Review Article

Narrowing uncertainties in the effects of elevated CO_2 on crops

Andrea Toreti, [1]

Email andrea.toreti@ec.europa.eu

Delphine Deryng, [2,3,4]

Email delphine.deryng@mail.mcgill.ca

Francesco N. Tubiello, [5]

Christoph Müller, [6]

Bruce A. Kimball, [7]

Gerald Moser, [8]

Ken Boote, [9]

Senthold Asseng, [9]

Thomas A. M. Pugh, [10,11,12]

Eline Vanuytrecht, [13,14]

Håkan Pleijel, [15]

Heidi Webber, [4]

Jean-Louis Durand, [16]

Frank Dentener, [1]

Andrej Ceglar, [1]

Xuhui Wang, [17,18]

Franz Badeck, [19]

Remi Lecerf, [1]

Gerard W. Wall, [7]

Maurits van den Berg, [1]

Petra Hoegy, [20]

Raul Lopez-Lozano, [21]

Matteo Zampieri, [1]

Stefano Galmarini, [1]

Garry J. O’Leary, [22]

Remy Manderscheid, [23]

Erik Mencos Contreras, [24,25]

Cynthia Rosenzweig, [24,25]

[1] European Commission, Joint Research Centre (JRC), Ispra, Italy

[2] NewClimate Institute, Berlin, Germany

[3] IRI THESys, Humboldt-Universität zu Berlin, Berlin, Germany

[4] Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany

[5] Statistics Division, Food and Agriculture Organization of the United Nations, Rome, Italy

[6] Potsdam Institute for Climate Impact Research PIK, Member of the Leibniz Association, Potsdam, Germany

[7] US Arid-Land Agricultural Research Center, USDA-ARS, Maricopa, AZ, USA

[8] Department of Plant Ecology, Justus Liebig University Giessen, Giessen, Germany

[9] University of Florida, Gainesville, FL, USA

[10] School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK

[11] Birmingham Institute of Forest Research, University of Birmingham, Birmingham, UK

[12] Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

[13] Flemish Institute for Technological Research (VITO), Mol, Belgium

[14] KU Leuven, Department of Earth and Environmental Science, Leuven, Belgium

[15] Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

[16] INRAE, URP3F, Lusignan, France

[17] Laboratoire des Sciences du Climat et de l'Environment LSCE, CEA-CNRS-UVSQ, Gif-sur-Yvette, France

[18] Sino-French Institute of Earth System Sciences, College of Urban and Environmental Sciences, Peking University, Beijing, China

[19] Council for Agricultural Research and Agricultural Economics, Research Centre for Genomics and Bioinformatics, CREA-GB, Fiorenzuola d'Arda, Italy

[20] University of Hohenheim, Stuttgart, Germany

[21] INRAE, Avignon Université, UMR EMMAH, UMT CAPTE, Avignon, France

[22] Agriculture Victoria, Horsham, Australia

[23] Thunen Institute of Biodiversity, Braunschweig, Germany

[24] NASA Goddard Institute for Space Studies, New York, NY, USA

[25] Center for Climate Systems Research, Columbia University, New York, NY, USA

Received: 13 February 2020 / Accepted: 6 November 2020

Abstract

Plant responses to rising atmospheric carbon dioxide (CO_2) concentrations, together with projected variations in temperature and precipitation will determine future agricultural production. Estimates of the impacts of climate change on agriculture provide essential information to design effective adaptation strategies, and develop sustainable food systems. Here, we review the current experimental evidence and crop models on the effects of elevated CO_2 concentrations. Recent concerted efforts have narrowed the uncertainties in CO_2-induced crop responses so that climate change impact simulations omitting CO_2 can now be eliminated. To address remaining knowledge gaps and uncertainties in estimating the effects of elevated CO_2 and climate change on crops, future research should expand experiments on more crop species under a wider range of growing conditions, improve the representation of responses to climate extremes in crop models, and simulate additional crop physiological processes related to nutritional quality.

Editor's Summary

Uncertainties in the estimation of the effects of elevated CO_2 on crops reduce trust in the underlying crop models, and hamper actions on climate change mitigation. This can be addressed by studying a wider variety of crop species under a wider range of growing conditions, improving the representation of responses to climate extremes in crop models and simulating additional crop physiological processes related to nutritional quality.

These authors contributed equally: Andrea Toreti, Delphine Deryng.

Main

Many countries under the Paris Agreement have committed to increasing their resilience to climate risks through adaptation and mitigation policies in their agricultural sectors. The scientific community produces relevant scientific information[1] for guiding the monitoring and evaluation of national climate policies and increasing their ambition as stipulated by the Global Stocktake component of the Paris Agreement[2].

AQ1

AQ2

AQ3

AQ4

AQ5

AQ6

AQ7

Crop models are among the key tools to generate such scientific sources[3]. Process-based crop models account for the impact of biophysical, climatic and environmental factors, including elevated CO_2 concentration (eCO_2) on plant growth processes[4], crop yield quantity and quality. Yet, despite decades of experiments robustly demonstrating the effects of eCO_2 (ref. [4]), climate change impact assessments have continued to use scenarios both with and without CO_2-fertilization effects[5, 6, 7]. Here we argue that this approach has produced more confusion than clarity, whereas current knowledge is sufficiently robust to make the scenario without CO_2 fertilization obsolete.

Available experimental evidence of eCO_2 effects

The role of eCO_2 in stimulating crop growth has been documented since 1804, when de Saussure[8] reported that peas exposed to eCO_2 grew better than control plants in ambient air. Since then, this effect has been exploited in commercial greenhouse production, while further scientific work has continued through many CO_2 enrichment experiments using greenhouses, growth chambers, gradient tunnels, open-top chambers (OTC), and Free-Air CO_2 Enrichment (FACE) techniques (Supplementary Tables 1 and 2). The understanding of eCO_2 effects on plant growth derived from those experiments has been synthesized in several topical and literature reviews, as summarized below[9, 10, 11].

The effects of eCO2 on crop productivity

Kimball et al.[12] assembled more than 70 reports and tabulated 430 prior observations of eCO_2-driven productivity changes in crops, concluding that yields of C_3 species under a full complement of water and nutrients significantly increase with a doubling of ambient CO_2 concentration (aCO_2; since that time the CO_2 mixing ratio has increased from 340 ppm to 412 ppm, which affects the degree of response to an experimental doubling). However, crop responses to eCO_2 vary by species and growing conditions[4]. Elevation of CO_2 concentration in FACE experiments (from a CO_2 mixing ratio of 353 ppm to 550 ppm) with ample water and nutrients increased yields of C_3 grains (for example, wheat, rice and barley) on average by 19% (ref. [4]). In contrast, the yield of C_4 crops (for example, maize and sorghum) did not change significantly when the crops were grown under ample water supply conditions. Variation in CO_2 responsiveness across genotypes within species[13, 14, 15] has also been demonstrated in rice, soybean and wheat[16, 17].

Beyond stimulating photosynthesis and growth, eCO_2 also causes reduced stomatal conductance by 19% to 22% (refs. [12, 18, 19]) and reduced crop transpiration[4, 20]. This leads to lower crop evapotranspiration (ET), as demonstrated by the average 10% ET reduction in FACE experiments for all investigated crops[4, 21] (Supplementary Information). Improved water-use efficiency under eCO_2 can enable crops to be more drought tolerant compared to crops grown in aCO_2. This effect is particularly important for C_4 crops, for which yield increases have been reported under water-limiting conditions in eCO_2. For example, FACE-sorghum[22, 23] and FACE-maize[24] experiments had average yield increases of 15% and 41%, respectively.

While under ample water and nutrient conditions, yields of most C_3 crops increase by 10% to 30% under eCO_2 in experiments, yield stimulation due to eCO_2 is generally smaller or insignificant when nutrients are limiting. Nutrient deficiencies, such as nitrogen (N) and probably also phosphorus deficiency, can minimize eCO_2 effects on crop productivity[4, 25]. While eCO_2 improves water-use efficiency, the eCO_2 growth stimulus, which accelerates leaf growth and may increase leaf area and root biomass, can lead to higher water use and nutrient limitation later in the growing season[26]. The modulating effects of N and seasonal rainfall on plant responses to eCO_2 have recently been demonstrated for a temperate C_3–C_4 grassland[27].

The effects of eCO_2 on crop quality

While eCO_2 has the potential to partly offset (and in some cases and conditions even compensate for) the negative effects of climate change on crop productivity (especially for C_3 crops such as wheat, rice and soybean[28]), a substantial body of work has shown that a CO_2-rich atmosphere also results in lowering food quality and potentially affecting nutrition security[29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43] (Supplementary Information).

A meta-analysis[33] of 228 pairs of experimental observations on barley, potato, rice and wheat reported reductions in protein concentrations ranging on average from –15.3% to –-9.8% under eCO_2, while the reduction was relatively small (–1.4%) in soybean[33]. A larger meta-analysis[43] done on 7,761 pairs of observations covering 130 species and cultivars reported an average 8% decline in mineral concentrations (except for Mn) and high agreement between FACE and non-FACE experiments. N fertilization and climate conditions may play a role in modulating the eCO_2-response in protein and mineral (Fe and Zn) concentrations[41, 42], entailing that processes such as mineralization should be taken into account to better understand this modulating role[42].

Declines in B vitamins (ranging from –30% to –13% for rice cultivars) under eCO_2 have been identified as well[30] (Supplementary Information). These changes in rice quality under eCO_2 may affect the nutrient status of about 600 million people[30] around the world.

Global-scale declines in minerals, such as Ca, Mg, protein concentrations and carotenoids under eCO_2 have been reported for many C_3 plants in general, including non-staple crops and vegetables[43, 44, 45]. A meta-analysis[46] on legumes and leafy vegetables found no changes in Fe, vitamin C and flavonoid concentrations under eCO_2; whereas antioxidant concentration tended to increase (although with high uncertainty). In another study, significant decreases in Fe concentration under eCO_2 were reported for leafy vegetables (-31%), fruit (–19.2%) and root vegetables (–8.2%), together with decreases in Zn concentration (–10.7% in stem vegetables, –18.1% in both fruit and root vegetables)[44]. Conversely, eCO_2 favours higher total antioxidant capacity in leafy vegetables (72.5%) but not in fruit vegetables (–14.4%)[44].

Decreases in protein concentration under eCO_2 are likely caused by nitrogen uptake not keeping up with carbon in biomass growth, an effect called carbohydrate dilution or growth dilution (Supplementary Information). However, recent studies have also found that lower protein concentrations may be triggered by reduced photorespiration and lower N-demand under eCO_2[43, 47, 48]. Indeed, slower photorespiration may induce a decrease in NO_3- assimilation and eventually lower protein concentration[48, 49]. However, changes in the ratio of manganese to magnesium may help to counterbalance this effect[48]. Leaf protein concentration is determined by the balance of Rubisco carboxylation or oxidation, with the former favoured by eCO_2, and by Rubisco content[50]. The reduction of Rubisco content and activity over time, being more pronounced under eCO_2, leads to lower leaf protein concentration. To date, no adaptation in agronomic management or phenotypic traits in FACE experiments[51, 52] has compensated for reduced protein concentration.

AQ8

AQ9

Thus, the negative impacts of eCO_2 on protein and nutrient availability may be such as to require important adjustments of future food systems[53, 54].

Future directions to improve experimental coverage

Although the overall number of eCO_2 experiments is large and the findings of the main effects on crops are unequivocal, more experimental work is still needed to improve the spatial (geographical) representativeness, temporal (timing and duration) distribution, numbers of crops and cultivars, and analyze components besides yield (for example, water use and nutrient concentrations).

As shown in Fig. 1a, eCO_2 experiments have been concentrated in Europe and the US, with some significant multi-year, large-scale FACE studies in South America, Asia (Japan, China and India), and Australia. There have been no eCO_2 experiments in Africa, where agriculture provides significant livelihoods. Furthermore, Fig. 1b highlights the need for more experiments in order to achieve better coverage of the diverse climatic conditions around the world. There is also a lack of multiple-year eCO_2 experiments, which are important for grasslands and perennials, especially tree crops, and for understanding long-term effects on soils and microbiota. A few long-term experiments have confirmed the ability of agro-ecosystems to acclimate (that is, reduced photosynthetic activity response compared to the initial response, known as down-regulation) to a CO_2-rich environment[55] (Supplementary Information). The results of these experiments suggest that eCO_2-induced effects in grasslands and perennial crops are highly dependent on climatic conditions and that acclimation may take more than 3–5 years[56, 57, 58, 59]. Although acclimation is of less relevance for the main food crops, it is still an important factor considering that it may act on shorter timescales and in light of recent studies on perennial grains[60] and the amplification of eCO_2 positive effects through crop generations by targeted selection[61].

Fig. 1

Overview of the eCO_2 experiments.

a, Global distribution of eCO_2 experiments on crops and grasslands. The distribution is derived from an updated version of the CLIMMANI Networking Group database (Supplementary Table 2) and other studies[43]. Colours indicate different agricultural crops: green, grassland and forages; ochre, cereals (barley, maize, sorghum and wheat); purple, woody crops (cotton and grape); turquois, forests and trees; light blue, natural ecosystems; red, other crops (apple, banana, cassava, coffee, cucumber, lemon, orange, pea, peach, potato, radish and spinach); gold, artificial crops (single or multiple species mixtures without agricultural use). **b**, The mean annual temperature versus annual precipitation (1981–2010) of the experimental sites and of the global cropland (grey area). The grey colour gets darker according to the cropland area falling into the temperature and precipitation bin. Data in panel **b** are taken from ref. [108] (experimental sites) and ref. [109] (global cropland).

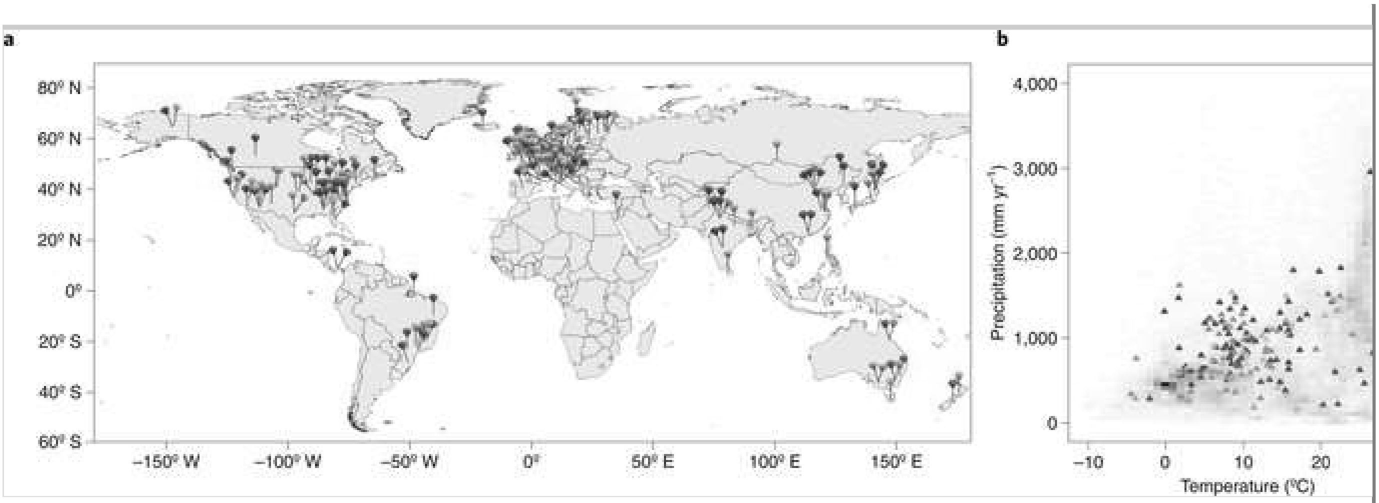
AQ12

AQ13

AQ14

AQ15

AQ16



AQ10

AQ11

Other types of experiments — including OTC, mini-FACE, climate control chambers and enclosures — can be cheaper and faster. These experiments can significantly reduce uncertainties by providing a larger number of replicates and sample sizes, covering a larger range of eCO_2 well above 550 ppm, and thus complementing and further supporting the evidence provided by the more expensive and time-consuming FACE experiments. OTC and mini-FACE may also help in addressing the role of eCO_2 at night[62], as many FACE experiments only enrich during daylight hours.

Approaches for modelling primary production

Crop growth models are key tools for scaling-up experimental evidence and assessing regional and global crops. We distinguish four basic approaches for modelling primary production[63]: complex with a biochemical basis; semi-complex involving leaf-level photosynthesis; based on radiation-use efficiency; and transpiration-efficiency based[64]. The choice of these modelling approaches largely determines how CO_2 responsiveness is implemented in crop models, either as simple response functions that scale productivity, or as components of the underlying mechanisms, such as Rubisco kinetics[65] (Supplementary Information).

AQ17

AQ18

While existing crop models include CO_2 responses in the simulation of primary production, they differ in the representation of transpiration and abiotic responses, such as N stress[64].

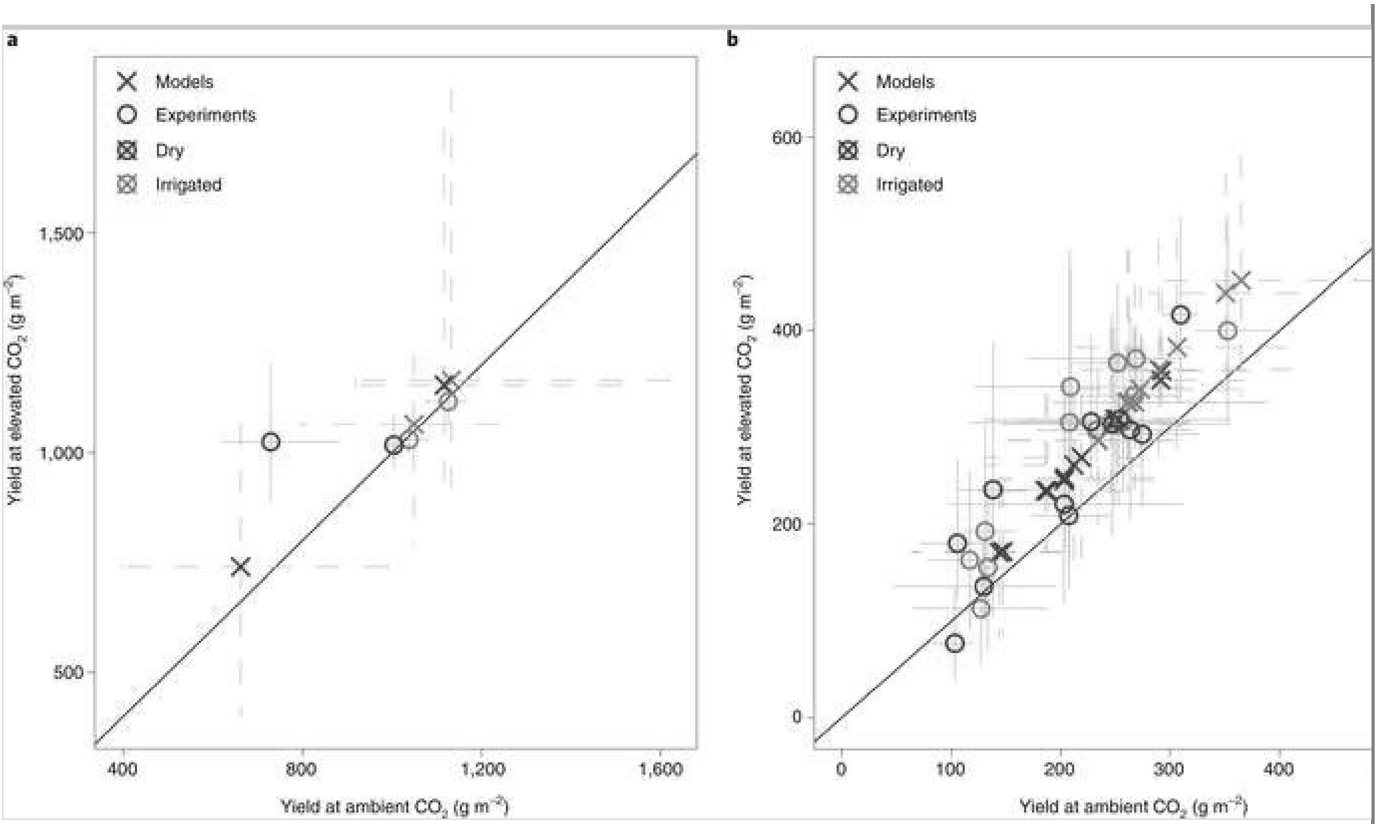
Many crop models have been tested against observations conducted with eCO_2 up to 600 ppm (FACE) and beyond (OTC). At the field scale under experimental conditions, crop models performed reasonably well[66] in reproducing the main effects of eCO_2 under both ample and limited water and N supplies, of higher temperatures on growth, harvestable yield, leaf area, water uptake, and of N dynamics for wheat[67, 68, 69], rice[70], maize[71], cotton[72], potatoes[73, 74] and pasture[75]. Figure 2 shows two examples of eCO_2 effects on yield of wheat and maize as simulated by crop models and measured in two dedicated experiments under different water and climatic conditions[24, 68, 71, 76]. Overall, good performance characterizes the modelling simulations, although some discrepancies remain (for example, in the case of maize under dry conditions).

Fig. 2

Yield responses to eCO_2 as measured in two FACE experiments and simulated by crop models.

a, Maize yield responses to eCO_2 from a mixing ratio of 387 ppm to 550 ppm measured in the 2007–2008 Braunschweig FACE experiment (northern Germany) under two levels of water supply: dry and irrigated. Uncertainty in measured crop yield response (given by replicates performed in the FACE experiment) is represented by grey solid lines. Uncertainty of the simulations, given by a 21-member ensemble of models, is represented by grey dotted lines. **b**, Wheat grain yield responses to eCO_2 from a mixing ratio of 365 ppm to 550 ppm measured in the 2007–2009 Horsham FACE experiment (south-eastern Australia) under different water supply conditions (dry and supplemental irrigation). Uncertainty in measured crop yield responses (given by replicates performed in the FACE experiment) is represented by grey solid lines. Uncertainty of the simulations, given by a six-member ensemble of models, is represented by grey dotted lines. Data in panel **a** are taken from ref. [24] (experiment) and ref. [71] (models). Data in panel **b** are taken from ref. [76] (experiment) and ref. [68] (models).

AQ19



Concerning the effects of N limitation in modulating the impacts of eCO$_2$, crop models in general reproduce how the lack of adequate N reduces yield gains induced by eCO$_2$, although uncertainties tend to be greater (Supplementary Fig. 1). In most cases, crop models also tend to underestimate yield gains induced by eCO$_2$ when N is adequate under experimental conditions (Supplementary Fig. 1).

Scaling-up crop simulations from field experiments

The high costs of running eCO$_2$ and climate change field experiments have prohibited the study of a representative sample with respect to the crop genetics (G), environmental conditions (E) and management regimes (M) in which farmers produce crops (G × E × M). Process-based crop models constitute an affordable solution to explore crop responses across a range of G × E × M combinations and at any scale of interest. More than twenty global-scale crop models[77] have been developed and many of them have been used in multi-model assessments[28, 78, 79, 80]. These global crop models follow the same dynamic process approaches of field-based models and have been increasingly used in economic and climate impact studies[5, 6, 7] that contribute to policy formulation[7, 81]. Large-scale crop simulations introduce additional uncertainty compared to field-scale crop models due to a lack of complete spatial and temporal data coverage on relevant agronomic information. Simulation and scenario approaches are used to fill current data gaps[82, 83, 84, 85, 86, 87], and relevant global data are being marshalled to address these challenges[88]. Trust in crop modeling capacity has been gained over the past five decades since models were first developed[28] based on widespread comparison of simulated yields and other variables against available field data, and from multi-model comparisons[89, 90, 91].

The effects of eCO_2 in crop model simulations

Past climate change assessments have routinely presented crop yield ‘with and without’ the effects of eCO_2[7, 92, 93], under the implicit assumption that the no-eCO_2-effects scenario represented an acceptable lower limit of the uncertainty range (Supplementary Table 3). That extremely cautious approach has, however, generated unnecessary misunderstanding of uncertainty regarding the current knowledge of eCO_2 on crops within climate change scenarios. As a result, some studies[94, 95] have used crop modelling results based on both ‘with’ and ‘without’ CO_2 simulations indistinguishably, potentially leading to misinterpretation of the ensemble median, range and causes for model (dis)agreement.

We demonstrate the issues in comparing crop model simulations with these different key settings (that is, with and without eCO_2) with global wheat and maize simulations under projected climate changes (Supplementary Fig. 2). The high uncertainties induced by the ‘without CO_2’ lower bound ultimately reduce trust in the underlying crop models, whereas experimental knowledge of the eCO_2 effect, as well as the ability of crop models to reproduce it, is substantial.

The large and growing body of experimental evidence has shown that current crop modelling approaches are increasingly able to capture the main effects of eCO_2 on crop growth and yield under a wide range of growing conditions at field scale. Hence, we argue that these effects should be included by default in climate change impact assessments: there is no longer a scientifically valid reason for expanding the range of model uncertainties to include a ‘without eCO_2’ scenario (other than quantifying the isolated effect). Under optimal growing conditions, ‘with eCO_2’ simulations should represent the upper bound of the uncertainty range. For the lower bound, rather than using a ‘without eCO_2’ scenario, levels responding to observed interactions of eCO_2 with abiotic stresses affecting crop growth — for example, soil N and water availability[70], temperature and O_3 (refs. [96, 97]) — should be assessed.

AQ20

Knowledge gaps in model development

Under complex growth-limiting environmental conditions, interactive processes are less well understood. A recent experiment on maize indicated that crop model results corresponded well to the observations under irrigated conditions[71, 98]. Nevertheless, some models had poor performance under certain drought conditions (due to underestimation of eCO_2 water savings), and therefore underestimated the associated crop yield stimulation[71]. Other nutrients, such as phosphorus (P) and potassium, are often neither considered in crop models nor fully measured or controlled in experiments, even though P is known to be a main limiting crop nutrient in many soils, particularly in Africa[99, 100, 101].

A serious gap in crop modelling tools is the scarcity of models for fruits and vegetables[64]. This situation is now improving, but models for many more fruits and vegetables with the full range of eCO_2 responses are needed. In addition, most existing crop models do not account for nutritional aspects other than protein concentration[67, 102], while recent work on the socio-economic impacts[54, 103] of reduced Fe and Zn concentration highlights the importance of including other key nutritional aspects, such as mineral concentrations. Finally, the upper range of projected CO_2 concentration by the end of the 21st century (for example, up to a CO_2 mixing ratio of 936 ppm in RCP8.5) greatly exceeds eCO_2 in current experiments. As the rate of C_3 crop responses declines with eCO_2, approaching 600 ppm (ref. [104]), and considering that the current atmospheric concentration is currently about 412 ppm and increasing by 2–3 ppm per year, key performance of crop models for long-term assessments will depend on the representation of this saturating response in interaction with other environmental variables, especially temperature,[18] and possible physiological limitations[105].

Key criteria for improving modelling protocols

We argue that research and assessment should better focus on critical issues in projecting the interactions of eCO_2 and climate change with crops. To this end, key criteria for selecting crop models for climate change impact assessments should advance the following representation:

1. Concurrent and interactive effects of eCO_2, temperature, water and nitrogen (CTWN) on crop processes;

2. Evaluation of simulated responses to CTWN variation compared to a range of observations from experiments (including at least crop cycle length, leaf area

index, harvestable yield, evapotranspiration) for C_3 and C_4 crops including staple grains, fruits and vegetables;

3. Comparison with observations to identify systematic biases in simulated baseline (that is, aCO_2) crop yields, which should then be either bias-corrected or excluded from the crop model ensemble.

AQ21

AQ22

The results of these evaluation tests should be made available as metadata in impact assessments, and crop models should be assessed in standardized evaluation exercises[106]. The proposed criteria-based model could improve the robustness of multi-model impact assessments.

Roadmap to advance future research on eCO_2

We outline here the main priorities for future research and point to existing barriers that must be addressed urgently to further improve scientific assessments of the effects of eCO_2 and climate change on crop productivity and quality (Table 1). We propose that the scientific community, through international initiatives such as the Agricultural Model Intercomparison and Improvement Project (AgMIP)[1], plays an important role in delivering scientific resources that helps assess the potential biophysical and socio-economic consequences to support national and international agricultural policies.

Table 1

Knowledge gaps, recommendations and requirements for research progress on eCO_2 and climate change

Data gaps and modelling inconsistencies	Recommendations	Main requirements to address
Data gap on crop nutritional quality, beyond N or protein AQ23	Include measurement of crop quality in experimental design	Funding
Data gap on crop types and cropping systems	Expand FACE, mini-FACE, OTC, climate control chambers and enclosures experiments to other crops and beyond high-input systems	Funding, expertise and infrastructure

Data gaps and modelling inconsistencies	Recommendations	Main requirements to address
Data gap in many agro-climatic regions of the world, especially Africa	Set up experiments in unstudied regions, especially in Africa	Funding, expertise and infrastructure
Data gap on interactions of eCO_2 effects, weather conditions and extreme events	More long-term (>10 years) FACE studies incorporating climate variables	Funding and infrastructure
Disparities in data measurements	Harmonization of measurement methods	Research method development
Limited sample sizes for testing experimental evidence	Increase replicates of experiments, especially non-FACE ones and those focused on nutrients	Funding and infrastructure
Lack of access to data	Set up and maintain an open-access data repository, for example, within Copernicus and AgMIP	Funding, communication and database development
Modelling uncertainty	Use multi-model ensembles, harmonization of variables and input data for modelling intercomparison exercises; display and discuss additional measures other than the ensemble median; use evaluation and validation criteria for inclusion of specific models AQ24	Research method and communication
Large uncertainty across scales	Harmonize available input data sets; identify an optimal set of global data to be used as input for large-scale model runs; create a common input data repository; develop a time-varying dataset of the main input parameters	Research method, funding, infrastructure and communication
Misleading scenarios using 'without eCO_2' as plausible AQ25	For policy purpose, use results that fully include eCO_2 effects (as well as N limitation) and are validated against recent eCO_2 experiments	Research method and communication
Effects on crop quality in modelling assessment are overlooked	Development of modelling components to simulate protein and mineral concentrations; set up AgMIP multi-modelling intercomparison activity for coordinated model development and improvement that includes nutrient quality	Funding, expertise and research method

Firstly, new eCO_2 experiments are needed for important crops in all agricultural regions of the world, particularly for cropping systems and agro-climatic regions in Africa, in order to capture the full diversity of responses. More experimental evidence on changes in crop quality and nutrition is needed for a wider range of crops to represent the threat for human health. All new studies describing results from specific CO_2-enrichment experiments should provide comprehensive and detailed weather, soil and management information to be easily integrated and used for crop model evaluation.

Synchronization of field experiments and modelling outputs should be enhanced to steadily improve crop models. Building connections among scientific disciplines will contribute to better access and use of experimental data to encourage continuous development of impact modelling tools.

Secondly, crop model improvements should focus with high priority on capturing the complex interactions of eCO_2, N, O_3, and varying climate and weather conditions, especially extreme events, and nutritional aspects. This crop model development will be fostered by an international initiative to be launched within AgMIP, but urgently requires research funding as well.

Thirdly, in addition to the inclusion of eCO_2 by default in impact assessments, the use of multi-model ensembles should be strongly encouraged to better capture modelling uncertainties[81]. Bias-correction techniques[107] should be applied to deal with potential biases in crop yield baseline simulations[28]

Finally, we propose to build an open-access web-repository (which could be hosted, for example, in the Copernicus C3S data store in conjunction with AgMIP and other agricultural modelling and data groups), containing information in standardized formats of experiments, model metadata and model simulations that are suitable for use in impact assessments, and to be made accessible to stakeholders across the science and policy spheres.

This roadmap will contribute to further narrowing the uncertainties that have long hampered actions on climate change mitigation and adaptation in agriculture, and facilitate major improvements in the conduct and use of climate change impact assessments in the agricultural sector.

Supplementary information

is available for this paper at https://doi.org/10.1038/s43016-020-00195-4.

Acknowledgements

We thank EC-JRC for hosting the ‘CO_2 Effects on Crops: Current Understanding, Modeling Needs, and Challenges’ workshop held in Ispra, Italy (8–10 October 2018), co-sponsored by AgMIP. S.A. acknowledges support by the CGIAR research programme on wheat agri-food systems (CRP WHEAT) and the CGIAR Platform for Big Data in Agriculture. T.A.M.P. acknowledges the Birmingham Institute of Forest Research (paper no. 50). C.R. acknowledges the AgMIP Coordination Unit at Columbia University Earth Institute. F.N.T. acknowledges funding from the FAO Regular Programme. The views expressed in this publication are those of the authors and do not necessarily reflect the views or policies of FAO and other organizations.

AQ26

Author contributions

A.T. and D.D. coordinated this community effort. All of the authors contributed to reviewing and interpreting the available literature, and writing the manuscript.

AQ27

Competing interests The authors declare no competing interests.

Supplementary information

Supplementary Information

Supplementary Tables 1 and 3, Figs. 1 and 2, and discussion.

Supplementary Table 2

List and details of all identified eCO_2 experiments shown in Fig. 1.

References

1. Rosenzweig, C. et al. The agricultural model intercomparison and improvement project (AgMIP): protocols and pilot studies. *Agric. For. Meteorol.* **170**, 166–182 (2013).

2. Hermwille, L., Siemons, A., Förster, H. & Jeffery, L. Catalyzing mitigation ambition under the Paris Agreement: elements for an effective global stocktake. *Clim. Policy* **9**, 988–1001 (2019).

3. Grassi, G. et al. Reconciling global-model estimates and country reporting of anthropogenic forest CO_2 sinks. *Nat. Clim. Change* **8**, 914–920 (2018).

4. Kimball, B. A. Crop responses to elevated CO_2 and interactions with H_2O, N, and temperature. *Curr. Opin. Plant Biol.* **31**, 36–43 (2016).

5. Wiebe, K. et al. Climate change impacts on agriculture in 2050 under a range of plausible socioeconomic and emissions scenarios. *Environ. Res. Lett.* **10**, 085010 (2015).

6. Stefanovic, M. et al. The impact of high-end climate change on agriculture welfare. *Sci. Adv.* **2**, e1501452 (2016).

7. Ciscar, J. C. et al. *Climate Impacts in Europe: Final Report of the JRC PESETA III Project* (European Union, 2018).

8. de Saussure, N. T. *Chemische Untersuchungen über die Vegetation* (trans. Wieler, A.) 22 (Engelmann, 1890).

9. Gamage, D. et al. New insights into the cellular mechanisms of plant growth at elevated atmospheric carbon dioxide concentrations. *Plant Cell Environ.* **41**, 1233–1246 (2018).

10. Bloom, A. J. Photorespiration and nitrate assimilation: a major intersection between plant carbon and nitrogen. *Photosynth. Res.* **123**, 117–128 (2015).

11. Franks, P. J. et al. Sensitivity of plants to changing atmospheric CO_2 concentration: from the geological past to the next century. *New Phytol.* **197**, 1077–1094 (2013).

12. Kimball, B. A. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agron. J.* **75**, 779–788 (1983).

13. Hasegawa, T. et al. Rice cultivar responses to elevated CO_2 at two free-air enrichment sites in Japan. *Funct. Plant Biol.* **40**, 148–159 (2013).

14. Aljazairi, S., Arias, C. & Nogues, S. Carbon and nitrogen allocation and partitioning in traditional and modern wheat genotypes under pre-industrial and future CO_2-conditions. *Plant Biol.* **17**, 647–659 (2015).

15. Bishop, K. A., Betzelberger, A. M., Long, S. P. & Ainsworth, E. A. Is there potential to adapt soybean (Glycine max Merr.) to future [CO_2]? An analysis of the yield of response of 18 genotypes to free-air CO_2-enrichment. *Plant Cell Environ.* **38**, 1765–1774 (2015).

16. Ziska, L. H. et al. Food security and climate change: on the potential to adapt global crop production by active selection to rising atmospheric carbon dioxide. *Proc. Royal Soc. B* **279**, 4097–4105 (2012).

17. Ziska, L. H. Three year field evaluation of early and late 20th century spring wheat cultivars to projected increase in atmospheric carbon dioxide. *Field Crops Res.* **108**, 54–59 (2008).

18. Ainsworth, E. A. & Rogers, A. The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant Cell Environ.* **30**, 258–270 (2007).

19. Purcell, C. et al. Increasing stomatal conductance in response to rising atmospheric CO_2. *Ann. Bot.* **121**, 1137–1149 (2018).

20. Manderscheid, R. et al. Effects of free-air carbon dioxide enrichment on sap flow and canopy microclimate of maize grown under different water supply. *J. Agron. Crop Sci.* **202**, 255–268 (2016).

21. Manderscheid, R., Dier, M., Erbs, M., Sickora, J. & Weigel, H.-J. Nitrogen supply – A determinant in water use efficiency of winter wheat grown under free air CO_2 enrichment. *Agr. Water Manag.* **210**, 70–77 (2018).

22. Ottman, M. J. et al. Elevated CO_2 increases sorghum biomass under drought conditions. *New Phytol.* **150**, 261–273 (2001).

23. Wall, G. W. et al. Elevated atmospheric CO_2 improved Sorghum plant water status by ameliorating the adverse effects of drought. *New Phytol.* **152**, 231–248 (2001).

24. Manderscheid, R., Erbs, M. & Weigel, H.-J. Interactive effects of free-air CO_2 enrichment and drought stress on maize growth. *Eur. J. Agron.* **52**, 11–21 (2014).

25. Dier, D. et al. Decreased wheat grain yield stimulation by free air CO_2 enrichment under N deficiency is strongly related to decreased radiation use efficiency enhancement. *Eur. J. Agron.* **101**, 38–48 (2018).

26. Gray, S. B. et al. Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. *Nat. Plants* **2**, 16132 (2016).

27. Hovenden, M. J. Globally consistent influences of seasonal precipitation limit grassland biomass response to elevated CO_2. *Nat. Plants* **5**, 167–173 (2019).

28. Rosenzweig, C. et al. Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proc. Natl Acad. Sci. USA* **111**, 3268–3273 (2014).

29. Loladze, I. Rising atmospheric CO_2 and human nutrition: toward globally imbalanced plant stoichiometry? *Trends Ecol. Evol.* **17**, 457–461 (2002).

30. Zhu, C. et al. Carbon dioxide (CO_2) levels this century will alter the protein, micronutrients, and vitamin content of rice grains with potential health consequences for the poorest rice-dependent countries. *Sci. Adv.* **4**, eaaq1012 (2018).

31. Müller, C., Elliott, J. & Levermann, A. Fertilizing hidden hunger. *Nat. Clim. Change* **4**, 540–541 (2014).

32. Myers, S. S. et al. Increasing CO_2 threatens human nutrition. *Nature* **510**, 139–142 (2014).

33. Taub, D. R., Miller, B. & Allen, H. Effects of elevated CO_2 on the protein concentration of food crops: a meta-analysis. *Glob. Change Biol.* **14**, 565–575 (2008).

34. Broberg, M. C., Högy, P. & Pleijel, H. CO_2-induced changes in wheat grain composition: meta-analysis and response functions. *Agronomy* **7**, 32 (2017).

35. Usui, Y. et al. Rice grain yield and quality responses to free-air CO_2 enrichment combined with soil and water warming. *Glob. Change Biol.* **22**, 1256–1270 (2016).

36. Shewry, P. R., Pellny, T. K. & Lovegrove, A. Is modern wheat bad for health? *Nat. Plants* **2**, 16097 (2016).

37. Fernando, N. et al. Intra-specific variation of wheat grain quality in response to elevated [CO_2] at two sowing times under rain-fed and irrigation treatments. *J. Cereal Sci.* **59**, 137–144 (2014).

38. Fernando, N. et al. Elevated CO_2 alters grain quality of two bread wheat cultivars grown under different environmental conditions. *Agric. Ecosyst. Environ.* **185**, 24–33 (2014).

39. Fares, C. et al. Increasing atmospheric CO_2 modifies durum wheat grain quality and pasta cooking quality. *J. Cereal Sci.* **69**, 245–251 (2016).

40. Beleggia, R. et al. Mineral composition of durum wheat grain and pasta under increasing atmospheric CO_2 concentrations. *Food Chem.* **242**, 53–61 (2018).

41. Verrillo, F. et al. Elevated field atmospheric CO_2 concentrations affect the characteristics of winter wheat (cv. Bologna) grains. *Crop Pasture Sci.* **68**, 713–725 (2017).

42. Dier, M. et al. Elevated atmospheric CO_2 concentration has limited effect on wheat grain quality regardless of nitrogen supply. *J. Agric. Food Chem.* **68**, 3711–3721 (2020).

43. Loladze, I. Hidden shift of the ionome of plants exposed to elevated CO_2 depletes minerals at the base of human nutrition. *eLife* **3**, e002245 (2014).

44. Dong, J., Gruda, N., Lam, S. K., Li, X. & Duan, Z. Effects of elevated CO_2 on nutritional quality of vegetables: a review. *Front. Plant Sci.* **9**, 924–924 (2018).

45. Loladze, I., Nolan, J. M., Ziska, L. H. & Knobbe, A. R. Rising atmospheric CO_2 lowers concentrations of plant carotenoids essential to human health: a meta-analysis. *Mol. Nutr. Food Res.* **63**, 1801047 (2019).

46. Scheelbeek, P. F. D. et al. Effect of environmental changes on vegetable and legume yields and nutritional quality. *Proc. Natl Acad. Sci. USA* **115**, 6804–6809 (2018).

47. Wujeska-Klause, A., Crous, K. Y., Ghannoum, O. & Ellsworth, D. S. Lower photorespiration in elevated CO_2 reduces leaf N concentrations in mature Eucalyptus trees in the field. *Glob. Change Biol.* **25**, 1282–1295 (2019).

48. Bloom, A. & Lancaster, K. M. Manganese binding to Rubisco could drive a photorespiratory pathway that increases the energy efficiency of photosynthesis. *Nat. Plants* **4**, 414–422 (2018).

49. Bahrami, H. et al. The proportion of nitrate in leaf nitrogen, but not changes in root growth, are associated with decreased grain protein in wheat under elevated [CO_2]. *J. Plant Physiol.* **216**, 44–51 (2017).

50. Gesch, R. W., Boote, K. J., Vu, J. C. V., Allen, L. H. & Bowes, G. Changes in growth CO_2 result in rapid adjustments of Ribulose-1,5-Bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiol.* **118**, 521–529 (1998).

51. Walker, C., Armstrong, R., Panozzo, J., Partington, D. & Fitzgerald, G. Can nitrogen fertiliser maintain wheat (Triticum aestivum) grain protein concentration in an elevated CO_2 environment? *Soil Res.* **55**, 518–523 (2017).

52. Walker, C. K. et al. Adaptive traits do not mitigate the decline in bread wheat quality under elevated CO_2. *J. Cereal Sci.* **88**, 24–30 (2019).

53. Medek, D. E., Schwartz, J. & Myers, S. S. Estimated effects of future atmospheric CO_2 concentrations on protein intake and the risk of protein

deficiency by country and region. *Environ. Health Perspect.* **125**, 087002 (2017).

54. Weyant, C. et al. Anticipated burden and mitigation of carbon-dioxide-induced nutritional deficiencies and related diseases: A simulation modeling study. *PLoS Med.* **15**, e1002586 (2018).

55. Pastore, M. A., Lee, T. D., Hobbie, S. E. & Reich, P. B. Strong photosynthetic acclimation and enhanced water-use efficiency in grassland functional groups persist over 21 years of CO_2 enrichment, independent of nitrogen supply. *Glob. Change Biol.* **25**, 3031–3044 (2019).

56. Reich, P. B., Hobbie, S. E., Lee, T. D. & Pastore, M. A. Unexpected reversal of C_3 versus C_4 grass response to elevated CO_2 during a 20-year field experiment. *Science* **360**, 317–320 (2018).

57. Yuan, N. et al. Extreme climatic events down-regulate the grassland biomass response to elevated carbon dioxide. *Sci. Rep.* **8**, 17758 (2018).

58. Andresen, L. C. et al. Biomass responses in a temperate European grassland through 17 years of elevated CO_2. *Glob. Change Biol.* **24**, 3875–3885 (2018).

59. Obermeier, W. A. et al. Reduced CO_2 fertilization in temperate C_3 grasslands under more extreme weather conditions. *Nat. Clim. Change* **7**, 137–141 (2017).

60. Crews, T. E. & Cattani, D. J. Strategies, advances, and challenges in breeding perennial grains. *Sustainability* **10**, 2192 (2018).

61. Li, X. et al. Effect of multigenerational exposure to elevated atmospheric CO_2 concentration on grain quality in wheat. *Environ. Exp. Bot.* **157**, 310–319 (2019).

62. Bunce, J. A. CO_2 enrichment at night affects the growth and yield of common beans. *Crop Sci.* **54**, 1744–1747 (2014).

63. Chen, T., van der Werf, G. R., Gobron, N., Moors, E. J. & Dolman, A. J. Global cropland monthly gross primary productivity in the year 2000. *Biogeosciences* **11**, 3871–3880 (2014).

64. Vanuytrecht, E. & Thorburn, P. J. Responses to atmospheric CO_2 concentrations in crop simulation models: a review of current simple and semicomplex representations and options for model development. *Glob. Change Biol.* **23**, 1806–1820 (2017).

65. Galmes, J. et al. Expanding knowledge of the Rubisco kinetics variability in plant species: environmental and evolutionary trends. *Plant Cell Environ.* **37**, 1989–2001 (2014).

66. Tubiello, F. N. et al. Crop response to elevated CO_2 and world food supply: A comment on “Food for Thought.” by Long et al., Science 312: 1918–1921, 2006. *Eur. J. Agron.* **26**, 215–223 (2007).

67. Asseng, S. et al. Climate change impact and adaptation for wheat protein. *Glob. Change Biol.* **25**, 155–173 (2019).

68. O’Leary, G. J. et al. Response of wheat growth, grain yield and water use to elevated CO_2 under a Free-Air CO_2 Enrichment (FACE) experiment and modelling in a semi-arid environment. *Glob. Change Biol.* **21**, 2670–2686 (2015).

69. Tubiello, F. N. et al. Testing CERES-Wheat with Free-Air Carbon Dioxide Enrichment (FACE) experiment data: CO_2 and water interactions. *Agron. J.* **91**, 247–255 (1999).

70. Hasegawa, T. et al. Causes of variation among rice models in yield response to CO_2 examined with Free-Air CO_2 Enrichment and growth chamber experiments. *Sci. Rep.* **7**, 14858 (2017).

71. Durand, J. L. et al. How accurately do maize crop models simulate the interactions of atmospheric CO_2 concentration levels with limited water supply on water use and yield? *Eur. J. Agron.* **100**, 65–75 (2018).

72. Wall, G. W., Amthor, J. S. & Kimball, B. A. $COTCO_2$: A cotton growth simulation-model for global change. *Agric. For. Meteorol.* **70**, 289–342 (1994).

73. Raymundo, R. et al. Climate change impact on global potato production. *Eur. J. Agron.* **100**, 87–98 (2018).

74. Wolf, J. & Van Oijen, M. 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. *Agric. Ecosyst. Environ.* **94**, 141–157 (2003).

75. Li, F. Y., Newton, P. C. D. & Lieffering, M. Testing simulations of intra- and inter-annual variation in the plant production response to elevated CO_2 against measurements from an 11-year FACE experiment on grazed pasture. *Glob. Change Biol.* **20**, 228–239 (2014).

76. Mollah, M., Norton, R. & Huzzey, J. Australian grains free-air carbon dioxide enrichment (AGFACE) facility: design and performance. *Crop Pasture Sci.* **60**, 697–707 (2009).

77. Müller, C. et al. The Global Gridded Crop Model Intercomparison phase 1 simulation dataset. *Sci. Data* **6**, 50 (2019).

78. Elliott, J. D. et al. Constraints and potentials of future irrigation water availability on agricultural production under climate change. *Proc. Natl Acad. Sci. USA* **111**, 3239–3244 (2014).

79. Mbow, C. et al. in *Climate Change and Land: an IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems* (eds Shukla, P. R. et al.) Ch. 5 (IPCC, 2019).

AQ28

80. Rosenzweig, C. et al. Climate change responses benefit from a global food system approach. *Nat. Food.* **1**, 94–97 (2020).

81. Rosenzweig, C. et al. Coordinating AgMIP data and models across global and regional scales for 1.5 °C and 2.0 °C assessments. *Philos. Trans. R. Soc. A* **376**, 20160455 (2018).

82. Hutchings, N. J. et al. A model for simulating the timelines of field operations at a European scale for use in complex dynamic models. *Biogeosciences* **9**, 4487–4496 (2012).

83. van Bussel, L. G. J., Stehfest, E., Siebert, S., Müller, C. & Ewert, F. Simulation of the phenological development of wheat and maize at the global

scale. *Glob. Ecol. Biogeogr.* **24**, 1018–1029 (2015).

84. Waha, K., van Bussel, L. G. J., Müller, C. & Bondeau, A. Climate-driven simulation of global crop sowing dates. *Glob. Ecol. Biogeogr.* **21**, 247–259 (2012).

85. Minoli, S., Egli, D. B., Rolinski, S. & Müller, C. Modelling cropping periods of grain crops at the global scale. *Glob. Planet. Change* **174**, 35–46 (2019).

86. Iizumi, T., Kim, W. & Nishimori, M. Modeling the global sowing and harvesting windows of major crops around the year 2000. *J. Adv. Model. Earth Syst.* **11**, 99–112 (2019).

87. Porwollik, V., Rolinski, S., Heinke, J. & Müller, C. Generating a global gridded tillage dataset. *Earth Syst. Sci. Data* **11**, 823–843 (2019).

88. Valdivia, R. O. et al. in *Handbook of Climate Change and Agroecosystems: The Agricultural Model Intercomparison and Improvement Project Integrated Crop and Economic Assessments, Part 1* (eds Rosenzweig, C. & Hillel, D.) 101–145 (Imperial College Press, 2015).

89. Asseng, S. et al. Rising temperatures reduce global wheat production. *Nat. Clim. Change* **5**, 143–147 (2015).

90. Bassu, S. et al. How do various maize crop models vary in their responses to climate change factors? *Glob. Change Biol.* **20**, 2301–2320 (2014).

91. Li, T. et al. Uncertainties in predicting rice yield by current crop models under a wide range of climatic conditions. *Glob. Change Biol.* **21**, 328–1341 (2015).

92. Moore, F. C., Baldos, U., Hertel, T. & Diaz, D. New science of climate change impacts on agriculture implies higher social cost of carbon. *Nat. Commun.* **8**, 1607 (2017).

93. Porter, J. R. et al. in *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on*

Climate Change (eds Field, C. B. et al.) Ch. 7 (IPCC, Cambridge University Press, 2014).

AQ29

94. Wheeler, T. & von Braun, J. Climate change impacts on global food security. *Science* **341**, 508–513 (2013).

95. Challinor, A. J. et al. A meta-analysis of crop yield under climate change and adaptation. *Nat. Clim. Change* **4**, 287–291 (2014).

96. Emberson, L. D. et al. Ozone effects on crops and consideration in crop models. *Eur. J. Agron.* **100**, 19–34 (2018).

97. Schauberger, B., Rolinski, S., Schaphoff, S. & Müller, C. Global historical soybean and wheat yield loss estimates from ozone pollution considering water and temperature as modifying effects. *Agr. For. Meteorol.* **265**, 1–15 (2019).

98. Kellner, J. et al. Response of maize biomass and soil water fluxes on elevated CO_2 and drought — From field experiments to process-based simulations. *Glob. Change Biol.* **25**, 2947–2957 (2019).

99. Van Straaten, P. in *Innovations as Key to the Green Revolution in Africa* (eds Bationo A. et al.) 31–47 (Springer, 2011).

AQ30

100. Sanchez, P. A. Soil fertility and hunger in Africa. *Science* **295**, 2019–2020 (2002).

101. Buresh, R. J., Smithson, P. C. & Hellums, D. T. in *Replenishing Soil Fertility in Africa* (eds Buresh, R. J. et al.) 111–149 (Soil Science Society of America, American Society of Agronomy, 1997).

AQ31

102. Nuttall, J. G. et al. Models of grain quality in wheat — a review. *Field Crops Res.* **202**, 136–145 (2017).

103. Beach, R. H. et al. Combining the effects of increased atmospheric carbon dioxide on protein, iron, and zinc availability and projected climate change on global diets: a modelling study. *Lancet Planet. Health* **3**, 307–317 (2019).

104. Broberg, M. C., Högy, P., Feng, Z. & Pleijel, H. Effects of elevated CO_2 on wheat yield: nonlinear response and relation to site productivity. *Agronomy* **9**, 243 (2019).

105. Sage, R. F. & Kubien, D. S. The temperature response of C_3 and C_4 photosynthesis. *Plant Cell Environ.* **30**, 1086–1106 (2007).

106. Müller, C. et al. Global gridded crop model evaluation: benchmarking, skills, deficiencies and implications. *Geosci. Model Dev.* **10**, 1403–1422 (2017).

107. Galmarini, S. et al. Adjusting climate model bias for agricultural impact assessment: how to cut the mustard. *Clim. Serv.* **13**, 65–69 (2019).

108. Ruane, A. C., Goldberg, R. & Chryssanthacopoulos, J. AgMIP climate forcing datasets for agricultural modeling: merged products for gap-filling and historical climate series estimation. *Agr. For. Meteorol.* **200**, 233–248 (2015).

109. Portmann, F. T., Siebert, S. & Döll, P. Mirca2000 — global monthly irrigated and rainfed crop areas around the year 2000: a new high-resolution data set for agricultural and hydrological modelling. *Glob. Biogeochem. Cy.* **24**, 1011 (2010).