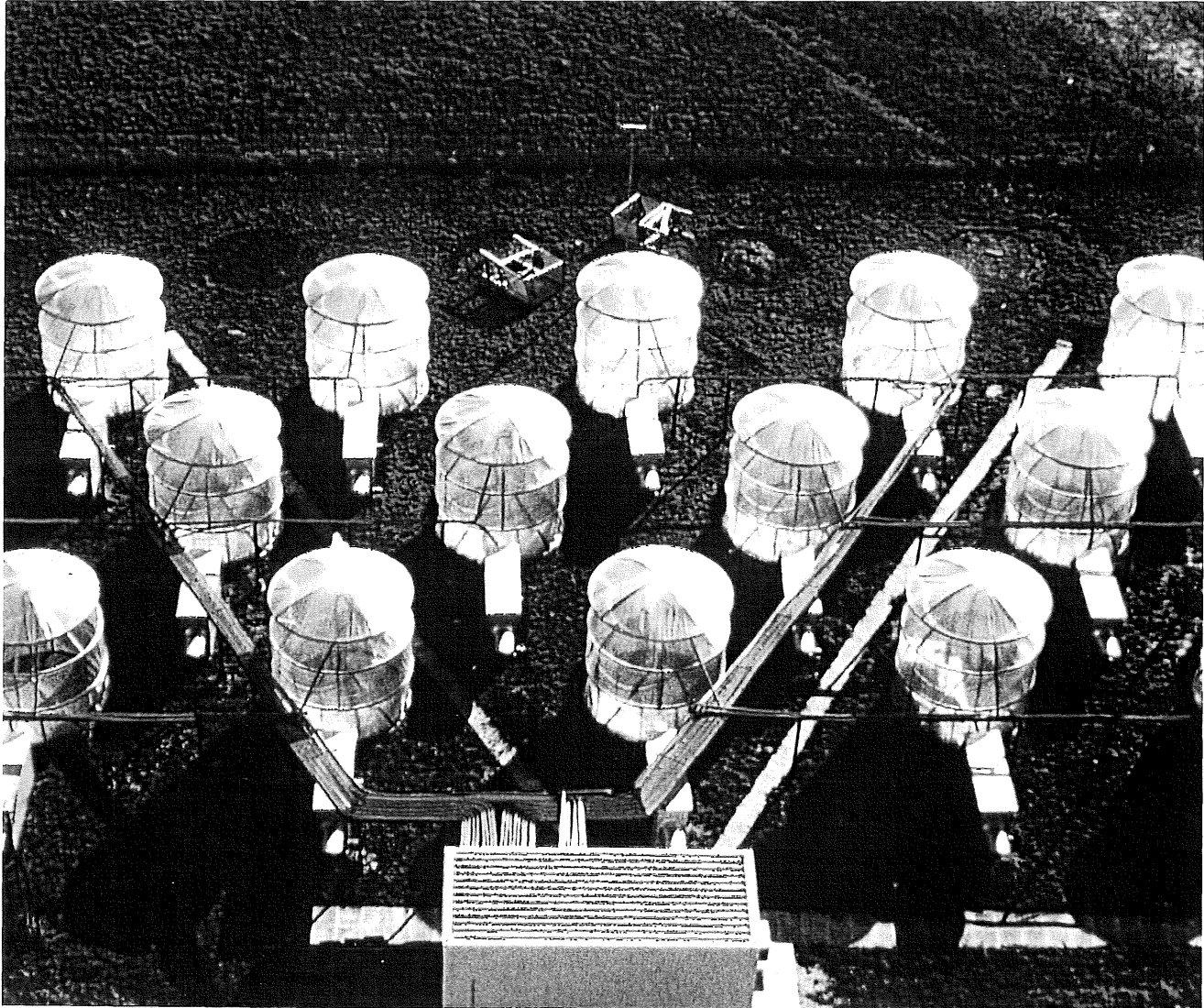


# MODEXCROP project

**Model evaluation of experimental variability  
to improve predictability of crop yields  
under climate change.**



**University of Essex, Department of Biological Sciences**



**The Royal Veterinary and Agricultural University, Dept. of Agricultural Sciences**



**Wageningen University and Research Center, Sub-dept. of Theoretical Production Ecology**



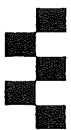
# **MODEXCROP project**

**Model evaluation of experimental variability to improve  
predictability of crop yields under climate change.**

## **Final report**

**Contract No. CT95-0142**

**August 1998**



**University of Essex, Department of Biological Sciences**



**The Royal Veterinary and Agricultural University, Dept. of Agricultural Sciences**



**Wageningen University and Research Center, Sub-dept. of Theoretical Production Ecology**

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Thanks are due to Marcel van Oijen (AB-DLO Research institute, Wageningen) for providing the photograph on the front cover. This photograph shows the open-top chamber experiments from the Justus-Liebig University, Giessen.



## Preface

The MODEXCROP project aimed at improving our understanding of the effects of climate change and increases in atmospheric CO<sub>2</sub> concentration on crop growth and food production. The research reported here was conducted over the period 1-2-1996 to 31-7-1998 under the European Commission's Environment Programme (Contract number: ENV4-CT95-0142). It was coordinated by the Sub-department of Theoretical Production Ecology of the Wageningen University and Research Center and was carried out by the following research institutions:

- Department of Biological Sciences, University of Essex, U.K.
- Department of Agricultural Sciences, Royal Veterinary and Agricultural University Copenhagen, Denmark.
- Sub-department of Theoretical Production Ecology, Wageningen University and Research Center, The Netherlands.

The following research institutions contributed significantly to the project by providing their experimental data sets:

- AB-DLO, DLO-Institute for Agrobiological and Soil Fertility, Wageningen, The Netherlands.
- Biochemistry and Physiology Department, IACR-Rothamsted Experimental Station, U.K.
- IATA-CNR, Institute of Agrometeorology and Environmental Analysis, National Research Council of Italy, Florence, Italy.
- INRA, Station d'Agonomie, Clermont Ferrand, France.
- Institut für Pflanzenökologie, Justus-Liebig University, Giessen, Germany.
- USDA-ARS, U.S. Water Conservation Laboratory, Phoenix, Arizona, USA.

This report presents first a summary of the main findings and conclusions from the research project. The aims of this project and the applied methods are described in the next section. This is followed by a short overview of the results. For detailed analyses crop growth models have been applied. This improves understanding of the causes for the observed variability in crop responses to climate change. The contribution of phenological and morphological development to the observed variability was mainly studied by the Copenhagen partner and the contribution of the physiological processes by the Essex partner. The overall analysis of collected data sets was done by the Wageningen partner. The summary report is followed by the reports from the Essex, Copenhagen and Wageningen partners, respectively.

The authors are grateful to European Commission's Environment Programme and in particular to Mr. Denis Peter.



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# **MODEXCROP project**

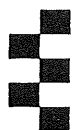
**Model evaluation of experimental variability to improve  
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## **Summary report**

**Research results**

**Contract No. CT95-0142**

**August 1998**



**University of Essex, Department of Biological Sciences**



**The Royal Veterinary and Agricultural University, Dept. of Agricultural Sciences**



**Wageningen University and Research Center, Sub-dept. of Theoretical Production Ecology**





## Summary of results

- ◆ Averaged over all collected wheat experiments, total biomass and grain yield increased per 100 ppmv of CO<sub>2</sub> enrichment by 7% of the yields under ambient atmospheric CO<sub>2</sub>. This corresponds well with the results found in other CO<sub>2</sub> response surveys.
- ◆ Averaged over all collected wheat experiments, the standard deviation of observed yield responses per 100 ppmv of CO<sub>2</sub> enrichment was 6% of the yields under ambient CO<sub>2</sub>. This indicates the strong variability in yield responses to CO<sub>2</sub> enrichment.
- ◆ The variability in yield responses to CO<sub>2</sub> enrichment was shown to be inherent to this type of experiments. Grouping of experimental results according to growing conditions and crop types did almost not reduce the standard deviation of the yield responses. In addition, yield response to CO<sub>2</sub> enrichment in the free-air CO<sub>2</sub> experiments in Arizona appeared to vary considerably within a week.
- ◆ Unexplained variation in leaf area dynamics is an important source of unexplained variation in the CO<sub>2</sub> effect on wheat growth and yield under different environmental conditions.
- ◆ Climate change experiments demand a high standardization in the experimental method (crop management, method for CO<sub>2</sub> enrichment, growth medium, etc.), as experimental differences may affect the yield responses to CO<sub>2</sub> enrichment. This is of importance when comparing and generalizing results from such experiments.
- ◆ A literature review showed that while the arguments for expecting positive temperature x CO<sub>2</sub> interactions on photosynthesis and plant growth are sound, the experimental evidence for it in long-term, acclimated plant growth is scant.
- ◆ When the temperature sensitivity of leaf photosynthesis (von Caemmerer and Farquhar model) was based on empirical relationships fitted to experimental data rather than making assumptions that the relationships fit an Arrhenius model, this resulted in a disappearance of the positive temperature x CO<sub>2</sub> interaction in photosynthesis.
- ◆ Increased temperatures reduced wheat growth duration and yields in the tunnel experiments at Reading. Increases of 1-2 °C during total growth period and of 2-3 °C during the reproductive phase were sufficient to negate the grain yield increase due to doubling of ambient atmospheric CO<sub>2</sub>.
- ◆ The temperature effect on yield was less variable and more certain than the CO<sub>2</sub> effect, as the standard deviation of the yield responses to 1 °C temperature rise was half (i.e. 3%) the standard deviation of yield responses to CO<sub>2</sub> enrichment and the mean temperature effect (yield decrease by 10%) was generally larger.

- ◆ Explanation of the variation in growth responses to CO<sub>2</sub> enrichment observed in open-top chamber experiments (from the ESPACE-Wheat project) was found to depend on the experimental performance. Wheat growth responses to CO<sub>2</sub> enrichment simulated with AFRCWHEAT2-O3 were in best agreement with observed responses for experiments performed closest to field conditions (plants grown in field with border plants). Simulations were poor and very poor for experiments with plants grown in the field without border plants and plants grown in pots without border plants, respectively.
- ◆ Understanding of the processes determining leaf area dynamics in response to climate change and crop management is limited and needs to be improved to allow more precise modelling of canopy development and crop growth under climate change.
- ◆ Crop variables were often more constant in the experiments than in the LINTULCC model simulations. This indicates that in situations without severe water or nutrient stress more simplified methods to simulate leaf area development and radiation interception, radiation use efficiency and grain growth may be applied to improve yield predictions.
- ◆ Crop responses are not easily predicted from short-term processes such as photosynthesis, because crop growth is affected by the complete time course of environmental conditions and key variables as temperature and CO<sub>2</sub> have different effects at different growth stages.

## **Aims and methods**

### **Background**

Since agricultural production is greatly affected by climate, any changes in climate which may result from increasing concentrations of so-called greenhouse gases in the atmosphere could have dramatic consequences for agricultural yield potential. Principal climate changes that are to be expected in Europe as based on the IPCC emission scenarios and the development of climate change scenarios for Europe (EU funded CLIVARA project), are a temperature rise of about 2 °C and an increase in atmospheric CO<sub>2</sub> concentration of about 200 ppmv over a period of 100 years.

A major problem in the correct estimation of future food supply under such changes in climate is the interpretation and extrapolation of the results from crop experiments under controlled and field conditions. Crop responses to changes in atmospheric CO<sub>2</sub> concentration and temperature greatly vary from experiment to experiment and from site to site. In the EU funded ESPACE-Wheat research project, for example, spring wheat experiments were carried out under ambient and elevated atmospheric CO<sub>2</sub> at a large number of sites over Europe. The wheat response to a doubling of atmospheric CO<sub>2</sub> varied from nil to more than 60% increase in grain yield, but this variation in CO<sub>2</sub> response could not be explained from the differences in climatic conditions between the different sites.

The aim of the project is an improved understanding of the causes for the variability in observed responses of wheat yields to changes in atmospheric CO<sub>2</sub> concentration and temperature. For this purpose, a large number of experimental data sets have been collected and analysed. Improved understanding from these analyses of the mechanisms that cause the variability in wheat responses may result in a more reliable prognosis of the impacts of climate change on future yields of wheat and other crops.

### **Approach**

The Essex partner has examined key aspects of the response of wheat to climate change, focussing in particular on the effects of temperature and CO<sub>2</sub> changes and their interaction. These effects were analysed using data from the Temperature Gradient Tunnel experiments at Reading. These winter wheat experiments were conducted during four consecutive years in tunnels with both ambient and almost doubled atmospheric CO<sub>2</sub> and with a temperature gradient superimposed on the ambient temperature variation. Subsequently, the results from a literature analysis of temperature x CO<sub>2</sub> interactions in crop growth were described. The reasons to expect a strong interaction between temperature and CO<sub>2</sub> in the growth of plants, such that growth stimulation by CO<sub>2</sub> enrichment is larger at higher temperatures, were given. This was followed by and compared with experimental data on this interaction in the literature. By developing a detailed leaf photosynthesis model, the importance of including different levels of detail in the simulation of crop physiology, particularly gas exchange and leaf photosynthesis, were examined. One of the key questions analysed was the temperature x CO<sub>2</sub> interaction in net photosynthesis.

The Copenhagen partner has analysed the hitherto unexplained variability in yield responses to CO<sub>2</sub> enrichment within the ESPACE-Wheat project. In ESPACE-Wheat open-top chamber (OTC) experiments with spring wheat were performed at nine sites throughout Western Europe. Reasons for unexplained variations in final biomass and grain yield and in the yield responses to CO<sub>2</sub> enrichment were identified by analysing the predictability of intermediate crop variables and underlying mechanisms. This analysis was performed using the wheat growth simulation model AFRCWHEAT2-O3. Simulated crop variables from this and other wheat models that had a major impact on the unexplained variation in biomass and grain yield, were compared. A relevant part of this model comparison was performed using results from a drought experiment with wheat in New Zealand. The adaptation of existing modules in AFRCWHEAT2-O3 to improve its performance is discussed.

The Wageningen partner has collected a large number of data sets from wheat experiments under CO<sub>2</sub> enrichment or temperature change. These data sets have been analysed to unravel the mechanisms behind the variability in the observed responses. Subsequently, the data sets have been analysed with the wheat growth simulation model LINTULCC, combining knowledge about crop characteristics and their interactions with the environment. This resulted in an improved explanation of the observed variability on the basis of crop characteristics and climatic conditions. For the large data sets from the free-air CO<sub>2</sub> enrichment experiments in Arizona these analyses have been carried out in more detail.

## Results

### Essex

Analysis of results from winter wheat crop experiments in Temperature Gradient Tunnels highlighted the variation in crop responses from year to year, and drew attention to the differences in responses shown by different varieties. Contrary to assumptions often made in the literature, increased CO<sub>2</sub> even affected canopy development and growth at low temperatures over winter. Both biomass and grain yield increased with doubling of ambient atmospheric CO<sub>2</sub>. This CO<sub>2</sub> effect, and in particular on grain yield, varied greatly between years and with temperature (range of 7 to 168% for grain yield). Both positive and negative interactions of temperature and CO<sub>2</sub> effects on yields occurred. When different cultivars were compared, they all showed substantial increases in biomass and grain yield with increased CO<sub>2</sub>. However, the interactions between temperature and CO<sub>2</sub> were different with two cultivars showing no difference in CO<sub>2</sub> response across the 2-3 °C range of mean seasonal temperature and the other two showing reduced CO<sub>2</sub> response at higher temperatures. Increased CO<sub>2</sub> had no effect on crop development. However, small changes in temperature had substantial effects on crop development, which were broadly in agreement with the simulated changes in crop development from the AFRCWHEAT model. Increased temperatures reduced growth duration and yields, and increases of 1-2 °C during total growth period and of 2-3 °C during the reproductive phase were sufficient to negate the grain yield increase due to doubling of ambient CO<sub>2</sub>. In addition, high temperature episodes during anthesis resulted in a marked decrease in harvest index and thus in grain yield.

A review of the literature showed that while the arguments for expecting positive temperature x CO<sub>2</sub> interactions on photosynthesis and crop growth are sound, the experimental evidence for it in long-term, acclimated plants is scant. Hence, it was concluded that CO<sub>2</sub> enrichment does not have a proportionally larger effect on yields at warmer temperatures. This shows that crop responses are not easily predicted from short-term processes such as photosynthesis, mainly because crop growth and development are affected by the complete time course of environmental conditions during growth and key variables as temperature and CO<sub>2</sub> have different effects at different growth stages.

A leaf photosynthesis model was used for examining the sensitivity of its predictions to the applied level of detail in physiology, particularly gas exchange. The standard biochemical model of von Caemmerer and Farquhar was used as starting point and a number of modifications were applied. When the temperature sensitivity of leaf photosynthesis was based on empirical relationships fit to the best available experimental data rather than making assumptions that the relationships fit an Arrhenius model, this resulted in a substantial difference in temperature sensitivity of photosynthesis and in a disappearance of its temperature x CO<sub>2</sub> interaction. This is potentially important as much of the arguments underlying the strongly positive temperature x CO<sub>2</sub> interaction in photosynthesis rely upon the widely used Arrhenius-model derived coefficients. Other modifications in the leaf photosynthesis model were (1) more detail on pathway for gas diffusion and the resistance analogue used, (2) a different stomatal model, and (3) a more complete leaf temperature feedback. This modified leaf photosynthesis model is to be validated with experimental data and will be used as basis for a crop growth model. In parallel with this detailed leaf photosynthesis model, a wheat growth version of the WIMOVAC model was developed, by

adding crop growth and development sub-models to the established leaf and canopy gas exchange model.

## **Copenhagen**

Unexplained variations in final biomass and grain yield and in the effect of CO<sub>2</sub> enrichment on yields were mainly caused by poor simulation with AFRCWHEAT2-O3 of leaf area dynamics (leaf area index and leaf area duration). Variation of LAI at anthesis was further analysed. AFRCWHEAT2-O3 did not simulate satisfactory the observed effects of plant density on leaf size and of CO<sub>2</sub> enrichment on leaf size and tiller number. These differences were identified as the main reasons for the poor simulation of LAI at anthesis. There are considerable differences among wheat models in their methods for simulating canopy development in response to changes in weather, CO<sub>2</sub> concentration and water supply. However, these other model approaches did not show improvement in the simulation of LAI.

Differences in the experimental method were found to have also contributed to the unexplained variation in the CO<sub>2</sub> effect on biomass production. The simulations of AFRCWHEAT2-O3 were in best agreement with observed results from the open-top chamber experiments (in ESPACE-Wheat project) which were performed closest to field conditions (plants grown in the field with border plants), and showed a smaller and much smaller agreement with results from experiments with plants grown in the field without border plants and plants grown in pots without border plants, respectively. For these last two groups of experiments the differences between simulated and observed effects of elevated CO<sub>2</sub> on total biomass at anthesis increased with a decrease in plant density and with temperature rise, whereas such relationships were not found for the experiments performed closest to field conditions. Apparently, the effect of CO<sub>2</sub> enrichment on the assimilation rate of plants grown in pots, small chambers or chambers without border plants was affected by temperature and plant density in a way which was different from that considered in the model. As in AFRCWHEAT2-O3 wheat growth is modelled for field conditions, the effects of temperature or radiation on growth and development as caused by missing border plants were not considered in the simulation. This shows that differences in method and management of open-top chamber experiments can affect the yield responses to CO<sub>2</sub> enrichment. This is an important consideration when comparing and generalizing results from such experiments.

## **Wageningen**

Averaged over all collected wheat experiments, total biomass and grain yield increased per 100 ppmv CO<sub>2</sub> enrichment by 7% of the yields under ambient CO<sub>2</sub> and the harvest index did not change. These results correspond well with the mean values found in other CO<sub>2</sub> response surveys. The standard deviation (SD) of the yield responses was 6% of the yields under ambient CO<sub>2</sub>. This indicates the strong variability in yield responses to CO<sub>2</sub> enrichment. For example in the free-air CO<sub>2</sub> enrichment (FACE) experiments in Arizona, the yield variability was so high that CO<sub>2</sub> enrichment did not result in a significant yield response. When experimental results were grouped according to growing conditions (pot or field; optimal or limited) or crop types (spring or winter wheat), SD of observed yield responses to CO<sub>2</sub> enrichment did almost not decrease. Apparently, variation in growing conditions and crop type was not the main cause for the high SD values. When results from the final harvest and a

one week earlier harvest in the FACE experiments were compared, total biomass and grain yield considerably changed from the earlier to the final harvest and often in different directions under ambient and elevated CO<sub>2</sub>. This resulted in different conclusions on the yield response to CO<sub>2</sub> enrichment from both harvests. This type of experimental variability (and also the high SD values mentioned above) was caused by the spatial variability in growing conditions and the uncertainty in yield measurements.

Simulation of the experimental data sets with the LINTULCC model showed that the relationship between the observed increases in total above-ground biomass due to CO<sub>2</sub> enrichment and the simulated increases was poor. This was mainly caused by the poor relationship between observed and simulated cumulative radiation interception (i.e. leaf area dynamics). In LINTULCC an increase in assimilate production by CO<sub>2</sub> enrichment generally resulted in a larger leaf area and thus more radiation interception, whereas in the experiments this increase in radiation interception almost did not occur. The relationship between simulated and observed changes in harvest index and thus grain yield was rather poor. It is not clear if this was mainly caused by experimental variability or that the relationship can be improved by replacing the actual (source-driven) model method for calculating grain production by a sink-driven (i.e. determined by growth of grains) method. In the FACE experiments for example, biomass production stopped before maturity with a considerable amount of green leaves left and the ratio between observed shoot biomass under elevated and ambient CO<sub>2</sub> showed a strong decrease near maturity. Both effects probably point to sink-limitation.

Averaged over all collected wheat experiments, total biomass and grain yield decreased by 8% and 11%, respectively per 1 °C temperature rise due to the shorter growth period. These yield decreases became smaller when the ambient atmospheric CO<sub>2</sub> concentration was doubled. The temperature effect is less variable and more certain than the CO<sub>2</sub> effect, as SD of yield responses to 1 °C temperature rise was half (i.e. 3%) the SD for yield responses to CO<sub>2</sub> enrichment and the mean temperature effect was generally larger. The relationship between simulated and observed decreases in total biomass by temperature rise was moderately good and was mainly determined by the good relationship between simulated and observed decreases in radiation interception during the shorter growth period. The relationship between simulated and observed changes in harvest index with temperature rise was nil, as the simulated changes were much larger than the observed changes (i.e. almost nil). This resulted in a poor relationship between simulated and observed changes in grain yield with temperature rise.

Comparison of experimental results with simulated results from LINTULCC showed that their correspondence might be improved in two opposite ways. The description of the morphological development (e.g. leaf area) of the crop and the limiting effects of available sinks (i.e. grains) on crop growth may be described in more detail. However, in many situations crop variables as observed in the experiments were more constant than simulated with LINTULCC. In that situation, a model approach may be applied which uses more simplified methods to simulate leaf area development and radiation interception, radiation use efficiency and grain yield. This only holds in situations without severe water or nutrient stress.

## **Final conclusions and recommendations**

### **Scientific conclusion important to agricultural policy**

The mean of all analyzed experimental results was in agreement with literature data: 7% increase in wheat yield for 100 ppmv increase in atmospheric CO<sub>2</sub>, and 10% yield reduction for 1 °C temperature rise. Increased temperatures reduced growth duration and yields, and increases of 1-2 °C during total growth period and of 2-3 °C during the reproductive phase were sufficient to negate the grain yield increase due to doubling of ambient CO<sub>2</sub>. In addition, high temperature episodes during anthesis resulted in a marked decrease in harvest index and thus in grain yield.

There was, however, a large variability in yield responses to CO<sub>2</sub> enrichment from experiment to experiment. There was no evidence for a temperature x CO<sub>2</sub> interaction, neither for any other interaction that could explain this large variability. It is remarkable that the experimental variability was much larger in CO<sub>2</sub> experiments than in temperature experiments. The cause of this phenomenon is not known.

### **Scientific conclusion important to science policy**

Crop growth simulation studies predicted a much more stable CO<sub>2</sub> effect than was found in the experiments. Lack of understanding of leaf area dynamics was a major source of disagreement between model results and experimental results. This was true for all present models that were investigated, such as AFRCWHEAT, SUCROS, LINTULCC, and CERES-Wheat. It was shown, that the agreement was best when the experimental situation approximated a closed canopy as normally found in the field. This requirement is rarely fulfilled in the experimental set-up for climatic change studies, such as OTC's or TGT's.

Future model development should proceed simultaneously along two opposite directions: one towards greater detail, especially in terms of morphology and leaf area dynamics, and the other one towards greater aggregation and simplification. An argument in favour of greater detail is the importance of the morphogenetic processes, whereas an argument in favour of less detail is the observed larger stability of some crop characteristics in the field than in the models. This phenomenon indicates unknown stabilizing feedback processes. While this stability could be well exploited for prognostic purposes, its cause is not known, and it is therefore not certain that it will stand up under conditions of climatic change. Therefore more detailed models should be simultaneously developed.

### **Recommendation important to design of climate-crop experiments**

The effect of CO<sub>2</sub> enrichment on the assimilation rate of plants grown in pots, small chambers or chambers without border plants was affected by temperature and plant density in a different way from that in a closed canopy as normally found in field conditions. This shows that variation in method and management of open-top chamber experiments may affect the observed yield responses to CO<sub>2</sub> enrichment. Hence, climatic change experiments should be designed in such a way that results can be compared and generalized. This means



that border effects should be minimized, and that management and growing conditions should be standardized.

### **Conclusion important to plant breeders**

There was some difference in the temperature x CO<sub>2</sub> interactions among different wheat varieties. Promising new varieties should be screened with respect to their future performance in a higher CO<sub>2</sub> environment.



# **MODEXCROP Project**

**Model evaluation of experimental variability to improve predictability of  
crop yields under climate change.**

**Report No. 1 from Department of Biological Sciences, University of Essex  
(United Kingdom)**

***Dr James I.L. Morison***

**August 1998**



**University of Essex**

**Department of Biological Sciences**

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## Summary

The work at Essex during MODEXCROP has examined key aspects of the response of wheat to climate change, focussing in particular on the effects of temperature and CO<sub>2</sub> changes, and their interaction.

Analysis of existing winter wheat crop response data from experiments in Temperature Gradient Tunnels highlighted the variation from year to year in effects, and drew attention to the differences in responses shown by different varieties. Contrary to assumptions often made in the literature, there were still effects of increased CO<sub>2</sub> on canopy development and growth, even at low temperatures over winter. There were only small effects of increased CO<sub>2</sub> on ontogenetic development, and these can probably be ignored in crop growth models. Both biomass and seed yield increased with doubling of CO<sub>2</sub>. Small changes in temperature had substantial effects on crop development, which were broadly in agreement with the AFRCWheat development sub-model. Increased temperatures generally reduced yields, and increases of 2-3°C during the reproductive phase were sufficient to negate the increase due to increased CO<sub>2</sub>. Generally, increased temperature reduced the absolute effect of increased CO<sub>2</sub>, contrary to what is usually expected.

A review of the literature indicated that while the argument for expecting positive  $T \times CO_2$  interactions are sound, the experimental evidence for it in long-term, acclimated plants is scant, so that the biomass enhancement in cooler conditions can be as large as that in warmer conditions. However, there are few extensive and strictly comparable comparisons available, particularly for cool temperature crops. The flexibility and adaptability in plant growth response, and the importance of the pattern of environmental conditions throughout the growing season were emphasised. There is as yet no coherent quantitative framework for understanding the controls on growth, and it is clear that it is the outcome of close linkage between photosynthate sources and growing sinks.

Modelling work examined the sensitivity of predictions to detail of physiology, particularly gas exchange. A key question highlighted was whether the use of the Arrhenius model for the RuBisCO coefficients is appropriate, as these necessarily result in strong  $T \times CO_2$  interactions in net photosynthesis. It is also necessary to include in crop models a realistic representation of stomatal responses to environment and water relations, and these may be important in determining leaf area which is not well represented. The fixed, empirical way in which most models partition biomass during growth is a major weakness. It is clear from experiments that wheat in particular is very flexible with different components of yield able to respond and "compensate" for effects of the environment throughout growth. This flexibility underlies much of the variability in observed responses of growth to CO<sub>2</sub> and temperature.

## 1.1 Introduction

Decisions on setting targets for reductions of greenhouse gas (GHG) emissions are driven by the balance between the direct costs of reduction and the benefits gained, in which both actual environmental damage, and the risk of damage must be considered. A key potential risk of altered atmospheric composition and consequent climate change is alteration of agricultural production. Given any scenario for GHG concentrations and consequent climate change the critical questions are for any particular area whether there will be changes in (a) the type (nature and quality of products), (b) the productivity (yields, both per area and in total), and (c) the reliability (variation from year to year) of production.

Prediction of such impacts of climate change on crop productivity require the integration of experiments and modelling. Experiments are essential to quantify sensitivity of crop growth to the key global environmental change (GEC) variables of temperature, carbon dioxide concentration [ $\text{CO}_2$ ] and water supply and to examine physiological processes and responses. Models are essential to incorporate understanding of crop processes derived from the experimental work and to extrapolate from the observed sensitivities in the necessarily limited number of experiments to the variety of conditions and scenarios possible. Models aid in interpretation and analysis of experiments, and experiments permit testing of models. There are now sufficient numbers of experiments on several major crops to expect that a synthesis should be possible, for example in rice (Baker et al., 1996), wheat (Kimball et al., 1995; Batts et al., 1997), soybean (Miller et al., 1998). However, there is a conundrum inherent in this approach to climate impact studies. Carrying out more realistic experiments involves moving to conditions more like the field, and away from controlled (and therefore well-defined and repeatable) conditions. By definition, field experiments are subject to year-to-year variations in conditions, particular in their day-to-day combination at particular stages during the crop life-cycle. Yield is the result of the integration by the crop of the responses of cells, organs, single plants, and the whole plant-soil-atmosphere system, to environmental conditions throughout the season. In addition, in the real world the final yield is also the integrated result of the influence of external variables such as management, pests and diseases. Clearly there is a limitless range of possibilities of weather combinations, and it is obvious that these different combinations result in differences in yield responses to changes in the key GEC variables of [ $\text{CO}_2$ ], temperature and water (e.g. Grashoff et al., 1995). This is evident in the range of responses of crops to modified temperature and  $\text{CO}_2$  seen in recent experiments using open-top chambers, temperature gradient tunnels (TGT) and other specialised enclosures (e.g. the Wageningen Rhizolab) and free air  $\text{CO}_2$  enrichment techniques (FACE).

Therefore, the overall objective of MODEXCROP was to try to understand the causes of this variation in crop responses, using crop growth models to assist in the analysis of the experimental results. The project concentrated on wheat, as there are established models and considerable information for wheat, reflecting its position globally and regionally as the most important food crop. However, using models to analyse experimental data presupposes that the models incorporate sufficient physiological detail to capture the interactions between crops and environmental conditions adequately. Over a century ago Lawes and Gilbert (1880) wrote "as yet the connection between meteorological phenomena and the progress of vegetation is not so clearly comprehended as to enable us to estimate with any accuracy the

yield of a crop by studying the statistics of the weather during the period of its growth". Clearly, our understanding has made massive advances since that time, but there is still doubt over whether we can adequately predict crop growth from weather information. A recent study found poor agreement between predictions from three major crop models and observed crop yields on some 150 experimental trials across the UK (Landau et al., 1998). The aims of the University of Essex component were (1) to analyse the 4 year data set from the TGT experiment at Reading to characterise and understand the variability in response to temperature and CO<sub>2</sub> (2) to review the literature for information on interactions between CO<sub>2</sub> and temperature and between CO<sub>2</sub> and other key variables (3) to study using physiologically detailed models of gas exchange, whether such detail is necessary and if inclusion alters the predictions in the standard crop growth models. The work concentrated on temperature and CO<sub>2</sub> interactions ("T x CO<sub>2</sub>") on crop growth because (a) these are the two most firm consequences of GEC (b) there are sound physiological reasons for interactions between these, as often cited in the literature (see Section 1.3.2 below) and (c) temperature is a key environmental factor determining wheat productivity in Europe, particularly in northern Europe.

## **1.2 Materials and methods**

### **1.2.1 Analysis of TGT experiments at Reading**

Data were available from four experiments in four consecutive seasons from 1991/92 to 1994/95 with winter wheat (*Triticum aestivum* L.) conducted at Reading, UK, in the TGT facility. The primary objective of these experiments (performed with previous UK research council funding) was to examine interactions between changes in temperature and [CO<sub>2</sub>]. The cultivar comparisons were based on different development rates, and different tillering propensities. Crops were grown in the field soil, at typical crop densities and fertiliser supply. The TGTs superimpose a temperature gradient on the ambient temperature variation at normal atmospheric (*c.* 370) or an increased [CO<sub>2</sub>] (*c.* 700  $\mu\text{mol CO}_2 \text{ mol}^{-1}$  air), producing many environments from one sowing date in each season at one location. In all four years one cv. (Hereward) was grown, in 1993/4 this was compared with 3 other cvs, and in 1994/5 it was compared with an early cv. Soissons. Mean seasonal temperatures varied by up to 4°C along the temperature gradient. The analysis during MODEXCROP has been reported in detail in 3 journal papers (Batts et al., 1997, 1998; Morison et al., 1998; see Appendix), but a brief summary is given in the Results section.

### **1.2.2 Review of literature for T x CO<sub>2</sub> interactions in crop growth**

The results from the experimental analysis above strongly suggested that understanding T x CO<sub>2</sub> interactions on wheat growth was important in understanding variation in crop responses, and it was essential to review the wider evidence available. Wheat is cultivated across the globe (from the Arctic Circle to the equator, e.g. Gooding and Davies, 1997) in an extremely wide range of conditions. In addition, there is a wide range of conditions within each growing season for the individual crops, particularly for the autumn sown crops grown in much of Europe. Temperatures during the over-winter period are low, (often below freezing), yet summer conditions during grain filling and maturation are typically warm or even hot. There are sound reasons to suggest that there should be a strong interaction between temperature and CO<sub>2</sub> in the growth of plants, such that growth stimulation by an increase in CO<sub>2</sub> will be larger at warm temperatures, and least (if not zero or even negative)

at low temperatures. The literature on these different aspects was reviewed, concentrating on recent papers, and trying to draw out areas where physiological understanding had advanced.

### **1.2.3 Physiological modelling - rationale**

It is important that models used in the evaluation of the observed variability in crop responses should be based on sound descriptions of the key physiological processes in crop growth and development, (i.e. models should “mechanistically sound”). Clearly, there are many areas of the models which could be examined and refined, but in view of the above analyses of data and the literature we concentrated on examining plant response to elevated CO<sub>2</sub> concentrations and temperature. In particular we sought to investigate potential weaknesses in current physiologically based models of photosynthesis and to develop and test improved algorithms.

We developed both a new physiological model to examine the consequences of different leaf gas exchange assumptions, and extended the WIMOVAC model to simulate wheat growth. WIMOVAC (Windows Intuitive Model of Vegetation response to Atmospheric and Climate Change) has been developed at Essex previously under a number of research projects to be a general physiological model of plant photosynthetic response to environment. This is a modular modelling system designed to facilitate the modelling of various aspects of plant photosynthesis with particular emphasis on the effects of global climate change. WIMOVAC allows the control of the simulation processes for photosynthesis through a standardized Windows user interface. WIMOVAC has been used to simulate grassland production, and investigate O<sub>3</sub> and CO<sub>2</sub> interactions in photosynthesis, and to model isoprene emissions, among other aspects.

## **1.3 Results**

### **1.3.1 Analysis of TGT experiments at Reading**

#### **1.3.1.1 Crop development**

While there was no effect of increased [CO<sub>2</sub>] on crop duration, nor on the rate of reproductive development, there were very large effects of temperature, which were the same across all years for cv. Hereward (Figure 1). A 2°C warming, on the 4-year ambient mean temperature (10°C), reduced crop duration by 42 days (from 254), and reduced the reproductive phase by 16 days (from 130). This has major implications for crop yields, as any reductions in duration, reduce time available for solar energy interception, and hence yield.

There were differences between cvs. in the temperature sensitivity of the rate of development, particularly when individual crop stages were analysed (Figure 2a and b). For example, in the earlier phase when the spike is developing (double ridges to terminal



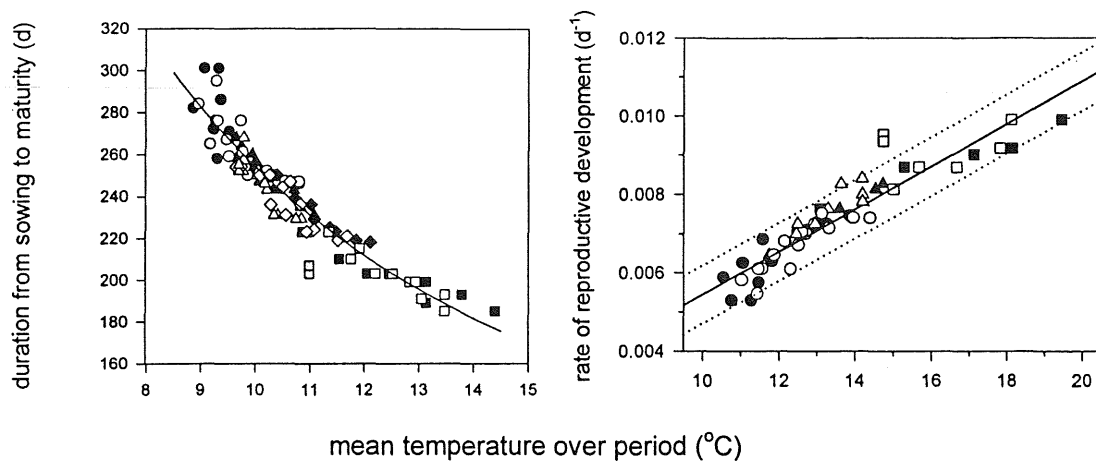


Figure 1 Relations between (*left*) crop duration from sowing to maturity, and (*right*) the rate of reproductive development and mean temperature during each phase for winter wheat crops cv. Hereward grown at increased (solid symbols) or normal (open symbols)  $[CO_2]$  during 1991/92 ( $\square$ ), 1992/93 ( $\Delta$ ), 1993/94 ( $\circ$ ), and 1994/95 ( $\diamond$ ). Results for crops grown in field plots in ambient conditions outside the tunnels are shown for comparison (shaded symbols).

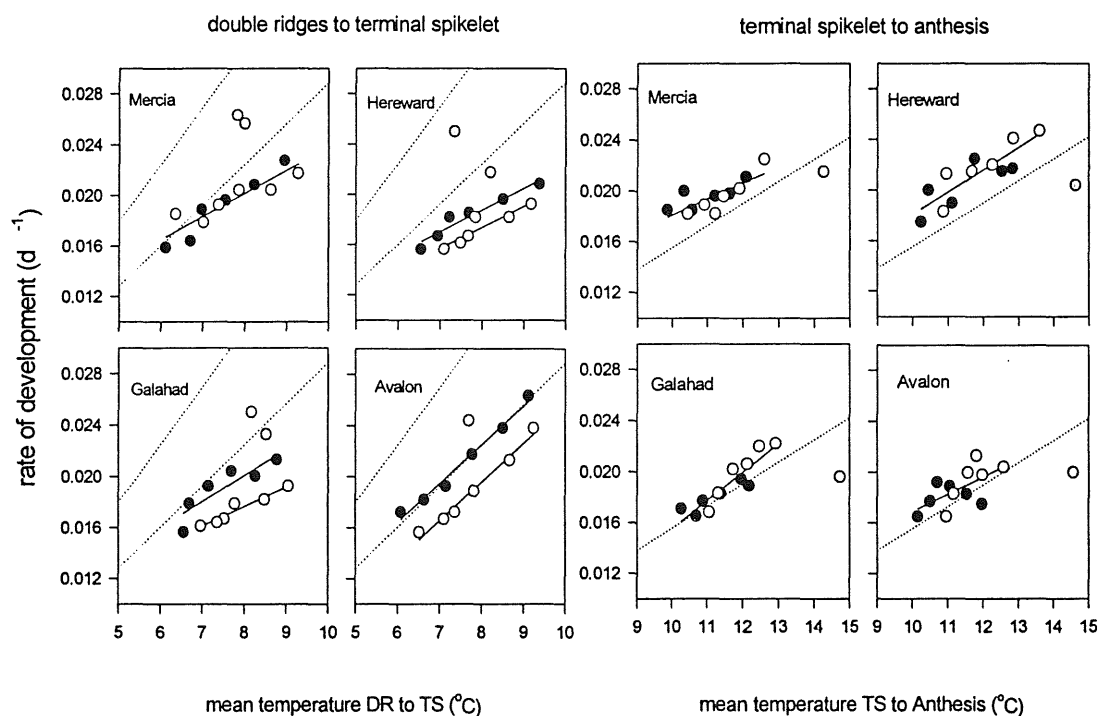


Figure 2 Relations for 4 wheat cvs. between developmental rate and mean temperature (a, left set of 4) during double ridges to terminal spikelet and (b, right set of 4) terminal spikelet to anthesis stage. Plants grown at increased (solid symbols) or normal (open symbols)  $[CO_2]$  during 1993/94. Results for crops grown in field plots in ambient conditions outside the tunnels are shown for comparison (shaded symbols).

spikelet), Mercia had the fastest rate of development, but least sensitivity to temperature, whereas Avalon had high sensitivity (Fig. 2a). Increased CO<sub>2</sub> increased the rate of development slightly during DR to TS in 3 of the cvs, but in the later TS to anthesis stage (Fig. 2b) there was no CO<sub>2</sub> effect in any cv. This difference between cultivars may be related to the different shapes of their apical meristems (Jitla et al., 1997). In both Figs 1 and 2, it is apparent that plants outside the TGTs do not fit the development patterns of those inside. This is partly due to the different relationship between air and plant temperature inside and outside the tunnel, but also partly because the outside plants were cooler earlier on, so were progressing through the later stages in a longer daylength regime.

Comparisons of the AFRC Wheat development model with the data for cv. Avalon from these experiments showed quite good agreement in predicting the shape of responses. However, predictions of duration of key phases (emergence to DR and DR to TS) were underestimates by 5-15 days, when using the observed daily maximum and minimum temperature data. When half hourly measured temperature data was used, the agreement between observed duration from sowing to maturity and predicted was much closer (Fig. 3), except at the coolest temperatures. This difference is caused by the assumption of sinusoidal temperature pattern in the model, while that observed in the tunnels had a much more pronounced peak.

The difference between using daily or half-hourly temperatures to drive the model emphasises that the temperature time course differs between experimental designs (e.g. TGT & OTC) and the effective temperature is unlikely to be properly estimated by models assuming typical field time courses. It also emphasises that models assume, or have implicit in them, a certain degree of coupling between the driving weather conditions (e.g. screen air temperature) and those the plant responds to, which may be affected by the experimental conditions.

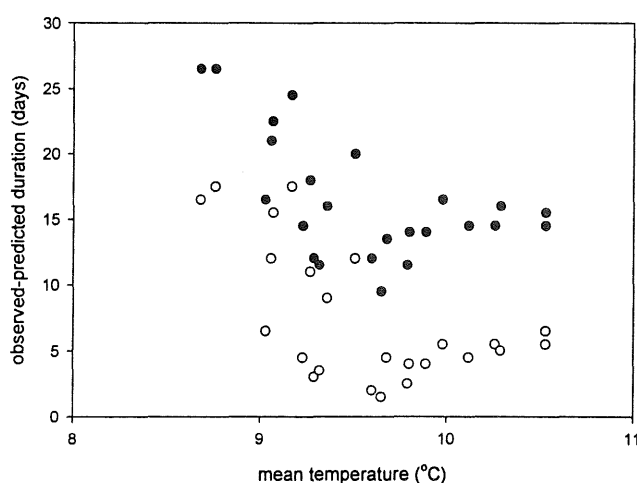


Figure 3 Difference between simulated (using AFRCWheat) and observed durations from sowing to harvest maturity for wheat cv. Avalon. Results when using daily maxima and minima (●), and when using half hourly means (○) are shown

### 1.3.1.2 Crop growth

Doubling the CO<sub>2</sub> concentration and increasing the temperature increased light interception by the crops of cv. Hereward (all 4 years). This was particularly important in the early growth where canopy expansion, and hence light interception was stimulated by increased [CO<sub>2</sub>] despite low temperatures (Fig. 4). For example, the leaf area index at the double ridge stage in Hereward was 0.9 at normal CO<sub>2</sub> and 1.3 with doubled CO<sub>2</sub> in 1994/5. The CO<sub>2</sub> stimulation was larger in the slower developing cv. Hereward than in the early cv. Soissons (1994/5 only). Later on there were no differences between these two cvs.

Analysis showed that  $2 \times \text{CO}_2$  increased mainstem mass, and that these heavier stems supported more tillers, which resulted in more shoots per unit area during vegetative growth, which in turn resulted in a more rapid increase in leaf area index, and hence a higher fractional interception of solar radiation. Therefore crop growth rate at the terminal spikelet stage was substantially increased by increased CO<sub>2</sub> (from 17 to 22 g m<sup>-2</sup> d<sup>-1</sup> in Hereward).

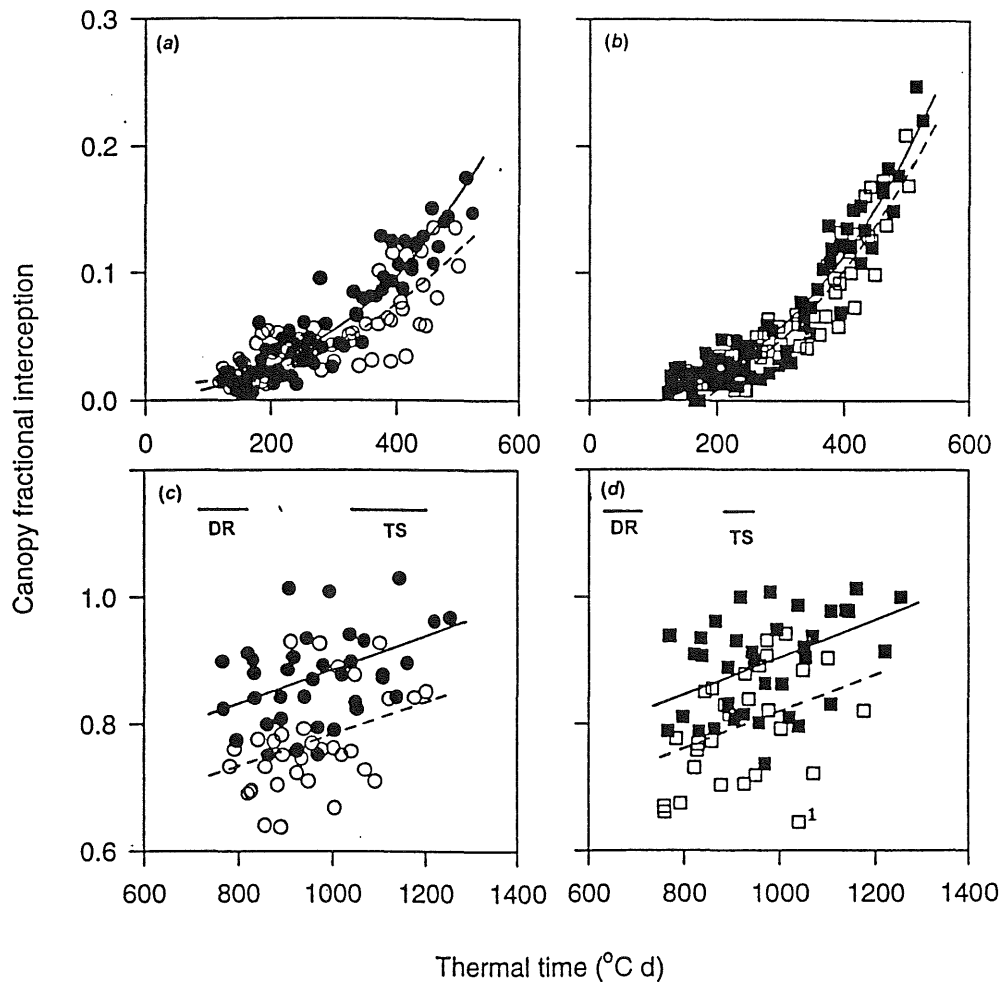


Figure 4 Canopy light interception by cvs. Hereward (left) and Soissons (right) grown at doubled (solid symbols) or normal (open symbol) [CO<sub>2</sub>], both early on during autumn/winter (top figures), and later in the season (bottom figures). Bars indicate periods of double ridge and terminal spikelet formation in the different temperature zones.

### 1.3.1.3 Crop biomass and yield

For cv. Hereward, crop biomass generally declined with increase in mean temperature, and was greater at increased  $[\text{CO}_2]$  (Fig. 5), with the effect of increased  $[\text{CO}_2]$  varying with temperature and between years (6-34% range in relative stimulation by increased  $[\text{CO}_2]$ ).

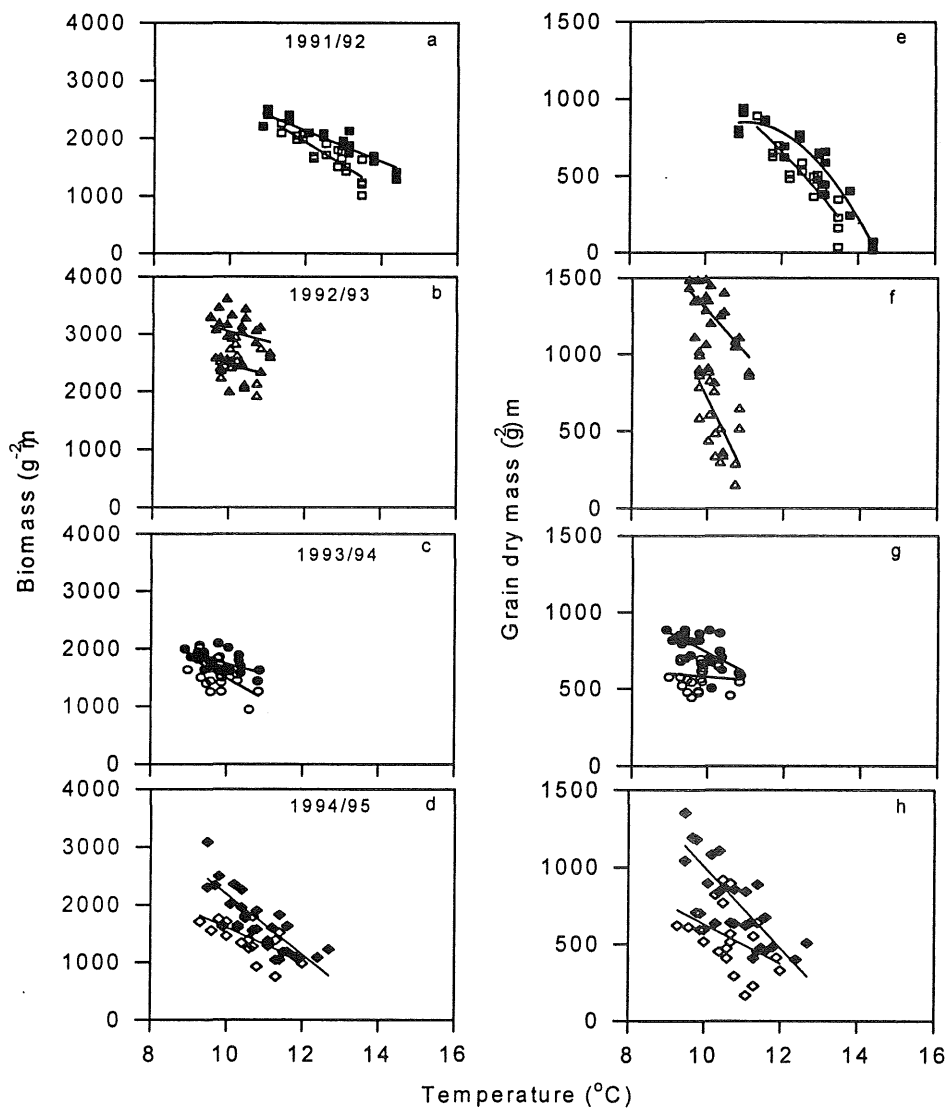


Figure 5. Relations between biomass (left column) and grain dry mass (right column) and the mean temperature from sowing to harvest maturity in 1991/92 (a,e), 1992/93 (b,f), 1993/94 (c,g) and 1994/95 (d,h) for crops grown at increased (solid symbols) or normal  $[\text{CO}_2]$  (open symbols). All regressions are significant ( $P < 0.05$ ), and where separate regressions are shown for the two  $\text{CO}_2$  treatments they are significantly different ( $P < 0.05$ ).

There were both positive and negative interactions of temperature and increased  $[\text{CO}_2]$  on biomass and grain yield (Table 1). While above ground biomass and grain yield showed a broadly similar pattern of response to temperature and  $[\text{CO}_2]$  in all years (Fig. 5), there were substantial changes in harvest index with temperature and with increased  $[\text{CO}_2]$  in most cases.

Table 1. Response of above ground biomass and yield to increased CO<sub>2</sub> concentration (approximately a doubling) in winter wheat crops grown in temperature gradient tunnels in the field in four seasons. The range shown is the range in relative effect of increased CO<sub>2</sub> between the coolest and warmest plots on biomass and yield. The absolute and relative effect of increased CO<sub>2</sub> on yield (g m<sup>-2</sup>) at 10°C is also shown<sup>1</sup> together with the warming above the ambient seasonal mean which negates the increase of grain yield by increased CO<sub>2</sub>.

Year	range		Grain yield at 10°C			
	Biomass (%)	Grain yield (%)	Normal [CO <sub>2</sub> ]	Increased [CO <sub>2</sub> ]	Grain yield (%)	Warming (°C)
1991/92	6-31	7-44	<sup>2</sup>	<sup>2</sup>	<sup>2</sup>	1.0
1992/93	34	72-168	683	1292	89	1.8
1993/94	8-17	46-7	580	738	27	2.0
1994/95	33-17	58-31	623	994	60	1.2

<sup>1</sup>4-year ambient mean temperature.

<sup>2</sup>Prediction beyond 1991/92 temperature range inadvisable.

The marked declines in harvest index that occurred in the first two years were when yields were affected by high temperature episodes during grain filling (Wheeler *et al.*, 1996a,b). Analyses of which yield components accounted for the observed variation of grain yield between treatments, showed that for all years the number of grain per unit area was a major determinant, and this arose either through variation in ear number m<sup>-2</sup> or grain number per ear (Table 2).

Table 2. Percentage variation accounted<sup>1</sup> for by linear regression analysis of grain yield (g m<sup>-2</sup>) on biomass or components of grain yield for all treatments in four years. Values in parentheses are the correlations when [CO<sub>2</sub>] is included as a factor in the regression.

Year	Biomass (g m <sup>-2</sup> )	Ears (m <sup>-2</sup> )	Grains (ear <sup>-1</sup> )	Grain mass (mg grain <sup>-1</sup> )	Grains (m <sup>-2</sup> )
1991/92	45.1 (----)	1.4 (65.6)	79.4 (82.5)	81.9 (----)	86.7 (----)
1992/93	66.6 (77.3)	6.21 (----)	62.4 (71.5)	8.6 (66.0)	80.5 (82.8)
1993/94	49.4 (68.5)	26.6 (69.8)	3.7 (46.4)	1.4 (48.5)	63.4 (78.4)
1994/95	86.1 (87.4)	81.0 (----)	0.0 (15.8)	89.5 (91.0)	77.4 (----)

<sup>1</sup>Percentage variation accounted for = [(Total MS-Residual MS)/Total MS]×100.

Degrees of freedom for 1991/92 to 1994/95 were 38,42, 46 & 46, respectively.

(----) indicates where correlation values are not significantly different (P>0.05) from those when [CO<sub>2</sub>] was included as a factor.

Grain size and its response to temperature and [CO<sub>2</sub>] differed between years, and in normal [CO<sub>2</sub>] was largest in years 2 and 3 (c. 45 mg at cooler temperatures), compared to c. 32 mg in equivalent temperatures in years 1 and 4, (see Batts *et al.* (1997) and Wheeler *et al.* (1996a)) clearly indicating different source-sink relations between years. The role of the ear number in determining yield varied between years, and the relative effect of increased [CO<sub>2</sub>] on ear number at maturity varied (9%, 0%, 12% and 20% increases, in years 1-4, respectively). The lack of [CO<sub>2</sub>] promotion of tillering in 1992/3 (Batts *et al.*, 1996) may have been caused by the low solar radiation flux during the vegetative development period in this year and this effect may have been exacerbated by the reduction in solar radiation within the temperature gradient tunnels. However, there was still a pronounced increase in yield in response to increased [CO<sub>2</sub>] in this year because of more grain per ear, and it should be noted that the grain filling rate of the cooler treatments at normal [CO<sub>2</sub>] was the same as that outside

(Wheeler *et al.*, 1996) indicating that the radiation regime in the tunnels was not too low. Clearly, wheat plants have substantial flexibility in the partitioning of the increased photosynthate supply in increased  $[\text{CO}_2]$ , and therefore increased tillering may not be a prerequisite for effects on grain yield.

When different cvs. were compared, they all showed substantial increases in biomass and in grain yield with increased  $\text{CO}_2$ . However, the interactions between temperature and  $\text{CO}_2$  were different so that two cultivars showed no difference in  $\text{CO}_2$  response across the 2-3 °C range of mean seasonal temperature, while the other two showed reduced stimulation by  $\text{CO}_2$  at higher temperatures – the opposite of the usually quoted  $T \times \text{CO}_2$  interaction (see below). Therefore maximum  $\text{CO}_2$  effect on yield was at the coolest effects, and in most cases mean seasonal temperature increases of 1-2°C were sufficient to negate the yield stimulation by a doubling of  $\text{CO}_2$ . However, it should be noted that these mean temperature increases, while apparently small, were not constant over the season, and mean increases in the grain filling period were of the order of 2-3 °C.

#### **1.3.1.4 Summary**

While there is considerable scatter in the observed results, indicating plot-plot variation, the design of the experiment, with two tunnels in each of the  $\text{CO}_2$  concentrations, and the 5 or 6 plots within each tunnel suggest that the differences between years are not simply due to measurement uncertainties. With this set of experimental data we were able to separate two aspects that may cause some of the substantial variation in  $\text{CO}_2$  response evident in the literature. Firstly, side-by side comparison of different cvs. in one year, showed that temperature and  $\text{CO}_2$  responses and their interactions were clearly different, so that interpretation of different experiments with different cvs. is difficult. Secondly, conducting similar (but not identical, due to small operational changes) experiments across 4 years has highlighted the importance in the exact weather patterns in each year, and the way they interact with growth stages. Effects of radiation supply and temperature on carbon balance, and on subsequent growth and yield (through effects on the development of different yield components) vary dependent on the growth stage, and the response to increased  $\text{CO}_2$  depends on all of these factors.

### **1.3.2 Review of literature for $T \times \text{CO}_2$ interactions in crop growth**

#### **1.3.2.1 Rationale and key arguments**

The basic argument for a  $T \times \text{CO}_2$  interaction (discussed in many papers) is based on the known responses of (1) photosynthesis and photorespiration, (2) respiration, and (3) tissue and organ growth to temperature and  $\text{CO}_2$ . Firstly, for photosynthesis, biochemical models predict that the response of net  $\text{CO}_2$  assimilation rate per unit area ( $A$ ) to increased  $\text{CO}_2$  for plants with  $\text{C}_3$  metabolism is largest at high temperatures and smallest at low (e.g. Long, 1991; Gifford, 1992; Bowes, 1996), providing a “fundamental basis for expecting an interactive effect of rising temperature and  $\text{CO}_2$  at the very point of entry of carbon in photosynthesis and into ecosystems” (Long, 1991). This biochemical understanding (along with earlier largely erroneous application of the concept of single limiting factors, see Gifford (1992)) has led to many suggestions that in colder conditions (<15°C) plant growth will not be stimulated by  $\text{CO}_2$ .

increase, and may even be inhibited. There is some experimental evidence for this (Idso and Kimball 1989).

Secondly, the response of plant growth to increasing CO<sub>2</sub> involves not only photosynthetic responses of leaves but also the whole-plant respiration (Gifford, 1992). As Lloyd and Farquhar (1996) have emphasised “it is incorrect to simply assume that the [CO<sub>2</sub>] and temperature dependencies of plant growth are well reflected by temperature and [CO<sub>2</sub>] dependencies of photosynthesis”. The growth response to CO<sub>2</sub> depends on the respiration rates per unit of dry matter, so that plants with high respiration per unit of photosynthesis show a higher relative sensitivity to CO<sub>2</sub> (Lloyd and Farquhar, 1996). Respiration rates increase with temperature, so there should be a higher sensitivity to CO<sub>2</sub> at warmer temperatures.

Thirdly, accumulation of plant biomass and its partitioning between different organs depends on both the net carbon balance (the difference between net photosynthesis and respiration) and the ordered initiation and expansion of organs. Expanding organs are sinks for assimilate which interact with the assimilate sources and understanding of this interaction is critical to understanding plant responses to environment (Lawlor and Keys, 1993; Farrar, 1996). As developmental and growth rates of sinks are strongly reduced at low temperatures, so is demand for assimilates. Therefore, as Rawson (1988) and Gifford (1992) have pointed out, at low temperatures sink growth and metabolism are the controlling processes and not carbohydrate supply, so plants may show very little response to increased CO<sub>2</sub>, depending on the response of CO<sub>2</sub> assimilation to temperature. As Paul, Driscoll and Lawlor (1994) have shown, low temperature generally results in accumulation of carbohydrates, indicating that growth or storage are limiting. Conversely, at high temperatures, sink demand is large and assimilate is depleted so there should be a marked positive response to increased CO<sub>2</sub>. However, temperature sensitivities and optima for photosynthesis, respiration, development, and for overall growth vary between species, ecotypes and varieties, and with acclimation and developmental stage. Biomass allocation patterns between organs are a key determinant of plant growth, and may profoundly influence CO<sub>2</sub> responsiveness as well as possibly be influenced by increased CO<sub>2</sub> (see e.g. Callaway *et al.* (1994) and Jitla *et al.* (1997)).

### 1.3.2.2 Summary of $T \times \text{CO}_2$ interaction

We have reviewed the arguments above and while we therefore expect positive  $T \times \text{CO}_2$  interactions, it is not clear from the results available in the literature that it does occur (Morison and Lawlor, 1998). In that review we could find no clear relationship between temperature and CO<sub>2</sub> responsiveness. The compilation of data (Fig. 6) particularly included studies where different temperatures were examined in the same experiment, or at least in the same experimental system, and where mean temperatures over the whole experiment were clearly defined or could be estimated from the information given. We expressed the growth response to increased CO<sub>2</sub> in two ways. Firstly, simply as the change in biomass ( $M$ ) due to increased [CO<sub>2</sub>] relative to the biomass at low [CO<sub>2</sub>], or  $R_b$  ( $= [M_{\text{high}} - M_{\text{low}}] / M_{\text{low}}$ ). As the range in CO<sub>2</sub> concentration used in these disparate experiments is large this cannot be ignored, so we have also used the “biotic growth factor”, or  $\beta$  value ( $= R_b / \ln[\text{CO}_{2 \text{ high}} / \text{CO}_{2 \text{ low}}]$ ), which has been widely used in modelling. Amthor and Koch (1996) have highlighted the problems in use of  $\beta$  in global change modelling, but here we are simply using it to summarise experimental data. It should also be noted that the experiments were of very different durations, and are for a mixture of experimental systems and conditions, some with spaced plants, some in stands.

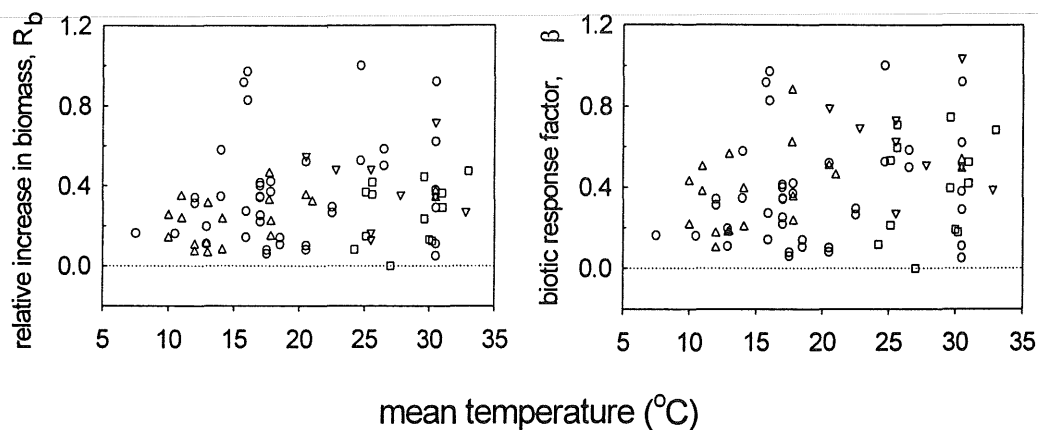


Figure 6 Relationship between a) relative stimulation of biomass,  $R_b$  by increased  $\text{CO}_2$  concentration and b) biotic growth factor,  $\beta$ , and mean growth temperature, derived from values in the literature. Symbols indicate :  $\square$  rice,  $\triangle$  wheat,  $\nabla$  soybean,  $\circ$  other species

Furthermore, the data used are a mixture of either just shoot biomass (above ground biomass) or total biomass. However, the studies used are not unrepresentative, as indicated by the overall average  $R_b$  and  $\beta$  values ( $0.32 \pm 0.02$ , s.e.m.] and  $0.52 \pm 0.4$ ], respectively), which are close to the average values usually reported for the growth increase with a doubling of  $[\text{CO}_2]$  (see e.g. Amthor and Koch, 1996). Two obvious points arise from Figure 6, firstly, there is little evidence of a  $T \times \text{CO}_2$  interaction, and secondly, there is a dearth of data at temperatures  $< 10^\circ\text{C}$ . The few studies at low temperatures are mostly those from longer term quasi-“field”, multi-year experiments, such as those in TGT, OTC and FACE that are the subject of MODEXCROP. A simple mean seasonal temperature as used in Figure 6 may be inappropriate because temperature varies substantially over the day and over the season. The question of what is the appropriate temperature to use is not clear in such syntheses of these whole-season results.

### 1.3.2.3 Conclusions

The conclusions from this review (Morison and Lawlor, 1998) were:

1. increased  $\text{CO}_2$  usually stimulates growth and biomass but in almost all situations the effect is limited, reducing as  $\text{CO}_2$  increases.
2. in many cases in elevated  $\text{CO}_2$  there is acclimation of net  $\text{CO}_2$  assimilation rate, but over the long term rates are still somewhat higher than in normal  $\text{CO}_2$ .
3. accumulation of carbohydrates is greater in elevated  $\text{CO}_2$ .
4. elevated  $\text{CO}_2$  increases the number of organs and size (the relative effects being highly specific to species) but in most cases does not affect development.
5. warmer temperatures accelerate the rate of organ development and expansion but decrease the duration so the total biomass produced is often reduced, depending on temperature range.
6.  $\text{CO}_2$  partially compensates for the effect of  $T$  on biomass but does not have a proportionately larger effect at elevated than at normal  $T$  (no  $T \times \text{CO}_2$  interaction).
7. warmer  $T$  may decrease the accumulation of carbohydrates but not consistently.
8. at very cool temperatures the stimulation of growth by  $\text{CO}_2$  may be decreased and may cease at low temperatures, though the effect will depend on plant adaptation.



Response of plant development, growth and biomass accumulation to elevated  $\text{CO}_2$  at different temperatures is not as expected from an analysis of the photosynthetic processes alone. In adapted and acclimated plants there is little firm evidence of  $\text{CO}_2 \times T$  interactions. Investigations in individual species or genotypes show little consistent pattern due largely to the many different interactions of temperature and assimilate supply (for example on carbon balance, meristem initiation and expansion rates, senescence, fertilisation, and carbohydrate storage and mobilisation) at different stages in the growth cycle or in different weather and edaphic conditions. The various processes affected by temperature and  $\text{CO}_2$  are highlighted in Figure 7. Extreme conditions (e.g. of temperature, nutrition) may affect processes independently of  $\text{CO}_2$  and thus prevent or modify the responses. This emphasises the importance of correctly incorporating into models and scenarios of climate change the detail of the changes to seasonal pattern of weather variables.

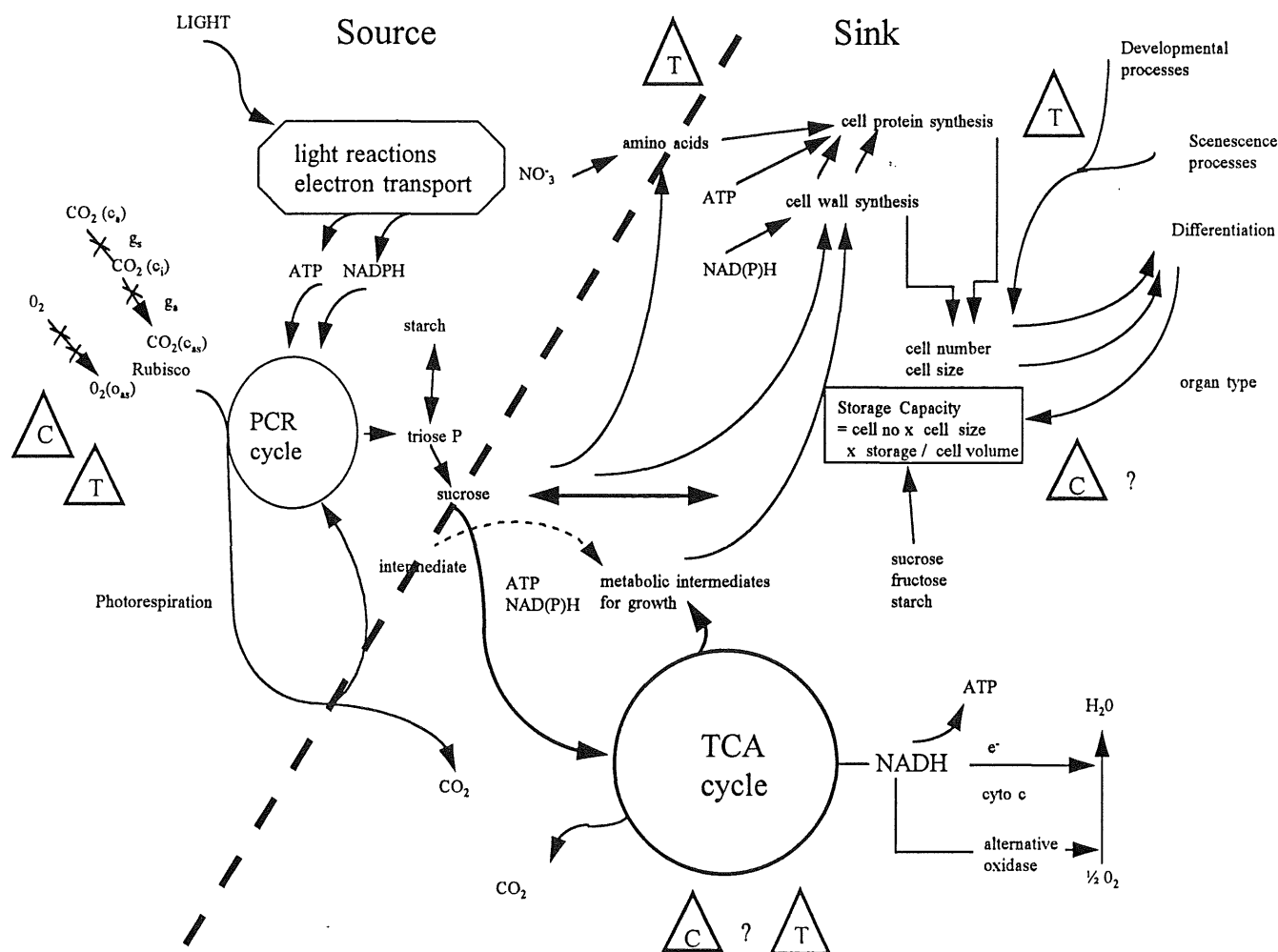


Figure 7. Diagram indicating processes determining, and linkages between, assimilate supply ("source") and assimilate demand ("sink") and the points of action of changing  $\text{CO}_2$  ("C") and temperature ("T").

### 1.3.3 Physiological modelling

#### 1.3.3.1 Outline

We investigated the importance of including different levels of detail in the simulation of CO<sub>2</sub> exchange of crops, by developing the McKee "MODEXCROP" model for leaf photosynthesis. This takes as its starting point the standard biochemical model of von Caemmerer and Farquhar (1983) and makes a hierarchy of modifications. These are (1) a different analysis of temperature sensitivity of the rubisco enzyme, (2) more detail on pathway for diffusion and the resistance analogue used, (3) a different stomatal model, and (4) a more complete leaf temperature feedback. The model is complete at the scale of the leaf, and a preliminary multilayer canopy model has been developed in order to simulate daily CO<sub>2</sub> exchange for comparison with more complete crop growth models. Some validation data are available from purpose-designed experiments on wheat, but more work is required.

In parallel with this detailed physiological model, we developed a wheat growth version of WIMOVAC, by adding empirical growth and development sub-models to the established leaf and canopy gas exchange model.

#### 1.3.3.2 Rubisco kinetics

The affinity constants of Rubisco for CO<sub>2</sub> and O<sub>2</sub> ( $K_c$  and  $K_o$ ) are central to the modelling of carbon assimilation, and are crucial to the modelling of responses to CO<sub>2</sub> concentration and temperature. A wide range of values for these constants appears in the literature. Reasons for this wide range include technical difficulties in early kinetic studies (Badger and Andrews, 1974) and misuse of kinetic models (McMurtrie and Wang, 1993). However, fitting empirical equations to the best available published data (Jordan and Ogren, 1984), validated in wheat (Brooks and Farquhar, 1985; McKee, unpublished), rather than making assumptions that the relationships fit an Arrhenius model, has highlighted a substantial difference, compared to the standard simulation of temperature sensitivity (Fig. 8). This is potentially important as much of the argument underlying the T x CO<sub>2</sub> interaction relies upon the widely used Arrhenius-model derived coefficients.

#### 1.3.3.3 Mesophyll resistance

The values for Rubisco kinetic parameters used in models of carboxylation are based *on in vitro* studies (Badger and Collatz, 1977). However, the values of CO<sub>2</sub> and O<sub>2</sub> concentration used in these models usually relate to gaseous substomatal concentrations (von Caemmerer and Farquhar, 1981). These values should be corrected for temperature dependent solubility (Long, 1991) and intercellular and cellular flux resistances between the sub-stomatal space and the chloroplast. These elements of the CO<sub>2</sub> transfer pathway are usually termed the mesophyll resistance,  $r_m$  (Evans and von Caemmerer, 1996), and have been shown to be important, particularly in low photosynthetic capacity leaves, where the values for  $r_m$  can be high. The new MODEXCROP model incorporates these corrections in a nested iteration (Fig. 9a).

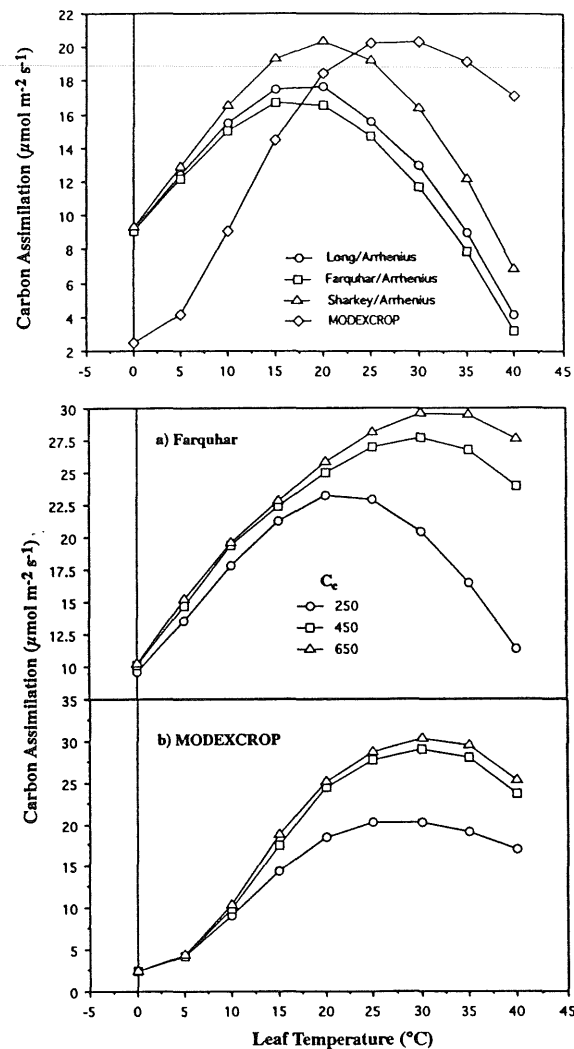


Fig. 8. Photosynthesis rate as a function of temperature calculated with different models (top); effect of chloroplast  $\text{CO}_2$  concentration on photosynthesis rate for Arrhenius-based RuBisCo temperature model (middle) and for MODEXCROP model with empirical temperature response (bottom).

#### 1.3.3.4 Stomatal conductance

At the level of whole leaf photosynthesis, feedbacks between photosynthesis and stomatal conductance are critical. Inevitably there is a high degree of empiricism in stomatal modelling. Some popular stomatal models (Ball et al., 1987) suffer from theoretical deficiencies which make them less robust for predictive purposes. Monteith (1995) has proposed a more reliable basis for stomatal modelling involving transpiration feedback. Advances in computing power mean that his model can now be used in a fully nested iteration with photoassimilation models, without excessive computation time problems (Fig. 9b). The Monteith approach has been used in the new MODEXCROP model, with several refinements. (1) stomatal responses to light and temperature have been modelled in terms of guard cell electron transport and respiration, (2) the  $\text{CO}_2$  response has been modelled with respect to solubility corrected substomatal  $\text{CO}_2$  concentration as distinct from the mesophyll chloroplastic  $\text{CO}_2$  concentration used in the photoassimilation model, and (3) the  $\text{CO}_2$  response has been modified with respect to the response to soil moisture to take account of the "root signal" abscisic acid feedback (Tardieu and Davies, 1993). The benefits of this model can be seen in the more realistic responses of conductance to  $\text{CO}_2$  and to relative humidity (Fig. 10).

Schematic of CO<sub>2</sub> flux into a leaf

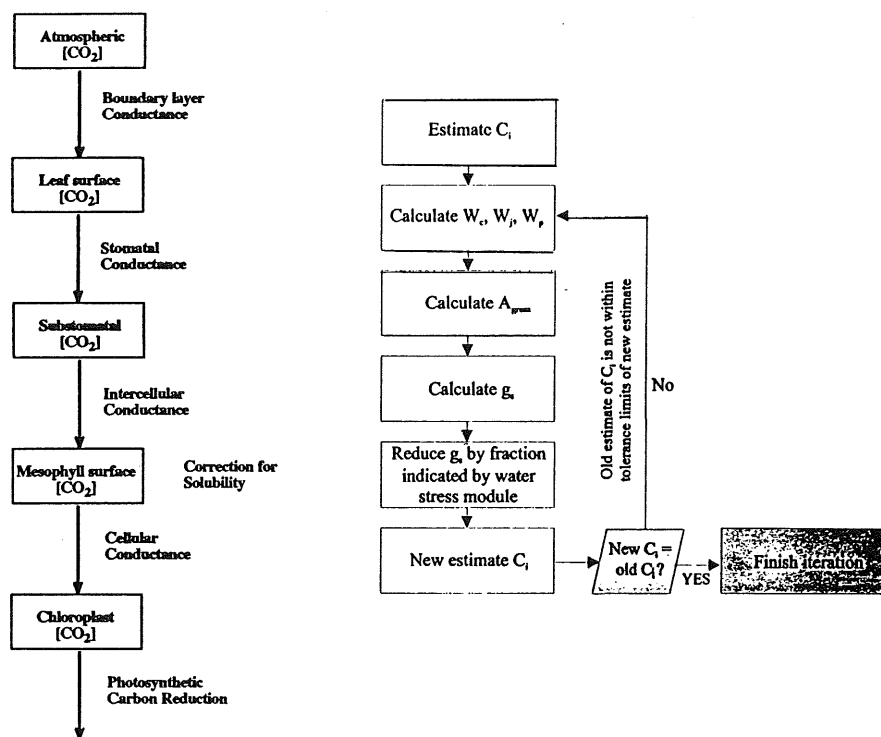


Fig. 9a. Diagram indicating the components considered in the MODEXCROP model in estimating CO<sub>2</sub> flux into the leaf.

Fig 9b. Diagram showing the iterative calculation procedure used for solving CO<sub>2</sub> assimilation rate, conductance and intercellular CO<sub>2</sub>.

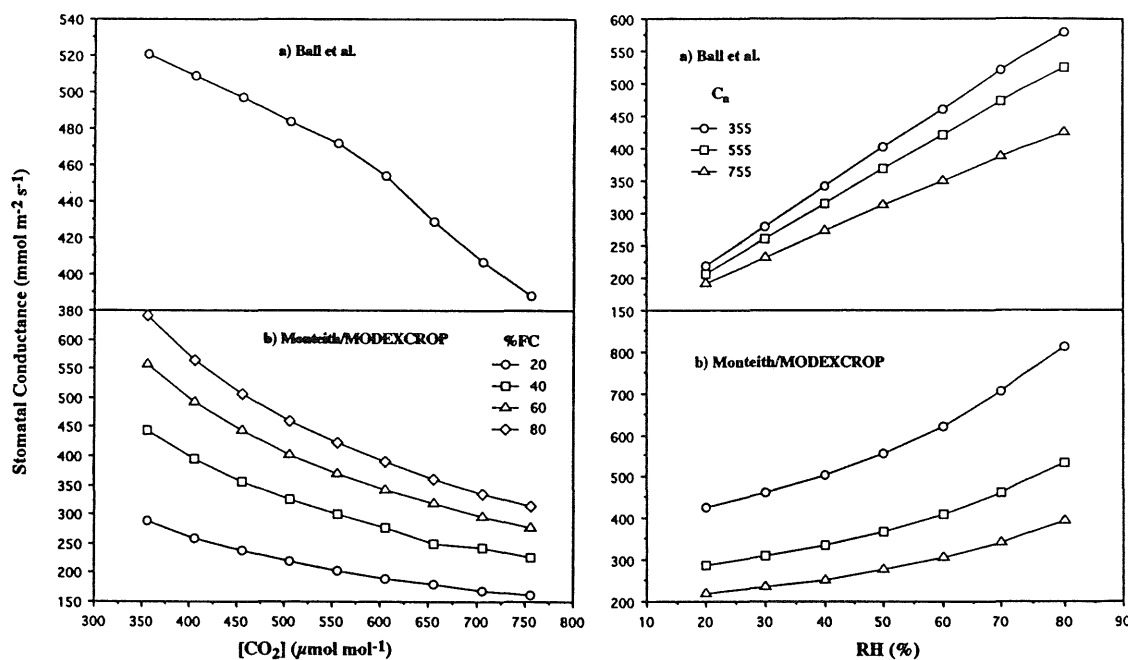


Fig. 10 Effect of different stomatal models on calculated response of stomatal conductance to (left) CO<sub>2</sub> at different soil water contents and (right) relative humidity at different CO<sub>2</sub> concentrations.

#### **1.3.3.5 Leaf temperature**

The calculation of leaf or canopy temperature using energy balance equations has long been a useful technique (Monteith, 1965) and the feedback on canopy water loss has often been analysed in this way (Choudhury and Monteith, 1986). The MODEXCROP model uses a reformulated, robust energy balance equation, dividing the radiation components, and avoiding the common but spurious "radiation resistance" term. This energy balance is used in a nested iteration with stomatal conductance and photoassimilation models, taking into account both feedback and feedforward responses of stomata to environment.

#### **1.3.3.6 Crop canopy model**

Scaling up from leaf to canopy, often involves "big leaf" assumptions with well understood drawbacks (e.g. de Pury and Farquhar, 1997). The modelling of canopy responses to CO<sub>2</sub> concentration and temperature ideally requires more detailed models of light vertical profile and gaseous flux within canopies. With regard to light profile, the new MODEXCROP model uses a layered canopy approach, splitting direct and diffuse components, and PAR and infra-red components, and treating direct sunlit and shaded components separately for each layer. A similar approach has recently been adopted by de Pury and Farquhar (1997). The flux of gases within a canopy can be modelled with respect to the flux of momentum. Traditional approaches model canopy boundary layer resistance with respect to a logarithmic wind speed profile (Grace, Ford and Jarvis, 1981). This does not adequately model the within-canopy components. We have used a multilayered canopy approach, treating canopy elements as momentum sinks. Combining this with free-convective models for individual elements and canopy surface produces a more robust model. This model is used in iteration with leaf-level models, still within reasonable computing times. Unfortunately, this model is not yet available for comparison with the simpler carbon assimilation routines in the other models used in MODEXCROP (e.g. SUCROS, AFRCWHEAT), due to lack of time for its development.

#### **1.3.3.7 WIMOVAC wheat version**

WIMOVAC was modified to allow the user (a) to explore consequences of different levels of detail, and (b) to include a growth module (Fig. 11). For example, it can be used to examine differences between models in the simulated responses of leaf or canopy photosynthesis to increased CO<sub>2</sub> (Fig. 12a). Or a multi-layer canopy model can be used to examine photosynthetic contributions from different layers to total canopy photosynthesis (Fig. 12b), as an alternative to the simple sun/shade leaf division. A multi-layer soil water budget was added, and when coupled with the stomatal model produced realistic patterns of soil and leaf water potential in response to drought (Fig 13). The effect of reduced transpiration in high [CO<sub>2</sub>] in slowing down the decline in soil water potential and reducing the fluctuations in leaf water potential is clear. In reality such improvements in water potential permit continued photosynthesis and leaf expansion. These are important effects, however several crop growth models do not explicitly include stomatal responses and leaf water status feedbacks on growth.

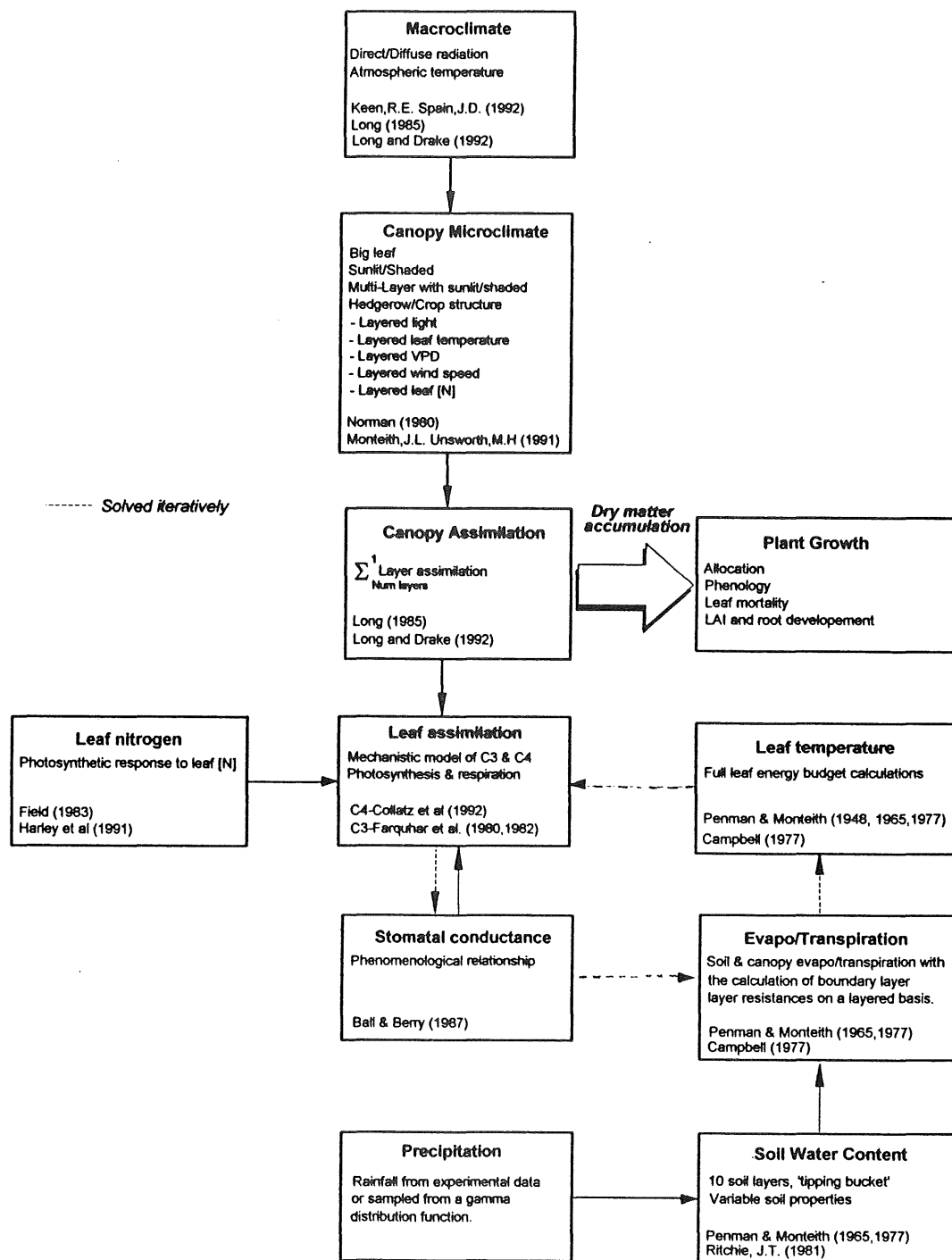


Fig. 11. Outline of the WIMOVAC model, indicating the main model components and the iterative nature of leaf photosynthesis, conductance, evapo-transpiration and energy balance calculations.

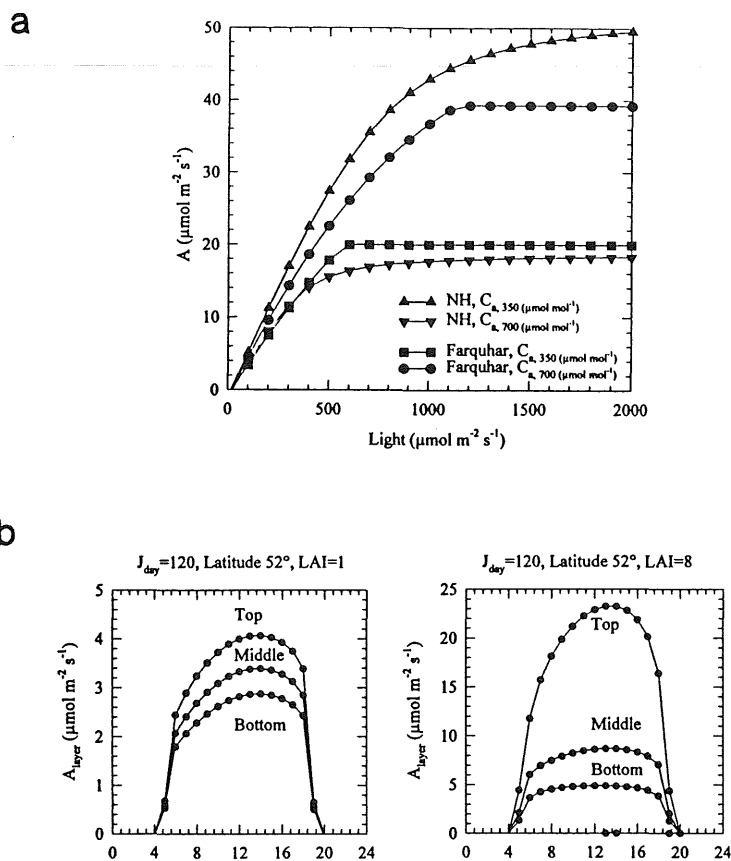


Fig. 12 (a) Effect of different  $\text{CO}_2$  concentration on the response of photosynthesis to light, using either a non-rectangular model (NH), or the von Cammerer and Farquhar (1981) model. (b) Photosynthesis rates over a clear spring day in different canopy layers for low (left) and high (right) leaf area index values (LAI)

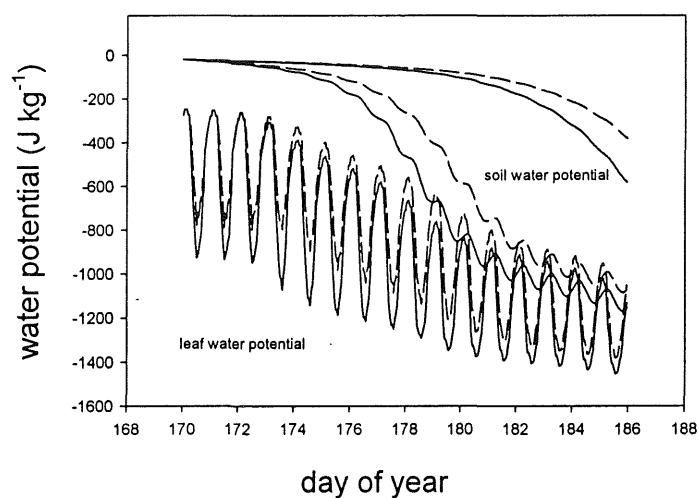


Figure 13. Simulated soil and leaf water potential during a dry period for a crop stand in  $350$  (solid line) or  $700 \mu\text{mol mol}^{-1}$   $\text{CO}_2$  (dashed lines)

A module was added to WIMOVAC to couple the detailed canopy  $\text{CO}_2$  assimilation and transpiration simulations to crop growth. This used a simple thermal time driven crop calendar, and empirical partitioning coefficients to divide current assimilate between different plant fractions (e.g. leaves, roots, stems, grain). Leaf death is simulated, again through a thermal time relation. The crop growth model was parameterised simply with appropriate values from the literature. However, the major problem remains with WIMOVAC and with all existing crop models, that the partitioning of assimilate between components is treated empirically, without any physiological detail. As was stressed in section 1.3.2. growth and assimilate partitioning in real plants is dynamic, and changes in response to conditions. Until progress is made on the physiological understanding of assimilate partitioning, and then on a satisfactory modelling approach perhaps through modelling availability of key assimilates (e.g. sucrose, see Farrar (1996)), this will remain a weak element of crop models.

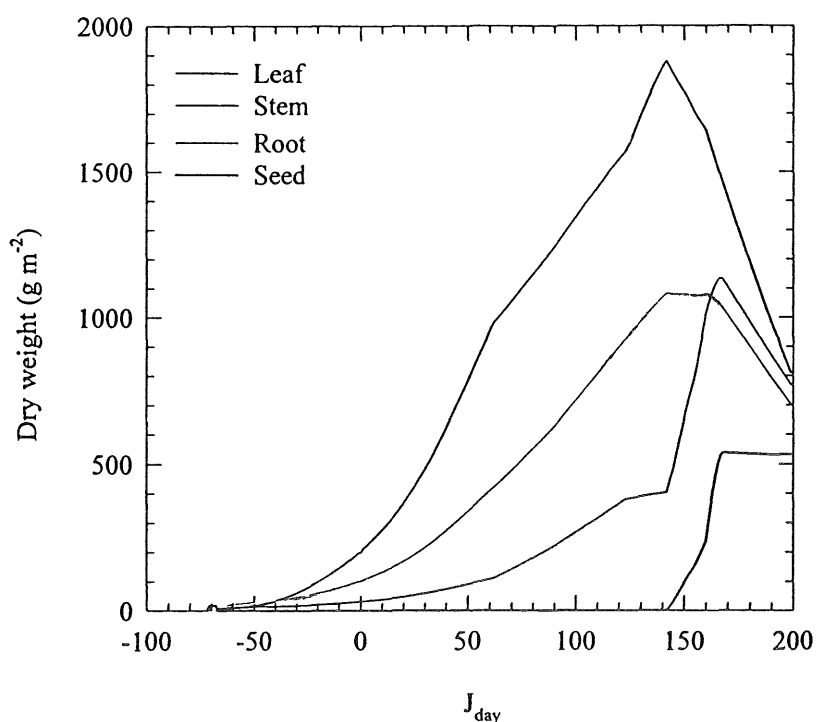


Fig. 14. Simulated growth of wheat over time using preliminary version of WIMOVAC Wheat model.

Preliminary tests of the WIMOVAC Wheat model showed some promise (Fig. 14), but the model needs more development and testing against the data sets that are now available before it can be confidently used to explore the effects of the physiological detail on the resulting yields. This work is continuing. The complete WIMOVAC package is available for download from the WWW (see <http://www.essex.ac.uk/bcs/downloads/> ).



### **1.3.3.8 Summary**

Modelling details of the physiology of wheat has shown some limitations in current models and information available. In particular, the relationship usually assumed for the effect of temperature on carbon fixation in C3 plants can be questioned and this has profound implications for the degree of the  $T \times \text{CO}_2$  interaction in photosynthesis. More experimental data on the temperature responses of the biochemistry is required. Secondly, the form of the stomatal sub-model is important and it is unlikely that models which simply correlate conductance with leaf  $\text{CO}_2$  assimilation rate can adequately represent the complexity of stomatal responses, and consequent feedbacks through water relations. More detailed approaches to solving energy balances for whole canopies are now possible, largely because of computational advances, but given other uncertainties in the models it is doubtful these are required (e.g. Wang and Leuning, 1998). While the simulation of canopy photosynthesis is now well advanced, and can be evaluated against direct measurement, the simulation of growth over longer periods has substantial difficulties. Assimilate partitioning remains a weak part of many if not all crop growth models, as we have yet to include a physiologically based understanding of what determines assimilate movement from sources (leaves) to sinks (e.g. roots, grain), and how assimilate availability determines activity and number of sinks.

## **1.4 Final discussion and conclusions**

The work at Essex during MODEXCROP combined analysis of existing winter wheat crop response data from experiments at Reading, with an extensive literature review and with examination of physiological models. One overall outcome that this work has emphasised is that observed crop responses are not easily predicted from short-term responses of readily measured and modelled characteristics, such as photosynthesis. For example, in the experiments examined temperature and  $\text{CO}_2$  effects on growth and yield were quite different in different years. Similarly, a detailed literature review could not find consistent evidence for the theoretical positive temperature  $\times$   $\text{CO}_2$  interaction on growth. Crop growth and development integrates the complete time courses of environmental variables during growth. Most importantly plants respond to the changing environmental conditions at a number of different scales. There are biochemical adjustments in metabolism, for example in temperature sensitivity of enzymes, and morphological and anatomical adjustments through leaf or stem cell expansion and through initiation of meristems and subsequent development of new organs. These adjustments then determine subsequent plant function and the effects of environmental conditions on final yield. We believe that it is these short and long-term responses of plants that lie behind the observed variations in growth and yield in the Reading TGT experiments with winter wheat. The responses may even differ between cultivars. In addition, the exact time courses of temperature and radiation during a season are important, and simple measures of average temperature may obscure important detail that affect plant metabolism. The crop components that contribute to the overall yield compensate and adjust throughout the growth of the crop, and this flexibility and adjustment is not at the moment incorporated into biomass partitioning in models.

Overall, we conclude that:

- it is difficult to generalise from the observed responses of crops examined in climate impact studies and to derive simple quantitative estimates of effects, because of the complexity of interactions between environmental factors and plant response.

- although theory suggest there should be a positive  $T \times CO_2$  interaction on growth of plants, there is no clear pattern evident across a wide range of experimental results due both to variation in experimental conditions and the acclimation and adaptation of plants to different temperature regimes.
- in experiments with winter wheat in temperature gradient tunnels, there were both positive and negative  $T \times CO_2$  interactions in different years, due largely to different combinations of weather conditions, and the responses of different yield components.
- small increases in temperature (2-4°C) cause major reductions in duration of wheat crop growth, reducing yields, which outweigh the yield increases from high  $CO_2$ .
- increased  $CO_2$  had only small effects on wheat ontogenetic development, which does not need to be considered in models.
- variability in crop responses to  $CO_2$  and temperature modification arises from several sources, some obvious and some not:
  - o differences in environmental conditions between different experiments;
  - o differences in experimental procedures;
  - o difference in plant material (species, cultivars);
  - o even within similar repeated experiments the exact time course of weather (critically temperature and radiation) affects the plant response and subsequent growth.
- the assumption that the temperature sensitivity of the key photosynthetic enzyme RuBisCo should be modelled by an Arrhenius-type model can be questioned, and without this assumption the modelled positive  $T \times CO_2$  interaction in  $CO_2$  fixation is much reduced.
- crop growth models should include details of stomatal responses and water relations in order to correctly simulate effects of water availability on photosynthesis and on leaf and root growth.
- the modelling of assimilate partitioning and morphogenetic changes (such as leaf appearance, mass and senescence) needs to be improved in order to be able to reproduce the observed sensitivities of wheat to changing conditions.

## References

- Amthor J.S. & Koch G.W., 1996. Biota growth factor  $\beta$ : stimulation of terrestrial ecosystem net primary production by elevated atmospheric  $CO_2$ . In: *Carbon dioxide and terrestrial ecosystems*, (eds G.W. Koch & H.A. Mooney), pp. 399-414. Academic Press, San Diego.
- Badger M.R. & Andrews T.J., 1974. *Biochem. Biophys. Res. Commun.* **60**, 204-210.
- Badger M.R. & Collatz G.J., 1977. Studies on the kinetic mechanism of ribulose-1,5-bisphosphate carboxylase and oxygenase reactions. *Carnegie Inst. Wash. Year Book* **76**, 355-361.
- Baker J.T., Allen L.H. Jr., Boote K.J. & Pickering N.B., 1996. Assessment of rice responses to global climate change:  $CO_2$  and temperature. In: *Carbon dioxide and terrestrial ecosystems*, (eds G.W. Koch & H.A. Mooney), pp. 265-282. Academic Press, San Diego.
- Ball J.T., Woodrow I.E. & Berry J.A., 1987. In *Progress in Photosynthesis Research, Vol. IV* (ed. J. Biggins), pp. 221-234 Martinus Nijhof Publishers, Dordrecht.
- Batts G.R., Wheeler T.R., Morison J.I.L., Ellis R.H. & Hadley, P., 1996. Developmental and

- tillering responses of winter wheat (*Triticum aestivum*) crops to elevated CO<sub>2</sub> concentration and temperature. *Journal of Agricultural Science* (Cambs) **127**, 23-35.
- Batts G.R., Morison J.I.L., Ellis R.H., Hadley P. & Wheeler T.R., 1997. Effects of CO<sub>2</sub> and temperature on growth and yield of crops of winter wheat over several seasons. *European Journal of Agronomy* **7**, 43-52.
- Batts G.R., Ellis R.H., Morison J.I.L. & Hadley P., 1998a. Canopy development and tillering of field-grown crops of two contrasting cultivars of winter wheat (*Triticum aestivum*) in response to CO<sub>2</sub> and temperature. *In press May 1998 Annals Applied Biology* vol **113**.
- Batts G.R., Ellis R.H., Morison J.I.L., Nkemka P.N., Gregory P.J. & Hadley P., 1998b. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO<sub>2</sub> and temperature in field studies using temperature gradient tunnels. *Journal of Agricultural Science*, (Cambs) **130**, 17-27.
- Bowes G., 1996. Photosynthetic responses to changing atmospheric carbon dioxide concentration. In: *Photosynthesis and the Environment*, (ed. N.R. Baker), pp. 387-407. *Advances in Photosynthesis* Vol. 5. Kluwer, Dordrecht.
- Brooks A. & Farquhar G.D., 1985. *Planta* **165**, 397-406.
- Callaway R.M., DeLucia E.H., Thomas E.M. & Schlesinger W.H., 1994. Compensatory responses of CO<sub>2</sub> exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO<sub>2</sub> and temperature regimes. *Oecologia* **98**, 159-166.
- Caemmerer S. von & Farquhar G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**, 376-387.
- Choudhury B.J. & Monteith J.L., 1986. Implications of stomatal response to saturation deficit for the heat balance of vegetation. *Agric. Forest Met.* **36**, 215-225.
- Farrar J.F., 1996. Sinks, integral parts of a whole plant. *Journal of Experimental Botany* **47**, 1273-1280.
- Evans J.R. & von Caemmerer S., 1996. Carbon dioxide diffusion inside leaves. *Plant Physiol.* **110**, 339-346.
- Gifford R.M., 1992. Interaction of carbon dioxide with growth-limiting environmental factors in vegetation productivity: implications for the global carbon cycle. *Advances in Bioclimatology* **1**, 24-58.
- Gooding M.J. & Davies W.P., 1997. Wheat production and utilization: systems, quality and the environment. CAB International, Walingford. 355pp.
- Grace J., Ford E.D. & Jarvis P.G., 1981. *Plants and their atmospheric environment*. Blackwells, Oxford.
- Grashoff C., Dijkstra P., Nonhebel S., Schapendonk A.H.C.M. & Van de Geijn, S.C., 1995. Effects of climate change on productivity of cereals and legumes; model evaluation of observed year-to-year variability of the CO<sub>2</sub> response. *Global Change Biology* **1**, 417-428.
- Idso S.B. & Kimball B.A., 1989. Growth responses of carrot and radish to atmospheric CO<sub>2</sub> enrichment. *Environmental and Experimental Botany* **29**, 135-9.
- Jitla D.S., Rogers G.S., Seneweera S.P., Basra A.S., Oldfield R.J. & Conroy J.P., 1997. Accelerated early growth of rice at elevated CO<sub>2</sub> Is it related to developmental changes in the shoot apex ? *Plant Physiology*, **115**, 15-22.
- Jordan D.B. & Ogren W.L., 1984. The CO<sub>2</sub> /O<sub>2</sub> specificity of ribulose-1,5- biphosphate concentration, pH and temperature *Planta* **161**, 308-313.
- Kimball, B. A., Pinter, P. J. Jr., Wall, G. W., Garcia, R. L., LaMorte, R. L., Jak, P. M. C., Frumau, K. F. A. and Vughts, H. F., 1997. Comparisons of responses of vegetation to elevated carbon dioxide in free-air and open-top chamber facilities. In: *Advances in*

- Carbon Dioxide Effects Research*. ASA Special Publication No. 61. ASA/CSSA/SSSA, Madison, Wisconsin, USA, pp.113-130.
- Landau, S., Mitchell R.A.C., Barnett V., Colls J.J., Craigon J., Moore K.L., Payne R.W., 1998. Testing winter wheat simulation models' predictions against observed UK grain yields. *Agricultural and Forest Meteorology*, 89:85- 99
- Lawes J.B. & Gilbert J.H., 1880. J. Roy. Soc. Agric England Series 2 16:173.
- Lawlor D.W. & Keys A.J., 1993. Understanding photosynthetic adaptation to changing climate. In: Plant Adaption to Environmental Stress (eds L. Fowden, T.A. Mansfield & J. Stoddart), pp. 85-106. Chapman and Hall, London.
- Lloyd J., & Farquhar G.D., 1996. The CO<sub>2</sub> dependence of photosynthesis, plant growth responses to elevated CO<sub>2</sub> concentrations and their interaction with soil nutrient status. 1. General principles and forest ecosystems. *Functional Ecology* 10, 4-32.
- Long S.P., 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentration: Has its importance been underestimated? *Plant, Cell & Environment* 14, 729-739.
- Miller J.E., Heagle A.S. & Pursley W.A., 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: II Biomass and development. *Crop Science* 38, 122-128.
- McMurtrie R.E. & Wang Y.P., 1993. Mathematical models of the photosynthetic response of tree stands to rising CO<sub>2</sub> concentrations and temperatures. *Plant, Cell & Env.* 16, 1-13.
- Monteith J.L., 1965. *Evaporation and Environment*. *Symposium of the S.E.B.*, 19. CUP, Cambridge.
- Monteith J.L., 1995. A reinterpretation of stomatal responses to humidity. *Plant, Cell & Env.* 18, 357-364.
- Paul M.J., Driscoll S.P. & Lawlor D.L., 1991. The effect of cooling on photosynthesis, amounts of carbohydrate and assimilate export in sunflower. *Journal of Experimental Botany* 42, 845-852.
- Pury D.G.G. de & Farquhar G.D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell & Env.* 20, 537-557.
- Rawson H.M., 1988. Effects of high temperatures on the development and yield of wheat and practices to reduce deleterious effects. In: *Wheat Production Constraints in Tropical Environments*, (ed. A.R. Klatt,) CIMMYT, Mexico D.F., pp. 44-63.
- Rawson H.M., 1992. Plant responses to temperature under conditions of elevated CO<sub>2</sub>. *Australian Journal of Botany* 40, 473-90.
- Rawson H.M., 1995. Yield responses of two wheat genotypes to carbon dioxide and temperature in field studies using temperature gradient tunnels. *Australian Journal of Plant Physiology* 22, 23-32.
- Tardieu F. & Davies W.J., 1993. Integration of hydraulic and chemical signaling in the control of stomatal conductance and water status of droughted plants *Plant, Cell & Environment*. 16, 341-349.
- Wang Y.-P. & Leuning R., 1998. A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. 1. model description and comparison with a multi-layered model. *Agricultural and Forest Meteorology*, 91:89-111.

## Appendix : List of references related to MODEXCROP

### *Original Journal papers*

1. Morison J.I.L., Batts G.R., Ellis R.H., Wheeler, T.W., M.C. Puche, Nkemka P.N., Hadley P., 1998. Effects of increased CO<sub>2</sub> on temperature responses of apical development in contrasting cultivars of winter wheat *submitted* to J. Expt. Botany July 1998.
2. Batts G.R., Ellis R.H., Morison J.I.L., Hadley P., 1998. Canopy development and tillering of field-grown crops of two contrasting cultivars of winter wheat (*Triticum aestivum*) in response to CO<sub>2</sub> and temperature. *In press May 1998 Annals Applied Biology* vol 113.
3. Batts G.R., Ellis R.H., Morison J.I.L., Nkemka P.N., Gregory P.J., Hadley P., 1998. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO<sub>2</sub> and temperature in field studies using temperature gradient tunnels. *J. Agric. Science, (Cambs)* 130: 17-27.
4. Batts, G.R., Morison, J.I.L., Ellis, R.H., Hadley, P. & Wheeler, T.R., 1997. Effects of CO<sub>2</sub> and temperature on growth and yield of crops of winter wheat over several seasons. *European J. Agronomy* 7: 43-52.

### *Review Articles:*

5. Morison, J.I.L. & Lawlor D.W., 1998. Interactions between increased CO<sub>2</sub> and temperature on plant growth. *Submitted* to Plant, Cell & Environment Special Issue.
6. Morison, J.I.L., 1996. Global Environmental Change impacts on crop growth and production in Europe. "Implications of Global Environmental Change for crops in Europe", *Aspects of Applied Biology* 45: 62-74, Association of Applied Biologists.
7. Morison, J.I.L., 1996. Climate Change and Crop Growth. in Special Issue of Environmental Management and Health, 7:24-27.



# **MODEXCROP project**

**Model evaluation of experimental variability to improve predictability of  
crop yields under climate change.**

**Report No. 2 from The Royal Veterinary and Agricultural University  
(Denmark)**

*Frank Ewert & John R Porter*

**August 1998**



**THE ROYAL VETERINARY & AGRICULTURAL UNIVERSITY**  
**Department of AGRICULTURAL SCIENCES, AGRO-ECOLOGY**

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## Summary

The present report analyses hitherto unexplained yield variability of the climate change experiment ESPACE-wheat which was performed in open-top chambers (OTC) at nine sites throughout Western Europe between 1994-96. Reasons for unexplained variations in final biomass and grain yield and in the response of final biomass and grain yield to elevated CO<sub>2</sub> are identified by analysing the predictability of intermediate variables and underlying mechanisms. This analysis is performed using the mechanistic crop simulation model AFRCWHEAT2-O3. Simulations of other wheat models were compared for processes which had a major impact on the unexplained variations in biomass and grain yield. A relevant part of this model comparison was performed using data from a drought experiment carried out in New Zealand in 1991/92. The adaptation of existing algorithms and modules is discussed and conclusion for future work are derived from the results of this analysis.

Unexplained variations in final biomass and grain yield in ambient air and CO<sub>2</sub> elevated chambers were mainly caused by poor simulation of leaf area dynamics (leaf area index and leaf area duration). Variation of LAI at anthesis was further analysed. Limitations of AFRCWHEAT2-O3 in not simulating the observed effects of plant density on leaf size and of CO<sub>2</sub> elevation on leaf size and tiller number were identified as the main reasons for the poor simulation of LAI at anthesis. However, other model approaches did not show improvement in the simulation of LAI. The complexity of the effects of weather, elevated CO<sub>2</sub> and crop management on leaf size and tiller number and a consideration of these effects in crop simulation models is discussed. Differences in the experimental procedure were found to have contributed to the unexplained variation of the CO<sub>2</sub> effect on biomass production. The effect of CO<sub>2</sub> elevation on biomass of plants grown in pots or chambers without border plants responded differently to plant density and chamber temperature from the model indicating that photosynthetic responses of wheat plants to elevated CO<sub>2</sub> can vary dependent on the experimental performance.

From the results of the present analysis we conclude that:

- Mechanistic crop simulation models are a useful tool to improve the understanding of unexplained variation in crop growth and yield.
- Unexplained variation in leaf area dynamics is the main source of the unexplained variation in crop growth and yield for a number of environmental conditions.
- Climate change experiments demand a high standardization in the experimental performance (soil properties, water and nutrient availability, crop management).
- There are considerable differences among wheat models in simulating canopy development in response to weather, CO<sub>2</sub> and drought.
- There is a general need to improve the modelling of canopy development for conditions of climatic change.
- Understanding of the complexity of processes determining leaf area dynamics in response to climate change and crop management is limited and needs to be improved. Understanding compensation and competition processes within the canopy might provide useful solutions applicable for crop simulation models.

## 2.1 Introduction

Experiments which aim to look at the effects of climate change on crop growth and yield have shown unexpected and, so far, unexplained variation.

It was the aim of the present project to use detailed mechanistic crop simulation models to analyse existing datasets, and give a clue to the origin of - and mechanism behind - the variability of crop growth and yield.

The aims of our group within this project were:

- further analysis of existing data sets on the effects of climate change on wheat.
- sensitivity analysis (CO<sub>2</sub>, temperature, light, nutrients) of model outcome with respect to underlying processes.
- model comparison and improvement (AFRCWHEAT2 and others).

Within the MODEXCROP project it was agreed that the work of our group would focus on analysing yield variability in the climate change experiment ESPACE-wheat. The ESPACE-wheat dataset has shown a high variability in growth and yield and in the responses of growth and yield to elevated CO<sub>2</sub>. Mechanistic crop simulation models could explain only part of this variation (Ewert and Porter, 1997; Ewert *et al.*, 1998; van Oijen and Ewert, 1998). In the present project we performed a detailed analysis of the unexplained yield variability observed in the ESPACE-wheat experiment. This analysis was based on the complex process-orientated crop simulation model AFRCWHEAT2-O3. Further, an extended model comparison was performed. The predictions of growth and developmental processes of five wheat simulation models were compared with data from a drought experiment performed at Lincoln, New Zealand.

The present report summarizes our work as follows:

- Identification of unexplained variability based on a process-orientated analysis of model predictions using AFRCWHEAT2-O3.
- Analysis of the causes of identified unexplained variability.
- Comparison of model simulations for processes which were simulated unsatisfactorily with AFRCWHEAT2-O3.
- Critical discussion of model improvement.

## 2.2 Materials and methods

### 2.2.1 Experiments

#### 2.2.1.1 ESPACE-Wheat

In ESPACE-wheat, a series of open-top chamber (OTC) experiments were performed to investigate the effects of CO<sub>2</sub> and physiological stresses on wheat growth and development for different climatic conditions. The experiments were at nine sites throughout Europe and in up to three years at each site (Table 1). All OTC experiments had a randomized design with two or three replicates and a number of treatments differing among sites. An extended description of all ESPACE-wheat experiments is given in Hertstein *et al.* (1998). The present analysis refers to the

ambient chamber and the high CO<sub>2</sub> treatment (2 x ambient). Temperature was an additional factor at one location (Table 1) and this treatment is also considered in the present analysis. Variation in the climatic conditions was achieved by the geographical distribution of the experimental sites and the performance of the experiments over a period of up to three years (Fig. 1a, b).

**Table 1.** Sites, geographical coordinates, years, treatment factors and experimental conditions of the ESPACE-wheat experiments considered in the present analysis. Standard experimental conditions were spring wheat *cv.* Minaret field sown in OTCs and surrounded by border plants. E, east; W, west; Pots, plants were grown in pots.

Site	Latitude; Longitude	Years	Treatment factors		Experimental conditions			
			CO <sub>2</sub>	T	Pots	Border plants	Chamber size (m)	
							Diameter	Height
Giessen, D	50.3; 8.41 E	94, 95, 96	x		x		3.1	2.4
Braunschweig, D	52.2; 10.3 E	94, 95, 96	x		x(94)		3.1	2.4
Carlow, Ire	52.5; 6.55 W	95, 96	x				3.0	2.8
Sutton Bonington, UK	52.8; 1.12 W	95, 96	x			x	3.1	2.4
Pau, F	43.2; 0.22 W	95, 96	x				3.0	2.8
Roskilde, DK	55.4; 12.1 E	94, 95, 96	x				1.5	1.8
Göthenburg, S <sup>1)</sup>	57.5; 12.0 E	95, 96	x				1.2	1.6
Tervuren, B	50.5; 4.31 E	94, 95, 96	x			x	3.0	2.8
Wageningen, NL	51.6; 5.39 E	95, 96	x	x		x	1.5	1.9

1) spring wheat *cv.* Dragon was grown in OTC instead of spring wheat *cv.* Minaret

Plants of spring wheat *cv.* Minaret were grown according to a standard protocol agreed between the partners of the ESPACE-wheat project. However, there were a series of factors which varied among experimental sites and years. Open-top chambers differed in height and diameter among the experimental sites (Table 1). Only few locations grew border plants around the OTC (Table 1). Sowing density was not constant among sites and years and varied from 120 to 380 plants m<sup>-2</sup> (Fig. 1c). Since it was not possible to use a standard soil in all experiments, each site had to use a local soil. However, in all selected treatments water and nutrients were supplied to avoid additional stresses. Pests and weeds were controlled as required. All chambers were supplied with non-filtered ambient air. CO<sub>2</sub> exposure started after plants had emerged and continued until maturity. CO<sub>2</sub> concentrations was recorded continuously in each treatment. Climate data, such as temperature, radiation and humidity were measured continuously inside and outside the chambers throughout all seasons.

The present study refers to selected measurements of crop growth and development which were performed at each site with a standard procedure. An area of fifty plants was marked in each

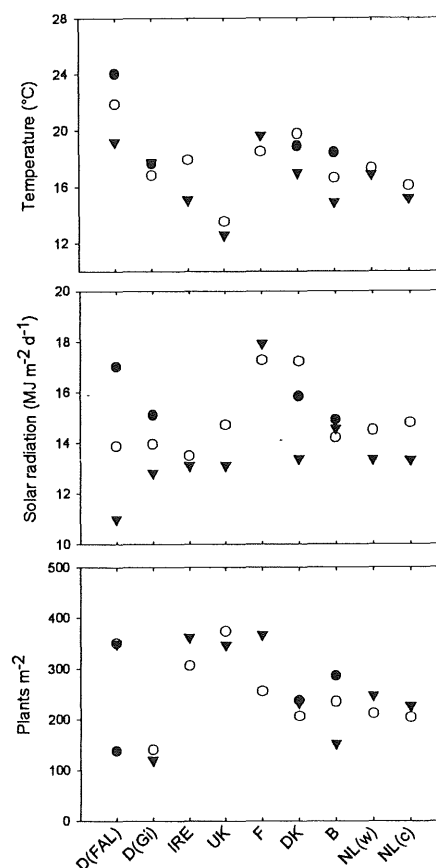
chamber to observe plant development non-destructively. Developmental stages were recorded according to a decimal code (Tottman and Broad, 1987). Five plants in the marked area were selected to record the cumulative leaf number on the main stem and the number of tillers per plant twice a week. Tiller number per plant, green leaf area index (LAI) and biomass per plant were measured destructively at growth stages DC31, anthesis and maturity for all OTCs. However, most sites performed two and more intermediate harvests to obtain additional measurements of plant growth. Finally, grain yield was measured destructively at maturity. A few sites were not able to perform all measurements in all years. Thus, the number of data slightly differ for the different growth and developmental variables analysed in this paper.

### 2.2.1.2 Drought experiment

A drought experiment with wheat (*cv.* Batten) sown in winter in New Zealand (8 June, 1991) in a mobile automatic rainshelter was performed at the New Zealand Institute for Crop and Food Research experimental station at Lincoln in Canterbury (latitude 43°38' S, longitude 172°30' E). The experiment is described in detail by Jamieson *et al.* (1995, 1998a).

The seven treatments chosen for analysis here are a subset of those reported by Jamieson *et al.* (1995), chosen for the greatest contrast, and excluding several treatments where performance did not differ from the control treatment. The treatments were:

- Control (1). Irrigated each week from August 29 until January 9.
- Early drought (3, 5). Irrigation of 20 mm on August 29, then no irrigation for 6 and 10 weeks respectively, then irrigated as the control. This meant irrigation recommenced about four weeks before anthesis in treatment 3, and four weeks after anthesis in treatment 5.
- Late drought (6,7,8). Irrigated for four, seven and ten weeks respectively from August 29 as for the control, and then no further irrigation. This meant the last irrigations were seven, four and one week before anthesis respectively.



**Figure 1.** Mean seasonal temperatures and solar radiations from sowing to maturity and plant densities for spring wheat *cv.* Minaret grown at different sites and years (●, 1994; ○, 1995; ▼, 1996) in ESPACE-Wheat.

- Full drought (11). This treatment received no irrigation.

In the present analysis we only refer to LAI data. Samples of 0.2 m<sup>2</sup> were taken at 2-week intervals until anthesis, and thereafter at approximately 5-day intervals. The leaf area and dry mass of a 10 tiller subsample were measured, and LAI calculated from the leaf area ratio (LAR) and total sample dry mass.

## 2.2.2 Model description

### 2.2.2.1 AFRCWHEAT2-O3

The present analysis was performed using the complex process-orientated crop simulation model AFRCWHEAT2 (Porter, 1993). The model comprises five submodels: phenological and canopy development, dry matter production and partitioning and grain growth (Weir *et al.* 1984, Porter, 1984) and includes subroutines that describe the movement of water and nitrogen within the soil profile and their uptake and effects on growth (Porter, 1993). AFRCWHEAT2 simulates phenology and canopy development on a high level of mechanistic detail considering the processes of leaf and tiller emergence, growth and senescence (Porter, 1984). The model was extended (AFRCWHEAT2-O3) to enable simulations to be made of the response of wheat to CO<sub>2</sub> and ozone (Ewert & Porter, 1997, 1998). The plant growth response to CO<sub>2</sub> is realized introducing the biochemical model of Farquhar *et al.* (1980) which is combined with a stomatal model (Leuning, 1995). The stomatal model also considers the effect of vapour pressure deficit on stomatal conductance (Leuning, 1995). Photosynthetic rate is considered to decline with leaf age and is calculated for every leaf age cohort assuming the youngest leaves at the top of the canopy. The radiation interception model is similar to that of Charles-Edwards (1978).

The time step of the model is one day except for the productivity submodule which simulates the assimilation rate in hourly steps. For the analysis of the ESPACE-wheat data water and nitrogen were assumed to be not limiting. The present version of the model runs with input data of temperature, radiation, vapour pressure deficit, CO<sub>2</sub> and ozone concentration.

### 2.2.2.2 Other models

It was one aim of the present analysis to compare the performance of different simulation models. We restrict our presentation of the results of the model comparison to processes of which the unpredicted variation was identified as a main contributor to the unexplained variation in final biomass and grain yield.

In ESPACE-wheat, a second model, LINTULCC, was used to simulate the effects of elevated CO<sub>2</sub> and physiological stresses on wheat growth and yield. The model is described and the simulation results are presented in van Oijen and Goudriaan (1997). LINTULCC simulates different processes, particularly leaf area dynamics with less mechanistic detail than AFRCWHEAT2-O3.

Data of the drought experiment described above were used to compare the predictions of five simulation models, AFRCWHEAT2 (Porter, 1993), CERES-Wheat (Ritchie and Otter, 1985;

version June 1994), Sirius (Jamieson *et al.*, 1998b), SWHEAT (van Keulen and Seligman, 1987) and SUCROS2 (van Laar *et al.*, 1992; version November 1994). These models differ considerably in complexity. Sirius is the simplest, treating the canopy as a single entity, producing biomass as the product of intercepted light and LUE, and making no calculation of yield components. At the other end of the scale, AFRCWHEAT2 is the most complex, particularly in simulating LAI, crop assimilation rate and grain population as a sink term determining grain yield. An extended description of model differences and similarities is given in Jamieson *et al.* (1998a).

## 2.3 Results

### 2.3.1 Analysis of yield variability in ESPACE-Wheat

#### 2.3.1.1 Variation in final biomass and grain yield

In ESPACE- wheat average final above-ground biomass and grain yield of the ambient chamber plots were 1230 g m<sup>-2</sup> and 596 g m<sup>-2</sup>, respectively (Table 2). However, both final biomass and grain yield varied greatly among sites and years (Table 2).

**Table 2.** Means and standard deviations of observed final grain yield (g m<sup>-2</sup>), total above-ground biomass (g m<sup>-2</sup>) at anthesis and maturity and LAI at anthesis from ambient air chambers and of the observed effects of elevated CO<sub>2</sub> (relative, 750/350) on biomass and grain of spring wheat cv. Minaret grown at different sites and years in ESPACE-Wheat.

Measurement	Ambient air					CO <sub>2</sub> effect				
	Observed		Simulated			Observed		Simulated		
	Mean	sd	Mean	sd	sd	Mean	sd	Mean	sd	sd
Grain yield	596	190	538	104	163	1.29	0.21	1.24	0.09	0.20
Biomass (mat.)	1230	315	1150	233	290	1.29	0.18	1.23	0.05	0.17
Biomass (an.)	824	263	973	167	248	1.28	0.31	1.18	0.04	0.32
LAI (an.)	3.7	1.53	4.9	1.07	1.78	1.15	0.39	1.02	0.01	0.39

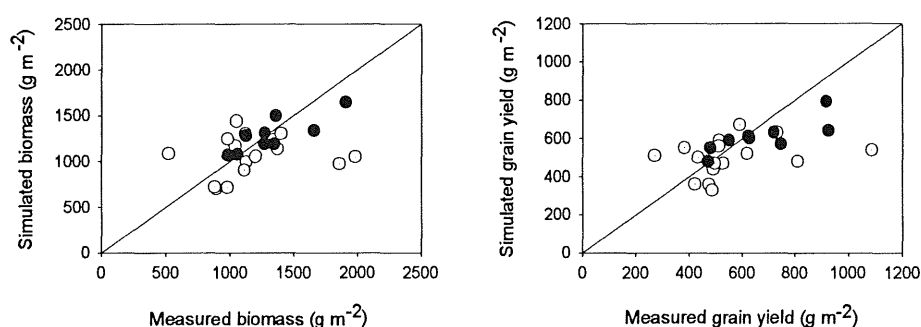
Doubling the ambient CO<sub>2</sub> concentration in the experiment increased final biomass and grain yield on average by about 29 percent and 31 percent, respectively (Table 2). Again, high variation in the effect of CO<sub>2</sub> on biomass and grain yield was observed among sites and years.

Variation in temperature, radiation and sowing density could neither explain variation in biomass and grain yield nor variation in the effects of elevated CO<sub>2</sub> on both, biomass and grain yield (Ewert and Porter, 1997). Obviously, factors varying in the experiment affected growth and yield of spring wheat cv. Minaret in a more complex way.

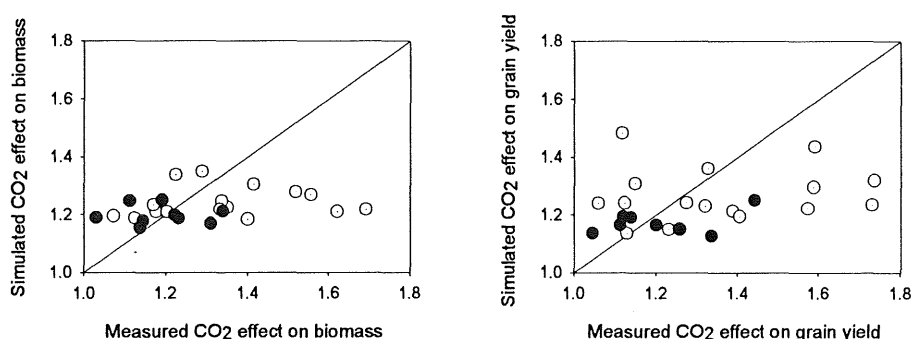
### 2.3.1.2 Identification of unexplained variability

#### 2.3.1.2.1 Experimental and model performance

AFRCWHEAT2-O3 was applied to simulate growth and yield of spring wheat *cv.* Minaret in the ESPACE-wheat project (Table 2, Fig. 2). The observed experimental averages of final total above-ground biomass and grain yield were simulated closely by the model (Table 2). However, the model could not reproduce satisfactorily the observed variation in final biomass and grain yield (Table 2, Fig. 2). The observed effects of elevated CO<sub>2</sub> on final biomass and grain yield were underestimated by the model and, again, simulations of the variation in the CO<sub>2</sub> effects on both, biomass and grain yield were poor (Table 2, Fig. 3).



**Figure 2.** Simulated vs. measured data of final above-ground biomass and grain yield for spring wheat *cv.* Minaret grown in ESPACE-Wheat. Full circles indicate experiments in which border plants were grown around the OTCs (see Table 1).



**Figure 3.** Simulated vs. measured data of the effects of elevated CO<sub>2</sub> (relative, 700/350) on final above-ground biomass and grain yield for spring wheat *cv.* Minaret grown in ESPACE-Wheat. For explanation of full and open circles see Fig. 2 and Table 1.

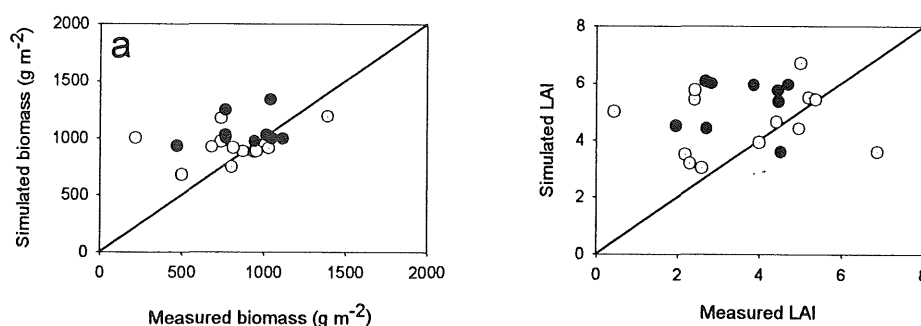
As a result of a first analysis of the model simulations Ewert *et al.* (1998) and van Oijen and Ewert (1998) concluded that factors such as water supply and chamber design, which were not supposed to vary among sites and years and were thus, not considered in the model, have caused the high level of unexplained variability in the ambient chamber plots. This conclusion was supported by the fact that simulations for experiments which reproduced field conditions best (i.e. plants were grown in the field and surrounded by border plants; Table 1) were close to the observations (Fig. 2).

### 2.3.1.2.2 Simulation of intermediate variables and underlying processes

Mechanistic crop simulation models offer the opportunity to analyse the simulations of intermediate variables and underlying processes. This helps to identify processes which were simulated poorly and which have thus caused poor prediction of site-specific yields. Generally, crop biomass production is physiologically determined by the rate of assimilation and the size of the assimilation area (canopy), (Lawlor, 1995). The structure of AFRCWHEAT2-O3 closely follows this approach. In ESPACE-wheat detailed measurements were available to analyse the simulation of biomass production and canopy development.

#### *Ambient CO<sub>2</sub> conditions*

In a first step we analysed the simulations of above-ground biomass and LAI at anthesis. AFRCWHEAT2-O3 overestimated total above-ground biomass at anthesis on average by about 150 g m<sup>-2</sup> (Table 2). Since final biomass was predicted closely this simulation also implies that the model underestimated the production of biomass between anthesis and maturity. Analysing the simulation of LAI at anthesis shows that AFRCWHEAT2-O3 overestimates LAI on average by about 1.2 m<sup>2</sup> m<sup>-2</sup> (Table 2). The results also show that not only the mean but the variation in both biomass and LAI at anthesis were simulated poorly even for experiments which were performed closest to field conditions (Table 2, Fig. 4).



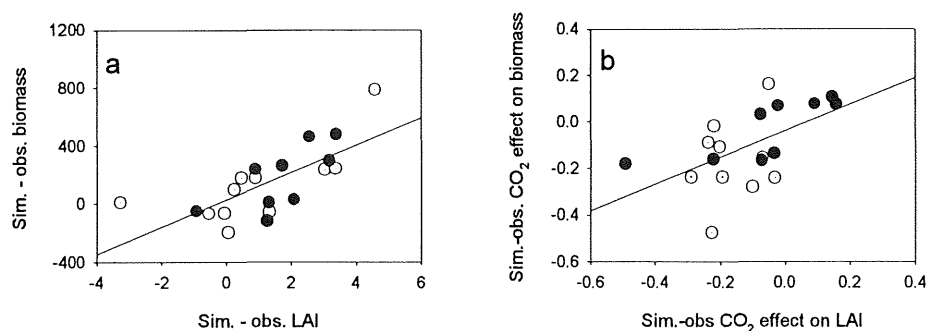
**Figure 4.** Simulated vs. measured data of above-ground biomass at anthesis and LAI at anthesis for spring wheat cv. Minaret grown in ESPACE-Wheat. For explanation of full and open circles see Fig. 2 and Table 1.



### *Elevated CO<sub>2</sub> conditions*

Above-ground biomass at anthesis was increased by about 28 percent (Table 2) due to doubling the ambient CO<sub>2</sub> concentration in ESPACE-wheat. This CO<sub>2</sub> effect was underestimated by the model. AFRCWHEAT2-O3 predicted an increase in biomass at anthesis of only 18 percent due to CO<sub>2</sub> elevation (Table 2). LAI at anthesis was observed to be increased due to CO<sub>2</sub> elevation by about 15 percent (Table 2). No such effect was simulated by the model since the corresponding mechanism has not been considered in the model (Table 2). Again, prediction of variation the CO<sub>2</sub> effect on biomass and LAI was poor (Table 2).

These results indicate that poor prediction of biomass and the effects of elevated CO<sub>2</sub> on biomass at anthesis was associated with poor prediction of LAI at anthesis. Corresponding relationships between the goodness of the simulations of biomass and LAI for ambient and elevated CO<sub>2</sub> conditions clearly confirm this finding (Fig. 5).

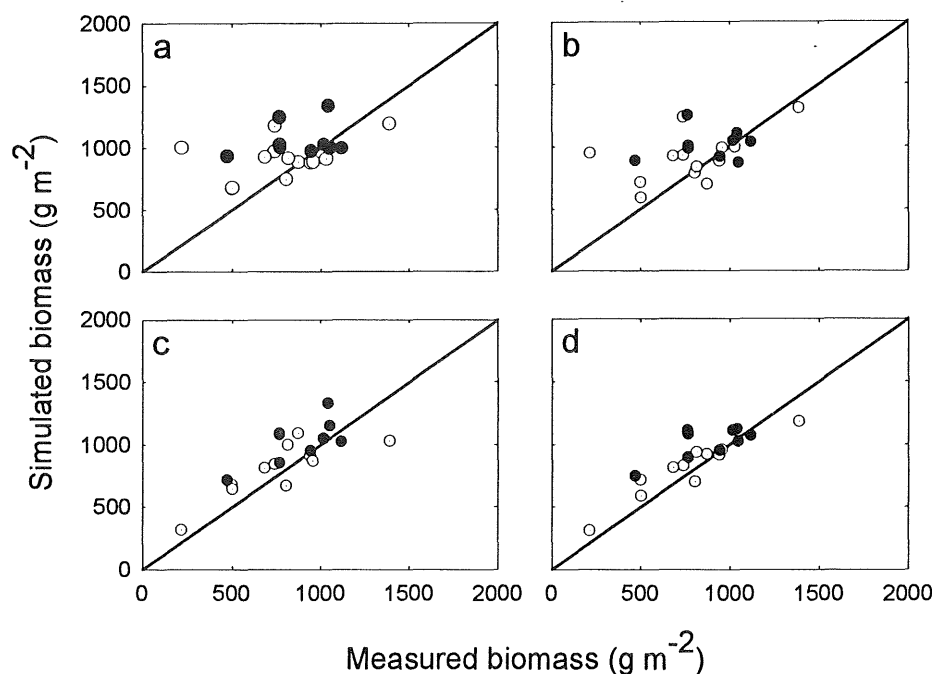


**Figure 5.** Relationships between a) the differences between simulated and observed biomass at anthesis and the differences between simulated and observed LAI at anthesis and b) the differences between simulated and observed CO<sub>2</sub> effect on biomass at anthesis and the differences between simulated and observed CO<sub>2</sub> effect on LAI at anthesis. The fitted regressions are of the form  $y=a+bx$ . Selected regression statistics are: a)  $p=0.00043$ ,  $r^2=0.51$ ; b)  $p=0.013$ ,  $r^2=0.31$ . For explanation of full and open circles see Fig. 2 and Table 1.

#### *2.3.1.2.3 Verification of identified unexplained variability*

We have identified the poor prediction of LAI as the main reason for the poor predictions of the variation in biomass at anthesis and for the poor prediction of the CO<sub>2</sub> effect and the variation of this effect on biomass at anthesis. Consequently, any improvement in the simulation of LAI should improve the simulation of biomass at anthesis and maturity as well as the simulation of the final grain yield. In ESPACE-wheat all sites recorded plant development and most sites performed several measurements of LAI throughout the growing season. These measurements enabled us to run the model with observed development and LAI data. We performed separate simulations

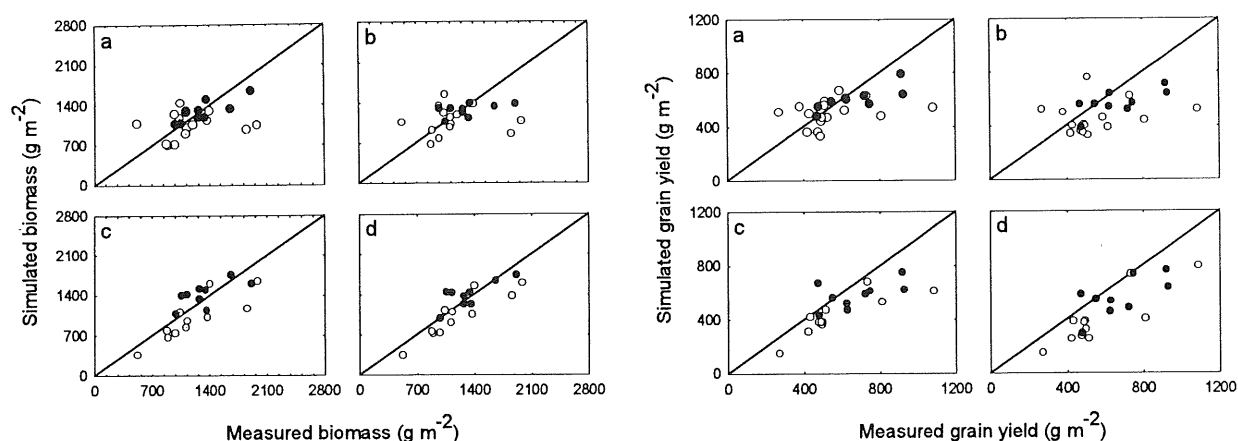
for above-ground biomass at anthesis (Fig. 6) and maturity and final grain yield (Fig. 7) using i) observed development data, ii) observed LAI data and iii) both, observed development and LAI data. This procedure to distinguish between the input of development and LAI data enabled us to clarify whether the poor predictions of the variations in biomass and grain yield were caused by unsatisfactory simulations of either the time course or the magnitude of LAI.



**Figure 6.** Simulated vs. measured above-ground biomass at anthesis using different input data for canopy development of spring wheat cv. Minaret grown in ESPACE-Wheat. a) simulated phenological stages and LAI, b) observed phenological stages and simulated LAI, c) simulated phenological stages and observed LAI and d) observed phenological stages and LAI. For explanation of full and open circles see Fig. 2 and Table 1.

#### *Ambient CO<sub>2</sub> conditions*

The simulations of the variation of above-ground biomass at anthesis (Fig. 6) and maturity (Fig. 7) improved when we used observed data of plant development and LAI. However, consideration of observed development stages had little effect on the simulations. We got the best improvement in the simulations when we used observed LAI data. Simulation of the variation in grain yield was



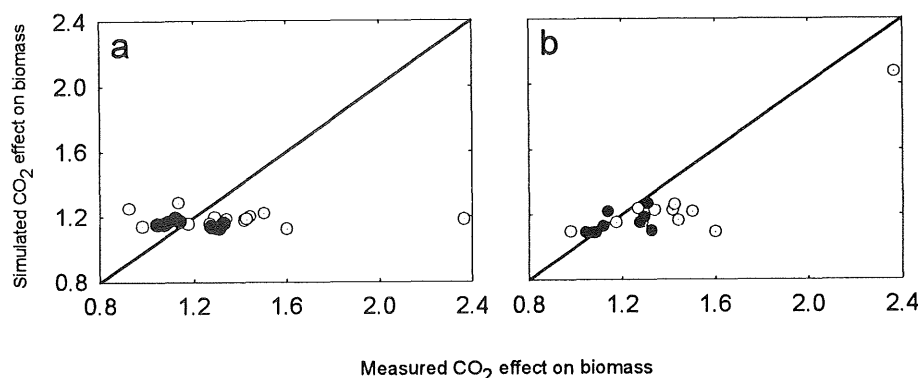
**Figure 7.** Simulated vs. measured data of above-ground biomass at maturity and grain yield using different input data for canopy development of spring wheat cv. Minaret grown in ESPACE-Wheat. For explanations see Fig. 6.

also improved using observed LAI and development data (Fig. 7). However, there was asystematic underestimation of the final grain yield (Fig. 7) which was basically due to poor simulation of the number of grains per ear by the model (not shown). The limitation of the current algorithm in the model to predict grain number per ear for varying climatic conditions has been discussed recently (Mitchell *et al.*, 1995, Jamieson, *et al.*, 1998a).

#### *Elevated CO<sub>2</sub> conditions*

We have shown that the present model underestimated mean and variation of the effect of elevated CO<sub>2</sub> on total above-ground biomass at maturity and grain yield (Table 2, Fig. 3). Similar results were obtained for the simulation of the CO<sub>2</sub> effect on biomass at anthesis (Table 2). There was no improvement in the simulations of the CO<sub>2</sub> effect on biomass at anthesis when we used observed LAI and development data of the ambient OTC as input data (not shown). This was not surprising since the model does not consider a CO<sub>2</sub> effect on LAI. Thus, we finally simulated biomass production in the elevated CO<sub>2</sub> treatments using observed development and LAI data as model input. Surprisingly, there was only little improvement in the simulations of the CO<sub>2</sub> effect on biomass at anthesis (Fig. 8). Consequently, the improvement in the simulation of total above-ground biomass at maturity and final grain yield were also rather small (not shown). However, poor simulations were mainly achieved for experiments where plants were grown in pots or without border plants (Fig. 8). Simulations of the CO<sub>2</sub> effect on biomass at anthesis were improved for experiments which were performed closest to field conditions (Fig. 8).

The present results identify poor simulation of LAI as the main reason for the poor simulation of the variation of biomass and grain yield among sites and years in the ambient chambers. AFRCWHEAT2-O3 also underestimated the average observed CO<sub>2</sub> effects on biomass and grain yield since the model does not account for a effect of CO<sub>2</sub> on LAI. Surprisingly, there was little improvement in the predictions of the observed effects of elevated CO<sub>2</sub> on biomass and grain yield using development and LAI data as model input which however was dependent on other experimental conditions. Thus, it remains to be clarified: i) why was LAI predicted poorly? and,



**Figure 8.** Simulated vs. measured effect of elevated CO<sub>2</sub> (relative, 700/350) on above-ground biomass at anthesis using different input data for canopy development of spring wheat *cv.* Minaret grown in ESPACE-Wheat. a) simulated phenological stages and LAI, b) observed phenological stages and LAI. For explanation of full and open circles see Fig. 2 and Table 1.

ii) why were the predictions of the CO<sub>2</sub> effects on biomass and grain yield unsatisfactory even when observed LAI data were used as model input?

### 2.3.1.3 Causes of unexplained variability

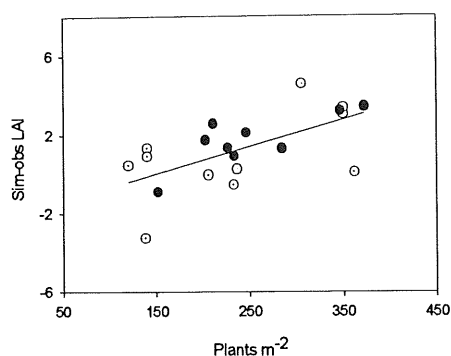
#### 2.3.1.3.1 Model limitations

Analysing the reasons for the poor prediction of LAI and the CO<sub>2</sub> effect on biomass and grain yield we generally distinguish between limitations in the model and in the experiment. AFRCWHEAT2-O3 simulates canopy development at a detailed level. LAI is simulated as the result of leaf and tiller emergence, growth and senescence (Porter, 1984). Most sites in ESPACE-wheat performed measurements of these processes which enabled us to analyse the model simulations in more detail.

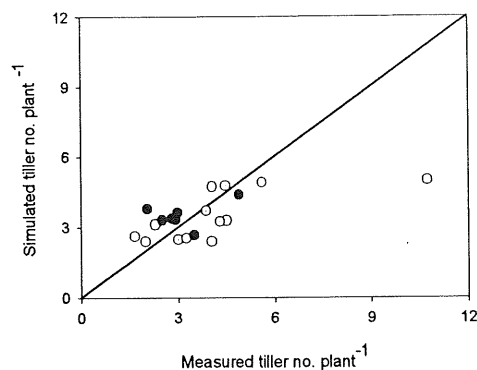
#### *Ambient CO<sub>2</sub> conditions*

We first analysed, for ambient chamber conditions, whether the poor prediction of LAI was related to other factors varying in ESPACE-wheat. There was variation in temperature, radiation and plant density among the experiments of ESPACE-wheat (Fig. 1). We found no relationships between the goodness of the site and year specific prediction of LAI at anthesis and the variation in mean temperature and mean solar radiation for the period from plant emergence until anthesis. However, there was a positive linear relationship between the differences in simulated and observed LAI and plant density (Fig. 9) indicating that prediction of LAI was particularly poor when plant densities were low or high (Fig. 9).

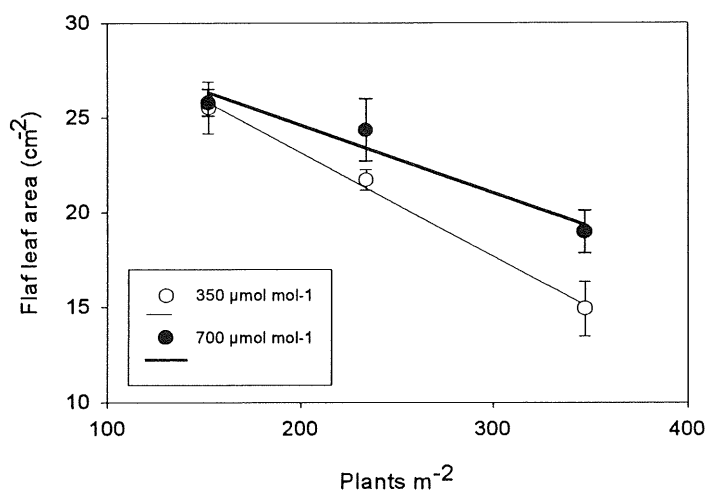
Detailed analysis of the underlying processes showed that the model simulated tiller (Fig. 10) and leaf number (Ewert *et al.*, 1998) at anthesis reasonably closely. LAI is determined by the number of leaves per unit area and the leaf size. In AFRCWHEAT2-O3, leaf size changes with leaf age



**Figure 9.** Differences between simulated and observed LAI at anthesis vs. plant density of spring wheat *cv.* Minaret grown in ESPACE-Wheat. For explanation of full and open circles see Fig. 2 and Table 1.



**Figure 10.** Simulated vs. observed number of tillers per plant of spring wheat *cv.* Minaret grown in ESPACE-Wheat. For explanation of full and open circles see Fig. 2 and Table 1.



**Figure 11.** Relationships between flag leaf area and plant density for ambient and elevated ( $2 \times$  ambient)  $\text{CO}_2$  of spring wheat *cv.* Minaret grown at selected sites in ESPACE-Wheat. The fitted regressions are for;  
 ambient  $\text{CO}_2$ :  $y = 34.07(\text{S.E.} = 0.99) - 0.055(\text{S.E.} = 0.0039)x$  ( $r^2 = 0.99$ ),  
 elevated  $\text{CO}_2$ :  $y = 31.71(\text{S.E.} = 2.15) - 0.036(\text{S.E.} = 0.0084)x$  ( $r^2 = 0.95$ ).

group (Porter, 1984). Within each leaf age group the size of the leaf is assumed to be constant and only decreases in water and nitrogen limited conditions (Porter, 1993). However, water and nitrogen were supposed to be non-limiting in the ESPACE-wheat experiments. Few ESPACE-wheat sites performed measurements of the size of the flag leaves. Interestingly, there was a large

variation in the size of the flag leaf among those experiments which we could explain by variation in plant density (Fig. 11). No such relationship is considered in the model.

#### *Elevated CO<sub>2</sub> conditions*

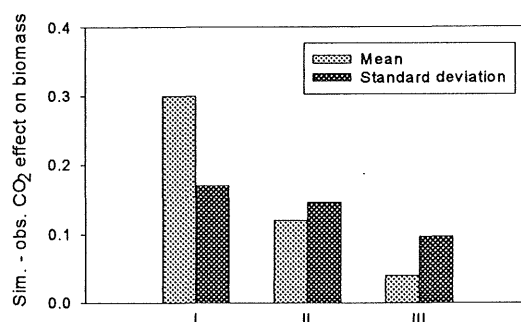
The analysis of the experimental data further indicated that leaf size increased with CO<sub>2</sub> elevation which, however, was also dependent on plant density (Fig. 11). Ewert and Pleijel (1998) have shown that CO<sub>2</sub> elevation also increased tiller number in ESPACE-wheat. However, they could not detect a relationship between the CO<sub>2</sub> effect on tiller number and the CO<sub>2</sub> effect on LAI. Thus, the CO<sub>2</sub> effect on LAI in ESPACE-wheat was a combined result of the CO<sub>2</sub> effects on tiller number and leaf size. AFRCWHEAT2-O3 does not predict an effect of elevated CO<sub>2</sub> on LAI since it does not account for the responses of tillering and leaf growth to CO<sub>2</sub> concentration.

#### *2.3.1.3.2 Experimental limitations*

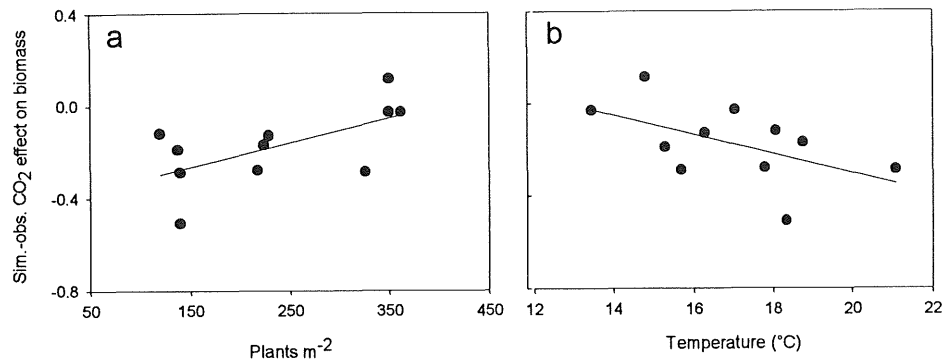
We have shown that the variation in plant density could explain much of the poor prediction of LAI, biomass and grain yield most likely via an effect of plant density on leaf size, a relationship not considered in the model.

Differences in the experimental performance might explain the rather poor prediction of the CO<sub>2</sub> effect on biomass (Fig. 8b) and grain yield of the simulations in which observed development and LAI data of the elevated CO<sub>2</sub> treatments were used as model input data. We separated the simulation results into three groups; i) experiments with plants grown in pots, ii) experiments sown in the field but without border plants, and iii) experiments sown in the field and surrounded by border plants. The simulations of the CO<sub>2</sub> effects on biomass at anthesis clearly differ among these groups (Fig. 12). The simulations were in best agreement with the observations for the experiments performed closest to field conditions and particularly poor for the experiments where plants were grown in pots (Fig. 12).

It remains to be clarified which factors are responsible for the poor simulations in the groups I and II. Interestingly, for these two groups we found a negative relationship between the goodness-of-fit of the simulations of the CO<sub>2</sub> effect on biomass at anthesis and the mean temperature of the period from emergence to anthesis (Fig. 13). There was also a positive relationship between the



**Figure 12.** Means and standard deviations of the differences between simulated and observed effects of elevated CO<sub>2</sub> (relative, 700/350) on total above-ground biomass at anthesis of three different groups of ESPACE-wheat experiments (I, plants grown in pots and without border plants; II, plants grown in the field and without border plants; III, plants grown in the field and with border plants). For experimental description see Table 1. Simulation conditions were the same as in Fig. 8a.



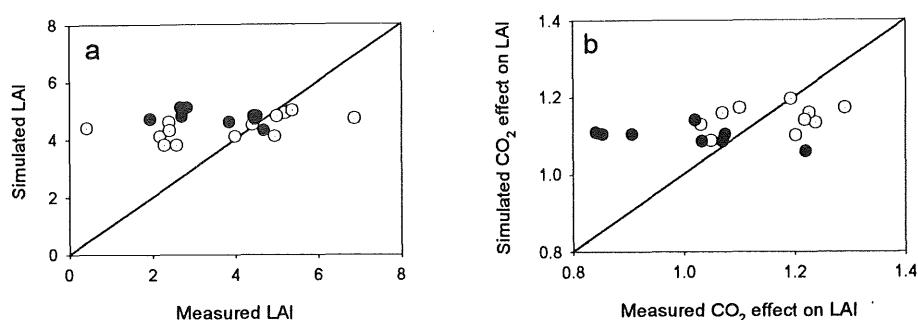
**Figure 13.** Differences between simulated and observed effects of elevated CO<sub>2</sub> (relative, 700/350) on total above-ground biomass at anthesis in relationship to a) plant density and b) mean temperature from plant emergence until anthesis of spring wheat *cv.* Minaret grown in ESPACE-wheat experiments considered in the groups I and II (see Fig. 12). The fitted regressions are of the form  $y=a+bx$ . Selected regression statistics are: a)  $p=0.05$ ,  $r^2=0.36$ ; b)  $p=0.097$ ,  $r^2=0.28$ .

simulation results and plant density (Fig. 13). No such relationships were found for the experiments performed closest to field conditions. Obviously, the CO<sub>2</sub> effect on the crop assimilation rate of plants grown in pots, small chambers or chambers without border plants respond differently to temperature and plant density as it is considered in the model. In AFRCWHEAT2-O3, wheat growth and development is modelled for field conditions. Thus, effects of temperature or radiation on growth and development caused by missing border plants are not considered in the model.

### 2.3.2 Model comparison

#### 2.3.2.1 ESPACE-Wheat

It was one aim of the present project to compare different models in their ability to simulate the variation of crop yield under climate change. A second model, LINTULCC, was used to simulate growth and yield in ESPACE-wheat (van Oijen and Goudriaan, 1997). LINTULCC simulates wheat growth and particularly canopy development with less detail than AFRCWHEAT2-O3. We have identified the poor simulation of LAI as the main reason for the poor simulation of biomass and grain yield in ambient and elevated CO<sub>2</sub> conditions. LINTULCC simulated the average LAI at anthesis and the CO<sub>2</sub> effect on LAI at anthesis closely (Ewert *et al.*, 1998). However, the model also failed to simulate the observed variation in LAI and in the effect of CO<sub>2</sub> elevation on LAI (Fig. 14). Again, poor simulation of LAI was the main reason for the poor simulation of biomass and grain yield (not shown). Since LAI is modelled rather empirically in LINTULCC, a detailed analysis of the poor simulation of LAI as it was performed for AFRCWHEAT2-O3 was not possible.



**Figure 14.** Simulated vs. measured data of LAI at anthesis and the effect of elevated CO<sub>2</sub> on LAI at anthesis for spring wheat cv. Minaret grown in ESPACE-Wheat. The simulations were performed with LINTULCC. For explanation of full and open circles see Fig. 2 and Table 1.

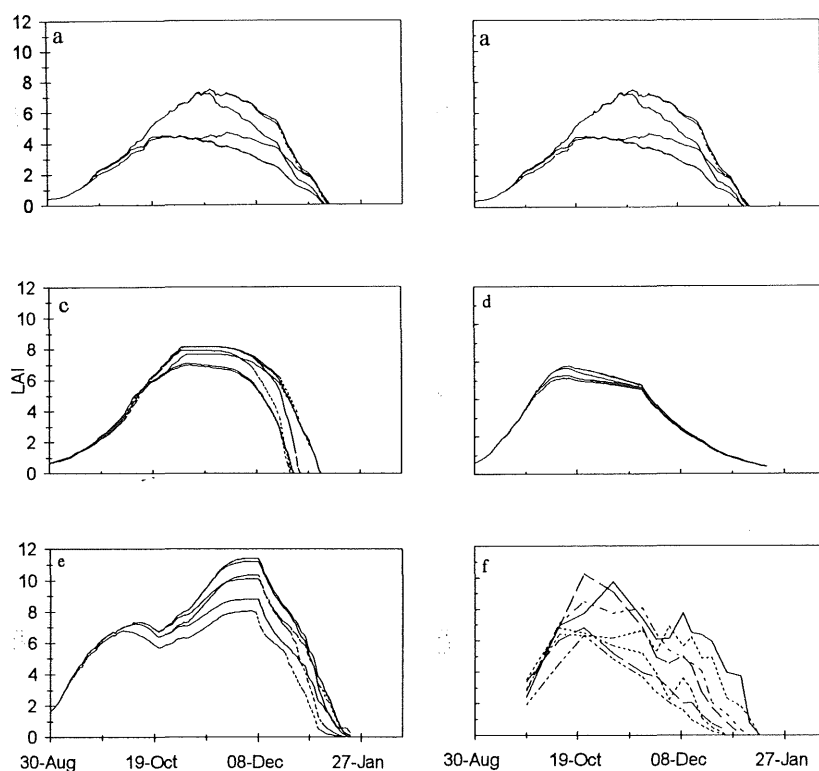
#### 2.3.2.2 Drought Experiment

An extended model comparison of the major, public-domain wheat models in the world was performed using data from a rainshelter experiment (Jamieson *et al.*, 1998a). Generally, the performance of all models in predicting both the time course and the final amount of above-ground biomass (not shown) and LAI (Fig. 15) varied substantially. As noted above, there is considerable variation in the way LAI is calculated among the models. However, none of the models could predict LAI satisfactorily (Fig. 15). The best predictions of LAI in the control treatment were given by AFRCWHEAT2 and Sirius (Fig. 15). Both models also resembled most closely the observed patterns of LAI development in response to different drought treatments (Fig. 15). However, the observations indicated that the drought effect on light interception, associated with changes in LAI was the main contributor to the drought induced reduction in the rate of biomass accumulation. In contrast, the models predicted, to varying degrees, that reduction in photosynthetic efficiency or light-use efficiency was the major cause. Again, AFRCWHEAT2 was a useful tool to perform this analysis, because it allows the testing of hypotheses about processes at the organ level.

#### 2.3.3 Discussion of new algorithms

It was an aim of the present project to adapt existing algorithms and modules in order to improve model performance and to reduce the proportion of unexplained variation. We have shown that the unexplained variations in biomass and grain yield in ESPACE-wheat were mostly due to variation in LAI, not simulated by AFRCWHEAT2-O3. Poor simulations of LAI in the ambient chambers were partly explained by variation in plant densities. From the ESPACE-wheat data we could derive a relationship between plant density and leaf size. Leaf size was also observed to be affected by CO<sub>2</sub> elevation which, however, depended on plant density. None of these responses





**Figure 15.** Time courses of LAI for (a) AFRCWHEAT2, (b), CERES-Wheat, (c) Sirius, (d) SUCROS2, (e) SWHEAT and (f) observed of wheat *cv.* Batten grown at Lincoln New Zealand in 1991/1992. The line styles represent treatments 1 (—), 3 (·····), 5 (---), 6 (— · — · — ·), 7 (— — — —), 8 (— · — · — ·) and 11 (— — — —).

were simulated by the model since it does not account for the relevant relationships or mechanisms. Poor prediction of the  $\text{CO}_2$  effect on LAI was also due to an observed effect of  $\text{CO}_2$  on tiller number. Again, this response is not considered in the model.

At present there is no sufficient algorithm available which could be used in a wheat simulation model to simulate the effect of elevated  $\text{CO}_2$  on LAI in response to weather and crop management satisfactory. An introduction of static relationships between plant density and leaf size (Fig. 11) and between  $\text{CO}_2$  elevation and leaf size (Fig. 11) and tiller number per plant into AFRCWHEAT2-O3 does not appear to improve the model performance. The ESPACE-wheat data indicate that the effects of  $\text{CO}_2$  concentration and plant density on canopy development are more complex than can be considered by simple empirical relationships. For instance, considering a simple relationship between tiller number and  $\text{CO}_2$  concentration in the model would increase simulated LAI with  $\text{CO}_2$  elevation. However, Ewert and Pleijel (1998) could not derive a relationship between the  $\text{CO}_2$  effect on tillering and the  $\text{CO}_2$  effect on LAI at anthesis from the ESPACE-wheat data. Obviously, in ESPACE-wheat, the  $\text{CO}_2$  effects on LAI were not simply an additive result of the  $\text{CO}_2$  effects on leaf size and tiller number. Further, generalization of the relationships we established between leaf size and plant density and  $\text{CO}_2$  elevation (Fig. 11)

appears risky since the data basis was very limited and refers only to flag leaves.

Our results have shown that attempts to model LAI in response to CO<sub>2</sub>, weather and crop management should consider the complexity of the effects of elevated CO<sub>2</sub> on tiller number and leaf size. However, the mechanistic detail of such approaches might be insufficient for crop simulation models particularly when applied for climate change assessment studies. One way to overcome this problem appears to be the introduction of relationships which account for compensation and competition processes within the canopy. However, our understanding of such processes in response to changes in CO<sub>2</sub> concentrations, weather and crop management is rather limited.

## 2.4 Final discussion and conclusions

The present analysis of the data of the climate change experiment ESPACE-wheat clearly identified the simulation of LAI at anthesis as the main source of the unexplained variation in biomass and grain yield among different sites and years and CO<sub>2</sub> concentrations. Although our analysis mainly refers to the simulation of the LAI from emergence until anthesis, the analysis has also indicated poor prediction of leaf area duration. In the drought experiment the variation in LAI was identified as the major contributor to the variation in biomass production and grain yield (Jamieson *et al.*, 1998a). The importance of LAI and leaf area duration as compared to photosynthetic rate per unit leaf area for wheat growth and yield has been described by Lawlor (1995). Reduction in biomass production of barley caused by water stress was found to be mainly caused by the drought affecting leaf area duration rather than the assimilation rate (Legg, *et al.*, 1979). Obviously, variation in wheat growth and yield is mainly explained by variation in leaf area dynamics for changing environmental conditions. Consequently, models which cannot predict variation in LAI fail to predict variation in biomass and yield. The comparison of model simulation has shown that different model approaches simulate different LAI. However, none of the algorithms in the models seems to be applicable to simulate LAI satisfactory for conditions of climate change.

The ESPACE-wheat data have shown that the increases in biomass production and grain yield due to CO<sub>2</sub> elevation were partly explained by the CO<sub>2</sub> effect on LAI. However, the response of LAI to elevated CO<sub>2</sub> varied dependent on other conditions related to climate and crop management. Variation in LAI and the effect of elevated CO<sub>2</sub> on LAI were simulated poorly by the models considered here. On the basis of the simulations performed with AFRCWHEAT2-O3 we found that poor predictions of LAI were mainly due to observed responses of leaf size to plant density and of leaf size and tiller number to CO<sub>2</sub> concentration. CO<sub>2</sub> effects on leaf size (Wheeler *et al.*, 1996) and tiller number (Mitchell *et al.*, 1993, 1995 and 1996; Batts *et al.*, 1996) have been reported several times. However, these effects are not simply additive and vary strongly depending on climatic conditions (Wheeler *et al.*, 1996) and crop management as it became clear from the ESPACE-wheat data. Our mechanistic understanding of the effects of elevated CO<sub>2</sub> on leaf area dynamics is still limited. The way of considering the complexity of processes determining LAI in crop simulation models is a subject for future modelling activities. To avoid insufficient mechanistic detail a better understanding of compensation and competition processes within the canopy might provide solutions applicable for crop simulation models.

We have shown that the unexplained variation of the CO<sub>2</sub> effect on biomass was only partly explained by the poor simulation of the CO<sub>2</sub> effect on LAI. Obviously, CO<sub>2</sub> had affected the rate of assimilation in a way which is not considered in the model. Interestingly, we could associate the remaining unexplained variation to differences in the experimental performance. The response of the assimilation rate to CO<sub>2</sub> elevation of plants grown in pots or chambers without border plants was additionally affected by plant density and chamber temperature. The diversity of OTC designs seems to affect the responses to CO<sub>2</sub> elevation of plants grown in OTCs. This is important to consider comparing and generalizing results from OTC studies.

From the results of the present analysis we conclude:

- Mechanistic crop simulation models are a useful tool to improve the understanding of unexplained variation in crop growth and yield.
- Unexplained variation in leaf area dynamics is the main source of the unexplained variation in crop growth and yield for a number of environmental conditions.
- Climate change experiments demand a high standardization in the experimental performance (soil properties, water and nutrient availability, crop management).
- There are considerable differences among wheat models in simulating canopy development in response to weather, CO<sub>2</sub> and drought.
- There is a general need to improve the modelling of canopy development for conditions of climatic change.
- Understanding of the complexity of processes determining leaf area dynamics in response to climate change and crop management is limited and needs to be improved. Understanding compensation and competition processes within the canopy might provide useful solutions applicable for crop simulation models.

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## References

- Batts, G.R., T.R. Wheeler, J.I.L. Morison, R.H. Ellis, and P. Hadley, 1996. Developmental and tillering responses of winter wheat (*Triticum aestivum*) crops to CO<sub>2</sub> and temperature. *J. agric. Sci., Camb.* 127: 23-35.
- Charles-Edwards, D.A., 1978. An analysis of the photosynthesis and productivity of vegetable crops in the United Kingdom. *Annals of Botany* 42: 717-731.
- Ewert, F. and J.R. Porter, 1997. Modelling the effects of CO<sub>2</sub> and ozone on growth and development of spring wheat in response to climatic conditions. Final report of The Royal Veterinary and Agricultural University (DK) to the European Stress Physiology and Climate Experiment - Project 1: Wheat, Contract No. EV5V-CT93-0301. 38 pp.

- Ewert, F. and H. Pleijel, 1998. Phenological development, leaf emergence, tillering and leaf area index and duration of spring wheat *cv.* Minaret grown at different sites across Europe in response to CO<sub>2</sub> and ozone. *Eur. J. Agron.* (submitted).
- Ewert F. and J.R. Porter, 1998. Modelling ozone effects on wheat in relation to elevated CO<sub>2</sub> and weather: Short-term to seasonal responses of leaf photosynthesis. *Global Change Biology* (submitted).
- Ewert F., M. van Oijen and J.R. Porter, 1998. Simulation of growth and developmental processes of spring wheat in response to CO<sub>2</sub> and ozone for different sites and years in Europe using mechanistic crop simulation models. *Eur. J. Agron.* (submitted).
- Farquhar, G.D., S. von Caemmerer and J.A. Berry, 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C3 species. *Planta* 149: 78-90.
- Hertstein, U., J. Colls, M.A. van Oijen and F. Ewert, 1998. General description of ESPACE-Wheat experimental investigations - sites, facilities and climatic conditions. *Eur. J. Agron.* (submitted).
- Jamieson, P.D., R.J. Martin and G.S. Francis, 1995. Drought influences on grain yield of barley, wheat and maize. *N.Z.J. Crop Hort. Sci.* 23: 55-66.
- Jamieson, P.D., J.R. Porter, J. Goudriaan, J.T. Ritchie, H. van Keulen and W. Stol. 1998a. A comparison of the models AFRCWHEAT2, CERES-Wheat, Sirius, SUCROS2 and SWHEAT with measurements from wheat grown under drought. *Field Crops Res.* 55: 23-44.
- Jamieson, P.D., M.A. Semenov, I.R. Brooking and G.S. Francis, 1998b. *Sirius*: a mechanistic model of wheat response to environmental variation. *Eur. J. Agron.* 8: 161-180.
- Lawlor D. W., 1995. Photosynthesis, productivity and environment. *Journal of Experimental Botany* 46: 1449-1461.
- Legg, B.J., W. Day, D.W. Lawlor and P.K. Parkinson, 1979. The effects of drought on barley growth: models and measurements showing the relative importance of leaf area and photosynthetic rate. *J. agric. Sci., Camb.* 92: 703-716.
- Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. *Plant Cell Environ.* 18: 339-355.
- Mitchell, R.A.C., V.J. Mitchell, S.P. Driscoll, J. Franklin, and D.W. Lawlor, 1993. Effects of increased CO<sub>2</sub> concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant Cell Environ.* 16: 521-529.
- Mitchell, R.A.C., D.W. Lawlor, V.J. Mitchell, C.L. Gibbard, E.M. White and J.R. Porter, 1995. Effects of elevated CO<sub>2</sub> concentration and increased temperature on winter wheat: test of ARCWHEAT1 simulation model. *Plant Cell Environ.* 18: 736-748.
- Mitchell, R.A.C., C.L. Gibbard, V.J. Mitchell and D.W. Lawlor, 1996. Effects of shading in different developmental phases on biomass and grain yield of winter wheat at ambient and elevated CO<sub>2</sub>. *Plant Cell Environ.* 19: 615-621.
- Porter, J.R., 1984. A model of canopy development in winter wheat. *J. agric. Sci., Camb.* 103: 383-392.
- Porter J.R. 1993. AFRCWHEAT2: A model of the growth and development of wheat incorporating responses to water and nitrogen. *Eur. J. Agron.* 2: 69-82.
- Ritchie, J.T. and S. Otter, 1985. Description and performance of CERES-Wheat: a user oriented wheat yield model. *United States Department of Agriculture, ARS* 38: 159-175.
- Tottman, D.R. and H. Broad, 1987. The decimal code for the growth stages of cereals, with illustrations. *Ann. Appl. Biol.* 110: 441-454.

- van Laar, H.H., J. Goudriaan and H. van Keulen, 1992. Simulation of crop growth for potential and water limited production situations (as applied to spring wheat). Simulation Reports CABO-TT, 27, CABO-DLO/TPE-WAU, Wageningen. 78 pp.
- van Keulen, H. and N.G. Seligman, 1987. Simulation of water use, nitrogen nutrition and growth of a spring wheat crop. Simulation Monographs, Pudoc, Wageningen. 310 pp.
- van Oijen, M. and J. Goudriaan, 1997. Final report of Wageningen Agricultural University (NL) to the European Stress Physiology and Climate Experiment - Project 1: Wheat, Contract No. EV5V-CT93-0301. 25 pp.
- van Oijen, M. and F. Ewert, 1998. The effects of climatic variation in Europe on the yield response of spring wheat *cv.* Minaret to elevated CO<sub>2</sub> and ozone: an analysis of open-top chamber experiments by means of two crop growth simulation models. Eur. J. Agron. (submitted).
- Weir A.H., P.L. Bragg, J.R. Porter and J.H. Rayner, 1984. A winter wheat crop simulation model without water or nutrient limitations. J. agric. Sci., Camb. 102: 371-382.
- Wheeler, T.R., G.R. Batts, R.H. Ellis, P. Hadley and J.I.L. Morison, 1996. Growth and yield of winter wheat (*Triticum aestivum*) crops in response to CO<sub>2</sub> and temperature. J. agric. Sci., Camb. 127: 37-48.

## List of references related to MODEXCROP

- Jamieson, P.D., Porter, J.R., Goudriaan, J., Ritchie, J.T., van Keulen, H. and Stol W. 1998a. A comparison of the models AFRCWHEAT2, CERES-Wheat, Sirius, SUCROS2 and SWHEAT with measurements from wheat grown under drought. Field Crops Res. 55: 23-44.
- Ewert F., van Oijen M. & Porter J.R. (1998) Simulation of growth and developmental processes of spring wheat in response to CO<sub>2</sub> and ozone for different sites and years in Europe using mechanistic crop simulation models. European Journal of Agronomy (submitted).
- van Oijen, M. and Ewert, F., 1998. The effects of climatic variation in Europe on the yield response of spring wheat *cv.* Minaret to elevated CO<sub>2</sub> and ozone: an analysis of open-top chamber experiments by means of two crop growth simulation models. European Journal of Agronomy (submitted).
- Ewert, F. and Pleijel, H., 1998. Phenological development, leaf emergence, tillering and leaf area index and duration of spring wheat *cv.* Minaret grown at different sites across Europe in response to CO<sub>2</sub> and ozone. European Journal of Agronomy (submitted).
- Porter, J.R. and Ewert, F., 1997: Modelling leaf and canopy response of wheat to CO<sub>2</sub> and ozone. *Report to the COST 619 Meeting*, Vienna, Austria, 25-28 September 1997.
- Ewert, F. and Porter, J.R., 1997: Climatic variability and the effects of CO<sub>2</sub> and ozone on spring wheat - experimental and modelling results. *Report to the 4th GCTE Wheat Network Workshop*, Arizona, U.S.A., 29 April - 2 May 1997.



# **MODEXCROP project**

**Model evaluation of experimental variability to improve predictability of  
crop yields under climate change.**

**Report No. 3 from the Wageningen University and Research Center  
(The Netherlands)**

*J. Wolf & C. Kempenaar*

**August 1998**



**Wageningen University and Research Center  
Sub-department of Theoretical Production Ecology**

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## Summary

A major problem in the correct estimation of future food supply under climate change is the interpretation and extrapolation of the results from crop experiments under controlled and field conditions. Crop responses to changes in atmospheric CO<sub>2</sub> concentration and temperature greatly vary from experiment to experiment and from site to site. To improve understanding of the causes for this variability in observed crop responses, a large number of data sets from wheat experiments under CO<sub>2</sub> enrichment or temperature change have been collected. These data sets for wheat have been analysed to unravel the mechanisms behind this variability. Subsequently, the data sets have been analysed with a crop growth simulation model, combining knowledge about crop characteristics and their interactions with the environment. This may result in an improved explanation of the observed variability on the basis of crop characteristics and climatic conditions. For the large data sets from the free-air CO<sub>2</sub> enrichment (FACE) experiments in Arizona these analyses have been carried out in more detail.

Averaged over all collected wheat experiments, total biomass and grain yield increased per 100 ppmv of CO<sub>2</sub> enrichment by 7% of the yields under ambient atmospheric CO<sub>2</sub>. The harvest index did not change with CO<sub>2</sub> enrichment. The standard deviation (SD) of the yield responses to 100 ppmv of CO<sub>2</sub> enrichment was 6% of the yields under ambient CO<sub>2</sub>. This indicates the strong variability in yield responses to CO<sub>2</sub> enrichment. For example in the FACE experiments, the yield variability was so high that CO<sub>2</sub> enrichment did not result in a significant yield response. When experimental results were grouped according to growing conditions (pot or field; optimal or limited) or crop types (spring or winter wheat), SD of observed yield responses to CO<sub>2</sub> enrichment did almost not decrease. Apparently, variation in growing conditions and crop type was not the main cause for the high SD values. When results from the final harvest and a one week earlier harvest in the FACE experiments were compared, total biomass and grain yield considerably changed from the earlier to the final harvest and often in different directions under ambient and elevated CO<sub>2</sub>. This resulted in different conclusions on the yield response to CO<sub>2</sub> enrichment from both harvests. This type of experimental variability (and also the high SD values mentioned above) is caused by the spatial variability in growing conditions and the uncertainty in yield measurements.

Simulation of the experimental data set with the LINTULCC growth model for wheat showed that the relationship between the observed increases in total above-ground biomass by CO<sub>2</sub> enrichment and the simulated increases was poor. This was mainly caused by the poor relationship between observed and simulated cumulative radiation interception. In LINTULCC an increase in assimilate production by CO<sub>2</sub> enrichment generally resulted in a larger leaf area and thus more radiation interception, whereas in the experiments this increase in radiation interception almost did not occur. The relationship between simulated and observed changes in harvest index and thus grain yield was rather poor. It is not clear if this was mainly caused by experimental variability or that the relationship can be improved by replacing the actual (source-driven) model method for calculating grain production by a sink-driven (i.e. determined by growth of grains) method. In the FACE experiments for example, biomass production stopped before maturity with a considerable amount of green leaves left and the ratio between observed shoot biomass under elevated and ambient CO<sub>2</sub> showed a strong decrease near maturity. Both effects probably point to sink-limitation.

Averaged over all collected wheat experiments, total biomass and grain yield decreased by 8% and 11%, respectively per 1 °C temperature rise due to the shorter growth period. These

yield decreases became smaller when the ambient atmospheric CO<sub>2</sub> concentration was doubled. The temperature effect is less variable and more certain than the CO<sub>2</sub> effect, as SD of yield responses to 1 °C temperature rise was half (i.e. 3%) the SD for yield responses to CO<sub>2</sub> enrichment and the mean temperature effect was generally larger. The relationship between simulated and observed decreases in total biomass by temperature rise was moderately good and was mainly determined by the good relationship between simulated and observed decreases in radiation interception during the shorter growth period. The relationship between simulated and observed changes in harvest index with temperature rise was nil, as the simulated changes were much larger than the observed changes (i.e. almost nil). This resulted in a poor relationship between simulated and observed changes in grain yield with temperature rise.

Comparison of experimental results with those simulated with LINTULCC showed that their correspondence might be improved in two opposite ways. The description of the morphological development (e.g. leaf area) of the crop and the limiting effects of available sinks (i.e. grains) on crop growth may be described in more detail. However, in many situations crop variables as observed in the experiments were more constant than simulated with LINTULCC. In that situation, a model approach may be applied which uses more simplified methods to simulate leaf area development and radiation interception, radiation use efficiency and grain yield. This only holds in situations without severe water or nutrient stress.

### 3.1 Introduction

Since agricultural production is greatly affected by climate, any changes in climate which may result from increasing concentrations of so-called greenhouse gases in the atmosphere could have dramatic consequences for agricultural yield potential. Principal climate changes that are to be expected in Europe as based on the IPCC emission scenarios (Second Assessment Report, Houghton et al., 1996) and the development of climate change scenarios for Europe (Barrow and Hulme, 1996), are a temperature rise of about 2 °C and an increase in atmospheric CO<sub>2</sub> concentration of about 200 ppmv over a period of 100 years.

A major problem in the correct estimation of future food supply under such changes in climate is the interpretation and extrapolation of the results from experiments under controlled and field conditions. The responses to changes in atmospheric CO<sub>2</sub> concentration and temperature of crop growth and yield greatly varies from experiment to experiment and from site to site. For example, literature reviews have shown that with doubling of atmospheric CO<sub>2</sub> concentration the wheat grain and biomass yields increase with about 35% (Cure and Acock, 1986; Idso and Idso, 1994). However, the variation around this average response is large, as for example shown in the ESPACE research project that was funded within the EU-ENVIRONMENT programme. In this project experiments were carried out with one spring wheat variety under enriched atmospheric CO<sub>2</sub> concentration at a large number of sites over Europe (Hertstein et al, 1996). The wheat response to a doubling of atmospheric CO<sub>2</sub> varied from nil to more than 60% increase in grain yield, but this variation in CO<sub>2</sub> response could not be explained from the differences in climatic conditions between the different sites (Van Oijen and Ewert, in prep.).

The aim of the project is an improved understanding of the causes for the variability in observed responses of wheat yields to changes in atmospheric CO<sub>2</sub> concentration and temperature. For this purpose, a large number of experimental data sets have been collected. These data sets have been analysed to unravel the mechanisms behind the variability in the observed responses. Subsequently, the data sets have been analysed with a crop growth simulation model, combining knowledge about crop characteristics and their interactions with the environment. This may result in an improved explanation of the observed variability on the basis of crop characteristics and climatic conditions. Prior to this model analysis, the sensitivity of modelled wheat growth to separately changed weather variables was determined. For the large data sets from the free-air CO<sub>2</sub> enrichment experiments in Arizona these analyses have been carried out in more detail. An improved understanding from these analyses of the mechanisms that cause the variability in wheat responses may result in a more reliable prognosis of the impacts of climate change on future yields of wheat and other crops.

### 3.2 Materials and methods

#### 3.2.1 Data

Six research groups contributed considerably to the project by providing the datasets from their wheat experiments under CO<sub>2</sub> enrichment and/or temperature change. These groups are: AB-DLO (Wageningen, Netherlands), IACR-Rothamsted (Harpenden, U.K.), IATA-CNR (Florence, Italy), INRA (Clermont Ferrand, France), Justus-Liebig University (Giessen, Germany), and USDA-ARS (Phoenix, Arizona, USA). The researchers involved and their addresses are listed as sub-contractors in Appendix P. Information about the methods and

treatments in the different experiments and some of their results are described below (see Section 3.3.1).

To analyse the effects of CO<sub>2</sub> enrichment and temperature change on wheat growth and yield, information was required on the dates of important phenological stages (e.g. anthesis, maturity), the leaf area, amount of biomass dry matter, and allocation of assimilates to crop organs over time, and the components of the grain yield at maturity. From most experiments the main part of this information was available.

For application of the crop growth model to analyse the experimental data sets, also climate data are required. These are daily values for minimum and maximum air temperature, solar radiation, and atmospheric CO<sub>2</sub> concentration. As the model simulations were only conducted for optimal conditions (i.e. no water stress or nitrogen shortage), information on the components of the water balance (e.g. rainfall and losses by crop transpiration and soil evaporation) and on the soil characteristics (e.g. water holding capacity and nitrogen supply from soil mineralization) was not required.

### 3.2.2 Model description

The LINTULCC model simulates wheat growth from crop emergence to maturity with a time-step of one day, taking into account the climatic conditions. Daily growth is computed as light interception multiplied by the crop light-use efficiency. The original version of this simple generic model (LINTUL) was described for growth of potato (Spitters, 1990). Light interception is calculated from the incoming photosynthetic active radiation and the light interception fraction, which fraction is calculated as an exponential function of LAI (i.e. leaf area index, m<sup>2</sup> leaf area per m<sup>2</sup> ground area) and approaches 1 at LAI values higher than 4. LAI is calculated from the amount of leaf dry matter and a constant value for specific leaf area during the whole growth period, except for the exponential increase in LAI during initial growth and the decrease in LAI due to senescence near crop maturity. In LINTULCC the effects of water shortage or nutrient limitation on crop growth are not taken into account.

The dates of the main phenological stages and thus the time course of the allocation of assimilates to the crop organs are determined by cumulative temperature sums from crop emergence. These sums determine, for example, the duration of leaf expansion and the start date and duration of grain filling. A new routine has been introduced in the original model to calculate the crop light-use efficiency as depending on light, temperature, atmospheric CO<sub>2</sub> and leaf rubisco concentration (Van Oijen and Goudriaan, 1997). The routine is based on biochemical photosynthesis equations for C3-plants (Farquhar and Von Caemmerer, 1982) and a temperature and CO<sub>2</sub> concentration independent ratio of the daily totals of crop respiration and photosynthesis (hence, fixed value for conversion efficiency CVF), as found for wheat (Gifford, 1995). A short description of this routine as based on Van Oijen and Goudriaan (1997) is given here. The crop light-use efficiency (LUE) is calculated with:

$$\text{LUE} = \text{EFF} * \text{PMAX} * \text{CVF} / (\text{EFF} * \text{K} * \text{PARAV} + \text{PMAX})$$

This equation is based on

1. PMAX and EFF, i.e. maximum and initial angle of the photosynthesis-light response curve, with their values derived from the biochemistry of leaf photosynthesis of C3 plants (Farquhar and Von Caemmerer, 1982);
2. Calculation of LUE from canopy photosynthesis and light interception, i.e.

$$LUE = P_c * CVF / ((1 - e^{-K * LAI}) * I_0)$$

with  $P_c$  daily integral of gross canopy photosynthesis, CVF efficiency of the conversion of assimilated  $CO_2$  to biomass,  $K$  extinction coefficient of irradiation, and  $I_0$  daily incoming amount of photosynthetic active radiation;

And this formula combined with:

3. a method for calculating the daily integral of gross canopy photosynthesis from leaf photosynthesis characteristics (Charles-Edwards, 1982), i.e.

$$P_c = I_0 * (1 - e^{-K * LAI}) * EFF * P_{MAX} / (EFF * K * PARAV + P_{MAX})$$

with PARAV average flux of photosynthetic active radiation during daytime.

For the details of this calculation method and the assumptions underlying this approach, see Van Oijen and Goudriaan (1997).

### 3.3 Results

#### 3.3.1 Experimental data sets

A short overview of the experiments used in this study, the main treatments applied in these experiments and some results are given here. For a list of the experiments with a short indication of crop and growing conditions, see Appendix A. For more information about the results from these experiments, see Appendices B to G.

##### 3.3.1.1 Arizona

USDA-ARS supplied three data sets from spring wheat field experiments. A free-air  $CO_2$  enrichment (FACE) system was applied for increasing the atmospheric  $CO_2$  concentration. In the first growing season 1992/93 the crop was grown under conditions of ambient and elevated atmospheric  $CO_2$  concentrations and ample and limited water supply. The experimental methods and the results were discussed by Hunsaker et al. (1996), Kimball et al. (1995), Li et al. (1997), and Pinter et al. (1996a). Final yield data from this experiment are given in Table B-1 and time courses of crop variables are shown in Figure B-1 (see Appendix B). In growing season 1993/94 the crop was grown under identical growing conditions as those in 1992/93. The experimental methods and the results from this experiment were discussed by Hunsaker et al. (1996) and Pinter et al. (1996a). Final yield data from this experiment are given in Table B-2 and time courses of crop variables are shown in Figure B-2. In growing season 1995/96 the crop was grown under ambient and elevated atmospheric  $CO_2$  concentrations, with the ambient treatment both with and without blower rings (for  $CO_2$  distribution), and low and high nitrogen supply. The experimental methods and the results were described by Pinter et al. (1996b). An important difference was the use of the blower rings in half of the ambient plots. The reason was the increase in minimum temperature by about  $1.5^\circ C$  when the blower rings were applied. This resulted in a combined  $CO_2$  enrichment plus blower effect in the previous growing seasons. Final yield data from this experiment are given in Table B-3. Time courses of crop variables are given in Figures B-3 and B-4, which show the separate  $CO_2$  enrichment and blower effects, respectively.

In growing season 1992/93  $CO_2$  enrichment (+180 ppmv) resulted in an increase in total biomass and grain yield by 9% and 14%, respectively, and in an increase (+5%) in harvest index (Table B-1). If water availability was limiting, the increases in biomass and grain yield

with CO<sub>2</sub> enrichment were halved (4% and 9%, respectively). CO<sub>2</sub> enrichment resulted in a slightly earlier date of maturity, an earlier final decrease in LAI and an earlier end of shoot growth (Figure B-1). This was caused by the use of the blower rings that gave an increase in minimum temperature and not by the higher atmospheric CO<sub>2</sub> concentration. If this blower ring effect was excluded, the CO<sub>2</sub> enrichment effect on yields should be higher. The ratio between grain yield with and that without CO<sub>2</sub> enrichment showed a considerable variation when based on their time courses during the 20 days before crop maturity (Figure B-1). This is probably an indication of the experimental variability in CO<sub>2</sub> response. Water limitation resulted in an earlier crop maturity and a much earlier decrease in LAI compared to the ample water supply treatments, and thus in an earlier end of biomass and grain production.

In growing season 1993/94 CO<sub>2</sub> enrichment (+ 180 ppmv) resulted in an increase in total biomass and grain yield by 7% and 12%, respectively, and in an increase (+5%) in harvest index (Table B-2). If water availability was limiting, the increases in biomass and grain yield with CO<sub>2</sub> enrichment were almost doubled (14% and 20%, respectively), contrary to the water limitation effect on yield increase in the previous growing season. CO<sub>2</sub> enrichment resulted in a slightly earlier date of maturity, an earlier final decrease in LAI and an earlier end of shoot growth (Figure B-2). This was also caused by the use of the blower rings (see above) that gave an increase in minimum temperature and not by the higher atmospheric CO<sub>2</sub> concentration. This may result in underestimation of the yield response to CO<sub>2</sub>. The ratio between grain yield with and that without CO<sub>2</sub> enrichment showed a considerable variation when based on their time courses during the 20 days before maturity (Figure B-2), as in the previous year. Water limitation resulted in earlier crop maturity and a much earlier decrease in LAI compared to the ample water supply treatments, and thus in an earlier end of biomass and grain production.

In growing season 1995/96 CO<sub>2</sub> enrichment (+ 200 ppmv) resulted in a decrease in total biomass and grain yield by 7% and 9%, respectively, and in a decrease (-2%) in harvest index (Table B-3). If nitrogen supply was limiting, the increases in biomass and grain yield with CO<sub>2</sub> enrichment were about similar to those in the previous growing seasons (16% and 19%, respectively). In the treatments without blowers total biomass and grain yield were expected to be higher because of the lower temperature than those in the treatment with blowers, however, this was only true for the treatment (nr. 6) with nitrogen limitation. When the blower ring effect was excluded, CO<sub>2</sub> enrichment did not result in a change in date of maturity, in an earlier final decrease in LAI and an earlier end of shoot growth (Figure B-3). The ratio between grain yield with and that without CO<sub>2</sub> enrichment showed a strong variation when based on their time courses during the 20 days before maturity (Figure B-3), as in the previous growing seasons. Nitrogen limitation resulted in a much earlier decrease in LAI compared to the ample nitrogen supply treatments, and thus in an earlier end of biomass and grain production. The higher minimum temperature due to the use of blower rings (without CO<sub>2</sub> enrichment) resulted in an earlier crop maturity, a much smaller LAI (mainly due to the lower specific leaf area), and an earlier final decrease in LAI (Figure B-4). Contrary to the expected result, however, this lower LAI resulted in a higher biomass and grain production in the treatment with ample nitrogen supply.

### **3.3.1.2 Clermont Ferrand**

INRA supplied one data set from a winter wheat experiment in growing season 1995/96 (Triboi, pers. comm.). The crop is grown outdoors in containers under ambient temperatures and ambient atmospheric CO<sub>2</sub> concentration. Four days after anthesis the containers were

transferred into transparent tunnels with controlled climatic conditions. In these tunnels the CO<sub>2</sub> exchange was measured continuously and the temperature, air humidity and CO<sub>2</sub> concentration were controlled. This experimental method was described by Triboi et al. (1996) and Blancal and Triboi (1993). The four different temperature regimes applied were ambient temperatures, and minimum and maximum temperatures of 10 and 18 °C, 20 and 28 °C and 10 and 34 °C, respectively (with these minimum and maximum temperatures during 6 and 12 hours, respectively per day). Atmospheric CO<sub>2</sub> was kept at the ambient concentration level. Final yield data from this experiment are given in Table C-1 and time courses of crop variables are shown in Figure C-1 (see Appendix C).

The temperature increase during grain filling resulted in a strong decrease in total biomass and grain yield by about 25 to 35% compared to the yields at ambient temperatures, whereas a temperature decrease resulted in an increase in grain yield and harvest index (Table C-1). These differences in grain yield corresponded with considerable differences in grain weight. Temperature increase during grain filling resulted in a faster decrease in LAI and in a strongly advanced end of biomass and grain production (Figure C-1).

### **3.3.1.3 Florence**

IATA-CNR supplied one data set from a winter wheat experiment in growing season 1997 (Miglietta, pers. comm.). The crop was grown in the field under conditions of ambient temperatures and ambient and elevated atmospheric CO<sub>2</sub> concentrations. For this elevated CO<sub>2</sub> treatment a simple system for free-air CO<sub>2</sub> enrichment (so-called Mini-Face system) was used, as described by Miglietta et al. (1996). Crop data from this experiment are shown in Figure D-1 in Appendix D. They show that CO<sub>2</sub> enrichment (+150 ppmv) resulted in changes in grain yield and total biomass of +19% and -3%, respectively.

### **3.3.1.4 Giessen**

The Institute for Plant Ecology from the Justus-Liebig University supplied three data sets from spring wheat experiments in pots in open-top chambers. In the first growing season 1994, the crop was grown under conditions of ambient and elevated atmospheric CO<sub>2</sub> concentrations with low and high nitrogen supply and ambient and elevated ozone concentrations. The results from the elevated ozone treatments were not used here. The experimental method and the results were discussed by Fangmeier et al. (1996; 1997a; 1997b). Final yield data from this experiment are given in Table E-1 and time courses of crop variables are shown in Figure E-1 (see Appendix E). In growing seasons 1995 and 1996 the experimental method was the same as that in 1994. The results of these experiments were discussed by Fangmeier et al. (1997b), however, the results from the elevated ozone treatments were not used in this study. Final yield data from the experiments in growing seasons 1995 and 1996 are given in respectively Table E-2 and E-3 and time courses of crop variables are shown in respectively Figure E-2 and E-3.

In growing season 1994, almost doubling (i.e. + 280 ppmv) of the ambient atmospheric CO<sub>2</sub> concentration resulted in an increase in total biomass and grain yield by 41% and 28%, respectively for spring wheat (see Table E-1). This yield increase was caused by the increasing number of grains per plant. The harvest index decreased with CO<sub>2</sub> enrichment. Nitrogen limitation resulted in a slightly smaller biomass increase and an identical grain yield increase with CO<sub>2</sub> enrichment. CO<sub>2</sub> enrichment did not change the dates of anthesis and maturity and resulted in a slightly higher LAI (Figure E-1).

In growing season 1995, almost doubling (i.e. +240 ppmv) of the ambient atmospheric CO<sub>2</sub> concentration resulted in an increase in total biomass and grain yield by 41% and 42%, respectively and in no change in harvest index (Table E-2). This yield increase was caused by both the increasing number of ears per plant and grains per ear. Nitrogen limitation resulted in a slightly smaller increase in biomass and grain yield with CO<sub>2</sub> enrichment. CO<sub>2</sub> enrichment did not change the dates of anthesis and maturity and resulted in a slightly higher LAI (Figure E-2). In growing season 1996, almost doubling (+285 ppmv) of the atmospheric CO<sub>2</sub> concentration resulted in an increase in total biomass and grain yield by 34% and 28%, respectively and in a small decrease in harvest index (Table E-3). The other effects of the increase in atmospheric CO<sub>2</sub> were identical to those mentioned above for growing season 1995, except for the LAI that did not change with CO<sub>2</sub> enrichment (Figure E-3).

### **3.3.1.5 Rothamsted**

The IACR-Rothamsted experimental station supplied three data sets from winter wheat experiments in pots in a greenhouse. In the first growing season 1990/91, the crop was grown under conditions of ambient and doubled atmospheric CO<sub>2</sub> concentrations, ambient temperatures and ambient + 4 °C temperatures, and low and high nitrogen supply. The experimental method and the results were discussed by Lawlor et al. (1993), Delgado et al. (1994) and Mitchell et al. (1993). Final yield data from this experiment are given in Tables F-1 and F-2 and time courses of crop variables are shown in Figures F-1 and F-2 (see Appendix F). In growing season 1991/92 the crop was grown under conditions of ambient and doubled atmospheric CO<sub>2</sub> concentrations and ambient temperatures and ambient + 4 °C temperatures. The experimental results were discussed and were compared with results from crop growth simulation models (Mitchell et al., 1995). Final yield data from this experiment are given in Table F-3 and time courses of crop variables are shown in Figure F-3. In growing season 1993/94 the crop was grown under conditions of ambient temperatures with shading during three different periods before and around anthesis and ambient and doubled atmospheric CO<sub>2</sub> concentrations. The experimental method and the results were discussed by Mitchell et al. (1996). Final yield data from this experiment are given in Figure F-4 and Table F-4 and time courses of crop variables are shown in Figure F-5.

In growing season 1990/91, doubling of atmospheric CO<sub>2</sub> resulted in an increase in total biomass and grain yield by 15% for winter wheat, both at ambient temperatures and ambient + 4 °C temperatures (see Table F-1). This yield increase was caused by the increasing number of ears per plant. The harvest index did not change with CO<sub>2</sub> enrichment. The temperature rise of 4 °C resulted in a decrease in total biomass and grain yield by 15% and 20%, respectively, both at ambient and doubled atmospheric CO<sub>2</sub> concentrations, and a small decrease in harvest index. The temperature rise strongly advanced the dates of anthesis and maturity and resulted in a much earlier leaf senescence and end of biomass production (Figure F-1), whereas CO<sub>2</sub> enrichment did almost not give such effects. With nitrogen limitation, doubling of atmospheric CO<sub>2</sub> resulted in a smaller increase in total biomass (+10%) and even in a decrease in grain yield (Table F-2). This may be the result of the higher biomass production with CO<sub>2</sub> enrichment that resulted in a larger amount of nitrogen kept in the vegetative parts. Van Kraalingen (1990) showed that with limiting nitrogen supply this CO<sub>2</sub> effect may result in a lower nitrogen translocation to the grains and thus in a lower grain production. Nitrogen limitation resulted in a much lower LAI and a slightly advanced date of crop maturity (Figure F-2).



In growing season 1991/92, CO<sub>2</sub> doubling resulted in an increase in total biomass and grain yield by 27% and about 40%, respectively, both at ambient temperatures and ambient + 4 °C temperatures (Table F-3). Hence, the harvest index increased by about 10%. The temperature increase by 4 °C resulted in a decrease in total biomass and grain yield by 16% and 35%, respectively, both at ambient and doubled atmospheric CO<sub>2</sub> concentrations, and thus in a considerable decrease in harvest index. The temperature increase strongly advanced the dates of anthesis and maturity and resulted in an much earlier leaf senescence and end of biomass production (Figure F-3), whereas CO<sub>2</sub> enrichment did almost not give such effects. In growing season 1993/94, CO<sub>2</sub> doubling resulted in increases in total biomass and grain yield by 25% and 21%, respectively without shading and in increases by about 15% averaged for the different shading treatments (Table F-4). The lowest yields were found for the longest period of shading which corresponds with the lowest amount of radiation (Treatments 8 and 16, see Figure F-4). However, there was no clear relation between the degree or period of shading and the CO<sub>2</sub> response of grain yield. CO<sub>2</sub> enrichment resulted in a very small increase in LAI but still in considerable increases in biomass and grain yield in the treatment without shading (Figure F-5). This indicates that the yield response to CO<sub>2</sub> enrichment was mainly caused by the increased photosynthetic rate. The dates of anthesis and maturity were not affected by the increase in atmospheric CO<sub>2</sub>.

### **3.3.1.6 Wageningen**

The AB-DLO research institute supplied five data sets from wheat experiments under elevated CO<sub>2</sub>. In the first two data sets spring wheat and winter wheat were grown in growing seasons 1991 and 1992/93, respectively under ambient and elevated CO<sub>2</sub> concentrations in climatized sun-lit crop enclosures. In these enclosures the CO<sub>2</sub> exchange rate and transpiration rates of the crops were measured at regular intervals. Dijkstra et al. (1993, 1994) described the experimental methods, discussed the results from the measurements and analysed the differences between spring wheat and faba bean in their responses to CO<sub>2</sub> enrichment of photosynthesis, growth and transpiration. These differences in CO<sub>2</sub> response between spring wheat, winter wheat and faba bean were analysed in more detail with crop growth models, calculating the interacting effects of weather conditions and CO<sub>2</sub> enrichment on crop growth (Dijkstra et al., 1996; Grashoff et al., 1995). In this study, however, only the final yield data (see Table G-1 in Appendix G) were used. In growing season 1993/94 winter wheat was grown in open-top chambers in the field at ambient and doubled atmospheric CO<sub>2</sub> concentration. Results from this experiment were discussed by Dijkstra et al. (in prep.) and the final yield data are given in Table G-2. In the last two experiments in growing seasons 1995 and 1996, spring wheat was grown in open-top chambers in the field, under both ambient and doubled atmospheric CO<sub>2</sub> concentrations and ambient and ambient + 2 °C temperatures. The experimental methods and the results were discussed by Van Oijen and Goudraan (1997), and Van Oijen et al. (1998a; 1998b). Final yield data from these experiments are given in Tables G-3 and G-4 and the time courses of crop variables are shown in Figures G-1 and G-2.

In growing season 1991, doubling of atmospheric CO<sub>2</sub> resulted in an increase in both total biomass and grain yield by 34% for spring wheat (see Table G-1). This yield increase was mainly caused by an increase in the number of ears per plant and to a less extent by the increasing number of grains per ear. The harvest index did not change with CO<sub>2</sub> enrichment. In growing season 1992/93, doubling of atmospheric CO<sub>2</sub> resulted in an increase in total biomass by 19% for winter wheat. However, the grain yield did not increase and the harvest index considerably decreased. In the open-top chamber experiment in growing season

1993/94, doubling of atmospheric CO<sub>2</sub> resulted in an identical increase in total biomass (+18%) for winter wheat (Table G-2). The increase in grain yield was slightly higher (+20%) and hence, the harvest index slightly increased (+2%). This yield increase was mainly caused by the increase in the number of ears per plant.

In the open-top chamber experiment in growing season 1995, doubling of atmospheric CO<sub>2</sub> resulted in an increase in both total biomass and grain yield by 11% for spring wheat at ambient temperatures and by 20% at ambient + 2 °C temperatures (Table G-3). The harvest index did not change. At ambient temperatures the yield increase was mainly caused by the increasing number of grains per ear and at ambient + 2 °C temperatures by the increasing grainweight and to a less extent by the increasing number of grains per ear and ears per plant. In growing season 1996, doubling of ambient atmospheric CO<sub>2</sub> resulted also in an increase in total biomass by about 20% and in grain yield by 14% (i.e. decrease in harvest index) at ambient + 2 °C temperatures (Table G-4). At ambient temperatures, however, doubling of ambient atmospheric CO<sub>2</sub> resulted again in a smaller increase in biomass and yield (about nil in 1996) than at ambient + 2 °C temperatures. This indicates a positive effect of temperature rise on the yield response to CO<sub>2</sub> enrichment, which may be due to an increased response with warming of both photosynthesis to CO<sub>2</sub> and of light interception to CO<sub>2</sub> (warming leads to crops with lower LAI (see Figures G-1 and G-2); in such crop increased leaf growth by CO<sub>2</sub> enrichment leads to considerably increased light interception and thus to extra growth enhancement), as analysed by Van Oijen et al. (1998b). Temperature increase by 2 °C resulted in a decrease in both total biomass and grain yield by 23% at ambient atmospheric CO<sub>2</sub> in both 1995 and 1996 (Table G-3 and G-4). Warming strongly advanced the dates of anthesis and maturity and caused an earlier decrease of the green, light intercepting foliage (Figures G-1 and G-2). This resulted in less cumulative light interception and thus in less biomass production. The harvest index did not change with the temperature change. The decrease in biomass and yield by temperature increase was less at elevated atmospheric CO<sub>2</sub>.

### 3.3.2 Analysis of experimental data sets

A summary of all experimental data sets that were collected for this project, was compiled. For each site, year and treatment the responses to CO<sub>2</sub> enrichment are given in Table H-1 (see Appendix H) and the responses to temperature change in Table H-2. These responses are: the change in growth duration, both from emergence until anthesis and from anthesis until maturity; total shoot dry matter at anthesis; LAI at anthesis; total shoot dry matter at maturity; grain dry matter yield at maturity; and harvest index. The responses to CO<sub>2</sub> enrichment are given as a percentage of the result at ambient conditions, except for the change in growth duration. In a following step, these responses were standardized per 100 ppmv increase in atmospheric CO<sub>2</sub> concentration. This assumes that the responses to CO<sub>2</sub> increase are linear, which is not completely true in all situations but will affect the result only to a limited extent. The responses to temperature change are given as a percentage of the result at ambient temperatures (except for the change in growth duration). Subsequently, these temperature responses were standardized per 1 °C temperature rise, again assuming that these responses are linear. The mean and standard deviation of these standardized responses to CO<sub>2</sub> enrichment were determined (Table 1) for results under different conditions (i.e. optimal, water-limited or nitrogen-limited conditions), for different crop types (i.e. winter or spring wheat) and for different growing media (i.e. field and container experiments versus pot experiments). This should indicate if the variation in CO<sub>2</sub> response becomes smaller when

experimental results are grouped according to these growing conditions and if the CO<sub>2</sub> response is affected by these growing conditions. The mean and standard deviation of the standardized responses to temperature change were determined for results under respectively ambient and elevated CO<sub>2</sub> concentration (Table 2). The means of the standardized responses to CO<sub>2</sub> enrichment and temperature change are based on all results given in Tables H-1 and H-2, respectively but it should be taken into account that each result in these tables was derived from a different number of replicates and from experiments with a different degree of reliability (field versus pots, size of plots, etc.).

### *3.3.2.1 CO<sub>2</sub> enrichment*

The growth duration from emergence to anthesis and from anthesis to maturity was not changed by an increase in atmospheric CO<sub>2</sub> concentration in most experiments (Table H-1). In the experiments from Rothamsted the date of anthesis is sometimes slightly earlier or later with CO<sub>2</sub> enrichment, however, the total growth duration does not change which probably indicates that there is not a real CO<sub>2</sub> effect. Only in the Arizona experiments the growth duration from emergence until anthesis becomes shorter with CO<sub>2</sub> enrichment. In this experiment the use of blower rings for CO<sub>2</sub> enrichment resulted in higher minimum temperatures (+ 1.5 °C) which caused this shortened duration.

The standardized CO<sub>2</sub> enrichment (+ 100 ppmv) resulted in an increase in both total biomass and grain yield of 7% , and in no change in harvest index, averaged for all wheat experiments (Table 1). The standard deviation (SD) was almost as large as the mean result, indicating a strong variation in yield increases between 1% and 13%. At anthesis the CO<sub>2</sub> enrichment resulted in a larger increase (+10%) in total biomass than at maturity, but in no change in LAI. The CO<sub>2</sub> enrichment resulted for spring wheat in a larger increase in total biomass at anthesis (+11%) than for winter wheat (+6%) and also in a larger increase in biomass at maturity but with a smaller difference between both crop types (+8% versus +5%). However, the increases in grain yield for spring and winter wheat were identical. The CO<sub>2</sub> enrichment resulted for pot experiments in an increase in total biomass at anthesis (+10%) that was identical to that for field experiments, but it resulted in increases in total biomass and grain yield at maturity (+10%) that were much higher than those for field experiments (+4%). This indicates that the response of yields to CO<sub>2</sub> enrichment in field experiments is much more limited.

The CO<sub>2</sub> enrichment resulted under optimal conditions in an increase in grain yield (+7%) that was identical to that for water- and nitrogen-limited conditions, and in an increase in total biomass at maturity that was lower and higher than that under nitrogen-limited and water-limited conditions, respectively. Finally, Table 1 shows that SD of the yield responses to standardized CO<sub>2</sub> enrichment did almost not decrease when experimental results were grouped according to growing conditions or crop types.

Table 1. Average (Av.) and standard deviation (SD) of responses of spring wheat or winter wheat to CO<sub>2</sub> enrichment under different conditions as based on results from all experiments collected for this project (see Table H-1). Response is calculated for 100 ppmv CO<sub>2</sub> increase and is given as a percentage of the result at ambient conditions.

Conditions, Crop		Total shoot at anthesis	LAI at anthesis	Total shoot at maturity	Grain yield At maturity	Harvest index
Optimal conditions, winter + spring wheat	Av.	+10.0	+1.2	+6.7	+6.9	+0.2
	SD	±6.5	±4.8	±5.4	±5.5	±3.8
Water-limited conditions, winter + spring wheat	Av.	+12.8	+1.9	+5.1	+7.9	2.5
	SD	±2.5	±4.0	±2.8	±3.1	±0.1
N-limited conditions, winter + spring wheat	Av.	+7.5	-4.8	+9.3	+7.0	-1.9
	SD	±3.4	±6.2	±6.2	±7.6	±2.4
Winter wheat, all conditions	Av.	+5.5	+3.3	+5.3	+6.3	+1.1
	SD	±3.8	±3.4	±3.1	±5.6	±5.5
Spring wheat, all conditions	Av.	+10.6	-1.6	+8.0	+7.0	-0.8
	SD	±5.7	±6.0	±6.3	±6.2	±2.2
Field/container experiments, winter + spring wheat	Av.	+9.4	-1.7	+3.1	+3.9	+0.9
	SD	±6.2	±6.8	±4.0	±5.7	±4.3
Pot experiments, winter + spring wheat	Av.	+9.5	+0.3	+10.6	+9.4	-1.0
	SD	±5.5	±5.1	±4.3	±5.1	±2.6
All experiments, winter + spring wheat	Av.	+9.5	-0.5	+7.3	+6.9	-0.2
	SD	±5.7	±5.9	±5.6	±6.0	±3.6

### 3.3.2.2 Temperature change

The duration from emergence to maturity considerably decreased with temperature rise (Table H-2), contrary to the nil response to CO<sub>2</sub> enrichment. For winter wheat at Rothamsted this total duration decreased per 1 °C temperature rise by 2.8%, for spring wheat at Wageningen by 5.0%, and for winter wheat at Clermont Ferrand by 2.6%. However, results from Clermont Ferrand apply only to the grain filling period. For winter wheat from Rothamsted the vegetative part of total growth duration is not only determined by temperature but by photoperiod and vernalization requirements too. Hence, these temperature effects on growth duration are not well comparable.

The standardized temperature increase (+ 1 °C) resulted in a decrease in total biomass and grain yield of 8% and 11%, respectively, and also in a decrease in harvest index (-3%), averaged for all wheat experiments (Table 2). SD was smaller (3%) than SD for the yield responses to CO<sub>2</sub> enrichment, whereas the mean temperature effect was generally larger. This indicates that the temperature effect is less variable and less uncertain than the CO<sub>2</sub> effect. The temperature increase also resulted in a decrease in total biomass and LAI at anthesis of 7% and 6%, respectively. The temperature increase resulted in smaller decreases in total biomass and grain yield under doubled atmospheric CO<sub>2</sub> concentrations (-7% and -9%, respectively) than under ambient CO<sub>2</sub> concentrations (-10% and -12%, respectively). Apparently, CO<sub>2</sub> enrichment partly counteracts the negative temperature effects on yields.

Table 2. Average (Av.) and standard deviation (SD) of responses of winter wheat and spring wheat to temperature change under optimal conditions as based on results from all experiments collected for this project (see Table H-2)<sup>a</sup>. Response is calculated for 1 °C temperature rise and is given as a percentage of the result at ambient temperatures.

Conditions, Crop		Total shoot at anthesis <sup>b</sup>	LAI at anthesis <sup>b</sup>	Total shoot at maturity	Grain yield at maturity	Harvest index
Ambient CO <sub>2</sub> concentration						
(≈370 ppmv)	Av.	-6.3	-5.9	-9.8	-11.9	-2.5
	SD	±8.9	±6.4	±3.4	±2.4	±3.8
Elevated CO <sub>2</sub> concentration						
(≈700 ppmv)	Av.	-7.0	-5.4	-6.9	-9.1	-2.7
	SD	±5.0	±3.3	±1.5	±2.7	±3.3
All experiments						
	Av.	-6.6	-5.7	-8.3	-10.5	-2.6
	SD	±7.2	±5.1	±3.0	±2.9	±3.6

<sup>a</sup> Experimental data from Clermont Ferrand were not taken in account.

<sup>b</sup> Response was determined for date of anthesis which date was advanced by temperature rise.

### 3.3.2.3 Detailed analysis of Arizona data sets

From the spring wheat FACE experiments at Maricopa, Arizona, experimental results were separately available for each replicate. Generally there were four replicates for each growing season and treatment, which results were used for a detailed analysis of their variability. To limit the variability from various stress factors, yield results from the experiments under optimal conditions (i.e. ample water and nitrogen supply) were only used. Differences in growth and yield response to CO<sub>2</sub> enrichment from one year to the other may be caused by variation in climatic conditions, which can be analysed by model simulation of wheat growth under identical conditions (see Sections 3.3.4 and 3.3.5). Variation in experimental results from one growing season and treatment can only be caused by the variability in growing conditions (e.g. soil structure and nutrient supply) and by the uncertainty in yield measurements (mainly determined by size of sampling plots and spatial variation in crop canopy). This variation cannot be analysed with LINTULCC, because growing conditions were assumed to be identical between replicates, however, it can be derived from the variability in results from the four replicates per treatment.

Figure 1 shows grain and total above-ground biomass yields of four replicates under both ambient and elevated CO<sub>2</sub> treatments in the three growing seasons. In the first two years (1992/93; 1993/94) no blower rings were used for the ambient treatment, which resulted in a slightly lower temperature and thus a slightly later end of crop growth than that under elevated CO<sub>2</sub>. However, there was no indication that this has influenced the results of this variation analysis. In the last year both an ambient CO<sub>2</sub> treatment with blower rings (to prevent the temperature effect) and the same treatment but without blower rings (with only two replicates) was applied. As the time courses of grain and biomass yield attained their maximum yield generally before maturity (Figures B-1, B-2 and B-3, see Appendix B), yield data were used that were determined at both the final date (near maturity) and one week before that date. This shows the variation that resulted from a repetition of the yield measurements. The variation in both total biomass and grain yields from one growing season and CO<sub>2</sub> treatment was large. However, this variation became even larger when results from one growing season and treatment were compared with results from the same season and treatment that were harvested one week earlier.

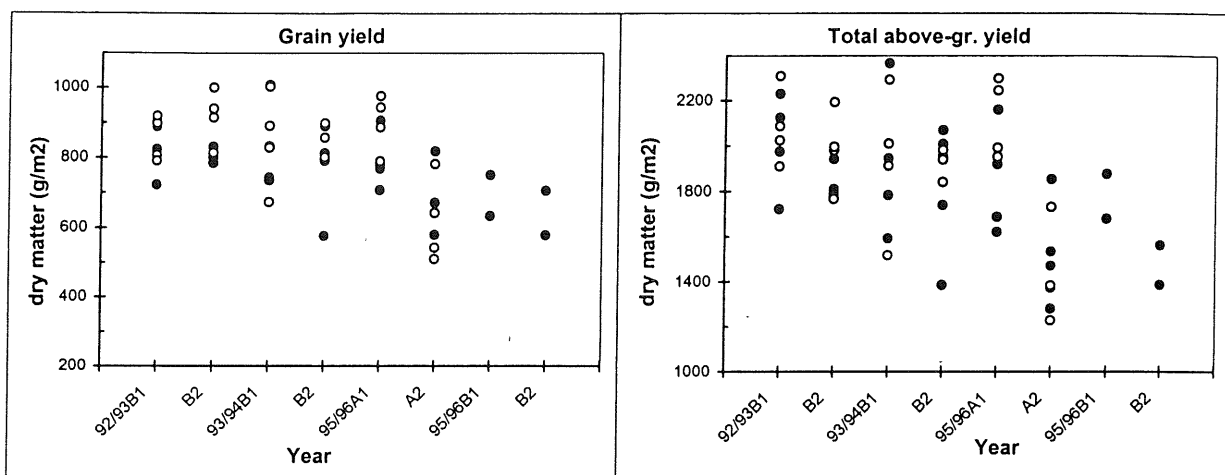


Figure 1. Grain and total above-ground biomass yields as observed in spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in different growing seasons under conditions of ample water and high nitrogen supply and ambient (•; in Year: A= ambient treatment with blowers; B= ambient treatment without blowers; 1= harvest one week before final harvest; 2= final harvest) and elevated (○; 550 ppmv in 1992/93 and 1993/94 and 570 ppmv in 1995/96) atmospheric CO<sub>2</sub> concentration (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a; 1996b). For each growing season and treatment there were four replicates except for 1995/96 B (i.e. 2 replicates).

Figure 2 shows for grain and total above-ground biomass yields the mean results under ambient and elevated CO<sub>2</sub> concentration, respectively in the different growing seasons. The mean results were given for the two harvest dates. The mean yield considerably changed from one harvest date to the other, and often in different directions under ambient and elevated CO<sub>2</sub>. This leads to different conclusions on the yield response to CO<sub>2</sub> enrichment depending on the harvest date. In addition to this uncertainty in mean yield, the standard deviation of the four replicate yields was large (roughly 50 to 100 g/m<sup>2</sup> for grains and 100 to 200 g/m<sup>2</sup> for total biomass) and almost identical to the mean yield response to CO<sub>2</sub> enrichment. The effect of CO<sub>2</sub> enrichment on both grain and total above-ground biomass yield was not significant at the five percent level, in particular if results from the two harvest dates were combined. This shows that the variability in experimental results from one season and treatment was so large that the mean effect of CO<sub>2</sub> enrichment became too small to obtain a significant yield response. This corresponds well with the results in Table 1 that also showed a high standard deviation of the yield responses to CO<sub>2</sub> enrichment from all experiments used in this study.

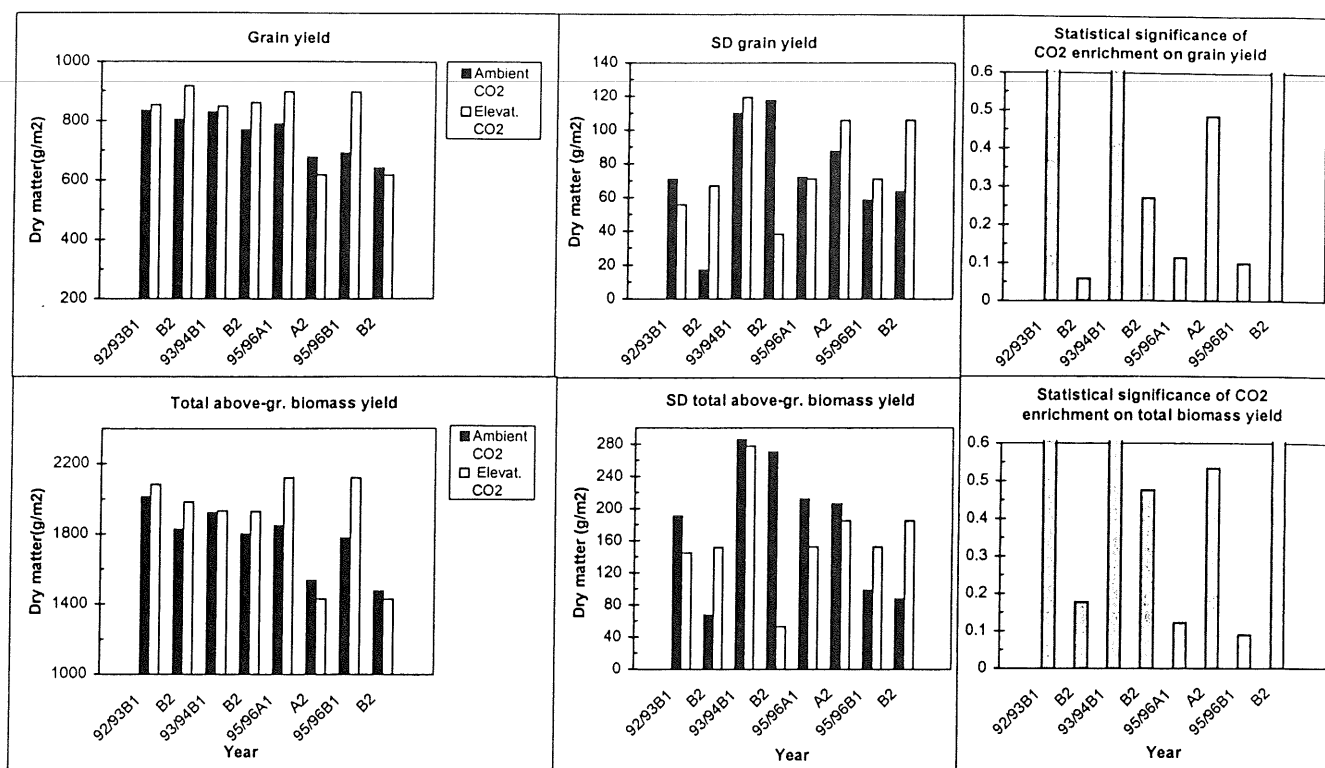


Figure 2. Mean and standard deviation of grain and total above-ground biomass yields as observed in spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in different growing seasons under conditions of ample water and high nitrogen supply and ambient (in Year: A= ambient treatment with blowers; B= ambient treatment without blowers; 1= harvest at one week before final harvest; 2= final harvest) and elevated (550 ppmv in 1992/93 and 1993/94 and 570 ppmv in 1995/96) atmospheric CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a; 1996b) and the statistical significance of CO<sub>2</sub> enrichment on grain and total above-ground biomass yields.

### 3.3.3 Sensitivity analysis of wheat growth with LINTULCC model

The sensitivity of the LINTULCC results to systematic changes in climate were analysed for optimal conditions (i.e. no water stress and no nutrient shortage). Weather variables were adjusted, in a stepwise manner, in order to gauge the sensitivity of model results to changing values of each variable. Sensitivity to changes in the following variables has been analysed: temperature, atmospheric CO<sub>2</sub> concentration, and solar radiation. The three variables were adjusted both independently and in different combinations, to calculate both their separate effects on wheat growth and the interacting effects of the three variables on growth. Results from this analysis can be used to explain both the results from simulations of the experiments and possibly the experimental results.

The model results showed a large positive interaction between the three variables. Doubling of the ambient atmospheric CO<sub>2</sub> concentration resulted in an increase in shoot growth rate of 35% at low light conditions, which increased to 55% at high light conditions (Figure 3). This light effect was mainly caused by the photosynthesis-light response curve, in which the positive effect of CO<sub>2</sub> enrichment on photosynthesis becomes larger at high light conditions (Grashoff et al., 1995). Doubling of ambient atmospheric CO<sub>2</sub> resulted in an increase in shoot growth rate of 35% at low temperatures, which increased to 60% at high temperatures. In the new routine to calculate the crop light-use efficiency (see Section 3.2.2) as based on the

biochemical photosynthesis equations (Farquhar and Von Caemmerer, 1982), the optimal temperature for photosynthesis shifts to a higher value with increasing atmospheric CO<sub>2</sub> concentration. This results in a positive effect of temperature rise on the growth response to CO<sub>2</sub> enrichment (Van Oijen and Goudriaan, 1997), as shown in Figure 3.

Temperature rise (e.g. from 10 to 30 °C) resulted in an increase in shoot growth rate of 45% at ambient atmospheric CO<sub>2</sub> concentration and of 65% at two times the ambient CO<sub>2</sub> concentration (Figure 3). However, this positive effect of temperature rise on the growth rate does generally not result in higher yields, as the temperature rise also results in a shortened duration of the growth period. This leads to a lower light interception and thus biomass production. For the experiments collected in this project, temperature rise always resulted in lower total biomass and grain yield (Tables 2 and H-2). Results from the experiments carried out within the ESPACE-Wheat programme also showed a negative yield response to temperature rise (Van Oijen and Goudriaan, 1997). At low light conditions a similar temperature rise (from 10 to 30 °C) resulted in an increase in shoot growth rate of 10% and at high light conditions of 60%. This shows that under low light conditions photosynthesis and thus growth rate are mainly determined by the amount of incoming radiation.

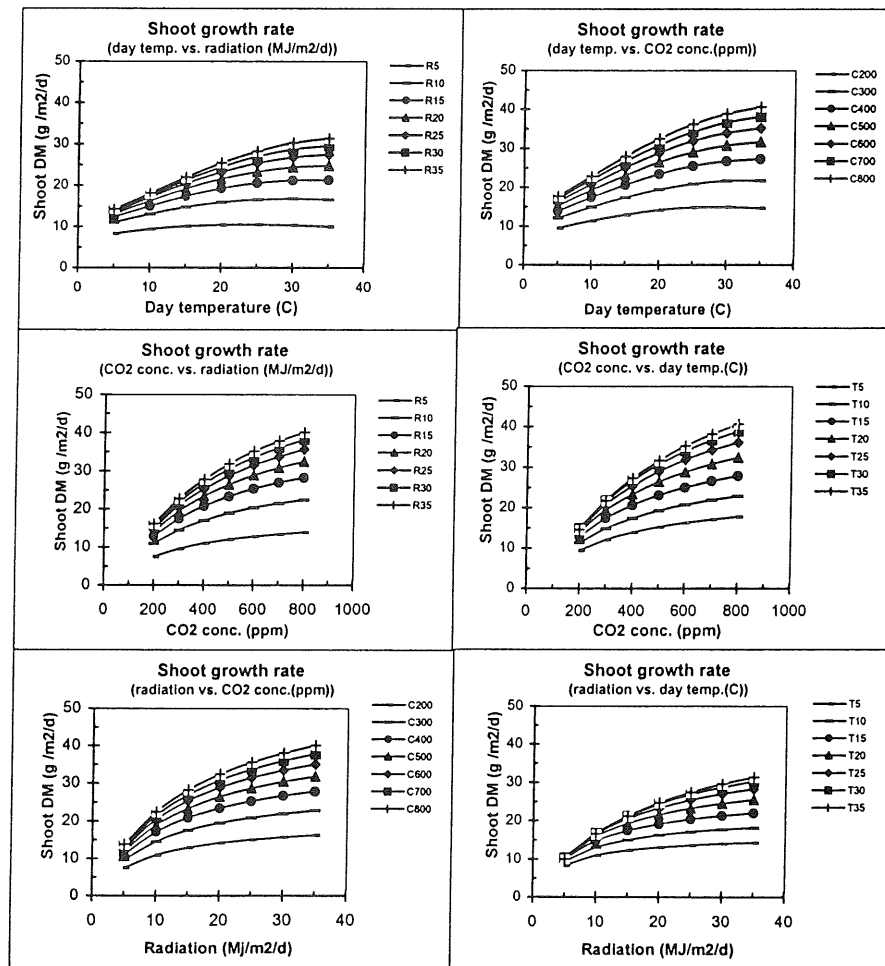


Figure 3. Sensitivity of the shoot growth rate of wheat to changes in temperature, atmospheric CO<sub>2</sub> concentration and solar radiation and its interaction with changes in temperature from 5 °C (T5) to 35 °C (T35), with changes in solar radiation from 5 (R5) to 35 MJ m<sup>-2</sup> d<sup>-1</sup> (R35) and with changes in atmospheric CO<sub>2</sub> concentration from 200 (C200) to 800 ppmv (C800), calculated with the LINTULCC model for a closed crop canopy (Van Oijen and Goudriaan, 1997). Standard values used were 20 °C, 350 ppmv CO<sub>2</sub> and 20 MJ m<sup>-2</sup> d<sup>-1</sup>.



The sensitivity of the shoot growth rate to changes in the three variables has also been determined for crops in three different growth phases. This may show if interactions occur between the growth responses to changes in the variables and the growth phase of the crop. The calculations have been done for a young crop ( $\text{LAI} = 1 \text{ m}^2 \text{ m}^{-2}$  and rubisco (RU) concentration =  $4 \text{ g m}^{-2} \text{ leaf}$ ), a closed crop with a productive canopy ( $\text{LAI} = 6 \text{ m}^2 \text{ m}^{-2}$  and  $\text{RU} = 4 \text{ g m}^{-2} \text{ leaf}$ ) and an old crop with a low productive canopy ( $\text{LAI} = 6 \text{ m}^2 \text{ m}^{-2}$  and  $\text{RU} = 2 \text{ g m}^{-2} \text{ leaf}$ ). Doubling of the ambient atmospheric  $\text{CO}_2$  concentration resulted in an increase in shoot growth rate of 50%, 50% and 55% for the young, closed, and old crop, respectively (Figure 4). The shoot growth rate was clearly lower for the young crop with its lower light interception (low LAI) and for the old crop with its lower maximum photosynthetic rate (low rubisco concentration), but the growth response to  $\text{CO}_2$  enrichment was not affected by the growth phase of the crop. Temperature rise (e.g. from  $10^\circ\text{C}$  to  $30^\circ\text{C}$ ) resulted in an increase in shoot growth rate of 50%, 50% and 70% for the young, closed and old crop, respectively. The growth response to the temperature rise was larger for the old crop with its lower maximum photosynthetic rate. An increase in incoming radiation (e.g. from 10 to  $30 \text{ MJ m}^{-2} \text{ d}^{-1}$ ) resulted in an increase in shoot growth rate of 55%, 55%, and 30% for the young, closed and old crop, respectively. The growth response to incoming radiation was smaller for the old crop, because the maximum of its photosynthetic rate was lower and was attained at a lower amount of incoming radiation.

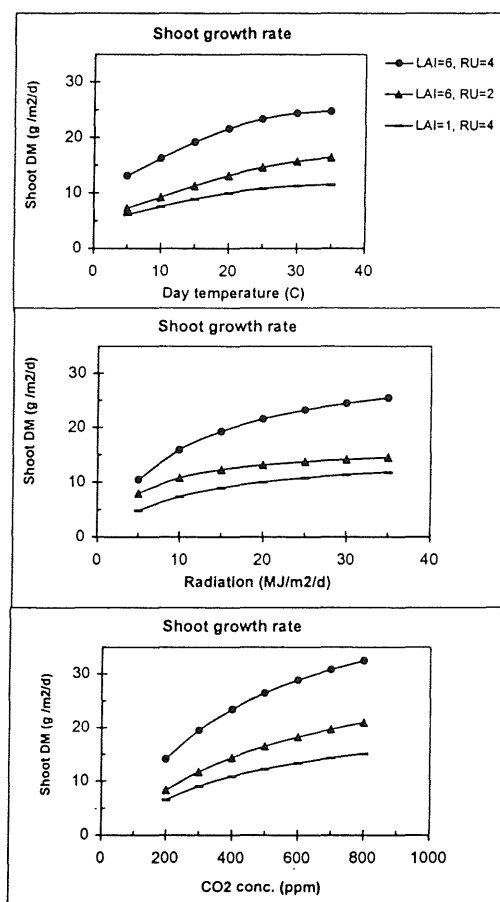


Figure 4. Sensitivity of the shoot growth rate of wheat to changes in temperature, solar radiation and atmospheric  $\text{CO}_2$  concentration for a crop with a closed and productive canopy ( $\text{LAI} = 6 \text{ m}^2 \text{ m}^{-2}$ , rubisco (RU) concentration =  $4 \text{ g m}^{-2} \text{ leaf}$ ), for an old and low productive crop canopy ( $\text{LAI} = 6$ ,  $\text{RU} = 2$ ), and for a young crop ( $\text{LAI} = 1$ ,  $\text{RU} = 4$ ), calculated with the LINTULCC model (Van Oijen and Goudriaan, 1997). Standard values used were  $20^\circ\text{C}$ , 350 ppmv  $\text{CO}_2$  and  $20 \text{ MJ m}^{-2} \text{ d}^{-1}$ .

### 3.3.4 Analysis of experimental data sets with LINTULCC model

The experimental data sets have been analysed with the LINTULCC model (see Section 3.2.2) by simulating crop growth under the environmental conditions found in the experiments. The crop growth simulations were made from crop emergence to maturity, taking into account the characteristics of the crop and its interaction with the environment. In this way the effects of changes in atmospheric CO<sub>2</sub> concentration and temperature on crop growth were analysed. The resulting changes in crop characteristics, growth and production from the growth simulations were compared with the observed changes. This may result in an improved explanation of the variability in observed responses of wheat growth and yield to changes in atmospheric CO<sub>2</sub> concentration and temperature.

For the analysis of the experimental data with LINTULCC, this model was calibrated on the basis of the experimental data set in three subsequent steps. In the first step (i.e. Simulat. A) the phenological development of the simulated crop in the ambient treatment (i.e. dates of anthesis and maturity) was made identical to that in the experiment. In the next step (i.e. Simulat. B) the phenological development in the model was calibrated separately for the ambient and the changed (i.e. change in atmospheric CO<sub>2</sub> concentration or temperature) treatment. In both step A and B the time course of LAI (m<sup>2</sup> leaf area m<sup>-2</sup> ground area) and thus of light interception was simulated. In the last step (i.e. Simulat. C) the phenological development in the model was calibrated separately for each treatment and the time course of LAI was made identical to the observed time course.

This calibration approach resulted in a step-wise improvement of the similarity between the simulated and observed durations of total crop growth and of grain filling and the simulated and observed cumulative radiation interception during the total growth period. These crop variables strongly determine the yield, as a higher radiation interception generally results in a higher biomass production and a longer grain filling period may result in a higher fraction of total biomass in the grains (i.e. harvest index). The step-wise approach shows the simulated responses to CO<sub>2</sub> enrichment and temperature change of crop variables and of total biomass and grain yields, to allow a comparison with the observed responses. This comparison may show for which reason the responses to CO<sub>2</sub> enrichment and temperature change differ between different experiments or years and in which crop variables (e.g. radiation use efficiency, light interception, or harvest index) the changes are mainly responsible for these different responses. Finally, this may show if the sensitivity to changes in atmospheric CO<sub>2</sub> concentration or temperature as observed in the experiments, is identical to that calculated with LINTULCC, or that this sensitivity is different or more complex.

Responses to CO<sub>2</sub> enrichment have been analysed for the experiments from Arizona, Florence, Giessen, Rothamsted and Wageningen and responses to temperature change for the experiments from Clermont Ferrand, Rothamsted and Wageningen. However, these analyses with LINTULCC have been performed only for experiments under optimal conditions (i.e. no water or nitrogen shortage). Summaries of the observed changes in crop variables and yields in response to changes in atmospheric CO<sub>2</sub> concentration against the simulated changes in these variables are given in Figures 5 (simulat. A) and 6 (simulat. C) and in response to temperature change are given in Figures 7(simulat. A) and 8 (simulat. C). Detailed information on the observed and simulated results for crop variables and yields under ambient conditions and their changes by CO<sub>2</sub> enrichment and temperature change are given in Appendices I upto N for the different experiments. For each site, year and treatment

information is given on the average growing conditions ( atmospheric CO<sub>2</sub> concentration, temperature and solar radiation), on crop variables such as temperature sums required for the total growth and grain filling periods, cumulative intercepted photosynthetically active radiation (MJ PAR m<sup>-2</sup>) from crop emergence to maturity, radiation use efficiency (g total above-ground biomass dry matter MJ<sup>-1</sup> PAR) and harvest index (g grain dry matter g<sup>-1</sup> total above-ground biomass dry matter), and on total above-ground biomass and grain yields.

#### 3.3.4.1 CO<sub>2</sub> enrichment

The increase in total above-ground biomass yield by CO<sub>2</sub> enrichment varied in the experiments between nil and 40% of total biomass under ambient conditions (Figure 5), whereas with calibration step A the simulated increase in total biomass varied between 20 and 60%. The relationship between the simulated and the observed increase in biomass yield was poor ( $R^2 = 0.31$  with  $\text{Obs} = 7.8 + 0.34 \cdot \text{Simul}$ ; result from linear regression analysis between simulated (Simul) and observed change (Obs; % of ambient value). The observed increases in radiation use efficiency by CO<sub>2</sub> enrichment were from 10% larger to 10% smaller than the simulated increases and a moderate relationship between observed and simulated increases occurred ( $R^2 = 0.40$  with  $\text{Obs} = 6.9 + 0.64 \cdot \text{Simul}$ ). In the experiments the change in intercepted radiation by CO<sub>2</sub> enrichment varied mainly between -5% and +5%, whereas in the simulation an increase by 5 to 10% occurred, resulting in nil relationship ( $R^2 = -0.16$ ). In the simulations an increase in assimilate production by CO<sub>2</sub> enrichment generally resulted in a larger leaf area and thus an increased radiation interception, whereas in the experiments this increase in radiation interception by CO<sub>2</sub> increase almost did not occur (see e.g. Appendix L for results from Giessen and Appendix N for results from Wageningen). This difference in radiation interception mainly caused the larger increase in total above-ground biomass by CO<sub>2</sub> enrichment in the simulations compared to the observed biomass increase. In the simulations the change in harvest index by CO<sub>2</sub> enrichment was small (i.e. increase of 0 to 8 %), whereas in the experiments the change in harvest index varied more strongly (i.e. -15% to +15%), resulting in a poor relationship ( $R^2 = 0.32$  with  $\text{Obs} = -6.6 + 1.36 \cdot \text{Simul}$ ). Consequently, the increase in grain yield by CO<sub>2</sub> enrichment in the simulations was almost similar to the increase in total biomass, whereas in the experiments the increases in total biomass and grain yield often differed. The simulated increase in grain yield varied between 25 and 65%, a much higher increase than that in the experiments (i.e. change of -5% to 40 %). The relationship between the simulated and observed increases in grain yield by CO<sub>2</sub> enrichment was poor ( $R^2 = 0.23$  with  $\text{Obs} = 6.8 + 0.26 \cdot \text{Simul}$ ).

The increase in total above-ground biomass by CO<sub>2</sub> enrichment varied in the experiments between nil and 40% of total biomass under ambient conditions (Figure 6), whereas with calibration step C the simulated increase in total biomass varied between 10 and 30%. The relationship between the simulated and observed increase in total biomass was much better than in step A ( $R^2 = 0.53$  with  $\text{Obs} = -4.8 + 1.06 \cdot \text{Simul}$ ). That was caused by the radiation interception in the simulation that was made identical to the observed interception. The observed increases in radiation use efficiency by CO<sub>2</sub> enrichment were from 10% higher to 10% lower than the simulated increases and a moderate relationship between observed and simulated increases occurred ( $R^2 = 0.40$  with  $\text{Obs} = 5.5 + 0.70 \cdot \text{Simul}$ ). This difference in the changes in radiation use efficiency caused the difference between simulated and observed increases in total biomass. The increase in radiation use efficiency by CO<sub>2</sub> enrichment and thus the increase in total biomass was underestimated in the growth simulation for Giessen (see also Appendix L) and was overestimated in the simulations for Wageningen and Arizona (see also Appendices N and I). In the simulations the change in harvest index by CO<sub>2</sub>

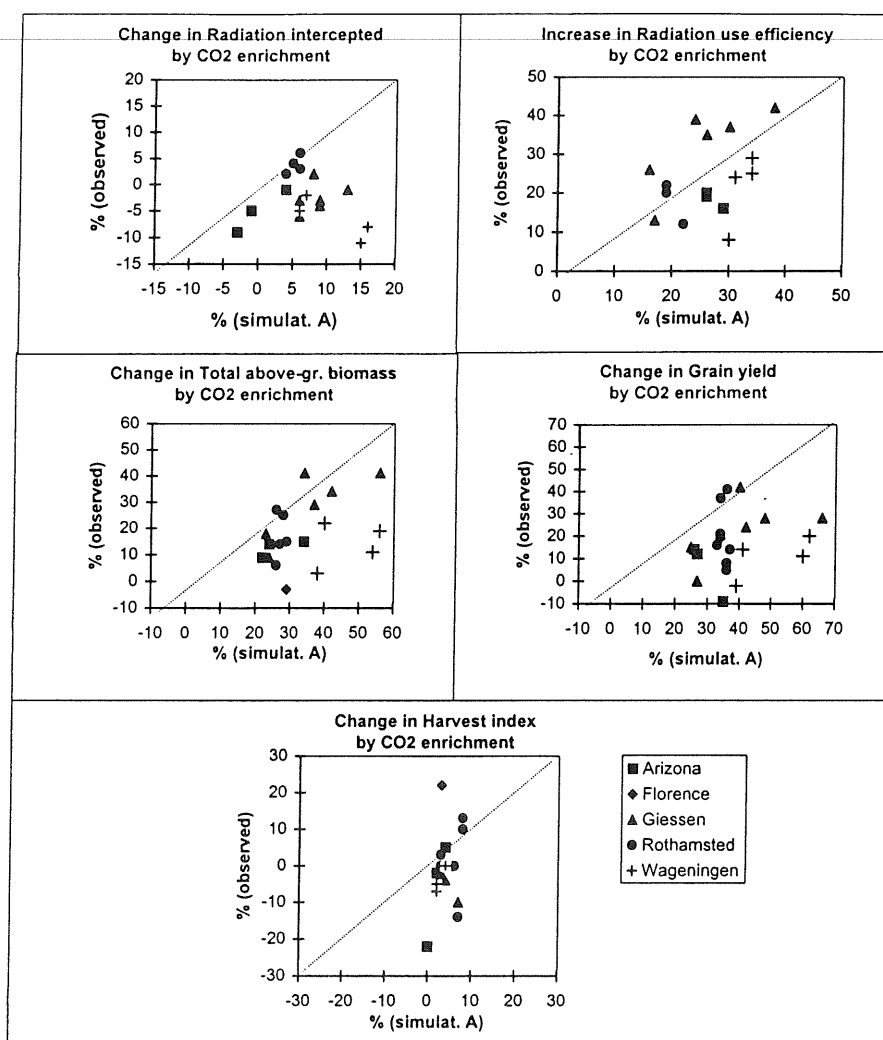


Figure 5. Responses of crop variables to atmospheric CO<sub>2</sub> enrichment as percentage of their values under ambient conditions, observed in experiments at the indicated locations versus simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A (i.e. simulat. A): phenology calibrated for ambient treatment and LAI simulated.

enrichment was much larger (i.e. change of -5% to +20 %) than in step A which was caused by the use of observed radiation interception data. In the experiments the range of changes in harvest index was slightly different (i.e. change of -10% to +10%), but the relationship between simulated and observed changes in harvest index was poor ( $R^2 = 0.18$  with  $\text{Obs} = -0.9 + 0.20 \cdot \text{Simul}$ ) This probably indicates for LINTULCC that simply calculated the grain production from the assimilate production during the period of grain filling, the need for a sink-determined calculation method (i.e. dependent on grain number and grain growth rate). However, it might also indicate experimental variability which cannot be reproduced by LINTULCC. The relationships between simulated and observed changes in total biomass and between simulated and observed changes in harvest index resulted together in a poor to moderate relation between simulated and observed changes in grain yield ( $R^2 = 0.40$  with  $\text{Obs} = 7.7 + 0.40 \cdot \text{Simul}$ ). The range of simulated changes in grain yield (0% to +40%), however, was similar to that of observed changes.

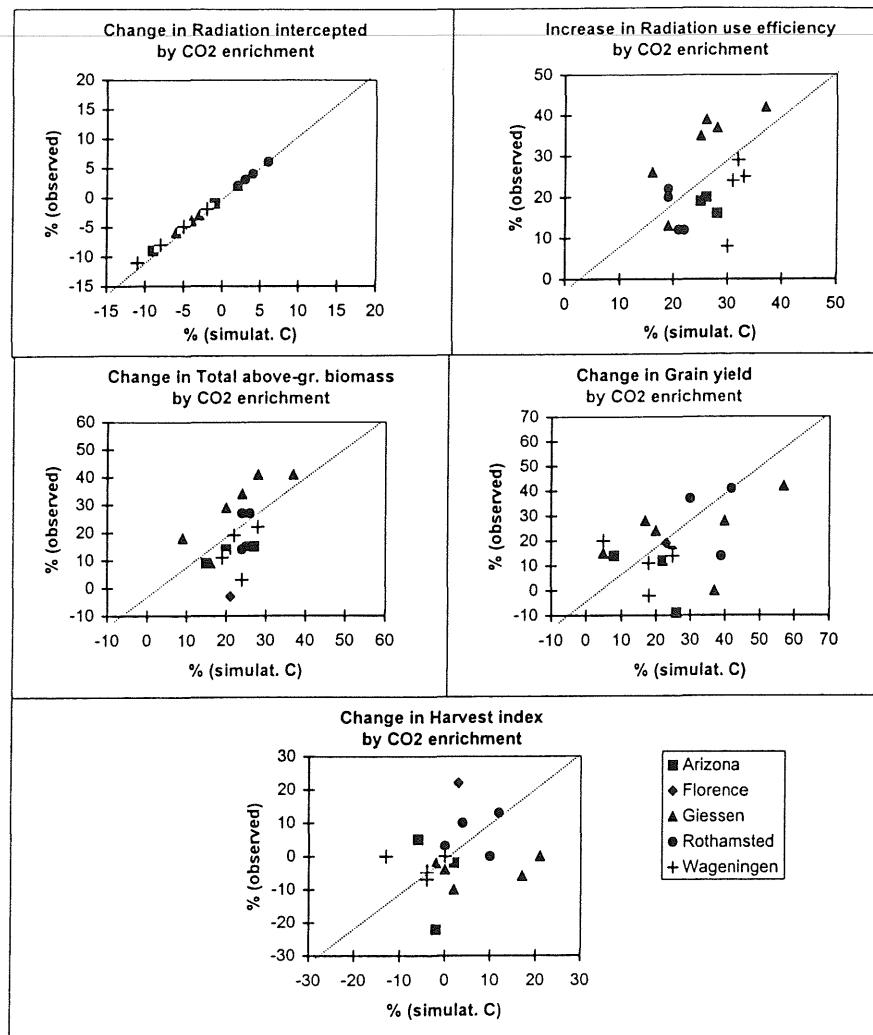


Figure 6. Responses of crop variables to atmospheric CO<sub>2</sub> enrichment as percentage of their values under ambient conditions, observed in experiments at the indicated locations versus simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C (i.e. simulat. C): phenology calibrated for each treatment and LAI as observed in the experiments.

#### 3.3.4.2 Temperature change

The decrease in total above-ground biomass by temperature rise (except for one treatment in Clermont Ferrand with lowered temperature) varied in the experiments between 10% and 30% of total biomass under ambient temperatures (Figure 7), whereas with calibration step A the simulated decrease in total biomass varied only between 5 and 10%. The relationship between the simulated and observed decreases in total biomass was poor ( $R^2 = 0.33$  with  $\text{Obs} = -13.6 + 0.62 \cdot \text{Simul}$ ). In the simulations the changes in intercepted radiation by temperature change were almost similar to the observed changes ( $R^2 = 0.89$  with  $\text{Obs} = -2.2 + 1.04 \cdot \text{Simul}$ ). The observed changes in radiation use efficiency by temperature change varied strongly (-25 to +5%), whereas in the simulations the change was almost nil and the variation in change was small. Hence, this relationship was poor ( $\text{Obs} = -15.0 + 4.1 \cdot \text{Simul}$ , although  $R^2 = 0.89$ ). The large variation in changes in observed radiation use efficiency caused the large variation in changes in observed total biomass and also caused the poor relation between observed and simulated changes in total biomass. In Clermont Ferrand the treatments with strong temperature increases (by 6.3 °C; see Appendix J) during grain filling

showed much stronger decreases in total biomass and radiation use efficiency than the experiments at the other sites and a much larger deviation from the simulated values. In the experiments the change in harvest index by temperature change was almost nil (i.e. change of -5 to +5 %) except for the large increase in harvest index at the lowered temperature treatment in Clermont Ferrand and the large decrease for two treatments in Rothamsted. The simulated changes in harvest index varied more strongly (i.e. -15 to +5%) and their relationship with the observed changes was poor ( $R^2 = 0.39$  with  $\text{Obs} = -1.0 + 0.72 \cdot \text{Simul}$ ). The simulated decrease in grain yield varied between 5 and 20% (except for the lowered temperature treatment), which decrease was smaller than that in the experiments (i.e. decrease of 15 to 35 %). The relationship between the simulated and observed decreases in grain yield by temperature change was poor ( $\text{Obs} = -6.2 + 1.42 \cdot \text{Simul}$ , although  $R^2 = 0.76$ ).

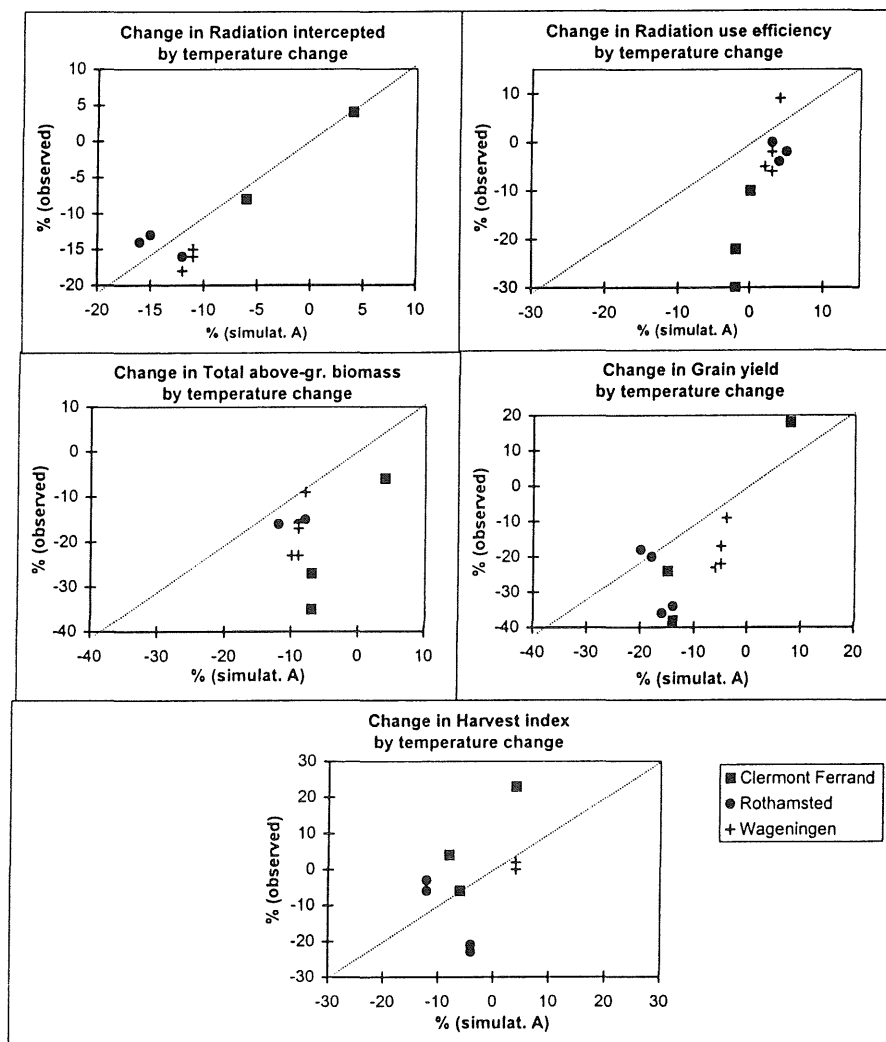


Figure 7. Responses of crop variables to temperature change as percentage of their values under ambient temperatures, observed in experiments at the indicated locations versus simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A (i.e. simulat. A): phenology calibrated for ambient treatment and LAI simulated.

The decrease in total above-ground biomass by temperature rise (except for the lower temperature treatment in Clermont Ferrand) varied in the experiments between 10 and 30% of total biomass under ambient temperatures (Figure 8), whereas with calibration step C the

simulated decrease in total biomass varied only between 10 and 15%. The relationship between the simulated and observed decreases in total biomass yield was just as poor ( $R^2 = 0.39$  with  $\text{Obs} = -12.1 + 0.57 \cdot \text{Simul}$ ) as in step A, although the radiation interception in the simulation was made identical to the observed interception. However, when the results from the experiments at Clermont Ferrand were left out because of their different experimental method, this relationship became much better ( $\text{CL.F.}: R^2 = 0.56$  with  $\text{Obs} = -4.5 + 0.94 \cdot \text{Simul}$ ). The observed changes in radiation use efficiency by temperature change were much more variable than the simulated changes and strongly differed ( $\text{Obs} = -11.9 + 3.71 \cdot \text{Simul}$ , although  $R^2 = 0.88$ ). This difference in changes in radiation use efficiency caused the poor relationship between simulated and observed changes in total biomass. If the results from the Clermont Ferrand experiments were left out, the relationship between simulated and

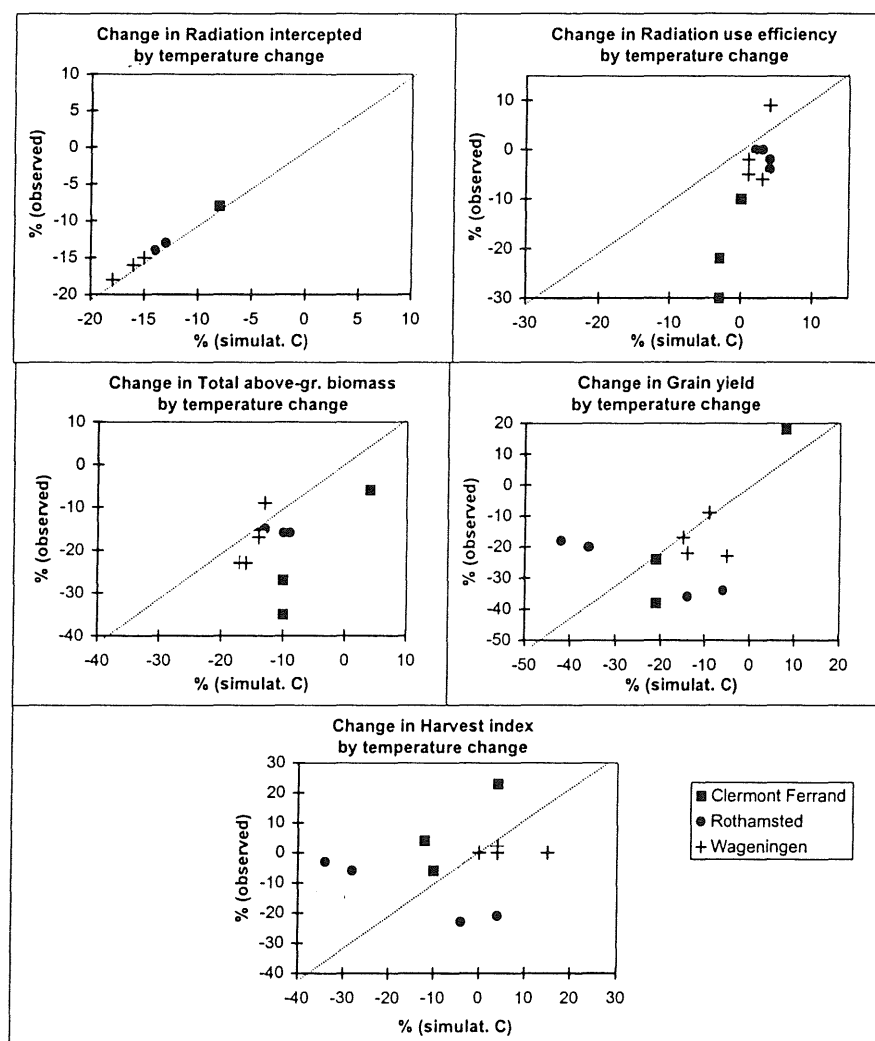


Figure 8. Responses of crop variables to temperature change as percentage of their values under ambient temperatures, observed in experiments at the indicated locations versus simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C (i.e. simulat. C): phenology calibrated for each treatment and LAI as observed in the experiments.

observed values for changes in radiation use efficiency was moderately improved ( $\text{CL.F.}: R^2 = 0.35$  with  $\text{Obs} = -4.7 + 1.26 \cdot \text{Simul}$ ) and thus also that for changes in total biomass (see above). However, temperature rise gave small increases in radiation use efficiency in the simulation (see Figure 3 for model sensitivity), whereas it generally gave small decreases in

the experiments. In the simulations the variation in changes in harvest index by temperature change was much larger (i.e. -30% to +10 %) than in step A which was caused by the use of observed radiation interception data. In the experiments the changes in harvest index were almost nil (i.e. -5% to + 5% mostly), and the relationship between simulated and observed changes in harvest index was nil and even worse than in step A (+Cl.F.:  $R^2 = 0.13$  with Obs =  $-2.2 + 0.11 \cdot \text{Simul}$ ; -Cl.F.:  $R^2 = 0.03$  with Obs =  $-6.3 + 0.02 \cdot \text{Simul}$ ). The moderate relationship between simulated and observed changes in total biomass and the very poor one between simulated and observed changes in harvest index resulted together in a poor relationship between simulated and observed changes in grain yield (+Cl.F.:  $R^2 = 0.39$  with Obs =  $-13.5 + 0.42 \cdot \text{Simul}$ ; -Cl.F.:  $R^2 = -0.25$  with Obs =  $-25.2 - 0.16 \cdot \text{Simul}$ ). This relationship between simulated and observed changes in grain yield would improve considerably, if the simulated harvest index was assumed to be constant with temperature change.

### 3.3.5 Detailed analysis of Arizona data sets with LINTULCC model

These experimental data sets have been analysed with the LINTULCC model by simulating crop growth under the environmental conditions at that location. The approach is partly identical to that described in Section 3.3.4. In that analysis the responses to CO<sub>2</sub> enrichment of different crop variables over the whole growth period and of the final yields were determined, whereas this approach goes more into details. Time courses of crop variables from crop emergence to maturity as observed in the experiments were compared with the time courses as simulated with LINTULCC for identical conditions. This gives information on the changes in these crop variables over time and their interactions with the environmental conditions, in particular the increase in atmospheric CO<sub>2</sub> concentration. This may show the time-dependent variability in observed and simulated responses of wheat growth to CO<sub>2</sub> enrichment and may improve the explanation of the variability in observed responses. For the analysis of the experimental data, LINTULCC was calibrated on the basis of the experimental data set in the three subsequent steps, as described above (Section 3.3.4).

The analyses with LINTULCC have been performed only for experiments in Arizona under optimal conditions (i.e. no water or nitrogen shortage). For growing season 1992/93 the time courses of crop variables under elevated atmospheric CO<sub>2</sub> and of the ratio between shoot growth under elevated and ambient CO<sub>2</sub>, both observed in the experiments and simulated with LINTULCC for calibration steps A and C, are given in Figures 9 and 10, respectively. The same time courses under elevated CO<sub>2</sub> but with simulated results for step B are given in Figure O-2 (see Appendix O). Under ambient CO<sub>2</sub> the time courses of observed crop variables were compared with simulated results for steps A and C in Figures O-1 and O-3, respectively. For growing season 1993/94 the time courses of crop variables under elevated atmospheric CO<sub>2</sub> and of the ratio between shoot growth under elevated and ambient CO<sub>2</sub>, both observed in the experiments and simulated with LINTULCC for calibration step C, are given in Figure 11. The same time courses under elevated CO<sub>2</sub> but with simulated results for steps A and B are given in Figures O-5 and O-6. Under ambient CO<sub>2</sub> the time courses of observed crop variables were compared with simulated results for steps A and C in Figures O-4 and O-7, respectively.

For growing season 1995/96 the time courses of crop variables under elevated atmospheric CO<sub>2</sub> and of the ratio between shoot growth under elevated and ambient CO<sub>2</sub> (both treatments with blower rings), both observed in the experiments and simulated with LINTULCC for calibration step C, are given in Figure 12. The same time courses under elevated CO<sub>2</sub> but



with simulated results for steps A and B are given in Figures O-9 and O-10 (see Appendix O). Under ambient  $\text{CO}_2$  (with blower rings), the time courses of observed crop variables were compared with simulated results for steps A and C in Figures O-8 and O-11, respectively. For ambient  $\text{CO}_2$  but without blower rings, being similar to the ambient treatment in the previous years, the time courses of observed crop variables were compared with simulated results for step C in Figure O-12 and the time course of the ratio between shoot growth under elevated and ambient  $\text{CO}_2$  (without blower ring) was shown too in this figure. Summaries of total biomass and grain yields at maturity and of the ratio between yields under elevated and ambient  $\text{CO}_2$ , as observed in the three growing seasons and as simulated with LINTULCC for identical conditions, are given in Figures 13 and 14, respectively.

### 3.3.5.1 Growing season 1992/93

For the ambient treatment the shoot growth, phenological development and maximum LAI in step A of the simulations were calibrated on the basis of the observed values (Figure O-1).

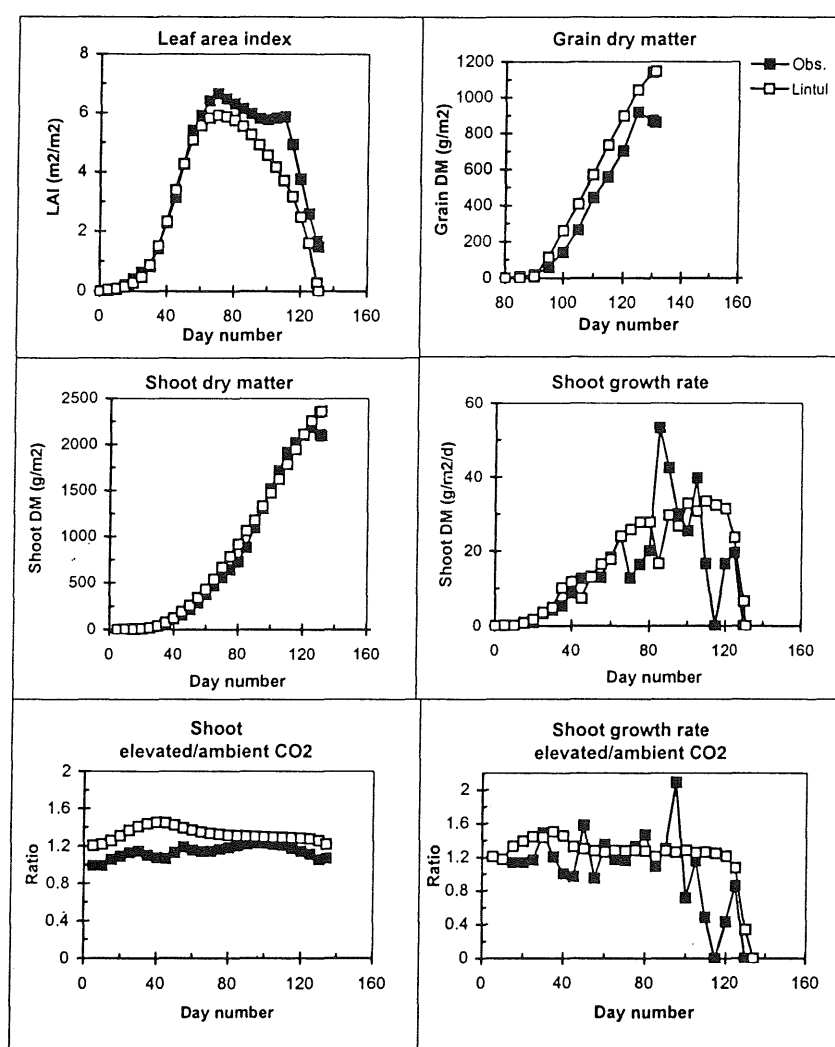


Figure 9. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1992/93 under conditions of ample water supply and elevated (550 ppmv) atmospheric  $\text{CO}_2$  concentration and the ratio between shoot growth under elevated and ambient (370 ppmv)  $\text{CO}_2$  concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A: phenology calibrated for ambient treatment and LAI simulated. Day number= Julian day.

The main difference between observed and simulated results was the higher simulated grain growth near maturity, although the observed LAI near maturity was higher. Under elevated CO<sub>2</sub> the shoot growth was simulated well, but the grain growth started too early in the simulation, resulting in a too high grain yield (Figure 9). The ratio between shoot dry matter under elevated and ambient CO<sub>2</sub> was initially higher in the simulation than in the experiment, became almost similar at day 100, and higher again near maturity. In step B the phenological development of the elevated CO<sub>2</sub> treatment was calibrated too and this resulted in improved simulation of grain growth (Figure O-2). In step C the observed LAI was used in the simulation. Shoot and grain growth under ambient CO<sub>2</sub> were simulated well, however the simulated final grain yield was much too high (Figure O-3). This was caused by the observed LAI that remained high upto maturity, resulting in a simulated growth rate that remained high too. In the experiment crop growth stopped earlier. Under elevated CO<sub>2</sub> the shoot growth was simulated well in step C, except for the last 10 days when the high values for observed LAI resulted in a higher growth rate than observed (Figure 10). Grain growth was clearly lower in

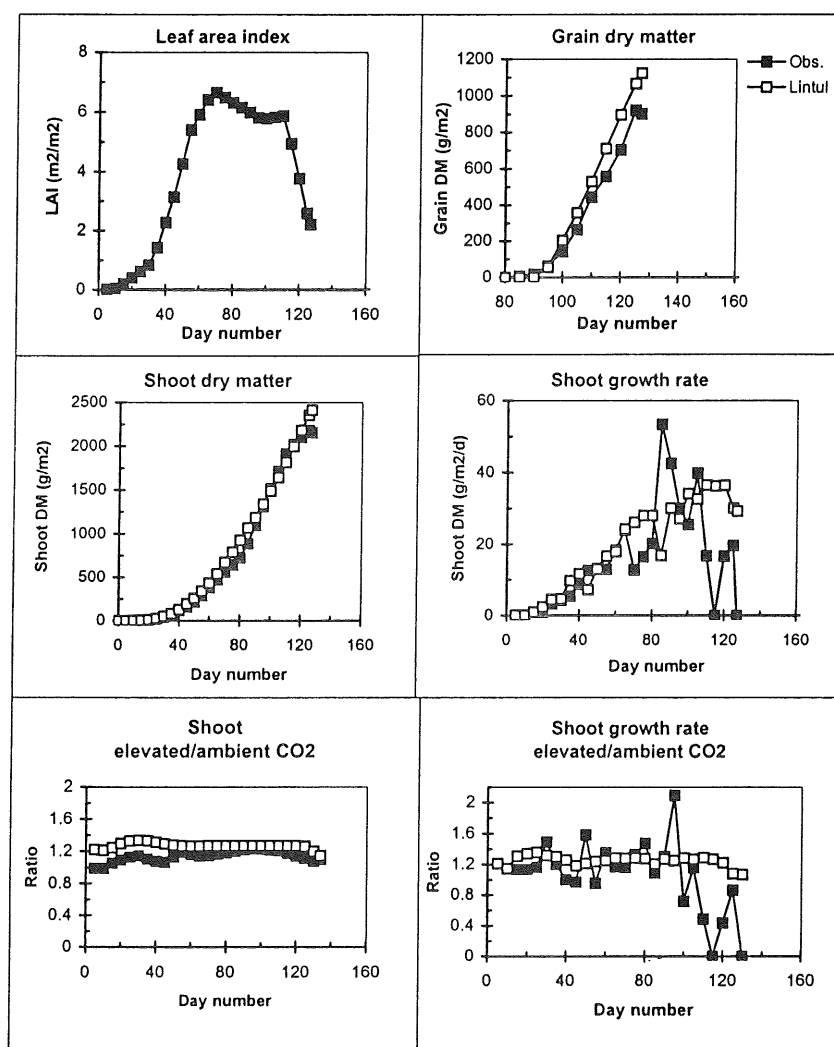


Figure 10. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1992/93 under conditions of ample water supply and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated and ambient (370 ppmv) CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C: phenology calibrated for each treatment and LAI as observed in the experiments. Day number= Julian day.

the experiment than in the simulation and stopped earlier. The ratio between shoot dry matter under elevated and ambient  $\text{CO}_2$  was initially higher in the simulation than in the experiment, became almost similar around day 100, and higher again near maturity. This last difference near maturity was mainly caused by the advanced end of shoot growth in the experiment under elevated  $\text{CO}_2$ .

### 3.3.5.2 Growing season 1993/94

For the ambient treatment and calibration step A shoot and grain growth were simulated well and the main difference between simulated and observed results was found for LAI (Figure O-4). Under elevated  $\text{CO}_2$  shoot and grain growth was simulated reasonably well. However, simulated shoot and grain growth stopped later than growth in the experiment, resulting in

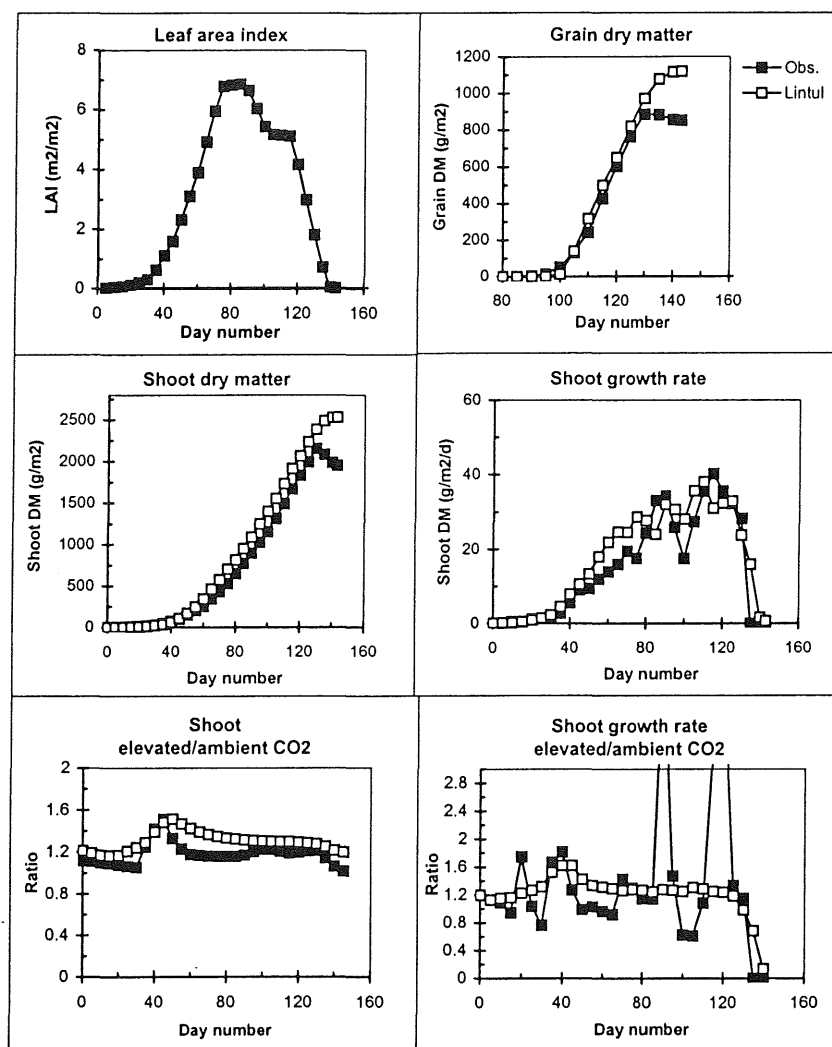


Figure 11. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1993/94 under conditions of ample water supply and elevated (550 ppmv) atmospheric  $\text{CO}_2$  concentration and the ratio between shoot growth under elevated and ambient (370 ppmv)  $\text{CO}_2$  concentrations (Source: Hunsaker et al., 1996; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C: phenology calibrated for each treatment and LAI as observed in the experiments. Day number= Julian day.

too high yields (Figure O-5). The ratio between shoot dry matter under elevated and ambient CO<sub>2</sub> was higher in the simulation than in the experiment during the whole growth period. In step B the calibration resulted in a slightly longer period of grain filling under elevated CO<sub>2</sub>, however, this did not improve the simulation of grain growth (Figure O-6). In step C the observed LAI was used in the simulation. Shoot and grain growth under ambient CO<sub>2</sub> were simulated reasonably well, however the simulated growth near maturity was too high (Figure O-7). This was caused by the observed LAI that remained high upto maturity, resulting in a simulated growth rate that remained high too (because radiation use efficiency in LINTULCC did not decrease near maturity). Under elevated CO<sub>2</sub> shoot and grain growth was simulated reasonably well in step C, except for the last 20 days before maturity. In this period the high values for observed LAI resulted in a considerable growth of shoot and grains, whereas in the experiment growth had stopped already (Figure 11). The ratio between shoot dry matter under elevated and ambient CO<sub>2</sub> was initially higher in the simulation than in the experiment, became almost similar around day 120, and higher again near maturity. This last difference near maturity was mainly caused by the advanced end of shoot growth in the experiment under elevated CO<sub>2</sub>.

### ***3.3.5.3 Growing season 1995/96***

For the ambient treatment and calibration step A shoot and grain growth and LAI were simulated well (Figure O-8). The main difference between simulated and observed results was the end of growth that in the experiment occurred 20 days before maturity. Under elevated CO<sub>2</sub> shoot and grain growth and LAI were simulated well. However, shoot and grain growth in the experiment stopped 20 days before maturity and even showed a strong decrease in biomass near maturity (Figure O-9). This resulted in a strong difference between simulated and observed shoot and grain yield. The ratio between shoot dry matter under elevated and ambient CO<sub>2</sub> was much higher in the simulation than in the experiment during the initial and the final part of the growth period. In step B calibration resulted in a slightly shorter period of grain filling but almost not in an improved simulation of grain growth (Figure O-10). In step C the observed LAI was used in the simulation. Shoot and grain growth under ambient CO<sub>2</sub> were simulated well, however the observed growth stopped 20 days before maturity (Figure O-11). Under elevated CO<sub>2</sub> the shoot growth was simulated well in step C but 20 days before maturity the observed growth stopped and total shoot dry matter strongly decreased (Figure 12). However, in this period the observed LAI was still quite high. The ratio between shoot dry matter under elevated and ambient CO<sub>2</sub> was initially higher in the simulation than in the experiment, became similar around day 80, and higher again near maturity. This difference near maturity was again caused by the advanced end of shoot growth in the experiment under elevated CO<sub>2</sub>. For the ambient treatment but without blower rings (resulting in lower minimum temperatures than with blower rings) and step C of the simulations, shoot and grain growth were simulated well, except again for the last 20 days (Figure O-12). The observed LAI increased and the growth duration should become longer at the lower temperatures in comparison to the ambient treatment with blower rings. The resulting higher light interception resulted in the simulation in higher yields, however, in the experiment this effect was not found (see Appendix I). Hence, the ratio between shoot dry matter under elevated and ambient CO<sub>2</sub> in the simulation (Figure O-12) was lower than the same ratio shown in Figure 12.

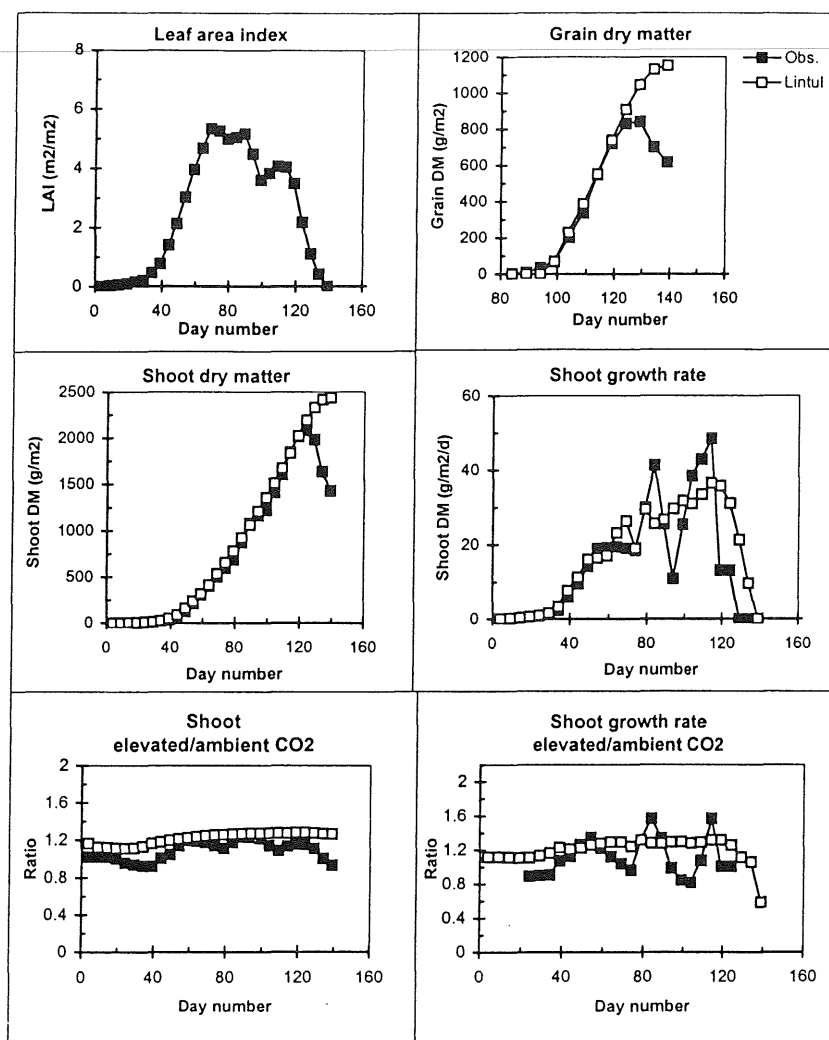


Figure 12. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of ample water supply and elevated (570 ppmv) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated and ambient (370 ppmv; with blower rings) CO<sub>2</sub> concentrations (Source: Pinter et al., 1996b) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C: phenology calibrated for each treatment and LAI as observed in the experiments. Day number= Julian day.

#### 3.3.5.4 Comparison of results from different growing seasons

Total above-ground biomass and grain yield at maturity as observed in the three growing seasons and as simulated with LINTULCC for the three calibration steps, were compared. In growing season 1992/93 total biomass under ambient CO<sub>2</sub> was simulated well in step A and total biomass under elevated CO<sub>2</sub> was also simulated well when in step B the time period of grain filling was shortened on the basis of the experimental results (Figure 13). In step C the actual LAI was used in the simulation but this did not improve correspondence with observed results, mainly because observed crop growth stopped earlier than was to be expected on the basis of LAI near maturity. This indicates a rapid decrease in the photosynthetic capacity and thus in radiation use efficiency near maturity, which was not incorporated in the model. The ratio between total above-ground biomass under elevated and ambient CO<sub>2</sub> was slightly overestimated in the simulations for steps B and C (Figure 14), mainly because the observed CO<sub>2</sub> effect on shoot dry matter was reduced near maturity (Figure 10). The ratio between

grain yield under elevated and ambient CO<sub>2</sub> was in the simulations for steps B and C lower than the ratio in the experiment (Figure 14). This was due to the shortened grain filling period under elevated CO<sub>2</sub>.

In growing season 1993/94 total biomass and grain yield under ambient CO<sub>2</sub> were simulated well in step A (Figure 13). Total biomass and grain yield increased with CO<sub>2</sub> enrichment more strongly in the simulation (steps A and B) than in the experiment (Figure 14). This difference was caused mainly by the decrease in cumulative radiation interception in the experiment, a decrease not found in the simulation. By using the actual LAI in the simulations (step C) the ratio between total biomass under elevated and ambient CO<sub>2</sub> was more in agreement with the observed ratio. However, in step C the total biomass under ambient CO<sub>2</sub> was overestimated in the simulation (Figure 13), mainly because observed crop growth decreased more rapidly than was simulated on the basis of the LAI near maturity. The ratio between total above-ground biomass under elevated and ambient CO<sub>2</sub> was overestimated in the simulation for step C (Figure 14), mainly because the observed CO<sub>2</sub> effect on shoot growth decreased near maturity (Figure 11).

In growing season 1995/96 total biomass under ambient CO<sub>2</sub> was simulated well in situation A (Figure 13) without blower effect (i.e. ambient treatment with blower rings that prevent temperature effect to be mixed with CO<sub>2</sub> enrichment effect). The ratio between total above-ground biomass under elevated and ambient CO<sub>2</sub> was higher in the simulations than the ratio in the previous growing seasons (Figure 14). This ratio was higher because the effect of temperature rise due to the blower rings in the elevated CO<sub>2</sub> treatment was removed. In the experiment, however, total biomass increased with CO<sub>2</sub> enrichment to the same extent as in the previous seasons and the grain yield even decreased. The prediction of the biomass increase with CO<sub>2</sub> enrichment was slightly improved (but still too high) from calibration step A to step C (Figure 14), taking into account the observed decrease in cumulative radiation interception. In growing season 1995/96 and situation B with blower effect (i.e. ambient treatment without blower rings as in previous growing seasons) simulated total biomass under ambient CO<sub>2</sub> was higher (Figure 13) than that in situation A because of the lower temperatures. This resulted in a smaller ratio between total above-ground biomass under elevated and ambient CO<sub>2</sub> (Figure 14). This ratio corresponded well with the observed ratio. However, because of the blower effect included, this observed ratio was expected to be smaller than the observed ratio in situation A without blower effect, but it was the opposite.

Summarizing, total biomass production in the experiments under ambient CO<sub>2</sub> almost did not vary between the three growing seasons (Figure 13). Total biomass increased by 10 to 20% with CO<sub>2</sub> enrichment (Figure 14), caused mainly by the increase in radiation use efficiency (RUE). Variation in total biomass increase was caused by the differences in decrease in radiation interception with CO<sub>2</sub> enrichment (see Appendix I). RUE remained almost constant from one growing season to the other for an identical CO<sub>2</sub> treatment. The harvest index was similar in the first two growing seasons and did almost not change with CO<sub>2</sub> enrichment, but it was more variable in the last season. RUE in the model was slightly higher than that observed and the increase in RUE with CO<sub>2</sub> enrichment was also slightly higher. As the simulated LAI and thus light interception were lower than their observed values (Figures O-1 and O-4), total biomass under ambient CO<sub>2</sub> was predicted well. The increase in total biomass by CO<sub>2</sub> enrichment was slightly overestimated in the simulation, mainly due to the stronger decrease in radiation interception and the smaller increase in RUE in the experiment. In the experiment the maximum LAI around anthesis did not change with CO<sub>2</sub> enrichment, whereas in the simulation LAI increased. Radiation interception decreased because of the small

temperature rise (blower effect), but this decrease was smaller in the simulation because of the LAI increase. When phenological development was calibrated for each treatment of the experiment (step B), this resulted in slight changes in growth period and thus in biomass production. However, this did almost not improve the correspondence with observed biomass production. Also the change in harvest index by CO<sub>2</sub> enrichment was not predicted better with step B (see Appendix I). When the time course of LAI and thus the actual radiation interception was used in the model (step C), this generally resulted in an improved agreement between the total biomass response to CO<sub>2</sub> enrichment in the simulation and the observed response (Figure 14), mainly by incorporating the reduced radiation interception in the elevated CO<sub>2</sub> treatment. Simultaneously, the actual radiation interception often resulted in higher values for total biomass in the simulation than observed (Figure 13), because observed crop growth already stopped before maturity with a considerable amount of green leaves left as shown above (e.g. Figure 11).

The end date of crop growth strongly determines the total biomass yield, but this end date could not be determined precisely from the observed dates of maturity (step B) or from the end of the time course of LAI (step C). This end of crop growth before maturity might indicate that growth and yield results were partly determined by the growth and grain filling potential of the crop (i.e. sink limitation). The time-courses of the ratio between observed shoot biomass under elevated and ambient CO<sub>2</sub> show a strong decrease in this ratio near maturity (Figures 10, 11 and 12), which also might point to sink-limitation.

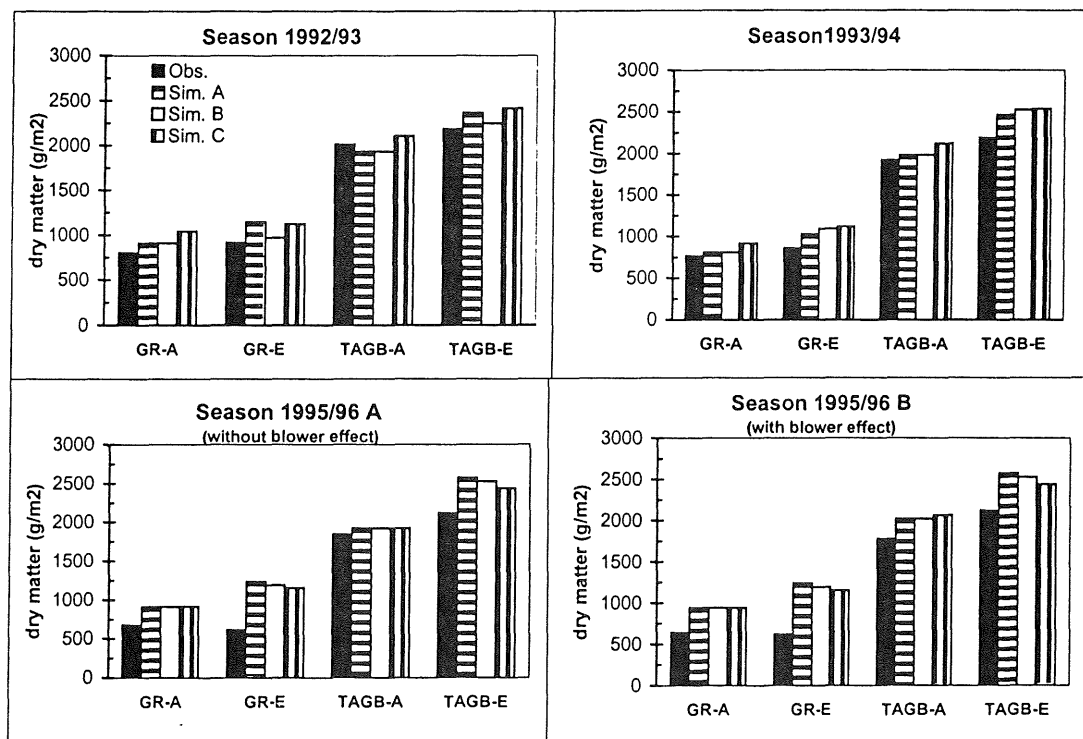


Figure 13. Total above-ground biomass (TAGB) and grain yield (GR) as observed (Obs.) in spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in different growing seasons under conditions of ample water and high nitrogen supply and ambient (A: 370 ppmv; without blower rings except for season 1995/96 A) and elevated (E: 550 ppmv in 1992/93 and 1993/94 and 570 ppmv 1995/96) atmospheric CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a; 1996b) and as simulated with the LINTULCC model for identical conditions. Calibration of LINTULCC was carried out in three steps: Sim. A= phenology calibrated for ambient treatment and LAI simulated; Sim. B= phenology calibrated for each treatment and LAI simulated; Sim. C= phenology calibrated for each treatment and LAI as observed in the experiments.

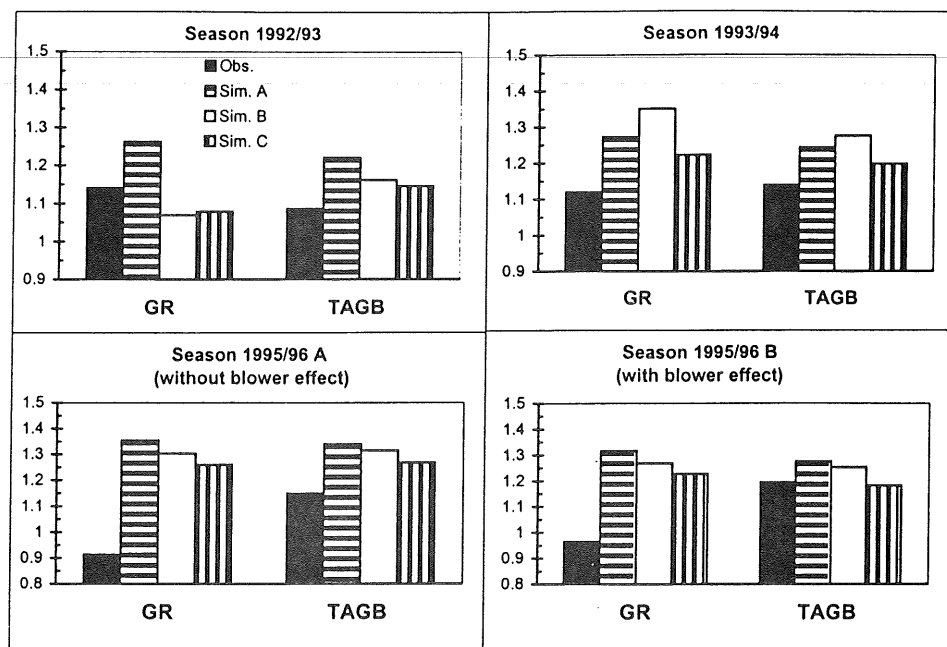


Figure 14. Ratio between total above-ground biomass (TAGB) and grain yields (GR) under elevated and ambient CO<sub>2</sub> concentration. Yields were observed (Obs.) in spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in different growing seasons under conditions of ample water and high nitrogen supply and ambient (370 ppmv; without blower rings except for season 1995/96 A) and elevated (550 ppmv in 1992/93 and 1993/94 and 570 ppmv 1995/96) atmospheric CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a; 1996b) and were simulated with the LINTULCC model for identical conditions. Calibration of LINTULCC was carried out in three steps: Sim. A= phenology calibrated for ambient treatment and LAI simulated; Sim. B= phenology calibrated for each treatment and LAI simulated; Sim. C= phenology calibrated for each treatment and LAI as observed in the experiments.

### 3.4 Final discussion and conclusions

The variability in observed responses of wheat yields to changes in atmospheric CO<sub>2</sub> concentration and temperature was studied. The experimental data sets collected for this project have been analysed to unravel the mechanisms behind this variability. Subsequently, crop growth in the various experiments has been simulated with the LINTULCC model. This may result in an improved explanation of the observed variability on the basis of crop characteristics and climatic conditions. For the large data sets from the free-air CO<sub>2</sub> enrichment experiments in Arizona these analyses have been carried out in more detail.

#### 3.4.1 CO<sub>2</sub> enrichment

A summary of all experimental data sets collected for this project, was compiled. In this summary the responses to CO<sub>2</sub> enrichment were given as percentage of the result at ambient conditions and were standardized per 100 ppmv increase in atmospheric CO<sub>2</sub> concentration. The mean and standard deviation (SD) of these standardized responses to CO<sub>2</sub> enrichment were determined for wheat growth under different conditions and for different crop types and growing media. This summary of standardized observed responses to CO<sub>2</sub> enrichment showed a number of effects. First, the duration from emergence to anthesis and from anthesis



to maturity did not change with CO<sub>2</sub> enrichment. Second, CO<sub>2</sub> enrichment by 100 ppmv resulted in an average increase in both total biomass and grain yield of 7% and in no change in the harvest index. Third, SD of the standardized yield responses was almost as large as the mean result, indicating a strong variation in yield increases between roughly 1% and 13%. Fourth, CO<sub>2</sub> enrichment by 100 ppmv resulted for spring wheat in a larger increase in total biomass at anthesis (+11%) than for winter wheat (+6%) and also in a larger increase in biomass for spring wheat at maturity but with a smaller difference between both crop types (+8% versus +5%). However, the increases in grain yield for spring and winter wheat were identical. Fifth, the CO<sub>2</sub> enrichment resulted for pot experiments in an increase in total biomass at anthesis (+10%) that was identical to that for field experiments, but it resulted in increases in total biomass and grain yield at maturity (+10%) that were much higher than those for field experiments (+4%). This indicates that the yield response to CO<sub>2</sub> enrichment in field experiments is much more limited which might be explained from more unfavourable soil conditions (water and nutrient shortage during grain filling), more extreme conditions (e.g. heat stress during anthesis which disturbs grain fertilisation and grain set (Ferris et al., 1997) and more disease infestation (resulting in advanced leaf senescence). Besides, the light conditions in pot experiments are often more favourable than in a crop canopy in the field, resulting in an overestimated CO<sub>2</sub> enrichment effect (e.g. Morison and Gifford, 1984; Wolf, 1996). Sixth, CO<sub>2</sub> enrichment by 100 ppmv resulted under optimal conditions in an increase in grain yield (+7%) that was identical to that for water- and nitrogen-limited conditions, and in an increase in total biomass at maturity that was lower and higher than that under nitrogen-limited and water-limited conditions, respectively. These results did not correspond well with results from literature reviews which with water limitation generally showed an identical or higher yield response to CO<sub>2</sub> enrichment and with nitrogen limitation a lower yield response (Cure and Acock, 1986). However the number of data sets from water- or nitrogen-limited conditions was small which limits the significance of these results. Finally, SD of the yield responses to standardized CO<sub>2</sub> enrichment did almost not decrease when experimental results were grouped according to growing conditions or crop types. This indicates that differences in growing conditions and crop types were not the main cause for the high SD.

Variation in experimental results from one growing season and treatment can only be caused by the variability in growing conditions and by the uncertainty in yield measurements. This type of experimental variation which can generally not be explained, is derived from results (four replicates for each season/treatment) of the spring wheat FACE experiments in Arizona. Results from three growing seasons were used and both from the final harvest and from the harvest at a one week earlier date. Only results from experiments under optimal conditions were used to limit the variability from various stress factors. The main results from this analysis were the following. First, the mean total biomass and grain yields considerably changed from the earlier to the final harvest, and often in different directions under ambient and elevated CO<sub>2</sub>. This leads to different conclusions on the yield response to CO<sub>2</sub> enrichment. Second, SD of the four replicate yields was large (roughly 50 to 100 g/m<sup>2</sup> for grain yield and 100 to 200 g/m<sup>2</sup> for total biomass) and almost identical to the mean yield response to CO<sub>2</sub> enrichment (about +200 ppmv) in this experiment. Third, the effect of this CO<sub>2</sub> enrichment on both grain and total biomass yield was not significant at the five percent level, and in particular if results from both harvest dates were combined. This shows that the variability in the experimental results from one season and treatment was so large that the mean effect of CO<sub>2</sub> enrichment became too small to obtain a significant yield response.

The experimental data sets have been analysed with the LINTULCC model by simulating crop growth under the conditions found in the experiments. This may result in an improved

explanation of the variability in observed responses of wheat growth and yield to CO<sub>2</sub> enrichment. Before applying LINTULCC, the sensitivity of its results to changes in the following variables has been analysed: temperature, atmospheric CO<sub>2</sub> concentration and solar radiation. The model results showed a considerably positive interaction between the three variables. For example, doubling of the ambient atmospheric CO<sub>2</sub> concentration resulted in an increase of shoot growth rate by 35% at low light conditions which increased to 55% at high light conditions, and in an increase of 35% at low temperatures which increased to 60% at high temperatures. The sensitivity of the shoot growth rate to changes in the three variables was also determined for crops in three different growth stages (i.e. young crop with low LAI, closed crop with productive canopy, and old crop with closed and low-productive canopy). Doubling of the ambient atmospheric CO<sub>2</sub> concentration resulted in similar increases in shoot growth rate for crops in the three growth stages.

Responses to CO<sub>2</sub> enrichment have been analysed with LINTULCC for the experiments from Arizona, Florence, Giessen, Rothamsted and Wageningen. These analyses have been performed only for experiments under optimal conditions. The calibration of LINTULCC was done on the basis of the experimental data set in three subsequent steps. This resulted first in similar durations of total crop growth and grain filling under ambient CO<sub>2</sub> in experiment and simulation (step A), next also in similar durations under elevated CO<sub>2</sub> (step B), and finally also in similar cumulative radiation interception in experiment and simulation (step C). The comparison between simulated and observed growth responses to CO<sub>2</sub> enrichment may show from which crop variables the changes are mainly responsible for different yield responses.

The increase in total above-ground biomass by CO<sub>2</sub> enrichment varied in the experiments between nil to 40% of total biomass under ambient conditions, whereas the simulated increase varied in step A between 20 and 60%. The relationship between the simulated and the observed increase in biomass yield was poor. In the experiment the change in intercepted radiation by CO<sub>2</sub> enrichment varied mainly between -5% and +5%, whereas in the simulation an increase by 5 to 10% occurred. In the simulations an increase in growth by CO<sub>2</sub> enrichment generally resulted in a larger leaf area and thus more radiation interception, whereas in the experiments this increase in radiation interception almost did not occur. This difference in radiation interception mainly caused the larger increase in total above-ground biomass by CO<sub>2</sub> enrichment in the simulations compared to the observed biomass increase. When the radiation interception in the simulation was made identical to the observed interception (step C), the relationship between the simulated (+10 to +30%) and the observed increase (0 to +40%) in total biomass by CO<sub>2</sub> enrichment was much better than in step A and became moderately good. The observed increases in radiation use efficiency (RUE) by CO<sub>2</sub> enrichment were from 10% higher to 10% lower than the simulated increases, but there was no systematical difference. This difference in RUE increases caused the difference between simulated and observed increases in total biomass. The simulated changes in harvest index (-5 to +20%) in step C slightly differed from the observed changes (-10 to +10%), but the relationship between these simulated and observed changes was rather poor. This might indicate that for calculating grain production LINTULCC needs to apply another method. The actual method that simply calculates the total assimilate production during the period of grain filling needs then to be replaced by a sink-determined calculation method (i.e. determined by the growth of grains). However, it might also indicate experimental variability that cannot be reproduced by LINTULCC. The relations between simulated and observed changes in total biomass and between simulated and observed changes in harvest index

resulted together in a poor to moderately good relation between simulated and observed changes (i.e. both 0 to +40%) in grain yield.

As described above, the experimental data sets have been analysed with LINTULCC. The results from the FACE experiments have been analysed in more detail. Time courses of crop variables from crop emergence to maturity as observed in the experiments were compared with these time courses as simulated with LINTULCC for identical conditions. This gives information on the changes in these crop variables over time and their interactions with CO<sub>2</sub> enrichment. This may show the time-dependent variability in observed and simulated responses of wheat growth to CO<sub>2</sub> enrichment. In the first two growing seasons total biomass and grain yield under ambient CO<sub>2</sub> were simulated well in step A. Total biomass and grain yield increased with CO<sub>2</sub> enrichment more strongly in the simulation than in the experiment, mainly because of the decrease in cumulative radiation interception in the experiment that was not simulated. By using the actual LAI in the simulations (step C) the ratio between total biomass under elevated and ambient CO<sub>2</sub> was more in agreement with the observed ratio. However, in step C total biomass yield under ambient CO<sub>2</sub> was overestimated in the simulation, mainly because observed crop growth near maturity decreased more rapidly than the growth simulated on the basis of observed LAI. This indicates a decrease in RUE near maturity that was not incorporated in LINTULCC. The observed effect of CO<sub>2</sub> enrichment on crop growth was almost identical to the simulated effect until the initial grain-filling period, but the observed effect decreased more strongly from that stage to maturity. Hence, the ratio between total biomass yield under elevated and ambient CO<sub>2</sub> was still overestimated in the simulations (step C). In the three growing seasons observed total biomass yields increased by 10 to 20% with CO<sub>2</sub> enrichment, caused mainly by the increased RUE. The variation in this yield increase was caused by the differences in decrease in radiation interception with CO<sub>2</sub> enrichment, as RUE remained almost constant from one growing season to the other (for identical CO<sub>2</sub> treatment).

The use of actual radiation interception data in LINTULCC resulted in higher values for total biomass yield than observed, because observed crop growth already stopped before maturity with a considerable amount of green leaves left. The end date of crop growth and the resulting total growth duration strongly determines total biomass yield, but this end date could not be derived precisely from the observed date of maturity or from the end of the time course of LAI. This end of crop growth before maturity might indicate that the final yield results were mainly determined by the growth and grain filling potential of the crop (i.e. sink limitation). The time-courses of the ratio between observed shoot biomass under elevated and ambient CO<sub>2</sub> show a strong decrease near maturity, which also might point to sink-limitation. This indicates that the wheat yield response to CO<sub>2</sub> enrichment in the experiment might become more positive and almost identical to the simulated response if this sink-limitation can be removed (e.g. by improving crop variety and growing conditions).

### 3.4.2 Temperature change

In a summary of all experimental data sets the responses to temperature change were given as percentage of the result at ambient temperatures and were standardized per 1 °C temperature rise. The mean and SD of these standardized responses to temperature change were determined for growth under respectively ambient and elevated CO<sub>2</sub> concentration. This summary of standardized responses showed a number of effects. First, the duration from emergence to maturity considerably decreased (between -3% for winter wheat to -5% for

spring wheat per 1 °C temperature rise). Second, the 1 °C temperature rise resulted in a decrease in total biomass and grain yield of 8 and 11%, respectively. Third, SD of the yield responses to 1 °C temperature rise was half (i.e. 3%) the SD value of the yield responses to CO<sub>2</sub> enrichment (+100 ppmv), whereas the mean temperature effect was generally larger. This indicates that the temperature effect is less variable and less uncertain than the CO<sub>2</sub> effect. However, the number of experimental data sets used was rather small. Fourth, the temperature increase resulted in smaller decreases in total biomass and grain yield under doubled atmospheric CO<sub>2</sub> (-7 and -9%, respectively) than under ambient CO<sub>2</sub> (-10 and -12%, respectively). Apparently, CO<sub>2</sub> enrichment may partly counteract the negative temperature effects on yields.

The experimental data sets have been analysed with the LINTULCC model by simulating crop growth under the conditions found in the experiments. This may result in an improved explanation of the variability in observed responses of wheat growth and yield to temperature change. Before applying LINTULCC, the sensitivity of its results to changes in the following variables has been analysed: temperature, atmospheric CO<sub>2</sub> concentration and solar radiation. The model results showed a considerable positive interaction between the three variables. For example, temperature rise from 10 to 30 °C resulted in an increase in shoot growth rate of 45% at ambient atmospheric CO<sub>2</sub> concentration and of 65% at two times the ambient CO<sub>2</sub> concentration. However, this positive effect of temperature rise on the growth rate does generally not result in higher yields, as the temperature rise also results in a considerably shortened growth duration. This leads to a much lower light interception and thus biomass production. For the experiments collected in this project, temperature rise always resulted in lower total biomass and grain yield. The wheat experiments within the ESPACE-Wheat programme also showed this negative yield response to temperature rise (Van Oijen and Goudriaan, 1997). At low light conditions LINTULCC calculated for a similar temperature rise (+20 °C) an increase in shoot growth rate of 10% and at high light conditions of 60%. This shows that under low light conditions photosynthesis and thus growth rate are mainly determined by the amount of incoming radiation. The sensitivity of the shoot growth rate to changes in the three variables was also determined for crops in three different growth stages (i.e. young, closed and productive, and old). Temperature rise resulted in roughly similar increases in shoot growth rate for crops in the three growth stages. In LINTULCC a fixed value for conversion efficiency (CVF) from assimilated CO<sub>2</sub> to biomass was used. If in practice CVF is not completely independent of temperature and CO<sub>2</sub> concentration, this may result in differences from these modelled sensitivities of shoot growth.

Responses to temperature change have been analysed with LINTULCC for the experiments from Clermont Ferrand, Rothamsted and Wageningen. These analyses have been performed only for experiments under optimal conditions. The calibration of LINTULCC was done in the way described earlier for the response to CO<sub>2</sub> enrichment. The comparison between simulated and observed growth responses to temperature change may show from which crop variables the changes were mainly responsible for different yield responses. The decrease in total above-ground biomass by temperature rise varied in the experiments between 10% and 30% of total biomass under ambient temperatures, whereas the simulated decrease varied in step A only between 5 and 10%. The relationship between the simulated and observed decreases in total biomass was poor. In the simulations the changes in intercepted radiation by temperature change were almost similar to the observed changes. When the radiation interception in the simulation was made identical to the observed interception (step C), the relation between the simulated and observed decrease in total biomass by temperature rise

was just as poor as in step A. The observed changes in RUE by temperature change were much more variable than the simulated changes and strongly differed. This difference in changes in RUE caused the poor relationship between simulated and observed changes in total biomass. If the results from the Clermont Ferrand experiments were left out because of their different experimental method, the relationship between simulated and observed changes in total biomass became moderately good. In the simulations small increases in RUE occurred with temperature rise, whereas in the experiments (without Clermont Ferrand results) small decreases generally occurred. This might indicate that the positive response of RUE to temperature rise, as calculated in the new routine of LINTULCC (see Section 3.2.2), does not occur in the experiments. The simulated changes in harvest index (step C) were much larger than the observed changes (i.e. almost nil) and hence, the relationship between these simulated and observed changes was nil. The moderate relationship between simulated and observed changes in total biomass and the very poor one between simulated and observed changes in harvest index resulted together in a poor relationship between simulated and observed changes in grain yield. This relationship between simulated and observed changes in grain yield would improve considerably, if the simulated harvest index was assumed to be constant under temperature change.

Comparison of the simulated results with the experimental results showed that an improved correspondence between experimental and LINTULCC results might be attained in two ways. The morphological development of the crop (in particular leaf area development and partitioning of assimilates among crop organs) and the effects of sink limitation on crop growth (i.e. grain yield determined by number of grains set and grain growth rate) may be described in more detail. However, crop variables as observed in the experiments were often more constant than simulated with LINTULCC. In that case, a more simplified model approach is probably possible (and perhaps even better) which uses a fixed value for the harvest index (i.e. grain yield as fixed fraction of total biomass, independent of temperature and atmospheric CO<sub>2</sub> concentration), a more simplified CO<sub>2</sub> assimilation-light response relation to calculate the RUE (i.e. dependent on atmospheric CO<sub>2</sub> concentration and radiation but not on temperature) and a simple calculation method for leaf area development and radiation interception that does not depend on assimilate production and allocation but only on cumulative temperature sums for crop development. This only holds in situations without severe water or nutrient stress.

### 3.4.3 Conclusions

Most results and conclusions from this study were already discussed in the earlier parts of this section. The main conclusions, in particular on the variability in observed responses of wheat yields to changes in atmospheric CO<sub>2</sub> concentration and temperature and the mechanisms behind this variability, are given in the following.

- Averaged over all collected wheat experiments, total biomass and grain yield increased per 100 ppmv of CO<sub>2</sub> enrichment by 7% of the yields under ambient CO<sub>2</sub>. The standard deviation (SD) of the yield responses was almost as large (i.e. 6%) as the mean result, indicating the strong variation in yield increases;
- SD of the observed yield responses to CO<sub>2</sub> enrichment did almost not decrease when experimental results were grouped according to growing conditions (pot or field; optimal or limited) or crop types (spring or winter wheat). Apparently, variation in growing conditions and crop type was not the main cause for the high SD value;

- The response of wheat yields to CO<sub>2</sub> enrichment was more limited in field experiments than in pot experiments. In pot experiments the soil and light conditions and the crop protection were probably more favourable;
- Results from the spring wheat FACE experiments in Arizona showed such a large variability between replicate yields that CO<sub>2</sub> enrichment by 200 ppmv was not sufficient to obtain a significant yield response;
- Results from the final harvest and from the harvest at a one week earlier date of the FACE experiments in Arizona greatly differed. Total biomass and grain yield considerably changed from the earlier to the final harvest and often in different directions under ambient and elevated CO<sub>2</sub>. This resulted in different conclusions on the yield response to CO<sub>2</sub> enrichment. This type of experimental variability is caused by the spatial variability in growing conditions and the uncertainty in yield measurements;
- The relationship between the observed increases in total above-ground biomass by CO<sub>2</sub> enrichment and the simulated increases was poor, which was mainly caused by the poor relationship between observed and simulated cumulative radiation interception. In the simulation with LINTULCC an increase in growth by CO<sub>2</sub> enrichment generally resulted in a larger leaf area and thus more radiation interception, whereas in the experiments this increase in radiation interception almost did not occur;
- The relationship between simulated and observed changes in grain yield was rather poor. To improve this relationship, LINTULCC needs to apply another method for calculating grain production, replacing the actual source-determined calculation method by a mainly sink-determined method. If however this rather poor relationship was mainly caused by experimental variability, the relationship cannot be improved;
- In the FACE experiments in Arizona the radiation use efficiency (RUE) between years was almost constant and the variation in total biomass increase with CO<sub>2</sub> enrichment between years was mainly caused by different changes in radiation interception;
- The use of actual LAI data in the simulation of the spring wheat FACE experiments in Arizona resulted in higher total biomass yields than observed, because observed crop growth already stopped before maturity with a considerable amount of green leaves left;
- The end date of crop growth strongly determines the total biomass yield, but this end date could not be determined precisely in the FACE experiments in Arizona from the observed dates of maturity or from the end of the time course of LAI;
- Yield results from the FACE experiments are probably affected by sink-limitation, i.e. by the growth and grain filling potential of the crop. Hence, the effect of CO<sub>2</sub> enrichment may become more positive if this sink-limitation can be removed. Indications for this sink-limitation are: 1. Time course of the ratio between observed shoot biomass under elevated and ambient CO<sub>2</sub> showed a strong decrease near maturity; 2. End of growth occurred before maturity with a considerable amount of green leaves left;
- Averaged over all collected wheat experiments, temperature rise resulted in a shorter growth period and hence total biomass and grain yield decreased by 8% and 11%, respectively per 1 °C of temperature rise;
- The temperature effect is less variable and more certain than the CO<sub>2</sub> effect, as SD of yield responses to 1 °C temperature rise was half (i.e. 3%) the SD for yield responses to CO<sub>2</sub> enrichment and the mean temperature effect was often larger;
- Temperature rise resulted in smaller decreases in total biomass and grain yield under doubled atmospheric CO<sub>2</sub> (-7% and -9%, respectively per 1 °C of temperature rise) than under ambient CO<sub>2</sub> (-10% and -12%, respectively);
- The relationship between simulated and observed decreases in total biomass by temperature rise was moderately good (without Clermont Ferrand results) and was mainly

determined by the good relationship between simulated and observed decreases in radiation interception during the shorter growth period;

- Temperature rise resulted in small increases in RUE in the simulations, whereas in the experiments it gave small decreases in RUE;
- The simulated changes in harvest index with temperature rise were much larger than the observed changes (i.e. almost nil). Hence, the relationship between these simulated and observed changes in harvest index was nil and resulted in a poor relationship between simulated and observed changes in grain yield. This last relationship would improve considerably, if the simulated harvest index was kept constant with temperature rise;
- Comparison of simulated with experimental results shows that an improved correspondence between experimental and LINTULCC results might be attained in two different ways. The morphological development (e.g. leaf area) of the crop and the limiting effect of available sinks (i.e. grains) on crop growth may be described in more detail. However, in many situations crop variables in the experiments were more constant than simulated with LINTULCC. In such a situation without severe water or nutrient stress, a simplified model approach may be applied.

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## References

- Bancal, P. & E. Triboi, 1993. Temperature effect on fructan oligomer contents and fructan-related enzyme activities in stems of wheat (*Triticum aestivum* L.) during grain filling. *New Phytologist* 123: 247-253.
- Barrow, E. & M. Hulme, 1996. Development of climate change scenarios at a range of scales. p. 13-17. In: Harrison, P.A., R.E. Butterfield & T.E. Downing (Eds.). Annual report of CLIVARA project: Climate change, climatic variability and agriculture in Europe, an integrated assessment. Environmental Change Unit, University of Oxford, Oxford, U.K.
- Cure, J.D. & B. Acock, 1986. Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology* 38: 127-145.
- Delgado, E., R.A.C. Mitchell, M.A.J. Parry, S.P. Driscoll, V.J. Mitchell & D.W. Lawlor, 1994. Interacting effects of CO<sub>2</sub> concentration, temperature and nitrogen supply on the photosynthesis and composition of winter wheat leaves. *Plant, Cell and Environment* 17: 1205-1213.
- Dijkstra, P., A.H.C.M. Schapendonk & K. Groenwold, 1993. Effects of CO<sub>2</sub> enrichment on canopy photosynthesis, carbon economy and productivity of wheat and faba bean under field conditions. p. 23-41. In: Van de Geijn, S.C., J. Goudriaan & F. Berendse (Eds.). *Climate change; crops and terrestrial ecosystems*. AB-DLO, Wageningen, Netherlands.
- Dijkstra, P., S. Nonhebel, C. Grashoff, J. Goudriaan & S.C. Van de Geijn, 1996. Response of growth and CO<sub>2</sub> uptake of spring wheat and faba bean to CO<sub>2</sub> concentration under semifield conditions: comparing results of field experiments and simulations. p. 251-264. In: Koch,

- G.W. & H.A. Mooney (Eds.). Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, USA.
- Dijkstra, P., A.H.C.M. Schapendonk & S.C. Van de Geijn, 1994. Response of spring wheat canopy photosynthesis to CO<sub>2</sub> concentration throughout the growing season: effect of developmental stage and light intensity. p. 53-62. In: Veroustraete, F., R. Ceulemans et al. (Eds). Vegetation, modelling and climate change effects. SPB Academic Publishing bv, The Hague, Netherlands.
- Dijkstra, P., A.H.C.M. Schapendonk, J. Groenwold & S.C. Van de Geijn., in prep. Response of winter wheat to elevated atmospheric CO<sub>2</sub> concentration in early spring under semi-field conditions. *Global Change Biology* (submitted).
- Fangmeier, A., U. Grüters, U. Hertstein, A. Sandhage-Hofmann, B. Vermehren & H.-J. Jäger, 1996. Effects of elevated CO<sub>2</sub>, nitrogen supply and tropospheric ozone on spring wheat. I. Growth and yield. *Environmental Pollution* 91: 381-390.
- Fangmeier, A., U. Grüters, P. Högy, B. Vermehren & H.-J. Jäger, 1997a. Effects of elevated CO<sub>2</sub>, nitrogen supply and tropospheric ozone on spring wheat. II. Nutrients (N, P, K, S, Ca, Mg, Fe, Mn, Zn). *Environmental Pollution* 96: 43-59.
- Fangmeier, A., U. Grüters, U. Hertstein, B. Vermehren & H.-J. Jäger, 1997b. ESPACE-Wheat (European Stress Physiology and Climate Experiment-Wheat) project. Final report. Institute für Pflanzenökologie, Justus-Liebig Universität Giessen, Giessen, Germany. 86 pp.
- Farquhar, G.D. & S. Von Caemmerer, 1982. Modelling of photosynthetic response to environmental conditions. p. 549-588. In: Lange, O.L., P.S. Nobel, C.B. Osmond & H. Ziegler (Eds.). *Physiological Plant Ecology. Encycl. Plant Physiol.*, Vol. 12B, Springer, Heidelberg, Germany.
- Ferris, R., T.R. Wheeler, R.H. Ellis, P. Hadley, B. Wollenweber, J.R. Porter, J. Schellberg, T.S. Karacostas & M. Papadopoulos, 1997. Effects of high temperature extremes on wheat. p. 31-49. In: Butterfield, R.E., K.G. Lonsdale & T.E. Downing (Eds.). Annual report of CLIVARA project: Climate change, climatic variability and agriculture in Europe, an integrated assessment. Environmental Change Unit, University of Oxford, Oxford, U.K.
- Gifford, R.M., 1995. Whole plant respiration and photosynthesis of wheat grown under increased CO<sub>2</sub> concentration and temperature: Long-term vs. short-term distinctions for modelling. *Global Change Biology* 1: 385-396.
- Grashoff, C., P. Dijkstra, S. Nonhebel, A.H.C.M. Schapendonk & S.C. Van de Geijn, 1995. Effects of climate change on productivity of cereals and legumes; model evaluation of observed year-to-year variability of the CO<sub>2</sub> response. *Global Change Biology* 1: 417-428.
- Hertstein, U., A. Fangmeier & H.-J. Jäger, 1996. ESPACE-Wheat (European Stress Physiology and Climate Experiment- project 1: wheat): Objectives, general approach and first results. *Journal of Applied Botany (Angewandte Botanik)* 70: 172-180.
- Houghton, J.T., L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg & K. Maskell, 1996. Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, U.K. 572 pp.
- Hunsaker, D.J., B.A. Kimball, P.J. Pinter, R.L. LaMorte & G.W. Wall, 1996. Carbon dioxide enrichment and irrigation effects on wheat evapotranspiration and water use efficiency. *Transactions of the ASAE* 39: 1345-1355.
- Idso, K.E. & S.B. Idso, 1994. Plant responses to atmospheric CO<sub>2</sub> enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agricultural and Forest Meteorology* 69: 153-203.
- Kimball, B.A., P.J. Pinter, R.L. Garcia, R.L. LaMorte, G.W. Wall, D.J. Hunsaker, G. Wechsung, F. Wechsung & T. Kartschall, 1995. Productivity and water use of wheat under free-air CO<sub>2</sub> enrichment. *Global Change Biology* 1: 429-442.



- Lawlor, D.W., R.A.C. Mitchell, J. Franklin, V.J. Mitchell, S.P. Driscoll & E. Delgado, 1993. Facility for studying the effects of elevated carbon dioxide concentration and increased temperature on crops. *Plant, Cell and Environment* 16: 603-608.
- Li, A.-G., A. Trent, G.W. Wall, B.A. Kimball, Y.-S. Hou, P.J. Pinter, R.L. Garcia, D.V. Hunsaker & R.L. LaMorte, 1997. Free-air CO<sub>2</sub> enrichment effects on rate and duration of apical development of spring wheat. *Crop Science* 37: 789-796.
- Miglietta, F., A. Giuntoli & M. Bindi, 1996. The effect of free air carbon dioxide enrichment (FACE) and soil nitrogen availability on the photosynthetic capacity of wheat. *Photosynthesis Research* 47: 281-290.
- Mitchell, R.A.C., C.L. Gibbard, V.J. Mitchell & D.W. Lawlor, 1996. Effects of shading in different developmental phases on biomass and grain yield of winter wheat ambient and elevated CO<sub>2</sub>. *Plant, Cell and Environment* 19: 615-621.
- Mitchell, R.A.C., D.W. Lawlor, V.J. Mitchell, C.L. Gibbard, E.M. White & J.R. Porter, 1995. Effects of elevated CO<sub>2</sub> concentration and increased temperature on winter wheat: test of ARCWHEAT1 simulation model. *Plant, Cell and Environment* 18: 736-748.
- Mitchell, R.A.C., V.J. Mitchell, S.P. Driscoll, J. Franklin & D.W. Lawlor, 1993. Effects of increased CO<sub>2</sub> concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant, Cell and Environment* 16: 521-529.
- Morison, J.I.L. & R.M. Gifford, 1984. Plant growth and water use with limited water supply in high CO<sub>2</sub> concentrations. II. Plant dry weight, partitioning and water use efficiency. *Australian Journal of Plant Physiology* 11: 375-384.
- Pinter, P.J., B.A. Kimball, R.L. Garcia, G.W. Wall, D.J. Hunsaker & R.L. LaMorte, 1996a. Free-air CO<sub>2</sub> enrichment: responses of cotton and wheat crops. p. 215-249. In: Koch, G.W. & H.A. Mooney (Eds.). *Carbon dioxide and terrestrial ecosystems*. Academic Press, San Diego, USA.
- Pinter, P.J., B.A. Kimball, G.W. Wall, R.L. LaMorte, F.J. Adamsen & D.J. Hunsaker, 1996b. FACE 1995-96: effects of elevated CO<sub>2</sub> and soil nitrogen on growth and yield parameters of spring wheat. p. 75-78. In: *Annual research report 1996*. U.S. Water Conservation Laboratory, USDA-ARS, Phoenix, Arizona, USA.
- Spitters, C.J.T., 1990. Crop growth models: their usefulness and limitations. *Acta Horticulturae* 267: 349-368.
- Triboi, E., A.M. Triboi, M. Martignac & R. Falcimagne, 1996. Experimental device for studying post-anthesis canopy functioning in relation to grain quality. p. 68-69. In: Van Ittersum, M.K., G.E.G.T. Venner, S.C. Van de Geijn & T.H. Jetten (Eds.). *Book of Abstracts of the fourth ESA congress*. European Society of Agronomy, Colmar, France.
- Van Kraalingen, D.W.G., 1990. Effect of CO<sub>2</sub> enrichment on nutrient-deficient plants. p. 42-45. In: Goudriaan, J., H. Van Keulen & H.H. Van Laar (Eds.). *The greenhouse effect and primary productivity in European agro-ecosystems*. Proceedings of the international workshop on primary productivity of European agriculture and the greenhouse effect. Pudoc, Wageningen, Netherlands.
- Van Oijen, M. & F. Ewert, in prep. The effects of climatic variation in Europe on the yield response of spring wheat cv. Minaret to elevated CO<sub>2</sub> and O<sub>3</sub>: an analysis of open-top chamber experiments by means of two crop growth simulation models. Submitted to *European Journal of Agronomy*.
- Van Oijen, M. & J. Goudriaan, 1997. ESPACE-Wheat (European Stress Physiology and Climate Experiment-Wheat) project. Final report. Sub-department of Theoretical Production Ecology, Wageningen University and Research Center, Wageningen, Netherlands. 25 pp.
- Van Oijen, M., A.H.C.M. Schapendonk, M.J.H. Jansen, C.S. Pot, J. Van Kleef & J. Goudriaan, 1998a. Effects of CO<sub>2</sub> on development and morphology of spring wheat grown

in cooled and non-cooled open-top chambers. *Australian Journal of Plant Physiology* 25: in press.

Van Oijen, M., A.H.C.M. Schapendonk, M.J.H. Jansen, C.S. Pot & R. Maciorowski, 1998b. Do open-top chambers overestimate the effects of rising CO<sub>2</sub> on plants? An analysis using spring wheat. *Global Change Biology*, in press.

Wolf, J., 1996. Effects of nutrient supply (NPK) on spring wheat response to elevated atmospheric CO<sub>2</sub>. *Plant and Soil* 185: 113-123.

## Appendix A: List of experimental data sets

### Atmospheric CO<sub>2</sub> increase :

Site	Year	Medium	Crop
Arizona	1992/93	Field (FACE)	Spring wheat
„	1993/94	„	„
„	1995/96	„	„
Florence	1997	Field (Mini FACE)	Winter wheat
Giessen	1994	Pots in OTC	Spring wheat
„	1995	„	„
„	1996	„	„
Rothamsted	1990/91	Pots in greenhouse	Winter wheat
„	1991/92	„	„
„	1993/94	„	„
Wageningen	1991	Container in enclosures	Spring wheat
„	1992/93	„	Winter wheat
„	1993/94	Field (OTC)	Winter wheat
„	1995	„	Spring wheat
„	1996	„	„

### Temperature change :

Site	Year	Medium	Crop
Clermont Ferrand	1995/96	Container in tunnel	Winter wheat
Rothamsted	1990/91	Pots in greenhouse	Winter wheat
„	1991/92	„	„
Wageningen	1995	Field (OTC)	Spring wheat
„	1996	„	„

## **Appendix B: Results from spring wheat experiments in Arizona**

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Spring wheat was grown during growing season 1992/93 in fields under conditions of ambient and elevated atmospheric CO<sub>2</sub> concentrations and ample and limited water supply. On the fields with elevated atmospheric CO<sub>2</sub> a free-air CO<sub>2</sub> enrichment (FACE) system was used. The blower rings of this FACE system resulted in an increase in minimum temperature by about 1.5 °C compared with the ambient CO<sub>2</sub> field (without blower rings). Final yield data are given in Table B-1 and time courses of crop variables are given in Figure B-1.

Spring wheat was grown during growing season 1993/94 in fields under conditions of ambient and elevated atmospheric CO<sub>2</sub> concentrations and ample and limited water supply. On the fields with elevated atmospheric CO<sub>2</sub> a FACE system was used (resulting in an increase in minimum temperature by about 1.5 °C compared with the ambient CO<sub>2</sub> field). Final yield data are given in Table B-2 and time courses of crop variables are given in Figure B-2.

Spring wheat was grown during growing season 1995/96 in fields under conditions of ambient and elevated atmospheric CO<sub>2</sub> concentrations, ample water supply and low and high nitrogen supply. On the fields with elevated atmospheric CO<sub>2</sub> a FACE system was used and also on half of the ambient fields (resulting in an increase in minimum temperature by about 1.5 °C compared with the ambient CO<sub>2</sub> field without FACE system). Final yield data are given in Table B-3 and time courses of crop variables are given in Figures B-3 (showing CO<sub>2</sub> enrichment effect) and B-4 (showing temperature effect from blower rings).

Table B-1. Yield component analyses of results (average and standard deviation of 4 replicates) from spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1992/93 under conditions of ample (Amp.) and limited (Lim.) water supply and ambient (370 ppmv) and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a). Treatments: Treatm. 1= 370 ppmv, Amp.; Treatm. 2= 370 ppmv, Lim.; Treatm. 3= 550 ppmv, Amp., Treatm. 4= 550 ppmv, Lim.; Ratio Amp.= Treatm. 3 / Treatm. 1; Ratio Lim.= Treatm. 4 / Treatm. 2

	Treatm.1	Treatm.2	Treatm.3	Treatm.4	Ratio Amp.	RatioLim.
Total biomass						
Above ground (g/m <sup>2</sup> )	1827.6 ±77.7	1491.3 ± 364.0	1983.2 ±175.0	1552.3 ±146.0	1.085	1.041
Grain yield (g/m <sup>2</sup> )	804.0 ±19.7	676.8 ±163.7	916.9 ±77.6	735.0 ±71.6	1.140	1.086
Harvest index	0.440 ±0.007	0.454 ±0.011	0.462 ±0.008	0.474 ±0.014	1.050	1.044
Plants/m <sup>2</sup>	108.8	108.8	108.8	108.8	-	-
Ears /plant	3.82 ±0.20	3.03 ±0.58	4.05 ±0.42	3.05 ±0.22	1.060	1.007
Grains /ear	-	-	44.3 ±1.0	47.6 ±1.3	-	-
Grain weight (mg)	-	-	47.1 ±1.9	46.5 ±1.4	-	-

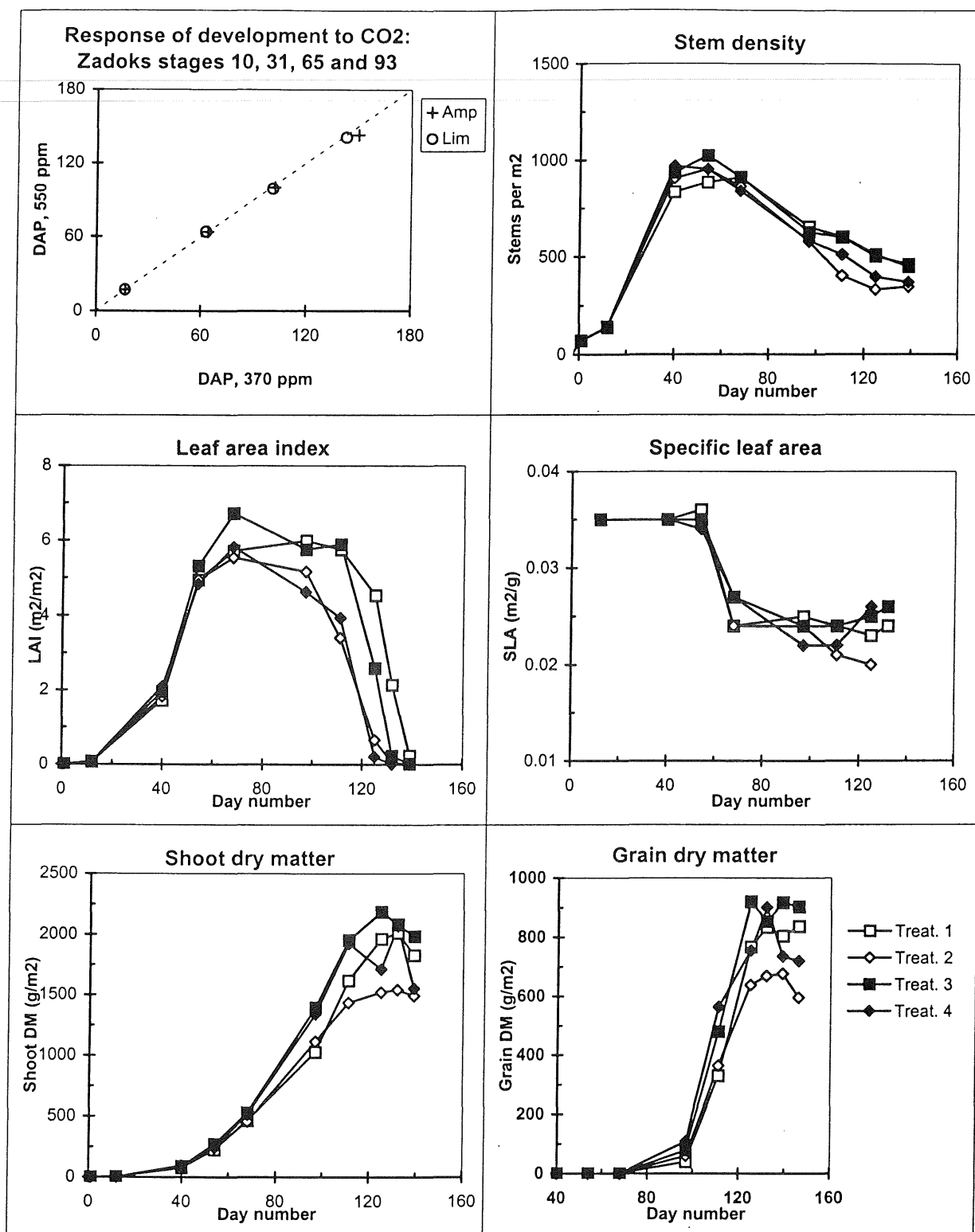


Figure B-1. Summary of results from spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1992/93 under conditions of ample (Amp.) and limited (Lim.) water supply and ambient (370 ppmv) and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 370 ppmv, Amp.; Treat. 2= 370 ppmv, Lim.; Treat. 3= 550 ppmv, Amp., Treat. 4= 550 ppmv, Lim.

*Arizona, growing season 1993/94*

Table B-2. Yield component analyses of results (average and standard deviation of 4 replicates) from spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1993/94 under conditions of ample (Amp.) and limited (Lim.) water supply and ambient (370 ppmv) and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Pinter et al., 1996a). Treatments: Treatm. 1= 370 ppmv, Amp.; Treatm. 2= 370 ppmv, Lim.; Treatm. 3= 550 ppmv, Amp., Treatm. 4= 550 ppmv, Lim.; Ratio Amp.= Treatm. 3 / Treatm. 1; Ratio Lim.= Treatm. 4 / Treatm. 2

	Treatm.1	Treatm.2	Treatm.3	Treatm.4	Ratio Amp.	RatioLim.
Total biomass above ground (g/m <sup>2</sup> )	1800.1 ±270.0	1385.7 ± 91.1	1927.7 ±52.9	1583.1 ±333.3	1.071	1.142
Grain yield (g/m <sup>2</sup> )	768.2 ±117.6	619.1 ±44.6	860.4 ±38.0	741.5 ±158.4	1.120	1.198
Harvest index	0.427 ±0.024	0.447 ±0.016	0.447 ±0.022	0.468 ±0.014	1.047	1.047
Plants/m <sup>2</sup>	153.6	153.6	153.6	153.6	-	-
Ears /plant	3.425 ±0.422	2.405 ±0.167	3.487 ±0.137	2.839 ±0.396	1.018	1.180
Grains /ear	-	-	37.31 ±0.96	37.25 ±2.77	-	-
Grain weight (mg)	-	-	43.11 ±2.10	45.26 ±1.47	-	-

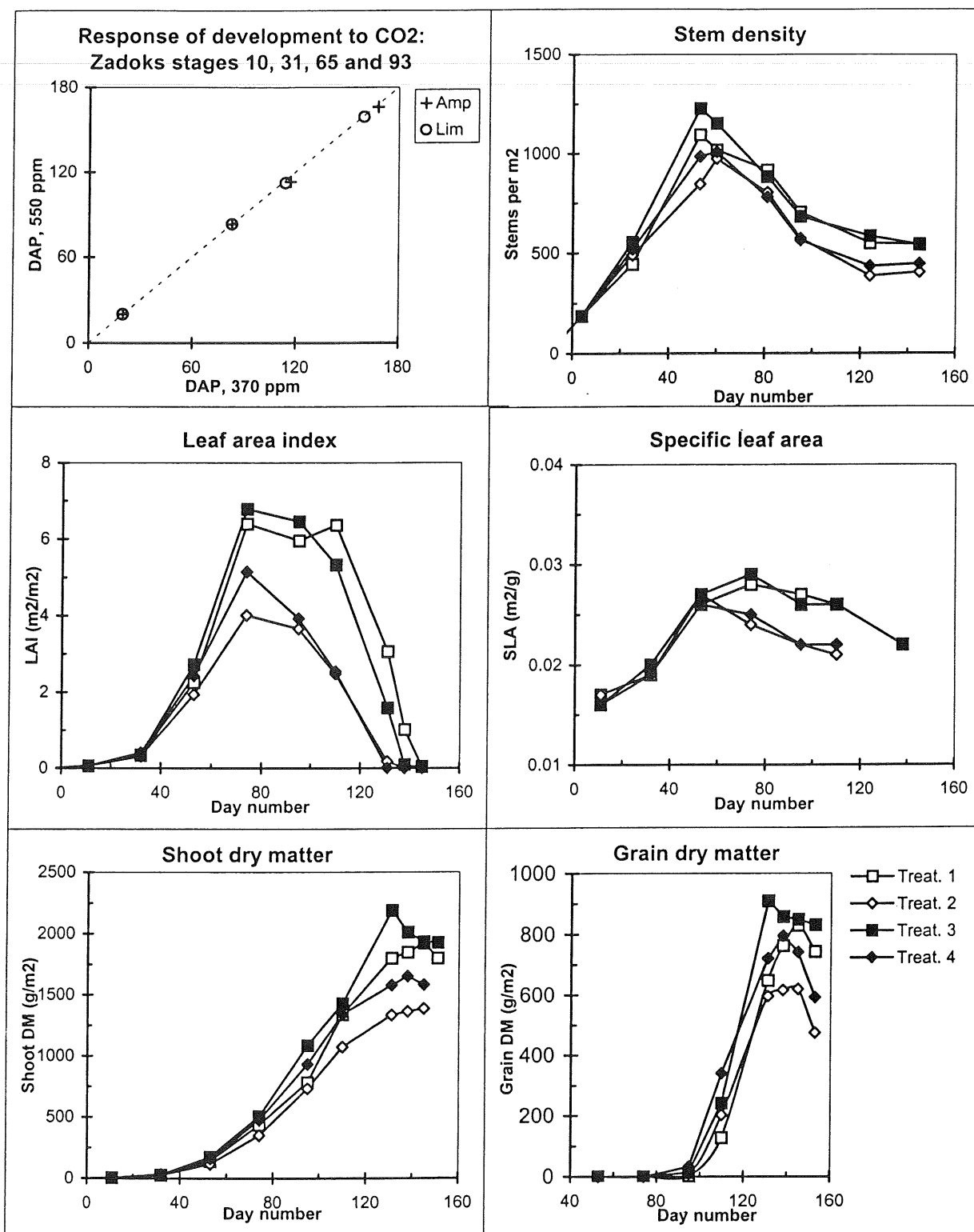


Figure B-2. Summary of results from spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1993/94 under conditions of ample (Amp.) and limited (Lim.) water supply and ambient (370 ppmv) and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Pinter et al., 1996a). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 370 ppmv, Amp.; Treat. 2= 370 ppmv, Lim.; Treat. 3= 550 ppmv, Amp., Treat. 4= 550 ppmv, Lim.



*Arizona, growing season 1995/96*

Table B-3. Yield component analyses of results (average and standard deviation of mostly 4 replicates) from spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of low (low N) and high nitrogen (high N) supply and elevated (570 ppmv) and ambient (370 ppmv) atmospheric CO<sub>2</sub> concentrations, with the ambient treatment both with (+Blow) and without (-Blow) blower rings (Source: Pinter et al., 1996b). Treatments: Treatm. 1= 370 ppmv, high N,+Blow; Treatm. 2= 370 ppmv, low N,+Blow; Treatm. 3= 570 ppmv, high N,+Blow; Treatm. 4= 570 ppmv, low N,+Blow; Treatm. 5= 370 ppmv, high N,-Blow; Treatm. 6= 370 ppmv, low N,-Blow; Ratio high N= Treatm. 3 / Treatm. 1; Ratio low N= Treatm. 4 / Treatm. 2

	Treatm.1	Treatm.2	Treatm.3	Treatm.4	Treatm.5	Treatm.6	Ratio high N	Ratio low N
Total biomass above gr. (g/m <sup>2</sup> )	1534.8 ±206.0	1085.9 ± 153.4	1429.3 ±184.6	1260.3 ±137.8	1474.5 ±87.5	1394.0 ±72.0	0.931	1.161
Grain yield (g/m <sup>2</sup> )	677.0 ±87.0	447.5 ±77.8	618.2 ±105.7	530.5 ±62.9	641.4 ±63.6	645.5 ±45.9	0.913	1.185
Harvest index	0.442 ±0.006	0.410 ±0.023	0.431 ±0.027	0.421 ±0.023	0.434 ±0.017	0.462 ±0.009	0.975	1.027
Plants/m <sup>2</sup>	184.1	184.1	184.1	184.1	184.1	184.1	-	-
Ears /plant	2.75 ±0.24	2.10 ±0.18	2.66 ±0.18	2.27 ±0.29	2.49 ±0.16	2.44 ±0.02	0.967	1.081
Grains /ear	29.72 ±3.04	25.18 ±2.76	27.91 ±3.18	27.64 ±1.80	32.79 ±0.87	32.45 ±1.91	0.939	1.098
Grain weight (mg)	45.11 ± 1.40	45.58 ±1.59	45.02 ±0.53	46.00 ±0.85	42.60 ±0.30	44.27 ±0.12	0.998	1.009

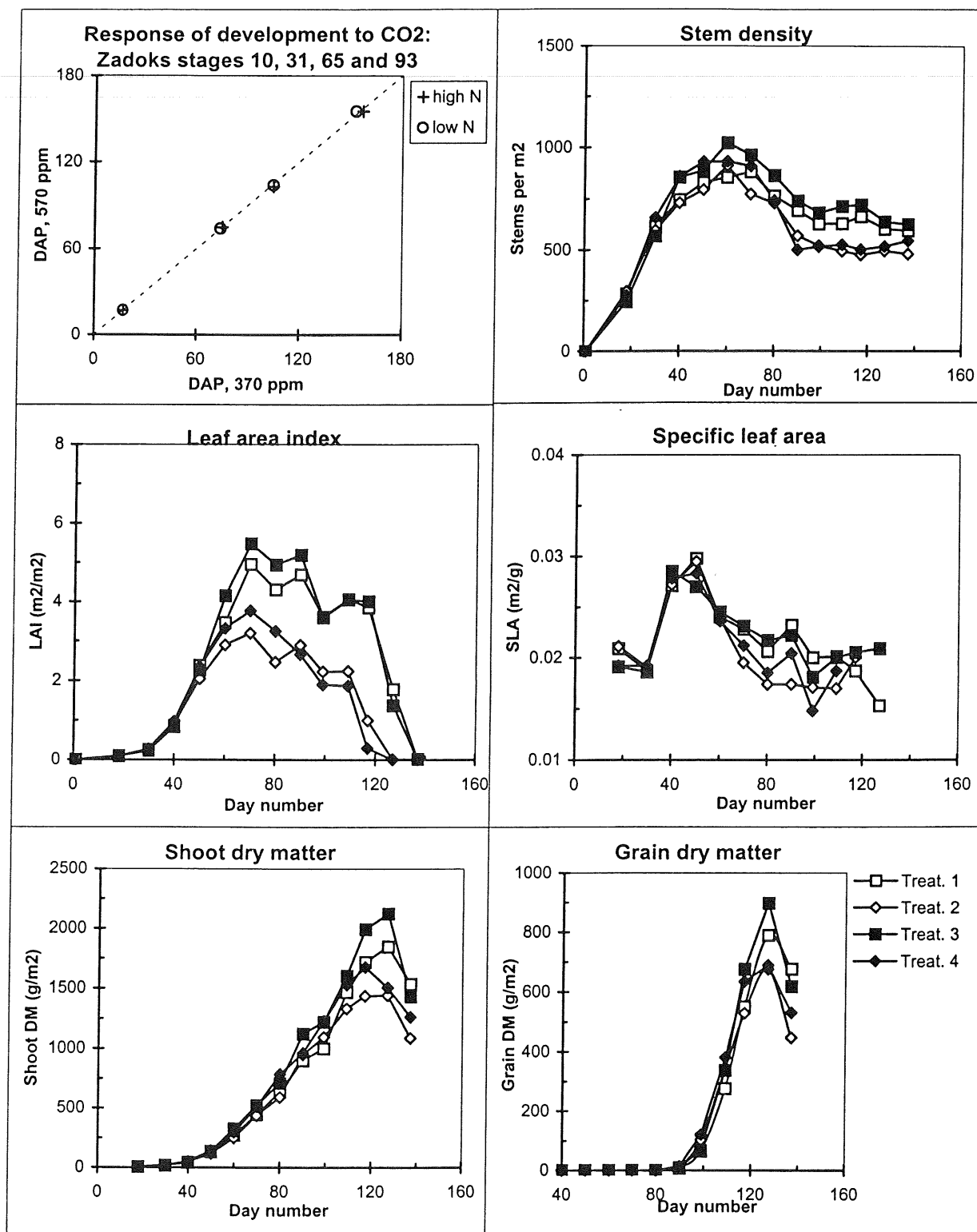


Figure B-3. Summary of results from spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of low (Low N) and high nitrogen (high N) supply and ambient (370 ppmv) and elevated (570 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Pinter et al., 1996b). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 370 ppmv, high N; Treat. 2= 370 ppmv, low N; Treat. 3= 570 ppmv, high N; Treat. 4= 570 ppmv, low N.

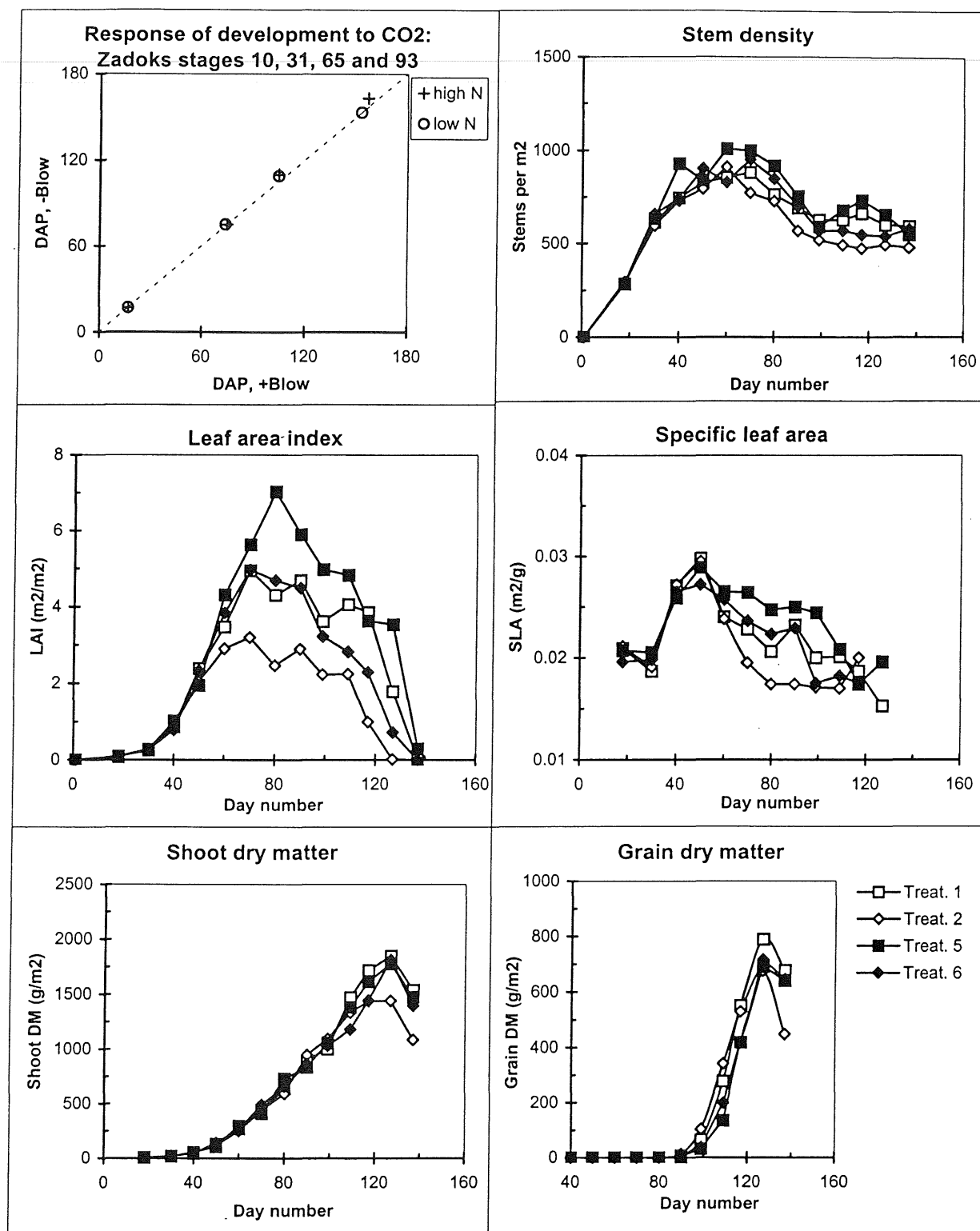


Figure B-4. Summary of results from spring wheat (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of low (Low N) and high nitrogen (high N) supply and ambient atmospheric CO<sub>2</sub> concentration with (+Blow) and without (-Blow) blower rings (Source: Pinter et al., 1996b). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= high N, +Blow; Treat. 2= low N, +Blow; Treat. 5= high N, -Blow; Treat. 6= low N, -Blow.

## Appendix C: Results from winter wheat experiment at Clermont Ferrand

Winter wheat was grown during growing season 1995/96 in containers in transparent tunnels under ambient atmospheric CO<sub>2</sub> concentration and different temperature regimes during the period of grain filling. Final yield data are given in Table C-1 and time courses of crop variables are given in Figure C-1.

### *Growing season 1995/96*

Table C-1. Yield component analyses of results (average of 5 replicates) from winter wheat (cv. These) experiments in containers in a transparent tunnels at Clermont Ferrand, France in growing season 1995/96 under conditions of ambient (Amb. T) temperatures and ambient atmospheric CO<sub>2</sub> concentration (Source: Triboi, pers. comm.), with different temperature regimes during the period of grain filling. Treatments: Treatm. 1= Amb. T; Treatm. 2= Amb. T but from end of anthesis (i.e. Julian day 155) minimum (Tmin) and maximum temperatures (Tmax) are set to respectively 10 and 18 °C; Treatm. 3= idem Treatm. 2 but Tmin= 20 °C and Tmax= 28 °C; Treatm. 4= idem Treatm. 2 but Tmin= 10 °C and Tmax= 34 °C; Ratio 2=Treatm. 2 / Treatm. 1; Ratio 3=Treatm. 3 / Treatm. 1; Ratio 4=Treatm. 4 / Treatm. 1

	Treatm.1	Treatm.2	Treatm.3	Treatm.4	Ratio 2	Ratio 3	Ratio 4
Total biomass above ground (g/m <sup>2</sup> )	1824	1714	1373	1212	0.940	0.753	0.664
Grain yield (g/m <sup>2</sup> )	849	1002	673	541	1.180	0.793	0.637
Harvest index	0.465	0.585	0.490	0.446	1.258	1.054	0.959
Plants/m <sup>2</sup> (initial)	520	520	520	520	-	-	-
Ears /plant	1.037	0.813	0.850	0.813	0.784	0.820	0.784
Grains /ear	36.9	39.5	39.0	38.4	1.070	1.057	1.041
Grain weight (mg)	42.7	58.5	36.9	31.6	1.370	0.864	0.740

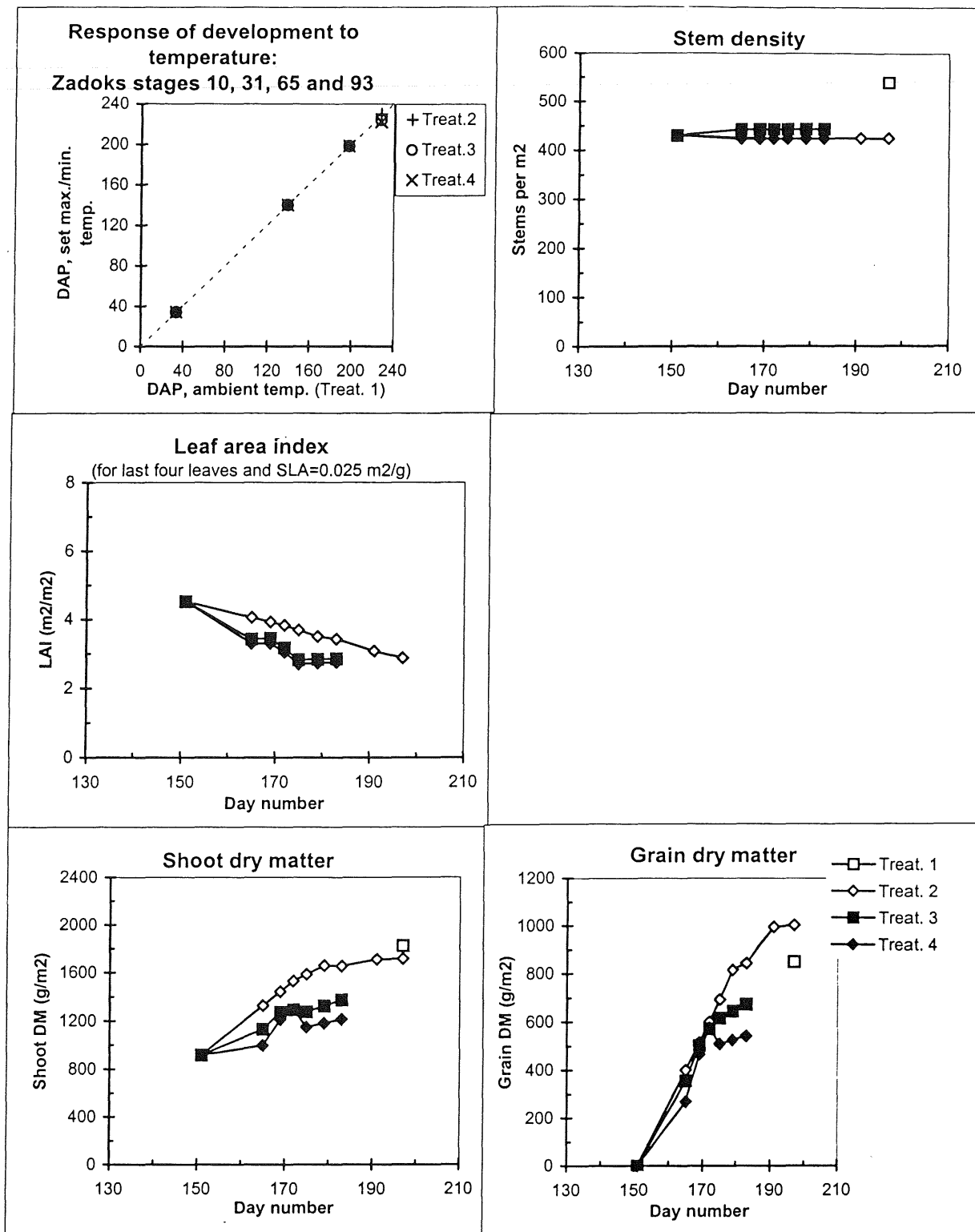


Figure C-1. Summary of results from winter wheat (cv. These) experiments in containers in transparent tunnels at Clermont Ferrand, France in growing season 1995/96 under conditions of ambient temperatures (Amb. T) and ambient atmospheric CO<sub>2</sub> concentration (Source: Triboi, pers. comm.). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= Amb. T; Treat. 2= Amb. T but from Julian day 155 minimum (Tmin) and maximum temperatures (Tmax) are set to respectively 10 and 18 °C; Treat. 3= idem Treat. 2 but Tmin= 20 °C and Tmax= 28 °C; Treat. 4= idem Treat. 2 but Tmin= 10 °C and Tmax= 34 °C.

## Appendix D: Results from winter wheat experiment at Florence

Winter wheat was grown during growing season 1997 in fields under ambient and elevated atmospheric CO<sub>2</sub> concentrations. A mini free-air CO<sub>2</sub> enrichment (MiniFACE) system was used. Crop data are given in Figure D-1.

### *Growing season 1997*

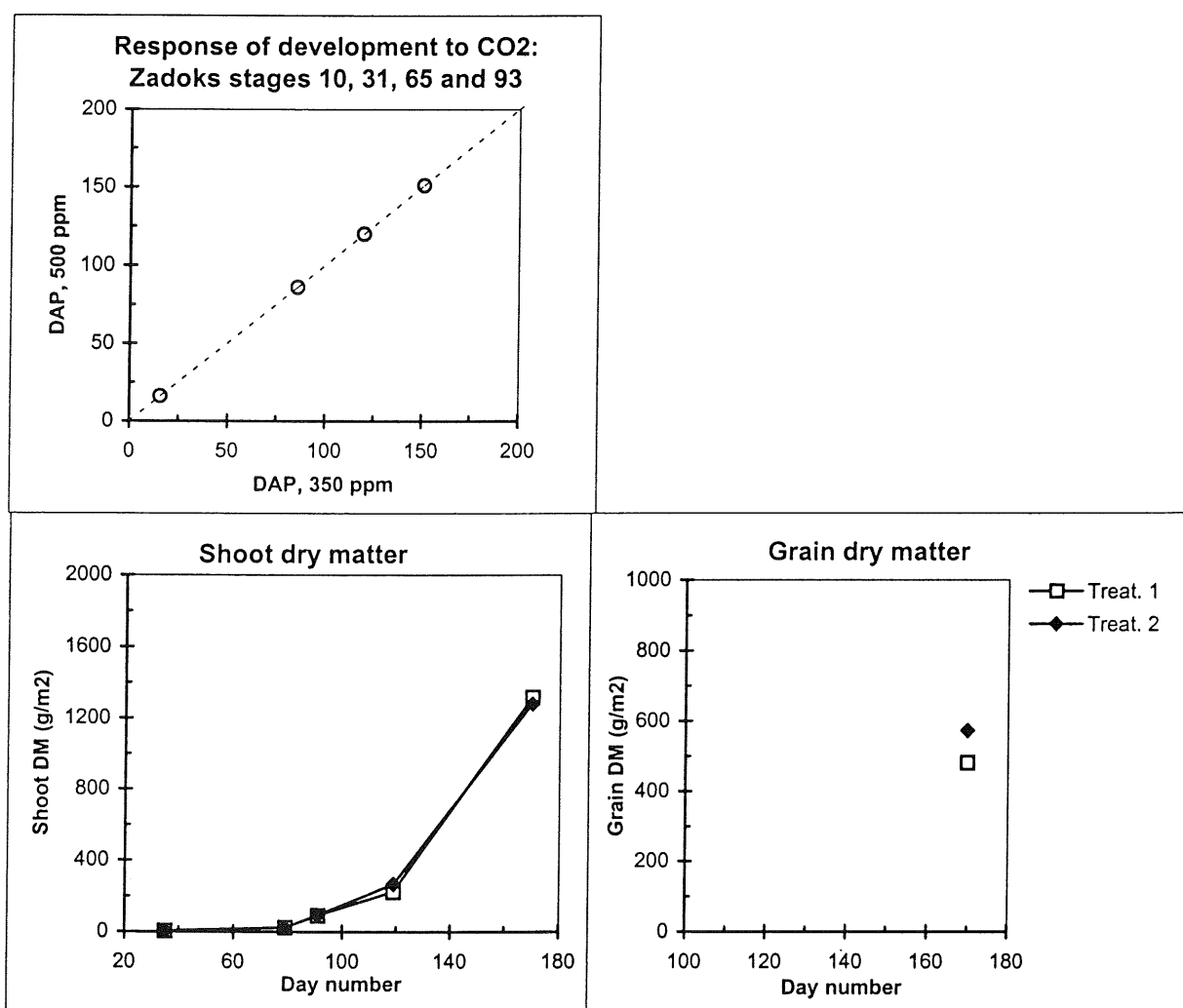


Figure D-1. Summary of results from winter wheat (cv. Golia) field experiments at Florence, Italy in growing season 1997 under conditions of ambient temperatures, ambient (350 ppmv) and elevated (500 ppmv; with MiniFACE system) atmospheric CO<sub>2</sub> concentrations and without irrigation (Source: Miglietta, pers. comm.). Legends: DAP= days after planting; Day number= Julian day; Treat. 1= 350 ppmv; Treat. 2= 500 ppmv.

## Appendix E: Results from spring wheat experiments at Giessen

Spring wheat was grown during growing season 1994 in pots in open-top chambers under ambient and elevated atmospheric CO<sub>2</sub> concentrations with low and high nitrogen supply. Final yield data are given in Table E-1 and time courses of crop variables are given in Figure E-1.

Spring wheat was grown during growing season 1995 in pots in open-top chambers under ambient and elevated atmospheric CO<sub>2</sub> concentrations with low and high nitrogen supply. Final yield data are given in Table E-2 and time courses of crop variables are given in Figure E-2.

Spring wheat was grown during growing season 1996 in pots in open-top chambers under ambient and elevated atmospheric CO<sub>2</sub> concentrations with low and high nitrogen supply. Final yield data are given in Table E-3 and time courses of crop variables are given in Figure E-3.

### *Giessen, growing season 1994*

Table E-1. Yield component analyses of results (average of 2 chamber replicates each consisting of the harvests from 5 pots) from spring wheat (cv. Minaret) experiments in pots in open-top chambers at Giessen, Germany in growing season 1994 under conditions of ambient (360 ppmv) and elevated (525 and 640 ppmv) atmospheric CO<sub>2</sub> concentration with low (-N) and high (+N) nitrogen supply (Source: Fangmeier et al., 1996; 1997a; 1997b). Treatments: Tr. 3= 360 ppmv, -N; Tr. 4= 360 ppmv, +N; Tr. 5= 525 ppmv, -N; Tr. 6= 525 ppmv, +N; Tr. 7= 640 ppmv, -N; Tr. 8= 640 ppmv, +N; Ratio 525, +N=Tr. 6 / Tr. 4; Ratio 525, -N=Tr. 5 / Tr. 3; Ratio 640, +N= Tr. 8 / Tr. 4; Ratio 640, -N=Tr. 7 / Tr. 3

	Tr. 3	Tr. 4	Tr. 5	Tr. 6	Tr. 7	Tr. 8	Ratio 525,+N	Ratio 525,-N	Ratio 640,+N	Ratio 640,-N
Total bio-mass above gr.(g/m <sup>2</sup> )	827	976	1015	1263	1119	1379	1.294	1.227	1.413	1.353
Grain yield (g/m <sup>2</sup> )	385	489	474	606	507	625	1.239	1.231	1.278	1.317
Harvest index	0.465	0.505	0.468	0.481	0.454	0.454	0.952	1.006	0.899	0.976
Plants/m <sup>2</sup>	140	140	140	140	140	140	-	-	-	-
Grains /plant	82.6	100.3	101.4	141.0	111.2	133.3	1.406	1.228	1.329	1.346
Grain weight (mg)	33.26	34.86	33.40	30.72	32.58	33.50	0.881	1.004	0.961	0.980

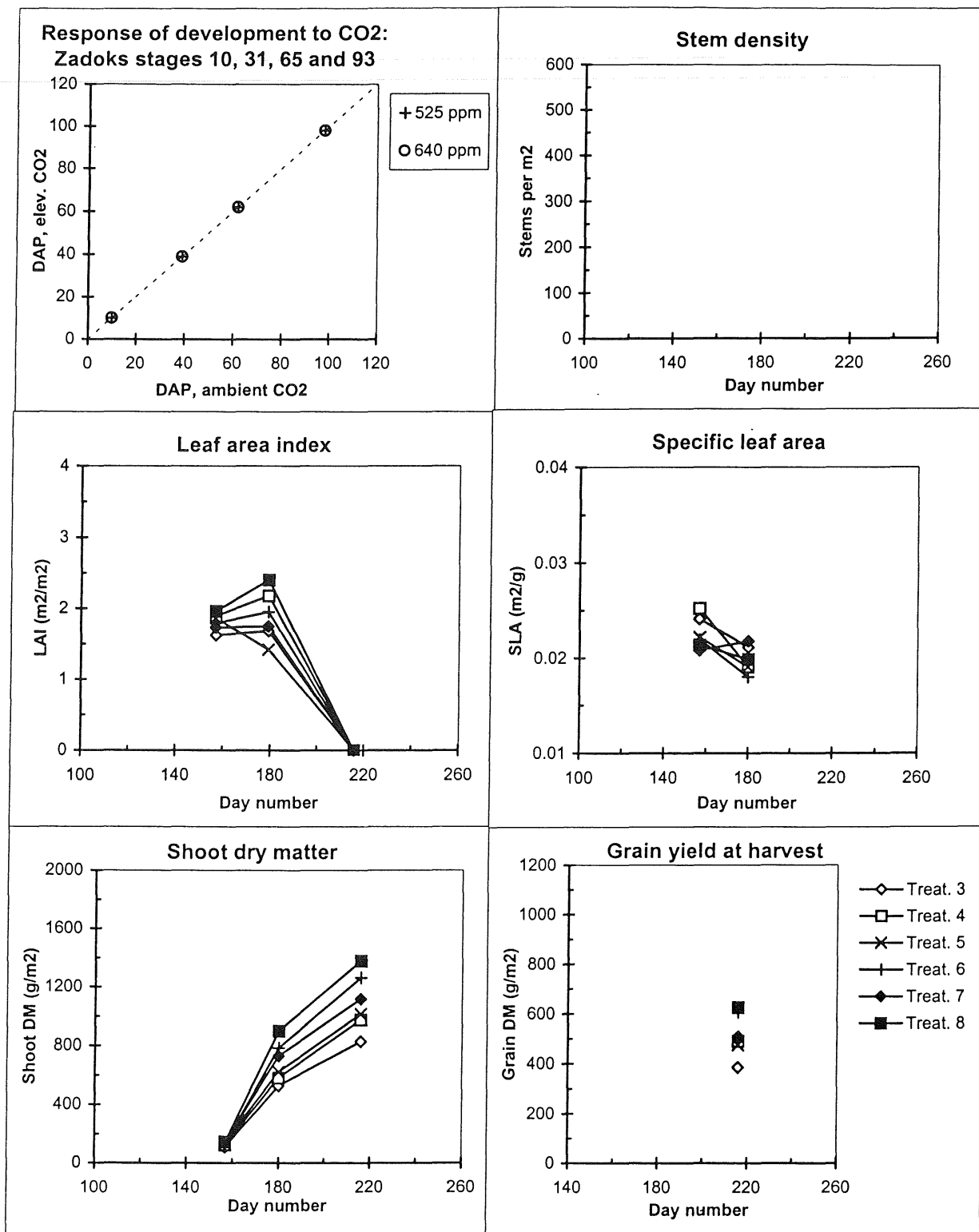


Figure E-1. Summary of results from spring wheat (cv. Minaret) in pots in open-top chambers at Giessen, Germany in growing season 1994 under conditions of ambient (360 ppmv) and elevated (525 and 640 ppmv) atmospheric CO<sub>2</sub> concentrations with low (-N) and high (+N) nitrogen supply (Source: Fangmeier et al., 1996; 1997a; 1997b). Legends: DAP= days after sowing; Day number= Julian day; Treat. 3= 360 ppmv, -N; Treat. 4= 360 ppmv, +N; Treat. 5= 525 ppmv, -N; Treat. 6= 525 ppmv, +N; Treat. 7= 640 ppmv, -N; Treat. 8= 640 ppmv, +N.



*Giessen, growing season 1995*

Table E-2. Yield component analyses of results (average of 2 chamber replicates each consisting of the harvests from 5 pots) from spring wheat (cv. Minaret) experiments in pots in open-top chambers at Giessen, Germany in growing season 1995 under conditions of ambient (400 ppmv) and elevated (540 and 640 ppmv) atmospheric CO<sub>2</sub> concentration with low (-N) and high (+N) nitrogen supply (Source: Fangmeier et al., 1997b). Treatments: Tr. 1= 400 ppmv, +N; Tr. 2= 400 ppmv, -N; Tr. 3= 540 ppmv, +N; Tr. 4= 540 ppmv, -N; Tr. 5= 640 ppmv, +N; Tr. 6= 640 ppmv, -N; Ratio 540, +N=Tr. 3 / Tr. 1; Ratio 540, -N=Tr. 4 / Tr. 2; Ratio 640, +N=Tr. 5 / Tr. 1; Ratio 640, -N= Tr. 6 / Tr. 2

	Tr. 1	Tr. 2	Tr. 3	Tr. 4	Tr. 5	Tr. 6	Ratio 540,+N	Ratio 540,-N	Ratio 640,+N	Ratio 640,-N
Total bio-mass above gr.(g/m <sup>2</sup> )	884	793	963	907	1250	1044	1.089	1.144	1.414	1.317
Grain yield (g/m <sup>2</sup> )	418	373	419	416	593	494	1.002	1.115	1.419	1.324
Harvest index	0.473	0.470	0.435	0.459	0.475	0.473	0.920	0.977	1.004	1.006
Plants/m <sup>2</sup>	140	140	140	140	140	140	-	-	-	-
Ears/plant	2.8	2.2	3.0	2.55	3.5	2.85	1.071	1.159	1.250	1.295
Grains /ear	36.93	41.41	44.0	44.31	44.94	45.86	1.191	1.070	1.217	1.107
Grain weight (mg)	29.16	29.25	22.74	26.40	26.95	26.97	0.780	0.903	0.924	0.922

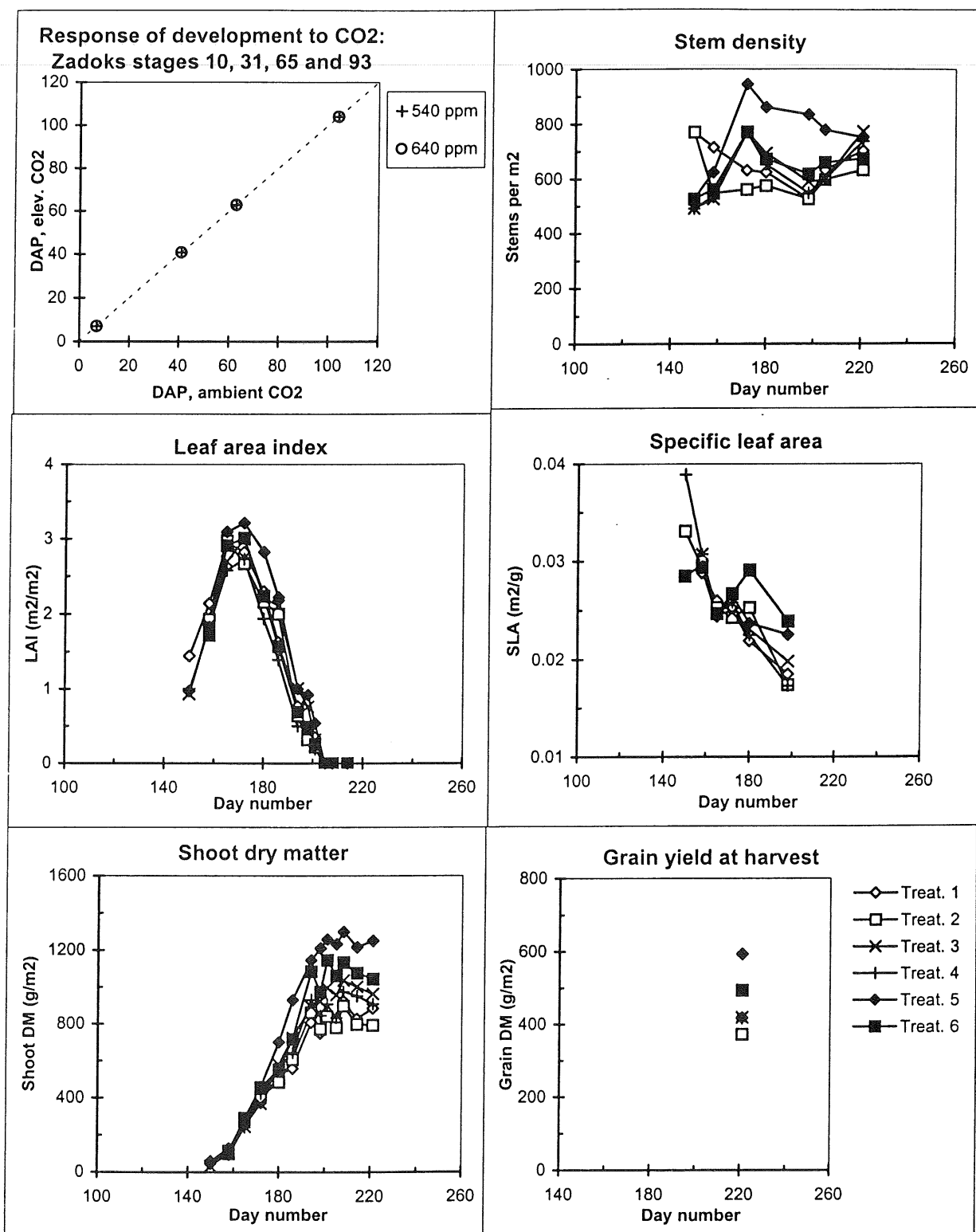


Figure E-2. Summary of results from spring wheat (cv. Minaret) in pots in open-top chambers at Giessen, Germany in growing season 1995 under conditions of ambient (400 ppmv) and elevated (540 and 640 ppmv) atmospheric CO<sub>2</sub> concentrations with low (-N) and high (+N) nitrogen supply (Source: Fangmeier et al., 1997b). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 400 ppmv, +N; Treat. 2= 400 ppmv, -N; Treat. 3= 540 ppmv, +N; Treat. 4= 540 ppmv, -N; Treat. 5= 640 ppmv, +N; Treat. 6= 640 ppmv, -N.

Table E-3. Yield component analyses of results (average of 2 chamber replicates each consisting of the harvests from 5 pots) from spring wheat (cv. Minaret) experiments in pots in open-top chambers at Giessen, Germany in growing season 1996 under conditions of ambient (380 ppmv) and elevated (515 and 665 ppmv) atmospheric CO<sub>2</sub> concentration with low (-N) and high (+N) nitrogen supply (Source: Fangmeier et al., 1997b). Treatments: Tr. 1= 380 ppmv, +N; Tr. 2= 380 ppmv, -N; Tr. 3= 515 ppmv, +N; Tr. 4= 515 ppmv, -N; Tr. 5= 665 ppmv, +N; Tr. 6= 665 ppmv, -N; Ratio 515, +N=Tr. 3 / Tr. 1; Ratio 515, -N=Tr. 4 / Tr. 2; Ratio 665, +N=Tr. 5 / Tr. 1; Ratio 665, -N= Tr. 6 / Tr. 2

	Tr. 1	Tr. 2	Tr. 3	Tr. 4	Tr. 5	Tr. 6	Ratio 515,+N	Ratio 515,-N	Ratio 665,+N	Ratio 665,-N
Total bio- mass above gr.(g/m <sup>2</sup> )	877	801	1037	985	1171	1026	1.182	1.230	1.335	1.281
Grain yield (g/m <sup>2</sup> )	486	440	560	515	621	526	1.152	1.170	1.278	1.195
Harvest index	0.554	0.549	0.540	0.523	0.531	0.512	0.975	0.953	0.958	0.933
Plants/m <sup>2</sup>	120	120	120	120	120	120	-	-	-	-
Ears/plant	2.95	2.68	3.20	3.23	3.55	2.9	1.085	1.205	1.203	1.082
Grains /ear	39.56	39.10	44.22	39.97	43.07	43.34	1.118	1.022	1.089	1.108
Grain weight (mg)	34.71	35.02	33.00	33.22	33.88	34.84	0.951	0.949	0.976	0.995

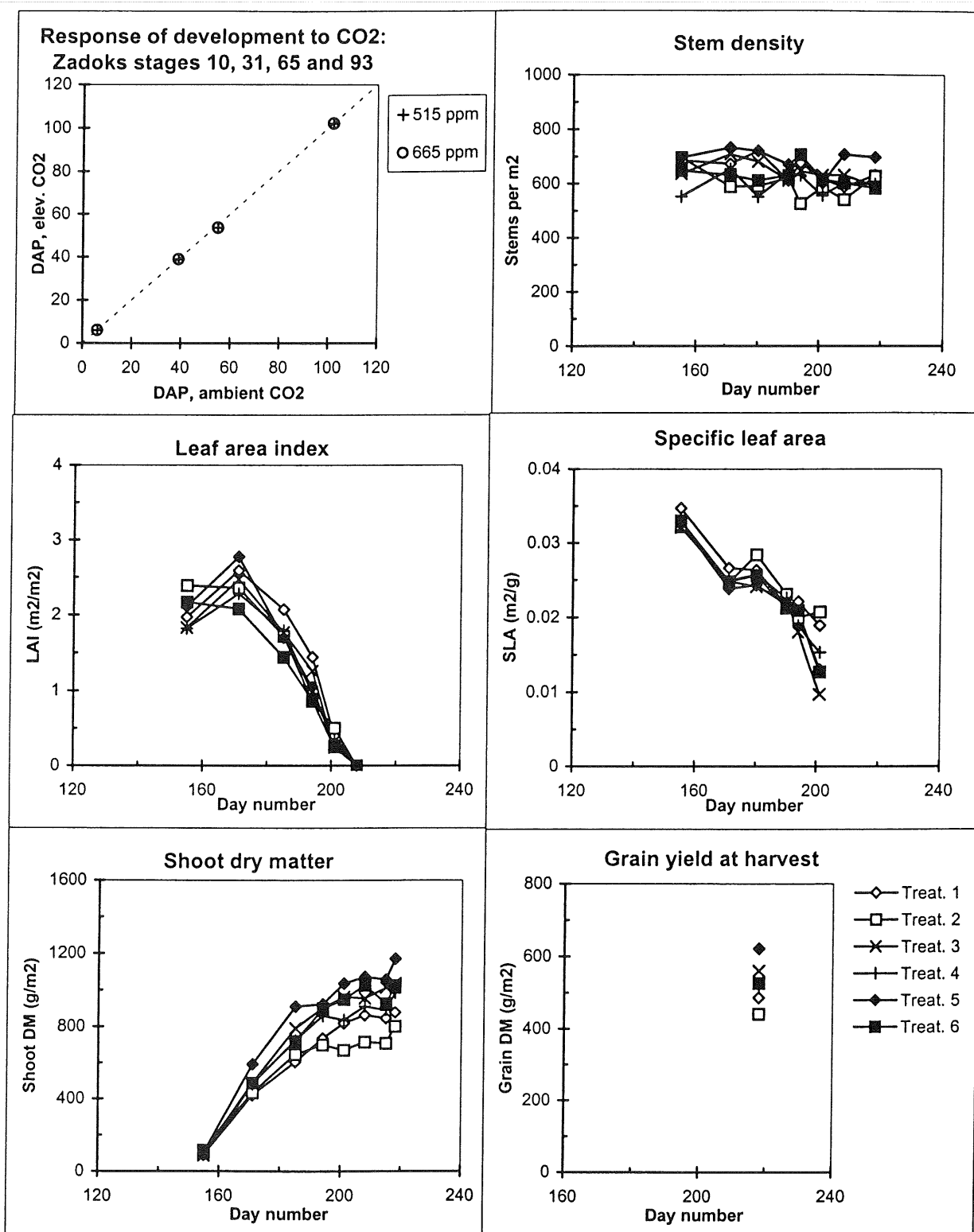


Figure E-3. Summary of results from spring wheat (cv. Minaret) in pots in open-top chambers at Giessen, Germany in growing season 1996 under conditions of ambient (380 ppmv) and elevated (515 and 665 ppmv) atmospheric CO<sub>2</sub> concentrations with low (-N) and high (+N) nitrogen supply (Source: Fangmeier et al., 1997b). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 380 ppmv, +N; Treat. 2= 380 ppmv, -N; Treat. 3= 515 ppmv, +N; Treat. 4= 515 ppmv, -N; Treat. 5= 665 ppmv, +N; Treat. 6= 665 ppmv, -N.

## Appendix F: Results from winter wheat experiments at Rothamsted

Winter wheat was grown during growing season 1990/91 in pots in a greenhouse under ambient and doubled atmospheric CO<sub>2</sub> concentrations and first combined with ambient and ambient + 4 °C temperatures and second with low and high nitrogen supply. Final yield data are given in Tables F-1 and F-2 and time courses of crop variables are given in Figures F-1 and F-2.

Winter wheat was grown during growing season 1991/92 in pots in a greenhouse under ambient and doubled atmospheric CO<sub>2</sub> concentrations and ambient and ambient + 4 °C temperatures. Final yield data are given in Table F-3 and time courses of crop variables are given in Figure F-3.

Winter wheat was grown during growing season 1993/94 in pots in a greenhouse under ambient and doubled atmospheric CO<sub>2</sub> concentrations with different degree of shading during three periods before and during anthesis. Final yield data are given in Table F-4 and Figure F-4 and time courses of crop variables are given in Figure F-5.

### *Rothamsted, growing season 1990/91*

Table F-1. Yield component analyses of results (average of 6 replicates) from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1990/91 under conditions of ambient (A) and ambient + 4 °C (A+4) temperatures and ambient (370 ppmv) and doubled (680 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Delgado et al., 1994; Mitchell et al., 1993). Treatments: Tr. 2= 370 ppmv, A; Tr. 4= 370 ppmv, A+4; Tr. 6= 680 ppmv, A; Tr. 8= 680 ppmv, A+4; Rat.A= Tr. 6 / Tr. 2; Rat.A+4= Tr. 8 / Tr. 4; Rat.370= Tr. 4 / Tr. 2; Rat.680= Tr. 8 / Tr. 6

	Tr. 2	Tr. 4	Tr. 6	Tr. 8	Rat.A, CO <sub>2</sub> effect	Rat.A+4, CO <sub>2</sub> effect	Rat.370, temp. effect	Rat.680, temp. effect
Total biomass above ground (g/m <sup>2</sup> )	3420	2879	3914	3310	1.144	1.150	0.842	0.846
Grain yield (g/m <sup>2</sup> )	1173	957	1361	1087	1.160	1.136	0.816	0.799
Harvest index	0.343	0.332	0.348	0.328	1.015	0.988	0.968	0.943
Plants/m <sup>2</sup>	192	192	192	192	-	-	-	-
Ears /plant	4.67	4.25	5.67	4.94	1.214	1.162	0.910	0.871
Grains /ear	31.8	23.53	32.17	21.07	1.012	0.895	0.740	0.655
Grain weight (mg)	41.17	49.84	38.88	54.36	0.944	1.091	1.211	1.398

Table F-2. Yield component analyses of results (average of 6 replicates) from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1990/91 under conditions of ambient temperatures with low (-N) and high (+N) nitrogen supply and ambient (370 ppmv) and doubled (680 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Delgado et al., 1994; Mitchell et al., 1993). Treatments: Treatm. 2= 370 ppmv, +N; Treatm. 1= 370 ppmv, -N; Treatm. 6= 680 ppmv, +N, Treatm. 5= 680 ppmv, -N; Ratio +N= Treatm. 6 / Treatm. 2; Ratio -N= Treatm. 5 / Treatm. 1

	Treatm.2	Treatm.1	Treatm.6	Treatm.5	Ratio +N	Ratio -N
Total biomass above ground (g/m <sup>2</sup> )	3420	1856	3914	2041	1.144	1.100
Grain yield (g/m <sup>2</sup> )	1173	619	1361	543	1.160	0.877
Harvest index	0.343	0.334	0.348	0.266	1.015	0.796
Plants/m <sup>2</sup>	192	192	192	192	-	-
Ears /plant	4.67	2.58	5.67	2.75	1.214	1.066
Grains /ear	31.8	29.44	32.17	25.95	1.012	0.881
Grain weight (mg)	41.17	42.40	38.88	39.64	0.944	0.935

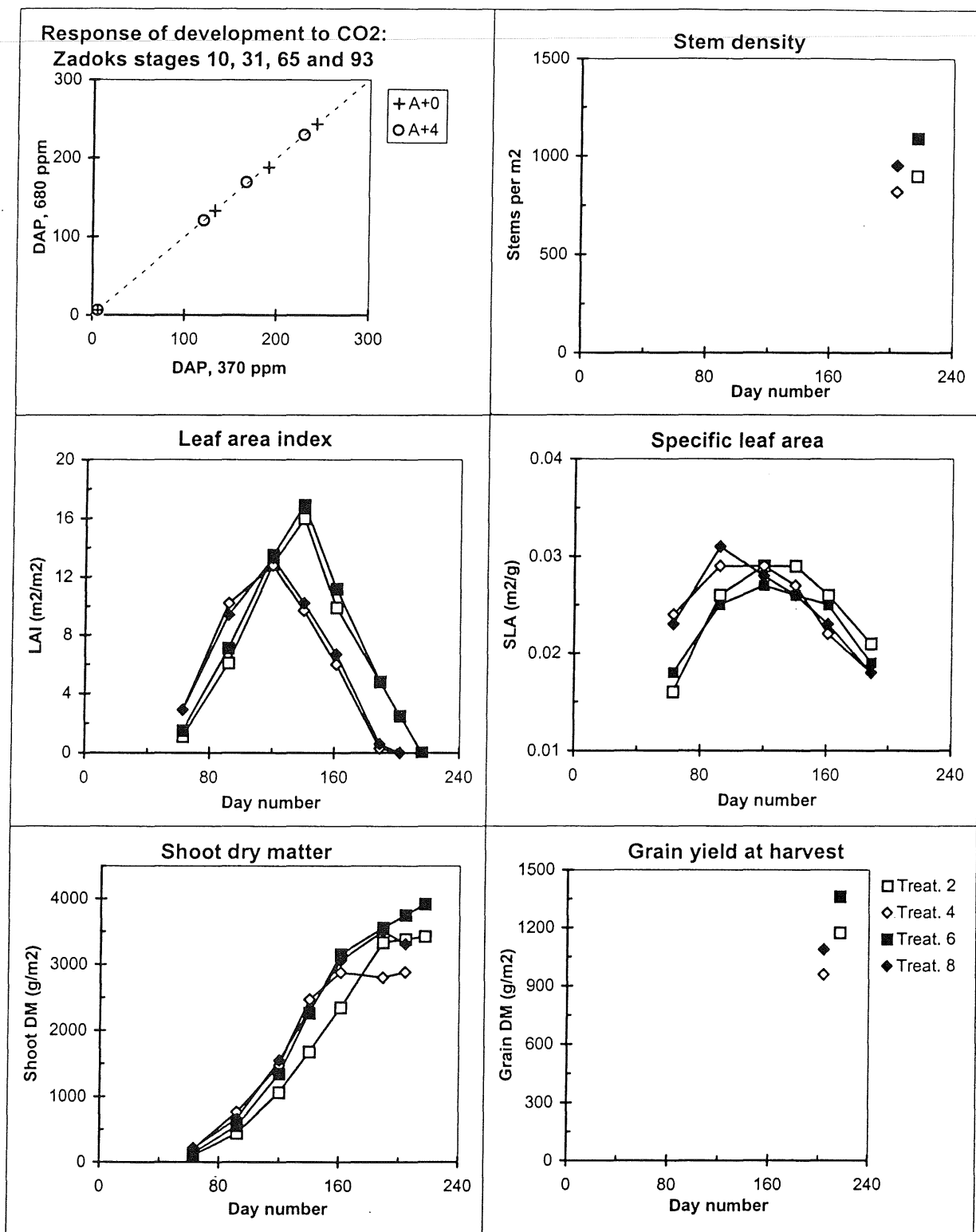


Figure F-1. Summary of results from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1990/91 under conditions of ambient (A) and ambient + 4 °C (A+4) temperatures and ambient (370 ppmv) and doubled (680 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Delgado et al., 1994; Mitchell et al., 1993). Legends: DAP= days after sowing; Day number= Julian day; Treat. 2= 370 ppmv, A; Treat. 4= 370 ppmv, A+4; Treat. 6= 680 ppmv, A; Treat. 8= 680 ppmv, A+4.

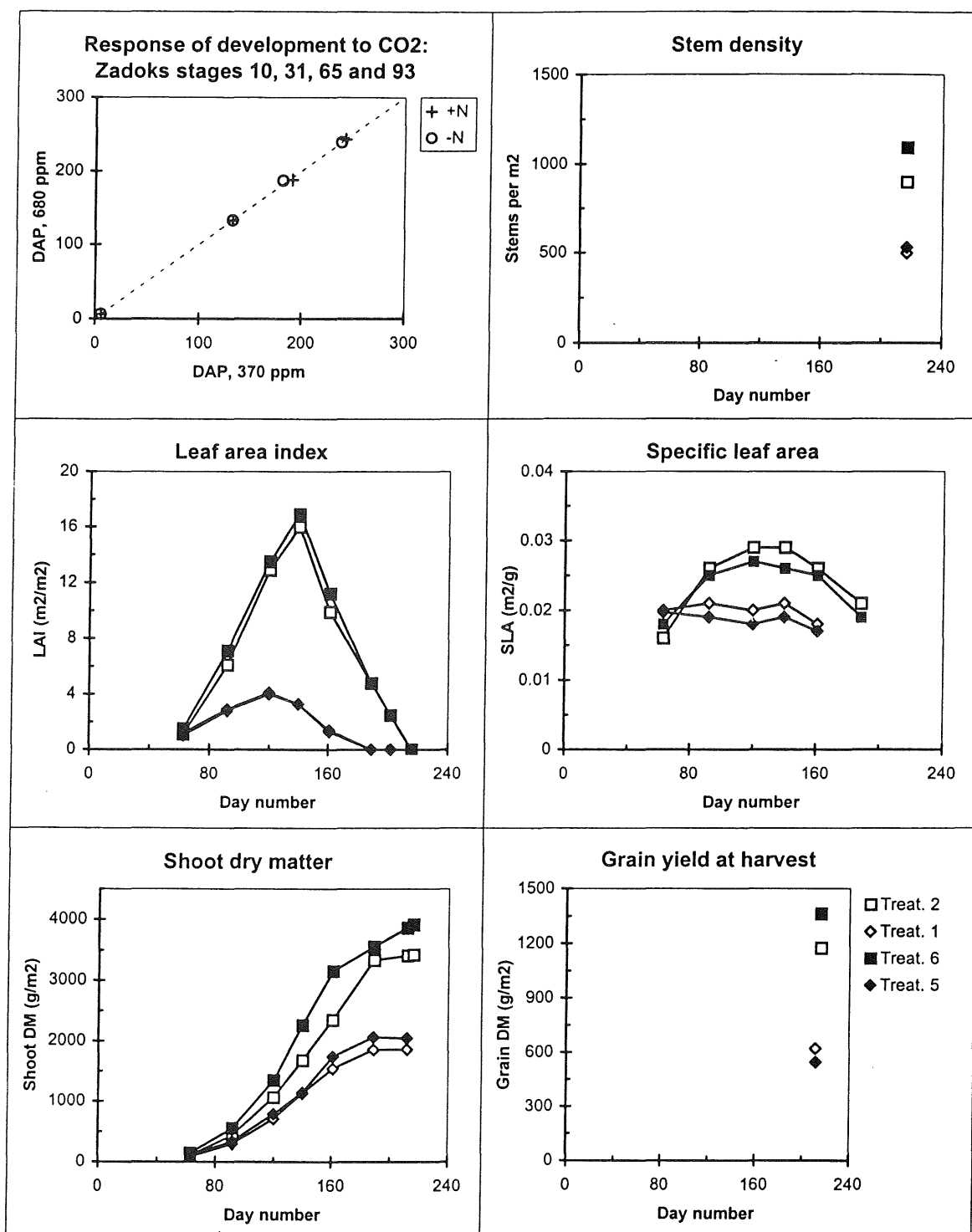


Figure F-2. Summary of results from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1990/91 under conditions of ambient temperatures with low (-N) and high (+N) nitrogen supply and ambient (370 ppmv) and doubled (680 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Delgado et al., 1994; Mitchell et al., 1993). Legends: DAP= days after sowing; Day number= Julian day; Treat. 2= 370 ppmv, +N; Treat. 1= 370 ppmv, -N; Treat. 6= 680 ppmv, +N; Treat. 5= 680 ppmv, -N.



*Rothamsted, growing season 1991/92*

Table F-3. Yield component analyses of results (average of 28 replicates) from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1991/92 under conditions of ambient (A) and ambient + 4 °C (A+4) temperatures and ambient (390 ppmv) and doubled (680 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Mitchell et al., 1995).  
Treatments: Tr. 1= 390 ppmv, A; Tr. 2= 390 ppmv, A+4; Tr. 3= 680 ppmv, A; Tr. 4= 680 ppmv, A+4; Rat. A= Tr. 3 / Tr. 1; Rat. A+4= Tr. 4 / Tr. 2; Rat. 390= Tr. 2 / Tr. 1; Rat. 680= Tr. 4 / Tr. 3.

	Tr.1	Tr.2	Tr.3	Tr.4	Rat.A, CO <sub>2</sub> effect	Rat.A+4, CO <sub>2</sub> effect	Rat.390, temp.effect	Rat.680, temp.effect
Total biomass above ground (g/m <sup>2</sup> )	2646	2226	3357	2819	1.269	1.266	0.841	0.840
Grain yield (g/m <sup>2</sup> )	800	514	1097	726	1.371	1.412	0.643	0.662
Harvest index	0.302	0.231	0.327	0.258	1.083	1.117	0.765	0.789
Plants/m <sup>2</sup>	300	300	300	300	-	-	-	-
Ears /plant	2.56	1.88	2.95	2.25	1.152	1.197	0.734	0.763
Grains /ear	30.77	35.75	34.35	34.22	1.116	0.957	1.162	0.996
Grain weight (mg)	33.90	25.45	36.09	31.43	1.065	1.235	0.751	0.871

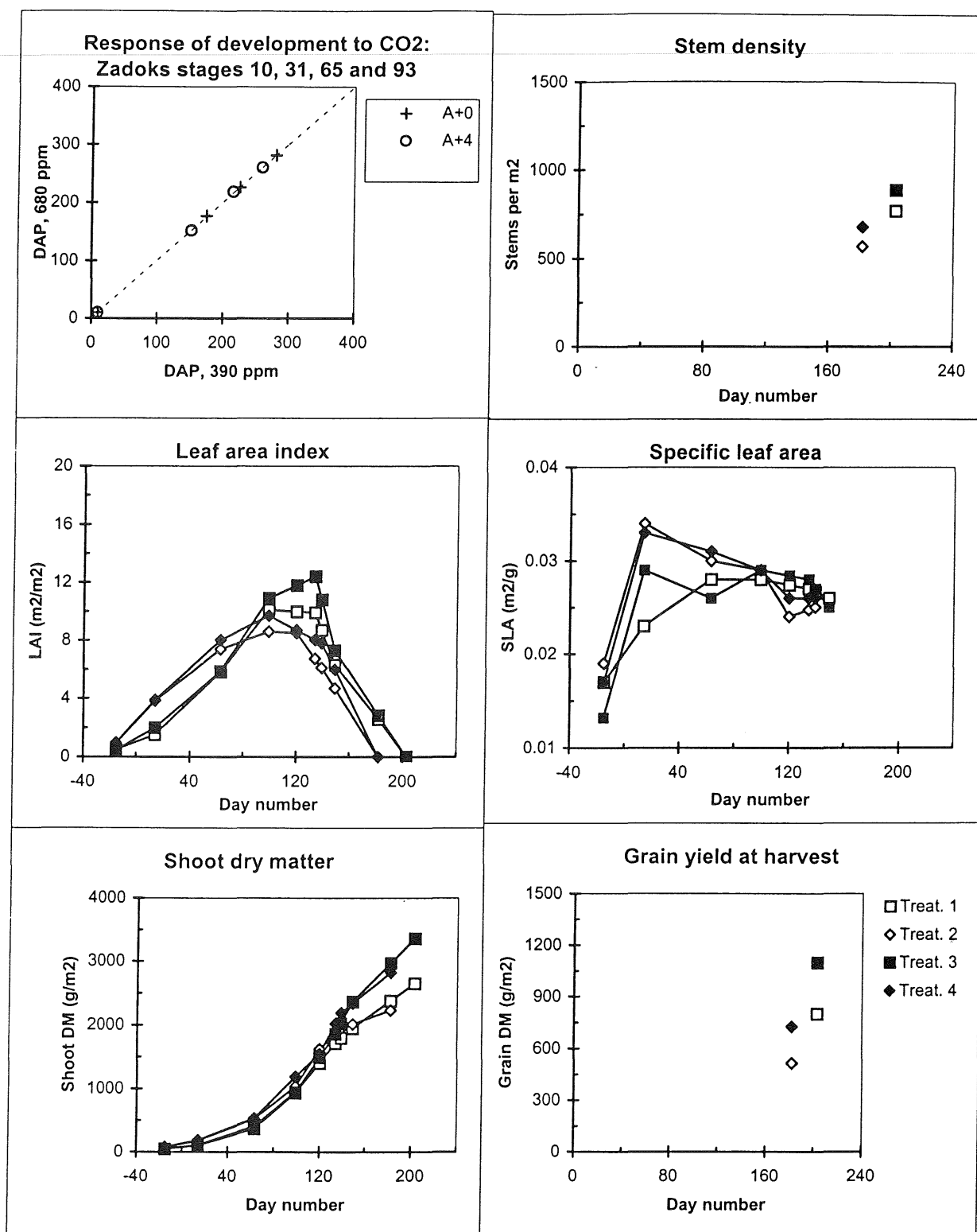
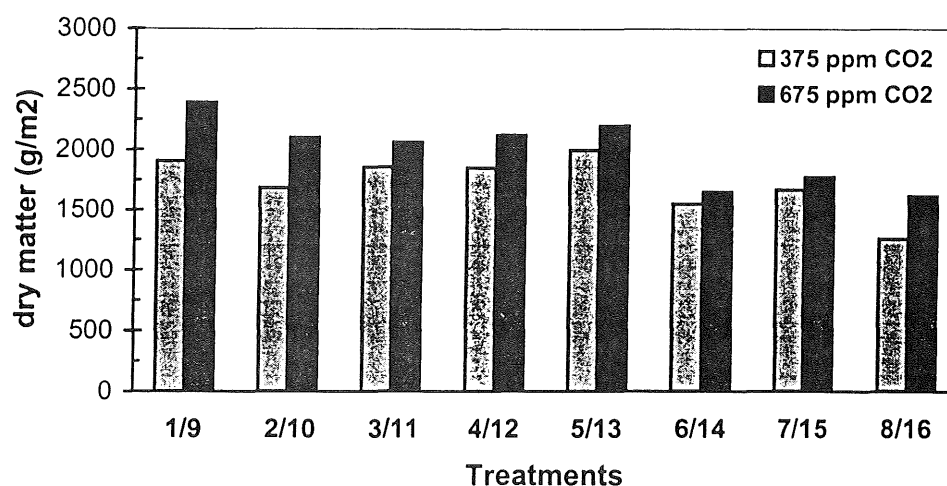


Figure F-3. Summary of results from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1991/92 under conditions of ambient (A) and ambient + 4 °C (A+4) temperatures and ambient (390 ppmv) and doubled (680 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Mitchell et al., 1995). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 390 ppmv, A; Treat. 2= 390 ppmv, A+4; Treat. 3= 680 ppmv, A; Treat. 4= 680 ppmv, A+4.

A.



B.

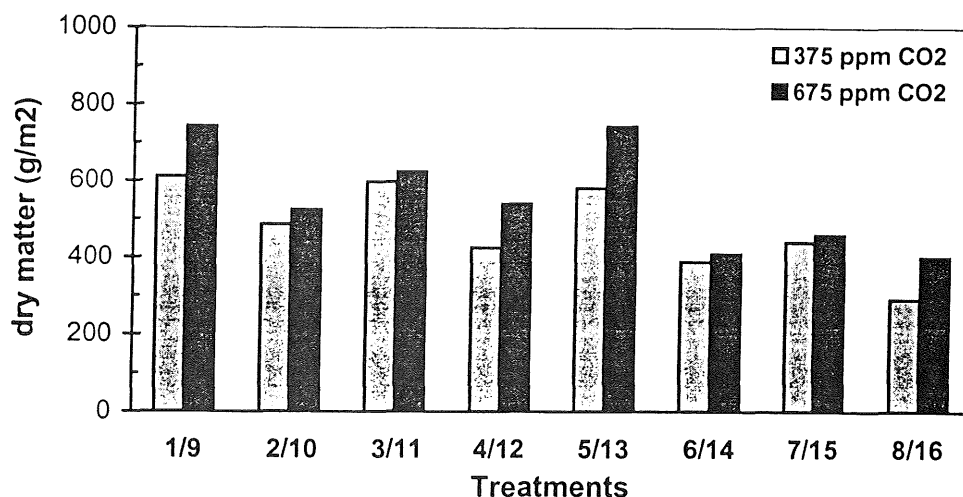


Figure F-4. Total above-ground biomass (A) and grain yield (B) from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1993/94 under conditions of ambient temperatures with shading during three different periods (SH1 and SH2 indicate shading during three-week periods of respectively 4 to 7 weeks and 1 to 4 weeks before 50% anthesis and SH3 is shading during 2.5 week around 50% anthesis) and ambient (375 ppmv) and doubled (675 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Mitchell et al., 1996). Treatments: TR 1= 375 ppmv, no shading; TR 2= 375 ppmv, SH3; TR 3= 375 ppmv, SH2; TR 4= 375 ppmv, SH2, SH3; TR 5= 375 ppmv, SH1; TR 6= 375 ppmv, SH1, SH3; TR 7= 375 ppmv, SH1, SH2; TR 8= 375 ppmv, SH1, SH2, SH3; TR 9= 675 ppmv, no shading; TR 10= 675 ppmv, SH3; TR 11= 675 ppmv, SH2; TR 12= 675 ppmv, SH2, SH3; TR 13= 675 ppmv, SH1; TR 14= 675 ppmv, SH1, SH3; TR 15= 675 ppmv, SH1, SH2; TR 16= 675 ppmv, SH1, SH2, SH3.

Table F-4. Yield component analyses of results (average of 12 replicates) from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1993/94 under conditions of ambient temperatures with shading during three different periods (SH1 and SH2 indicate shading during three-week periods of respectively 4 to 7 weeks and 1 to 4 weeks before 50% anthesis and SH3 is shading during 2.5 week around 50% anthesis) and ambient (375 ppmv) and doubled (675 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Mitchell et al., 1996). Treatments: TR 1= 375 ppmv, no shading; TR 2= 375 ppmv, SH3; TR 3= 375 ppmv, SH2; TR 4= 375 ppmv, SH2, SH3; TR 5= 375 ppmv, SH1; TR 6= 375 ppmv, SH1, SH3; TR 7= 375 ppmv, SH1, SH2; TR 8= 375 ppmv, SH1, SH2, SH3; TR 9= 675 ppmv, no shading; TR 10= 675 ppmv, SH3; TR 11= 675 ppmv, SH2; TR 12= 675 ppmv, SH2, SH3; TR 13= 675 ppmv, SH1; TR 14= 675 ppmv, SH1, SH3; TR 15= 675 ppmv, SH1, SH2; TR 16= 675 ppmv, SH1, SH2, SH3.

	TR 1 / 9	TR 2 / 10	TR 3 / 11	TR 4 / 12	TR 5 / 13	TR 6 / 14	TR 7 / 15	TR 8 / 16	Average of ratios
Total biomass above ground (g/m <sup>2</sup> ), TR 1 - 8	1907	1682	1854	1848	2000	1550	1666	1260	
Idem, TR 9 - 16	2392	2102	2061	2123	2198	1650	1772	1614	
<b>Ratio TR9 / TR1etc.</b>	<b>1.254</b>	<b>1.250</b>	<b>1.112</b>	<b>1.149</b>	<b>1.099</b>	<b>1.065</b>	<b>1.064</b>	<b>1.281</b>	<b>1.159</b>
Grain yield (g/m <sup>2</sup> ), TR 1 - 8	612	487	598	426	582	389	441	292	
Idem, TR 9 - 16	743	525	624	541	743	410	460	402	
<b>Ratio TR9 / TR1etc.</b>	<b>1.214</b>	<b>1.078</b>	<b>1.043</b>	<b>1.270</b>	<b>1.277</b>	<b>1.054</b>	<b>1.043</b>	<b>1.377</b>	<b>1.170</b>
Harvest index, TR 1 - 8	0.321	0.290	0.323	0.231	0.291	0.251	0.265	0.232	
Idem, TR 9 - 16	0.311	0.250	0.303	0.255	0.338	0.248	0.260	0.249	
<b>Ratio TR9 / TR1etc.</b>	<b>0.969</b>	<b>0.862</b>	<b>0.938</b>	<b>1.104</b>	<b>1.162</b>	<b>0.988</b>	<b>0.981</b>	<b>1.073</b>	<b>1.010</b>
Plants / m <sup>2</sup> , TR1 and TR 9, etc.	225	225	225	225	225	225	225	225	
Ears /plant, TR 1 - 8	2.876	2.302	2.889	3.071	2.947	2.311	3.098	2.147	
Idem, TR 9 - 16	3.444	3.364	3.120	3.467	2.840	2.484	2.827	2.778	
<b>Ratio TR9 / TR1etc.</b>	<b>1.197</b>	<b>1.461</b>	<b>1.080</b>	<b>1.129</b>	<b>0.964</b>	<b>1.075</b>	<b>0.913</b>	<b>1.294</b>	<b>1.139</b>
Grains /ear, TR 1 - 8	26.89	22.20	23.08	16.06	24.43	19.81	21.23	16.36	
Idem, TR 9 - 16	25.29	19.02	20.51	16.79	26.92	19.32	23.11	15.68	
<b>Ratio TR9 / TR1etc.</b>	<b>0.940</b>	<b>0.857</b>	<b>0.889</b>	<b>1.045</b>	<b>1.102</b>	<b>0.975</b>	<b>1.089</b>	<b>0.958</b>	<b>0.982</b>
Grain weight (mg), TR 1 - 8	35.17	42.35	39.87	38.38	35.93	37.77	29.80	36.96	
Idem, TR 9 - 16	37.91	36.46	43.33	41.30	43.20	37.96	31.29	41.02	
<b>Ratio TR9 / TR1etc.</b>	<b>1.078</b>	<b>0.861</b>	<b>1.087</b>	<b>1.076</b>	<b>1.202</b>	<b>1.005</b>	<b>1.05</b>	<b>1.110</b>	<b>1.059</b>

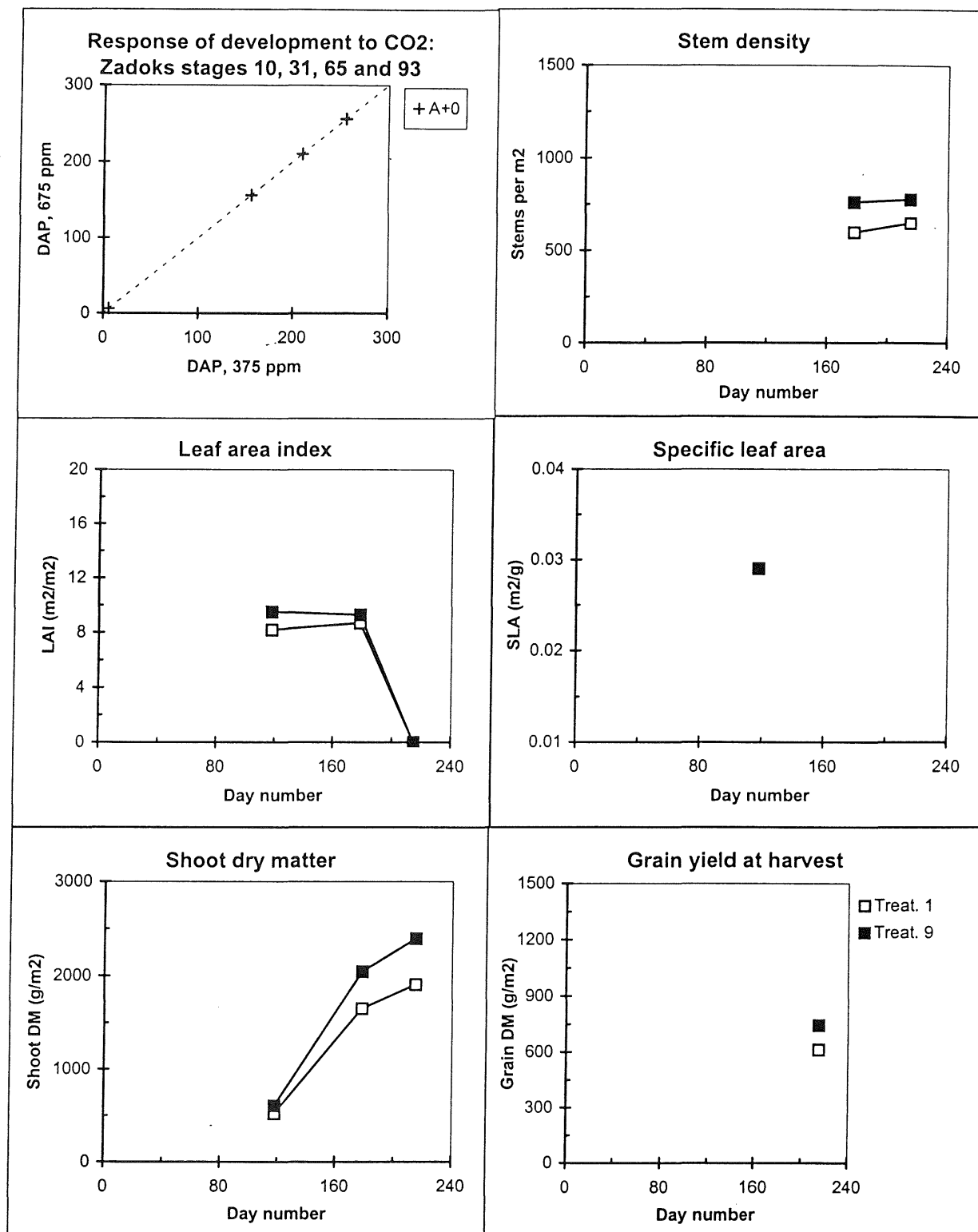


Figure F-5. Summary of results from winter wheat (cv. Mercia) experiments in pots in a greenhouse at Rothamsted, Harpenden, U.K. in growing season 1993/94 under conditions of ambient temperatures, ambient (375 ppmv) and doubled (675 ppmv) atmospheric CO<sub>2</sub> concentrations and no shading (Source: Mitchell et al., 1996). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 375 ppmv; Treat. 9= 675 ppmv.

## Appendix G: Results from wheat experiments at Wageningen

Spring wheat and winter wheat were grown in containers in climatized sun-lit enclosures during growing seasons 1991 and 1992/93, respectively under ambient and doubled atmospheric CO<sub>2</sub> concentrations. Final yield data are given in Table G-1.

Winter wheat was grown during growing season 1993/94 in the field in open-top chambers under ambient and doubled atmospheric CO<sub>2</sub> concentrations. Final yield data are given in Table G-2.

Spring wheat was grown during growing seasons 1995 and 1996 in the field in open-top chambers under ambient and doubled atmospheric CO<sub>2</sub> concentrations and ambient and ambient + 2 °C temperatures. Final yield data are given in Tables G-3 and G-4 and time courses of crop variables are given in Figures G-1 and G-2.

### *Wageningen, growing seasons 1991 and 1992/93*

Table G-1. Yield component analyses of results from spring wheat (cv. Minaret) and winter wheat (cv. Ritmo; 2 replicates) experiments in containers in climatized (ambient temperatures) sun-lit enclosures at Wageningen, the Netherlands during growing seasons 1991 and 1992/93, respectively under conditions of ambient (350 ppmv) and doubled (750 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Dijkstra et al., 1993; 1994). Ratio 2\*CO<sub>2</sub> S.W.= Spring wheat 750 ppmv / Spring wheat 350 ppmv; Ratio 2\*CO<sub>2</sub> W.W. = Winter wheat 750 ppmv / Winter wheat 350 ppmv.

	Spring wheat, 350 ppmv	Spring wheat, 750 ppmv	Winter wheat, 350 ppmv	Winter wheat, 750 ppmv	Ratio 2*CO <sub>2</sub> S.W.	Ratio 2*CO <sub>2</sub> W.W.
Total biomass above ground (g/m <sup>2</sup> )	1308	1750	2175	2589	1.338	1.190
Grain yield (g/m <sup>2</sup> )	438	588	964	929	1.342	0.964
Harvest index	0.335	0.336	0.443	0.359	1.003	0.810
Plants/m <sup>2</sup> (initial)	235	235	220	220	-	-
Ears /plant	2.48	2.98	3.14	3.52	1.202	1.121
Grains /ear	15.29	16.53	27.30	23.83	1.081	0.873
Grain weight (mg)	49.10	50.87	51.07	50.41	1.036	0.987

*Wageningen, growing season 1993/94*

Table G-2. Yield component analyses of results from winter wheat (cv. Ritmo; 3 replicates) field experiments in open-top chambers at Wageningen, the Netherlands during growing seasons 1993/94 under conditions of ambient (370 ppmv) and doubled (700 ppmv) atmospheric CO<sub>2</sub> concentrations (Source: Dijkstra et al., in prep.). Ratio 2\*CO<sub>2</sub> = Winter wheat 700 ppmv / Winter wheat 370 ppmv.

	Winter wheat, 370 ppmv	Winter wheat, 700 ppmv	Ratio 2*CO <sub>2</sub>
Total biomass above ground (g/m <sup>2</sup> )	2302	2709	1.177
Grain yield (g/m <sup>2</sup> )	1009	1206	1.195
Harvest index	0.438	0.445	1.016
Plants/m <sup>2</sup> (initial)	360	360	-
Ears /plant	1.858	2.100	1.130
Seed /ear	34.37	35.46	1.032
Grain weight (mg)	40.82	41.95	1.028

*Wageningen, growing season 1995*

Table G-3. Yield component analyses of results from spring wheat (cv. Minaret; 3 replicates) field experiments in open-top chambers at Wageningen, the Netherland in growing season 1995 under conditions of ambient (370 ppmv) and doubled (720 ppmv) atmospheric CO<sub>2</sub> concentrations and ambient (A) and ambient + 2 °C temperatures (A+2) (Source: Van Oijen et al., 1998a; 1998b). Treatments: Tr. 1= 370 ppmv, A; Tr. 2= 370 ppmv, A+2; Tr. 3= 720 ppmv, A; Tr. 4= 720 ppmv, A+2; Ratio A= Tr. 3 / Tr. 1; Ratio A+2= Tr. 4 / Tr. 2; Ratio 370= Tr. 2/Tr. 1; Ratio 720= Tr. 4 / Tr. 3

	Tr. 1	Tr. 2	Tr. 3	Tr. 4	Ratio A, CO <sub>2</sub> effect	Ratio A+2, CO <sub>2</sub> effect	Ratio 370, temp.effect	Ratio 720, temp.effect
Total biomass above ground (g/m <sup>2</sup> )	1271	985	1413	1174	1.112	1.192	0.775	0.831
Grain yield (g/m <sup>2</sup> )	624	479	694	575	1.112	1.200	0.768	0.829
Harvest index	0.491	0.486	0.491	0.490	1.000	1.008	0.990	0.998
Plants/m <sup>2</sup>	210	210	210	210	-	-	-	-
Ears /plant	2.419	2.224	2.462	2.319	1.018	1.043	0.919	0.942
Grains /ear	37.4	34.3	41.0	36.0	1.096	1.050	0.917	0.878
Grain weight (mg)	32.8	30.0	32.7	32.8	0.997	1.093	0.915	1.003



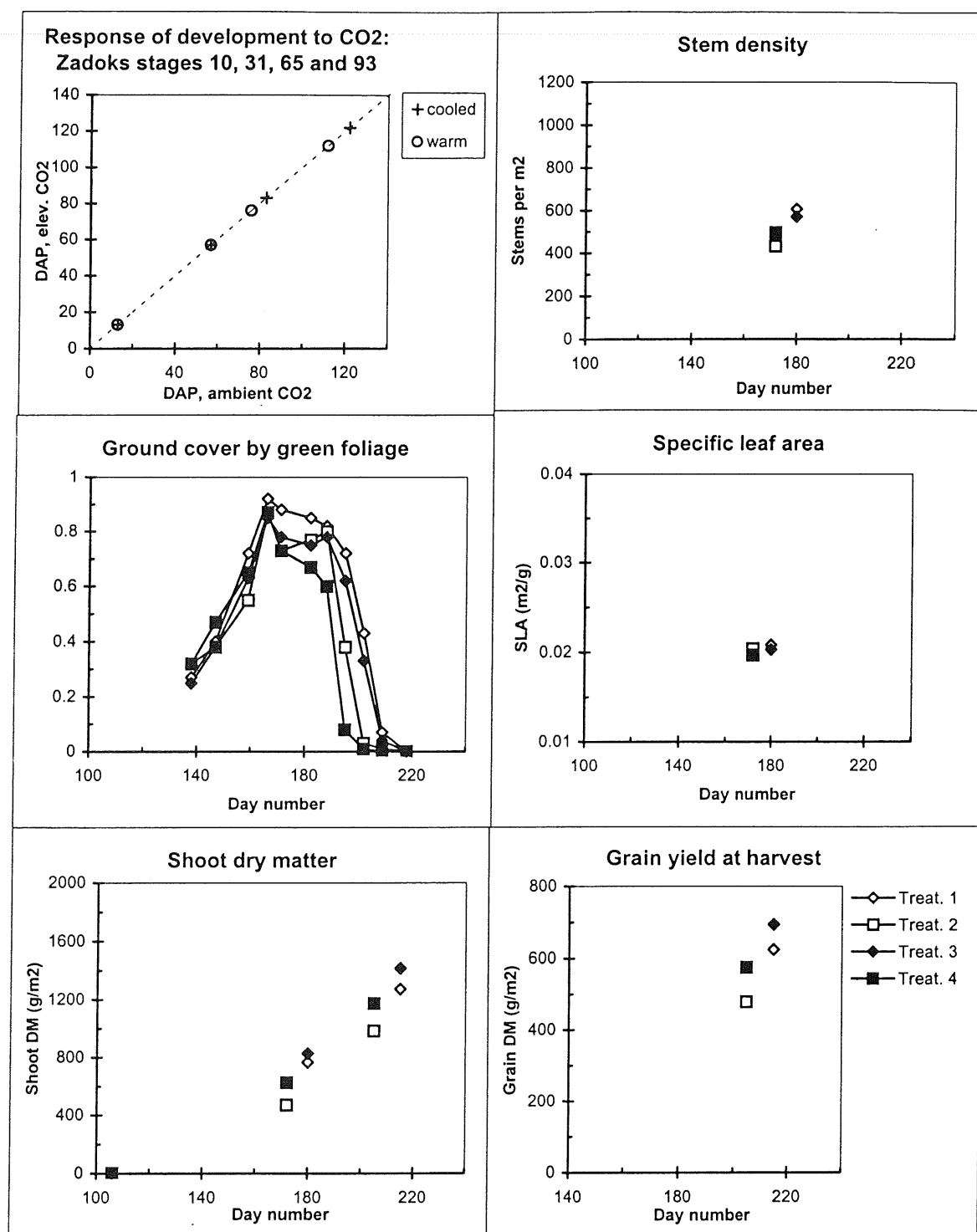


Figure G-1. Summary of results from spring wheat (cv. Minaret) field experiments in open-top chambers at Wageningen, the Netherlands in growing season 1995 under conditions of ambient (370 ppmv) and doubled (720 ppmv) atmospheric CO<sub>2</sub> concentrations, ambient (A) and ambient + 2 °C temperatures (A+2) and ample water and nutrient supply (Source: Van Oijen et al., 1998a; 1998b). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 370 ppmv, A; Treat. 2= 370 ppmv, A+2; Treat. 3= 720 ppmv, A; Treat. 4= 720 ppmv, A+2.

*Wageningen, growing season 1996*

Table G-4. Yield component analyses of results from spring wheat (cv. Minaret; 3 replicates) field experiments in open-top chambers at Wageningen, the Netherlands in growing season 1996 under conditions of ambient (380 ppmv) and doubled (750 ppmv) atmospheric CO<sub>2</sub> concentrations and ambient (A) and ambient + 2 °C temperatures (A+2) (Source: Van Oijen et al., 1998a; 1998b). Treatments: Tr. 1= 380 ppmv, A; Tr. 2= 380 ppmv, A+2; Tr. 3= 750 ppmv, A; Tr. 4= 750 ppmv, A+2; Ratio A= Tr. 3 / Tr. 1; Ratio A+2= Tr. 4 / Tr. 2; Ratio 380= Tr. 2/Tr. 1; Ratio 750= Tr. 4 / Tr. 3 .

	Tr. 1	Tr. 2	Tr. 3	Tr. 4	Ratio A, CO <sub>2</sub> effect	Ratio A+2, CO <sub>2</sub> effect	Ratio 380, temp.effect	Ratio 750, temp.effect
Total biomass above ground (g/m <sup>2</sup> )	1660	1272	1710	1553	1.030	1.221	0.766	0.908
Grain yield (g/m <sup>2</sup> )	927	721	908	822	0.980	1.140	0.778	0.905
Harvest index	0.558	0.567	0.531	0.529	0.952	0.933	1.016	0.996
Plants/m <sup>2</sup>	235	235	235	235	-	-	-	-
Ears /plant	2.306	1.838	2.285	2.021	0.991	1.100	0.797	0.884
Grains /ear	41.3	43.4	42.0	48.3	1.017	1.113	1.051	1.150
Grain weight (mg)	41.6	38.5	40.1	36.0	0.964	0.935	0.925	0.898

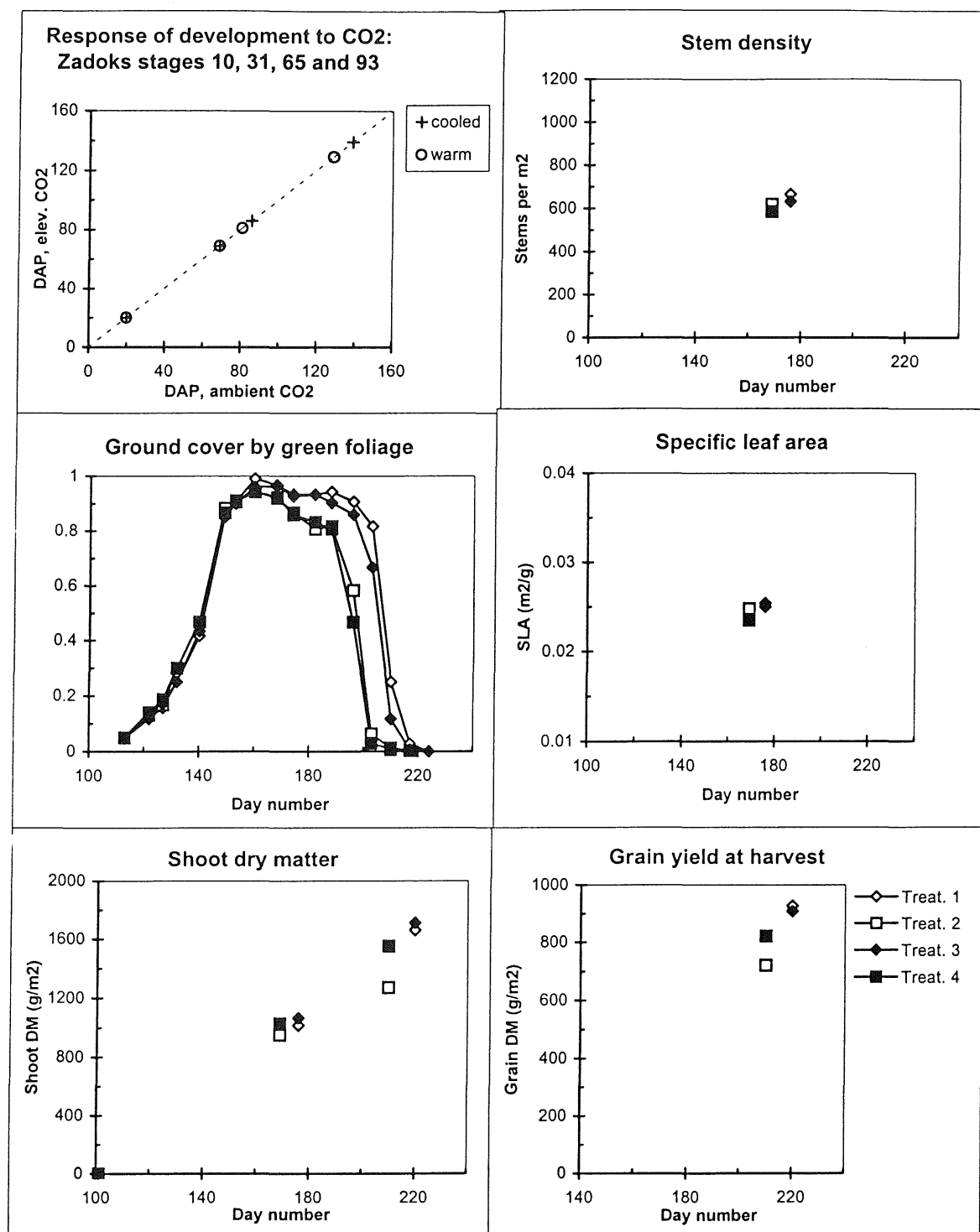


Figure G-2. Summary of results from spring wheat (cv. Minaret) field experiments in open-top chambers at Wageningen, the Netherlands in growing season 1996 under conditions of ambient (380 ppmv) and doubled (750 ppmv) atmospheric CO<sub>2</sub> concentrations, ambient (A) and ambient + 2 °C temperatures (A+2) and ample water and nutrient supply (Source: Van Oijen et al., 1998a; 1998b). Legends: DAP= days after sowing; Day number= Julian day; Treat. 1= 380 ppmv, A; Treat. 2= 380 ppmv, A+2; Treat. 3= 750 ppmv, A; Treat. 4= 750 ppmv, A+2.

## Appendix H: Summary of wheat responses to CO<sub>2</sub> enrichment and temperature change

Responses of spring wheat and winter wheat to increases in atmospheric CO<sub>2</sub> concentration are given in Table H-1. This table includes all results from experiments with CO<sub>2</sub> enrichment collected for this project, both under optimal and sub-optimal conditions. Responses to CO<sub>2</sub> enrichment are given as a percentage of the result at ambient conditions, except for the change in growth duration. Subsequently, these responses are standardized per 100 ppmv CO<sub>2</sub> increase. This assumes that the responses to CO<sub>2</sub> increase are linear, which is not completely true in all situations but will affect the result only to a limited extent.

Responses of spring wheat and winter wheat to changes in temperature are given in Table H-2. This table includes all results from experiments with temperature change collected for this project. Responses to temperature change are given as a percentage of the result at ambient conditions, except for the change in growth duration. Subsequently, these responses are standardized per 1 °C temperature rise. This assumes that the responses to temperature change are linear, which is not completely true in all situations but will affect the result only to a limited extent.

Table H-1. Summary of the response of spring wheat (SW) or winter wheat (WW) to CO<sub>2</sub> enrichment under optimal (O), water-limited (W) or nitrogen-limited (N) conditions in a number of experiments at various locations. Response is given as a percentage of the result at ambient conditions (except for the change in growth duration (Ch/Dur, in days)) with the standardized response (per 100 ppmv CO<sub>2</sub> increase) as subsequent value within brackets. Temperature change is indicated as (e.g. +1.0) if its effect is mixed up with the CO<sub>2</sub> effect and as (e.g. T+1.0) if its effect is kept separate and does not influence CO<sub>2</sub> effect.

Site Year/ Crop	Medi- um	Condi- tions	CO <sub>2</sub> increa- se (ppmv)	Temp. change (°C)	Ch/Dur Emerg. till anthesis <sup>a</sup>	Ch/Dur Anthe- sis till matur. <sup>a</sup>	Total shoot at an- thesis <sup>b</sup>	LAI at an- thesis <sup>b</sup>	Total shoot at matur.	Grain yield at matur.	Har- vest Index
<b>Arizona</b>											
1992/93 SW	field	O	180	+0.75 <sup>c</sup>	-2/85	-5/48	+30.3 (+16.8)	+4.7 (+2.6)	+8.5 (+4.7)	+14.0 (+7.8)	+5.0 (+2.8)
1992 /93 SW	field	W	180	+0.75 <sup>c</sup>	-2/84	0/42	+18.5 (+10.3)	-3.8 (-2.1)	+4.1 (+2.3)	+8.6 (+4.8)	+4.4 (+2.4)
1993/94 SW	field	O	180	+0.75 <sup>c</sup>	-4/97	+2/51	+36.9 (+20.5)	+8.2 (+4.6)	+7.1 (+3.9)	+12.0 (+6.7)	+4.7 (+2.6)
1993/94 SW	field	W	180	+0.75 <sup>c</sup>	-2/94	+1/46	+27.6 (+15.3)	+10.5 (+5.8)	+14.2 (+7.9)	+19.8 (+11.0)	+4.7 (+2.6)
1995/96 SW	field	O	200	+0.0	-2/88	0/52	+22.6 (+11.3)	+11.4 (+5.7)	-6.9 (-3.5)	-8.7 (-4.4)	-2.5 (-1.3)
1995/96 SW	field	N	200	+0.0	-1/88	+3/48	+5.8 <sup>c</sup> (+2.9)	-1.0 (-0.5)	+16.1 (+8.1)	+18.5 (+9.3)	+2.7 (+1.4)
1995/96 SW	field	O	200	+0.75 <sup>c</sup>	-7/93	-1/53	+27.7 (+13.9)	-16.2 (-8.1)	-3.1 (-1.6)	-3.6 (-1.8)	-0.1 (-0.1)
1995/96 SW	field	N	200	+0.75 <sup>c</sup>	-5/92	+7/44	+12.5 (+6.3)	-38.7 (-19.4)	-9.6 (-4.8)	-17.8 (-8.9)	-8.9 (-4.5)
<b>Florence</b>											
1997 WW	field	O	150	0.0	0	-?	+1.7? (+1.1?)	? (-1.9)	-2.8 (-1.9)	+18.9 (+12.6)	+22.3 (+14.9)

Table H-1 (continued)

Site Year/ Crop	Medi- um	Condi- tions	CO <sub>2</sub> increa- se (ppmv)	Temp. change (°C)	Ch/Dur Emerg. till anthesis <sup>a</sup>	Ch/Dur Anthe- sis till matur. <sup>a</sup>	Total shoot at an- thesis <sup>b</sup>	LAI at an- thesis <sup>b</sup>	Total shoot at matur.	Grain yield at matur.	Har- vest Index
<b>Giessen</b>											
1994 SW	pots	O	165	0.0	0	0	+34.6 (+21.0)	-10.5 (-6.4)	+29.4 (+17.8)	+23.9 (+14.5)	-4.8 (-2.9)
1994 SW	pots	O	280	0.0	0	0	+54.6 (+19.5)	+10.3 (+3.7)	+41.3 (+14.8)	+27.8 (+9.9)	-10.1 (-3.6)
1994 SW	pots	N	165	0.0	0	0	+17.8 (+10.8)	-15.5 (-9.4)	+22.7 (+13.8)	+23.1 (+14.0)	+0.6 (+0.4)
1994 SW	pots	N	280	0.0	0	0	+38.5 (+13.8)	+3.7 (+1.3)	+35.3 (+12.6)	+31.7 (+11.3)	-2.4 (-0.9)
1995 SW	pots	O	140	0.0	0	0	+10.7 (+7.6)	-3.9 (-2.8)	+8.9 (+6.4)	+0.2 (+0.1)	-8.0 (-5.7)
1995 SW	pots	O	240	0.0	0	0	+34.0 (+14.2)	+22.6 (+9.4)	+41.4 (+17.3)	+41.9 (+17.5)	+0.4 (+0.2)
1995 SW	pots	N	140	0.0	0	0	+15.1 (+10.8)	-10.2 (-7.3)	+14.4 (+10.3)	+11.5 (+8.2)	-2.3 (-1.6)
1995 SW	pots	N	240	0.0	0	0	+14.3 (+6.0)	+3.7 (+1.5)	+31.7 (+13.2)	+32.4 (+13.5)	+0.6 (+0.3)
1996 SW	pots	O	135	0.0	-1/49	?	+16.5 (+12.2)	-4.6 (-3.4)	+18.2 (+13.5)	+15.2 (+11.3)	-2.5 (-1.9)
1996 SW	pots	O	285	0.0	-1/49	?	+41.1 (+14.4)	+6.9 (+2.4)	+33.5 (+11.8)	+27.8 (+9.8)	-4.2 (-1.5)
1996 SW	pots	N	135	0.0	-1/49	?	+10.6 (+7.9)	-3.4 (-2.5)	+23.0 (+17.0)	+17.0 (+12.6)	-4.7 (-3.5)
1996 SW	pots	N	285	0.0	-1/49	?	+12.7 (+4.5)	-11.9 (-4.2)	+28.1 (+9.9)	+19.5 (+6.8)	-6.7 (-2.4)
<b>Rothamsted</b>											
1990/91 WW	pots	O	310	T+ 0.0	-3/185	+3/52	+34.3 (+11.1)	+13.1 (+4.2)	+14.4 (+4.6)	+16.0 (+5.2)	+1.5 (+0.5)
1990/91 WW	pots	O	310	T+ 2.4	+2/161	-2/62	-6.9 (-2.2)	+5.2 (+1.7)	+15.0 (+4.8)	+13.6 (+4.4)	-1.2 (-0.4)
1990/91 WW	pots	N	310	T+ 0.0	+5/176	-5/57	+13.0 (+4.2)	-7.1 (-2.3)	+10.0 (+3.2)	-12.3 (-4.0)	-20.4 (-6.6)
1991/92 WW	pots	O	290	T+ 0.0	0/216	0/55	+21.4 (+7.4)	+15.9 (+5.5)	+26.9 (+9.3)	+37.1 (+12.8)	+8.3 (+2.9)
1991/92 WW	pots	O	290	T+ 2.6	+2/206	-2/44	+12.5 (+4.3)	+27.9 (+9.6)	+26.6 (+9.2)	+41.2 (+14.2)	+11.7 (+4.0)
1993/94 WW	Pots	O	300	0.0, No Sh. <sup>d</sup>	0	0	+23.8 (+7.9)	+6.9 (+2.3)	+25.4 (+8.5)	+21.4 (+7.1)	-3.1 (-1.0)
1993/94 WW	Pots	O	300	0.0, Av. Sh. <sup>d</sup>	0	0	+18.0 (+6.0)	+6.9 (+2.3)	+14.6 (+4.9)	+16.3 (+5.4)	+1.5 (+0.5)
1993/94 WW	Pots	O	300	0.0, Max.Sh. <sup>d</sup>	0	0	? ?	? ?	+28.1 (+9.4)	+37.7 (+12.6)	+7.3 (+2.4)

Table H-1 (continued)

Site Year/ Crop	Medi- um	Condi- tions	CO <sub>2</sub> increa- se (ppmv)	Temp. change (°C)	Ch/Dur Emerg. till anthesis <sup>a</sup>	Ch/Dur Anthe- sis till matur. <sup>a</sup>	Total shoot at an- thesis <sup>b</sup>	LAI at an- thesis <sup>b</sup>	Total shoot at matur.	Grain yield at matur.	Har- vest inde
<b>Wageningen</b>											
1991 SW	Contai	O	400	0.0	?	?	?	?	+33.8 (+8.5)	+34.2 (+8.6)	+0.3 (+0.1)
1992/93 WW	Contai	O	400	0.0	?	?	?	?	+19.0 (+4.8)	-3.6 (-0.9)	-19.0 (-4.8)
1993/94 WW	Field	O	330	0.0	?	?	?	?	+17.7 (+5.4)	+19.5 (+5.9)	+1.6 (+0.5)
1995 SW	Field	O	354	T+ 0.0	0	0	+7.8 (+2.2)	-9.3 (-2.6)	+11.2 (+3.2)	+11.2 (+3.2)	0 (0.0)
1995 SW	Field	O	350	T+ 1.8	0	0	+32.6 (+9.3)	+7.1 (+2.0)	+19.2 (+5.5)	+20.0 (+5.7)	+0.8 (+0.2)
1996 SW	Field	O	377	T+ 0.0	0	0	+4.8 (+1.3)	-14.6 (-3.9)	+3.0 (+0.8)	-2.0 (-0.5)	-4.8 (-1.3)
1996 SW	Field	O	372	T+ 1.7	0	0	+8.1 (+2.2)	-15.8 (-4.2)	+22.1 (+5.9)	+14.0 (+3.8)	-6.7 (-1.8)

<sup>a</sup> Ch/Dur is the change (Ch) in growth duration (days) from emergence until anthesis and from anthesis until maturity by CO<sub>2</sub> enrichment and the growth duration (Dur, in days) at ambient atmospheric CO<sub>2</sub> concentration, respectively.

<sup>b</sup> Response was determined for identical date.

<sup>c</sup> Blowers for CO<sub>2</sub> distribution resulted in an increase in minimum temperature by roughly 1.5 °C

<sup>d</sup> Shading was or was not applied during three-weeks periods before and around anthesis depending on the shading treatment. No Sh.= no shading treatment; Av. Sh.= average result of the seven different shading treatments; Max. Sh.= shading during all three shading periods.

Table H-2. Summary of the response of spring wheat (SW) or winter wheat (WW) to temperature change under optimal (O) conditions in a number of experiments at various locations. Response is given as a percentage of the result at ambient temperatures (except for the change in growth duration (Ch/Dur, in days)) with the standardized response (per 1 °C temperature rise) as subsequent value within brackets.

Site Year/ Crop	Medi- um	Condi- tions	CO <sub>2</sub> conc. (ppmv)	Temp. change (°C)	Ch/Dur. Emerg. till an- thesis <sup>a</sup>	Ch/Dur Anthe- sis till matur. <sup>a</sup>	Total shoot at an- thesis <sup>b</sup>	LAI at an- thesis <sup>b</sup>	Total shoot at matur.	Grain yield at matur.	Har- vest Index
<b>Clermont Ferrand</b>				Tmin/ max=							
1995/96 WW	Contai- ners	O	360	10/18 <sup>c</sup>	0	+2/30	0.0	0.0	-6.0 (+1.6)	+18.0 (-4.9)	+25.8 (-7.0)
1995/96 WW	Contai- ners	O	360	20/28 <sup>c</sup>	0	-4/30	0.0	0.0	-24.7 (-3.9)	-20.7 (-3.3)	+5.4 (+0.9)
1995/96 WW	Contai- ners	O	360	10/34 <sup>c</sup>	0	-6/30	0.0	0.0	-33.6 (-5.3)	-36.3 (-5.8)	-4.1 (-0.7)
<b>Rothamsted</b>											
1990/91 WW	Pots	O	370	+2.4	-24/185	+10/52	+0.7 (+0.3)	+3.2 (+1.3)	-15.8 (-6.6)	-18.4 (-7.7)	-3.2 (-1.3)
1990/91 WW	Pots	O	680	+2.4	-19/182	+5/55	-24.8 (-10.3)	-11.6 (-4.8)	-15.4 (-6.4)	-20.1 (-8.4)	-5.7 (-2.4)
1991/92 WW	Pots	O	390	+2.6	-10/216	-11/55	-0.3 (-0.1)	-4.7 (-1.8)	-15.9 (-6.1)	-35.7 (-13.7)	-23.5 (-9.0)
1991/92 WW	Pots	O	680	+2.6	-8/216	-13/55	-5.5 (-2.1)	-0.4 (-0.2)	-16.0 (-6.2)	-33.8 (-13.0)	-21.1 (-8.1)
<b>Wageningen</b>											
1995 SW	Field	O	366	+1.8	-7/70	-3/39	-38.5 (-21.4)	-27.7 (-15.4)	-22.5 (-12.5)	-23.2 (-12.9)	-1.0 (-0.6)
1995 SW	Field	O	718	+1.8	-7/70	-3/39	-24.3 (-13.5)	-14.6 (-8.1)	-16.9 (-9.4)	-17.1 (-9.5)	-0.2 (-0.1)
1996 SW	Field	O	379	+1.7	-5/66	-5/53	-6.4 (-3.8)	-13.3 (-7.8)	-23.4 (-13.8)	-22.2 (-13.1)	+1.6 (+0.9)
1996 SW	Field	O	754	+1.7	-5/66	-5/53	-3.5 (-2.1)	-14.5 (-8.5)	-9.2 (-5.4)	-9.5 (-5.6)	-0.4 (-0.2)

<sup>a</sup> Ch/Dur is the change (Ch) in growth duration (days) from emergence until anthesis and from anthesis until maturity by temperature change and the growth duration (Dur, in days) at ambient temperatures, respectively.

<sup>b</sup> Response was determined for date of anthesis which date was advanced by temperature rise.

<sup>c</sup> From the end of anthesis until maturity the minimum and maximum temperatures were set to the indicated values. This resulted in an average change in temperature during the period of grain filling of respectively -3.7, +6.3 and +6.3 °C compared to ambient conditions.

**Appendix I.** Summary of results from spring wheat FACE experiments under ambient and elevated CO<sub>2</sub> concentrations and optimal conditions at Maricopa, Arizona, USA as observed (Obs.; Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a; 1996b) and as simulated with LINTULCC model for identical conditions. Response to CO<sub>2</sub> enrichment is given within brackets as percentage of the result at ambient conditions. Calibration of LINTULCC was carried out in three steps: Sim. A= phenology calibrated for ambient treatment and LAI simulated; Sim. B= phenology calibrated for each treatment and LAI simulated; Sim. C= phenology calibrated for each treatment and LAI as observed in experiment.

Year	Medium	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. change (°C)	T <sub>av</sub> <sup>a</sup>	Rad <sub>av</sub> <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1992/93</b>	Field	Obs.	370	-	14.8	18.6	1960	810	1023	1.97	2012	804	0.40
Idem	Idem	Obs.	550	+0.75 <sup>b</sup>	15.0	18.0	1880	695	934	2.34	2186	917	0.42
									(-9)	(+19)	(+9)	(+14)	(+5)
Idem	Idem	Sim. A	370	-	14.8	18.6	1960	810	942	2.05	1935	909	0.47
Idem	Idem	Sim. A	550	+0.75 <sup>b</sup>	15.3	18.4	1960	810	913	2.59	2362	1148	0.49
									(-3)	(+26)	(+22)	(+26)	(+4)
Idem	Idem	Sim. B	550	+0.75 <sup>b</sup>	15.0	18.0	1880	695	873	2.58	2248	972	0.43
									(-7)	(+26)	(+16)	(+7)	(-9)
Idem	Idem	Sim. C	370	-	14.8	18.6	1960	810	1023	2.06	2105	1043	0.50
Idem	Idem	Sim. C	550	+0.75 <sup>b</sup>	15.0	18.0	1880	695	934	2.58	2412	1125	0.47
									(-9)	(+25)	(+15)	(+8)	(-6)
<b>1993/94</b>	Idem	Obs.	370	-	14.8	20.1	2180	880	1034	1.86	1921	768	0.40
Idem	Idem	Obs.	550	+0.75 <sup>b</sup>	15.4	20.1	2230	930	981	2.23	2188	860	0.39
									(-5)	(+20)	(+14)	(+12)	(-2)
Idem	Idem	Sim. A	370	-	14.8	20.1	2180	880	970	2.04	1981	809	0.41
Idem	Idem	Sim. A	550	+0.75 <sup>b</sup>	15.3	19.9	2180	880	957	2.57	2462	1029	0.42
									(-1)	(+26)	(+24)	(+27)	(+2)
Idem	Idem	Sim. B	550	+0.75 <sup>b</sup>	15.4	20.1	2230	930	980	2.58	2525	1093	0.43
									(+1)	(+26)	(+27)	(+35)	(+5)
Idem	Idem	Sim. C	370	-	14.8	20.1	2180	880	1034	2.05	2117	916	0.43
Idem	Idem	Sim. C	550	+0.75 <sup>b</sup>	15.4	20.1	2230	930	981	2.58	2534	1120	0.44
									(-5)	(+26)	(+20)	(+22)	(+2)
<b>1995/96</b>	Idem	Obs.	370	-	16.2	20.6	2320	1040	1005	1.77	1776	641	0.36
Idem	Idem	Obs.	370	+0.75 <sup>b</sup>	16.7	20.4	2320	1040	928	1.99	1846	677	0.37
Idem	Idem	Obs.	570	+0.75 <sup>b</sup>	16.5	20.2	2280	1000	921	2.30	2121	618	0.29
									(-8, -1) <sup>c</sup>	(+30, +16) <sup>c</sup>	(+19, +15) <sup>c</sup>	(-4, -9) <sup>c</sup>	(-19, -22) <sup>c</sup>
Idem	Idem	Sim. A	370	-	16.2	20.6	2320	1040	982	2.06	2019	940	0.47
Idem	Idem	Sim. A	370	+0.75 <sup>b</sup>	16.7	20.4	2320	1040	928	2.07	1922	913	0.48
Idem	Idem	Sim. A	570	+0.75 <sup>b</sup>	16.7	20.4	2320	1040	969	2.66	2574	1237	0.48
									(-1, +4) <sup>c</sup>	(+29, +29) <sup>c</sup>	(+27, +34) <sup>c</sup>	(+32, +35) <sup>c</sup>	(+2, 0) <sup>c</sup>
Idem	Idem	Sim. B	570	+0.75 <sup>b</sup>	16.5	20.2	2280	1000	954	2.65	2528	1191	0.47
									(-3, +3) <sup>c</sup>	(+29, +28) <sup>c</sup>	(+25, +32) <sup>c</sup>	(+27, +30) <sup>c</sup>	(0, -2) <sup>c</sup>
Idem	Idem	Sim. C	370	-	16.2	20.6	2320	1040	1005	2.05	2062	940	0.46
Idem	Idem	Sim. C	370	+0.75 <sup>b</sup>	16.7	20.4	2320	1040	928	2.07	1922	915	0.48
Idem	Idem	Sim. C	570	+0.75 <sup>b</sup>	16.5	20.2	2280	1000	921	2.65	2437	1153	0.47
									(-8, -1) <sup>c</sup>	(+29, +28) <sup>c</sup>	(+18, +27) <sup>c</sup>	(+23, +26) <sup>c</sup>	(+2, -2) <sup>c</sup>



## Appendix I (continued)

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<sup>a</sup> T-av= average temperature from crop emergence to maturity ( $^{\circ}\text{C}$ ).

Rad-av= average daily amount of solar radiation from crop emergence to maturity ( $\text{MJ}/\text{m}^2/\text{d}$ ).

Tsum Total= cumulative temperature sum (above base temperature of  $0^{\circ}\text{C}$ ) from crop emergence to maturity ( $^{\circ}\text{C.d}$ ).

Tsum Grain= cumulative temperature sum (above base temperature of  $0^{\circ}\text{C}$ ) from start of grain filling to maturity ( $^{\circ}\text{C.d}$ ).

RI= cumulative intercepted photosynthetically active radiation (PAR) from crop emergence to maturity ( $\text{MJ}/\text{m}^2$ ).

RUE= radiation use efficiency, i.e.  $\text{TAB} / \text{RI}$  ( $\text{g dry matter}/\text{MJ PAR}$ ).

TAB= maximum total above-ground biomass ( $\text{g dry matter}/\text{m}^2$ ); in experiments maximum occurs before maturity.

GR= grain yield ( $\text{g dry matter}/\text{m}^2$ ) at maturity.

HI= harvest index, i.e.  $\text{GR}/\text{TAB}$  ( $\text{g dry matter}/\text{g dry matter}$ ).

<sup>b</sup> Blowers for  $\text{CO}_2$  distribution resulted in an increase in minimum temperature by roughly  $1.5^{\circ}\text{C}$ . This increase is taken into account in simulations.

<sup>c</sup> Response to  $\text{CO}_2$  enrichment is first calculated from results at ambient conditions without blowers and next from results at ambient conditions with blowers (see <sup>b</sup> for effect of blowers).

**Appendix J.** Summary of results from winter wheat experiments in transparent tunnels under different temperature regimes (from the end of anthesis) and optimal conditions at Clermont Ferrand, France as observed (Obs.; Source: Triboi, pers. comm.) and as simulated with LINTULCC model for identical conditions. Response to temperature change is given within brackets as percentage of the result at ambient conditions. Calibration of LINTULCC was carried out in two steps: Sim. A= phenology calibrated for treatment with Tmin/Tmax=10/18 and LAI simulated; Sim. C= phenology calibrated for treatment with Tmin/Tmax=10/18 and LAI simulated but with a stronger decrease in LAI near maturity in treatments with Tmin/Tmax= 20/28 and 10/34.

Year	Medium	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. T- chan- av <sup>a</sup> ge(°C)	T- av <sup>a</sup>	Rad- av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
				Tmin/ Tmax=									
1995/96	Containers	Obs.	360	Ambient <sup>b</sup>	9.9	11.5	1810	820	752 <sup>c</sup>	2.43	1824	849	0.47
Idem	Idem	Obs.	Idem	10/18 <sup>b</sup>	9.5	11.4	1810	820	784 <sup>c</sup> (+4)	2.18 (-10)	1712 (-6)	998 (+18)	0.58 (+23)
Idem	Idem	Obs.	Idem	20/28 <sup>b</sup>	10.3	11.5	1810	820	692 <sup>c</sup> (-8)	1.91 (-22)	1324 (-27)	645 (-24)	0.49 (+4)
Idem	Idem	Obs.	Idem	10/34 <sup>b</sup>	10.3	11.5	1810	820	692 <sup>c</sup> (-8)	1.71 (-30)	1181 (-35)	525 (-38)	0.44 (-6)
Idem	Idem	Sim. A	Idem	Ambient <sup>b</sup>	9.9	11.5	1810	820	752	2.39	1795	886	0.49
Idem	Idem	Sim. A	Idem	10/18 <sup>b</sup>	9.5	11.4	1810	820	784 (+4)	2.38 (0)	1866 (+4)	957 (+8)	0.51 (+4)
Idem	Idem	Sim. A	Idem	20/28 <sup>b</sup>	10.3	11.5	1810	820	710 (-6)	2.35 (-2)	1665 (-7)	756 (-15)	0.45 (-8)
Idem	Idem	Sim. A	Idem	10/34 <sup>b</sup>	10.3	11.5	1810	820	710 (-6)	2.35 (-2)	1669 (-7)	760 (-14)	0.46 (-6)
Idem	Idem	Sim. A	Idem	Ambient <sup>b</sup>	9.9	11.5	1810	820	752	2.39	1795	886	0.49
Idem	Idem	Sim. C	Idem	20/28 <sup>b</sup>	10.3	11.5	1810	820	692 (-8)	2.32 (-3)	1607 (-10)	698 (-21)	0.43 (-12)
Idem	Idem	Sim. C	Idem	10/34 <sup>b</sup>	10.3	11.5	1810	820	692 (-8)	2.33 (-3)	1611 (-10)	702 (-21)	0.44 (-10)

<sup>a</sup> T-av= average temperature from January 1 to maturity (°C).

Rad-av= average daily amount of solar radiation from January 1 to maturity (MJ/m<sup>2</sup>/d).

Tsum Total= cumulative temperature sum (above base temperature of 0 °C) from January 1 to maturity (°C.d).

Tsum Grain= cumulative temperature sum (above base temperature of 0 °C) from start of grain filling to maturity (°C.d).

RI= cumulative intercepted photosynthetically active radiation (PAR) from January 1 to maturity (MJ/m<sup>2</sup>).

RUE= radiation use efficiency, i.e. TAB / RI (g dry matter/MJ PAR).

TAB= total above-ground biomass (g dry matter/m<sup>2</sup>) at maturity.

GR= grain yield (g dry matter/m<sup>2</sup>) at maturity.

HI= harvest index, i.e. GR/TAB (g dry matter/g dry matter).

<sup>b</sup> From the end of anthesis until maturity the minimum and maximum temperatures were set to the indicated values. This resulted in an average change in temperature during the period of grain filling of respectively -3.7, +6.3 and +6.3 °C compared to ambient conditions.

<sup>c</sup> Radiation intercepted as calculated with model calibrated on the basis of observed leaf weights.

**Appendix K.** Summary of results from winter wheat experiments under ambient and elevated (with Mini FACE system) CO<sub>2</sub> concentrations and optimal conditions at Florence, Italy as observed (Obs.; Source: Miglietta, pers. comm.) and as simulated with LINTULCC model for identical conditions. Response to CO<sub>2</sub> enrichment is given within brackets as percentage of the result at ambient conditions. Calibration of LINTULCC was carried out in two steps: Sim. A= phenology calibrated for ambient treatment and LAI simulated; Sim. C= phenology calibrated for ambient treatment and LAI identical for both treatments .

Year	Medium	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. change (°C)	T-av <sup>a</sup>	Rad-av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
1997	Field	Obs.	350	-	10.1	16.8? <sup>c</sup>	1350	550	672 <sup>b</sup>	1.96? <sup>b</sup>	1316	482	0.37
Idem	Idem	Obs.	500	-	10.1	16.8? <sup>c</sup>	1350	550	672 <sup>b</sup> (0)	1.90? <sup>b</sup> (-3)	1279 (-3)	573 (+19)	0.45 (+22)
Idem	Idem	Sim. A	350	-	10.1	16.8? <sup>c</sup>	1350	550	674? <sup>c</sup>	1.90	1282	497	0.39
Idem	Idem	Sim. A	500	-	10.1	16.8? <sup>c</sup>	1350	550	716? <sup>c</sup> (+6)	2.31 (+22)	1654 (+29)	667 (+34)	0.40 (+3)
Idem	Idem	Sim. C	350	-	10.1	16.8? <sup>c</sup>	1350	550	672? <sup>c</sup>	1.90	1277	491	0.38
Idem	Idem	Sim. C	500	-	10.1	16.8? <sup>c</sup>	1350	550	672? <sup>c</sup> (0)	2.30 (+21)	1545 (+21)	603 (+23)	0.39 (+3)

<sup>a</sup> T-av= average temperature from crop emergence to maturity (°C).

Rad-av= average daily amount of solar radiation from crop emergence to maturity (MJ/m<sup>2</sup>/d).

Tsum Total= cumulative temperature sum (above base temperature of 0 °C) from crop emergence to maturity (°C.d) .

Tsum Grain= cumulative temperature sum (above base temperature of 0 °C) from start of grain filling to maturity (°C.d).

RI= cumulative intercepted photosynthetically active radiation (PAR) from crop emergence to maturity (MJ/m<sup>2</sup>).

RUE= radiation use efficiency, i.e. TAB / RI (g dry matter/MJ PAR).

TAB= total above-ground biomass (g dry matter/m<sup>2</sup>) at maturity.

GR= grain yield (g dry matter/m<sup>2</sup>) at maturity.

HI= harvest index, i.e. GR/TAB (g dry matter/g dry matter).

<sup>b</sup> Radiation intercepted based on simulation with LINTULCC model, as observed values for LAI or light interception are missing.

<sup>c</sup> Radiation data are not reliable.

**Appendix L.** Summary of results from spring wheat experiments in open-top chambers under ambient and elevated CO<sub>2</sub> concentrations and optimal conditions at Giessen, Germany as observed (Obs.; Source: Fangmeier et al., 1996; 1997a; 1997b) and as simulated with LINTULCC model for identical conditions. Response to CO<sub>2</sub> enrichment is given within brackets as percentage of the result at ambient conditions. Calibration of LINTULCC was carried out in two steps: Sim. A= phenology calibrated for ambient treatment and LAI simulated (calibrated for ambient treatment); Sim. C= phenology calibrated for ambient treatment (i.e. no CO<sub>2</sub> effect on phenology) and in year 1994 LAI simulated after calibration for different CO<sub>2</sub> treatments and in 1995 and 1996 LAI as observed in experiments .

Year	Medium	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. change (°C)	T <sub>av</sub> <sup>a</sup>	Rad <sub>av</sub> <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1994</b>	Pots	Obs.	360	-	24.0	17.1	2100	1100	374 <sup>b</sup>	2.61	976	489	0.50
Idem	Idem	Obs.	525	-	24.0	17.1	2100	1100	358 <sup>b</sup>	3.53	1263	606	0.48
									(-4)	(+35)	(+29)	(+24)	(-4)
Idem	Idem	Obs.	640	-	24.0	17.1	2100	1100	372 <sup>b</sup>	3.71	1379	625	0.45
									(-1)	(+42)	(+41)	(+28)	(-10)
Idem	Idem	Sim. A	360	-	24.0	17.1	2100	1100	374	2.76	1033	469	0.45
Idem	Idem	Sim. A	525	-	24.0	17.1	2100	1100	408	3.47	1417	667	0.47
									(+9)	(+26)	(+37)	(+42)	(+4)
Idem	Idem	Sim. A	640	-	24.0	17.1	2100	1100	423	3.81	1613	777	0.48
									(+13)	(+38)	(+56)	(+66)	(+7)
Idem	Idem	Sim. C	525	-	24.0	17.1	2100	1100	358	3.46	1238	563	0.45
									(-4)	(+25)	(+20)	(+20)	(0)
Idem	Idem	Sim. C	640	-	24.0	17.1	2100	1100	372	3.79	1411	656	0.46
									(-1)	(+37)	(+37)	(+40)	(+2)
<b>1995</b>	Idem	Obs.	400	-	21.9	14.1	2100	1100	286	3.09	884	418	0.47
Idem	Idem	Obs.	540	-	21.9	14.1	2100	1100	277	3.48	963	419	0.44
									(-3)	(+13)	(+9)	(0)	(-6)
Idem	Idem	Obs.	640	-	21.9	14.1	2100	1100	291	4.30	1250	593	0.47
									(+2)	(+39)	(+41)	(+42)	(0)
Idem	Idem	Sim. A	400	-	21.9	14.1	2100	1100	311	3.21	999	409	0.41
Idem	Idem	Sim. A	540	-	21.9	14.1	2100	1100	330	3.76	1240	518	0.42
									(+6)	(+17)	(+24)	(+27)	(+2)
Idem	Idem	Sim. A	640	-	21.9	14.1	2100	1100	337	3.97	1338	574	0.43
									(+8)	(+24)	(+34)	(+40)	(+5)
Idem	Idem	Sim. C	400	-	21.9	14.1	2100	1100	286	3.09	883	255	0.29
Idem	Idem	Sim. C	540	-	21.9	14.1	2100	1100	277	3.69	1022	349	0.34
									(-3)	(+19)	(+16)	(+37)	(+17)
Idem	Idem	Sim. C	640	-	21.9	14.1	2100	1100	291	3.89	1131	401	0.35
									(+2)	(+26)	(+28)	(+57)	(+21)

# Appendix L (continued)

Year	Medium	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. change (°C)	T-av <sup>a</sup>	Rad-av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
1996	Pots	Obs.	380	-	19.3	11.0	1840	1040	262	3.35	877	486	0.55
Idem	Idem	Obs.	515	-	19.3	11.0	1840	1040	246	4.22	1037	560	0.54
									(-6)	(+26)	(+18)	(+15)	(-2)
Idem	Idem	Obs.	665	-	19.3	11.0	1840	1040	255	4.59	1171	621	0.53
									(-3)	(+37)	(+34)	(+28)	(-4)
Idem	Idem	Sim. A	380	-	19.3	11.0	1840	1040	270	3.31	894	483	0.54
Idem	Idem	Sim. A	515	-	19.3	11.0	1840	1040	286	3.84	1099	603	0.55
									(+6)	(+16)	(+23)	(+25)	(+2)
Idem	Idem	Sim. A	665	-	19.3	11.0	1840	1040	294	4.31	1266	713	0.56
									(+9)	(+30)	(+42)	(+48)	(+4)
Idem	Idem	Sim. C	380	-	19.3	11.0	1840	1040	262	3.24	849	411	0.48
Idem	Idem	Sim. C	515	-	19.3	11.0	1840	1040	246	3.75	922	433	0.47
									(-6)	(+16)	(+9)	(+5)	(-2)
Idem	Idem	Sim. C	665	-	19.3	11.0	1840	1040	255	4.14	1056	482	0.46
									(-3)	(+28)	(+24)	(+17)	(-4)
Idem	Idem	Sim. A	380	-	19.3	11.0	1840	1040	270	3.31	894	483	0.54
Idem	Idem	Sim. D <sup>c</sup>	515	-	19.3	11.0	1840	1040	263	3.83	1006	540	0.54
									(-3)	(+16)	(+13)	(+12)	(0)
Idem	Idem	Sim. D <sup>c</sup>	665	-	19.3	11.0	1840	1040	270	4.29	1159	639	0.55
									(0)	(+30)	(+30)	(+32)	(2)

<sup>a</sup> T-av= average temperature from crop emergence to maturity (°C).

Rad-av= average daily amount of solar radiation from crop emergence to maturity (MJ/m<sup>2</sup>/d).

Tsum Total= cumulative temperature sum (above base temperature of 0 °C) from crop emergence to maturity (°C.d).

Tsum Grain= cumulative temperature sum (above base temperature of 0 °C) from start of grain filling to maturity (°C.d).

RI= cumulative intercepted photosynthetically active radiation (PAR) from crop emergence to maturity (MJ/m<sup>2</sup>).

RUE= radiation use efficiency, i.e. TAB / RI (g dry matter/MJ PAR).

TAB= total above-ground biomass (g dry matter/m<sup>2</sup>) at maturity.

GR= grain yield (g dry matter/m<sup>2</sup>) at maturity.

HI= harvest index, i.e. GR/TAB (g dry matter/g dry matter).

<sup>b</sup> Intercepted radiation was derived from simulations with LINTULCC model that was calibrated for observed LAI values.

<sup>c</sup> Sim. D is similar to Sim. A except for LAI for elevated CO<sub>2</sub> treatments which was simulated after calibration for LAI data observed in the 665 ppm CO<sub>2</sub> treatment (in Sim. A LAI calibrated for data from ambient treatment). In Sim. D leaf senescence near maturity was less severe than that in the observed LAI data.

## Appendix M: Simulated versus experimental results from Rothamsted

Responses to CO<sub>2</sub> enrichment as observed in the winter wheat experiments at Rothamsted and as simulated with the crop growth model, are given in Table M-1 and the responses to temperature change are given in Table M-2.

Table M-1. Summary of results from winter wheat experiments in pots in a greenhouse under ambient and elevated CO<sub>2</sub> concentrations and optimal conditions at Rothamsted, U.K. as observed (Obs.; Source: Delgado et al., 1994; Mitchell et al., 1993; Mitchell et al., 1995; Mitchell et al., 1996) and as simulated with LINTULCC model for identical conditions. Response to CO<sub>2</sub> enrichment is given within brackets as percentage of the result at ambient conditions. Calibration of LINTULCC was carried out in two steps: Sim. A= phenology calibrated for ambient CO<sub>2</sub> treatment and LAI simulated; Sim. C= phenology calibrated for ambient CO<sub>2</sub> treatment and LAI as observed in experiment.

Year, Treatment	Medi- um	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. change (°C)	T- chan- av <sup>a</sup>	Rad- av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1990/91,</b>													
<b>Cool</b>	Pots	Obs.	370	-	11.1	10.4	2380	870	824	4.15	3420	1173	0.34
Idem	Idem	Obs.	680	-	11.1	10.4	2380	870	844	4.64	3914	1361	0.35
									(+2)	(+12)	(+14)	(+16)	(+3)
Idem	Idem	Sim. A	370	-	11.1	10.4	2380	850	856	4.20	3597	1174	0.33
Idem	Idem	Sim. A	680	-	11.1	10.4	2380	850	893	5.12	4574	1556	0.34
									(+4)	(+22)	(+27)	(+33)	(+3)
Idem	Idem	Sim. C	370	-	11.1	10.4	2380	870	824	4.20	3457	1097	0.32
Idem	Idem	Sim. C	680	-	11.1	10.4	2380	870	844	5.09	4299	1370	0.32
									(+2)	(+21)	(+24)	(+25)	(0)
<b>1990/91,</b>													
<b>Warm</b>	Idem	Obs.	370	+2.4	13.0	10.1	2600	850	695	4.14	2879	957	0.33
Idem	Idem	Obs.	680	+2.4	13.0	10.1	2600	850	714	4.64	3310	1087	0.33
									(+3)	(+12)	(+15)	(+14)	(0)
Idem	Idem	Sim. A	370	+2.4	13.0	10.1	2600	850	755	4.33	3266	937	0.29
Idem	Idem	Sim. A	680	+2.4	13.0	10.1	2600	850	797	5.28	4212	1281	0.30
									(+6)	(+22)	(+29)	(+37)	(+3)
Idem	Idem	Sim. C	370	+2.4	13.0	10.1	2600	850	695	4.30	2990	633	0.21
Idem	Idem	Sim. C	680	+2.4	13.0	10.1	2600	850	714	5.24	3740	878	0.23
									(+3)	(+22)	(+25)	(+39)	(+10)
<b>1991/92,</b>													
<b>Cool</b>	Pots	Obs.	390	-	12.1	9.0	2610	920	736	3.60	2646	800	0.30
Idem	Idem	Obs.	680	-	12.1	9.0	2610	920	766	4.38	3357	1097	0.33
									(+4)	(+22)	(+27)	(+37)	(+10)
Idem	Idem	Sim. A	390	-	12.1	9.0	2610	920	735	4.44	3261	857	0.26
Idem	Idem	Sim. A	680	-	12.1	9.0	2610	920	773	5.30	4095	1145	0.28
									(+5)	(+19)	(+26)	(+34)	(+8)
Idem	Idem	Sim. C	390	-	12.1	9.0	2610	920	736	4.44	3268	850	0.26
Idem	Idem	Sim. C	680	-	12.1	9.0	2610	920	766	5.29	4052	1106	0.27
									(+4)	(+19)	(+24)	(+30)	(+4)

**Table M-1 (continued)**

Year, Treatment	Medi- um	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. chan- ge(°C)	T- av <sup>a</sup>	Rad- av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1991/92,</b>													
<b>Warm</b>	Idem	Obs.	390	+2.6	14.0	8.9	2740	910	632	3.52	2226	514	0.23
Idem	Idem	Obs.	680	+2.6	14.0	8.9	2740	910	669	4.21	2819	726	0.26
									(+6)	(+20)	(+27)	(+41)	(+13)
Idem	Idem	Sim. A	390	+2.6	14.0	8.9	2740	910	617	4.64	2863	719	0.25
Idem	Idem	Sim. A	680	+2.6	14.0	8.9	2740	910	654	5.52	3613	980	0.27
									(+6)	(+19)	(+26)	(+36)	(+8)
Idem	Idem	Sim. C	390	+2.6	14.0	8.9	2740	910	632	4.63	2925	730	0.25
Idem	Idem	Sim. C	680	+2.6	14.0	8.9	2740	910	669	5.51	3689	1035	0.28
									(+6)	(+19)	(+26)	(+42)	(+12)
<b>1993/94,</b>													
<b>No</b>													
<b>Shading</b>	Pots	Obs.	375	-	10.3	6.6	2180	830	527? <sup>b</sup>	3.62	1907	612	0.32
Idem	Idem	Obs.	675	-	10.3	6.7	2180	830	563? <sup>b</sup>	4.25	2392	743	0.31
									(+7?)	(+17)	(+25)	(+21)	(-3)
Idem	Idem	Sim. A	375	-	10.3	6.6	2180	830	527	4.48	2361	703	0.30
Idem	Idem	Sim. A	675	-	10.3	6.7	2180	830	563	5.35	3014	942	0.31
									(+7)	(+19)	(+28)	(+34)	(+3)
<b>1993/94,</b>													
<b>Sha-</b>													
<b>ding 1<sup>c</sup></b>	Idem	Obs.	375	-	10.3	6.1	2180	830	478? <sup>b</sup>	3.52	1682	487	0.29
Idem	Idem	Obs.	675	-	10.2	6.2	2180	830	513? <sup>b</sup>	4.10	2102	525	0.25
									(+7?)	(+16)	(+25)	(+8)	(-14)
Idem	Idem	Sim. A	375	-	10.3	6.1	2180	830	478	4.56	2182	659	0.30
Idem	Idem	Sim. A	675	-	10.2	6.2	2180	830	513	5.43	2787	895	0.32
									(+7)	(+19)	(+28)	(+36)	(+7)
<b>1993/94,</b>													
<b>Sha-</b>													
<b>ding 2<sup>c</sup></b>	Idem	Obs.	375	-	10.3	5.8	2180	830	439? <sup>b</sup>	3.53	1550	389	0.25
Idem	Idem	Obs.	675	-	10.2	5.8	2180	830	466? <sup>b</sup>	3.54	1650	410	0.25
									(+6?)	(0)	(+6)	(+5)	(0)
Idem	Idem	Sim. A	375	-	10.3	5.8	2180	830	439	4.63	2032	644	0.32
Idem	Idem	Sim. A	675	-	10.2	5.8	2180	830	466	5.52	2570	874	0.34
									(+6)	(+19)	(+26)	(+36)	(+6)

- <sup>a</sup> T-av= average temperature from January 1 (in season 1991/1992 from December 16) to maturity (°C).  
Rad-av= average daily amount of solar radiation from January 1 (in season 1991/92 from December 16) to maturity (MJ/m<sup>2</sup>/d).  
Tsum Total= cumulative temperature sum (above base temperature of 0 °C) from January 1 (in season 1991/1992 from December 16) to maturity (°C.d).  
Tsum Grain= cumulative temperature sum (above base temperature of 0 °C) from start of grain filling to maturity (°C.d).  
RI= cumulative intercepted photosynthetically active radiation (PAR) from January 1 (in season 1991/1992 from December 16) to maturity (MJ/m<sup>2</sup>).  
RUE= radiation use efficiency, i.e. TAB / RI (g dry matter/MJ PAR).  
TAB= total above-ground biomass (g dry matter/m<sup>2</sup>) at maturity.  
GR= grain yield (g dry matter/m<sup>2</sup>) at maturity.  
HI= harvest index, i.e. GR/TAB (g dry matter/g dry matter).
- <sup>b</sup> Simulated time course of LAI, calibrated on the basis of few observed LAI data, was used as an observed time course of LAI was not available.
- <sup>c</sup> Shading 1= 17 days of shading around anthesis; Shading 2= 17 days of shading around anthesis and 21 days of shading at 40 days before anthesis.

Table M-2. Summary of results from winter wheat experiments in a greenhouse at ambient and increased temperatures and optimal conditions at Rothamsted, U.K. both at ambient and doubled CO<sub>2</sub> concentration (1\*CO<sub>2</sub>/2\*CO<sub>2</sub>) as observed (Obs.; Source: Delgado et al., 1994; Mitchell et al., 1993; Mitchell et al., 1995) and as simulated with LINTULCC model for identical conditions. Response to temperature change is given within brackets as percentage of the result at ambient temperatures. Calibration of LINTULCC was carried out in two steps: Sim. A= phenology calibrated for ambient CO<sub>2</sub> treatment and LAI simulated; Sim. C= phenology calibrated for ambient CO<sub>2</sub> treatment and LAI as observed in experiment.

Year, Treatment	Medium	Observed or Simulat.	CO <sub>2</sub> Conc. (ppmv)	Temp. change (°C)	T <sub>av</sub> <sup>a</sup>	Rad <sub>av</sub> <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1990/91, 1*CO<sub>2</sub></b>													
Cool	Pots	Obs.	370	-	11.1	10.4	2380	870	824	4.15	3420	1173	0.34
Warm	Idem	Obs.	370	+2.4	13.0	10.1	2600	850	695	4.14	2879	957	0.33
									(-16)	(0)	(-16)	(-18)	(-3)
Cool	Idem	Sim. A	370	-	11.1	10.4	2380	850	856	4.20	3597	1174	0.33
Warm	Idem	Sim. A	370	+2.4	13.0	10.1	2600	850	755	4.33	3266	937	0.29
									(-12)	(+3)	(-9)	(-20)	(-12)
Cool	Idem	Sim. C	370	-	11.1	10.4	2380	870	824	4.20	3457	1097	0.32
Warm	Idem	Sim. C	370	+2.4	13.0	10.1	2600	850	695	4.30	2990	633	0.21
									(-16)	(+2)	(-14)	(-42)	(-34)
<b>1990/91, 2*CO<sub>2</sub></b>													
Cool	Idem	Obs.	680	-	11.1	10.4	2380	870	844	4.64	3914	1361	0.35
Warm	Idem	Obs.	680	+2.4	13.0	10.1	2600	850	714	4.64	3310	1087	0.33
									(-15)	(0)	(-15)	(-20)	(-6)
Cool	Idem	Sim. A	680	-	11.1	10.4	2380	850	893	5.12	4574	1556	0.34
Warm	Idem	Sim. A	680	+2.4	13.0	10.1	2600	850	797	5.28	4212	1281	0.30
									(-11)	(+3)	(-8)	(-18)	(-12)
Cool	Idem	Sim. C	680	-	11.1	10.4	2380	870	844	5.09	4299	1370	0.32
Warm	Idem	Sim. C	680	+2.4	13.0	10.1	2600	850	714	5.24	3740	878	0.23
									(-15)	(+3)	(-13)	(-36)	(-28)
<b>1991/92, 1*CO<sub>2</sub></b>													
Cool	Pots	Obs.	390	-	12.1	9.0	2610	920	736	3.60	2646	800	0.30
Warm	Idem	Obs.	390	+2.6	14.0	8.9	2740	910	632	3.52	2226	514	0.23
									(-14)	(-2)	(-16)	(-36)	(-23)
Cool	Idem	Sim. A	390	-	12.1	9.0	2610	920	735	4.44	3261	857	0.26
Warm	Idem	Sim. A	390	+2.6	14.0	8.9	2740	910	617	4.64	2863	719	0.25
									(-16)	(+5)	(-12)	(-16)	(-4)
Cool	Idem	Sim. C	390	-	12.1	9.0	2610	920	736	4.44	3268	850	0.26
Warm	Idem	Sim. C	390	+2.6	14.0	8.9	2740	910	632	4.63	2925	730	0.25
									(-14)	(+4)	(-10)	(-14)	(-4)
<b>1991/92, 2*CO<sub>2</sub></b>													
Cool	Idem	Obs.	680	-	12.1	9.0	2610	920	766	4.38	3357	1097	0.33
Warm	Idem	Obs.	680	+2.6	14.0	8.9	2740	910	669	4.21	2819	726	0.26
									(-13)	(-4)	(-16)	(-34)	(-21)
Cool	Idem	Sim. A	680	-	12.1	9.0	2610	920	773	5.30	4095	1145	0.28
Warm	Idem	Sim. A	680	+2.6	14.0	8.9	2740	910	654	5.52	3613	980	0.27
									(-15)	(+4)	(-12)	(-14)	(-4)
Cool	Idem	Sim. C	680	-	12.1	9.0	2610	920	766	5.29	4052	1106	0.27
Warm	Idem	Sim. C	680	+2.6	14.0	8.9	2740	910	669	5.51	3689	1035	0.28
									(-13)	(+4)	(-9)	(-6)	(+4)



Table M-2 (continued)

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<sup>a</sup> T-av= average temperature from January 1 (in season 1991/1992 from December 16) to maturity ( $^{\circ}\text{C}$ ).  
 Rad-av= average daily amount of solar radiation from January 1 (in season 1991/92 from December 16) to maturity ( $\text{MJ}/\text{m}^2/\text{d}$ ).  
 Tsum Total= cumulative temperature sum (above base temperature of  $0^{\circ}\text{C}$ ) from January 1 (in season 1991/1992 from December 16) to maturity ( $^{\circ}\text{C.d}$ ).  
 Tsum Grain= cumulative temperature sum (above base temperature of  $0^{\circ}\text{C}$ ) from start of grain filling to maturity ( $^{\circ}\text{C.d}$ ).  
 RI= cumulative intercepted photosynthetically active radiation (PAR) from January 1 (in season 1991/1992 from December 16) to maturity ( $\text{MJ}/\text{m}^2$ ).  
 RUE= radiation use efficiency, i.e. TAB / RI (g dry matter/MJ PAR).  
 TAB= total above-ground biomass (g dry matter/ $\text{m}^2$ ) at maturity.  
 GR= grain yield (g dry matter/ $\text{m}^2$ ) at maturity.  
 HI= harvest index, i.e. GR/TAB (g dry matter/g dry matter).

## Appendix N: Simulated versus experimental results from Wageningen

Responses to CO<sub>2</sub> enrichment as observed in the spring wheat experiments at Wageningen and as simulated with the crop growth model, are given in Table N-1 and the responses to temperature change are given in Table N-2.

Table N-1. Summary of results from spring wheat experiments in open-top chambers under ambient and elevated CO<sub>2</sub> concentrations and optimal conditions at Wageningen, the Netherlands as observed (Obs.; Source: Van Oijen et al., 1998a; 1998b) and as simulated with LINTULCC model for identical conditions. Response to CO<sub>2</sub> enrichment is given within brackets as percentage of the result at ambient conditions. Calibration of LINTULCC was carried out in three steps: Sim. A= phenology calibrated for ambient treatment and light interception simulated; Sim. B= phenology calibrated for each treatment and light interception simulated; Sim. C= phenology calibrated for each treatment and light interception as observed in experiment.

Year, Treatment	Medium	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. change (°C)	T- av <sup>a</sup>	Rad- av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1995,</b>													
<b>Cool</b>	Field	Obs.	366	-	16.0	14.8	1740	810	384	3.31	1271	624	0.49
Idem	Idem	Obs.	720	-	16.0	14.8	1740	810	342	4.13	1413	694	0.49
									(-11)	(+25)	(+11)	(+11)	(0)
Idem	Idem	Sim. A	366	-	16.0	14.8	1740	810	395	3.19	1259	618	0.49
Idem	Idem	Sim. A	720	-	16.0	14.8	1740	810	454	4.27	1940	989	0.51
									(+15)	(+34)	(+54)	(+60)	(+4)
Idem	Idem	Sim. C	366	-	16.0	14.8	1740	810	384	3.17	1215	563	0.46
Idem	Idem	Sim. C	720	-	16.0	14.8	1740	810	342	4.21	1440	667	0.46
									(-11)	(+33)	(+19)	(+18)	(0)
<b>1995,</b>													
<b>Warm</b>	Idem	Obs.	366	+1.8	17.2	14.4	1700	770	315	3.13	985	479	0.49
Idem	Idem	Obs.	716	+1.8	17.2	14.4	1700	770	291	4.03	1174	575	0.49
									(-8)	(+29)	(+19)	(+20)	(0)
Idem	Idem	Sim. A	366	+1.8	17.4	14.6	1740	810	348	3.26	1135	581	0.51
Idem	Idem	Sim. A	716	+1.8	17.4	14.6	1740	810	404	4.38	1769	943	0.53
									(+16)	(+34)	(+56)	(+62)	(+4)
Idem	Idem	Sim. B	366	+1.8	17.2	14.4	1700	770	341	3.25	1110	555	0.50
Idem	Idem	Sim. B	716	+1.8	17.2	14.4	1700	770	395	4.37	1727	901	0.52
									(+16)	(+34)	(+56)	(+62)	(+4)
Idem	Idem	Sim. C	366	+1.8	17.2	14.4	1700	770	315	3.21	1012	537	0.53
Idem	Idem	Sim. C	716	+1.8	17.2	14.4	1700	770	291	4.25	1238	565	0.46
									(-8)	(+32)	(+22)	(+5)	(-13)
<b>1996,</b>													
<b>Cool</b>	Idem	Obs.	379	-	15.3	13.4	1820	890	466	3.56	1660	927	0.56
Idem	Idem	Obs.	756	-	15.3	13.4	1820	890	445	3.84	1710	908	0.53
									(-5)	(+8)	(+3)	(-2)	(-5)
Idem	Idem	Sim. A	379	-	15.3	13.4	1820	890	534	3.28	1750	913	0.52
Idem	Idem	Sim. A	756	-	15.3	13.4	1820	890	566	4.27	2419	1271	0.53
									(+6)	(+30)	(+38)	(+39)	(+2)
Idem	Idem	Sim. C	379	-	15.3	13.4	1820	890	466	3.31	1543	820	0.53
Idem	Idem	Sim. C	756	-	15.3	13.4	1820	890	445	4.30	1914	969	0.51
									(-5)	(+30)	(+24)	(+18)	(-4)

Table N-1 (continued)

Year, Treatment	Medi- um	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. chan- ge (°C)	T- av <sup>a</sup>	Rad- av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1996,</b>													
Warm	Idem	Obs.	379	+1.7	16.8	13.3	1820	890	380	3.35	1272	721	0.57
Idem	Idem	Obs.	751	+1.7	16.8	13.3	1820	890	372	4.17	1553	822	0.53
									(-2)	(+24)	(+22)	(+14)	(-7)
Idem	Idem	Sim. A	379	+1.7	16.8	13.3	1820	890	472	3.37	1592	866	0.54
Idem	Idem	Sim. A	751	+1.7	16.8	13.3	1820	890	503	4.43	2229	1222	0.55
									(+7)	(+31)	(+40)	(+41)	(+2)
Idem	Idem	Sim. C	379	+1.7	16.8	13.3	1820	890	380	3.42	1299	709	0.55
Idem	Idem	Sim. C	751	+1.7	16.8	13.3	1820	890	372	4.49	1669	885	0.53
									(-2)	(+31)	(+28)	(+25)	(-4)

<sup>a</sup> T-av= average temperature from crop emergence to maturity (°C).

Rad-av= average daily amount of solar radiation from crop emergence to maturity (MJ/m<sup>2</sup>/d).

Tsum Total= cumulative temperature sum (above base temperature of 0 °C) from crop emergence to maturity (°C.d).

Tsum Grain= cumulative temperature sum (above base temperature of 0 °C) from start of grain filling to maturity (°C.d).

RI= cumulative intercepted photosynthetically active radiation (PAR) from crop emergence to maturity (MJ/m<sup>2</sup>).

RUE= radiation use efficiency, i.e. TAB / RI (g dry matter/MJ PAR).

TAB= total above-ground biomass (g dry matter/m<sup>2</sup>) at maturity.

GR= grain yield (g dry matter/m<sup>2</sup>) at maturity.

HI= harvest index, i.e. GR/TAB (g dry matter/g dry matter).

Table N-2. Summary of results from spring wheat experiments in open-top chambers at ambient and increased temperatures and optimal conditions at Wageningen, the Netherlands both at ambient and doubled CO<sub>2</sub> concentration (1\*CO<sub>2</sub>/2\*CO<sub>2</sub>) as observed (Obs.; Source: Van Oijen et al., 1998a; 1998b) and as simulated with LINTULCC model for identical conditions.

Response to temperature change is given within brackets as percentage of the result at ambient temperatures. Calibration of LINTULCC was carried out in three steps: Sim. A= phenology calibrated for ambient treatment and light interception simulated; Sim. B= phenology calibrated for each treatment and light interception simulated; Sim. C= phenology calibrated for each treatment and light interception as observed in experiment.

Year, Treatment	Medi- um	Observed or Simulat.	CO <sub>2</sub> conc. (ppmv)	Temp. chan- ge (°C)	T- av <sup>a</sup>	Rad- av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1995,</b>													
<b>1*CO<sub>2</sub></b>													
Cool	Field	Obs.	366	-	16.0	14.8	1740	810	384	3.31	1271	624	0.49
Warm	Idem	Obs.	366	+1.8	17.2	14.4	1700	770	315	3.13	985	479	0.49
									(-18)	(-5)	(-23)	(-23)	(0)
Cool	Idem	Sim. A	366	-	16.0	14.8	1740	810	395	3.19	1259	618	0.49
Warm	Idem	Sim. A	366	+1.8	17.4	14.6	1740	810	348	3.26	1135	581	0.51
									(-12)	(+2)	(-10)	(-6)	(+4)
Warm	Idem	Sim. B	366	+1.8	17.2	14.4	1700	770	341	3.25	1110	555	0.50
									(-14)	(+2)	(-12)	(-10)	(+2)
Cool	Idem	Sim. C	366	-	16.0	14.8	1740	810	384	3.17	1215	563	0.46
Warm	Idem	Sim. C	366	+1.8	17.2	14.4	1700	770	315	3.21	1012	537	0.53
									(-18)	(+1)	(-17)	(-5)	(+15)

Table N-2 (continued)

Year, Treatment	Medi- um	Observed or Simulat.	CO <sub>2</sub> Conc. (ppmv)	Temp. chan- ge (°C)	T- av <sup>a</sup>	Rad- av <sup>a</sup>	Tsum Total <sup>a</sup>	Tsum Grain <sup>a</sup>	RI <sup>a</sup>	RUE <sup>a</sup>	TAB <sup>a</sup>	GR <sup>a</sup>	HI <sup>a</sup>
<b>1995, 2*CO<sub>2</sub></b>													
Cool	Idem	Obs.	720	-	16.0	14.8	1740	810	342	4.13	1413	694	0.49
Warm	Idem	Obs.	716	+1.8	17.2	14.4	1700	770	291	4.03	1174	575	0.49
									(-15)	(-2)	(-17)	(-17)	(0)
Cool	Idem	Sim. A	720	-	16.0	14.8	1740	810	454	4.27	1940	989	0.51
Warm	Idem	Sim. A	716	+1.8	17.4	14.6	1740	810	404	4.38	1769	943	0.53
									(-11)	(+3)	(-9)	(-5)	(+4)
Warm	Idem	Sim. B	716	+1.8	17.2	14.4	1700	770	395	4.37	1727	901	0.52
									(-13)	(+2)	(-11)	(-9)	(+2)
Cool	Idem	Sim. C	720	-	16.0	14.8	1740	810	342	4.21	1440	667	0.46
Warm	Idem	Sim. C	716	+1.8	17.2	14.4	1700	770	291	4.25	1238	565	0.46
									(-15)	(+1)	(-14)	(-15)	(0)
<b>1996, 1*CO<sub>2</sub></b>													
Cool	Field	Obs.	379	-	15.3	13.4	1820	890	466	3.56	1660	927	0.56
Warm	Idem	Obs.	379	+1.7	16.8	13.3	1820	890	380	3.35	1272	721	0.57
									(-18)	(-6)	(-23)	(-22)	(+2)
Cool	Idem	Sim. A	379	-	15.3	13.4	1820	890	534	3.28	1750	913	0.52
Warm	Idem	Sim. A	379	+1.7	16.8	13.3	1820	890	472	3.37	1592	866	0.54
									(-12)	(+3)	(-9)	(-5)	(+4)
Cool	Idem	Sim. C	379	-	15.3	13.4	1820	890	466	3.31	1543	820	0.53
Warm	Idem	Sim. C	379	+1.7	16.8	13.3	1820	890	380	3.42	1299	709	0.55
									(-18)	(+3)	(-16)	(-14)	(+4)
<b>1996, 2*CO<sub>2</sub></b>													
Cool	Idem	Obs.	756	-	15.3	13.4	1820	890	445	3.84	1710	908	0.53
Warm	Idem	Obs.	751	+1.7	16.8	13.3	1820	890	372	4.17	1553	822	0.53
									(-16)	(+9)	(-9)	(-9)	(0)
Cool	Idem	Sim. A	756	-	15.3	13.4	1820	890	566	4.27	2419	1271	0.53
Warm	Idem	Sim. A	751	+1.7	16.8	13.3	1820	890	503	4.43	2229	1222	0.55
									(-11)	(+4)	(-8)	(-4)	(+4)
Cool	Idem	Sim. C	756	-	15.3	13.4	1820	890	445	4.30	1914	969	0.51
Warm	Idem	Sim. C	751	+1.7	16.8	13.3	1820	890	372	4.49	1669	885	0.53
									(-16)	(+4)	(-13)	(-9)	(+4)

<sup>a</sup> T-av= average temperature from crop emergence to maturity (°C).

Rad-av= average daily amount of solar radiation from crop emergence to maturity (MJ/m<sup>2</sup>/d).

Tsum Total= cumulative temperature sum (above base temperature of 0 °C) from crop emergence to maturity (°C.d)

Tsum Grain= cumulative temperature sum (above base temperature of 0 °C) from start of grain filling to maturity (°C.d).

RI= cumulative intercepted photosynthetically active radiation (PAR) from crop emergence to maturity (MJ/m<sup>2</sup>).

RUE= radiation use efficiency, i.e. TAB / RI (g dry matter/MJ PAR).

TAB= total above-ground biomass (g dry matter/m<sup>2</sup>) at maturity.

GR= grain yield (g dry matter/m<sup>2</sup>) at maturity.

HI= harvest index, i.e. GR/TAB (g dry matter/g dry matter).

## **Appendix O: Detailed analysis of Arizona data sets: simulated versus experimental results**

Spring wheat was grown during growing seasons 1992/93, 1993/94 and 1995/96 in fields at Maricopa, Arizona, USA under conditions of ambient and elevated atmospheric CO<sub>2</sub> concentrations and ample and limited water supply (1992/93 and 1993/94) or high and low nitrogen supply (1995/96). On the fields with elevated atmospheric CO<sub>2</sub> a free-air CO<sub>2</sub> enrichment (FACE) system was used. The blower rings of this FACE system resulted in an increase in minimum temperature by about 1.5 °C compared with the ambient CO<sub>2</sub> fields (without blower rings). Only in 1995/96 blower rings were also used on half of the ambient CO<sub>2</sub> fields. Results from the experiments under optimal conditions (i.e. no water or nitrogen shortage) were compared with results as simulated with the LINTULCC model for identical conditions. Calibration of LINTULCC was carried out in three steps: step A= phenology calibrated for ambient treatment and LAI simulated; step B= phenology calibrated for each treatment and LAI simulated; step C= phenology calibrated for each treatment and LAI as observed in the experiments.

Time courses of crop variables as observed in experiment in 1992/93 under ambient atmospheric CO<sub>2</sub> concentration and as simulated with LINTULCC for identical conditions and calibration steps A and C, are given in Figures O-1 and O-3, respectively. Time courses of crop variables as observed in 1992/93 under elevated CO<sub>2</sub> and as simulated with LINTULCC for identical conditions and step B, are given in Figure O-2. Figure O-2 also shows the ratio between shoot growth under elevated and ambient CO<sub>2</sub>.

Time courses of crop variables as observed in experiment in 1993/94 under ambient atmospheric CO<sub>2</sub> concentration and as simulated with LINTULCC for identical conditions and calibration steps A and C, are given in Figures O-4 and O-7, respectively. Time courses of crop variables as observed in 1993/94 under elevated CO<sub>2</sub> and as simulated with LINTULCC for identical conditions and steps A and B, are given in Figures O-5 and O-6, respectively. Figures O-5 and O-6 also show the ratio between shoot growth under elevated and ambient CO<sub>2</sub>.

Time courses of crop variables as observed in experiment in 1995/96 under ambient atmospheric CO<sub>2</sub> concentration (with blower rings) and as simulated with LINTULCC for identical conditions and calibration steps A and C, are given in Figures O-8 and O-11, respectively. Time courses of crop variables as observed in 1995/96 under elevated CO<sub>2</sub> and as simulated with LINTULCC for identical conditions and steps A and B, are given in Figures O-9 and O-10, respectively. Time courses of crop variables as observed in 1995/96 under ambient CO<sub>2</sub> but without blower rings and as simulated with LINTULCC for identical conditions and step C, are given in Figure O-12. Figures O-9, O-10 and O-12 also show the ratio between shoot growth under elevated and ambient CO<sub>2</sub>.

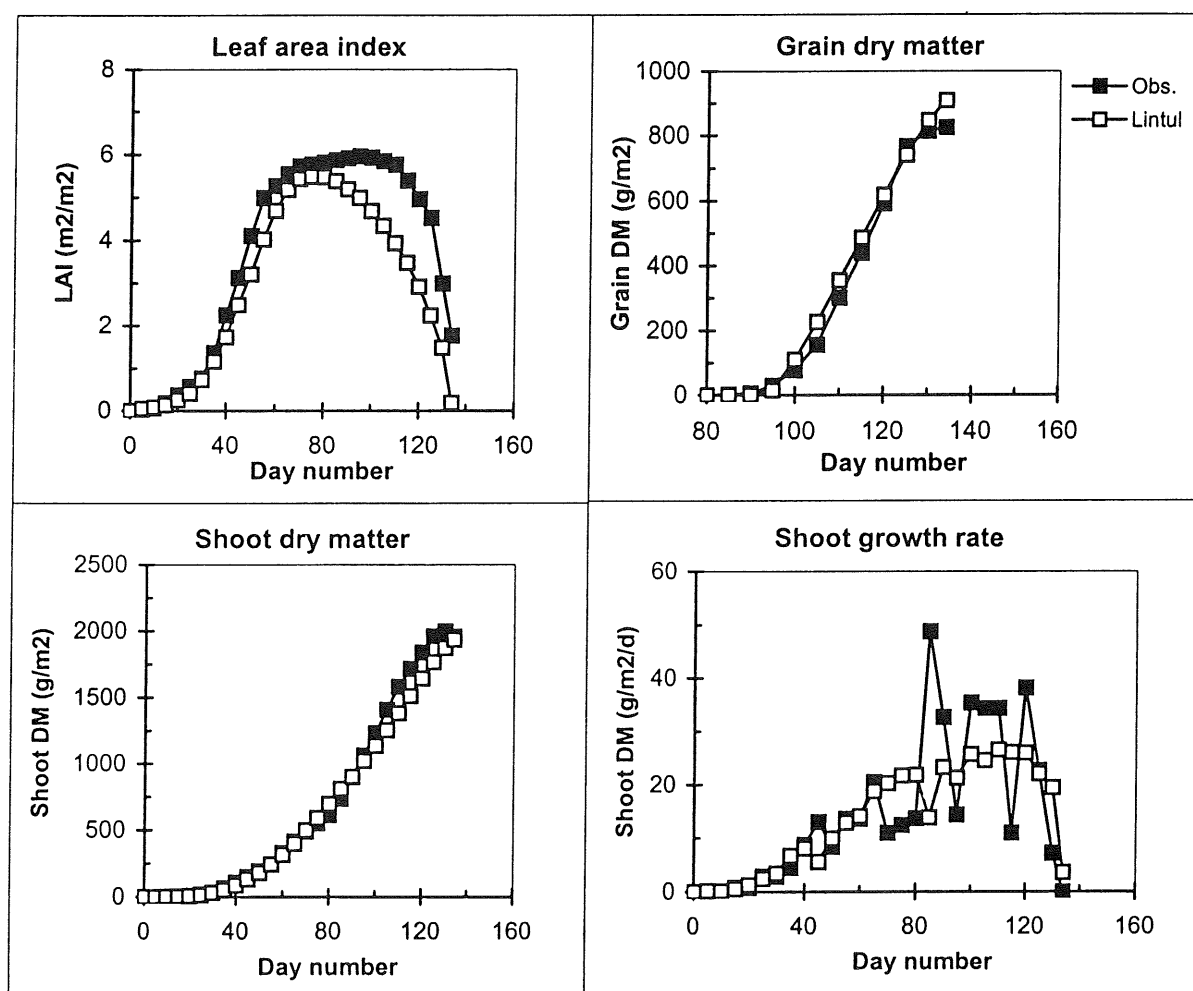


Figure O-1. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1992/93 under conditions of ample water supply and ambient (370 ppmv) atmospheric CO<sub>2</sub> concentration (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A: phenology calibrated for ambient treatment and LAI simulated. Day number= Julian day.

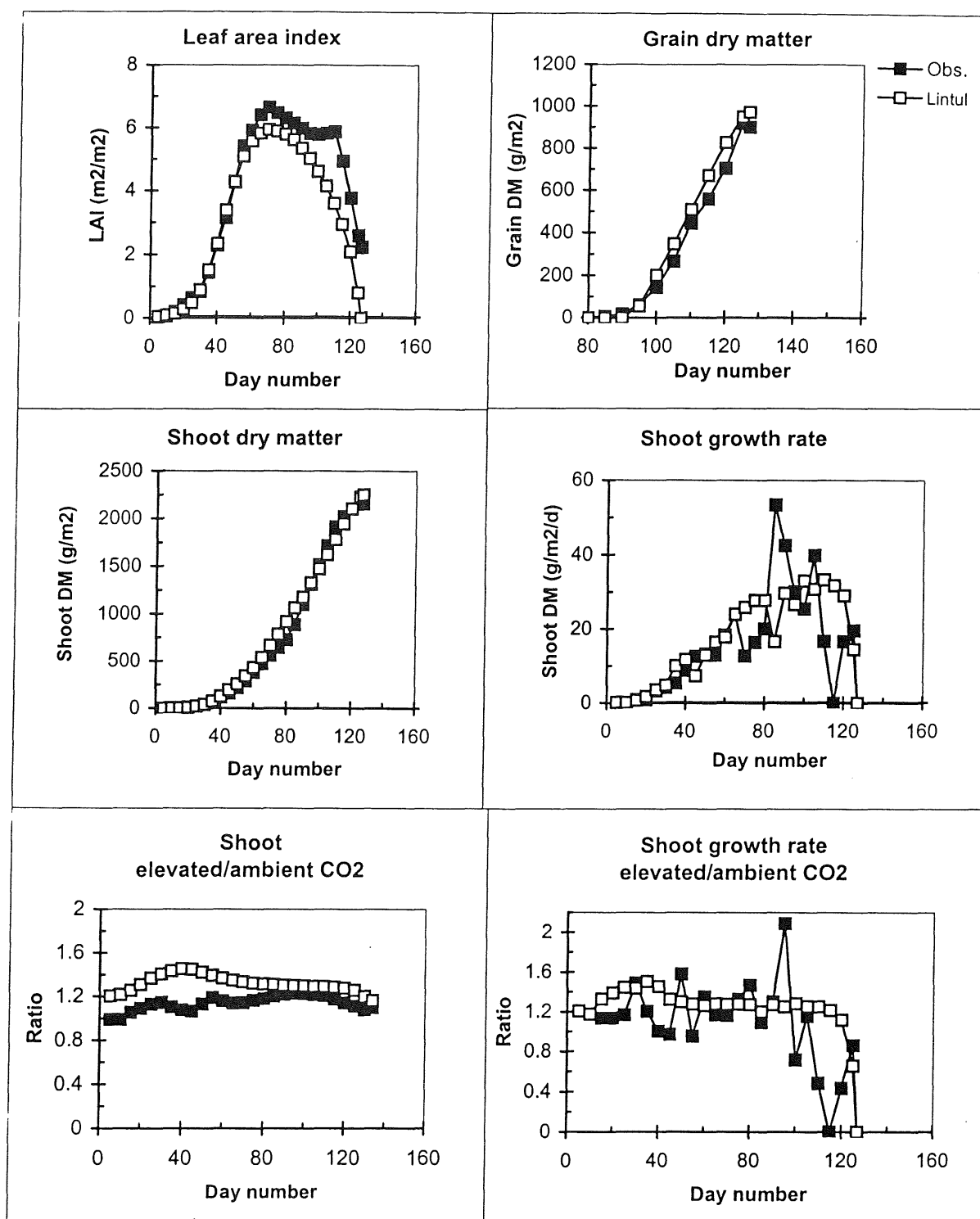


Figure O-2. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1992/93 under conditions of ample water supply and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated and ambient (370 ppmv) CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step B: phenology calibrated for each treatment and LAI simulated. Day number= Julian day.

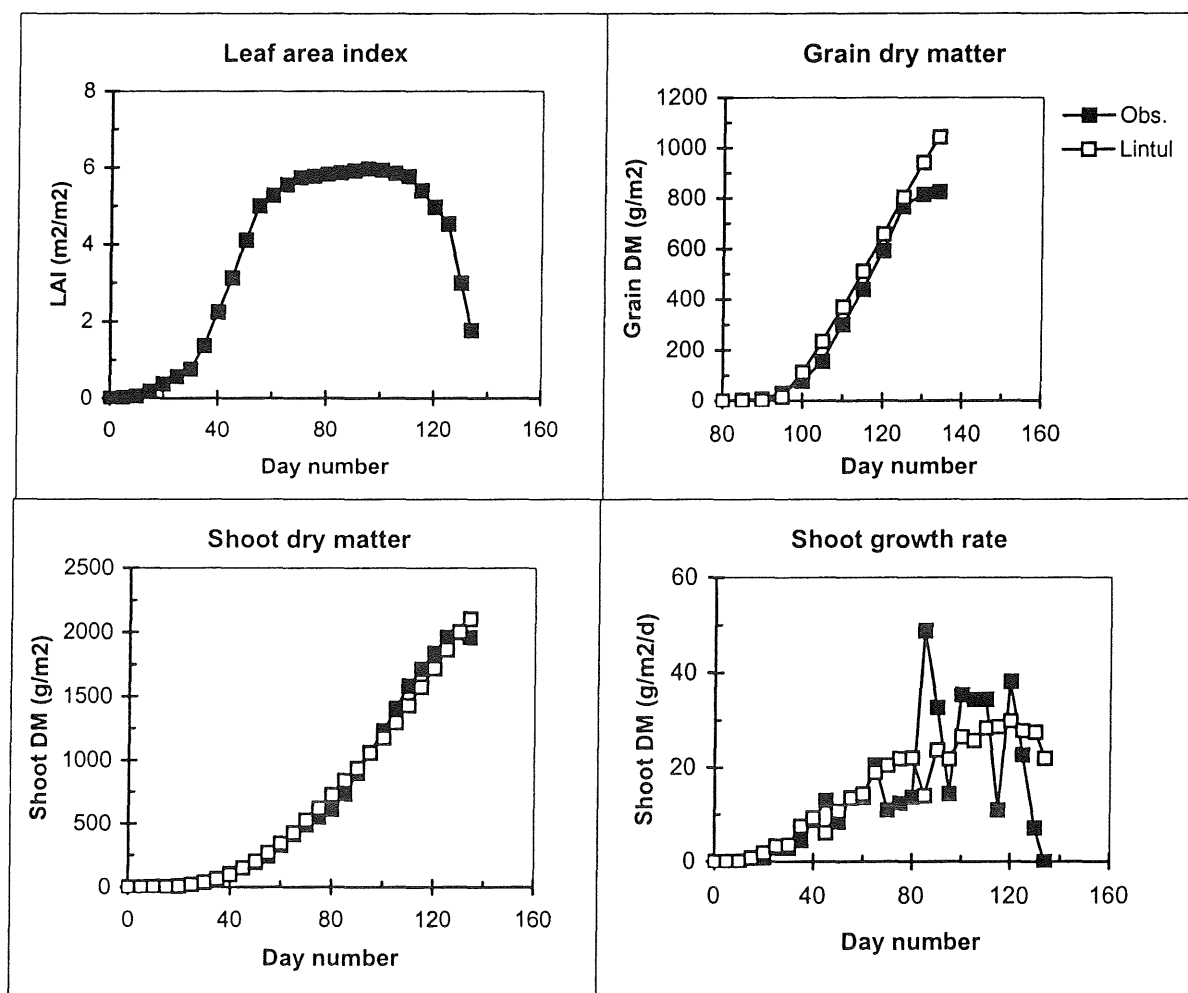


Figure O-3. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1992/93 under conditions of ample water supply and ambient (370 ppmv) atmospheric CO<sub>2</sub> concentration (Source: Hunsaker et al., 1996; Kimball et al., 1995; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C: phenology calibrated for each treatment and LAI as observed in the experiments. Day number= Julian day.



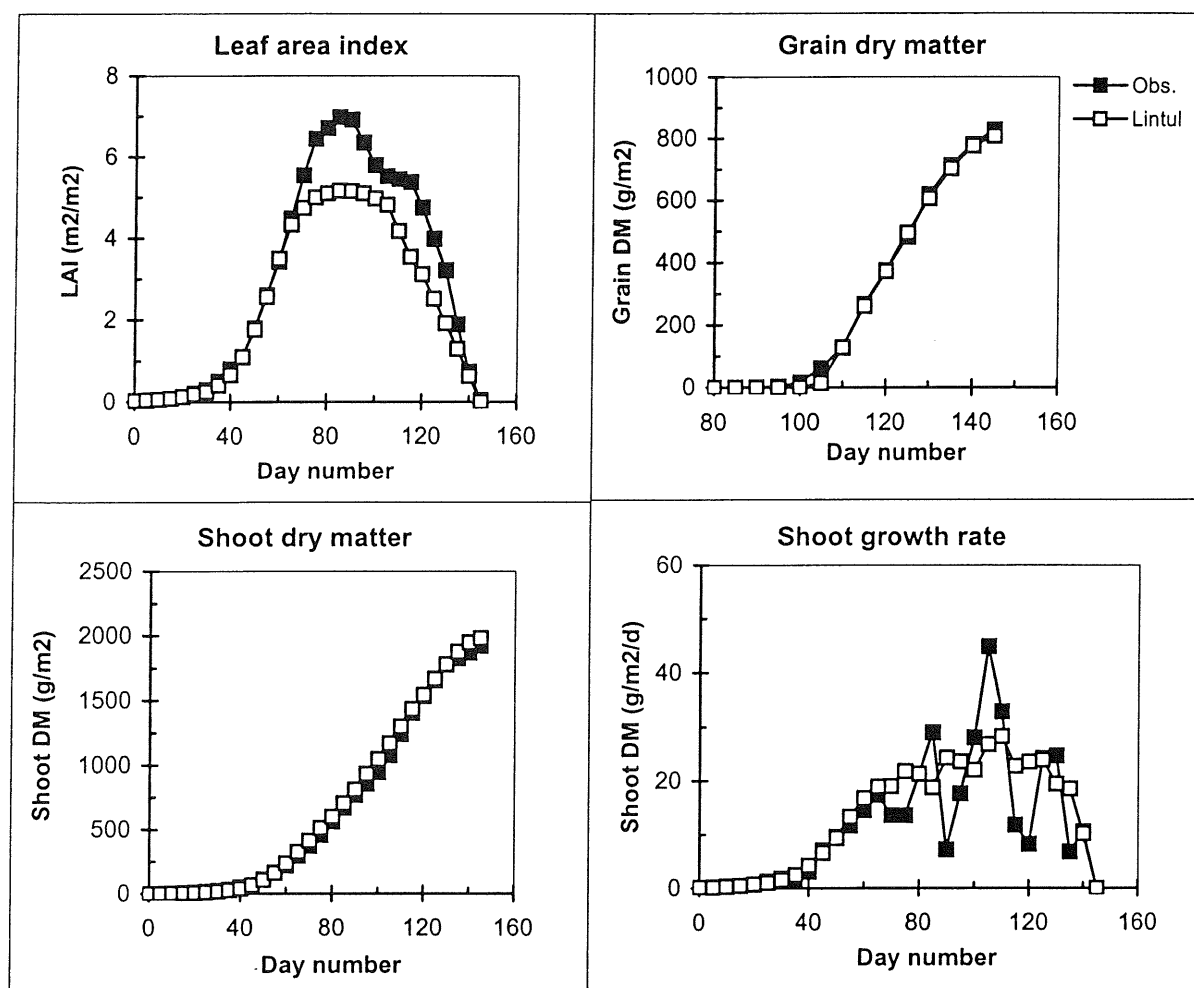


Figure O-4. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1993/94 under conditions of ample water supply and ambient (370 ppmv) atmospheric CO<sub>2</sub> concentration (Source: Hunsaker et al., 1996; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A: phenology calibrated for ambient treatment and LAI simulated. Day number= Julian day.

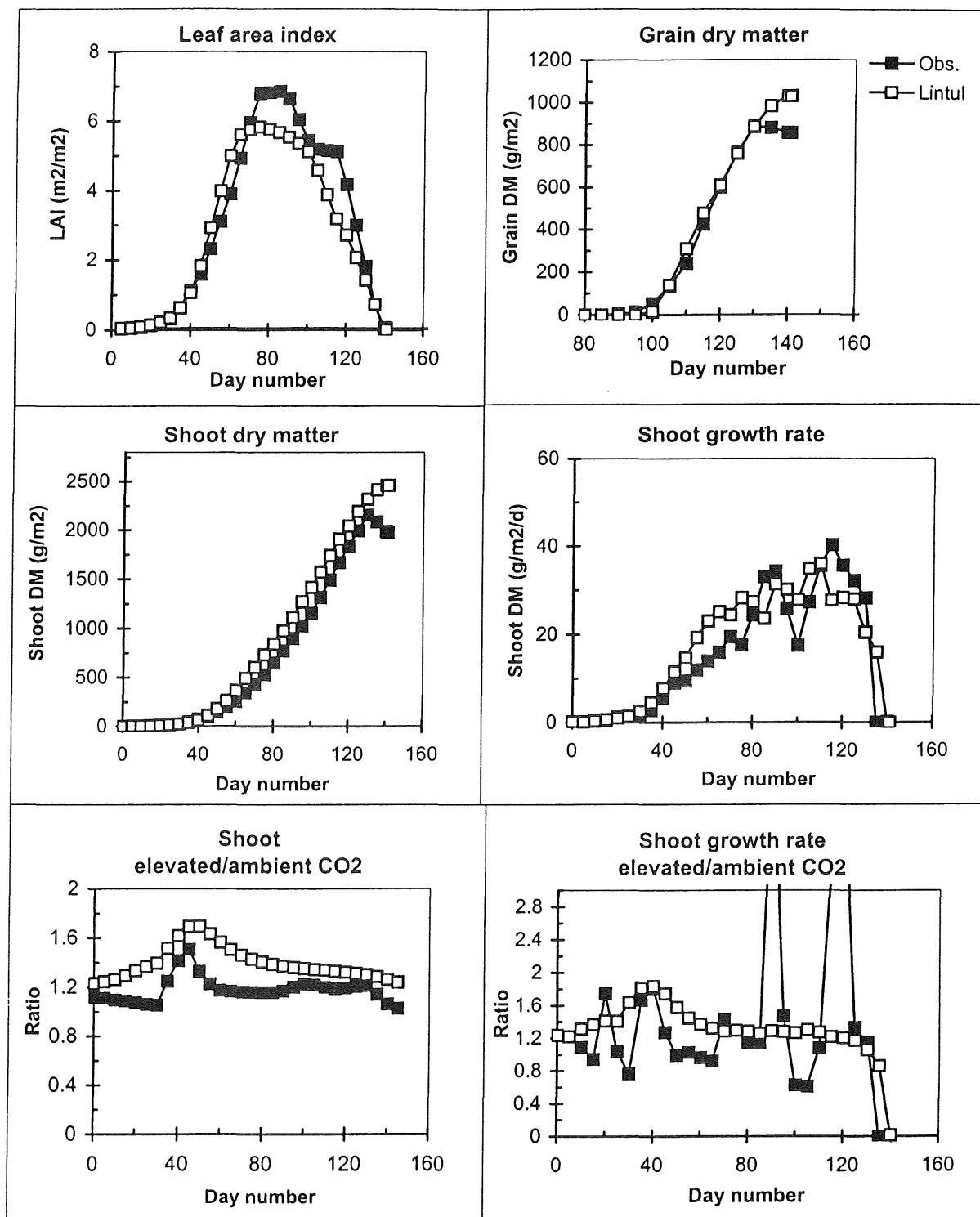


Figure O-5. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1993/94 under conditions of ample water supply and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated and ambient (370 ppmv) CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A: phenology calibrated for ambient treatment and LAI simulated. Day number= Julian day.

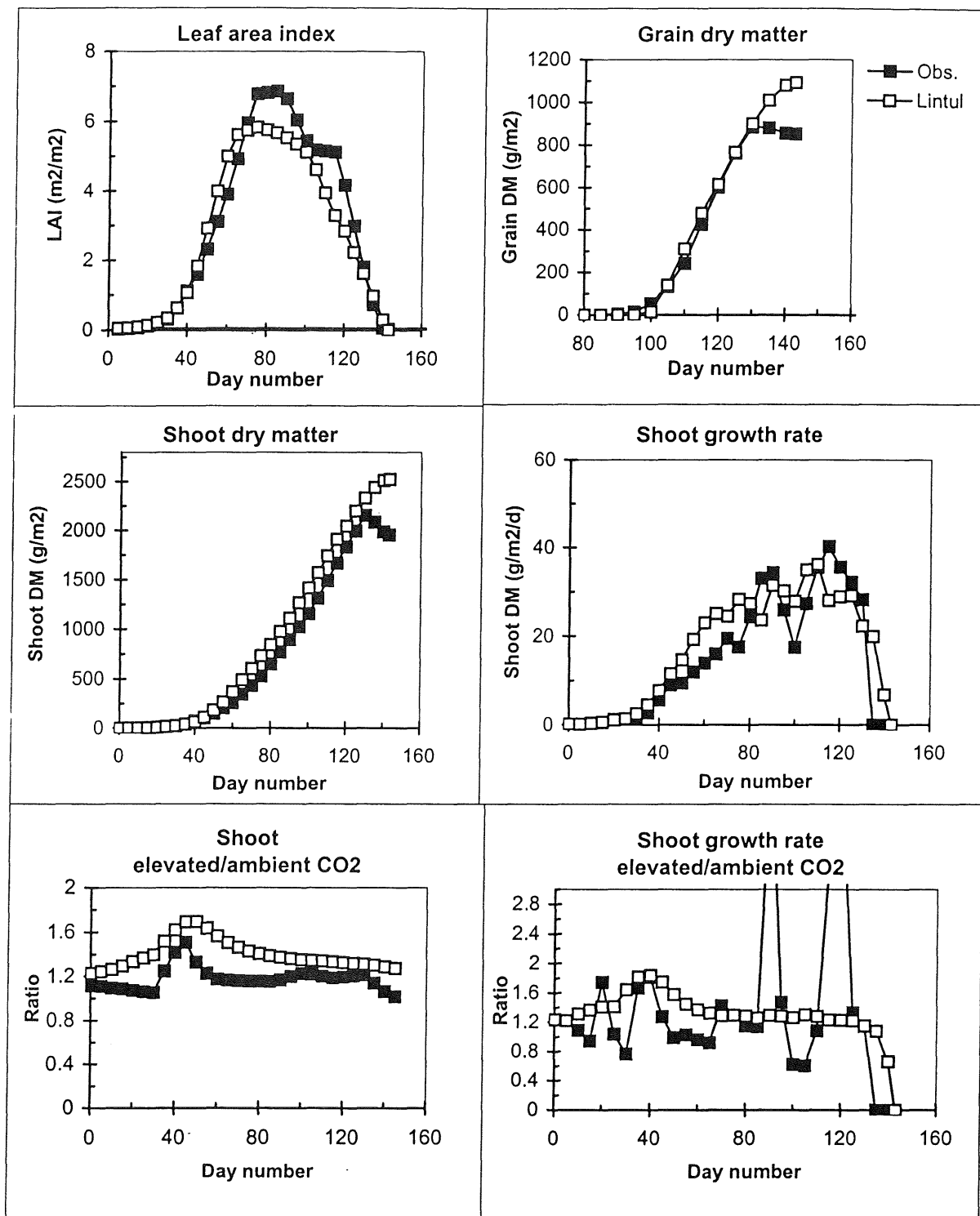


Figure O-6. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1993/94 under conditions of ample water supply and elevated (550 ppmv) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated and ambient (370 ppmv) CO<sub>2</sub> concentrations (Source: Hunsaker et al., 1996; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step B: phenology calibrated for each treatment and LAI simulated. Day number= Julian day.

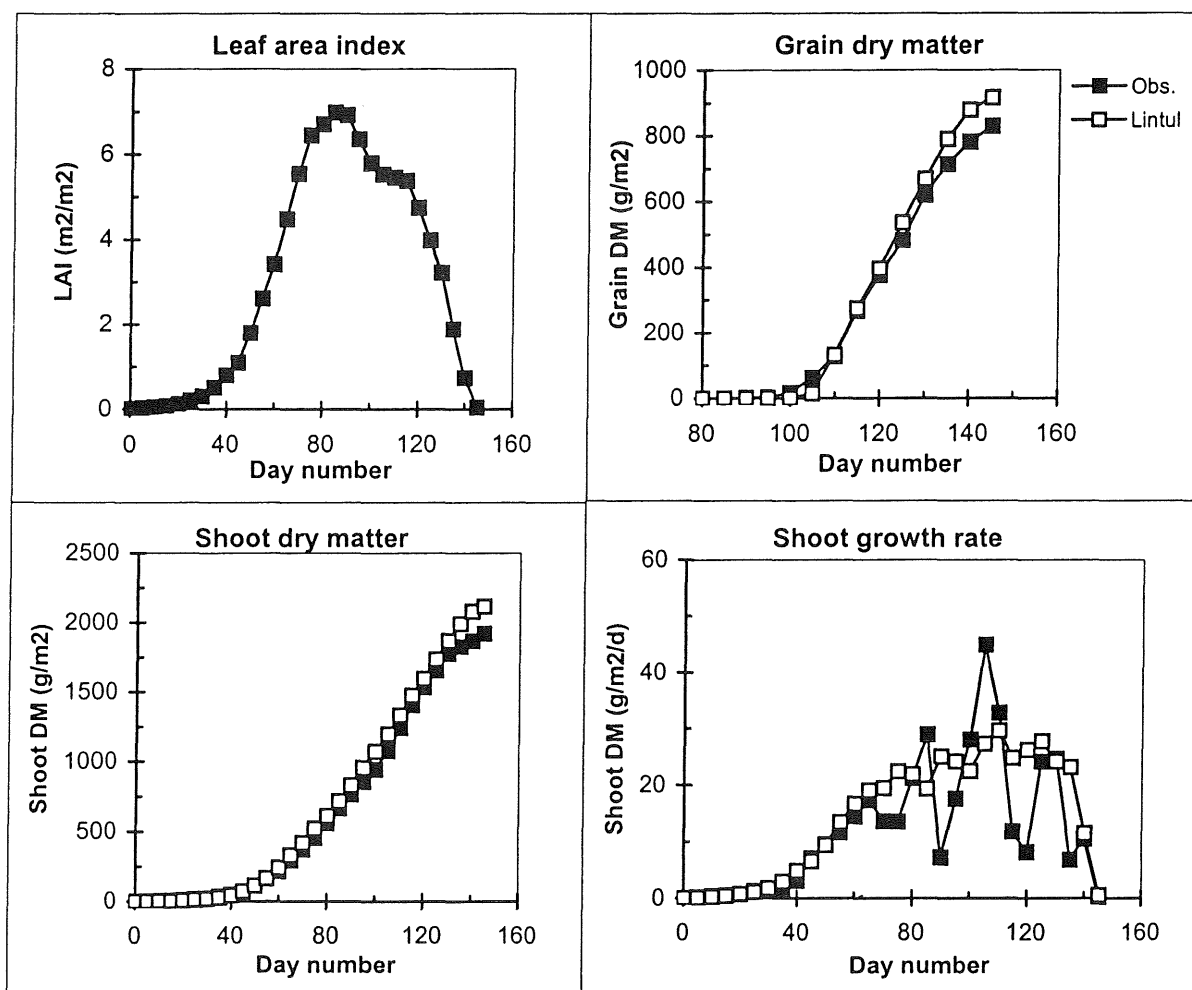


Figure O-7. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1993/94 under conditions of ample water supply and ambient (370 ppmv) atmospheric CO<sub>2</sub> concentration (Source: Hunsaker et al., 1996; Pinter et al., 1996a) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C: phenology calibrated for each treatment and LAI as observed in the experiments. Day number= Julian day.

Arizona, growing season 1995/1996

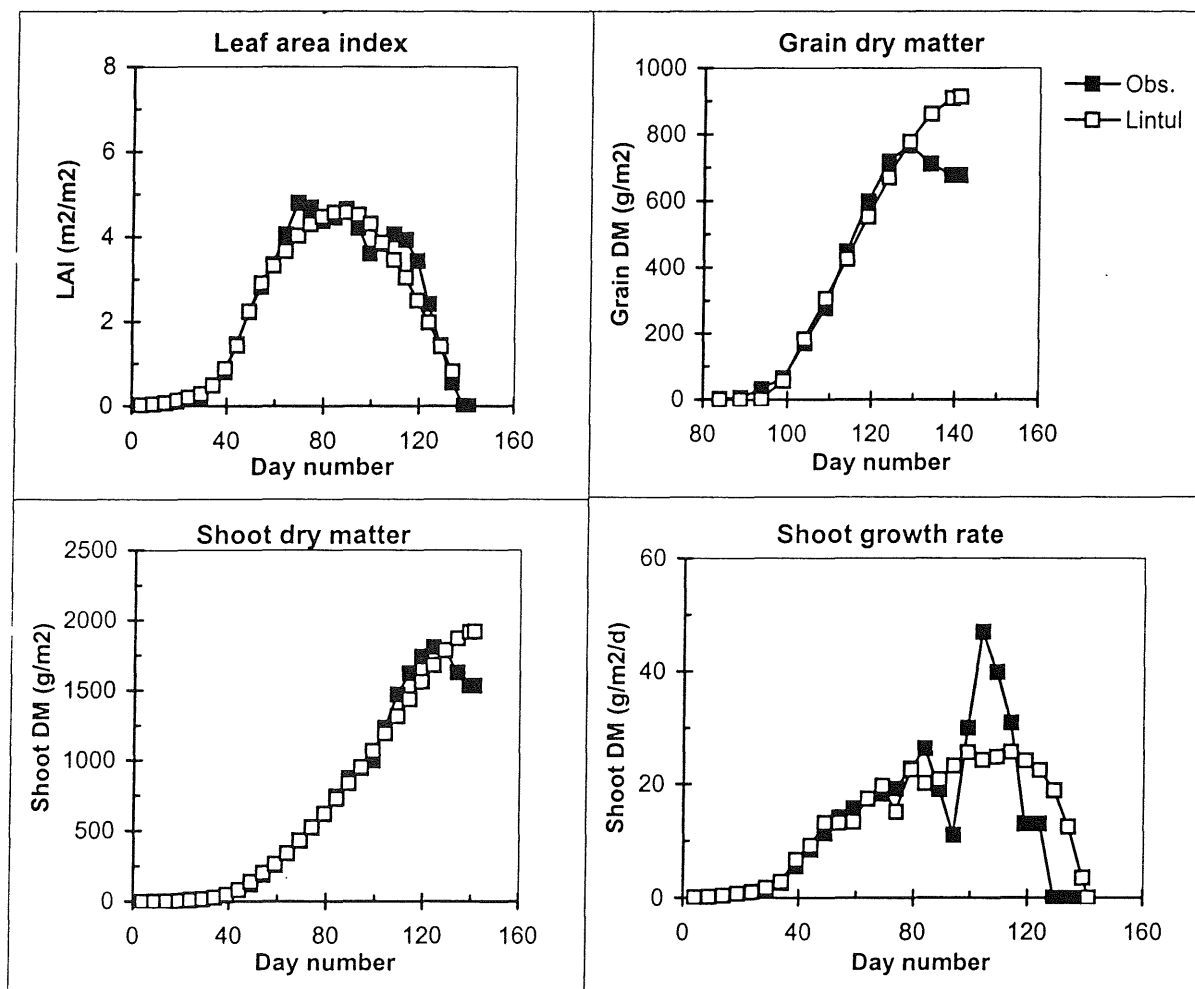


Figure O-8. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of ample water and high nitrogen supply and ambient (370 ppmv; with blower rings) atmospheric CO<sub>2</sub> concentration (Source: Pinter et al., 1996b) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A: phenology calibrated for ambient treatment and LAI simulated. Day number= Julian day.

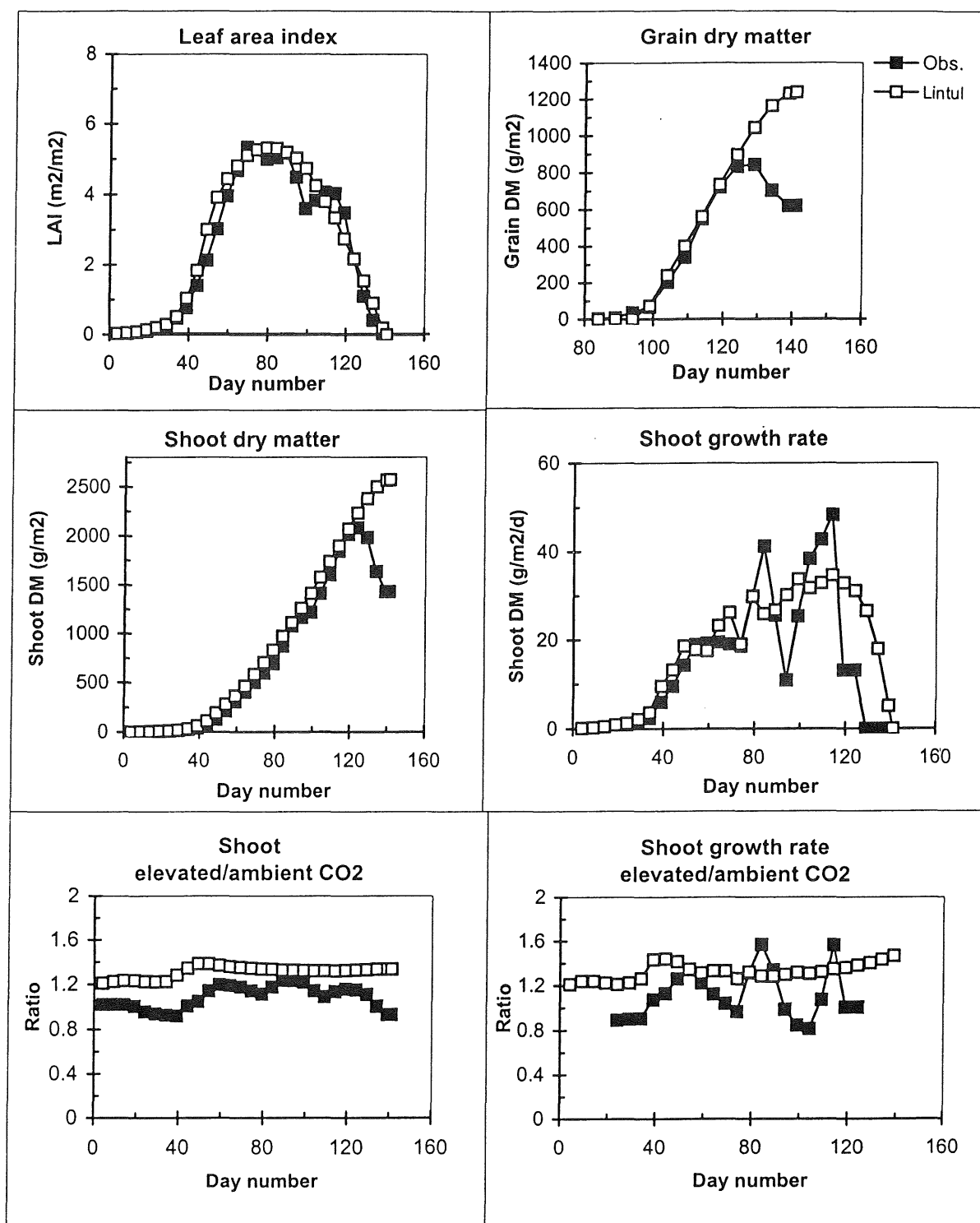


Figure O-9. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of ample water and high nitrogen supply and elevated (570 ppmv) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated and ambient (370 ppmv; with blower rings) CO<sub>2</sub> concentrations (Source: Pinter et al., 1996b) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step A: phenology calibrated for ambient treatment and LAI simulated. Day number= Julian day.

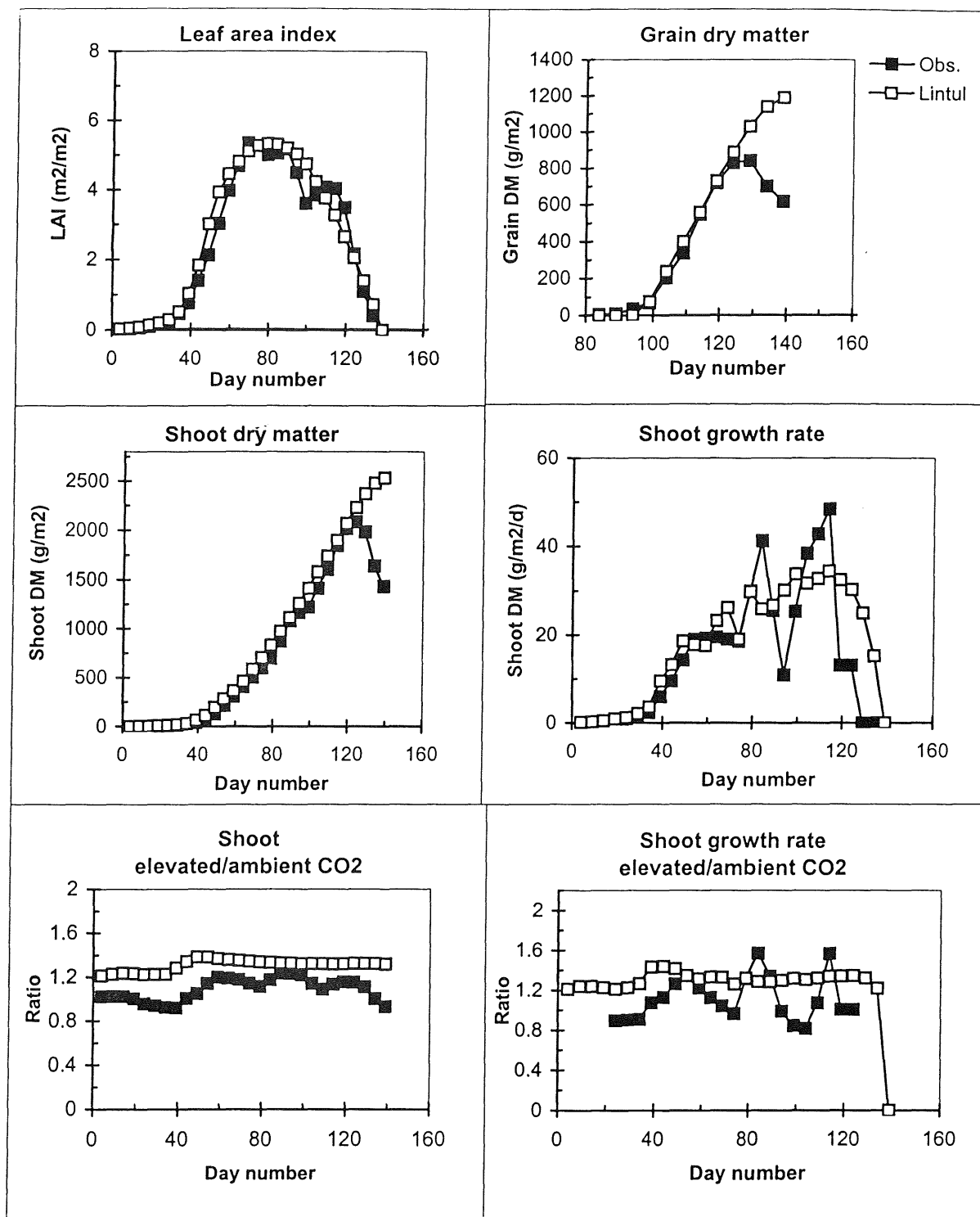


Figure O-10. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of ample water and high nitrogen supply and elevated (570 ppmv) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated and ambient (370 ppmv; with blower rings) CO<sub>2</sub> concentrations (Source: Pinter et al., 1996b) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step B: phenology calibrated for each treatment and LAI simulated. Day number= Julian day.

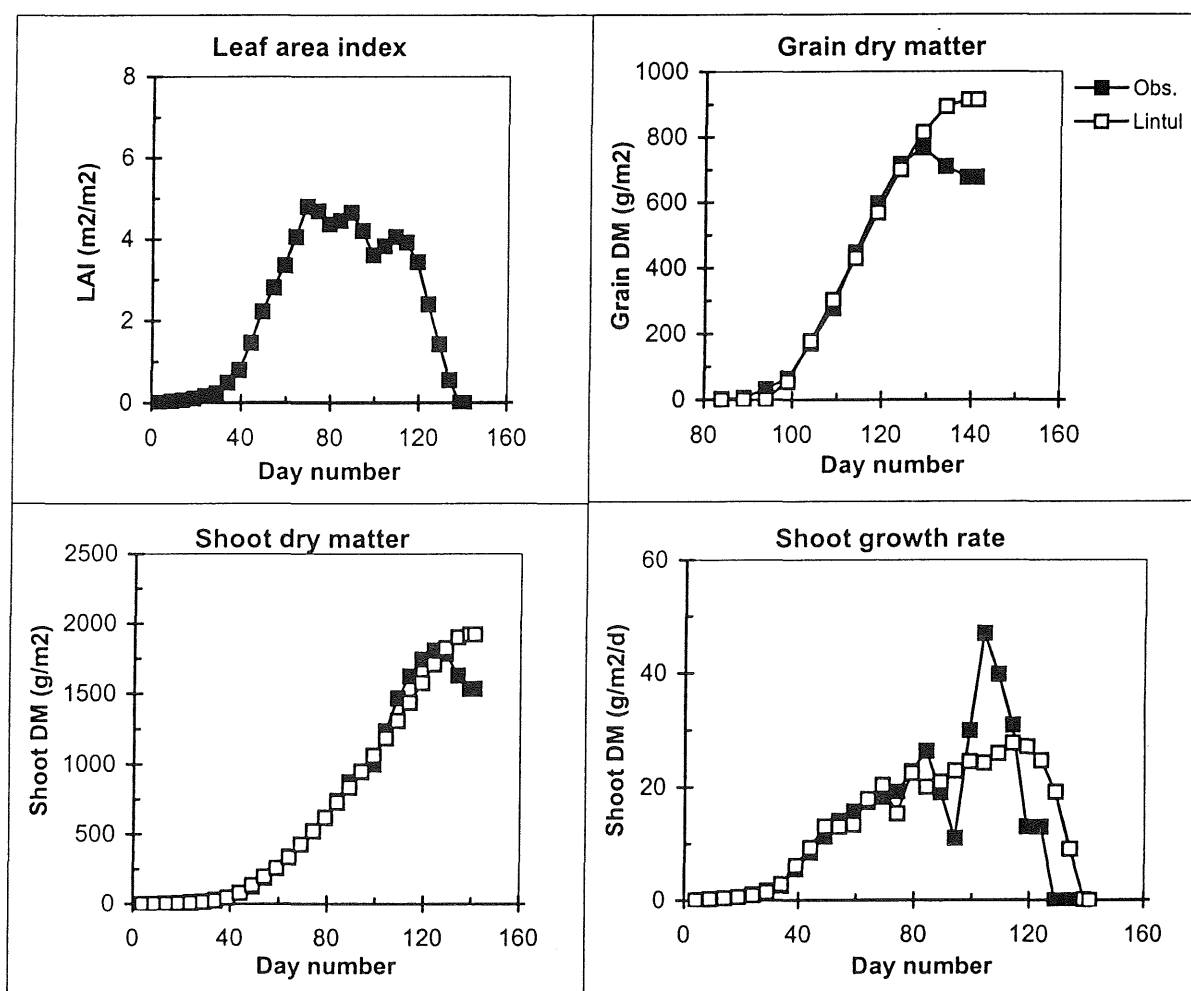


Figure O-11. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of ample water and high nitrogen supply and ambient (370 ppmv; with blower rings) atmospheric CO<sub>2</sub> concentration (Source: Pinter et al., 1996b) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C: phenology calibrated for each treatment and LAI as observed in the experiments. Day number= Julian day.



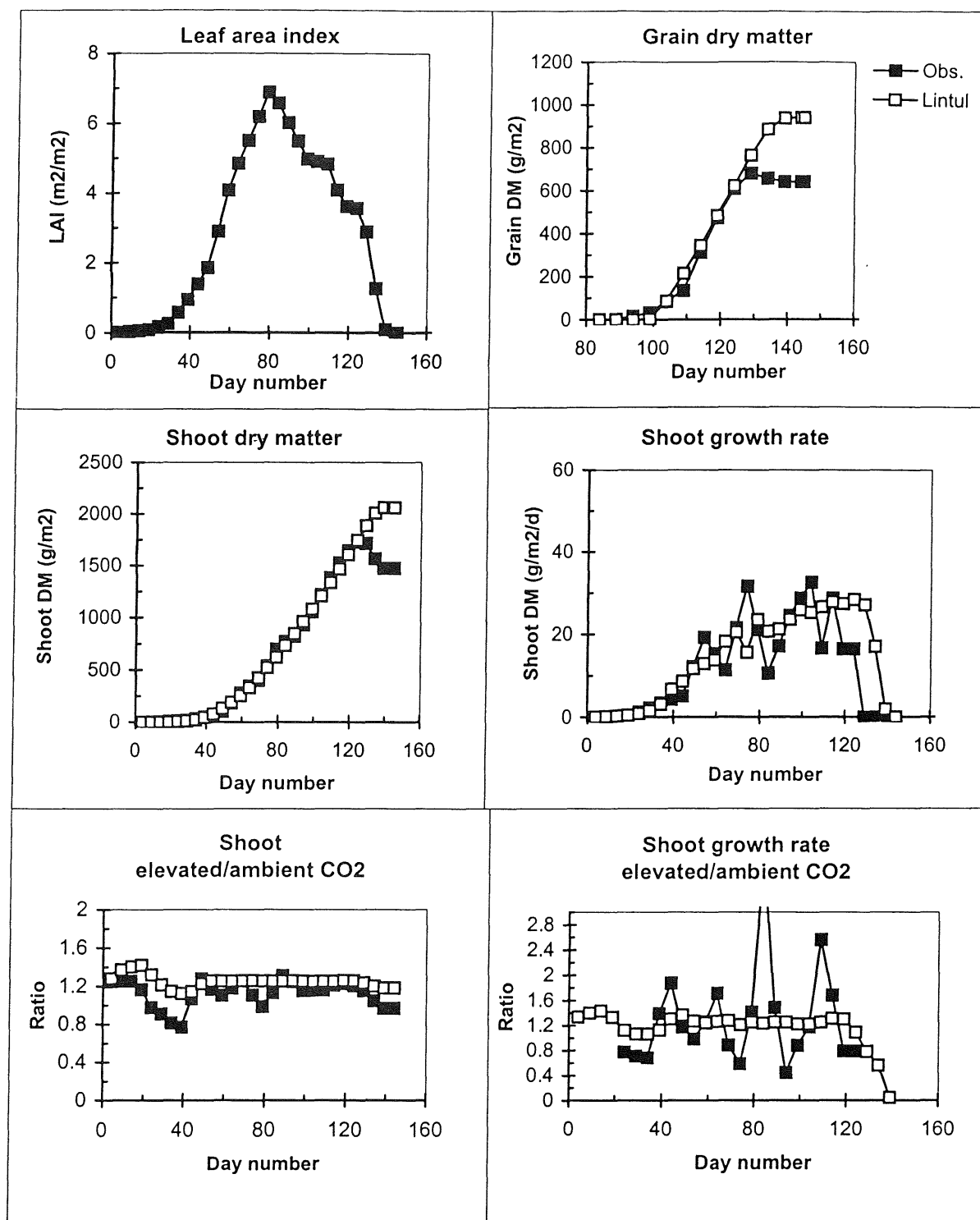


Figure O-12. Results from spring wheat experiments (cv. Yecora Rojo) FACE experiments at Maricopa, Arizona, USA in growing season 1995/96 under conditions of ample water and high nitrogen supply and ambient (370 ppmv; without blower rings) atmospheric CO<sub>2</sub> concentration and the ratio between shoot growth under elevated (570 ppmv) and ambient CO<sub>2</sub> concentrations (Source: Pinter et al., 1996b) versus the results simulated with the LINTULCC model for identical conditions. Growth simulations were made for calibration step C: phenology calibrated for each treatment and LAI as observed in the experiments. Day number= Julian day.

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