



Genetic progress battles climate variability: drivers of soybean yield gains in China from 2006 to 2020

Li Zhang¹ · Haoyu Zheng¹ · Wenjie Li¹ · Jørgen Eivind Olesen² · Matthew Tom Harrison³ · Zhiyuan Bai¹ · Jun Zou¹ · Axiang Zheng¹ · Carl Bernacchi⁴ · Xingyao Xu¹ · Bin Peng⁴ · Ke Liu³ · Fu Chen¹ · Xiaogang Yin¹

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Abstract

While improvement of soybean productivity under a changing climate will be integral to ensuring sustainable food security, the relative importance of genetic progress attributed to historical yield gains remains uncertain. Here, we compiled 16,934 cultivar-site-year observations from experiments during the period of 2006–2020 to dissect effects of genetic progress and climate variability on China's soybean yield gains over time. Over the past 15 years, mean yields in the Northeast China (NEC), Huang-Huai-Hai Plain (HHH), and Southern Multi-cropping Region (SMR) were 2830, 2852, and 2554 kg ha⁻¹, respectively. Our findings show that genetic progress contributed significantly to yield gains, although underpinning mechanisms varied regionally. Increased pod number per plant (PNPP) drove yield gains in the NEC, while both PNPP and 100-grain weight (100-GW) contributed to yield gains in the HHH. In all regions, incremental gains in the reproductive growing periods increased PNPP, 100-GW, and yields. While heat stress in the reproductive period reduced average yields in all regions, superior yielding cultivars (top 25%) in the HHH and SMR were less sensitive to heat stress during the reproductive phases, indicating that the higher yielding cultivars benefited from genetic improvement in heat stress tolerance. Our results highlight the importance of genetic improvements in enabling sustainable food security under global warming and increasingly frequent heat stress.

Keywords Yields · Cultivar · Genetic progress · Phenology · Extreme weather · Heat stress

1 Introduction

Soybean is a globally vital food and non-food product crop (Fodor et al. 2017; Fuchs et al. 2019). China is the largest soybean importer globally due to anthropogenic consumption (USDA 2019; Wu et al. 2020), with imports accounting over 80% of Chinese domestic demand (Ren et al. 2021).

The increasing global demand for protein, as well as global warming and increased frequencies of extreme weather events have together exacerbated the risk in soybean production (Hamed et al. 2021; Zhang et al. 2021; Zhao et al. 2021). Current and historical yield gains of soybean in China have been much lower than yield gains seen in other nations over the last few decades (Yin and Chen 2019). Although China has adopted a series of policies and invested in research enabling soybean production, many questions remain unsolved. For instance, genetic progress through introduction of novel cultivars has played a fundamental role in improving soybean yield (Bai et al. 2023; Kumagai et al. 2022), but the extent to which soybean yields are driven by genotype versus environment under global warming remains to be elucidated.

It is near certain the global temperatures will rise in the coming decades, causing intensification of the global water cycle and more frequent extreme events, such as heat stress (Harrison 2021; IPCC 2021). Temperature is one of the most important climatic factors driving soybean yields through both developmental and photosynthetic rates (Lobell and Field 2007; Yan et al. 2022). Previous studies

✉ Xiaogang Yin
xiaogangyin@cau.edu.cn

¹ College of Agronomy and Biotechnology, and Key Laboratory of Farming system, Ministry of Agriculture and Rural Affairs of China, China Agricultural University, Beijing 100193, China
² Department of Agroecology, Aarhus University, Blichers Alle 20, 8830 Tjele, Denmark
³ Tasmanian Institute of Agriculture, University of Tasmania, Newnham Drive, Launceston, Tasmania 7250, Australia
⁴ Institute for Sustainability, Energy and Environment, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

have shown that an increase in global mean temperature by 1 °C would decrease soybean yields by 3% (Zhao et al. 2017). When temperature exceeds 30 °C, soybean development processes, such as flowering and grain filling, are inhibited (Deryng et al. 2014; Jin et al. 2017; Thomey et al. 2019), and can result in severe yield penalties (Kimm et al. 2021; Siebers et al. 2015; Zhang et al. 2016a). However, previous experiments have generally been limited in scale and scope, with additional analyses needed to extend site-specific results to regional scales in order to provide insight into general and long-term trends. Panel regression analysis, which includes both site and temporal dimensions, is suitable for evaluating yield responses to climate variability and is widely used to aggregate site scale to regional scale (Lobell 2017; Zhang et al. 2016b). Furthermore, the available research related to soybean production is mainly focused on a global scale or the USA, with limited information available for China (Jin et al. 2017; Schlenker and Roberts 2009; Zhao et al. 2017).

Genetic progress through crop breeding is a fundamental pillar for closing the attainable yield gap between China and other major soybean production countries, such as the USA (Vogel et al. 2021). Soybean genetic yield gains in China have been attributed to various traits improvement, including optimization of yield components and extension of the reproductive growth period (Jin et al. 2010; Wang et al. 2016; Xu et al. 2020). However, genetic sensitivity to temperature varies substantially among soybean cultivars (Kumagai and Sameshima 2014). Genetic adaptation is essential in the quest to breed crops better adapted and more resilient to a changing climate (Zabel et al. 2021), although the extent of adaptation is mediated by site-specific genotype, by environment, and by management interactions (Ibrahim et al. 2019). Development of new cultivars together with contextualized management may enable place-based climate change adaptation, enabling resilience to extreme heat exposure and/or crop heat stress (He et al. 2020; Zhang et al. 2021; Zhao et al. 2022).

To enable evidence-based decision making, China has established an integrated system for soybean cultivar assessment and comparison, including data from multiple cultivar-environment traits. Compared with previous work, this database consists of extensive multi-point cultivar trials enabling insight into interactions between cultivars, management, and environment (www.natesc.org.cn). Here, we utilize these data together with climatic data to determine how soybean productivity has responded to genetic progress and changes in climate. Specifically, the objectives of this study were to (1) evaluate the genetic contribution to China's historical soybean yield gains, (2) estimate the sensitivity of soybean yields to temperature variability and heat stress, and (3) determine defining characteristics of heat resilience and superior yield performance in contemporary cultivars.

2 Materials and methods

2.1 Data sources

Measured data, including yield, sowing dates, flowering dates, maturity dates, pod number per plant (PNPP), grain number per pod (GNPP), and hundred-grain weight (100-GW), were obtained from the national unified variety testing of China (NUSVT) annual reports from 2006 to 2020 (www.natesc.org.cn). The National Agro-Tech Extension and Service Center (NATESC) coordinated the NUSVT to select genotypes with high yield, high quality, and high resilience across agroecological regions. Cultivars were evaluated using a consistent protocol that was repeated every year for each NUSVT station, no other treatments were applied in the trial (NATESC 2020). The NUSVT was conducted using a randomized block design with each block repeated in triplicate at each site for each cultivar, variables reported represent averages of the three repetitions. Plot sizes were 15–20 m² with 10–12 m² harvested, depending on location. There were 6–12 rows in each plot, sowing density ranged from 180,000 to 260,000 plants per hectare following the local soybean agronomic recommendations. Although all agronomic practices were not provided in the annual reports, tillage practices and water and fertilizer management were the same as practices used for local soybean production. In general, herbicides were applied only after seedling emergence, weeds were controlled through manual weeding over the entire growth period, while insecticides, fungicides, and plant growth regulators were not applied. All observations were collected by experts following standardized protocols of the NATESC. Flowering date was recorded when more than 50% of plants exhibited anthers, and maturity date was recorded when 95% of pods per plant attained maturity color. Flowering and maturity dates were deemed the R1 and R8 stages of soybean development, respectively (Fehr and Caviness 1977). The annual report for 2019 was unavailable due to COVID-19.

Strict rules were used in the NUSVT to select exemplary cultivars (NATESC 2020). Generally, cultivar evaluation continued for 1 to 3 years, with new cultivars entering the evaluation while earlier cultivars cease to be evaluated each year. A new cultivar will be dropped at the end of the first year if it did not perform well, but will continue to be tested in the subsequent years if its performance meets the selection criteria. Depending on performance, cultivars could be dropped from the trial at the end of the second year, continue to be tested in the third year, or be recommended for further production trials based on performance in the second year. As such, only cultivars tested for more than 1 year were included in the present study. This dataset comprised 1659 cultivars with 16,934 observations (Table S1); cultivar-year-site combinations are shown in Tables S1 and S2, detailed information for a selected dataset is illustrated in Table S3.

The study area is transverse to all major soybean growing regions in China, and these regions were subdivided into the sub-regions shown Fig. 1a following Xu et al. (2020), including Northeast China (NEC), Huang-Huai-Hai Plain (HHH), and the Southern Multi-cropping Region (SMR). The NEC and HHH together cover more than 80% of national soybean cultivated area. Cultivars were divided into spring (generally sowing from March to May depending on region) and summer (generally sowing in June) based on the sowing dates of soybean. In summary, spring soybean was cultivated in the NEC and SMR, and summer soybean was grown in the HHH and SMR. More information about the treatments for either spring or summer cultivars is depicted in Table S4. Daily minimum temperature, mean temperature, maximum temperature, and precipitation in each NUSVT site were obtained from the China Meteorological Data Sharing Service System (<http://data.cma.cn>). Detailed soybean-related records from the NUSVT and the daily climatic data were compiled to build a comprehensive dataset for further analyses detailed below.

2.2 Data analysis

2.2.1 Yield, yield components, growth periods, and climatic resources

A mixed linear model was adopted to evaluate the trends of yield, yield components, growth periods, and climatic resources in each region during the study period. Due to the maturity groups varied across the NEC and other regions shown in Table S5, differences between groups were considered in the mixed linear model. Generally, the lmerTest R package was applied to calculate each variable included in

the study (Kuznetsova et al. 2017). Ambient temperature and precipitation during each growing period were calculated using the actual soybean growth phase in each year recorded by NUSVT. Each variable was expressed as trend per decade computed as 10 times the regression coefficient of the model. Cultivars were categorized in three discrete levels according to average yield as shown in Fig. S1, with yields the top 25% defined as high-yielding cultivars, the bottom 25% low yielding cultivars and others mid yielding cultivars.

2.2.2 Contribution of genetic progress to historical yield gains

The contribution of genetic progress to yield was first quantified by evaluating genetic trend of each cultivar. Selected representative datasets (Table S3) were used to evaluate the genetic trends in each region using a three-way model with year, site and cultivar factors (Hartung et al. 2023; Laidig et al. 2008, 2014):

$$y_{ijt} = \mu + G_i + S_j + Y_t + (GS)_{ij} + (GY)_{it} + (SY)_{jt} + (GSY)_{ijt} + e_{ijt} \quad (1)$$

where y_{ijt} is the mean yield of cultivar i in the site j and year t ; μ is a fixed intercept; G_i , S_j , and Y_t are the main effects of cultivar i , site j , and year t ; $(GS)_{ij}$ is the interaction effect of cultivar i and site j ; $(GY)_{it}$ is the interaction effect of cultivar i and year t ; and $(SY)_{jt}$ is the interaction effect of site j and year t ; $(GSY)_{ijt}$ represents interaction effects of the three factors; and e_{ijt} is a random error. For the SMR, $(GSY)_{ijt}$ was not included in the analysis as the number of observations at this sub-region was equal to the number of cultivar-by-year-by-site combinations, so the terms $(GS)_{ij}$, $(GY)_{it}$, and $(SY)_{jt}$ were used instead of $(GSY)_{ijt}$. Genetic and non-genetic trends

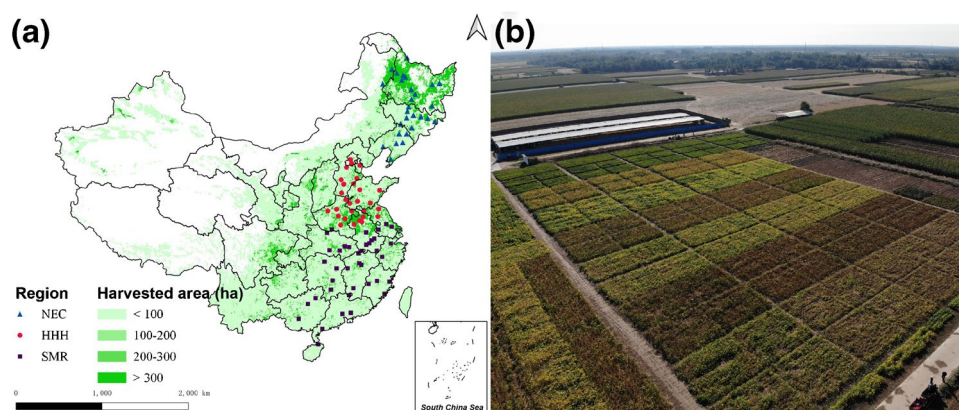


Fig. 1 Spatial distribution of the national unified soybean variety testing (NUSVT) sites between the period of 2006 and 2020 across China (a). Effects of the interactions of cultivars, sowing dates and nitrogen inputs on soybean performance in the field experiment (b, photograph by the authors). NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping

Region, respectively. The background image represents the harvested soybean area in 2010, which was obtained from the Spatial Production Allocation Model provided by International Food Policy Research Institute (<https://www.mapspam.info/>). The field experiment represented the interactions of 2 cultivars, 3 sowing dates, and 4 nitrogen managements.

were estimated by extension of Eq. (1) as follows (Piepho et al. 2014):

$$G_i = \beta r_i + H_i \tag{2}$$

$$Y_t = \gamma t_t + Z_t \tag{3}$$

where r_i is the first testing year for cultivars i , and t_t is the numeric variable for the year of testing. β is a fixed regression coefficient for genetic trend, and γ is a fixed regression coefficient for non-genetic trend. H_i and Z_t respectively represent the random normal residual of G_i and Y_t in each model. Genetic and non-genetic trends per decade were quantified as the regression coefficients β and γ multiplied by 10.

As structural equation modeling can be used to explore the causal relationships of different variables (Fan et al. 2016), we used this approach to analyze how agronomic traits influenced yield based on mean records per cultivar over multi-environments. Causalities between agronomic traits (e.g., length of vegetative growth period, the length of reproductive growth period, PNPP, GNPP, 100-GW) and yield were analyzed in the past work with parameters, such as P -values, comparative fit index (CFI), and root mean square error of approximation (RMSEA), to evaluate quality of model fit (Fan et al. 2016; Li et al. 2022). Here, CFI represents the discrepancy function adjusted for sample size and ranges from 0 to 1, higher values represent better model performance (Fan et al. 2016; Hu and Bentler 1999). RMSEA is associated with residual and range from 0 to 1, smaller values indicate better model performance (Fan et al. 2016; Hu and Bentler 1999). The lavaan R package was applied for structural equation model analysis (<https://lavaan.ugent.be>).

2.2.3 Response of yield to temperature

Cumulative temperature effects on yield over the growth period was evaluated following Hadasch et al (2020) and Schlenker and Roberts (2009):

$$Y_{ijt} = E(Y_{ijt}) + G_i + S_j + Y_t + (GS)_{ij} + (GY)_{it} + (SY)_{jt} + (GSY)_{ijt} + e_{ijt} \tag{4}$$

$$E(Y_{ijt}) = \mu + \beta r_i + \gamma t_t + \sum_{k=1}^n \alpha_k ATE_{kijt} + \theta_1 P_{ijt} + \theta_2 P_{ijt}^2 \tag{5}$$

where Y is the natural logarithmic of yield, i is the cultivar, j is the site, and t is the year. G_i , S_j , Y_t , $(GS)_{ij}$, $(GY)_{it}$, $(SY)_{jt}$, $(GSY)_{ijt}$, and e_{ijt} are defined as in Eq. (1). μ is a fixed intercept, β is a fixed regression coefficient for genetic trend, and γ is a fixed regression coefficient for non-genetic trend. ATE_{kijt} represents accumulated temperature in days to the k^{th} temperature interval in each region, n is the number of intervals in each region and α_k is estimated coefficient of temperature exposure. The quadratic function of growing

season precipitation denoted with P_{ijt} and P_{ijt}^2 were added to capture nonlinear effects of precipitation based on the preliminary analyses; θ_1 and θ_2 are estimated coefficients. We conducted a preliminary analysis (temperature ranging from 1 to 5 °C) to select the temperature optima based on the temperature distribution in different regions, arriving on the 4 °C step to calculate ATE_{kijt} :

$$ATE_{kijt} = \frac{1}{24} \times \sum T_{hkijt} \tag{6}$$

where T_{hkijt} represents hourly temperature for the k^{th} temperature interval. The hourly temperature was computed by interpolating the daily maximum temperature and daily minimum temperature with a sine function (Lobell et al. 2013).

2.2.4 Sensitivity of yield to heat stress

The combined effects of heat stress and thermal accumulation are thought to be key factors affecting yield (Butler and Huybers 2015), hitherto this has only been analyzed at the plot/field scale. Heat stress is represented by high temperature degree days (HDD) and thermal accumulation is quantified with growing degree days (GDD). GDD and HDD in the vegetative growth period and reproductive growth period at each site were respectively calculated using the following equations based on hourly temperature:

$$GDD = \sum_{t=1}^N GDD_t \tag{7}$$

$$GDD_t = \begin{cases} 0, T_h \leq 10 \\ (T_h - 10)/24, 10 < T_h \leq 30 \\ \frac{30-10}{24}, T_h > 30 \end{cases} \tag{8}$$

$$HDD = \sum_{t=1}^N HDD_t \tag{9}$$

$$HDD_t = \begin{cases} 0, T_h \leq 30 \\ (T_h - 30)/24, T_h > 30 \end{cases} \tag{10}$$

where T_h is the hourly temperature, GDD_t represents the value of GDD in t hour, HDD_t is the value of HDD in t hour, and N is the number of hours in each period. The threshold maximum temperature was defined as 30 °C and the threshold minimum temperature was set as 10 °C for soybean following measurements made previously (Schlenker and Roberts 2009; Yin et al. 2016a).

A regression model was applied to estimate the sensitivity of yield to HDD and GDD during different growth periods. The analysis was conducted for each region.

$$Y_{ijt} = E(Y_{ijt}) + G_i + S_j + Y_t + (GS)_{ij} + (GY)_{it} + (SY)_{jt} + (GSY)_{ijt} + e_{ijt} \quad (11)$$

$$E(Y_{ijt}) = \mu + \beta r_i + \gamma t_t + \alpha_1 GDD_{ijt}^V + \alpha_2 GDD_{ijt}^R + \theta_1 HDD_{ijt}^V + \theta_2 HDD_{ijt}^R + \sigma_1 P_{ijt}^V + \sigma_2 P_{ijt}^R \quad (12)$$

where Y is the yield; G_i , S_j , Y_t , $(GS)_{ij}$, $(GY)_{it}$, $(SY)_{jt}$, $(GSY)_{ijt}$, and e_{ijt} are defined as in Eq. (1). μ is a fixed intercept, β is a fixed regression coefficient for genetic trend, and γ is a fixed regression coefficient for non-genetic trend. V indicates the vegetative growth period, R is the reproductive growth period; α_1 , α_2 , θ_1 , and θ_2 correspond to model coefficients of yield to GDD and HDD in each growth period, respectively; P_{ijt} is the precipitation in each growth stage. In all cases, the variance inflation factor (VIF) in each sub-region was less than 10, suggesting an absence of multicollinearity between variables (Thompson et al. 2017). The sensitivity of yield to GDD and HDD was calculated referring to Zhang et al. (2016b):

$$Sen_{a,c} = \frac{Coeff_c}{Yield_a} \quad (13)$$

where a represents the sub-region, c represents either GDD or HDD in the vegetative and reproductive stages; $Sen_{a,c}$ is yield sensitivity to climate factor c in region a shown in Fig. 1a; $Coeff_c$ represents the climatic factor c and $Yield_a$ is the average yield across region a . The sensitivity of yield to heat stress was further explored for cultivars of different yield levels, providing insight into genotypic response to heat stress, in particular whether high yield is linked with heat resilience.

3 Results

3.1 Yield and yield components

Average yield was higher in the NEC and HHH than SMR, and the high-yielding sites were mainly located in the southern NEC,

central HHH, and northern SMR (Fig. 2a). Average yields over the last 15 years were 2852, 2830, and 2554 kg ha⁻¹ in the HHH, NEC, and SMR, respectively (Fig. 2b). Mean summer cultivar yields were higher than that of spring cultivars in the SMR and at the national scale (Figs. S2 and S3). Yield increased in each cultivation zone from 2006 to 2020 with rates of 332, 389, and 185 kg ha⁻¹ per decade in the NEC, HHH, and SMR, respectively. There were considerable differences between yield, the average of the high yielding cultivars was 3129, 3086, and 3050 kg ha⁻¹ in the NEC, HHH, and SMR, respectively (Fig. S4).

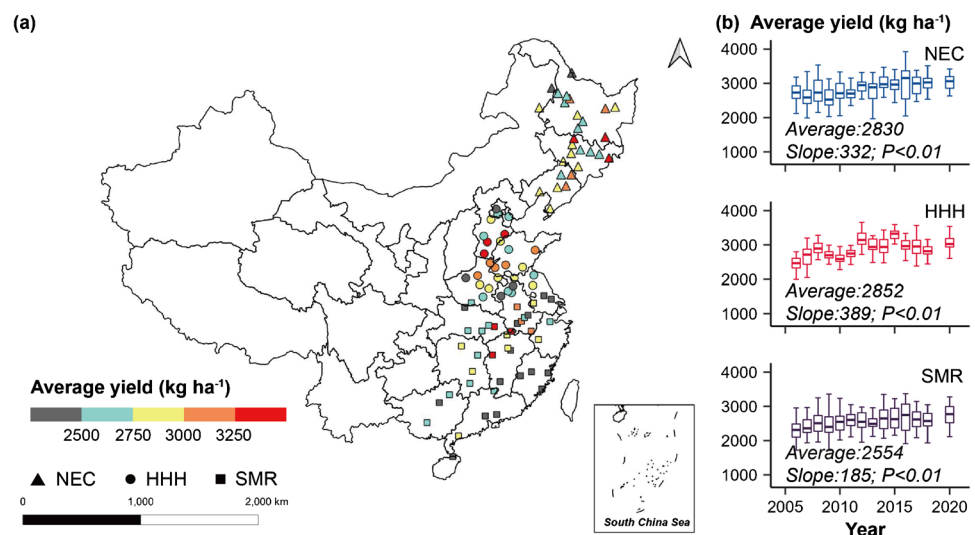
Yield components varied considerably across regions (Fig. 3). Pod number per plant (PNPP) was higher in the NEC and HHH than in the SMR. PNPP increased faster in the NEC and HHH as the rate of 2.14 and 3.28 per decade, respectively (Fig. 3a and d), compared with the SMR where no change in PNPP was identified. Grain number per pod (GNPP) was higher in the NEC with mean value of 2.16, followed by HHH and SMR; no differences in GNPP trends among the three regions were observed (Fig. 3b and e). 100-GW was lower in the NEC than in the HHH and SMR, it only showed significantly (increasing) trend in the HHH with a rate of 1.48 per decade (Fig. 3c and f). Yield components tended to be higher for the high yielding cultivars compared with the lower yielding cultivars (Fig. S5).

3.2 Phenology

Phenology varied among regions, especially for the reproductive growth period (Fig. 4), with average vegetative growth periods from 40 to 56 days, being longest in the NEC. Mean reproductive growth period was 62 to 82 from south to north and with largest values in the NEC, which led to the longest growing season in the NEC (Fig. 4a). Sowing times were earlier in the NEC and later in the HHH; similar trends were observed for the flowering and maturity times in the two regions (Fig. S6).

Sowing times were delayed while flowering times advanced significantly in the NEC and SMR leading to shorter

Fig. 2 Spatial distribution of the multi-year average soybean yield per experimental site (a) and the temporal changes of soybean yield in each cultivation zone (b) during the experimental period. Boxplots show the median (horizontal line in each box), the 25th and 75th percentiles (boxes), and the 5th and 95th percentiles (whiskers) of average observed soybean yield. NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.



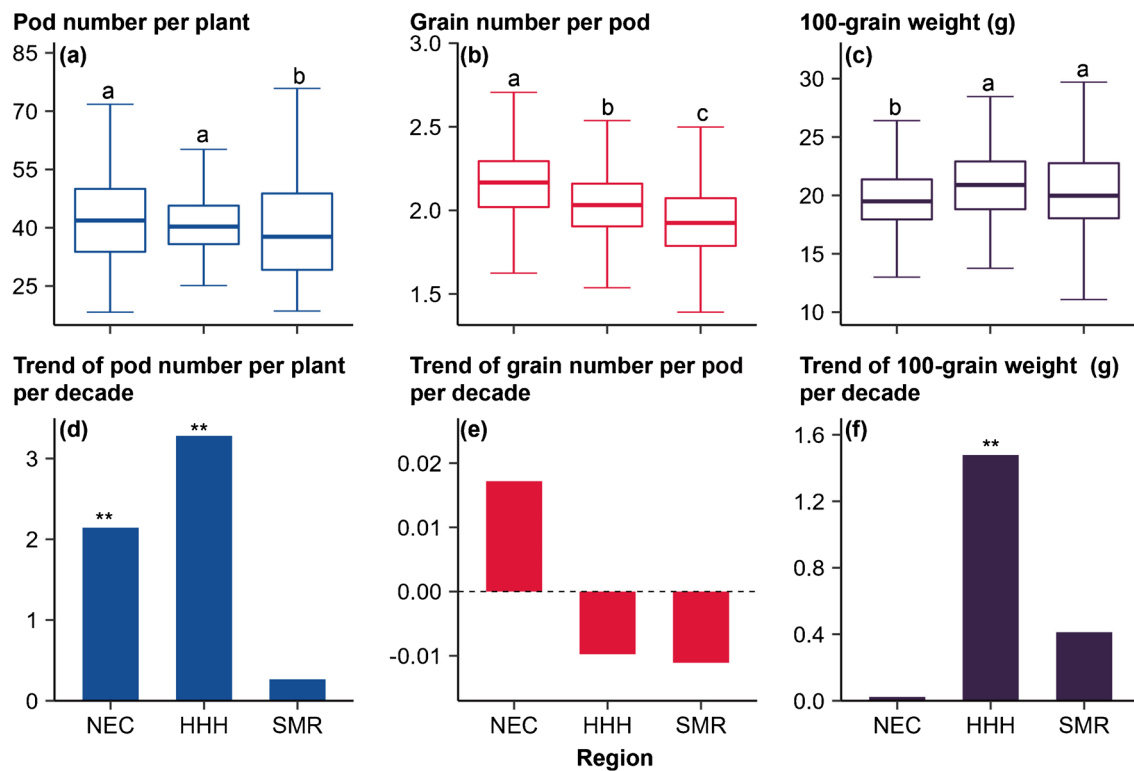


Fig. 3 Variations of soybean pod number per plant (PNPP, **a**), grain number per pod (GNPP, **b**), and 100-grain weight (100-GW, **c**) across soybean cultivation zones over the study period. The changing trends of PNPP (**d**), GNPP (**e**), and 100-GW (**f**) per decade in different soybean cultivation zones over the study period.

Different letters in the boxplots indicate statistically significant difference between each zone (a–c), and the trends with a mark “**” are significant at 0.01 level (d–f). NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.

vegetative periods of 2.5 and 2.6 days per decade in these two regions (Fig. S6 and Fig. 4b). Maturity times were delayed significantly with 3.8 days per decade in the NEC, but were more stable in the SMR, thus extending the reproductive growth period significantly with 4.4 and 1.4 days per decade in the NEC and SMR, respectively. On the other hand, sowing, flowering, and maturity times in the HHH were delayed significantly, with 2.2, 1.9, and 2.8 days per decade, respectively, thus shortening the vegetative growth period and extending the reproductive growth period. Maturity was delayed more compared with the sowing time in the NEC and HHH, prolonging the whole growth period while advanced maturity date and delayed sowing date shortened the growth period in SMR. The reproductive period was longer for the high yielding cultivars than for the low yielding cultivars (Fig. S7).

3.3 Effects of genetic progress on soybean yield

Genetic progress contributed positively to yield gains as estimated by Eqs. (1–3) (Table 1), advancing by 213, 150, and 155 kg ha⁻¹ per decade for the NEC, HHH, and SMR, respectively. Non-genetic trends also increased in the NEC and HHH, with mean values of 203 and 241 kg ha⁻¹,

respectively (Table S6) suggesting that non-genetic drivers contributed more to yield gains than genetic factors. Contributions of genetic progress to yield were different between spring and summer soybean (Tables S7 and S8).

Generally, differences in growth periods and yield components explain cultivar differences in yield (Fig. 5). Each yield component had positive effects on yield, despite the negative relationship among these yield components. The vegetative period and the reproductive period were negatively related. With the exception of SMR, both growth periods had positive effects on PNPP and 100-GW, while negatively affecting GNPP. In the NEC and HHH, the vegetative period had the largest effect on PNPP and the reproductive period had the largest effect on 100-GW. The PNPP had the largest effects on yield in each region. The magnitudes of the effects of GNPP and 100-GW on yield were similar in the NEC and SMR, while the contribution of 100-GW to yield was higher than GNPP in the HHH (Fig. 5).

3.4 Climatic changes during the growing season

Our results clearly illustrated the spatial variability in mean temperature, GDD, and HDD for each of the growth periods,

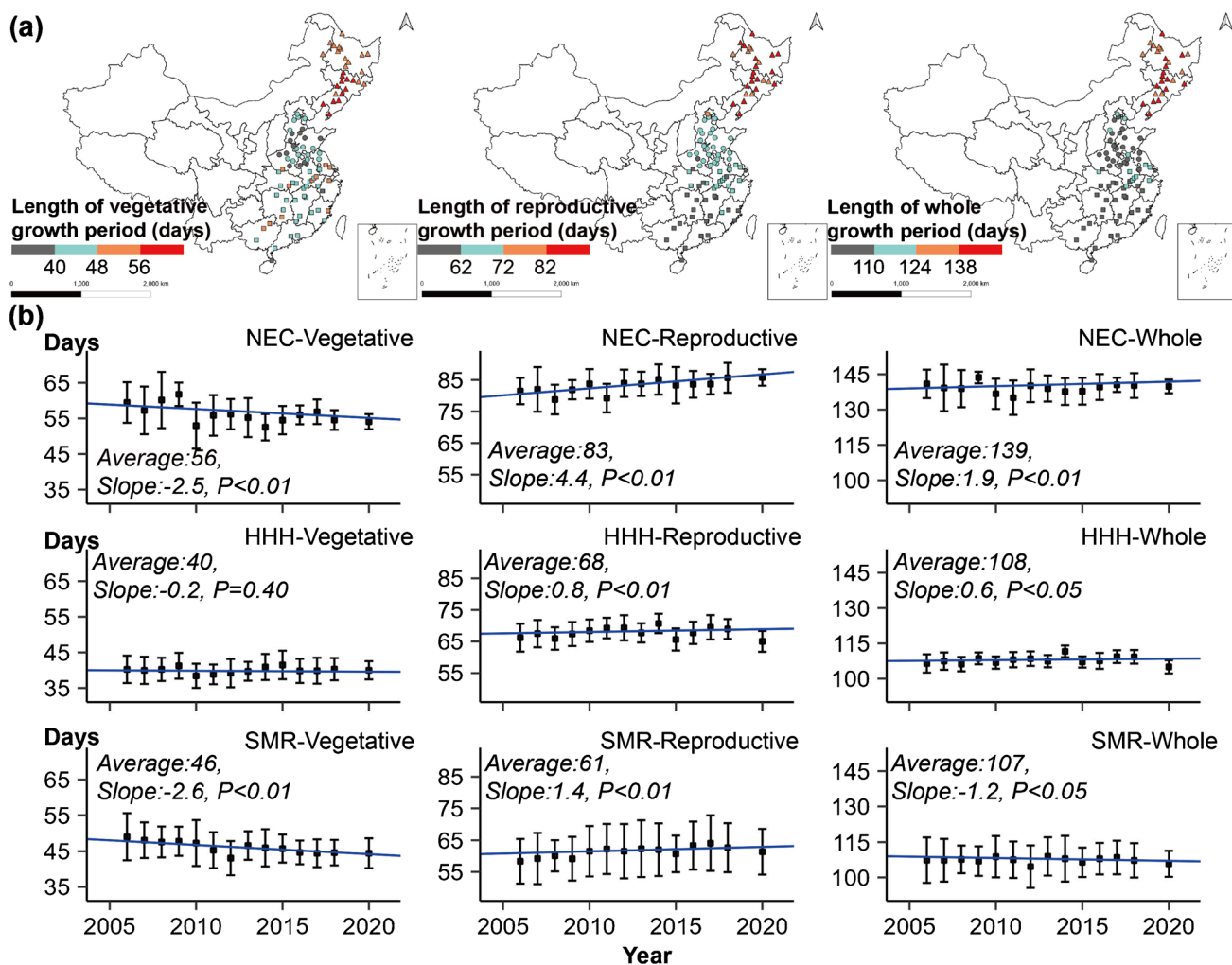


Fig. 4 Spatial distribution of the length of the vegetative growth period, reproductive growth period, and whole growth period (a), and their temporal changes for each soybean cultivation

zone (b). NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.

especially for the HDD and mean temperature in the reproductive growth period (Fig. 6). The HDD in the reproductive growth period was higher in the southern NEC and southern HHH; similar trends were obtained for mean temperature.

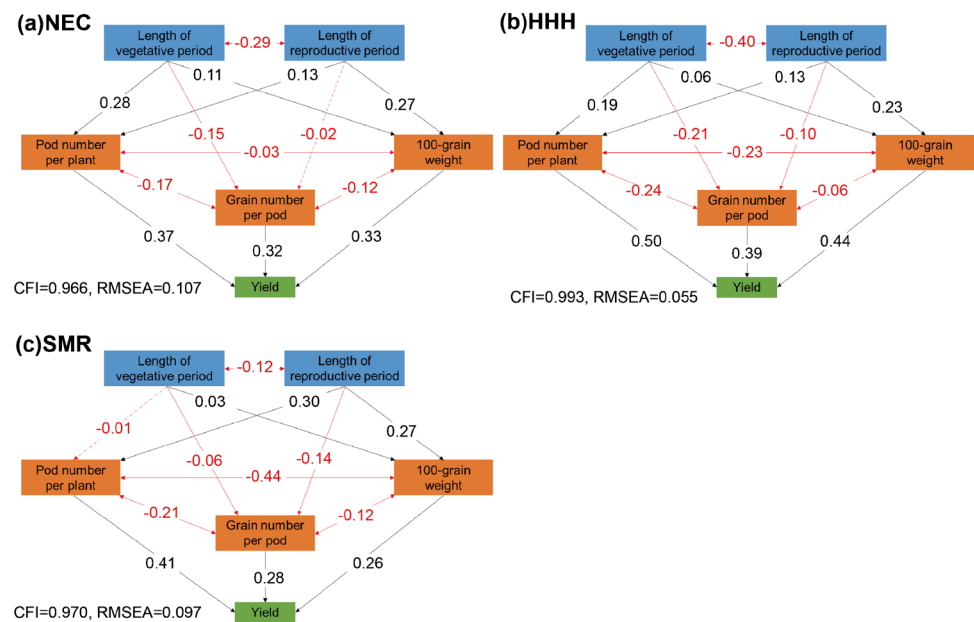
Table 1 Estimates of the genetic trend of soybean cultivars from 2006 to 2020 using Eqs. (1–3). Specially, SE is standard error, superscript “**” represents significant at 0.05 level, and superscript “***” represents significant at 0.01 level. NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.

Region	Estimate of the genetic trend (kg ha ⁻¹ decade ⁻¹)	
	Absolute	SE
NEC	212.9**	43.5
HHH	149.6**	39.9
SMR	155.2*	71.4

Mean temperature in the vegetative period tended to be higher in the HHH than NEC and SMR, while the mean temperature in the reproductive growth period was highest in the SMR, followed by the HHH and NEC (Fig. 6a and b). In addition, the GDD in the vegetative period was lower in the NEC and southern HHH, while northern SMR had higher GDD in the reproductive period (Fig. 6d and e). HDD was higher in the HHH in both growth periods (Fig. 6g and h). The precipitation in the HHH was lower than in other regions (Fig. S8).

During the last 15 years, HDD in the reproductive growth period increased significantly in the NEC and HHH at a rate of 4.6 and 10.4 °Cd per decade (Fig. 6i). Mean temperature in the reproductive stage in the HHH also significantly increased (Fig. 6c). GDD in the vegetative growth period decreased over time in NEC and SMR at rates of 30 and 27 °Cd per decade, while GDD in the reproductive period increased significantly at 52, 35, and 22 °Cd in the NEC, HHH, and SMR,

Fig. 5 Structural equation models of soybean yield in the NEC (a), HHH (b), and SMR (c). Black and red solid arrows respectively indicate positive and negative effects, and the dashed arrows mean no significant relationships at the $P = 0.05$ level. NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.



respectively (Fig. 6f). Precipitation increased in both soybean growth phases in the NEC and decreased in the vegetative growth period in the HHH (Fig. S8).

3.5 Sensitivity of yield to temperature and heat stress

Temperature exposure during the growing season was distributed between 12 and 28 °C in the NEC and 20–32 °C in the HHH and SMR (Fig. 7). Generally, the sensitivity of yield to temperature was evaluated by Eqs. (4–5). The duration of high temperature exposure was greater in the HHH and SMR than in the NEC. The clear temperature response was observed in the NEC, where yield declined when temperatures exceeded 28 °C, similar trends were also found in the SMR when temperature larger than 32 °C.

A multiple linear regression model (Eqs. 11–12) was adopted to evaluate the impacts of heat stress on yield in each growth period (Table S9). Yield responded more negatively to heat stress in the reproductive growth period compared with heat stress during the vegetative growth period in all regions (Fig. 8a). Heat stress caused the highest yield penalties in the reproductive period in the NEC (Fig. 8a). Cultivars had negative sensitivity to heat stress in the reproductive stage in the NEC, the largest sensitivity was observed for high yielding cultivars (Figs. 8b and S9; Table S10). All types of cultivars were adversely affected by HDD in the HHH, and high yielding cultivars were least sensitive to heat stress in this region. Nevertheless, heat stress in the reproductive stage did not tend to reduce yield of the highest yielding cultivars in the SMR (Fig. 8b; Table S10).

4 Discussion

4.1 Genetic progress contributed to yield gains over time

Our results showed that genetic progress contributed to yield gains over the last 15 years (Table 1), which is a finding aligned with previous studies (Rincker et al. 2014; Wang et al. 2016; Xu et al. 2020). Other studies have attributed these breeding gains due to increased yield floor rather than yield ceiling (de Felipe and Alvarez Prado 2021), probably because newer cultivars have longer growing seasons, higher photosynthetic rates, less lodging, higher biomass production, and greater partitioning of biomass into seed compared with older cultivars (Jin et al. 2010; Koester et al. 2014; Lopez et al. 2021).

Improved yield components translated to yield gains, although the extent of which varied between regions (Figs. 3, 5, and S5). For instance, PNPP was the dominant contributor to yield in the NEC, increasing at a rate of 2 pods per plant per decade (Figs. 3d and 5a). The PNPP for the high yielding cultivars was 1.8 times higher than that of the low yielding cultivars, while differences between GNPP and 100-GW were much smaller compared with PNPP between different yield-levels in the NCP (Fig. S5). Other study has shown that yield gains were attributed to seed number per plant, with PNPP being the most important contributor to yield stability in the NEC from 1960 to 2006 (Jin et al. 2010). Here, we found that both PNPP and 100-GW drove yield gains in the HHH (Figs. 5 and S5), similar to a previous study that showed increased seed weight and seeds per pod rather than pods per plant contributed more to genetic yield gain in the HHH (Wang et al. 2016). Moreover, both PNPP and 100-GW increased in the HHH, which explained the yield gains in the region (Fig. 3). PNPP and GNPP contributed to yield

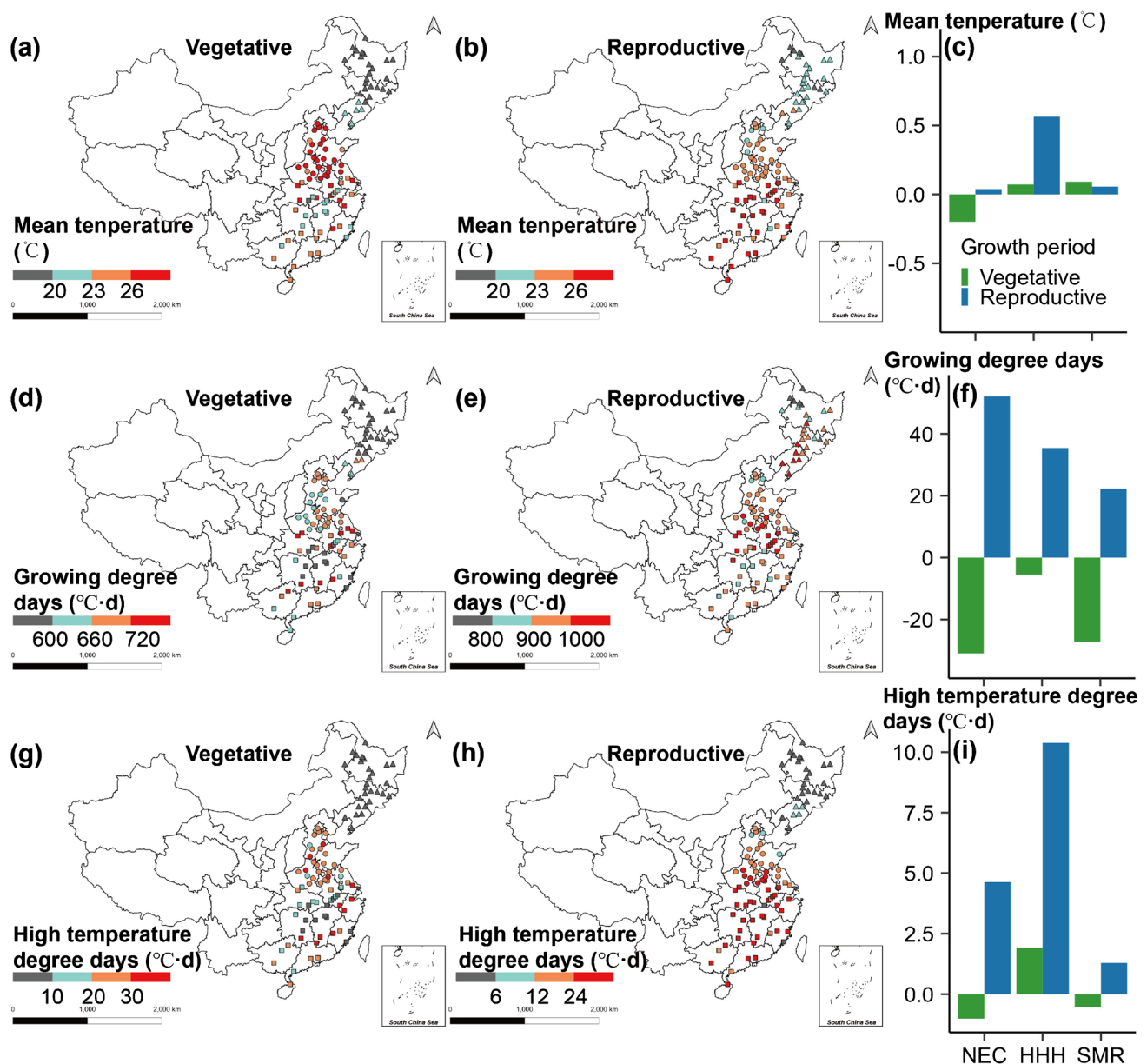


Fig. 6 The spatial pattern of mean temperature (**a** and **b**), growing degree days (GDD; **d** and **e**), and high temperature degree days (HDD; **g** and **h**) in the vegetative growth period and reproductive growth period, respectively. Trends in mean temperature (**c**), GDD (**f**), and HDD (**i**) per decade in each soybean cultivation zone dur-

ing the vegetative and reproductive growth stages. “*” means significance at $P=0.05$ level, while “**” denotes significance at the $P=0.01$ level. NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.

gains in the SMR, in line with previous conclusions showing that the pod number and seed number per plant increased in the southern China for the cultivars released between 1995 and 2016 (Yang et al. 2022). Despite this, changes in PNPP, GNPP, and 100-GW were not significant in the SMR over the last 15 years, probably because assessed alternative breeding goals in different periods (Qin et al. 2017; Yang et al. 2022). As well, soybeans tend to have greater sensitivity to climate vagaries than other crop types (Wu et al. 2019).

Our results showed that the extension of reproductive growth period was a key factor affecting the performance of cultivars in each region. Phenological observations at agrometeorological stations have demonstrated that the reproductive growth period has extended over time (He et al. 2020; Liu and Dai 2020), which can increase shoot biomass and yield (Yang et al. 2022). The duration of the reproductive period increased in each region in the study, contributing to increased PNPP and 100-GW (Figs. 4 and 5; Wang et al. 2016).

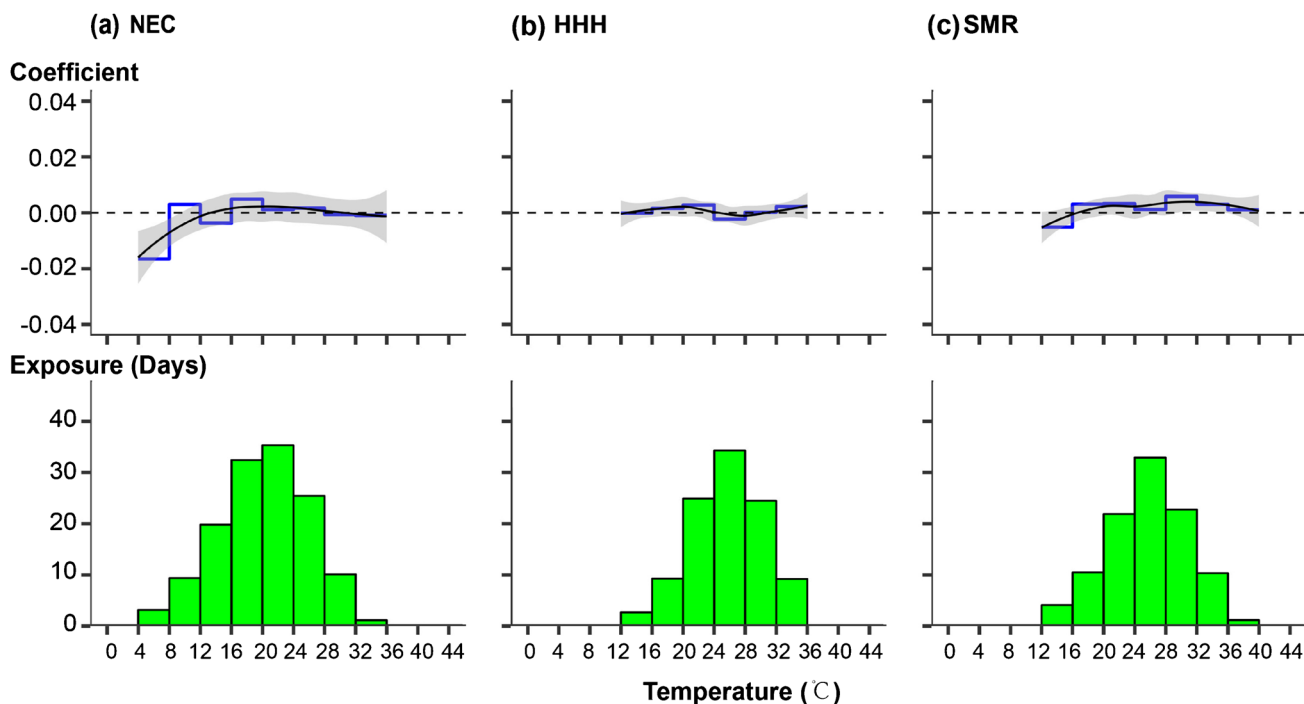


Fig. 7 Nonlinear relation between temperature and yield in the NEC (a), HHH (b), and SMR (c). Upper panels display changes in log yield for 4 °C temperature increments, shown in blue lines (the estimated coefficient α_k in the Eq. 4). The black line is the fitted curve (using locally weighted regression) for the regression coefficients,

and grey area represents 95% confidence interval. Lower panels represent the mean accumulated duration of thermal exposure to each 4 °C temperature bin in each region. NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.

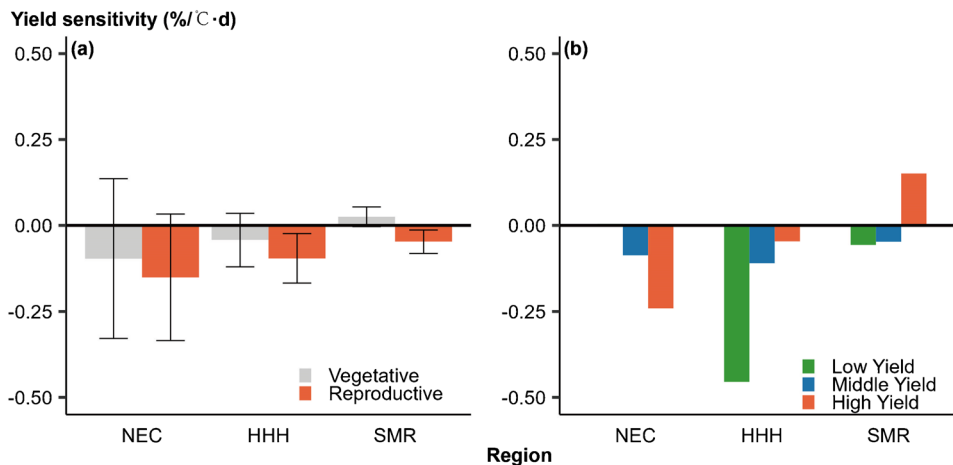
4.2 Impacts of global warming and heat stress on crop productivity

4.2.1 Global warming

China has experienced significant atmospheric warming during recent decades, similar to the majority of other regions in the world, which has temperature projections of warmer future climates (Jiang et al. 2021; You et al. 2021). Recent

studies have highlighted temperature as the most important climatic factor influencing soybean growth and development (Liu and Dai 2020; Zhao et al. 2017). In theory, global warming would extend the soybean growing season and provide better sowing and harvest conditions, especially in cold regions such as the NEC (Yin et al. 2016b). Similar to other crop types, how to best adapt soybean to a changing climate remains a challenge, but success in this endeavor will be vital to ensure sustainable food security (Muleke et al. 2022).

Fig. 8 Sensitivity of soybean yield to high temperature degree days (HDD) in either vegetative or reproductive growth period in the NEC, HHH, and SMR (a), and the responses of different levels of soybean yield to HDD in the reproductive growth period in each region (b). NEC, HHH, and SMR represent Northeast China, Huang-Huai-Hai Plain, and Southern Multi-cropping Region, respectively.



Our results found that soybean is most sensitive to climate warming in the NEC, where the maturity date was delayed more than the sowing dates thus extending the growing season (Fig. S6). On the other hand, increased temperature would accelerate soybean development, thus shortening the growth period and leading to decreased yield, unless the cultivar is adapted to counteract this (He et al. 2020; Liu and Dai 2020; Ruiz-Vera et al. 2018; Yin et al. 2016a). However, our results indicated that the whole soybean growth period was only shortened in the SMR while it was extended significantly in the NEC and HHH (Fig. 4). This suggests that modern soybean cultivars are well adapted to climate warming through shortening the vegetative growth period and extending the reproductive growth period for the regions in the study, thus making better use of the reproductive growing period to improve soybean yield (Figs. 4 and 5).

4.2.2 Heat stress

Previous studies showed that the frequency and degree of heat stress increased along with climate warming, especially in the summer season (Chen et al. 2018; Yin et al. 2016b). Our results indicated that the heat stress risks were much higher in the reproductive growth period than the vegetative growth period in all regions, and this risk was much greater in the reproductive period in the NEC and HHH (Fig. 6). Soybean growth could be adversely affected once the temperature exceeded the optimal range (Alsajri et al. 2019; Djanaguiraman et al. 2011; Jumrani and Bhatia 2018). The exposure of high temperature led to soybean yield reduction in each region, and heat stress in the reproductive growth period was the major driver for yield losses in the NEC and HHH (Figs. 7 and 8), which is in line with recent studies (Jha et al. 2017; Siebers et al. 2015; Thomey et al. 2019).

Previous studies have demonstrated that heat stress severely reduced PNPP, GNPP, and 100-GW, thus reducing soybean yield by affecting physiological processes, such as leaf photosynthetic rate, stomatal conductance, and the dry matter accumulation (Sima et al. 2020; Tacarindua et al. 2013). Generally, the flowering and pod filling phases are particularly critical to heat stress during the reproductive growth period (Thomey et al. 2019; Yin et al. 2016a). Past work has shown that soybean may recover from heat stress during the flowering stage due to the longer growth period of this phase in soybean, while the yield loss caused by heat stress in the late reproductive stages affecting pod setting cannot be mitigated (Siebers et al. 2015). Thus, the timing of heat stress is crucial and heat stress in the grain filling stage is particularly harmful for soybean production. Furthermore, heat stress is associated with vapor pressure deficit that promotes drought, which elevates leaf temperatures and exacerbates soybean yield losses (Tacarindua et al. 2013).

Generally, the sensitivities of soybean yield to heat stress varied massively across regions and cultivars (Fig. 8). The

climatic conditions and the breeding strategies could be the most important factors making the differences of heat sensitivity between three regions. Soybean in the NEC is mainly produced under rainfed agriculture, which is particularly sensitive to temperature variability (Hamed et al. 2021; Yin et al. 2016a). The soybean yield in cool areas of the NEC was positively correlated with temperature, while opposite in the warm areas of NEC (Zhang et al. 2021). The southern part of NEC is characterized by higher soybean yield and higher temperature with frequently occurring heat stress, which could explain the strongly negative sensitivity of high-yield cultivars to heat stress in the NEC (Figs. 6 and 8). Previous studies have documented the largest anticipated increase of heat stress in the warmer areas of NEC, which negatively affects soybean yield (Yin et al. 2016b). Thus, we concluded that increased utilization of thermal resource has been identified as an important strategy to promote yield gains in the NEC; thus, the high-yield cultivars tend to be more sensitive to temperature and eventually the heat stress. On the other hand, the heat stress risk was much higher in the HHH than NEC, mainly because the soybean growing season was concentrated in the summer season and the high temperate conditions in the HHH (Figs. 6 and S6). Moreover, our results also showed that soybean yield was most sensitive to heat stress in the reproductive growth period in the HHH, particularly the low yield level cultivars with the mean value around 2300 kg ha⁻¹ (Fig. 8). Additionally, evidence from field warming experiments in the HHH showed that warming significantly decreased 100-GW and soybean yield by 21% and 45%, respectively (Zhang et al. 2016a). Thus, reducing the adverse effects of heat stress is essential for yield increasing. The sensitivity of the high yield-level cultivars to heat stress was less than others, which means the cultivars with both higher heat-tolerant and high-yielding traits were relatively well adapted to heat stress in the HHH. This is probably because high yielding soybean cultivars with stronger heat stress tolerance have been historically selected in the HHH.

The SMR generally had higher temperatures and higher precipitation (Figs. 6 and S8; Song et al. 2016). High temperatures caused greater yield losses in dry conditions than in wet conditions, with heat stress resulting in greater penalties to soybean yield during dry conditions than wet conditions (Hamed et al. 2021; Luan et al. 2021). The climate may help explain why soybean in the SMR was less affected by heat stress even though the higher HDD (Fig. 8): it is plausible that abundant water in the SMR maintained water supply and sustained evaporative cooling, mediating the detrimental effects of supraoptimal temperatures on soybean.

4.3 Implications and perspectives

Our results underscore the importance of implementing multiple cultivar-environment traits to evaluate yield responses to genetic progress and climate variability. Detailed records of agronomic

traits helped reveal the effects of genotypic improvement on yield, and explained why yield increased over time. Our results also exemplified trends in adapting to global warming, with high yielding cultivars in the HHH generally demonstrating superior performance under heat stress. Our panel regression model dissected the genetic and non-genetic influences on yield gains over time, deeper, mechanistic insights into how crop traits and canopy biophysics contribute to yields in individual years could further be investigated using process-based models. In summary, this study should be useful for advancing soybean production and cultivar breeding in China under global warming.

5 Conclusions

This study aims to determine how China's soybean productivity responded to genetic progress and changes in climate during the last 15 years. Our results demonstrated that new genetics contributed to yield gains over 2006 to 2020. While yields were higher in the NEC and HHH compared with SMR, all regions exhibited yield gains over time. Incremental gains in PNPP were primarily attributed to yield gains observed in the NEC, while increments in PNPP and 100-GW were dominant contributors to yield improvements in the HHH. Reproductive stages in all regions increased over time, leading to increased PNPP and 100-GW. The non-linear response of yield to temperature emphasized the negative implications associated with heat stress on yield during the reproductive growth period in the NEC and HHH. Our findings highlight the importance of improving genotypic tolerance and resilience to extreme heat exposure, while increasing GDD to maintain growing duration, biomass production, and yield.

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Data availability The data analyzed during the study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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