

Comparison of two soya bean simulation models under climate change. I. Model calibration and sensitivity analyses

Joost Wolf*

Department of Soil and Land Use, ALTERRA, PO Box 47, 6700 AA Wageningen, The Netherlands

ABSTRACT: To analyse the effects of climate change on soya bean growth and production, both a simple growth model, SOYBEANW, and a comprehensive model, CROPGRO, have been applied. Both models were calibrated and tested against results from soya bean trials at Toulouse, France. The sensitivity of model results to changed values of weather variables was determined. The comparison of the results from both models indicated the sort of conditions in which model results differed and may become less reliable. The start date of seed filling at Toulouse was predicted well by both models, but the simulated duration of seed filling from both models was too short in most years. Irrigated seed production was calculated reasonably well by both models, although in some years simulated yields were rather high. Seed yields from SOYBEANW were strongly dependent on the soil nitrogen supply, whereas in CROPGRO this dependence was almost nil. Without irrigation, the yield reduction due to water shortage in dry years as simulated with CROPGRO was stronger than the observed yield reduction. For SOYBEANW the opposite applied (i.e. too small reduction). Irrigated seed yields from both models increased with both increasing solar radiation and atmospheric CO₂. The optimum for irrigated production from SOYBEANW was at present temperatures in Toulouse and from CROPGRO at 2 to 4°C higher temperatures. Water-limited seed yields from both models were almost insensitive to temperature, increased with an increase in atmospheric CO₂ and precipitation, and decreased with increasing solar radiation for CROPGRO but did not change for SOYBEANW.

KEY WORDS: Climate change · Model comparison · Sensitivity analyses · Simulation model · Soya bean

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1. INTRODUCTION

Since agricultural production is greatly affected by climate, any changes in climate which may result from increasing concentrations of greenhouse gases in the atmosphere (Mearns 2000) could have dramatic consequences for agricultural yield potential. In this study the effects of climate change on the yield potential of soya bean were analysed.

The relationship between climate, crop growth and yield is complicated since a large number of climate, soil, management and crop characteristics are involved. In addition, crop growth mainly appears to re-

spond to changing conditions in a non-linear way (Nonhebel 1994). For example, crop yields may decrease with an increase in temperature variability (i.e. temperatures more often outside of optimum range for crop growth) or rainfall variability (i.e. longer dry spells), as shown by Semenov & Porter (1995) and Semenov et al. (1996). As a consequence, the effects of climate change on crop yield cannot be described in terms of simple and average relationships between the two. In the last 2 decades methods have been developed for calculating yield levels of crops under well-specified conditions. These methods are based on the application of crop growth simulation models, combining knowledge about crop characteristics and their interactions with the environment.

*E-mail: j.wolf@alterra.wag-ur.nl

In this way, the effects of climate change in the USA on the yields of a large number of crops, such as wheat, maize and alfalfa, and the efficacy of management responses to climate change have been calculated and examined (Wilks 1988, Adams et al. 1990, Cooter 1990, Easterling et al. 1992a,b). For soya bean too, the effects of climate change on the yields at a large number of sites in the USA have been studied (Curry et al. 1990, 1995, Sinclair & Rawlins 1993, Haskett et al. 1997, Phillips et al. 1996). Such studies for soya bean under climate change have also been done, for example, for Madhya Pradesh in India (Lal et al. 1999) and the pampayan region of Argentina (Magrin et al. 1997). Soya bean is worldwide the most important grain legume and its production ranked number 5 among the most important food crops (Allen & Boote 2000). In Europe, however, soya bean is a crop of minor importance (FAO statistical data bases, available at <http://apps.fao.org>), although this may change in future. The effects of climate change in Europe on the yields of a number of crops, such as wheat (Wolf 1993, Nonhebel 1996, Semenov et al. 1996), maize (Wolf & Van Diepen 1994, 1995), potato (Carter et al. 2000, Olesen et al. 2000, Wolf 2000a) and grapevine (Bindi et al. 1996, Bindi & Fibbi 2000) have been analysed, but this has not yet been done for soya bean.

A detailed soya bean growth model, CROPGRO, which has been tested and applied in a large range of environmental conditions, was used in this climate change impact study under European conditions. This model was first calibrated and tested against results from soya bean trials. Subsequently, the sensitivity of soya bean production to separately changed weather variables was determined. These analyses were also done with a more simplified model, SOYBEANW. Both models were also applied to analyse the possible effects of climate change, change in climatic variability and change in crop management in response to climate change on soya bean production at a number of sites in the EU (Wolf 2002, in this issue). For analyses at the larger (e.g. national and European) scale, simple models such as SOYBEANW are preferred, as they can be applied more easily. More information on this study, which formed part of the EU project CLIVARA (focussed on the effects of climate change and climatic variability on the growth and yield of 4 crop species in Europe), is given in the final report of this project (Downing et al. 2000, Wolf 2000b).

2. METHODOLOGY

CROPGRO contains more elaborate descriptions of crop growth, assimilate allocation, leaf area expansion, phenology, organ formation, senescence of crop

organs, water balance, sink limitation, stress effects on assimilate production and allocation and on senescence than does SOYBEANW. A schematic of both models and their main differences is shown in Fig. 1. The main characteristics of both models and their input data requirements are described in the following.

2.1. Description of SOYBEANW

SOYBEANW has been based on the simple model developed by Sinclair (1986) for simulating soya bean growth, and it has been changed for this study. The model calculates growth from sowing to maturity with a time-step of 1 d and takes into account the effects of weather conditions, water supply and nitrogen supply. The main processes included in the model are leaf expansion and senescence, crop growth, soil evaporation and crop transpiration, water inflow from precipitation and irrigation, water losses by drainage, and biological nitrogen fixation.

The original model has been applied and tested under ambient conditions in Argentina (Sinclair et al. 1992), Japan (Spaeth et al. 1987) and Australia (Muchow & Sinclair 1986) and has also been applied to projected future changes in climatic conditions in the USA (Sinclair & Rawlins 1993).

2.1.1. Crop phenology

The duration between sowing and crop emergence depends on thermal time. After emergence, the period up to the end of leaf growth and the start of seed filling (i.e. vegetative period) is calculated on the basis of thermal time and photoperiod, as based on the approach and data given by Grimm et al. (1993), Jones et al. (1991), and Hesketh et al. (1973). This relationship between thermal time and photoperiod, and the phenological development is cultivar-specific. The duration of seed filling till crop maturity is also calculated on the basis of thermal time and photoperiod (Jones et al. 1991, Grimm et al. 1994), but in general, the end of seed filling and crop maturity is calculated to occur at an earlier date due to advanced canopy senescence. This so-called self-destruction of the plant is caused by the translocation of large amounts of nitrogen from the canopy. This nitrogen is required for the growth of the seeds (Sinclair & de Wit 1976). In the original model (Sinclair 1986) the duration of the vegetative period was not based on thermal time and photoperiod but was an input and the duration of seed filling was only determined by self-destruction.

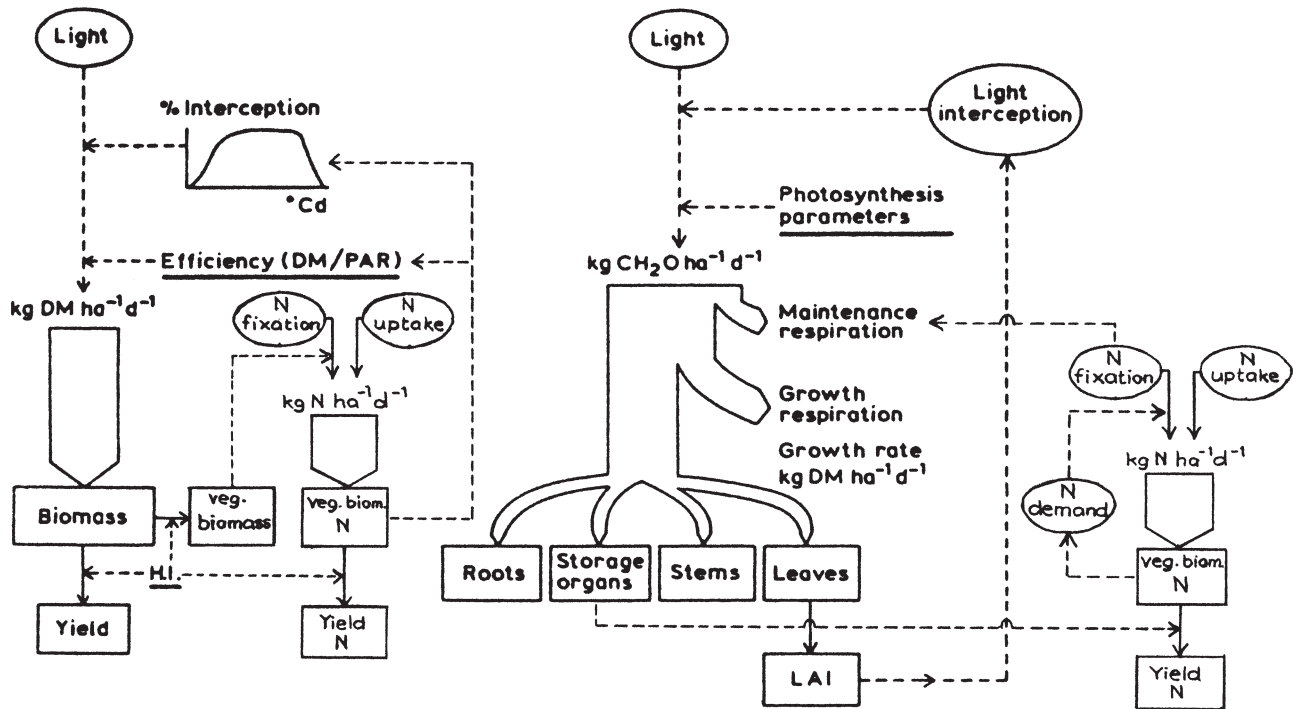


Fig. 1. Schematic representation of the calculation of crop growth according to: Left: SOYBEANW model based on light interception (function of leaf area index and thus of thermal time and leaf nitrogen), light use efficiency, harvest index, and biological N fixation (function of vegetative biomass). Right: CROPGRO model based on light interception (function of leaf area index and thus leaf mass), photosynthesis and respiration characteristics, dry matter partitioning, and biological N fixation (mainly function of crop nitrogen demand). (Source: Spitters 1990, with additions for soya bean)

2.1.2. Crop growth

Daily growth is computed as light interception multiplied by light use efficiency. Leaf area expansion, which determines the fraction of incoming light intercepted, is mainly a linear function of the plastochron index. This index is about equal to cumulative temperature sum above a base value (Sinclair 1984). The increase in leaf area is limited by both water stress and nitrogen shortage. Light use efficiency is corrected for sub-optimal temperature (with optimal day-time temperature between 24 and 34°C), soil moisture content and leaf nitrogen content and for a change in atmospheric CO₂ (there were no CO₂ and temperature corrections in the original model). Seed yield is calculated as a fraction of total biomass (i.e. accumulated crop growth), taking conversion losses into account. This fraction (i.e. harvest index) linearly increases with the duration of the seed filling period since its start date. Further information concerning these model concepts can be found in Sinclair (1986).

2.1.3. Water balance

Available soil moisture in the root zone is calculated from the water balance, which includes precipitation,

irrigation, losses by runoff, soil evaporation and crop transpiration, and leaching from the root zone. Potential rates of soil evaporation and crop transpiration are calculated using the Penman approach (Frère & Popov 1979). A correction factor is incorporated to calculate transpiration rates that are essentially similar to those from the Penman-Monteith method (Smith 1992). The actual transpiration rate is calculated from its potential rate by using a correction for the degree of light interception by the crop and the available soil moisture fraction in the root zone. The actual evaporation rate is calculated from its potential rate by using a correction for the degree of light interception by the soil and the time since last rain (Ritchie 1972). This differs from the original model (Sinclair 1986), where transpiration was calculated from biomass production and crop water-use efficiency.

2.1.4. Nitrogen supply

Nitrogen supply to the crop is determined by both the amount of available nitrogen in the soil and biological nitrogen fixation. As the processes that determine the nitrogen availability in the soil, such as organic matter decomposition, nitrogen mineralization and nitrogen leaching, are not described in the

model, the soil nitrogen supply is given as an input value. This value is based on the nitrogen uptake by a non-leguminous crop under identical field conditions without nitrogen application. Biological nitrogen fixation is calculated as a linear function of total vegetative biomass, and it decreases with a decrease in available soil moisture and becomes nil after heavy rainfall (Sinclair 1986). As the nitrogen supply becomes limiting during seed filling, a large amount of nitrogen is then translocated from the canopy to the seeds (see Section 2.1.1).

2.1.5. Direct effects of increased atmospheric CO₂

In the model, doubling of atmospheric CO₂ results in an increase in light use efficiency of 35% and practically in a similar biomass increase. This increase has been based on experimental results (Jones et al. 1984, Cure 1985, Cure & Acock 1986, Allen & Boote 2000). Potential transpiration is reduced by 5% for a doubling of CO₂ (see Pickering et al. 1995 for CROPGRO), representing a large decrease in stomatal conductance, which is largely compensated for by the larger amount of leaves (not calculated in model) and in particular by the micrometeorological feedback (i.e. increases in leaf temperature and vapour pressure gradient as shown by Valle et al. 1985). In the original model these CO₂ effects were not included.

2.2. Description of CROPGRO

SOYGRO has been developed at the University of Florida (Wilkerson et al. 1983, Jones et al. 1989) for the simulation of soya bean growth (Hoogenboom et al. 1992). SOYGRO has been integrated into a generic grain legume module, called CROPGRO, which makes use, together with the CERES models for grain crops, of a software shell for input and output handling (Tsuji et al. 1994, Hoogenboom et al. 1995). CROPGRO version 3.0 was used in this study.

The growth simulation is carried out from sowing to maturity with a time-step of 1 d. It describes soya bean growth, its nitrogen and water uptake, and the nitrogen and water dynamics in the soil. The main processes included in the model are photosynthesis, respiration, partitioning of assimilates to plant organs, phenological development, soil evaporation and crop transpiration, water inflow from precipitation and irrigation, water losses by runoff and drainage, change in inorganic and organic soil nitrogen, crop nitrogen uptake and nitrogen leaching.

CROPGRO has been validated and applied under ambient conditions (Jones & Ritchie 1991, Egli & Bru-

ening 1992, Hoogenboom et al. 1992, Nagarajan et al. 1993) and has also been applied to projected future changes in climatic conditions in the USA (Curry et al. 1990, 1995, Pickering et al. 1995). CROPGRO has also been used under European conditions, for analysing the modelled phenological development, growth, reproductive development and seed yield versus measured results from soya bean experiments and for testing its predictive potential (Brisson et al. 1989, Colson et al. 1995a,b).

The subsequent description of modules of the CROPGRO model was mainly based on its technical documentation (J. W. Jones pers. comm.). More detailed descriptions of CROPGRO were given by Boote et al. (1998a,b).

2.2.1. Crop phenology

This routine calculates the phenological development through the different growth stages, as partly based on the description by Fehr & Caviness (1977). The development rate is determined mainly by the temperature during vegetative growth phases and is also dependent on photoperiod during the reproductive phases (i.e. seed filling), and both relationships are cultivar-specific. The effects of water and nitrogen shortage on development rate are also included. Water shortage results in retarded development in all growth phases except seed filling. Both water and nitrogen shortage give an increase in development rate during seed filling and, hence, an advancement of physiological maturity. The timing of different growth stages is determined by the development rate and is important in establishing changes in dry matter partitioning in the plant. For more information on this phenology model, see Jones et al. (1991).

2.2.2. Crop growth

Gross assimilation of the canopy is a function of the intercepted photosynthetically active radiation (PAR), and its rate is modified for suboptimal temperatures (with optimal day-time temperature between 22 and 34°C), water stress and nitrogen shortage. The fraction of incoming PAR intercepted by the canopy is an exponential function of leaf area index (LAI). Maintenance respiration losses, which depend on biomass dry weight, daily gross assimilation and temperature, are subtracted from the daily gross assimilation. During the vegetative growth phase the remaining assimilates are allocated to crop organs dependant upon the developmental stage of the crop. Allocated assimilates are converted to structural plant material by taking

into account conversion losses. During the reproductive growth phase the allocation of assimilates is determined by the potential seed and pod growth and the environmental conditions. The allocation to pods and seeds increases with increasing drought stress and becomes less under suboptimal temperatures. Low temperatures, for example, result in decreased pod formation and seed production.

2.2.3. Water balance

The soil is treated as a multi-layered system. For each layer, daily changes in soil moisture content are the result of infiltration, soil evaporation, crop transpiration, and downward movement to the lower layer. Precipitation is a daily input. Runoff is a function of soil type, soil moisture content and precipitation. Infiltration is equal to precipitation minus runoff and drainage occurs when soil moisture exceeds the water-holding capacity of the bottom soil layer. Potential transpiration is calculated by the Priestley-Taylor relation (Priestley & Taylor 1972), and actual transpiration is modified by the LAI, soil evaporation and soil water deficit. Actual evaporation is a function of potential evaporation, LAI and time (Ritchie 1972).

2.2.4. Nitrogen supply

Nitrogen supply is critical for growth of new tissues, in particular the seeds. Initially the model calculates the nitrogen available from the mobilization of older tissue. If this is insufficient to satisfy the nitrogen demand, the possible nitrogen uptake from the soil is calculated. If both sources are sufficient, crop growth proceeds at its potential rate, using all the available carbohydrates. If there is still a nitrogen deficit, the remaining nitrogen demand is satisfied by biological nitrogen fixation. The model assumes that at all times just enough nitrogen is made available for the potential growth rate, and that the required amount of carbohydrates, if available, is used for nitrogen fixation in the nodules.

2.2.5. Direct effect of increased atmospheric CO₂

Modifications to photosynthesis and evapo-transpiration routines in CROPGRO, which account for the effects of increases in atmospheric CO₂, were described by Pickering et al. (1995). Doubling of ambient CO₂ results in an increase in photosynthetic rate of about 30% and a decrease in the potential evapo-transpiration rate of about 5%.

2.3. Data requirements for both models

For application of SOYBEANW, data that specify crop growth and phenological development are required. Data that determine phenological development and partitioning are thermal time sums for emergence, vegetative development, seed filling, critical day lengths for photoperiod effect, and the daily increase in harvest index. These data are cultivar-specific. Data that determine crop growth are the light use efficiency and its sensitivity to changes in temperature and atmospheric CO₂.

For application of CROPGRO, data that determine assimilation and respiration processes, dry matter allocation, growth of plant organs, and the temperature sensitivity of various growth processes are required. These data are stable and generally do not need to be changed (i.e. not cultivar-specific). Data that determine phenological development are thermal time for each vegetative growth phase, photo-thermal time (inclusive day length effect) for each reproductive growth phase, critical day length below which no day length effect occurs, and the slope of the relative day length response. These data are cultivar-specific and should be determined for the various cultivars and environmental conditions on the basis of experimental results.

Soil input data required for growth simulations with SOYBEANW are the initial and maximum available soil moisture fractions, the maximum effective rooting depth, the fraction of precipitation lost by surface runoff, the maximum amount of available soil nitrogen, and the nitrogen fixation coefficient. Such information can be derived from the European soil map (King et al. 1995) and field trials. For CROPGRO practically the same soil input data (except nitrogen fixation coefficient) are required but the soil moisture characteristics, mineral nitrogen and organic matter contents are specified for each soil layer. Besides, the applications of fertilizer nitrogen, organic material and irrigation water can be specified in more detail.

Daily minimum and maximum air temperatures, atmospheric CO₂ concentration and solar radiation are required for both models to calculate the CO₂ assimilation rates. To calculate the components of the water balance, for CROPGRO daily precipitation and for SOYBEANW precipitation, wind speed and vapour pressure are also required. Historical or generated sets of daily weather data were used.

3. RESULTS

CROPGRO and SOYBEANW were calibrated and tested against results from soya bean trials. For analyz-

ing the possible effects of climate change, the sensitivity of modelled soya bean production to separately changed values of weather variables was determined.

3.1. Model testing and comparison of modelling results

Both models were calibrated and tested against soya bean (cultivar Weber) trials at Toulouse, France (Colson 1992, Colson et al. 1995a). These experiments were conducted over 4 years (1986–1989), both with and without irrigation. Observed seed yields and dates of phenological stages (i.e. flowering, first pods, physiological maturity) were given. For application of both models, the data that are cultivar-specific (see Section 2.3), and in particular thermal time sums for different phenological phases, were calibrated against these experimental data sets. For supplementary information on the calibration of CROPGRO against these data sets and on the possibilities of application of CROPGRO for yield prediction, see the studies by Colson et al. (1995a,b).

Seed yield is affected by the duration between the start of seed filling and physiological maturity. The simulated start date of seed filling from both models

corresponded well in 3 out of 4 years with the observed date (Fig. 2A), as calculated from the observed date of first pods. This correspondence was not improved if the start of seed filling from SOYBEANW was not only determined by thermal time but also by photoperiod. The simulated duration of seed filling from both CROPGRO and SOYBEANW (version with maturity determined by nitrogen limitation) was too short in most years, compared to the observed duration (Fig. 2B). If the duration of seed filling from SOYBEANW was only determined by thermal time and photoperiod (assuming that nitrogen supply was not limiting), this duration corresponded well with the observed duration. However, for such a non-limiting nitrogen supply SOYBEANW calculated seed yields that were much too high (Fig. 3A). Hence, in the subsequent analyses with SOYBEANW crop maturity is determined by nitrogen limitation and the start of seed filling only by thermal time.

From irrigated soya bean trials at Toulouse with different management (i.e. differences in soil type, irrigation and nitrogen supply), the mean of 2 highest seed yields in each year was used for comparison with the simulated yields, assuming that crops in these experiments experienced the weakest yield reductions by pest and disease infestation, nutrient shortage and

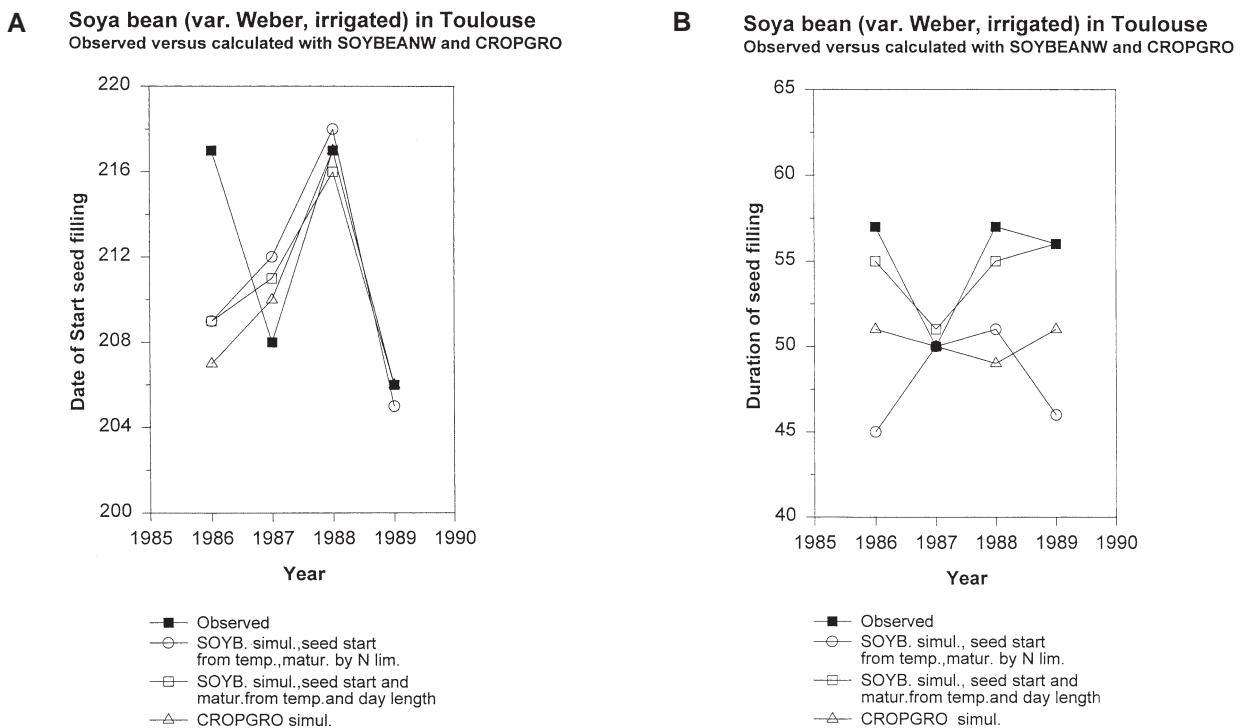


Fig. 2. (A) Date (Julian day) of the start of seed filling and (B) duration of the period of seed filling for soya bean as observed in field experiments at Toulouse, France (Colson 1992, Colson et al. 1995a) and as simulated with respectively CROPGRO and SOYBEANW (SOYB; dates of start of seed filling and of maturity determined either by respectively required temperature sum and nitrogen limitation or by required temperature sums with day length effect included)

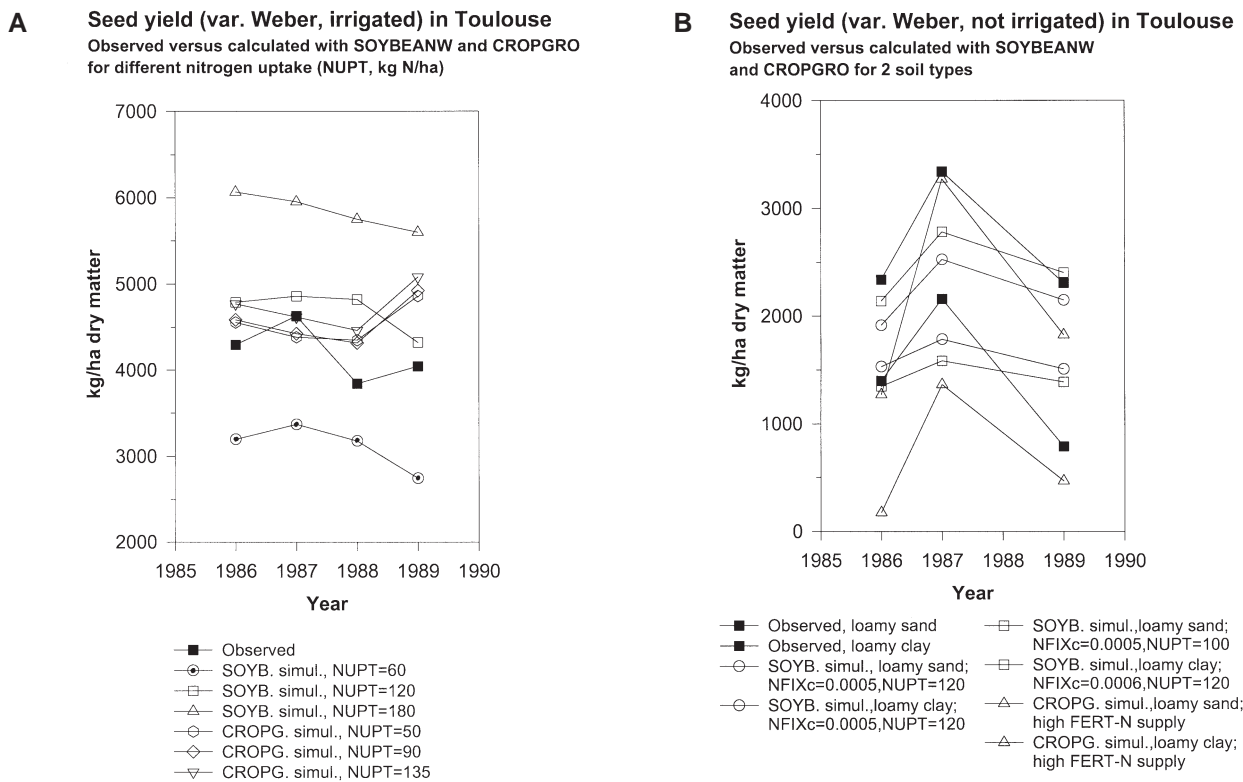


Fig. 3. Seed yield for respectively (A) irrigated and (B) non-irrigated soya bean (on loamy sand and loamy clay soils with respectively lower and higher yields) as observed in field experiments at Toulouse, France (Colson 1992, Colson et al. 1995a) and as simulated with CROPGRO (CROPG.) and SOYBEANW (SOYB.) for different N uptake from soil (NUPT in kg N ha⁻¹) and nitrogen fixation coefficient (NFIxc in kg N kg⁻¹ vegetative dry biomass d⁻¹)

other soil limitations. Growth simulations were carried out for different values for soil nitrogen supply and thus nitrogen uptake (NUPT) from the soil. The difference in seed yield for different NUPT values with CROPGRO was very small (Fig. 3A). As described earlier (Section 2.2), a lower value for NUPT resulted in more biological nitrogen fixation, and thus a greater carbohydrate use for this process and a slightly lower yield. The simulated yields from CROPGRO corresponded well with the observed yields in the first 2 years but were higher in the last 2 years. Although the simulated duration of seed filling from CROPGRO was shorter than observed (Fig. 2B), this did not result in the yields being too low. With SOYBEANW the difference in simulated seed yield for different values for NUPT was very large. In this model a larger soil nitrogen supply resulted in more vegetative biomass and in more biological nitrogen fixation (Section 2.1). This in turn resulted in a strong increase in nitrogen availability and a much higher seed yield (the yield being strongly limited by nitrogen). If NUPT was set at 120 kg N ha⁻¹, the correspondence between simulated yields from SOYBEANW and observed yields was moderately good. However, the value for NUPT, as

based on the calibration, strongly affected the yield level from SOYBEANW.

Soya bean experiments at Toulouse without irrigation were conducted during the same years. These experiments were carried out on both a loamy sand and a loamy clay soil. The initial and maximum available amounts of soil moisture were estimated on the basis of soil information from these trials (Colson 1992). Seed yield simulated with CROPGRO for the loamy clay soil corresponded well with the observed yield in 1987, but was too low in the other 2 years (Fig. 3B: higher and lower yield for respectively loamy clay and loamy sand). This indicated that the simulated reduction of the seed yield by water shortage in relatively dry years was too strong. The seed yields simulated for the loamy sand were lower than the observed yields, which also was caused by a too strong yield reduction by water shortage in the simulation. Seed yields on both soil types were simulated with SOYBEANW first with identical values for the nitrogen fixation coefficient and NUPT (Fig. 3B). In that case, the simulated yield difference between the 2 soil types was too small. The SOYBEANW simulations were, therefore, repeated with values for the nitrogen fixation coefficient

and NUPT that were lower for loamy sand than for loamy clay. The observed seed yields were then calculated moderately well by SOYBEANW for years 1986 and 1989; however, they were underestimated for year 1987. Hence, the inter-annual variation of non-irrigated yields from SOYBEANW was weaker and from CROPGRO stronger than observed.

The available information from soya bean experiments in Europe appeared to be limited, which caused the need for additional testing of both models. Hence, the simulation results from the 2 models were compared in more detail in the following, assuming that CROPGRO has been applied and tested for a large range of environmental conditions and can be considered a standard model for simulating soya bean growth. Simulated courses of growth variables during one growing season, both with and without irrigation, at Toulouse were compared (Fig. 4). The time courses of total biomass from the 2 models were different, with a later increase and maximum for total biomass and a stronger decrease near maturity from CROPGRO, in particular for irrigated production. The time courses of seed production were also different, with the CROPGRO time course starting later, resulting in particular for irrigated production in a lower seed yield. The time courses of biological nitrogen fixation for non-irrigated production were practically similar for both models. With irrigation, however, the final nitrogen fixation from SOYBEANW was larger due to the large vegetative biomass near maturity and due to disregard of the actual nitrogen demand. The time courses of LAI from both models were similar for irrigated production, but near maturity the depletion of leaf nitrogen for seed growth in SOYBEANW resulted in a more rapid decrease in leaf area than in CROPGRO. For water-limited production, in particular on the loamy sand, CROPGRO simulated a lower maximum LAI and an advanced leaf senescence compared with irrigated production. These changes by increasing water limitation were not simulated with SOYBEANW.

For irrigated production with different values for NUPT, the results from growth simulations with the 2 models were compared (Fig. 5). SOYBEANW calculated for increased NUPT a later leaf senescence near crop maturity (mainly determined by nitrogen limitation). This resulted in a higher seed production near maturity and thus a larger seed yield. If NUPT decreased to 60 kg N ha^{-1} , SOYBEANW calculated a lower LAI, a lower biomass production and thus also a lower biological nitrogen fixation. The resulting lower nitrogen availability resulted in an earlier leaf senescence and a much lower seed production. CROPGRO calculated identical time courses for biomass and seed production and for LAI with different values for NUPT. If NUPT is low (i.e. 50), CROPGRO calculated during

the initial growth period a high biological nitrogen fixation to cover the nitrogen demand of the crop. Hence, according to CROPGRO the soil nitrogen supply and the resulting values for NUPT have a negligible effect on biomass and seed production.

3.2. Sensitivity analyses

For both irrigated and water-limited soya bean production at Toulouse the sensitivity of model results to systematic changes in climate were analysed. Growth simulations were conducted with both CROPGRO and SOYBEANW over a time period of 20 yr (1970–1989) for a historical climate data set from Toulouse. Weather variables in this data set were adjusted independently, in a stepwise manner, in order to gauge the sensitivity of model results to changing values of each variable. Sensitivity to changes in temperature, atmospheric CO_2 concentration, precipitation, solar radiation, vapour pressure and windspeed was analysed. Values for each output variable are the mean result of 20 yr of growth simulations.

The optimum temperature for both total above-ground biomass and seed yield was 2 to 4°C above present temperatures at Toulouse for irrigated production from CROPGRO but was equal to present temperatures for SOYBEANW (Fig. 6). Without irrigation, the yields from CROPGRO were much lower and were almost insensitive to temperature change. An increase in temperature caused an increase in growth rate, the effect of which was undone by increasing water shortage. SOYBEANW calculated the highest water-limited biomass yield at the lowest temperature (due to potential evapo-transpiration being at the lowest); however, as with CROPGRO the seed yield almost did not change with temperature change. The reduction in seed yield due to water limitation was smaller from SOYBEANW than from CROPGRO compared to irrigated production. As the differences in evapo-transpiration and in total biomass between irrigated and non-irrigated production were practically similar for both models (Fig. 6A,D), CROPGRO apparently applied a stronger sensitivity of seed production to water shortage. The coefficient of variation ($\text{CV} = \text{standard deviation}/\text{mean yield}$) of the seed yields (Fig. 6C) indicates the degree of inter-annual yield variation. Both models calculated a low CV for irrigated production that increased rapidly with a decrease in temperature (i.e. more years with growth reduction due to low temperatures). Note that this strong increase in CV is partly caused by the strong decrease in mean seed yield. Without irrigation, CV of seed yield was moderately and very high for respectively SOYBEANW and CROPGRO, indicating the difference in the modelled yield sensitivity to water shortage.

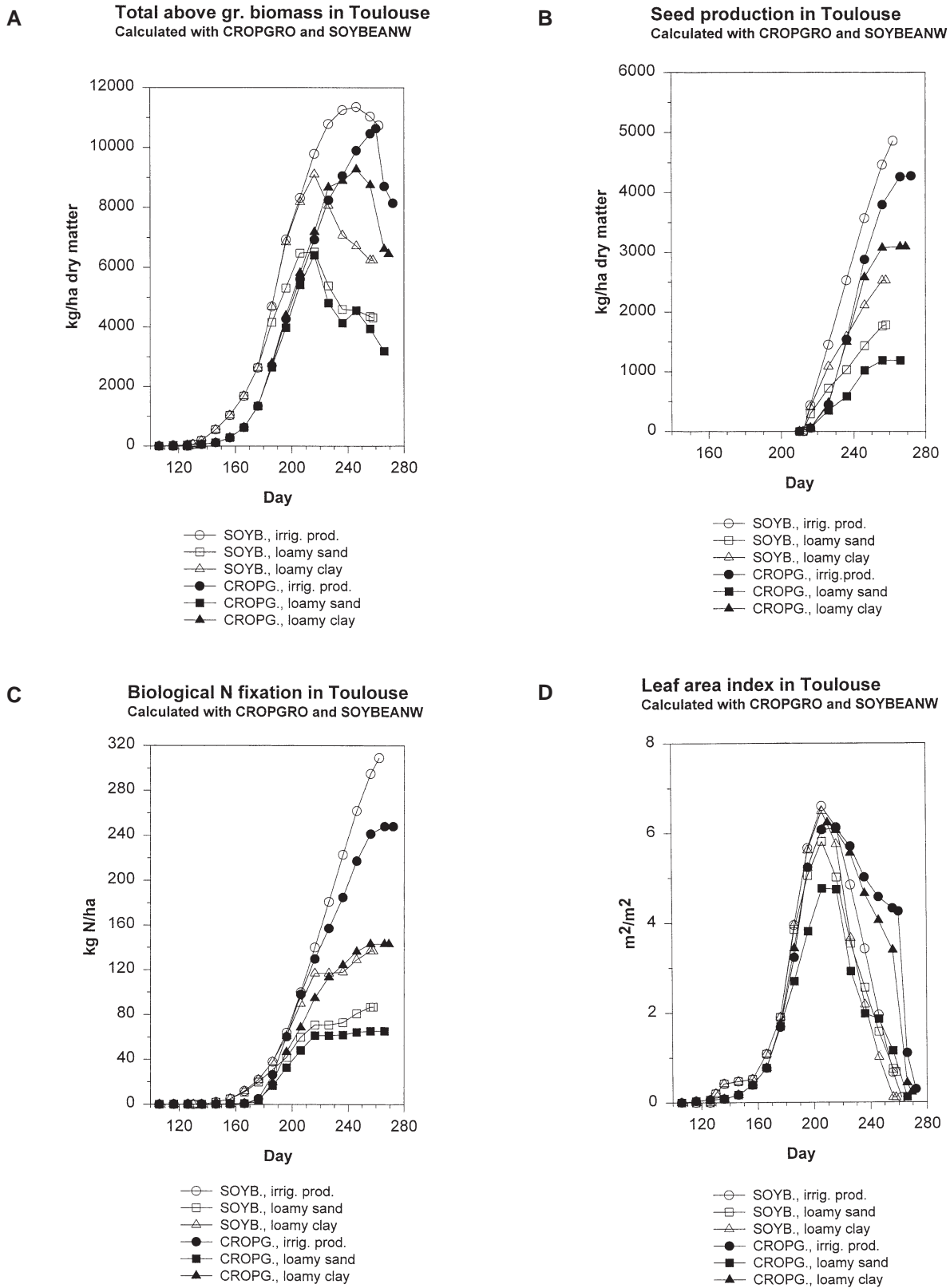


Fig. 4. Time course of (A) total above-ground biomass, (B) seed production, (C) biological nitrogen fixation, and (D) leaf area index for soya bean as simulated with CROPGRO (CROPG.) and SOYBEANW (SOYB.) for irrigated and water-limited production (on 2 soil types) in 1987 at Toulouse, France

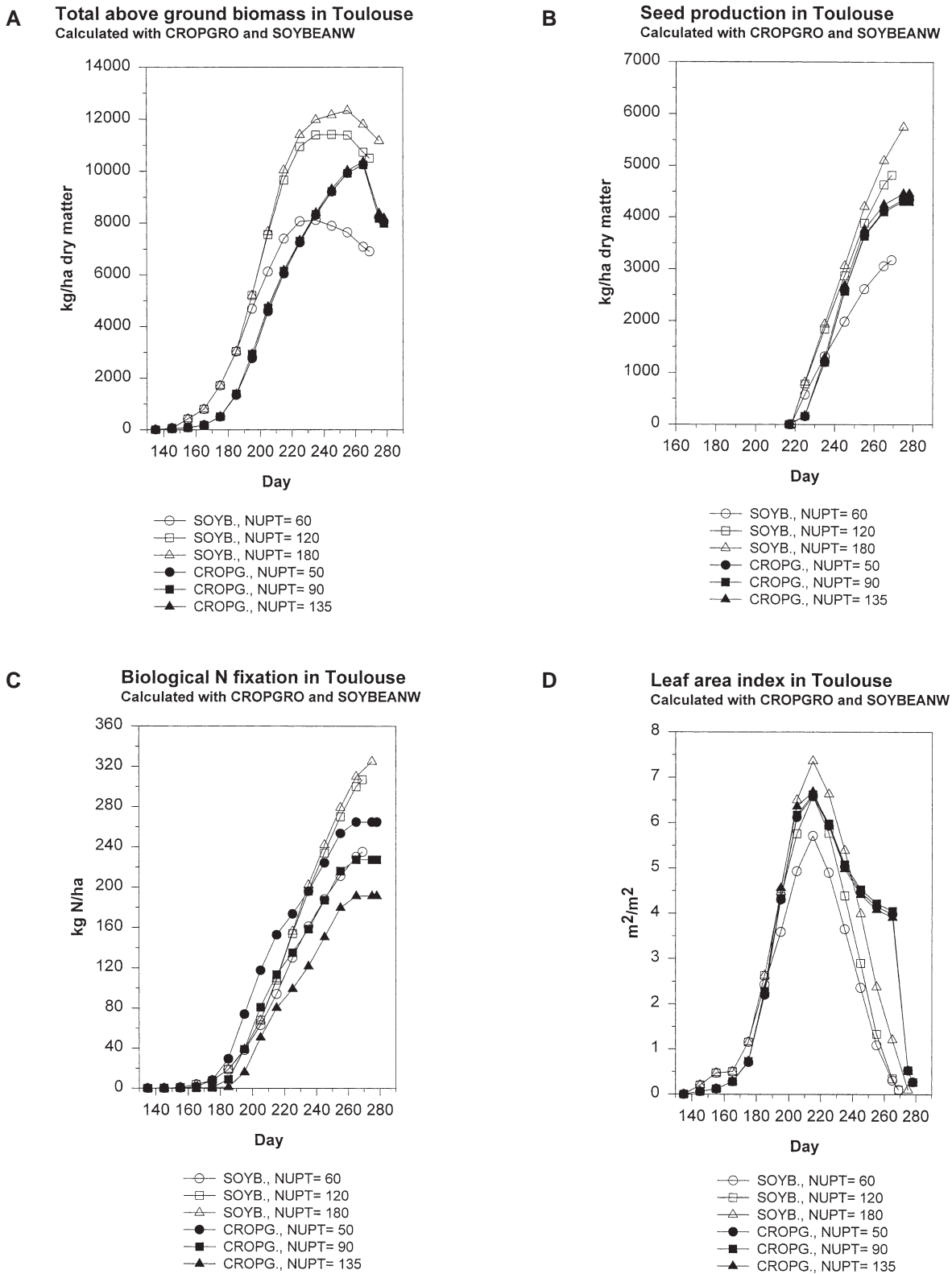


Fig. 5. Time course of (A) total above-ground biomass, (B) seed production, (C) biological nitrogen fixation, and (D) leaf area index for soya bean as simulated with CROPGRO (CROPG.) and SOYBEANW (SOYB.) for irrigated production and different N uptake from soil (Nupt in kg N ha^{-1}) in 1988 at Toulouse, France

Seed yield considerably increased with precipitation (as a result of increasing water supply) when no irrigation was applied (Fig. 7). This yield increase from both models was similar, although CROPGRO calculated a

stronger yield reduction compared with irrigated production. The increase in irrigated seed yield with increasing solar radiation was moderate for CROPGRO and considerable for SOYBEANW, and with an in-

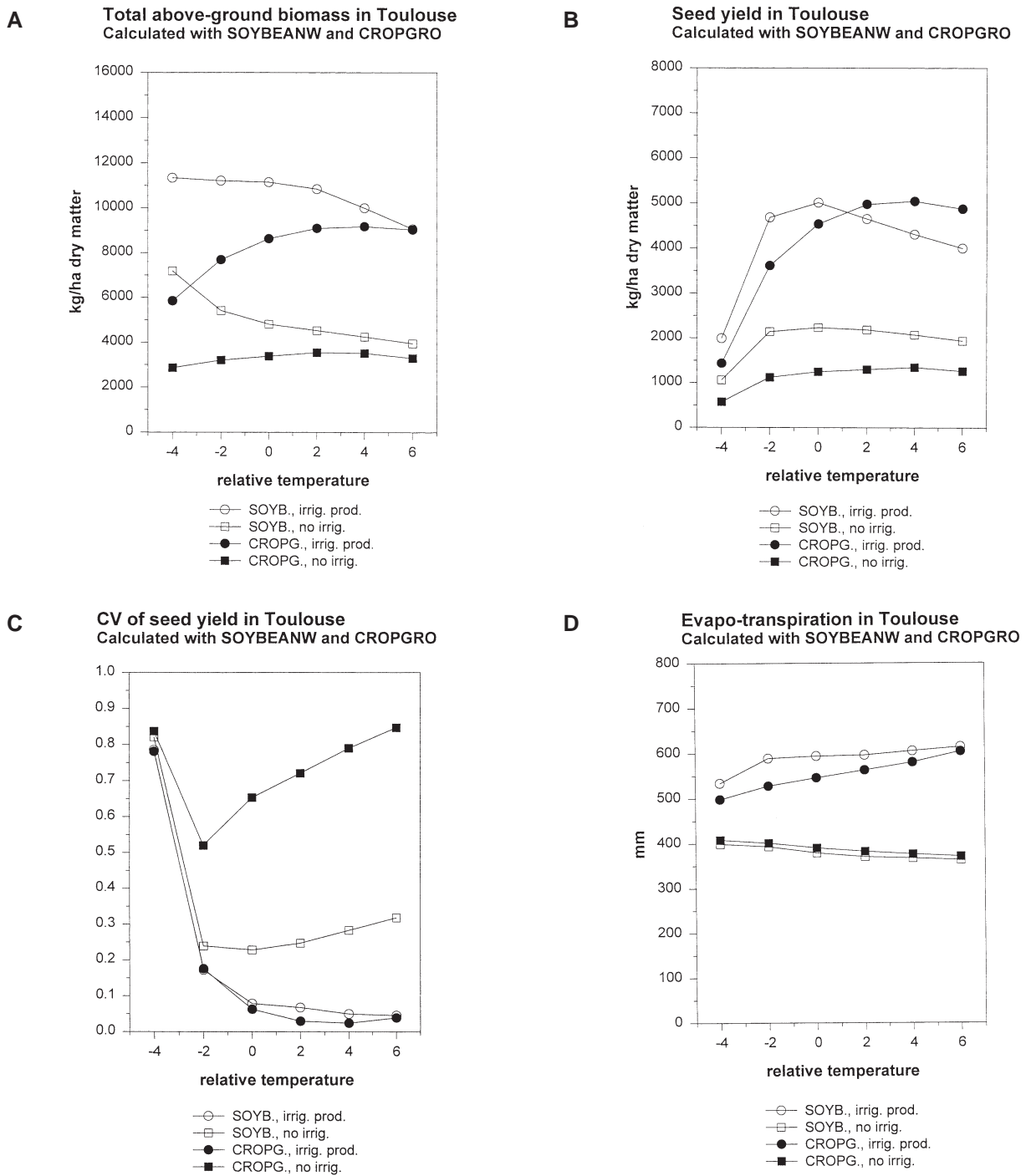


Fig. 6. Sensitivity to change in temperature of (A) total above-ground biomass, (B) seed yield, (C) coefficient of variation (CV) of seed yield, and (D) cumulative evapo-transpiration from sowing to maturity for soya bean as simulated with CROPGRO (CROPG.) and SOYBEANW (SOYB.) for irrigated and non-irrigated production at Toulouse, France. Results were established for 20 yr (1970–1989) of historical weather data, for which temperature values were changed as indicated

crease in atmospheric CO₂ the yield increase was considerable for both models. Without irrigation, the decrease in seed yield with increasing solar radiation was considerable for CROPGRO (as a result of increasing

water limitation) and nil for SOYBEANW. For both models an increase in atmospheric CO₂ caused a moderate increase in non-irrigated seed yield. Increasing vapour pressure and decreasing windspeed caused a

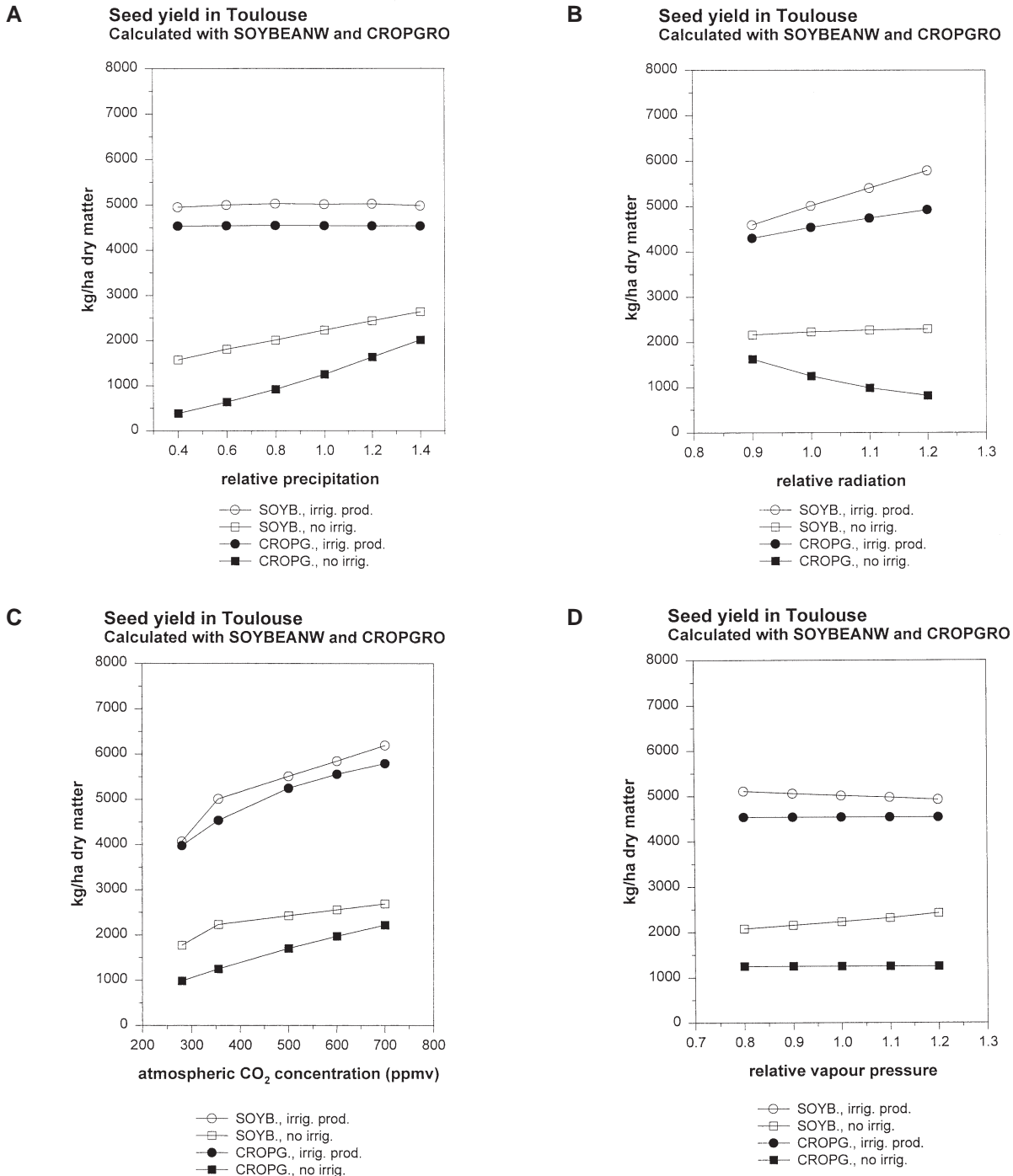


Fig. 7. Sensitivity to changes in (A) precipitation, (B) solar radiation, (C) atmospheric CO₂ concentration, and (D) vapour pressure of seed yield for soya bean as simulated with CROPGRO (CROPG.) and SOYBEANW (SOYB.) for irrigated and non-irrigated production at Toulouse, France. Results were established for 20 yr (1970–1989) of historical weather data, for which values for 1 weather variable were changed as indicated

decrease in potential evapo-transpiration and thus an increase in non-irrigated seed yield from SOYBEANW, but no change from CROPGRO (these weather variables were not used in its evapo-transpiration method).

4. FINAL DISCUSSION AND CONCLUSIONS

To analyse the effects of climate change on soya bean growth and production, 2 different soya bean models were applied. The SOYBEANW model has a limited degree of detail in the description of growth processes. Hence, the number of model relations that needed to be tested, the number of parameters that needed calibration to site-specific conditions, and the required data base of inputs were more limited than in the CROPGRO model. In addition, the results from such a simple model are often more stable than those from a more comprehensive model. These model characteristics are an advantage for use in regional scale studies (Boote et al. 1996). On the other hand in a more detailed model, such as CROPGRO, the growth processes, the responses of these processes to changes in environmental conditions and the interactions between these responses are described in a more mechanistic and more realistic way. The comparison of the results from the 2 models indicated the differences in their model approaches and the sort of environmental conditions in which the model results differed and may become less reliable.

Results from both SOYBEANW (version with physiological maturity determined by nitrogen limitation) and CROPGRO were compared with results from soya bean experiments at Toulouse, France. The start date of seed filling was predicted well by both models, but the simulated period from start of seed filling to maturity from both models was too short in most years. This may give simulated seed yields that are too low. However, results from other experiments (Egli et al. 1984) showed that the effective seed filling period for soya bean (as of importance for simulating seed production) was much shorter than the total period from start of seed filling to maturity. SOYBEANW was able to predict the duration from start of seed filling to maturity well on the basis of photoperiod and thermal time (with approach from Grimm et al. 1994). However, this only applied to situations where the nitrogen supply was large and, hence, advanced crop senescence by nitrogen shortage did not occur. This would result in unrealistically high yields from SOYBEANW compared to the observed yields.

Irrigated seed yields were calculated reasonably well by both models, although in some years simulated yields were rather high. Seed yields from SOYBEANW were strongly dependent on the soil nitrogen supply,

whereas in CROPGRO this dependence was almost nil. Without irrigation, the yield reduction due to water shortage in dry years as simulated with CROPGRO was stronger than the observed yield reduction. For SOYBEANW the opposite applied (i.e. the yield reduction in dry years was too small). Hence, the interannual (water-limited) yield variation was too small with SOYBEANW and too large with CROPGRO. A comparison of CROPGRO with a more detailed model showed that the water use and hence the yield reduction by water shortage from CROPGRO could severely be overestimated at high temperatures (Pickering et al. 1995). However, the sensitivity analyses (Section 3.2) of this study showed that CROPGRO and SOYBEANW calculated identical evapo-transpiration, both with and without irrigation, and that CROPGRO apparently applied a stronger sensitivity of seed production to water shortage.

Simulation results from both models for both irrigated and water-limited production at Toulouse were compared in more detail. The time courses of total biomass from both models were different, with a later increase and maximum for total biomass and a stronger decrease near maturity from CROPGRO, in particular for irrigated production. This made it difficult to compare the final total biomass from both models. As shown in the sensitivity analyses (Section 3.2), CROPGRO assumed a more negative effect of cool temperatures (during the initial part of the growing season) on biomass production than SOYBEANW. This may explain the slower increase in total biomass from CROPGRO. The time courses of seed production were also different between the 2 models, with the CROPGRO time course starting later. This resulted in particular for irrigated production in a lower seed yield with CROPGRO. However, the differences between the time courses of biological nitrogen fixation from the 2 models and between the time courses of LAI were small.

Simulations for irrigated production were done for different soil nitrogen supplies. Results from both models clearly showed the difference in model concept. CROPGRO assumed that a soil nitrogen supply that was much lower than the nitrogen demand for optimal crop growth did not result in reduced growth (except for the small assimilate use for nitrogen fixation) due to a strong increase in biological nitrogen fixation. SOYBEANW assumed that crop growth was not only limited by the assimilate production but also by the nitrogen supply. In this model a lower soil nitrogen supply gave a lower biomass production during initial growth and thus a lower nitrogen fixation. The resulting lower nitrogen availability caused advanced leaf senescence and a much lower seed production. The complicated interactions between assimilate and nitrogen availability for soya bean growth were discussed by Sinclair

(1989), showing that it was difficult to determine which of the 2 model approaches was best. It may be concluded that CROPGRO is probably too optimistic about the potential for biological nitrogen fixation on poor soils, especially during initial growth. The assumption in SOYBEANW that a larger soil nitrogen supply, for example, from fertilizer nitrogen application, results in more biomass production and thus more biological nitrogen fixation is only true for initially low soil nitrogen supply. Increasing the soil supply of mineral nitrogen was often observed to result in a reduction of the nitrogen fixation, so that the total amount of nitrogen available to the crop and hence the seed yield did not increase (Herridge & Brockwell 1988). Therefore, an increase in seed yields of soya bean has been attempted by increasing the rate of nitrogen fixation (Ronis et al. 1985, Herridge & Rose 1994).

The sensitivity of seed production to systematic changes in climate was calculated with both models for Toulouse. These climate effects that were largely determined by the model approaches were already discussed in the sensitivity analyses (Section 3.2). Hence, mainly the conclusions of these analyses are given here. Irrigated seed yields from both models increased with increases in both solar radiation (stronger increase with SOYBEANW) and atmospheric CO₂ and had an optimum at present temperatures in Toulouse and 2 to 4°C above these temperatures for SOYBEANW and CROPGRO, respectively. Pickering et al. (1995) showed that CROPGRO overestimated the negative effect of cool temperatures on biomass production and, hence, the benefits of temperature rise under climate change. Without irrigation, the seed yield was reduced more strongly by water limitation with CROPGRO than with SOYBEANW. Water-limited seed yields from both models were almost insensitive to temperature change but increased with an increase in both atmospheric CO₂ and precipitation. These increases were of the same magnitude for both models. Water-limited seed yields increased with increasing vapour pressure and decreasing wind speed for SOYBEANW but did not change for CROPGRO, and decreased with increasing solar radiation for CROPGRO but did not change for SOYBEANW.

A comparable sensitivity analysis was done with CROPGRO for water-limited soya bean production in Iowa, USA (Curry et al. 1995). Yield sensitivities to increases in atmospheric CO₂ and precipitation were similar to those calculated in the present study for Toulouse. However, seed yields in Iowa decreased with rising temperature, whereas yields at Toulouse did not change. Apparently, present mean seasonal temperature in Iowa was at or above the optimum for seed production and was higher than the mean temperature at Toulouse.

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LITERATURE CITED

- Adams RM, Rosenzweig C, Peart RM, Ritchie JT, McCarl BA, Glycer JD, Curry RB, Jones JW, Boote KJ, Allen LH (1990) Global climate change and US agriculture. *Nature* 345: 219–223
- Allen LH, Boote KJ (2000) Crop ecosystem responses to climatic change: soybean. In: Reddy KR, Hodges HF (eds) *Climate change and global crop productivity*. CABI Publishing, Wallingford, p 133–160
- Bindi M, Fibbi L (2000) Modelling climate change impacts at the site scale on grape vine. In: Downing TE, Harrison PA, Butterfield RE, Lonsdale KG (eds) *Climate change, climatic variability and agriculture in Europe: an integrated assessment*. Research report no. 21, Environmental Change Institute, University of Oxford, p 117–134
- Bindi M, Fibbi L, Gozzini B, Orlandini S, Miglietta F (1996) Modelling the impacts of future climate scenarios on yield and yield variability of grapevine. *Clim Res* 7:213–224
- Boote KJ, Jones JW, Pickering NB (1996) Potential uses and limitations of crop models. *Agron J* 88:704–716
- Boote KJ, Jones JW, Hoogenboom G (1998a) Simulation of crop growth: CROPGRO model. In: Peart RM, Curry RB (eds) *Agricultural systems modeling and simulation*. Marcel Dekker Inc, New York, p 651–692
- Boote KJ, Jones JW, Hoogenboom G, Pickering NB (1998b) The CROPGRO model for grain legumes. In: Tsuji GY, Hoogenboom G, Thornton PK (eds) *Understanding options for agricultural production*. Kluwer Academic Publishers, Dordrecht, p 99–128
- Brisson N, Bona S, Bouniols A (1989) Adaptation of a soybean crop simulation model (SOYGRO) to southern European conditions. In: Pascale AJ (ed) *Proc World Soybean Research Conference IV*, Buenos Aires, p 279–284
- Carter TR, Saarikko RA, Joukainen SKH (2000) Modelling climate change impacts on wheat and potato in Finland. In: Downing TE, Harrison PA, Butterfield RE, Lonsdale KG (eds) *Climate change, climatic variability and agriculture in Europe: an integrated assessment*. Research report no. 21, Environmental Change Institute, University of Oxford, p 289–312
- Colson J (1992) *Developpement reproducteur du soja—impact des conditions de culture et modelisation du potentiel de production varietal*. PhD thesis, University Paul Sabatier, Toulouse
- Colson J, Bouniols A, Jones JW (1995a) Soybean reproductive development: adapting a model for European cultivars. *Agron J* 87:1129–1139
- Colson J, Wallach D, Bouniols A, Denis JB, Jones JW (1995b)

- Mean squared error of yield prediction by SOYGRO. *Agron J* 87:397–402
- Cooter EJ (1990) The impact of climate change on continuous corn production in the southern USA. *Clim Change* 16: 53–82
- Cure JD (1985) Carbon dioxide doubling responses: a crop survey. In: Strain BR, Cure JD (eds) Direct effects of increasing carbon dioxide on vegetation. DOE/ER-0238, US Dept of Energy, Washington, DC, p 99–116
- Cure JD, Acock B (1986) Crop responses to carbon dioxide doubling: a literature survey. *Agric For Meteorol* 38: 127–145
- Curry RB, Peart RM, Jones JW, Boote KJ, Allen LH (1990) Response of crop yield to predicted changes in climate and atmospheric CO₂ using simulation. *Trans Am Soc Agric Eng* 33:1383–1390
- Curry RB, Jones JW, Boote KJ, Peart RM, Allen LH, Pickering NB (1995) Response of soybean to predicted climate change in the USA. In: Climate change and agriculture: analysis of potential international impacts. ASA special publication number 59, American Society of Agronomy, Madison, p 163–182
- Downing TE, Harrison PA, Butterfield RE, Lonsdale KG (eds) (2000) Climate change, climatic variability and agriculture in Europe: an integrated assessment. Research report no. 21, Environmental Change Institute, University of Oxford
- Easterling WE, McKenney MS, Rosenberg NJ, Lemon KM (1992a) Simulations of crop response to climate change: effects with present technology and no adjustments (the 'dumb farmer' scenario). *Agric For Meteorol* 59:53–73
- Easterling WE, Rosenberg NJ, Lemon KM, McKenney MS (1992b) Simulations of crop responses to climate change: effects with present technology and currently available adjustment (the 'smart farmer' scenario). *Agric For Meteorol* 59:75–102
- Egli DB, Bruening W (1992) Planting date and soybean yield: Evaluation of environmental effects with a crop simulation model: SOYGRO. *Agric For Meteorol* 62:19–29
- Egli DB, Orf JH, Pfeiffer TW (1984) Genotypic variation for duration of seedfill in soybean. *Crop Sci* 24:587–592
- Fehr WR, Caviness CE (1977) Stages of soybean development. Cooperative Extension Service, Agriculture and Home Economics Experiment Station, Special Report 80, Iowa State University, Ames
- Frère M, Popov GF (1979) Agrometeorological crop monitoring and forecasting. FAO Plant Production and Protection Paper 17, FAO, Rome
- Grimm SS, Jones JW, Boote KJ, Hesketh JD (1993) Parameter estimation for predicting flowering date of soybean cultivars. *Crop Sci* 33:137–144
- Grimm SS, Jones JW, Boote KJ, Herzog DC (1994) Modeling the occurrence of reproductive stages after flowering for four soybean cultivars. *Agron J* 86:31–38
- Haskett JD, Pachepsky YA, Acock B (1997) Increase of CO₂ and climate change effects on Iowa soybean yield, simulated using GLYCIM. *Agron J* 89:167–176
- Herridge DF, Brockwell J (1988) Contributions of fixed nitrogen and soil nitrate to the nitrogen economy of irrigated soybean. *Soil Biol Biochem* 20:711–717
- Herridge DF, Rose IA (1994) Heritability and repeatability of enhanced N₂ fixation in early and late inbreeding generations of soybean. *Crop Sci* 34:360–367
- Hesketh JD, Myhre DL, Willey CR (1973) Temperature control of time intervals between vegetative and reproductive events in soybeans. *Crop Sci* 13:250–254
- Hoogenboom G, Jones JW, Boote KJ (1992) Modeling growth, development, and yield of grain legumes using SOYGRO, PNUTGRO, and BEANGRO: a review. *Trans Am Soc Agric Eng* 35:2043–2056
- Hoogenboom G, Tsuji GY, Pickering NB, Curry RB, Jones JW, Singh U, Godwin DG (1995) Decision support system to study climate change impacts on crop production. In: Climate change and agriculture: analysis of potential international impacts, ASA special publication no. 59, American Society of Agronomy, Madison, p 51–75
- Jones JW, Ritchie JT (1991) Crop growth models. In: Management of farm irrigation systems. American Society of Agricultural Engineers, St. Joseph, p 69–98
- Jones JW, Boote KJ, Hoogenboom G, Jagtap SS, Wilkerson GG (1989) SOYGRO V5.42, Soybean crop growth simulation model, User's guide. Florida Agric Exp Stn Journal no. 8304, International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT) and University of Florida, Gainesville
- Jones JW, Boote KJ, Jagtap SS, Mishoe JW (1991) Soybean development. In: Modelling plant and soil systems, American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, p 71–90
- Jones P, Allen LH, Jones JW, Boote KJ, Campbell WJ (1984) Soybean canopy growth, photosynthesis, and transpiration responses to whole-season carbon dioxide enrichment. *Agron J* 76:633–637
- King D, Le Bas C, Daroussin J, Thomasson AJ, Jones RJA (1995) The EU map of soil water available for plants. In: King D, Jones RJA, Thomasson AJ (eds) European land information systems for agro-environmental monitoring, EUR 16232, Agriculture series, European Commission, Luxembourg, p 131–141
- Lal M, Singh KK, Srinivasan G, Rathore LS, Naidu D, Tripathi CN (1999) Growth and yield responses of soybean in Madhya Pradesh, India to climate variability and change. *Agric For Meteorol* 93:53–70
- Magrin GO, Travasso MI, Diaz RA, Rodriguez RO (1997) Vulnerability of the agricultural systems of Argentina to climate change. *Clim Res* 9:31–36
- Mearns LO (2000) Climatic change and variability. In: Reddy KR, Hodges HF (eds) Climate change and global crop productivity. CABI Publishing, Wallingford, p 7–35
- Muchow RC, Sinclair TR (1986) Water and nitrogen limitations in soybean grain production. II. Field and model analyses. *Field Crop Res* 15:143–156
- Nagarajan K, O'Neil RJ, Lowenberg-DeBoer J, Edwards CR (1993) Indiana Soybean system model (ISSM): I. Crop model evaluation. *Agric Syst* 43:357–379
- Nonhebel S (1994) The effects of use of average instead of daily weather data in crop growth simulation models. *Agric Syst* 44:377–396
- Nonhebel S (1996) Effects of temperature rise and increase in CO₂ concentration on simulated wheat yields in Europe. *Clim Change* 34:73–90
- Olesen JE, Jensen T, Bøcher PK (2000) Modelling climate change impacts on wheat and potato in Denmark. In: Downing TE, Harrison PA, Butterfield RE, Lonsdale KG (eds) Climate change, climatic variability and agriculture in Europe: an integrated assessment. Research report no. 21, Environmental Change Institute, University of Oxford, p 313–332
- Phillips DL, Lee JJ, Dodson RF (1996) Sensitivity of the US corn belt to climate change and elevated CO₂. 1. Corn and soybean yields. *Agric Syst* 52:481–502
- Pickering NB, Jones JW, Boote KJ (1995) Adapting SOYGRO V5.42 for prediction under climate change conditions. In: Climate change and agriculture: analysis of potential international impacts, ASA special publication no. 59,

- American Society of Agronomy, Madison, p 77–98
- Priestley CHB, Taylor RJ (1972) On the assessment of surface heat and evaporation using large-scale parameters. *Mon Weather Rev* 100:81–92
- Ritchie JT (1972) Model for predicting evaporation from a row crop with incomplete cover. *Water Resour Res* 8: 1204–1212
- Ronis DH, Sammons DJ, Kenworthy WJ, Meisinger JJ (1985) Heritability of total and fixed N content of the seed in two soybean populations. *Crop Sci* 25:1–4
- 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. II. Application of climate change scenarios. *Clim Res* 7:271–281
- Sinclair TR (1984) Leaf area development in field-grown soybeans. *Agron J* 76:141–146
- Sinclair TR (1986) Water and nitrogen limitations in soybean grain production. I. Model development. *Field Crop Res* 15:125–141
- Sinclair TR (1989) Simultaneous limitation to soybean yield increase by carbon and nitrogen. In: Pascale AJ (ed) *Proc World Soybean Research Conference IV*, Buenos Aires, p 183–188
- Sinclair TR, De Wit CT (1976) Analysis of the carbon and nitrogen limitations to soybean yield. *Agron J* 68:319–324
- Sinclair TR, Rawlins SL (1993) Inter-seasonal variation in soybean and maize yields under global environmental change. *Agron J* 85:406–409
- Sinclair TR, Salado-Navarro L, Morandi EN, Bodrero ML, Martignone RA (1992) Soybean yield in Argentina in response to weather variation among cropping seasons. *Field Crop Res* 30:1–11
- Smith M (1992) Report of expert consultation on revision of FAO methodologies for crop water requirements. FAO, Land and Water Development Division, Rome
- Spaeth SC, Sinclair TR, Ohnuma T, Konno S (1987) Temperature, radiation, and duration dependence of high soybean yields: measurement and simulation. *Field Crop Res* 16: 297–307
- Spitters CJT (1990) Crop growth models: their usefulness and limitations. *Acta Horticult* 267:349–368
- Tsuji GY, Uehara G, Balas S (1994) DSSAT version 3, a decision support system for agrotechnology transfer. International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT), University of Hawaii, Honolulu
- Valle R, Mishoe JW, Jones JW, Allen LH (1985) Transpiration rate and water use efficiency of soybean leaves adapted to different CO₂ environments. *Crop Sci* 25:477–482
- Wilkerson GG, Jones JW, Boote KJ, Ingram KT, Mishoe JW (1983) Modeling soybean growth for crop management. *Trans Am Soc Agric Eng* 26:63–73
- Wilks DS (1988) Estimating the consequences of CO₂-induced climatic change on North American grain agriculture using general circulation model information. *Clim Change* 13:19–42
- Wolf J (1993) Effects of climate change on wheat production potential in the European Community. *Eur J Agron* 2: 281–292
- Wolf J (2000a) Modelling climate change impacts at the site scale on potato. In: Downing TE, Harrison PA, Butterfield RE, Lonsdale KG (eds) *Climate change, climatic variability and agriculture in Europe: an integrated assessment*. Research report no. 21, Environmental Change Institute, University of Oxford, p 135–154
- Wolf J (2000b) Modelling climate change impacts on soya bean in south-west Spain. In: Downing TE, Harrison PA, Butterfield RE, Lonsdale KG (eds) *Climate change, climatic variability and agriculture in Europe: an integrated assessment*. Research report no. 21, Environmental Change Institute, University of Oxford, p 217–237
- Wolf J (2002) Comparison of two soya bean simulation models under climate change. II. Application of climate change scenarios. *Clim Res* 20:71–81
- Wolf J, Van Diepen CA (1994) Effects of climate change on silage maize production potential in the European Community. *Agric For Meteorol* 71:33–60
- Wolf J, Van Diepen CA (1995) Effects of climate change on grain maize yield potential in the European Community. *Clim Change* 29:299–331

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