	1991	1992	1961-1990	1991	1992
April	8.0	10.0	10.4	12.9	14.6	11.8
May	12.3	10.7	16.9	16.8	15.4	20.0
June	15.2	13.8	18.0	17.9	11.0	16.2
July	16.8	20.0	20.0	16.7	17.8	16.2
August	16.7	18.9	19.1	14.7	14.8	11.6

yield and biomass to CO_2 concentrations have been found in these experiments, it remains unclear whether these are real differences between species, or due to year-year variability in weather conditions.

2.3.2 *Year-effects*

The early part of the growth period of the year 1992 was characterized by a much higher averaged daily temperature and radiation than 1991 (Table 2.3). In the later part of the season, the differences between the years were small. From a comparison with the 30-year average daily mean temperatures in De Bilt, it is clear that the temperature for 1991 was comparatively low, and for 1992 very high for May and June with corresponding higher light intensities (Table 2.3).

2.3.3 *Single day analysis*

A first impression of the effects of CO_2 concentration on spring wheat and faba bean can be derived from an exemplary day in both years. Julian day 188 of both years was selected.

Both days were clear days, with radiation levels over 400 W m^{-2} PAR (Figure 2.1). Total PAR radiation was 12.7 MJ m^{-2} d^{-1} and 12.9 MJ m^{-2} d^{-1} for 1991 and 1992 respectively. Mean temperature was more than 5 °C higher in 1991 (24.6 versus 19.0 °C). Photosynthetic rates closely followed the radiation pattern (Figure 2.2A, B), and were higher under elevated CO_2 in both years: 40 % for spring wheat and 46 % for faba bean (Table 2.4). Rearrangement of the data into light response curves revealed a striking resemblance between the crops (Figure 2.2C, D).

Canopy dark respiration was 58 % and 69 % higher for wheat and faba bean growing under elevated CO_2 concentration, respectively (Table 2.4). Soil-root respiration rates (SRR) for day 188 were available for 1992 only. SRR increased with 50 % for faba bean growing under elevated CO_2 concentration (Table 2.4).

Approximately 8 % of the carbon fixed during the light period was lost during the night by canopy dark respiration (CDR) for both crops. This fraction was slightly higher under elevated CO_2 (9 %), due to a stimulation of CDR with 58 % (Table 2.4).

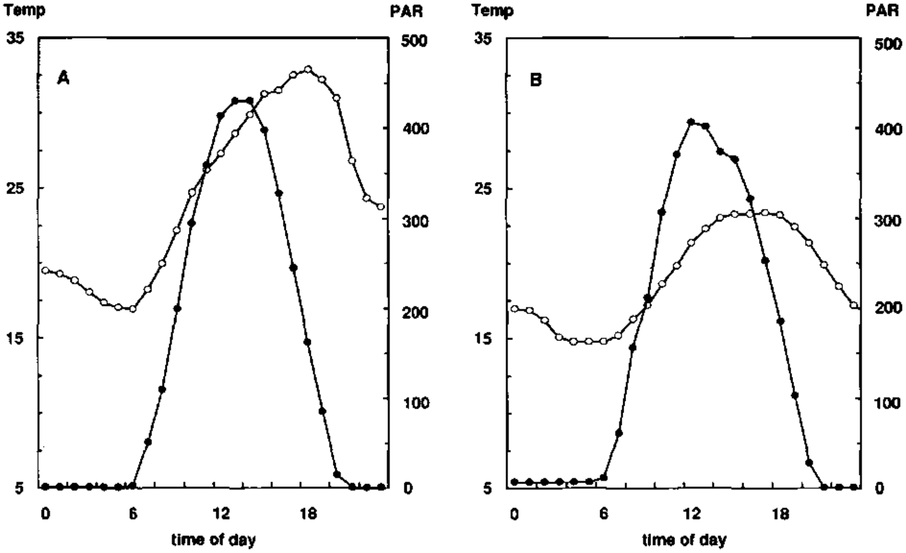

Figure 2.1. Hourly mean values for temperature (°C, ○) and PAR radiation (W m^{-2}, ●) on day 188 for (A) 1991 and (B) 1992.

The positive effect of CO_2 on CCER was partly decreased by the relatively greater enhancement of CDR.

The SRR of faba bean was about equal to CDR, but accumulated over the full 24 h, it represented a much larger fraction of the daily nett carbon balance. On this very clear day, 23 % of the total nett carbon fixation during the day was lost by SRR. Overall, about 31 to 32 % of the carbon fixed was respired for faba bean.

As an indicator of the response to CO_2 concentration, the ratio between elevated CO_2 and normal CO_2 (response factor) is often used. When determined at maximum light intensity, this response factor was 1.40 and 1.46 for wheat and faba bean respectively. When determined over the light period (PAR>100 W m^{-2}) this ratio became respectively 1.42 and 1.48. When considering the whole day canopy carbon balance, this factor was 1.40 for spring wheat and 1.46 for faba bean.

Maximum Canopy EvapoTranspiration rate (CET) was slightly higher for wheat (Figure 2.3, Table 2.4). For faba bean, elevated CO_2 concentration increased CET at maximum light intensity (+6 %), while for spring wheat a slight reduction was found under elevated CO_2 concentration (-8 %). Total transpiration over 24 h was 7 % lower for spring wheat and 2 % higher for faba bean for elevated CO_2 treatment.

Table 2.4 Effect CO_2 concentration on gas exchange parameters for spring wheat/1991 and faba bean/1992 on day 188

	spring wheat			faba bean		
µmol CO_2 m^{-2} s^{-1}	350	750	750/350	350	750	750/350
CCER max	50.22	70.38	1.40	45.57	66.85	1.47
CDR	-3.80	-6.03	1.59	-3.85	-6.51	1.69
SRR	n.a.	n.a.	n.a.	-4.18	-6.28	1.50
mg CO_2 m^{-2} d^{-1}						
CCER light period	67.5	95.6	1.42	67.7	100.7	1.49
CDR dark period	-5.4	-8.6	1.59	-5.5	-9.3	1.69
Nett CCER shoot	62.1	87.0	1.40	62.2	91.4	1.47
Gross CCER shoot	76.5	109.9	1.44	76.9	116.2	1.51
SRR	n.a.	n.a.	n.a.	-15.9	-23.9	1.50
Nett CCER plant	n.a.	n.a.	n.a.	46.3	67.5	1.46
CET max (mmol m^{-2} s^{-1})	9.55	8.77	0.92	7.29	7.71	1.06
Total transpiration (mm d^{-1})	5.24	4.90	0.94	5.50	5.60	1.02

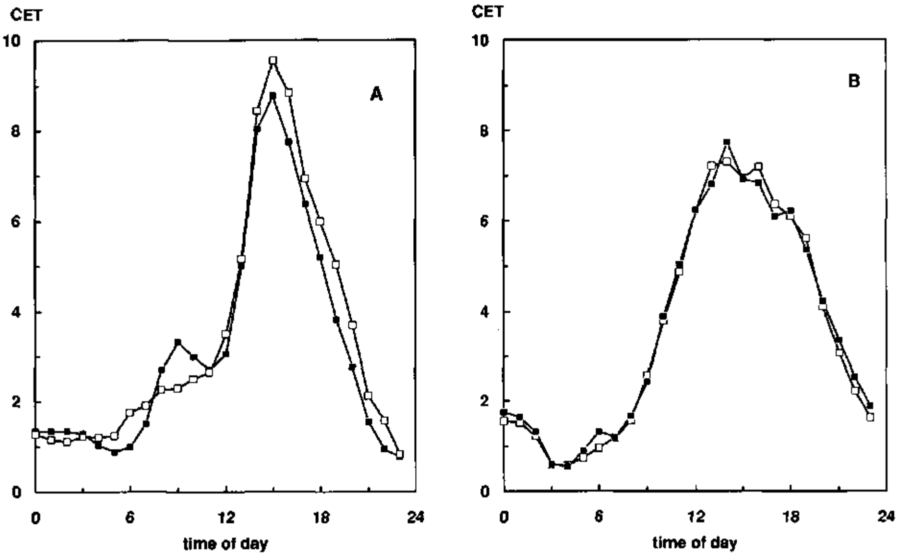

Figure 2.3. Effect of ambient (□) and elevated (■) CO_2 concentration on CET (Canopy EvapoTranspiration rate, mmol m^{-2} s^{-1}) on (A) spring wheat and (B) faba bean on day 188.

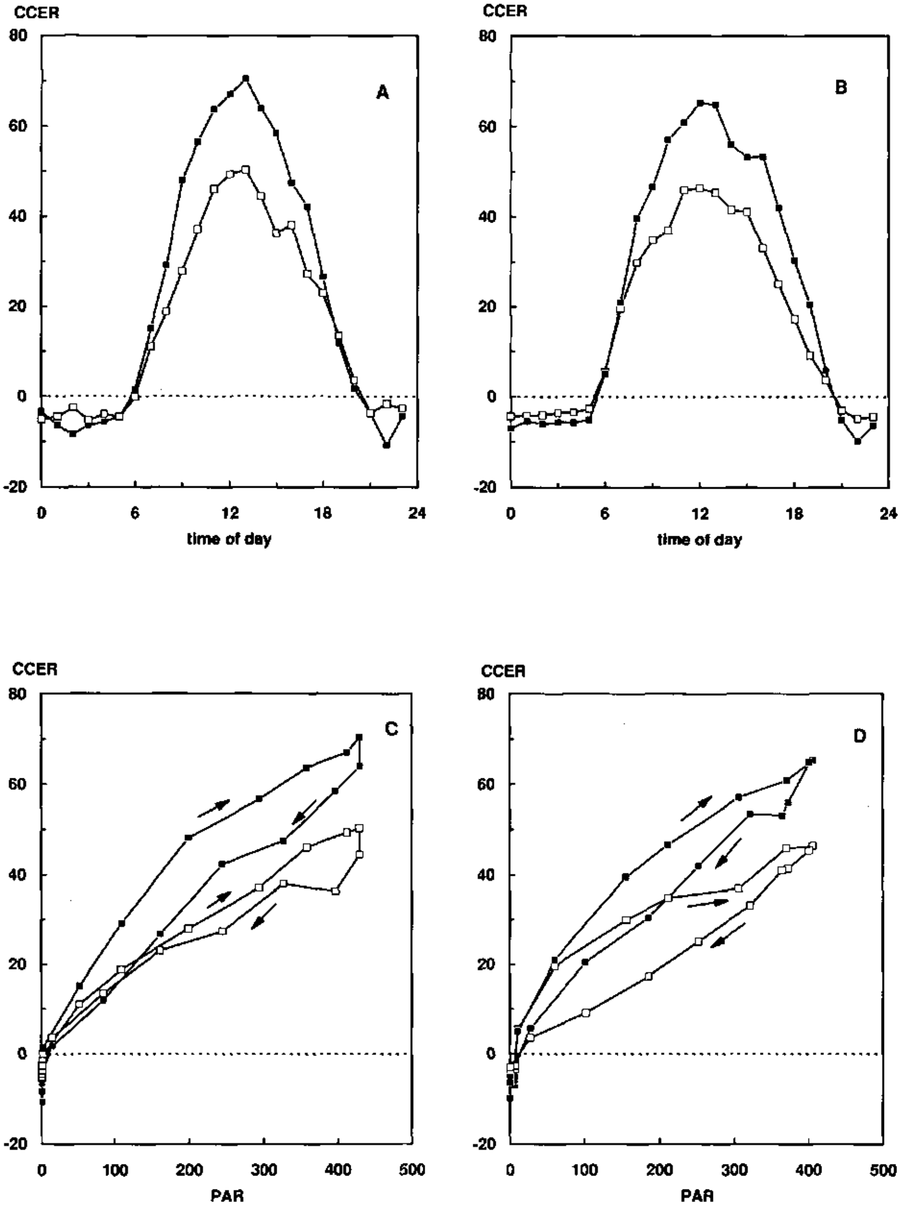

Figure 2.2. Effect of ambient (❑) and elevated (■) CO_2 concentration on CCER (canopy CO_2 exchange rate, μmol m^{-2} s^{-1}) on (A) spring wheat and (B) faba bean on day 188; and (C) the relationship between CCER and light intensity for (C) spring wheat and (D) faba bean on day 188. (Arrows indicate the daily course of CCER).

It was concluded that

- Canopy photosynthesis was stimulated by CO_2 concentration in both crops, but more so in faba bean.
- The response factor for canopy dark respiration was higher than for CCER for both crops.
- The response factor for soil-root respiration was higher than for CCER for faba bean.
- Soil-root respiration constitutes an substantial fraction of the daily carbon balance of the soil-crop system.

Although these data on C-balance of day 188 seem to reflect the response of yield and biomass to CO_2 concentration quite adequately, important variability in the response to CO_2 may exist over the growing period.

2.3.4 Whole season analysis

The daily canopy photosynthetic rate at maximum light intensity ($CCER_{max}$) was increased by CO_2 concentration during the entire season (Fig 4). The initial growth of faba bean was slower than that for spring wheat, as could be derived from $CCER_{max}$ between Julian days 120 and 140. At the end of the season, $CCER_{max}$ did not decline to zero. This was caused by survival of green leaf tissue up to harvest, even though seeds were completely matured. Additionally, for faba bean growth of new shoots at the base of the old plants took place.

The slope of $CCER_{max}$ under elevated versus ambient CO_2 concentration showed that the overall stimulation by CO_2 was larger for faba bean than for spring wheat (Figure 2.5A). This difference is also evident from values of $CCER_{max}$, averaged over the complete growing season: 32.1 (elevated) versus 21.8 (ambient) $\mu mol\ m^{-2}\ s^{-1}$ for spring wheat, yielding a 51 % stimulation by CO_2, and 30.3 (elevated) versus 17.8 (ambient) $\mu mol\ m^{-2}\ s^{-1}$ for faba bean, yielding 71 % stimulation by CO_2 concentration.

However, any time- or development related shifts in the response factor can be detected only when this factor is expressed for each day (Figure 2.5B). Apparently, there was no clear seasonal drift in the relative stimulation, with two exceptions. The first is the greater variability at the start of the season. This very important period (Grashoff & Nonhebel, 1993) did not yield any accurate estimates for the relative stimulation. The second exception is the response to CO_2 at the end of the growing season. In both years, the effect of CO_2 increased during the last two weeks of the growing season.

Mean daily values for CDR, averaged over the growing season, were stimulated by CO_2 concentration with 42 % for spring wheat and 87 % for faba bean (Figure 2.6). No clear seasonal or developmental trend in the response factor could be detected (results not shown).

Transpiration rates of the two crops were very similar, although large fluctuations, probably due to variation in temperature, light and RH, were found (Figure 2.7). Effects of CO_2 concentration on this parameter were moderate.

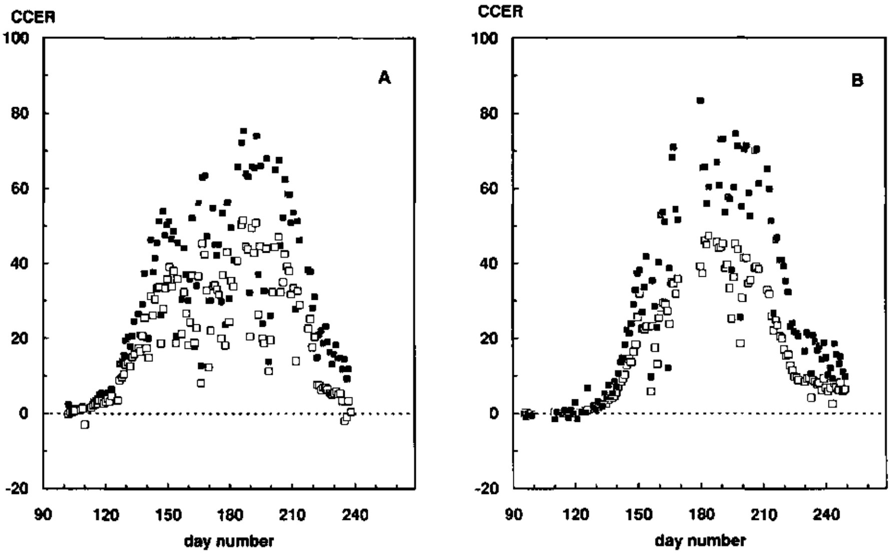

Figure 2.4. Effect of ambient (□) and elevated (■) CO_2 concentration on $CCER_{max}$ (canopy CO_2 exchange rate at max light intensity, μmol m^{-2} s^{-1}) on (A) spring wheat and (B) faba bean.

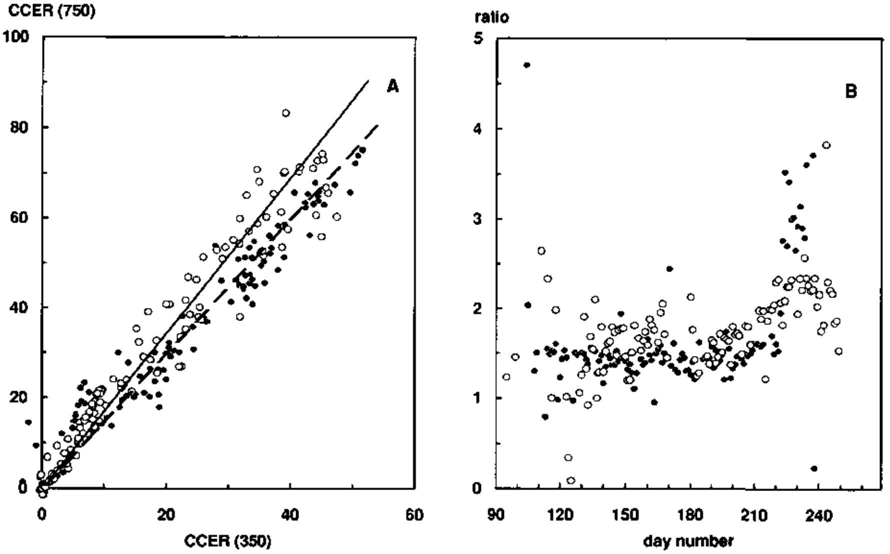

Figure 2.5. Relationship between $CCER_{max}$ values (μmol m^{-2} s^{-1}) of plants grown at ambient ($CCER_{350}$) and elevated ($CCER_{750}$) (A) and response factor of $CCER_{max}$ in time (B) for spring wheat (●) and faba bean (○).

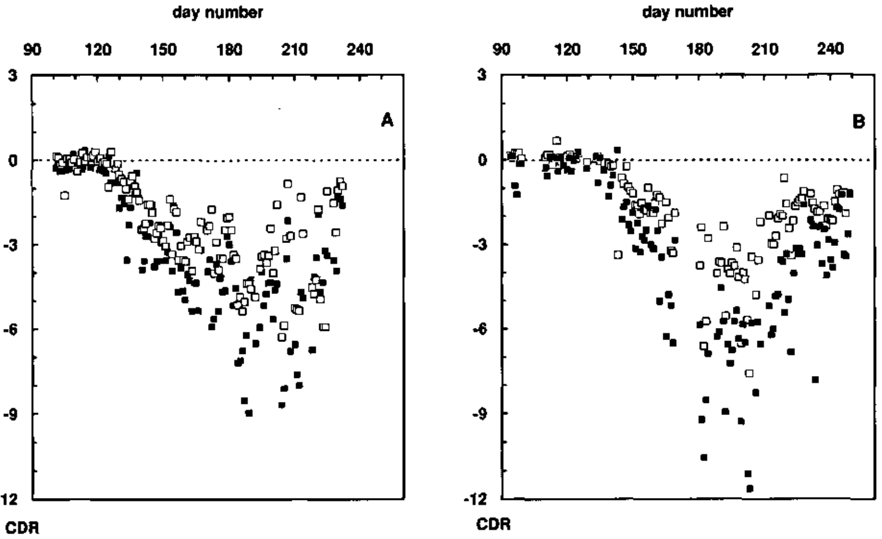

Figure 2.6. Effect of ambient (❑) and elevated (■) CO_2 concentration on CDR (canopy dark respiration rate, µmol m^{-2} s^{-1}) on (A) spring wheat and (B) faba bean.

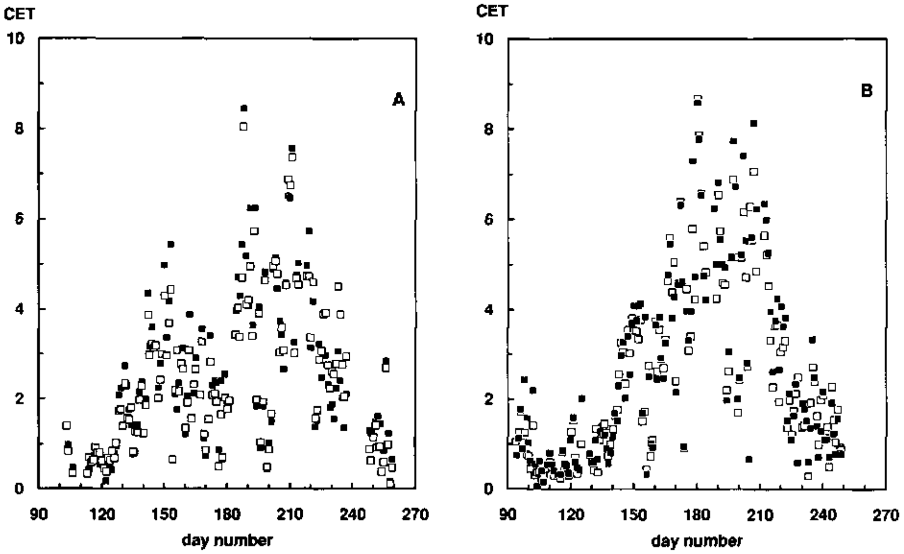

Figure 2.7. Effect of ambient (❑) and elevated (■) CO_2 concentration on CET (canopy evapotranspiration, mmol m^{-2} s^{-1}) on (A) spring wheat and (B) faba bean.

Conclusions:

No indication could be found for seasonal- or developmentally-related shifts in the response factor, except at the end of the season. The CDR and SRR were stimulated to a greater extent than $CCER_{max}$. CET remained largely unaffected by CO_2 concentration for most of the season.

2.4 Discussion

2.4.1 Relating biomass and yield increase to canopy C-balance.

The purpose of these experiments is to understand how gas-exchange characteristics, biomass and yield of two crop species respond to CO_2 enrichment in a 'real-life' situation. It should be realized, however, that a complete evaluation between carbon-balance data and biomass production is almost impossible to attain at this scale. This is not only caused by the technical limitations of the measuring equipment, but also by inaccuracies with which the biomass production can be measured. Losses due to volatiles, pollen, root exudation, decay and decomposition into soil organic matter are very difficult to determine. Perhaps the most important limitation is the practical difficulty to sample a large soil volume for root biomass.
With these restrictions in mind, we will now discuss the photosynthetic characteristics, yield and biomass data. Furthermore, possible changes in the effect of CO_2 concentration over the season are discussed

2.4.2 Biomass productivity under elevated CO_2 concentration and species variability

Kimball (1983) was one of the first to compile an extensive literature data-set on the effect of CO_2 concentration on biomass and yield. This was followed by many reviews (of reviews) afterwards. While Kimball still stressed the averaged response of all C_3-crop species to CO_2 concentration, later reviews recognized the differences between the different crop species. A recent review by Rogers & Dahlman (1993), updated from Cure & Acock (1986), estimated that wheat total biomass increased with 31 % in response to CO_2 doubling, while for related graminee species aboveground biomass responses to CO_2 doubling were 30 % (barley) and 27 % (rice). Yield increased with 35 % (wheat), 70 % (barley) and 15 % (rice). Soybean gave 29 % yield increase and 39 % increased biomass, while alfalfa exhibited a 57 % increased biomass (Rogers & Dahlman, 1993). Our result with spring wheat (35 %) are in the range of the results mentioned above, while that of faba bean (58 %) seems somewhat higher.
Nodulated plants were more responsive to CO_2 concentration than non-nodulated plants (Arnone & Gordon, 1990). This was also found in this study. A similar conclusion was drawn from a literature review of the effects of CO_2 concentration during the early vegetative period (Poorter, 1993). Although his data indicated that the response factor of faba bean was in the same range as that for wheat, the differ-

ence between the group of N_2-fixing species versus other C_3 species was significant, with the N_2-fixing species being the more responsive.

In all these reviews, the range of values obtained for weight or yield stimulation was very large (e.g. 7 % to 97 % for wheat; Poorter, 1993). It is obvious that environmental factors are important, especially under field conditions (Lawlor & Mitchell, 1991). The consequence of this is that species variability should be evaluated against common environmental backgrounds. This may very well result in disappearance of many of the so-called species or genotypical differences. Our approach is to use crop growth models to calculate the influence of year-to-year variability and interpret the differences between species against the background of a common temperature-light data-set (Grashoff & Nonhebel, 1993).

2.4.3 Canopy net photosynthesis

Differences between canopy CO_2-uptake or -production per unit ground area can be caused by differences in biomass and/or in specific rate. However, in the period of canopy closure, this effect of biomass is different for CCER and CDR. CCER is, at LAI above 3 almost not dependent on biomass (or LAI). Respiration rates, on the other hand, remain dependent on biomass. This may be the most straightforward explanation for the differential effect of CO_2 concentration on CCER versus CDR/SRR (however, see below).

CO_2 concentration increased photosynthesis at the leaf level (review Stitt, 1991; Ammerlaan & De Visser, 1993) and at the canopy level (Lawlor & Mitchell, 1991; this study). CCER was stimulated with 44 % for rice (Baker & Allen, 1993) and 89 % (26 °C) or 78 % (36°C) for soybean (Campbell *et al.*, 1990). The difference in response was attributed to a difference in canopy structure, and acclimation of canopy photosynthesis for rice, but not for soybean (Baker & Allen, 1993). A smaller difference in CCER was observed in our studies, where the nett CO_2 fixation of the grain crop increased with approx. 40 % and faba bean with 47 % on day 188 (Table 2.4). Acclimation at the canopy level was not observed for spring wheat (Dijkstra, Groenwold & van de Geijn unpublished).

2.4.4 Dark respiration

We found higher dark respiration rates per unit ground area under elevated CO_2 concentration for both crops. This may have been caused by a difference in shoot biomass, and/or by a difference in specific respiration rates (per unit dry weight). With the assumption that the biomass increase found at harvest (Table 2.2) reflected the biomass increase at any other stage of growth, it can be concluded that, since respiration increased more by CO_2 concentration than biomass, the specific respiration rate per unit of biomass increased somewhat, especially for faba bean.

Effects of CO_2 concentration on dark respiration rate were reviewed by Amthor (1991). Direct inhibiting effects of high CO_2 concentration on respiration rates per unit dry weight were found (Amthor, 1991; Bunce, 1990; Bunce & Caulfield, 1991; Butzelaar, 1991; Mousseau, 1993), and may involve regulation of the alternative oxidase (Palet *et al.*, 1991). Bunce (1990) and Mousseau (1993) found greater changes in respiration rates in response to short-term changes in CO_2 concentration than due long-term change. Dark respiration rate per unit leaf area increased after long-term adaptation to elevated CO_2 concentration (Bunce & Caulfield, 1991; Thomas *et al.*, 1993). Baker *et al.* (1992b) investigated the effect of CO_2 concentration on canopy dark respiration of rice, and found that rates were increased per unit ground area, but decreased per unit plant dry weight. A reduction of the respiration rate per unit dry weight is expected in the situation of closed canopies: maintenance respiration increases proportionally with biomass, while respiration for new growth is a constant or declining. Therefore, the larger the biomass, the more respiration for new growth gets diluted by the larger maintenance costs. This conclusion may be further complicated by changes in the chemical composition of the material, affecting the maintenance costs.

Thomas *et al.* (1993) found a 15 % increased dark respiration rate per unit leaf area of cotton. They concluded that the growth component of leaf respiration was unaffected by CO_2 concentration, but that the maintenance component of respiration increased. On the other hand, Baker *et al.* (1992b) found a decreased maintenance component of respiration, associated with the decreased protein content.

In this study, CDR increased more than CCER and yield. For the total C-balance, the great unknown remains the soil respiration rate, which on day 188 was 23 % of the total carbon fixed. This percentage will definitively be higher on cloudy days.

2.4.5 Transpiration and WUE

Transpiration per unit leaf area (Eamus, 1991; Tyree & Alexander, 1993) and stomatal conductance (Mott, 1990) are often decreased under higher CO_2 concentrations. This was partly explained by a reduction of the stomatal aperture, partly by a long-term decrease in number of stomata per unit leaf area (Oberbauer *et al.*, 1985; Woodward, 1987). Apparently, transpiration rates of C_3- and C_4-species respond similarly to CO_2 concentration (Morison, 1985)

Canopy evapotranspiration (per unit ground area) is much less affected by CO_2 concentration (this paper), probably because the decreased transpiration rate per unit leaf area is compensated for by the increase in leaf area per unit ground area (Goudriaan & Unsworth, 1990). Jones *et al.* (1985a) found similar canopy transpiration rates for soybean. However, CO2 concentration increasingly reduced the transpiration rate for rice in the course of the season (Baker *et al.* 1990a) . In the case of rice and soybean, and the species studied in this paper, the water use efficiency was greatly increased, due mainly to the increased photosynthetic rate and yield.

2.4.6 Response to CO_2 concentration in time

It is often found that the increased photosynthetic rate is not sustained, but decreased after some time (Ammerlaan & De Visser, 1993). This feedback mechanism is fairly well understood at the proces level (Stitt, 1991), but the whole-plant regulation is still rather speculative (Farrar & Williams, 1991). Downton *et al.* (1987) suggested that feedback at the leaf level is caused by an insufficient sink activity. Experimentally changing source-sink relations by manipulations of the leaf area or fruit number of soybean resulted in changing photosynthetic rates (Clough *et al.*, 1981)

An interesting observation was made by Arp (1991) and Thomas & Strain (1991), who suggested that growing plants in small pots would limit the sink in the roots, thereby inducing a negative feedback on photosynthesis. A literature review by Arp (1991) revealed a correlation between acclimation of photosynthesis in reponse to elevated CO_2 concentration and the size of the pots in which plants were grown. Thomas & Strain (1991) gave the experimental evidence. However, rice exhibited acclimation at the leaf level (Rowland-Bamford *et al.*, 1991) as well as at the canopy level (Baker *et al.*, 1990a). The hypothesis of the induction of feedback by root confinement does not seem to hold under field conditions. Supplementary explanations are needed.

Acock *et al.* (1985) found large fluctuations in the rate of photosynthesis depending on the developmental stage of the crop. However, the response factor for canopy photosynthesis did not change much, except a sudden increase just before flowering. Jones *et al.* (1984) found a constant stimulation of soybean canopy photosynthesis over the year. For *Scirpus olneyi* an increase of the ratio of canopy photosynthesis of elevated to ambient CO_2 from 1.34 to 1.78 was found, followed by an increase to 4.0 at the end of the season (Drake & Leadley, 1991). The latter value was influenced by a delayed senescence under elevated CO_2-concentration. For tundra vegetation, the period of positive stimulation of vegetation photosynthesis was limited to three weeks; thereafter no effect of CO_2 concentration was evident (Grulke *et al.*, 1990). An increase in the response factor in time from 1.8 to 2.8 was found by Havelka *et al.* (1984b) for winter wheat. The lower stimulation corresponded with the period before flowering, during which non-structural carbohydrates accumulated. In our experiments, the response factor remained constant during the growing season, except for the period, when leaves exhibited senescence and leaf area index decreased sharply.

The stimulation by CO_2 enrichment disappeared at the end of the growing season for soybean (Havelka *et al.* 1984a), cotton (Radin *et al.*, 1987) and sweet potato (Bhattacharya *et al.*, 1985), but increased for wheat (Havelka *et al.*, 1984b, Kendall *et al.*, 1992). Results from studies with wild vegetations indicate that CO_2 enrichment delayed senescence (Curtis *et al.*, 1989a; Grulke *et al.*, 1990), just as was found in our experiments.

The contradictory results of the response of canopy photosynthesis to CO_2 concentration during the period of senescence are difficult to explain. A direct effect of CO_2 concentration on leaf senescence and LAI (e.g. on ethylene sensitivity) cannot be ruled out. Secondly, the onset of senescence may have to do with carbon- and water-balances of individual leaves. Thirdly, an indirect effect may influence the development of the crop (e.g. tuber maturity, grain ripening), which triggers senescence in some way or other. Finally, it may be the result of the declining leaf area index itself: the lower the leaf area index, the more the canopy photosynthesis reflects the effects of CO_2 concentration on leaf photosynthesis, which is usually much greater than that of CCER (Grashoff & Nonhebel, 1993).

The increased responsiveness at the end of the season seems of little importance for the total carbon balance of the crop. However, competition between species which depend on growth late in the season may be affected by a later leaf fall.

It is concluded that CO_2 concentration stimulated canopy photosynthesis for most part of the season with a constant factor. Canopy dark respiration and soil-root respiration increased with a greater percentage than canopy photosynthesis, probably mainly due to the increased biomass. These results indicated that adaptations to long-term elevated CO2 concentration, such as found for leaves or single plants, appear to be of minor importance for the carbon-balance of the crop. However, this is not sure for the period until canopy closure, a period during which no accurate estimates of the response factor could be made.

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3 Effect of CO_2 increase on the productivity of cereals and legumes; model exploration and experimental evaluation

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Summary

The effect of an increased atmospheric CO_2 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 CO_2 concentration (350 ppm) and also with a concentration of 700 ppm. The results were compared with those of experiments with increased CO_2 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 CO_2 concentration showed an increase of above-ground biomass of 35-50 % and the experiment showed an increase of 35 %. Faba bean showed a larger CO_2 response, both in the simulations (+ 47-56 %) and in the experiment (+ 58 %).

Model explorations further showed that the experimental difference in CO_2 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 CO_2 concentration in the atmosphere and the associated probable rise of temperature may affect the functioning of crops and agro-ecosystems in future. Various crop physiological processes are affected by climatic change. CO_2 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 CO_2 increase on photosynthesis often compensates for the negative effect of temperature rise on crop longevity.

However, the large positive effect of CO_2 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 CO_2 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 CO_2 concentration, may reduce the positive effect (Wong, 1979; Rowland-Bamford et al., 1991). Differences in CO_2 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 CO_2 response of spring wheat and faba bean (Nonhebel, 1993a; Grashoff et al., 1993) agree with the CO_2 response measured in recent long-term experiments. Crops were grown under high CO_2 concentration with radiation and temperature similar to the field situation. Moreover, we investigate if there are differences in CO_2 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 CO_2 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 CO_2 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 CO_2 concentration. According to Goudriaan (1985), the value of AMAX is almost proportional to the CO_2 concentration but the value of EFF is less sensitive. At an average temperature of 20 °C, doubling the CO_2 concentration increases EFF by 15 % and AMAX by 100 % (Figure 3.1)(Goudriaan & Unsworth, 1990).

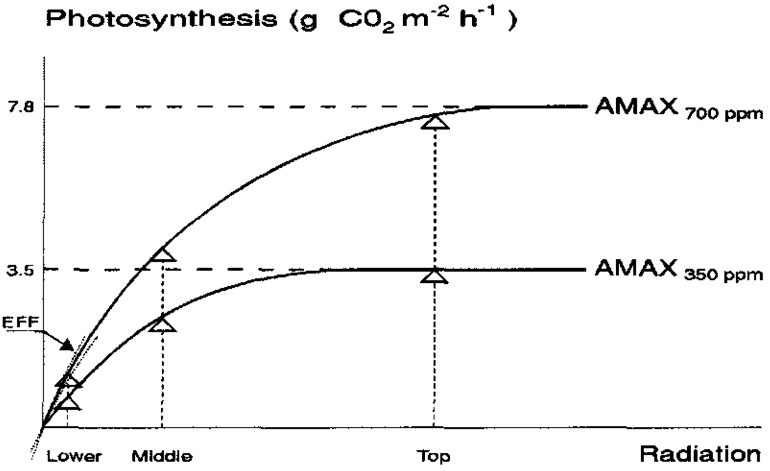

Figure 3.1. The photosynthesis/light response curve for individual leaves with a CO_2 concentration of 350 ppm and with a concentration of 700 ppm. EFF=initial light use efficiency; AMAX=maximum photosynthetic rate; L, M, T = maximum radiation levels at a clear day for leaves placed at a low level in 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 CO_2 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 CO_2

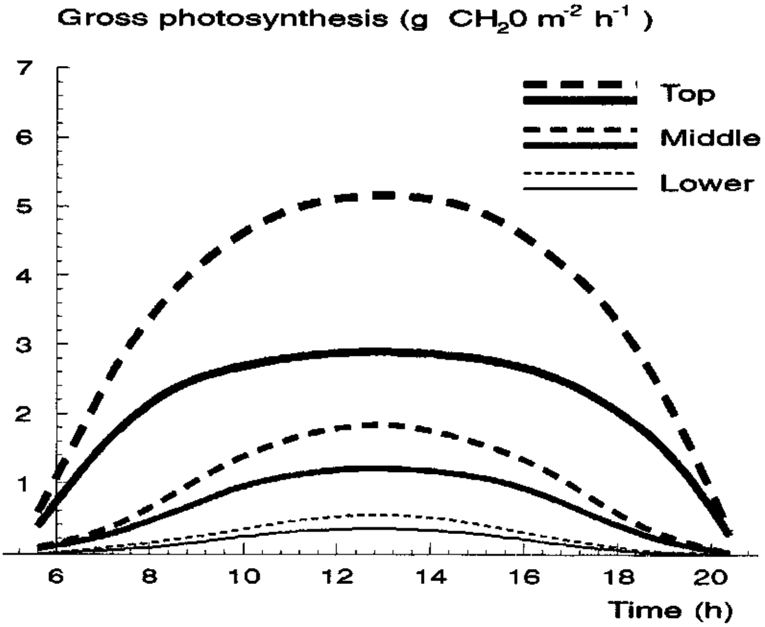

Figure 3.2. The theoretical course of photosynthesis of three levels in a closed canopy on a clear day under CO_2 concentrations of 350 ppm (—) and 700 ppm (---).

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 C_3 plants, a doubling of the CO_2 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

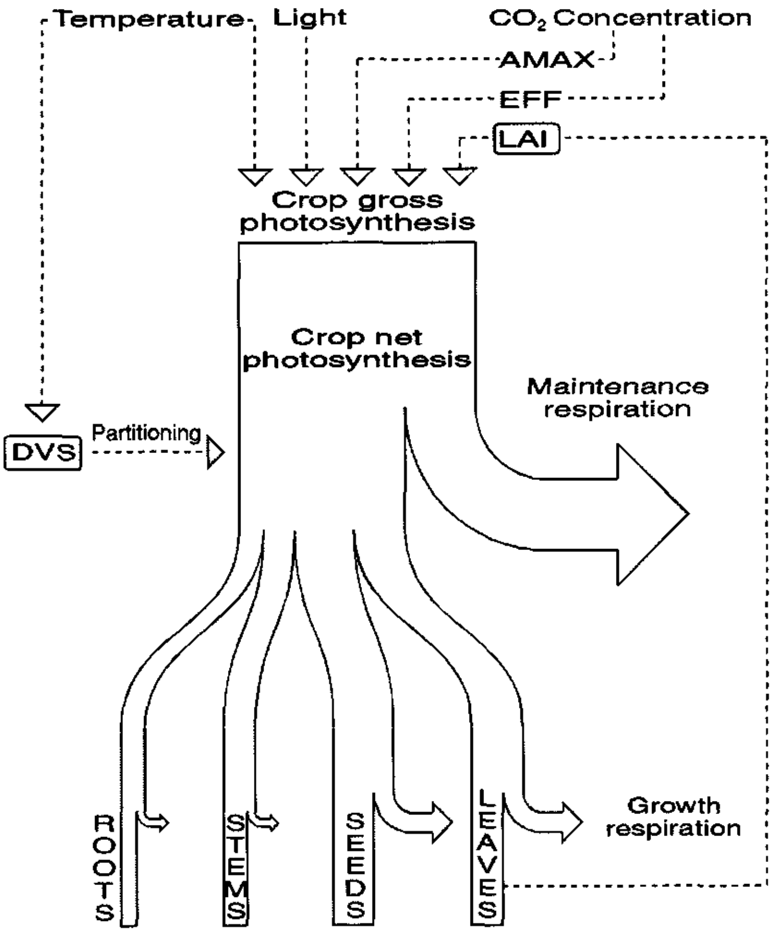

Figure 3.3. Schematic representation of crop growth. Dotted lines indicate information lines.

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 CO_2 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 CO_2 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 CO_2 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 CO_2 concentrations of 350 ppm (control) and 700 ppm (C700). The average CO_2 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	--

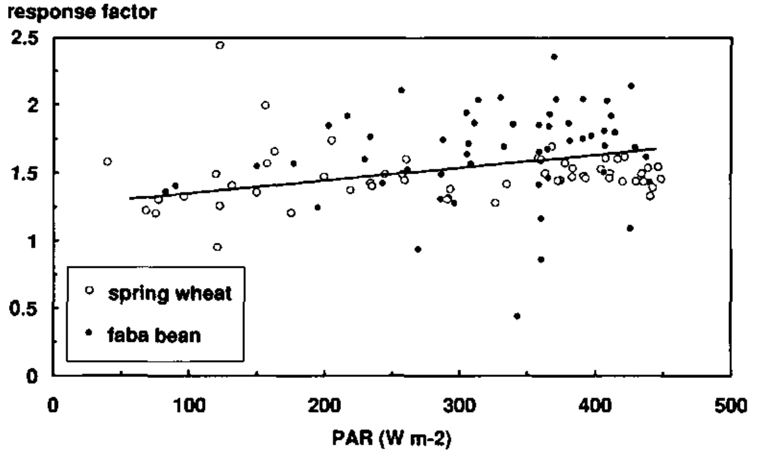

Figure 3.4. Measured (symbols) and simulated (line) values of the ratio between maximum rates of crop photosynthesis at 350 and 700 ppm CO_2 at various light intensities during the period of a closed canopy

Both in the simulation studies and in the experiments, spring wheat showed 10 % less response to CO_2 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 CO_2 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 CO_2 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 CO_2 concentration of 700 ppm and CO_2 response (%-increase) on above-ground biomass for spring wheat and faba bean (1975-1988) with early and late dates of emergence (Julian daynumber).

	Spring wheat		Faba bean	
Emergence	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**

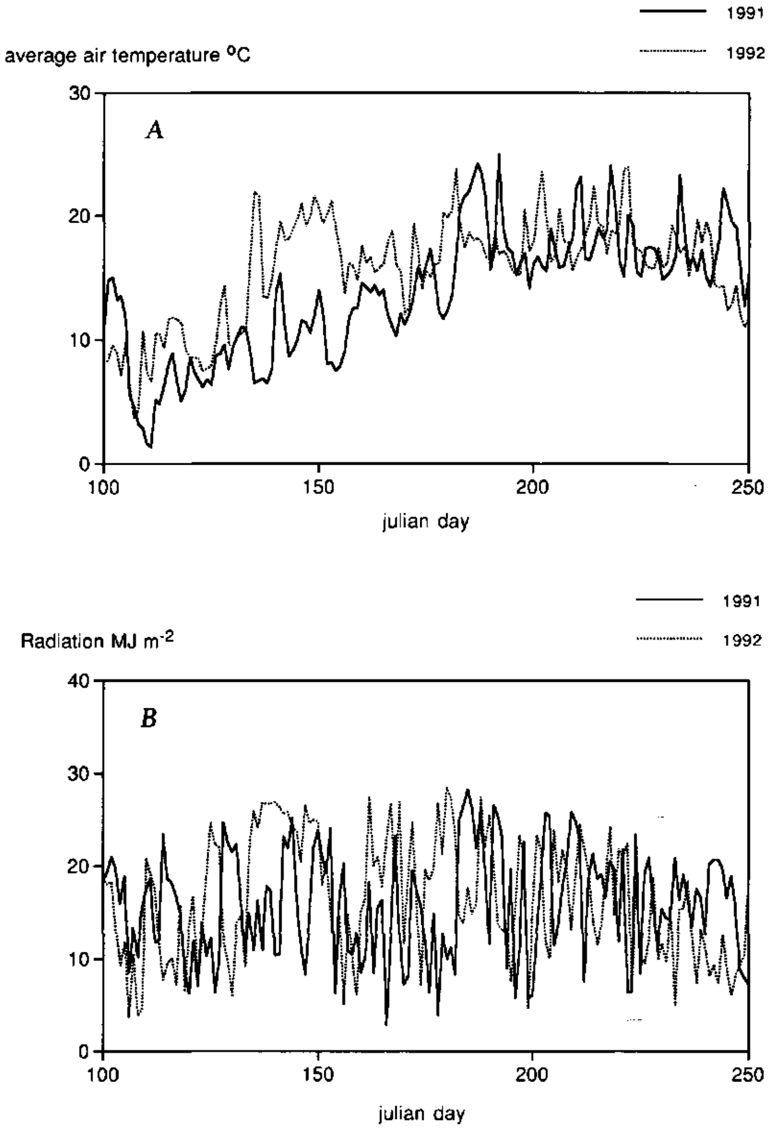

Figure 3.5. Daily weather data for 1991 and 1992. a: Average air temperature; b: Total radiation.

however, were much lower than in 1992 (Figures 3.5a and 3.5b). The simulations for both crops showed a smaller CO_2 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 CO_2 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 (C700/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 CO_2 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 CO_2 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 CO_2 concentration (Table 3.1). This shows that the simulation modeling approach for assessments of the effects of CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 concentration. Pot experiments with wheat showed almost no increase of AMAX, due to CO_2 (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 CO_2 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 CO_2 concentration in the field may be more representative for the actual CO_2 response of crops than the results from pot or greenhouse experiments.

Another question is the importance of processes which progressively reduce the effect of CO_2 increase on crop photosynthesis during the season, such as a reduction of AMAX after a prolonged period of exposure to a high CO_2 concentration. Baker

& Allen (1993) found no negative feed-back of a long-term CO_2 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 CO_2 increase in future, at least not for cereals and leguminous crops under optimum nutrient supply.

Our simulations showed that the difference in CO_2 response between spring wheat and faba bean is not likely based on a fundamental physiological difference. It was shown that the smaller CO_2 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 CO_2 increase, which is confirmed by the experimental results (Dijkstra, pers comm.) and experiments with soya bean (Lieth et al., 1986). Theoretically, a doubled CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 response curve (Figure 3.6b). This additional effect probably explains why the simulated differences in CO_2 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 CO_2 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

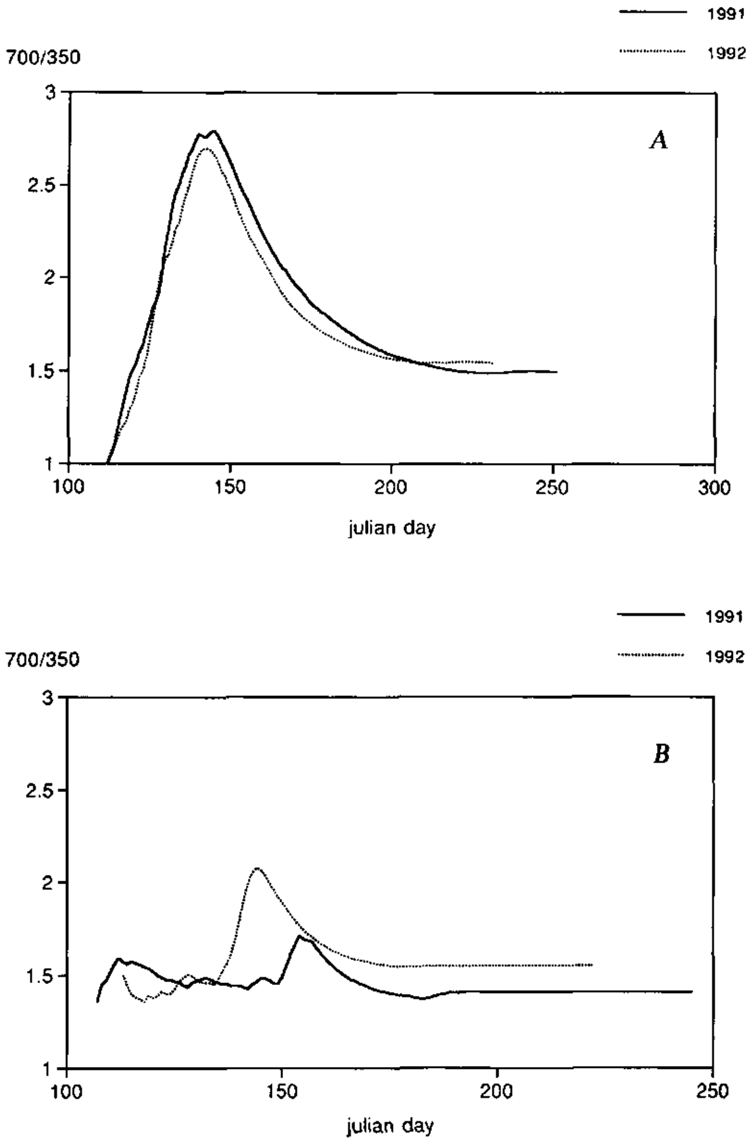

Figure 3.6. The relative CO_2 response of cumulative biomass (C700/C350) versus time for simulations in a season with low temperatures (1991) and a season with higher temperatures (1992). a: faba bean; b: spring wheat

the relative CO_2 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 CO_2 concentration on crop growth and yields. Moreover, it was

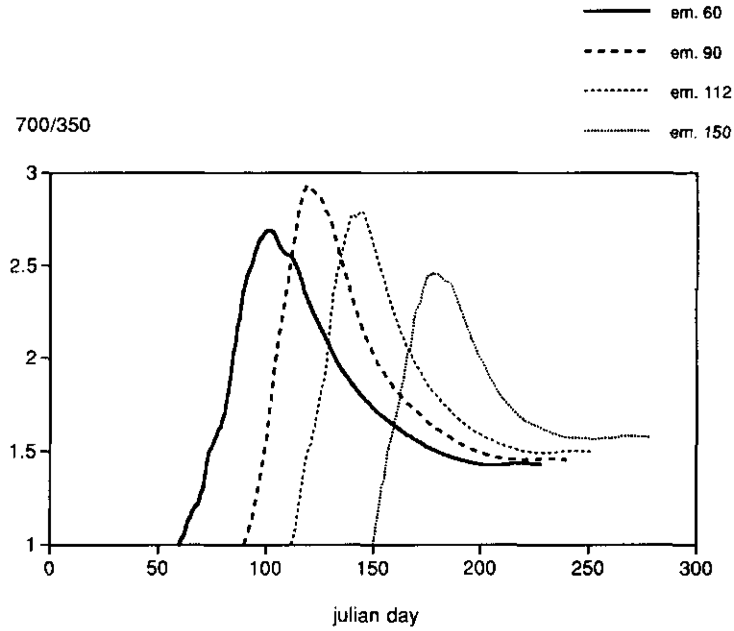

Figure 3.7. The relative CO_2 response of cumulative biomass (C700/C350) versus time for four faba bean simulations with increasing emergence dates in 1991.

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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4 Influence of air pollution on carbon dioxide effects on plants

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Summary

Air pollution can have a major impact on ecosystems. Despite the implementation of emission abatement measures, ambient concentrations of O_3, *NO_x and NH_y are still well above effect thresholds and are increasing in many regions. On a more global scale, the CO_2 concentration is increasing as well. This paper discusses the importance of taking air pollution into account when evaluating the effects of elevated CO_2. The results of experiments with CO_2 and pollutant combinations has shown that effects were generally additive. An exception may be the combination of CO_2 and NH_3. In a preliminary experiment the growth of several plant species was stimulated by both compounds when applied singly but not when applied in combination. The growth stimulating effect of CO_2 was also counteracted by NO_x. The effect threshold of O_3 was found to increase in the presence of elevated CO_2. In more general terms, it appeared that the the stimulating effect of elevated CO_2 concentration is reduced by "conventional" air pollutants. This might mean that reductions of O_3, NO_x and NH_y enhance the effects of CO_2 and that in polluted regions the growth stimulating effect of elevated CO_2 may be smaller than generally assumed. It is obvious from these results that to properly evaluate the impact of elevated CO_2 and air pollution, both have to be taken into account.*

In: S.C. van de Geijn, J. Goudriaan & F. Berendse (eds), 1993, Climate change: crops and terrestrial ecosystems. Agrobiologische Thema's 9, CABO-DLO, Wageningen; 59 - 70.

4.1 Introduction

During the next decades, the CO_2 concentration will probably continue to increase on a worldwide scale. The present rate of increase is about 2 ppm per year. This elevated CO_2 concentration will result in growth stimulation in vegetations where CO_2 is a dominant growth limiting factor. This is the case in many agricultural systems.

However, in natural vegetations there may be other key factors (nutrient deficiency, biomass turn over, competition etc.).

To meet with the present definitions, the expression "elevated CO_2" in addition to "air pollutants", i.e. O_3, NH_3 and SO_2, will be used in this paper, although elevated CO_2 concentrations are usually undesired as well.

Currently, ambient O_3 concentrations are well above effect thresholds for many plant species (Tonneijck, 1989). These concentrations are even increasing in many European countries, by 1-3 % annually (Guicherit, 1989) due to the increased emission of precursors (NO_x and hydrocarbons) and photochemical activity in the atmosphere combined with higher temperatures. On a regional scale, other pollutants are added to this mixture. Excessively high concentrations of SO_2 and HF, for instance, which in the past have caused serious damage, have been substantially decreased. However, the NO_x concentration (NO+ NO_2) has been more or less constant over the past ten years (RIVM, 1992), but might increase in the future if emission abatement does not compensate the expected increase in road traffic emissions.

Due to intensification of livestock farming, concentrations of NH_y (NH_3 + NH_4^+) have increased substantially since the sixties, but will probably decrease in the coming decade as a result of emission abatement. In many countries at the present, a substantial part of the atmospheric nitrogen deposition in rural areas is caused by NH_y. In the Netherlands, roughly 50 % of the nitrogen deposition is made up of NH_3 and 15 % of NH_4^+ (Heij & Schneider, 1992). When evaluating the effects of CO_2, which is rather uniformly dispersed over a wide scale, one might question whether pollutants of a more local nature have to be taken into account. On the other hand, one might also question the relevance of small increases in the CO_2 concentration on the effects of other air pollutants on plants. This is especially relevant in the case of pollutant interactions.

Generally, O_3 (Lefohn *et al.*, 1992) and NO_x (Wellburn 1990) cause growth and yield reduction, although near-to-background levels might act as a growth stimulator (Schulze 1989). Growth stimulation is shown for CO_2 (Kimball 1983) and NH_y (van der Eerden *et al.* 1991). Only high concentrations of NH_y have proven to directly reduce growth (van der Eerden 1982). The concentration level at which growth stimulation turns into reduction of growth is much higher for NH_y than for NO_x. This may be due to differences in manner of detoxification and cellular acidification of the pollutants (Raven, 1988; Pearson *et al.*, 1993). O_3, NH_y and NO_x can also induce secondary effects, such as increased stress sensitivity, changes in flowering and in competitive ability (Lefohn, 1992; Dueck *et al.*, 1990; van der Eerden *et al.* 1991; Wellburn 1990).

Information on combination effects including CO_2 is fragmentary and thus hypotheses on interactions between pollutants must be based on results from experiments with the single pollutants only. Both NO_x (Wellburn, 1990) and NH_3 (van der Eerden and Pérez-Soba, 1992) can stimulate stomatal opening and thus increase the uptake of other gases. On the other hand, exposures to O_3 and CO_2 generally result in stomatal closure, thereby decreasing the uptake of other air pollutants. Whether these effects will be of an additive nature is largely unknown, and will likely depend on the concentrations of the individual pollutants.

The growth stimulating effect of CO_2 will be limited by the availability of other nutrients. Nitrogen can be such a limiting factor and therefore a nitrogen fertilizer like NH_y (and possibly NO_x as well) may have a more-than-additive interaction with CO_2. In 1991 we started a modest research programme to study the combined effects of CO_2 with O_3, NH_y and NO_x. With respect to NH_y, we focused on NH_3 as this compound has by far the highest contribution to the nitrogen deposition in the Netherlands. Results on combinations with NO_x are largely based on literature data. Although many combinations of compounds can be made and the entire air pollution cocktail is relevant for evaluation of the field situation, for practical reasons we decided to start by studying the effects of combinations of two compounds. The first results are presented and briefly discussed in this paper.

4.2 Experimental procedures

Fumigation experiments with CO_2, O_3, NH_3 and their combinations were performed in 1991 and 1992 in climate controlled chambers, described by Mooi & Jolink (1990). Results on combination effects of CO_2 and NO_x have been taken from the literature. Temperature, relative humidity and light intensity were 17 °C, 75 % and 60 W m^{-2} PAR during the day (8-19 h) and 11 °C, 90 % and 0 W m^{-2} during the night. The concentration of CO_2 is expressed in ppm (1 ppm = 550 µg m^{-3}); that of the other gases are in µg m^{-3}). The O_3 concentrations were 110 µg m^{-3} from 10 to 18 h and 40 µg m^{-3} during the remaining hours. Concentrations of NH_3 (100 and 40 µg m^{-3}, in 1991 and 1992 respectively) and of elevated CO_2 (650 ppm) were kept constant over day and night. Saplings of *Fagus sylvatica* and *Pinus sylvestris* were grown in sandy, nutrient poor soil and were two and three years old, respectively, when fumigated. The experiment commenced just after the leaves were fully expanded. *Nicotiana tabacum* cv. Bel W3 (6 weeks old) and *Trifolium subterraneum* cv. Geralton (directly after sowing) in commercial potting soil were also used in these experiments.
This paper focuses mainly on *F. sylvatica* and *T. subterraneum*, while *P. sylvestris* and *N. tabacum* are only briefly mentioned.

4.3 Results

4.3.1 CO_2+O_3

Leaf injury in *Trifolium* due to O_3 was reduced in the presence of elevated CO_2. This reduction was the strongest 15 to 20 days after the start of the fumigation. After 25 days the difference in injury between plants exposed to O_3 and O_3+CO_2 was small, but remained constant over the remaining 15 days of exposure. This indicates that O_3-induced leaf injury was both reduced and delayed by CO_2. Exposure to O_3 also reduced the shoot and root growth of *Trifolium* and reduced the shoot/root ratio, while exposure to CO_2 stimulated shoot and root growth equally (Figure 4.1).The impact of CO_2 and O_3 on shoot and root growth was additive and

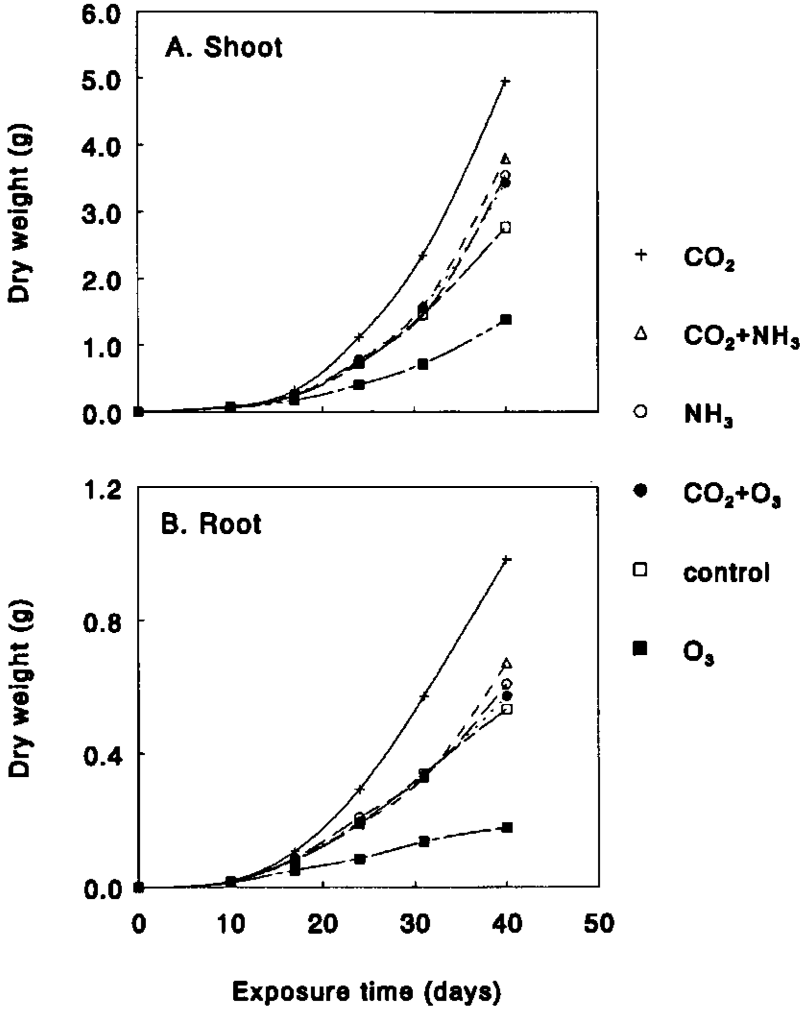

Figure 4.1. Mean shoot and root weight (g dry wt) of *Trifolium subterraneum* cv. Geralton exposed to O_3, NH_3, CO_2 and some combinations for 40 days.

no interaction was found. With respect to leaf injury and shoot growth of *Nicotiana*, the response was very similar to that of *Trifolium*. No leaf or needle injury was observed in either tree species.

Because the spring flush of *Fagus* was completed prior to fumigation, neither treatment influenced the leaf biomass production. A negative effect of O_3 was observed on the fine roots (diameter less than 2 mm) largely formed during the fumigation. This reduced the specific root length (length per unit dry weight; SRL), implying shorter and thicker roots, impairing the capacity to take up nutrients and water. While the CO_2 treatment did not affect the SRL, the CO_2+O_3 treatment reduced SRL more than the O_3 treatment alone. The influence of the treatments on the SRL and transpiration were comparable, but differed from those on the photo-

Table 4.1 Effects of exposures to CO_2, O_3, NH_3 and some combinations for 90 days on root growth and gas exchange of *Fagus sylvatica*. SE indicates the standard error, n=10. Significant treatment effects are indicated in the ANOVA's below by: *** $P<0.001$; ** $P<0.01$; * $P<0.05$; NS = not significant at $P<0.05$.

	Roots (<2mm)	Specific root length	Net photosynthesis	Daily transpiration
	(g dry wt)	(m g^{-1})	(mg CO_2 m^{-2} s^{-1})	(g H_2O g^{-1} leaf dwt)
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Control	1.83 ± 0.18	9.05 ± 0.46	0.12 ± 0.00	20.1 ± 1.94
CO_2	2.40 ± 0.35	9.77 ± 1.31	0.16 ± 0.02	17.0 ± 1.52
O_3	2.55 ± 0.40	7.80 ± 0.73	0.11 ± 0.01	8.07 ± 0.55
NH_3	1.54 ± 0.25	7.22 ± 0.47	0.18 ± 0.02	29.3 ± 2.21
CO_2+O_3	1.10 ± 0.21	5.30 ± 0.22	0.14 ± 0.01	7.14 ± 1.00
CO_2+NH_3	1.25 ± 0.15	6.88 ± 0.68	0.13 ± 0.01	23.1 ± 3.22
ANOVA for O_3 + CO_2				
O_3	NS	**	NS	***
CO_2	NS	NS	*	NS
O_3 x CO_2	***	NS	NS	NS
ANOVA for NH_3 + CO_2				
NH_3	**	**	NS	**
CO_2	NS	NS	NS	NS
NH_3 x CO_2	NS	NS	**	NS

synthesis (Table 4.1). The experiment with *Fagus* was repeated in 1992 and generally gave the same results. The fine root biomass was reduced by O_3 and increased by CO_2 and the strongest reduction in SRL was found in the combination of O_3+CO_2. With respect to root growth, *Pinus* reacted somewhat differently than *Fagus*. CO_2 also increased the root biomass of *Pinus*, but reduced root branching. O_3 slightly increased root branching while the combination of O_3+CO_2 did not affect it. The responses on photosynthesis in pine were not significant.

4.3.2 CO_2+NH_3

Root and shoot growth of *Trifolium* were stimulated by both NH_3 and CO_2 alone and in combination, but the combination effect was less than additive (Figure 4.1). This applied to the root length as well. Obviously, there was a strong negative interaction between the two compounds in their impact on biomass production.

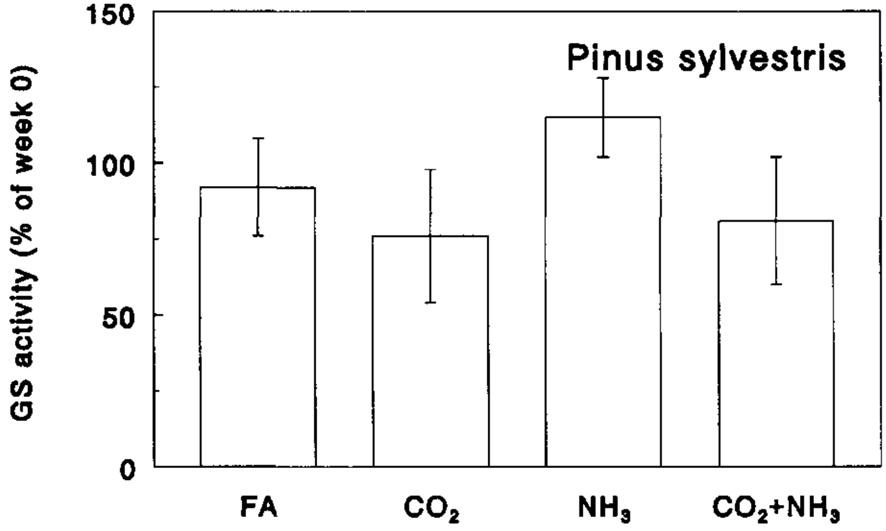

Figure 4.2 Change in specific activity of GS (% of initial activity in needles of *Pinus sylvestris* exposed to filtered air (350 ppm CO_2), to elevated CO_2 (650 ppm), to NH_3 (100 µg m^{-3}) and to the combination of CO_2+NH_3 for 8 weeks. Changes with respect to initial activity were calculated per individual tree, n=4.

The reaction of *Nicotiana* plants differed from that of *Trifolium* in that the leaf biomass of *Nicotiana* was equally stimulated by CO_2 and CO_2+NH_3, but was not influenced by NH_3 alone.

Photosynthesis of *Fagus* was stimulated by both compounds singly but not by their combination. The photosynthesis of *Pinus* was also stimulated by NH_3 and CO_2, while their combination reduced photosynthesis.

As far as the effects on needles are concerned, the effect of the combination of CO_2 and NH_3 on *Pinus* was less than additive with respect to needle biomass, net photosynthesis, soluble proteins and glutamine synthetase (GS) activity (Figure 4.2). It would appear that NH_3 alters the effects of elevated CO_2. The activity of the enzymes peroxidase and glutamate dehydrogenase were the only parameters that showed an interactive effect between and elevated CO_2.

The needle biomass of *Pinus* was not affected by NH_3, but was increased slightly by CO_2+NH_3 and increased significantly by CO_2 alone (Figure 4.3). The trees exposed to elevated CO_2 had significantly lower concentrations of nitrogen in their needles than those exposed to NH_3, although the total nitrogen content between trees fumigated with NH_3 and CO_2 did not significantly differ, indicating dilution by growth. A linear relationship was found between biomass and total needle nitrogen in trees fumigated with filtered air or NH_3. This relationship does not exist however, in trees exposed to CO_2, alone or in combination with NH_3 (Figure 4.3). Belowground, a slightly negative effect of NH_3 and NH_3+CO_2 on the fine root growth of

Fagus was found, while CO_2 increased it (Figure 4.4). The fine root growth of *Pinus* was not affected by NH_3 and was again stimulated by CO_2, while in contrast to *Fagus*, the combination more than additively increased fine root growth.

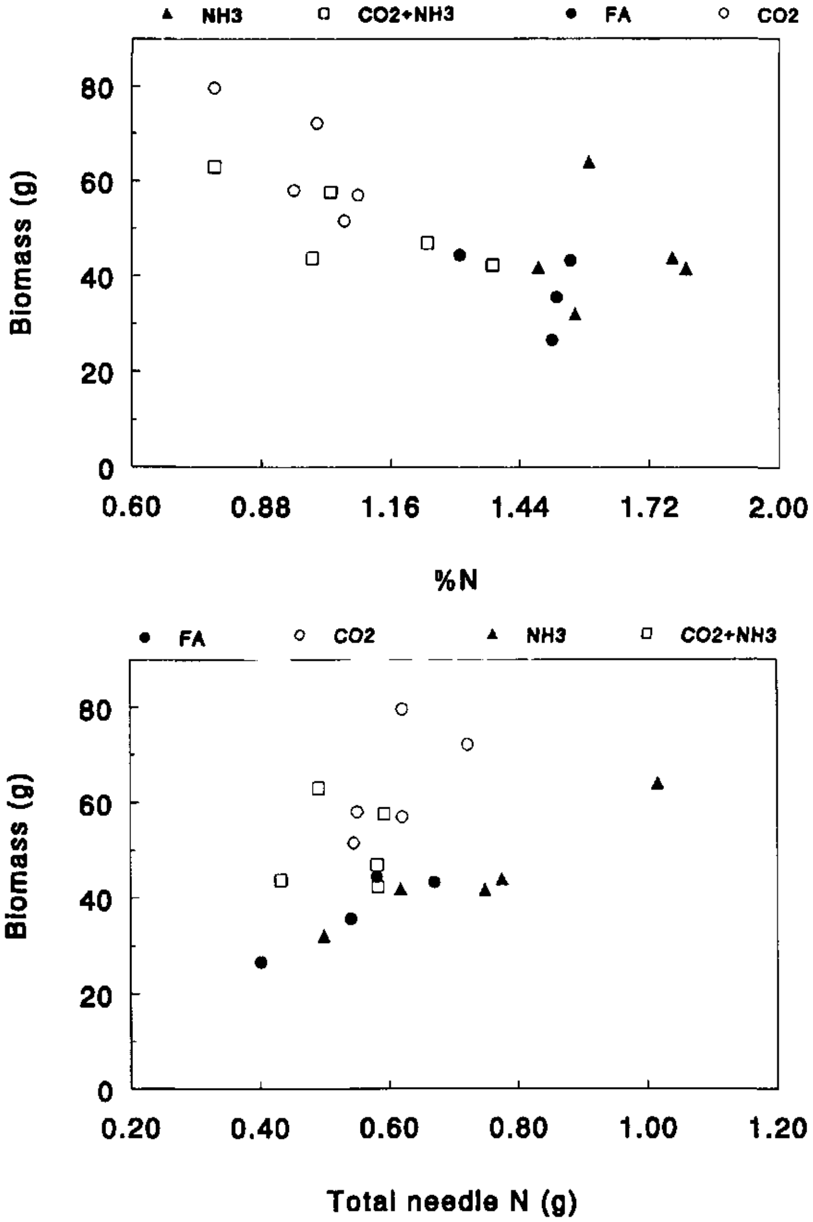

Figure 4.3 The relationship between needle biomass and nitrogen concentration (top) and total nitrogen content (bottom) in *Pinus sylvestris* exposed to filtered air (350 ppm CO_2), to elevated CO_2 (700 ppm), to NH_3 (40 µg m^{-3}) and to the combination of CO_2+NH_3 for 12 weeks.

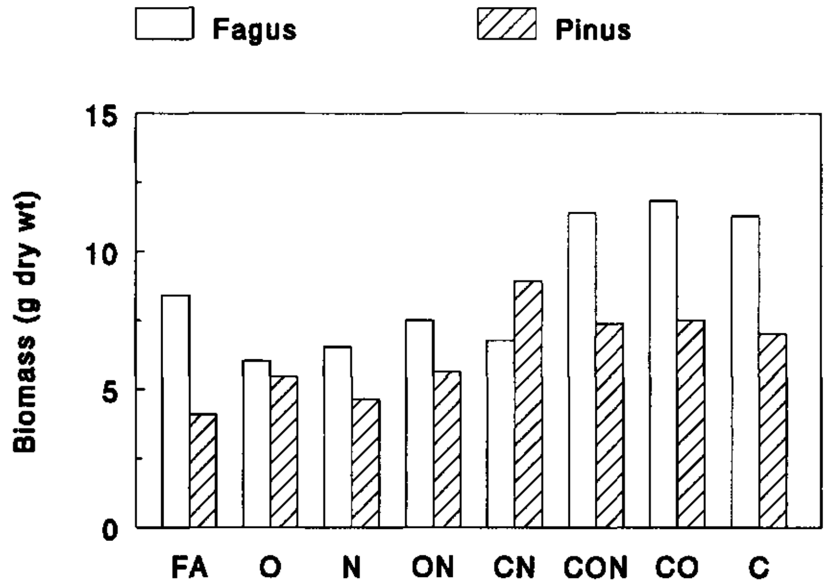

Figure 4.4. Mean fine root biomass of *Fagus sylvatica* and *Pinus sylvestris* exposed to filtered air (350 ppm CO_2), to O_3 (110 µg m^{-3}), to elevated CO_2 (700 ppm), to NH_3 (40 µg m^{-3}) and to all combinations for 12 weeks.

4.3.3 CO_2+NO_x

In order to make the review more complete, some literature data on the effects of CO_2+NO_x will be mentioned. Effects of this combination have not yet been studied within the scope of global climate change research programmes. Some relevant information however, can be gained from literature dealing with CO_2 enrichment in glasshouses. In using flue gas from the heating system as a CO_2 source, NO_x (in which NO is dominant) becomes a major contaminant. To evaluate the impact of this contamination, Mortensen (1985) grew tomato (eight cultivars) and lettuce (six cultivars) in CO_2 enriched air (1000 ppm), with and without addition of 700-900 ppb NO_x. The yield increase by CO_2 was completely eliminated by the addition of NO_x in most of the tomato cultivars, but not in lettuce. Anderson & Mansfield (1979) and Saxe & Voight Christensen (1984) also found that NO_x inhibited the growth stimulation due to CO_2 in tomato and several species of ornamentals. Bruggink *et al.* (1988) evaluated this phenomenon in tomato in terms of gas exchange (Figure 4.5). They found that photosynthesis and growth were reduced by NO, irrespective of the level of CO_2, while NO did not affect stomatal conductance and did not cause any visible injury. Contrary to the results of Bruggink *et al.* (1988), who found an additive effect of CO_2 and NO, Saxe (1986) reported that the NO_x effect was slightly reduced in the mixture due to a CO_2-induced increase in stomatal resistance. This seems to indicate that growth stimulation by CO_2 is reduced by NO_x.

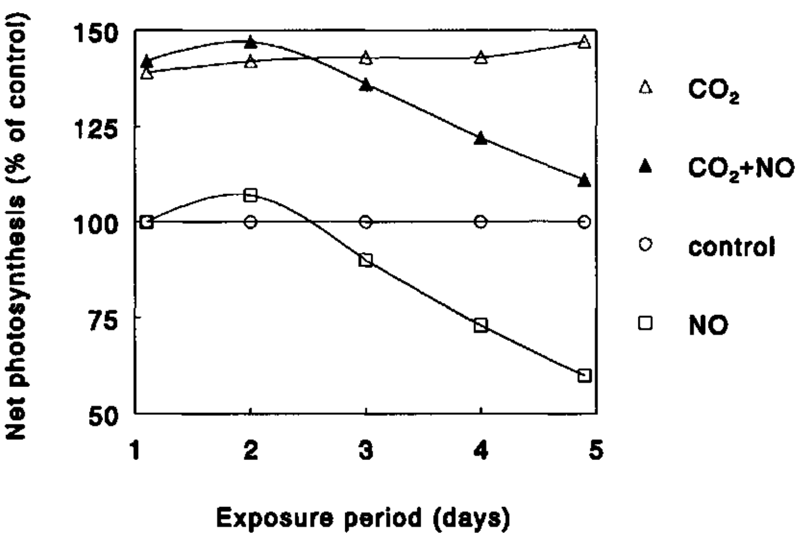

Figure 4.5. Net photosynthesis (% of control) of tomato plants exposed to NO (1150 µg m^{-3}), CO_2 (1000 ppm) and their combination for five days. Control plants were exposed to filtered air (350 ppm CO_2). After Bruggink *et al.* (1988).

4.5 Discussion

Results from our experiments were in agreement with data reported in literature, that O_3 generally reduces growth whereas CO_2 and NH_3 act as growth stimulators. The growth stimulation by CO_2 in *Trifolium* is in the upper part of the range found in other experiments (Rozema *et al.*, 1993). Pfirrman & Barnes (1993) studied the effects of O_3*CO_2 on *Raphanus sativus* and measured responses which were basically similar to ours with *Trifolium*. In terms of biomass production *Trifolium* and *Nicotiana* responded more strongly than *Pinus* and *Fagus* to the treatments in our experiments. This may partly be due to species differences, but also by differences in soil type. The tree saplings grew in nutrient poor soil, which generally reduces the plant's response to elevated CO_2.

With respect to combination effects, interactions seem to be an exception rather than a rule. This does not mean that mixtures causing additive effects are of little relevance. For instance, the effect threshold of O_3 is probably higher in the presence of elevated CO_2. Thus, O_3 damage may increase if abatement of CO_2 emission is successful, or in other words, O_3 damage may be reduced if CO_2 concentrations continue to rise. Our results showed that the responses of the plants to the pollutant combinations were generally additive. However, this was not true for the combined effects of NH_3 and CO_2. Both NH_3 and CO_2 stimulated growth or photosynthesis in all four tested species, but stimulation largely disappeared when the gases were combined. This interaction due to NH_3xCO_2 has not been found for NO_xxCO_2, which indicates differences in response of the plant to NH_3 compared to NO_x. Moreover, there is evidence that the effects of NH_3 and NH_4^+ are different, both qualitatively and quantitatively (Raven, 1988; van der Eerden *et al.* 1991, van der Eerden & Pérez-Soba, 1992). This is probably true for NO an NO_2 as well (Saxe, 1993). Wellburn (1990) assumes NO to be the most toxic nitrogenous air pollutant. Therefore, one has to be aware that in most cases the combined effects of elevated CO_2 and nitrogen deposition can not simply be simulated by soil fertilisation during CO_2 enrichment. The NO_x concentrations used in experiments described above were 10-20 times higher than ambient levels outdoors, but the CO_2 concentrations were unusually high as well. Even taking this into consideration, growth reductions due to NO_x should not be ignored when estimating the growth stimulating effects of elevated CO_2.

The data in this paper and from the literature show that NO_x, O_3, NH_3 reduce the growth stimulating effect of CO_2. This may be true for other pollutants as well. Therefore, reductions of O_3, NO_x and NH_y may enhance the effects of CO_2 and in polluted regions the stimulatory effect of CO_2 on biomass production may be less than in cleaner regions.

Doubling of the CO_2 concentration may occur in the next 75-150 years, depending on the rate with which the concentration of CO_2 rises. However, for the present and near future, we should be more concerned with increases of 5-15 % in CO_2 concentration in combination with effects of 'conventional' air pollutants. It is not yet known whether the CO_2 effect in those combinations is linear to its concentration. The quantitative importance of CO_2 effects during the coming few decades should not be overestimated, compared to 'conventional' air pollutants (and the relative impact of both kinds of changes due to air quality are probably small compared changes due to climatic fluctuations). This can be illustrated by the following example. While elevated CO_2 concentrations increase crop yield, air pollution reduces it. In the Netherlands, crop loss due to air pollution is estimated to be 5 % (van der Eerden *et al.*, 1988). Comparing the effects of CO_2 and O_3 for the near future, it appears that the O_3 effect may dominate. For instance, assuming that a 1 % increase in CO_2 concentration results in a 0.5 % increase in crop production, the crop loss in the Netherlands due to O_3 is estimated to be higher for the next 15-20 years than the gain in yield due to increased CO_2. This however, applies to crops, which are reseeded annually. In natural vegetations, air pollutant effects may dominate those of elevated CO_2 for an even longer period. Therefore, when assessing the current and near-future impact of changes in air quality, it might be better to focus on the "conventional" air pollutants and to evaluate the influence of addition of CO_2, rather than to fully concentrate on the effect of elevated CO_2 alone.

Because of its complexity, it is not yet possible to quantitatively assess the effects of the air pollution "cocktail" including elevated CO_2, on vegetations in the field. Generalizations and simplifications should be made and a proper philosophy has to be developed to select the relevant air pollution climates, the types of vegetation and effects, and the exposure conditions. Mechanistic simulation models may become powerful tools to generalize results from various air pollution experiments (van de Geijn *et al.*, 1993). However, too much knowledge on biochemical and physiological mechanisms is still lacking to incorporate the impact of air pollution on vegetations in these models. This applies especially to natural vegetations where stress sensitivity and rates of senescence are key factors in competition and survival. In general, air pollutants have to be taken into account when the impact of elevated CO_2 need to be evaluated. Otherwise the estimates of CO_2-induced effects may not only be inaccurate, but may even be systematically incorrect.

Acknowledgements

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5 Effects of climate change on crop production and land use in the Rhine basin

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Summary

Changes in climate affect the hydrological cycle of river basins. This results in a changed annual course of river discharge which might cause problems in future. To attain a better understanding of the effects of climate change on the course of discharge of the river Rhine, a hydrological model for the Rhine basin is to be developed. As part of this project the effects of climate change on production and water use of crops in the Rhine basin and on the land use were analyzed. Information on land use was derived from the literature. Crop production levels and water use were calculated with a crop growth simulation model WOFOST. These calculations were done for winter wheat, permanent grassland and silage maize and both for current and future climate conditions. Also the sensitivity of production and water use to separately changed weather variables were determined. According to these analyses, the expected climate change in the Rhine basin will result in a higher level of production for most crops, will reduce the risk for water shortage and will allow the cultivation of crops with higher temperature sum requirements.

In: S.C. van de Geijn, J. Goudriaan & F. Berendse (eds), 1993, Climate change: crops and terrestrial ecosystems. Agrobiologische Thema's 9, CABO-DLO, Wageningen; 71 - 96.

5.1 Introduction

Considerable changes in the climate on this planet might occur within a limited period of time as a result of rising concentrations of so-called 'greenhouse' gases in the atmosphere. The climate changes that are to be expected for the Rhine basin, are mainly an increase in air temperature and a change in annual rainfall distribution. As higher temperatures may result in less snowfall and an earlier snow melting, it is to be expected that in winter and early spring river discharge will become

larger and that high water will occur more frequently and will attain higher levels and that in the summer the discharge will become smaller (CHR, 1989).
Changes in climate conditions may also result in changes in the level of crop production and in the use of agricultural land in the Rhine basin. This may affect for example the degree of soil coverage and hence the amounts of rainfall discharged by runoff, and the water use by evapo-transpiration and hence the amount of water leached to deeper soil layers. In this way climate change will cause changes in the course of discharge of the river Rhine too.
A change in the annual course of discharge might cause problems with respect to supply of drinking and irrigation water, shipping, etc. in future. A better understanding of the effects of climate change on the hydrological processes is needed to take purposeful actions for minimizing such negative effects. Hence, the international Comittee for the Hydrology of the Rhine basin (CHR) initiated in 1989 a project 'Effects of climate change on the discharge of the Rhine'. The main part of this project is the development of a hydrological model for the Rhine basin (CHR, 1989).
Rijkswaterstaat RIZA has taken responsibility for the development of the lowland part of this hydrological model and besides, of scenarios for changing land use in the Rhine basin as a result of climate change. In a preliminary phase of these projects the effects of climate change on crop production, water balance and land use in the Rhine basin have been analyzed. Information on changes in land use have been derived from agricultural statistics and information on changes in crop production and water balance have been calculated with a crop growth simulation model. These calculations have been carried out for a limited number of crops, meteorological stations and for artificially derived soil characteristics. This gives a first impression of the possible effects of climate change on land use and crop production in the Rhine basin.

5.2 Land use

The use of land for agriculture depends on environmental, socio-economic and other factors. Environmental factors that set limitations to land use, are mainly climate, soil, landscape and hydrology. For example, low temperatures may prevent maturing of the crop, for example of grain maize in the Netherlands, frost in late spring may damage orchards, and drought periods in summer may reduce yields, particularly on shallow or gravelly soils with small amounts of available water. Soils may set limitations to agriculture, being for example too heavy for cultivation of root crops or too gravelly. Landscapes with steep slopes cannot be used for arable cropping, as without permanent coverage erosion takes place at a too high rate. High groundwater levels and insufficient natural or artificial drainage generally prevent use of land for arable cropping.
Other factors that determine land use, are the size of the consumer market, market regulations of the European Community and hence, the prices for the various agricultural products, the historical development of agriculture per region, the distance to consumer markets and processing industries, the infra- and marketing structure, transport facilities and transport costs, the fodder demand of the animal husbandry sector, and the introduction of new crop species that produce raw material for non-food use (energy, paper, oil, plastic, medicines, etc.). In addition, a further increase

Table 5.1 Change in use of agricultural and arable land (cultivated area in 10^4 ha)in the Netherlands (CBS, 1986).

	1930	1950	1970	1987
Agricultural land	225	234	213	201
Permanent grassland	132	132	133	113
Horticulture	8	9	11	12
Arable land	85	93	69	77
Cereals	43	48	36	18
Root crops	26	30	27	30
Silage maize	0	0	0	20
Other crops[1]	16	16	6	9

[1] Pulses, rape seed, lucerne, etc.

in production per unit of land area in combination with a policy to curb the production of surplusses in the EC may lead to a concentration of farm production on a much smaller area of land than that currently under cultivation (Latensteijn & Rabbinge, 1992; WRR, 1992). Such a contraction of the agricultural area has occurred periodically in the past (periods 1350-1475 and 1650-1750) and may lead to abandonment of marginal farmlands and possibly to extensive reforestation in the next future (van der Woude, 1990).

The examples mentioned above indicate that a possible change in climate can only be just one of the many factors that together determine the changes in land use. Climate change may have only a minor impact compared to the effects of other future changes in agriculture (Rabbinge *et al.*, 1993). Also at present weather conditions, land use can already change quite rapidly as shown in Table 5.1. The areas of permanent grassland and cereals in the Netherlands appeared to decrease quite rapidly. Simultaneously, the area of arable land cultivated with silage maize increased strongly over the last 20 years.

5.2.1 Actual land use in the Rhine basin

For the regions that drain to the river Rhine, data on land use were derived from statistics (Eurostat, 1987, 1988). For each region it was also estimated which fraction of the area drains to the Rhine. Multiplication of the areas in use for specified types of agriculture per region by the draining fraction of the region resulted in data on the land use in regions that drain to the Rhine.

In 1985 the relative use of agricultural land in the regions draining to the Rhine was as follows in:

	Arable crops	Permanent crops	Permanent grassland
Netherlands	35 %;	3 %;	62 %
Germany	61 %;	3 %;	36 %
France	52 %;	5 %;	43 %
Luxemburg	43 %;	1 %;	56 %

The overall use of agricultural land in the Rhine basin, largely corresponding to the land use in the German regions and to less extent to that in the French regions, was: arable cropping 58 % ; permanent crops 4 % ; and permanent grassland 38 % .

In 1985 the relative use of arable land in the regions draining to the Rhine was as follows in:

	Cereals	Root crops	Oil seeds	Other crops
Netherlands	22 %;	26 %;	4 %;	48 %
Germany	70 %;	7 %;	3 %;	20 %
France	67 %;	1 %;	8 %;	24 %
Luxemburg	62 %;	2 %;	1 %;	35 %

The overall use of arable land in the Rhine basin, largely corresponding to the land use in German regions, was: cereals 69 % ; root crops 6 % ; oilseed crops 4 % ; other crops 21 % . From statistics (Eurostat, 1987, 1988) it can be derived that cereals cultivated in the Rhine basin were mainly wheat, barley, oats and rye and that the main oil seed crops cultivated were rapeseed and turnip rapeseed.

5.2.2 Actual land use in southern France and nothern Italy

Increasing atmospheric CO_2 might result in changes in climate conditions. For example, according to the Bultot scenario (Section 5.5.1) temperatures rise with 3 °C, precipitation increases but not much more than the evapo-transpiration, and the other weather variables remain identical. Such climate conditions can be found at present in southern France and in northern Italy. For example, the average temperatures in Bordeaux, France and in Milan and Turin, Italy are 12.3, 13.1 and 13.0 °C and the annual amounts of rainfall are 900, 963 and 845 mm, respectively. The average temperatures in de Bilt, Netherlands and Freiburg, Germany are 9.3 and 10.3 °C and the annual amounts of rainfall 765 and 903 mm, respectively (Müller, 1987).

In 1985 the relative use of agricultural land was as follows in:

	Arable crops	Permanent crops	Permanent grassland
southern France	53 %;	9 %;	38 %
northern Italy	62 %;	8 %;	30 %

Compared to the overall land use in the Rhine basin, the relative area used for permanent crops in these regions is larger (8 % compared to 4 % in the Rhine basin) and the relative area in use for permanent grassland is smaller, particularly in northern Italy (compared to 38 % in the Rhine basin). Besides, the fraction of the area in use for permanent crops that is used as vineyards, increases from about half the area in the Rhine basin to three fourth of the area in southern France and northern Italy (Eurostat, 1987).

In 1985 the relative use of arable land was as follows in:

	Cereals	Root crops	Oil seeds	Other crops
southern France	50 %;	1 %;	11 %;	38%
northern Italy	59 %;	3 %;	0 %;	38%

Comparing these land use data with those for the Rhine basin, the relative areas used for cereals are smaller (compared to 69 % in the Rhine basin), for root crops are smaller too (compared to 6 % in the Rhine basin) and for other crops are larger (compared to 21 % in the Rhine basin). From statistics (Eurostat, 1987, 1988) it can be derived that the areas cultivated in southern France and northern Italy with other crops, are mainly used for green fodder production (about 30 % of the arable land area), that cereals cultivated in southern France and northern Italy are mainly wheat, barley and grain maize and that the main oil seed crop cultivated in southern France is sunflower and in Italy soyabean.

5.2.3 Effects of climate change on land use

Future climate conditions for the Rhine basin can be found at present in southern France and northern Italy. In all these European regions agriculture functions within the same system of market regulations of the European Community. Hence, socio-economic conditions do not differ too much and comparison of the land use in southern France and northern Italy with that in the Rhine basin may give good indications of the possible changes in land use that are to be expected from climate change.

The following changes in land use in the Rhine basin may be expected:

- decrease in area of permanent grassland;
- increase in area of permanent crops;
- increasing part of the area with permanent crops used as vineyards;
- smaller areas cultivated with oats and rye and larger areas with grain maize;
- smaller areas cultivated with root crops;
- smaller areas cultivated with rapeseed and turnip rapeseed and larger areas cultivated with sunflower and soyabean.

5.3 Methodology

5.3.1 Model description

A dynamic crop growth simulation model, WOFOST, developed for calculating agricultural production potential on the basis of physiological, physical and agronomic information, was used. This model can be easily applied to a large number of combinations of different weather data, soil characteristics and crop species. The principles underlying this model have been discussed in detail by van Keulen & Wolf (1986), and the implementation and structure have been described by van Diepen *et al.* (1988, 1989). Its application for quantitative land evaluation and for regional analysis of the physical potential of crop production has been described by van Keulen *et al.* (1987) and van Diepen *et al.* (1990) and its use for analysis of the effects of climate on crop production has been discussed by van Diepen *et al.* (1987) and Wolf (1993).

In the model, the growth of a crop is simulated from emergence to maturity on the basis of physiological processes as determined by the crop response to environmental conditions. The simulation is carried out in time steps of one day. The major processes considered are CO_2 assimilation, respiration, partitioning of assimilates to various plant organs, transpiration and phenological development.

Two levels of crop production are calculated. Firstly, the potential production which is determined by crop characteristics, solar radiation and temperature, and can be realised in situations where the supply of water and plant nutrients, and crop management are optimal. Secondly, the water-limited production which is determined by crop characteristics, temperature, solar radiation and water availability (dictated by rainfall pattern and soil physical properties), and can be realised in situations where the supply of plant nutrients and crop management are optimal.

Available soil moisture in the root zone follows from quantification of the water balance including rainfall, surface runoff, soil surface evaporation, crop transpiration, and leaching from the root zone. If the moisture content in the root zone is too low or too high, water uptake by the plant roots is reduced, stomata close and the water-limited growth is reduced: in a dry soil due to water shortage, in a wet soil due to oxygen shortage.

5.3.2 Data

Effects of climate change on crop production have been calculated for three crops, winter wheat, silage maize and permanent grassland, growing on different soil types and in different climates of the Rhine basin. In order to apply the model, data that specify crop growth and phenological development are required, including information on initial crop weight, properties that determine assimilation and respiration processes and response to moisture stress, partitioning of assimilates to plant organs, life span of leaves, and death rates of plant organs. For the most part a standard crop data set was used (van Heemst, 1988). Data from the literature and field experiments (for winter wheat: Alblas et al, 1987; Darwinkel, 1985; Darwinkel, 1988; van Keulen *et al.*, 1988; PAGV, 1987; for silage maize: Alblas *et al.*, 1987; PAGV, 1985; de Jong, 1985; Sibma, 1987; for permanent grassland: PR, 1988; Wieling & de Wit, 1987; Lantinga, 1985; Noy, 1989; van Dijk, 1989) were used to assess the rate of phenological development, the partitioning of assimilates to the plant organs, the effective growth duration that determines the level of production, and the regrowth retardation after mowing of permanent grassland. For locations in Germany the same crop data as derived for wheat, maize and grass varieties in the Netherlands, were used in the calculations.

For the calculation of CO_2 assimilation rates, daily minimum and maximum air temperatures, CO_2 concentration and solar radiation are required (Goudriaan & van Laar, 1978). To calculate the components of the water balance data on daily rainfall, windspeed and vapour pressure are also required. For example, the calculations of potential rates of evaporation and transpiration that are made with the Penman formula, require data on radiation, average daily air temperature, vapour pressure and windspeed (Frère & Popov, 1979). Daily weather data over a period of 20 years (1969 - 1988) for three meteorological stations (i.e. de Bilt, the Netherlands; Frankfurt and Freiburg, Germany) that cover the variation in the Rhine basin, have been used.

In order to calculate the soil water balance, the soil's infiltration, retention and transport properties must be known. These soil physical characteristics are defined by soil moisture characteristics (notably soil porosity and volumetric moisture contents at field capacity and wilting point, respectively), effective soil depth, maximum infiltration rate or surface runoff fraction and the hydraulic conductivity of the subsoil. Four soil types were specified for the calculations. They cover the extent of variation in soil water-holding capacity that can be expected in the Rhine basin, but they are theoretical concepts representing a sandy soil, a sandy loam soil, a loamy soil and an optimum soil. For each soil it was assumed that no groundwater influence occurs, that excess water may drain rapidly to the subsoil so that growth reduction due to oxygen shortage does not occur, that the infiltration rate is so large that no surface runoff may occur, and that the effective rooting depth is 100 cm for the cultivation of winter wheat and silage maize and also for permanent grassland on optimum soils, and 50 cm for permanent grassland on the other soils. This results in maximum amounts of available soil water for cultivation of winter wheat and silage maize on sandy, sandy loam, loamy and optimum soils of 7, 14, 21 and 50 cm , respectively and for permanent grassland of 3.5, 7, 10.5 and 50 cm, respectively. The optimum soil is fictive but allows to calculate the potential level of production (i.e. no water shortage during crop growth).

5.3.3 Model adaption to increasing atmospheric CO_2

For plants as wheat and grass that belong to the C_3 plant type, the atmospheric CO_2 concentration at present is generally suboptimal. In the model, the CO_2 assimilation - light response curve was therefore changed at increasing atmospheric CO_2 in the following way. Up to a CO_2 concentration of about three times the present one, the maximum assimilation rate of light-saturated individual leaves increased about proportionally to the atmospheric CO_2 concentration. Secondly, the initial light use efficiency, i.e. the initial angle of the CO_2 assimilation - light response curve, increased with increasing atmospheric CO_2 (Goudriaan *et al.*, 1984; Goudriaan *et al.*, 1985; Goudriaan, 1990; Goudriaan & Unsworth, 1990). For C_4 plants such as maize and other tall tropicall grasses, such as millet, sorghum and sugarcane, the photosynthetic response to CO_2 is very steep until an atmospheric CO_2 concentration of one third of the present one. At the natural range of atmospheric CO_2 at present (about 350 µmol/mol) the CO_2 assimilation - light response curve practically does not change with increasing CO_2, even under high light intensities (Goudriaan & Unsworth, 1990) and hence, at increasing CO_2 this curve was not changed in the model for maize. These photosynthetic responses to CO_2 are in agreement with the results from literature reviews by Cure (1985) and Cure & Acock (1986).

The effect of increasing CO_2 on leaf area development is rather difficult to quantify, as indicated in comparable studies on the effects of climate change (van Diepen *et al.*, 1987; Jansen, 1990). It has been observed that increased assimilate availability at increasing atmospheric CO_2 results partly in thicker leaves, rather than in increased leaf area growth (Goudriaan & de Ruiter, 1983; Goudriaan & Bijlsma, 1987). In agreement with these observations the specific leaf areas of wheat and grass have been reduced at increasing atmospheric CO_2.

High atmospheric CO_2 may result in a high CO_2 assimilation rate. In such a situation formation of plant organs may become more limiting for crop growth than the rate of the CO_2 assimilation process. In this study, however, it is assumed that also at high CO_2 concentrations and light intensities, the rate of organ formation never is the limiting factor for crop growth. This includes the assumption that plant breeding will be able to produce new crop varieties that are very well adapted to a possibly changed climate and increased atmospheric CO_2 in future.

The simulation model calculates the potential rates of evaporation and transpiration by way of the Penman formula. In a situation of soil water shortage, the actual transpiration rate becomes lower than its potential value. This reduction in transpiration is caused by the partial closure of stomatal pores in the leaves, resulting in a decrease in stomatal conductance. The stomata permit at the same time uptake of CO_2 from the ambient air and escape of water vapour, leading to transpiration. When ambient CO_2 is raised, CO_2 assimilation may increase and/or transpiration losses may be reduced, depending on how the stomata react. In both ways the water use efficiency of plants may be stimulated considerably. Typically in C_3 plants transpiration is reduced to a limited extent and the CO_2 assimilation is stimulated considerably and in C_4 plants that have a much higher affinity for CO_2, the transpiration is reduced considerably and the CO_2 assimilation does not change (Goudriaan & Unsworth, 1990). These changes in the transpiration rate due to changing stomatal conductance and closure at increasing atmospheric CO_2 cannot be handled with the simple method used in the WOFOST model.

A stratified micrometeorological model (Goudriaan, 1977; Chen, 1984) that includes detailed profiles of radiation and aerial conditions in the canopy and uses the Penman - Monteith equation for calculating the energy balances of canopy and soil surface, has been applied for simulating the effects of doubled atmospheric CO_2 concentration on the transpiration rate (Goudriaan & Unsworth, 1990). For C_4 plant species the CO_2 assimilation rate was not affected but the stomatal resistence almost doubled, proportional to the increased CO_2 concentration. The transpiration rate, however, was not about halved because of a negative feedback in two ways. First,

Table 5.2 Changes in specific leaf area (SLA), in initial light-use efficiency of CO_2 assimilation of single leaves (EFF), in maximum leaf CO_2 assimilation rate (AMAX) and in the reduction factor for potential transpiration (RTRA) for adaptation of the model to doubled atmospheric CO_2 concentration.

	SLA ($m^2\ kg^{-1}$	EFF ($kg\ ha^{-1}\ h^{-1}$)/($J\ m^{-2}s^{-1}$)	AMAX ($kg\ ha^{-1}\ h^{-1}$)	RTRA (-)
Winter wheat				
1*CO_2	18.0	0.45	40	1.00
2*CO_2	14.4	0.55	80	0.90
Silage maize				
1*CO_2	26.0	0.45	70	1.00
2*CO_2	26.0	0.45	70	0.74
Grass				
1*CO_2	25.0	0.45	40	1.00
2*CO_2	20.0	0.55	80	0.90

the reduced transpiration rate caused an increase in leaf temperature. Secondly, the reduced transpiration rate affected air conditions inside the canopy. Both effects resulted in a transpiration rate of 74 % of that at the actual CO_2 concentration. For C_3 plant species the CO_2 assimilation rate is mainly affected by doubled atmospheric CO_2. In that case model simulations resulted in a transpiration rate of 90 % of that at current CO_2. These fractions of the transpiration rate calculated for a situation of doubled atmospheric CO_2, for which almost identical values were given in literature reviews by Cure (1985) and Cure & Acock (1986), have been used in the present study as overall reduction factors for calculating the transpiration rates at changing atmospheric CO_2. Changes in crop parameters of the model that reflect the changes in plant behaviour at increasing atmospheric CO_2 as discussed above, are summarized in Table 5.2 .

5.4 Sensitivity analyses

Weather variables that determine crop production directly are solar radiation and temperature. Those that affect the water balance and hence the duration and degree of drought stress are rainfall, windspeed, vapour pressure, and again solar radiation and temperature. The atmospheric CO_2 concentration also has direct and indirect effects on crop production. These variables were adjusted separately in a stepwise manner, in order to gauge the sensitivity of crop production and components of the water balance to changing values of each. These analyses have been done for the three crops of which each can be considered representative for a separate crop group. Winter wheat is a C_3 crop with a determinate growth cycle (shorter growth period at higher temperatures), silage maize is a C_4 crop with a determinate growth cycle, and grass is a C_3 crop with an indeterminate growth cycle (longer growth period at higher temperatures).

5.4.1 Crop production

The sensitivity analyses were carried out for the three crops on sandy loam and loamy soils in de Bilt, the Netherlands, using historical weather data for a period of 20 years (1969 - 1988). Table 5.3 summarizes the sensitivity of water-limited production to changing values of each weather variable. For winter wheat the grain production appears to increase with increasing atmospheric CO_2, rainfall, solar radiation and vapour pressure, and to decrease with rising temperature and increasing windspeed. Both increasing solar radiation and CO_2 positively affect the assimilation rate and thus production. Increasing rainfall and vapour pressure limit the degree of water shortage and hence result in a larger production too. Increasing windspeed results in a higher evapo-transpiration rate and longer periods with water shortage and hence, in a smaller production. At higher temperatures the growth period of wheat is reduced, which also results in a smaller production. For silage maize the total water-limited production appears to increase with increasing atmospheric CO_2, solar radiation, rainfall and vapour pressure, and to decrease with increasing temperature and windspeed. Increasing CO_2 results in a more efficient water use and hence a larger production for maize. Rising temperature results in a shorter growth period but also in a higher rate of CO_2 assimilation. This explains the much smaller, negative effect of rising temperatures compared to that for winter wheat. The sensitivity of silage maize to the other weather variables can be explained in the same way as done above for winter wheat. For permanent grassland the total water-limited production appears to increase with increasing atmospheric CO_2, temperature, rainfall, vapour pressure and solar radiation, and to decrease with increasing windspeed. Rising temperatures result in a longer growth period for grass and thus in a higher level of production. Increasing solar radiation causes a higher rate of CO_2

Table 5.3 Sensitivity of crop production[1] in de Bilt, the Netherlands, on sandy loam and loamy soils to increasing values for atmospheric CO_2 concentration (C), temperature (T), rainfall (R), solar radiation (S), windspeed (W) and vapour pressure (V) (expressed in relative change in production per unit change in temperature (°C) or per relative change in one of the other weather variables).

Crop	C	T	R	S	W	V
Winter wheat	+0.523	-0.034	+0.128	+0.600	-0.114	+0.312
Silage maize	+0.045	-0.004	+0.127	+0.691	-0.084	+0.239
Permanent grassland	+0.454	+0.027	+0.300	+0.240	-0.143	+0.480

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[1] Production refers for winter wheat to grain production, for silage maize to total crop production and for grassland to grass production.

Table 5.4 Changes in crop production[1] (as a percentage of production at current climate) in de Bilt, the Netherlands on sandy loam and loamy soils if atmospheric CO_2 concentration (C) increases with 100 %, temperature (T) rises with 3 °C, rainfall (R) or windspeed (W) increases with 30 %, solar radiation (S) or vapour pressure (V) increases with 10 %.

Crop	C	T	R	S	W	V
Winter wheat	+52 %	-10 %	+4 %	+6 %	-3 %	+3 %
Silage maize	+5 %	-1 %	+4 %	+7 %	-3 %	+2 %
Permanent grassland	+45 %	+8 %	+9 %	+2 %	-4 %	+5 %

[1] Production refers for winter wheat to grain production, for silage maize to total crop production and for grassland to grass production.

assimilation but also a higher evapo-transpiration rate and thus longer periods with water shortage. This explains the smaller positive effect of increasing solar radiation compared to that for winter wheat. The sensitivity of grassland to the other weather variables can be explained in the same way as done above for winter wheat. As in reality the various weather variables do not change to the same extent, sensitivities of water-limited production are also given for specified changes in weather variables (Table 5.4). This gives an indication of the changes in production that might be expected for a changed climate.

5.4.2 Evapo-transpiration and leaching

The sensitivity analyses for crop production in de Bilt, the Netherlands have also been used to determine the sensitivity of cumulative water losses by evapo-transpiration to changing weather variables. The results of these analyses are summarized in Table 5.5. For the cultivation of winter wheat cumulative evapo-transpiration during the growth period appears to increase with increasing windspeed, solar radiation, and rainfall, and to decrease with increasing atmospheric CO_2, temperature and vapour pressure. With increasing solar radiation and windspeed the rate of evapo-transpiration increases and for increasing vapour pressure the opposite applies. Increasing atmospheric CO_2 results in a reduced crop transpiration rate. With increasing rainfall cumulative evapo-transpiration increases with the increasing amount of available soil water. Rising temperatures result in shorter growth periods and hence in reduced cumulative evapo-transpiration. For the cultivation of silage maize cumulative evapo-transpiration during the growth period appears to increase with increasing rainfall, solar radiation, and windspeed, to remain almost constant at rising temperature, and to decrease with increasing atmospheric CO_2 and vapour pressure. Increasing atmospheric CO_2 results in major reduction of the rate of crop transpiration. Rising temperatures cause a shorter growth period and thus a smaller cumulative evapo-transpiration, but this effect is about counterbalanced by the increase in evapo-transpiration rate as a result of a greater vapour pressure deficit at higher temperatures. For silage maize the sensitivity of cumulative evapo-transpiration to the other weather variables can be explained in the same way as done above for the cultivation of winter wheat. For permanent grassland cumulative evapo-transpiration during one year appears to increase at increasing temperature, rainfall, solar radiation and windspeed, and to decrease at increasing atmospheric CO_2 and vapour pressure. Rising temperatures result in a longer growth period and thus in an increase in cumulative evapo-transpiration. With increasing solar radiation cumulative evapo-transpiration increases but much less than that for winter wheat or silage maize. This can be explained from the fact that on grasslands water availability limits evapo-transpiration more strongly. The sensitivity of evapo-transpiration to the other weather variables can be explained in the same way as done above

Table 5.5 Sensitivity of cumulative evapo-transpiration[1] in de Bilt, the Netherlands on sandy loam and loamy soils to increasing values for atmospheric CO_2 concentration (C), temperature (T), rainfall (R), solar radiation (S), windspeed (W) and vapour pressure (V) (expressed in relative change in evapo-transpiration per unit change in temperature (°C) or per relative change in one of the other weather variables).

Crop	C	T	R	S	W	V
Winter wheat	-0.036	-0.046	+0.122	+0.489	+0.201	-1.007
Silage maize	-0.174	+0.001	+0.136	+0.496	+0.152	-0.805
Permanent grassland	-0.057	+0.026	+0.235	+0.105	+0.213	-1.360

[1] For winter wheat and silage maize cumulative values for evapo-transpiration during the growth period (dependent on temperature) are compared and for permanent grassland cumulative values during one year.

Table 5.6 Changes in cumulative evapo-transpiration[1] (as a percentage of evapo-transpiration at current climate) in de Bilt, the Netherlands on sandy loam and loamy soils if atmospheric CO_2 concentration (C) increases with 100 % , temperature (T) rises with 3 °C, rainfall (R) or windspeed (W) increases with 30 % , solar radiation (S) or vapour pressure (V) increases with 10 % .

Crop	C	T	R	S	W	V
Winter wheat	-4%	-14%	+4%	+5%	+6%	-10%
Silage maize	-17%	+2%	+4%	+5%	+5%	-8%
Permanent grassland	-6%	+8%	+7%	+1%	+6%	-14%

[1] For winter wheat and silage maize cumulative values for evapo-transpiration during the growth period (dependent on temperature) are compared and for permanent grassland cumulative values during one year.

for winter wheat. As in reality the various weather variables do not change to the same extent, sensitivities of cumulative evapo-transpiration are also given for specified changes in weather variables (Table 5.6). This indicates the degree of changes in evapo-transpiration that might be expected for a changed climate.

The water balance for permanent grassland was calculated for a period of one year. The change in available soil water over this period is about zero. As a consequence, an increase in evapo-transpiration as a result of for example an increase in solar radiation results in a decrease in the amount of water leached from the root zone, if the amount of rainfall is not changed. In this way, leaching from permanent grassland is calculated to increase at increasing atmospheric CO_2, rainfall, and vapour pressure, and to decrease at increasing temperature, solar radiation and windspeed.

5.5 Results for climate changed according to Bultot scenario

Average potential and water-limited production levels and the coefficient of variation (CV) of the productions

were calculated for the sets of historical weather data and for the same data sets changed on the basis of a climate scenario. Results are given for the three crops, for the different soil types and for three locations, i.e. de Bilt, Frankfurt and Freiburg. They cover the degree of variation in climate in the Rhine basin. De Bilt has a relatively low average temperature, a small temperature variation over the year and an average rainfall, Franfurt has also a rather low average temperature but a a larger temperature variation over the year and less rainfall, and Freiburg has the highest average temperature and a larger temperature variation and more rainfall than de Bilt. Results calculated for the optimum soil represent the potential level of crop production. Average results for the sandy loam and loamy soils that are about representative for the waterholding capacity of soils in the Rhine basin, represent the water-limited level of production (without irrigation).

5.5.1 Bultot scenario

Best information on the response of the atmosphere to increasing concentrations of so-called greenhouse gasses is provided by general circulation models. These models are detailed, three-dimensional numerical simulation models that describe atmospheric motions, heat exchanges and land - ocean - ice interactions. However, the spatial resolution of the output of general circulation models is too coarse to be of interest for hydrologic studies of river basins. In addition, results from various general circulation models appear to differ considerably, both in magnitude and in geographical distribution, as shown for the U.S.A. (Croley, 1990) and for Europe (Barrow, 1993). So the output of general circulation models should be received with caution.

Scenarios on climate change have been developed for use in hydrological studies. In such scenarios weather variables are changed to various extents to test their effects on future water resources. But the internal consistency in the changed weather variables is often a weak point (Gleick, 1989). For river basins in Belgium a scenario of the climate change induced by doubling the actual atmospheric CO_2 concentration, has been reported (Bultot *et al.*, 1988). This scenario applies to an area close to the Rhine basin, was compiled in a consistent way and hence, is used for calculating 'future' climate conditions in the Rhine basin. It can be considered representative for the situation in the year 2080, if the 'Business-as-usual' emission scenario of the IPCC (Houghton *et al.*, 1990) comes true. It should be realized that in this situation there is not yet an equilibrium between the temperature rise and the increased radiative forcing on the earth-atmosphere system.

'Future' climate conditions are calculated from historical weather data (period 1969 - 1988) by changing the weather data for each location according to the Bultot scenario. The following changes are applied:

- change in air temperature + 3 °C;
- change in precipitation in November, December and January + 10 % ;
- „ „ „ „ February, March and April + 16 % ;
- „ „ „ „ May, June, July and August - 3 % ;
- „ „ „ „ September + 0 % ;
- „ „ „ „ October + 7 % ;
- no change in relative air humidity and hence, vapour pressure corrected for increased temperature;
- no change in windspeed (no information in Bultot scenario);
- no change in solar radiation because relative humidity does not change;
- doubling of current atmospheric CO_2 concentration.

5.5.2 Winter maize

Crop growth and the components of the water balance were simulated from January 1 till the date of maturing. Actually sowing occurs in October or November. After about two weeks crop emergence finds place, so that at January 1 a limited amount of crop material is already formed. An estimate for this amount is used as start weight in the crop growth simulation. The initial amount of available soil water at January 1 was set at the maximum per soil type.

Potential grain production calculated for current climate conditions is more than 9 t ha^{-1} in de Bilt and more than 8 t ha^{-1} in Frankfurt and Freiburg (Figure 5.1). For the climate change according to the Bultot scenario potential production increases to almost 13 t ha^{-1} in de Bilt, to 11 t ha^{-1} in Frankfurt and 10 t ha^{-1} in Freiburg. Increases in water-limited production by climate change are almost identical to those in potential production (Figure 5.1). They are mainly caused by the doubled atmospheric CO_2 concentration that results in a larger assimilate production of the leaves. The growth period of winter wheat decreases if the average temperature rises. At locations with relatively high temperatures (Freiburg) and thus rather short growth periods, production increases as a result of climate change appear to be much lower than those on locations with relatively lower temperatures (Figure 5.1: de Bilt).

The CV is a good indicator of production variability and the risk of a relatively low production. Climate change may cause changes in the CV. Calculated increases or decreases in the CV indicate that the agricultural risks in future may increase or decrease. For potential production the CV appears to remain almost identical with

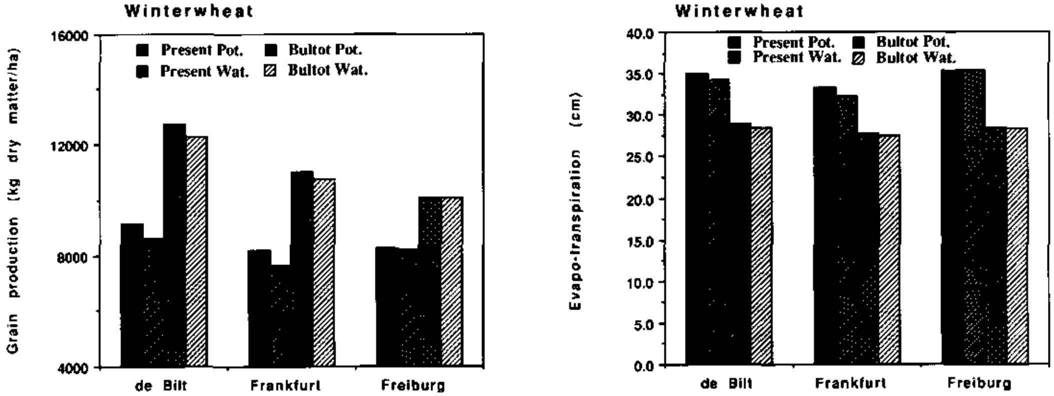

Figure 5.1 Average potential (Pot.) and water-limited (Wat.) grain production (kg dry matter/ha) and evapo-transpiration (cm) during the growth period of winter wheat in current and scenario climate conditions. Average values have been established for historical weather data over a period of twenty years (1969 - 1988) from de Bilt, the Netherlands, and Frankfurt and Freiburg, Germany without and with changes on the basis of the Bultot scenario, and for cultivation on optimum (Pot.) and on sandy loam and loamy soils (Wat.).

climate change for all locations and for water-limited productions the CV decreases (Table 5.7). This indicates that the risk for a low production in relatively dry years that at present is small to moderately large (e.g. Frankfurt) in the Rhine basin, decreases as a result of climate change.

Cumulative water losses by evapo-transpiration during the growth period decrease considerably by climate change (Figure 5.1). This can be explained from the rise in temperature that results in a shorter growth period (Table 5.7). The amount of rainfall during the growth period decreases with climate change too but slightly less than the decrease in evapo-transpiration, which results in less depletion of available soil water. However, such a comparison of water balances over different periods of time can only be of limited value. For water-limited production the water losses by evapo-transpiration are almost identical to those of potential production (Figure 5.1) which indicates that evapo-transpiration and thus production are almost not limited by water availability.

Table 5.7 Average values (AV) and coefficients of variation (CV) for potential (POT) and water-limited (WAT) grain productions[1] and the components of the water balance[2] during the growth period of winter wheat at current and scenario climate conditions in de Bilt, the Netherlands, and in Frankfurt and Freiburg, Germany; average values have been established for historical weather data over a period of 20 years (1969 - 1988) without and with changes on the basis of the Bultot scenario.

Location,	Climate	Duration growth period[2] (d)	Dry matter production (kg ha^{-1})				Rainfall (cm)	Transpiration (cm)	Evaporation (cm)	Leaching (cm)	Change Soil water[3] (cm)
			POT		WAT						
			AV	CV	AV	CV					
de Bilt,	Present	228	9170	0.09	8640	0.17	46.8	25.2	9.0	20.4	-7.8
de Bilt,	Bultot	195	12740	0.09	12310	0.13	42.9	21.3	7.1	20.9	-6.4
Frankfurt,	Present	218	8190	0.12	7680	0.22	38.6	24.0	8.3	15.3	-9.0
Frankfurt,	Bultot	191	10990	0.09	10740	0.12	36.0	20.5	6.9	15.5	-6.9
Freiburg,	Present	207	8290	0.11	8220	0.13	56.9	25.4	9.9	24.9	-3.3
Freiburg,	Bultot	181	10090	0.14	10080	0.14	51.7	19.4	9.0	25.3	-2.0

[1] Average water-limited production situation on sandy loam and loamy soils.

[2] Growth period was considered from January 1 till moment of crop maturing and components of the water balance (on sandy loam and loamy soils) were calculated for the indicated duration.

[3] Initial amount of available soil water at January 1 was set at the maximum amount.

Table 5.8 Average values (AV) and coefficients of variation (CV) for potential (POT) and water-limited (WAT) total productions[1] and the components of the water balance[2] during the growth period of silage maize at current and scenario climate conditions in de Bilt, the Netherlands, and in Frankfurt and Freiburg, Germany; average values have been established for historical weather data over a period of 20 years (1969 - 1988) without and with changes on the basis of the Bultot scenario.

Location,	Climate	Duration growth period[2] (d)	Dry matter production (kg ha^{-1})				Rainfall (cm)	Transpiration (cm)	Evaporation (cm)	Leaching (cm)	Change Soil water[3] (cm)
			POT		WAT						
			AV	CV	AV	CV					
de Bilt,	Present	138	19790	0.10	18900	0.11	29.9	22.9	6.5	3.4	-2.9
de Bilt,	Bultot	118	19080	0.08	18720	0.09	24.3	18.5	6.5	3.2	-3.9
Frankfurt,	Present	126	19730	0.10	17940	0.16	25.4	23.6	6.4	2.9	-7.5
Frankfurt,	Bultot	110	16310	0.13	16010	0.16	22.0	16.4	6.7	3.1	-4.2
Freiburg,	Present	114	20190	0.07	19920	0.08	38.8	27.2	6.6	7.8	-2.8
Freiburg,	Bultot	104	16500	0.13	16010	0.12	35.0	17.4	7.6	10.3	-0.3

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[1] Average water-limited production situation on sandy loam and loamy soils.

[2] Growth period was considered from crop emergence (May 15 and April 25 for de Bilt and May 8 and April 18 for Frankfurt and Freiburg for current and scenario climate conditions respectively) till date of crop maturing or date of harvest (set at October 2 when crop is not yet mature at that date) and components of the water balance (on sandy loam and loamy soils) were calculated for the indicated duration.

[3] Initial amount of available soil water at crop emergence was set at the maximum amount minus 3 cm water.

Table 5.9 Average values (AV) and coefficients of variation (CV) for potential (POT) and water-limited (WAT) productions[1] and the components of the water balance[2] for mown permanent grassland at current and scenario climate conditions in de Bilt, the Netherlands, and in Frankfurt and Freiburg, Germany; average values have been established for historical weather data over a period of 20 years (1969 - 1988) without and with changes on the basis of the Bultot scenario.

Location,	Climate	Dry matter production (kg ha^{-1})				Rainfall (cm)	Transpiration (cm)	Evaporation (cm)	Leaching (cm)	Change Soil water[3] (cm)
		POT		WAT						
		AV	CV	AV	CV					
de Bilt,	Present	18190	0.04	15820	0.16	79.4	28.3	12.1	38.8	+0.2
de Bilt,	Bultot	27790	0.04	24860	0.11	84.1	28.1	13.5	42.2	+0.3
Frankfurt,	Present	17870	0.04	14400	0.24	63.3	28.3	12.0	23.0	0.0
Frankfurt,	Bultot	26900	0.03	22450	0.18	66.6	28.0	13.1	25.5	0.0
Freiburg,	Present	19660	0.05	19020	0.07	96.3	39.2	14.7	42.4	0.0
Freiburg,	Bultot	28590	0.04	27870	0.06	100.7	38.2	16.6	45.9	0.0

[1] Average water-limited production situation on sandy loam and loamy soils.

[2] Production and components of the water balance (on sandy loam and loamy soils) were calculated for a period of one year.

[3] Initial amount of available soil water at January 1 was set at the maximum amount.

5.5.3 Silage maize

Crop growth and the components of the water balance were simulated from the date of crop emergence, i.e. May 15 and April 25 for de Bilt and May 8 and April 18 for Frankfurt and Freiburg for current and 'future' climate conditions respectively, till the date of maturing or the date of harvest. If the maize crop is not yet mature at October 2, it is assumed to be harvested on that date anyway. With climate change the date of emergence is advanced by three weeks, which can be explained from the rise in average temperature by 3 °C. The initial amount of available soil water at crop emergence was set at the maximum amount per soil type minus 3 cm water.

Potential production calculated for current climate conditions, is about 20 t ha^{-1} in de Bilt, Frankfurt and Freiburg (Figure 5.2). With climate change potential production decreases to 19 t ha^{-1} in de Bilt and to about 16 t ha^{-1} in Frankfurt and Freiburg. Particularly on locations with a relatively high average temperature (e.g. Freiburg), the negative effect of temperature rise on the growth duration and hence on production, appears to be large. Decreases in water-limited production by climate change are generally smaller than those in potential production (Figure 5.2). Particularly in Frankfurt where the water supply may limit production at present, the increased water use efficiency of maize at doubled atmospheric CO_2 reduces the decrease in production by climate change.

For potential and water-limited production the CV remains about identical with climate change for all locations (Table 5.8). This indicates that the risk for low production in relatively dry years that at present is very small in the Rhine basin, does not change as a result of climate change.

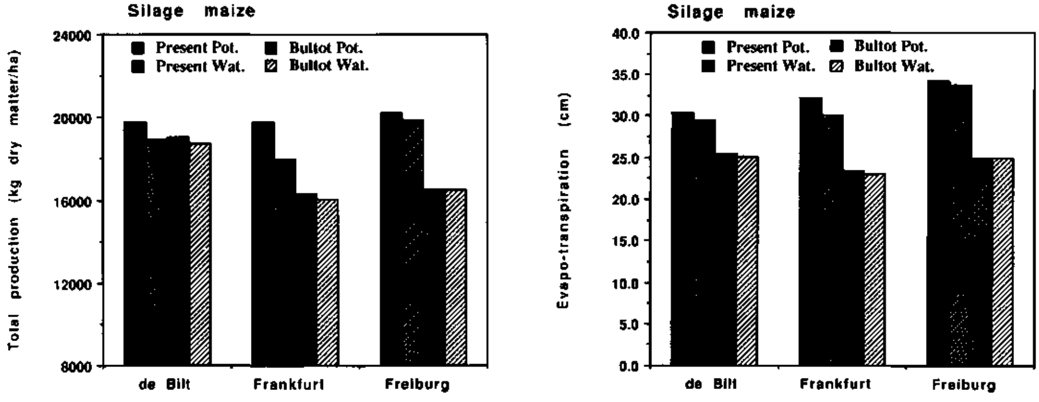

Figure 5.2 Average potential (Pot.) and water-limited (Wat.) total production (kg dry matter/ha) and evapo-transpiration (cm) during the growth period of silage maize in current and scenario climate conditions. Average values have been established for historical weather data over a period of twenty years (1969 - 1988) from de Bilt, the Netherlands, and Frankfurt and Freiburg, Germany without and with changes on the basis of the Bultot scenario, and for cultivation on optimum (Pot.) and on sandy loam and loamy soils (Wat.).

Cumulative water losses by evapo-transpiration during the growth period decrease considerably by climate change (Figure 5.2). This can be explained from the rise in temperature that results in a shorter growth period (Table 5.8) and from the decreased transpiration rate at doubled atmospheric CO_2. The cumulative amount of rainfall decreases as a result of climate change and the shorter growth period too. In Frankfurt and Freiburg the decrease in evapo-transpiration is larger than that in rainfall, which results in a decreased depletion of available soil water. However, such a comparison of water balances over different periods of time can only be of limited value. For water-limited production the water losses by evapo-transpiration are almost identical to those of potential production (Figure 5.2). This indicates that evapo-transpiration and thus production are almost not limited by water availability, with only Frankfurt at present as an exception.

5.5.4 Permanent grassland

Growth of regularly mown grassland and the components of the water balance were simulated over one year.

The initial amount of available water at January 1 was set at the maximum amount per soil type.

Potential productions of mown permanent grassland calculated for current climate conditions are 18 t ha^{-1} in de Bilt and Frankfurt and 20 t ha^{-1} in Freiburg (Figure 5.3). Highest productions are found on locations where the temperature is relatively high and hence the period of grass growth is relatively long. For the changed climate potential productions increase to between 27 and 29 t ha^{-1}.

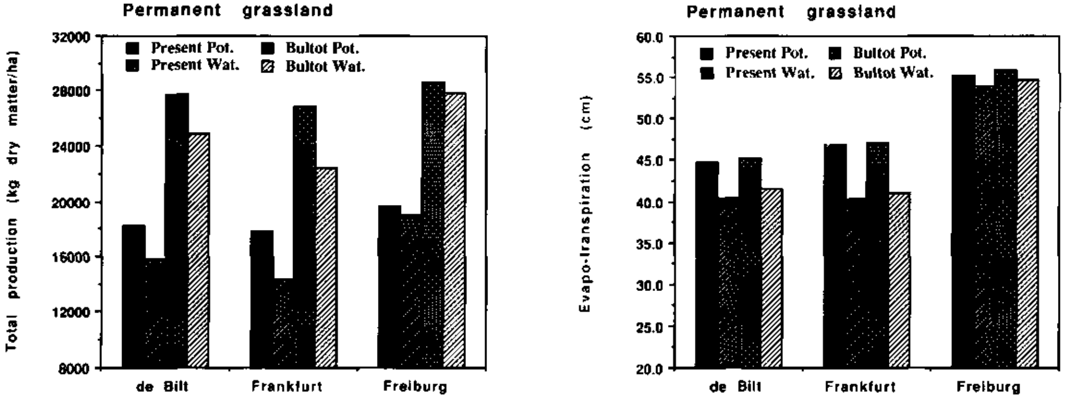

Figure 5.3 Average potential (Pot.) and water-limited (Wat.) total production (kg dry matter/ha) and evapo-transpiration (cm) per year of mown permanent grassland in current and scenario climate conditions. Average values have been established for historical weather data over a period of twenty years (1969 - 1988) from de Bilt, the Netherlands, and Frankfurt and Freiburg, Germany without and with changes on the basis of the Bultot scenario, and for grasslands on optimum (Pot.) and on sandy loam and loamy soils (Wat.).

Increases in water-limited production by climate change are about identical to those in potential production (Figure 5.3). They are mainly caused by the doubled atmospheric CO_2 concentration that results in a larger assimilate production of the leaves, and by the longer growth duration at higher temperatures.
For potential production the CV remains about identical with climate change for all locations (Table 5.9). For water-limited production the CV decreases considerably with climate change in Frankfurt, where at present the CV of water-limited production is much higher than that of potential production. In Freiburg no water shortage occurs at present and with climate change and consequently, the CV of water-limited production remains almost identical with climate change. In de Bilt the CV decreases slightly with climate change, as the degree of water shortage is in between those for Frankfurt and Freiburg. As indicated by these changes in CV, the risk for a low production in relatively dry years that at present is small to moderately large (e.g. Frankfurt) in the Rhine basin, decreases as a result of climate change.
Cumulative water losses by evapo-transpiration over one year increase slightly with climate change (Figure 5.3). This can be explained from the rise in temperature that results in increases in evaporation and in transpiration (via longer growth period and larger vapour pressure deficit) which are largely counterbalanced by a reduction in transpiration rate (via decreased stomatal conductance) at doubled atmospheric CO_2 (Table 5.9). For water-limited production the increase in evapo-transpiration by climate change is almost identical to that for potential production. The annual amount of rainfall increases with climate change too and to a larger extent than the increase in evapo-transpiration. As over a period of one year the change in available soil water is about nil, leaching from the root zone appears to increase by about 10 % as a result of climate change. For water-limited production the water losses by evapo-transpiration are smaller than those of potential production in de Bilt and particularly in Frankfurt (Figure 5.3) which indicates that evapo-transpiration and thus grass production are limited by water availability on these locations.

5.6 Conclusions

Future climate conditions in the Rhine basin according to the applied climate change scenario can be found at present in southern France and northern Italy. Socio-economic conditions in the Rhine basin and in southern France and northern Italy do not differ much and consequently, the effects of climate change on future land use in the Rhine basin may be derived from the comparison of actual land use in the Rhine basin and that in southern France and northern Italy, respectively. The derived changes in land use are mainly an increase in area for permanent crops and for arable crops with large temperature sum requirements (e.g. grain maize and sunflower) and a decrease in area for permanent grassland and for root crops.
For the three crops, winter wheat, silage maize and permanent grass, that can be considered representative for determinate C_3 crops, determinate C_4 crops and indeterminate C_3 crops, the sensitivity to separately changed weather variables has been calculated. Rising temperatures have a positive effect on the production of indeterminate crops but a negative one on the production of determinate crops. By growing crop varieties with higher temperature sum requirements this negative effect can be avoided. Increasing rainfall and vapour pressure have a positive effect

on the production of all crops by increasing water supply or decreasing water use. Increasing windspeed has a negative effect on the production of all crops by increasing water use. Increasing atmospheric CO_2 results in a higher assimilation rate of the leaves for C_3 crops and a higher water use efficiency for C_4 crops, which causes a larger crop production in both cases. Also increasing solar radiation has a positive effect on production of all crops.
For the three crops the effects of climate change on their production in the Rhine basin have been calculated. The main changes in climate included are an increase in temperature, a doubling of atmospheric CO_2 and a moderately increased amount of annual rainfall with a changed distribution over the year. This results for permanent grassland in a slightly increased annual evapo-transpiration. As the annual amount of rainfall increases more strongly by climate change, water losses by leaching from the root zone increase and the risk for water shortage decreases. Climate change also results in less water limitation for the production of winter wheat and silage maize in the Rhine basin. With climate change grain production of winter wheat was calculated to become roughly 35 % higher, production on permanent grassland 50 % higher and production of silage maize 10 % lower. The negative effects of higher temperatures on the production of determinate crops can be avoided by growing better adapted crop varieties. This means that in reality maize production will not decrease with climate change. Largest increases in production have been calculated for grassland which can be explained from the higher assimilation rate at doubled atmospheric CO_2 and the extended growth period at higher temperatures.

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6 Carbon fluxes and organic matter transformations in plant-soil-systems

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Summary

Plants are the primary suppliers of substrate for life in soil and thus play a key role in the control of the dynamics of microbial populations and organic matter in soil. The complex interactions between plants and microbial activity in soil are discussed in view of the expected climate change. The predicted higher atmospheric CO_2 *concentration will likely result in higher primary production as well as higher rhizodeposition of organic carbon. Since this rhizodeposition is a quantitatively important source, accumulation of soil organic matter is anticipated. Whether such an accumulation will occur and will turn soil organic matter into a significant sink for atmospheric* CO_2 *depends on the rates of microbial transformations of rhizodeposited compounds and mineralization of plant nutrients. The complex nature of these plant/soil interactions and of predictions on the future equilibrium levels for carbon content of terrestrial ecosystems is further illustrated by the effects of mineral nitrogen concentrations on microbial utilization of soil organic matter. A reduction of the decomposability of plant residues as a consequence of a wider C:N ratio that is anticipated at an elevated atmospheric* CO_2 *concentration, might result in accumulation of organic matter in soil. However, soil organic matter has a narrower C:N ratio than plants and their residues and a reduction of the decomposition rate might eventually lead to a reduced potential carbon conservation in terrestrial ecosystems if primary production is hampered by the availability of nutrients.*

In: S.C. van de Geijn, J. Goudriaan & F. Berendse (eds), 1993, Climate change: crops and terrestrial ecosystems, Agrobiologische Thema's 9, CABO-DLO, Wageningen, 97 - 108.

6.1 Introduction

The terrestrial ecosystem is an important component of the global carbon cycle. The reservoir of C in vegetation and soils is estimated to be approximately 2100 Pg C (1 Pg = 10^{15} g) of which 75 % is in soils (Eswaran *et al.*, 1993).

Plants are the major primary producers in terrestrial ecosystems and most organic matter in terrestrial ecosystems originates from them. Photoassimilated carbon is distributed over all plant parts including roots. Via litter fall, translocation and exudation and root turnover, organic carbon enters the soil. Rhizodeposition in many ecosystems is a major flow of carbon into the soil. Rhizodeposition is defined as the total amount of carbon originating from the roots and includes gases and organic materials. For plants upto a few weeks old, rhizodeposition can account for about 40 % of the total dry matter production by the plant (Whipps, 1987; Merckx *et al.*, 1985).

In soil, organic matter is transformed by soil biota into a wide variety of compounds or returned to the atmosphere as CO_2. Decomposition of (soil) organic matter and respiration of the vegetation are the major contributing processes of CO_2 release from terrestrial ecosystems into the atmosphere.

Soil organic matter is a chemically strongly heterogeneous material. A major part is humic materials which are relatively difficult to decompose and therefore have turnover times of upto several thousand years.

Microorganisms are the principle transformers of rhizodeposited organic materials and producers of soil organic matter. Microbes therefore play a crucial role in determining the nature of the soil organic matter.

The global carbon cycle is being perturbed significantly during the last century. Human activities such as the use of fossil fuels for energy production and agricultural practices and other changes in land use, i.e. deforestation increased the production of CO_2. This has resulted in a gradually increasing concentration of CO_2 in the atmosphere (Woodwell *et al.*, 1983). The increase in the atmospheric CO_2 concentration may lead to substantial changes in the carbon cycling in terrestrial ecosystems. Elevation of the CO_2 concentration in the atmosphere is expected to increase the primary production. This may ultimately change the rate of subsequent processes in soil such as mineralization of carbon as well as nitrogen and so have major consequences for primary production through changes in nutrient availability.

Since the observed atmospheric CO_2 increase is less than expected on the basis of the calculated emissions, several reports (Tans *et al.*, 1990; Musselman and Fox, 1991) argued that terrestrial ecosystems in the northern hemisphere must be responsible for sequestering substantial amounts of carbon dioxide. The current global annual exchange between the atmosphere and the terrestrial ecosystems is estimated to be roughly 100 Pg C but considerable differences and disagreement exists on the quantification of these fluxes among different ecosystems. Dixon and Turner (1991) compared several General Circulation Models and calculated that soils could either serve as a sink 41 Pg) or a source (101 Pg) for carbon.

In this paper, we will discuss the effects of plant roots and rhizodeposition on soil organic matter dynamics as a basis for prediction of the impact of an elevated CO_2 concentration and changes in plant growth on carbon fluxes in terrestrial ecosystems.

6.2 Carbon translocation via roots into soil

Contrary to aboveground litter production and crop residues left after harvest, the input rates of carbon into the soil are hard to quantify, particularly for natural ecosystems, and to a lesser extend for agricultural ecosystems. Ten to forty percent of the total net carbon assimilation of arable crops is released from the roots into the soil either as root respired CO_2 or as organic compounds. Large variations exist with plant species, plant development, growing season and environmental conditions. Estimations of annual carbon input to soil range from 900 to 3000 kg ha^{-1} a^{-1} (van Veen *et al.*, 1989) for arable crops and for forest stands. These data were mainly derived from direct measurements in ^{14}C-labelling experiments under controlled conditions in the laboratory or greenhouse and mostly on relatively young plants or from indirect measurements on the basis of observations on intact root systems.

Martin and Merckx (1992) studied the carbon dynamics in field grown wheat continuously labelled with ^{14}C-CO_2 and confirmed the conclusion that were drawn from earlier growth-cabinet experiments on the high proportion of photosynthetically fixed carbon translocated belowground and released from roots into the soil from the early growth stages on.

Swinnen *et al.* (in press) calculated on the basis of pulse-labelling wheat and barley under field conditions that over the entire growing season 1900 kg C. ha^{-1} was translocated belowground. Their carbon budget further showed that 1000 kg C ha^{-1} was released as CO_2 and 500 kg C ha^{-1} as rhizodeposition from the living roots and 400 kg C ha^{-1} was found in the roots at harvest. Part of the latter two fractions will be respired by microbial metabolism during and after the growing season so the net-input of carbon into soil will be less than 900 kg C ha^{-1} a^{-1}.

In a field experiment in which wheat was pulse-labelled with ^{14}C-CO_2, Martin and Merckx (1992) recovered approximately 40 % of the total residual soil ^{14}C from acid stable humic substances. This could reflect an extensive decomposition of root material and indicate a relatively fast formation of more or less stable soil organic materials during wheat growth upto the stage of flowering.

6.3 Interactions between plants and soil organic matter

Plants are the primary suppliers of substrate and energy for life in soil and thus play a key role in the control of the dynamics of microbial populations especially in the rhizosphere. Plants affect microbial activity through uptake and thus depletion of water and nutrients, which are as important to microbes as they are to plants, and through other physical and chemical changes in the environment.

The effects of mineral nutrients such as nitrogen in soil on microbial activity and decomposition processes is poorly understood. Fog (1988) reviewed the knowledge on the effects of soil nitrogen availability on the decomposition of organic material and also concluded that rather conflicting data exist with regard to the influence of plants on the decomposition of organic matter is soils.

Despite the relatively high C:N ratio of plant litter and rhizodeposition, microbial activity is generally stimulated in the root environment or rhizosphere (Curl and Truelove, 1986). It has been postulated that this readily decomposable rhizodeposition is used as an energy source to acquire nutrients from soil organic matter with far narrower C:N ratios (Coleman *et al.*, 1983 and Clarholm, 1985).

There is evidence that plants affect mineralization of soil organic matter by influencing microbial metabolism in the rhizosphere through the release of organic substances (Cheng and Coleman, 1990). Alternatively, other workers suggest that plants, rather than stimulating nitrogen mineralization, reduce the immobilization of nitrogen through effective competition with microbes for mineral nitrogen (Jingguo and Bakken, 1989). This explanation was based on the observation that plants did not affect mineralization of nitrogen from N-rich plant residues, but reduced immobilization of nitrogen in N-poor straw residues. This phenomenon was highly dependent on the spatial distribution of N-rich and N-poor sites in soil (Jingguo and Bakken, 1989).

6.4 Interactions between carbon and nitrogen dynamics in soil

In a series of experiments we tested the hypothesis that i) sufficient mineral nitrogen allows larger microbial populations that yield a higher immobilizing capacity and ii) insufficient mineral nitrogen enhances decomposition/mineralization of soil organic matter through input of rhizodeposition as substrates for the decomposing organisms. Liljeroth *et al.* (1990) observed that the apparent utilization efficiency of rhizodeposited organics by microbes was affected by the availability of mineral nutrients. The ^{14}C-labelled microbial biomass as well as the number of bacteria in the rhizosphere of wheat was significantly higher in soils amended with relatively high amounts of mineral N. As compared to soils which received smaller amounts of mineral N, remarkably, the relative increase in ^{14}C-labelled microbial biomass was larger than the relative increase in release of ^{14}C-labelled rhizodeposited, residual organic material grown in the high N amended soils. This indicates that at relatively *high mineral N concentrations in soil, the rhizodeposition was more efficiently used* as biosynthates by the microbes. Simultaneously, the decomposition of native, non ^{14}-labelled, soil organic matter was retarded in the high mineral N soils as compared to the decomposition rates in soils planted to the same crops but receiving smaller amounts of mineral nitrogen. The observations were made in a phytotron that enables growing (and labelling) plants with ^{14}C-CO$_2$ at a constant specific activity and subtracting CO$_2$ derived from root respiration and from the decomposition of ^{14}C-labelled rhizodeposition from the total CO$_2$-evolution. For this purpose, the soil-root atmosphere was separated from the surrounding atmosphere by growing plant in air-tight columns.

Interestingly, recovery of N by plants that were grown in the N limited soils exceeded the amount of N supplied with fertilizer and this was not the case in the regular N fertilized soils (Table 6.1). This observation means that in the case of fertil-

Table 6.1 Nitrogen uptake by plants as percentage from fertilizer addition (mg N in plants (mg N as fertilizer)$^{-1}$ x 100 %) (unpublished results from the experiment reported in Liljeroth *et al.*, 1990).

Plant age (d)	Low N	High N
40 days	123	114
61 days	106	83

izer-N-limitations, plants were able to efficiently utilize N derived from mineralization of native soil organic matter. In the case of sufficient fertilizer-N, plants were not able to recover all nitrogen added with fertilizer and microbes competed succesfully and immobilized upto 20 % of the fertilizer nitrogen. This available mineral nitrogen also enabled microbes to utilize rhizodeposited carbon with a relatively wide C:N ratio. This hypothesis is supported by observations that high nutrient levels in soils can simulate the turnover of added ^{14}C-labelled glucose but decrease both the decomposition rate of added ^{14}C-labelled crop residues (van Veen *et al.*, 1989) and the decomposition rate of native soil organic matter (Figure 6.1). In the latter case, the addition of both glucose and mineral nitrogen strongly stimulated the SIR potential microbial activity (Figure 6.1).

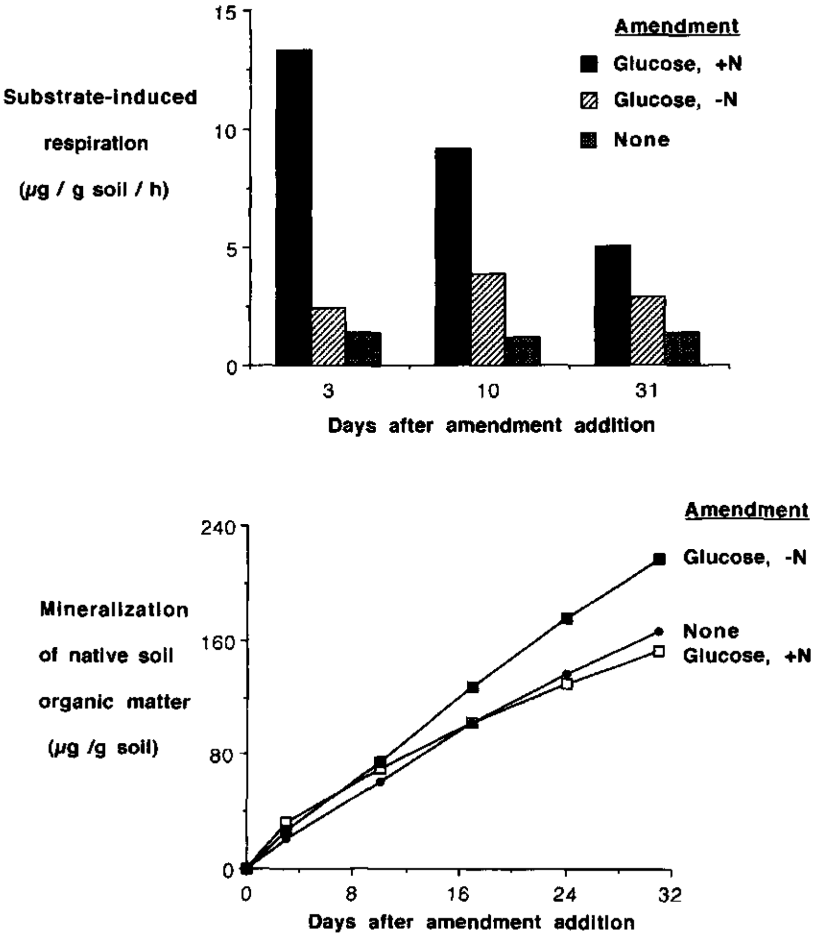

Figure 6.1 Potential activity of microorganisms, as measured by substrate-induced respiration according to Anderson and Domsch (1978) and mineralization of native soil organic matter, after addition of glucose (580 µg C g^{-1} soil) with or without mineral nitrogen.

6.5 Carbon partitioning between plant and soil at elevated atmospheric CO_2 concentrations

The same experimental approach as applied by Liljeroth *et al.* (1990) was used to study the effects of plants that were grown in an atmosphere with 350 and 700 ppm CO_2, respectively (Lekkerkerk *et al.*, 1990).

The dry weight of shoots of plants grown at 700 ppm CO_2 was up to 50 % higher after 49 days compared to that of plants grown at 350 ppm CO_2 (Table 6.1). The relative distribution of ^{14}C between shoot, root, soil/root respiration and soil did not differ significantly between plants grown at 700 ppm CO_2 or 350 ppm CO_2. This suggests that the distribution pattern of carbon within the plant, including the translocation to below-ground parts, is not changed by an elevated CO_2 level in the atmosphere. Our latest results, however, indicate that the increase in plant biomass production depends on the availability of nutrients in soil. At low soil mineral nitrogen contents, the relative increase in plant biomass at 700 ppm CO_2 compared to that at 350 ppm CO_2, was much smaller than at high soil mineral nitrogen contents (Table 6.2).

Part of the CO_2 collected from the soil columns during the experiment originated from the decomposition of native soil organic matter, already present in the sieved soil at the start of the experiment. The contribution of this unlabelled material was calculated from the specific activity of the plant material and the specific activity of the respired CO_2 (Table 6.3). Up to 21 days of growth, unlabelled soil organic matter was decomposed at the same rate at both CO_2-levels, and contributed 25-40 % of the total soil/root respiration. After 49 days, the turnover of unlabelled organic matter was responsible for 27 % and 10 % of the total amount of respired CO_2 for 350 and 700 ppm CO_2, respectively. It is striking, that the total respiration of unlabelled CO_2 from the soil/root compartment was less enhanced by an increasing CO_2 level than was the respiration of plant derived ^{14}C-material. At the end of the incubation, 53 % more total-CO_2 and 74 % more ^{14}C had been respired from soils exposed to 700 ppm CO_2 than soils exposed to 350 ppm CO_2, respectively.

Table 6.2 Relative changes in dry mass (mg per column, 2370 g dry soil) of wheat grown at 350 and 700 ppm CO_2 in the atmosphere at two nitrogen fertilizer applications (Low N: 50 mg N per kg soil and High N: 150 mg N per kg soil) at a plant age of 83 days.

	Shoot		Root	
	Low N	High N	Low N	High N
CO_2 content of the atmosphere				
350 ppm	100	126	100	150
700 ppm	100	153	113	121

Table 6.3 Dry mass (mg per column, 2370 g dry soil) of wheat grown at 350 and 700 ppm CO_2, and ^{14}C-CO_2- and ^{12}C-CO_2-evolution, respectively.

	350 ppm	700 ppm
Shoot	14020	20960**
Root	4150	4870
Total	18170	25830**
^{14}C-CO_2	847	1544**
Total CO_2	1090	1707**

**: $P<0.01$

Table 6.4 Carbon budget for a soil planted with wheat and exposed to either 350 or 700 ppm CO_2. Input, output, net change and root biomass after 49 days are given as mg C per column, 2.37 kg dry soil.

	350 ppm	700 ppm
Input ^{14}C residue	198	247
Output $^{12}CO_2$ from SOM	243	163
Net change (after 49 days)	- 45	+ 84
Root biomass	1606	2054

Kuikman *et al.* (1991) calculated a net soil carbon balance (Table 6.4) for the soil, by comparing the carbon coming from the roots plus that remaining in the soil as ^{14}C-labelled material (as determined by digestion of the soil) with the output of carbon by microbial decomposition of native soil organic matter ($^{12}CO_2$ respiration) (Table 6.4). After 49 days, a net decrease of soil organic matter was found when plants were exposed to 350 ppm CO_2 (-45 mg C per column), and a net increase in soil organic matter when plants were grown at 700 ppm CO_2 (+84 mg C per column). Moreover, the root biomass at 700 ppm was larger than the biomass at 350 ppm CO_2. Since only the first part of the growing season, before flowering, is considered here, these short term effects of elevated CO_2 on soil organic matter dynamics should not be extrapolated to long-term carbon fixation in arable soils. It is known, from pulse labelling with ^{14}C-CO_2 of wheat plants in the field, that the pattern of carbon allocation changes drastically during the growing season. In plants older than about 8-10 weeks, 80-90 % of the photosynthetically fixed carbon remains aboveground which is much more than in young plants (Swinnen *et al.*, in press). Despite these uncertainties, the increased primary production will enhance the input of carbon into the soil, both during the growth of plants, as well as through root turnover and root litter production.

We have further studied the impact of elevated atmospheric CO_2 concentration on allocation of assimilates of Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Gorissen, unpublished results). Juvenile 3- and 4-year-old trees were pre-treated for 14 months at 350 and 700 ppm CO_2 ans subsequently transferred to the ESPAS phytotron and treated with 350 and 700 ppm CO_2 for three weeks in an atmosphere continuously labelled with $^{14}CO_2$. Total net uptake of $^{14}CO_2$ increased during the treatment with 700 ppm CO_2 by 22 % compared to the treatment with 350 ppm CO_2. Also, the $^{14}CO_2$ in root/soil respiration increased in the 700 ppm CO_2 treatment. This was accompanied by a higher specific activity of the root/soil respiration and indicates a preferential use of recent assimilates by the root system or by the microbial biomass in the elevated atmospheric CO_2 treatment (cf. Liljeroth *et al.*, 1990).

6.6 Concept formulation

The input of readily decomposable root-derived material to the soil was higher when wheat plants were exposed to 700 ppm CO_2 than to 350 ppm CO_2. Because microorganisms pre-ferred this material as their energy source, the turnover of the more resistent native soil organic matter was reduced at 700 ppm CO_2. The non-soluble ^{14}C-residue in the soil was also increased at the highest CO_2 level. At 700 ppm CO_2, a conserving effect on the organic matter level in soil was observed. These observations are quite similar to those observed by Liljeroth *et al.* (1990) for the effects of mineral nitrogen on organic matter dynamics in soil.
On the basis of our results (Liljeroth *et al.*, 1990; Lekkerkerk *et al.*, 1990; Kuikman *et al.*, 1991), we formulated the so-called preferential substrate utilization concept (Figure 6.2). It comprises that i) root released organic substances have a relative high C/N-ratio and provide an energy rich source for energy and biosynthesis processes, ii) microbes prefer root released organic substances over native soil organic matter provided that sufficient nutrients are available to match the microbial requirements for nutrients and iii) when supplies of nutrients are insufficient for microbial metabolism, microbes will utilize native soil organic substances, with a relatively lower C/N-ratio in order to secure a sufficient nutrient supply. Thus, this concept assumes that the decomposition of native soil organic in planted soils depends on the presence or absence of inorganic nutrients.

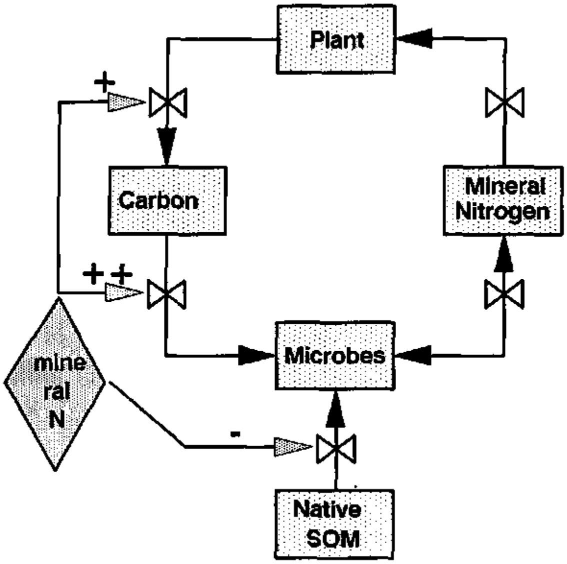

Figure 6.2 Conceptual diagram of substrate utilization.

6.7 Concluding remarks

The effects of climatic changes on C-fluxes in the plant/soil-ecosystem as a result of indirect, plant mediated effects have been discussed. The effects of plants will depend on soil related factors such as land-use and agricultural practices (inputs and soil management), soil structure and texture and mineral nutrient availability. Plant may have a conserving effect on soil organic matter through a continuous input of organic materials and their hypothesized suppressing effect on soil organic matter decomposition. This latter effect seems to be enhanced by a stimulated plant growth and input of carbon to soil at relatively high mineral nitrogen concentrations in soil as well as under elevated atmospheric CO_2 concentrations. This may lead to an accumulation of soil organic matter as long as sufficient plant nutrients are available.

Diaz *et al.* (1993) suggested that a feed-back mechanism might exist where elevated carbon dioxide causes an increase in substate release into the rhizosphere which will result in immobilisation of nutrients in microbial biomass. Consequently, plant growth will be limited by nutrients, particularly in nutrient-poor ecosystems.

These interactions need further research, as changes in soil organic matter could play a quantitatively important role in the global carbon budget. Investigations will particularly focuss on the possible feed-back mechanisms, such as those influenced by the nutrient status of the soil and by temperature, on carbon dynamics in plant/soil ecosystems.

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7 Plant growth and nutrient cycling in nutrient-poor ecosystems

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Summary

The response to elevated CO_2 levels of natural, nutrient-limited ecosystems depends on the long-term availabilty of nutrients to support an increase in biomass. Four hypotheses are discussed why nitrogen-limited ecosystems should not respond to an increase in the CO_2 concentration: 1) Not CO_2, but nutrients are the limiting factors in these systems. 2) The C/N ratio of plant tissue will increase, which will limit the decomposition rate and reduce the availability of nutrients in the soil. 3) The concentration of secondary metabolites will increase. 4) Plants with low growth rates respond less to elevated CO_2 than potentially fast growing species. Also, the effects of a temperature increase on growth, rates of decomposition and water balance in nutrient-limited ecosystems are discussed. It is concluded that the consequences of a global climate change for nutrient-limited ecosystems depend on the balance between the increase in nutrient loss, the enhanced availability of nutrients, and the reduction of the nutrient requirement of the plants in high CO_2. So far there is no evidence that the change in this balance will negatively affect nitrogen-limited ecosystems. An increase in temperature and nitrogen deposition will both directly affect this balance and enhance the stimulation of growth in elevated CO_2.

In: S.C. van de Geijn, J. Goudriaan & F. Berendse (eds), 1993, Climate change: crops and terrestrial ecosystems. Agrobiologische Thema's 9, CABO-DLO, Wageningen: 109 - 124.

7.1 Introduction

While an increase in atmospheric carbon dioxide and temperature is expected to enhance the growth of crops and wild plants under favourable conditions, there are serious doubts whether global change will have a lasting effect on the productivity of natural, nutrient-limited ecosystems. The ability of these ecosystems to respond depends on the long-term availability of nutrients to support an increase in biomass. In these systems the carbon and nitrogen cycles are closely linked, and changes in the carbon cycle will affect processes of the nitrogen cycle and vice versa. How elevated CO_2 and an increase in temperature may affect the carbon and nitrogen cycles, and what the consequences are for a long term growth response will be discussed in this paper.

7.2 Effects of elevated CO_2 on nitrogen-limited ecosystems

7.2.1 Why nitrogen limited ecosystems should not respond to an increase in the CO_2 concentration

Increased levels of CO_2 increase photosynthesis and growth of almost all crops and wild species (Cure & Acock, 1986; Poorter, 1993). However, the long term effects on natural ecosystems are of an increased CO_2 concentration may only be small (Field *et al.*, 1992). Several reasons for the predicted lack of response have been put forward, including both direct and indirect effects of elevated CO_2:

- In these systems CO_2 is not a limiting factor, but nitrogen or phosphorus. An increase in CO_2 will have no effect on growth.
- The C/N ratio of plant tissue will increase, which will limit the decomposition rate and reduce the availability of nutrients in the soil.
- The increase in the concentration of secondary metabolites will limit the decomposition rate.
- Plants with low growth rates (plants adapted to nutrient-limited environments) respond less to elevated CO_2 than potentially fast growing species.

What evidence is there to support these hypotheses? The last several years a large amount of data has been collected and reported in the literature. Unfortunately, it is often difficult to extrapolate these data to plants growing in natural ecosystems. We will examine to what extent the different hypotheses are verified by the available data, and how important these interactions are for the effects of elevated CO_2 on nutrient-limited vegetation.

7.2.1.1 "Not CO_2, but nutrients are the limiting factor in these systems. An increase in CO_2 will have no effect on growth"

The majority of studies show that nitrogen limitation does not prevent CO_2 from increasing the growth of plants. Although there are differences between species, most plants grown at low nitrogen supply rates do respond as much or more to elevated CO_2 as plants supplied with sufficient nitrogen (Bowes, 1993). The response to elevated CO_2 at low nitrogen is the result of an increase in the nitrogen use efficiency in photosynthesis (more C fixed per unit of N in the leaf). This is caused by an increase in photosynthesis due to higher substrate levels of CO_2, by a reduction of carbon loss in photorespiration, which also makes nitrogen available from the photorespiratory cycle (Conroy, 1992), and by reducing dark respiration (Bunce, 1990). Furthermore, nitrogen uptake can be stimulated by enhanced root growth, increased rhizobium growth and increased allocation of carbohydrates to mycorrhiza.

7.2.1.2 *"The C/N ratio of plant tissue will increase, which will limit the decomposition rate and reduce the availability of nutrients in the soil"*

It has been stated that CO_2 fertilisation lowers the concentration of N in the plant organs and increases the C/N ratio of the plant material to the soil (Bottner & Couteaux, 1991), which will then affect the decomposition rate. This theory actually consists of 3 hypotheses:

a] The C/N ratio of plant tissue will increase

One of the most frequently reported effects of growing plants in a high CO_2 concentration is the increase in the C/N ratio, or similarly, a decrease in the nitrogen concentration of the plant (Cure *et al.*, 1988; Johnson & Lincoln, 1990). However, when the C/N ratios of different plant parts are compared, it is often found that only the C/N ratio of the leaves is increased by high CO_2 (Cure *et al.*, 1988; Den Hertog & Stulen, 1990).

Elevated CO_2 can cause an increase in the C/N ratio in different ways. First, the C/N ratio of leaves will increase when nitrogen is used more efficiently in photosynthesis. Nitrogen that becomes available under high CO_2 conditions can be more effectively allocated to other processes, or to increased growth (Hilbert *et al.*, 1991; Pearcy & Bjorkman, 1983). However, this does not apply to the nitrogen concentration of non-photosynthetic plant parts. CO_2 may also increase the C/N ratio of these tissues is if the production of lignin, cellulose, and secondary metabolites is stimulated by an increased availability of carbohydrates. The quantity of these products in the litter will also negatively affect the decomposition rate. Finally, the C/N ratio will increase when non-structural carbohydrates accumulate in high CO_2. Due to the

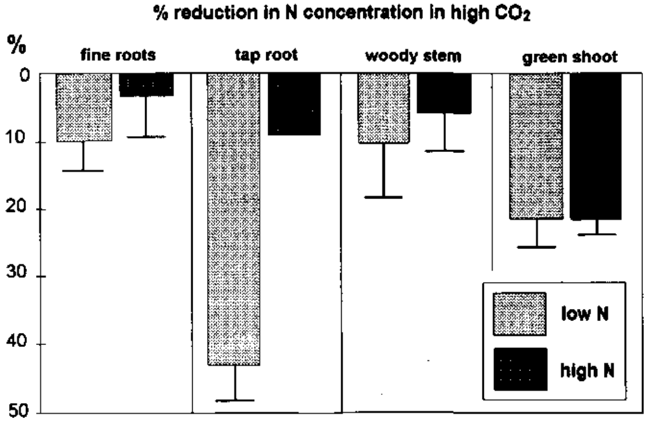

Figure 7.1. The effect of elevated CO_2 on the nitrogen concentration of four different plant parts. The 'tap root'category consist of data for both tap roots and coarse roots, while data for green stems, leaves and green shoots are combined under 'green shoot' . For each category the data are separated for plants grown in low and high nitrogen. The average values and the standard errors are shown. The complete set of data with their sources is given in Table 7.1.

Table 7.1 A compilation of data from the literature on the nitrogen concentration plants grown in elevated CO_2. The data are separately shown for different plant parts, and for plants grown in high and in low nitrogen. For experiments with more than one 'high CO_2 concentration', the different CO_2 concentrations are given in ppm.

% increase in N concentration in high CO_2			fine roots		coarse roots		tap roots		woody stem		green stem		leaves		green shoot		leaf litter	
author	species	CO_2	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high
Couteaux *et al.* '91	chestnut		6.0		-33.0		-45.0		-25.3								-47.9	
Curtis *et al.* '89	*Scirpus olneyi*															-15.4		
Den Hertog & Stulen	*Plantago major*			1.8												-22.1		
'90	*Urtica dioica*			3.4												-9.2		
Diaz *et al.* '93	*Rumex obtusifolius*														-23.4	-40.8		
Gries *et al.* '93	sour orange					-8.9								-13.0				
Hocking & Meyer '85	*Xanthium occidentale*		-14.7	28.1							-23.7	-18.2	-26.5	-41.4				
Hocking & Meyer '91	wheat														-21.8	-36.7		
Johnson & Lincoln '91	sagebrush												-15.3	-25.8				
Larigauderie *et al.* '88	*Bromus mollis*												-27.1	-19.8			-4.9	-1.4
Norby *et al.* '86	*Quercus alba*		-17.2				-51.1		-26.5				-19.2					
Norby & O'Neill '91	*Liriodendron*	493	-8.9	-3.6					-6.9	-5.3			-13.5	-13.5				
	tulipifera													-17.2				
		787	-14.4	-27.7					-10.3	-17.5			-28.1	-33.3				
														-34.5				
Oberbauer *et al.* '86	*Carex bigelowii*												38.9	1.9				
	Betula nana												-18.7	-5.6				
	Ledum palustre												-14.3	-4.8				
Reddy *et al.* '89	soybean			-9.09								0.0		-22.9				0.0
Williams *et al.* '86	mixed trees	500		0.5						9.5				-24.4				
		700		-18.6						-9.7				-28.9				
Wong '79	cotton														-52.3	-43.4		
Wong *et al.* '92	*Eucalyptus camaldulensis*												-31.2	-26.2				
	E. cypellocarpa												-29.8	-25.0				
	E. pulverulenta												-18.1	-17.5				
	E. pauciflora												-22.0	-21.0				
Woodin *et al.* '92	Calluna vulgaris								18.2				-40.4					
	mean		**-9.8**	**-3.1**	**-33.0**	**-8.9**	**-48.1**		**-10.2**	**-5.7**	**-23.7**	**-9.1**	**-19.0**	**-20.7**	**-32.5**	**-27.9**	**-26.4**	**-0.7**
	number of observations		5	8	1	1	2	0	5	4	1	2	14	18	3	6	2	2
	standard error		4.2	5.9			3.0		8.1	5.7		9.1	4.9	2.6	9.9	5.8	21.5	0.7

increased production, more carbohydrates can be allocated to storage organs such as tap roots or rhizomes. When the sink for carbohydrates is limited, starch may also accumulate in the leaves.

When these different effects are combined, one would expect an increase in the C/N ratio of leaves and other photosynthetically active parts, caused by an increased NUE and a possible accumulation of starch. The C/N ratio of storage organs will increase because of increased accumulation of carbohydrates, while Increased lignification may primarily affect the woody parts of the plant. The nitrogen concentration of roots is not expected to change in high CO_2.

A survey of the available data confirms this theory (Figure 7.1, Table 7.1). The reduction in nitrogen concentration is larger in leaves and green stems than in woody stems. The difference in N concentration is smallest in the fine roots, but very large for tap roots and coarse roots. For this reason, the separate effects on the different plant parts must be distinguished when referring to the effect of elevated CO_2 on the C/N ratio of plants. A consequence of this finding is that a change in the biomass allocation pattern in elevated CO_2 will also influence the effect on the C/N ratio of the whole plant. Another difference which becomes apparent is that for roots and stems the relative reduction in N content is larger for plants grown in low N, while it appears that intermediate CO_2 concentrations lead to a smaller reduction than high CO_2 concentrations (Table 7.1). It appears that an increasing imbalance between the C and the N supply to the plant results in a larger reduction in the nitrogen concentration in elevated CO_2. However, the differences in N concentration between plant parts remain.

b] A higher C/N ratio in the plant will lead to an increase of the C/N ratio of litter

Often the connection is made between an increased C/N ratio in the plant and its effect on decomposition, while ignoring the possibility that the C/N ratio of litter may differ from that of living plants. Plants will try to conserve the scarce nutrients, and withdraw nitrogen from the senescing leaves. If the efficiency in withdrawing nitrogen from the dying leaves is not affected by elevated CO_2, then the difference in the C/N ratio between plants grown in high and low CO_2 will be retained in the litter. However, if the efficiency is lower in elevated CO_2, then the difference in C/N ratio will be smaller for the litter than for the living plant.

Why would the efficiency of reallocating nitrogen be different in high CO_2? The increase in NUE may allow the plant to allocate less nitrogen to the photosynthetic apparatus which has a low C/N ratio, and more to new permanent structureswith a high C/N ratio. While nitrogen in photosynthetic enzymes can easily be reused by the plant, it may not be possible to recycle nitrogen allocated to permanent plant structures. In the extreme case that all of the non-structural N is reused and none of the structural N, there will be no difference in C/N ratio of the litter.

There are only few data available in the literature that provide the C/N ratio of the green leaves as well as the C/N ratio of the litter. However, these data points show a clear trend, with nitrogen withdrawal being consistingly less efficient in high CO_2 than in ambient CO_2, with the exception of a C_4 species (Figure 7.2, Table 7.2). This lower reallocation efficiency may even cause the difference in leaf N concentration between treatments to disappear during senescence (Curtis *et al.*, 1989; Larigauderie *et al.*, 1988). The statement that a low N status as induced by elevated CO_2 either

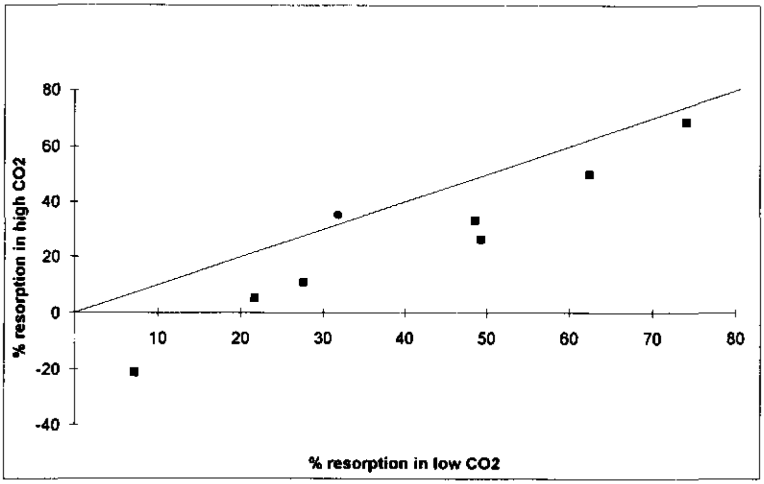

Figure 7.2. A comparison of the efficiency of nitrogen reallocation between plants grown in low and in high CO_2. The squares represent C_3 species and the circle stands for a C_4 species. The complete dataset and references are given in Table 7.2.

has no effect or enhances N resorption efficiency (Field *et al.*, 1992) is therefore not correct.

In annual plants, nitrogen is not being recovered for growth in the next season, but for reallocation to seeds. When too much N is invested in structural vegetative biomass, less can be reallocated towards reproduction. A lower seed set in annual plants in elevated CO_2 has indeed been found when N is limiting (Mitchell *et al.*, 1993; Sionit *et al.*, 1981; Van Kraalingen, 1990). Because reallocation of N may not be of great importance to the plant when N is not limiting growth, the resulting C/N ratio of the litter may be difficult to predict.

Plants adapted to nutrient-poor conditions invest relatively more in structure and less in the photosynthetic apparatus compared to fast growing plants. Elevated CO_2 may therefore cause only a relatively small shift in the C/N ratio of slow growing plants because the pool from which they can reallocate nitrogen is smaller.

c] The increase in the C/N ratio of the litter will limit the decomposition rate

A high C/N ratio of the litter usually leads to a reduction in the decomposition rate (Berendse *et al.*, 1987). However, not only the nitrogen content but also the type of carbon compounds determines how fast litter will decompose. When the lignin concentration is increased, decomposition of litter is reduced (van Vuuren, 1992). While it is possible that excess carbon will be used for the production of secondary metabolites, an accumulation of starch in elevated CO_2 has often been documented. The effects of the different carbon compounds on decomposition will be discussed in the next paragraph.

Table 7.2 A compilation of data from the literature showing the effect of elevated CO_2 on the nitrogen reallocation effciency

reallocation efficiency			live material									dead material									resorption	
			low CO_2			high CO_2			% increase			low CO_2			high CO_2			% increase			of N (%)	
authors	species	comment	%C	%N	C:N	%C	%N	C:N	%C	%N	C/N	%C	%N	C:N	%C	%N	C:N	%C	%N	C/N	low CO_2	high CO_2
Curtis et al 1989	*Scirpus olneyi*	pure	41.3	1.13	36.7	42.1	0.95	44.2	2.11	-15.4	20.6			83.1			86.0			3.6	74.1	68.7
		mixed	40.6	1.23	33.2	41.2	0.87	47.3	1.5	-28.8	42.6			47.5			51.7			8.9	49.2	26.4
	Spartina patens	C_4	42.1	0.72	58.1	42.8	0.62	69.1	1.71	-14.5	19										31.8	35.3
Larigauderie *et al.* 1988	*Bromus mollis*	low N		2.21			1.61			-27.1			2.05			1.95			-4.9		7.24	-21.1
		high N		3.84			3.08			-19.8			2.78			2.74			-1.4		27.6	11.0
Norby *et al.* 1986	*Quercus alba*			1.20			0.97			-19.2			0.94			0.92			-2.1		21.7	5.15
Reddy *et al.* 1989	soybean	leaves		3.5			2.7			-22.9			1.8			1.8			0.0		48.6	33.3
		stems		1.6			1.6			0			0.6			0.8			33.3		62.5	50.0

7.2.1.3 "The concentration of secondary metabolites will increase"

The increased production of carbohydrates may promote synthesis of carbon-based secondary metabolites such as lignin, cellulose and phenolics (Field *et al.*, 1992). These products give rise to low quality, slowly decomposing litter. So far there is little evidence for a direct effect of elevated CO_2 on the production of secondary metabolites in elevated CO_2. However, indirect effects are possible when nitrogen becomes more limiting, resulting in increased production of secondary compounds. For a review on this subject see Lambers (1993). The production of allelopathic compounds (which inhibit mycorrhizal and root growth of other species) can affect the interaction between species in nutrient-poor environments (Nilsson *et al.*, 1993). It is unknown what the effects of elevated CO_2 will be on the production of these compounds.

More likely than the increase in secondary metabolites is the accumulation of non-structural carbohydrates in the plant. When the carbohydrate sinks are limited, much of this will end up in the litter. Although accumulation of starch will increase the C/N ratio, its effect on decomposition will be different from that of structural carbon. While secondary metabolites will suppress the decomposition process, non-structural carbohydrates can be easily used by the decomposers, and may stimulate microbial growth. Microbes will prefer these energy rich and easily decomposable compounds over recalcitrant organic matter, but to meet their requirement of nitrogen they are forced to decompose the relatively nitrogen-rich soil organic matter (van de Geijn & van Veen, 1993). Simultanuously, the availability of this energy source may facilitate the decomposition of lignin. The net effect may be a stimulation of the decomposition rate.

Greater below ground C inputs through root exudation and turnover at elevated CO_2 have been shown to increase the soil microbial biomass (Diaz *et al.*, 1993; Zak *et al.*, 1993). It is not clear how an increase in the microbial biomass in the soil will affect the availability of nutrients for the plants. While the decomposition rate will increase, more nitrogen is required and tied up by the soil microbes. In one study this resulted in an increased N availability under N-limited conditions (Zak *et al.*, 1993), while in a nutrient rich soil the increased soil microbial biomass reduced the N availability (Diaz *et al.*, 1993). How a rapid growth of micro-organisms will affect the availability of nitrogen in the soil may be dependent on the release of nitrogen from the microbial biomass through grazing by other soil organisms (de Ruiter *et al.* 1993). The decomposition rate appears to be dependent on the complexity of the soil fauna. In a complex community of soil organisms low quality litter grown in elevated CO_2 decomposes faster than in a system with only a few species of decomposers (Couteaux *et al.*, 1991).

7.2.1.4 "Plants with low growth rates respond less to elevated CO_2 than potentially fast growing species"

Recent papers (Hunt *et al.*, 1991; Poorter, 1993) show that slow growing species (adapted to nutrient-limited ecosystems) respond less to elevated CO_2 than potentially faster growing species. A review of the literature shows the average increase in biomass at elevated CO_2 of 'slow growing species' to be 23%, while 'medium fast growing species' increase biomass by 38%, and fast growing species by 54% on average (Poorter, 1993).

There are several difficulties in extrapolating these results to natural ecosystems. First, most experiments are short-term, ranging from a few weeks to a few months. It may take longer for slower growing species to show a response to elevated CO_2 (Bowler & Press, 1993). Second, most experiments are conducted under conditions favourable for the faster growing species (non-limiting nutrients and water). In nutrient-limited conditions the slower growing species may show a different response to an increased CO_2 concentration (Wong *et al.*, 1992).

The presence of mycorrhiza may favour slow growing species in the response to elevated CO_2. Mycorrhiza provide a large sink for carbohydrates, and provide nutrients in return. It may also prevent a large stimulation of other soil organisms by carbohydrates that may tie up the available nitrogen in the soil. Fast growing species (often non-mycorrhizal) may become severely N-limited as a result of a large increase of micro-organisms caused by increased loss of carbohydrates by the roots (Diaz *et al.*, 1993).

7.2.2 The effect of elevated CO_2 on the nitrogen cycle

Will nutrient-limited ecosystems respond to an increase in CO_2 concentration? There is a clear need for information on how CO_2 levels affect the different aspects of the nitrogen cycle in these ecosystems. However, the data that are available show that elevated CO_2 will enhance growth even when nitrogen is limited. Also, the response of slow growing plants to elevated CO_2 may be larger than found in short term experiments when they are grown for a longer period under natural, nutrient-limited conditions. Ultimately, the response of nutrient-limited ecosystems to elevated CO_2 will be based on the effect of CO_2 on three processes: the nitrogen use efficiency of the plant; the loss of nutrient from the plant and the availability and uptake of nutrients.

7.2.3 The availability of nutrients may not meet the nutrient requirement

The availability of nutrients in the soil is determined by the rate of decomposition. An increase in the C/N ratio and a higher concentration of secondary compounds which are difficult to decompose will slow down the decomposition rate, and in due time will reduce the nutrient availability. Even if the total loss of nitrogen doesn't increase, the growth will eventually be limited by the reduced availability of nutrients.

However, as shown above, the C/N ratio in some plant parts may not increase and the reallocation efficiency of nitrogen is reduced at high CO_2. The C/N ratio of litter will therefore not increase as much as the C/N ratio of green leaves. An important consequence of this is that the combination of a 'relatively high' nitrogen concentration and an increased growth rate in elevated CO_2 will result in an increase in the total amount of nitrogen lost through the production of litter (Curtis *et al.*, 1989). In order to obtain a similar biomass during the following growing season, the plant will have to take up an equivalent amount of nutrients (Berendse *et al.*, 1987).

Because the nitrogen lost through litter will only become available to the plant slowly through the decomposition process, it will not be readily accessible again. In this case the rate at which nitrogen becomes available to the plant remains the same while the loss of nitrogen increases, resulting in an increased nutrient limitation during the following years which will limit the CO_2 response.

In both scenario's the expected initial growth response cannot be not sustained because a larger fraction of the nutrients is tied up in the decomposition process. The long term responses are dominated by the slow changes in turnover of soil C and N pools (Rastetter *et al.*, 1991). To maintain a lasting effect of CO_2 on growth, either an external input of nutrients is required, or the release of nutrients from the decomposition process must be accelerated.

7.2.4 Elevated CO_2 may increase the N availability and uptake

The possibility that elevated CO_2 may stimulate nitrogen uptake is often overlooked in long term predictions (Rastetter *et al.*, 1991). Increased root growth and an increased capacity for nutrient uptake per unit root may increase the uptake per plant (Field *et al.*, 1992). Stimulation of microbial activity and recycling of microbial N at elevated CO_2 may increase the N availability for plants (Lekkerkerk *et al.*, 1990; Zak *et al.*, 1993). Allocation of carbohydrates to rhizobium or other nitrogen fixing symbionts may provide another effective way to permanently increase the nutrient availability (Norby, 1987). Plants may also allocate more carbon to the mycorrhiza, which will stimulate mycorrhizal infection (Diaz *et al.*, 1993; O'Neill *et al.*, 1987). Ericoid mycorrhiza, which form mutualistic associations with many of the dominant species of nutrient-limited ecosystems, are able to actively participate in the mobilisation of nitrogen from organic matter, and supply their hosts with nitrogen (Leake & Read, 1989; 1990). These different processes may all enhance the nitrogen availability in high CO_2, even in the absence of a temperature rise. Because they will partly determine whether CO_2 will affect growth in nutrient-poor ecosystems, it is important to study the interactions between elevated CO_2 and these different processes.

Nitrogen deposition will likewise increase the nitrogen availability and stimulate production in nutrient-limited ecosystems (Berendse & Elberse, 1990). The potential for increased production will be even higher in combination with elevated CO_2 (Field *et al.*, 1992).

7.3 Effects of a temperature increase on nutrient-limited ecosystems

Like elevated CO_2, an increase in temperature may affect nutrient-limited ecosystems in several different ways. In combination with an increase in atmospheric CO_2 the effects of climate change on these ecosystems may be even more pronounced.

7.3.1 The effect of temperature on growth

In areas where the ambient temperatures are below the optimum temperatures for growth, a direct enhancement of growth by temperature can be expected. In addition, higher temperatures in early spring and late fall will extend the growing season. However, an increase in winter temperatues will enhance the respiration rate, while deciduous plants will have no means to benefit from the higher temperatures through fotosynthesis after leaf fall. Evergreen species may be able to balance this loss with an increased carbon gain provided the light levels are sufficiently high. Plants may be subjected to an increase in heat stress during the warmest periods. However, the damaging effect may be less when a temperature increase is combined with higher CO_2 levels, which has been shown to mitigate the negative effects of high temperatures (Kriedemann *et al.*, 1976). An increase in temperature can also affect the winter hardening of plants, while the shorter and less severe cold period during the winter may affect the vernalization of plants.
Higher temperatures often stimulate the effect of elevated CO_2 on growth (Idso *et al.*, 1987). However, there does not seem to be a threshold temperature below which CO_2 will have no effect. Plants from temperate regions have been shown to respond to elevated CO_2 even at low temperatures (Mitchell *et al.*, 1993).

7.3.2 Increased rates of decomposition with increased temperature

Increased temperatures will speed up the decomposition rate (provided the soil moisture content does not decrease), and will increase the availability of nutrients. In nutrient-limited ecosystems on organic soils, most of the N is held in the soil and is released very slowly. A potential increase in the mineralization of this N may provide a long-term boost in the nutrient supply (Rastetter *et al.*, 1991). This increase in nutrient availability will directly enhance plant growth, and in addition will counteract the nutrient limitation induced by elevated CO_2.
Higher winter temperatures can create the possibility that the mineralization rate is increased, while the (deciduous) plants are not able to take up the extra nutrients. This may enhance leaching, and result in a permanent loss of nitrogen from the system (Rastetter *et al.*, 1991). Enhanced mineralization may favour evergreen species in these systems if they are capable of increasing nutrient uptake during a warm spell in the winter.

7.3.3 Effect of CO_2 and temperature on the water balance

Higher temperatures will enhance evaporation and transpiration. While an increase in CO_2 concentration will increase the WUE, this may be partly offset by an increase in leaf area. It is difficult to predict whether a combination of higher temperature and high CO_2 will result in increased or reduced evapotranspiration. A decrease in soil moisture will reduce both decomposition and plant growth, while an increase in soil moisture will stimulate both processes. The effect of drought on the balance between nitrogen release and nitrogen requirement is therefore difficult to predict. A possible change in the amount of precipitation as a result of global warming can have a large impact on these ecosystems, and will interact with the change in temperature and CO_2 concentration. At the present, it is very uncertain if and how precipitation will be affected.

7.4 Conclusions

The increase in the C/N ratio and the level of secondary metabolites in plant litter as a result of growth in high CO_2 is probably not as large as previously predicted. Moreover, a large fraction of the increase in the C/N ratio is very likely caused by starch accumulation. Litter produced in high CO_2 may therefore have only a slightly lower ratio of nitrogen to secondary compounds, which is a measure of decomposability. However, the total amount of nitrogen in litter will increase with a higher biomass production, while the content of energy rich, easily decomposable compounds is enhanced. When a stimulation of plant symbionts is also taken into account, clearly the general notion that elevated CO_2 will retard the decomposition process will need to be reconsidered.

The consequences of global change for nutrient-limited ecosystems depend on the balance between the increase in nutrient loss, the enhanced availability of nutrients, and the reduction of the nutrient requirement of the plants in high CO_2. So far there is no evidence that the change in this balance will negatively affect ecosystems where nitrogen is the most limiting factor. In addition, an increase in temperature and nitrogen deposition will both directly affect this balance and enhance the stimulation of growth in elevated CO_2.

7.5 An experiment to study the effects of climate change on a nutrient-limited ecosystem

Controlled environment studies are neccessary in order to separate the effects of CO_2 and temperature on the different interacting processes between the carbon and the nutrient cycles. These studies will indicate the importance of the different factors, and provide valuable data for ecosystem models. However, because of the complexity of the carbon and nitrogen cycles in the system, controlled environment studies will not be able to provide definitive answers on how ecosystems will respond to climate change. Simultaneous large scale ecosystem studies are essential for predicting the effects of global warming and CO_2 increase on natural vegetation.

A large scale study on the effects of increased CO_2 and temperature on whole catchment areas has recently started in a nutrient-limited ecosystem in southern Norway (the CLIMEX project). Several European research groups participate in this project, which aims to investigate how the different ecosystem processes respond to climate change and CO_2 increase. Among the processes studied are catchment hydrology, soil water chemistry, soil fauna and decomposition, mineralization, growth and turnover of trees and dwarf shrubs, photosynthesis, and nutrient content and allocation of the vegetation.

Effects of temperature on soil processes such as decomposition, root growth and nutrient uptake will be studied in a separate catchment exposed to soil heating, with no increase in CO_2 concentration.

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8 Carbon cycle and ecosystem productivity on a global scale

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Summary

The annual rate of increase of atmospheric CO_2 *by fossil fuel combustion is only about 60% of the annual* CO_2 *emission rate. Most of the remaining* CO_2 *is absorbed by the ocean, but a smaller part also by the terrestrial biosphere. The use of carbon isotopes as a tracer has shown that annually almost one tenth of the atmospheric carbon dioxide reservoir is exchanged with the ocean. Another one tenth is exchanged with the terrestrial biosphere. The rate of absorption of* CO_2 *in the ocean is limited by sluggish exchange of surface water with the deep sea. Increasing atmospheric* CO_2 *stimulates plant growth worldwide, both by increased photosynthesis and improved water use efficiency. This biotic* CO_2 *enrichment effect has delayed the rising atmospheric* CO_2 *curve by about ten years, and probably also explains the fate of* CO_2 *released by deforestation, the so-called "missing carbon". On a time scale of hundreds of years ocean and biosphere together will be able to absorb much more than they do now, about 85% of the total* CO_2 *emission. Climatic change can alter this picture in ways that are necessarily strongly diverse for different climatic zones.*

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8.1 Introduction

The concentration of greenhouse gases in the atmosphere is unmistakably increasing at a fast rate, and will double at the timescale of a few human generations. This increase may induce climatic changes that will exceed the adaptive capacity of nature, and indeed of the human society. The mere existence of something like a greenhouse effect is a good thing: without it we would be frozen, but its intensification is a cause of concern, and may lead to temperature increases of the order of a few degrees centigrade. Other climatic consequences such as for precipitation or storm events are hardly known.

The most abundant greenhouse gas is not CO_2, but water vapour. Yet, CO_2 has a central role because it is less dependent on climate than water vapour. Water vapour acts more like a passive companion, enhancing a warming up by CO_2 once begun. There is usually a higher water vapour content in warmer air and therefore also a larger greenhouse effect. This sounds like a circular argument, but in fact it is the expression of a positive feed-back mechanism that destabilizes the climate system and makes prediction much more difficult. Surely, negative feed-backs also exist, such as increased cloud formation, that might weaken an initial warming. The uncertainty of the net result of the combined effects is considerable. For this reason most of the attention in this article will be given to CO_2 and the carbon cycle.

8.2 The global carbon cycle

Atmospheric CO_2 increases at a rather steady rate, at least on a decadal time scale. During the last 50 years its rate of increase has grown exponentially at a rate of about 2.4% per year, which has been about 60 % of the rate of emission of CO_2 from fossil fuel burning. The size of this fraction is not a natural constant, on the contrary, it depends on the activity and absorptive capacity of the sinks for CO_2, the ocean in the first place and the biosphere in the second place. On longer time scales, there has been a rather stable level at about 280 ppm for the last thousands of years until the effects of the industrial revolution became noticeable. Further back in time, during the last glacial period, atmospheric CO_2 was much lower and even dropped to about 200 ppm. This alternation of about 200 ppm during a glacial period and 280-300 ppm during an interglacial period has probably been repeated several times during the last one million years, when glacial periods returned about every 100 000 years. The causes of these glacial periods are still debated, and probably consist of many cooperating factors. Glacial periods are triggered by the Milankovich cycle, that is caused by precession in the planetal orbit of the earth around the sun. This cycle itself already existed during the Tertiary period but it did not cause glacials yet. Probably a slowly declining CO_2 concentration, and accompanying global cooling, passed a critical threshold so that the positive feedback mechanism of increased snow cover and glacial cap formation could take over. Only then could the Milankovich cycle trigger a run-away "ice-house" condition, signifying the beginning of the Pleistocene period.

Surely, on different time scales, different processes are important. On a shorter time scale than the decadal one, seasonal or even diurnal fluctuations dominate. The seasonal effect of carbon uptake by plant growth is quite outspoken in atmospheric CO_2 records that have been obtained during the past 30 years, such as the well-known record of Mauna Loa. Most remarkably, this seasonal fluctuation is almost absent on the southern hemisphere. The best explanation is that carbon uptake by algal growth in the oceans is buffered by the large carbonate content of seawater. The alternative explanation that carbon uptake in the ocean is simply much smaller than that on land, has recently been disproven by simultaneous measurements of atmospheric oxygen. Until recently the corresponding seasonal cycle of atmospheric oxygen could not be measured, due to the very high back

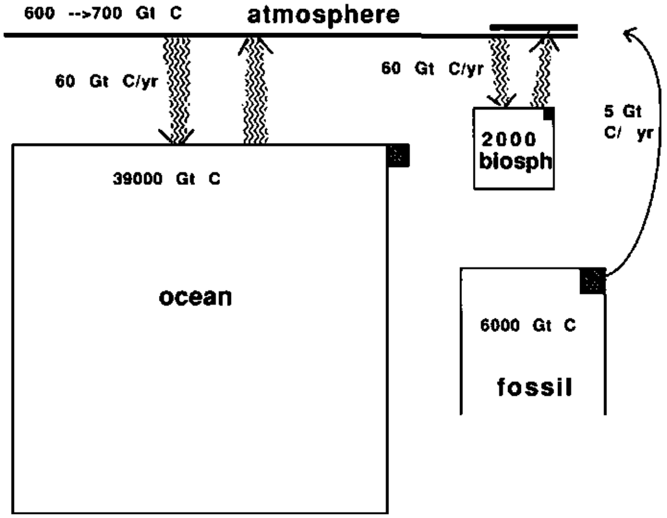

Figure 8.1 Major global reservoirs and fluxes of carbon, expressed in Pg (or Gt).

ground concentration, but now it has been shown that the cycle is present both above the continents and the oceans. Oxygen is not buffered in seawater the same way as CO_2 is, and so it does follow the annual cycle.

On the whole, the terrestrial and marine annual fluxes of biotic carbon uptake and release are of the same order of magnitude and equal to about 60 Pg of carbon (1 Pg = 10^{15} g = 1 Gt) each (Figure 8.1). The total flux of about 120 Pg is drawn from the atmosphere that contains about 700 Pg of C in total. Therefore the whole CO_2 content of the atmosphere is recycled once per six years. This is such a short period of time that it seems as if any disturbance by injecting CO_2 from fossil fuel should be absorbed without difficulty. This impression is even reinforced when one considers the large size of the ocean pool of carbon: almost 40 000 Pg of C, but it is a false impression as we will see.

8.3 The limited absorption capacity for CO_2 in the carbon cycle

On a geological time scale the largest carbon reservoir on earth is rock carbonate. This huge reservoir does participate in the global carbon cycle, but very slowly. During a process of granite rock weathering, carbonate and SiO_2 are formed from silicate and CO_2 drawing down atmospheric CO_2. Eventually this process will absorb practically all CO_2 from fossil fuel burning, but it will only do so at a time scale of tens of thousands of years (Berner and Lasaga, 1989). The largest next reservoir of carbon in the carbon cycle is the dissolved bicarbonate in the ocean, and this reservoir is active on a decadal time scale. In comparison to carbon in the ocean, fresh water of lakes and rivers can be totally ignored. The amount of CO_2 that can be dissolved in water is proportional to the partial pressure in the air above it. This holds for both fresh water and seawater, but in seawater bicarbonate ions have a much higher concentration than dissolved CO_2, because of the high pH (about 8.1). In fact, a chemical equilibrium exists in the chain $CO_2 <-> HCO_3^- \leftrightarrow (CO_3)^{2-}$, which shifts to the right with increasing pH (Butler, 1982). When the CO_2 concentration in the air increases, more CO_2 gets dissolved and an equilibrium shift occurs towards HCO_3^-, which will release H^+ ions. Therefore the pH goes down, offering a strong negative feed-back to further absorption. The net result is that in seawater the incremental absorption is not proportional to partial pressure of CO2 and total amount (about 25 g m^{-3}) of carbon dissolved, but to only about 1/10 of this product. Therefore, effectively the pool size of ocean carbon is only about 4000 Pg , and 36 000 Pg can be considered as being chemically locked up.

Still, 4000 Pg is much more than what the biosphere contains. However, the second reason for limited absorptive capacity is the slowness of mixing of deep ocean water and surface water. The upper few hundred meters of the ocean are in good contact with the atmosphere, but the deeper layers are separated by a thermal inversion and the exchange rate with them is slow. The average residence time of water in the deep Pacific is several hundreds of years. The water of the Atlantic is recirculated at a much faster rate, in less than 100 years time. The overall effect is that out of the 4000 Pg chemically accessible, only about one tenth is immediately in contact with the atmosphere. The other nine tenth will absorb its portion in due time, but only after hundred of years.

These two facts tell a lot about the global carbon cycle. In the long run (a thousand years) redistribution of emitted CO_2 will occur between the atmospheric reservoir of 700 Pg and the oceanic effective reservoir of 4000 Pg. A fraction of about 700/(700 + 4000) or about 15 % will remain in the atmosphere. On the short decadal time scale, this remanent fraction is much higher due to lack of time for mixing. A similar calculation gives a remanent fraction of about 700/(700 + 400) or about 64 %. This value is very close to the observed remanent fraction, and can serve as a first guideline for scenario studies.

8.4 The role of the terrestrial biosphere

Deforestation as an additional source of CO_2 release to the atmosphere is estimated to amount to a rate between 1 and 2 Pg of C per year. When this rate is added to the known emission rate of fossil fuel burning, atmospheric CO_2 should rise faster than it actually does. This in a nutshell is the problem of the so-called "missing carbon". In Figure 8.1 the total biosphere reservoir is given, as well as the annual exchange flux of carbon with the atmosphere. The size of this exchange flux is of the order of 50 Pg of C per year, but it is worthwhile to consider this flux and its definition in more detail.

This flux can be identified with the Net Primary Productivity, the annual sum of the daily net growth rates of plant dry matter (expressed in carbon). This definition means that the own respiration of the vegetation has been taken into account , and is not included any more. The flux *before* subtraction of respiration is the Gross Primary Productivity (*GPP*), which can be considered as the sum of gross CO_2 assimilation rates. However, the calculation of this gross flux is even more imprecise

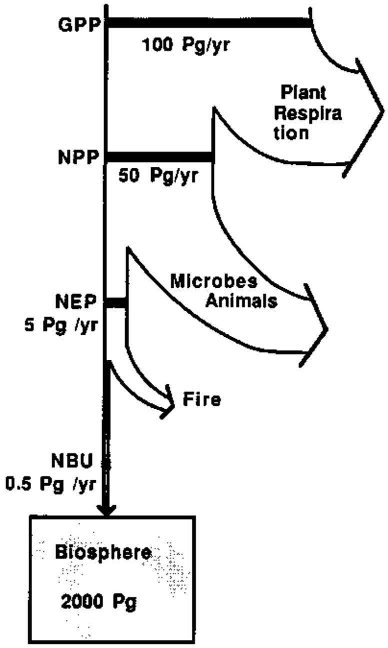

Figure 8.2 Major terrestrial carbon fluxes, as consumed by the plants themselves, by heterotrophic organisms and by fire. Net biospheric uptake is the remainder of large positive and negative fluxes.

than that of the *NPP*, and based on rough guesses of the rate of respiration. The estimate of *NPP* is based on field observations of production rates of new leaves, twigs, branches and roots and is therefore somewhat more reliable. The order of magnitude of global *NPP* is 50 Pg of C per year, whereas that of *GPP* is about twice as much (Figure 8.2). The Net Primary Productivity is largely consumed by grazers, such as insects and various kinds of mammals, or left over to be decomposed by fungi and microbes. Live biomass is estimated to be about 500 Pg , mainly in the form of wood. After death it turns to litter and eventually to soil organic matter (about 1500 Pg of C). The magnitudes of the pools of organic matter in various forms and of the fluxes of formation and consumption are related by residence times and partitioning coefficients. Their basic relationship is given in Figure 8.3 as a scheme driven by *NPP*. The outflow of each state variable in this scheme is calculated as content divided by longevity, so that its equilibrium content is simply the product of longevity and inflow. The outflows cascade down to litter, humus, and resistent soil carbon. From biomass to humus a considerable fraction of carbon is lost by respiratory processes, and also from humus to resistant soil carbon. The complement of this fraction returns to the atmosphere as respiratory CO_2. More complex approaches to decomposition of organic matter (Janssen, 1992) may be needed, but were not considered here.

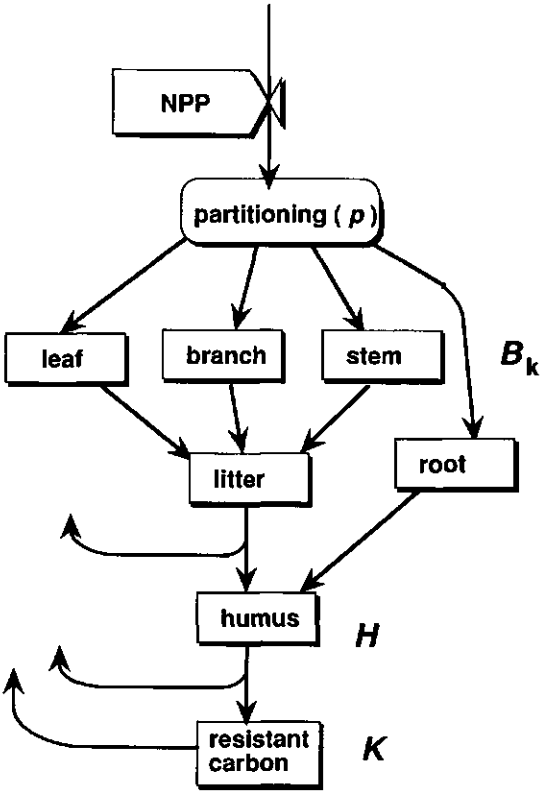

Figure 8.3 Simplified model structure for an ecosystem. Each box itself is described by first order decay. Characteristics such as *NPP*, its allocation, reservoir longevities and transfer (respiratory) losses depend on ecosystem type.

Above-ground biomass consists of leaves, stemwood, roots, branches and litter. Combination of the driving forces and residence times leads to a steady state distribution of surface densities of carbon for a biosphere model consisting of six different ecosystem types as presented in Figure 8.4 (Goudriaan 1990). In this figure the width of each bar represents the area of the vegetation type, and the height of each bar the carbon areal density. The high areal density of soil carbon in temperate forest and in grasslands as compared with agricultural land and tropical forests is noteworthy.

Many ecosystems in the world, however, are not in a steady state, but they accumulate dry matter during a number of years and are then disrupted by fire or other drastic events, so that they go through a saw tooth-like life cycle. Fire is often a natural process, and necessary for rejuvenation of ecosystems. Locally, disruption by fire is a discontinuous event, but summed over the entire globe there is a con-

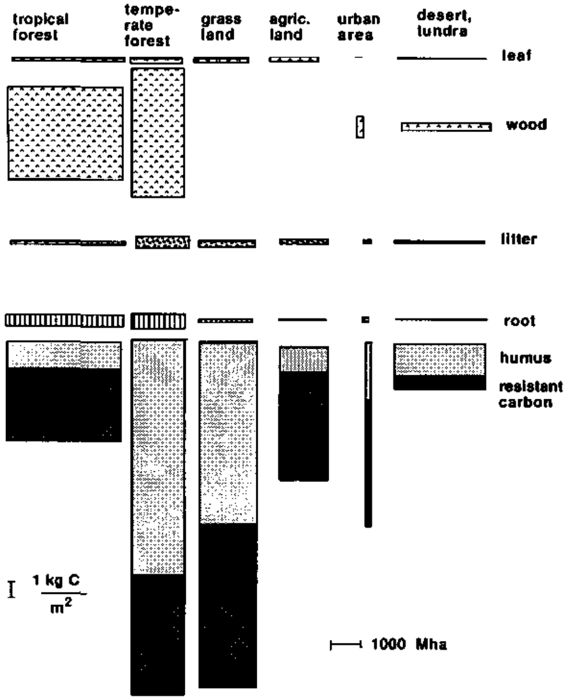

Figure 8.4 Simulated carbon areal density (heights of the columns) and land area for each vegetation type (widths of the columns). In this representation the areas of the columns are proportional to the simulated amounts of carbon.

tinuous release of CO_2 by fire, which is practically compensated by regrowth at theother places. The total carbon release flux due to fire is of the order of 4 - 7 Pg of carbon per year. The largest portion in this flux is on account of periodic burning of tropical grasslands (Hall and Scurlock 1991). Although this flux is almost as large as the rate of fossil fuel consumption, grassland burning does not contribute to the increase of atmospheric CO_2. Within a time span of one year most of the biomass turns to CO_2 anyway, if not by fire then by decomposition. Moreover, fire residues such as charcoal are added to resistant soil carbon.

On a global scale, grasslands occupy about 20% of the well vegetated land area, contributing about 23% to both annual carbon flux and total carbon storage. The surprisingly large share in terms of carbon storage is entirely due to the large amount of organic matter that is maintained in grassland soils, owing to a combination of large partitioning of dry matter to below-ground parts and to a relatively slow rate of decay of soil organic matter. When a forest is turned into land used for agriculture, the standing biomass is removed (often partly burned), and the disturbance of the soil will give rise to enhanced decomposition of soil organic matter and so to a strong efflux of CO_2. In arable land, the disturbance is repeated annually by ploughing and after a few decades the soil carbon content has declined to a much lower level than originally present in the virgin soil. In grassland, however, the situation is different. The soil is much less disturbed, the crop is perennial, and the remnants of leaves, stolons, roots, stubble and of cattle manure accumulate and give rise to a soil organic matter level as high as in the original forest soil. At present grasslands are extended far beyond their natural range. In the Holdridge diagram (Holdridge,1967; Monserud and Leemans, 1992) the term "cool temperate steppe" is used to indicate the climatic zone where grasslands naturally occur. This zone is a rather dry one, with annual potential evapotranspiration exceeding annual precipitation. These truly natural grasslands occur in the prairie zone of North America, the chernozem zone of the Ukraine and in the pampas of Argentina. Their combined area is about 900 Mha, containing a total amount of soil carbon of 120 Pg (Post et al. 1985) In the actual man-made situation, the most productive grasslands are found in the zone with a larger moisture supply, indicated by the term "moist temperate forests". These natural forests have long ago been replaced by agricultural land, and indeed also by pasture land. The area of these man-made grasslands is also about 900 Mha, but their soil carbon content is higher than that of natural grasslands, probably around 200 Pg.

8.5 The use of carbon isotopes as a tracer

Ammerlaan and de Visser (1993) demonstrate the usefulness of carbon isotopes in plant physiological research. On a global scale as well, time courses of carbon isotopes are utilized to yield important information. The largest global tracer "experiment" ever came from the hydrogen bomb experiments that peaked around 1962. Due to these experiments the concentration of ^{14}C in the atmosphere was approximately doubled. After the international ban in 1965 this peak gradually declined by dilution of ^{14}C in the ocean and biosphere. The rate of this decline offers a method to estimate the exchange rate. In early studies the exchange rate with the biosphere was ignored, and the estimated rate was totally ascribed to the ocean. This yielded exchange rates of the order of 100 Pg C per year. In fact, part of the exchange is with the biosphere, and only the remainder is with the ocean. Therefore the best method is to use a model that allows for both exchange rates, to impose the exchange rate of the biosphere (*NPP*) and then to find the exchange rate at the ocean surface by curve fitting. This method yields a lower rate of exchange (50 Pg per year) than the one normally assumed, but it describes very well the measured decline rate of ^{14}C in the atmosphere (Figure 8.5).

The second man-made global tracer experiment is the emission of fossil carbon. No ^{14}C remains in fossil fuel at all, and therefore the atmospheric ^{14}C content before 1960 gradually declined ("Suess effect"). Later the hydrogen bomb experiments completely swamped this effect, and made it impossible to follow it any further. However, the other carbon isotope, ^{13}C, was not disturbed by the nuclear experiments and remained available as a tracer. Naturally, about 1% of carbon is in the form of ^{13}C, but in several processes a slight discrimination occurs. The process of photosynthetic CO_2 assimilation (in C_3 plants at least) discriminates against the heavier ^{13}C, so that the ^{13}C concentration in plant biomass is about 25 per thousand lower than in the atmospheric source. This has been the case ever since photosynthesis started, and so the depletion is equally present in fossil carbon. Additional discrimination in methanogenesis has further depleted ^{13}C content in

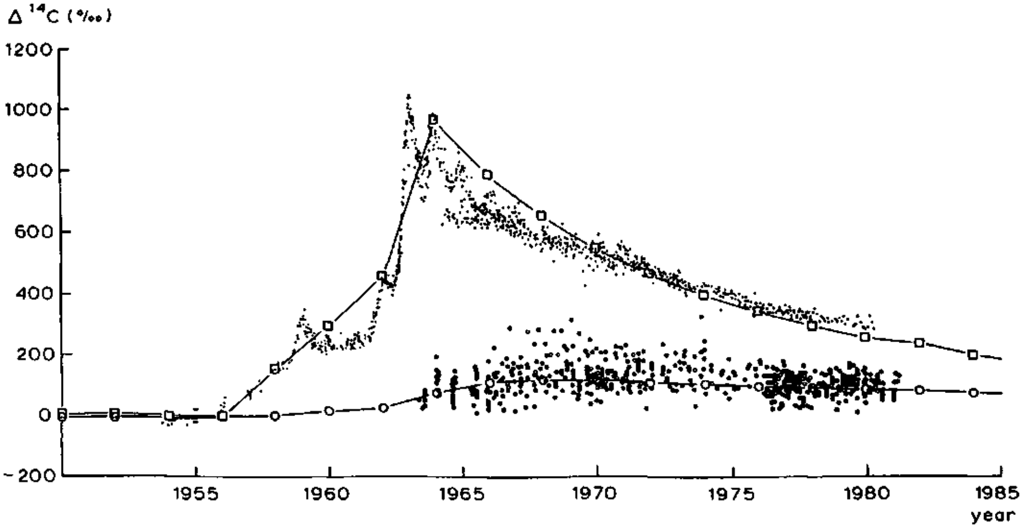

Figure 8.5 Simulated and observed time courses of $\Delta^{14}C$ in the atmosphere (squares) and in the sea surface water at low latitudes (circles), for the period around the nuclear tests. Data from Bolin (1986) in his Figure 3.6.

natural gas reserves, down to about -40 per thousand. The release of isotopically depleted CO_2 by fossil fuel burning is visible in various records of atmospheric CO_2 and also in tree rings. This decline serves as a validation of model runs for the global carbon cycle (Goudriaan,1989; Goudriaan, 1992).

8.6 The biosphere as a sink for carbon

The increase of atmospheric CO_2 itself induces an increase in net CO_2 assimilation and also in plant growth. Since industrialization, this effect by itself has stimulated biospheric uptake rate by about 1 Pg of C per year, which is at present equivalent to 20 % of the global emission rate of CO_2. As another comparison, this CO_2-induced absorption is just about equal to the fluxes released in large scale deforestation. This is a coincidental compensation, but it explains why a model with just the ocean, and without biosphere at all, still works reasonably well. Such a model will obviously fail to explain effects of deforestation or afforestation.
This role of the biosphere as a sink cannot be directly measured, but the circumstantial evidence is very strong, indicating a strong stimulation of plant growth by increased atmospheric CO_2, not only in agricultural crops but also in natural vegetation (Strain and Cure, 1985). According to a summary of Kimball (1983), there is a mean 40% increase of dry matter in C_3 crops upon doubling of CO_2, and of 15% for C_4 crops. This effect of CO_2 not only occurs in crop plants, but is a general phenomenon (Lemon 1984). The primary physiological effect of increased CO_2-concentration is a stimulation of the rate of CO_2 assimilation, and also the respiration rate might be reduced (Amthor 1991). The CO_2 enrichment effect is main-

tained when growth is limited by water (Gifford 1979), which can be explained by control of both water loss and CO_2 assimilation by stomatal resistance. Any increase in ambient CO_2 will then stimulate CO_2 uptake without raising water loss. Nutrient shortage, especially of phosphorus and of potassium, tends to impose a more absolute limitation to crop growth without leaving much room for stimulation by CO_2. Nitrogen, however,differs from other nutrients in that it permits a small positive CO_2 effect, even under rather severe nitrogen shortage (see also Arp and Berendse, 1993).

Arp (1991) showed that part of the conflicting evidence in literature on adaptation of plants during growth can be explained by differences in pot size used in the reported experiments, the disappearance of the CO_2 effect on growth being associated with small pot size. In the field, a primary CO_2 stimulus can lead to better exploration of the soil (Rosenberg 1981), so that nutrient uptake may go up even under nutrient limited circumstances. Indeed, in an experimental study during 4 years of continued exposure of a natural salt marsh vegetation to high CO_2, Arp et al.(1991) found no decline in increased photosynthesis and no decline in water use efficiency .

8.7 Deforestation and CO_2 fertilization

The CO_2-induced sink effect must be separated from the effect of land-use changes, because the latter is independent of atmospheric CO_2. The precise definition of emission due to deforestation is full of pitfalls: next to direct removal and burning of wood, it contains also a stimulated oxidation of soil carbon. This process takes many years to reach a new steady state, and during that period the soil is still releasing a flux of CO_2 larger than it used to do before. This continued flux increase was represented in the carbon cycle model by decreased longevity for humus after land is turned into arable land. Another factor included in the model was incomplete biomass burning, leading to partial charcoal formation (10 - 20% of the above ground biomass). The net effect of these factors is expressed in the total amount of simulated biospheric carbon. Comparison of total biospheric carbon for model runs with and without land use changes (deforestation in particular) resulted in a difference, due to deforestation, of 90 Pg C over the period 1780 - 1980 (Table 8.1, first column for $\beta = 0$). The correct order of magnitude of this number is confirmed by a comparison with the amount of biomass that was present on the total forest area lost during this period. For tropical forests almost 800 Mha was lost with a mean biomass of 8 kg C m^{-2} (64 Pg C) and for temperate forests 200 Mha with a mean biomass of 11 kg C m^{-2} (22 Pg C).

However, deforestation and CO_2 fertilization occur at the same time. Therefore the true effect of land use changes must be determined from model results *without* this CO_2 enrichment effect (left hand column in Table 8.1). As the next step, the CO_2 enrichment effect must be estimated *with* the land use changes going on (lower row in Table 8.1).

The sequence is important, as there appeared to be a strong interaction between the effects of deforestation and CO_2 enrichment. The positive CO_2 enrichment effect was larger when deforestation was included, and on the other hand the biomass removal by deforestation became smaller when CO_2 fertilization occurred.

Table 8.1 Simulated total amount of carbon in Pg C in the terrestrial biosphere for the year 1980. Without any land use changes and without any CO_2 effect ($\beta = 0$), the biosphere would have remained identical to that in the starting year 1780. The separate effects of these two factors and of their combination showed a strong interaction. The arrows indicate the correct sequence for determining the effects of land use changes and of CO_2 enrichment respectively (bold). Their combined effect gave a net loss of carbon of 39 Pg C.

	$\beta = 0$	$\beta = 0.5$	Enrichment effect
No land use changes	1894 Pg$^{(1780AC)}$	1926 Pg	32 Pg
	↓		
With land use changes	1804 Pg ⟶	1855 Pg $^{(1980AC)}$	**51** Pg
			↓
Land use effect	– **90** Pg	– 71 Pg	– **39** Pg

This interaction can be understood as follows: By deforestation the dynamics in the biosphere is enhanced, and the CO_2 enrichment effect is more effectively transferred into the slow compartments.

The other interaction is more straighforward: CO_2 fertilization will reduce the net effect of deforestation, simply by negative feedback. The baseline of deforestation emission was 90 Pg C. The CO_2 fertilization effect itself will recycle about 20% of this emission into the biosphere, which leaves about 71 Pg C as effective emission. This number is however not a good estimate for the size of the source itself, since the negative feedback is already included. The combined effect of CO_2 fertilization and deforestation is a simulated biospheric carbon loss of 39 Pg between 1780 and 1980 (diagonal transition in Table 8.1).

Summarizing, the total emission of 249 Pg C (159 fossil and 90 biospheric) was partitioned to the three major reservoirs as 88 Pg to the ocean, 51 Pg to the biosphere and 110 Pg remaining in the atmosphere. For the biosphere, the net result was a loss of 39 Pg of carbon, which was added to the release of 159 Pg of fossil carbon. The time course of total emission followed an approximately exponential increase at a relative growth rate of about 2.4% a^{-1}.

8.8 Redistribution of current fluxes

The almost exponential increase of fluxes is still going on. The rate of deforestation in the year 1980 was about 12 Mha per year, and with a loss or carbon (including soil carbon) of about 14 kg C m^{-2}, a flux of release of carbon due to deforestation can be expected of about 1.7 Pg C a^{-1} (including soil carbon losses). This figure is well within the range of a recent estimate of Houghton(1991).

There are, however, a number of processes that reduce the rate of emission from the biosphere as a whole. First, loss of soil carbon does not occur instantaneously but it is delayed in time. A dynamic simulation model takes such a delay into account, in contrast with statistical calculations that assume immediate release. To give an impression of the effect of this delay: assuming a time coefficient of 20 years for soil carbon and a relative growth rate of deforestation of 2% per year, the rate of release is reduced by a factor 1.5. Surely the soil carbon will eventually be released, but the model deals with the *current* rates. Secondly, not all standing biomass is immediately oxidized, part of it is even conserved in the form of charcoal, which has a much longer longevity than biomass. As a third factor, regrowth of forests occurs in particular in the temperate parts of the world (Brouwer et al. 1991). The total rate of regrowth is probably of the order of one third of the rate of tropical deforestation. In the model these processes together reduced the net rate of global carbon release due to land use changes to about 0.6 Pg C a^{-1}.

This net rate of release was counteracted by a current CO_2 fertilization flux of 1.1 Pg C a^{-1}, which was derived from model output using the same method as for the accumulated amounts, given in Table 8.1. This model result can be approximately understood as follows:

The annual rate of increase of atmospheric CO_2 is about 0.4% per year, leading to an assumed CO_2 fertilization effect of 0.2% per year for *NPP*. In the simple biosphere model explained in the beginning of this text, the resulting annual increase of equilibrium should then be 4 Pg a^{-1}, based on 2000 Pg present. The effect of the slowness of the different compartments reduces this rate to about 1.1 Pg a^{-1}.

The result for the terrestrial biosphere as a whole is *a net uptake rate of carbon of 0.5 Pg* a^{-1}. The rate of emission due to fossil fuel burning was about 5.2 Pg C a^{-1}. When this flux is added to the biospheric release rate of 0.6 Pg a^{-1} , we find a total emission rate of about 5.8 Pg C a^{-1} . The rate of absorption by the ocean was simulated to be 2.0 Pg C a^{-1} , and so the remaining rate of accumulation in the atmosphere was 2.7 Pg C a^{-1}. The remanent fraction based on *current* emission rates is now found to be 0.46, very close to the figure based on accumulated amounts over the past 200 years. This small difference emphasizes that the actual increase over time for the combined fossil/biosphere emission has been very close to an exponential one. Yet, the time patterns of biospheric emission and fossil fuel emission separately have not been identical. Around the turn of the century the biospheric emission was larger than the fossil fuel emission was, whereas nowadays the situation has reversed. Over the past 200 years together the biosphere has been a net source, but somewhere during the past decades it must have turned into a net sink. This switch is the result of the steadily increasing CO_2 fertilization effect.

The dual character of the biosphere in being both a source and a sink is undeniable. The biosphere may not be quite as strong a sink as the ocean is, but it is well capable of counteracting its own role as a source (Lugo & Brown, 1986).

8.9 Final remarks

There are different ways to calculate the remanent fraction in the atmosphere. The classical method is simply to take the ratio of atmosphere increment divided by fossil fuel emission, which yields a value of 0.69. This number is too high, since the biospheric emission is not included. But which contribution should we use? Based on *total* biospheric emission (159 + 90) we find a value of 0.44 , but based on *net* biospheric emission (159 + 39) we find a value of 0.55. When biospheric emission is taken for granted and only the ocean is considered as a sink interacting with the atmosphere, the value of the remanent fraction is 0.55. When the sink response of the biosphere is included, the remanent fraction is smaller and arrives at a value of 0.46.

Biospheric release fluxes of CO_2 that are caused by periodic fires in savannas e.g. should not be added to the base of the calculation. These fluxes do not constitute a permanent transfer of carbon from the biosphere to the atmosphere, but are part of the system itself in much the same way as decomposition and respiration are.

Climatic change *per se* was not discussed yet in this manuscript. Warming, if it occurs, will almost certainly have various effects. In some places enhanced decomposition of soil organic matter will prevail, such as is most likely the case in the tundra regions. Simultaneously, this enhanced decay in the soil compartments may be compensated by increased formation of above ground dry matter (Esser, 1987). In other places, extension of the duration of the climatic growing season will be more important and the net carbon storage will increase. Agricultural zones will shift (Parry,1990; Leemans and Solomon, 1993; Cramer and Solomon,1993).

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Frank Berendse worked as lecturer at the University of Utrecht within the Department of Ecology and Evolutionary Biology (1977-1987). Thereafter he coordinated the research group Vegetation Ecology and Nature Restoration within the DLO Centre for Agrobiological Research (CABO-DLO). From 1 January 1994 he will be Professor of Systems Ecology and Nature Management at the Wageningen Agricultural University.

C.A. van Diepen MSc

Kees van Diepen graduated at the Agricultural University Wageningen in Tropical Land and Water Engineering in 1975. From 1975-1987 he was engaged in regional land use planning projects in Thailand and Benin, land evaluation research at ISRIC and research on regionally distributed crop production potential of tropical countries at the Wageningen Agricultural University and the DLO Centre for Agrobiological Research (CABO-DLO). In 1988 he moved to the Soil Survey Institute, Land Use section, now Winand Staring Centre for Integrated Land, Soil and Water Research (SC-DLO), and became head of the section of Land Evaluation Methods in 1991. There he participated in the study on the assessment of crop production potential at the European scale, 'Grounds for Choices', undertaken by the Netherlands

Scientific Council for Government Policy. He is currently leading an EC project to develop an information system for regional crop yield forecasting across the EC. In the field of studies into the effects of climate change on crop production he participated in crop simulation studies when at the CABO-DLO in 1986 on wheat and rice in a climosequence from Wageningen, Migda (Israel), Hyderabad (India), and Los Baños (Philippines), and is currently involved in a study on the Rhine basin, focussing on effects of changes in climate and in land use on crop production and water use.

Dr. Paul Dijkstra

The author studied Plant Breeding at the Agricultural University of Wageningen. In 1980 and 1981 he worked at the Department of Plant Pathology of the Agricultural University on methods for screening for resistance against *Phytophthora cinnamomi* in *Cinchona ledgeriana*. In 1990 he finished his PhD at the Department of Plant Physiology at the State University of Groningen on the physiological background of differences in relative growth rate between two subspecies of *Plantago major*. This research was continued in 1990 and 1991 at the CPRO-DLO (DLO Centre for Plant Breeding and Reproduction Research) in Wageningen, where he studied the growth characteristics and water-relations of wild relatives of *Lycopersicon esculentum*. In 1991 he started to work at the present project. This included, in addition to the presented work, the development of an Open Top Chamber facility at the CABO-DLO.

Dr. Th.A. Dueck

Tom Dueck studied biology at the Free University, Amsterdam, majoring in plant ecology with plant physiology and phytopathology. He graduated in 1982, after which he began his doctorate at the Department of Plant Ecology and Ecotoxicology. His doctorate entailed the study of soil and air pollutant effects on plant population genetics and resulted in a dissertation entitled "Impact of heavy metals and air pollution on plants". Following his doctorate he became a member of the project group on air pollution at the DLO Research Institute for Plant Protection (IPO-DLO), where he worked on the effects of ammonia, sulphur dioxide and ozone on natural vegetations and forest trees. In 1993, together with the project group on air pollution, he joined CABO-DLO, where he studies the detoxification and effects of ammonia in combination with ozone effects on forest trees.

Dr. L.J. van der Eerden

Ludger van der Eerden studied Environmental Sciences at the Wageningen Agricultural University. Since 1978 he studied the effects of air pollution (in particular NH_3, HF, SO_2 and NO_2) on crops and natural vegetations at IPO-DLO. In 1992 he wrote his PhD thesis on the fertilizing effects of NH_3 and $(NH_4)_2SO_4$ on semi-natural vegetations. Since 1991 he is head of the project group on air pollution (which moved to CABO-DLO in April 1993). His special interest is ecotoxicology.

Dr. S.C. van de Geijn

Siebe van de Geijn graduated in physics at Utrecht State University in 1968 and obtained his PhD there in 1976. From 1968 till 1981 he studied methodological and physiological aspects of transport processes in plants at the Institute for Application of Atomic Energy in Agriculture in Wageningen. From 1981 till 1987 he was in charge of research in soil biology and rhizospere processes. In 1987 he was appointed head of the Department of Crop and Grassland Science at CABO-DLO. Since 1991 he holds here the position of head of the Department of Plant Physiology. Since 1989 he is involved in coordination and planning of climate change research in the Netherlands and in International programmes like IGBP-GCTE (Global Change and Terrestrial Ecosystems). He is Project coordinator of an International research project (CROPCHANGE: 10 partners in 6 EC countries) funded under the EC ENVIRONMENT Programme. He is task leader "Temperate Crops" in IGBP-GCTE Focus 3 and invited Lead Author (Wgr IID, Agriculture) for the 1995 Scientific Assessment Report of IPCC (Intergovernmental Panel on Climate Change). In the Dutch National Programme on Global Air Pollution and Climate Change (NOP-MLK) he is member of the Programme Committee and coordinator of the theme "Land Use and Terrestrial Ecosystems". He is also Programme leader of the DLO programme Climate Change, Agriculture and Nature (DLO-122 Klimaatverandering, Landbouw en Natuur).

Dr. A. Gorissen

Ton Gorissen graduated from the Wageningen Agricultural University in Phytopathology. Since 1987, he studied the effects of acid rain and ozone on microbial activity in the rhizosphere of Douglas-fir trees at the Research Institute Ital. This project resulted in a PhD thesis, which he defended in 1991 at the Free University of Amsterdam. Since 1990, he is responsible at the DLO Institute for Soil Fertility Research (IB-DLO) for research projects on effects of climate change and elevated atmospheric CO_2 levels on carbon dynamics in plant-soil systems.

Prof.dr. J. Goudriaan

Since 1970, Jan Goudriaan is staff member of the Department of Theoretical Production-Ecology (TPE) of the Wageningen Agricultural University and since 1992 as personal professor. His research fields comprise micrometeorology, crop physiology, CO_2 effects on plant growth and on climate, global carbon cycle, climate and agriculture. In 1992 he received the Akzo Award. He is also a member of the Scientific Steering Committee of the Core project GCTE of IGBP.

Dr. C. Grashoff

In 1984, Kees Grashoff received his MSc in Biology with a major in Ecophysiology and minors in Theoretical Production Ecology, Crop Ecology and Didactics in Biology. In July 1984, he received a position at CABO-DLO, from 1985 as member of the permanent staff, where his main task is to perform experimental and simulation research into the effects of environmental factors on productivity, yield stability and quality of cereals and leguminous plants. On 11 November 1992 he graduated at the Wageningen Agricultural University with his PhD thesis on the variability in yield of faba beans (*Vicia faba* L.).

J. Groenwold BSc

Ko Groenwold studied Land and Water Management for three years at the Wageningen Agricultural University. He continued his studies at the Utrecht State University, where he obtained his Bachelor Degree in Biology. In 1971 he got a position at the Centre for Plant Physiological Research, at present CABO-DLO. From 1973-1987 he was involved in research on effects of crop rotation, especially the effects of crop residues on root growth. He also studied the background of urine scorch in pastures. In the following years, he was involved in a project studying the relationship between root growth and activity, soil factors and crop growth. The experience gained with the experimental set-up formed a basis for the development of the Wageningen Rhizolab. At present he is managing this facility with special emphasis on methods for soil-root processes.

Dr. P.J. Kuikman

In 1985 Peter Kuikman graduated at the Utrecht State University in Systems Ecology and Microbial Ecology. He received his PhD at the Wageningen Agricultural University in Microbiology in 1990 with the thesis "Mineralization of nitrogen by protozoan activity in soil". Since 1989, he is responsible for research at the DLO Institute for Soil Fertility Research (IB-DLO) on the regulation of soil microbial activity by carbon and nitrogen availability in the rhizosphere and related mineralization of nitrogen and decomposition of rhizodeposition. He is involved in a research project on the quantification of carbon fluxes in grasslands as related to climate change and an elevated atmospheric CO_2 level.

Mrs. Dr. S. Nonhebel

Sanderine Nonhebel studied Plant Pathology at the Wageningen Agricultural University. In 1986 and 1987 she was employed by the Department of Physical Geography of the State University Groningen where she studied water use of forests in the Netherlands. From 1987 to 1993 she worked on her doctoral thesis at the Department of Theoretical Production Ecology (TPE) of the Wageningen Agricultural University. In May 1993 she received her degree with the PhD thesis: "The importance of weather data in crop growth simulation models and assessment of climatic change effects". Since June 1993 she works at TPE and studies the possibilities for growing so called "energy crops" in Europe.

Mrs. M. Pérez-Soba MSc

Marta Pérez-Soba was born November 26, 1961 in Madrid (Spain). She studied Agricultural Engineering at the Superior Politechnical School of Madrid, specializing in plant science. During the summer of 1985, she went to the Netherlands for a two-months practical training on the effects of air pollution on plants performed at IPO-DLO in Wageningen. She graduated in 1986, after which she worked for a private consultancy in Madrid on redistribution of farmland for half a year. In 1987, she was appointed for a grant by the National Institute of Agricultural Research of Spain (INIA), in order to do research for a PhD thesis in a foreign country. In 1988, she started her research on the effects of atmospheric ammonia on forest trees, in a collaborative project between the DLO Research Institute for Plant Protection (IPO-DLO), the State University of Groningen (RUG) and INIA. Her work focused on the response of nitrogen metabolism to gaseous ammonia in combination with sulphur dioxide, elevated carbon dioxide and ozone. In 1993, together with the project group on air pollution, she joined CABO-DLO, where she finishes her doctoral thesis.

Dr. A.H.C.M. Schapendonk

Ad Schapendonk studied Biology at the Agricultural University of Wageningen, with main subject 'Physical Aspects of Plant Physiology'. In 1980 he got his PhD at the Wageningen Agricultural University on "Electrical events associated with primary photosynthetic reactions in chloroplast membranes". In 1980 he started to work at the Centre for Agrobiological Research (CABO-DLO) on physiological aspects associated with climate control in protected cultivation. This project was a combination of plant physiology and technology. In 1985 he became head of the Department 'Grasses and Maize' at the CPRO-DLO (DLO Centre for Plant Breeding and Reproduction Research), with the assignment of introducing knowledge of crop physiology and simulation in the breeding programmes. From 1990 he is working at the CABO-DLO, assigned with the coordination of the photosynthesis research.

Dr. A.J.C. de Visser

Ries de Visser studied Biology at the University of Groningen, with majors in Biochemical Genetics and Plant Physiology. In 1984, he received his PhD for research with Hans Lambers, Rinie Hofstra and Piet Kuiper on photosynthesis and efficiency of root respiration in *Pisum sativum* as affected by nitrate reduction, ammonium assimilation or symbiotic N_2-fixation. He continued his studies on root activities in *Pisum sativum* as a NSERC post-doc with prof. Mary Spencer at the University of Alberta, Edmonton, Canada. His research focussed on the control of root ethylene production and root respiration, till 1986, when he obtained a position at the DLO Centre for Agrobiological Research (CABO-DLO) in Wageningen, where research was started on respiration in relation to maintenance processes in plants, and on the physiological mechanisms of genotypic variation in growth rate and nitrogen utilization in *Lolium perenne*.

J. Wolf MSc

Joost Wolf studied Soil Science at the Wageningen Agricultural University and specialised in Soil physics and chemistry. After short-term positions at the WAU Department of Soil Science and Plant nutrition (simulation study of phosphate transport) and the Environmental Service of the province Gelderland (research on soil pollution), he was a research scientist at the Centre for World Food Studies from 1982 to 1989. In this period he developed simulation models of nitrogen and phosphorus cycling and contributed to the development and application of the WOFOST model for regional analysis of the potential for crop production. Since 1990 he is employed by the WAU Department of Theoretical Production Ecology, where he studies the effects of climate change on arable production in the EC by means of simulation models.