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Title: Evaluating the ability of four crop models to predict different environmental impacts on spring wheat grown in open-top chambers

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Abstract: In this study, we used the modelling package Expert-N to investigate the ability of four generic-mechanistic crop models, which were originally developed under fi eld conditions, to simulate plant growth of spring wheat grown in open-top chambers (OTC) under different environmental conditions. Thereby we focus on the impacts of drought stress and elevated atmospheric CO2-concentration on biomass production. Expert-N facilitates the comparison of the components of agro-ecosystem models, as it allows exchanging single modules while leaving the rest of the model unchanged. Here the crop growth part of the models SPASS, CERES-Wheat, SUCROS and GECROS were combined with the Penmen-Monteith equation for potential evapotranspiration, the HYDRUS-1D model for water transport and the LEACH-N model for nitrogen transport and turnover simulation. The models were applied to a data set provided by OTC experiments with spring wheat (Triticum aestivum L. cv. 'Minaret') which was grown under two atmospheric CO2-concentration levels (ambient/elevated), two irrigation schemes (unlimited water supply/water limitation) and two soil types (Cambisol/Chernosem) in two subsequent vegetation periods (1998/1999). We show that the crop models are able to simulate CO2 effects on spring wheat growth on organ level under the conditions of the OTC experiments. Based on model calibration using experimental and literature data, the best simulation results describing the impact of the considered environmental conditions were obtained using the model SPASS followed by the models SUCROS, GECROS and CERES. A more sensitive response of atmospheric CO2-concentrations on crop growth was simulated using GECROS and SPASS.

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To whom it may concern,

Enclosed you find the manuscript by Christian J. Biernath et al. titled "Evaluating the ability of four crop models to predict different environmental impacts on spring wheat grown in open-top chambers," which is being submitted for possible publication in the journal *Agricultural Systems*.

This manuscript is new and is not being considered elsewhere. We would be pleased if our manuscript would be to your complete satisfaction.

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Sincerely,
Christian J. Biernath

Research highlights

- unique is the test of the four crop growth models also on the organ level by a complete data set
- the four crop models were able to simulate crop growth under the conditions of open-top chambers
- mechanistic models simulated the impact of CO2 and other environmental factors more sensitively

Evaluating the ability of four crop models to predict different environmental impacts on spring wheat grown in open-top chambers

Agricultural Systems

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Abstract

In this study, we used the modelling package Expert-N to investigate the ability of four generic-mechanistic crop models, which were originally developed under field conditions, to simulate plant growth of spring wheat grown in open-top chambers (OTC) under different environmental conditions. Thereby we focus on the impacts of drought stress and elevated atmospheric CO_2-concentration on biomass production. Expert-N facilitates the comparison of the components of agro-ecosystem models, as it allows exchanging single modules while leaving the rest of the model unchanged. Here the crop growth part of the models SPASS, CERES-Wheat, SUCROS and GECROS were combined with the Penmen-Monteith equation for potential evapotranspiration, the HYDRUS-1D model for water transport and the LEACH-N model for nitrogen transport and turnover simulation. The models were applied to a data set provided by OTC experiments with spring wheat (*Triticum aestivum* L. cv. 'Minaret') which was grown under two atmospheric CO_2-concentration levels (ambient/elevated), two irrigation schemes (unlimited water supply/water limitation) and two soil types (Cambisol/Chernosem) in two subsequent vegetation periods (1998/1999). We show that the crop models are able to simulate CO_2 effects on spring wheat growth on organ level under the conditions of the OTC experiments. Based on model calibration using experimental and literature data, the best simulation results describing the impact of the considered environmental conditions were obtained using the model SPASS followed by the models SUCROS, GECROS and CERES. A more sensitive response of atmospheric CO_2-concentrations on crop growth was simulated using GECROS and SPASS.

Keywords: Triticum aestivum L., wheat, elevated CO_2, crop growth simulation, crop model

1. Introduction

In plants carbon is assimilated from atmospheric CO_2 via photosynthesis. Coming from a pre-industrial level of approx. 280 ppm (Siegenthaler et al., 2005) recent CO_2 concentrations amount to 390 ppm (Tans, 2009) and are predicted to yield 450 ppm in the year 2030 (Alcamo et al., 2007; OECD EO, 2008). Since CO_2 is not substrate saturated at current CO_2 concentrations, atmospheric CO_2 enrichment is commonly seen to boost crop yields of C_3 cereals such as wheat and thus food and feed production. Throughout the last two decades, this view is supported by various experiments by using climate chamber, open-top chamber (OTC) and free-air-carbon-enrichment (FACE) technology (Amthor, 2001; Fangmeier et al., 1999; Högy et al., 2009; Wullschleger et al., 1992). While most studies demonstrated positive effects of aboveground biomass production under CO_2 enrichment (Ewert et al., 2002; Fangmeier et al., 2000; Poorter et al., 1996), several studies suggested that even a reduction of biomass under elevated CO_2 in interaction with other environmental factors is possible (Long et al., 2005, 2006). Long et al. (2006) and Schimmel (2006) summarized that CO_2 fertilization effects on plant production have been overestimated as they sum up to 13% for wheat grown in FACE experiments in contrast to 31-36% that were observed in chamber-based studies. Nevertheless, Ziska and Bunce (2007) show that differences of the CO_2 response on plant production between different experimental systems are less significant if the data are normalized to the different levels of CO_2 elevation. Moreover, CO_2 enrichment inhibits the nitrate assimilation from soil (Bloom et al., 2010), which in turn decreases biomass production and grain yield quality (Högy and Fangmeier, 2008). Furthermore CO_2 fertilization effects on plants using the C_3 metabolism are only expected if the environment is not limited by temperature or water supply. Thus, extreme weather events like longer moisture or drought periods as predicted by future climate scenarios for Europe (McGregor et al., 2005; Parizek et al., 2004) could affect crop growth stronger than elevated atmospheric CO_2 concentration.

Throughout the last decades, various crop models have been developed describing physiological processes and cycling of water and nutrients in terrestrial agro-ecosystems. Model types can be characterized as static or dynamic, deterministic or stochastic and empirical or mechanistic (Dent and Blackie, 1979; Thornley and France, 2007). Up to date, model development for complex system simulations aims to be rather dynamic than static, rather deterministic than stochastic and rather mechanistic than empirical. Examples for models are SPASS (Wang, 1997; Wang and Engel, 2000), GECROS (Yin and van Laar, 2005) and CROPSIM-CERES (Hunt and Pararajasingham, 1995). Mechanistic models are usually much more complex than empirical models and input data can be less well adapted, because structural constraints are incorporated by model assumptions. Mechanistic models basically offer more options to improve the system and to understand processes and their interactions. Empirical models are basically direct descriptions of measurements and define the characteristics of a system in a simple way. Usually a basic advantage of empirical models is the little effort for calibration (Thornley and France, 2007).

The four crop models in this study were chosen because of their different degree of including mechanistic approaches to model genotype-by-environment interactions and because of the different approaches to simulate elevated CO_2 effects on crop growth. In SUCROS and CERES this is simply controlled by an empirical increase of the light use efficiency. In SPASS a constant initial slope where photosynthesis is entirely CO_2 limited with a switch to a horizontal maximum photosynthesis rate is assumed, while in GECROS the non-rectangular hyperbolic response to CO_2 concentrations of the Farquhar model (Farquhar et al., 1980) is applied. The objective of this study was to test the four crop growth models CERES-Wheat 2.0 (Ritchie and Godwin, 1987; Ritchie et al., 1987), SUCROS2 (Goudriaan and van Laar, 1994; Groot, 1987; Spitters et al., 1989; van Keulen et al., 1992; van Keulen and van Laar, 1982), SPASS (Wang, 1997; Wang and Engel, 2000) and GECROS (Yin and van Laar, 2005) which have been implemented into the Expert-N modelling package, in terms of their ability to simulate spring wheat aboveground biomass growth, grain yield and yield quality under various environmental conditions. For comparison only the plant models were exchanged while the models of water flow, nitrogen transport and heat transfer were the same for all four crop models. We therefore analyzed

i) if the impact of atmospheric CO_2 and water shortage on crop growth can be adequately simulated by each of the four different crop growth models and

ii) if a mechanistic modelling approach for the responses of crop growth on elevated atmospheric CO_2 concentrations is an improvement compared to the established models that include empirical assumptions.

2. Material and methods

2.1. The Expert-N model package

The model package Expert-N was developed to provide models for the simulation of soil-plant-atmosphere systems. Its modular design helps to combine simulation models from available components that were implemented into the Expert-N package. These components include sub-models to simulate soil water flow, soil heat transfer, turnover and transport of soil carbon and nitrogen, soil management and crop growth (Priesack, 2006; Priesack and Bauer, 2003). Different crop growth sub-models describe phenological development, photosynthesis, canopy formation, growth of aboveground and root biomass, crop senescence, transpiration and nitrogen uptake. They include corresponding routines of the generic plant models CERES-Wheat, SUCROS, SPASS and GECROS. In contrast to the original crop growth models, the sub-models to calculate soil processes such as water flow, heat transfer and nitrogen transport were replaced within the Expert-N package by corresponding sub-models based on different numerical simulation methods. For example, the different capacity type soil water flow models of the plant models CERES, SPASS, SUCROS and GECROS were substituted by a model based on a numerical solution of the Richards equation similar to that of the HYDRUS 1D model (Simunek et al., 1998). In this way, the model package Expert-N facilitates the comparison of crop growth models, since they can now be based on the same model components that represent the soil processes. In the following simulations we applied the soil water flow model similar to HYDRUS 1D (Simunek et al., 1998), the soil heat transfer and soil nitrogen transport description using the methods of the model LEACHN (Tillotson et al., 1980) and the soil carbon and nitrogen turnover simulation method after the approach of the SOILN model (Johnsson et al., 1987).

For the comparison of the crop growth models therefore in each case only the model components that describe plant processes were taken from the corresponding crop model, i.e. either from CERES, SUCROS, SPASS or GECROS.

2.2. Crop growth sub-models

CERES-Wheat is a process-oriented model that was developed for agricultural practice to simulate crop development and grain yield (Ritchie and Godwin, 1987; Ritchie et al., 1987). The model has been designed so that it can be used under extremely different environments, including those with limited water availability (Otter-Nacke et al., 1986; Otter-Nacke and Ritchie, 1989). A number of cultivar specific coefficients explain the variability between cultivars. As the original CERES model does not take into account the effect of the atmospheric CO_2 concentration on plant growth the model was modified to increase the light saturated photosynthetic capacity by 20% as the CO_2 concentration increases by 200 ppm (Tubiello et al., 1999).

The aim of the SUCROS model development was to quantify the aboveground biomass production of crops. While in SUCROS1 plant growth was dependent on temperature and radiation, it is further limited by the availability of water in SUCROS2. The SUCROS version implemented in Expert-N also considers nitrogen-limited growth, assuming for each crop species a maximal uptake and partitioning of nitrogen according to the partitioning key given by van Keulen and Seligman (1987). To consider the effect of CO_2 concentration, SUCROS was changed similar to CERES.

The SPASS model is a hybrid model composed by parts of both, the CERES-Wheat and the SUCROS models. For example, senescence of crops is simulated using the relative death rate based on the SUCROS model and partitioning of nitrogen follows the parameterization according to Penning de Vries et al. (1989). The maximum photosynthesis rate at light saturation is affected by the three factors nitrogen content of the leaf, air temperature and atmospheric CO_2 concentration. The factor correcting for the atmospheric CO_2 concentration is calculated on the base CO_2 concentration of 340 ppm with respect to the CO_2 compensation point and the CO_2 concentration within the leaf. In C_3 species the maximum rate of leaf photosynthesis is nearly proportional to the atmospheric CO_2 concentration and holds up to a level of about 700 ppm (Penning de Vries et al., 1989).

The GECROS model is a successor model of the SUCROS models. It was developed to better describe the interactions between genotype and environment. The input parameters therefore are mainly genotype-by-environment specific measurable parameters. The model is designed to deal with interactions of CO_2 and other environmental factors on photosynthesis based on the Farquhar model (Farquhar et al., 1980). Furthermore an optimal criterion for the root-shoot ratios of nitrogen and carbon is assumed. Thus, apart from temperature, radiation and water availability crop growth is also determined by the nitrogen supply.

2.3. Data sets for model input and testing

The experimental data used in this study are part of the "IMPETUS" project that are presented in Fangmeier et al. (1999) and Schütz (2002). The data were obtained from open-top-chamber (OTC) experiments carried out at the Justus-Liebig-Universität, Gießen, Germany. The OTC system is described in detail by

Fangmeier et al. (1991). The environmental conditions of the treatments were applied as presented in Table 1.

In the experiments, spring wheat was exposed to two different atmospheric CO_2 concentrations (ambient, elevated) and two different water supply levels (wet, dry). In the first year the influences of two soil types on crop growth (Cambisol, Chernozem) were also studied (Table 1). In both experimental years, the target plant density was 350 plants per square meter.

2.4. Model calibration

The four crop models were originally developed to simulate crop growth under field conditions. As the plots in 1999 were larger in surface area and in depth than the pots in 1998, we assumed that the experimental conditions in 1999 were closer to field conditions. Therefore we parameterized the model using the available measurements of the reference treatment (ambient CO_2, unlimited water supply, and Cambisol soil) in 1999 and data from literature if the experiments could not provide the required parameters.

According to Hunt et al. (1993) the model calibration was conducted iteratively. First, the crop phenological development of the four crop models was calibrated to the reference treatment. This was subsequently followed by adjusting the coefficients describing crop growth and grain development. The adapted parameter values are presented in Table 2. Genotype-specific parameters were used when measurements were available from the experiment or could be obtained from the literature. The rest of the model parameters were taken from the original model documentations. Subsequently, calibrated models were applied to the remaining treatments of 1998 and 1999.

2.5. Statistical measures

The ability of the model to match the observations was tested by two statistical criteria, the model efficiency index (ME) and the normalized root mean square error (NRMSE).

1. We define the ME after Willmott (1982) as

$$ME = 1 - \frac{\sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}(|P_i - \overline{O}| + |O_i - \overline{O}|)^2} \qquad (1)$$

where $\overline{O}$ denote for the mean values of the measured values O_i. The corresponding simulated values to O_i are P_i.

The ME is a method to evaluate the modelling performance results in a range between -∞ and 1. A value above 0 indicates that the simulation is better than a simulation of the mean of the measurements.

2. The NRMSE is given by

$$NRMSE = \frac{\sqrt{\frac{1}{n}\sum_{i=1}^{n}(P_i - O_i)^2}}{\overline{O}} \tag{2}$$

The NRMSE describes the average relative deviation between the simulation and the measurements. It evaluates the relative difference between simulation and measurement in a range between 0 for a perfect match of simulation and measurement and +∞ indicating no match at all.

ME and NRMSE were calculated for each model and each treatment for the observables growth stage, total aboveground biomass and leaf area index. In order to include variability of ME and NRMSE between the single treatments also the arithmetic means $\overline{ME}$ and $\overline{NRMSE}$, for the single examined plant variable over all treatments were calculated. In addition, the arithmetic means of the statistical measures over all considered plant variables and treatments, $\overline{\overline{ME}}$ and $\overline{\overline{NRMSE}}$, were calculated to provide aggregated indices, which facilitate comparison of model performance. In case of the yield parameters grain yield, thousand grain weight and grain number per square meter, which were measured once per year at the end of the vegetation period, only $\overline{ME}$ and $\overline{\overline{ME}}$ were calculated.

3. Simulation results

Figure 1 shows for the reference treatment the simulation results of all four models together with measured data. The results of the statistical evaluation of those output variables which were measured repeatedly during the vegetation period are presented for all treatments in Table 3. Simulation results as well as corresponding measurements of model outputs for which only one measurement at the end of the vegetation exists, are listed in Table 4. In Table 4 also the values of $\overline{ME}$ for these variables are shown.

3.1. Overall behaviour and model performance

Based on the values of $\overline{\overline{ME}}$ and $\overline{\overline{NRMSE}}$, a rough assessment of the performance of the models with respect to the crop growth variables presented in Table 3 is possible:

$\overline{\overline{ME}}$: SUCROS (0.85) > GECROS (0.84) > CERES (0.82) > SPASS (0.80)

$\overline{\overline{NRMSE}}$: SPASS (0.28) < SUCROS (0.30) < GECROS (0.43) < CERES (0.56)

For the grain yield parameters presented in Table 3, results:

$\overline{\overline{ME}}$: SPASS (0.73) > CERES (0.49) > GECROS (0.40) > SUCROS (0.22)

The development stages are well (within the standard deviations of the measurements (Figure 1), $\overline{ME}$>0.96 and $\overline{NRMSE}$<0.15 (Table 3)) simulated by all four crop models. However, due to the absence of measurements before development stage 50 in 1999 the pre-anthesis development could not be calibrated. For example, CERES reached development stage 20 two weeks earlier than GECROS. The simulation of the total aboveground biomass was within the standard deviations of the measurements except for the final harvest which was underestimated (Figure 1). In case of both, green leaf biomass and leaf area index (LAI) the variability of the measurements, particularly for the first harvest, was high. The four models do not generally agree with the measurements, in particular in the case of some high NRMSE values (above 1.00). These were observed in the cases of CERES and GECROS simulations concerning the state variables stem biomass, green leaf biomass and LAI, in case of SPASS simulations for stem biomass and in case of SUCROS simulations for total aboveground and stem biomass. None of the four crop models could simulate significant treatment effects on stem biomass. In case of the reference treatment the four models match the grain yield in the range of the measured variability (Figure 1). Nevertheless, simulations for different environmental conditions show some inaccurate results of grain yield which is indicated by comparably low $\overline{ME}$ values (Table 4).

CERES simulations under various environmental conditions are good in case of total aboveground biomass (Table 3). In case of LAI, the CERES simulations are not as good, although the ME and NRMSE values observed by CERES simulations are accurate for the reference treatment (and also for the corresponding treatment under elevated CO_2 concentration, Table 3). This is indicated by some high NRMSE values above 1.0 in 1998. Yet, the corresponding ME values are above 0.75 for most of the considered environmental conditions. The explanation is the steep slope of the LAI curve. Already a small phase shift due to both accelerated and slowed down LAI development can lead to high NRMSE values. Green and senescent leaf biomasses were generally inadequately simulated by CERES. This was due to rather poor simulations of leaf senescence which did not distinguish between both, environmental conditions and the amount of green leaf biomass available for senescence. Regarding the simulation of grain yield parameters the CERES simulations are neither the best nor the worst of the investigated crop models. This is indicated by $\overline{ME}$

values between 0.44 and 0.52 (Table 4).

GECROS simulations of total aboveground biomass under the different environmental conditions in the OTCs were the best ($\overline{ME}$=0.75, $\overline{NRMSE}$=0.31) but only slightly better than the simulation results of CERES (Table 3). The simulation results for stem biomass of the treatments in 1998 were rather poor and ME values ranged from 0.00 to 0.11, although in 1999 the quality of the simulation results of stem biomass exceeded those of the three other models and ranged from 0.48 to 0.90. GECROS is the best model for the simulations of the grain numbers per square meter because all simulation results are within the standard deviations of the measurements (Table 4). However, the weak $\overline{ME}$ value disagrees with this statement because the GECROS simulation results in 1999 do not reflect the high variation of the measurement means.

The *SPASS* simulations of the crop variables listed in Table 3 for the different environmental conditions are almost as accurate as the simulations using the SUCROS model, for which the $\overline{\overline{ME}}$ value is slightly better. Notably, there was a good performance of the SPASS simulations in case of the leaf senescence simulations under the different environmental conditions ($\overline{ME}$=0.82, $\overline{NRMSE}$=0.34). Results of comparable quality were simulated by none of the three other models. SPASS simulations are the best compared to the simulations of the other three models in the cases of grain yield ($\overline{ME}$=0.69) and the important grain yield parameters thousand grain weight ($\overline{ME}$=0.83) and grain number per square meter ($\overline{ME}$=0.67, Table 4).

Basically, *SUCROS* gives good results when vegetative aboveground crop organs are to be simulated under different environmental conditions. Based on the parameters analysed in Table 3 the SUCROS simulations in this case are the best ($\overline{ME}$=0.85 and $\overline{NRMSE}$=0.28), which is basically due to the substantially good simulation results of LAI under the different environmental conditions in the OTC experiments ($\overline{ME}$=0.92). Also green leaf biomass is well simulated by SUCROS for all considered environmental conditions ($\overline{ME}$=0.91). A major weakness of SUCROS is the simulation of grain yield under the different environmental conditions ($\overline{ME}$=0.22). Moreover, the variables thousand grain weight and grain number per square meter cannot be simulated by the SUCROS model.

Good simulation results using the SUCROS model were only achieved when the parameterization for nitrogen allocation to the crop organs of van Keulen and Seligman (1987) was applied. In case of SPASS it was necessary to apply the parameterization of Penning de Vries et al. (1989). At first glance this is surprising, however, the models have been developed by the respective parameterization.

3.2. Environmental conditions

In Table 5, the relative effects of increased CO_2 concentrations and water shortage on both, measured and simulated aboveground biomass are expressed as the ratios between of the results with and without the respective treatment. This is indicated in the header of the first column, whereas the parameters which were not changed are the entries of this column.

3.2.1. Atmospheric CO_2 concentration

Generally the four crop models were in agreement with the assumption that elevated atmospheric CO_2 concentrations increase plant growth. Nevertheless, some weaknesses were obtained for the accuracy of the simulations with any of the four crop models. The strong variation of the CO_2 response on total aboveground biomass, which was measured in the OTC with respect to the development stage in 1999 could not be simulated by any of the four crop models. The slightly earlier development of green leaf biomass under elevated CO_2, which was observed for barley by Fangmeier et al. (2000), was also simulated using GECROS, CERES and SPASS. Leaf senescence under elevated CO_2 concentrations was delayed in the simulations of each of the four crop models compared to the OTC measurements. Simulations show an increase of senescent leaf biomass under elevated CO_2 conditions for both, SPASS and GECROS simulations. While the best simulations for senescent leaf biomass were obtained by the SPASS model under all different environmental conditions, the best response of leaf senescence to CO_2 elevation was simulated using GECROS.

The simulations using of the four models under different CO_2 concentrations basically increased the total aboveground biomass and the grain yield. While a more sensitive response was observed for the GECROS and SPASS simulations, the response of the *CERES* and *SUCROS* simulations to elevated CO_2 increased grain yields and total aboveground biomass rather constantly by 18% (CERES) and 16% (SUCROS). This increase was unaffected by environmental conditions or the development stage of the crop.

In *SPASS* simulations, elevated CO_2 increased total aboveground biomass and grain yields by 53% on average. Especially the impact of CO_2 elevation on grain yields ranged from minimum increases of 43% up to 71%. On average, the CO_2 response on grain yield was much stronger expressed in 1999 (68%) than in 1998 (49%). In interaction with other environmental factors the response on elevated CO_2 was of higher flexibility than that observed for SUCROS and CERES simulations.

Obviously, *GECROS* simulations show a higher CO_2 fertilization effect on grain yield when the water supply is limited. The highest sensitivity to CO_2 concentration on grain yields was simulated using GECROS. Elevated CO_2 increased grain yields on average by 42%, however the degree of the CO_2 response interacted strongly with the availability of water and nitrogen, resulting in a decrease by 2% up to an increase by 97%. Thus, elevated CO_2 increased grain yields on average by 53% under water limited conditions, but only by 31% when water supply was unlimited. The increase observed in the measurements of total aboveground biomass resembles the average increase simulated by applying the GECROS model being about 26% on average for all treatments. However, in 1998 total aboveground biomass at development stage 65 was overestimated by 25% on average compared to the measurements, while the simulations correspond to the measurements at crop maturity. In 1999, the GECROS simulations clearly indicate that the observed CO_2 effect depended on the development stage and occurred stronger in the earlier development stages (DC 44-65) compared to the results at later development stages (DC 77-92). Thus, in GECROS simulations in both years the increase of total aboveground biomass was smaller under elevated CO_2, with ongoing plant development by 16% on average from 48% at heading to 34% at maturity in 1998 and from 36% to 18% in 1999. Moreover, GECROS also indicated a slightly increased CO_2 fertilization effect on total aboveground biomass when the water supply was limited. Despite the sensitivity of GECROS to respond to CO_2 concentration, similar to the other growth models the strong variation of the CO_2 response measured in the OTC experiments with respect to the development stage could not be simulated.

The positive CO_2 fertilization effect on the thousand grain weight obtained under Cambisol soil conditions was also simulated by GECROS. Also the measured negative CO_2 fertilization effect of Chernozem soil conditions could be found by GECROS simulations, however to a lesser extent than by the measurements (Table 4).

3.2.2. Water supply

The total aboveground biomass and the grain yield were differently affected by dry (water limited) and wet (unlimited water supply) conditions in the two experimental years. The significant reductions of total aboveground biomass and grain yields, which were observed in the OTCs under water limited conditions in 1998, could not be simulated by any of the four crop models. Moreover, in 1998 the models showed no different response to dry or wet conditions on total aboveground biomass and grain yields. In 1999, the simulation results of all models are in agreement with the observation that limited water supply decreases the grain yield. In 1999, the measured reduction of total aboveground biomass under water limited conditions was continuously simulated by CERES, SPASS and *SUCROS* models throughout the vegetation period. In the *GECROS* simulations this reduction did not occur until flowering, but then a drop of 22% was simulated for the dry treatments until maturity. In all models no response of grain yield simulations on the amount of water supply was observed. While the number of grains per square meter was underestimated using CERES and SPASS, overestimations occurred in the simulations with both models for the thousand grain weights. The simulations of thousand grain weights by GECROS agree well with the measurements in the OTC. Although a poor $\overline{ME}$ value was observed for the simulation of number of grains per square meter, the best simulation results were observed using GECROS because all simulations were accurate within the range of the standard deviations of the measurements (Tables 4 and 5).

3.2.3. Soil type

Due to the experimental setup only the two soils in 1998 are compared in this section. (Table 1).

No or only small soil effects on total aboveground biomass were simulated by CERES, SUCROS and SPASS. GECROS simulations, however, indicate that total aboveground biomass production is 19% higher on Chernozem than on Cambisol soil (Table 5).

In the measurements on average 30% lower grain yields were observed on Chernozem than on Cambisol soil (Schütz, 2002; Schütz and Fangmeier, 2001). CERES and SPASS simulations also show lower grain yields on Chernozem soil. Using SUCROS no effects were obtained while the opposite soil effect on grain yield was simulated by GECROS.

4. Discussion

The NRMSE and ME values for the comparison between simulated and measured crop growth parameters are comparable to other simulation studies (Niu et al., 2009; Priesack et al., 2006; Wegehenkel and Mirschel, 2006). The ME values are generally above 0.00, indicating better model performance than a model which only predicts the mean of the measurements. Using the applied parameterization some high NRMSE values show that the four models tested in the present study cannot reliably predict all plant variables under the different environmental conditions of the OTCs.

Rather poor simulations were observed in case of green leaf biomass and LAI by CERES, SPASS and GECROS. This is due to the calibration of the models which was done predominantly with respect to the measured grain yield and total aboveground biomass but restricted to available measurements and the range of literature values. Nevertheless, as indicated by the ME values, the dynamics of green leaf biomass and LAI are yet well simulated by SPASS and GECROS for most of the environmental conditions. The explanation for the weak NRMSE, but better ME values is that the slope of the curves for green leaf biomass and LAI are generally steep. Thus, at one and the same date an early or delayed onset of leaf growth or senescence causes strong differences between the measurements and the simulations. Ewert (2004) shows the necessity of LAI modelling for a better understanding of substrate allocation and aboveground biomass growth, especially for agricultural crops that have large temporal variability in LAI. We found that the simulated qualitative development of LAI is of higher importance for the simulation of crop growth than its temporal dynamic. This means a time shift of LAI by some days does not significantly affect crop growth.

If only total aboveground biomass and grain yields have to be estimated and impacts of environmental factors can be neglected, the application of the model CERES leads to simulations of high quality based on a minor parameterization effort. Even though the somewhat weaker overall quality of the CERES simulations the model gave good results for development stage, total aboveground biomass and grain yield. The little effort required for parameterization is very attractive. Later versions of CERES (e.g. DSSAT (Jones et al., 2003) and CROPSIM (Hunt and Pararajasingham, 1995)) allow for a more detailed parameterisation of crop varieties and follow a more physical approach.

GECROS requires the highest effort for parameterization of all four models. This is basically due to two reasons: Firstly, the high number of parameters that have to be set and secondly, the sensitivity of the model on some of these parameters.

Both, chamber and pot effects (Arp, 1991; Passioura, 2002; Pinter et al., 2000) can not be ruled out in this study because no comparable measurements under field conditions are available. The absence of more detailed information on soil properties causes uncertainties with the interpretation of the simulation results of the four crop models. A detailed description on possible reasons for disagreements between measurements and simulation results, based on OTC data is given by van Oijen and Ewert (1999). Indeed the four crop models were developed to predict crop growth under field conditions, which might not directly cause errors in the OTC simulations, but to some extent a different parameterization would be obtained using field data.

4.1. Environmental conditions

4.1.1. Atmospheric CO_2 concentration

In agreement with Goudriaan et al. (1999) we doubt that an almost constant increase of the light use efficiency in the way it is implemented in our SUCROS and CERES versions is a meaningful way to account for a positive CO_2 fertilization effect. The constant increase assumption basically ignores possible interactions with other environmental factors affecting plant growth. The measurements by Schütz (2002) show that elevated CO_2 increased grain yields on average by 48% in 1998 and by 35% in 1999. Findings of several authors who analysed OTC experiments indicate that the CO_2 fertilization effect on total aboveground biomass and on grain yield varies strongly from approximately 10 to 120% with even stronger variations if measurements throughout the vegetation period are considered (Bender et al. (1999); Fangmeier et al. (1999); Schütz (2002); Schütz and Fangmeier (2001); van Oijen and Ewert (1999)). Such a more sensitive CO_2 response was observed by simulations of the two more mechanistically based modelling approaches of GECROS and SPASS. The models are better if the impact of various CO_2 concentrations and its interactions with other environmental factors on physiological aspects of crop growth such as water supply are considered (Table 3). The biochemical photosynthesis model of Farquhar et al. (1980) which is implemented in GECROS with modifications by Yin et al. (2004) was better than the simpler response in SPASS. The latter model assumes a constant initial slope when photosynthesis is entirely CO_2-limited and then switches to a horizontal maximum photosynthesis rate (Wang, 1997).

In most studies on the effects of elevated CO_2 on C_3 species positive effects on aboveground biomass production were observed (Ewert et al., 2002; Fangmeier et al., 2000; Poorter et al., 1996). Our simulation results do mostly indicate a surplus of CO_2 enrichment on biomass production and on grain yield. Only in case of GECROS simulations a few negative CO_2 fertilization effects occurred. Mainly the highest sensitivity of the CO_2 response was observed in the mechanistic approaches implemented in the SPASS and GECROS models.

4.1.2. Interactions of CO_2 and water supply

Ainsworth et al. (2008) argue that the CO_2 response algorithms are up to now based on enclosure studies where the CO_2 effect was experienced higher than in field experiments. However, in this study the simulated range of CO_2 responses and its interactions with water supply were within the range of the measurements. We can neither agree nor disagree the statement by Ainsworth et al. (2008). Following Ziska and Bunce (2007), who found that differences of the CO_2 effects on crop growth between field and enclosure studies are small, the algorithms should work in either case. In this study, often the more mechanistically approaches of GECROS and SPASS matched or even overestimated the CO_2 response on total aboveground biomass that was measured in the OTC under water limitation as well as under unlimited water supply. This shows that the mechanistic algorithms worked well at least in case of the OTCs in this study. Ewert et al. (2002), Manderscheid and Weigel (2007) and Tubiello and Ewert (2002) found that summer drought effects can be weakened by increasing atmospheric CO_2 concentration. The GECROS simulations of total aboveground biomass agree with this finding, but the remaining models did not show this trend.

Piikki et al. (2008) observed no significant CO_2 effect on the thousand grain weight of wheat, but they show that elevated CO_2 increases grain yields mainly by an increase of the grain number per square meter. The measurements of thousand grain weights by Schütz (2002) and Schütz and Fangmeier (2001) show a strong variability and may support both conclusions, either that elevated CO_2 increases the grain numbers per square meter or that this parameter is rather unaffected by CO_2 elevation. Simulation results by both models, CERES and SPASS, also showed a CO_2 effect on the grain numbers per square meter and thus support the findings by Piikki et al. (2008). However, both models underestimated the grain numbers per square meter strongly. The rather stable grain numbers per square meter which were simulated using GECROS were the best to simulate this grain yield parameter under the different environmental conditions. In contrast to both, CERES and SPASS, which similarly calculate the grain number per square meter from the stem weight at the start of flowering, in GECROS, the grain numbers per square meter are a function of the estimated soluble nitrogen in vegetative organs, which are replaceable for grain growth, the achieved nitrogen-to-carbon ratio in the grain, the achieved grain weight and the proportion of grain nitrogen, which is accumulated before the end of the grain number determining period that comes from non-structural nitrogen pools in vegetative organs. This nitrogen reserve limited grain number determination and grain filling approach obviously works good enough to adequately simulate the measurements in the special case of the analysed OTC system. However, in absence of measurements of nitrogen contents we cannot decide whether the mechanism implemented in GECROS is correct or if it just works in the special case analysed in this study.

4.1.3. Soil type

The soil hydraulic properties were estimated by Expert-N with respect to the soil texture, the content of organic carbon and the estimated soil density to simulate transpiration and soil water flow. Therefore the calculated hydraulic properties could be at some degree different from those in the experimental soils and may have influenced the simulation accuracy to some unknown extent.

The Cambisol soil was characterized as a low fertility soil based on the lower contents of organic carbon and macro nutrient contents than the Chernozem soil (Schütz, 2002). Although nutrients other than nitrogen are not taken into account by any of the four crop models we would expect spring wheat growth on the different soils in the OTC system similar to the results simulated by the GECROS model where grain yields were higher on the Chernozem soil.

5. Conclusions

Decoupled from the original models to calculate water, nitrogen and heat transfer but embedded into a uniform model environment provided by Expert-N four crop models were tested for the ability to simulate the special cases of environmental conditions of an OTC study. The NRMSE and ME values show that the best simulation results were achieved for the development stages. The qualities of the simulations of the other crop parameters were mostly of comparable accuracy as observed in other studies. Some simulation results however were at the lower limit of accuracy (NRMSE values above 0.75 and ME values below 0.5). SUCROS simulations are good in case of simulated vegetative crop organs, but grain yield simulations are not as good. The CERES model is attractive for the little effort of parameterization and the good results in total aboveground biomass and grain yield. In case of GECROS significantly better simulation results were observed in 1999 than for the treatments in 1998. Similar to simulations with SUCROS the simulations of grain yield are not good using the GECROS model. However, the variability of the CO_2 fertilization effect on grain yields is most sensitive using GECROS. Based on a parameterization using values obtained by Penning de Vries et al. (1989) the SPASS model combines the positive properties of CERES and SUCROS. Using SPASS most impressing were the good simulation results for the different environmental conditions in 1998, where simulation outliers were more frequent for the other models.

The impact of atmospheric CO_2 and its high variability due to interactions with other environmental factors were more sensitively simulated by the two different mechanistic modelling approaches in GECROS and SPASS. Nevertheless, neither the dynamics at different development stages nor the relative effects between ambient and elevated CO_2 conditions were consistently adequately simulated in comparison with the OTC measurements. The empirical approaches that constantly increase the elevated CO_2 response are in most cases too static and not sensitive enough to adequately respond to interactions with other environmental factors. Although the mechanistic approaches were more substantial, we conclude that neither the static nor the mechanistic approaches are good enough for adequate simulations of interactions between CO_2 and other environmental factors on plant growth. Whether this is due to the special conditions of the OTC or due to insufficient understanding of elevated CO_2 response remains unclear. The results of this study suggest that further research is needed to improve the understanding of the CO_2 response of crop growth under different environmental conditions especially with regard to realistic field conditions.

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figure caption

figure 1: Simulation results and dynamic of the reference treatment (wet, ambient CO_2, Cambisol, 1999) after calibration. Numbers of x-axis indicate the days after sawing. Abbreviations: DW - dry weight, TAGB - total aboveground biomass, LAI - leaf area index. Error bars are standard deviations of the measurements.

Table 1: Experimental conditions of the applied data sets (Schütz, 2002).

Cultivar	*Triticum aestivum* L. cv. 'Minaret'		
Year	1998	1998	1999
Soil type	Chernozem	Cambisol	Cambisol
Soil texture	Clay loam (Lt)	Loamy sand (Sl)	Loamy sand (Sl)
Soil depth [cm]	40 cm (pot system)	40 cm (pot system)	50 cm (plot system)
N-Fertilization [kg N ha^{-1}]	200	200	200
Irrigation (wet) [mm]	718±67	789±115	433±5
Irrigation (dry) [mm]	377±40	477±48	102±2
ambient CO_2 [ppm]	Ø380.4±27.1	Ø380.4±27.1	Ø383.7±32.3
elevated CO_2 [ppm]	Ø634.1±69.2	Ø634,1±69.2	Ø672.7±120.0
Organic C content [%]	2.44	0.812	0.812
Organic N content [%]	0.24	0.081	0.081
Texture (S/U/C) [%]	35/44/21	67/22/11	67/22/11
Porosity [%]	57	52	52
Field capacity (pF 1.8)	45	40	40
Wilting point (pF 4.2)	30	17	17
Plot size [m^2]	0.27	0.27	1.765
Lateral canopy border conditions	Shading fences	Shading fences	Border strip
Average PAR [MJ m^{-2} d^{-1}]	9.9±4.6	9.9±4.6	10.2±3.6
Location of the experiments	50.6°N, 8.7°E. Gießen, Germany.		

Soil type according to FAO classification. Soil textures as described in AG Boden (1994). Air flow rate within the OTC amounted to 19000 m^3h^{-1}.

Table 2: Crop growth model parameter values.

Model	Parameter		Unit	Spring wheat	Reference
CERES	P5	grain filling period coefficient		4	
	P1D	day length coefficient		3.25	
	P1V	vernalization coefficient		0.3	
	fPhint	phyllochrome interval		80	Ritchie and Godwin (1987)
	G1	kernel number coefficient		4	Godwin et al. (1990)
	G2	Kernel weight coefficient		3	Godwin et al. (1990)
	LUE	light use efficiency		ambient CO_2: 7.5	Ritchie and Godwin (1987)
				elevated CO_2: 9.0	Ritchie and Godwin (1987)
GECROS	YGV	growth efficiency of vegetative organs	g C g^{-1} C	0.79	Penning de Vries et al. (1989)
	CFV	carbon fraction in vegetative-organ biomass	g C g^{-1} dw	0.45	Tubiello et al. (1999)
	LWIDTH	leaf width	m	0.012	Bos and Neuteboom (1998)
	LNCI	initial critical shoot nitrogen concentration	g N g^{-1} dw	0.0555	Brooks et al. (2000)
	RNCMIN	minimum nitrogen concentration in root	g N g^{-1} dw	0.0076	Rroco and Mengel (2000)
	STEMNC	minimum nitrogen concentration in stem	g N g^{-1} dw	0.005	Abreu et al. (1993)
	SEEDW	weight of a single seed	g $seed^{-1}$	0.038	Diepenbrock et al. (1999)
	SEEDNC	standard seed N concentration	g N g^{-1} dw	0.0242	Weigel and Manderscheid (2005)
	HTMX	Maximum plant height	m	0.9	
	CDMHT	proportionality factor between stem biomass and plant height	g m^{-2} m^{-1}	450	
	MTDV	Minimum thermal days for vegetative phase	day	22	
	MTDR	Minimum thermal days for reproductive (seed fill)	day	32	
	EAJMAX	Activation energy of J_{max} (photosynthesis whole-chain electron transport)	J mol^{-1}	23100	Alonso et al. (2009)
	BLD	Leaf angle from horizontal		25°	Simon (1999)
	NUPTX	Maximal N-uptake rate	g N $m^{-2}d^{-1}$	0.5	
	SLNMIN	minimum specific leaf nitrogen	g N g^{-1}	0.2	
	RDMX	maximum root depth	cm	1998: 40; 1999: 50	
SPASS	D_v	physiological development days before anthesis	day	37	
	D_r	physiological development days after anthesis	day	24	
	V_{nd}	vernalization requirement	day	0	
	Ω	photoperiod sensitivity factor	day^{-1}	0.25	
	$R_{gfill,max}$	maximum grain filling rate	mg $grain^{-1}$ day^{-1}	1.75	
	ξ_{grain}	number of grains	g grains $stem^{-1}$	25	
	basis parameterization for Nitrogen allocation according to				Penning de Vries et al. (1989)
SUCROS	TbaseV	base temperature of development rate before anthesis	°C	0	
	DVRV	development rate before anthesis	°C day^{-1}	0.4	
	TbaseR	base temperature of development rate after anthesis	°C	0	
	$DVRR^{-1}$	development rate after anthesis	(°C day^{-1})	0.48	
	LUE	light use efficiency	g MJ^{-1}	ambient CO_2: 0.45	Ritchie and Godwin (1987)
				elevated CO_2: 0.54	Ritchie and Godwin (1987)
	basis parameterization of Nitrogen allocation according to				van Keulen and Seligman (1987)
		specific leaf weight	g m^{-2}	45.4	Spitters and Kramer (1986)

Table 3: Model efficiency index (ME) and normalized root mean square error (NRMSE) of the simulations with the respective model for the development stage, the total aboveground biomass (TAGB) and the leaf area index (LAI). $\overline{ME}$ and $\overline{NRMSE}$ represent the arithmetic means of each column, while $\overline{\overline{ME}}$ and $\overline{\overline{NRMSE}}$ represent the arithmetic mean of the observed ME and NRMSE values of a single crop model.

Treatment	Growth stage	TAGB	LAI	Growth stage	TAGB	LAI
	ME/NRMSE	ME/NRMSE	ME/NRMSE	ME/NRMSE	ME/NRMSE	ME/NRMSE
		CERES			SPASS	
wet/aCO_2/Ch/1998	0.95/0.23	0.81/0.14	0.86/0.66	0.98/0.13	0.81/0.14	0.76/0.77
wet/eCO_2/Ch/1998	0.97/0.17	0.75/0.18	0.53/2.72	0.99/0.10	0.59/0.29	1.00/0.13
wet/aCO_2/Ca/1998	0.97/0.16	0.68/0.27	0.90/0.49	0.99/0.12	0.55/0.31	0.68/0.94
wet/eCO_2/Ca/1998	0.98/0.15	0.64/0.37	0.91/0.52	0.99/0.11	0.52/0.50	0.70/0.90
dry/aCO_2/Ch/1998	0.95/0.21	0.34/0.75	0.60/2.17	0.98/0.12	0.00/0.27	1.00/0.12
dry/eCO_2/Ch/1998	0.97/0.18	0.64/0.38	0.55/2.55	0.99/0.11	0.07/0.31	0.99/0.16
dry/aCO_2/Ca/1998	1.00/0.16	0.59/0.28	0.57/2.40	1.00/0.12	0.39/0.26	0.99/0.14
dry/eCO_2/Ca/1998	0.98/0.15	0.98/0.04	0.67/1.72	0.99/0.11	0.44/0.31	0.94/0.40
wet/aCO_2/Ca/1999 *	0.97/0.16	0.93/0.14	0.91/0.33	0.99/0.12	0.79/0.21	0.86/0.35
wet/eCO_2/Ca/1999	0.94/0.09	0.86/0.23	0.88/0.38	1.00/0.02	0.74/0.35	0.89/0.53
dry/aCO_2/Ca/1999	0.94/0.09	0.80/0.24	0.76/0.75	1.00/0.04	0.61/0.32	0.91/0.32
dry/eCO_2/Ca/1999	0.94/0.09	0.83/0.22	0.84/0.56	0.99/0.04	0.68/0.33	0.86/0.45
$\overline{ME}$ (Mean±SD)	0.96±0.02	0.74±0.17	0.75±0.15	0.99±0.01	0.52±0.26	0.88±0.11
$\overline{NRMSE}$ (Mean±SD)	0.15±0.04	0.27±0.18	1.27±0.96	0.09±0.04	0.30±0.09	0.42±0.30
	$\overline{\overline{ME}} = 0.82\pm0.17$. $\overline{\overline{NRMSE}} = 0.56\pm0.75$			$\overline{\overline{ME}} = 0.80\pm0.26$. $\overline{\overline{NRMSE}} = 0.28\pm0.22$		
		GECROS			SUCROS	
wet/aCO_2/Ch/1998	0.98/0.17	0.73/0.31	0.63/0.84	0.98/0.23	0.79/0.15	0.81/0.67
wet/eCO_2/Ch/1998	0.98/0.16	0.74/0.28	0.65/2.04	0.99/0.17	0.75/0.15	0.97/0.39
wet/aCO_2/Ca/1998	0.96/0.21	0.48/0.61	0.62/1.07	0.99/0.16	0.64/0.22	0.73/0.82
wet/eCO_2/Ca/1998	0.97/0.17	0.56/0.60	0.67/0.78	0.99/0.15	0.58/0.36	0.77/0.74
dry/aCO_2/Ch/1998	0.97/0.17	0.65/0.39	0.85/0.56	0.98/0.21	0.26/1.04	0.98/0.30
dry/eCO_2/Ch/1998	0.98/0.16	0.95/0.10	0.65/2.00	0.99/0.18	0.52/0.56	0.98/0.32
dry/aCO_2/Ca/1998	0.99/0.21	0.70/0.27	0.76/0.66	0.98/0.16	0.41/0.48	0.98/0.27
dry/eCO_2/Ca/1998	0.97/0.18	0.73/0.27	0.86/0.84	0.99/0.15	0.83/0.11	1.00/0.12
wet/aCO_2/Ca/1999 *	0.96/0.21	0.89/0.19	0.87/0.35	0.99/0.16	0.80/0.20	0.90/0.36
wet/eCO_2/Ca/1999	1.00/0.02	0.78/0.29	0.96/0.24	1.00/0.09	0.70/0.30	0.92/0.33
dry/aCO_2/Ca/1999	1.00/0.04	0.93/0.18	0.90/0.33	1.00/0.09	0.70/0.27	0.98/0.18
dry/eCO_2/Ca/1999	1.00/0.02	0.90/0.20	0.93/0.36	0.99/0.09	0.71/0.26	0.95/0.29
$\overline{ME}$ (Mean±SD)	0.98±0.01	0.75±0.15	0.78±0.13	0.99±0.01	0.64±0.17	0.92±0.09
$\overline{NRMSE}$ (Mean±SD)	0.14±0.07	0.31±0.15	0.84±0.61	0.15±0.04	0.34±0.26	0.40±0.22
	$\overline{\overline{ME}} = 0.84\pm0.15$. $\overline{\overline{NRMSE}} = 0.43\pm0.46$			$\overline{\overline{ME}} = 0.85\pm0.19$. $\overline{\overline{NRMSE}} = 0.30\pm0.22$		

* indicates the reference treatment; wet: unlimited water supply; dry: water limited conditions; aCO_2: ambient; eCO_2: elevated atmospheric CO_2 concentrations; Ch: Chernozem soil; Ca: Cambisol soil.

Table 4: Comparison of measurements and simulations of grain yield parameters.

Yield parameters	Treatment	Measured ± SD	CERES Simulated	GECROS Simulated	SPASS Simulated	SUCROS Simulated
Grain yield [g m^{-2}]	wet/aCO_2/Ch/1998	575±84	537.2	433.3	498.2	594.8
	wet/eCO_2/Ch/1998	809±146	639.3	422.7	779.1	743.0
	wet/aCO_2/Ca/1998	790±50	569.3	290.4	550.2	620.4
	wet/eCO_2/Ca/1998	1107±180	682.9	522.8	785.9	705.2
	dry/aCO_2/Ch/1998	301±40	539.3	446.2	514.9	684.2
	dry/eCO_2/Ch/1998	441±239	640.7	619.1	765.7	791.2
	dry/aCO_2/Ca/1998	401±29	569.6	320.5	530.2	684.1
	dry/eCO_2/Ca/1998	657±63	682.9	630.1	777.6	772.8
	wet/aCO_2/Ca/1999 *	566±98	582.1	557.3	479.2	608.3
	wet/eCO_2/Ca/1999	832±241	681.5	648.5	819.1	705.5
	dry/aCO_2/Ca/1999	530±145	372.0	540.1	302.4	479.0
	dry/eCO_2/Ca/1999	648±120	448.0	661.2	501.2	542.9
	$\overline{ME}$		0.50	0.33	0.69	0.22
Thousand grain weight [g]	wet/aCO_2/Ch/1998	42.3±1.5	41.2	32.1	42.0	-
	wet/eCO_2/Ch/1998	41.9±0.3	40.7	38.0	42.8	-
	wet/aCO_2/Ca/1998	36.9±2.9	43.5	38.0	42.7	-
	wet/eCO_2/Ca/1998	40.0±1.8	43.5	37.9	43.7	-
	dry/aCO_2/Ch/1998	38.5±2.2	41.2	37.4	40.0	-
	dry/eCO_2/Ch/1998	37.1±2.7	40.7	34.8	42.6	-
	dry/aCO_2/Ca/1998	35.9±1.9	43.5	37.8	41.6	-
	dry/eCO_2/Ca/1998	39.4±0.9	43.5	34.6	43.5	-
	wet/aCO_2/Ca/1999 *	32.9±4.8	43.9	32.2	39.7	-
	wet/eCO_2/Ca/1999	35.9±2.3	42.8	38.0	42.0	-
	dry/aCO_2/Ca/1999	33.4±2.8	36.2	31.3	32.4	-
	dry/eCO_2/Ca/1999	37.1±1.5	37.6	37.9	32.5	-
	$\overline{ME}$		0.44	0.55	0.83	-
Grain number m^{-2} [m^{-2}]	wet/aCO_2/Ca/1999 *	17143±1386	13382	17378	12162	-
	wet/eCO_2/Ca/1999	22957±5732	16072	17143	19664	-
	dry/aCO_2/Ca/1999	15645±3308	10364	17391	9421	-
	dry/eCO_2/Ca/1999	17434±1352	12027	17472	15564	-
	$\overline{ME}$		0.52	0.31	0.67	-

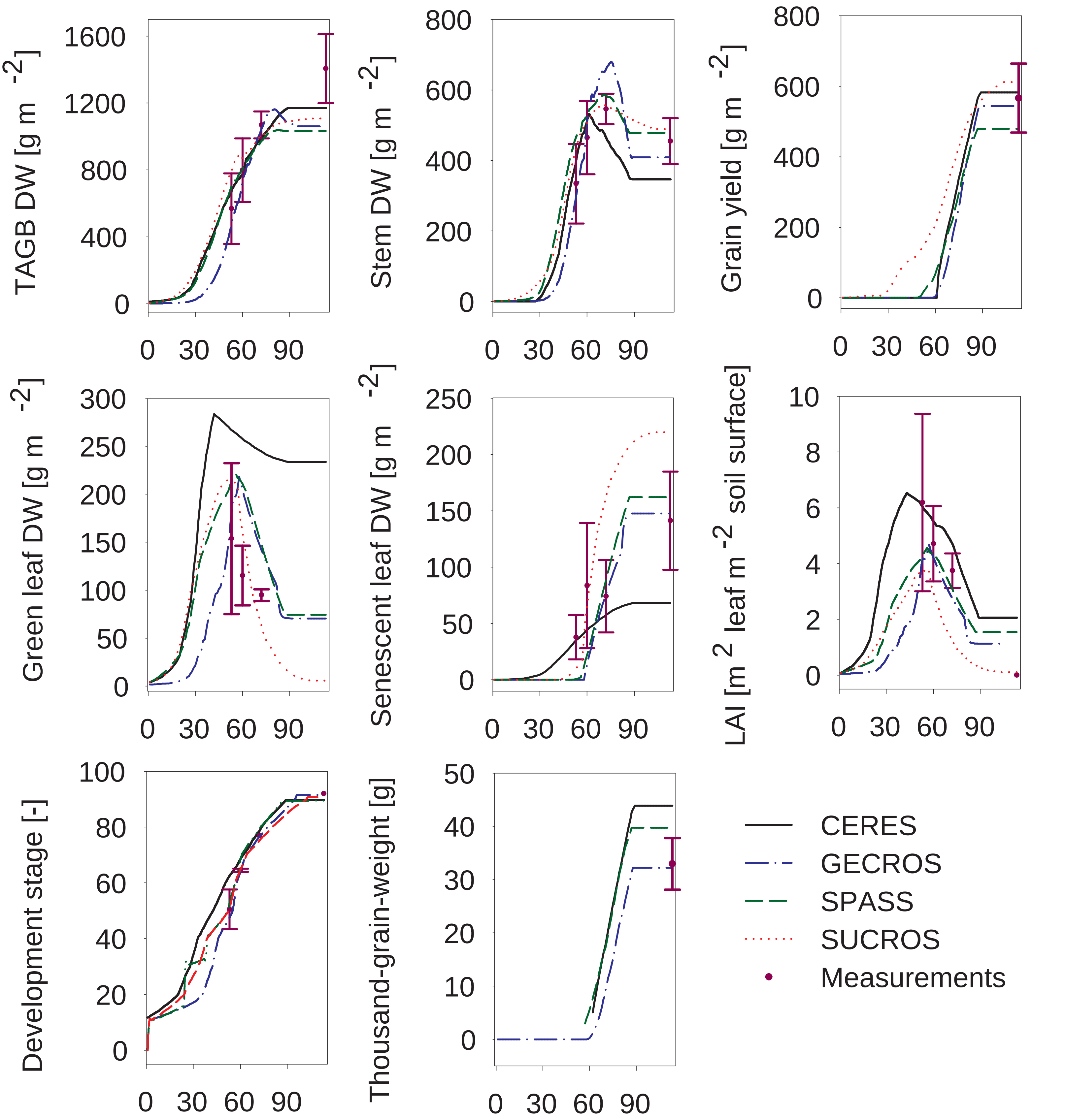
* indicates the reference treatment. wet: unlimited water supply; dry: water limited conditions; aCO_2: ambient, eCO_2: elevated atmospheric CO_2 concentrations; Ch: Chernozem; Ca: Cambisol. SD: Standard deviation.

Table 5: Fraction of the relative effects of each environmental condition on total aboveground biomass for the measurements and for the four crop models.

		Measurement	CERES	GECROS	SPASS	SUCROS
Relative effect of CO_2 (eCO_2 vs. aCO_2)	Development stage	Ratio of the corresponding eCO_2 vs. aCO_2 treatment				
wet/Ch/1998	65	1.28	1.18	1.49	1.45	1.36
	92	1.27	1.19	1.26	1.58	1.30
wet/Ca/1998	65	1.12	1.18	1.45	1.36	1.14
	92	1.38	1.18	1.36	1.43	1.15
dry/Ch/1998	65	1.35	1.17	1.49	1.37	1.14
	92	1.63	1.19	1.26	1.49	1.16
dry/Ca/1998	65	1.50	1.18	1.51	1.37	1.14
	92	1.58	1.18	1.49	1.45	1.14
wet/Ca/1999 *	44-57	1.14	1.18	1.36	1.58	1.14
	64-65	1.05	1.18	1.28	1.56	1.14
	77	1.00	1.19	1.18	1.57	1.15
	92	1.31	1.18	1.17	1.64	1.16
dry/Ca/1999	44-57	0.96	1.16	1.37	1.61	1.11
	64-65	1.43	1.15	1.29	1.56	1.11
	77	1.10	1.16	1.26	1.60	1.12
	92	1.10	1.18	1.20	1.64	1.12
Relative effect of water supply (dry vs. wet)		Ratio of the corresponding dry vs. wet treatment				
aCO_2/Ch/1998	65	0.58	1.01	0.99	1.05	1.18
	92	0.51	1.00	0.96	1.04	1.16
eCO_2/Ch/1998	65	0.61	1.00	0.99	0.99	1.00
	92	0.65	1.00	0.96	0.98	1.04
aCO_2/Ca/1998	65	0.68	1.00	1.07	0.99	1.00
	92	0.55	1.00	1.31	0.97	1.06
eCO_2/Ca/1998	65	0.92	1.00	1.12	0.99	1.00
	92	0.64	1.00	1.43	0.99	1.05
aCO_2/Ca/1999 *	44-57	0.90	0.88	1.00	0.82	0.82
	64-65	0.67	0.81	1.00	0.77	0.77
	77	0.79	0.86	0.84	0.81	0.79
	92	0.88	0.76	0.77	0.74	0.79
eCO_2/Ca/1999	44-57	0.76	0.86	1.00	0.84	0.80
	64-65	0.90	0.79	1.00	0.77	0.75
	77	0.88	0.84	0.90	0.83	0.77
	92	0.74	0.76	0.79	0.73	0.76

* indicates the reference treatment; development stages according to Zadok et al. (1974); wet: unlimited water supply; dry: water limited conditions; aCO_2: ambient; eCO_2: elevated atmospheric CO_2 concentrations; Ch: Chernozem soil; Ca: Cambisol soil.

Figure



TAGB DW [g m -2]
1600
1200
800
400
0
0 30 60 90
Stem DW [g m -2]
800
600
400
200
0
0 30 60 90
Grain yield [g m -2]
800
600
400
200
0
0 30 60 90
Green leaf DW [g m -2]
300
250
200
150
100
50
0
0 30 60 90
Senescent leaf DW [g m -2]
250
200
150
100
50
0
0 30 60 90
LAI [m 2 leaf m -2 soil surface]
10
8
6
4
2
0
0 30 60 90
Development stage [-]
100
80
60
40
20
0
0 30 60 90
Thousand-grain-weight [g]
50
40
30
20
10
0
0 30 60 90
CERES
GECROS
SPASS
SUCROS
Measurements