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Improved Estimates of Regional Rice Yield Responses to Elevated CO2 by Considering Sub-Species Discrepancies

Songhan Wang[1, 8*], Kees Jan van Groenigen[2], Christoph Müller[3], Xuhui Wang[4], Lian Song5, Yunlong Liu[1], Yu Jiang[1*], Josep Peñuelas[6, 7], Yanfeng Ding[1*],

[1]Jiangsu Collaborative Innovation Center for Modern Crop Production/Key Laboratory of Crop Physiology and Ecology in Southern China, College of Agriculture, Nanjing Agricultural University, Nanjing 210095, China.
[2]Department of Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK.
[3]Potsdam Institute for Climate Impact Research, Member of the Leibniz Association, Potsdam, Germany.
[4]Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing, China.
[5]State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing, China.
[6]CSIC, Global ecology Unit CREAF-CSIC-UAB, Bellaterra 08193, Catalonia, Spain.
[7]CREAF, Cerdanyola del Vallès 08193, Catalonia, Spain.
[8]Lead contact

***Corresponding author**:
Songhan Wang, Yu Jiang, Yanfeng Ding
College of Agriculture
Nanjing Agricultural University
NO.1 Weigang Road, Xuanwu District, Nanjing, Jiangsu Province, China
Email: wangsonghan@njau.edu.cn yujiang@njau.edu.cn dingyf@njau.edu.cn

Summary

Increased rice yields due to rising atmospheric carbon dioxide (CO_2), known as the CO_2 fertilisation effect (CFE), play as one of the important factors in sustaining global food security. However, model projections on future rice yields are still largely uncertain, partly owing to the lack of how CFE varies between rice species. Here, through synthesis of hundreds of field observations, we found the experimental evidence of 12.8% yield increase per 100 ppm CO_2 increase for Indica, but only about a half for Japonica. This difference in CFE between sub-species was possibly due to their different photosynthetic acclimation during reproductive stages. After accounting for differences in sub-species, crop model projections showed substantial regional discrepancies of CFE, which are not captured by original models. More importantly, the spatial and temporal variations of rice yield could be better projected after considering this sub-species difference. Together, these results suggest strong influences of genotype on rice yield responses to CO_2, and highlight the need for crop models to consider genotypes for improving projections of global crop yield.

Keywords

Global crop yield, rice yield, CO_2 fertilisation effect, rice sub-species, crop models

Introduction

Achieving zero-hunger, a key sustainable development goal[1], requires increasing crop yields to feed the ever-growing global population[2,3]. Rice (*Oryza sativa L.*) is one of the most widely planted and consumed crops worldwide, especially in developing countries[4], and plays a crucial role in ensuring global food security[5]. One critical threat to global rice production is climate change[6-8]. Field experiments, crop models, and historical data analysis all suggest that global rice yield is largely affected by changes in climatic factors such as increasing temperature[9-11].

Continuously rising levels of atmospheric carbon dioxide (CO_2) concentration, one of the causes of climate change[12], will generally increase the rice yields[13]. This benefit from elevated CO_2 on crop yield, also known as the CO_2 fertilisation effect (CFE), results from an enhanced net photosynthetic rate and the increased water-use-efficiency for typical C_3 plants such as rice[14]. Except for CO_2, other climate factors including temperature and precipitation also had significant impacts on rice yield[11,15]. Global increased temperature due to climate change generally had negative impacts on rice yield[11]. However, it is still unclear whether the positive effect of CO_2 on rice yield will compensate for the negative effects from other climate change factors, making it difficult to project future changes in global rice yield[10]. Addressing this issue requires accurate quantification of the influence of CFE on rice yield.

Process-based crop models are widely used to quantify the CFE on crop yield at regional to global scales[10,16,17]. By scaling up the CO_2 effects on crop physiology from foliar to canopy and regional levels, or based on the radiation-use-efficiency approach at the canopy scale, these models predict CO_2 impacts on crop yield in the context of future climate change. In recent decades, several crop models have been developed and applied in the Agricultural Model Intercomparison and Improvement Project (AgMIP)[18] and the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP)[19] to simulate global crop yield under climate change. Multi-model ensemble mean or median values from these models generally match observed CFE on crop yield more closely than individual models[20,21]. However, substantial variation in CFE predictions between models, and discrepancies between model predictions and results from field experiments, still exist[10,16,22]. This is possibly because that most of current models did not explicitly parametrize the CO_2 effects between various cultivars[16].

Genotype is one of the most important factor determining the inherent yield potential of crops[16,23], and it largely affects the yield response to rising levels of CO_2[24,25]. For instance, field experiments suggest that Indica and Japonica, the two main sub-species of rice, respond differently to enhanced CO_2[26]. Rice growing regions are usually dominated by one of these two sub-species[27], suggesting the potential for large regional differences in CFE. However, species-dependent responses of rice yield to elevated CO_2 have not been comprehensively analysed and considered in current crop models.

Here, we present a comprehensive study to assess the variation in CO_2 response between rice sub-species and cultivars. First, we compiled a dataset including results from field-based CO_2 enrichment experiments, covering the main rice planting areas and various cultivar types (Fig. S1), including 167 site-years of CO_2 enhancement experiments (see Methods), which is, as far as we know, the most complete datasets that conducted at field conditions. We then used meta-analysis to compare rice yield responses to elevated CO_2 between the two main different rice sub-species (i.e., Japonica and Indica). Second, we conducted the field experiments covered with 50 various cultivars at the same site to test the above finding. We also conducted a pot experiment to evaluate the mechanisms underlying the CFE differences between rice sub-species. Finally, we used our findings to inform a suite of crop models, based on the hypothesis that current models would not be able to account for the CFE differences between sub-species. We aimed to show that whether the large regional differences in CFE, and the spatial and temporal variations of regional rice yield, could be better projected after considering this difference.

Results

CFE differences between rice sub-species

Averaged across the studies in our dataset, elevated CO_2 increased rice yield by 9.2 ± 0.5% 100 ppm^{-1} (Fig. 1a). However, the CFE on Indica rice (12.8 ± 0.8% 100 ppm^{-1}) was significantly higher than that for Japonica rice (6.3 ± 0.5% 100 ppm^{-1}; Fig. 1a, b). Despite a substantial spread of CFE between cultivars (Fig. 1c), the CFE of almost all Japonica cultivar types was < 10% 100 ppm^{-1}, while the CFE for most Indica cultivar types was > 10% 100 ppm^{-1} (Fig. 1c).

The CFE on rice yield may vary with environmental and experimental factors other than cultivar types[12]. Thus, in theory the difference in CFE between cultivars could also be caused by differences in environmental conditions between sites. To check that this was not the case, we conducted two additional analyses. First, we combined a mixed-effects meta-analysis with model selection analysis to identify the most important predictors of CFE on rice yield (see Methods). Among a wide range of environmental and experimental factors, rice sub-species was the most important predictor of CFE (Fig. S2a), followed by nitrogen (N) fertilization rate. Again, the effect of CO_2 was significantly higher for Indica than Japonica, after excluding the impacts from other confounding factors (e.g., N fertilizer, duration, temperature etc.) (Fig. S2). The average N fertilization rate were similar for studies on both sub-species (Figs. S3), indicating that the differences between Indica and Japonica could not be attributed to this factor.

Second, we compared the CFE between Japonica and Indica across the four experiments that grew both sub-species side-by-side, thereby ensuring that all environmental and experimental factors for both sub-species were identical. Within this subset of studies, CFE on Indica rice was again significantly higher than that on Japonica rice (Fig. S4). More importantly, to further verify the significant CFE difference between Japonica and Indica was robust, we also conducted the field experiment at the same site with a large spread of rice varieties, i.e., overall 50 cultivars with 25 belonging to Japonica and the other 25 Indica (see Methods). Results showed that the averaged CFE for these 25 Indica cultivars was 11.5 % 100 ppm^{-1}, more than twice larger than that for the 25 Japonica cultivars planted at the same site (5.3 % 100 ppm^{-1}, Fig. S5 & Table. S1). Besides, several previous studies based on meta-analysis that collected more than hundreds of field observations also suggested the remarkable differences of Japonica and Indica sub-species response to enhanced CO_2[26,28]. These above evidences from either the same site or from previous independent analyses, provide further and solid support for our interpretation that CFE differs largely between rice sub-species.

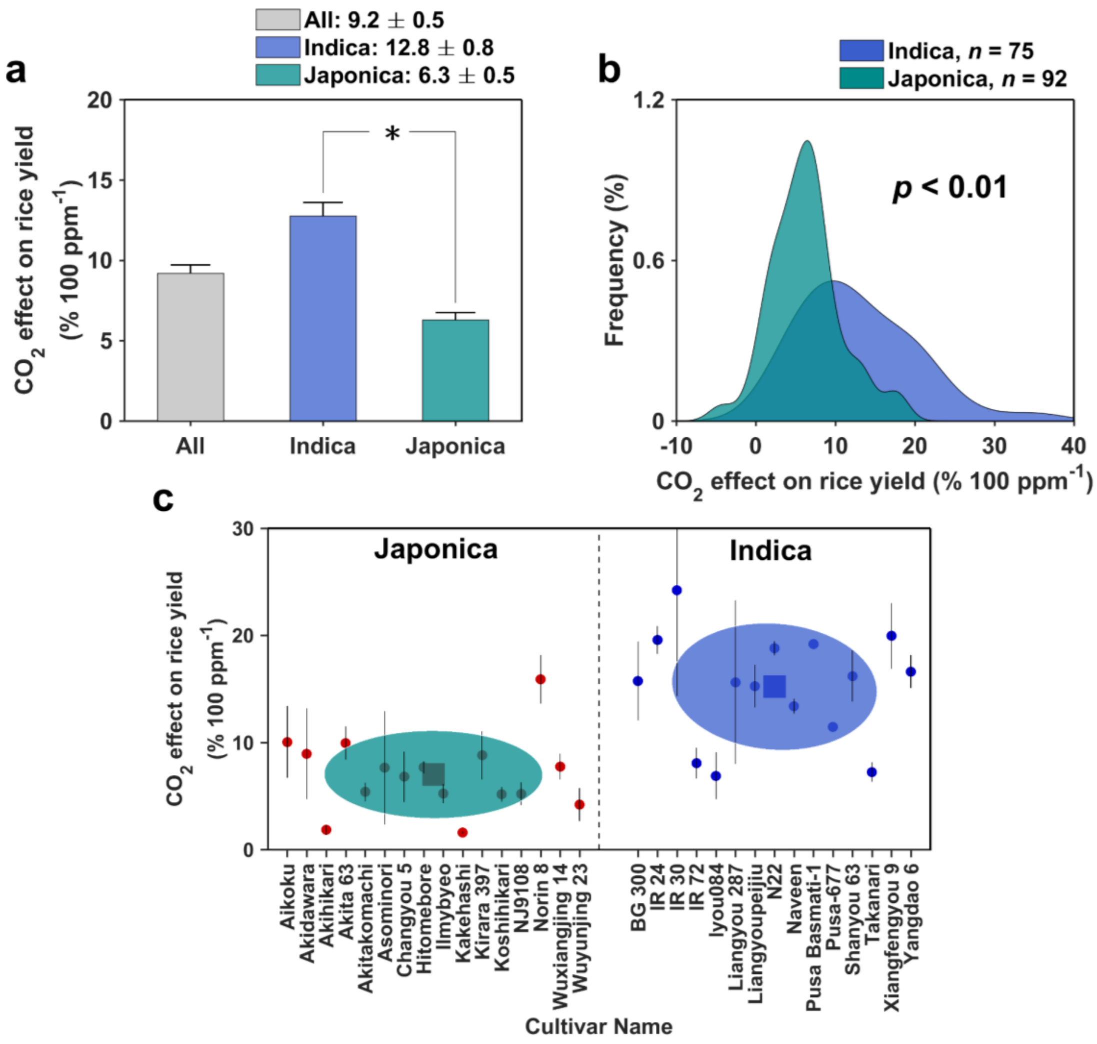

Fig. 1. Differences in rice yield responses to elevated CO_2 between Indica and Japonica sub-species based on field observations. a, The CFE on rice yield for Indica and Japonica, based on 167 field observations. Bars and error bars represent the mean value of CFE and the standard error, respectively. Asterisks indicate a significantly different CFE between Indica and Japonica using a two-sample t-test at $p < 0.01$. **b**, Histogram distribution of CFE for Indica and Japonica rice. The statistical significance (*p*-value) between CFE of Indica and Japonica rice was estimated using a two-sample t-test (*n* represents the number of observations). **c**, The influence of CFE on rice yield for various cultivar types. Solid dots and solid black lines represent the mean value of CFE and the standard error for each cultivar type, respectively. Solid squares represent the average CFE for Japonica and Indica sub-species, respectively. Ellipses show the uncertainty ranges of CFE on rice yield for Japonica and Indica.

Possible mechanisms for CFE differences

To determine the mechanisms underlying the difference in CFE between rice sub-species, we conducted a pot experiment using popular Japonica and Indica cultivars in open-top-chambers and measured physiological parameters throughout the growing season (see Methods). This pot experiment was conducted at two CO_2 levels (ambient and enhanced) and nine field N application levels (see Methods). Net photosynthetic rates (A_n) at the leaf-level of both sub-species responded similarly to elevated CO_2 during the pre-heading stage, but Indica responded more strongly than Japonica during the post-heading stage (Fig. 2a). This phenomenon was observed across multiple N application rates (Fig. S6). During the post-heading stage, the positive effect of elevated CO_2 on A_n remained significant for Indica rice, but largely disappeared for Japonica (Figs. 2a, S6b). These findings are consistent with field experiments showing that CFE during the reproductive stage for Japonica rice was lower than that for Indica rice[26]. The lower CO_2 impacts on photosynthesis during the post-heading stage implies a lower rate of biomass accumulation for Japonica than for Indica rice[29]. Photosynthates formed during the post-heading stage are effectively stored in grains[30], which may explain the differential CO_2 effect on rice yield between these two sub-species.

To investigate why the CFE on A_n was higher for Indica than Japonica rice during the post-heading stage, we also estimated two key photosynthetic parameters, i.e., the maximum carboxylation rate (V_{cmax}) and the maximum electron transport rate (J_{max}), through the leaf-level gas exchange measurements. Elevated CO_2 reduced V_{cmax} both for Japonica and Indica rice (Fig. 2b), consistent with vegetation photosynthetic acclimation to increasing CO_2[14]. However, the reduction in V_{cmax} for Japonica rice was 22.5%, about twice that for Indica rice (11.9%) (Fig. 2b). Similarly, the reduction in J_{max} for Japonica rice was 26.2%, while J_{max} for Indica rice did not change significantly (Fig. 2b). Differential photosynthetic acclimation to elevated CO_2 for Japonica and Indica rice occurred across a range of N application rates (Fig. S7), although the difference between sub-species was most pronounced for moderate N application rates (Fig. S7). This may be because that the remobilization of N occurred earlier developmental cycle for Indica than Japonica. Together, these findings suggest that the difference in CFE between Japonica and Indica rice is related to differences in photosynthetic acclimation rate to enhanced CO_2 during the post-heading stage.

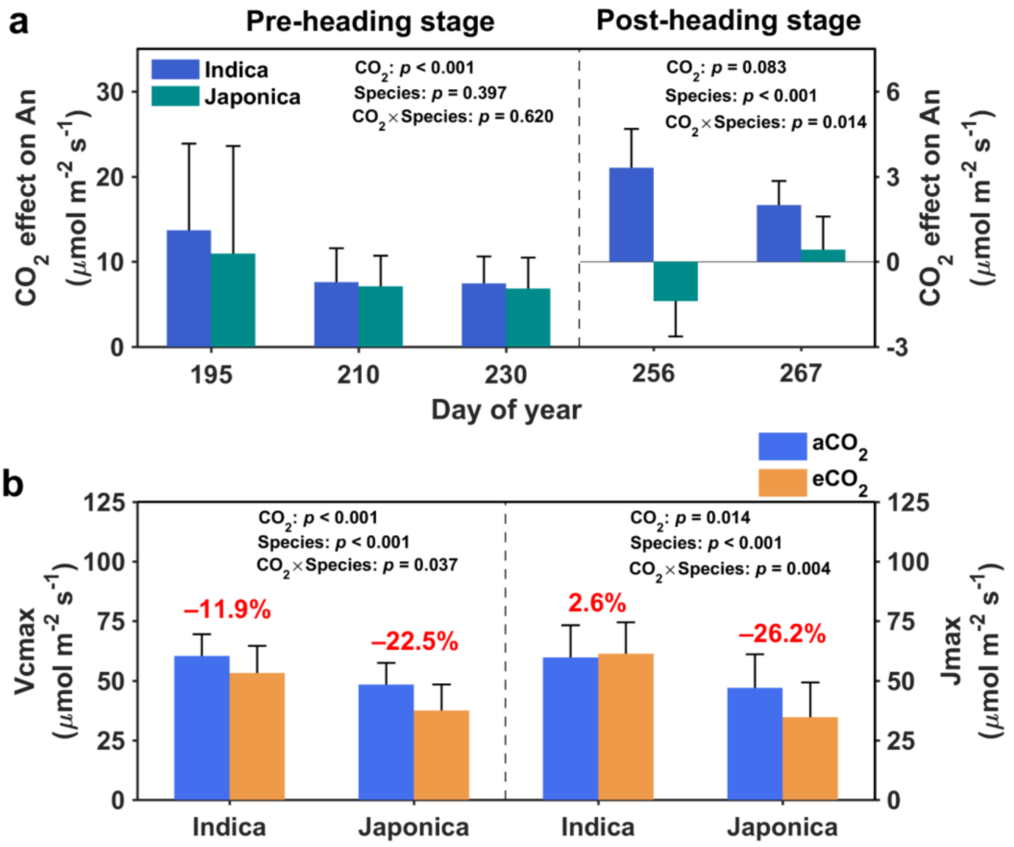

Fig. 2. A comparison of the CFE on the net photosynthetic rate (A_n), the maximum carboxylation rate (V_{cmax}) and the maximum electron transport rate (J_{max}) between Japonica and Indica rice. **a**, The CFE on A_n during the pre-heading stage and the post-heading stage for Japonica and Indica rice ($n = 3$). Bars and error bars represent the mean value of the CFE on A_n and their standard deviation (SD) respectively, across various N application rates. The significance of the impacts of CO_2 enhancement and rice sub-species on A_n were assessed using two-way analysis of variance (ANOVA). **b**, The CFE on V_{cmax} and J_{max} during the post-heading stage for Japonica and Indica rice. Bars and error bars represent the mean value of the CFE on V_{cmax} and J_{max} and their SD respectively, across various N application rates. Numbers above the bars represent the response of V_{cmax} and J_{max} to the increase in CO_2. The significance of the impacts of CO_2 enhancement and rice sub-species on V_{cmax} and J_{max} were assessed using two-way analysis of variance (ANOVA).

Comparing observed CFE to model estimates

We compared the CFE estimates from field experiments to predictions made by eight state-of-the-art process-based crop models that belong to the Global Gridded Crop Model Intercomparison Phase 2 (GGCMI-2) ensemble[31], which estimated the CFE on global rice yield through scenario simulations (see Methods). We extracted the model simulations for each observation in our dataset by maintaining the environmental factors to be the similar between observations and models (see Methods), resulting in 167 pairs of CFE from field observations and corresponding model estimates. Model estimates of CFE had a smaller spread than the CFE observed in experiments (Fig. 3a & S8), and were centred around 10% 100 ppm^{-1} for both Japonica and Indica rice (Fig. 3a & S8). Generally, no clear differences in CFE between various cultivar types were found from models (Fig. S8c). Moreover, current crop models were not able to reproduce the observed CFE on rice yield in field experiments (Fig. 3). Using field experiments as benchmark, models underestimated the CFE on rice yield for Indica sub-species but overestimated the CFE for Japonica sub-species (Fig. 3b).

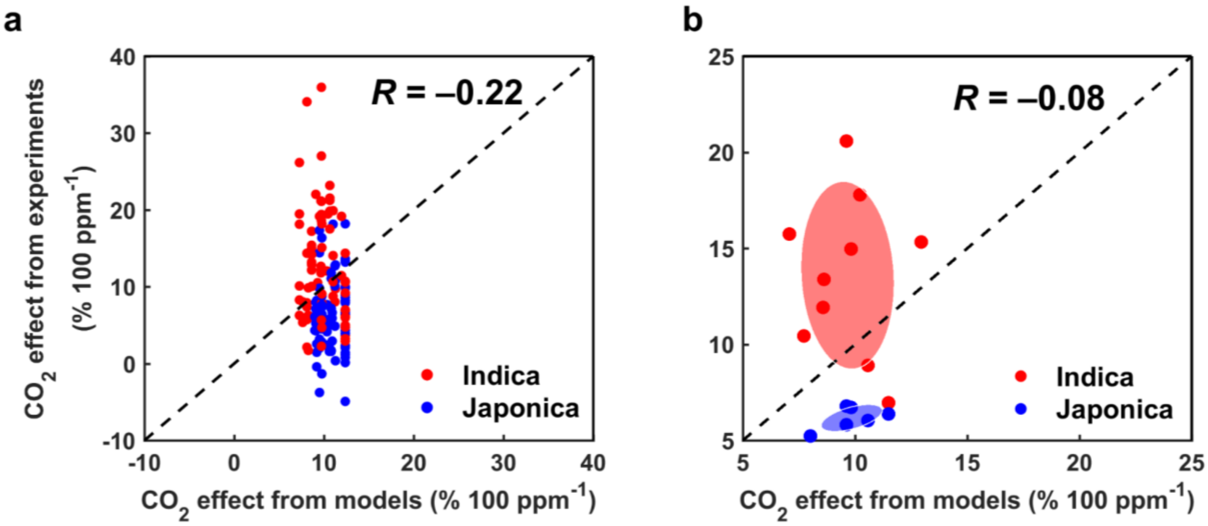

Fig. 3. The CFE on rice yield as observed in field experiments versus CFE predicted by crop models a, Comparison of CFE on rice yield between observations and models for all the 167 observations. The black dashed line represents the 1:1 line. **b**, Comparison of CFE on rice yield between observations and models for all 12 sites. Ellipses show the uncertainty ranges of CFE for Japonica and Indica sites.

Further analysis based on individual crop models verified this finding. All eight models significantly overestimated CFE for Japonica rice (Fig. S9b), and most of the models significantly underestimated CFE for Indica rice (Fig. S9c). The models' inability to capture the observed CFE differences between rice sub-species may be because most models in the GGCMI-2 ensemble do not explicitly consider the physiological differences in cultivars' response to elevated CO_2[31]. Therefore, to improve the accuracy of regional to global rice yield predictions, models need to account for the differences in CFE between rice sub-species and cultivars.

Improving CFE predictions by considering rice sub-species

We analysed the impact of sub-species discrepancies on model predictions of CFE, given that the uncertainties of CFE on crop yields are still large and need to be narrowed[14]. We conducted this analysis through a 'data-model fusion' framework to adjust the modelled CFE estimates to be consistent with results from field experiments (see Methods). This analysis was conducted with China as an example, because China has the largest rice planting areas for both Japonica and Indica rice, and the prior-information of Japonica and Indica sub-species in China is well-documented (Fig. S10). We generated two scenarios: a) modelled CFE after considering differences between Japonica and Indica (termed 'Japonica + Indica'); b) the original estimated CFE from the multi-model mean values (termed 'Original models', see Methods).

After accounting for the CFE differences between Japonica and Indica rice, the projected CFE was consistent with the results from field experiments (R^2 = 0.38 for observation level and R^2 = 0.93 for site level; Fig. S11). The averaged estimates of CFE for China were ~11.9 ± 3.0% 100 ppm^{-1} for the 'Japonica + Indica' scenario, similar to the value of 10.1 ± 1.4% 100 ppm^{-1} from the 'Original models' scenario (Fig. 4a). However, the spatial distribution of CFE differed strongly between these two scenarios (Fig. 4b, c). The original models generally showed no clear spatial variation, with a value around 10% 100 ppm^{-1} (Fig. 4b). By contrast, the updated CFE estimates in the 'Japonica + Indica' scenario was notably higher for areas planted with Indica rice (e.g., Southeast China) than areas with Japonica rice, which are generally located in Northeast China (Fig. 4c). Compared to the 'Japonica + Indica' scenario, the 'Original models' scenario largely underestimated the CFE for traditional Indica planted regions (Fig. 4d). Similarly, the projections from 'Original models' scenario heavily overestimated the CFE values at many traditional Japonica planted regions (Fig. 4d). Therefore, compared with the 'Original models' scenario that predicted the regional CFE with generally non-spatial variation (Fig. 4b), the 'Japonica + Indica' scenario showed a two-peaked shape (around 7% and 14% 100 ppm^{-1}; Fig. 4a), more consistent with the results from field controlled experiments (Fig. S11). These results suggest that the regional CFE estimations could be improved by considering the differences between rice sub-species.

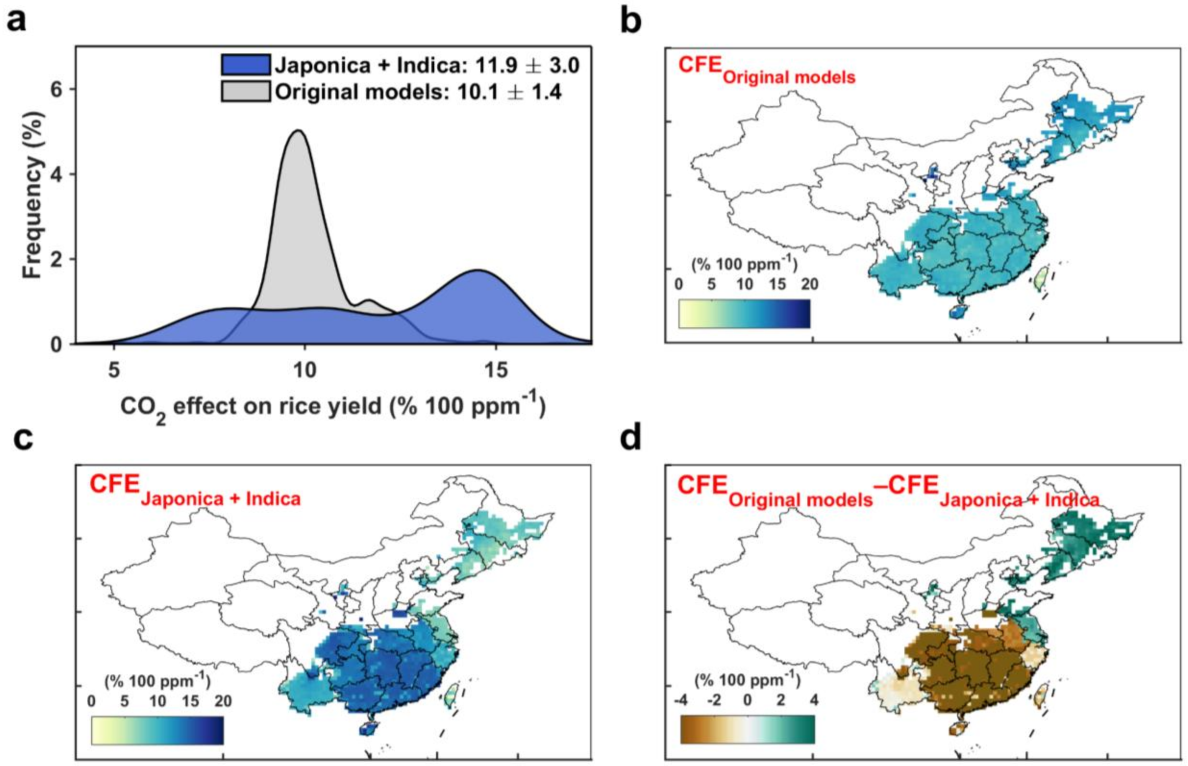

Fig. 4. Estimation of CFE on rice yield across rice planting areas in China after considering the differential CO_2 effect for Japonica and Indica rice. a, Histogram distribution of CFE for two scenarios, namely the estimated CFE after considering the Japonica and Indica differences (termed 'Japonica + Indica') and the original estimated

CFE from multi-model mean values ('Original models'). Mean values and their standard deviation (SD) are given in the figure. **b**, Spatial distribution of CFE estimates in the 'Original models' scenario. **c**, Spatial distribution of CFE estimates in the 'Japonica + Indica' scenario. **d,** difference in CFE estimates between the 'Original models' and 'Japonica + Indica" scenarios.

Improved regional rice yield projections by considering rice sub-species

Improving the regional estimations of CFE is only the first step, and further, the resulting improved projections of regional and global rice yield is our final goal, which is the basis for formulating mitigation polies to ensure global food security. Based on the improved regional CFE estimations, we then simulated the rice yield across China's rice planting areas using the emulator approach during the past four decades (see Methods), and also extend this approach to project the future rice yield during 2020-2050 (Fig. 5). Using the global rice yield estimations from EarthStat as the benchmark, on the grid level, we found that the simulation result from the 'Original models' scenario largely underestimated the rice yield in China (R^2=0.12, Fig. S12a). On the contrary, after incorporating the CFE differences between Japonica and Indica, the regional rice yield simulations have been improved, with a R^2 value of 0.48 (Fig. S12b).

Beyond the rice yield simulations at the grid level, more importantly, the yearly mean rice yield and its temporal trend could be largely improved after considering the sub-species difference. Compared to the yearly rice yield statistics from National Bureau of Statistics of China, most of the original GGCMI-2 models generally underestimate the yearly mean rice yield in China (Fig. S13a). Averaging the rice yields from these models, the underestimation of yearly mean rice yield was more clear, with a slope of 0.32 and a RMSE value of 1.42 t ha^{-1} (Fig. 5b). On the contrary, after considering the CFE differences between Japonica and Indica into the emulators, the yearly mean rice yield from models and observations was generally consistent (slope=0.72, RMSE=0.27 t ha^{-1}, Fig. 5b). Before adjusting, the linear trend of rice yield from original GGCMI-2 models during 1980-2019 (21.7 kg ha^{-1}) was significantly lower than that from the rice yield statistics (58.0 kg ha^{-1}, Fig. 5a & Fig. S13b). While, after considering the CFE difference between Japonica and Indica, the trend from model simulation increased to 47.0 kg ha^{-1}, close to the result from observations (Fig. 5a). Extending this approach to the future rice yield projections under the SSP245 scenario, the mean rice yield in China may increase at a rate of 28.0 kg ha^{-1} during 2020-2050, which is almost three times higher than that from the original models (8.6 kg ha^{-1}, Fig. 5a). These results not only suggest that the regional rice yield could be estimated with high accuracy based on the emulator approach, but also prove the importance of considering species differences of rice yield response to CO_2 when we need the accurate simulations and projections of global rice yield.

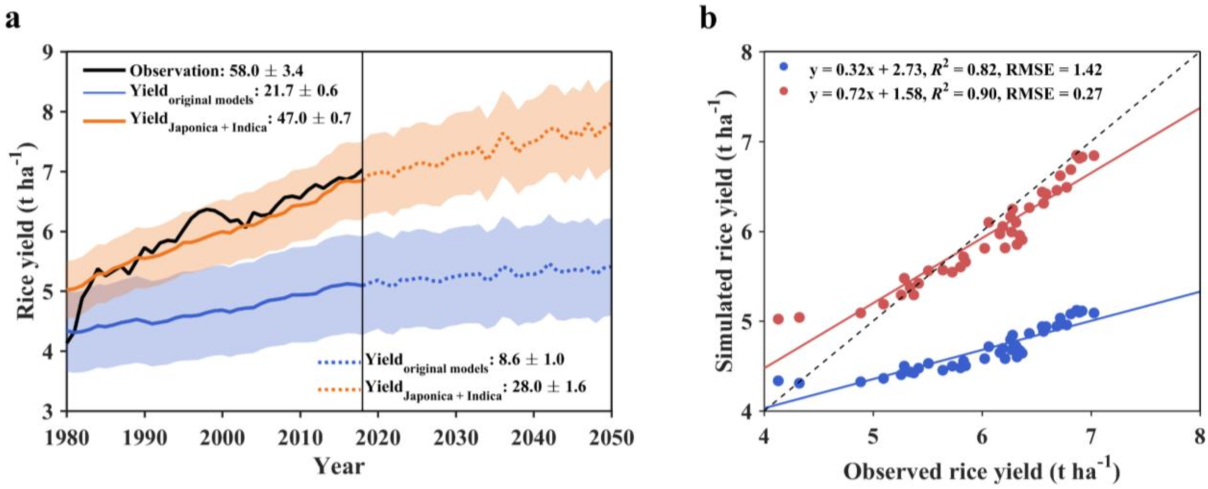

Fig. 5. Rice yield simulations (1980-2019) and projections (2019-2050) across rice planting areas in China before and after considering the differential CO_2 effect for Japonica and Indica rice. a, Yearly mean rice yield simulations and projections for two scenarios, namely after considering the CFE differences between Japonica and Indica (termed '$\text{Yield}_{\text{Japonica + Indica}}$') and from multi-model mean values ('$\text{Yield}_{\text{Original models}}$'). Solid lines represent the yield simulations during 1980-2019, and dotted lines represent the yield projections during 2020-2050 at the SSP245 scenario (see Methods). The shaded areas represent the standard deviations (SD). Mean rice yield observations from the statistics from National Bureau of Statistics of China were used as the benchmark (solid black line). The linear trends of the two scenarios and the observations were calculated and presented (numbers represent the linear trends and their standard errors, with a unit of kg ha^{-1}). **b**, Comparisons of the rice yield simulations from these two scenarios ($\text{Yield}_{\text{Japonica + Indica}}$ and $\text{Yield}_{\text{Original models}}$) with the observations from China's statistics during 1980-2019. Solid lines represent the linear regressions and dotted black lines represent the 1:1 lines. R^2, determination coefficient; RMSE, root-mean-square error.

Discussion

The positive effect of elevated CO_2 on rice yield originates from the direct stimulation of foliar photosynthetic rate[14,32], which is then amplified to the canopy scale through changes in leaf area[33,34], and is also affected by the allocation of biomass to crop grains[24]. On this basis, several plant traits and processes, including foliar photosynthesis, soil nutrient acquisition, nutrient use efficiency and biomass allocation, may contribute to the differential CFE on Japonica and Indica rice. We found a significantly different response of foliar photosynthetic rate to elevated CO_2 between these two rice sub-species during the reproductive stage, which may fundamentally affect the biomass accumulation of rice growth (Fig. 2a). Our data further suggest that this difference between sub-species can be explained by different photosynthetic acclimation rate to higher CO_2 between Japonica and Indica rice (Fig. 2b). Plant photosynthetic capacity is mainly controlled by foliar N concentration[35], suggesting that the different responses of V_{cmax} and J_{max} between rice sub-species are related to their acquisition efficiency of N from soils[36]. This explanation was supported by our finding that the difference in CO_2 responses between Japonica and Indica rice for both photosynthetic capacities and rice yield were more pronounced at moderate N application rates (Figs. S7 & S14). At moderate N availability, differences in N acquisition efficiency from soils may result in large differences in foliar N concentrations[37]. By contrast, under zero or extremely high N application rates, the foliar N concentration of rice is not largely affected by the ability of rice to acquire N from soils, and the response of rice yield to CO_2 are similar between sub-species (Fig. S14). The divergence in N acquisition capability for different rice cultivars may result from their different key genes (e.g., *NRT1.1B*)[38,39], which suggests the potentials to improve the CFE on rice yield through gene-editing techniques[40]. In addition, the differences in the sink capacity between various rice cultivars also possibly be an important factor leading to the divergent response of rice yield to enhanced CO_2[24,41].

To simulate the CO_2 effect on crop yield, process-based crop models generally represent the plant processes such as photosynthesis at the foliar and canopy scale, and consider the impact of biomass allocation[16]. The key process that influences the CO_2 effect on crop yield, that is, the photosynthetic rate, is generally simulated through a series of biochemical equations[42], or based on the radiation-use efficiency or transpiration-efficiency approaches[16]. Among these models, several key parameters still have large uncertainties, especially at large spatial scales. For example, in the popular Farquhar biochemical model[42], V_{cmax} and J_{max} are the most important factors to directly affect both net photosynthetic rate and the magnitude of CO_2 effects[43,44]. These parameters in crop models were generally obtained from the leaf gas-exchange data at non-stress conditions and then extended to large spatial scales. Alternatively, V_{cmax} and J_{max} can also be estimated by an empirical function of foliar N concentrations[35,45] and then upscaled to regional scales. These parameters are possibly converged for some crops, however, clearly it is not the case for rice given the tremendous genetic diversity of rice cultivars. Therefore, the sub-species and cultivars dependent V_{cmax} and J_{max} values are needed to be considered when we used crop models to predict regional and global rice yield.

Many rice models predict similar CFE for both Japonica and Indica rice planted areas (Fig. 3) and do not capture spatial variation (Fig. 4b). This is not surprising, since most of these models do not explicitly consider differences between rice sub-species and cultivars, and need the calibration of cultivar-based specific values[31]. This is partly because of a lack of data on the spatial distribution of rice sub-species and cultivars at large scales, which is an urgent knowledge gap to fill. To better represent different sub-species in crop models, their soil N acquisition efficiency and different photosynthetic acclimation rates need to be considered[26,36]. In this regard, more field experiments and data synthesis are needed to inform crop models, better describe the soil nutrients acquisition process, and to estimate the key parameters more accurately[16,24]. Additionally, the parameterisation of crop models could also be improved through the ‘data-model fusion’ approach, with the aid of either the field experiments network or remote sensing observations[43,46].

Accounting for differences in CFE between rice sub-species may only be the first step towards the improved yield predictions, since CFE also varies between cultivars within the same sub-species (Fig. 1c). Further analysis of CFE at the cultivar level may be useful to improve model performance, but currently limited field observations do not fully cover the popular cultivars planted in global rice areas[24]. On this aspect, our study here provides an alternative approach (i.e., data-model fusion) to calibrate the CFE values across difference rice sub-species. And through this approach, together with the emulation method, we could enhance the modelled accuracy of regional rice yield with the synchronously changed CO_2, temperature and other climate factors (Fig. 5). Besides, we also argued that more CO_2 enhancement experiments covering a wider range of cultivars are needed, especially in developing countries with few observations[16]. Also, we suggest that an open-access platform and a repository containing standard field observations and metadata are needed to provide immediate and free access to data. Moreover, although current experiments and models are beginning to consider the complex interactions between genotypes, CO_2 and other environmental factors (temperature, radiation, ozone) on rice and crop yield, both the underlying mechanisms and modelling approaches remain poorly understood[16,47]. One caveat of this study is that we did not consider the interaction of other factors (temperature, precipitation etc.) on the CFE when we project the regional rice yield. On this aspect, to better simulate and project global crop yield in the context of climate change, these factors need to be investigated and considered in future modelling efforts.

Conclusion

In summary, we report a substantial difference in the response of rice yield to CO_2 enrichment between two major rice sub-species, with CFE for Indica rice about twice that for Japonica rice. This finding is based on hundreds of field observations, and on results of side-by-side comparisons between Indica and Japonica rice conducted at the same locations. The differences in CFE for Japonica and Indica rice may originate from the differential responses of photosynthetic rate to increasing CO_2 at the reproductive stage, which in turn is related to differences in photosynthetic acclimation rate. Current process-based crop models do not consider these differences, causing erroneous estimates of the spatial distribution of rice yield responses to elevated CO_2. By considering the differences in CFE between Japonica and Indica, regional estimates of CFE on rice yield can be modified and become more consistent with field observations. More importantly, after considering the CFE between rice sub-species, the modelled accuracy of regional rice yield has been largely enhanced. These results emphasize the impact of genotypes on the response of crop yield to climate change, highlight the need to consider genotypes in current crop models, and may ultimately inform breeding programs and adaptation efforts to maintain and enhance global crop yield as our climate continues to change.

Experimental procedures

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Dr. Songhan Wang (wangsonghan@njau.edu.cn).”

Materials availability

This study did not generate new unique materials.

Data and code availability

The collected field experiment data and the pot experiment data are available at https://figshare.com/s/971479b6006d220484da. The GGCMI-2 data are available from the public links from Table. 4 of [31] (e.g., the outputs of APSIM-UGOE rice model is available at https://doi.org/10.5281/zenodo/2582533). The GGCMI-2 emulators are available at https://zenodo.org/record/3592453. The rice yield from EarthStat is available at http://www.earthstat.org/. The rice yield statistics in China are available from http://data.stats.gov.cn. The global averaged atmospheric CO_2 concentrations are available at https://gml.noaa.gov/ccgg/trends/data.html. The CRU TS4.03 climate data are available at https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.03/. The code used in this study are available at https://figshare.com/s/971479b6006d220484da.

Data from field experiments

We collected data from previous studies to compare CFE between rice sub-species. We used Web of Science to search literature published before 2020 that used field artificial CO_2 enhancement facilities to assess the CO_2 effect on rice yield. We only included experiments conducted at field environment conditions, using field chambers, open-top-chambers (OTC) and free-air CO_2 enhancement (FACE) facilities in our analysis. We only considered experiments that spanned at least one whole growing season and reported both rice yields and the CO_2 concentrations. We avoided the confounding effects of other climate factors on rice yield by collecting the pairs of data acquired under the same experimental conditions for other factors (e.g., temperature) and differing only in CO_2 concentration. Following the above criteria, we collected data from 12 experimental sites (Fig. S1), covering the main global rice planting areas, resulting in 167 site-years of observations (92 for Japonica rice and 75 for Indica rice; Fig. 1). Among these 12 experimental sites, two of them were planted with all Japonica cultivars (Japonica sites), six were planted with all Indica cultivars (Indica sites), and the remaining four were planted with both sub-species (Mixed sites). Ambient and elevated CO_2 concentration, field N application rate, rice yield and rice cultivar data were extracted from the literature. The CO_2 effect on rice yield (CFE, % 100 ppm^{-1}) was used to represent the sensitivity of rice yield to CO_2

concentration changes. To compare experimental observations with model predictions, CFE values were normalised to a +100 ppm impact by dividing the effect value by ΔCO_2 using the following equation:

$$\mathrm{CFE} = \frac{\Delta \mathrm{Yield}}{\Delta \mathrm{CO_2}} \times 100 \qquad (1)$$

where ΔYield and ΔCO_2 represent differences in rice yield (%) and CO_2 concentration (ppm) between the elevated CO_2 treatment and the ambient CO_2 treatment. Although the response of rice yield to CO_2 is nonlinear at various CO_2 concentrations[14], the average ambient and elevated CO_2 concentrations for different rice sub-species (i.e., Japonica and Indica) were similar (Fig. S15). Therefore, normalisation of CFE is unlikely to affect the main findings of this study.

Data from crop model simulations

We compared the CFE estimates between field experiments and crop models. Overall, eight process-based crop models (APSIM-UGOE, CARAIB, EPIC-IIASA, EPIC-TAMU, GEPIC, LPJmL, PEPIC, pDSSAT) belonging to the Gridded Crop Model Intercomparison Phase 2 experiment (GGCMI-2) were used in this study[31]. As part of the Agricultural Model Intercomparison and Improvement Project (AgMIP), GGCMI-2 was designed to provide a systematic assessment of the crop yield response to changes in climate change factors and soil fertilisers. These models used the same simulation protocol and similar input datasets, e.g., they all used the AgMERRA daily climate data, and most of them used the FAO or ISRIC-WISE database to describe the soils[31]. For rice simulations, most of the models did not calibrate for various sub-species and cultivars. Validations against the FAO historical yields and site-specific experimental data showed the reasonable fidelity of these models at capturing year variations[31]. However, it should be noted that the GGCMI-2 models were not designed to capture the realistic crop yield, but to simulate the rice yield response to environmental factors (CO_2, temperature etc.). Therefore, the comprehensive simulations with varying atmospheric CO_2 level, temperature, water supply and applied nitrogen scenarios conducted from a previous study that based on the GGCMI-2 models[31], providing ideal datasets for assessing CFE on rice yield in this study, not only at the site-level, but also at the regional to global scales.

In this study, we used rice yield simulations from eight models conduced at two different CO_2 levels (360 and 660 ppm) from a previous study[31], with other factors remaining constant (temperature, water supply and applied N fertilizer). We used these two CO_2 levels to make fair comparisons between field experiments and models, since their ambient and elevated CO_2 concentrations were similar (Fig. S15). We also analysed the CFE from models at 360 and 510 ppm and compared them with experiments. Using both approaches, crop models did not project a difference in CFE between Japonica and Indica rice (Fig. S16). To make fair comparisons with experiments, among the three levels of N fertilizer simulations from GGCMI-2 models (10, 60 and 200 kg ha^{-1})[31], we used the scenarios of 200 kg ha^{-1}, which is the closest to the averaged N fertilizer rate used for field experiments (Fig. S3). Other environmental factors (temperature, precipitation, soil properties, N fertilizer etc.) between the models and experiments should be the similar, since the GGCMI-2 models used the realistic climate, soil, planting dates and N fertilizers as the input[31]. The standard and harmonized input datasets ensure the environmental factors in GGCMI-2 models to be the similar with those of the experimental sites. The CO_2 effect on rice yield for each pixel from models was then calculated using Eq. (1) and normalised to the same units (% 100 ppm^{-1}). Since model simulations were conducted at a spatial resolution of 0.5°, we extracted the modelled CFE using the results from the pixel nearest each site.

Pot experiments

To identify the possible mechanism underlying CFE differences between Japonica and Indica rice, we conducted pot experiments using an OTC facility[48]. Pot experiments were conducted in Danyang (31°54′N, 119°28′E), China, in 2021. The experimental site has a subtropical monsoon climate, with a mean annual temperature of 16.4°C and a mean precipitation of ~1056 mm. Rice-wheat crop rotation is the main cropping system at this area, hence we conducted experiments during the rice season from mid-June to mid-October. Pot experiments were conducted using the OTC platform, which consists of two open top boxes, a control system and a gas supply system. The open top box is a hexagonal prism with sides 1.5 m long and 1.8 m high constructed by plexiglass. The control system includes the GMM220 CO_2 sensors, a valve control module and a data acquisition module, which enables the real-time monitoring and adjustment of CO_2 concentrations at a frequency of 30 seconds.

We used 54 pots in one ambient CO_2 chamber and 54 pots in another elevated CO_2 chamber. These 54 pots included two rice sub-species, nine N fertiliser gradients, and three replicates ($54 = 2\times9\times3$). Each plastic pot (20 cm long, 15 cm wide, 15 cm high) was filled with 4 kg of air-dried clay soil. We employed two widely-used rice cultivars; *Wuyungeng* representing the Japonica sub-species and *Y-liangyou-900* representing the Indica sub-species. We also used nine N application rate gradients (urea) ranging from 0–400 kg ha^{-1} with a step of 50 kg ha^{-1}, 60% of the N fertiliser was applied at transplanting stage, 20% of N fertiliser was applied at the tillering stage, and the remaining N was applied at the young panicle differentiation stage. The phosphorus fertilizer (120 kg P_2O_5 ha^{-1}) was applied at soil tillage stage, and potassium fertilizer (80 kg K_2O ha^{-1}) was applied at soil tillage stage. Rice seedlings were transplanted into each pot in mid-June, moved into the OTC platform, and grown until harvest under two levels of atmosphere CO_2 concentration (ambient ~410 ppm; elevated ~600 ppm). We maintained the water layer (3–5 cm) before the tillering stage, and used the intermittent flooding practice, i.e., did not add water until the water filled pore space of soils (0–5 cm depth) decreased to ~75%. Other field practices were followed the local recommendations.

The net foliar photosynthetic rate during the whole growing season, V_{cmax} and J_{max} during the post-heading stage, and the grain yield after harvest were measured. We measured the net foliar photosynthetic rate of each pot for these various treatments using an LI-6400 Portable Photosynthesis System (LI-COR Inc., Lincoln, USA). Measurements were conducted during the key growing stage of rice with three replicates (Fig. S6). We also measured the photosynthetic capabilities (V_{cmax} and J_{max}) of rice leaves during the post-heading stage by measuring A-Ci curves using the LI-6400 instrument (Fig. S7). We oven-dried the rice grains to achieve a moisture content of about 13%, and then measured the grain yield of each plot. All values used in the analysis were averaged across three replicates.

In order to further check the robustness of the significant CFE differences between Japonica and Indica, we also conducted the pots experiments using the same OTC facility with a total of 50 typical cultivars at the same site (Danyang). Overall 50 cultivars including 25 Japonica cultivars and 25 Indica cultivars, and four replicates, were planted at four ambient and enhanced chambers respectively. As far as we know, this experiment was the largest number of cultivars tested for the same site at the same time, which could further test the CFE differences between Japonica and Indica. We measured the grain yields at maturity and then calculated the CFE for each cultivar (Table. S1).

Data synthesis

We firstly analysed the differences in CFE on rice yield between rice sub-species (Japonica and Indica) based on the collected data from previous field experiments. Individual site-year observations were separated into two groups (Japonica and Indica). We then calculated and compared the averaged CO_2 effect for Japonica and Indica. Differences between CFE of Japonica and Indica rice were evaluated using a two-sample t-test. The CFE on rice yield for each individual rice cultivar were also analysed.

To test the robustness of our analysis, we also conducted a meta-analysis to investigate the CFE on rice yield between rice sub-species. For each experiment, we quantified the CFE on rice yield by calculating the natural logarithm of the response ratio (R), $\ln R = \ln (Y_e / Y_a)$, where Y_e and Y_a represent the rice yield under elevated CO_2 and ambient CO_2 treatments respectively. We weighted lnR by the inverse of the study variance, estimating missing variances using the average coefficient of variance across the whole dataset. The following environmental factors that affected rice yield were used, including rice sub-species (Japonica or Indica), N application rate, study duration, soil organic carbon (SOC), temperature of the rice season, water regimes, facility, and the degree of CO_2 enrichment ($\triangle CO_2$). Then, the relative importance of the environmental factors in affecting the CFE on rice yield was determined using the "glmulti" package in R[49,50]. We used a Wald test[51] to determine whether treatment effects were statistically different between experimental classes. We perform a mixed-effects meta-analysis in R using the rma.mv function in the "metafor" package[52]. We included "site" as a random effect, because each sites contributed multiple observations to the dataset. We conducted the meta-analysis for the full dataset, and for the subset of data derived from the four ‘Mixed’ sites respectively. To ease interpretation, we back-transformed the results of lnR and reported as the percentage change [(R − 1) × 100].

We then compared the CFE on Japonica and Indica rice yield from the results of field experiments and crop models. At the individual observation level, CFE values estimated from crop models were extracted as the pixel nearest the site during the same observation year. This procedure resulted in the same 167 estimated CFE values for each crop model, of which 92 values were for Japonica and 75 for Indica. We then compared the modelled CFE values between Japonica and Indica rice using the same method with field observation data. Since there may be multi-observations at one field site, at the site level, we aggregated the multiple CFE estimations of a site into a single value. CFE values estimated from field experiments and crop models at these 12 sites were then compared with each other.

Finally, using China as an example, we estimated regional CFE on rice yield after considering the CFE differences between rice sub-species. The rice planting areas in China were extracted from a widely-used high spatial resolution (10 km) global crop distribution dataset (Fig. S1)[53]. Across the rice planting areas in China, two regional CFE scenarios were estimated. The first scenario was the original values of CFE estimated from the eight GGCMI-2 models (termed ‘Original models’ scenario). The second scenario was based on the improved regional CFE estimates using the optimal-fingerprint method[54], to consider the CFE differences between Japonica and Indica and to adjust the modelled CFE estimates to be consistent with the results from field experiments (termed ‘Japonica + Indica’ scenario). Simply speaking, the method just used the empirical factors to directly adjust the CO_2 effects from original model outputs, but did not need other data inputs. Based on the original CFE outputs from GGCMI-2 models, we could easily modify the CFE estimation through this data-model fusion approach and considered the CFE differences between rice-species, but did not need to modify the source code and re-run the models. The optimal-fingerprint method was conducted as follows:

$$\begin{cases} \mathrm{CFE}_{\mathrm{obs\_Japonica}} = \sum_{\mathrm{i}=1}^{\mathrm{n}} \beta_{\mathrm{Japonica}}^{\mathrm{i}} \mathrm{CFE}_{\mathrm{model}}^{\mathrm{i}} \\ \mathrm{CFE}_{\mathrm{obs\_Indica}} = \sum_{\mathrm{i}=1}^{\mathrm{n}} \beta_{\mathrm{Indica}}^{\mathrm{i}} \mathrm{CFE}_{\mathrm{model}}^{\mathrm{i}} \end{cases} \quad (2)$$

where $\mathrm{CFE}_{\mathrm{obs\_Japonica}}$ and $\mathrm{CFE}_{\mathrm{obs\_Indica}}$ represent the CFE on Japonica and Indica from field observations, $\mathrm{CFE}^{\mathrm{i}}_{\mathrm{model}}$ represents the CO_2 effect on rice yield based on crop models, $\beta^{\mathrm{i}}_{\mathrm{Japonica}}$ and $\beta^{\mathrm{i}}_{\mathrm{Indica}}$ represent the scaling factors for Japonica and Indica rice, and i refers to the different crop models ($n = 8$). Based on the observation data from previous studies, the scaling factors (β) for Japonica rice and Indica rice in Eq. (2) were estimated using maximum likelihood analysis. Through the above optimal-fingerprint method applied separately to Japonica and Indica, we adjusted the modelled CFE to be consistent with the results from field observations, and took into consideration the CFE differences between rice sub-species.

After calculating the scaling factors using Eq. (2), we estimated the actual regional CFE across planting areas in China after accounting for the CFE differences between Japonica and Indica rice. We first obtained the planting areas of rice in each province of China through the China Agricultural Statistics Yearbook, then obtained the planting areas of Japonica rice from a previous study[55]. The percentages of Japonica rice in each province were estimated (Fig. S10), and the remaining areas were deemed as Indica rice planting regions. Note that hybrid-rice cultivars that originate from Japonica were considered Japonica rice, and the same was true for Indica. We then calculated the improved CFE estimates of each pixel ('Japonica + Indica' scenario) as follows:

$$\mathrm{CFE}_{\mathrm{Japonica+Indica}} = \mathrm{R}_{\mathrm{Japonica}} \sum_{i=1}^{n} \beta^{i}_{\mathrm{Japonica}} \mathrm{CFE}^{i}_{\mathrm{model}} + \mathrm{R}_{\mathrm{Indica}} \sum_{i=1}^{n} \beta^{i}_{\mathrm{Indica}} \mathrm{CFE}^{i}_{\mathrm{model}} \tag{3}$$

where $\mathrm{CFE}_{\mathrm{Japonica+Indica}}$ represents the CFE estimates at each pixel for the 'Japonica + Indica' scenario, and $\mathrm{R}_{\mathrm{Japonica}}$ and $\mathrm{R}_{\mathrm{Indica}}$ represent the percentage of Japonica and Indica rice in each pixel. Finally, the regional CFE values across China from these two scenarios were compared with each other.

Regional rice yield simulations and projections

In order to analyze the regional CFE differences impacts on rice yield, we used the emulation approach together with the GGCMI-2 models to simulate and project the rice yields in China. To simplify the simulation of global crop yield, a previous study has proposed this emulation approach, which used the statistical model to represent the crop yield as a function of various environmental factors[56]. They used a third-order polynomial basis function to represent the global rice yield as the function of four main factors, i.e., atmospheric CO_2, temperature, precipitation and applied nitrogen (CTWN). In general, the rice yield could be expressed as:

$$\mathrm{Y} = \sum \mathrm{K}_i * \mathrm{f}(\mathrm{C}, \mathrm{T}, \mathrm{W}, \mathrm{N}) \tag{4}$$

where Y represents the rice yield, f represents the three-order polynomial functions of CO_2, temperature, precipitation and applied nitrogen; K_i represents the coefficients, i.e., the emulators. Detailed information of the functions can be found at[56]. Based on this approach, the previous study has demonstrated that the resulting GGCMI-2 emulators can reproduce the global rice yields under various climate conditions[56].

Therefore, we followed this emulation approach, to investigate the regional CFE differences impacts on rice yield. Two scenarios were generated, of which the first one was based on the rice yield simulations from the GGCMI-2 emulators (termed 'Original models' scenario). In this study, we used six models that has fitted the emulators, including CARAIB, EPIC-TAMU, GEPIC, LPJmL, pDSSAT and PEPIC. We also generated the second scenario which considered the CFE differences between Japonica and Indica (termed 'Japonica + Indica' scenario), by adjusting the emulators corresponding to the CO_2 term in Eq. (4):

$$Y = R_{Japonica}\beta_{Japonica}K_C f(C) + R_{Indica}\beta_{Indica}K_C f(C) + \sum K_i * f(T, W, N) \quad (5)$$

where $\beta_{Japonica}$ and β_{Indica} represent the scaling factors for Japonica and Indica rice from Eq. (2), $R_{Japonica}$ and R_{Indica} represent the percentage of Japonica and Indica rice in each pixel, K_C represent the emulators corresponding to the CO_2 term in Eq. (4). By applying this approach, the CO_2 impacts on rice yield (represented by K_C) could be improved and the CFE differences between Japonica and Indica have been incorporated into the rice yield simulations.

We then simulated the rice yield across China pixel by pixel for the above two scenarios during the past four decades (1980-2019), with a spatial resolution of 0.5 degree. The input datasets include the yearly global averaged atmospheric CO_2 concentrations, the gridded growing-season mean temperature from CRU TS4.03, and the yearly gridded applied nitrogen fertilizers[57]. The rice yield simulations were firstly generated from the six individual GGCMI-2 models, and then the multi-model mean values were calculated ($Yield_{Original\ models}$). Finally, based on Eq. (5), the improved rice yield simulations were also generated ($Yield_{Japonica+Indica}$).

We validated both the spatial and temporal accuracies of the rice yield simulations. The spatial distributions of the rice yield simulations were validated against the rice yield data from EarthStat, which provided the geographic distribution of global rice yield in the year of about 2000[53]. The rice yield simulations of these two scenarios at 2000 were compared to EarthStat data respectively (Fig. S12). We also validated the temporal variations of the rice yield simulations, using the yearly mean rice yield observations during 1980-2019 from the National Bureau of Statistics of China (http://data.stats.gov.cn) as the benchmark. The temporal trends of the rice yield simulations of the two scenarios were estimated, and then compared to the observations (Fig. 5 & Fig. S13).

Finally, we also predicted the rice yield for these two scenarios to 2050, based on the same emulation approaches. The input data including the future CO_2 concentrations, temperature and nitrogen fertilizers. Here in this study, we used a medium-emission scenario, i.e., the SSP245 scenario. The future CO_2 concentration prediction under SSP245 was obtained from[58]. The future temperature predictions were the averages based on eight CMIP6 models (CanESM5, CNRM-CM6-1, INM-CM5-0, HadGEM3-GC31-LL, NESM3, MRI-ESM2-0, IPSL-CM6A-LR, ACCESS-ESM1-5). The applied nitrogen fertilizers were assumed to be unchanged for future predictions, since there are no reliable predictions of nitrogen fertilizers at long time-period. After the projections of rice yield based on these two scenarios, their temporal trends during 2020-2050 were calculated then compared with each other.

Supplementary information: Figures S1–S16 & Table. S1

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References:

1. UN, Transforming Our World: The 2030 Agenda for Sustainable Development (UN, New York, 2015); http://bit.ly/TransformAgendaSDG-pdf.
2. H. C. J. Godfray *et al.*, Food security: the challenge of feeding 9 billion people. *Science* **327**, 812-818 (2010).
3. J. A. Foley *et al.*, Solutions for a cultivated planet. *Nature* **478**, 337-342 (2011).
4. P. A. Seck, A. Diagne, S. Mohanty, M. Wopereis, Crops that feed the world 7: Rice. *Food Security* **4**, 7-24 (2012).
5. N. Bandumula, Rice production in Asia: Key to global food security. *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences* **88**, 1323-1328 (2018).
6. D. B. Lobell *et al.*, Prioritizing climate change adaptation needs for food security in 2030. *Science* **319**, 607-610 (2008).
7. C. Rosenzweig, M. L. Parry, Potential impact of climate change on world food supply. *Nature* **367**, 133-138 (1994).
8. A. J. Challinor *et al.*, A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change* **4**, 287-291 (2014).
9. D. B. Lobell, W. Schlenker, J. Costa-Roberts, Climate trends and global crop production since 1980. *Science* **333**, 616-620 (2011).
10. C. Rosenzweig *et al.*, Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proceedings of the national academy of sciences* **111**, 3268-3273 (2014).
11. C. Zhao *et al.*, Temperature increase reduces global yields of major crops in four independent estimates. *Proceedings of the National Academy of Sciences* **114**, 9326-9331 (2017).
12. IPCC. *Summary for Policymakers. In: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (IPCC, 2021).

13. E. A. Ainsworth, Rice production in a changing climate: a meta-analysis of responses to elevated carbon dioxide and elevated ozone concentration. *Global Change Biology* **14**, 1642-1650 (2008).
14. E. A. Ainsworth, A. Rogers, The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant, Cell & Environment* **30**, 258-270 (2007).
15. J. Fu et al., Extreme rainfall reduces one-twelfth of China's rice yield over the last two decades. *Nature Food*, 1-11 (2023).
16. A. Toreti *et al.*, Narrowing uncertainties in the effects of elevated CO_2 on crops. *Nature Food* **1**, 775-782 (2020).
17. D. Deryng *et al.*, Regional disparities in the beneficial effects of rising CO_2 concentrations on crop water productivity. *Nature Climate Change* **6**, 786-790 (2016).
18. C. Rosenzweig *et al.*, The agricultural model intercomparison and improvement project (AgMIP): protocols and pilot studies. *Agricultural and Forest Meteorology* **170**, 166-182 (2013).
19. L. Warszawski *et al.*, The inter-sectoral impact model intercomparison project (ISI–MIP): project framework. *Proceedings of the National Academy of Sciences* **111**, 3228-3232 (2014).
20. P. Martre *et al.*, Multimodel ensembles of wheat growth: many models are better than one. *Global Change Biology* **21**, 911-925 (2015).
21. T. Li *et al.*, Uncertainties in predicting rice yield by current crop models under a wide range of climatic conditions. *Global Change Biology* **21**, 1328-1341 (2015).
22. E. A. Ainsworth, A. D. Leakey, D. R. Ort, S. P. Long, FACE-ing the facts: inconsistencies and interdependence among field, chamber and modeling studies of elevated [CO_2] impacts on crop yield and food supply. *New Phytologist*, 5-9 (2008).
23. B. Peng *et al.*, Towards a multiscale crop modelling framework for climate change adaptation assessment. *Nature Plants* **6**, 338-348 (2020).
24. E. A. Ainsworth, S. P. Long, 30 years of free-air carbon dioxide enrichment (FACE): what have we learned about future crop productivity and its potential for adaptation? *Global Change Biology* **27**, 27-49 (2021).
25. B. A. Kimball, Crop responses to elevated CO_2 and interactions with H_2O, N, and temperature. *Current opinion in plant biology* **31**, 36-43 (2016).
26. C. Lv, Y. Huang, W. Sun, L. Yu, J. Zhu, Response of rice yield and yield components to elevated [CO_2]: a synthesis of updated data from FACE experiments. *European Journal of Agronomy* **112**, 125961 (2020).
27. R. M. Gutaker *et al.*, Genomic history and ecology of the geographic spread of rice. *Nature Plants* **6**, 492-502 (2020).
28. S. Hu *et al.*, Response of rice yield traits to elevated atmospheric CO_2 concentration and its interaction with cultivar, nitrogen application rate and temperature: a meta-analysis of 20 years FACE studies. *Science of the Total Environment*, 764, 142797 (2021).
29. N. Fageria, Yield physiology of rice. *Journal of plant nutrition* **30**, 843-879 (2007).
30. H. Sasaki *et al.*, Effect of free-air CO_2 enrichment on the storage of carbohydrate fixed at different stages in rice (Oryza sativa L.). *Field Crops Research* **100**, 24-31 (2007).
31. J. A. Franke *et al.*, The GGCMI Phase 2 experiment: global gridded crop model simulations under uniform changes in CO_2, temperature, water, and nitrogen levels (protocol version 1.0). *Geoscientific Model Development* **13**, 2315-2336 (2020).
32. A. P. Walker *et al.*, Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO_2. *New Phytologist* **229**, 2413-2445 (2021).
33. Y. Luo, S. Niu, The fertilization effect of CO_2 on a mature forest. *Nature* **580**, 191-192 (2020).

34. Q. Li *et al.*, Leaf area index identified as a major source of variability in modeled CO_2 fertilization. *Biogeosciences* **15**, 6909-6925 (2018).

35. J. Kattge, W. Knorr, T. Raddatz, C. Wirth, Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* **15**, 976-991 (2009).

36. Q. Jiang, J. Zhang, X. Xu, G. Liu, J. Zhu, Effects of free-air CO_2 enrichment (FACE) and nitrogen (N) supply on N uptake and utilization of indica and japonica cultivars (Oryza sativa L.). *Ecological Processes* **9**, 1-12 (2020).

37. L. Yuan *et al.*, Responses of rice production, milled rice quality and soil properties to various nitrogen inputs and rice straw incorporation under continuous plastic film mulching cultivation. *Field Crops Research* **155**, 164-171 (2014).

38. B. Hu *et al.*, Variation in NRT1. 1B contributes to nitrate-use divergence between rice subspecies. *Nature Genetics* **47**, 834-838 (2015).

39. Z. Zhang, C. Chu, Nitrogen-use divergence between indica and japonica rice: variation at nitrate assimilation. *Molecular Plant* **13**, 6-7 (2020).

40. J. Bailey-Serres, J. E. Parker, E. A. Ainsworth, G. E. Oldroyd, J. I. Schroeder, Genetic strategies for improving crop yields. *Nature* **575**, 109-118 (2019).

41 Yoshinaga, S. *et al.* Analysis of factors related to varietal differences in the yield of rice (Oryza sativa L.) under Free-Air CO_2 Enrichment (FACE) conditions. *Plant Production Science* **23**, 19-27 (2020).

42. G. D. Farquhar, S. v. von Caemmerer, J. A. Berry, A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149**, 78-90 (1980).

43. Y. Zhang *et al.*, Estimation of vegetation photosynthetic capacity from space-based measurements of chlorophyll fluorescence for terrestrial biosphere models. *Global Change Biology* **20**, 3727-3742 (2014).

44. S. Wang *et al.*, Recent global decline of CO_2 fertilization effects on vegetation photosynthesis. *Science* **370**, 1295-1300 (2020).

45. A. P. Walker *et al.*, The relationship of leaf photosynthetic traits-Vcmax and Jmax-to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecology and evolution* **4**, 3218-3235 (2014).

46. L. He *et al.*, Diverse photosynthetic capacity of global ecosystems mapped by satellite chlorophyll fluorescence measurements. *Remote Sensing of Environment* **232**, 111344 (2019).

47. E. A. Ainsworth, J. M. McGrath, in *Climate change and food security*. (Springer, 2010), pp. 109-130.

48. Y. Wan et al., Applied effect of improved open-top chamber on simulation in situ of elevating air temperature and CO_2 concentration in early rice field. *Transactions of the Chinese Society of Agricultural Engineering* 30, 123-130 (2014).

49. C. Terrer, S. Vicca, B. A. Hungate, R. P. Phillips, I. C. Prentice, Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science* **353**, 72-74 (2016).

50. K. J. van Groenigen *et al.*, Faster turnover of new soil carbon inputs under increased atmospheric CO_2. *Global Change Biology* **23**, 4420-4429 (2017).

51. D. Juan J., H. Lütkepohl, Making Wald tests work for cointegrated VAR systems. *Econometric reviews* **15**, 369-386 (1996).

52. W. Viechtbauer, Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**, 1-48 (2010).

53. C. Monfreda, N. Ramankutty, J. A. Foley, Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles* **22**, GB1022 (2008).

54. M. R. Allen, S. F. Tett, Checking for model consistency in optimal fingerprinting. *Climate Dynamics* **15**, 419-434 (1999).
55. W. Chen, W. Pan, Z. Xu, Current situation and trends in production of Japonica rice in China. *Journal of Shenyang Agricultural University* **37**, 801-805 (2006).
56. J. A. Franke. *et al.*, The GGCMI Phase 2 emulators: global gridded crop model responses to changes in CO_2, temperature, water, and nitrogen (version 1.0). *Geoscientific Model Development* **13**, 3995-4018 (2020).
57. C. Lu, H. Tian, Global nitrogen and phosphorus fertilizer use for agriculture production in the past half century: shifted hot spots and nutrient imbalance. *Earth System Science Data* **9**, 181-19(2017).
58. M. Malte. *et al*. The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. Climatic change **109**, 213-241 (2011).