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1 Quantitative synthesis of temperature, CO₂, rainfall, and adaptation
2 effects on global crop yields

3

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12

13 Abstract

14 Climate change is known to impact crop yields, mainly through increased temperatures,
15 changing rainfall patterns and increasing CO₂ concentration in the atmosphere. Although the
16 potential effects of each of these factors have been discussed in a number of separate
17 studies, no recent synthesis has been published to provide quantitative estimates of climate
18 change impacts on crop yields, with or without adaptation strategies. In this paper, we
19 synthesize a broad range of experimental or modeling studies to estimate, at the global
20 scale, crop yield changes resulting from the marginal and combined effects of temperature,
21 CO₂ concentration and precipitation, with and without adaptation strategies. Crop yield
22 sensitivities are estimated by distinguishing between C3 and C4 crops. For C3 crops, our
23 results show that the positive effects of adaptation (+7.25%) and CO₂ (+9% for +100ppm) are
24 high enough to offset the negative effects of temperature increase (-2.4% for +1°C), even at
25 +4°C. On the other hand, for maize (i.e., the only C4 plant species in our database) the
26 somewhat low positive effect from increased CO₂ concentration and the absence of a
27 significant effect of adaptation lead to higher yield losses, in the order of -10% for +4°C. The
28 minimum level of CO₂ concentration increase requested to achieve a yield gain under
29 increased temperature conditions is much higher for maize than for C3 crops, in particular
30 for wheat. The estimated effects of adaptation are uncertain, especially for soybean and
31 rice, but also for maize, where the absence of a significant adaptation effect is probably at
32 least partly due to limited data availability. Our results demonstrate that CO₂ effects on crop
33 yields should not be overlooked in foresight studies on the impacts of climate change. Our
34 analysis also highlights the importance of improving the reliability of estimating the effects
35 of adaptation strategies on crop yields.

36

37 **Keywords:** Adaptation, Climate change, CO₂, ensemble modelling, meta-analysis, yield

38

39 1. Introduction

40 Many studies on the impact of climate change on crop yields, mainly through increased
41 temperatures, changing rainfall patterns and increasing CO₂ concentration have been
42 published in recent years. They are based on the results of experiments (Ainsworth and Long
43 2005, Long et al. 2006, Zhao et al. 2016, Zhao et al. 2017a), on simulations from single or
44 ensemble of mechanistic crop models (Asseng et al. 2013, Bassu et al. 2014, Makowski et al.
45 2015), or on statistical or machine learning models (Crane-Droesch 2018, Lobell & Asseng
46 2017, Lobell et al. 2011, Roberts et al. 2017). These studies provide a better understanding
47 of the impact of climate change on yields, in particular, of the magnitude of the so-called
48 "fertilizing" effect of atmospheric CO₂ concentration on biomass production (Long et al.
49 2006). It is now well established that C3 crops (e.g., wheat, soybean, rice) benefit more from
50 CO₂ concentration increase (Ainsworth and Long 2005; Fitzgerald et al. 2016; Long et al.
51 2006) than C4 crops (e.g., maize, sorghum). However, in practice, the effect of CO₂ on crop
52 yields is often ignored when assessing impact of climate change on crop yield of C3 crops,
53 both in scientific papers (Zhao et al. 2017a, b) and in reports presenting results of foresight
54 studies on climate change (FAO 2018).

55 Climate change impacts crop yields through other factors than CO₂, in particular through
56 temperature and rainfall changes. The rate of crop development and growth strongly
57 responds to temperature (Bonhomme et al 1994, Bonhomme 2000, Soltani and Sinclair
58 2012). Under conditions of increased temperature, the sum of temperature required for

59 development will be met more rapidly, hence reducing the amount of intercepted solar
60 energy and penalizing potential plant growth (Brisson and Levrault 2010). In addition to its
61 effect on the length of the growth cycle, temperature can have deleterious effects on crops
62 when it becomes higher than some thresholds, penalizing yields (Hunt et al. 2018) or
63 accelerating plant senescence by altering its photosystem (De la Haba et al. 2014) or
64 reproductive processes (Lizaso et al 2018). Several studies have shown that the effect of
65 rainfall on yields depends on various factors, related to its total amount and distribution
66 within the growing season, soil characteristics, in particular initial soil water conditions,
67 useful soil reserve, and soil rooting depth (Schlenker and Lobell 2010; Ray et al. 2015, Lobell
68 and Asseng 2017). Rainfall effects vary according to agricultural practices, in particular to
69 irrigation but also to the specific water requirements of species and varieties. In fact, various
70 adaptation strategies can be implemented by farmers to mitigate the negative effects of
71 temperature and rainfall changes on yields, including irrigation (Li and Troy 2018, Saadi et al.
72 2015), varietal improvement (Olesen et al. 2011, Nuccio et al. 2018) or changes in harvesting
73 or sowing dates (Caubel et al. 2018).

74 Although the potential effects of each of these factors have been discussed in a number of
75 separate studies, only a few syntheses have been published to provide quantitative
76 estimates of crop yield changes resulting from changes in temperature, CO₂, and rainfall
77 with or without adaptation strategy. Two meta-analyses published in 2014 synthesized
78 results of several studies (Challinor et al. 2014, Wilcox and Makowski 2014) but these two
79 papers did not include the most recent studies based on ensemble of crop models or global
80 experimental datasets.

81 The objective of our work is to provide a quantitative synthesis of the effects of changes in
82 temperature, CO₂ concentration and precipitation on crop yields from key scientific sources
83 of information. In our analysis, we estimate the yield losses or gains associated with
84 different levels of temperature increase, CO₂ increase, and changes in precipitation patterns,
85 while taking the crop photosynthetic pathway and adaptation strategies into account. We
86 report these effects both individually (i.e., for one variable at a time, with all others set to
87 zero) and in combination. Based on our results, we are hence able to disentangle the effects
88 of temperature, CO₂, rainfall and adaptation.

89 Given the high variability of estimated yield responses between sites or between models
90 (Asseng et al. 2013, Bassu et al. 2014, Li et al. 2015, Makowski et al. 2015), we chose to focus
91 only on bibliographic references that present the results from several sources of information
92 in the same analysis (e.g., three or more models). Our synthesis thus includes results from
93 ensembles of crop models (such as those from the AgMip project, Rosenzweig et al. 2014)
94 and from meta-analyses (e.g., Challinor et al. 2014, Wilcox and Makowski 2014, Zhao et al.
95 2016, Zhao et al. 2017a). The articles included in our analysis are systematically selected
96 according to a procedure based on explicit criteria. The data extracted from these articles
97 are analyzed using statistical models commonly used in meta-analysis. The levels of
98 uncertainty associated with our estimates are systematically presented to allow for a
99 transparent assessment of the robustness of our conclusions.

100 By adopting this approach, we are able to synthesize a large number of studies each using
101 several sources of information to estimate the impact of climate change on yields for a
102 group C3 species as a whole and for four major C3 and C4 crops separately (i.e., maize,
103 wheat, soybean, rice), and to analyze uncertainties associated. Our synthesis is based on

104 aggregated estimates provided by simulations of model ensembles and meta-analyses. As
105 these aggregated estimates are generally less uncertain than those provided by individual
106 studies or models (Koricheva et al. 2013, Wallach et al. 2016, 2019), our synthesis is
107 expected to produce robust conclusions that could be relevant for foresight studies on
108 climate changes, such as those produced by the Intergovernmental Panel on Climate Change
109 or the FAO.

110

111 2. Material and method

112 2.1. Systematic literature review

113 A bibliographic search was conducted in the web of science according to the following
114 research equation:

115 **TITLE:** ((Climat* and (change* or event* or condition* or factor* or variability or
116 regime*)) or future or trend* or projecti* or "warming" or forecast* or 2030 or 2040 or
117 2050 or 2100)

118 **AND TITLE:** (Crop or Cereal* or Maize or corn or wheat or rice or barley or sorghum or
119 oat* or rye or triticale or "Sugar plant*" or sugarbeet or sugarcane or beet* or "sugar
120 cane" or Oilcrop* or oleaginous or proteaginous or "oilseed crop*" or Rape* or Soya* or
121 soybean* or Sunflower or "Protein crop*" or pulse* or pea* or "faba bean*" or lupin* or
122 alfalfa or Forages or Grass or fodder or pasture* or canola or bean or grass* or "grain
123 legume*")

124 **AND TOPIC:** (meta-analys* OR (meta NEAR analys*) OR meta-model* OR (model*
125 NEAR inter-comp*) OR (model* NEAR intercomp*) OR (model* NEAR ensemble*))

126 **NOT TITLE:** (peak or beetle)

127 This bibliographic search allowed us to retrieve 113 articles as of 14/05/2018.

128 2.2. Study selection

129 To be selected, an item must meet the following criteria: (i) it must involve an analysis of the
130 climate change impact on crop yield, (ii) it must present the results of at least three different
131 yield estimation methods and/or at least three different crop models, (iii) it must present
132 yield values and the characteristics of the climate change scenarios tested (temperature
133 change, CO₂, precipitation). After application of the selection criteria, the final corpus
134 contains 16 review articles, published between 2008 and 2018 (Supplementary 1). The crops
135 represented are wheat (6 items), maize (5), soya (5), rice (7), barley (1) and grassland (1).
136 Depending on the case, these studies are carried out on the scale of a large geographical
137 region (e.g. Europe), a country, or a local site. The most represented countries are China (4
138 articles), Brazil (4 articles), USA (3 articles), India (3 articles) and France (2 articles). In total,
139 15 distinct geographical areas covering both temperate and tropical regions are concerned.
140 The results published in the articles are based on mechanistic (11) or statistical (5)
141 modelling. Two articles analyze a set of experiments. Some articles use several approaches.
142 The number of selected articles is relatively small, but each of them includes several
143 individual studies (3 to 346) and several scenarios.

144 2.3. Data extraction

145 The following information has been extracted from the selected articles:

146 - article references (title, authors, date of publication)

147 - geographical coordinates for site studies or countries or regions

- 148 - the crop species concerned
- 149 - scenarios of changes in temperature, precipitation and CO₂
- 150 - the future horizons considered and the reference period
- 151 - the average impacts of climate change on yields (relative change in yield in % of
- 152 baseline estimated by combining all available individual models/studies)
- 153 - information about the uncertainty of the average impacts reported in the articles
- 154 (standard deviations or confidence intervals)
- 155 - the number of individual studies or models analyzed
- 156 - the adaptation strategies considered (change of sowing dates, irrigation, varietal
- 157 improvement, when tested).

158 Data were extracted from the text or tables of the selected articles. When the data was not
159 directly accessible, the web plot digitizer software was used to extract it from the figures.
160 Finally, some missing data were retrieved directly from the authors. The total number of
161 relative yield change values extracted from the 16 items is 310 (about 40% in temperate
162 areas, 44% in tropical areas, 16% in both). These data are presented in Figure 1 as a function
163 of changes in temperature, precipitation, and CO₂ concentrations considered in the selected
164 articles. The majority of the relative change in yield values are between -10% and +10%.
165 Note that, for maize and rice, the number of scenarios of increasing precipitation is very
166 small (two and one, respectively), and that no scenario of decreasing precipitation is
167 considered in the selected references for these two crops. The file including the data is
168 available on request.

169

170 2.4. Statistical analysis

171 The objective of our statistical analysis is to estimate the relative change in yield due to
172 climate change (Y) as a function of changes in temperature (T), precipitation (P), metabolic
173 pathways of carbon fixation (i.e., C3 or C4 plants), atmospheric CO₂ concentration (C) and
174 adaptation to climate change (i.e., change in planting date, varietal choice, and/or
175 irrigation). Given the available data, a global binary variable indicating the application (or
176 not) of adaptation strategies was considered (I), without distinguishing between different
177 types of adaptation.

178 The analysis is performed with a mixed model including a random effect associated with the
179 different studies (defined by the combinations Articles*Sites because the same article can
180 contain several sites). The random effect allows for the heterogeneity between the different
181 studies included in our database. This type of model is often used to manage heterogeneity
182 in meta-analysis (i.e., quantitative synthesis of data collected in different situations). A global
183 model was adjusted for all C3 crops, and other models were adjusted species by species for
184 wheat, maize, soybean and rice. As the only C4 species included in our database is maize, it
185 was not necessary to define a C4 model in addition to the maize model.

186 The model for C3 crops (as a group) is defined by:

$$187 Y_{ij} = a_{Ti}T_{ij} + a_P P_{ij} + a_C C_{ij} + a_{CT} C_{ij} T_{ij} + a_A I_{Aij} + \varepsilon_{ij} \quad (1)$$

188 Y_{ij} is the relative change in yield in % with respect to site reference i for scenario j, a_{Ti}
189 corresponds to the effect of the increase of one degree Celsius on yield for study i, a_P is a
190 parameter describing the effect of the 1% increase in precipitation on yield, a_C is a
191 parameter describing the effect of increasing by one ppm of CO₂, a_A is the parameter
192 corresponding to the effect of adapting to climate change, a_{CT} is a parameter describing the

193 interaction between the effect of increasing temperature and of increasing CO₂. Variable I_{Aij}
194 is a dummy variable equal to 1 for situations where adaptation is present, and equal to zero
195 otherwise. The variables T_{ij} , P_{ij} and C_{ij} are the changes of temperature, rainfalls and CO₂
196 concentrations on site i and scenario j , respectively. The sites considered are well suited for
197 each crop, and our model does not cover regions out of the current cropping area of the
198 respective species. The temperature effect a_{Ti} is assumed to vary from one study to another
199 according to a Gaussian distribution $a_{Ti} \sim N(\mu_T, \sigma_T^2)$, with μ_T the global expected value of
200 a_{Ti} and σ_T the between-study standard deviation of a_{Ti} . This random term recognizes that
201 the effect of temperature on yield is likely to vary depending on the characteristics of the
202 environment and crop, but also on the method used (e.g., selected crop models). The term
203 ε_{ij} is a random error distributed according to a Gaussian distribution $\varepsilon_{ij} \sim N(0, \tau_{ij}^2)$,
204 describing intra-study variability, with τ_{ij} the residual standard deviation for study i and
205 scenario j . The values of τ_{ij} are assumed to be proportional to the standard deviations
206 extracted from the selected articles in order to give less weight to the most uncertain
207 studies.

208 Our statistical model cannot be used to simulate the effects of a specific heat stress or
209 drought occurring at certain stages or on certain date because it does not explicitly take into
210 account the dates of occurrence of heat and water stresses. However, the parameters of our
211 statistical models are estimated from data mostly generated by process-based crop models
212 that do simulate the timing of these stresses (albeit imperfectly). Thus, the estimated
213 parameter values of our model are indirectly dependent on the dates of occurrence of heat
214 and water stresses and their corresponding crop growth stages.

215 Several variants of the model (1) were tested under the following assumptions: (i) the effects
216 of precipitation, CO₂, and adaptation vary between studies (such as the temperature effect
217 a_{Ti} presented above), (ii) interactions exist between temperature and precipitation, and
218 between precipitation and CO₂. These variants of the global model (1) were not retained;
219 either they could not be adjusted to the data because of identifiability problems (model too
220 complex compared to available data), or they led to higher AIC values (Akaike information
221 criterion) reflecting a less optimal compromise between likelihood and complexity than that
222 offered by the initial model, or they included non-statistically significant effects. The residual
223 analysis does not reveal any particular issue (Supplementary 2). Quality of fit is similar for
224 both considered sources of data (i.e., model ensembles and meta-analyses), and is better for
225 wheat ($R^2=0.85$), maize ($R^2=0.84$) and soybean ($R^2=0.89$) than for rice ($R^2=0.5$). The lower
226 quality of fit obtained for rice is due to the relatively large residuals obtained for
227 temperature change of +6°C. Results obtained for this level of temperature change should
228 thus be interpreted with caution for rice. We tried to fit the model for each continent
229 separately, but the results were not conclusive due to a lack of data.

230 The species-by-species analyses were carried out using the model (1) by estimating its
231 parameters based on the data reported specifically for the species in question. For some
232 species, simplified versions of the model (1) were selected because they led to a reduction in
233 the AIC criterion. Depending on the crop species, the effects of P_{ij} , $C_{ij}T_{ij}$ interaction and/or
234 I_{Aij} adaptation were significant or not (Supplementary 3). The interaction between
235 temperature change and CO₂ change was significant ($p<0.001$) for the C3 model and for the
236 rice model. This means that, in these models, the effect of CO₂ depends on the level of
237 temperature change. Since the interaction parameter here is negative, the positive effect of
238 CO₂ on yield decreases as the temperature change increases.

239 The parameters μ_T , σ_T , a_P , a_C , a_A et a_{CT} were estimated by restricted maximum likelihood
240 using the R lme4 package. All the estimated parameter values of the selected models are
241 available in Supplementary 3. Once the parameters estimated, the global C3 model and the
242 models selected species by species were used to compute the relative change in yield
243 resulting from temperature increases of +0, +2, +3, +4°C, for CO₂ content increases of +0,
244 +100, and +200ppm, precipitation decreases of 0 and -10%, with and without adaptation to
245 climate change. The proposed models can easily be reused to test other temperature and
246 CO₂ combinations than those considered here. In particular, it is possible to compute the
247 frontier describing the minimum levels of CO₂ concentration increase requested to achieve a
248 yield gain. Thus, based on model (1), a yield gain is expected when the CO₂ concentration
249 increase exceeds the value calculated from

$$250 \frac{-1}{a_C + a_{CT} T_{ij}} (\mu_T T_{ij} + a_P P_{ij} + C_{ij} + a_{CT} C_{ij} T_{ij} + a_A I_{Aij}) \quad (2)$$

251 Uncertainty was analyzed by computing 95% confidence intervals by bootstrap for all
252 relevant quantities.

253

254 3. Results

255 In this section we present first the results of the marginal effects of changes in temperature,
256 precipitation, CO₂ and adaptation (3.1) and then the combined effects of these factors (3.2).

257

258 3.1. Marginal effects of changes in temperature, precipitation, CO₂ and adaptation

259 The estimated values of the parameters μ_T , a_P , a_C , a_{CT} , and a_A respectively describe the
260 marginal effects of temperature, precipitation, CO₂ concentration, CO₂-temperature

261 interaction, and climate change adaptation. Each marginal effect quantifies the impact on
262 yield of a unit increase in one of the factors taken individually, i.e., without taking the effect
263 of the other factors into account (all set equal to zero). The estimated values of these effects
264 are presented in Figures 2 and 3.

265 For temperature (Figure 2A), the estimated values range from -1.42% (for rice, C3) to -4.52%
266 (for maize, C4) yield for an increase of +1°C. The overall estimate for all C3 crops is -2.40%.
267 The estimated values are all significant ($p < 0.05$) except for soybean where the estimated
268 impact of temperature is highly uncertain.

269 For CO₂ (Figure 2B), the effect of an increase of +1ppm is significant and positive in all cases,
270 but is significantly lower for maize (C4) (+0.02% yield per ppm, or 2% for 100 ppm) than for
271 C3 crops. In average over all C3, the effect is about +9% for +100ppm (+0.09 per ppm). The
272 interaction between temperature and CO₂ is significant for rice (Figure 2C). This interaction
273 is negative, indicating that the positive effect of CO₂ is hampered by temperature increases.
274 For example, this interaction induces an additional rice yield decrease of -0.02% for +1ppm
275 and +1°C or, equivalently, -2% for +100ppm and +1°C.

276 The effect of a 1% increase in growing season cumulated rainfall on crop yield is significant
277 and positive for the group of C3 crops (+0.27%), as well as for wheat (+0.43%) and soybean
278 (+0.32%) separately (Figure 2D). For maize, this effect is close to zero and not significant,
279 partly because maize is either cultivated in regions exhibiting rainy growing seasons or
280 irrigated by default in most of the selected studies. For rice, the uncertainty is high and does
281 not allow to robustly conclude.

282 The effect of adaptation (all types of adaptation combined) (Figure 3) is significant when all
283 C3 crops are analyzed simultaneously (+7.25%) and for wheat (+10.4%). The effect is close to

284 zero for maize. For rice and soybean, the results are very uncertain and do not allow us to
285 conclude.

286

287 3.2. Estimation of the combined effect of temperature and CO₂ changes

288 The model (1) was used to estimate the effects of different combinations of temperature
289 and CO₂ concentration increases, with/without adaptation, and with/without a decrease in
290 precipitation for all C3 crops altogether (Figures 4 and 5). Without adaptation, significant C3
291 yield gains of +5.1 to +7.8% (depending on whether rainfall is reduced or not) are obtained
292 when the temperature increase is limited to +2°C and associated with a +200ppm increase in
293 CO₂ (Figure 4A,B). On the other hand, yield losses ranging from -5.1 to -12.2% are estimated
294 in case of a temperature increase of +4°C combined with a 10% decrease in precipitation
295 (Figure 4B).

296 For C3, the increase in CO₂ has a positive effect on yield, but this positive effect could be
297 partly offset by stronger temperature increase (Figure 5). This is due to the interaction
298 between temperature and CO₂, estimated at -0.01% for +1°C and +1ppm for all C3 crops
299 combined (Figure 2). When temperature increase reaches +4°C, the interaction effect equals
300 -0.04% and partially compensates for the positive CO₂ effect estimated for C3 at +0.09% per
301 ppm. Thus, the level of yield increase due to the positive effect of CO₂ on photosynthesis is
302 smaller at +4°C than at +2°C (Figure 5).

303 As we said before, adaptation could have a strong effect on yields (+7.25% for C3 in Figure
304 3). The effect of a +2 and +3°C temperature increase combined with respectively a +100 and
305 +200ppm CO₂ concentration increase become positive and significantly different from zero

306 when adaptation is considered and assuming no or small rainfall decrease (Figure 4C
307 compared to 4A and 4D compared to 4B).

308 The selected statistical model for maize (C4) includes a temperature effect and a CO₂ effect,
309 but no precipitation effect, interaction or adaptation (not significant, see Figures 2-3). The
310 absence of effect of precipitation on maize yields is unexpected and could be due to the
311 limited number of scenarios considering water stress in our dataset. For this crop, the
312 combined effect of temperature and CO₂ increases is systematically negative; estimated
313 yield losses range from -4.6% to -17.3% depending on the scenario considered (Figure 6).
314 The estimated losses for +4°C systematically exceed -13% but the levels of uncertainty
315 obtained for this temperature increase are high and significantly higher than those obtained
316 for +2 and +3°C.

317 For wheat (C3), the selected model includes all the effects of model (1) except the
318 temperature/CO₂ interaction which is not significant (Figure 2). When there is no adaptation,
319 the temperature increase is associated with significant yield gains if the CO₂ increase
320 exceeds 200ppm, but it can lead to yield losses when the CO₂ increase is lower (Figure 7AB).
321 Losses are higher in the event of a 10% decrease in rainfall, but despite the negative effect of
322 a rainfall decrease, the yield loss for wheat is not statistically significant when combined with
323 an increase of +4°C and 200ppm of CO₂ (Figure 7B). When an adaptation strategy is applied,
324 no significant yield loss is estimated for wheat, with the only exception of a – physically
325 unlikely - situation corresponding to a temperature increase of +4°C but without any CO₂
326 increase (Figure 7CD). For a CO₂ increase of +200ppm associated with a temperature
327 increase of +4°C, a yield gain of 9 to 13% is estimated for wheat if adapted.

328 Based on the fitted maize and wheat models, we computed the minimum levels of CO₂
329 increase requested to obtain a positive yield change (yield gain) for +0 to +6°C (Figure 8) and
330 we determined frontiers of CO₂ increase level above (below) which a yield gain (loss) is more
331 likely than not (Eq.2). Here, we assume that no adaptation strategy is applied. Results show
332 that the CO₂ frontier obtained for maize is well above the one obtained for wheat. Thus, at
333 +2°C, an increase in CO₂ concentration of more than +300 ppm would be necessary to obtain
334 a yield gain in maize crops. But, for wheat without adaptation, a yield gain is expected as
335 soon as the CO₂ concentration increases by +50ppm at +2°C and by +150ppm at +4°C (Figure
336 8). The frontier is even lower for wheat in case of adaptation (not shown).

337 For soybean (C3), the selected model includes temperature, CO₂ and precipitation effects,
338 but no adaptation or temperature/CO₂ interaction effects (no significant effect at 5%, see
339 Figures 2-3). The estimates obtained are quite similar to those obtained for wheat without
340 adaptation with slightly lower losses and slightly stronger gains for the same temperature
341 and CO₂ combinations (Figure 9). For CO₂ increases of +200ppm, the estimated yield gain
342 exceeds 10% for +2°C, even if precipitation decreases by 10%. The gain also exceeds 10% for
343 a temperature increase of +3°C if rainfall is not reduced. On the other hand, soybean yield
344 gain becomes not statistically significant at +4°C (Figure 9).

345 For rice (C3), the selected model includes temperature, CO₂, temperature/CO₂ interaction
346 and adaptation effects, but no precipitation effect (non-significant effect, see Figure 2).
347 Without adaptation, yield losses of -3 to -5% are estimated for a temperature increase of
348 +4°C, but a yield gain is estimated when CO₂ increases by +100 ppm and temperature
349 increases by +2°C (Figure 10A). A slight gain is also estimated if temperature increases by
350 +3°C and CO₂ by +200 ppm. With adaptation, no significant yield loss is estimated for

351 temperature increases less than or equal to +4°C; yield gains can even reach 15% if the
352 temperature only increases by +2°C and the CO₂ content increases by +200ppm or more
353 (Figure 10B).

354

355 4. Discussion

356 The difference in CO₂ yield response between C3 and C4 plants is consistent with known
357 photosynthesis mechanisms. C4 plants (e.g., maize, sorghum, millet, and sugar cane) have a
358 mechanism for supplying CO₂ to leaf sites where it is fixed on sugars and it is therefore the
359 concentration of photosynthetic enzymes that limits photosynthesis and not the
360 concentration of CO₂. Their photosynthesis rate hence does not strongly respond to CO₂
361 variations at values higher than current concentration levels. On the contrary, under optimal
362 growing conditions, C3 plants do not have these concentration processes in the leaf and are
363 instead limited by atmospheric CO₂ concentration (Ainsworth 2008, Gao et al 2015).
364 However, to benefit from the positive effect of increasing CO₂ concentrations, C3 plants
365 require a concomitant increase in nitrogen supply from the soil (Weigel and Manderscheid
366 2012, Manderscheid et al 2010). If nitrogen supplies are not adjusted, then the positive
367 impact of CO₂ increase is reduced (Lakshmi et al 2017), except for leguminous plants that
368 use part of the photosynthesized sugars to feed their nitrogen fixing symbionts (Li et al 2017,
369 Matsunami et al, 2009, Oikawa et al 2010). In addition, for C3 crops and in particular for rice,
370 we found a negative interaction between CO₂ and temperature change revealing that the
371 positive effect of CO₂ on yield is partly offset by an increase in temperature. For rice, the
372 negative interaction between temperature and CO₂ may come from the fact that the
373 increase in CO₂ itself generates a temperature increase in the rice vegetation cover (Li et al.

374 2015). The divergent effects of CO₂ between C3 and C4 estimated in our study are consistent
375 with the results of Webber et al. (2018) who indicated that climate change could result in
376 yield losses for grain maize but gains for winter wheat.

377 The ability of adaptation strategies to mitigate the potential negative impact of climate
378 change is discussed in a number of published studies (Challinor et al., 2014; Li and Troy,
379 2018; Lipper et al., 2014; Wilcox and Makowski, 2014). The strong effect of adaptation that
380 we found on wheat yields is partly due to the meta-analysis of Challinor et al (2014) which
381 reports a high estimated value for this parameter. Irrigation (when allowed by local water
382 availability) is a direct way to protect against climate change induced droughts (Li and Troy
383 2018). However, irrigation can increase greenhouse gas emissions through energy use,
384 creating a negative feedback on the long term (Lipper et al. 2014). In addition, water
385 availability and water quality (e.g. salinization) are expected to decrease in some areas. An
386 increase in the quantity of water used for irrigation can also generate water use conflicts,
387 e.g., as in California (Grantham and Viers 2014). Its use can be improved by more efficient
388 technologies such as precision irrigation and more efficient deficit irrigation strategies
389 (Wolfe et al. 2018).

390 Varietal improvement is another adaptation strategy and mostly relies on the use of earlier
391 or later varieties, the modification of the photoperiod (Olesen et al. 2011) or, more rarely,
392 the use of drought-tolerant varieties (Nuccio et al. 2018). Farmers can also adapt to climate
393 change by changing sowing dates, harvesting dates or plant density without necessarily
394 changing the varieties themselves (Caubel et al. 2018). These types of adaptation can be
395 already observed in many parts of the world, for example for French vines with increasingly

396 early harvest dates (Webb et al. 2012, Jones et al. 2005) and for maize in central United
397 States with increasingly early planting dates (Kucharik 2008).

398 The effectiveness of a few adaptation strategies has been assessed in previous studies
399 (Basso et al. 2015, Challinor et al. 2014, Wilcox and Makowski 2014), including changes in
400 sowing dates, crop varieties or irrigation. The results of these studies show that these
401 strategies partially offset the negative impacts of climate change on crop yields. Other more
402 systemic adaptation strategies exist; they are based on profound changes in agricultural
403 systems e.g., adoption of soil conservation systems (Powlson et al. 2016) or systems based
404 on agroforestry (Verchot et al. 2007), changes in the composition of rotations or substitution
405 between species (Olesen et al. 2011).

406 It is important to keep in mind that the effectiveness of these strategies depends on the
407 socio-economic context, and may present heterogeneous results at the global level (Hoegh-
408 Guldberg et al. 2018). In modeling studies, adaptation strategies are tested under optimal
409 conditions, and simulated benefits should thus be considered as potential. Practical or social
410 constraints could reduce the effectiveness of adaptation strategies such as irrigation, and
411 could limit farmers' ability to obtain high yields in the future. Also, extreme weather events
412 and development of pests and diseases induced by climate change could reduce the
413 expected benefit of adaptation strategies (Gouache et al., 2013; Webber et al., 2018).

414 Our approach has several limitations. We present here only a single global statistical model
415 for each crop species, without any regional differentiation. We attempted to fit our
416 statistical models for each continent separately, but the confidence intervals were very large
417 and the estimated values were not informative. Note that our global statistical models could
418 nevertheless be implemented regionally using regional climate data as inputs. Spatialized

419 yield gain/loss resulting from climate change are available in a number of published reports
420 but these studies usually rely on a small number of model outputs. For example, the report
421 of the Joint Research Center (Donatelli et al., 2012) assesses the effects of several climate
422 change scenarios on maize, wheat, rice, rape and sunflower yields in Europe. Some of their
423 results have been taken up and completed in Donatelli et al (2015). This study was carried
424 out both at national level and at the level of NUTS2 regions for all countries of the European
425 Union. Two climate models HadCM3 ("warm scenario") and ECHAM5 ("cold scenario") were
426 used, but only one crop model (BIOMA) was run. No adaptation strategy was considered.
427 Yield projections were made at time horizons close to 2020 (+45ppm CO₂) and 2030
428 (+65ppm CO₂) compared to a reference period corresponding to 1996-2005. For maize, yield
429 simulations indicate a gain of +10% and a loss of -9% for the "cold" and "warm" scenarios,
430 respectively. Apart from sunflower, the average losses are therefore somewhat low, and
431 close to zero for maize and rice, -1% for wheat and -2.5% for rapeseed. These average values
432 are close to those obtained for the +2°C and +100ppm CO₂ scenario for wheat and rice in our
433 own study. However, these averages hide significant regional disparities within Europe.

434 Another limit of our study is that it covers a limited number of crop species. Only four major
435 crop species are indeed considered here, namely wheat, maize, soybean, and rice. Some
436 previous studies assessing climate change impacts consider a higher number of crop species,
437 but others studies present aggregated results for large groups of crop species. For example,
438 in the report by Müller et al (2010), yield projections are performed on average over a wide
439 range of crops (wheat, rice, maize, millet, millet, peas, sugar beet, sweet potato, soya,
440 groundnut, sunflower, rape) but simulated yields are averaged over all species and are not
441 presented crop by crop. The results obtained for C3 and C4 plants are therefore not
442 presented separately in this report. About thirty climate scenarios are considered and yields

443 are simulated with the LPJmL model directly at the global scale. Two series of simulations
444 are carried out successively, first without any effect on yields of CO₂ concentration increase,
445 and then taking its effect into account. With CO₂ effect, the results show an average yield
446 gain of 12.4% worldwide. On the other hand, without CO₂ effect, an average loss of -6.5%
447 was estimated. This result is consistent with the strong positive effects of CO₂ on the yields
448 estimated in our study for C3 plants.

449 In our analysis, the effects of temperature, precipitation and CO₂ on crop yields are
450 calculated for a large variety of soil types in different geographical areas. Yield variations
451 presented in our study should therefore be interpreted as average responses and it is
452 important to keep in mind that local values of these responses may be significantly different
453 from the average values under particular soil conditions (Kersebaum and Nendel, 2014). This
454 is particularly true for yield response to precipitation, which is known to be dependent on
455 initial soil water conditions, soil water holding capacity and on plant rooting depth (He and
456 Wang, 2019) and may hence differ from aggregate values across several soil types (Lobell
457 and Burke 2010). It has been shown that the local sensitivity of yields to changes in
458 precipitation may differ from aggregate values across several soil types (Lobell and Burke
459 2010). In addition, in our study, we were unable to explore in detail the effect of rainfall
460 changes on maize and rice yields due to the limited number of scenarios considering rainfall
461 changes for these two crops. For rice and maize, the uncertainty is high and does not allow
462 for robust conclusions on the effect of rainfall changes on yields.

463 Our approach does not directly quantify yield losses due to pests and diseases. However, the
464 effects of climate variables on pests and diseases are multiple and are difficult to estimate.
465 Relative air and soil humidity impact the survival and reproduction of pests and diseases

466 (Roos et al. 2011). Winter temperatures can have a significant impact on the survival of
467 pathogens and insect pests (Gouache et al. 2013, Bale et al. 2002, Roos et al. 2011).
468 Additional effects on the spatial distribution of insect populations cannot be ruled out (Bale
469 et al. 2002). Recently, it has been shown that climate change could strongly impact the level
470 of crop destruction by insects (between 10 and 25% additional losses for wheat, maize and
471 rice per degree Celsius of warming) via an effect of temperature on insect metabolism
472 (Deutsch et al. 2018).

473 Despite these limitations, we were able to establish simple analytical functions quantifying
474 the individual and combined effect of temperature, CO₂, precipitation and adaptation of
475 practices on yields of several major crop species. Our results show that it is not reasonable
476 to overlook the effect of CO₂ on yields when studying the effect of climate change on crop
477 production. Yet, this effect was disregarded in several recent articles (Zhao et al. 2017a,b)
478 and reports (FAO, 2018). Thus, FAO (2018) estimates the impacts of climate change on the
479 yields of different types of crops by 2050 at a global scale. The estimated impacts are
480 derived from FAO-IIASA GAEZ simulations obtained using a set of climate data from five
481 different climate models. RCP scenarios 4.5, 6 and 8.5 were considered successively and
482 these scenarios correspond to temperature increases of about 2.5, 3.5 and 4.5°C
483 respectively. The results of these models suggest that climate change will mainly have
484 negative impacts on yields, with reductions of about 5% globally by 2050 compared to 2012
485 for all crops combined. According to this report, the effect of climate change is negative on
486 wheat yields, including in Europe. However, it is important to note that these results were
487 obtained while neglecting the CO₂ effect, which has a positive effect on yields, particularly
488 on wheat yields, as shown in our study. We believe that our simple models could be used in
489 future foresight studies to take CO₂ effect on crop yields into account.

490

491 5. Conclusion

492 Our work is based on a quantitative synthesis of a wide range of studies assessing the impact
493 of climate change on crop yields and could be relevant for future foresight studies on
494 climate change.

495 For C3 plants, our results show that the positive effects of adaptation (+7.25% for all C3) and
496 CO₂ (+9% for +100ppm for all C3) are high enough to offset the negative effects of a
497 temperature increase, even at +4°C (-2.4% for +1°C). On the other hand, for maize (the only
498 C4 plant represented in our database), the low positive effect of CO₂ and the absence of
499 significant effect of adaptation strategies lead to yield losses, in the order of -10% for +4°C.
500 Our results thus clearly demonstrate that effect of CO₂ should not be overlooked when
501 studying climate change impacts on crop yields.

502 Our analysis also highlights the need for more reliable estimates of the effects of key factors
503 influencing crop yields, in particular of climate change adaptation strategies. The effects of
504 adaptation are somewhat uncertain, especially for soybean and rice, but also for maize,
505 where the absence of a significant adaptation effect is probably at least partly due to the
506 limited data available. The mechanisms underlying the interaction between temperature
507 and CO₂ should also be studied more precisely, in particular for rice, a crop for which this
508 interaction is significant.

509

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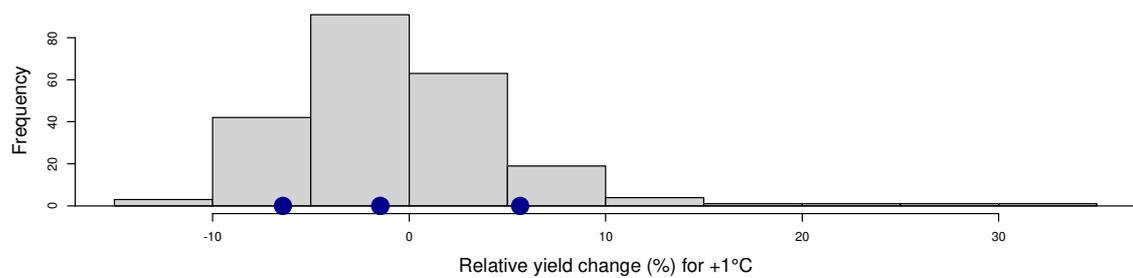
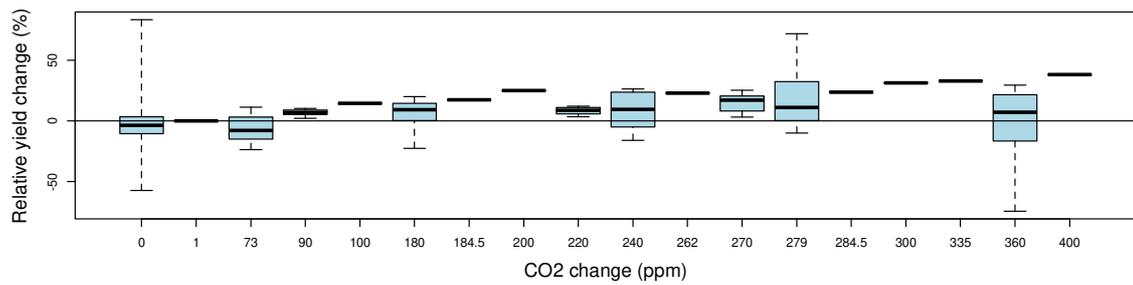
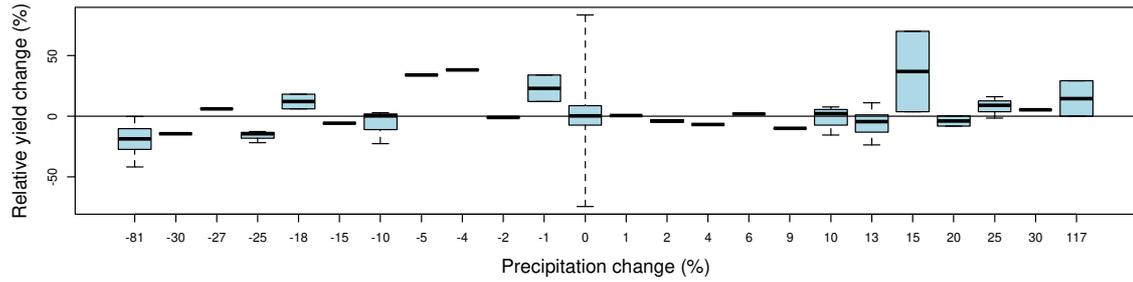
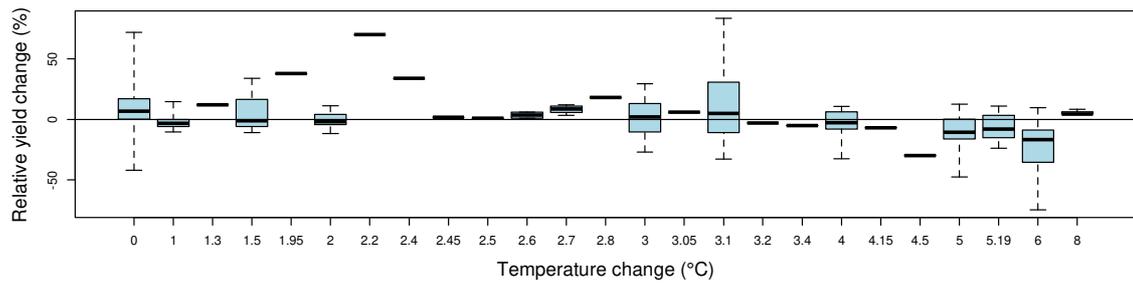
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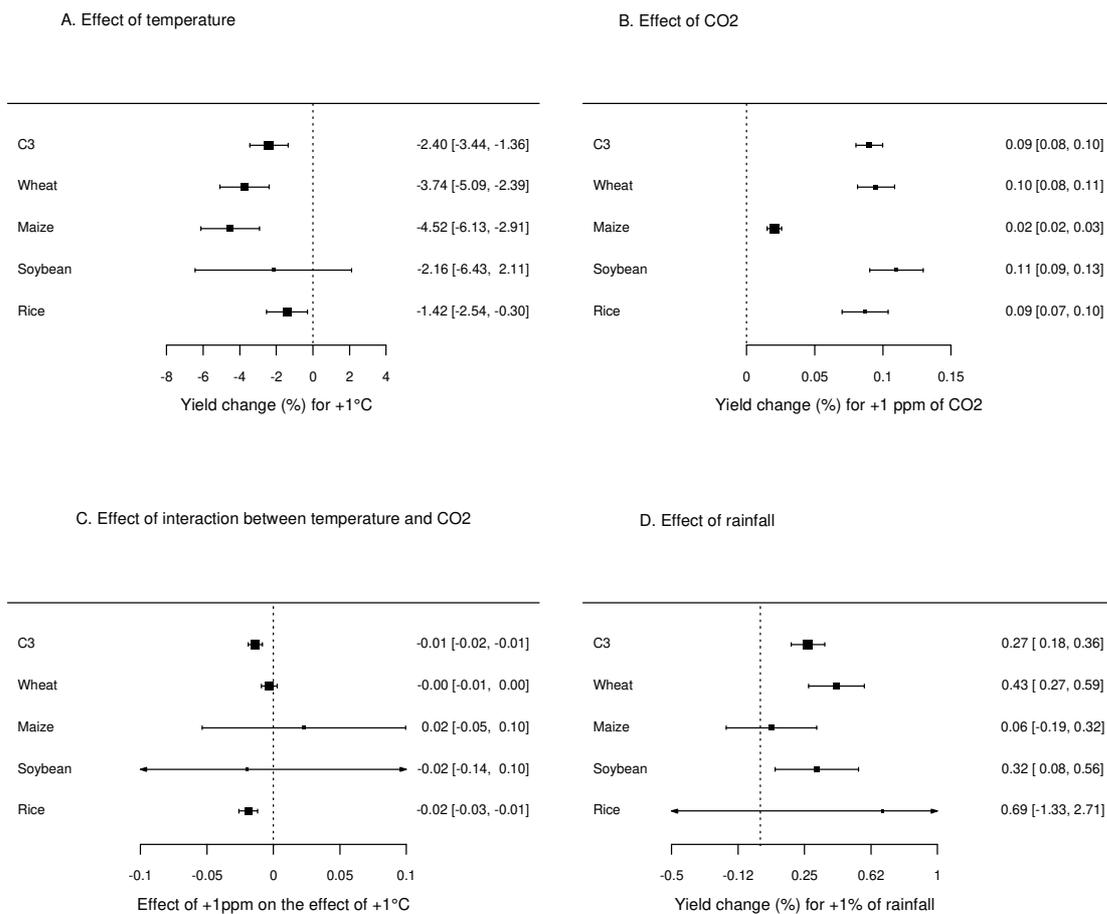


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687 **Figure 1.** Data from the literature. Relative change of yield (%) as a function of a temperature
 688 increase from 0 to +8°C, a change in precipitation from about -100 to +100%, an increase in CO2
 689 concentration up to +400ppm compared to the reference period considered in the studies. Each box
 690 describes the minimum, 1st quartile, median, 3rd quartile, and maximum values determined through
 691 all available data. When only one data is available, it is indicated by a horizontal black dash. Low:
 692 distribution of relative yield changes for +1°C, median and quartiles of the distribution (blue dots).

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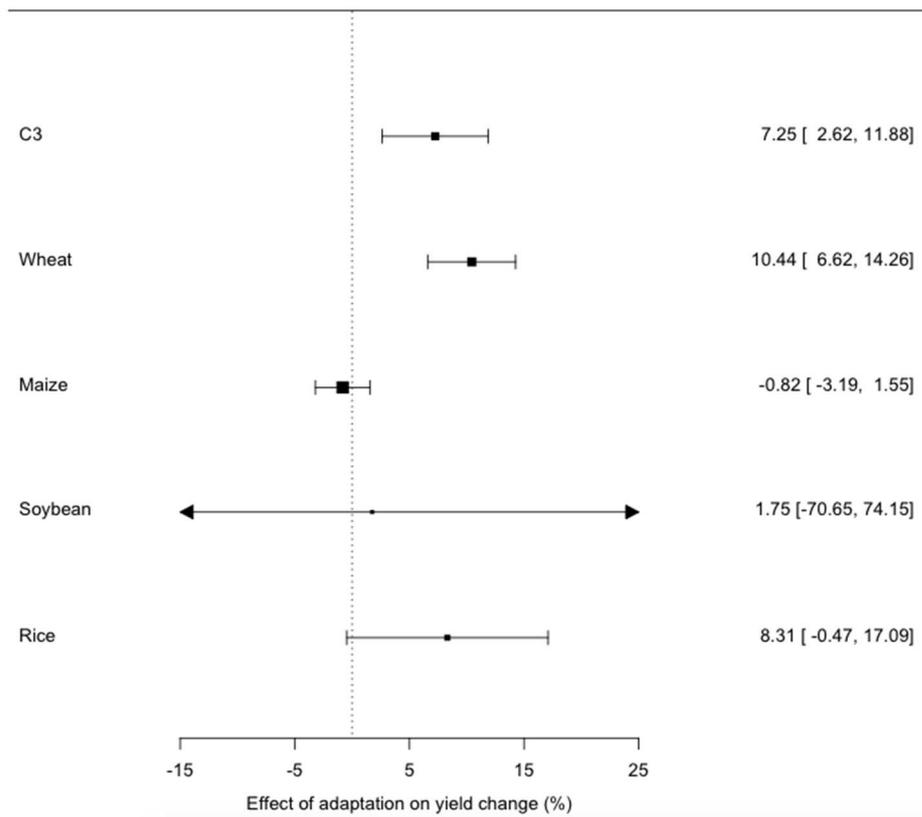
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696 **Figure 2.** Marginal effects (regardless of the level of adaptation) on yield of temperature (A), CO₂ (B),
 697 temperature-CO₂ (C) interaction, and precipitation (D) for all C3 crops combined and for each major
 698 species (wheat, maize, soybean, rice). The squares correspond to the estimated values and the
 699 horizontal bars represent the 95% confidence intervals. Each estimated value is obtained by
 700 increasing the corresponding factor by one unit with all others set equal to zero. The size of the
 701 square is proportional to the accuracy of each estimate. Numerical values are presented on the right.

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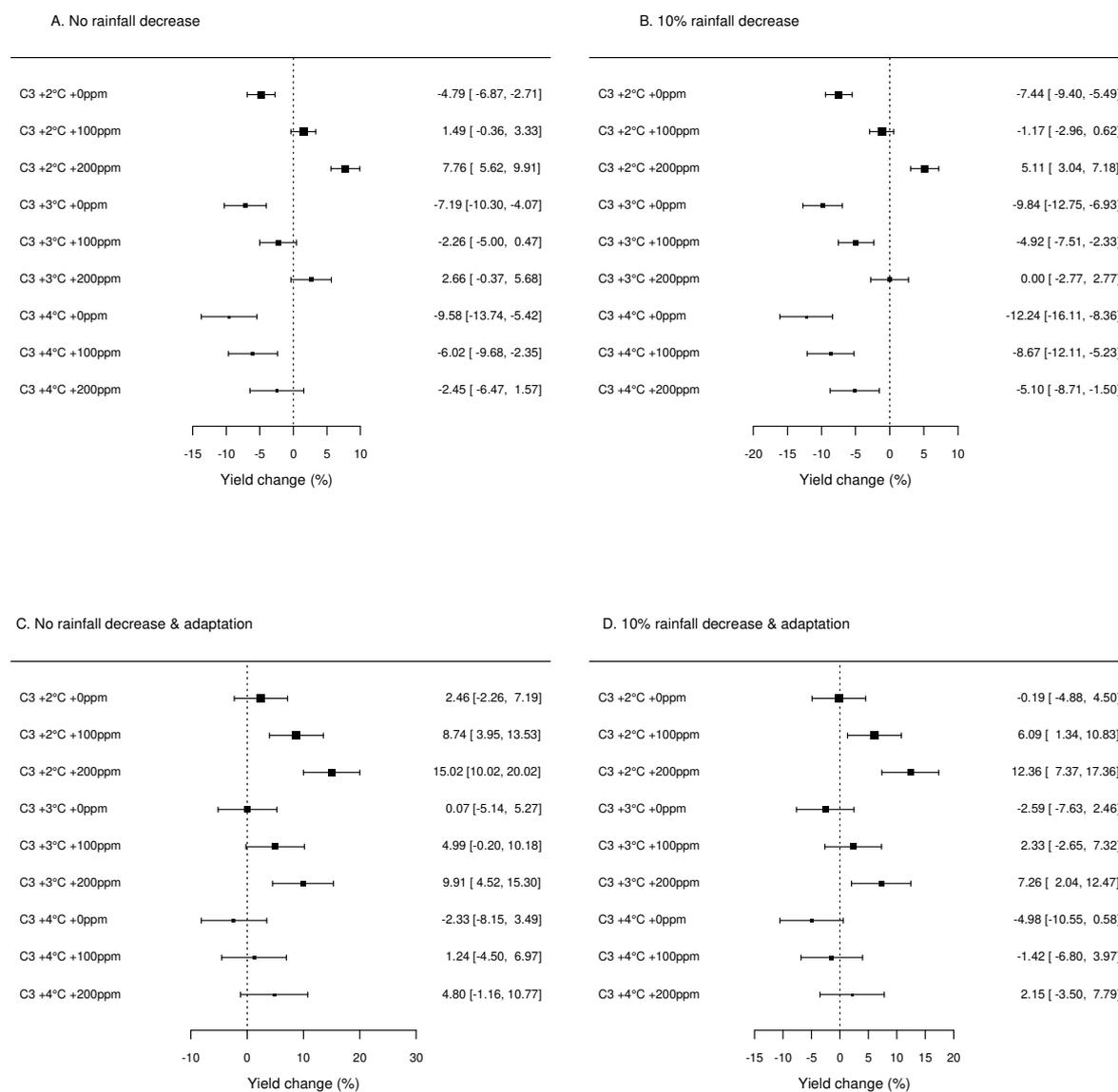
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Figure 3. Estimated parameter values quantifying the effect of climate change adaptation on relative yield variation for all C3 crops combined, and for major species. The squares correspond to the estimated values and the horizontal bars represent the 95% confidence intervals. The size of the squares is proportional to the accuracy of the estimates. Numerical values are presented on the right.



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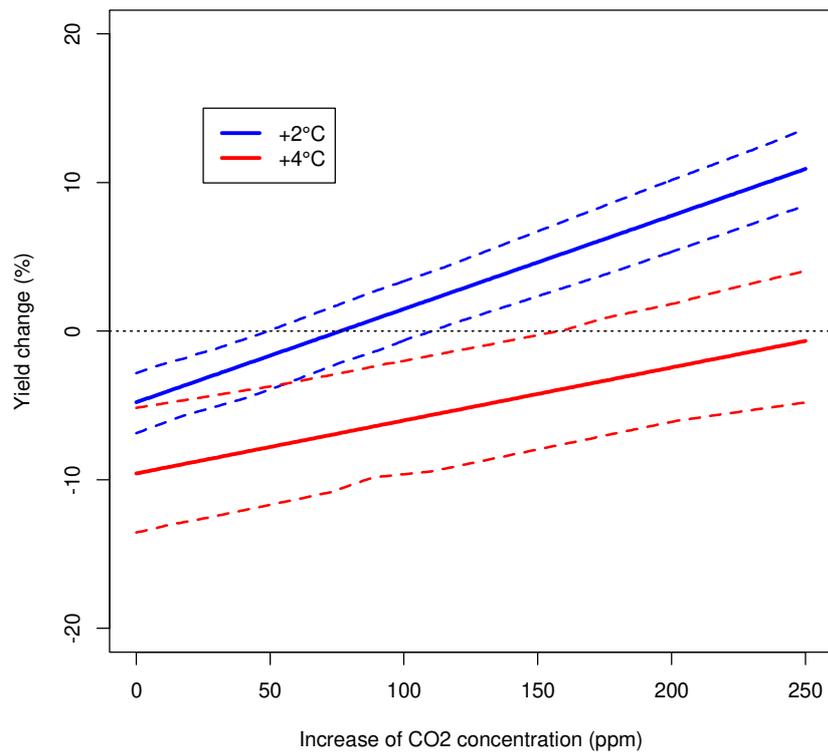
711 **Figure 4.** Combined effects of different levels of temperature (+2, +3, +4°C) and CO₂ concentration
 712 increase (+0, +100, +200ppm) on C3 crop yields. No decrease in precipitation and no adaptation (A),
 713 10% decrease in precipitation without adaptation (B), no decrease in precipitation with adaptation
 714 (C), 10% decrease in precipitation with adaptation (D). The squares correspond to the estimated
 715 values and the horizontal bars represent the 95% confidence intervals. The size of the squares is
 716 proportional to the accuracy of the estimates. Numerical values are presented on the right of the
 717 graphs.

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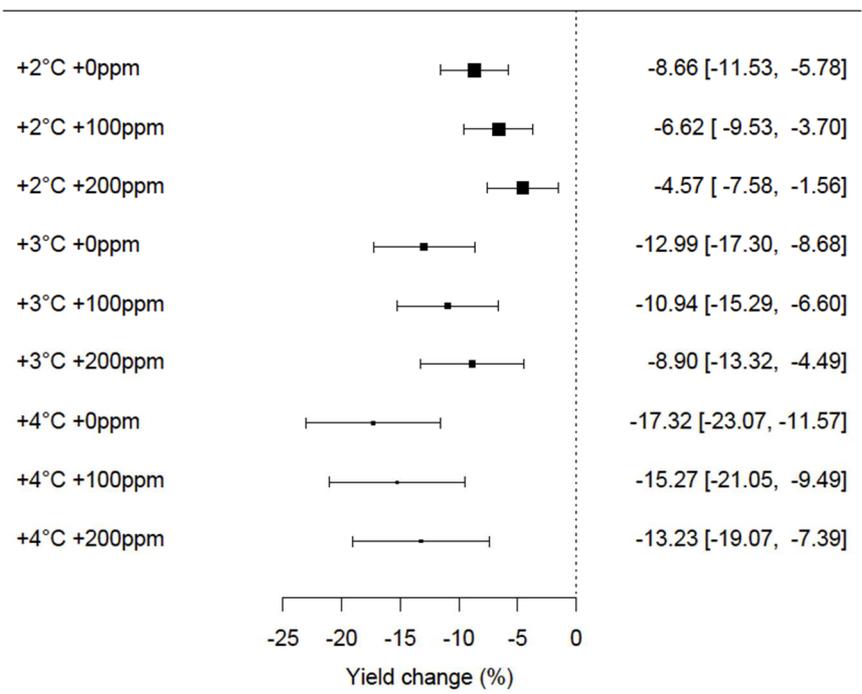
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724 **Figure 5.** Response of the relative change in C3 crop yield to an increase in CO₂ concentration (+0 to
 725 +250ppm) for two levels of temperature increase (+2 or +4°C), without decrease in precipitation and
 726 without adaptation. The dashed lines represent the 95% confidence intervals. The effect of CO₂ is
 727 smaller for large temperature increases.

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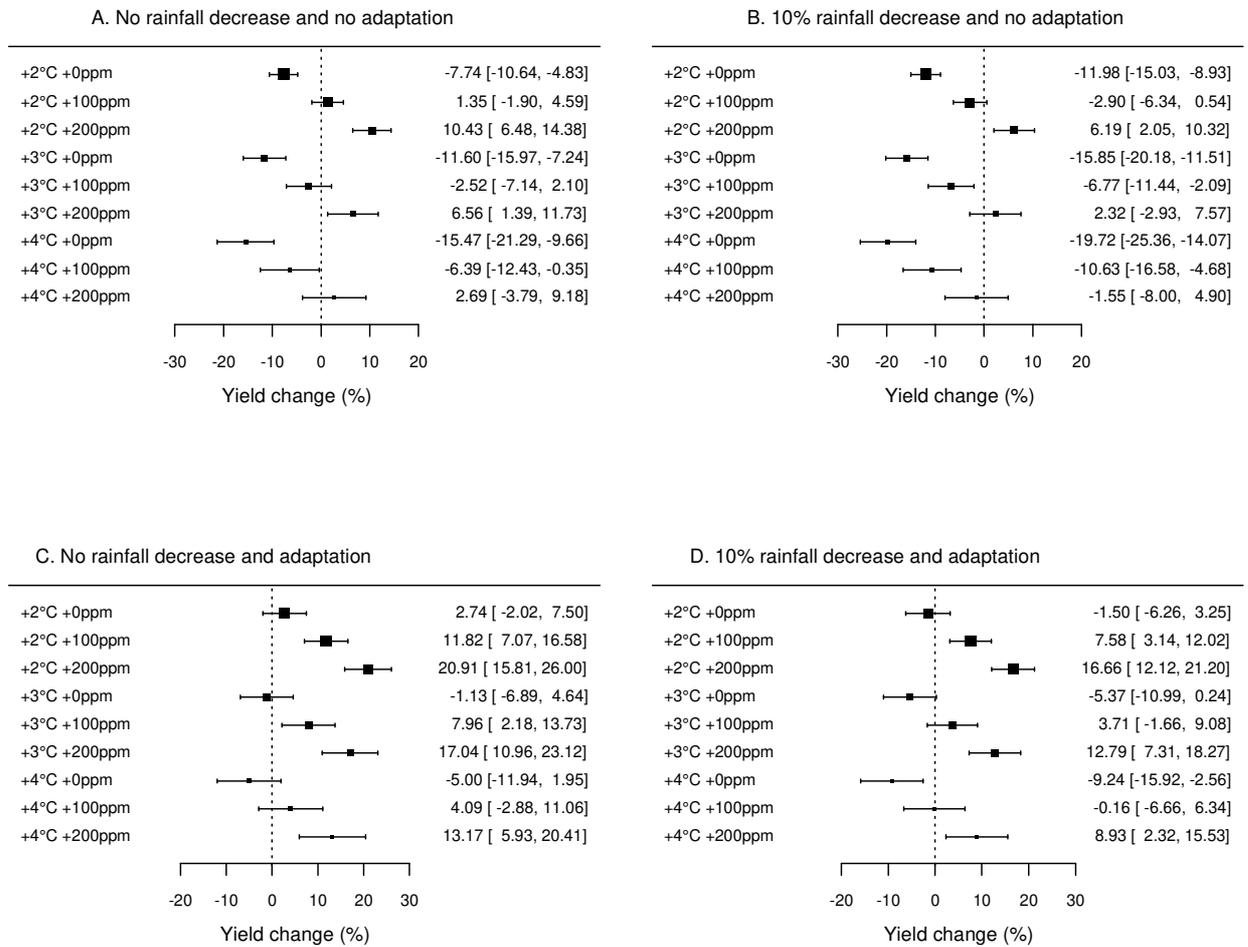
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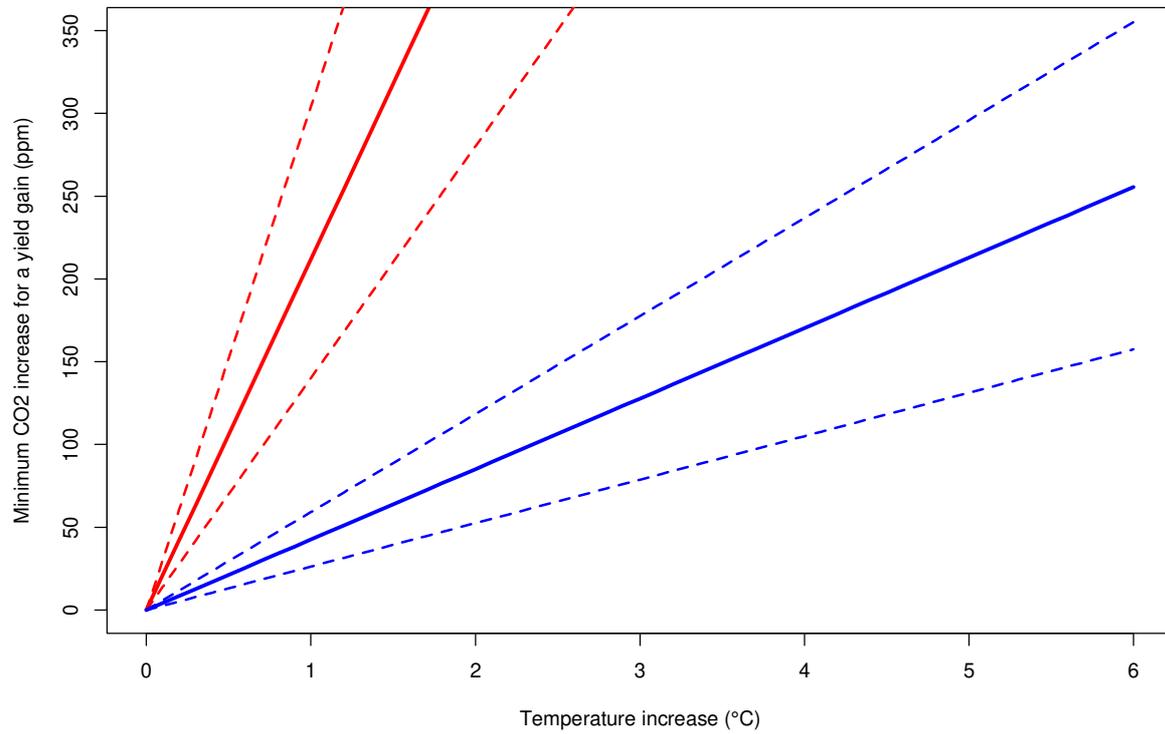
Figure 6. Effect of different levels of temperature and CO₂ concentration increase on maize yields. Note that some combinations are physically unlikely (e.g., an increase of +4°C for 0 ppm). The squares correspond to the estimated values and the horizontal bars represent the 95% confidence intervals. The size of the squares is proportional to the accuracy of the estimates. Numerical values are presented on the right.



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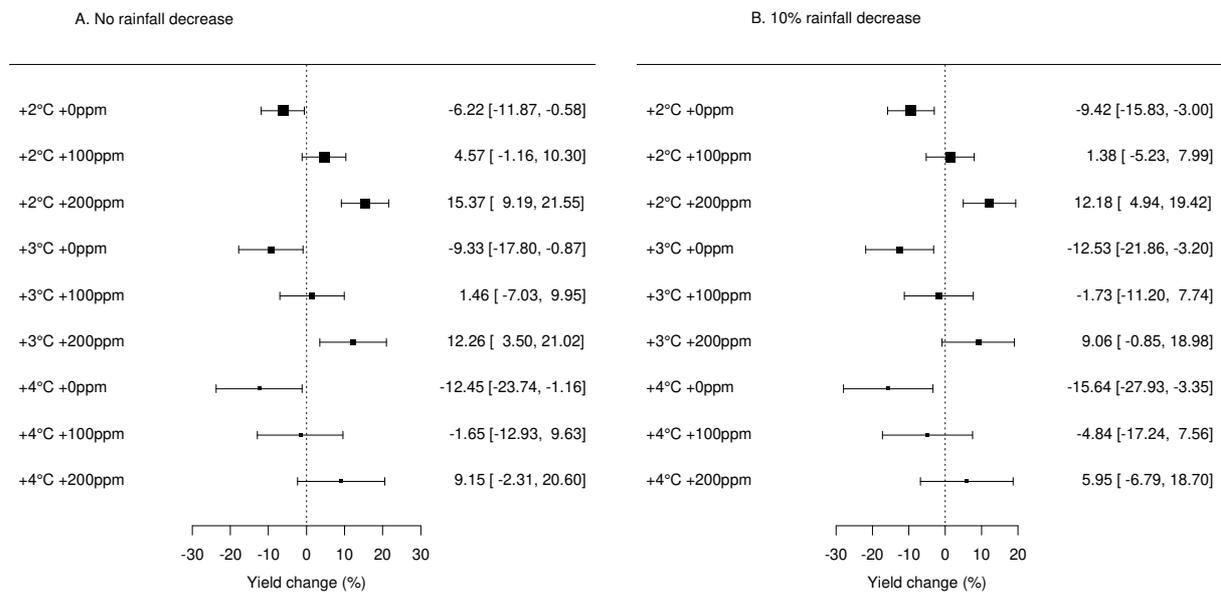
744 **Figure 7.** Effect of different levels of temperature increase (+2, +3, +4°C), CO₂ content (+0, +100,
 745 +200ppm) and precipitation on wheat yields. No decrease in precipitation and no adaptation (A),
 746 10% decrease in precipitation without adaptation (B), no decrease in precipitation with adaptation
 747 (C), 10% decrease in precipitation with adaptation (D). The squares correspond to the estimated
 748 values and the horizontal bars represent the 95% confidence intervals. The size of the squares is
 749 proportional to the accuracy of the estimates. Numerical values are presented on the right.

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752 **Figure 8.** Frontiers of CO₂ increase levels above (below) which a yield gain (loss) is expected
 753 for wheat (blue) and maize (red). Dotted lines represent 95% confidence intervals.

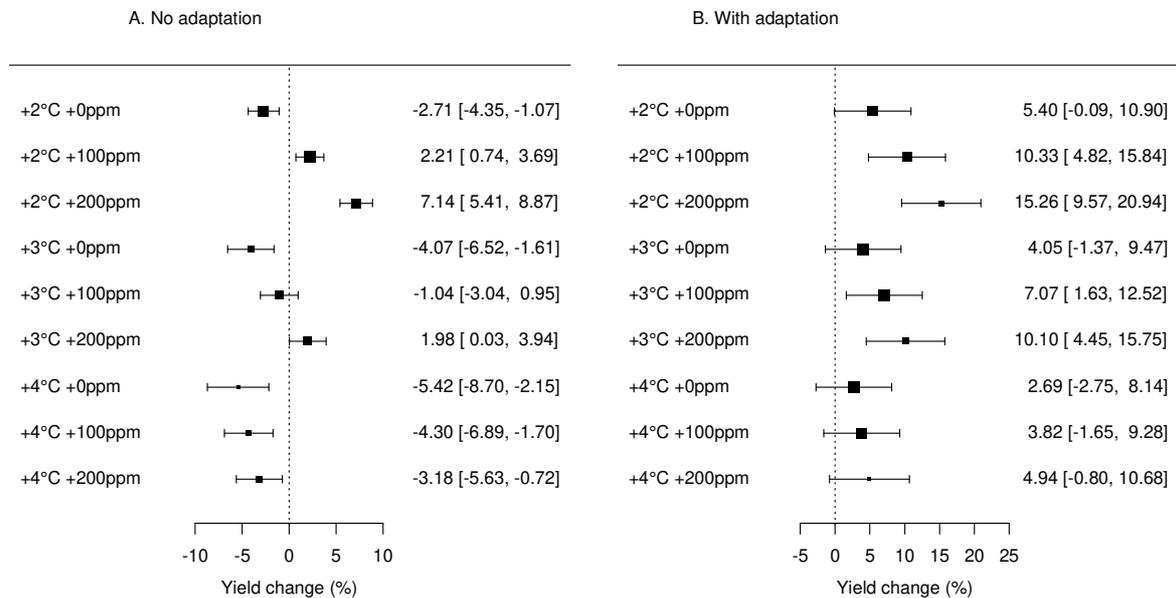


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756 **Figure 9.** Effect of different levels of temperature increase (+2, +3, +4°C), CO₂ content (+0, +100,
 757 +200ppm) and precipitation on soybean yields. No decrease in precipitation (A), 10% decrease in
 758 precipitation (B). The effect of adaptation is not presented because it is not significant for the
 759 soybean model. The squares correspond to the estimated values and the horizontal bars represent
 760 the 95% confidence intervals. The size of the squares is proportional to the accuracy of the
 761 estimates. Numerical values are presented on the right.

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763

764 **Figure 10.** Effect on rice yield of different levels of temperature increase (+2, +3, +4°C), and CO₂
 765 content (+0, +100, +200ppm) with and without adaptation. The effect of a change in precipitation is
 766 not presented here because it is not significant. The squares correspond to the estimated values and
 767 the horizontal bars represent the 95% confidence intervals. The size of the squares is proportional to
 768 the accuracy of the estimates. Numerical values are presented on the right.

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