



Optimized irrigation and fertilization can mitigate negative CO₂ impacts on seed yield and vigor of hybrid maize

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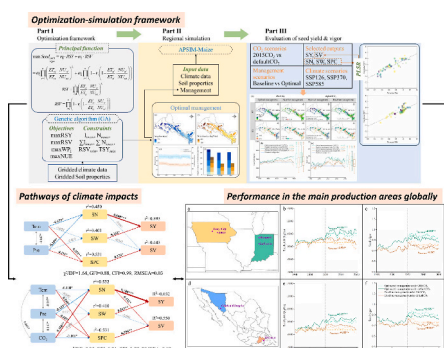
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HIGHLIGHTS

- Elevated CO₂ is beneficial to seed yield of hybrid maize by increasing seed number.
- Elevated CO₂ is detrimental to seed vigor by decreasing seed protein concentration.
- Optimized management can lead to seed yield improvement.
- Optimized management can mitigate 24.7–35.7 % risk of seed vigor reduction globally.

GRAPHICAL ABSTRACT



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ABSTRACT

Seed yield and vigor of hybrid maize determine the planting, yield, and quality of maize, and consequently affect food, nutrition, and livelihood security; however, the response of seed yield and vigor to climate change is still unclear. We established an optimization-simulation framework consisting of a water-nitrogen crop production function, a seed vigor and a gridded process-based model to optimize irrigation and nitrogen fertilization management, and used it to evaluate seed yield and vigor in major seed production locations of China, the USA, and Mexico. This framework could reflect the influence of water and nitrogen inputs at different stages on seed yield and vigor considering the spatio-temporal variability of climate and soil properties. Projected seed yield and vigor decreased by 5.8–9.0 % without adaptation by the 2050s, due to the 1.3–5.8 % decrease in seed number and seed protein concentration. Seed yield was positively correlated with CO₂ and negatively correlated with temperature, while seed vigor depended on the response of components of seed vigor to climatic factors. Under optimized management, the direct positive effects of temperature on seed protein concentration and CO₂ on seed number were strengthened, and the direct negative effects of temperature on seed number and CO₂ on seed protein concentration were weakened, which mitigated the reductions in both seed yield and vigor. Elevated CO₂ was projected to exacerbate the 2.6 % seed vigor reduction and mitigate the 2.9 % seed yield loss without adaptation, while optimized management could increase seed yield by 4.1 % and mitigate the 2.2 % seed vigor

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reduction in the Hexi Corridor of China, and decrease the seed yield and vigor reduction by 2.4–5.8 % in the USA and Mexico. Optimized management can strengthen the positive and mitigate the negative effects of climate change on irrigated hybrid maize and inform high-yield and high-quality seed production globally.

1. Introduction

As a multipurpose crop, maize provides 15 % of global human protein, 80 % of feed grain trade, and ~ 20 % of production for non-food demands (e.g., industrial alcohol, fuel ethanol, and glue) (Ranum et al., 2014; Erenstein et al., 2022). Demand for maize is increasing in the context of social development and population growth (Ulfat et al., 2022; van Dijk et al., 2021). However, climate change may bring big challenges to maize production, e.g., decreases in maize yield and protein concentration (Abramoff et al., 2023; Jägermeyr et al., 2021; Schmidhuber and Tubiello, 2007). Therefore, safeguarding maize production is a global concern in the context of climate change.

Maize production includes hybrid maize (mainly for seed production) and field maize (mainly for food and feed purposes). Hybrid maize differs markedly from field maize in several aspects, including growth processes, yield, and harvest index (Dalil et al., 2010; Ran et al., 2017; Yan et al., 2021). A number of previous studies have indicated substantial impacts of climate change on the yield and quality of field maize. For instance, rising temperature increases or (Perdomo et al., 2017; Li et al., 2020) decreases (Kimball et al., 2002; Cunniff et al., 2017) field maize yield, but the effect on protein concentration tends to be the opposite (Abebe et al., 2016; Qiao et al., 2019). On the other hand, increasing CO₂ concentration has limited effects on field maize yield due to the photosynthetic pathway (Manderscheid et al., 2014; Abebe et al., 2016), but is negatively correlated with protein concentration (Taub et al., 2008; Myers et al., 2014; Beach et al., 2019). However, impacts of climate change on the production and quality of hybrid maize remain largely unclear – in particular, the effect of increasing CO₂, and previous results for field maize may not be applicable to hybrid maize. Maize yield and quality are crucial for food security, but bigger challenges are related to obtaining sufficient high-quality maize seed to ensure future maize cultivation (Erenstein et al., 2022). Significant differences in the intensity and quantity of water and nutrient requirements between field and hybrid maize are caused by earlier sowing and harvesting, shorter reproductive periods, and greater planting densities in hybrid maize than in field maize (Ran et al., 2017; Zou et al., 2020). Therefore, it is of relevance to understand the responses of yield and quality of hybrid maize to climate change.

Globally, China (23 %), the USA (9 %), and Mexico (5 %) are the largest producers of hybrid maize (Arisnabarreta and Solari, 2017). The Hexi Corridor located in Northwest China produces >70 % of China's production of hybrid maize (NBSC, 2022). Evaluating future seed yield and vigor of hybrid maize and developing high yield and high quality management in these regions are critical to regional and global maize production. Seed yield and vigor of hybrid maize and agricultural resource use efficiency associated with hybrid maize can be improved by optimized agricultural managements, e.g., irrigation and nitrogen fertilization (N-fertilization) (Chen et al., 2020; Shi et al., 2020). However, the effects of elevated CO₂, rising temperature, and uncertain precipitation patterns on hybrid maize yield and vigor, and whether such effects vary under different agricultural managements have rarely been reported.

Here, we aimed to clarify the individual and combined effects of changing CO₂, temperature, and precipitation on seed yield and vigor of hybrid maize and explore the effects of optimized irrigation and N-fertilization on mitigating possible negative effects. An optimization-simulation framework, which adapts seasonal water and N inputs to crop demand, was combined with a crop model (the Agricultural Production Systems sIMulator, APSIM) to evaluate spatial and temporal variabilities of seed yield and vigor under four climate and management

scenarios. The four simulation scenarios consider the intersections of two managements (optimized and baseline) and two CO₂ scenarios (defaultCO₂ and 2015CO₂), including optimized under projected increasing CO₂ concentration from three socio-economic scenarios (defaultCO₂) or static CO₂ holding the level of 2015 (2015CO₂). We set these two CO₂ trajectories in order to clearly show the effect of CO₂ on hybrid maize. The optimization-simulation framework, developed for the Hexi Corridor and tested in the USA and Mexico, could be further applied to any regions important for hybrid maize production. Spatio-temporal variability in seed yield and vigor under climate change would be characterized and innovatively quantified the pathways of future climate factor impacts on seed yield and vigor, in order to specify potential improvement strategies for seed yield and vigor in different regions globally.

2. Methods

2.1. Study area

The Hexi Corridor spans over 1000 km from east to west and covers an area of 2.7×10^5 km² (37°17'–42°48'N, 92°12'–104°20'E) in the arid region of Gansu Province, Northwest China (Chen et al., 2021, 2023a). Abundant light and heat resources (annual sunshine hours is 2550–3500 and average temperature is 5.8–9.3 °C) make this area an important base for maize seed production, supporting over 70 % of China's maize seed. However, the scarcity of water resources (50–200 mm of average annual precipitation and 1500–2000 mm of average pan evaporation) induces a significant constraint on the seed of hybrid maize production (Li et al., 2015).

Six sites in the USA and Mexico were selected to test optimization-simulation framework applicability: Story City and Ames in Iowa, Lafayette in Indiana, and Wanatah in Indiana of the USA, and Texcoco in State of Mexico and Ciudad Obregón in Sonora of Mexico. The field experimental data collected at these sites are shown in Table S1.

2.2. Data collection

Gridded maize harvested areas were collected from the 5'-resolution spatial production allocation model 2010 (SPAM2010) data (IFPRI, 2019; Yu et al., 2020). The harvested areas of hybrid maize were obtained based on the proportion of hybrid maize to total maize areas in the Hexi Corridor (Chen et al., 2023a). Soil properties, including bulk density, field capacity, wilting point, saturated water content, saturated hydraulic conductivity, alkali-hydrolysable N, and soil organic matter, were obtained from the Soil Database of China for Land Surface Modeling (Shangguan et al., 2013) with 138.3-cm depth and 30" spatial resolution.

Historical climate data (during 1981–2020) were collected from the China Meteorological Forcing Dataset (Yang and He, 2019) (0.1°-resolution) retrieved from the National Tibetan Plateau Data Center (TPDC) for Hexi Corridor, and for the USA and Mexico were retrieved from the National Oceanic and Atmospheric Administration (NOAA, <https://www.nci.noaa.gov/maps/daily/>) (observations from meteorological sites). Future climate data (during 2021–2060) were collected from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) bias-adjusted and downscaled from the Coupled Model Intercomparison Project Phase 6 (CMIP6) climate model outputs with a 0.5°-resolution, including five global circulation model datasets (CanESM5, CNRM-CM6-1, CNRM-ESM2-1, EC-Earth3, and GFDL-ESM4) and three socio-economic scenarios (SSP126, SSP370, and SSP585) (Lange and

Büchner, 2022). Annual CO₂ concentration data was accessed from ISIMIP3a atmospheric composition input data with the range of 337–400 ppm during 1979–2020. Future CO₂ concentration data during 2021–2060 was accessed from ISIMIP3b, ranging from 400 to 474 ppm for SSP126, to 593 ppm for SSP370, and to 643 ppm for SSP585 (Matthias and Christopher, 2022). In this study, the projected annual CO₂ concentration trajectory was named defaultCO₂. Correspondingly, 2015CO₂ means that annual CO₂ during 2021–2060 remained constant at the 2015 level (400 ppm). The first-order conservative remapping procedure in Climate Data Operators (<https://code.mpimet.mpg.de/projects/cdo>) was used to resample the soil and climate input data to a 5'-resolution.

2.3. Optimization-simulation framework

An optimization-simulation framework was developed to evaluate the spatial and temporal variability of seed yield and vigor under different management and CO₂ emission scenarios, which consisted of three parts (Fig. 1). In the optimization framework (Part I), the gridded optimization for seed yield and vigor was used to optimize irrigation and N-fertilization management for each grid cell and year by using the water-N production functions of seed yield and vigor. Then, the gridded and N-fertilization management obtained from Part I, climate data, and soil properties were used as inputs to simulate seed yield, seed number, seed weight, and seed protein concentration of hybrid maize for each grid cell by using APSIM (Part II, regional simulation). Finally, in the evaluation of seed yield & vigor part (Part III), the partial least squares regression (PLSR, detailed information is shown in Section 2.3.3) for simulating seed vigor was first developed based on seed number, seed weight, and seed protein concentration (obtained from Part II), followed by quantifying the effects of climatic factors on the spatial and temporal variability of seed yield, seed vigor, and their components under different simulation scenarios. Detailed information for Part I, II, and III is shown in Section 2.3.1, 2.3.2, 2.3.3 respectively.

To test the applicability of the optimization-simulation framework, we evaluated seed vigor of hybrid maize with measured data at 6 sites in the USA and Mexico, optimized the irrigation and N-fertilization management, and further simulated the future seed vigor of hybrid under four simulation scenarios (see Section 2.3.2) with different managements (baseline vs. optimal management) and CO₂ concentration trajectories (2015CO₂ vs. defaultCO₂). The experimental data were obtained from 6 peer-reviewed published papers in 6 sites of the USA and

Mexico (Table S1), which were selected based on the same criteria as in Section 2.3.3 and were all conducted in irrigated fields.

2.3.1. Optimization framework

Crop water production functions can characterize the relationship between water consumption and seed yield, and between water consumption and seed vigor of hybrid maize under different irrigation treatments (Shi et al., 2020), and based on that, adding N uptake and water-N interaction sensitivity coefficients for each growth stage also performs well (Chen et al., 2023b). In this study, we selected the best performing water-N production function for seed yield and vigor of hybrid maize based on R² and nRMSE (Chen et al., 2023b), the Jensen-based and Rao-based functions, as the core of optimization of water and N management, and grid-running to make decisions for each grid cell in the study area:

$$\frac{SY_a}{SY_{max}} = \prod_{i=1}^n \left(\frac{ET_{ai} NU_{ai}}{ET_{ci} NU_{mi}} \right)^{\lambda_i} \quad (1)$$

$$\frac{SV_a}{SV_{max}} = \prod_{i=1}^n \left(1 - \nu_i \left(1 - \frac{ET_{ai} NU_{ai}}{ET_{ci} NU_{mi}} \right) \right) \quad (2)$$

where SY_a and SY_{max} are actual and maximum seed yield, kg/ha; SV_a and SV_{max} are actual and maximum seed vigor; ET_{ai} and ET_{ci} are the actual and maximum water consumption in stage i, mm; NU_{ai} and NU_{mi} are the actual and maximum N uptake in stage i, kgN/ha; λ_i and ν_i are the interactive sensitivity coefficient of water and N in stage i for Jensen- and Rao-based functions, respectively. Seedling, jointing, heading, filling, and maturity are five stages for hybrid maize represented by 1–5 in the equations.

There were four objectives including maximizing seed yield, seed vigor, and water and N use efficiency that were converted to a single objective using the analytic hierarchy process (AHP):

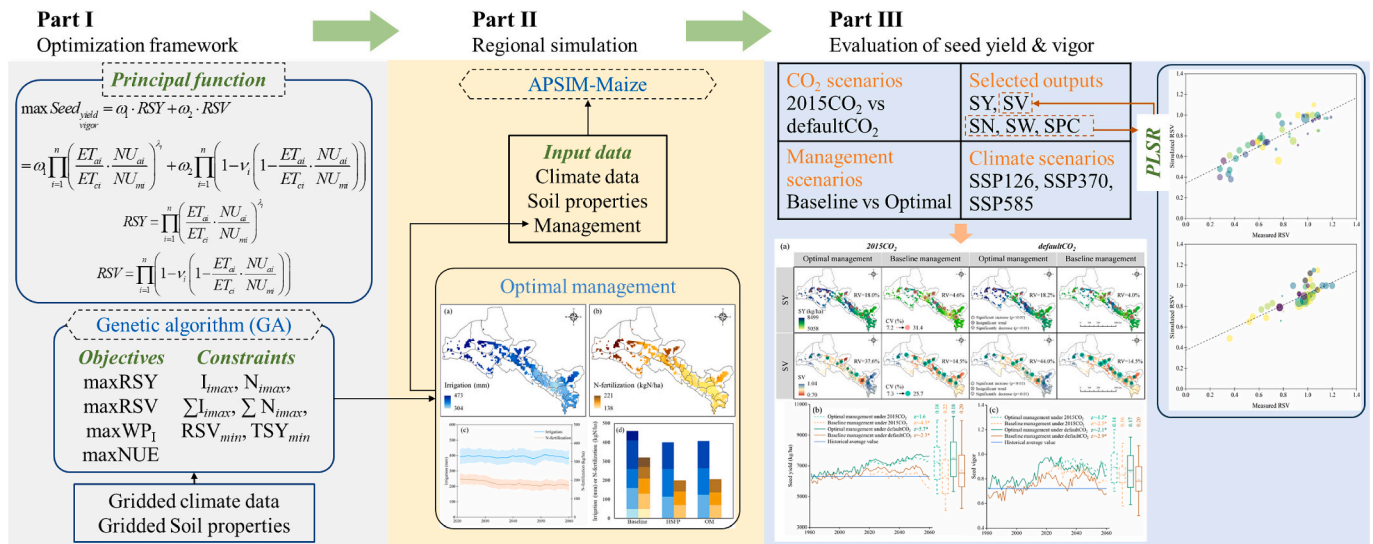


Fig. 1. Optimization-simulation framework. SN, SW, SPC, SY, and SV are seed number, seed weight, seed protein concentration, seed yield, and seed vigor, respectively. PLSR is partial least squares regression for evaluating seed vigor.

$$F = \omega_1 \times \frac{SY_a}{SY_{max}} + \omega_2 \times \frac{SV_a}{SV_{max}} + \omega_3 \times \frac{WP_I}{WP_{I_{max}}} + \omega_4 \times \frac{PFP_N}{PFP_{N_{max}}}$$

$$\begin{cases} \max SY_a = f_1(I_i, P_i, N_{feri}, SY_{max}) \\ \max SV_a = f_2(I_i, P_i, N_{feri}, SV_{max}) \\ \max WP_I = SY_a / \left(\sum_{i=1}^n I_i \times 10 \right) \\ \max PFP_N = SY_a / \sum_{i=1}^n N_{feri} \end{cases} \quad (3)$$

where I_i , P_i , and N_{feri} are irrigation, precipitation, and N-fertilization in stage i , respectively; WP_I is irrigation water productivity, kg/m^3 ; PFP_N is partial factor productivity from applied N-fertilization, kg/kgN . WP_I and PFP_N were used to evaluate the water and N use efficiency. The optimization framework was run to obtain optimized irrigation and N-fertilization management in each grid cell of Hexi Corridor (Fig. S2 and Fig. S3) and sites in the USA and Mexico.

The genetic algorithm was used for determining the optimized irrigation and N-fertilization management in each grid cell, which was implemented using the scikit-opt package (Head et al., 2020) in Python v 3.9, and settings were: the population size was 500, the maximum number of generations was 1000, the proportional selection and single-point crossover were selected, the crossover probability was 0.75, and the probability of variance was 0.01. Water consumption and N uptake at different stages were characterized based on initial soil water and N content in the 30-cm depth soil layer, irrigation inputs, and N-fertilization inputs. Constraints of the optimization framework included the range of irrigation and N-fertilization at each growth stage, the range of total irrigation and N-fertilization, and the solubility of urea in irrigation water (see Supporting Information).

2.3.2. Regional simulation part

In this part, we used APSIM to simulate seed number, seed weight, seed protein concentration, and seed yield of hybrid maize under different scenarios. APSIM (Holzworth et al., 2014) is a process-based simulator of crops and cropping systems, and here was used to simulate seed number, seed weight, seed protein concentration, and seed yield under different scenarios. CROPTIMIZR package was used for calibrating phenology parameters of hybrid maize in APSIM (Buis et al., 2021) based on the collected experimental data, and the calibrated values are shown in Table S2 referred to Chen et al. (2023a). The gridded irrigation and N-fertilization management obtained in the optimization framework (see Section 2.3.1) would be one of the inputs to APSIM, other inputs included climate data (gridded data during 1981–2060 with SSP126, SSP370, and SSP585), soil properties (gridded and layered), and CO_2 concentration trajectory (not gridded with SSP126, SSP370, and SSP585) (see Section 2.2). The calibrated APSIM was run in the harvest area of hybrid maize transformed from SPAM2010. Four simulation scenarios were set for each SSP, consisting of different CO_2 trajectories with or without the optimized management: with or without the optimized irrigation and N-fertilization under default CO_2 and with or without the optimized irrigation and N-fertilization under 2015 CO_2 .

2.3.3. Evaluation of seed yield & vigor

Seed yield, vigor, and their components were evaluated and analyzed on both temporal and spatial scales in this part. Partial least squares regression (PLSR) is a method of reducing an independent variable with co-linearity to a few non-correlated latent variables and building a regression model to maximize the covariance with the dependent variable (Geladi and Kowalski, 1986). Seed vigor of hybrid maize is significantly correlated with germination percentage, germination index, pollen viability, seed number, seed weight, and seed protein

concentration (Shi et al., 2020). The protein concentration can be calculated using a conversion factor of 6.25 based on the N concentration (William, 2006). Considering that seed number, seed weight, and seed protein concentration were easier and faster to measure than others (germination percentage, germination index, and pollen viability), we selected them as the independent variables of PLSR for evaluating seed vigor and collected 6 peer-reviewed published papers containing seed number, seed weight, and seed protein concentration, and at least one of germination percentage, germination index, or pollen viability as sources of measured data (Table S1). Since the seed vigor was a comprehensive evaluation index and the evaluation variables used varied across different field experiments from the published papers, we re-calculated the seed vigor using principal component analysis (PCA) (Chen et al., 2023b) based on seed number, seed weight, seed protein concentration, germination percentage, germination index, and pollen viability as potentially available variables. The collected experimental data were randomly allocated to the calibration and the validation sets (1:1 ratio), which were used for the calibrating and validating PLSR, respectively. We implemented PLSR using the sklearn package in Python version 3.9 and selected the normalized root mean square error (nRMSE) and coefficient of determination (R^2) for evaluating the accuracy of PLSR:

$$R^2 = 1 - \frac{\sum_{i=1}^n (M_i - S_i)^2}{\sum_{i=1}^n (M_i - \bar{M})^2} \quad (4)$$

$$nRMSE = \frac{\sqrt{\sum_{i=1}^n (M_i - S_i)^2 / n}}{\bar{M}} \times 100 \quad (5)$$

where M_i , S_i , and \bar{M} are measured values, simulated values, and the mean of the measured values, and n the total number of measured samples.

Regional seed yield was obtained from APSIM and seed vigor was estimated using the established PLSR based on the APSIM-simulated seed number, seed weight, and seed protein concentration (obtained from Part II). Spatio-temporal variability of seed yield, seed vigor, seed number, seed weight, and seed protein concentration of hybrid maize was evaluated under four simulation scenarios (see Section 2.3.2).

2.4. Correlation and effect analysis

The Spearman correlation was used to evaluate the relationship between simulation outputs (seed number, seed weight, seed protein concentration, seed yield, and seed vigor) and climate factors (temperature, precipitation, and CO_2) to initially identify climatic factors that were significantly correlated with the simulation outputs. We used Spearman for correlation analysis instead of Pearson because of the non-normality of the simulations in this study. Further, through building structural equation models (SEMs), the direct and indirect (i.e., mediated) effects of climate factors on seed number, seed weight, seed protein concentration, seed yield and seed vigor were quantified. SEM is a statistical procedure used to study complex and multivariate relationships, where the weight of each factor's contribution to the objective and the paths between related factors can be clearly delineated (Boslaugh and McNutt, 2008). Different from traditional regression models, SEM can simultaneously evaluate all relevant regression pathways as independent and/or dependent factors contributing to the state of the objective. Standard criteria were used to assess the statistical fit of the SEM models to the data, including chi-square test (χ^2/DF), goodness-of-fit index (GFI), comparative fit index (CFI), and root mean square error of approximation (RMSEA). A good fit generally has the following criteria: $\chi^2/\text{DF} < 2$, CFI and GFI are close to 1 (range 0–1), and RMSEA is close to 0 (Karin et al., 2003).

2.5. Statistical analysis and model validation

The coefficient of variation (CV, the ratio of mean to standard deviation) was used to quantify the temporal variability (Warrick and Nielsen, 1980) of the simulation outputs, and the random variance (RV) obtained from the geostatistical analysis was used to quantify the spatial variability (Tsefahunegn et al., 2011). RV was the ratio of nugget and sill values, where the nugget and sill value reflected variance between samples that are closely spaced and total possible variance in the variable, respectively. Higher CV values represent higher variance, which higher RV represent weaker spatial variability. The significance of differences for outputs (seed number, seed weight, seed protein concentration, seed yield, and seed vigor) between management, CO₂, and managements × CO₂ interactions were estimated based on two-way ANOVA using Tukey's HSD test.

3. Results

3.1. Impacts of increasing CO₂ concentration on seed yield and vigor

For seed yield, there was a significant positive relationship between the 2015CO₂ and defaultCO₂ scenarios under the baseline management during 2021–2060, with the Spearman correlation coefficients being 0.43–0.79 (Fig. 2). Whereas, seed vigor under the baseline management presented insignificant positive or even negative correlations in about 35.5 % of the study region with the range being 30.9–38.1 %. These results indicate that elevated CO₂ would have substantial impacts on seed vigor rather than seed yield of hybrid maize under the baseline management, which was further confirmed by the Spearman correlation of aggregated regional yield and vigor values under the two management scenarios. On the other hand, we found that optimized management could improve the correlation of yield and vigor between the two CO₂ scenarios. In particular, correlations of vigor between the two CO₂ scenarios under optimized management increased by –0.26–0.42 compared with baseline management, with only 25.3 % of the study region showing insignificant or negative correlation.

Seed number and seed weight showed significant positive correlations between 2015CO₂ and defaultCO₂ scenarios under both baseline and optimized management scenarios (0.76–0.98) spatially (Fig. 2). Whereas, spatial mean correlations for seed protein concentration between 2015CO₂ and defaultCO₂ scenarios were only –0.05 and 0.19 under baseline and optimized management scenarios, with 42.4 % and 25.4 % of the study area being insignificant or negative, respectively. Temporally, there were significantly positive correlations between defaultCO₂ and 2015CO₂ scenarios (0.73–0.94) for seed number, seed weight, and seed yield, with higher correlation coefficients appearing under optimized management. Optimized management temporally increased the correlation between defaultCO₂ and 2015CO₂ scenarios for seed vigor compared to baseline management scenario, which was mainly influenced by the change in seed protein concentration from a negative to a positive correlation. Detailed information of Spearman correlation coefficients for all annual outputs between 2015CO₂ and defaultCO₂ scenarios under SSP126, SSP370, and SSP585 is shown in Table S3.

During 2021–2060, seed yield increased by 4.1 % from 2020s to 2050s under optimized management and decreased by 5.8 % under baseline management, with higher increases and lower decreases for defaultCO₂ than 2015CO₂ (Fig. 2). However, seed vigor decreased by 5.7–10.3 % under all scenarios temporally, which were –6.8 % and –9.0 % under optimized and baseline management scenarios, respectively. From 2020s to 2050s, seed number (7.2 %) and seed weight (1.5 %) increased under optimized management during 2021–2060, while seed protein concentration still decreased under optimized management. But optimized management could mitigate 20.0 % of the reduction risk of seed protein concentration compared to baseline management.

3.2. Spatial and temporal variability of outputs of hybrid maize under baseline and optimized management

Seed yield and vigor under the optimized management were 10.5–15.4 % higher than the baseline management, with a 2.9–3.9 % decrease in coefficient of variation (CV) and a 13.8–26.6 % increase in random variation (RV). This means that optimized management could greatly improve the spatial and temporal stabilities (Fig. 3 and Fig. S4). Changes in management scenarios affected seed number, seed weight, and seed protein concentration as well: 10.4–14.3 % higher under optimized management than the baseline management, with a 4.0–5.8 % decrease in CV and an 18.1–30.3 % increase in RV (Fig. S5). Moreover, elevated CO₂ led to higher seed number and seed yield, and lower seed protein concentration and seed vigor on the spatial and temporal scales (Fig. 2). We could infer that seed number and seed protein concentration may dominate yield and vigor of hybrid maize, respectively. Seed yield under defaultCO₂ was 4.0 % higher than 2015CO₂, still influenced by seed number (defaultCO₂ 4.3 % higher than 2015CO₂) over seed weight (defaultCO₂ 0.4 % higher than 2015CO₂) (Fig. 3, Fig. S4, and Fig. S5). However, seed vigor under defaultCO₂ was 5.6 % lower than 2015CO₂, mainly influenced by seed protein concentration (defaultCO₂ 5.2 % lower than 2015CO₂).

3.3. Relationships and pathways between climate factors and seed yield and vigor

Temperature was significantly positively correlated with seed protein concentration and seed vigor, and was significantly negatively correlated with seed yield and seed number, which was completely opposite to the performance of CO₂ (Fig. 4). Higher coefficients and more significant levels between climate factors and outputs of hybrid maize were found under optimized management than baseline management. The correlation between precipitation and outputs was inconsistent across management scenarios. From a CO₂ emission scenario perspective, the negative correlation between temperature and seed weight was weakened in defaultCO₂ compared to 2015CO₂, while the negative correlation between temperature and seed vigor was strengthened. Essentially, consistent correlations appeared separately under SSP126, SSP370, and SSP585 (Fig. S6).

The coefficients of the direct pathways varied with managements and CO₂ emission trajectories during 2021–2060 by using structural equation models (SEMs) under SSP126, SSP370, and SSP585, of which all were well fitted in this study (Fig. 5 and Fig. S7). Optimized management weakened the direct negative effect of temperature on seed number but strengthened the direct positive effect temperature to seed protein concentration compared to the baseline management. Oppositely, the direct positive effect of CO₂ on seed number was strengthened and the negative effect on seed protein concentration was weakened by optimized management. Furthermore, the positive effects of climate factors on seed number, seed weight, and seed protein concentration were strengthened and the negative effects were weakened by optimized management rather than baseline management. The direct path coefficients of seed weight on seed yield and seed protein concentration on seed vigor were higher in defaultCO₂ than in 2015CO₂ (Fig. S7). Detailed information about direct pathways under each SSP (SSP126, SSP370, and SSP585) is shown in Table S4.

The significant indirect effect of CO₂ on seed yield was positive and on seed vigor was negative, but the opposite for temperature, with higher significance levels under optimized management (Table 1). Seed yield and seed vigor under optimized management could benefit from CO₂ and temperature, respectively, and the negative response of seed vigor to CO₂ was weakened compared to the baseline management. Similar indirect pathways for climate factors affecting seed yield and seed vigor were found under SSP125, SSP370, and SSP585 (Table S4).

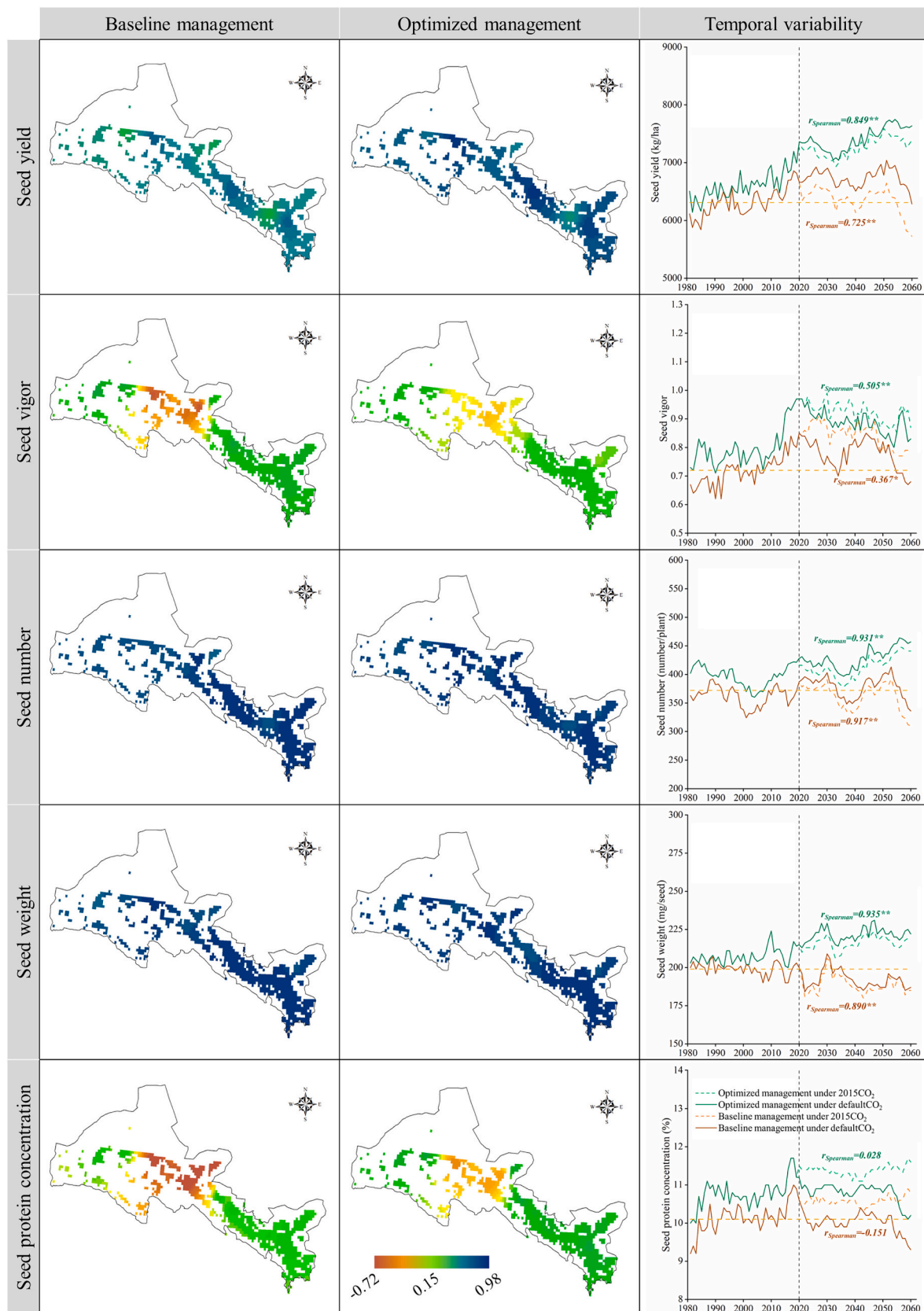


Fig. 2. Spearman correlation coefficients of seed yield, vigor, seed number, seed weight, and seed protein concentration between 2015CO₂ and defaultCO₂ scenarios under baseline and optimized managements for the period 2021–2060. Saffron solid line is the mean value based on outputs for defaultCO₂ under baseline management during 1981–2020. Spatial spearman correlation coefficients are determined from the outputs between 2015CO₂ and defaultCO₂ in each grid cell during 2021–2060. Spearman correlation coefficients ($r_{Spearman}$) in the spatial and temporal plots are estimated from the averaged outputs between 2015CO₂ and defaultCO₂ during 2021–2060 under SSP126, SSP370, and SSP585. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

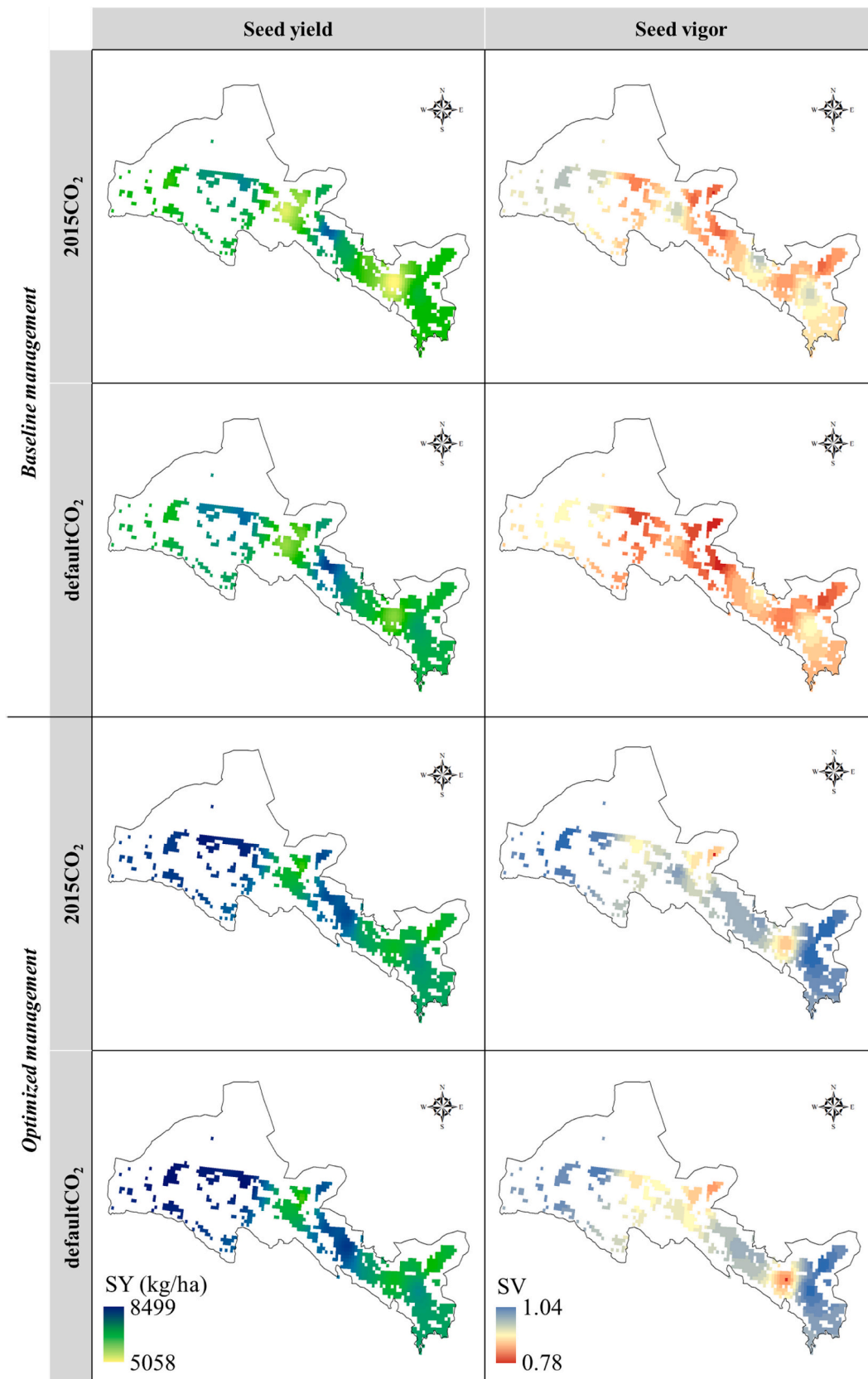


Fig. 3. Comparison of seed yield and vigor between 2015CO₂ and defaultCO₂ scenarios under baseline and optimized managements during 2021–2060. Data in the spatial distribution maps are mean values for 2021–2050 in the grid cells under SSP126, SSP370, and SSP585.

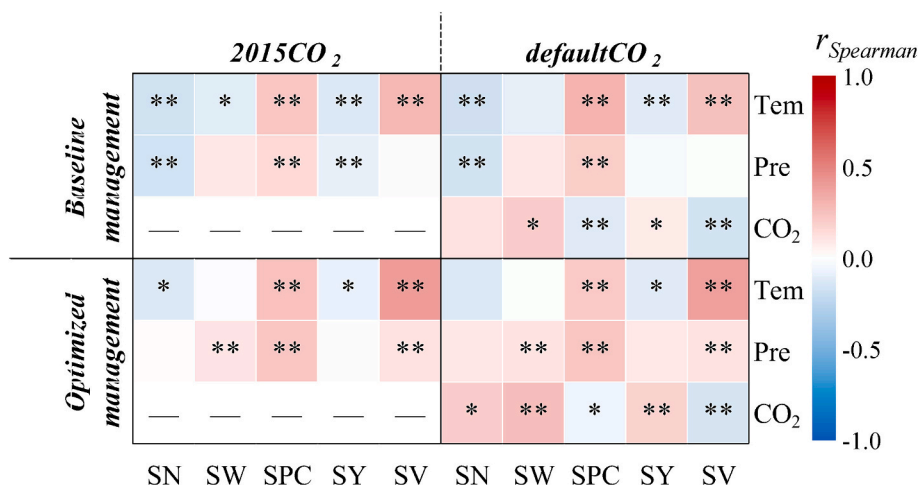


Fig. 4. Spearman correlation coefficients between climate factors (temperature, precipitation, and CO₂) and hybrid maize outputs (SN, SW, SPC, SY, and SV) under SSP126, SSP370, and SSP585. Positive and negative relationships are in red and blue, respectively. *, $p < 0.05$; **, $p < 0.01$. Tem, pre, SN, SW, SPC, SY, and SV are temperature, precipitation, seed number, seed weight, seed protein concentration, seed yield, and seed vigor, respectively.

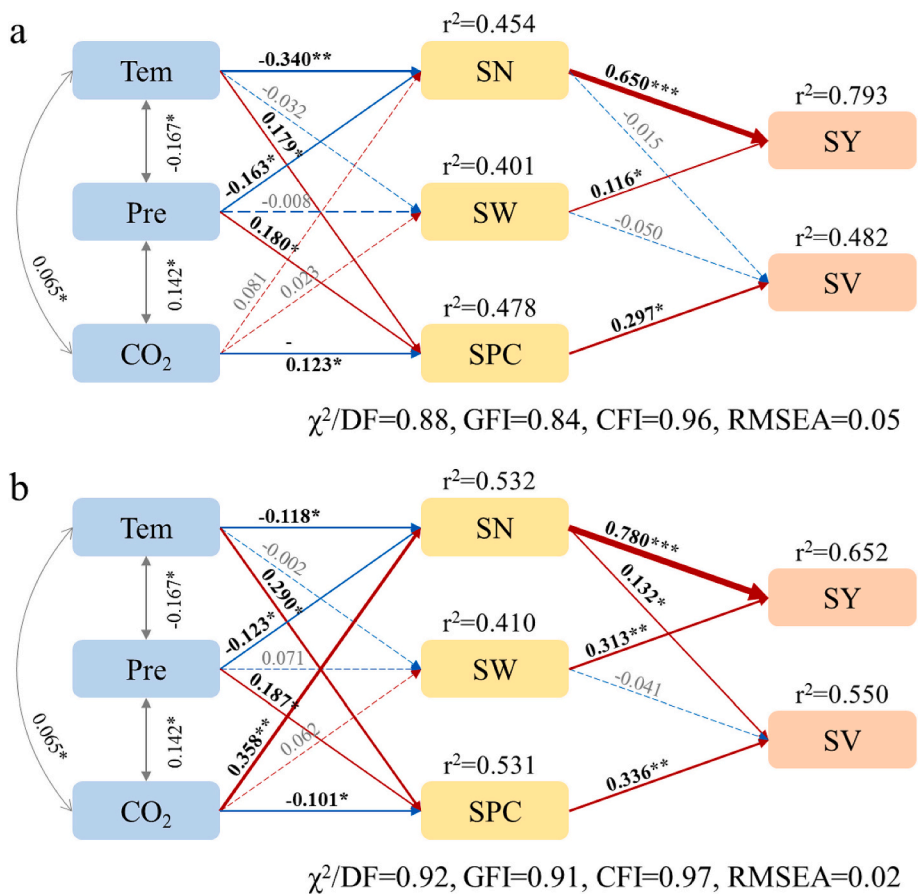


Fig. 5. Direct pathways for climate factors affecting seed yield and seed vigor of hybrid maize under defaultCO₂. Structural equation models (SEMs) were conducted for baseline (a) and optimized (b) managements. Single-headed arrows indicate the hypothesized direction of causality, with positive and negative effects in red and blue, respectively. Solid lines with black bolded numbers indicate statistical significance (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$), and dashed lines with gray numbers indicate statistical insignificance ($p > 0.05$). Arrow thickness is proportional to the standardized path coefficient adjacent to each arrow. Explained variance (r^2) is labeled alongside each response variable. Tem, pre, SN, SW, SPC, SV, and SY are temperature, precipitation, seed number, seed weight, seed protein concentration, seed yield, and seed vigor, respectively.

Table 1

Indirect pathways for climate factors affecting seed yield and vigor of hybrid maize under optimized management.

Items	Baseline management		Optimized management	
	2015CO ₂	defaultCO ₂	2015CO ₂	defaultCO ₂
Tem- > SY	-0.132*	-0.111*	-0.118*	-0.020
Tem- > SV	0.106*	0.117*	0.228**	0.368***
Pre- > SY	-0.171*	0.007	-0.030	0.133*
Pre- > SV	0.017	0.027	0.115*	0.287**
CO ₂ - > SY	-	0.097	-	0.141*
CO ₂ - > SV	-	-0.466***	-	-0.204**

Note: Tem, pre, SN, SW, SPC, SV, and SY are temperature, precipitation, seed number, seed weight, seed protein concentration, seed yield, and seed vigor, respectively. *, **, and *** indicate statistical significance at $p < 0.05$, $p < 0.01$, $p < 0.001$.

3.4. Seed yield and vigor in the USA and Mexico under future climate change

Our optimization-simulation framework was successfully applied to the major seed production regions in the USA and Mexico. Similar to the simulations in the Hexi Corridor, optimized management decreased the risk of seed vigor reduction by 35.7 % in 2021–2060, but did not change the decreasing trend (Fig. 6). However, seed yield did not increase (-0.1 %) with optimized management and remained at a level similar to the 2020s. For components of seed yield and vigor, higher seed number and seed weight could be obtained under optimized management and elevated CO₂, while seed protein concentration only responded positively to optimized management and negatively to elevated CO₂ (Fig. S8).

4. Discussion

4.1. Impact of future climate change on seed yield and vigor of hybrid maize

In this study, we simulated future seed yield, vigor, and their components by setting up scenarios considering different CO₂ and management combinations, and quantified the effects of climate factors on seed yield and vigor. This serves as a guide for obtaining sufficient high-vigor seeds and developing potential adaptation strategies under future climate change. We found that elevated CO₂ and temperature could decrease seed yield and vigor by 4.3 %–10.3 % without adaptations in Hexi Corridor, respectively, whereas seed yield increased by 4.8 % and seed vigor decreased by -7.9 % under the optimized management (Fig. 2 and Fig. S5). As well, the optimized management remains optimistic in the USA and Mexico: seed yield is stable while the risk of seed vigor decrease is reduced by >24.7 % during 2021–2060 (Fig. 6 and Fig. S8). CO₂ was significantly negatively correlated with seed vigor, and temperature was significantly negatively correlated with seed yield in this study. This required analyzing the pathways of CO₂ and temperature effects.

As a C4 crop, the response of maize yield to elevated CO₂ is still unclear: rather significantly increasing yield as for C3 crops (such as wheat and rice), maize yield may increase (Abebe et al., 2016; Long et al., 2006; Manderscheid et al., 2014) or decrease (Cunniff et al., 2017; Kimball et al., 2002; Leakey et al., 2004). With elevated CO₂, RuBisCO of maize saturates, theoretically limiting the CO₂ uptake (von Caemmerer and Furbank, 2003) and subsequent yield benefits. On the one hand, reduced stomatal conductance and thus improved water use efficiency make yield improvement possible (Long et al., 2004). For the yield development processes, elevated CO₂ can increase the number of flowers, promote pollen formation, and in turn increase the yield

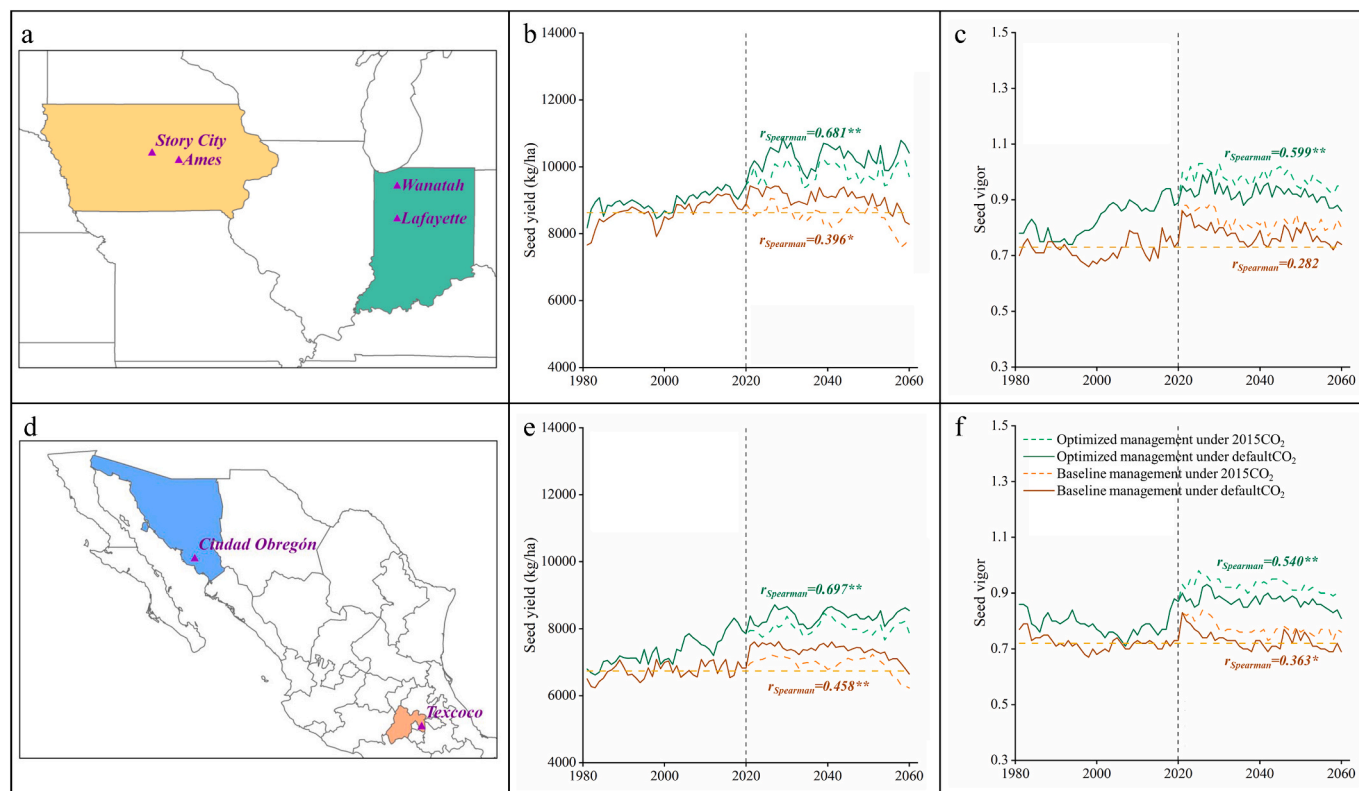


Fig. 6. Temporal variability of seed yield and vigor in the USA and Mexico during 2021–2060 under SSP126, SSP370, and SSP585. Locations of studied experiments are given in subplot a (the USA) and b (Mexico). Annual mean seed yield (b in the USA and e in Mexico) and seed vigor (c in the USA and f in Mexico) during 1981–2060 with Spearman correlation coefficients (r_{Spearman}) between 2015CO₂ and defaultCO₂ based on outputs from 2021 to 2060.

components (grain number and weight) by 8–72 % (Jablonski et al., 2002; Abebe et al., 2016), but decrease grain quality (protein, oil, and nutrient concentrations in grains) of cereals due to the dilution effect from carbohydrate accumulation (Jablonski et al., 2002; Taub et al., 2008). Our results confirmed that CO₂ was negatively correlated with seed vigor, caused by a decrease in seed protein concentration, but positively correlated with seed yield, caused by an increase in seed number, especially under optimized management (Fig. 4 and Fig. 5). Notably, seed protein concentration was almost independent of management, which was related to temperature and precipitation and caused strong spatial and temporal variability of seed vigor.

High temperature reduces maize yield and yield components by reducing photosynthesis (Li et al., 2020; Moore et al., 2021) and shifting carbon away from reproduction (Ruiz Vera et al., 2015). Increased grain protein concentration due to high-temperature-induced protein synthesis adaptation and mitigate the negative effects of elevated CO₂ (Abebe et al., 2016; Erda et al., 2005; Qiao et al., 2019). However, whether grain yield and protein concentration of maize benefit or not depends on whether the temperature change exceeds the optimal range (Naveed et al., 2014; Perdomo et al., 2017; Li et al., 2020). Temperature was negatively correlated with seed yield, caused by a decrease in seed number, but positively correlated with seed vigor, caused by an increase in seed protein concentration in this study (Fig. 4 and Fig. 5). Seed vigor increased tortuously (Fig. 2) due to the inconsistent spatio-temporal variability of the components used to evaluate seed vigor under climate change (Fig. 3 and Fig. S5).

The sensitivity of maize growth, yield, and grain protein concentration in response to precipitation varies with region (humid and arid regions) and farming type (rainfed and irrigated) (Li and Troy, 2018; Rosegrant and Cline, 2003). Irrigation decouples crop yields from precipitation buffering the negative effects (Schauberger et al., 2017; Troy et al., 2015) and stabilizes crop yield under climate variability (Leng, 2017). Precipitation was significantly correlated with seed vigor but not seed yield under optimized management (Fig. 4) due to the low precipitation remaining in the future (Chen et al., 2023a) and the widespread irrigated agriculture in the Hexi Corridor. We inferred that low future increases in precipitation and irrigation diminished the response of seed yield to precipitation, but the response of seed vigor was clearly more sensitive due to the positive effects of precipitation on seed protein concentration.

4.2. Adaptation and mitigation strategies to safeguard seed yield and vigor

Optimized agronomic management practices (e.g., planting management, fertilization management, and genotype selection) are feasible options (Zhang et al., 2020; Yu et al., 2022) for solving the issue of low grain protein concentrations under climate change (Schmidhuber and Tubiello, 2007). Ran et al. (2017) recommended 298 mm of irrigation and 175 kgN/ha of N-fertilization could achieve high yield and high water use efficiency of hybrid maize based on field experiments, but the limitations of the experimental location and period made it difficult to provide guidance for hybrid maize production over a large area and for a long period. In this study, we focused on two aspects of optimized management: irrigation and N-fertilization in grid cells and at different growth stages. Spatial effects of climate and soil properties on water consumption and N uptake was considered in this optimization-simulation framework, ensuring adequate supply at stages with high impacts on seed yield and vigor and applying appropriate deficits at other stages (Fig. S2 and Fig. S3), to achieve high yield, high vigor, and high resource use efficiency. Seed vigor was consistently significantly negatively correlated in parts of the Hexi Corridor with constant CO₂ (2015CO₂) and evaluated CO₂ (defaultCO₂) and so was seed protein concentration, which we postulated to be a result of uncertainty (Fig. S9) in the changes in warming range and precipitation patterns (Fig. S10). We found that optimized management could achieve a –

0.1–4.1 % increase in seed yield from 2020s to 2050s and a 24.7–35.7 % reduction in the risk of seed vigor decrease in major seed production regions around the world with evaluated CO₂ and temperature (Fig. 2 and Fig. 6). This suggests that the optimized management obtained by using the optimization-simulation framework have strong applicability to guide future management and production of hybrid maize globally. We clarified that optimized management was beneficial for future seed yield and seed vigor of hybrid maize, remedying the limitation of previous research that generalizes adaptation strategies instead of specifying the domain practice.

4.3. Limitations of the research

We also acknowledge limitations of this study. First, the effects of ozone concentration (Cao et al., 2009) and N deposition (Churkina et al., 2009) to enhance or counteract the effects of CO₂ under climate change, which may negatively impact photosynthesis and growth (Guarin et al., 2023), were not considered in this study. Second, elevated CO₂ may shorten the phenological development (especially the vegetative stages not the reproductive stage) (Erda et al., 2005; Reyes-Fox et al., 2014; Vanaja et al., 2017), but the phenological development of crops in most crop models is determined only by temperature. The effects of CO₂ on crops (e.g., photosynthesis, yield, and biomass) may be overestimated (Asseng et al., 2004; Yin, 2013) or underestimated (Bloom et al., 2010) in crop models. Third, the adaptation strategy in this study (optimized management) was unable to prevent the decreasing trend in seed vigor, which was related to the complex response of seed protein concentration to CO₂, temperature, and precipitation (Fig. 4 and Fig. 5). Nevertheless, our framework was applicable to important seed producers in China, the USA, and Mexico. The quality and yield of maize seed would be guaranteed under the optimized irrigation and N-fertilization management (Fig. 6 and Fig. S8). In addition, more FACE experiments should be carried out and new cultivars need to be bred for hybrid maize to address the adverse effects of evaluated CO₂ and temperature on seed yield and vigor, in order to ensure the high-yield and high-quality production of maize seed.

5. Conclusion

In this study, we developed an optimization-simulation framework to project the spatial and temporal variabilities of seed yield and vigor of hybrid maize to ensure the high-quality maize seed supply. The risk of future reductions in seed yield and vigor will affect China's maize planting and production, and consequently global maize supply. Our study revealed that seed vigor benefits from elevated temperature, but suffers from elevated CO₂, while seed yield responses to temperature and CO₂ are opposite, due to the complex response of seed number, seed weight, and seed protein concentration to climate change. Optimized irrigation and N-fertilization management could strengthen the positive effects of CO₂ on seed number and mitigate the negative effects of CO₂ on seed protein concentration. We found that optimization led to a 24.7 % decrease in the risk of seed vigor reduction, and a shift in seed yield from a decrease of –5.8 % to an increase of 4.1 % in Hexi Corridor. Our optimized management was also applicable to the USA and Mexico, achieving 5.7 % and 2.5 % lower reductions in seed yield and vigor, respectively. This optimization-simulation framework and the adaptation strategy are applicable to other irrigated hybrid maize planting regions and can provide a valuable reference for the important maize seed producers of the world.

CRediT authorship contribution statement

Shichao Chen: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Wenfeng Liu:** Writing – review & editing, Methodology, Conceptualization. **David Parsons:** Writing – review & editing. **Taisheng Du:** Writing – review &

editing, Supervision, Project administration, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.175951>.

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