Modelling CO₂ effects on wheat with varying nitrogen supplies

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Abstract

Crop simulation models are an essential tool for testing whether predicted global atmospheric changes are likely to have impact on food production. Any confidence in model predictions must be based on their ability successfully to predict performance in experiments. Accordingly, the predictions of three daily time step wheat simulation models (AFRCWHEAT2, FASSET and Sirius) were tested against data from wheat (Triticum aestivum L.) experiments in AZ in which the amount of applied N and the atmospheric CO₂ concentration were both varied. Although there were differences between predicted and observed yields, all the three models predicted yield trends with treatments very similar to those observed. They all predicted, both in absolute terms and in the magnitude of responses, very similar effects of the variations on green area index (GAI), shoot and grain biomass accumulation, and shoot and grain biomass yield to observations and to each other. Comparison of simulated and observed results showed that CO₂ effects were expressed through effects on light use efficiency (LUE), whereas N effects were expressed by causing variations in GAI. The exercise showed that the models used have potential for assessing climate change impacts on wheat production. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The one certainty of atmospheric changes in the next century is that atmospheric CO₂ concentration ([CO₂]) will increase. Along with this there is likely to be an increase in temperature where most crops are grown. These effects combined, along with associated changes in rainfall patterns, are likely to have substantial effects on food production, and it is uncertain whether production enhancing effects of CO₂ fertilisation will be balanced by any production reducing effects of elevated temperature (Baker and Allen, 1993; Rawson, 1995). There have been several simulation studies of the effects of climate change on food production (e.g., Rosenzweig and Hillel, 1998), but confidence in these would be substantially enhanced if the models used could be shown to mimic the effects of [CO₂] in particular, and any interactions with other variables such as N and water supply.

Much of the foregoing has been the focus of the large free air CO₂ enhancement (FACE) experiments performed at University of Arizona, Maricopa Agricultural Center, over the past several years (Hendrey and Kimball, 1994), and the interaction of the scientists there with other members of the Global Change
Terrestrial Ecosystems (GCTEs) International Wheat Network. The data generated in those experiments have been used to validate assumptions incorporated in several models working at various levels of detail (Grant et al., 1995; Grossman et al., 1995), and to test the capabilities of the models to predict the performance of wheat crops in scenarios where atmospheric [CO₂] is increased and conditions are warm (Kartschall et al., 1995; Tubiello et al., 1999). In this paper, the performance of three models, Sirius 99 (Jamieson and Semenov, 2000), AFRCWHEAT2 (Porter, 1993) and FASSET (Jacobsen et al., 1998) are tested against data from 2 years of FACE experiments where [CO₂] and N fertiliser were varied. The models incorporate different assumptions about the effect of N shortage on canopy development and growth, and different levels of detail on processes within the crop. The major characteristic that the three models have in common is that their major computational time-step is 1 day, although some processes are calculated using a shorter-time step in AFRCWHEAT2. The major objective of this paper is to test whether the assumptions incorporated into the three models are supported by experimental evidence, and whether or not these models are suitable for assessing the impacts of global atmospheric change on wheat production.

2. Model descriptions

The models used in this simulation study are described in detail elsewhere. Only brief descriptions of major processes are given here, with an emphasis on the differences among the models. The descriptions are given in the order of Sirius, AFRCWHEAT2 and FASSET.

Sirius 99 (Jamieson and Semenov, 2000) is an updated version of Sirius (Jamieson et al., 1998a) that uses a new description of N distribution and responses. Shoot biomass accumulation is calculated as the product of intercepted photosynthetically active radiation (PAR) and light use efficiency (LUE), incremented daily. The LUE is constant at 2.2 g MJ⁻¹, except in extreme water stress, a condition that did not occur in these experiments. Light interception is related to green area index (GAI) via Beer’s law, with an extinction coefficient of 0.45 (Jamieson et al., 1998a). Variations in N supply have no effect on the LUE. CO₂ effects are simulated by increasing the LUE linearly so that at double current [CO₂], LUE is increased by 30%. Hence for an increase in [CO₂] from 350 to 550 ppm, LUE is increased by 16% to 2.55 g MJ⁻¹. Note that no biomass is assigned to roots, giving a lower LUE than otherwise. Any N in roots is considered to be part of the unavailable soil pool.

GAI is calculated at the canopy level as a function of thermal time, modified by stress. In the new N description Sirius 99 uses, green area (leaf laminae, exposed leaf sheaths, exposed stem surface) is assumed to require 1.5 g of N per m². New increments of GAI can expand to their potential size only if enough N is available. Non-leaf tissue (enclosed leaf sheaths, interior of true stem, interior of thick leaves, but excluding grain, collectively identified as “stem”) is maintained above a minimum N concentration ([N]) of 0.5%, but may store excess N up to 1.5%. If the minimum N requirement for a new increment of “stem” cannot be met from storage or from the soil, then green area may be sacrificed to supply it. Crop demand for N on any day is calculated from the need to expand GAI and grow “stem”.

Partitioning of biomass to grain is calculated assuming that all new biomass from the beginning of grain growth is grain, and a pool of 25% of anthesis biomass is translocated to the grain at a constant rate in thermal time, so that it is all transferred by the potential end of grain filling. Should grain growth be prematurely curtailed, not all the pool is transferred. Grain demand for N is set at the beginning of grain fill so that 80% of the N in the plant at that time will be transferred to the grain, again by the potential end of grain filling (Jamieson and Semenov, 2000). The source of N for this is first, N in storage in “stem” (some of which is released into the “stem” by naturally senescing GAI), second, any mineral N available in the soil, and third, from premature senescence of green area. This last effect can cause an early end to grain filling through more rapid removal of GAI. Grain growth is assumed to end when GAI has reduced to zero.

In contrast, daily biomass accumulation in AFRCWHEAT2 (Porter, 1993) is calculated using a photosynthesis equation applied at hourly intervals during daylight to unit GAI layers of the canopy, and summed over GAI layers and the day. This is the one exception to the daily time-step, which is used to calculate everything else, although even in this
case simulation still uses daily weather data as input. The rate of photosynthesis depends on the light level at each layer, calculated from Beer’s law using an extinction coefficient of 0.6 [CO2] and stomatal resistance (calculated as a function of the vapour pressure deficit (VPD)). Respiration losses are also calculated so that the biomass increment is the difference between what is gained and what is lost. This means that late in crop life total biomass may fall.

The calculation of GAI is also done in more detail than in Sirius. The current sizes of leaves on the mainstem and tillers is calculated each day, and GAI is calculated by summing these per unit ground area. Leaves have finite lifetimes, and expand and contract at constant rates in thermal time. Hence, changes in GAI reflect the balance of births and deaths of both leaves and tillers. Drought reduces leaf extension rates and lifetimes.

Accounting for N is done differently from Sirius. N demand is set assuming that there is a maximum [N] on a whole plant basis, and this decreases from 4.5% at emergence to 1.5% at the beginning of grain filling as a function of development stage. Minimum required [N] is set at 1.5% reducing to 0.3% in the same fashion, and optimum [N] is assumed to be midway between the maximum and minimum levels. N in excess of the optimum concentration is labile N in storage. If [N] is above optimum levels, then growth processes are unlimited by N. Below this level, a set of stress factors based on the ratio of current to optimum [N] is used to reduce tiller production rates, leaf expansion rates and lifetimes, and to reduce photosynthesis. Thus, AFRCWHEAT2 treats N-stress in very much the same way as it treats water stress.

Both biomass and N demand per grain are constant in thermal time, so that grain growth and N uptake depend on grain population and temperature. The sources of biomass for grain growth are current assimilate, and a pool of carbohydrate that is initially calculated as 20% of the shoot biomass at anthesis, and increased by a fraction of the biomass accumulated between anthesis and the beginning of grain filling. Grain growth is unrestricted by assimilate provided this latter exceeds demand, in which case excess assimilate is added to the carbohydrate pool. The existence of the pool means grain growth can continue after the canopy dies.

FASSET is a whole farm simulation model (Jacobsen et al., 1998), which includes a soil–plant–atmosphere model that simulates N turn-over and crop production as affected by availability of water and N (Olesen et al., 1996). The soil model has a one-dimensional vertical structure and simulates the daily movement and plant availability of N. The downward movement of water and N in the soil profile is simulated using the concepts of the SLIM model (Addiscott and Whitmore, 1991) that is also incorporated into AFRCWHEAT2. Soil temperature is simulated using an extended heat flow equation. The turn-over of soil organic matter in the soil is simulated using the structure of the DAISY model (Hansen et al., 1991). A simplified version of the DAISY model is used to simulate crop water and N uptake.

The crop model has three biomass pools: shoot biomass, below ground biomass and biomass in grains. The daily increase in biomass is proportional to the intercepted radiation. The LUE is reduced by drought, by low temperatures and by low N status in the crop according to the function by Sinclair and Horie (1989). The N status is the current N uptake scaled between a minimum and a maximum N uptake, which depend on both crop biomass and GAI. The crop GAI is assumed to increase up to the date of anthesis as a function of vegetative biomass and the nitrogen status. This function was estimated using data from growth analysis experiments in winter wheat in Denmark. The senescence of the GAI follows crop development, but is hastened by drought stress. The extinction coefficient for light interception is 0.44. Crop phenology follows the Sirius approach with modifications as described by Olesen et al. (1999). Partitioning to grain is similar to Sirius.

3. Experimental

The experiment was conducted over 2 years at the University of Arizona, Maricopa Agricultural Center, AZ (latitude 33.1°N), and is described in detail by Kimball et al. (1999). Wheat (cv. “Yecoro Rojo”) was sown in 1995 and 1996 on 15 December in 25 cm rows at a population of approximately 200 plants per m². Irrigation water was applied from a subsurface irrigation system. There were four FACE rings kept at 200 μmol/mol CO₂ above the concentration of four Blower rings, which had similar air movement but no added CO₂. The Blower rings were the primary
experimental controls. All rings (or main plots) were split into high and low N treatment subplots. A profile of mineral N in the soil was determined at planting time in each treatment, and was used to set the initial conditions for all the models. The N-content of irrigation water was sufficiently high that it needed to be accounted for in N-balance calculations (30 kg ha\(^{-1}\), 1995/1996; 33 kg ha\(^{-1}\), 1996/1997). In 1995/1996, an additional 70 kg N ha\(^{-1}\) was added to the low N treatment, and this treatment had 15 kg N ha\(^{-1}\) added in the second experiment. The high N treatments received additional N of 350 kg ha\(^{-1}\) each year, in four applications, plus 33 and 38 kg N ha\(^{-1}\) in 1995/1996 and 1996/1997, respectively, from the irrigation water. Measurements of biomass, leaf area, stem area, tiller number and, once grain filling was underway, grain biomass were made on each plot at intervals of about 10 days throughout growth. Final harvest results were recorded from large samples from an area adjacent to the one from which the sequential biomass measurements were made. Measurements of Haun stage (Haun, 1973) on the mainstem were made at each harvest, and the anthesis dates were determined.

In the 1995/1996 experiment, two extra rings had no extra CO\(_2\) or air movement. These plots were added because the fans associated with the FACE treatment tended to increase foliage temperatures at night. Measurements comparing the extra plots with the FACE and Blower plots showed that the air mixing caused a rise in foliage temperature equivalent to an increase in minimum air temperature in the FACE and Blower plots of 1.2°C. Biomass results from these plots are not reported here, but phenological observations from them were used to calibrate the models for pheno-logy. These extra plots flowered 4 days later than the Blower plots.

4. Model calibration

Each of the models requires some cultivar information, and the cultivar used in these experiments had not been used in these models before. The major requirement in each case was to specify phenological response to temperature and day-length so that the anthesis date could be accurately simulated. Some other minor adjustments were also made, but all changes were based on one treatment in the first year, and applied universally across treatments in both years.

Yecoro Rojo is a day-length insensitive spring wheat cultivar. Such cultivars are characterised by their production of a constant number of leaves on the mainstem, usually about eight (Jamieson et al., 1998b). Observations from these experiments confirmed this. Phenological development in Sirius is based on the prediction of the leaf appearance rate in response to temperature, and final mainstem leaf number in response to daylength. In this case, the final leaf number was fixed at eight, and the phyllochron (thermal time interval between the appearance of successive leaves) was adjusted so that the anthesis dates were matched in the “ambient” plots described above. The result was a close match of observed and simulated anthesis dates across all treatments in both years, and a close match between observed and predicted Haun stages (Fig. 1). Results for FASSET and AFR-CWHEAT2 were very similar to the Sirius results.

Two other calibration procedures were used with Sirius. The initial trajectory of GAI increase in Sirius is exponential in thermal time, controlled by two parameters (Jamieson et al., 1998a). These were adjusted so that the first few observations of GAI in the high-N ambient CO\(_2\) treatment (1995/1996) were matched. Additionally, the maximum value of GAI was reduced from its usual value of 8.5 to a value of 6.0, to allow for the wide row spacing. The 8.5 value usually used was based on row spacings of 15 cm. Interplant com-

![Fig. 1. Observed Haun stage for low (○) and high (□) N high CO\(_2\) treatment in 1996/1997 based on calibration from 1995/1996. Sirius predictions (line) were identical for both treatments.](image_url)
petition for a similar population in wider rows will result in a smaller maximum GAI.

Phenological calibration in AFRCWHEAT2 involves fixing the duration of a sequence of phenophases in thermal time modified by vernalisation and photoperiod factors. Because Yecoro Rojo is a spring cultivar, the vernalisation factor was set to unity. Hence, the duration of the period from emergence to anthesis was constant in photothermal time, giving a calibration very similar to that for Sirius. The effect of photoperiod variation (implicit in the photothermal time calculation) was negligible between the two years.

Two other changes were made to ARFCWHEAT2 for these simulations. The sensitivity of stomatal resistance to VPD was reduced by one-third, to allow for the very large values common in the desert environment. Additionally, the maximum inflow rate of N to roots was doubled from its original value, which was shown to be too small by Porter (1993).

The calibration for FASSET was similar to the calibration for Sirius. The cultivar used was assumed to be daylength insensitive and to develop a total of eight leaves. The soil water retention curves and the hydraulic conductivity were taken from observed data, and the observed soil carbon and nitrogen contents were used directly to derive soil organic matter and N pools. The LUE under optimal conditions was set to 2.66 g MJ⁻¹, which is 20% lower than the value used for Danish conditions (this is larger than the value used in Sirius because FASSET simulates below-ground biomass, Sirius does not). The increase in LUE due to elevated CO₂ was assumed to be an increase of 17% for the applied increase in [CO₂], corresponding to the mean observed increase in total biomass for CO₂ increase in experiments (Olesen et al., 1999).

5. Comparisons of simulations with observations

In this section, we confine time course comparisons to the 1996/1997 experiment, because these data are completely independent and were not used in the calibrations.

5.1. GAI

Characteristics of the data were that N increased peak GAI, there were small increases in peak GAI with increased [CO₂] at high N, and small decreases in peak GAI with increased [CO₂] at low N. All the three models produced time courses of GAI that were broadly similar to those observed (Fig. 2), particularly the reductions in peak GAI caused by N shortage. The nearest fit to the observations was from Sirius; both AFRCWHEAT2 and FASSET initially underestimated GAI and then tended to overestimate peak GAI in the low N treatments. There were differences among the models and to the data in the effect of CO₂. Neither AFRCWHEAT2 nor Sirius explicitly account for [CO₂] in the calculation of GAI, but there can be an effect when N is limiting because of an N dilution effect at high [CO₂]. This meant that neither model predicted the observed small increase in peak GAI with increased [CO₂] at high N. However, Sirius did predict a reduction of peak GAI with increased [CO₂] at low N of similar magnitude to that observed (Fig. 3, data replotted from Fig. 2), but the N dilution was not sufficient in AFRCWHEAT2 to have much influence. FASSET links GAI directly to biomass, so it showed an increase of peak GAI at both low N (not supported by the data) and high N (as shown in the data).

5.2. Biomass accumulation

Growth rates for shoot biomass were very similar among the models and very similar to the data. This was especially true through the middle period of rapid growth, where time courses of observed and simulated data are very close to parallel (Fig. 4). Differences in the simulations of absolute biomass at any time were mostly associated with those that occurred very early in growth when simulations of light interception varied substantially among the models. Both AFRCWHEAT2 and FASSET substantially overestimated peak GAI in the low N treatments. The overestimates were sufficient that, without compensation, growth rates during these periods should have been overestimated by 10–15%. However, there was compensation through underestimates of LUE or photosynthesis per unit GAI, through reduction of these factors in response to N shortage. This means that the models were getting the right answers for the wrong reasons, and means that both models need to adjust the balance of effects of N shortage on processes at the canopy and unit GAI levels. Similar imbalances were shown by all of the models tested by Jamieson et al. (1998c) in response
Fig. 2. Comparison of simulated GAI time courses from the three models with observations (○) from the four treatments in 1996/1997: (a) low N ambient CO2, (b) high N ambient CO2, (c) low N high CO2, (d) high N high CO2. AFRCWHEAT2 (— – – – – –), FASSET (– – – – – –), Sirius (— –).

Fig. 3. The effect of [CO2] on GAI at low N. Observations, high CO2 (○), low CO2 (□). Simulations from Sirius, high CO2 (full line), low CO2 (broken line).

to water deficits, and portions of those responses have been adjusted in AFRCWHEAT2 (Jamieson and Ewert, 1999) and Sirius (Jamieson and Semenov, 2000). Differences in grain yield predictions are associated with differences in the descriptions of biomass partitioning to grain, which result in slightly different rates and durations of grain filling, and not with substantially different predictions of biomass accumulation.

In the high N treatments, both GAI and biomass accumulation predictions of AFRCWHEAT2 and FASSET were very similar. Hence, the LUE implied by the photosynthesis calculations in AFRCWHEAT2 are close to values of LUE chosen for FASSET.

5.3. Grain yield

In the experiments, increases in both N and [CO2] caused grain yield to increase. The fractional increase in yield caused by increased [CO2] was lower (much lower in the 1996/1997 season) at low N than at high N. The effect on yield of the N variation at high [CO2] was about twice as big as the effect of [CO2] at high N. There were differences between simulated and observed yields. In particular, all three models showed a tendency to overestimate yield (Fig. 5). This was most obvious for FASSET, where the overestimate was quite large and systematic, but its magnitude meant that in the graph comparing model output
Fig. 4. Comparison of simulated and observed shoot and grain biomass accumulation with observations: (a) low N ambient CO₂, (b) high N ambient CO₂, (c) low N high CO₂, (d) high N high CO₂. AFRCWHEAT2 (--- ● --- ●), FASSET (---- •), Sirius (-- - - - - -).

Fig. 5. Comparison of simulated with observed grain yield (t ha⁻¹) from (a) AFRCWHEAT2, (b) FASSET and (c) Sirius for 1995/1996 (○) and 1996/1997 (□), filled symbols are for high CO₂.
Table 1  
Goodness of fit of simulated final grain yields compared with observations

<table>
<thead>
<tr>
<th></th>
<th>AFRCWHEAT2</th>
<th>FASSET</th>
<th>Sirius</th>
</tr>
</thead>
<tbody>
<tr>
<td>RSMD(a)</td>
<td>2.01</td>
<td>3.90</td>
<td>1.32</td>
</tr>
<tr>
<td>Bias(a)</td>
<td>0.33</td>
<td>1.2</td>
<td>0.11</td>
</tr>
<tr>
<td>Intercept(b)</td>
<td>-1.62</td>
<td>1.75</td>
<td>-0.31</td>
</tr>
<tr>
<td>Slope(b)</td>
<td>1.30</td>
<td>0.91</td>
<td>1.06</td>
</tr>
<tr>
<td>S.E. of slope</td>
<td>0.25</td>
<td>0.20</td>
<td>0.17</td>
</tr>
<tr>
<td>(R^2)</td>
<td>0.87</td>
<td>0.69</td>
<td>0.87</td>
</tr>
</tbody>
</table>

\(a\) From regression.

(Fig. 5b), points were gathered parallel but above the 1:1 line. AFRCWHEAT2 tended to overestimate by progressively more as yield increased. However, even accounting for these differences, the predicted responses (i.e., changes in yield) to N and [CO\(_2\)] of all the three models were similar to those observed. All the three models produced predictions that were well correlated with observations, and regression slopes for Sirius and FASSET were within 10% of and not significantly different from unity (Table 1), but the slope for the AFRCWHEAT2 regression was high. Root mean square deviations (RMSDs) of simulated from observed yields were smallest for Sirius and AFRCWHEAT2, and the bias (tendency to over- or underestimate, calculated as the difference in mean predicted yield and mean observed yield) was low for these two models. The larger RMSD for FASSET contained a large bias component (Table 1).

5.4. Grain N

Grain N results are presently available only for the 1996/1997 experiment (Table 2). The largest effect on grain N concentration (N%) was N supply. Increased [CO\(_2\)] had little effect on grain N% at high N, but did cause a significant reduction at low N. All three models simulated a response of grain N% to N supply of the same order of magnitude as observed, but Sirius and FASSET underestimated grain N% at low N, and Sirius overestimated grain N% at high N, whereas FASSET overestimated at high N, high [CO\(_2\)], and underestimated at high N, low [CO\(_2\)].

Table 2  
Observed and simulated grain N contents (%) for the 1996/1997 experiment

<table>
<thead>
<tr>
<th></th>
<th>Observed</th>
<th>Sirius</th>
<th>FASSET</th>
<th>AFRCWHEAT2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low CO(_2) low N</td>
<td>1.82</td>
<td>1.57</td>
<td>1.52</td>
<td>1.91</td>
</tr>
<tr>
<td>Low CO(_2) high N</td>
<td>2.78</td>
<td>3.09</td>
<td>2.53</td>
<td>2.34</td>
</tr>
<tr>
<td>High CO(_2) low N</td>
<td>1.65</td>
<td>1.53</td>
<td>1.49</td>
<td>1.79</td>
</tr>
<tr>
<td>High CO(_2) high N</td>
<td>2.74</td>
<td>2.98</td>
<td>2.97</td>
<td>2.34</td>
</tr>
<tr>
<td>LSD 5%</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

6. Interactions between CO\(_2\) and N

An observation from the experiments was that, particularly when N was limiting, increases in grain yield associated with high CO\(_2\) were smaller than the increases in shoot biomass. Also, fractional increases in grain yield were smaller at low N than at high N, in both observations and simulations. To test the way the three models handled this situation, simulations were run for N fertiliser supplied at various rates from 0 to 200 kg N ha\(^{-1}\) at both 350 and 550 ppm [CO\(_2\)], using the 1995/1996 conditions with all N applied on 22 February. These showed that two of the three models (Sirius and FASSET) predicted rather smaller grain yield responses to [CO\(_2\)] than biomass responses, especially at low N (Figs. 6 and 7). Indeed, in the case of Sirius, there was little or no predicted increase in grain yield to [CO\(_2\)] until N-supply exceeded 100 kg ha\(^{-1}\) (Fig. 6c). AFRCWHEAT2 predicted a very similar response of both final biomass and grain yield to an N-supply of less than about 100 kg ha\(^{-1}\), although grain yield response was smaller than biomass response at higher N-supply (Fig. 7a).

The description of the plant N balance and resultant effects in Sirius is based on a quantitative N-balance, and is the most mechanistic of the three models (Grindlay, 1997; Jamieson and Semenov, 2000). Even though it is not completely accurate, it provides some insight into the reason that the grain response to [CO\(_2\)] is different from the biomass response. As stated above, the extra biomass produced in response to increased [CO\(_2\)] when N is limiting means more is required for non-leaf biomass, and less is available to
Fig. 6. Simulated response of final above-ground biomass (upper lines) and grain yield (lower lines) (t ha\(^{-1}\)) to applied N (kg ha\(^{-1}\)) at two [CO\(_2\)] for (a) AFRCWHEAT2, (b) FASSET, and (c) Sirius, broken lines are for high CO\(_2\) and full lines for ambient CO\(_2\).

Fig. 7. Simulated fractional response of final biomass (broken line) and grain yield (full line) to [CO\(_2\)] increase from 350 to 550 ppm at various levels of applied N (kg ha\(^{-1}\)).
support green area. In addition, the demand for N by growing grain when there is insufficient plant N will result in the sacrifice of some green area to supply the necessary N (Sinclair and Amir, 1992; Jamieson and Semenov, 2000). Hence, the canopy senesces rather faster, less light is intercepted, so that both the grain growth rate and duration are reduced. Both the experimental data and the simulations show that the extra biomass generated in response to increased [CO2] is not necessarily expressed as increased GAI or grain.

In high CO2 conditions and low N-supply, AFRCWHEAT2 can also reduce GAI compared with similar conditions under ambient CO2, also through dilution of N by extra biomass. However, AFRCWHEAT2 does not have the feedback that Sirius uses to reduce GAI during grain filling, and this causes it to overestimate the effect of CO2 on grain yield in N-stressed conditions (Fig. 7).

Overall, Sirius provides the closest match to the observations of both GAI and biomass accumulation. The major assumptions in the model about [CO2] and N effects are that the direct effect of [CO2] is to vary the LUE with no direct effect on GAI, and that the direct effect of N variation is to vary GAI with no direct effect on LUE. Interactions can cause GAI to vary when [CO2] is changed. The very close correspondence of predicted and measured light interception and biomass accumulation strongly supports these hypotheses. Hence, the model showed, quite conclusively, that CO2 effects were expressed almost entirely on a per unit green area basis (through changes in LUE), whereas N effects were expressed almost entirely through influences on GAI.

7. Conclusions

The experiment used to test the models here was performed in a warm environment, even though temperature was not a treatment. The models tested were all developed in temperate regions, and have performed very well in a warm one. There are differences among the models, and clear pointers to where each could be improved, e.g., there needs to be some re-balancing of N effects on the canopy vs. its effects on LUE. They will remain separate models because they emphasise different processes. The detailed leaf and tiller based canopy model in AFRCWHEAT2 will not be replaced by the aggregated GAI models of FASSET and Sirius because it is very useful for studying processes at the level of organisation it represents.

Although there was, and always is, some “local calibration” of the models, this amounted to little more than adjustment to phenology to ensure timing was correct. It did not involve any “fitting” of the experimental data on biomass accumulation and grain growth. Effects of N and [CO2] are based on hypotheses implicit in the models and completely independent of these experiments. Although the experiments here were restricted to two levels each of [CO2] and N over two years, they produced a wide range of yields. These were reasonably well matched by the simulations, particularly in the changes caused by treatments. Hence, our major conclusion is that day time step models can mimic the behaviour of crops growing at high CO2 levels. Despite some differences in the detail of the description of mechanisms, and some systematic overestimation of yield, the three models mimicked the response of wheat crops to variation in both N-supply and [CO2] in a hot, dry (though well watered) environment. This adds to the demonstrated success of such models to reproduce growth and yield of wheat in response to substantial variations of environment and management (Jamieson et al., 1998a,c; Jamieson and Semenov, 2000). It gives a clear demonstration that climate change issues are of the same order of complexity as other issues addressed by such models, such as water supply (Jamieson et al., 1998c) and nitrogen supply (Jamieson and Semenov, 2000). In addition, the models give insights into mechanisms of response to variation in the environment.

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