

# Sensitivity of field-scale winter wheat production in Denmark to climate variability and climate change

Jørgen E. Olesen<sup>1,\*</sup>, Tom Jensen<sup>2</sup>, Jens Petersen<sup>1</sup>

<sup>1</sup>Department of Crop Physiology and Soil Science and <sup>2</sup>Department of Agricultural Systems, Danish Institute of Agricultural Sciences, PO Box 50, 8830 Tjele, Denmark

**ABSTRACT:** A simulation model of the direct effects of climate on winter wheat production and grain yield is presented. The model was calibrated using data from field experiments in Denmark. The model was validated using data from near optimally managed experimental plots with winter wheat from The Netherlands and Denmark. The model was further evaluated using data from 1971 to 1997 for 7 sites in Denmark. The model explained from 0 to 20% of the variation in detrended observed yields, depending on soil type. A regression analysis of observed yields against monthly climate data showed a positive effect of temperature in October, November and January on grain yield, a positive effect of radiation in April and a strongly negative effect of precipitation in July. Only the positive effect of radiation in April was predicted by the simulation model, probably because the indirect effects of climate are not taken into account by the model (e.g. effects of rainfall on lodging or *Septoria* disease). The sensitivity of simulated grain yield to changes in mean temperature, temperature variability, precipitation, length of dry spells and CO<sub>2</sub> concentration was analysed for 4 soil types using generated climate data from 1 site in Denmark. Yield decreased with increasing temperature. This decrease was strongly non-linear with temperature change when using a fixed sowing date, but almost linear for the optimal sowing date. There was only a very small response to changes in temperature variability. Increasing precipitation increased yields with the largest response on the sandy soils. Large changes in grain yield were also seen on sandy soils with changes in the length of dry spells. A comparison of the simulated responses to the direct effects of temperature and rainfall with those to the indirect effects of these variables as estimated from the regression analysis showed that the indirect and the direct effects had opposite effects and that they may almost cancel each other out. The simulated increase in grain yield due to increasing CO<sub>2</sub> concentration in most cases exceeded the simulated responses to changes in climate variables.

**KEY WORDS:** Global change · Temperature · Precipitation · CO<sub>2</sub> concentration · Grain yield · Sowing date

—Resale or republication not permitted without written consent of the publisher—

## 1. INTRODUCTION

Winter wheat has become one of the most important small grain cereal crops throughout Europe due to its high grain productivity. In Denmark the winter wheat area increased from 3.0% of the agricultural area in 1971 to 25.0% in 1997. This has also increased the farmer's reliance on the productivity of this crop.

Climate influences crop production directly through effects on crop development, crop leaf area develop-

ment, radiation interception and carbon fixation. Such effects may be modified by water shortage or occurrence of high or low temperatures. These processes are commonly included in wheat simulation models (Goudriaan 1996), although the damaging effects of high or low temperatures are seldom taken into account (Porter & Gawith 1999).

There are also indirect effects of climate on crop production. These are the effect of weather on the availability of nutrients and the occurrence of weeds, pests and diseases. Most importantly perhaps is the effect of weather on the possibilities of management of these

\*E-mail: jorgene.olesen@agrsci.dk

factors and of the crop in general. Weather may thus also indirectly affect the final outcome through effects on lodging or wet harvest conditions, which reduce yield and yield quality (Easson et al. 1993). These indirect effects are generally not included in crop models, although there are some studies on effects of climate on yield limitation by individual factors, e.g. nitrogen (Porter et al. 1995) and pests (Teng et al. 1996).

Changes in the global climate will affect temporal patterns of temperature and rainfall at the regional level (Houghton et al. 1996), and this will have important consequences for crop production (Parry 1990). Several studies have examined the sensitivity of wheat yield potential to temperature changes using simulation models (Stockle et al. 1992, Wang et al. 1992, Nonhebel 1993, 1996). Comparisons of wheat models and of their sensitivity to climate change have been performed for Europe (Semenov et al. 1996, Wolf et al. 1996). The models have also been used to study the sensitivity of crop production to daily and interannual climatic variability (Semenov & Porter 1995, Mearns et al. 1996, Moot et al. 1996, Riha et al. 1996) and to differential day and night warming (Dhakwa & Campbell 1998).

Recently criticism has been raised on the use of these crop simulation models in climate change impact assessment (Landau et al. 1998). This critique stems from the often poor results of comparison of simulation results against yields obtained from agronomic field experiments including fertiliser and variety trials. Sub-optimal management and indirect climate effects often result in sub-optimal yields. This does not necessarily mean that the simulated relative response to climate change is erroneous, but it shows that further studies of the sensitivity of crops to climate change under realistic farming conditions are needed. The results of simulation models should be interpreted as effects on production potential (Jamieson et al. 1999). Actual yields will be constrained by the production potential as well as by indirect effects of climate and by inadequacies in the management of the crop. The indirect effects of climate may have a dominating influence in many environments.

This paper describes a simulation model developed for analysis of the sensitivity of winter wheat production in Denmark to climate change. The model includes the direct effects of climate on crop production, but not the indirect effects. A simple model structure was used as this simplifies interpretation of the simulation results when detailed information on crop management is not available. The model was validated by comparing simulation results with observed crop development and grain yield from well-managed crops. The model results were further evaluated by comparison with observations of grain yield from experimental plots with standard management, and

the sensitivity of simulated grain yield to changes in climate was explored and compared with observed sensitivities. This was done in order to separate the direct and indirect effects of climate on grain yield variation.

## 2. MATERIAL AND METHODS

**2.1. Model description.** The winter wheat model presented here is part of the CLIMCROP suite of crop models, which share a common soil water and soil temperature model (Olesen et al. 2000a). A description of the model is given below with the emphasis on the processes that differ from other models.

The phenology submodel is identical to that of the SIRIUS wheat model (Brooking et al. 1995, Brooking 1996, Robertson et al. 1996, Jamieson et al. 1998) with a few exceptions. Soil temperature at 10 cm depth is used as the driving variable until the beginning of stem elongation, which is set to 3.5 phyllochrons prior to flag leaf ligule appearance. Thereafter air temperature is used as the driving variable. The duration of a phyllochron is set to 90°C d with a base temperature of 0°C. The duration from flag leaf ligule appearance to anthesis is calculated using a temperature sum of  $S_a$  (°C d) with a base temperature of 0°C. The duration of the period from anthesis to the end of grain-filling is calculated using a temperature sum of  $S_m$  (°C d) with a base temperature of 6°C (Porter et al. 1987). Grain-filling is assumed to start 60°C d after anthesis using a base temperature of 6°C (Amir & Sinclair 1991).

The development of the green area index is described by a logistic equation prior to start of senescence. Thereafter a linear decline in green area index is assumed along with a similar but lower increase in dead area index. The growth of green area index from emergence to 1 March is described by a linear function of soil temperature sum. The rate of crop area expansion is affected by winter survival and by drought. This gives the following equation for green area index:

$$L_d = \begin{cases} L_{d-1} + a_1(T - T_{bl})_+(1 - f_w) \frac{E_{aT}}{E_{pT}} & \text{for } d < 1 \text{ March} \\ & \text{and } 9 \leq \text{GS} \\ L_{d-1} + a_2(T - T_{bl})_+ L_{d-1} \frac{L_x - L_{d-1}}{L_x} (1 - f_w) \frac{E_{aT}}{E_{pT}} & \text{for } d \geq 1 \text{ March} \\ & \text{and } 9 \leq \text{GS} < 65 \\ L_a \max[1 - (S_g / S_{gR}), 0] & \text{for } \text{GS} \geq 65 \end{cases} \quad (1)$$

where  $L_d$  is green area index ( $\text{m}^2 \text{m}^{-2}$ ) on day  $d$ ,  $T$  is mean daily temperature (°C),  $T_{bl}$  is the base temperature for crop area expansion (°C),  $f_w$  is a winter kill factor,  $E_{aT}$  is the actual transpiration ( $\text{mm d}^{-1}$ ),  $E_{pT}$  is the potential transpiration ( $\text{mm d}^{-1}$ ),  $L_x$  is the maximum obtainable green area index ( $\text{m}^2 \text{m}^{-2}$ ),  $L_a$  is the simu-

lated green area index at anthesis ( $\text{m}^2 \text{m}^{-2}$ ),  $S_g$  is the temperature sum accumulated from beginning of grain fill ( $^\circ\text{C d}$ ),  $S_{gr}$  is the temperature sum requirement for the grain filling period ( $^\circ\text{C d}$ ), and GS is the crop growth stage according the BBCH scale (Lancashire et al. 1991). A growth stage of 9 corresponds to emergence and 65 corresponds to anthesis.  $a_1$  and  $a_2$  are empirical rate constants. The subscripted + denotes that only positive contributions are considered.  $L_x$  is set to 5 (Aslyng & Hansen 1982), and the base temperature  $T_{bl}$  is set to  $0^\circ\text{C}$ . Soil temperatures are used for  $T$  until the beginning of stem elongation, and air temperatures are used thereafter.

The winter kill function is calculated starting at emergence as

$$f_{w,d} = \min[f_{w,d-1} + a_3(1-f_{w,d-1})(T_{bw} - T_n)_+, 1] \quad (2)$$

where  $f_{w,d}$  is the factor on day  $d$ ,  $T_n$  is minimum soil temperature at 10 cm depth ( $^\circ\text{C}$ ), and  $T_{bw}$  is the base temperature for winter kill ( $^\circ\text{C}$ ).  $T_{bw}$  is set to  $-6^\circ\text{C}$  until 2 phyllochrons after formation of the flag leaf primordium, after which  $T_{bw}$  is set to  $-4^\circ\text{C}$ . This reflects an increasing sensitivity to frost damage in older plants, which is often observed as dehardening (Fujita et al. 1992, Griffith & McIntyre 1993).  $a_3$  is an empirical factor that determines the rate at which low temperatures affect crop winter survival.

The total above-ground biomass ( $W$ ) ( $\text{g m}^{-2}$ ) at any time is the integral of the daily growth rate ( $\Delta W$ ). The daily growth rate is proportional to the intercepted radiation modified by drought and low temperatures. This is calculated as

$$\Delta W = \varepsilon Q [1 - \exp(-kL)] f_T f_C \frac{E_{aT}}{E_{pT}} \quad (3)$$

where  $\varepsilon$  is the radiation use efficiency ( $\text{g MJ}^{-1}$ ),  $Q$  is the incident PAR ( $\text{MJ d}^{-1}$ ),  $k$  is the extinction coefficient,  $L$  is the green area index ( $\text{m}^2 \text{m}^{-2}$ ),  $f_T$  is a function of air temperature and  $f_C$  is a function of atmospheric  $\text{CO}_2$  concentration.  $\varepsilon$  is set to  $2.8 \text{ g MJ}^{-1}$  (Kiniry et al. 1989).  $k$  is set to 0.45 (Thorne et al. 1988).  $f_T$  is a function which increases linearly with air temperature from 0 at  $4^\circ\text{C}$  to 1 at  $10^\circ\text{C}$  and above (Hansen et al. 1991). Similar functions for temperature dependency of radiation use efficiency have been used by Christensen & Goudriaan (1993) for spring barley and estimated by Olesen & Grevsen (1997) for *Brassica* species. The functional dependency on  $\text{CO}_2$  concentration was estimated from data presented by Weigel et al. (1994):

$$f_C = \exp(0.4537 - 170.97/C) \quad (4)$$

where  $C$  is  $\text{CO}_2$  concentration (ppm).

In the senescence phase dead crop area index ( $L_y$ ) ( $\text{m}^2 \text{m}^{-2}$ ) is assumed to increase by 40% of the reduction in green area index (Aslyng & Hansen 1982).

Grain dry matter is calculated as the sum of assimilation in the period from the beginning of grain-filling to maturity plus a pool of reserves, which is set to 30% of the assimilation from flag leaf ligule appearance to anthesis and to 90% from anthesis to beginning of grain-filling. These factors are in accordance with observations on storage and remobilisation of stem reserves in wheat (Davidson & Chevalier 1992, Gent 1994). The reserve pool is transferred to the grain at a constant rate, so that all will have been transferred at end of grain filling. Grain dry matter is converted to grain yield with 85% dry matter.

The soil is characterised by the depth of the topsoil and by the capacity for plant-available water in the topsoil and in the subsoil (Olesen & Plauborg 1995). The water balance model has a root zone and a sub-zone. The root zone extends from the soil surface to the effective root depth. The sub-zone extends from the current effective root depth to the maximum effective root depth. Both the maximum root depth and the capacity for plant-available water are assumed to vary between soil types. Evaporation from the soil can only occur from the root zone reservoir, either through crop transpiration or soil evaporation. The capacity of plant-available water in the root zone and sub-zone is calculated from topsoil and subsoil texture. The interception reservoir contains the water which is retained on the surface of the vegetation. Root depth is calculated as a function of soil temperature sum from emergence or from growth start in spring (Hansen et al. 1991).

Soil temperature at 10 cm depth is modelled using a simple resistance approach where air temperature and global radiation drive the changes in soil temperature. The resistance to change is affected by snow depth and by ice formation in the soil. The model was parameterised using daily data from 1987 to 1997 for a bare soil at Research Centre Foulum in Denmark ( $56^\circ 30' \text{N}$ ,  $9^\circ 35' \text{E}$ ).

Potential evapotranspiration ( $E_p$ ) ( $\text{mm d}^{-1}$ ) is partitioned between the crop and the soil as

$$E_{ps} = E_p \exp[-k_E (L + L_y)] \quad (5)$$

where  $E_{ps}$  is potential soil evaporation, and  $k_E$  is an extinction coefficient which is set to 0.6 (Aslyng & Hansen 1982).

The potential transpiration from the crop ( $E_{pT}$ ) is assumed to depend on the size of the canopy and on  $\text{CO}_2$  concentration:

$$E_{pT} = (E_p - E_{ps}) f_a (a_4 - a_5 C) \quad (6)$$

where  $a_4$  and  $a_5$  are empirical constants that are set to  $a_4 = 1.11$  and  $a_5 = 0.00029 \text{ ppm}^{-1}$  based on calculations by Goudriaan & Unsworth (1990). This relation reduces the transpiration by about 10% for a doubling of current atmospheric  $\text{CO}_2$  concentration, which is

within the range observed at the crop level (Samarakoon et al. 1995).  $f_a$  is a function that accounts for the increasing evaporation demand of taller crops with higher roughness lengths.  $f_a$  is set to 1 before stem elongation, and to  $1 + 0.02(L + L_v)$  after stem elongation (Andersen et al. 1992).

Irrigation is assumed to follow the principles of the MARKVAND irrigation scheduling programme (Plauborg et al. 1996). A maximum of 25 mm is applied in each irrigation event, and there must be at least 7 d between each application.

The model is updated in daily time steps, and it requires daily data on minimum and maximum air temperature, global radiation, precipitation and potential evapotranspiration.

## 2.2. Calibration

Data on obtained dates of emergence (GS 9), flag leaf ligule appearance (GS 39), anthesis (GS 65) and hard dough (GS 87) were collected from experiments on winter wheat carried out at 5 agricultural research stations in Denmark during 1992 to 1997 (Table 1). The temperature sum requirements from flag leaf appearance to anthesis ( $S_a$ ) and from anthesis to maturity ( $S_m$ ) were estimated by linear regression of the rate of development against the mean temperature over the period using the REG procedure of SAS with the NOINT option (SAS Institute 1996). For the period from anthesis to maturity 6°C were subtracted from the mean temperature. The requirements were taken as the inverse of the estimated slopes.

Data on the increase of green area index were obtained from experiments carried out at Research Centre Foulum. Winter wheat cultivar Sleipner was grown for 4 seasons (September 1988 to August 1992) using a plant density of 300 plants  $m^{-2}$  and a split nitrogen dressing. Winter wheat cultivar Gawain was grown for 2 seasons (September 1991 to August 1993) in 4 treatments, which were combinations of 150 or 450 plants  $m^{-2}$  and single or split nitrogen dressing. Above-ground biomass was sampled 8 to 16 times per season during the period from early spring to anthesis. The area of leaves, stems and ears were measured using a

LICOR LI-3100 area meter. Logistic growth curves were fitted to the measurements of green area index ( $L$ ):

$$L = \frac{L_x}{1 + \exp(b - a_2 S)} \quad (7)$$

$$b = \ln\left(\frac{L_x - L_0}{L_0}\right) \quad (8)$$

where  $S$  is the temperature sum from 1 March with a base temperature of 0°C, and  $L_0$  is the crop area index on 1 March.  $L_x$  and  $a_2$  are described in Eq. (1). The parameters were estimated using the NLIN procedure of SAS (SAS Institute 1996).  $a_2$  was assumed to be constant, but separate values of  $L_0$  and  $L_x$  were estimated for each experiment and treatment. The  $a_1$  parameter in Eq. (1) was subsequently estimated by linear regression of  $L_0$  on temperature sum from emergence to 1 March.

Data on winter survival of winter wheat varieties were obtained from variety trials at 9 Danish agricultural research stations during 3 seasons (September 1984 to August 1987), where severe winter damage occurred. There were 15 to 22 varieties in each experiment. The experiments were assessed for winter damage in April and each variety given a score for winter survival. A score of 0 corresponded to no surviving plants and 10 to no winter damage. An overall score ( $s$ ) was calculated for each site and year as the mean of all varieties. This overall score varied from 4.6 to 10. The observations of winter survival were used to estimate the  $a_3$  parameter in Eq. (2) by linear regression of  $(1 - s)/10$  against  $\sum(T_{bw} - T_n)_+$  using the REG procedure of SAS with the NOINT option. This implies that the effect of winter damage on crop area expansion is proportional to the fraction of plants surviving in early spring.

Meteorological data for model calibration, validation and evaluation were obtained as daily observations on minimum and maximum air temperature, global radiation, precipitation, mean wind speed and mean relative humidity from official meteorological stations within 1 km of the experiments (6 km for Bouwing in The Netherlands). Potential evapotranspiration was calculated using a modified Penman equation (Mikkelsen & Olesen 1991).

Table 1. Locations, varieties and sowing dates for experiments used for calibration of the development model

Site	Latitude	Longitude	Varieties	Sowing dates	No. of observations
Flakkebjerg	55° 20' N	11° 23' E	Gawain, Kraka	17 Sep–22 Oct	8
Foulum	56° 30' N	9° 35' E	Gawain, Pepital	18 Sep–25 Sep	3
Jyndevad	54° 54' N	9° 08' E	Obelisk, Pepital, Hussar	19 Sep–21 Sep	3
Roskilde	55° 37' N	12° 03' E	Haven, Kraka, Pepital	18 Sep–22 Sep	4
Rønhave	54° 57' N	9° 46' E	Gawain, Obelisk	20 Sep–21 Sep	3

### 2.3. Validation

Two independent data sets on winter wheat were used for model validation. These data sets originated from 2 different experiments, each covering 2 yr and having several measurements of above-ground biomass during the growing season. The first data set covered the growing seasons 1982-1983 and 1983-1984 at Bouwing (51° 57' N, 5° 45' E) in The Netherlands (Groot & Verberne 1991). The soil type at Bouwing is a silty clay loam. The second data set covered the growing seasons 1995-1996 and 1996-1997 at Jyndevad (54° 54' N, 9° 08' E) in Denmark (Olesen et al. 2000b). This site has a sandy soil, and the experiment covered treatments with and without irrigation. Both experiments had different levels of nitrogen application, but data were taken only from the highest nitrogen rate and from plots where insecticides and fungicides had been applied to control pests and diseases. This pest and disease control was fully effective at Bouwing, but not at Jyndevad, where epidemics of mildew and *Septoria* developed in 1996 and 1997, respectively. The disease attack occurred primarily after anthesis in both years. The effect of the disease was therefore simulated by using a fixed factor to reduce the radiation use efficiency after anthesis. The attack of mildew in 1996 varied between irrigation treatments and the radiation use efficiency was reduced according to observations by 10% in the non-irrigated treatment and by 15% in the irrigated treatment. The attack of *Septoria* in 1997 did not vary between treatments, and the radiation use efficiency was reduced by the observed disease level of 20%. The actual sowing date was used in the simulations.

### 2.4. Evaluation

Data on harvested grain yield in winter wheat were obtained during 1971 to 1997 from 7 agricultural research stations in Denmark. The observed yield data

represent yields from experimental plots which were treated according to normal agricultural practice in the region (Olesen 1991). These represent other experiments and plots than those used for the model validation, even though data were taken from some of the same years at Jyndevad research station. The sites represent different soil types, and some of the observations represent irrigated treatments (Table 2). The stations were grouped into 4 soil type classes (I to IV, Table 2). The soil water capacities of the different soil types were estimated from measurements of soil texture and soil water retention curves (Hansen 1976). Yield data were not available from all years at all sites as shown in Table 2. The observed yields were detrended using the same linear time trend for all sites estimated by multiple linear regression with fixed effects of site and irrigation by the GLM procedure of SAS (SAS Institute 1996). These detrended yields were corrected to 1990 level. The estimated linear increase in yield was 0.10 t ha<sup>-1</sup> yr<sup>-1</sup>, and the regression model captured 44% of the yield variation. A regression on year alone captured 20% of the yield variation.

The simulation model was used to estimate grain yield of both irrigated and unirrigated crops for all years and sites shown in Table 2. A standard sowing date of 20 September was used in all cases due to incomplete information on crop management. This is the sowing date generally recommended in Denmark. The simulated and detrended yields were compared using correlation analysis.

The yield levels differed between the 7 sites, not only due to climatic and soil conditions, but also due to management. This sub-optimal management is often caused by insufficient nutrients and incomplete control of weeds, pests and diseases. The effect on crop production is most often mediated through reduced light interception caused by a lower effective crop area index (Olesen et al. 2000c). This management effect was therefore estimated as a specific value of the maximum crop area index ( $L_x$ ) for each site by minimising the squared difference between observed and simu-

Table 2. Characteristics of the agricultural research stations where data on grain yield in normal treated plots of winter wheat have been recorded. SWC is the soil capacity for plant-available water at maximum effective root depth

	Soil type	Site	Latitude	Longitude	SWC (mm)	No. of observations	
						Not irrigated	Irrigated
(I)	Coarse sand	Jyndevad	54° 54' N	9° 08' E	61	8	22
(II)	Fine sand	Tylstrup	57° 11' N	9° 57' E	120	5	4
(III)	Loamy sand	Askov	55° 28' N	9° 07' E	153	24	2
	Loamy sand	Foulum	56° 30' N	9° 35' E	153	13	1
(IV)	Sandy loam	Roskilde	55° 37' N	12° 03' E	179	24	0
	Sandy loam	Tystofte	55° 15' N	11° 20' E	179	24	0
	Sandy loam	Ødum	56° 18' N	10° 08' E	179	19	0

lated grain yield using the downhill simplex method (Nelder & Mead 1965).

### 2.5. Regression analysis

The yield data from the 7 sites (Table 2) partly reflect effects of sub-optimal management. To investigate whether this would cause differences in general yield response to climate, regression modelling of yields on various monthly climate variables was used. A regression model was selected from all 146 yield observations using the STEPWISE procedure of SAS (SAS Institute 1996). A forward selection combined with a backward elimination method was used, and only variables significant at the 5% level were finally retained in the model. The explanatory variables investigated were year, soil-water-holding capacity, irrigation, mean monthly temperatures from October to July, monthly precipitation from April to July and monthly global radiation from April to July. Monthly values were chosen as a reasonable compromise between the desire to represent seasonal effects of climate on yield and the need to reduce spurious effects that may occur from inclusion of too many variables representing short time periods. The use of monthly values almost eliminates the problem of autocorrelation in the climate variables.

### 2.6. Sensitivity analyses

The effect of changes in climatic variables was analysed using sets of 200 yr of climate data generated by the LARS-WG stochastic weather generator (Semenov & Barrow 1997). The parameters for LARS-WG were calibrated using daily observed climate data from Ødum (56° 18' N, 10° 08' E) for 1961 to 1997. The weather generator did not provide estimates of humidity and wind speed. The potential evapotranspiration was therefore calculated using a modified Priestly-Taylor formula calibrated against the Penman equation (Aslyng & Hansen 1982).

Changes were applied to the 4 parameters in LARS-WG describing mean air temperature, temperature variability (standard deviation), mean precipitation and duration of dry spells. The change in mean temperature was varied from –2 to 5°C in steps of 0.5°C. The changes in temperature variability, precipitation and duration of dry spells were varied from 50 to 200% of baseline conditions in steps of 10%. The response of simulated yield was calculated for the 4 soil types shown in Table 2. Both the mean yield and coefficient of variation of yield were calculated for each change in climatic parameters on the basis of 200 individual years of model runs.

The results of the change in climate parameters can be affected by the sowing date used. This is especially the case for changes in temperature. All the scenarios for temperature changes were therefore run for sowing dates varying from 1 September to 30 October. All other scenarios were run for a constant sowing date of 20 September. The scenarios for response to precipitation were run for 3 different atmospheric CO<sub>2</sub> concentrations: 360, 540 and 720 ppm. All other scenarios were run at a CO<sub>2</sub> concentration of 360 ppm.

The observed climate data from Ødum for 1961 to 1997 were also used directly as input to the simulation model for comparison with the use of generated weather data.

The regression analysis described in Section 2.5 was supplemented with a sensitivity analysis using the simulation model. For each significant monthly climate variable in the regression analysis LARS-WG was used to generate 200 yr of weather data for both a decrease and an increase in this climate variable in the specific month. The sensitivity of the simulated change in yield to change in the climatic parameter was then calculated by dividing the mean yield change by the change in the climatic parameter.

## 3. RESULTS

### 3.1. Calibration

The temperature sum requirement from flag leaf appearance (GS 39) to anthesis (GS 65) was estimated as  $S_a = 274$  (SE 10) °C d, and the requirement from anthesis to yellow ripeness (GS 87, hard dough) was estimated as  $S_m = 420$  (SE 8) °C d. The model was subsequently used to simulate 4 growth stages using the actual sowing dates. The result of this comparison is shown in Fig. 1. The simulated dates of GS 39, 65 and 87 were generally in agreement, except for Rønhave in 1992, where the simulated dates were about 2 wk earlier than the observed dates.

The parameters for the green area function (Eq. 1) were estimated as  $a_1 = 2.8 \times 10^{-4}$  (SE  $0.5 \times 10^{-4}$ ) (°C d)<sup>-1</sup> and  $a_2 = 81 \times 10^{-4}$  (SE  $3 \times 10^{-4}$ ) (°C d)<sup>-1</sup>. The parameter for effect of winter damage on crop area expansion (Eq. 2) was estimated as  $a_3 = 0.005$ .

### 3.2. Validation

The result of the validation of the simulation model is shown in Fig. 2. The simulated total dry matter and grain dry matter followed observations closely for both years at Bouwing. The development of total dry matter at Jyndevad was underestimated by the model, espe-

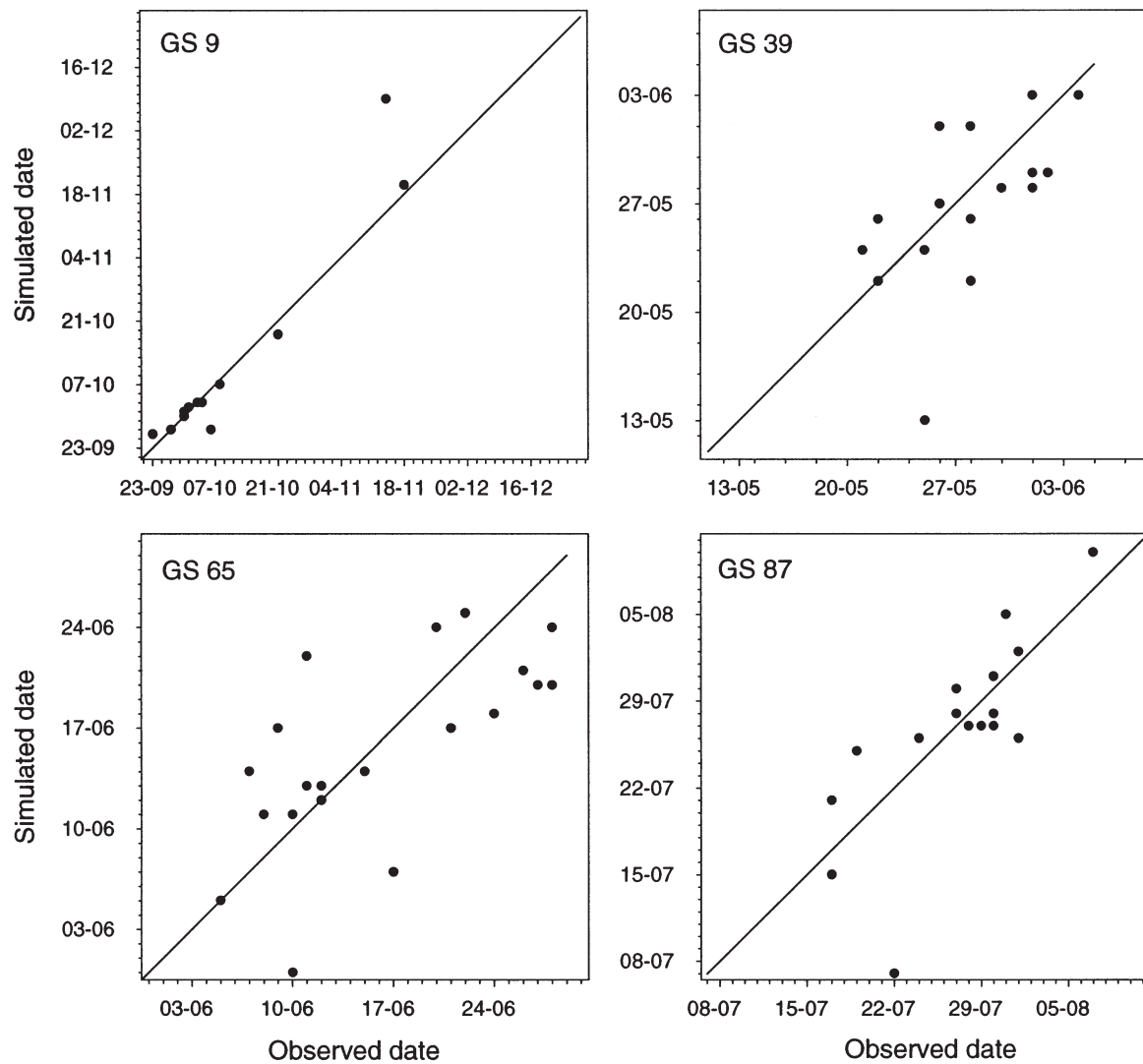


Fig. 1. Simulated versus observed dates (dd-mm) of selected developmental stages for the calibration data set (Table 1). Four developmental stages are compared: emergence (GS 9), flag leaf ligule appearance (GS 39), anthesis (GS 65) and hard dough (GS 87)

cially for the irrigated treatments. Final simulated total dry matter yields and grain yields were, however, close to the observed values. The model thus captured the main differences between years, locations and treatments.

### 3.3. Evaluation

Fig. 3 shows the simulated versus detrended grain yields for the 7 agricultural research stations. The results from the different stations are grouped according to the estimated soil water capacities of the different sites (Table 2). Most of the simulated grain yields were higher than the detrended yields, indicating that

other factors may have been limiting yield. There were, however, a few cases, especially at Foulum and Tystofte, where detrended yields were higher than the simulated ones (Fig. 3c,d).

Linear regressions of simulated yield on detrended yield were performed for the 4 soil types separately. The  $R^2$  values for a linear regression of measured yield on simulated yield were 0.13, 0.18, 0.00 and 0.20 for the 4 groups (I to IV), respectively. The regression coefficient was only significantly different from zero for group IV. The regression coefficients from linear regressions for the individual sites are shown in Table 3. The  $R^2$  was especially low at Askov and Foulum. The slopes of the regressions for all other sites were positive, but only significantly for Roskilde and Tystofte.

The detrended yields were generally lower than the simulated yields, possibly due to effects of weeds, pests or diseases or due to sub-optimal nutrient management. In a model context this may be expressed by a change in the maximum attained green area index ( $L_x$ ). The value of  $L_x$  that would match the detrended

yields was estimated for each site (Table 3), and new simulated values were calculated using these revised estimates of  $L_x$ . The effect of this on the slope and goodness of fit of the relationship between detrended and simulated yields is shown in Table 3. Compared to the fixed  $L_x$  of 5, the revised estimates resulted in

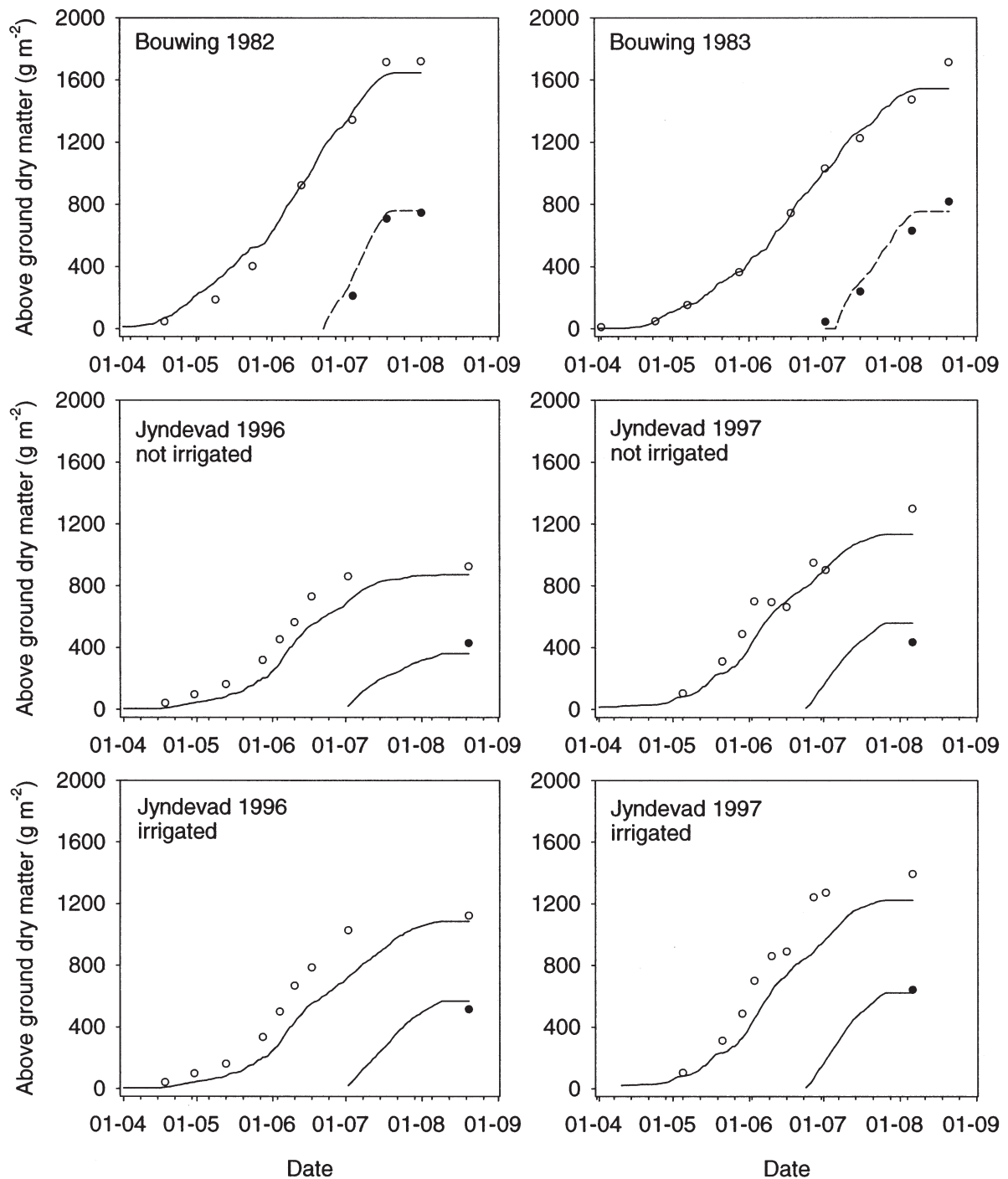


Fig. 2. Simulated (lines) and observed total above-ground biomass (○) and grain biomass (●) for 2 growing seasons at Bouwing in The Netherlands and 2 growing seasons with and without irrigation at Jynde vad in Denmark. Dates given as dd-mm



higher absolute values of the slope, whereas there was no consistent change in  $R^2$ .

Table 3. Validation of the winter wheat model using yields from normally treated plots at 7 research stations for 1971 to 1997. The  $R^2$  of a linear regression of simulated yields on detrended yields are shown both for unchanged maximum leaf area index ( $L_x$ ) and for  $L_x$  adjusted for site. \*Significant at the 95% confidence level

Site	Unadjusted $L_x$		Adjusted $L_x$		
	Slope	$R^2$	$L_x$	Slope	$R^2$
Jynde vad	0.39	0.13	3.93	0.46	0.10
Tylstrup	0.69	0.18	3.56	1.14	0.36
Askov	0.15	0.02	3.18	0.28	0.02
Foulum	-0.23	0.03	4.33	-0.36	0.04
Roskilde	0.54*	0.24	3.75	0.69*	0.26
Tystofte	0.75*	0.22	4.46	0.80*	0.24
Ødum	0.65	0.19	3.99	0.65	0.17

### 3.4. Regression analysis

Table 4 shows the result of the regression analysis of grain yields on monthly climate variables. Temperatures in autumn (October and November) and winter (January) had a positive influence on yields. Increasing global radiation in April increased yields, whereas increasing precipitation in July decreased yields. Global radiation in April and precipitation in July were the climatic variables that contributed most to the explanation of the variability in observed yields.

The simulation model was used to calculate the sensitivities to change in the climate parameters (Table 4). In all cases simulated yield responded positively to increasing temperature in October through January, but the response was much smaller than the response estimated from regression analysis. There was a positive simulated response to increasing precipitation in July, but a negative response in the regression analy-

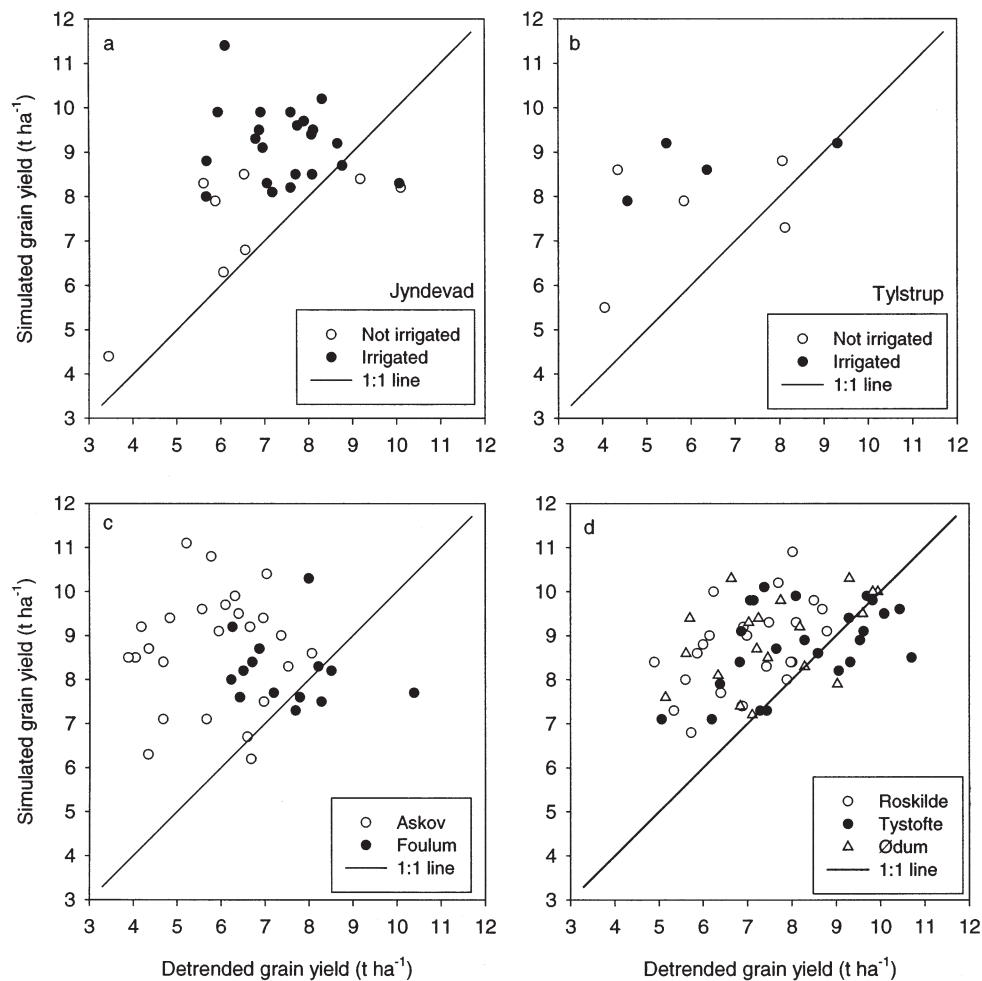


Fig. 3. Simulated versus measured grain yield detrended to the 1990 level in winter wheat at 7 Danish agricultural research stations for the period 1971 to 1997, grouped according to their estimated soil-water-holding capacity: (a) Jynde vad (coarse sand), (b) Tylstrup (fine sand), (c) Askov and Foulum (loamy sand), and (d) Roskilde, Tystofte and Ødum (sandy loam)

Table 4. Regression models fitted to observed grain yields after selection of monthly explanatory variables by forward selection and backward elimination. The  $R^2$  of the model was 0.42 based on 146 observations of grain yield from 7 research stations from 1971 to 1997. The importance of each variable was calculated as its contribution to the sum of squares explained by the model. The response of simulated increase in grain yield with the simulation model is shown as t per unit change of the specified parameter estimated from simulation runs based on 200 yr of generated weather data

Variable	Coefficient	Standard error	Importance (%)	Simulated response
Intercept ( $\text{t ha}^{-1}$ )	-196.5	31.3		
Year	0.10	0.016	36.6	
Mean temperature in October ( $^{\circ}\text{C}$ )	0.24	0.097	5.9	0.004
Mean temperature in November ( $^{\circ}\text{C}$ )	0.19	0.087	4.4	0.006
Mean temperature in January ( $^{\circ}\text{C}$ )	0.09	0.037	5.5	0.009
Precipitation in July (mm)	-0.014	0.003	18.9	0.003
Global radiation in April ( $\text{MJ m}^{-2}$ )	0.012	0.002	28.7	0.008

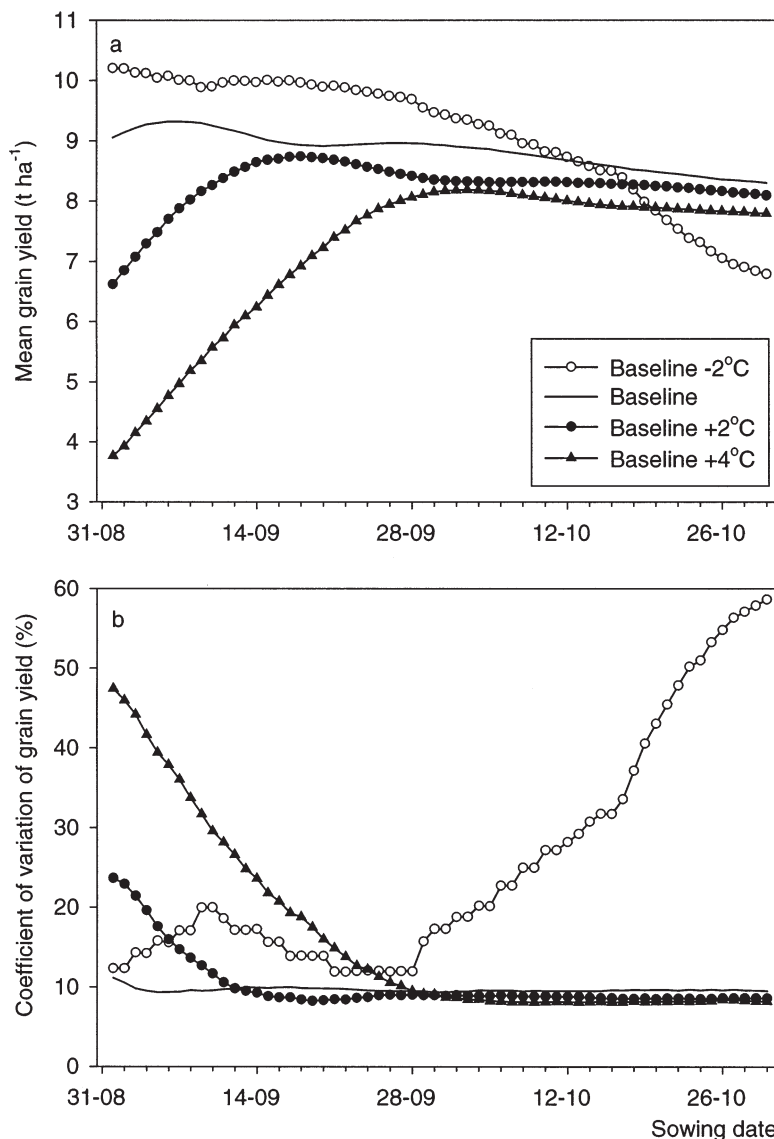


Fig. 4. Response of simulated (a) mean rainfed winter wheat grain yield and (b) coefficient of variation of yield on a sandy loam to changes in sowing date (dd-mm) for 4 different temperature scenarios; -2, 0, 2 and  $4^{\circ}\text{C}$  relative to baseline conditions

sis. The simulated response to radiation in April was very close to the response estimated in the regression analysis.

### 3.5. Sensitivity to climate change

The model includes an effect of soil minimum temperature on winter survival. This is controlled by a rate parameter  $a_3$ , which was estimated as 0.005. A value of  $a_3 = 0$  corresponds to full winter survival irrespective of winter temperatures. The effect of increasing  $a_3$  from 0 to 0.005 on change in simulated yield was  $-0.003 \text{ t ha}^{-1}$  for 200 yr of generated baseline weather data and  $-0.027 \text{ t ha}^{-1}$  for the observed climate at Ødum during 1991 to 1997.

The response of simulated grain yield (mean and CV) to change in sowing date is shown in Fig. 4 for 4 different temperature scenarios. The curves for mean yield for all temperature scenarios show a very small, but consistent bimodal response with 2 maximums, of which the early maximum is the largest. There was only a very small simulated response to changing sowing dates under the baseline climate. This was the case not only for the 200 yr of generated weather data, but also for simulations based on actual observed weather data from Ødum 1961 to 1997 (Table 5). A comparison in Table 5 of these simulated responses with data from sowing date experiments in Denmark indicates that the actual response may be slightly larger. This was especially the case in the experiment reported by Thomsen et al. (1994), whereas the

response found by Andersen & Olsen (1992) is very close to the simulated response.

Fig. 4a shows that a cooling of 2°C gave a moderate yield reduction for sowing dates in late October, whereas a warming of 2 or 4°C caused a severe yield reduction for sowing dates in early September. These yield reductions were associated with increases in CV, indicating that the frequency of years with very low yields may increase in these situations. The sowing

date giving the highest yield was delayed by about 7 d for each 1°C increase in mean temperature.

Fig. 5 shows that the response of grain yield to temperature change depends on whether the evaluation is performed using a fixed sowing date or whether the optimal sowing date is used in each case. This is a result of the differential yield response to sowing time for the different temperature scenarios shown in Fig. 4. There was a strongly non-linear response to a fixed

Table 5. Simulated grain yield on a sandy loam using either 200 yr of generated baseline climate data or observed climate data from 1961 to 1997, and observed grain yield from experiments in Denmark for 3 different sowing times shown relative to sowing on 1 September (= 100)

Sowing date	Simulated		Observed		
	200 yr	1961–1997	Olsen (1984), 1979–1983	Andersen & Olsen (1992), 1986–1988	Thomsen et al. (1994), 1992–1994
1 September	100	100	100	100	100
20 September	98	100	98	101	92
10 October	96	98	88	97	82

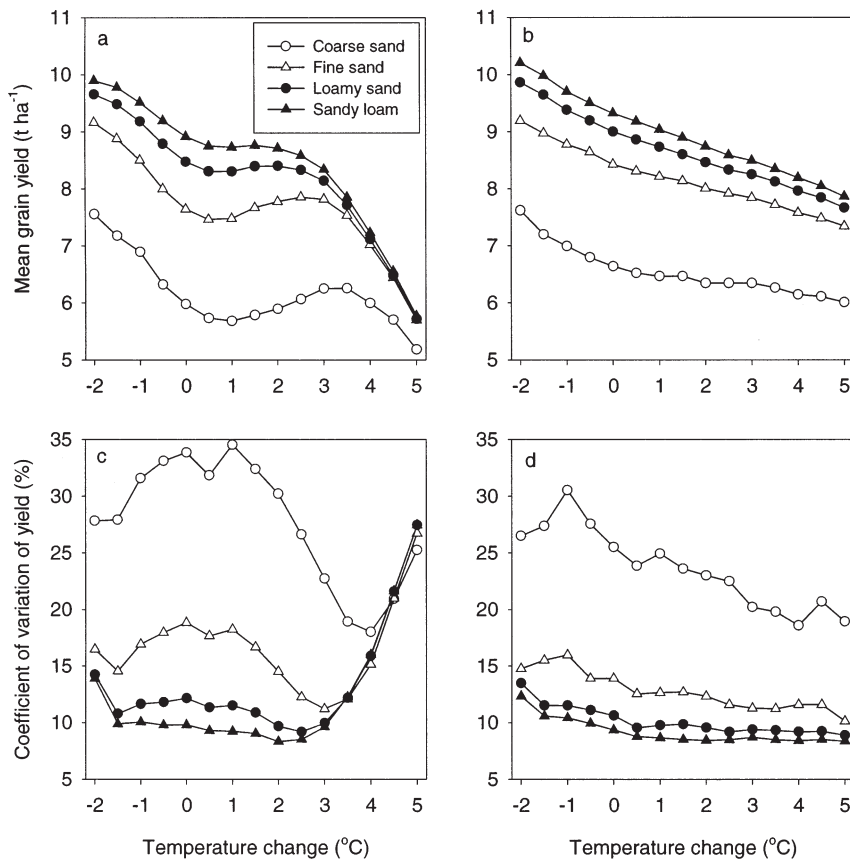


Fig. 5. Response of simulated rainfed winter wheat grain yield to changes in mean air temperature for 4 different soils. (a, b) Effects on mean yield; (c, d) coefficient of variation of yield. The results are shown both for a constant sowing date of 20 September (a, c) and for the sowing date giving the highest mean yield for each temperature scenario and soil type (b, d)

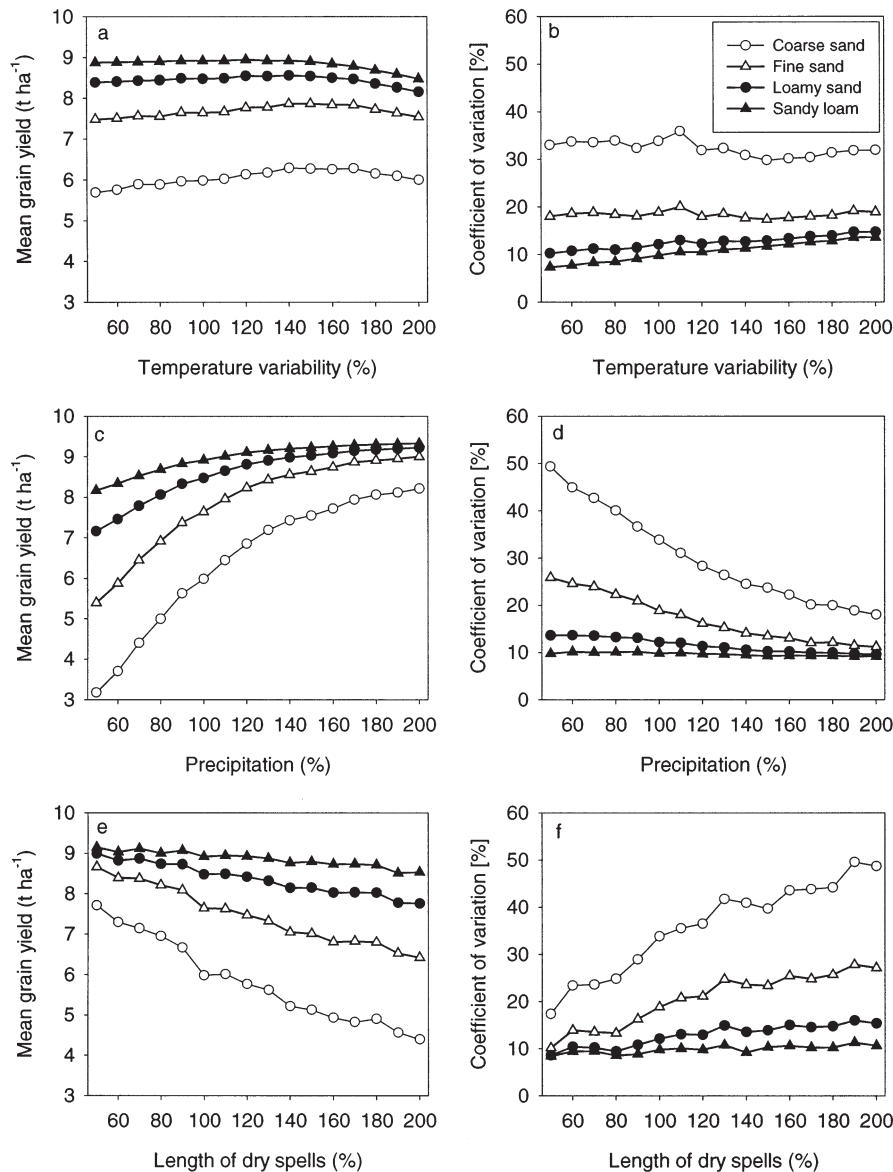


Fig. 6. Response of simulated rainfed winter wheat grain yield to changes in (a, b) temperature variability, (c, d) precipitation and (e, f) duration of dry spells for 4 different soils. The changes in climatic parameters are shown relative to the baseline climate. (a, c, e) Effects on mean yield; (b, d, f) coefficient of variation of yield

sowing time of 20 September (Fig. 5a). In this case yield may even increase with increasing temperature, especially on the sandy soils. For sowing at the optimal time derived from curves similar to Fig. 4a, there was a reduction in mean yield of about  $0.29 \text{ t ha}^{-1} \text{ }^{\circ}\text{C}^{-1}$  for sandy loam and  $0.13 \text{ t ha}^{-1} \text{ }^{\circ}\text{C}^{-1}$  for coarse sandy soils. The change in CV with increasing temperature was much larger for a constant compared with the optimal sowing date (Fig. 5).

Fig. 6 shows the effect of temperature variability (standard deviation), precipitation amount and length

of dry spells on mean yield and variability of yield. All yields were estimated for a constant sowing date of 20 September, as the interaction of these factors with sowing date was considered to be marginal.

There was a small increase in mean grain yield for minor increases in temperature variability on the sandy soils (Fig. 6a), whereas the yield on the sandy loam was largely unaffected. On the other hand, CV of grain yield increased with increasing temperature variability on the sandy loam and loamy sand soils, but was unaffected on the sandy soils (Fig. 6b).

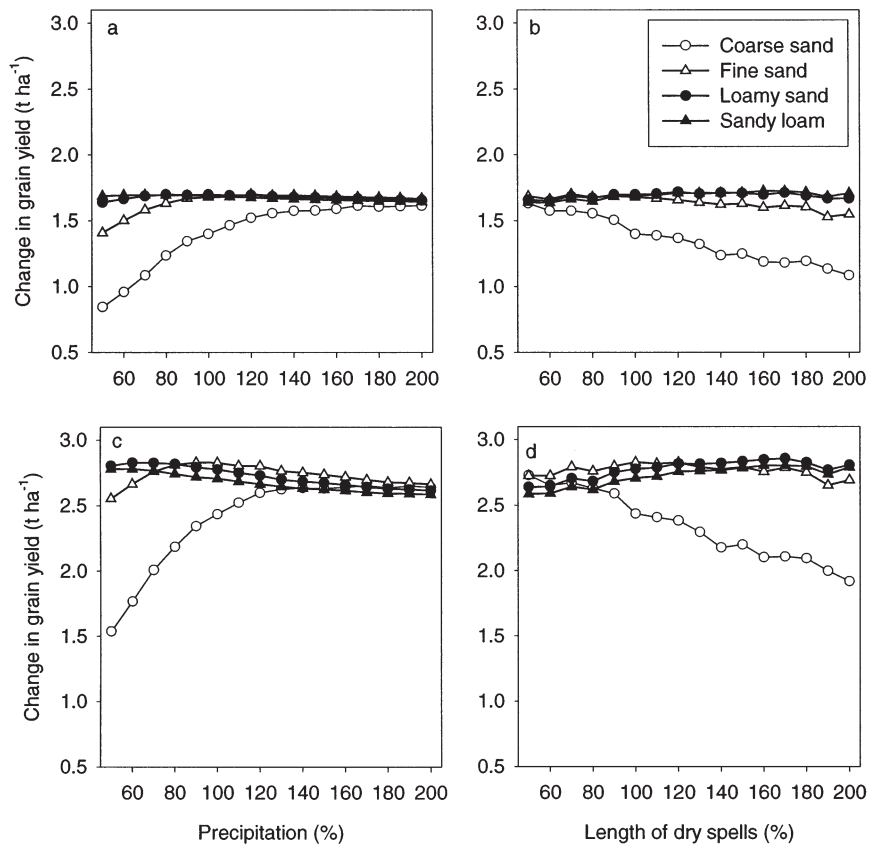


Fig. 7. Response of CO<sub>2</sub>-induced increase in rainfed winter wheat grain yield to change in (a, c) precipitation and (b, d) duration of dry spells for 4 different soils. The increase in grain yield was calculated as the difference between yields at CO<sub>2</sub> concentrations of (a, b) 360 and 540 ppm, and (c, d) 360 and 720 ppm

The yield increased with increasing precipitation levels, but to a smaller extent on the soils with a larger water-holding capacity (Fig. 6c). The CV of grain yield decreased with increasing precipitation level, but it was largely unaffected by precipitation on the loamy sand and sandy loam soils (Fig. 6d). Similar differences between soil types were observed for the responses to change in length of dry spells (Fig. 6e,f).

The effect of CO<sub>2</sub> concentration on mean grain yield is shown in Fig. 7 as the difference between yield for increased CO<sub>2</sub> concentration and for a concentration of 360 ppm at different levels of precipitation and length of dry spells. The yield increase was almost constant for the fine sand, loamy sand and sandy loam soils for all precipitation levels and duration of dry spells, despite the change in yield level at baseline CO<sub>2</sub> concentration shown in Fig. 6c,e. Figs. 6 & 7 show that the relative increase in grain yield for increasing CO<sub>2</sub> concentration decreases with increasing soil-water-holding capacity and precipitation level or with decreasing length of dry spells.

#### 4. DISCUSSION

The crop model presented here (CLIMCROP) uses the same approach to simulation of crop development as the SIRIUS model (Jamieson et al. 1998). CLIMCROP, however, uses a slightly different approach to simulation of green area index and dry matter assimilation and partitioning, and CLIMCROP does not directly include effects of nitrogen on crop growth. The approaches applied in CLIMCROP are much simpler than those applied in wheat models like AFRCWHEAT (Porter 1993), CERES-Wheat (Ritchie & Otter 1985) and SUCROS (van Laar et al. 1992), which have often been used in climate change impact assessments. However, CLIMCROP includes effects of low temperatures during winter on the survival and vitality of the crop.

The validation of CLIMCROP indicates moderately good performance for the crop development (Fig. 1). The most accurate simulations were obtained for date of maturity, where only 1 data point deviated consider-

ably from the 1:1 line. The scatter was larger for date of flag leaf emergence and for anthesis. This scatter is probably largely caused by variety differences unaccounted for and by inadequacies in the simulation of vernalisation, which has been shown to be one of the weak points in the current understanding of crop development in winter wheat (Kirby et al. 1999). The validation of dry matter production shows that the model was able to capture differences between years, location and irrigation treatments in terms of both total above-ground biomass and grain yield when corrections were made for observed disease levels (Fig. 2).

The correlations between simulated and detrended yields at agricultural research stations were very low, with  $R^2$  in the range of 0.02 to 0.24 (Table 3). The highest correlation was seen for the sandy loam soils, which are the soil types where winter wheat is traditionally grown in Denmark. The larger variation and lack of correlation between simulated and detrended yields at Askov and Foulum may be due to a larger variation in soil texture and rooting depth at these locations (Hansen 1976, Heidmann 1989). Such effects combined with possible effects of management (e.g. sowing time) may partly explain the higher observed versus simulated yields at Foulum and Tystofte (Fig. 3). The correlation between simulated and detrended yield in this study was higher than those obtained for winter wheat in UK using 3 different simulation models (Landau et al. 1998). The data used by Landau et al. (1998) were obtained from a much larger geographical area also covering widely differing soils. This may also have caused larger differences in management not taken account of in the simulation models. Nonhebel (1993) found a small positive correlation between simulated and observed yields of spring wheat from several years at 1 site in The Netherlands.

The use of a reduced maximum green area index to match the detrended yields increased the  $R^2$  values only slightly (Table 3). This shows that sub-optimal management inputs are not the direct source of lack of match between observed and simulated inter-annual yield variation.

A regression analysis of detrended yields on monthly climate variables showed that temperatures in October, November and January had a positive influence on yields. Similar results were found by Landau et al. (1998) in an analysis of winter wheat yields for the UK. Both studies showed a strong negative influence of rainfall in July on grain yields. The current study also indicated radiation in April as a positive contributor to yield. This was not found in the regression analysis by Landau et al. (1998). Empirical studies from both the UK and Denmark thus point to winter temperatures and rainfall in July as being important for current yield variability. None

of these effects were sufficiently captured by the CLIMCROP model (Table 4).

The positive effect of higher winter temperatures on grain yield may have been caused both by better winter survival and by better general establishment of the crop. The results of the sensitivity analysis with the CLIMCROP model do not indicate that winter survival is a major contributor to this effect, as the yield loss when including the winter damage effect on average was very small. It is more likely that the positive effects of winter temperature are caused by crops in the spring being better established, having a higher leaf area and having more extensive root systems, resulting in a more effective resource capture.

The normal sowing date for winter wheat in Denmark is between 15 and 20 September, which is 1 to 2 wk later than suggested as optimal by the response function shown in Fig. 4 and by field experiments (Table 5). The later sowing is used because other agronomic factors influence the date of sowing, such as availability of seed and the higher risk of disease and weed problems with early sowings (Prew et al. 1986, Jørgensen et al. 1997). Simulated yield reductions for late sowings were not as marked as often observed in practice (Table 5). This may be related to the positive response of warm October and November temperatures on grain yield from the regression analysis, which was not captured by the simulation model.

There was a strongly non-linear response of mean grain yield to temperature change for a fixed sowing date, but an almost linear decline for the optimal sowing date (Fig. 5). The non-linear response was strongest for the sandy soil, where the simulated yields increased for an increase of  $3^\circ\text{C}$  in mean temperature above baseline. The yield decreases for sowing on the optimal date were  $3\% \text{ }^\circ\text{C}^{-1}$  on sandy loam and  $2\% \text{ }^\circ\text{C}^{-1}$  on sand. The positive effects of the autumn and winter temperatures from the regression analysis (Table 4) are of the same magnitude as this decrease in simulated yield with increasing temperature. This indicates that small changes in temperature may not have any discernible effect on winter wheat yield in Denmark.

Most other studies on the effect of temperature change on wheat yield have assumed a fixed sowing date, and studies have often been conducted for a single soil type only. Wolf et al. (1996) compared the response of 4 winter wheat models to temperature change at Rothamsted in the UK and found that the decrease in grain yield varied between 0.33 and 0.54  $\text{t ha}^{-1} \text{ }^\circ\text{C}^{-1}$  depending on the model used. Mitchell et al. (1995) observed a reduction in measured grain yield of 35%, but a reduction in total biomass of only 16% for a temperature increase of  $3^\circ\text{C}$  using growth chambers following the observed climate at Rothamsted. Nonhebel (1996) found reductions in simulated water-

limited grain yield for spring wheat of 10 to 20% for a temperature increase of 3°C for sites in the UK, Germany and The Netherlands. Simulation results from the Great Plains in the USA show yield decreases of about 7% for each °C increase in temperature (Stockle et al. 1992, Brown & Rosenberg 1997). The estimated yield decrease in this study was lower than the results reported in literature. This is mostly a result of using the optimal sowing date instead of fixed sowing date, and it shows the importance of considering both sowing time and soil type when evaluating effects of temperature on grain yield in winter wheat.

There was only a small simulated effect of changes in temperature variability on grain yield (Fig. 6a). There was a small initial yield increase with increasing temperature variability on the sandy soils, but a decrease in yield for higher increases in variability on all soil types. The latter effect is probably caused by a reduction in winter survival with increasingly variable winter temperatures (results not shown). Simulation studies for wheat in the USA have generally shown reductions in yield with increasing variability of temperatures (Mearns et al. 1996, Riha et al. 1996). The differences in effects may be due to differences in both baseline climates and in models used.

The sensitivities to changes in climate parameters shown in Figs. 4 to 6 are based on generated weather data. Simulations with actual weather data gave sensitivities to the winter survival parameter which were about 10 times larger than those obtained with generated weather data. The sensitivities to temperature change shown in Figs. 4 & 5 may therefore not truly represent Danish climate. This is probably caused by the fact that LARS-WG assumes a constant autocorrelation coefficient for minimum temperature throughout the year (Semenov et al. 1998), whereas this autocorrelation coefficient has been shown to vary considerably during the year for sites in Denmark, with higher autocorrelation during the winter (Olesen & Mikkelsen 1983). A higher autocorrelation will increase the frequency of successive days with severe frosts, which then causes a larger accumulative effect on crop damage in Eq. (2).

There are several possible causes of the negative effect of rainfall in July. Heavy rainfall during this period may cause lodging, which will reduce harvested yield (Easson et al. 1993). It is, however, more likely that the negative effect of precipitation in July on yields are caused by *Septoria* disease, which is favoured by wet conditions during this period (Hansen et al. 1994).

Fig. 6 shows substantially different responses of both mean and CV of grain yield to changes in precipitation and length of dry spells for the different soil types. These results are in agreement with results of other

simulation studies (Stockle et al. 1992, Brown & Rosenberg 1997), although Wolf et al. (1996) found that the response varied considerably between simulation models. Similar differences in response of wheat yield to climate change for different soil types have been found for a Mediterranean environment (Wassenaar et al. 1999).

The simulated increase in grain yield with increasing precipitation (Fig. 6) outweighs the negative effect of July rainfall estimated from the regression analysis (Table 4), but only for the coarse sand and fine sand soils. This comparison indicates that the indirect effects of precipitation may be larger than the direct effects for the sandy loam soil.

The simulated effects of increased CO<sub>2</sub> concentration on grain yield were dependent on soil type and rainfall (Fig. 7). The relative increase in grain yield under current climate varied from 23% (coarse sand) to 19% (sandy loam) for a 50% increase in CO<sub>2</sub> concentration and from 41% (coarse sand) to 30% (sandy loam) for a 100% increase in CO<sub>2</sub> concentration. The yield increase for a doubling of CO<sub>2</sub> concentration was 28% when water was not limiting growth. This is within the range generally assumed in crop models (Melkonian et al. 1998). The higher relative increase in grain yield on the sandy soils are due to reduced transpiration (Eq. 6) with increasing CO<sub>2</sub> concentration. Similar effects on yield have also been simulated for the Midwestern USA (Brown & Rosenberg 1997). The results in Fig. 7 demonstrate that such effects are important also for sandy soils in Northern Europe.

The simulated yield increase for a 50% increase in CO<sub>2</sub> concentration could be counteracted by a temperature increase of 7°C or a precipitation decrease of 60% for a loamy sand soil (Figs. 5, 6 & 7). For a coarse sand soil a temperature increase of more than 10°C and a precipitation decrease of about 20% would be required to counteract the CO<sub>2</sub> effect. The climate changes estimated from GCM runs for the period 2035–64 are generally considerably smaller than these values (Hulme et al. 1999). It is therefore likely that the effect of global change on winter wheat yield in Denmark is going to be mediated mainly through the effect of CO<sub>2</sub> concentration on carbon assimilation.

The sensitivities to change in climatic parameters presented here were determined for a model that includes only the direct effects of weather on crop production. This does not necessarily invalidate the assessments of crop production using current models, as partly suggested by Landau et al. (1998), but these assessments should only be considered as effects on production potential. An indication that the model may perform fairly well in this respect can be seen from the agreement between simulated and observed phenology (Fig. 1), from the relatively good results from the

validation of the model against data from well-managed crops (Fig. 2), and from the fact that the effect of temperature on yield is mainly a result of different timing of crop developmental stages. More effort should, however, be put into the understanding of the interaction of crop management and the indirect effects of climate on crop production. For winter wheat the regression analyses presented here point to autumn and winter temperatures and mid-summer rainfall as being important in this respect. There is a need to study the importance of such indirect climate effects in a climate change context. This may be approached either by developing more complex simulation models that incorporate the mechanisms behind these effects or by developing correction factors to be included in a simulation model like CLIMCROP. Given the complexity of the winter wheat cropping system and the intricate interactions with management, the latter option is probably the only one that is feasible over the short term. Developing such correction factors would, however, require a data set spanning a wider range of environmental conditions than that which was available for this study.

*Acknowledgements.* The work was supported by the European Union under contract ENV4-CT95-0154. The model is programmed in Delphi, and the source code may be obtained from <http://www.agrsci.dk/pvj/dyste/climcrop/>.

#### LITERATURE CITED

- Amir J, Sinclair TR (1991) A model of the temperature and solar-radiation effects on spring wheat growth and yield. *Field Crops Res* 28:47–58
- Andersen A, Olsen CC (1992) Sätid, såmængde og kvælstofgødskning i forskellige sorter af vinterhvede. *Tidsskr Planteavl* 96:441–451
- Andersen MN, Jensen CR, Löscher R (1992) The interaction effects of potassium and drought in field-grown barley. I. Yield, water use efficiency and growth. *Acta Agric Scand Sect B Soil and Plant Sci* 42:34–44
- Aslyng HC, Hansen S (1982) Water balance and crop production simulation. The Royal Veterinary and Agricultural University, Copenhagen
- Brooking IR (1996) Temperature response and vernalization in wheat: a developmental analysis. *Ann Bot* 78:507–512
- Brooking IR, Jamieson PD, Porter JR (1995) The influence of daylength on final leaf number in spring wheat. *Field Crops Res* 41:155–165
- Brown RA, Rosenberg NJ (1997) Sensitivity of crop yield and water use in a range of climatic factors and CO<sub>2</sub> concentrations: a simulation study applying EPIC to the central USA. *Agric For Meteorol* 83:171–203
- Christensen S, Goudriaan J (1993) Deriving light interception and biomass from spectral reflectance ratio. *Remote Sens Environ* 43:87–95
- Davidson DJ, Chevalier PM (1992) Storage and remobilization of water-soluble carbohydrates in stems of spring wheat. *Crop Sci* 32:186–190
- Dhakhwa GB, Campbell CL (1998) Potential effects of differential day-night warming in global climate change on crop production. *Clim Change* 40:647–667
- Easson DL, White EM, Pickles SJ (1993) The effects of weather, seed rate and cultivar on lodging and yield in winter wheat. *J Agric Sci Camb* 121:145–156
- Fujita M, Kawada N, Tahir M (1992) Relationship between cold resistance, heading traits and ear primordia development of wheat cultivars. *Euphytica* 64:123–130
- Gent MPN (1994) Photosynthate reserves during grain filling in winter wheat. *Agron J* 86:159–167
- Goudriaan J (1996) Predicting crop yields under global change. In: Walker BW, Steffen WL (eds) *Global change and terrestrial ecosystems*. International Geosphere-Biosphere Book Series 2. Cambridge University Press, Cambridge, p 260–274
- Goudriaan J, Unsworth MH (1990) Implications of increasing carbon dioxide and climate change for agricultural production and water resources. In: Kimball BA, Rosenberg NJ, Allen LH (eds) *Impact of carbon dioxide, trace gases and climate change on global agriculture*. ASA Special Publication 53, American Society for Agronomy (ASA), Madison, WI, p 71–82
- Griffith M, McIntyre HCH (1993) The interrelationship of growth and frost tolerance in winter rye. *Physiol Plant* 87: 335–344
- Groot JJR, Verberne ELJ (1991) Response of wheat to nitrogen fertilisation, a data set to validate simulation models for nitrogen dynamics in crop and soil. *Fert Res* 27: 349–383
- Hansen JG, Secher BJM, Jørgensen LN, Welling B (1994) Thresholds for control of *Septoria* spp. in winter wheat based on precipitation and growth stage. *Plant Pathol* 43: 183–189
- Hansen L (1976) Jordtyper ved statens forsøgsstationer. *Tidsskr Planteavl* 80:742–758
- Hansen S, Jensen HE, Nielsen NE, Svendsen H (1991) Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model DAISY. *Fert Res* 27:245–259
- Heidmann T (1989) Startkarakterisering af arealer til systemforskning. II. Resultater fra arealet ved Foulum. *Tidsskr Planteavl Specialserie S2007*
- Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (1996) *Climate change 1995: the science of climate change*. Cambridge University Press, Cambridge
- Hulme M, Barrow EM, Arnell NW, Harrison PA, Johns TC, Downing TE (1999) Relative impacts of human-induced climate change and natural climate variability. *Nature* 397:688–691
- Jamieson PD, Semenov MA, Brooking IR, Francis GS (1998) Sirius: a mechanistic model of wheat response to environmental variation. *Eur J Agron* 8:161–179
- Jamieson PD, Porter JR, Semenov MA, Brooks RJ, Ewert F, Ritchie JT (1999) Comments on 'Testing winter wheat simulation models predictions against observed UK grain yields' by Landau et al. (1998). *Agric For Meteorol* 96: 157–161
- Jørgensen LN, Secher BJM, Olesen JE, Mortensen J (1997) Need for fungicide treatment when varying agricultural parameters. *Asp App Biol* 50:285–292
- Kiniry JR, Jones CA, O'Toole JC, Blanchet R, Cabelguenne M, Spanel DA (1989) Radiation-use efficiency in biomass accumulation prior to grain-filling for five grain-crop species. *Field Crops Res* 20:51–64
- Kirby EJM, Spink JH, Frost DL, Sylvester-Bradley R, Scott RK,



- Foulks MJ, Clare RW, Evans EJ (1999) A study of wheat development in the field: analysis by phases. *Eur J Agron* 11:63–82
- Lancashire PD, Bleiholder H, van den Boom T, Langelüddeke P, Strauss P, Weber E, Witzemberger A (1991) A uniform decimal code for growth stages of crops and weeds. *Ann Appl Biol* 119:561–601
- Landau S, Mitchell RAC, Barnett V, Colls JJ, Craigon J, Moore KL, Payne RW (1998) Testing winter wheat simulation models' predictions against observed UK grain yields. *Agric For Meteorol* 89:85–99
- Mearns LO, Rosenzweig C, Goldberg R (1996) The effect of changes in daily and interannual climatic variability on CERES-wheat: a sensitivity study. *Clim Change* 32: 257–292
- Melkonian J, Riha SJ, Wilks DS (1998) Simulation of elevated CO<sub>2</sub> effects on daily net canopy carbon assimilation and crop yield. *Agric Syst* 58:87–106
- Mikkelsen HE, Olesen JE (1991) Sammenligning af metoder til bestemmelse af potentiel vandfordampning. *Tidsskr Planteavl Specialserie S2157*
- Mitchell RAC, Lawlor DW, Mitchell VJ, Gibbard CL, White EM, Porter JR (1995) Effects of elevated CO<sub>2</sub> concentration and increased temperature on winter wheat: test of AFCWHEAT1 simulation model. *Plant Cell Environ* 18: 736–748
- Moot DJ, Henderson AL, Porter JR, Semenov MA (1996) Temperature, CO<sub>2</sub> and the growth and development of wheat: changes in the mean and variability of growing conditions. *Clim Change* 33:351–368
- Nelder JA, Mead R (1965) A simplex method for function minimization. *Comput J* 7:308–315
- Nonhebel S (1993) Effects of changes in temperature and CO<sub>2</sub> concentration on simulated spring wheat yields in the Netherlands. *Clim Change* 24:311–329
- Nonhebel S (1996) Effects of temperature rise and increase in CO<sub>2</sub> concentration on simulated wheat yields in Europe. *Clim Change* 34:73–90
- Olesen JE (1991) *Jordbrugsmeteorologisk årsoversigt 1990*. *Tidsskr Planteavls Specialserie S2130*
- Olesen JE, Grevsen K (1997) Effects of temperature and irradiance on vegetative growth of cauliflower (*Brassica oleracea* L. *botrytis*) and broccoli (*Brassica oleracea* L. *italica*). *J Exp Bot* 48:1591–1598
- Olesen JE, Mikkelsen SA (1983) Description and prediction of night minimum temperature by means of statistical methods. *Tidsskr Planteavl* 87:97–110
- Olesen JE, Plauborg F (1995) MVTOOL version 1.10 for developing MARKVAND. Danish Institute of Agricultural Sciences, Foulum. SP report 27-1995
- Olesen JE, Jensen T, Bøcher PK (2000a) Modelling climate change impacts on crop wheat and potato in Denmark. In: Downing TE, Harrison PA, Butterfield RE, Lonsdale KG (eds) *Climate change, climate variability and agriculture in Europe: an integrated assessment*. Environmental Change Unit, University of Oxford, Oxford, p 313–332
- Olesen JE, Mortensen JV, Jørgensen LN, Andersen MN (2000b) Irrigation strategy, nitrogen application and fungicide control in winter wheat on a sandy soil. I. Yield, yield components and nitrogen uptake. *J Agric Sci Camb* 134:1–11
- Olesen JE, Jørgensen LN, Mortensen JV (2000c) Irrigation strategy, nitrogen application and fungicide control in winter wheat on a sandy soil. II. Radiation interception and conversion. *J Agric Sci Camb* 134:13–23
- Olsen CC (1984) Såtid og såmængde vinterhvede og vinterbyg. *Tidsskr Planteavl* 88:557–569
- Parry ML (1990) *Climate change and world agriculture*. Earthscan, London
- Plauborg F, Andersen MN, Heidmann T, Olesen JE (1996) MARKVAND: a decision support system for irrigation scheduling. In: Camp CR, Sadler EJ, Yoder RE (eds) *Evaporation and irrigation scheduling*. Proceedings of International Evapotranspiration and Irrigation Scheduling Conference. November 3–6, San Antonio, TX. American Society for Agricultural Engineers (ASAE), St. Joseph, MO, p 257–535
- Porter JR (1993) AFRCWHEAT2: A model of the growth and development of wheat incorporating responses to water and nitrogen. *Eur J Agron* 2:19–22
- Porter JR, Gawith M (1999) Temperatures and the growth and development of wheat: a review. *Eur J Agron* 10:23–36
- Porter JR, Kirby EJM, Day W, Adam JS, Appleyard M, Ayling S, Baker CK, Beale P, Belford RK, Biscoe PV, Chapman A, Fuller MP, Hampson J, Hay RKM, Hough MN, Matthews S, Thompson WJ, Weir AH, Willington VBA, Wodd DW (1987) An analysis of morphological development stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. *J Agric Sci Camb* 109:107–121
- Porter JR, Leigh RA, Semenov MA, Miglietta F (1995) Modelling the effects of climatic change and genetic modification on nitrogen use by wheat. *Eur J Agron* 4:419–429
- Prew RD, Beane J, Carter N, Church BM, Dewar AM, Lacey J, Penny A, Plumb RT, Thorne GN, Todd AD (1986) Some factors affecting the growth and yield of winter wheat grown as a third cereal with much or negligible take-all. *J Agric Sci Camb* 107:639–671
- Riha SJ, Wilks DS, Simoens P (1996) Impact of temperature and precipitation variability on crop model predictions. *Clim Change* 32:293–311
- Ritchie JT, Otter S (1985) Description and performance of CERES-Wheat: a user oriented wheat yield model. US Department of Agriculture, ARS 38:159–175
- Robertson MJ, Brooking IR, Ritchie JT (1996) The temperature response of vernalization in wheat: modelling the effect on the final number of meristem leaves. *Ann Bot* 78: 371–381
- Samarakoon AB, Müller WJ, Gifford RM (1995) Transpiration and leaf area under elevated CO<sub>2</sub>: effects of soil water status and genotype in wheat. *Aust J Plant Physiol* 22:33–44
- SAS Institute (1996) SAS/STAT Software: changes and enhancements through release 6.11. SAS, Cary, NC
- Semenov MA, Barrow EM (1997) Use of stochastic weather generator in the development of climate change scenarios. *Clim Change* 35:397–414
- Semenov MA, Porter JR (1995) Climatic variability and the modelling of crop yields. *Agric For Meteorol* 73:265–283
- Semenov MA, Wolf J, Evans LG, Eckersten H, Iglesias A (1996) Comparison of wheat simulation models under climate change scenarios. *Clim Res* 7:271–281
- Semenov MA, Brooks RJ, Barrow EM, Richardson CW (1998) Comparison of the WGEN and LARS-WG stochastic weather generators for diverse climates. *Clim Res* 10: 95–107
- Stockle CO, Dyke PT, Williams JR, Jones CA, Rosenberg NJ (1992) A method for estimating direct and climatic effects of rising atmospheric carbon dioxide on growth and yield of crops: Part II—Sensitivity analysis at three sites in the Midwestern USA. *Agric Syst* 38:239–256
- Teng PS, Heong KL, Kroppf MJ, Nutter FW, Sutherst RW (1996) Linked pest-crop models under global change. In: Walker BH, Steffen WL (eds) *Global change and terrestrial ecosystems*. International Geosphere-Biosphere Book Se-

- ries 2. Cambridge University Press, Cambridge, p 291–316
- Thomsen SV, Voss J, Schou O, Kjærsgaard JF (1994) Planteavlsberetning 1994. Tureby-Køge og Omegns Landboforening, Ringsted
- Thorne GN, Pearman L, Day W, Todd AD (1988) Estimation of radiation interception by winter wheat from measurements of leaf area. *J Agric Sci Camb* 110:101–108
- van Laar HH, Goudriaan J, van Keulen H (1992) Simulation of crop growth for potential and water limited production situations. Simulation reports CABO-TT 27, CABO-DLO/TPE-WAU, Wageningen
- Wang YP, Handoko J, Rimmington GM (1992) Sensitivity of wheat growth to increased air temperature for different scenarios of ambient CO<sub>2</sub> concentration and rainfall in Victoria—a simulation study. *Clim Res* 2:131–149
- Wassenaar T, Lagacherie P, Legros JP, Rounsevell MDA (1999) Modelling wheat yield responses to soil and climate variability at the regional scale. *Clim Res* 11:209–220
- Weigel HJ, Manderscheid R, Jäger HJ, Mejer GJ (1994) Effects of season-long CO<sub>2</sub> enrichment on cereals. I. Growth performance and yield. *Agric Ecosyst Environ* 48: 231–240
- Wolf J, Evans LG, Semenov MA, Eckersten H, Iglesias A (1996) Comparison of wheat simulation models under climate change. I. Model calibration and sensitivity analyses. *Clim Res* 7:253–270

*Editorial responsibility: Mike Hulme,  
Norwich, United Kingdom*

*Submitted: September 16, 1999; Accepted: March 29, 2000  
Proofs received from author(s): August 10, 2000*