Simulated wheat growth affected by rising temperature, increased water deficit and elevated atmospheric CO₂

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Abstract

The cropping systems simulation model APSIM-Nwheat was tested against detailed field measurements representing possible growing conditions under future climate change scenarios. Increasing average temperatures by 1.7 °C observed over several seasons at Obregon, Mexico reduced the time to flowering by 11 days and resulted in a decline of total biomass and grain yield. These effects were reproduced by the model, except when the observed total biomass inexplicably rose again in the fourth and fifth year, despite higher temperature and a much shorter growing time. In a water stress experiment, the effects of different timing and duration of water deficit on crop growth and yield were reproduced with the model for a rain-shelter experiment at Lincoln, New Zealand where observed grain yields were reduced from 10 to 4 t ha⁻¹ due to increased water deficit. In experiments from Western Australia, reduced growth and yields due to extreme terminal water deficit were also reproduced with the model where measured yields fall below 0.5 t ha⁻¹. In the Maricopa Free Air Carbon-Dioxide Enrichment (FACE) experiment in Arizona, USA, the largest yield increase occurred with elevated CO₂ in the dry and high N treatments, whereas little or no response was observed in the wet and low N supply treatments, as simulated with the model. Combining elevated CO₂ with increased temperature in a sensitivity analysis, two levels of water supply and a range of N applications indicated a positive effect of elevated CO₂ on yield as long as N was not limiting growth. Increased temperature and reduced water supply reduced yields and the yield response to N supply under ambient and elevated CO₂. Grain protein concentrations were reduced under elevated CO₂, but the difference was minor with ample N fertiliser. Evapotranspiration was reduced under elevated CO₂. Higher temperatures increased evapotranspiration with low N input, but reduced it with ample N fertiliser, resulting in a reduction and an increase, respectively, in drainage below the root zone. In the Mediterranean environment of Western Australia the impact of elevated CO₂ and increased temperature on grain yield was in average positive, but varied with seasonal rainfall distribution. Based on the range of model testing experiments and the sensitivity analysis, APSIM-Nwheat was found suitable for studies on directional impacts of future climate change on wheat production. Due to some large discrepancies

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between simulated and observed data, field experiments representing only a limited range of possible climate change scenarios and the large possible range of factorial interactions not tested, simulated quantitative effects with the model should be interpreted cautiously.

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1. Introduction

Scenarios for future global and regional climate change will include elevated atmospheric CO₂ (Jones, 1996), but could also mean warmer average air temperatures and increased water deficit in rainfed agriculture due to changes in rainfall amount and distribution (Whetton, 2001). While elevated CO₂ might stimulate growth in some situation, e.g. under water deficit (e.g., Kimball et al., 1995), higher temperatures will usually shorten the growth cycle of a given cultivar (e.g., Sayre et al., 1997) and together with reduced water supply are likely to reduce crop production (Turner, 1997). These effects of climate change on growth processes in the context of natural climatic and soil variability, and a large range of crop management options (e.g. N management) make it extremely difficult to foresee and quantify any consequences of future climate change on crop production.

Simulation models are a means to analyse the potential effects of climate change on crop growth, but testing model performance against measured data under such scenarios is essential for such an analysis to be meaningful. Some efforts have been made to test crop models under elevated atmospheric CO₂ with data from the Maricopa Free Air Carbon-Dioxide Enrichment (FACE) experiment in Arizona, USA (e.g. Grant et al., 1995; Kartschall et al., 1995; Tubiello et al., 1999; Jamieson et al., 2000; Grossman-Clarke et al., 2001); and experiments with elevated CO₂ in open top chambers (Ewert et al., 1999; Rodriguez et al., 2001). However, most of this work concentrated on elevated CO₂. Only few models have been tested with different levels and duration of water stress periods (e.g. Jamieson et al., 1998). None of these models were ever compared with severe terminal water limitations nor rising air temperatures, although these factors are important components of future climate change scenarios affecting crop production.

The APSIM-Nwheat model comprises crop growth, soil water, nitrogen and crop residue modules (Keating et al., 2001) and enables simulation of their interactions in an atmosphere–crop–soil system. APSIM-Nwheat and its different components have been successfully tested against a range of field experiments. These field experiments included treatments of variable N management, sowing date, cultivars, tillage, irrigation, seasons and occurred in different climatic regions. The tests indicated transferability and robustness of individual model components, but also the model as a whole (Keating et al., 1995; Probert et al., 1995, 1998; Meinke et al., 1998; Asseng et al., 1998b, 2000). The analysis of simulation studies of cropping systems under variable growing conditions using long-term historical weather data had further confirmed the reliable performance of APSIM-Nwheat (e.g., Asseng et al., 1998a, 2001b).

To capture the effect of elevated CO₂ on crop growth, radiation use efficiency (RUE) and transpiration efficiency (TE) coefficients in APSIM-Nwheat were modified, based on an independent RUE–CO₂—temperature function and an independent CO₂—TE function (Reyenga et al., 1999). Before employing this model for climate change scenario studies, the capability of the model to reproduce climate change experiments needs to be tested. This paper aims to evaluate the performance of the APSIM-Nwheat model against a range of detailed field measurements and in a sensitivity analysis representing possible climate change scenarios of rising air temperatures, increased levels of water deficit and elevated atmospheric CO₂.

2. Material and methods

2.1. The APSIM-Nwheat model

The Agricultural Production Systems Simulator (APSIM) (McCown et al., 1996) for wheat (Triticum
*Triticum aestivum* L.) (APSIM-Nwheat version 1.55s) is a crop simulation model, consisting of modules that incorporate aspects of soil water, nitrogen, crop residues, crop growth and development and their interactions within a wheat crop/soil system that is driven by daily weather data. It calculates the potential yield, which is the maximum yield reached by a crop in a given environment that is not limited by pests, diseases, weeds and lodging, but is limited by temperature, solar radiation, water and nitrogen supply. Parts of APSIM-Nwheat (Keating et al., 2001) have evolved from experiences in Australia with the CERES family of crop and soil models (Ritchie et al., 1985; Jones and Kiniry, 1986), and the PERFECT model (Littleboy et al., 1992), as modified by Probert et al. (1995, 1998). The main differences between the APSIM-Nwheat model and the CERES-Wheat model are described by (Keating et al., 2001).

APSIM-Nwheat has been rigorously tested against field measurements in various studies under a large range of growing conditions (Turpin et al., 1996; Probert et al., 1995, 1998; Asseng et al., 2000) and in particular in the Mediterranean climatic regions of Western Australia (Asseng et al., 1998a,b, 2001a, 2002).

In APSIM-Nwheat (Keating et al., 2001), air temperature affects several processes including leaf area growth, photosynthesis, senescence, root depth elongation and phenology. Increasing temperatures accelerate the phenological development, which results in a shorter growth period. If the mean temperatures is <11 and >24 °C leaf area growth is reduced. Maximum temperatures >34 °C hastens senescence of the leaf area. If the weighted mean temperatures (=0.25T_{min} + 0.75T_{max}) is <17 and >19 °C photosynthesis is reduced. Potential root depth elongation is 2.2 mm °Cd^{-1} (degree-day).

Water stress (Fw, water deficit stress) is calculated as a fraction of available soil water (fasw) in the root zone (root depth at a given time) and reduces leaf growth (when fasw < 0.45), tillering (when fasw < 1.0, stops when fasw < 0.5), photosynthesis and root depth elongation (when fasw < 0.25). When Fw for photosynthesis falls below 0.8, leaf senescence is enhanced (Keating et al., 2001).

The crop nitrogen routines are described by Keating et al. (2001). Critical and minimum crop N concentrations are calculated in the model as a function of the growth stage, both declining over time. Crop N demand is the difference between critical and actual N content plus the N amount required for new growth at a given day. When N concentration falls below the critical concentration, a N stress factor (F_N) is calculated based on the ratio of actual and critical N concentration and analogue to water stress reduces leaf area growth, tillering (when F_N < 1.0), photosynthesis (when F_N < 0.66), increases leaf area senescence (when F_N < 0.66) and the root–shoot ratio for carbon partitioning (when F_N < 1.0). Crop N content cannot fall below the minimum N concentration in the model.

Nitrogen uptake follows the approach used by Ritchie et al. (1985) and is a function of potential N uptake capacity of the root system and crop N demand. The potential N uptake capacity is a function of root length density distribution, NO3 and NH4 concentration and soil water content. Low soil mineral N concentrations reduce the amount of available N for uptake. NO3 and NH4 can be taken up at the same amount, but relative more NO3 is taken up than NH4 when both are available at the same amount at a low soil N concentration (<10 ppm). An empirical upper limit for daily N uptake exists in APSIM-Nwheat at 6 kg ha^{-1} per day.

Documented model source code in hypertext format can be obtained by writing to Dr. B.A. Keating, email: Brian.Keating@csiro.au, or can be viewed at http://www.apsim-help.tag.csiro.au.

Elevated CO2 has two main effects on crop growth. It increases the intercellular CO2 concentration leading to increased net photosynthesis rates and at the same time reduces stomatal conductance resulting in reduced transpiration (Farquhar et al., 1978). While the increased net photosynthesis rates affect directly radiation use efficiency (RUE), the increased net photosynthesis under reduced crop transpiration has an impact on transpiration efficiency (TE). To consider these effects in APSIM-Nwheat for the FACE experiment at Maricopa, USA, with elevated CO2 of 550 ppm (and an average growing season temperature of 21.8 °C at this location), RUE (the net above-ground biomass accumulation per unit intercepted radiation based on a radiation dependent function after CERES-Wheat, Ritchie et al. (1985)) was increased by 15% based on Eq. (1) after Reyenga et al. (1999):

$$\Phi_p = \frac{(C_e - \Gamma)(C_{350} + 2\Gamma)}{(C_e + 2\Gamma)(C_{350} - \Gamma)}$$

(1)
with $\Phi_p$ being the ratio of the light limited photosynthetic response calculated according to Goudriaan et al. (1985) at the enhanced CO$_2$ concentration compared with the current level (350 ppm; assumed to be the CO$_2$ concentration when the model was developed) for scaling RUE. $C_{350} =$ current CO$_2$ concentration (=350 ppm), $C_e =$ elevated CO$_2$ concentration (ppm). The temperature dependent CO$_2$ compensation point ($T$) is calculated as $T = (163 - T)/(5 - 0.17)$, $T =$ temperature (°C), according to Bykov et al. (1981).

TE (the net above-ground biomass accumulation per unit crop water transpiration) was linearly scaled (by a factor that increases linearly from 1 to 1.37 when the CO$_2$ concentration increases from 350 to 700 ppm) according to increased TE under elevated CO$_2$ after Gifford and Morison (1993). This scaling of TE captures, though not explicitly, the effects of elevated CO$_2$ on the ratio between internal and external CO$_2$ concentration. For simulating the effects of 550 ppm, TE (constant for wheat concentration. For simulating the effects of 550 ppm, TE (constant for wheat) was increased by 21%. No other model changes were made for any of the simulations. Note, that water stress, N stress and temperature affect RUE and TE indirectly through the above described processes (e.g. through their effects on photosynthesis).

To test the validity of this approach independently, calculated RUE and TE using the Reyenga et al. (1999) functions were compared with measured RUE (Table 1) and measured TE. Linear regression of observed versus calculated RUE with intercept set to zero indicated no significant bias ($y = 1.022x$; Mallows $C_p$ statistic = 1). For the FACE experiment at Maricopa, enhancement of ambient levels of CO$_2$ by 200 ppm increased observed TE by 26% for the dry treatment and 25% for the wet treatment in 1993–1994, whilst the calculated increase for a CO$_2$ level of 550 ppm according to the Reyenga et al. (1999) TE function is 21%.

When using a plant physiological method for estimating TE after Farquhar et al. (1982) (assuming an average daily reduction of stomatal conductance with elevated CO$_2$) resulted in a similar value of TE under elevated CO$_2$ (data not shown) compared to Reyenga et al. (1999). This confirmed the reasonable change in TE under elevated CO$_2$ based on the Reyenga et al. (1999) approach.

### Table 1

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Observed</th>
<th>Calculated</th>
</tr>
</thead>
<tbody>
<tr>
<td>FACE dry 1992–1993</td>
<td>15.8</td>
<td>12.4</td>
</tr>
<tr>
<td>FACE wet 1992–1993</td>
<td>15.5</td>
<td>12.4</td>
</tr>
<tr>
<td>FACE low N 1995–1996</td>
<td>10.5</td>
<td>13.7</td>
</tr>
<tr>
<td>FACE high N 1995–1996</td>
<td>12.9</td>
<td>13.7</td>
</tr>
<tr>
<td>Gifford and Morison (1993)</td>
<td>20.0</td>
<td>22.1</td>
</tr>
<tr>
<td>Morison and Gifford (1984)</td>
<td>17.0</td>
<td>22.0</td>
</tr>
<tr>
<td>Rudorff et al. (1996)</td>
<td>14.7</td>
<td>12.1</td>
</tr>
<tr>
<td>Rudorff et al. (1996)</td>
<td>8.1</td>
<td>11.9</td>
</tr>
<tr>
<td>Total mean</td>
<td>14.3</td>
<td>14.8</td>
</tr>
</tbody>
</table>

*Note, for simplicity the same constant factor (based on the mean temperature at the experimental site) was used for all simulations of the FACE experiments, not the individual calculated changes in RUE presented here.

### 2.2. Experimental data

To test the performance of the APSIM-Nwheat model under different possible climate change scenarios, including rising air temperature, various levels and periods of increased water limitations and elevated atmospheric CO$_2$, field measurements from a range of experiments (Table 2) were compared to outputs of the model. All simulations were set up using measured soil characteristics, initial soil water and N conditions and recorded management.

#### 2.2.1. Rising air temperature—Obregon, Mexico

Each growing season from 1989–1990 to 1994–1995 wheat cv. Yecora70 (Table 3) was sown at CIANO, near Obregon in Sonora, Mexico (Table 2). The experiment was planted in the same location at the

<table>
<thead>
<tr>
<th>Location</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Soil type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Obregon, Mexico</td>
<td>26.6°N</td>
<td>109.4°W</td>
<td>Clay loam</td>
</tr>
<tr>
<td>Maricopa, USA</td>
<td>33.1°N</td>
<td>112.0°W</td>
<td>Clay loam</td>
</tr>
<tr>
<td>Lincoln, NZ</td>
<td>43.4°S</td>
<td>172.3°E</td>
<td>Sandy loam</td>
</tr>
<tr>
<td>Wongan Hills, Western Australia</td>
<td>31.0°S</td>
<td>116.7°E</td>
<td>Sand</td>
</tr>
<tr>
<td>Cunderdin, Western Australia</td>
<td>31.4°S</td>
<td>117.4°E</td>
<td>Clay</td>
</tr>
</tbody>
</table>
same time of the year (within 15 days in late November or early December) and management was standardised (optimal water and nutrient supply) to give maximum yields. Hence, the main variable in this experiment was mean air temperature, which varied for unexplained reasons on average by up to 1.7°C for parts of the growing season over the course of the 6 years. A detailed description of the experiment is given by Sayre et al. (1997).

2.2.2. Increased levels of water deficit—Lincoln, New Zealand

The experiment under a mobile rain-shelter was located on the New Zealand Institute for Crop and Food Research experiment station at Lincoln in Canterbury (Table 2). Wheat cv. Batten (Table 3) was sown in the rain-shelter on 8 June 1991. About 150 kg N ha$^{-1}$ was applied through the irrigation system as urea dissolved in the irrigation water. The seven treatments chosen for analysis here are a subset of those reported by Jamieson et al. (1995), chosen for the greatest contrast. A detailed description of the experiment is given by Jamieson et al. (1995).

2.2.3. Increased late water deficit—Cunderdin and Wongan Hills, Western Australia

Crops at Cunderdin, Western Australia were sown 6 June (sowing 1), 8 July (sowing 2) and 20 July (sowing 3) 1997. Sowing 3 was outside to normal sowing time (normally between May and June) to increase water deficit conditions during grain filling, similar to possible climate change scenarios. The same experiment was repeated at Wongan Hills, Western Australia with crops sown 4 June (sowing 1), 7 July (sowing 2) and 20 July (sowing 3) 1997. Cultivars Amery at Wongan Hills and Wilgoyne at Cunderdin (early maturing) and Spear at both locations (late maturing) were grown. Fertiliser treatments (zero and 50 kg N ha$^{-1}$) were applied at the different sowing dates and (zero and 30 kg N ha$^{-1}$) at booting.

Irrigation treatments (total of 105 mm) were applied at weekly intervals for 7 weeks commencing prior to anthesis at the early time of sowing (late September) across all selected treatments at Cunderdin only to offset the water deficit effect while keeping the impact of increased temperature during grain filling in the later sowing treatments. Initial soil water conditions were estimated from a simulation which started before the summer fallow season, initial soil N was estimated based on previous crop residues.

2.2.4. Elevated atmospheric CO$_2$—Maricopa, USA

Two experiments were conducted during the 1992–1993 and 1993–1994 growing seasons to determine the interactive effects of elevated atmospheric CO$_2$ concentration (550 μmol mol$^{-1}$ CO$_2$) and limited soil

<table>
<thead>
<tr>
<th>Explanation</th>
<th>Coefficient</th>
<th>Yecora$^a$</th>
<th>Batten$^b$</th>
<th>Amery$^c$</th>
<th>Wilgoyne$^d$</th>
<th>Spear$^e$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sensitivity to vernalisation (1 (lowest)–5 (highest))</td>
<td>p1v</td>
<td>1.0</td>
<td>1.0</td>
<td>1.6</td>
<td>1.4</td>
<td>1.5</td>
</tr>
<tr>
<td>Sensitivity to photoperiod (1 (lowest)–5 (highest))</td>
<td>p1d</td>
<td>1.2</td>
<td>2.0</td>
<td>1.8</td>
<td>1.6</td>
<td>3.5</td>
</tr>
<tr>
<td>Thermal time (base 0°C) from beginning of grain filling to maturity (Cd)</td>
<td>p5</td>
<td>660</td>
<td>600</td>
<td>680</td>
<td>680</td>
<td>740</td>
</tr>
<tr>
<td>Coefficient of kernel number per stem weight at the beginning of grain filling (kernels (g per stem))</td>
<td>Gno</td>
<td>24</td>
<td>20</td>
<td>22</td>
<td>22</td>
<td>24</td>
</tr>
<tr>
<td>Potential kernel growth rate (mg per kernel per day)</td>
<td>Fillrate</td>
<td>1.9</td>
<td>1.6</td>
<td>1.9</td>
<td>1.9</td>
<td>2.1</td>
</tr>
<tr>
<td>Potential final dry weight of a single stem, excluding grain (g per stem)</td>
<td>Stwt</td>
<td>3.0</td>
<td>3.0</td>
<td>3.0</td>
<td>3.0</td>
<td>3.0</td>
</tr>
<tr>
<td>Phyllochron interval</td>
<td>Phint</td>
<td>120</td>
<td>130</td>
<td>100</td>
<td>100</td>
<td>110</td>
</tr>
</tbody>
</table>

$^a$ Same parameters as Yecora Rojo; no vernalisation requirements; no or little sensitivity to photoperiod; phyllochron fitted to 1992–1993 dry ambient CO$_2$ treatment of FACE experiment; other parameter estimated based on similar cultivars.

$^b$ No vernalisation requirements; little sensitivity to photoperiod; phyllochron fitted to control treatment of Lincoln experiment; other parameter estimated based on similar cultivars.

$^c$ Same as cv. Kulin (after Asseng et al., 1998b).

$^d$ Slightly less vernalisation requirements and sensitivity to photoperiod than cv. Amery.

$^e$ After Asseng et al. (1998b).
water supply on spring wheat cv. Yecora Rojo (same cv. as Yecora 70) at the University of Arizona Maricopa Agricultural Center (MAC), Maricopa, Arizona, USA (Table 2). Two additional experiments were similarly conducted to determine the interactive effects of elevated CO$_2$ (550 μmol mol$^{-1}$CO$_2$) and limited soil nitrogen during the 1995–1996 and 1996–1997 growing seasons. Wheat crops were planted at mid-December in all seasons (Kimball et al., 1999). A field plot plan for the 1992–1993 and 1993–1994 experiments is presented by Wall and Kimball (1993) and for the 1995–1996 and 1996–1997 experiments by Kimball et al. (1999). Additional details about the methodology are given by Kimball et al. (1995), Hunsaker et al. (1996), and Pinter et al. (1996, 2000) and about measurements by Kimball et al. (1995), Tubiello et al. (1999) and Jamieson et al. (2000).

2.3. Sensitivity analysis

In the absence of measured data sets for full factorial scenarios of climate change impacts in combination with N supply, a sensitivity study was conducted with the model to analyse the interactive effects. To qualitatively test the modelled interactions of CO$_2$, water deficit, temperature and N, a simulation experiment was carried out which included elevated CO$_2$ (550 ppm), water deficit (50% of full irrigation), increased air temperature (+3 °C) and N supply (0–400 kg N ha$^{-1}$). Crop growth, grain yields, grain protein, evapotranspiration (ET) and drainage below the potential root zone of 130 cm were simulated for the Maricopa site with the initial conditions and irrigation of the low N treatment in the 1996–1997 experiment. The same fertiliser regime was used for the N applications as in the high N treatment in the 1996–1997 experiment.

To capture the interactions of climate change impact on grain yield in a low rainfall environment with large seasonal rainfall variability, a simulation experiment was carried out with 90 years of historical rainfall data for a clay soil (109 mm plant available soil water in the potential root zone) at Wongan Hills (390 mm long-term average annual rainfall), Western Australia. Sowing time in the simulation experiment was controlled by a sowing rule in the model. Sowing was set between 5 May and 20 July, but did not occur before at least 25 mm of rainfall within 10 days before 5 June or 10 mm thereafter. A late maturing variety was simulated as being sown before 5 June, otherwise an early maturing variety was assumed. A total of 150 kg N ha$^{-1}$ was applied at sowing and 40 days later. Simulations with elevated CO$_2$ (550 ppm) and increased air temperature (+3 °C) were compared with unchanged climate conditions.

3. Results

3.1. Rising temperature

Rising average temperatures of 1.7 °C over a period of 40 days after sowing in the first 4 years of the experiment at Obregon, Mexico, accelerated the observed anthesis date by 11 and crop maturity by 3 days (Fig. 1). The shorter growth period due to warmer temperatures reduced total biomass growth and grain yields and were reproduced by APSIM, except for the total biomass in 1992–1993 and 1993–1994. In these 2 years, total biomass increased inexplicably in the experiment despite a shorter growth period, whereas the model simulated a lower accumulated growth. Also the grain yield in 1992–1993, the highest recorded in the experiment during the shorter growth period, was underestimated by the model.

3.2. Increased water stress

APSIM reproduced wheat crop growth and yield affected by different periods and durations of water deficit observed at the rain-shelter at Lincoln, New Zealand (Fig. 2, Table 4). However, the model underestimated the late biomass accumulation in the severe water stress treatment (Fig. 2a).

APSIM tended to overestimate low LAI and underestimated high LAI at the rain-shelter experiment, however total biomass was closely simulated. The model reproduced the variation in grain yields observed in this experiment according to the treatments, which ranged from 4 to 10 t ha$^{-1}$ (Table 4).

In experiments at Cunderdin and Wongan Hills, Western Australia, the model simulated the range of biomass dynamics with different sowing dates, cultivars, N and irrigation treatments (Table 4). Of particular interest were the late sown crops which completed
their growth cycle during a period of little rainfall and increasing temperatures (higher ET demand) (Fig. 3a and b). As a result, the late sown crops suffered severe terminal water deficit and produced significantly less observed biomass at both sites and this reduction was simulated by the model (data not shown). However, the largest effects of the severe terminal water deficit were on grain yields.Delaying the sowing date in this environment reduced grain yields drastically to <0.5 t ha⁻¹ (Fig. 3c).

3.3. Elevated atmospheric CO₂

Elevated atmospheric CO₂ showed variable effects on crop growth, depending on water and N supply in the FACE experiment at Maricopa, USA. The largest positive growth effects were recorded under water limitation and high N supply. Smaller effects occurred when crops were well watered and little or no effects were recorded under N limited growing conditions. Using the modified model with increased RUE and TE for elevated CO₂ conditions, these directional responses of biomass growth to elevated CO₂ were reproduced (Fig. 4). Elevated atmospheric CO₂ of 550 ppm in the dry treatment of 1993–1994 increased biomass growth (however, more in the simulation than in the observed data), LAI and grain yield compared to normal CO₂. Fig. 4c and d shows the model performance for all biomass and LAI data from the FACE experiment including dry and wet, low and high N supply with ambient and elevated CO₂. Final biomass, particularly under elevated CO₂ tended to be overestimated in most treatments. The model was able to reproduce the different yields as a response to water and N supply with and without elevated atmospheric CO₂ (Fig. 5).

The FACE water deficit experiments in 1992–1993 and 1993–1994 showed no major change in green leaf N% as a result of interactions between elevated CO₂ and water deficit (Sinclair et al., 2000) and was reproduced as such with the model (data not shown). The FACE N deficit experiments in 1995–1996 and 1996–1997 showed that the main effects on leaf N% were due to N supply. The low N treatment had significant less green leaf N% compared to the high N treatments. Green leaf N% was also reduced by elevated CO₂, but significantly only at some sampling dates in the low N treatments (Sinclair et al., 2000). Similar treatment differences have been simulated with the model (Fig. 6), however, in general at a smaller scale. Note, that some of the smaller absolute treatment difference, the steeper N% decline and the

![Fig. 1. (a) Measured average temperature from sowing until 40 days after sowing (●) and until 120 days after sowing (■). (b) Observed (symbols) and simulated (lines) 50%-anthesis date (●) and maturity date (▲), (c) grain yield (●) and total above-ground biomass (▲) at Obregon, Mexico. Bars in (c) indicate 1.s.d. Observed data after Sayre et al. (1997).](image-url)

lower final N% in the simulations were due to the inclusion of dead leaves and stems into the simulated above-ground N%.

3.4. Sensitivity analysis

A stepwise simulated increase in N supply for well watered conditions for the Maricopa site showed that grain yields were not different between normal and elevated atmospheric CO2 under very low N supply with up to 200 kg N ha\(^{-1}\), when N was still limiting growth. An application of 100 kg N ha\(^{-1}\) even reduced the grain yield by 8% with elevated CO2 compared to ambient CO2. Since water was not limit-
duration with higher temperature reduced the yields mainly due to less biomass accumulation. In addition, increased temperature also resulted in a higher vapour pressure deficit, which reduced TE of the crop. The latter together with higher evapotranspiration demand led to an increased water deficit (also in the fully irrigated treatment). As a consequence, higher N input led to a decline (up to 4%) of yields with increased N applications (Fig. 7b) in the increased temperature treatment.

Reducing the irrigation by 50% increased the yields in the N0 treatment compared to the fully irrigated treatment by 37–48% due to less N leaching (i.e. simulated N leaching was higher in the fully irrigated treatment), since N was the limiting factor for yield under full irrigation at low N. However, this increase was on a very low absolute yield level (0.3 t ha⁻¹). Increasing N applications increased the grain yield to a maximum of 2.9 t ha⁻¹ with 100 kg N ha⁻¹ under normal CO₂ and to a maximum of 3.3 t ha⁻¹ with 200 kg N ha⁻¹ under elevated CO₂. The maximum yield under elevated CO₂ was at a higher N rate due to the increased TE under elevated CO₂ conditions. Further increases of N applications resulted in larger vegetative growth (data not shown) which led to a decline of yields (15% under normal CO₂ and 10% under elevated CO₂) due to more early water use and hence increased water deficit at later growth stages (Fig. 7c). A similar effect, but on a lower yield level was simulated for the combination of 50% irrigation

### Table 4
Summary of the APSIM-Nwheat model performance

<table>
<thead>
<tr>
<th>Model attribute</th>
<th>Number of paired data points</th>
<th>Observed range</th>
<th>$r^2$ (1:1)^a</th>
<th>$m^b$</th>
<th>RMSD^c</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Obregon, Mexico</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grain yield (t ha⁻¹)</td>
<td>6</td>
<td>5.4–7.8</td>
<td>n.a. d</td>
<td>0.98</td>
<td>1.0</td>
</tr>
<tr>
<td>Kernel (m⁻²)</td>
<td>6</td>
<td>14120–20514</td>
<td>n.a. d</td>
<td>0.89</td>
<td>2824</td>
</tr>
<tr>
<td>Kernel weight (mg)</td>
<td>6</td>
<td>38.1–44.7</td>
<td>n.a. d</td>
<td>1.08</td>
<td>4.8</td>
</tr>
<tr>
<td>Biomass (t ha⁻¹)</td>
<td>6</td>
<td>12.3–17.6</td>
<td>n.a. d</td>
<td>0.89</td>
<td>2.8</td>
</tr>
<tr>
<td><strong>Lincoln, NZ</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grain yield (t ha⁻¹)</td>
<td>7</td>
<td>3.6–9.9</td>
<td>n.a. d</td>
<td>1.07</td>
<td>1.2</td>
</tr>
<tr>
<td>Kernel (m⁻²)</td>
<td>7</td>
<td>10335–21473</td>
<td>n.a. d</td>
<td>1.11</td>
<td>3015</td>
</tr>
<tr>
<td>Kernel weight (mg)</td>
<td>7</td>
<td>34.2–41.7</td>
<td>n.a. d</td>
<td>0.99</td>
<td>7.1</td>
</tr>
<tr>
<td>Biomass (t ha⁻¹)</td>
<td>84</td>
<td>1.6–25.9</td>
<td>0.90</td>
<td>0.96</td>
<td>1.9</td>
</tr>
<tr>
<td>LAI (m m⁻²)</td>
<td>93</td>
<td>0.2–10.3</td>
<td>0.53</td>
<td>0.98</td>
<td>1.3</td>
</tr>
<tr>
<td><strong>WA, Australia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grain yield (t ha⁻¹)</td>
<td>28</td>
<td>0.5–4.0</td>
<td>0.77</td>
<td>0.93</td>
<td>0.5</td>
</tr>
<tr>
<td>Kernel (m⁻²)</td>
<td>28</td>
<td>2677–9878</td>
<td>0.54</td>
<td>1.10</td>
<td>2311</td>
</tr>
<tr>
<td>Kernel weight (mg)</td>
<td>28</td>
<td>20.0–53.0</td>
<td>0.86</td>
<td>0.87</td>
<td>11.6</td>
</tr>
<tr>
<td>Biomass (t ha⁻¹)</td>
<td>131</td>
<td>0.1–9.5</td>
<td>0.86</td>
<td>0.94</td>
<td>1.1</td>
</tr>
<tr>
<td><strong>Maricopa, USA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grain yield (t ha⁻¹)</td>
<td>16</td>
<td>5.3–9.2</td>
<td>0.72</td>
<td>1.02</td>
<td>1.1</td>
</tr>
<tr>
<td>Kernel (m⁻²)</td>
<td>12</td>
<td>12458–19958</td>
<td>n.a. d</td>
<td>1.17</td>
<td>3462</td>
</tr>
<tr>
<td>Kernel weight (mg)</td>
<td>12</td>
<td>38.3–47.1</td>
<td>n.a. d</td>
<td>0.92</td>
<td>6.1</td>
</tr>
<tr>
<td>Biomass (t ha⁻¹)</td>
<td>276</td>
<td>0.02–21.9</td>
<td>0.94</td>
<td>1.02</td>
<td>1.6</td>
</tr>
<tr>
<td>LAI (m m⁻²)</td>
<td>242</td>
<td>0.001–7.1</td>
<td>0.73</td>
<td>0.88</td>
<td>0.9</td>
</tr>
<tr>
<td><strong>Total mean</strong></td>
<td></td>
<td></td>
<td>0.76</td>
<td>0.99</td>
<td>0.95^f</td>
</tr>
</tbody>
</table>

^a $r^2(1 : 1) = r^2$ for the 1 to 1 line ($y = x$).
^b Slope of linear regression (forced through origin).
^c Root mean square deviation.
^d Insufficient data.
^e Only final biomass harvest.
^f For grain yield (in t ha⁻¹) only.
and increased temperature with increasing N applications (Fig. 7d).

The grain protein concentration response (Fig. 8) was similar to the grain yield response to elevated CO₂. At zero N, grain protein concentration was low with grain protein at about 8% under normal temperature and at about 9% under increased temperature. Under both temperature regimes, grain protein concentrations increased with higher N rates. The grain protein concentration was usually lower under elevated CO₂ treatments than under normal CO₂ with low N rates, but similar with high N rates. Grain protein concentrations reached a maximum of about 12% with high N rates regardless of other treatments.

Evapotranspiration (ET) increased from 200 to 500 mm in the full irrigation treatment when N rates increased from 0 to 400 kg N ha⁻¹. ET was lower under elevated CO₂ treatments than under normal CO₂, particularly with N rates of 100 to 300 kg N ha⁻¹ (data not shown). With increased temperature, ET was higher with lower N supply, but lower with ample N fertiliser (>200 kg N ha⁻¹). When analysing the seasonal pattern, cumulative ET was up to 18 mm higher during the growth period under increased temperature (and ample N fertiliser), but the crop matured 13 days earlier and therefore had less total crop water uptake which resulted in less overall ET (data not shown). As a result, deep drainage below the potential root zone of 130 cm declined with N rates, but was higher under elevated CO₂ treatments than under normal CO₂ until high N rates reduced drainage to zero (Fig. 9). Increased temperature reduced drainage under low N supply, but increased drainage under high N supply.

When extending the sensitivity analysis to a large number of variable rainfall seasons the average impact of elevated CO₂ plus increased temperatures (3 °C) on grain yield was similar as described above. However, the yield response to these changes in any particular season ranged from a yield reduction to a large yield increase, depending on annual rainfall and seasonal rainfall distribution (Fig. 10). In most seasons, earlier flowering, as a result of increased temperature and faster phenology helped to avoid all or part of the terminal water deficit conditions, which are characteristic for the Mediterranean environment in Western Australia. However, TE was usually reduced due to increased temperature resulting in a higher vapour pressure deficit. And, in some seasons with sufficient rainfall during grain filling, earlier flowering was a disadvantage due to the shorter growing time with less biomass accumulation. An additional increase in the efficiency of radiation and transpiration use under
elevated CO$_2$ had a positive but variable effect on grain yield in all seasons. Interesting are the different slopes of grain yield versus rainfall for the climate change and the normal scenario (Fig. 10a). The steeper slope of grain yield versus rainfall under elevated CO$_2$ plus increased temperature indicated that a decline in rainfall would cause a larger yield reduction under such climate change than under current CO$_2$ and temperature. In addition, elevated CO$_2$ plus increased temperatures had a consistently small impact on evapotranspiration (in average <1% increase) across all seasons, which translated into an average 13% (4 mm) reduction of deep drainage below the root zone (data not shown).

4. Discussion

The results of model testing have shown that APSIM-Nwheat was able to simulate, in principle (directional changes), a range of experiments with rising temperatures, various levels and periods of water deficit and elevated atmospheric CO$_2$ in combination with water and N supply. RMSD for grain yields were on average 18% of the mean and errors for other model components were in a reasonable range of field experimental variability. However, large discrepancies between simulated and measured results occurred for some aspects of the crop and needs further investigation. One of these discrepancies...
was in relation to LAI with no clear indication for the cause. However, while LAI simulations often reflected the measurements poorly, crop biomass was well simulated with the model. Similar outcomes for LAI and biomass have been reported with the same model in other growing environments (Asseng et al., 1998b, 2000). Although biomass growth is related to LAI and intercepted radiation, biomass growth is less sensitive to variation in LAI due to little effect of increases in LAI on intercepted radiation with LAI >3. Other limitations to biomass growth rather than light interception at a given LAI (e.g., low temperature, water and/or N deficit) also reduce the sensitivity to LAI. As a consequence, perfect LAI simulations are not critical in simulating crop growth and yields under a wide range of growing conditions. LAI simulations are also not critical for the simulation of crop N dynamics and transpiration, since N and transpiration are both linked to biomass in APSIM-Nwheat rather than leaf area. The crop N and transpiration dynamics have been tested in other studies and shown to work reasonably well (Asseng et al., 1998a,b, 2000). The simulated effect of elevated CO₂ in combination with N supply on the dynamics of above-ground biomass N concentrations for the FACE experiment gave the same dynamics and treatment differences as for observed leaf N concentrations reported by Sinclair et al. (2000) for the same experiments. The largest treatment differences occurred due to N supply with the highest N concentration in the high N input treatments. A lower simulated N concentration in the elevated CO₂ treatments was due to dilution of N concentration with elevated CO₂ and occurred mainly under low N input (Sinclair et al., 2000), a finding also supported by Fangmeier et al. (1999).

When testing the model in different climates with different mean temperatures, APSIM-Nwheat reproduced observed phenology, biomass growth and yield adequately. However, discrepancy between the model and some observations occurred when simulating the Obregon experiment with the gradual increase of air temperature over the course of the six seasons. For the
first three simulated years the model did reproduce the
effect of rising temperature on phenology, biomass
and grain yield as observed in the experiment and as
expected with such a temperature change. The lowest
biomass would have been expected for the warmest
average temperature and shortest growing season as in
the previous seasons of the experiment (Sayre et al.,
1997) and as suggested by the simulation. Since all six
seasons were managed for optimal growing conditions
with no water or nutrient limitations (Sayre et al.,
1997), it is not clear what caused the high yield in the
warmest season in the field with the shortest period of
biomass accumulation. This apparent lack in under-
standing of temperature effects on crop growth raises
some concern, since even larger temperature changes
than observed in this experiment can be expected with
greater water limitations. Higher canopy temperatures, which enhanced phenological
devolution and reduced the duration for biomass
accumulation, could be one reason for these dif-
ferences. Taking into account canopy rather than
air temperatures under water de
fi
fi
deficit conditions (Kartschall et al., 1995) may remove this discrepancy.

Using canopy temperature could also be necessary
in simulating elevated atmospheric CO₂ since some
of the elevated CO₂ treatments showed an increased
canopy temperature and more rapid phenological
development in the elevated CO₂ plots (Kartschall

Fig. 7. Simulated grain yields versus N application rates for ambient CO₂ (cross-hatched bars) and elevated CO₂ of 550 ppm (filled bars) for
the 1996–1997 irrigation regime at the FACE experiment, Maricopa, USA: (a) full irrigation, (b) full irrigation and 3 °C temperature increase,
(c) 50% irrigation and (d) 50% irrigation and 3 °C temperature increase.

et al., 1995). However, increasing the water deficit conditions to such extremes as in the sowing experiments of Western Australia normally increases spatial heterogeneity of crops, indicated by the large variability in some of the measurements. Improvements under such situations are limited by the homogenous considerations of cropping systems by the model, but also by most field experimentation. Spatial aspects of soil conditions and crop canopies may therefore be required to deal with severe water stress conditions, but this will also increase the parameter requirement for such a model, which is often not available from field measurements.

When combining elevated CO₂ with increased temperature, water deficit and a range of N applications in a sensitivity analysis, the model gave reasonable directional changes (Fig. 7), similar to reports by Seligman and Sinclair (1995) and Jamieson et al. (2000). In addition, the here presented results indicated a small yield decline with high N rates under both CO₂ levels together with increased temperature and reduced irrigation, a feature (“haying off”) commonly observed in rainfed wheat with high N applications (van Herwaarden et al., 1998). Results showed a positive effect of elevated CO₂ on yield as long as N was not limiting growth. Increased temperature and reduced water supply reduced yields and the yield response to N supply under ambient and elevated CO₂. Grain protein concentrations were lower with elevated CO₂ than ambient CO₂, but the difference was minor with ample N fertiliser, a similar response was observed under field conditions by Kimball et al. (2001). Elevated CO₂ in the sensitivity analysis for Maricopa resulted in a small reduction of simulated ET in particular with higher rates of N fertiliser, which is consistent with observations reported by Kimball et al. (1995, 1999). As a consequence, drainage below the potential root depth was higher under elevated
CO₂. Interesting was the simulated effect of increased temperature on ET. While cumulative ET increased during crop growth due to increased temperature and also over the season with low N supply, it was reduced by the end of the season with ample N fertiliser due to the shorter crop growth and earlier maturity with higher temperatures. An increase in ET, but small (in average <1%), was simulated when combining elevated CO₂ with increased temperature in the sensitivity analysis for the Mediterranean environment of

![Graph](image)

**Fig. 9.** Simulated drainage below the potential root depth versus N application rates for ambient CO₂ (cross-hatched bars) and elevated CO₂ of 550 ppm (filled bars) for the 1996–1997 irrigation regime at the FACE experiment, Maricopa, USA: (a) full irrigation and (b) full irrigation and 3 °C temperature increase. Note, drainage below the potential root depth was zero for each treatment in combination with 50% irrigation.

![Graph](image)

**Fig. 10.** Simulated grain yields versus annual rainfall for: (a) ambient CO₂ (C) and climate change (△) (elevated CO₂ of 550 ppm plus 3 °C temperature increase) for 1907–1996 at Wongan Hills, Western Australia, (b) absolute yield difference and (c) relative difference. Linear regression lines are shown.
Western Australia, resulting in a small reduction of drainage below the potential root depth. These results indicated the complex nature of crop response to climate change and its interaction with management (water and N) and rainfall seasons. Acclimation effects not considered in the model may be important under climate change and can further complicate its actual impact on crop production. In addition, some of the interactions have not been tested with measurements (e.g., elevated CO2 and increased temperature) due to lack of data and therefore the magnitude of the model response should be treated cautiously. The yield response to increased temperature can vary depending on the impact of reduced biomass accumulation, earlier flowering avoiding terminal drought conditions and reduced TE due to higher VPD on grain yield. An increase in the temperature optimum for assimilation rate under elevated CO2 (Farquhar et al., 1980) is considered in APSIM-Nwheat when RUE changes (Reyenga et al., 1999). Other impacts of elevated CO2 on crop growth, like increased root biomass (but not root depth growth) (Wechsung et al., 1995) or different cultivar response (Manderscheid and Weigel, 1997) could be important for such simulation experiments but are currently not included.

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