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Simulating the effects of elevated CO_2 on crops: approaches and applications for climate change

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Abstract

Several crop models may be used to simulate the effects of elevated CO_2 on crop productivity. Yet no summary exists in the literature attempting to describe differences among models and how simulations might differ under climate change conditions. We provide an introductory review focusing on simulating the impacts of elevated CO_2 on crops. We describe and discuss modeling approaches, component modules, applications to climate change and model validation and inter-comparison studies. By searching the recent peer-reviewed literature from 1995 to present, we found that about 20% of published crop modeling studies have focused on climate change impacts. About half of these studies explicitly analyzed the effects of elevated CO_2 on crop growth and yield. Our analysis further suggested that the crop models that have been used the most in climate change assessments are also those that have been evaluated the least using available data from elevated CO_2 experiments. Based on our review, we identify a set of recommendations aimed at improving our confidence in predictions of production under elevated CO_2 and climate change conditions. These include continued model evaluation with existing field experiment data; increased focus on limiting factors such as pest, weeds, and disease; and attention to temporal and spatial scaling issues.

Keywords: Elevated CO_2; Crops; Agriculture; Modeling; Climate change

1. Introduction

Atmospheric CO_2 concentration is today at 375 μl/l, or 30% higher than during pre-industrial times, and is increasing at about 0.5% per annum. Trends in global energy and land use suggest that anthropogenic emissions of CO_2 and of other greenhouse gases will continue to be substantial for many decades. As a result, atmospheric CO_2 concentration is projected to be in the range of 550–750 μl/l by the end of this century, the lower range depending on whether or not climate policy agreements such as the Kyoto Protocol are soon put in place (e.g., www.unfccc.org, IPCC, 2001). Increasing concentrations of CO_2 in the atmosphere are linked to a high probability of climate change, characterized by increased surface temperatures, by changed global and regional patterns of precipitation, and by climatic shifts in both

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mean and variability that could threat ecosystems functions and human welfare.

In particular, elevated CO_2 and associated climate change may greatly affect agricultural production worldwide (IPCC, 1995). It is thus not surprising that a large body of work has been devoted to analyzing potential impacts on future local, regional and global crop production (e.g., Rosenberg, 1993; Rosenzweig and Parry, 1994; Rosenzweig et al., 1995; Jones et al., 2000; Fischer et al., 2001; Reilly et al., 2001). In the majority of such studies, crop models were employed to assess the simultaneous effects on crop growth and yield of future elevated CO_2, regional climate change, and crop management (with or without adaptation). It is in fact well-recognized that CO_2 concentration and management factors will interact in complex ways to determine the ultimate impacts of climate change on crop production. While elevated CO_2 alone tends to increase growth and yield of most agricultural plants (Kimball, 1983; Cure and Acock, 1986; Allen et al., 1997; Kimball et al., 2002), warmer temperatures and changed precipitation regimes may either benefit or damage agricultural systems (e.g., Rosenzweig and Hillel, 1998). Water and fertilizer application regimes will further modify crop responses to elevated CO_2 (e.g., Reilly et al., 2001).

Because of such multi-factor interactions, the simulated increase in productivity under elevated CO_2 often determines not only the magnitude, but even the sign, of the overall changes in crop yields in global warming scenarios (Tubiello et al., 2002). The dependence of agricultural assessment studies on the simulated CO_2 response makes it thus pertinent to ask the following questions: (i) How are key plant processes, and their responses to elevated CO_2, implemented in current agricultural crop models? (ii) How have different approaches been evaluated and/or compared? (iii) How have the models been used?

The modeling state-of-the art with respect to plant responses to elevated CO_2 has already been reviewed (e.g., Boote and Loomis, 1991; Allen et al., 1997). However, there is little overview about the variety of crop models and incorporated approaches to modeling the effects of elevated CO_2. Although many of these models are quite routinely used in climate change studies, we do not fully understand the impacts that different methods may have on projected results.

Clearly, most agricultural crop models used in climate change studies were not originally developed with the intention to model plant responses to elevated CO_2 under climate change conditions, but rather to provide, under current climate: (a) decision support to farmers, regional or national authorities; (b) insight into specific physiological processes; (c) agronomic relationships among crops and cropping systems; or (d) analyses of environmental effects at various spatial scales (e.g., plot, field, ecosystem, regional or even global). Therefore, while a few models already contained relationships that accounted for effects of elevated CO_2 on individual processes, many had to be specifically modified.

In the following sections, we analyze differences among crop models widely used in climate change studies. In detail, we describe approaches to modeling effects of CO_2 on crops, we perform a literature search on model applications and analyze studies on models testing and inter-comparison that have used high-quality data from elevated CO_2 experiments. Finally, we identify specific modeling and methodological issues that require attention in order to increase confidence in the simulations of the effects of elevated CO_2 and climate change conditions on crop production.

2. Crop response to elevated CO_2: background

Irrespective of climate change issues, the positive impacts of elevated CO_2 on plant growth and yield were well understood and put into practice by greenhouse vegetable growers since the 1930s, leading to elevated CO_2 large-scale commercial operations within a few decades (Nederhoff, 1994). The scientific recognition and rudimentary theoretical understanding of the positive role of CO_2 on plant photosynthesis had of course developed much earlier (1770–1850), while the first plant growth controlled experiments with enriched CO_2 were performed at the beginning of the 20th century (Browne and Escombe, 1902). Progress in biochemistry and plant physiology subsequently led to the discovery of the C3 carbon fixation pathway by Calvin in the 1940s; of the interactions of CO_2 and transpiration via effects on leaf stomata by Gaastra (1959) in the 1950s; of C4 and CAM photosynthesis pathways in the 1960s (see, e.g., Hatch, 1992). Improved measurements of O_2 evolution and isotope discrimination characterized progress in the 1970s and 1980s, leading to measurements of photosynthetic quantum yield and increased understanding of stomatal dynamics (Koh and Kumura, 1971; McCree, 1972; Farquhar et al., 1982; Bjorkman and Demmig, 1987).

In the last decade, great effort was devoted to further understand the effects of elevated CO_2 on growth and yield of most agricultural plants (Kimball, 1983; Cure and Acock, 1986; Bowes, 1993; Allen et al., 1997; Kimball et al., 2002). Mechanisms regulating the interactions of CO_2 with other environmental conditions, e.g., light, temperature, soil quality, soil water status, nutrient supply, exposure to air pollutants, weeds and pests, have been investigated extensively (Allen, 1990; Lawlor and Mitchell, 1991; Idso and Idso, 1994; Morison and Lawlor, 1999). Recent research has focused greatly on the effects of elevated CO_2 on key plant and ecosystem processes such as community-level carbon assimilation and respiration; stomatal conductance and transpiration; partitioning to grain and fruit; above- and below-ground partitioning; phenological development; root and soil processes; and on the potential for acclimation of individual processes to elevated CO_2 conditions (e.g., Amthor and Loomis, 1996; Allen et al., 1997; Norby et al., 2001).

3. Modeling approaches of crop responses to CO_2

3.1. Development in crop modeling

Plant models were historically developed following the accumulation of knowledge and the progressive availability of experimental data. Leaf-level models of photosynthesis were developed early last century (Blackman, 1919) to describe photosynthesis-light response curves. It was not until the early 1950s and 1960s, however, that models computing canopy-level light interception and carbon assimilation rates were built (Monsi and Saeki, 1953; de Wit, 1965; Duncan et al., 1967; Hesketh and Baker, 1967). The simplifying concept of crop radiation-use efficiency (RUE) was developed and applied to agronomic crop modeling in the 1970s (Sinclair et al., 1976; Monteith, 1977; Norman, 1979); during the same period, maintenance respiration was quantified and implemented in plant growth models (Penning de Vries, 1975; de Wit, 1978). The first crop photosynthesis models to include CO_2 as an explicit variable were built in the 1970s and early 1980s, and included rectangular hyperbolae describing leaf photosynthesis dependence on light and CO_2 concentration, scaled to canopy level (Acock et al., 1971; Thornley, 1976; Acock et al., 1978; Charles-Edwards, 1981; Acock and Allen, 1985; Goudriaan et al., 1985). Finally, leaf-level biochemical models of photosynthesis including direct CO_2 effects on photosynthesis were published in the early 1980s (Charles-Edwards, 1981; Farquhar et al., 1980; Farquhar and von Caemmerer, 1982; Ball et al., 1987).

More recent developments in crop modeling have aimed at harmonizing and improving these various approaches, from better scaling routines from leaf to canopy (or even from cell to canopy) to the introduction of leaf nitrogen distributions affecting photosynthetic capacity; to refining temperature–CO_2 and water–CO_2 interactions (e.g., see for further details: Long, 1991; Boote and Loomis, 1991; Norman, 1993; Boote et al., 1997).

3.2. Types of models and scale issues

Integration into crop models of experimental knowledge on the effects of elevated CO_2 on plant growth and yield is required for predicting crop productivity under scenarios of global change. Many crop models have been modified to this end, yet there is no summary in the literature documenting today's state-of-the art approaches, or discussing how model performances compare across models and against experimental data. One problem for compiling such a summary is certainly represented by the large number of models—and

Table 1
Example of studies in which crop simulation models were used to predict effects of elevated CO_2 on wheat

Study/Model	Country/Region[a]	Reference
Impact assessment studies		
AFRCWHEAT2	United Kingdom, France	Semenov et al. (1993)
CropSyst	Italy	Tubiello et al. (2000)
CERES	Argentina	Magrin et al. (1997)
	Bangladesh	Karim et al. (1996)
	Bulgaria	Alexandrov and Hoogenboom (2000)
	Canada	Brklacich and Stewart (1995)
		El Maayar et al. (1997)
	China	Shi et al. (2001)
	Commonwealth of Independent States	Menzhulin et al. (1995)
	India	Lal et al. (1998)
	France	Delecolle et al. (1995)
	Romania	Cuculeanu et al. (1999)
	Uruguay, Argentina	Baethgen and Magrin (1995)
	USA	Adams et al. (1990)
		Tubiello et al. (2002)
EPIC	USA	Easterling et al. (1992a)
		Easterling et al. (1992b)
		McKenney et al. (1992)
		Easterling et al. (1993)
		Brown and Rosenberg (1999)
		Brown et al. (2000)
		Easterling et al. (2001)
EuroWheat	Europe	Harrison and Butterfield (1996)
GAEZ	Global	Fischer et al. (2001)
SUCROS87	Europe	Nonhebel (1996)
WOFOST	Europe	Wolf (1993)
APSIM	Australia	Reyenga et al. (1999)
Other studies[b]		
AFRCWHEAT2, LINTULCC2, Sirius	Spain	Ewert et al. (2002)
AFRCWHEAT2, AFRCWHEAT3S	United Kingdom	Porter et al. (1995)
AFRCWHEAT2, CERES, NWHEAT, Sirius, SOILN	United Kingdom, Spain	Semenov et al. (1996)
		Wolf et al. (1996)
AFRCWHEAT2-O3, LINTLCC	Europe	van Oijen and Ewert (1999)
CENTURY	USA	Paustian et al. (1996)
CERES	USA	Rosenzweig and Tubiello (1996)
CERES, EPIC, Stewart and Sinclair models	Canada	Touré et al. (1995)
CLIMCROP	Denmark	Olesen et al. (2000)
EPIC	USA	Stöckle et al. (1992)
	USA	Brown and Rosenberg (1997)
SOIL/SOILN	Sweden	Eckersten et al. (2001)
Wheat model	Australia	Wang and Connor (1996)

[a] Simulations were performed either for selected sites or entire regions, r countries.
[b] Studies with more focus on sensitivity analysis (e.g., model components, input data), model inter-comparison etc.

model versions—used in assessment studies. An example for wheat models is given in Table 1. Particularly, the existence of many different modeling approaches, including differences in models structure and modeling detail[fe1] make any such comparison difficult.

As shown in Fig. 1a, two kinds of models can be generally identified: statistical models, used to empirically predict large-scale (county to region) agricultural yields from regression analyses based on monthly or annual variables; and process-oriented models, further referred to as process

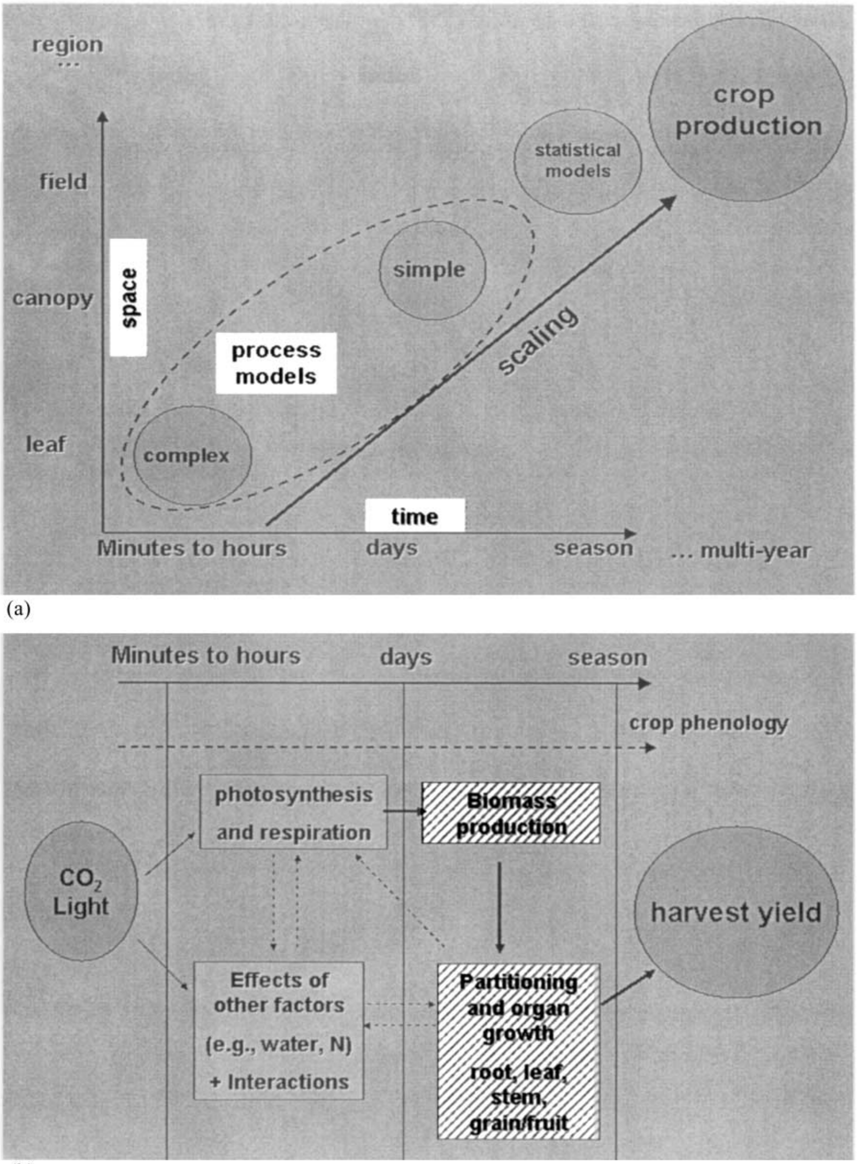


Fig. 1. Schematic illustrations of crop modeling approaches of (a) types of models in relation to levels of spatial (leaf, canopy, field) and temporal (minutes to hour, days, seasons) scales and (b) CO_2 effects on different processes. Note that processes are simulated with different time-steps, e.g. leaf level photosynthesis in minute to hour intervals, crop biomass production in days and harvest yield in season or multi-year steps (see text for further explanation). The bold arrow lines among boxes indicate the flow of carbon from leaf to canopy production to harvest yield. Important feedbacks (dotted lines among boxes) link many of these processes across timescales.

models, used to compute crop dynamics at smaller spatial scales (leaf to canopy and/or field levels), based on deterministic equations and simulation of underlying processes at timescales of minutes to days. Process models can be further grouped into ‘*complex*’ and ‘*simple*’. Complex models compute processes at the level of organs or lower; for example, the dynamics of carbon and water calculated at the leaf-level, requiring time-steps ranging from minutes to hours. Simple models are more holistic and compute canopy-level dynamics directly, using empirical relationships without consideration of underlying processes, typically using daily time-steps (for a discussion on simple vs. complex modeling issues, see Passioura, 1979; Thornley, 1980; Charles-Edwards et al., 1986; Sinclair and Seligman, 2000).

In general, both statistical and process models adequately predict agronomic yields at given scales. Statistical models were intrinsically designed to operate at the multi-seasonal, regional scale, and are thus best suited for analyzing inter-annual variability of regional production. Process crop models were developed to simulate crop responses to environmental conditions at the plot and field level and can be used to analyze inter-seasonal dynamics of field-level crops. [fe2]Many assessment studies have employed process models to project the impacts of climate change and elevated CO_2 on crops from field-scale to regional and even global levels. Yet, no clearly defined methodologies exist for extending field-level yields computed with process models to large regions.

3.3. Model components and responses to CO_2

We focus on process crop models, as these [fe3]capture the dynamics of crop response to elevated CO_2, and because they have widely been used in climate change studies. These models have different components that can be simplistically grouped into those computing: plant phenology as a function of accumulated temperature and day-length; photosynthesis and respiration; water balance, N-uptake and distribution and effects of other factors; partitioning, biomass accumulation and organ growth (Fig. 1b). These components may operate at different timescales. For instance, photosynthesis and water exchange are resolved at timescales from minutes to hours (complex process models) to days (simple process models). Biomass production and partitioning, and ultimately yield, are generally computed at daily (process models) to seasonal (statistical models) time-steps. Thus, linkages among model components are often across timescales. For instance, 'long-term' patterns of root partitioning may affect soil-water dynamics, which in turn may modify 'short-term' stomatal dynamics and photosynthesis; patterns of biomass accumulation and growth of reproductive organs may trigger source-sink relations, also capable of modifying leaf photosynthetic rates, etc.

Simulating the effects of elevated CO_2 on crop growth and yield within process models involves the introduction and/or modification of specific components. Previous reviews have focused on theoretical aspects of such modifications, describing in detail model equations, especially focusing on leaf and canopy photosynthesis (e.g., Boote et al., 1997; Long, 1991). We provide herein a summary of modeling solutions implemented in current crop models, following the simplified list of components illustrated in Fig. 1b (see also Table 2).

3.3.1. Light interception and photosynthesis

Process models have some component to simulate light interception of the canopy. The approach taken largely depends on the concept used to simulate carbon assimilation or biomass production; e.g. whether a big-leaf model (Boote and Loomis, 1991), a sunlit/sunshade two-box model (Boote and Loomis, 1991) or a multiple-layered model is used, and whether or not leaf-angular distributions and crop geometries and other factors are accounted for (i.e., Spitters, 1986). Radiation absorption is often computed separately for direct and diffuse radiation.

Many crop models employ equations written at leaf or canopy level to explicitly simulate gross photosynthesis rates from absorbed light. The photosynthesis response to light is often calculated using exponential or rectangular hyperbolic functions with parameters representing quantum efficiency and light saturated rate of photosynthesis; examples are AFRCWHEAT2 (Weir et al., 1984; Porter, 1993), CROPGRO (Hoogenboom et al., 1992), SUCROS (Goudriaan and van Laar, 1994) and WOFOST (Boogard et al., 1998). Effects of atmospheric CO_2, temperature and other factors, depending on the model, on quantum efficiency and light saturated rate of photosynthesis are realized via empirical relationships. Few crop

Table 2
Summary of modeling approaches of CO_2 effects on plant processes considered in crop models. Note, that implementation of modeling approaches differ among models

Processes	CO_2 effect	Modeling Approaches
Assimilation	Increase	Direct effect using: (a) Biochemical model of leaf photosynthesis (b) Photosynthesis-light response curve (c) RUE which empirically increases with CO_2
Respiration[a]	Increase	Not considered[b]
Stomatal conductance	Decrease	(a) Direct effect via empirical reduction of stomatal conductance (b) Indirect effect via coupling of models for photosynthesis and stomatal conductance
Partitioning	Variable responses	Indirect effect via source-sink relationships
Organ growth	Increase	Indirect effect via increase in assimilation
Phenological development	Variable responses (Mostly acceleration)	Indirect effect via increase in canopy temperature
Soil water balance		
(a) Transpiration[c]	Decrease	(a) Direct effect via empirical reduction in transpiration with CO_2 (b) Indirect effect via reduction in stomatal conductance
(b) Water uptake	Decrease[d]	Indirect effect via reduction in stomatal conductance and transpiration[c], and acceleration of crop development
(c) Water use efficiency	Increase	Indirect effect via reduction in transpiration
Nitrogen dynamics		
N-concentration in biomass	Decrease	Indirect effect via increase in biomass
N-uptake	Increase	Indirect effect via increase in N demand

See text for explanation.
[a] Respiration rate per unit dry weight.
[b] Respiration may increase via increase in canopy temperature under elevated CO_2.
[c] Transpiration per unit leaf area.
[d] Water uptake may also increase via increase in canopy size and root growth at elevated CO_2. The net result will depend on the specific environmental conditions.

models use more detailed, biochemical equations, such as the ones described by Farquhar et al. (1980); examples are DEMETER (Kartschall et al., 1995) and LINTULCC2 (Rodriguez et al., 2001). However, these equations have many coefficients that must be derived from leaf measurements and parameterization of such equations remains difficult (Boote et al., 1997).

In these models, gross photosynthesis is often computed at minute to hourly intervals and scaled to canopy levels. In addition, respiration losses and conversion units are calculated and used to finally compute daily biomass accumulation. By contrast, simple models often calculate net biomass production directly, typically in daily time-steps, by multiplying the light intercepted by the crop's RUE. In many such models RUE is a constant that is empirically derived by comparing seasonal data of crop biomass accumulation versus light totals (e.g., Sinclair and Horie, 1989). However, in some models RUE may be dependent on light intensity and plant age (Ritchie and Otter-Nacke, 1985). The effects of elevated CO_2 on RUE are modeled empirically, using simple linear or curvilinear multipliers. Examples of simple approaches are the modeling systems CERES (Ritchie and Otter-Nacke, 1985; Tsuji et al., 1994), EPIC (Williams et al., 1989), APSIM (Reyenga et al., 1999) or the wheat model Sirius (Jamieson et al., 2000).

RUE models can hardly be evaluated against leaf-level data, so that validation of the RUE response to CO_2 remains difficult. By contrast, complex model predictions of leaf or canopy-level instantaneous photosynthesis rates can be shown to perform well against a range of environments. Nonetheless, as we discuss in a following section, several simple and complex models alike, evaluated using above-ground biomass and yield data under ambient and elevated CO_2, were found in agreement with observed data.

3.3.2. Respiration

Complex models that simulate photosynthesis also compute maintenance and growth respiration. Respiration is not explicitly considered in the more simple RUE models. None of the models we considered included direct effects of elevated CO_2 on respiration, although some experiments have indicated the importance of such effects (Amthor, 1997). Indirect increases in simulated maintenance and growth respiration rates under elevated CO_2 are computed in complex models only as a consequence of larger standing biomass and higher growth rates, from which respiration rates typically depend.

3.3.3. Water balance

In some complex models simulations of photosynthetic carbon uptake are linked with calculations of leaf stomatal conductance. Based on mechanisms that optimize carbon fixation and water loss, leaf stomates can close under water stress, automatically reducing the flow of CO_2 into the leaf/canopy, and limiting photosynthetic rates (e.g., Ball et al., 1987; Leuning, 1995). Alternatively, increasing CO_2 concentration may also induce stomatal closure and, thus, reduce water loss through transpiration. These dynamics require computation of leaf or canopy level energy balances and simulation time-steps are from minutes to hours, substantially increasing the number of calculations per model run. Examples of models implementing such an approach are CROPGRO (Hoogenboom et al., 1992), LINTULCC2 (Rodriguez et al., 2001) and DEMETER (Kartschall et al., 1995; Grossman-Clarke et al., 2001). A simpler approach used in a number of crop models is to simulate effects of water stress on photosynthesis via empirically calculated factors. Using daily time-steps, these models first compute canopy potential transpiration. Based on the assumption that stomatal closure is controlled by the balance between available plant root water uptake and potential transpiration demand (Tubiello et al., 1995; Ewert et al., 2002), a working assumption is made that, if actual transpiration—at most equal to available root water uptake—is less than the potential demand, ‘stomates will have adjusted over the course of a day to account for that imbalance’ (Ritchie and Otter-Nacke, 1985). This implies that the actual reduction of daily biomass production depending on that water stress must be proportional to the ratio of actual to potential evapotranspiration (Ritchie, 1972). Some models may further limit biomass production under water-limiting conditions by means of a transpiration efficiency coefficient, TE, dependent on air relative humidity, multiplied by daily total canopy transpiration to obtain daily total biomass accumulation. In these models, actual biomass production is computed as the minimum between RUE- and TE-dependent quantities (e.g., Stöckle et al., 1992; Reyenga et al., 1999).

The adjustment for elevated CO_2 conditions in these models is made empirically, by reducing potential transpiration demand via a multiplier, representing reduction of maximum stomatal conductance as a function of CO_2. Examples of crop models following such approach include the DSSAT-CERES and EPIC family of models (e.g., Peart et al., 1989; Stöckle et al., 1992).

As in the case of photosynthesis modeling, simple approaches to transpiration cannot be evaluated against leaf-level data. Only few data exist of crop canopy gas exchange measurements (e.g., Rodriguez et al. 2001) so that it is difficult to validate modeled CO_2 impacts on transpiration and photosynthesis. However, many authors have often incorrectly assumed that the carbon–water relations observed under elevated CO_2 could only be captured by complex modeling (e.g., Grant et al., 1995). As shown in a later section, comparisons with observed data for biomass and yield have rather shown that complex and simple approaches alike could well reproduce these dynamics.

3.3.4. Phenological development

Elevated CO_2 may affect crop development via effects on leaf temperature via CO_2-induced stomatal closure. Complex models compute such an effect via energy balance calculations, affecting leaf temperature and enhancing plant senescence (e.g., DEMETER, ecosys). Simple models do not include such an effect, which is nonetheless thought to be small in most environments.

3.3.5. Biomass partitioning and yield

The degree of complexity of process crop models relative to partitioning of biomass depends on their ability to dynamically allocate carbon among roots, stems, leaves, and grain or fruit, as a function of resource status. Under elevated CO_2, feedbacks between photosynthesis rates and organ growth/size, known as source-sink relations, may significantly modify photosynthesis rates, partitioning and biomass accumulation over time (Boote et al., 1997; Grace, 1997). Most crop models used in current studies do not simulate source-sink relations, lacking dynamic partitioning rules. Constant allocation fractions for allocating carbon among organ groups are used instead. In some models allocation fractions change empirically with crop development. Among the reviewed crop models, the simplest computed harvest yield from final above-ground biomass, via a harvest index coefficient that could be reduced as a function of water stress accumulated during the growing season. Examples are EPIC (Williams et al., 1989); GAEZ (Fischer et al., 2001); and Cropsyst (Stöckle et al., 1994). More complex approaches were those computing partitioning to roots, leaves, stem and grain or fruit, via coefficients that depended on phenology and, in some cases, on water stress. Examples were the DSSAT models. With these models, simulations under elevated CO_2 were capable of generating dynamic feedbacks between root systems, water uptake, and biomass accumulation (e.g., Tubiello et al., 1995).

3.3.6. Interaction with other conditions

The effects of CO_2 on crop growth and yield can greatly vary depending on other environmental and management factors. The interactive effects of CO_2 and air temperature on crop photosynthesis are one notable example. Elevated CO_2 levels tend to shift the leaf-level photosynthetic optimum towards higher temperatures (Long, 1991). Simulating such interactions can best be resolved by complex models that account for bio-chemical relationships of leaf photosynthesis and for feedbacks among photosynthesis, water and energy balance (see photosynthesis and water balance sections above). Models such as CROPGRO and DEMETER capture the complexity of these effects, while simple approaches such as those implemented into DSSAT and EPIC do not. However, comparison of simulations from complex and simple models showed that such interactions between CO_2 and temperature on leaf photosynthesis may be small when averaged over the whole growing season (Boote et al., 1997).

Water and nutrients also affect crop responses to CO_2. Experimental data suggest that the relative effects of elevated CO_2 on crop growth and yield is more pronounced under water-limited as compared to well-watered conditions (Chaudhuri et al., 1990; Kimball et al., 1995). The contrary is true for nitrogen: well-fertilised crops respond more positively to CO_2 than less fertilised ones (Sionit et al., 1981; Mitchell et al., 1993). Such effects have been included in crop models indirectly, via effects on stomatal closure and/or transpiration and canopy development. As discussed in the next section, both simple and complex crop models have shown some ability to mimic the interactions of elevated CO_2 with water and N.

Effects of CO_2 on crops also vary depending on presents of air pollutants, such as tropospheric ozone, which may limit CO_2 effects by reducing stomatal conductance and/or by decreasing biochemical activity due to cell damage. Such effects have been included into a few mechanistic models (e.g., Ewert et al., 1999). Current crop models do not yet include other important factors that could limit crop response to CO_2 in the field, such as soil quality, competition with weeds, pests and disease.

Finally, biochemical acclimation of plant photosynthesis to elevated CO_2 was not implemented in the crop models considered.

4. Model applications: elevated CO_2 and climate change assessments

How are the crop models modified for elevated CO_2 used? We have used the science portal Scirus (www.scirus.com) for searching the peer-reviewed literature published since 1995, in order to derive information on the number of studies assessing the effects of elevated CO_2 and climate change on crop production. A preliminary search indicated about 1000 published articles that used crop modeling to investigate a variety of issues, e.g., field-level to regional crop production, soil and water quality, land-use and economic assessments. Of the total number of references found, roughly 20% were climate change assessment studies. Those concerned with elevated CO_2 were 8% of the total, irrespective on whether or not climate change issues were considered (Fig. 2).

Our search also indicated that the crop models that have been most widely used both in general applications as well as to predict future crop yields under climate change and elevated CO_2 concentrations, were decision support systems. These modeling environments cover many crop types, often including the major cereal (wheat, maize, rice, barley, sorghum, millet), soybean, potato, oil crops (peanut, rape oil) and some vegetable crops (tomato). Our web search showed that three decision support models, DSSAT, EPIC, and SUCROS–WOFOST, were those most widely used in the literature. The percent of climate change and/or elevated CO_2 studies performed with these three models was higher than the general average. Roughly 35% of all crop modeling studies published with these three models were climate change assessments. The percent of studies involving the effects of elevated CO_2 was 14%.

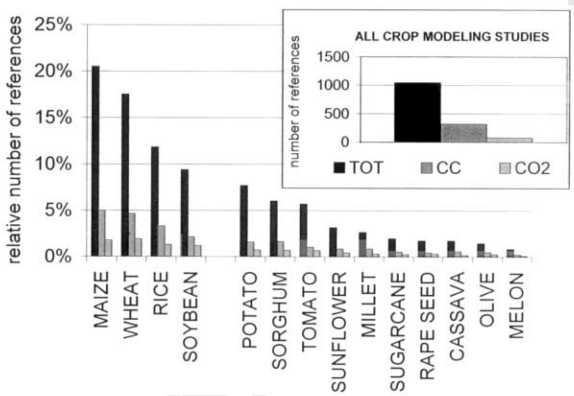


Fig. 2. Number of references from the peer-reviewed literature since 1995 dealing with crop modeling obtained from a web search using Scirus (www.scirus.com). Results refer to total number of crop modeling studies found (TOT); those explicitly concerned with climate change impacts (CC); and those considering effects of elevated CO_2 (CO_2) for all crops (inserted graph) and individual crops (large graph).

We next searched for single-crop modeling studies. As also shown in Fig. 2, we found that 60% of all studies published in the last 6 years involved analyses of wheat, maize, soybean, and rice. Of the remaining, potato, sorghum, tomato, sunflower, millet were among the crops most simulated. Within each crop, the percentage of climate change assessment studies with or without CO_2 effects was close to that found overall.

A more detailed analysis on model applications was performed for wheat. Our web search found a group of nine models as the most cited over the last 6 years, of which CERES-Wheat, EPIC and SUCROS represented three-quarters of all crop modeling studies in wheat. AFRCWHEAT2, Sirius, Cropsyst, SWHEAT, LINTUL, APSIM were among the models most used in the remaining group. The differences among models in the frequency of usage were the same for climate change studies. When refining our search by considering CO_2 effects some sharp asymmetries emerged among models. The percentage of the CO_2 studies that were also performed in conjunction with climate change impact analyses was close to 100% for EPIC, and about 40% for CERES-Wheat. By contrast, SUCROS, SWHEAT, Sirius, and AFRCWHEAT2 were by far more frequently used in studies investigating the effects of elevated CO_2 alone and evaluating models with experimental data and without connections to climate change assessments. These differences plainly indicate that some of the wheat models most widely used in climate impact studies are not those evaluated under elevated CO_2! It has been argued that successful validation of sub-routines or model components, as extensively done for leaf photosynthesis, provide sufficient evidence for crop model validity and justify its application in climate change studies. However, effects of elevated CO_2 on crop growth and yield are complex, including responses of different growth and development processes (e.g., Kimball et al., 2002). Consequently, crop models require testing against a range of data from experiments in which effects of elevated CO_2 on crops' growth and yield were investigated.

In the following section we focus on the availability and suitability of experimental data for model evaluation and on published results on model testing and inter-comparison. Again, we restricted our analysis to wheat because it has been investigated and modeled most extensively.

5. Model testing and inter-comparison

About a decade ago, many authors had recognized that experimental data of the effects of elevated CO_2 on crop plants, particularly in combination with other factors, was needed in order to advance model development (see e.g., Lawlor and Mitchell, 1991). Since then a number of studies were performed using different experimental approaches (Table 2). A large number of experiments were performed within controlled environment chambers (e.g., Mitchell et al., 2001); under semi-controlled conditions using greenhouses (e.g., Gifford and Morison, 1993; Lawlor and Mitchell, 1993); inside temperature gradient tunnels (e.g., Conroy et al., 1994; Rawson, 1995); or within open-top chambers (e.g., Mulholland et al., 1998; Hertstein et al., 1999). More recently, elevated CO_2 experiments were designed under more realistic field conditions, using free-air carbon dioxide enrichment facilities (e.g., Kimball et al., 1995; Norby et al., 2001; Bindi et al., 2001; Miglietta et al., 2001; Weigel and Dämmgen, 2000).

Several attempts have been made to use data from controlled (e.g., Mitchell et al., 1995) or semi-controlled conditions for model testing in wheat grown under elevated CO_2 (e.g., Ewert et al., 1999; van Oijen and Ewert, 1999; Ewert and Porter, 2000; Ewert et al., 2002). Modification of growing conditions in controlled or semi-controlled environments were, however, reported to limit the applicability of these data for model testing (Ewert et al., 2002). A number of factors related to the microclimatic conditions with chambers and restricted rooting volume, caused additional variation in growth and yield which could not be reproduced by models (van Oijen and Ewert, 1999; Ewert et al., 2002).

Further data have become available from FACE experiments during the last 6 years and have been used most extensively for model testing and inter-comparison under conditions of elevated CO_2, together with the interactions of either water (e.g., ecosys, Grant et al., 1995; DEMETER, Kartschall et al., 1995; Wechsung et al., 1999; mC-Wheat, Tubiello et al., 1999; AFRC-WHEAT2, Sirius, LINTULCC2, Ewert et al., 2002) or N (AFRCWHEAT2, Sirius, and FASSET, Jamieson et al., 2000). The crop models tested using FACE data had different approaches to the modeling of both biophysical and agronomic variables, but all showed good agreement, under both ambient and elevated CO_2, with a large number of observed variables such as time courses of phenology, above-ground biomass, LAI, in addition to final above-ground biomass and grain yield (Table 3). Both simple and complex approaches were able to capture the observed interactions of elevated CO_2 with both water and N (e.g., Jamieson et al., 2000; Ewert et al., 2002). For example, Fig. 3 shows that several models well captured the observed increase in the relative CO_2 effect on grain yield underwater-limited compared to well-watered conditions, provided some effects of elevated CO_2 on stomates and/or transpiration were included. Furthermore, as shown in Fig. 4, model inter-comparison studies underlined that differences among tested models were often larger than those computed between single models and observations.

A number of issues were identified in these studies in order to improve model evaluation and inter-comparison with data from elevated CO_2 studies (e.g., Ewert et al., 2002). Firstly, even in the case of high-quality datasets such as those developed under FACE, there was often a disconnection between the nature of collected data and the format ideally required for model testing. For example, while models need exact dates of pheno-

Table 3
Selected experiments and treatments used to test crop model simulations of wheat responses to elevated CO_2

Treatments		Model	Reference
CO_2	Others		
Free-air carbon dioxide experiments			
Ambient, ambient × 1.5	Water (well-watered, water-stressed), 2 seasons	mC-Wheat	Tubiello et al. (1999)
		AFRCWHEAT2, LINTULCC2, Sirius	Ewert et al. (2002)
		DEMETER	Kartschall et al. (1995), Grossman-Clarke et al. (2001)
		ecosys	Grant, et al., (1995, 1999)
Ambient, ambient × 1.5	N (optimal, limited), 2 seasons	Sirius, AFRCWHEAT2, FASSET	Jamieson et al. (2000)
Open-top chamber experiments			
Ambient, ambient × 2	Ozone (ambient, ambient × 1.5), 3 seasons, 8 sites (across Europe)	AFRCWHEAT2-O3, LINTULCC	Ewert et al. (1999), Ewert and Porter (2000), van Oijen and Ewert (1999)
Ambient, ambient × 2	Water (well-watered, water-stressed), 2 seasons	AFRCWHEAT2, LINTULCC2	Ewert et al. (2002), Rodriguez et al. (2001)
Controlled environment experiments			
Ambient, ambient × 2	Temperature (ambient, ambient + 4 °C)	ARCWHEAT1	Mitchell et al. (1995)

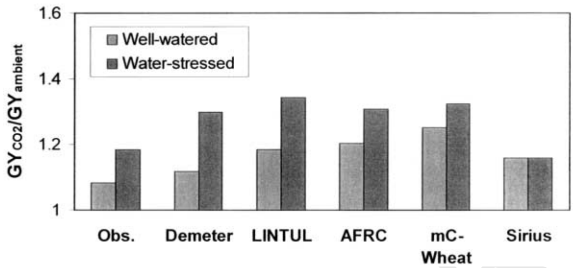
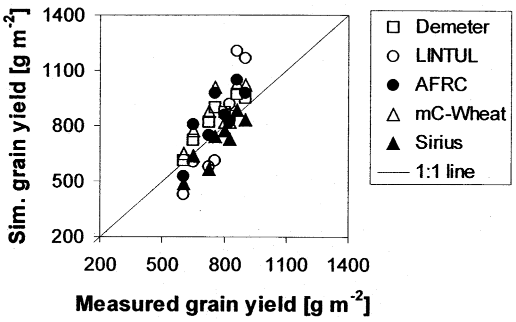


Fig. 3. Comparison of simulated relative CO_2 effects on grain yield (GY) from different crop models with observations (Obs.) from free-air CO_2 enrichment experiments in Maricopa, Arizona in 1992/93 and 1993/94. Relative effects were calculated from the data presented in Fig. 4.

logical development, pre-scheduled measurement campaigns were such that Zadoks growth stages had to be estimated in the field often in between key growth stages, and then interpolated to date phenological events. Additionally, most wheat models predicted exact grain maturity, while data collected in the field included mass decrease after maturity, due to physical and respiratory losses, prior to actual harvest. Secondly, differences in model structure and linkages among sub-components made it inherently difficult to thoroughly compare overall model performance. Thirdly, the existence of only a few field experiments available to date for evaluation studies and the use of a narrow range of elevated CO_2 concentrations (~ 550 μl/l), may have contributed to hide larger model differences than observed, ones that could become more apparent at elevated CO_2 concentrations and for a wider range of conditions. A few recent efforts have indeed attempted to extend the range of model development using observed datasets, elevated CO_2 and/or climate change scenarios (e.g., Paustian et al., 2000; Reilly et al., 2001; Ewert et al. 2002).

6. Recommendations and conclusions

Based on the reviewed material, we elaborate a set of recommendations of importance to the use of crop models for studies that involve elevated



	RMSD (g m^{-2})				
	Measured	Demeter	LINTUL	AFRC	mC-Wheat
Demeter	82	-	-	-	-
LINTUL	185	191	-	-	-
AFRC	123	82	186	-	-
mC-Wheat	135	62	219	69	-
Sirius	84	141	187	151	188

Fig. 4. Comparison of simulated grain yield from different crop models with observed data from free-air CO_2 enrichment experiments in Maricopa, Arizona in 1992/93 and 1993/94. Simulations were taken from Tubiello et al. (1999), Grossman-Clarke et al. (2001), Ewert et al. (2002). Data refer to two [CO_2] (ambient and 1.5 × ambient CO_2) and two drought (well-watered and water-stressed) treatments. Models simulate [CO_2] effects on assimilation with different detail in the order of DEMETER and LINTULCC2 (most detailed), AFRC-WHEAT2, mC-Wheat and Sirius. Simulations were compared using root mean squared deviated (RMSD) between observed and simulated and between simulated data. Note that RMSDs are often larger between models than between simulated and observed data.

CO_2 and/or climate change conditions. Firstly, those models that have been used extensively in climate change assessment studies but have not yet been sufficiently tested using the available field experimental data need to undergo renewed evaluation. Secondly, successful model testing under a restricted set of CO_2, climate and management conditions does not warrant unlimited ability to perform equally well under an extended range of climate change and management conditions. To this end, model evaluation studies should also include, in addition to model testing against standard sets of experimental data, sensitivity simulations with a range of climate scenarios, management, and CO_2 concentrations. Thirdly, current field experiments on crop responses to CO_2 should also address the effects of factors that are known to determine farm-level yield variability. Such experiments will provide better understanding of effects of soil quality, competition with weeds and pests and diseases on crop responses to CO_2 and will improve our ability to assess CO_2 impacts at larger scales.

However, not only spatial but temporal issues of model predictions require attention, such as reproducing inter-annual variability of yield over historical periods. For instance, point-level simulations from process-oriented crop models show larger inter-annual yield variations than evident from reported regional production data. Aside from key socio-economic issues that shape year-to-year agronomic decisions, factors like geographic heterogeneity, pests and diseases, and even mathematical methods used to calculate yield averages affect inter-annual yield variations in ways that models presently do not account for. Clearly, crop models need to be evaluated with multi-year datasets and the implication of models performances for predicting CO_2 effects under climate change needs to be assessed. In this respect, developments in agro-technology that have been a major determinant of changes in crop yields in the last century (e.g., Amthor, 1998), but have largely been ignored in current crop modeling, require particular attention.

Previous review studies have focused on describing specific aspects, mostly photosynthesis, important to modeling the effects of elevated CO_2 on crops. This review focused on process-level agronomic models capable of predicting harvest yield as a function of environmental and management factors. Our conclusions can be summarized as follows:

i) Increase model testing under field conditions and elevated CO_2;
ii) Increase model inter-comparison, including sensitivity studies employing ranges of CO_2 concentration and climate change scenarios;
iii) Focus on issues of temporal and spatial scale;
iv) Clearly indicate limits of crop models used in climate change assessments.

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