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REVIEW PAPER

Improving the use of modelling for projections of climate change impacts on crops and pastures

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Abstract

Projections of climate change impacts on global food supply are largely based on crop and pasture modelling. The consistency of these models with experimental data and their ability to simulate the effects of elevated CO_2 and of increased climate variability has been debated. The effects of high temperatures, of increased climate variability and of several limiting factors which interact with elevated CO_2 such as soil nutrients, pests and weeds are neither fully understood nor well implemented in leading models. Targeted model developments will be required based on experimental data concerning: (i) the role of extreme climatic events, (ii) the interactions between abiotic factors and elevated CO_2, (iii) the genetic variability in plant CO_2 and temperature responses, (iv) the interactions with biotic factors, and (v) the effects on harvest quality. To help make better use of the available knowledge, it is envisioned that future crop and pasture modelling studies will need to use a risk assessment approach by combining an ensemble of greenhouse gas emission (or stabilization) scenarios, of regional climate models and of crop and pasture models, as well as an ensemble of adaptation options concerning both management practices and species/varieties.

Key words: Agriculture, ecophysiology, FACE, global change, livestock.

Introduction

For many key parameters, the climate system is already moving beyond the patterns of natural variability within which our society and economy have developed and thrived. There is a significant risk that many of the trends will accelerate, leading to extreme climatic events and to an increasing risk of abrupt or irreversible climatic shifts (IPCC, 2007*a*; University of Copenhagen, 2009).

Global climate change can be expected to threaten food supply, for example, through changing patterns of rainfall, increasing incidence of extreme weather, and the changing distribution of diseases and their vectors (Tubiello *et al.*, 2007). Increased incidences of extreme climate events could lead to greater variability of production, increased price volatility and changes in trade flows (Lobell *et al.*, 2008). A consensus has emerged that developing countries are more vulnerable to climate change than developed countries because of the predominance of agriculture in their economies, the scarcity of capital for adaptation measures, their warmer baseline climates, and their heightened exposure to extreme events (Parry *et al.*, 2001). Thus, climate change may have particularly serious consequences in the developing world (Nelson *et al.*, 2009) where about one billion people are currently undernourished (FAO, 2009).

Even in temperate regions, there are some early warning signs of climate change impacts on the yields of some major crops like wheat. A slower increase in grain yields compared to past decades has been reported in a range of countries, including Europe and India. For example, since 1990, winter wheat yields have been increasing at a significantly slower rate in France than over previous decades (Gate, 2009) and this change has foremost been attributed to an increased variability in climate (Gate 2007, 2009). By contrast, circumstantial evidence for climate-induced increasing grain yield of winter wheat (*Triticum aestivum* L.)

from 1981 to 2005 at two locations in China has been challenged by a recent re-analysis (White, 2009).

The Intergovernmental Panel on Climate Change report (IPCC, 2007*b*) has reviewed model projections of climate change impacts at the plot level. Moderate warming (i.e. in the first half of this century) may benefit crop and pasture yields in temperate regions, while it would decrease yields in semiarid and tropical regions. Modelling studies indicate small beneficial effects on crop yields in temperate regions corresponding to local mean temperature increases of 1–3 °C and associated CO_2 increases and rainfall changes. By contrast, in tropical regions, models indicate negative yield impacts for the major cereals even with moderate temperature increases (1–2 °C). Further warming has negative impacts in all regions.

These conclusions are based on modelling studies which most often do not account adequately for the impacts of an increased climatic variability (Tubiello *et al.*, 2007; Orlandini *et al.*, 2008). The projected rise in climatic variability will tend to be associated with more extreme weather patterns (IPCC, 2007*a*), leading to a potential for negative surprises that has not been fully explored, thus reducing the level of confidence in regional and global projections. Moreover, several key interactions are currently poorly described by crop and pasture models including: (i) non-linearity and threshold effects in response to extreme weather events; (ii) modification of weed pest and disease incidence; (iii) field response of crops to elevated CO_2 concentration; and (iv) interactions of climate and management variables with elevated CO_2 (Tubiello *et al.*, 2007).

It is thus imperative to continue to advance the fundamental knowledge of crop and pasture species responses to climate change, reduce uncertainties in impact projections, and assess future risks (IPCC, 2007*a*). Stakeholders have increasing demands concerning adaptation to climate change of agricultural management (Howden *et al.*, 2007). Adaptation requires detailed understanding of the likely impacts of climate change in small agricultural regions, which further increases the need for modelling.

Some of the key sources of uncertainties for future crop and pasture productivity under climate change are reviewed here; how they could be better reflected in model results, how they could be reduced in the future, and the extent to which conclusions from these models can already be used to provide outlook and guidance for adapting agriculture to climate change are discussed.

An uncertainty cascade in future climate change drivers

Socioeconomic scenarios (SRES) projecting greenhouse gas emissions in CO_2 equivalents are the backbones of impact studies, providing the basis for assessing the impact of climate change on human activities, including agriculture (Parry *et al.*, 2005). Scenarios are neither predictions nor forecasts in a traditional sense; rather they are images of the future, or alternative futures that are meant to assist in climate change analysis (Nakicenovic, 2000). As an alternative, mitigation scenarios can be used with atmospheric CO_2 concentrations stabilized by 2100 (Arnell *et al.*, 2002; Tubiello and Fischer, 2007).

Global and regional climate models

The best available tool for predicting climatic change from greenhouse gas (GHG) emission scenarios is the atmosphere–ocean general circulation model (AOGCM) (Giorgi and Mearns , 2002). The atmospheric component of an AOGCM (the atmospheric GCM) is coupled to a land-surface scheme and used to predict changes in land-based state variables (e.g. soil moisture). GCMs compute future climates under anthropogenic forcing (i.e. present and projected future emissions of GHGs (IPCC, 2001*a*). Their use in impact assessment studies of climate change is widespread (IPCC, 2001*b*; Reilly *et al.*, 2001). These models provide internally coherent climate dynamics by solving globally all climate-relevant physical equations. Yet it is recognized that GCM projections present significant uncertainties, in part through issues of scale resolution, and in part through imperfect understanding of key climate dynamics (IPCC, 2001*a*). Even among GCMs with similar temperature-change simulations, predictions of regional precipitation responses may vary significantly, in part because of the intrinsic chaotic nature of climate and in part because of differences in model approach to resolving local to regional atmospheric dynamics.

For example, GCM predictions of the magnitude and location of soil moisture changes often disagree and are often difficult to compare with one another, since the land-surface schemes employed by the various AOGCMs differ considerably, and their accuracy is questionable (Cornwell and Harvey, 2007). This presents a problem when assessing the impacts of climatic change on crops. For example, many studies project impacts using a single GCM (IPCC, 2007*a*), thus neglecting a major source of uncertainty. Moreover, the spatial resolution of most GCMs is low, which much reduces the realism of local projections of climate change, especially in areas with complex terrain.

Among the methods used to provide insight on climate description at regional scales, regional climate models forced by GCMs have become a widely used tool for regional climate studies (Giorgi and Mearns, 1999; IPCC, 2007*a*). Since new information is added to the regional climate models by modelling GCM-subgrid processes, the RCMs' fields may have different statistical properties that those of the original GCM (Mearns *et al.*, 1999). This is especially apparent with highly anisotropic fields such as precipitation (Machenhauer *et al.*, 1998).

Downscaling methods

While working with scenarios, difficulties have often been encountered in relation to the disparity of scales between global and regional climate models (RCM) on the one hand and the local application of models on the other hand. For this reason, GCM or RCM results are usually downscaled with the help of high resolution atmospheric models (dynamical downscaling) and/or statistical models and stochastic weather generators (statistical downscaling). Dynamical downscaling is most demanding in terms of computational resources. Statistical downscaling has the advantage of being computationally fast, but tends to introduce additional uncertainties into the scenarios (Calanca *et al.*, 2008).

The uncertainty originating from the choice of global and regional model formulation in climate-change downscaling experiments has been analysed (Beniston *et al.*, 2007), by conducting a co-ordinated set of climate modelling experiments. While there are a number of contrasted approaches for statistical downscaling (e.g. anomalies, variable corrections, Déqué *et al.*, 2005; statistical disaggregation, Boé *et al.*, 2006), they all require accurate climatic data and long time series and are therefore most applicable in regions with a high density of weather stations. Moreover, it should be noted that the validation of a statistical downscaling algorithm for present day climate conditions does not necessarily imply the validity of its climate change projections, the plausibility of which needs to be compared with direct GCM model outputs (Boé *et al.*, 2006). The task of deriving better estimates of changing variability and extreme events is thus still intrinsically difficult (IPCC, 2007*a*) and this limits the confidence in climate model projections.

Finally, it should be noted that a number of past impact studies with a focus on agriculture have taken arbitrary ad hoc incremental annual, seasonal or monthly anomalies for the long-term mean temperature and precipitation. Therefore, part of the literature does not reflect the likely range of climate change impacts but only the effects of a certain degree of temperature and/or precipitation change.

In order to assess uncertainties arising from future climatic and atmospheric drivers on crop and pasture productivity better, an ensemble of regional climate models carefully downscaled to reflect better the local distribution of key climatic variables like rainfall is needed (Challinor *et al.*, 2007, 2009). This approach could be generalized by comparing several crop and pasture models for a range of greenhouse gas emission scenarios and/or of mitigation scenarios in order to quantify the probability of avoided impacts brought by greenhouse gas mitigation.

Statistical and mechanistic models of crop and pasture impacts

Assessment studies of the impacts of climate change on agriculture at farm to regional levels need to analyse complex interactions of climate, agro-ecosystem function, and human management. To this end, researchers typically link climate predictions to crop models and land management decision tools (Tubiello *et al.*, 2002). For instance, Decision Support System for Agrotechnology Transfer (DSSAT) (Rosenzweig *et al.*, 1995, Tsuji *et al.*, 1995), Erosion Product Impact Calculator (EPIC) (Williams, 1995), Terrestrial Ecosystem Model (TEM) (Felzer *et al.*, 2004), and the AEZ model (Tubiello and Fischer, 2007) have been used at the global scale. Simulation models often provide the only available tool to investigate complex interactions and feedbacks of many variables.

Process-based models

Most studies have made use of process-based crop and pasture models to evaluate the impacts of climate change scenarios either at a local or at the global scale (Rosenzweig and Parry, 1994; IFPRI, 2009) for crop and pasture species. However, substantial time, data, and expertise are needed to calibrate these models for particular locations (Wallach *et al.*, 2006) and the lack of process-based models for many minor crops, restricts the scope of this approach. Nevertheless, mechanistic models have recently been expanded in the context of climate change studies to cover an extended range of crop species, including potato (Wolf and Van Oijen, 2003), sugar beet (Launay *et al.*, 2009), cassava, sorghum, millet (Liu *et al.*, 2008), and quinoa (Lebonvallet *et al.*, 2009).

Generic models

An intermediate approach uses detailed agronomic-based knowledge to simulate availability and use of land resources, farm-level management options, and crop production potentials as a function of climate (AEZ, Fischer *et al.*, 2002, 2005). It computes potentially attainable, rather than actual, crop yields. Thus, wherever the gap between actual and potential yields is large, such as in many developing countries, there is uncertainty in translating the calculated impacts of climate change into changes in actual crop productivity. In those regions with large yield gaps, this approach may predict larger positive impacts of climate change on crop production than is actually possible in real fields (Tubiello and Fischer, 2007). It should be noted that results from such approaches, as well as of some of the generic crop modelling (e.g. CROPSYST; Stöckle *et al.*, 2001), can be used to compare the future suitability of land for a range of crops, which allows mapping of the likely future climatic envelopes of the main cropping systems.

Statistical models

Statistical models of crop responses to climate change, based on historical datasets of crop and climate variables have recently been used (Lobell *et al.*, 2008; Paeth *et al.*, 2008; Schlenker and Roberts, 2009) to address climatic change impacts on food security in developing countries. This approach can be used for all crops and all regions, but has several deficiencies (as acknowledged by the authors): (i) errors in statistical data of production and in gridded climate data, and (ii) in some instances, low weight of climatic factors for the between year variation in crop yields. Moreover, statistical models cannot be extrapolated without further assumptions to predict production impacts for future conditions (e.g. higher temperature than any historical year, elevated CO_2 concentration).

Modelling the incidence of extreme climatic events

Increased frequency of heat stress, droughts, and floods (IPCC, 2007*a*; Beniston *et al.*, 2007) negatively affect crop yields and livestock beyond the impacts of mean climate change, with impacts that are larger, and occurring earlier, than predicted using changes in mean variables alone (IPCC, 2007*b*).

High temperatures

In Europe, during the summer of 2003, temperatures were up to 6 °C above long-term means, and precipitation deficits up to 300 mm. Crop and pasture yields were reduced by 20–36% in regions affected, leading to uninsured economic losses for the agriculture sector in the European Union which were estimated at 36 billion euros (IPCC, 2007*b*). It is highly likely (more than 90% chance) that growing season temperatures by the end of the 21st century will exceed even the most extreme seasonal temperatures recorded from 1900 to 2006 for most of the tropics and subtropics (Battisti and Naylor, 2009). High seasonally averaged temperatures will challenge food production in the future, unless major adaptations are made. Indeed, above-optimal temperatures have been reported to induce severe damages to corn and soybean crops in the US, leading to large potential negative impacts in the future (Schlenker and Roberts, 2009).

Yield damaging climate thresholds spanning periods of just a few days for cereals and fruit trees include absolute temperature levels linked to particular developmental stages that condition the formation of reproductive organs, such as seeds and fruits (Wheeler *et al.*, 2000; Wollenberg *et al.*, 2003). Three research needs were identified by Wheeler *et al.* (2000) in order to provide a framework for predicting the impact of episodes of hot temperatures on the yields of crops: (i) reliable seasonal climate projections, (ii) robust predictions of crop development, and (iii) crop simulation models which are able to quantify the effects of brief episodes of hot temperatures on seed yield. Crop simulation models often do not, at present, capture the effects of brief hot temperature episodes on the number of reproductive structures (Wheeler *et al.*, 2000). Inclusion of detailed phenology and above-optimal temperature effects on crops is therefore required to address this problem (Porter and Semenov, 2005).

Variability in temperature can also affect yield quality. Heat damage effects on wheat grains quality caused by episodes of hot temperatures are reasonably well documented (Wheeler *et al.*, 2000), but we are not aware of any crop model that explicitly simulates such effects, despite the increasingly large impacts of these damages on grain price and on bread making. Moreover, information on the effects of variability in temperature on the yield and quality of other annual and perennial crops is sparse, which prevents the development of models.

Drought

During the 20th century a major drought index has increased over a number of regions, including Southern Europe and most of Africa (Bates *et al.*, 2008). Further drying of a large part of the subtropics is likely by the end of this century (IPCC, 2007*a*) as a result of elevated greenhouse gas concentrations. Amplification of the hydrological cycle as a consequence of global warming is forecast to lead to more extreme intra-annual precipitation regimes characterized by larger rainfall events and longer intervals between events (IPCC, 2007*a*). More extreme rainfall regimes are expected to increase the duration and severity of soil water stress in mesic ecosystems as intervals between rainfall events increase (Knapp *et al.*, 2008). Drought in particular plays an important role in pasture dynamics and can lead to long-term degradation (Briske *et al.*, 2005).

Plant strategies to cope with drought normally involve a mixture of stress avoidance and tolerance 'strategies' that vary with species and with genotype. For instance, to survive severe droughts, most perennial pasture species exhibit a combination of responses. An increased senescence of mature shoots leads to a reduction in leaf transpiration surface. An increase in rooting depth and water uptake at low soil water potential (Durand *et al.*, 2007) contributes to a delay in dehydration. The accumulation of carbohydrates and dehydrins in basal tissues, including buds and meristems that ensure perenniality, allows tolerating dehydration in the surviving organs (Volaire, 2002). The genotypes surviving best in the most arid conditions exhibit responses associated with summer dormancy (Norton *et al.*, 2008, 2009). The combination of these plant strategies confers very contrasting inter- and intra-specific adaptations to drought. An example of threshold effect is the abrupt cessation of the ascending sap flow, which occurs as a result of xylem cavitation. With herbaceous plants this process has been evidenced in maize, rice, sunflower, and sugar-cane (Tyree *et al.*, 1986; Cochard *et al.*, 2002).

Moreover, drought has a number of interactive effects on plant–soil processes. For example, it sharply reduces microbial biomass in soils, leading to the transient accumulation of soluble forms of N and to high N uptake when rainfall resumes (Lemaire and Denoix, 1987). Longer-term effects will be affected by the increase in the atmospheric CO_2 concentration (Loiseau and Soussana, 2000; Pinay *et al.*, 2007) and may include shifts in functional microbial types (e.g. nitrifiers, denitrifiers, heterotrophs) (Barnard *et al.*, 2006), increased nutrients losses and, hence, changes in biogeochemical cycles and carbon sequestration.

Furthermore, a number of potential feedbacks that may increase water stress and vulnerability have not yet been simulated at the scale of a river basin. For example, a decline in vegetation cover and soil organic matter as a result of warming and drought would increase run-off and reduce soil water storage, thereby accentuating water-related extremes. Contrasted conclusions may be obtained with crop models depending on the assumptions made, or not, on changes in capillary rise and in groundwater level which may provide a substantial part of evapotranspiration, especially during low precipitation periods. Scaling up individual processes such as run-off, infiltration, soil water redistribution, is uneasy since the boundaries of the system are at a higher scale than the field (Schulze, 2000). Process-oriented ecosystem and crop simulation models do not adequately represent the rise in plant mortality that may occur as a result of climatic variables exceeding thresholds and the resulting complex plant–soil interactions described above.

The ability of current crop and pasture models to simulate future summer heat and drought events could be tested by using severe heat and drought pulses like the summer 2003 event in Europe as a benchmark. Further benchmarks could be obtained through the development of crop and ecosystem manipulation experiments imposing extreme climatic events of the same magnitude as that predicted by downscaled climate scenarios.

Modelling interactions between elevated CO_2 and abiotic factors

Crop and pasture models used in impact assessment studies simulate the effects of elevated CO_2 on growth and yield with a variety of methods (reviewed by Tubiello and Ewert, 2002), ranging from simple multipliers of final biomass and yield or variable multipliers of daily growth, based on, for example, water and nutrient stress, phenological stage, leaf area feedback, etc. Only a few models have mechanistic equations of leaf photosynthesis scaled to canopy. For instance, the AEZ-simulated crop response to elevated CO_2 is modelled rather simply, as a multiplier of the harvest yield obtained under current CO_2 levels (Tubiello and Fischer, 2007). In the AEZ assessment, these factors are applied to land units without production limitations. Where suitability is limited, the multipliers are reduced proportionally to the magnitude of the limitations. While this type of approach is generic and robust it does not necessarily cover the main interactions between elevated CO_2 and environmental drivers which have been demonstrated experimentally.

Modelled versus observed effects of elevated CO_2

Some concerns have also been expressed (Long *et al.*, 2006; Ainsworth *et al.*, 2008*b*) that most simulation models would overestimate the CO_2 effect compared with Free Air Carbon dioxide Enrichment (FACE) experiments.

Tubiello *et al.* (2007) reported that some key models used in climate change impact assessments have not been evaluated against FACE data, but where this has been carried out, the models reproduce FACE results well. This statement was based on a previous assessment of five widely used crop models with wheat grain yield data from the Maricopa FACE experiment (Tubiello and Ewert, 2002). However, this conclusion was challenged by Long *et al.* (2006) and Ainsworth *et al.* (2008*b*) who showed experimental mean response ratios of 1.08 and 1.18 under well-watered and water-stress conditions, respectively, whereas the average model outputs estimated response ratios of 1.18 and 1.28, respectively. Thus, wheat crop models which were compared to the Maricopa FACE data would overestimate the CO_2 fertilization effect both under well-watered conditions and under water-stress conditions (Ainsworth *et al.*, 2008*a*).

There is, however, no consensus yet in the literature on the experimental reference to be used for model calibration. By scaling the relative yields to a ratio of 700 to 370 μmol mol^{-1} CO_2, Ziska and Bunce (2007) have shown that relative yield stimulations in response to future CO_2 concentrations obtained using a number of enclosure methodologies are quantitatively consistent with FACE results for three crops of global importance: rice, soybean, and wheat. By contrast, a direct approach was taken by Ainsworth *et al.* (2008*a*) who limited the comparison of FACE experiments and chamber studies to those with similar ambient [CO_2] and similar elevated [CO_2]. It should be stressed, however, that ambient CO_2 concentration itself has changed appreciably during the experimental era (e.g. from 320 in early enhancement studies to a current concentration of 380 μmol mol^{-1}). This could cause a higher response ratio in earlier studies conducted with enclosures than in more recent studies with FACE technology.

In any case, the best test of model parameterization and model design is validation of model output against observed experimental data comparisons. Therefore, a greater number of comparisons with elevated CO_2 and warming experiments would be valuable since the magnitude of the CO_2 effect may vary among sites, according to crop types, as well as to environment and management drivers.

Interactions between elevated CO_2 and temperature

As an increase in temperature enhances photorespiration in C_3-species (Long, 1991), the positive effects of atmospheric CO_2 enrichment on photosynthetic productivity are usually greater when temperature rises close to optimal values. However, the CO_2 effect for seed yield would be lower at above-optimal temperatures (Matsui *et al.*, 1997; Batts *et al.*, 1998; Amthor, 2001). For rice, increasing CO_2 and temperature may, in fact, negate any yield enhancement related to increasing CO_2 (Ziska *et al.*, 1996; Moya *et al.*, 1998) as a result, in part, of reductions in transpirational cooling, higher canopy temperatures and increased pollen sterility (reviewed by Ziska and Bunce, 2007). This decline in the magnitude of the CO_2 effect at high temperatures is not necessarily well captured by current simulation crop models and would require more research, since above-optimal temperatures may become prevalent by the end of the century for a number of crops and of regions (Lobell *et al.*, 2008).

Interactions between elevated CO_2 and nutrients

Over a number of studies it has been found that plants grown in conditions of high nutrient supply respond more strongly to elevated atmospheric CO_2 concentrations than nutrient-stressed plants (Poorter, 1998; Schneider *et al.*, 2004; Soussana and Lüscher, 2007). FACE experiments confirm that high soil N contents increase the relative response to elevated atmospheric CO_2 concentrations (Nowak *et al.*, 2004). With a temperate pasture grass, in the Swiss FACE experiment, the response in above-ground dry matter (DM) yield to elevated atmospheric CO_2 concentrations increased from being not significant to a significant positive proportional response of 0.17 when the rate of application of N fertilizer was increased (Schneider *et al.*, 2004). The CO_2-induced N limitation was alleviated in the high N-fertilizer treatment only by supplying a significant external input of N. These results confirm that N is a major limiting factor in the response of grasslands to elevated atmospheric CO_2 concentrations.

As a result of these interactions with soil processes, experiments which impose sudden changes in temperature or atmospheric CO_2 concentrations, and which last only a few years are unlikely to predict the magnitude of the long-term responses in crop productivity, soil nutrients (Thornley and Cannell, 2000) and C sequestration. This may imply that the actual impact of elevated atmospheric CO_2 concentrations on yields in farmers' fields could be less than earlier estimates which did not take into account limitations in availability of nutrients and plant–soil interactions.

When other nutrients are not strongly limiting, a decline in N availability may be prevented by an increase in biological N_2-fixation under elevated atmospheric CO_2 concentrations (Gifford, 1994). Indeed, in fertile grasslands, legumes benefit more from elevated atmospheric CO_2 concentrations than non-fixing species (Hebeisen *et al.*, 1997; Lüscher *et al.*, 1998) resulting in significant increases in symbiotic N_2 fixation (Soussana and Hartwig, 1996; Zanetti *et al.*, 1997). Nevertheless, other nutrients, such as phosphorus, may act as the main limiting factor restricting growth and responses in yield in legumes to atmospheric CO_2 concentrations. This has been demonstrated both in calcareous grasslands (Stöcklin *et al.*, 1998) and under controlled environmental conditions (Almeida *et al.*, 2000).

Such experimental results underline the need to model nutrients cycling under climate change and not just plant growth. This can be best achieved by coupling crop/pasture models with soil models (Thornley and Cannell, 2000). However, simpler approaches have been used in some models like AEZ where multipliers of yield are reduced proportionally to the magnitude of the limitations. This conclusion is extended by the model to interactions between CO_2, nitrogen, and other major nutrients (P, K, and S) which are widespread limiting factors especially in tropical crops and pastures.

Interactions between elevated CO_2 and water

Most crop and pasture models (Tubiello and Ewert, 2002) include an interaction between elevated atmospheric CO_2 and water availability. An increased productivity from increased water-use efficiency is the major response to elevated atmospheric CO_2 concentrations in C_3- or C_4-crops that are exposed frequently to water stress (Casella and Soussana, 1997; Drake *et al.*, 1997; Aranjuelo *et al.*, 2005). Moreover, elevated atmospheric CO_2 concentrations can reduce depletion in soil moisture content (Morgan *et al.*, 2004). These results support a general view that elevated atmospheric CO_2 concentration reduces the sensitivity to low precipitation in grassland ecosystems (Volk *et al.*, 2000; Morgan *et al.*, 2004). However, it is still unclear whether, or not, elevated CO_2 can reduce mortality and increase recovery during severe water stress events and further research will be needed in order to model the impacts of such episodes on annual crops and perennial vegetation better.

Interactions between elevated CO_2 and atmospheric O_3 concentration

Another uncertainty is the role of air pollution and especially of increased ozone exposure. IPCC emission scenarios for many cropland regions project elevated mean ozone levels in surface air for 2050 and beyond. At the same time, crop sensitivity may decline in areas where warming is accompanied by drying (e.g. in southern and central Europe). Besides uncertainties in climate projections, parameters in models for ozone risk assessment are also uncertain and model improvements are necessary to define specific targets for crop improvements to identify regions most at risk from ozone in a future climate and to set robust effect-based ozone standards (Fuhrer *et al.*, 2009).

Semi-empirical versus mechanistic models of photosynthesis

The complexity of crop ecophysiology under elevated CO_2, the large range of interactions with abiotic factors, and the possibility for substantial between (Kimball *et al.*, 2002; Nowak *et al.*, 2004) and within (Ziska and George, 2004) species variation in plant responses clearly challenge crop and pasture modellers.

Although, semi-empirical models may seem robust and easily applicable, they tend to oversimplify interactions between elevated CO_2 and abiotic factors which may create concerns for their accuracy. On the other hand, mechanistic models based on physical and biochemical laws are theoretically valid for any combination of soil, climate and crop conditions but are difficult to parameterize. For instance, responses of leaf photosynthesis to variations of light, temperature, and CO_2 concentration have been successfully represented by the biochemical model of C_3 photosynthesis by Farquhar *et al.* (1980), which has pioneered the mechanistic representation of the dark (Wc) and light (Wj) biochemical processes. It assumes that the carboxylation/oxygenation of RuBP by the enzyme Rubisco, and the regeneration of RuBP by the electron transport chain are the main limitations of photosynthesis. Possibly because of the large effort required for parameterizing such detailed photosynthetic models, we are not aware of any crop model being currently used for climate change impact simulation that incorporates the equations for leaf photosynthesis by Farquhar *et al.* (1980) and upscales these equations from leaf to canopy level. Nevertheless, some comparisons between simplified photosynthetic equations with Farquhar's equations have sometimes been performed successfully (e.g. for the CROPGRO model; Alagarswamy *et al.*, 2006), but for a limited range of environmental conditions. Incorporating detailed ecophysiological knowledge in widely used crop models would help in reducing the probability for surprises caused by possible failures of semi-empirical models of photosynthesis outside the environmental domain for which they were calibrated.

Modelling biotic interactions under elevated CO_2 and climate change

Growth-reducing factors reduce or hamper crop growth and comprise biotic factors such as weeds, pests, and diseases (Van Ittersum *et al.*, 2003). Biotic yield-reducing factors such as insects, pathogens, and weeds have long been ignored in climate change impact simulations (Coakley *et al.*, 1999).

Pests and diseases

CO_2–temperature interactions are recognized as a key factor determining plant damage from pests in future decades; CO_2–precipitation interactions will also be important (Stacey and Fellows, 2002; Zvereva and Kozlov, 2006). Most studies continue to investigate pest damage as a separate function of either CO_2 (Agrell *et al.*, 2004; Chen *et al.*, 2005) or climate, mostly temperature (Bale *et al.*, 2002; Salinari *et al.*, 2006). Importantly, increased climate extremes may promote plant disease and pest outbreaks (Alig *et al.*, 2002; Gan *et al.*, 2004) and such interactions are not yet included in modelling approaches.

The development of linked disease–crop models is still an important objective within the overall goal of developing a predictive capability for agricultural impact assessment (IPCC, 2007*a*). In recent years only, models of plant disease have been developed to incorporate more sophisticated climate predictions. Several approaches have been used for modelling the effect of climate change on disease. Climate matching is applied by quantifying the climatic features of locations so that the success of an organism in a reference climate can be used to predict the success of that organism in other locations with similar climates. Empirical models, such as regression models with climatic variables as predictors and epidemic parameters as response variables, can be used to predict the success of organisms across the range of conditions studied (Garrett *et al.*, 2006). Simulation models are based on theoretical relationships and can predict outcomes under a range of scenarios. However, there are continuing problems with the application of models for predicting climate change effects on disease, including the lack of data on the geographic distribution of disease, non-linear relationships and thresholds in the relationship between climatic variables and epidemiological responses, and the potential for adaptation by plants and pathogens that is often ignored in models (Scherm, 2004).

Weeds

Increases in high temperatures (above 32 °C) have been reported to enhance weed competitiveness in soybean crops (Tungate *et al.*, 2007). Recent research has also highlighted the key role of competition between C_3 crop and C_4 weed species under different climate and CO_2 concentrations. Ziska and Bunce (2006) reviewed the role of weeds under elevated CO_2, showing only a handful of weed/crop competition studies with respect to soybean (Ziska, 2000; Ziska and Goins, 2006), one study with respect to rice (Alberto *et al.*, 1996) and no studies with respect to wheat, where the effects of projected changes in CO_2/climate on seed yield have been quantified. To our knowledge, there has been no research specifically to examine the potential for agricultural weeds to adapt rapidly to climate change and elevated CO_2. Phenological changes in agricultural weeds could significantly alter crop–weed interactions and recent work by Franks and Weis (2007) has shown the potential for rapid life-history evolution in response to climate change in annual weedy plants. Demo-genetic models that incorporate demographic and environmental stochasticity with quantitative genetics may have utility for predicting population level responses of weed species under changing management and climatic conditions (Neve *et al.*, 2010).

Multi-species grasslands and intercropping

Mechanistic bases for establishing the differential responses of plant species to elevated CO_2 have been thought of. However, the relative growth responses to elevated atmospheric CO_2 concentrations obtained for isolated plants cannot be used to predict the response in multi-species mixtures although the CO_2 response of monocultures may be a better predictor (Poorter and Navas, 2003). Studies of between-species competition among three grasses, showed that grasses that capture relatively more light per unit leaf area in mixtures than their competitors become increasingly dominant under elevated atmospheric CO_2 concentrations (Teyssonneyre *et al.*, 2002*b*). Moreover, a high N-use efficiency can confer a competitive advantage under elevated atmospheric CO_2 concentrations to mixed grasses (Soussana *et al.*, 2005). Such experiments suggest that the inclusion in models of mechanisms of resource capture and use among plant functional types may help simulate plant species dynamics in multi-species grasslands under elevated CO_2 (Soussana and Oliveira Machado, 2000; Lazzarotto *et al.*, 2009) and climate change. In the same way, intercrop models (Corre-Hellou *et al.*, 2009) could be applied to future climatic conditions.

Modelling adaptation to climate change

Adaptation to climate change will require changes in genotype (G) and management (M) to match the climate-induced changes in environment (E). For rainfed crops in dry areas, evidence shows that variation due to E far outweighs the variation of grain yield that is due to M or

G, or the interactions between these factors, and between these factors and E (Anderson, 2010). As shown by a review of modelling studies, there is a tendency for most of the benefits of adapting the existing systems to be gained under moderate warming (<2 °C) then to level off with increasing temperature changes (Howden *et al.*, 2007). In addition, the yield benefits tend to be greater under scenarios of increased than decreased rainfall, reflecting that there are many ways of more effectively using more abundant resources, whereas there are fewer and less-effective options for significantly ameliorating risks when conditions become more limiting (Howden *et al.*, 2007).

Most field-scale crop and pasture simulation models can test the effects of changes in farming practices, such as changes in planting and harvest dates, in the timing and amount of fertilizer and/or water supply. By contrast, there are only few examples of modelling studies (but see Challinor *et al.*, 2007), which have tried to alter varieties/species to those with more appropriate thermal time and vernalization requirements and/or with increased resistance to heat shock and drought to maintain crop productivity and quality consistent with the prevailing climate. In the same way, improving the effectiveness of pest, disease, and weed management practices through wider use of integrated pest and pathogen management, development, and use of varieties and species resistant to pests and diseases are effective adaptation measures (Howden *et al.*, 2007) which, however, have not yet been tested in the context of climate change modelling studies.

Climate change alters breeding targets. Increasing emphasis needs to be placed on the identification of the most CO_2-responsive genotypes (Ainsworth *et al.*, 2008*a*) and of drought- and salinity-tolerant genotypes (Tester and Langridge, 2010) in order to provide starting lines for breeding programmes. Modelling can be used to facilitate plant breeding by dissecting and integrating the role of traits in an altered climate (Hammer *et al.*, 2002).

Conclusions

There is no single approach to the complex task of modelling the impacts of climate change on agriculture and food security. In climate sciences, with the development of computer capacities, simpler models have not disappeared; on the contrary, a stronger emphasis has been given to the concept of a 'hierarchy of models' as the only way to provide a linkage between theoretical understanding and the complexity of realistic models (Held, 2005). In the same way, a hierarchy of models ranging from simple 'theoretical' models to complex models is useful for crop and pasture modelling, which will have a continuing central, heuristic role to support scientific investigation of climate change impacts on agriculture and to facilitate adaptative decision making by farmers and land managers.

To approach the vulnerability to climate change of crops and pastures better, we envision that future modelling studies will need to develop a risk assessment approach by combining ensembles of:

- downscaled regional climate models and GHG emissions (or stabilization) scenarios,
- improved crop models tested against available experimental evidence (e.g. in FACE studies) in a large range of climatic conditions (including extreme climatic events),
- adaptation options, including both changes in management practices and in varieties/species.

Moreover, uncertainties in projections will need to be better assessed, separating climate projection-related, crop model-related, and adaptation-related uncertainties. While such approaches would help make better use of the available knowledge in simulation studies, there is also a need to reduce epistemic uncertainties by further developing research to reduce some of the knowledge gaps in terms of agronomy, ecology, and ecophysiology which have been highlighted in this review. Compared with past studies, targeted model developments will be required based on experimental data designed to reduce uncertainties in areas such as: (i) the role of extreme climatic events, (ii) the interactions between abiotic factors and elevated CO_2, (iii) the genetic variability in CO_2 and temperature responses, (iv) the interactions with biotic factors, and (v) the effects on harvest quality.

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References

Agrell J, Anderson P, Oleszek W, Stochmal A, Agrell C. 2004. Combined effects of elevated CO_2 and herbivore damage on alfafa and cotton. *Journal of Chemical Ecology* **30,** 2309–2324.

Ainsworth EA, Beier C, Calfapietra C, *et al*. 2008*a*. Next generation of elevated [CO_2] experiments with crops: a critical investment for feeding the future world. *Plant, Cell and Environment* **31,** 1317–1324.

Ainsworth EA, Leakey ADB, Ort DR, Long SP. 2008*b*. FACE-ing the facts: inconsistencies and interdependence among field, chamber and modeling studies of elevated [CO_2] impacts on crop yield and food supply. *New Phytologist* **179,** 5–9.

Alagarswamy G, Boote KJ, Allen LH, Jones JW. 2006. Evaluating the CROPGRO–Soybean model ability to simulate photosynthesis response to carbon dioxide levels. *Agronomy Journal* **98,** 34–42.

Alberto AMP, Ziska LH, Cervancia CR, Manalo PR. 1996. The influence of increasing carbon dioxide and temperature on competitive interactions between a C_3 crop, rice (*Oryza sativa*) and a C_4 weed (*Echinochloa glabrescens*). *Australian Journal of Plant Physiology* **23,** 795–802.

Alig RJ, Adams DM, McCarl BA. 2002. Projecting impacts of global climate change on the US forest and agriculture sectors and carbon budgets. *Forest Ecology and Management* **169,** 3–14.

Almeida JPF, Hartwig UA, Frehner M, Nösberger J, Lüscher A. 2000. Evidence that P deficiency induces N feedback regulation of symbiotic N_2 fixation in white clover *Trifolium repens* L.). *Journal of Experimental Botany* **51,** 1289–1297.

Amthor JS. 2001. Effects of atmospheric CO_2 concentration on wheat yield: review of results from experiments using various approaches to control CO_2 concentration. *Field Crops Research* **73,** 1–34.

Anderson WK. 2010. Closing the gap between actual and potential yield of rainfed wheat. The impacts of environment, management and cultivar. *Field Crops Research* **116,** 14–22.

Aranjuelo I, Irigoyen JJ, Perez P, Martinez-Carrasco R, Sanchez-Diaz M. 2005. Response of nodulated alfalfa to water supply, temperature and elevated CO_2: productivity and water relations. *Environmental and Experimental Botany* **55,** 130–141.

Arnell NW, Cannell MGR, Hulme M, Kovats RS, Mitchell JFB, Nicholls RJ, Parry ML, Livermores TJ, White A. 2002. The consequences of CO_2 stabilization for the impacts of climate change. *Climatic Change* **53,** 413–446.

Bale JS, Masters GJ, Hodkinson ID, *et al*. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8,** 1–16.

Barnard R, Barthes L, Leadley PW. 2006. Short-term uptake of ^{15}N by a grass and soil micro-organisms after long-term exposure to elevated CO_2. *Plant and Soil* **280,** 91–99.

Bates BC, Kundzewicz ZW, Wu S, Palutikof JP, eds. 2008. *Climate change and water. Technical Paper of the Intergovernmental Panel on Climate Change*. Geneva: IPCC Secretariat.

Battisti DS, Naylor RL. 2009. Historical warnings of future food insecurity with unprecedented seasonal heat. *Science* **323,** 240–244.

Batts GR, Ellis RH, Morison JIL, Nkemka PN, Gregory PJ, Hadley P. 1998. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO_2 and temperature in field studies using temperature gradient tunnels. *Journal of Agricultural Science* **130,** 17–27.

Beniston M, Stephenson DB, Christensen OB, *et al*. 2007. Future extreme events in European climate: an exploration of regional climate model projections. *Climatic Change* **81,** 71–95.

Boé J, Terray L, Habets F, Martin E. 2006. A simple statistical-dynamical downscaling scheme based on weather types and conditional resampling. *Journal of Geophysical Research* **111,** D23106doi:10.1029/2005JD006889.

Briske DD, Fuhlendor SD, Smeins EE. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management* **58,** 1–10.

Calanca P, Kaifez Bogataj L, Halenka T, Cloppet E, Mika J. 2008. Use of climate change scenarios in agrometeorological studies: past experiences and future needs. *COST Action 734: impact of climate change and variability on European Agriculture: survey of agrometeorological practices and applications in Europe regarding climate change impacts* 237–266.

Casella E, Soussana JF. 1997. Long-term effect of CO_2 enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany* **48,** 1309–1321.

Challinor AJ, Wheeler TR, Craufurd PQ, *et al*. 2007. Adaptation of crops to climate change through genotypic responses to mean and extreme temperatures. *Agriculture Ecosystems and Environment* **119,** 190–204.

Challinor AJ, Wheeler T, Hemming D, *et al*. 2009. Ensemble yield simulations: crop and climate uncertainties, sensitivity to temperature and genotypic adaptation to climate change. *Climate Research* **38,** 117–127.

Chen F, Wul G, Ge F, Parajulee MN, Shrestha RB. 2005. Effects of elevated CO_2 and transgenic Bt cotton on plant chemistry, performance, and feeding of an insect herbivore, the cotton bollworm. *Entomologia Experimentalis et Applicata* **115,** 341–347.

Coakley SM, Scherm H, Chakraborty S. 1999. Climate change and plant disease management. *Annual Review of Phytopathology* **37,** 399–426.

Cochard H, Lluis C, Le Roux X, Améglio T. 2002. Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. *Plant Physiology* **128,** 282–290.

Cornwell AR, Harvey ADD. 2007. Soil moisture: a residual problem underlying AGCMs. *Climatic Change* **84,** 313–336.

Corre-Hellou G, Faure M, Launay M, *et al*. 2009. Adaptation of the STICS intercrop model to simulate crop growth and N accumulation in pea-barley intercrops. *Field Crops Research* **113,** 72–81.

Déqué M, Jones RG, Wild M, Giorgi F, *et al*. 2005. Global high resolution versus Limited Area Model climate change projections over Europe: quantifying confidence level from PRUDENCE results. *Climate Dynamics* **25,** 653–670.

Drake BG, Gonzalez-Meler MA, Long SP. 1997. More efficient plants: a consequence of rising atmospheric CO_2? *Annual Review of Plant Physiology and Plant Molecular Biology* **48,** 607–637.

Durand JL, Bariac T, Ghesquiere M, Biron P, Richard P, Humphreys M, Zwierzykowski Z. 2007. Ranking of the depth of water extraction by individual grass plants, using natural 18O isotope abundance. *Environmental and Experimental Botany* **60,** 137–144.

Farquhar GD, Von Caemmer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149,** 78–90.

Felzer B, Kicklighter DW, Melillo JM, Wang C, Zhuang Q, Prinn RG. 2004. Effects of ozone on net primary production and carbon sequestration in the conterminous United States using a biogeochemistry model. *Tellus* **56B,** 230–248.

Fischer G, Tubiello FN, van Velthuizen H, Wiberg D. 2006: Climate change and wateruse in agriculture. *Technical Forecasting and Society Change* (in press).

Fischer G, Shah M, Tubiello FN, van Velthuizen H. 2005. Socio-economic and climate change impacts on agriculture: an integrated assessment, 1990–2080. *Philosophical Transactions of the Royal Society, London Series B* **360,** 2067–2083.

Food and Agricultural Organization of the United Nations (FAO). 2009. *The state of food insecurity in the world: economic crises: impacts and lessons learned*. Electronic Publishing Policy and Support Branch Communication Division, FAO.

Franks SJ, Weis AE. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences, USA* **104,** 1278–1282.

Fuhrer J. 2009. Ozone Risks for crops and pastures in present and future climates. *Naturwissenschaften* **96,** 173–194.

Gan J. 2004. Risk and damage of southern pine beetle outbreaks under global climate change. *Forest Ecology and Management* **191,** 61–71.

Garrett KA, Dendy SP, Frank EE, Rouse MN, Travers SE. 2006. Climate change effects on plant disease: genomes to ecosystems. *Annual Review of Phytopathology* **44,** 489–509.

Gate P. 2007. Dossier 'Le blé face au changement climatique'. *Perspectives Agricoles* **336,** 20–56.

Gate P. 2009. Les raisons du plafonnement des rendements. *Perspectives Agricoles* **365,** 6–12.

Gifford RM. 1994. The global carbon cycle: a viewpoint on the missing sink. *Australian Journal of Plant Physiology* **21,** 1–15.

Giorgi F, Mearns LO. 1999. Regional climate modeling revisited. An introduction to the special issue. *Journal of Geophysical Research* **104,** 6335–6352.

Giorgi F, Mearns LO. 2002. Calculation of average, uncertainty range and reliability of regional climate changes from AOGCM simulations via the 'reliability ensemble averaging' (REA) method. *Journal of Climate* **15,** 1141–1158.

Hammer GL, Kropff MJ, Sinclair TR, Porter JR. 2002. Future contributions of crop modelling: from heuristics and supporting decision making to understanding genetic regulation and aiding crop improvement. *European Journal of Agronomy* **18,** 15–31.

Hebeisen T, Lüscher A, Zanetti S, *et al*. 1997. Growth response of *Trifolium repens* L. and *Lolium perenne* L. as monocultures and bi-species mixture to free air CO_2 enrichment and management. *Global Change Biology* **3,** 149–160.

Held IM. 2005. The gap between simulation and understanding in climate modelling. *Bulletin of the American Meteorological Society* **86,** 1609–1614.

Howden SM, Soussana JF, Tubiello FN, Chhetri N, Dunlop M, Meinke H. 2007. Adapting agriculture to climate change. *Proceedings of the National Academy of Sciences, USA* **104,** 19691–19696.

Intergovernmental Panel on Climate Change (IPCC). 2001*a*. *Climate change 2001: the scientific basis.* Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

Intergovernmental Panel on Climate Change (IPCC). 2001*b*. *Climate change 2001: impacts, adaptation, and vulnerability.* Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

Intergovernmental Panel on Climate Change (IPCC). 2007*a*. *Climate change 2007: the physical science basis* Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

Intergovernmental Panel on Climate Change (IPCC). 2007*b*. *Climate change: impacts, adaptation and vulnerability.* Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

International Food Policy Research Institute (IFPRI). 2009. *Climate change impact on agriculture and costs of adaptations*. Food Policy Report.

Kimball BA, Kobayashi K, Bindi M. 2002. Responses of agricultural crops to free-air CO_2 enrichment. *Advances in Agronomy* **77,** 293–368.

Knapp AK, Beier C, Briske DD, *et al*. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience* **58,** 811–821.

Launay M, Graux AI, Brisson N, *et al*. 2009. Carbohydrate remobilization from storage root to leaves after a stress release in sugar beet (*Beta vulgaris* L.): experimental and modelling approaches. *Journal of Agricultural Science* **147,** 669–682.

Lazzarotto P, Calanca P, Fuhrer J. 2009. Dynamics of grass–clover mixtures. An analysis of the response to management with the productive grassland simulator (PROGRASS). *Ecological Modelling* **220,** 703–724.

Lebonvallet S, Brisson N, Raffaillac JP, *et al*. 2009. Establishment of quinoa (*Chenopodium quinoa* Willd.) and simulation of its cultivation with the STICS crop model. *Proceedings of the conference on integrated assessment of agriculture and sustainable development: Setting the Agenda for Science and Policy (AgSAP 2009)*. The Netherlands: Egmond aan Zee, 10–12 March 2009, 224–225.

Lemaire G, Denoix A. 1987. Croissance estivale en matière sèche de peuplement s de fétuque élevée (*Festuca arundinacea* Schreb.) et de dactyle (*Dactylis glomerata* L.) dans l'Ouest de la France. I. Etude en conditions de nutrition azotée et d'alimentation hydrique non limitantes. *Agronomie* **7,** 373–380.

Liu JG, Fritz S, van Wesenbeeck CFA, *et al*. 2008. A spatially explicit assessment of current and future hotspots of hunger in Sub-Saharan Africa in the context of global change. *Global and Planetary Change* **64,** 222–235.

Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL. 2008. Prioritizing climate change adaptation needs for food security in 2030. *Science* **319,** 607–610.

Loiseau P, Soussana F. 2000. Effects of elevated CO_2, temperature and N fertilization on nitrogen fluxes in a temperate grassland ecosystem. *Global Change Biology* **6,** 953–965.

Long SP. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: has its importance been underestimated? *Plant, Cell and Environment* **14,** 729–739.

Long SP, Ainsworth EA, Leakey ADB, Nösberger J, Ort DR. 2006. Food for thought: lower-than-expected crop yield stimulation with rising CO_2 concentrations. *Science* **312,** 1918–1921.

Lüscher A, Hendrey GR, Nösberger J. 1998. Long-term responsiveness to free-air CO_2 enrichment of functional types, species and genotypes of plants from fertile permanent grassland. *Oecologica* **113,** 37–45.

Machenhauer B, Windelband M, Botzet M, Christensen JH, Déqué M, Jones J, Ruti PM, Visconti G. 1998. *Validation and analysis of regional present-day climate and climate change simulations over Europe.* Max-Planck Institut für Meteorologie.

Matsui T, Namuco OS, Ziska LH, Horie T. 1997. Effects of high temperature and CO_2 concentration on spikelet sterility in Indica rice. *Field Crops Research* **51,** 213–221.

Mearns LO, Bogardi I, Matyasovsky I, Palecki M. 1999. Comparison of climate change scenarios generated from regional climate model experiments and statistical downscaling. *Journal of Geophysical Research* **104,** 6603–6621.

Morgan JA, Pataki DE, Korner C, *et al*. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia* **140,** 11–25.

Moya TB, Ziska LH, Namuco OS, Olszyk D. 1998. Growth dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide and temperature. *Global Change Biology* **4,** 645–656.

Nakicenovic N. 2000. Greenhouse gas emissions scenarios. *Technological Forecasting and Social Change* **65,** 149–166.

Nelson GC, Rosegrant MW, Koo J, *et al*. 2009. *Climate change. Impact on agriculture and costs of adaptation*. Washington DC: International Food Policy Research Institute. doi: 0.2499/0896295354.

Neve P, Vila-Aiub M, Roux F. 2010. Evolutionary-thinking in agricultural weed management. *New Phytologist* **184,** 783–793.

Norton MR, Lelièvre F, Fukai S, Volaire F. 2008. Measurement of summer dormancy in temperate perennial pasture grasses. *Australian Journal of Agricultural Research* **59,** 498–509.

Norton MR, Volaire F, Lelièvre F, Fukai S. 2009. Identification and measurement of summer dormancy in temperate perennial grasses. *Crop Science* **49,** 2347–2352.

Nowak RS, Ellsworth DS, Smith SD. 2004. Functional responses of plants to elevated atmospheric CO_2: do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* **162,** 253–280.

Orlandini S, Nejedlik P, Eitzinger J, Alexandrov V, Toulios L, Calanca P, Trnka M, Olesenh JE. 2008. Impacts of climate change and variability on european agriculture. Results of inventory analysis in COST 734 countries. *Trends and Directions in Climate Research* **1146,** 338–353.

Paeth H, Capo-Chichi A, Endlicher W. 2008. Climate change and food security in tropical West Africa: a dynamic-statistical modelling approach. *Erdkunde* **62,** 101–115.

Parry ML, Arnell NW, McMichael AJ, Nicholls RJ, Martens P, Kovats RS, Livermore MTJ, Rosenzweig C, Iglesias A, Fischer G. 2001. Millions at risk: defining critical climate change threats and targets. *Global Environmental Change* **11,** 181–183.

Parry M, Rosenzweig C, Livermore M. 2005. Climate change and risk global food supply and hunger. *Philosophical Transactions of the Royal Society B-Biological Sciences* **360,** 2125–2138.

Pinay G, Barbera P, Carreras-Palou A, Fromin N, Sonié L, Couteaux MM, Roy J, Philippot L, Lensi R. 2007. Impact of atmospheric CO_2 and plant life forms on soil microbial activities. *Soil Biology and Biochemistry* **39,** 33–42.

Poorter H. 1998. Do slow-growing and nutrient-stresses plants respond relatively strongly to elevated CO_2? *Global Change Biology* **4,** 693–697.

Poorter H, Navas ML. 2003. Plant growth and competition at elevated CO_2: on winners, losers and functional groups. *New Phytologist* **157,** 175–198.

Porter JR, Semenov MA. 2005. Crop responses to climatic variation. *Philosophical Transactions of the Royal Society B-Biological Sciences* **360,** 2021–2035.

Reilly J, Tubiello FN, McCarl B, Melillo J. 2001. Climate change and agriculture in the United States. In: Melillo J, Janetos G, Karl T, eds. *Climate change impacts on the United States.* Foundation, United States Global Change Research Program. Cambridge: Cambridge University Press.

Rosenzweig C, Parry ML. 1994. Potential impact of climate change on world food supply. *Nature* **367,** 133–138.

Rosenzweig C, Ritchie JT, Jones JW, Tsuji GY, Hildebrand P. 1995. *Climate change and agriculture: analysis of potential international impacts*. Madison WI: ASA Special Publication No. 59. American Society of Agronomy.

Salinari F, Giosue S, Tubiello FN, Rettori A, Rossi V, Spanna F, Rosenzweig C, Gullino ML. 2006. Downy mildew (*Plasmopara viticola*) epidemics on grapevine under climate change. *Global Change Biology* **12,** 1–9.

Scherm H. 2004. Climate change: can we predict the impacts on plant pathology and pest management? *Canadian Journal Plant Pathology* **26,** 267–273.

Schlenker W, Roberts MJ. 2009. Nonlinear temperature effects indicate severe damages to US crop yields under climate change. *Proceedings of the National Academy of Sciences, USA* **106,** 15594–15598.

Schneider MK, Luscher A, Richter M, Aeschlimann U, Hartwig UA, Blum H, Frossard E, Nösberger J. 2004. Ten years of free-air CO_2 enrichment altered the mobilization of N from soil in *Lolium perenne* L. swards. *Global Change Biology* **10,** 1377–1388.

Schulze R. 2000. Transcending scales of space and time in impact studies of climate and climate change on agrohydrological responses. *Agriculture, Ecosystems and Environment* **82,** 185–212.

Soussana JF, Hartwig UA. 1996. The effects of elevated CO_2 on symbiotic N_2 fixation: a link between the carbon and nitrogen cycles in grassland ecosystems. *Plant and Soil* **187,** 321–332.

Soussana JF, Lüscher A. 2007. Temperate grasslands and global atmospheric change: a review. *Grass and Forage Science* **62,** 127–134.

Soussana JF, Oliveira Machado JL. 2000. Modelling the dynamics of temperate grasses and legumes in cut mixtures. In: Lemaire G, Hodgson JG, Moraes A, Nabinger C, Carvalho F, eds. *Grassland ecophysiology and grazing ecology*. Curitiba, Parana, Brazil: CABI Publishing, 169–190.

Soussana JF, Teyssonneyre F, Picon-Cochard C, Dawson L. 2005. A trade-off between nitrogen uptake and use increases responsiveness to elevated CO_2 in infrequently cut mixed C_3 grasses. *New Phytologist* **166,** 217–230.

Stacey DA, Fellows MDE. 2002. Influence of elevated CO_2 on interspecific interactions at higher trophic levels. *Global Change Biology* **8,** 668–678.

Stöckle CO, Donatelli M, Nelson R. 2001. CropSyst, a cropping systems simulation model. *European Journal of Agronomy* **18,** 289–307.

Stöcklin J, Schweizer K, Körner C. 1998. Effects of elevated CO_2 and phosphorus addition on productivity and community composition of intact monoliths from calcareous grassland. *Oecologia* **116,** 50–56.

Tester M, Langridge P. 2010. Breeding technologies to increase crop production in a changing world. *Science* **327,** 818–822.

Teyssonneyre F, Picon-Cochard C, Soussana JF. 2002. How can we predict the effects of elevated CO_2 on the balance between perennial C_3 grass species competing for light? *The New Phytologist* **154,** 53–64.

Thornley JHM, Cannell MGR. 2000. Dynamics of mineral N availability in grassland ecosystems under increased [CO_2]: hypotheses evaluated using the Hurley Pasture Model. *Plant and Soil* **224,** 153–170.

Tsuji GY, Uehara G, Balas S. 1995. *DSSAT v3*. Honolulu: University of Hawaii.

Tubiello FN, Ewert F. 2002. Modeling the effects of elevated CO_2 on crop growth and yield: a review. *European Journal of Agronomy* **18,** 57–74.

Tubiello FN, Fischer G. 2007. Reducing climate change impacts on agriculture: global and regional effects of mitigation, 2000–2080. *Technological Forecasting and Social Change* **74,** 1030–1056.

Tubiello FN, Rosenzweig C, Goldberg RA, *et al*. 2002. Effects of climate change on US crop production: simulation results using two different GCM scenarios. I. Wheat, potato, maize, and citrus. *Climate Research* **20,** 259–270.

Tubiello FN, Soussana JF, Howden MS. 2007. Crop and pasture response to climate change. *Proceedings of the National Academy of Sciences, USA* **104,** 19686–19690.

Tungate KD, Israel DW, Watson DM, *et al*. 2007. Potential changes in weed competitiveness in an agroecological system with elevated temperatures. *Environmental and Experimental Botany* **60,** 42–49.

Tyree MT, Fiscus EL, Wullschleger SD, Dixon MA. 1986. Detection of xylem cavitation in corn under field conditions. *Plant Physiology* **82,** 597–599.

University of Copenhagen. 2009. *Synthesis report from climate change global risks, challenges and decisions*, 2009, 2nd edn. Copenhagen: 10–12 March.

Van Ittersum MK, Leffelaar PA, Van Keulen H, Kropff MJ, Bastiaans L, Goudriaan J. 2003. On approaches and applications of the Wageningen crop models. *European Journal of Agronomy* **18,** 201–234.

Volaire F. 2002. Drought survival, summer dormancy and dehydrin accumulation in contrasting cultivars of *Dactylis glomerata*. *Physiologia Plantarum* **116,** 42–52.

Volk M, Niklaus PA, Korner C. 2000. Soil moisture effects determine CO_2 responses of grassland species. *Oecologia* **125,** 380–388.

Wallach D, Makowski D, Jones J. 2006. *Working with dynamic crop models: evaluation, analysis, parameterization, and applications*. Amsterdam, The Netherlands: Elsevier.

Wheeler TR, Craufurd PQ, Ellis RH, Porter JR, Vara Prasad PV. 2000. Temperature variability and the yield of annual crops. *Agriculture, Ecosystems and Environment* **82,** 159–167.

White JW. 2009. Comments on a report of regression-based evidence for impact of recent climate change on winter wheat yields. *Agriculture, Ecosystems and Environment* **129,** 147–148.

Williams JR. 1995. The EPIC model. In: Singh VP, ed. *Computer models of watershed hydrology*. Highlands Ranch: CO Water Resources Publications.

Wolf J, Van Oijen M. 2003. Model simulation of effects of changes in climate and atmospheric CO_2 and O_3 on tuber yield potential of potato (cv. Bintje) in the European Union. *Agriculture, Ecosystems and Environment* **94,** 141–157.

Wollenweber B, Porter JR, Schellberg J. 2003. Lack of interaction between extreme high-temperature events at vegetative and reproductive growth stages in wheat. *Journal of Agronomy and Crop Science* **189,** 142–150.

Zanetti S, Hartwig UA, van Kessel C, Lüscher A, Hebeisen T, Frehner M, Fischer BU, Hendrey GR, Blum H, Nösberger J. 1997. Does nitrogen nutrition restrict the CO_2 response of fertile grassland lacking legumes? *Oecologia* **112,** 17–25.

Ziska LH. 2000. The impact of elevated carbon dioxide on yield loss from a C_3 and C_4 weed in field grown soybean. *Global Change Biology* **6,** 899–905.

Ziska LH, Bunce JA. 2006. Plant responses to rising atmospheric carbon dioxide. In: Morison JIL, Morecroft MD, eds. *Plant growth and climate change*. Oxford, UK: Blackwell Publishing, 17–47.

Ziska LH, Bunce JA. 2007. Predicting the impact of changing CO_2 on crop yields: some thoughts on food. *New Phytologist* **175,** 607–618.

Ziska LH, George K. 2004. Rising carbon dioxide and invasive, noxious plants: Potential threats and consequences. *World Resource Review* **16,** 427–447.

Ziska LH, Goins EW. 2006. Elevated atmospheric carbon dioxide and weed populations in glyphosate treated soybean. *Crop Science* **46,** 1354–1359.

Ziska LH, Manalo PA, Ordonez RA. 1996. Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars. *Journal of Experimental Botany* **47,** 1353–1359.

Ziska LH, Morris CF, Goins EW. 2004. Quantitative and qualitative evaluation of selected wheat varieties released since 1903 to increasing atmospheric carbon dioxide: can yield sensitivity to carbon dioxide be a factor in wheat performance? *Global Change Biology* **10,** 1810–1819.

Zvereva EL, Kozlov MV. 2006. Consequences of simultaneous elevation of carbon dioxide and temperature for plant–herbivore interactions: a meta-analysis. *Global Change Biology* **12,** 27–41.