Uncertainty in simulating wheat yields under climate change

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Projections of climate change impacts on crop yields are inherently uncertain[1]. Uncertainty is often quantified when projecting future greenhouse gas emissions and their influence on climate[2]. However, multi-model uncertainty analysis of crop responses to climate change is rare because systematic and objective comparisons among process-based crop simulation models[1,3] are difficult[4]. Here we present the largest standardized model intercomparison for climate change impacts so far. We found that individual crop models are able to simulate measured wheat grain yields accurately under a range of environments, particularly if the input information is sufficient. However, simulated climate change impacts vary across models owing to differences in model structures and parameter values. A greater proportion of the uncertainty in climate change impact projections was due to variations among crop models than to variations among downscaled general circulation models. Uncertainties in simulated impacts increased with CO_2 concentrations and associated warming. These impact uncertainties can be reduced by improving temperature and CO_2 relationships in models and better quantified through use of multi-model ensembles. Less uncertainty in describing how climate change may affect agricultural productivity will aid adaptation strategy development and policymaking.

Uncertainties in projections of climate change impacts on future crop yields derive from different sources in modelling. The trajectories of future greenhouse gas emissions cannot be projected easily as they are strongly influenced by political and socio-economic development. A range of plausible projections (scenarios) of emissions are used instead[2]. Projecting the effects of emissions on climate and the downscaling of climate data themselves, are both inherently uncertain, because different general circulation model ensembles[5] and downscaling methods[6] give different results. Finally, uncertainty in simulating the response of crops to altered climate can be attributed to differences in the structures of crop models and how model parameters are set. Process-based crop models account for many of the interactions among climate, crop, soil and management effects and are the most common tools for assessing climate change impacts on crop productivity. Many crop model impact assessments have been carried out for specific locations[7], agricultural regions[8] and the globe[9]. Statistical methods have also been used to analyse trends in yields driven by climate[10], but interactions between climate and non-climate factors confound results[11]. This hinders the attribution of causality[12] and development of appropriate adaptation strategies.

Uncertainty, any departure from the unachievable ideal of completely deterministic knowledge of a system[13], has been addressed by the climate science community through probabilistic projections based on multiple general circulation models (GCMs) or regional climate model ensembles[14]. However, most climate change agricultural impact assessments have used a single crop model[3], limiting the quantification of uncertainty[15]. As crop models differ in the way they simulate dynamic processes, set parameters and use input variables[3], large differences in simulation results have been reported[16]. Although uncertainty of crop model projections is sometimes assessed by using more than one crop model[16] or by perturbing crop model parameters[17], coordinating comprehensive assessments has proved difficult[4].

To estimate the uncertainty associated with studies of climate impacts on crop yields, we used 27 different wheat crop models (Supplementary Tables S1 and S2) at four sites representing very different production environments (Fig. 1a). Simulated grain yields varied widely, although median values were close to observed grain yields across single-year experiments for four representative environments (Supplementary Table S3) in the Netherlands, Argentina, India and Australia (Fig.1a, b). This phenomenon was previously reported in another multi-model comparison with fewer models[16], and is comparable to the improved seasonal climate simulations produced with multiple GCMs (ref. 18). The range of simulated yields was reduced significantly after full calibration, such that >50% of yields from calibrated models were within the mean coefficient of variation (CV%) (±13.5%) of >300 wheat field experiments[19] (Fig. 1c). Similar patterns were found for other simulated aspects of wheat growth (Fig. 1d). Hence, crop models are able to simulate measured grain yield and other crop components accurately under diverse environments if input information is sufficient.

To illustrate the possible changes in uncertainty of simulated impacts, we analysed the sensitivity of models to a combination of changes in precipitation and increases in both temperature and atmospheric CO_2 concentration (734 ppm, compared with baseline at 360 ppm) based on a location-specific scenario that best approximated the ensemble of high-emission late-century climate projections (Supplementary Table S3). Simulated climate change yield responses of all partially calibrated crop models had CV values between 20 and 30% (Fig. 2a); these were reduced by 2–7% when models were fully calibrated. However, the CV of simulated impacts using the 50% best-performing calibrated models (based on root mean square errors (r.m.s.e) across all locations) was about 2% higher than using all models, and this decreased only when the 50% of models closest to observed yields at each location were used (Fig. 2a). Uncertainty in simulated climate change impacts differed across the environments (Fig. 2a). In addition, uncertainty in simulated impacts varied with soil (Fig. 2b) and crop management (Fig. 2c,d). Hence, the overall

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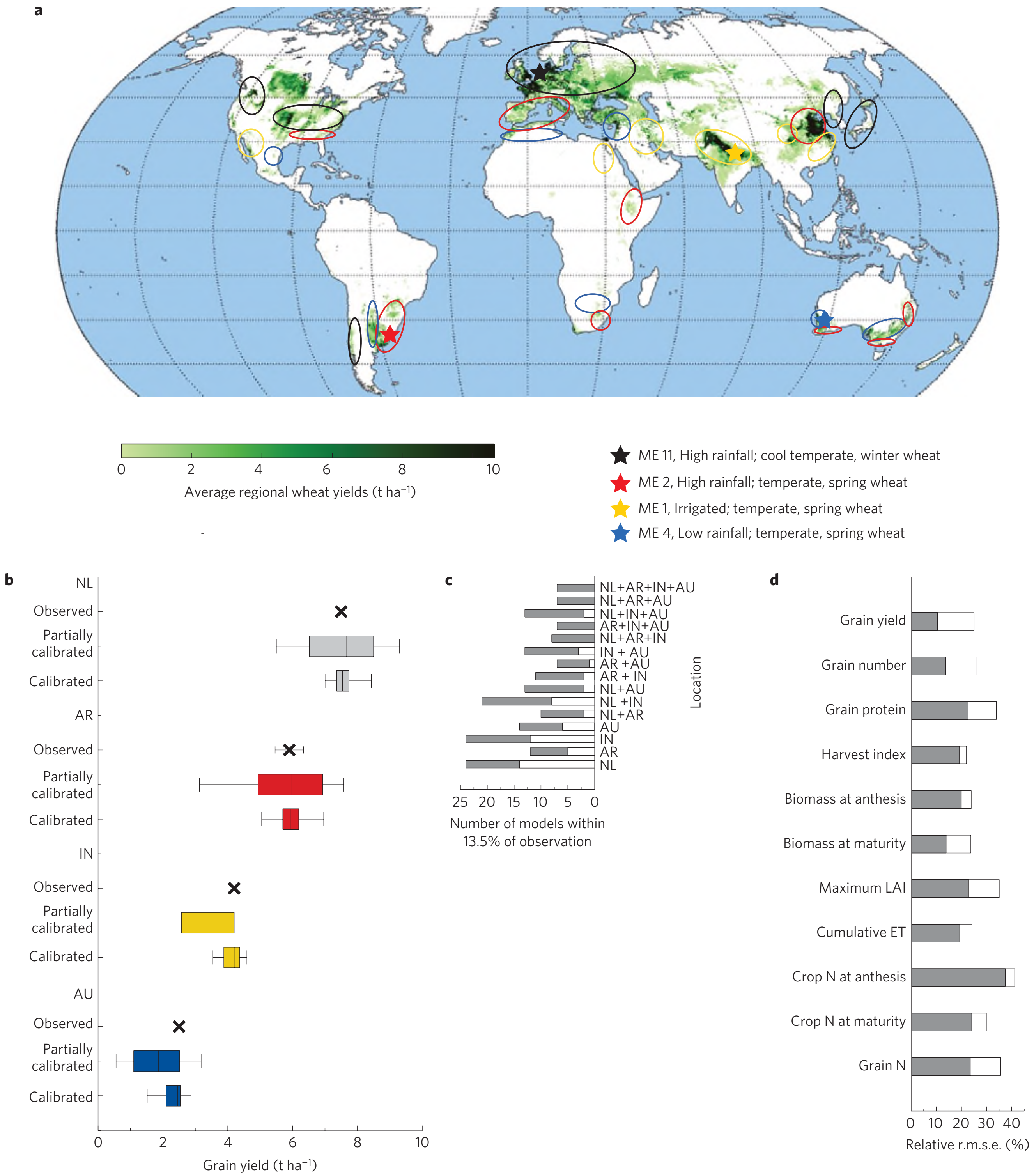

Figure 1 | Wheat model-observation comparisons. a, Global map of wheat production[30] showing experimental sites (stars) representative of CIMMYT mega-environments (ME, broadly indicated by ovals, http://wheatatlas.cimmyt.org). **b**, Observed (cross mark) and simulated (box plots) grain yields from single-year experiments for the Netherlands (NL), Argentina (AR), India (IN) and Australia (AU). Simulated yields are from 27 different wheat crop models. Partially calibrated simulated yields (larger boxes)—researchers had no access to observed grain yields and growth dynamics (blind test). Calibrated simulated yields (smaller boxes)—researchers had access to observed grain yields and growth dynamics. In each box plot, vertical lines represent, from left to right, the 10th percentile, 25th percentile, median, 75th percentile and 90th percentile of simulations. Standard deviation for observed yields (based on measurements of four replicates) is shown as an error bar if known. **c**, Number of models within mean field experimental variation (13.5%; ref. 19) for partially calibrated (open bars) and fully calibrated models (grey bars) for single locations (NL, AR, IN and AU for each country) and combinations of locations. **d**, Relative r.m.s.e. of simulation–observation comparisons for partially calibrated (open bar) and fully calibrated models (grey bars) of grain yield components across all four locations. LAI, leaf area index; ET, evapotranspiration.

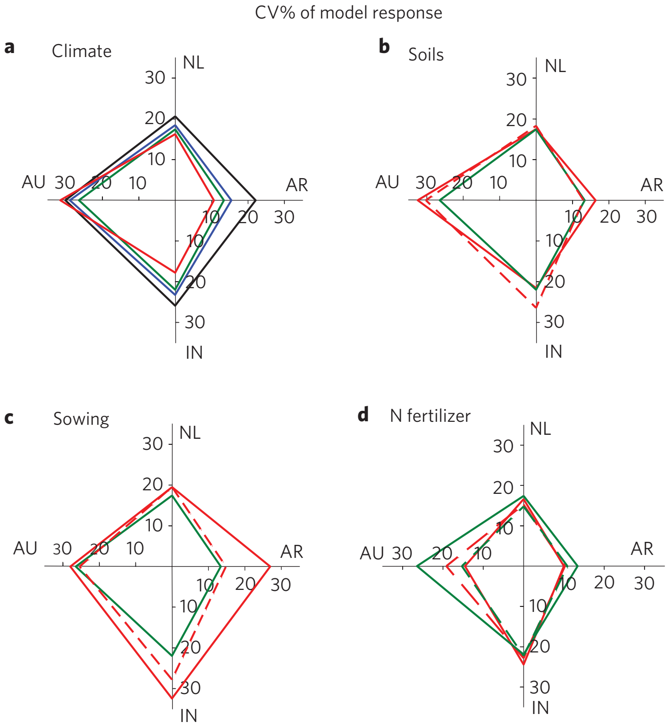

Figure 2 | Variability in impact model uncertainty. a, CV% for simulated yield response to a location-specific scenario representing GCM projections for the high-emission (A2) scenario for the late century (in relation to baseline 1981–2010, Supplementary Table S3) with 27 crop models. Models were partially calibrated (black) or fully calibrated (green). In addition, 50% of models with the closest simulations to the observed yields across all locations (blue) and 50% of models with the closest simulations to the observed yields per location are shown (red). **b–d**, CV% of simulated yield response to the climate change scenario with 27 fully calibrated crop models with increased (solid red) and reduced (dashed red) soil water holding capacity (**b**), early (solid red) and delayed (dashed red) sowing dates (**c**) and increased (solid red) and reduced (dashed red) N fertilizer applications (**d**; only 20 models included N dynamics); fully calibrated 20 models that included N dynamics (dashed green). The fully calibrated simulation (green) from **a** is reproduced in **b–d** for comparison. The Netherlands (NL), Argentina (AR), India (IN) and Australia (AU).

growing environment, in particular the soil and crop management, affects the range of simulated grain yields across models, thus adding to uncertainty in responses coming from individual models. Therefore, selecting a subset of models that perform best in present environments does not reduce uncertainty in simulated climate change impacts.

Changes in atmospheric CO_2, temperature and precipitation are key drivers of the responses of crops to climate change[20]. Simulated impacts of elevated CO_2 on yields varied relatively little across models (50% of model results were within ±20% of the median response; Fig. 3a–d and Supplementary Fig. S5), but the variation across 80% of the crop models increased under elevated CO_2 concentration mostly in the low-yielding environment of Australia (see box-plot whiskers in Fig. 3d). The uncertainty in simulated yields did not increase with increasing CO_2 in the other environments. This is not surprising as elevated CO_2 affects fewer processes than increased temperature and because several of the wheat models have used observations from free-air CO_2 enrichment experiments to improve model processes related to high CO_2 (refs 21,22). However, none of the models has been tested with elevated CO_2 in combination with high temperature. Most simulated yield responses to a 180 ppm CO_2 increase at present temperatures (Fig. 3a–d) were within the range of measured responses, ranging from 8% to 26% with elevated atmospheric CO_2 concentrations (Fig. 3e) across experiments conducted in the USA, Germany and China[23,24] (Supplementary Information, page 11 last paragraph).

In contrast to the mean response of yields to CO_2, uncertainty in simulated yield showed a strong dependency on temperature, particularly when the temperature increase exceeded 3 °C with associated changes in atmospheric CO_2. The median model response to a 3 °C increase in temperature (Fig. 3a–d and Supplementary Fig. S5) is consistent with general field observations (Fig. 3e); observed wheat grain yields declined by 3–10% $°C^{-1}$ increase in mean temperature[10,24] (Supplementary Information, page 11 last paragraph). The increased range of impacts at high temperatures (50% of models were between 20 and 40% of the median response on either side) indicated an increased model uncertainty with increasing temperature. This is partly related to simulated phenology (Supplementary Fig. S3). For example, phenology is often enhanced with increasing temperature resulting in less time for light interception and photosynthesis and consequently less biomass and yield. In addition, the increased model uncertainty is also partly due to an increased frequency of high-temperature events and its simulated impact on crop growth[25] (Supplementary Fig. S4), and high-temperature interactions with elevated CO_2 (Fig. 3). However, accounting for a process such as high-temperature stress impact in a model does not necessarily result in correctly simulating that effect (Supplementary Fig. S4), as the modelled process itself, for example, leaf area or biomass growth, interacts with other model processes in determining the final yield response of a model. Precipitation affected simulated yields, but precipitation change had little impact on the range of simulated responses (Supplementary Fig. S2).

If averaging multi-model simulations is superior to a single crop[4] or climate[26] model simulation because the ratio of signal (mean change) to noise (variation) increases with the number of models and errors tend to cancel each other out, we should be able, with caution[27], to estimate how many models would be required for robust projections. We assessed this by randomly choosing 260 subsets of the crop models, and computing the mean and spread of simulated results (Supplementary Fig. S1). As the variation in yields was about 13.5% around the mean in field experiments[19], we considered projections to be robust if the range of projections was within 13.5% of the mean. The number of models required for robust assessments of climate change varied depending on the magnitude of temperature change and interactions with the change in atmospheric CO_2 (Fig. 4a). For example, at least five models are needed for robust assessments of yield impacts for increases of up to 3 °C and 540 ppm of CO_2. Fewer models are needed for smaller changes and more models for greater changes in temperature (Fig. 4a).

When simulating impacts assuming a mid-century A2 emissions scenario (556 ppm of CO_2) for climate projections from 16 downscaled GCMs using 26 wheat models, a greater proportion of the uncertainty in yields was due to variations among crop models than to variations among the downscaled GCMs (Fig. 4b). In contrast, GCM uncertainty tends to dominate in perturbed single crop model parameter studies[28]. The variation of simulated yields for the scenario ensemble was greater for low-yielding environments and absolute values were similar to observations across yield levels and within the range of field experimental variation[19]. Smaller projected climate changes, for example, for low emissions or early-century time frames, result in less variation in simulated impacts; larger climate changes result in more variation (Fig. 3).

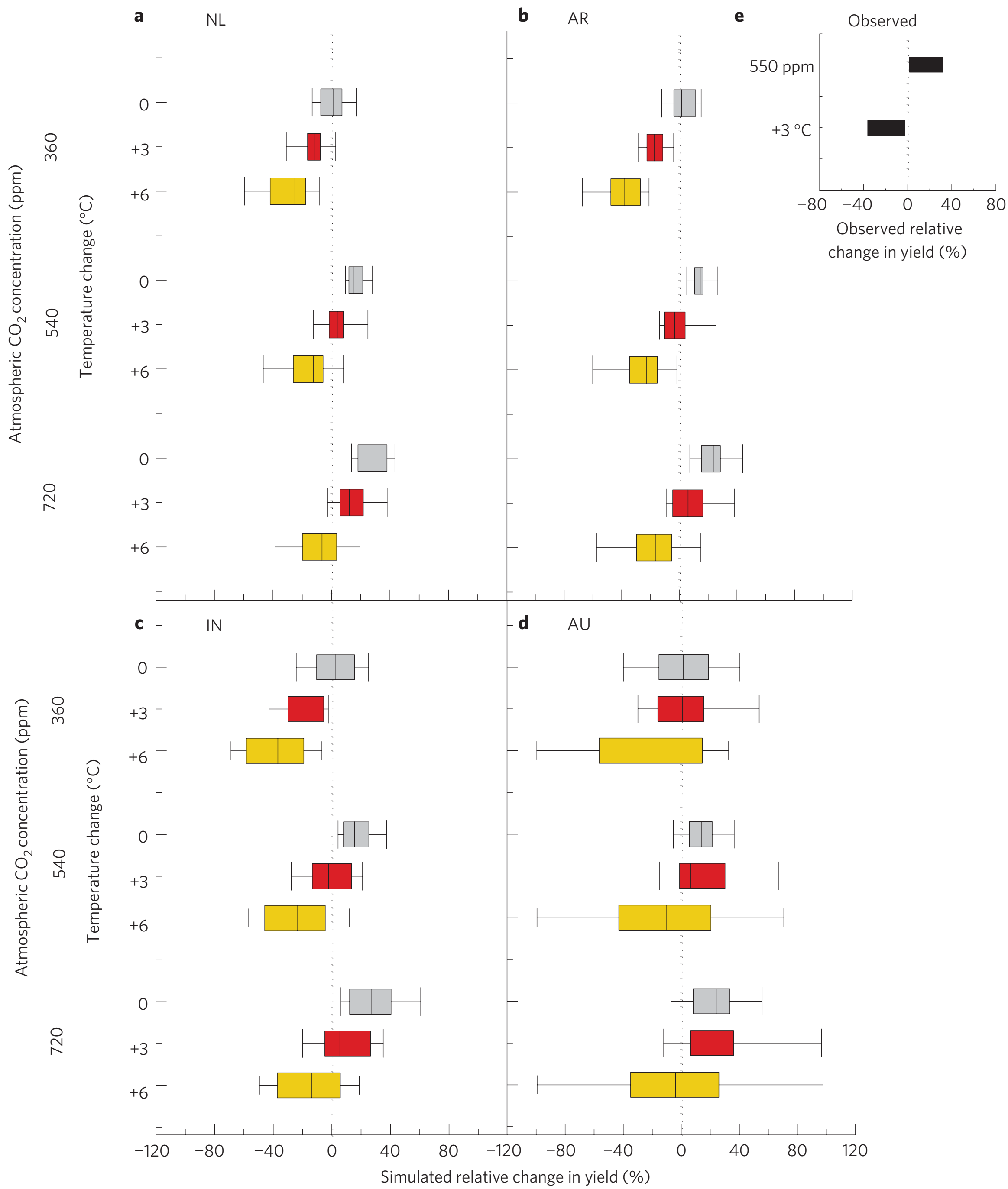

Figure 3 | Sensitivity of simulated and observed wheat to temperature and CO_2 change. a–d, Simulated relative mean (30-year average, 1981–2010) grain yield change for increased temperatures (no change, grey; +3 °C, red; +6 °C, yellow) and elevated atmospheric CO_2 concentrations for the Netherlands (NL; **a**), Argentina (AR; **b**), India (IN; **c**) and Australia (AU; **d**). For each box plot, vertical lines represent, from left to right, the 10th percentile, 25th percentile, median, 75th percentile and 90th percentile of simulations based on multi-models. **e**, Observed range of yield impacts with elevated CO_2 (refs 23,24). Observed range of yield impacts with increased temperature[10,24] (extrapolated, based on separate experiments with 40–345 ppm elevated CO_2 and 1.4–4.0 °C temperature increase, Supplementary Information).

We conclude that projections from individual crop models fail to represent the significant uncertainties known to exist in crop responses to climate change. On the other hand, model ensembles have the potential to quantify the significant, and hitherto uncharacterized, crop component of uncertainty. Crop models need to be improved to more accurately reflect how heat stress and high-temperature-by-CO_2 interactions affect plant growth and yield formation.

Methods

Twenty-seven wheat crop simulation models (Supplementary Tables S1 and S2) were tested within the Agricultural Model Intercomparison and Improvement Project[29] (www.agmip.org), with data from quality-assessed field experiments (sentinel site data) from four contrasting environments using standardized protocols, including partial and full model calibration experiments, to assess the role of crop model-based uncertainties in projections of climate change impacts (Fig. 1a and Supplementary Information). Model simulations were executed by individual modelling groups.

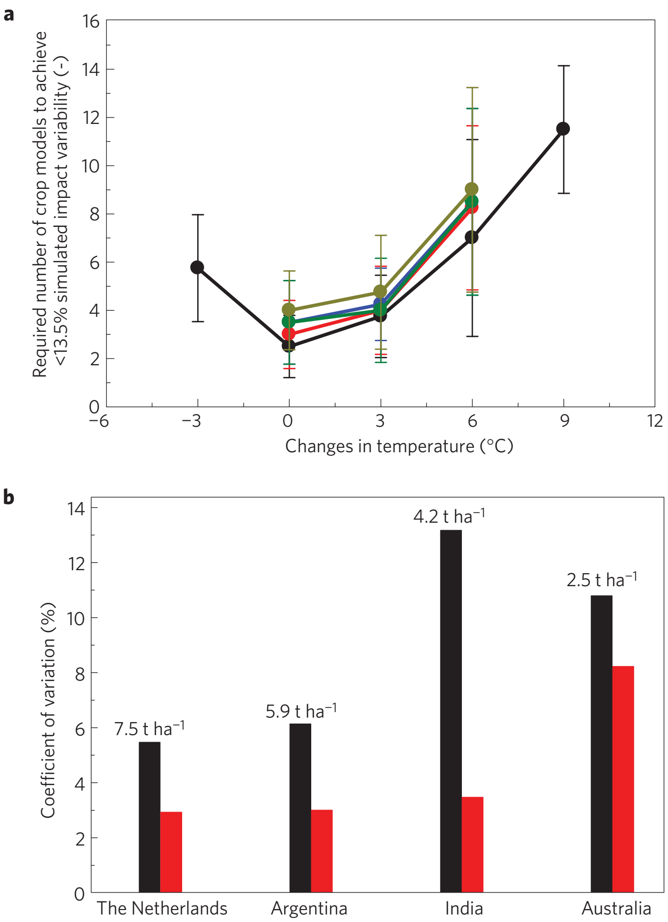

Figure 4 | Size of model ensembles and impact model uncertainty. **a**, Average number of crop models across locations required to reduce the simulated yield impact variation to within the mean field experimental CV% of 13.5% (ref. 19). Different colours indicate elevated atmospheric CO_2 concentrations (black, 360 ppm; red, 450 ppm; blue, 540 ppm; green, 630 ppm; dark yellow, 720 ppm) in combinations with temperature changes. Error bars show s.d. **b**, CV due to crop model uncertainty (using 10th percentile to 90th percentile of simulations based on 26 crop models) in simulated 30-year average climate change yield impact (black) and due to variation in 16 downscaled GCM (red, Supplementary Tables S6 and S7) mid-century A2 emission scenarios (2040–2069). Numbers indicate present yields at each location (Supplementary Table S3).

References

1. Godfray, H. C. J. *et al.* Food security: The challenge of feeding 9 billion people. *Science* **327,** 812–818 (2010).
2. Moss, R. H. *et al.* The next generation of scenarios for climate change research and assessment. *Nature* **463,** 747–756 (2010).
3. White, J. W., Hoogenboom, G., Kimball, B. A. & Wall, G. W. Methodologies for simulating impacts of climate change on crop production. *Field Crops Res.* **124,** 357–368 (2011).
4. Rötter, R. P., Carter, T. R., Olesen, J. E. & Porter, J. R. Crop-climate models need an overhaul. *Nature Clim. Change* **1,** 175–177 (2011).
5. Meehl, G. A. *et al.* The WCRP CMIP3 multimodel dataset—A new era in climate change research. *Bull. Am. Meteorol. Soc.* **88,** 1383–1394 (2007).
6. Wilby, R. L. *et al.* A review of climate risk information for adaptation and development planning. *Int. J. Clim.* **29,** 1193–1215 (2009).
7. Semenov, M. A., Wolf, J., Evans, L. G., Eckersten, H. & Iglesias, A. Comparison of wheat simulation models under climate change. 2. Application of climate change scenarios. *Clim. Res.* **7,** 271–281 (1996).
8. Tao, F., Zhang, Z., Liu, J. & Yokozawa, M. Modelling the impacts of weather and climate variability on crop productivity over a large area: A new super-ensemble-based probabilistic projection. *Agric. Forest Meteorol.* **149,** 1266–1278 (2009).
9. Rosenzweig, C. & Parry, M. L. Potential impact of climate change on world food supply. *Nature* **367,** 133–138 (1994).
10. Lobell, D. B., Schlenker, W. & Costa-Roberts, J. Climate trends and global crop production since 1980. *Science* **333,** 616–620 (2011).
11. Lobell, D. B. & Burke, M. B. On the use of statistical models to predict crop yield responses to climate change. *Agric. Forest Meteorol.* **150,** 1443–1452 (2010).
12. Gifford, R. *et al.* Climate change and Australian wheat yield. *Nature* **391,** 448–449 (1998).
13. Harris, G. R., Collins, M., Sexton, D. M. H., Murphy, J.M. & Booth, B. B. B. Probabilistic projections for twenty first century European climate. *Nature Hazards Earth Syst. Sci.* **10,** 2009–2020 (2010).
14. Semenov, M. A. & Stratonovitch, P. Use of multi-model ensembles from global climate models for assessment of climate change impacts. *Clim. Res.* **41,** 1–14 (2010).
15. Müller, C. Agriculture: Harvesting from uncertainties. *Nature Clim. Change* **1,** 253–254 (2011).
16. Palosuo, T. *et al.* Simulation of winter wheat yield and its variability in different climates of Europe: A comparison of eight crop growth models. *Eur. J. Agron.* **35,** 103–114 (2011).
17. Challinor, A. J., Simelton, E. S., Fraser, E. D. G., Hemming, D. & Collins, M. Increased crop failure due to climate change: Assessing adaptation options using models and socio-economic data for wheat in China. *Environ. Res. Lett.* **5** (2010).
18. Hagedorn, R., Doblas-Reyes, F. J. & Palmer, T. N. The rationale behind the success of multi-model ensembles in seasonal forecasting—I. Basic concept. *Tellus A* **57,** 219–233 (2005).
19. Taylor, S. L., Payton, M. E. & Raun, W. R. Relationship between mean yield, coefficient of variation, mean square error, and plot size in wheat field experiments. *Commun. Soil Sci. Plant Anal.* **30,** 1439–1447 (1999).
20. Hatfield, J. L. *et al.* Climate impacts on agriculture: Implications for crop production. *Agron. J.* **103,** 351–370 (2011).
21. Long, S. P., Ainsworth, E. A., Leakey, A. D. B., Nosberger, J. & Ort, D. R. Food for thought: Lower-than-expected crop yield stimulation with rising CO_2 concentrations. *Science* **312,** 1918–1921 (2006).
22. Ewert, F., Porter, J. R. & Rounsevell, M. D. A. Crop models, CO_2, and climate change. *Science* **315,** 459–459 (2007).
23. Kimball, B. A. in *Handbook of Climate Change and Agroecosystems—Impacts, Adaptation, and Mitigation* (eds Hillel, D. & Rosenzweig, C.) 87–107 (Imperial College Press, 2011).
24. Amthor, J. S. Effects of atmospheric CO_2 concentration on wheat yield: Review of results from experiments using various approaches to control CO_2 concentration. *Field Crops Res.* **73,** 1–34 (2001).
25. Asseng, S., Foster, I. & Turner, N. C. The impact of temperature variability on wheat yields. *Glob. Change Biol.* **17,** 997–1012 (2011).
26. Tebaldi, C. & Knutti, R. The use of the multi-model ensemble in probabilistic climate projections. *Phil. Trans. R. Soc. A* **365,** 2053–2075 (2007).
27. Knutti, R. The end of model democracy? *Climatic Change* **102,** 395–404 (2010).
28. Challinor, A. J., Wheeler, T., Hemming, D. & Upadhyaya, H. D. Ensemble yield simulations: Crop and climate uncertainties, sensitivity to temperature and genotypic adaptation to climate change. *Clim. Res.* **38,** 117–127 (2009).
29. Rosenzweig, C. *et al.* The Agricultural Model Intercomparison and Improvement Project (AgMIP): Protocols and pilot studies. *Agr. Forest Meteorol.* **170,** 166–182 (2013).
30. Monfreda, C., Ramankutty, N. & Foley, J. A. Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Glob. Biogeochem. Cycles* **22** (2008).

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S.A., F.E., C.R., J.W.J., K.J.B. and J.L.H. motivated the study; S.A. and F.E. coordinated the study; S.A., F.E., D.W., P.M., D.C. and A.C.R. analysed data; D.C., A.C.R., K.J.B., P.J.T., R.P.R., N.B., B.B., D.R., P.B., P.S., L.H., M.A.S., P.S., C.S., G.O.L., P.K.A., S.N.K., R.C.I., J.W.W., L.A.H., R.G., K.C.K., T.P., J.H., T.O., J.W., I.S., J.E.O., J.D., C.N., S.G., J.I., E.P., T.S., F.T., C.M., K.W., R.G., C.A., I.S., C.B., J.R.W. and A.J.C. carried out crop model simulations and discussed the results; M.T. and S.N.K., provided experimental data; S.A., F.E., C.R. and J.W.J. wrote the paper.

Competing financial interests

The author declares no competing financial interests.

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