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Toreti, Andrea; Deryng, Delphine; Tubiello, Francesco; Müller, Christoph; Kimball, Bruce; Moser, Gerald; Boote, Kenneth; Asseng, Senthold; Pugh, Thomas; Vanuytrecht, Eline; Pleijel, Hakan; Webber, Heidi; Durand, Jean-Louis; Dentener, Frank; Ceglar, Andrej; Wang, Xuhui; Badeck, Franz; Lecerf, Remi; Wall, Gerald; van den Berg, Maurits

DOI:
10.1038/s43016-020-00195-4

Document Version
Peer reviewed version

Citation for published version (Harvard):
Toreti, A, Deryng, D, Tubiello, F, Müller, C, Kimball, B, Moser, G, Boote, K, Asseng, S, Pugh, T, Vanuytrecht, E, Pleijel, H, Webber, H, Durand, J-L, Dentener, F, Ceglar, A, Wang, X, Badeck, F, Lecerf, R, Wall, G, van den Berg, M, Hoegy, P, Lopez-Lozano, R, Zampieri, M, Galmarini, S, O'Leary, G, Manderscheid, R, Mencos Contreras, E & Rosenzweig, C 2020, 'Narrowing the uncertainties in the effects of elevated CO_2 on crops', *Nature Food*, vol. 1, pp. 775–782 . https://doi.org/10.1038/s43016-020-00195-4

Narrowing the uncertainties in the effects of elevated CO_2 on crops

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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 crops

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.

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 produce relevant scientific information 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].

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*, hereafter) on plant growth processes[4], crop yield quantity and quality. Yet, despite decades of experiments robustly demonstrating the effects of *eCO_2*[4], climate change impact assessments have continued to use scenarios both with and without CO_2-*fertilization effects*[5-7]. Here we argue that this approach has produced more confusion than clarity, whereas current knowledge is sufficiently robust to make the *without CO_2-fertilization* scenario 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 S1 and S2). 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[9-11].

The effects of eCO₂ on crop productivity. Kimball et al.[12] assembled more than 70 reports and tabulated 430 prior observations of *e*CO_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 (*a*CO_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 *e*CO_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 (e.g., wheat, rice, barley) on average by 19%[4]. In contrast, the yield of C_4 crops (e.g., maize, sorghum) did not change significantly when the crops were grown under ample water supply conditions. Variation in CO_2 responsiveness across genotypes within species[13-15] has also been demonstrated in rice, soybean, and wheat[16-17].

Beyond stimulating photosynthesis and growth, *e*CO_2 also causes reduced stomatal conductance by 19% to 22%[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 Material S.1.1). Improved water-use efficiency under *e*CO_2 can enable crops to be more drought tolerant compared to crops grown in *a*CO_2. This effect is particularly important for C_4 crops, for which yield increases have been reported under water-limiting conditions in *e*CO_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 *e*CO_2 in experiments, yield stimulation due to *e*CO_2 is generally smaller or insignificant when nutrients are limiting. Nutrient deficiencies, such as nitrogen (N) and probably also phosphorus (P) deficiency, can minimize *e*CO_2 effects on crop productivity[4,25]. While *e*CO_2 improves water-use efficiency, the *e*CO_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 potential affecting nutrition security[29-43] (Supplementary Material S.1.2).

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 Material S.1.2). 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 mineral, 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[43-45]. 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 favors 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 Material S.1.3). 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-magnesium may help to counterbalance this effect[48]. Leaf protein concentration is determined by the balance of Rubisco carboxylation-oxidation, with the former one favored 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.

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 (e.g., water use and nutrient concentrations).

As shown in Figure 1a, *eCO_2* experiments have been concentrated in Europe and the U.S., 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, Figure 1b highlights the need for more experiments in order to achieve a 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 (i.e., reduced photosynthetic activity response compared to the initial response, known as down-regulation) to a CO_2-rich environment[55] (Supplementary Material S.1.4). Their results 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[56-59]. Although acclimation is of less relevance for the main food crops, it is still an important factor considering that it may act on shorter time scale and also looking at recent studies on perennial grains[60] and the amplification of *eCO_2* positive effects through crop generations[61].

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 larger number of replicates and sample sizes, covering a larger range of *eCO_2* well above 550ppm, 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.

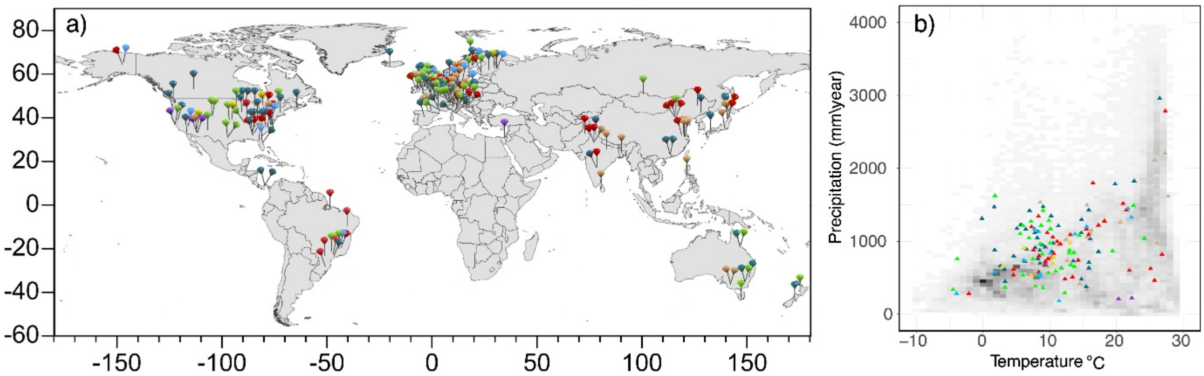

***Figure 1. Overview of the eCO₂ experiments**. a). Global distribution of eCO_2 experiments on crops and grasslands. The distribution is derived from an updated version of the CLIMMANI Networking Group database (https://climmani.org, access date: October 2018; Table S2 in Supplementary Material) and other studies[43]. Colors indicate different agricultural crops: green – grassland/forages, ochre – cereals (barley, maize, sorghum, wheat), purple – woody crops (cotton, grape), light blue – natural ecosystems, red – other crops (apple, banana, cassava, coffee, cucumber, lemon, orange, pea, peach, potato, radish, spinach), gold – artificial crops (single or multiple species mixtures without agricultural use). b). The mean annual temperature vs annual precipitation[63] (1981-2010) of the experimental sites and of the global cropland[64] (grey area). The grey color gets darker according to the cropland area falling into the temperature/precipitation bin.*

Approaches for modeling primary production

Crop growth models are key tools for scaling-up experimental evidence and assessing regional and global crop. We distinguish four basic types of approaches for modeling primary[65]: complex with a biochemical basis; semi-complex involving leaf-level photosynthesis; radiation-use efficiency (RUE)-based; and transpiration-efficiency based[66]. The choice of these modeling 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[67] (Supplementary Material S.2).

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[66]. 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[68] 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[69-71], rice[72], maize[73], cotton[74], potatoes[75-76], and pasture[77]. 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[24,70,73,78]. Overall, good performance characterizes the modeling simulations, although some discrepancies remain (e.g. in the case of maize under dry conditions).

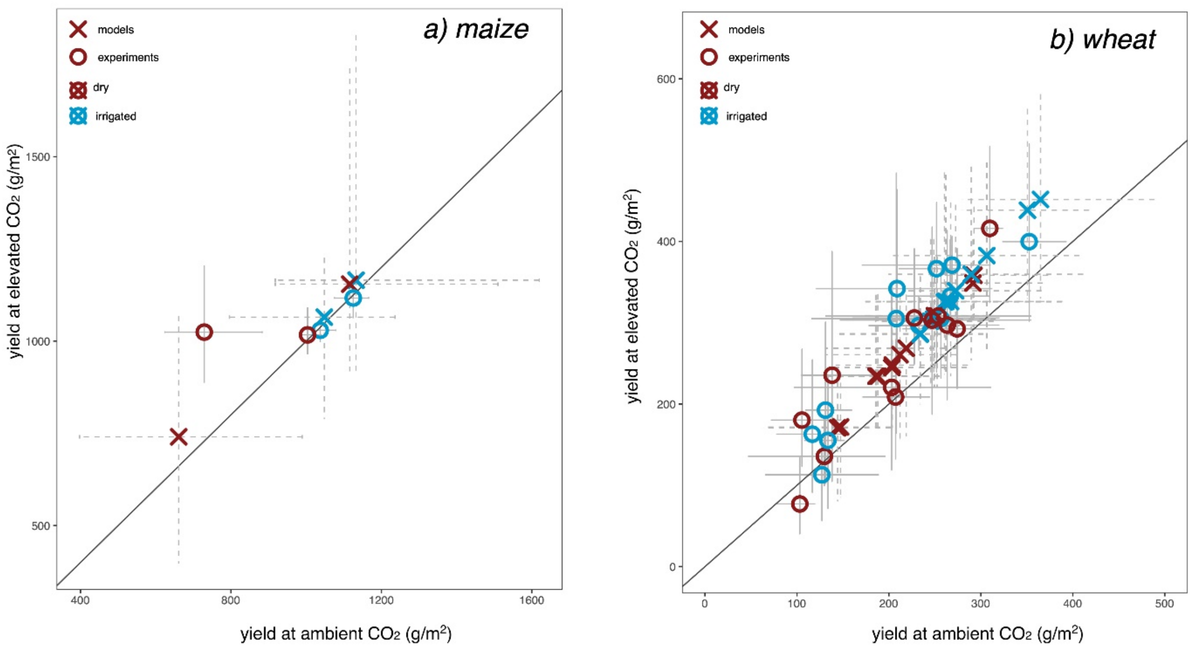

Figure 2. Yield responses (g/m²) to eCO_2 as measured in two FACE experiments[24,78] and simulated by crop models[70,73]. *a): maize yield responses to eCO_2 from a mixing ratio of 387 ppm to 550 ppm measured in the 2007-8 Braunschweig-FACE experiment[24] (northern Germany) under two levels of water 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[73], 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 2007-9 Horsham-FACE experiment[78] (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 6-member ensemble of models[70], is represented by grey dotted lines.

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 Figure S1). In most cases, crop models also tend to underestimate yield gains induced by eCO_2 when N is adequate under experimental conditions (Supplementary Figure S1).

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 (E) conditions and management (M) regimes (G×E×M) in which farmers produce crops. 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[79] have been developed and many of them have been used in multi-model assessments[28,80-82]. 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[5-7] that contribute to policy formulation[7,83]. Large-scale crop simulations introduce additional uncertainty compared to field-scale crop models due to lack of complete spatial and temporal data coverage on relevant agronomic information. Simulation and scenario approaches are used to fill current data gaps[84-

[89], and relevant global data are being marshalled to address these challenges. 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[91-93].

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 [7,94-95], under the implicit assumption that the no-eCO_2-effects scenario represented an acceptable lower limit of the uncertainty range (Supplementary Table S3). 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[96-97] 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 (i.e., with and without eCO_2) with global wheat and maize simulations under projected climate changes (Supplementary Figure 2). The high uncertainties induced by the 'without CO_2' lower bound ultimately reduce trust in the underlying crop models, whereas experimental knowledge on the eCO_2 effect, as well as crop models' ability to reproduce it, is substantial.

The large and growing body of experimental evidence has shown that current crop modeling 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, e.g., soil N and water availability[72], temperature and O_3[98-99] should be assessed.

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[73,100]. 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[73]. Other nutrients, such as phosphorus (P) and potassium (K), 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[101-103].

A serious gap in crop modeling tools is the scarcity of models for fruits and vegetables[66]. 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[69,104], while recent work on the socio-economic impacts[54,105] 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 (e.g., 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[106], 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[107].

Key criteria for improving modeling protocols

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

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 (i.e., aCO_2) crop yields, which should then be either bias-corrected or excluded from the crop model ensemble.

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[108]. 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 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 modeling inconsistencies	**Recommendations**	**Main requirements to address**
Data gap on crop nutritional quality, beyond N/protein	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, Infrastructure
Data gap in many agro-climatic regions of the world, especially Africa	Set up experiments in unstudied regions, especially in Africa	Funding, Expertise, 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; 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, Infrastructure
Lack of access to data	Set up and maintain an open-access data repository, e.g. within Copernicus and AgMIP	Funding, Communication, Database development
modeling uncertainty	- Use multi-model ensembles - Harmonization of variables and input data for modeling intercomparison exercises - Display and discuss additional measures other than the ensemble median - Use evaluation and validation criteria for inclusion of specific models	Research method, 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 time-varying dataset of the main input parameters	Research method, Funding, Infrastructure, Communication
Misleading scenarios using *without eCO_2* as plausible	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, Communication
Effects on crop quality in modelling assessment are overlooked	- Development of modeling components to simulate protein and mineral concentrations - Set up AgMIP multi-modelling inter-comparison activity for coordinated	Funding, Expertise, Research method

	model development and improvement that includes nutrient quality	

First, 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 modeling 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 modeling tools.

Secondly, crop model improvements should focus with high priority on capturing the complex interactions of eCO_2, N, O_3, and varying climate/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 modeling uncertainties[83]. Bias-correction techniques[109] 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 modeling 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.

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Acknowledgements

We thank EC-JRC for hosting the 'CO_2 Effects on Crops: Current Understanding, Modeling Needs, and Challenges' Workshop 8-10 October 2018 held in Ispra (Italy) co-sponsored by AgMIP.

AT and DD coordinated this community effort. All the authors contributed in writing, reviewing and interpreting the available literature. SA acknowledges support by the CGIAR research program on wheat agri-food systems (CRP WHEAT) and the CGIAR Platform for Big Data in Agriculture. TP acknowledges the Birmingham Institute of Forest Research. CR acknowledges the AgMIP Coordination Unit at Columbia University Earth Institute. FNT 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 organisations.

The authors declare no competing interests.