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Plant responses to rising atmospheric carbon dioxide (CO₂) 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 CO₂ concentrations. Recent concerted efforts have narrowed the uncertainties in CO₂-induced crop responses so that climate change impact simulations omitting CO₂ can now be eliminated. To address remaining knowledge gaps and uncertainties in estimating the effects of elevated CO₂ 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 (*eCO₂*, hereafter) on plant growth processes[4], crop yield quantity and quality. Yet, despite decades of experiments robustly demonstrating the effects of *eCO₂*[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 CO₂-fertilization* scenario obsolete.

Available experimental evidence of *eCO₂* effects

The role of *eCO₂* in stimulating crop growth has been documented since 1804, when De Saussure[8] reported that peas exposed to *eCO₂* 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 *eCO₂* effects on plant growth derived from those experiments has been synthesized in several topical and literature reviews as summarized below[9-11].

77   ***The effects of eCO₂ on crop productivity***. Kimball et al.[12] assembled more than 70 reports and

78   tabulated 430 prior observations of *eCO₂*-driven productivity changes in crops, concluding that

79   yields of C_3 species under a full complement of water and nutrients significantly increase with

80   a doubling of ambient CO_2 concentration (*aCO₂*; since that time, the CO_2 mixing ratio has

81   increased from 340 ppm to 412 ppm, which affects the degree of response to an experimental

82   doubling). However, crop responses to *eCO₂* vary by species and growing conditions[4].

83   Elevation of CO_2 concentration in FACE experiments (from a CO_2 mixing ratio of 353 ppm to

84   550 ppm) with ample water and nutrients increased yields of C_3 grains (e.g., wheat, rice, barley)

85   on average by 19%[4]. In contrast, the yield of C_4 crops (e.g., maize, sorghum) did not change

86   significantly when the crops were grown under ample water supply conditions. Variation in

87   CO_2 responsiveness across genotypes within species[13-15] has also been demonstrated in rice,

88   soybean, and wheat[16-17].

89   Beyond stimulating photosynthesis and growth, *eCO₂* also causes reduced stomatal

90   conductance by 19% to 22%[12,18-19] and reduced crop transpiration[4,20]. This leads to lower crop

91   evapotranspiration (ET), as demonstrated by the average 10% ET reduction in FACE

92   experiments for all investigated crops[4,21] (Supplementary Material S.1.1). Improved water-use

93   efficiency under *eCO₂* can enable crops to be more drought tolerant compared to crops grown

94   in *aCO₂*. This effect is particularly important for C_4 crops, for which yield increases have been

95   reported under water-limiting conditions in *eCO₂*. For example, FACE-sorghum[22-23] and

96   FACE-maize[24] experiments had average yield increases of 15% and 41%, respectively.

97   While under ample water and nutrient conditions, yields of most C_3 crops increase by 10% to

98   30% under *eCO₂* in experiments, yield stimulation due to *eCO₂* is generally smaller or

99   insignificant when nutrients are limiting. Nutrient deficiencies, such as nitrogen (N) and

100   probably also phosphorus (P) deficiency, can minimize *eCO₂* effects on crop productivity[4,25].

101   While *eCO₂* improves water-use efficiency, the *eCO₂* 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

152 (geographical) representativeness, temporal (timing and duration) distribution, numbers of

153 crops and cultivars, and analyze components besides yield (e.g., water use and nutrient

154 concentrations).

155 As shown in Figure 1a, *eCO2* experiments have been concentrated in Europe and the U.S., with

156 some significant multi-year, large-scale FACE studies in South America, Asia (Japan, China

157 and India), and Australia. There have been no *eCO2* experiments in Africa, where agriculture

158 provides significant livelihoods. Furthermore, Figure 1b highlights the need for more

159 experiments in order to achieve a better coverage of the diverse climatic conditions around the

160 world. There is also a lack of multiple-year *eCO2*-experiments, which are important for

161 grasslands and perennials, especially tree crops, and for understanding long-term effects on

162 soils and microbiota. A few long-term experiments have confirmed the ability of agro-

163 ecosystems to acclimate (i.e., reduced photosynthetic activity response compared to the initial

164 response, known as down-regulation) to a CO_2-rich environment[55] (Supplementary Material

165 S.1.4). Their results suggest that *eCO2*-induced effects in grasslands and perennial crops are

166 highly dependent on climatic conditions and that acclimation may take more than 3-5 years[56-

167 59]. Although acclimation is of less relevance for the main food crops, it is still an important

168 factor considering that it may act on shorter time scale and also looking at recent studies on

169 perennial grains[60] and the amplification of *eCO2* positive effects through crop generations[61].

170 Other types of experiments – including OTC, mini-FACE, climate control chambers and

171 enclosures – can be cheaper and faster. These experiments can significantly reduce

172 uncertainties by providing larger number of replicates and sample sizes, covering a larger range

173 of *eCO2* well above 550ppm, and thus complementing and further supporting the evidence

174 provided by the more expensive and time-consuming FACE experiments. OTC and mini-

175 FACE may also help in addressing the role of *eCO2* at night[62], as many FACE experiments

176 only enrich during daylight hours.

177
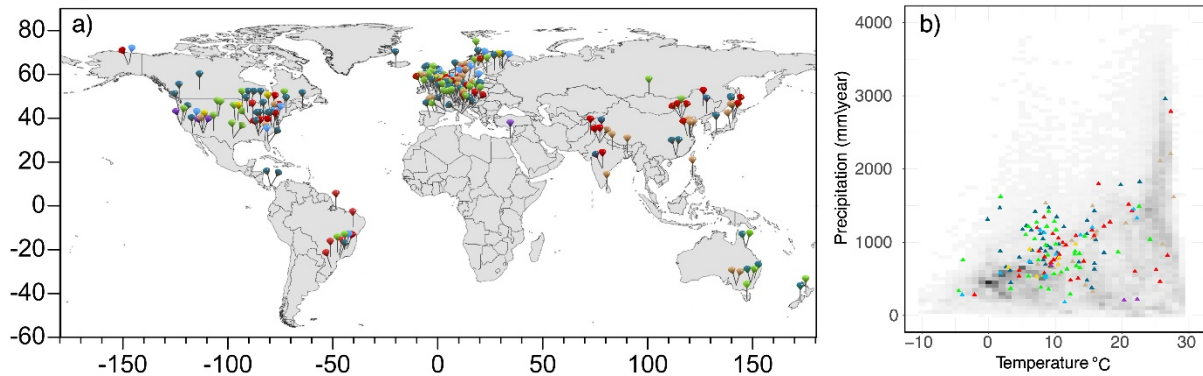
Figure 1. Overview of the eCO₂ experiments. *a). Global distribution of eCO₂ experiments on crops and grasslands. The distribution is derived from an updated version of the CLIMMANI Networking Group database (https://climmani.org, access date: October 2018; Table S2 in Supplementary Material) and other 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).

198 While existing crop models include CO_2 responses in the simulation of primary production,

199 they differ in the representation of transpiration and abiotic responses such as N stress[66].

200 Many crop models have been tested against observations conducted with eCO_2 up to 600 ppm

201 (FACE) and beyond (OTC). At the field scale under experimental conditions, crop models

202 performed reasonably well[68] in reproducing the main effects of eCO_2 under both ample and

203 limited water and N supplies, of higher temperatures on growth, harvestable yield, leaf area,

204 water uptake, and of N dynamics for wheat[69-71], rice[72], maize[73], cotton[74], potatoes[75-76], and

205 pasture[77]. Figure 2 shows two examples of eCO_2 effects on yield of wheat and maize as

206 simulated by crop models and measured in two dedicated experiments under different water

207 and climatic conditions[24,70,73,78]. Overall, good performance characterizes the modeling

208 simulations, although some discrepancies remain (e.g. in the case of maize under dry

209 conditions).
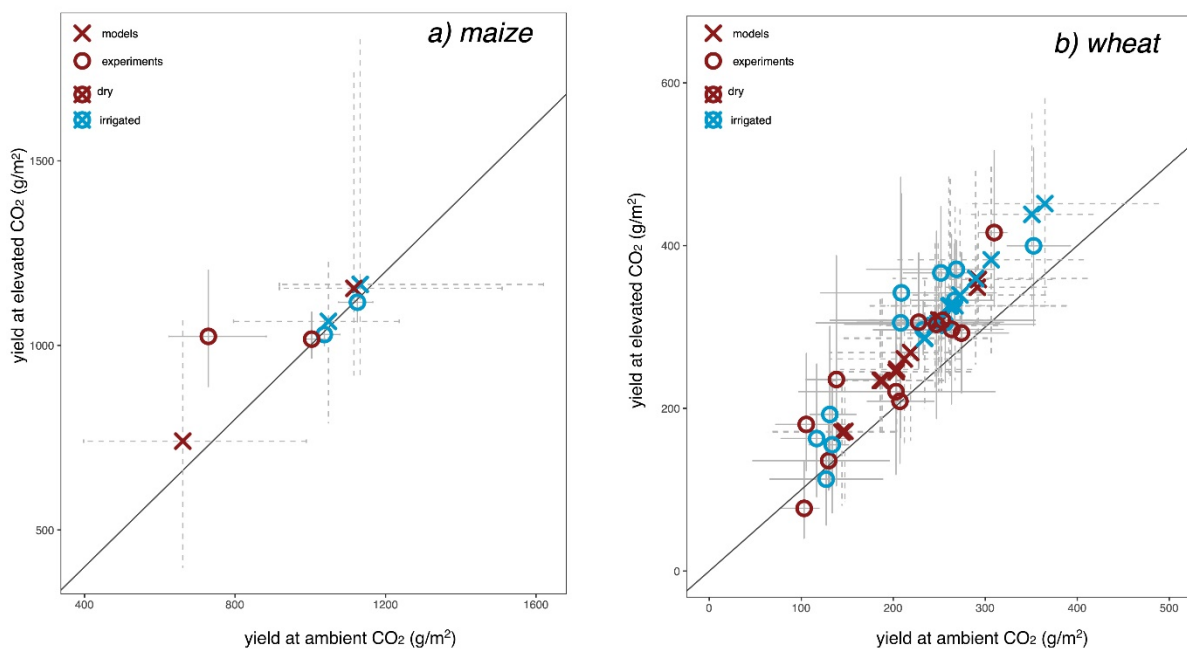
210

211 *Figure 2. Yield responses (g/m²) to eCO_2 as measured in two FACE experiments[24,78] and simulated by crop*

212 *models[70,73]. a): maize yield responses to eCO_2 from a mixing ratio of 387 ppm to 550 ppm measured in the 2007-*

213 *8 Braunschweig-FACE experiment[24] (northern Germany) under two levels of water supply: dry and irrigated.*

214 *Uncertainty in measured crop yield response (given by replicates performed in the FACE experiment) is*

221

222 Concerning the effects of N limitation in modulating the impacts of eCO_2, crop models in

223 general reproduce how the lack of adequate N reduces yield gains induced by eCO_2, although

224 uncertainties tend to be greater (Supplementary Figure S1). In most cases, crop models also

225 tend to underestimate yield gains induced by eCO_2 when N is adequate under experimental

226 conditions (Supplementary Figure S1).

227

228 **Scaling-up crop simulations from field experiments**

229

230 The high costs of running eCO_2 and climate change field experiments have prohibited the study

231 of a representative sample with respect to the crop genetics (G), environmental (E) conditions

232 and management (M) regimes (G×E×M) in which farmers produce crops. Process-based crop

233 models constitute an affordable solution to explore crop responses across a range of G×E×M

234 combinations and at any scale of interest. More than twenty global-scale crop models[79] have

235 been developed and many of them have been used in multi-model assessments[28,80-82]. These

236 global crop models follow the same dynamic process approaches of field-based models and

237 have been increasingly used in economic and climate impact studies[5-7] that contribute to policy

238 formulation[7,83]. Large-scale crop simulations introduce additional uncertainty compared to

239 field-scale crop models due to lack of complete spatial and temporal data coverage on relevant

240 agronomic information. Simulation and scenario approaches are used to fill current data gaps[84-]

241 [89], and relevant global data are being marshalled to address these challenges. Trust in crop

242 modeling capacity has been gained over the past five decades since models were first

243 developed[28] based on widespread comparison of simulated yields and other variables against

244 available field data and from multi-model comparisons[91-93].

The effects of eCO_2 in crop model simulations

247 Past climate change assessments have routinely presented crop yield 'with and without' the

248 effects of eCO_2 [7,94-95], under the implicit assumption that the no-eCO_2-effects scenario

249 represented an acceptable lower limit of the uncertainty range (Supplementary Table S3). That

250 extremely cautious approach has, however, generated unnecessary misunderstanding of

251 uncertainty regarding the current knowledge of eCO_2 on crops within climate change scenarios.

252 As a result, some studies[96-97] have used crop modelling results based on both 'with' and

253 'without' CO_2 simulations indistinguishably, potentially leading to misinterpretation of the

254 ensemble median, range, and causes for model (dis)agreement.

256 We demonstrate the issues in comparing crop model simulations with these different key

257 settings (i.e., with and without eCO_2) with global wheat and maize simulations under projected

258 climate changes (Supplementary Figure 2). The high uncertainties induced by the 'without

259 CO_2' lower bound ultimately reduce trust in the underlying crop models, whereas experimental

260 knowledge on the eCO_2 effect, as well as crop models' ability to reproduce it, is substantial.

262 The large and growing body of experimental evidence has shown that current crop modeling

263 approaches are increasingly able to capture the main effects of eCO_2 on crop growth and yield

264 under a wide range of growing conditions at field scale. Hence, we argue that these effects

265 should be included by default in climate change impact assessments: there is no longer a

266 scientifically valid reason for expanding the range of model uncertainties to include a 'without

267 eCO_2' scenario (other than quantifying the isolated effect). Under optimal growing conditions,

268 'with eCO_2' simulations should represent the upper bound of the uncertainty range. For the

269 lower bound, rather than using a 'without eCO_2' scenario, levels responding to observed

270 interactions of eCO_2 with abiotic stresses affecting crop growth, e.g., soil N and water

271 availability[72], temperature and O_3[98-99] should be assessed.

272

273 **Knowledge gaps in model development**

274 Under complex growth-limiting environmental conditions, interactive processes are less well

275 understood. A recent experiment on maize indicated that crop model results corresponded well

276 to the observations under irrigated conditions[73,100]. Nevertheless, some models had poor

277 performance under certain drought conditions (due to underestimation of eCO_2 water savings),

278 and therefore underestimated the associated crop yield stimulation[73]. Other nutrients, such as

279 phosphorus (P) and potassium (K), are often neither considered in crop models nor fully

280 measured or controlled in experiments, even though P is known to be a main limiting crop

281 nutrient in many soils, particularly in Africa[101-103].

282

283 A serious gap in crop modeling tools is the scarcity of models for fruits and vegetables[66]. This

284 situation is now improving, but models for many more fruits and vegetables with the full range

285 of eCO_2 responses are needed. In addition, most existing crop models do not account for

286 nutritional aspects other than protein concentration[69,104], while recent work on the socio-

287 economic impacts[54,105] of reduced Fe and Zn concentration highlights the importance of

288 including other key nutritional aspects, such as mineral concentrations. Finally, the upper range

289 of projected CO_2 concentration by the end of the 21st century (e.g., up to a CO_2 mixing ratio of

290 936 ppm in RCP8.5) greatly exceeds eCO_2 in current experiments. As the rate of C$_3$ crop

291 responses declines with *eCO₂* approaching 600 ppm[106], and considering that the current

292 atmospheric concentration is currently about 412 ppm and increasing by 2-3 ppm *per* year, key

293 performance of crop models for long-term assessments will depend on the representation of

294 this saturating response in interaction with other environmental variables, especially

295 temperature,[18] and possible physiological limitations[107].

296

297 **Key criteria for improving modeling protocols**

298 We argue that research and assessment should better focus on critical issues in projecting the

299 interactions of *eCO₂* and climate change on crops. To this end, key criteria for selecting crop

300 models for climate change impact assessments should advance the representation as listed

301 below.

    1. Concurrent and interactive effects of eCO_2, temperature, water and nitrogen (CTWN) on crop
302

303   processes;

304   2. Evaluation of simulated responses to CTWN variation compared to a range of observations

305   from experiments (including at least crop cycle length, leaf area index, harvestable yield,

306   evapotranspiration) for C_3 and C_4 crops including staple grains, fruits, and vegetables;

307   3. Comparison with observations to identify systematic biases in simulated baseline (i.e., *aCO₂*)

308   crop yields, which should then be either bias-corrected or excluded from the crop model

309   ensemble.

310 The results of these evaluation tests should be made available as metadata in impact

311 assessments, and crop models should be assessed in standardized evaluation exercises[108]. The

312 proposed criteria-based model could improve the robustness of multi-model impact

313 assessments.

314

315 **Roadmap to advance future research on *eCO₂***

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 eCO₂ 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 eCO₂* 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	

326

327 First, new *eCO₂* experiments are needed for important crops in all agricultural regions of the

328 world, particularly for cropping systems and agro-climatic regions in Africa, in order to capture

329 the full diversity of responses. More experimental evidence on changes in crop quality and

330 nutrition is needed for a wider range of crops to represent the threat for human health. All new

331 studies describing results from specific CO_2-enrichment experiments should provide

332 comprehensive and detailed weather, soil and management information to be easily integrated

333 and used for crop model evaluation.

334 Synchronization of field experiments and modeling outputs should be enhanced to steadily

335 improve crop models. Building connections among scientific disciplines will contribute to

336 better access and use of experimental data to encourage continuous development of impact

337 modeling tools.

338 Secondly, crop model improvements should focus with high priority on capturing the complex

339 interactions of *eCO₂*, N, O_3, and varying climate/weather conditions, especially extreme events,

340 and nutritional aspects. This crop model development will be fostered by an international

341 initiative to be launched within AgMIP, but urgently requires research funding as well.

342 Thirdly, in addition to the inclusion of *eCO₂* by default in impact assessments, the use of multi-

343 model ensembles should be strongly encouraged to better capture modeling uncertainties[83].

344 Bias-correction techniques[109] should be applied to deal with potential biases in crop yield

345 baseline simulations[28]

346 Finally, we propose to build an open-access web-repository (which could be hosted, for

347 example, in the Copernicus C3S data store in conjunction with AgMIP and other agricultural

348 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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