

WHEAT BREEDING IMPROVED STABILITY OF YIELD UNDER CLIMATE CHANGE

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Abstract

Food security is affected by limited arable land, growing food demand and environmental degradation. Therefore, the selection of high-yield, stable-yield and climate-resistant varieties is essential to increase and maintain wheat yield. In this study, the contribution of wheat breeding was analyzed by the data of yield of wheat in production, yield and yield composition trait of wheat regional testing, annual average temperature and annual average precipitation in Sichuan Province over 40 years. The average yield per hectare (YH) of wheat lines of regional testing increased from 4.14 t ha⁻¹ in 1981 to 5.81 t ha⁻¹ in 2021. By 2020, the wheat yield and planting area in Sichuan, China were 59.70 10⁴ ha and 246.70 10⁴ t, and the yield per hectare increased from 0.82 t ha⁻¹ in 1952 to 4.13 t ha⁻¹ in 2020. The lower limits of yield determinants including spikes number per hectare (SNH), grain number per spike (GNS) and thousand grain weight (TGW) were significantly increased. And the obviously shortened growth period (GD) was more beneficial for wheat to cope with the complex climate in Sichuan. These results indicate that wheat breeding has significantly elevated the stability and sensitivity of wheat to climate change, which is helpful in maintaining stability and high yield under environmental anomalies. In addition, the formation of wheat varieties has been accelerated in part on the development of breeding technology. Diversifying wheat varieties is expected to mitigate some of the negative effects of climate change.

Key words: Wheat breeding; Wheat yield; Climate change; Annual temperature; Annual precipitation.

Introduction

Wheat (*Triticum aestivum* L.) has the widest distribution in the world, and provides about 20% of the daily calories and protein for humans (Dixon *et al.*, 2009; Shiferaw *et al.*, 2013; Curtis & Halford, 2014). China, which increased its wheat production by approximately 30.6 million tons from 2000 to 2018 (Li *et al.*, 2019), is the world's major wheat producer, with about 17% of the total global production (FAO, 2018). As populations grow and urbanize, the demand for wheat will continue to increase (Yang, 2013; Lu *et al.*, 2015; Ji-kun *et al.*, 2017).

Wheat yield is controlled by genes and environment (Araki *et al.*, 1999). In production, there were many related traits that determine grain yield, such as spike numbers per hectare (SNH), grain number per spike (GNS), thousand grain weight (TGW), growth duration (GD) and plant height (PH), etc., (Ain *et al.*, 2015). In previous studies, yield was significantly correlated with SNH, GNS and TGW, and the relationship between these three components was often studied (Zhang *et al.*, 2016). GD and PH affected grain weight through vegetative growth process (Zapata *et al.*, 2004). At present, many researchers have studied the genes or QTL that control SNH, GNS, TGW, GD and PH, and accumulated some genes or QTL that could contribute to wheat breeding and improvement.

The growth and development of wheat mainly depend on climate resources such as temperature, solar radiation and precipitation, etc., (Bos & Neuteboom, 1998; Evers *et al.*, 2006). Some biological processes of wheat, such as photosynthesis, respiration and substance conversion, are significantly affected by temperature, and the restriction of these processes will affect the yield and quality. The rise of temperature leads to the weakening of the vernalization of

wheat and the shortening of the growth period, which in turn shortens the time of photosynthesis and material accumulation of wheat, making it inevitable to reduce production (Zhang *et al.*, 2013; Zhang *et al.*, 2015). Since the 1960s, the annual average temperature in China has risen gradually, with the range of 0.24°C / decade (Piao *et al.*, 2010). Similarly, the annual average temperature in Sichuan Province also showed a gradual rising trend, with an increasing range of about 0.15°C / decade (Fig. 1a), The dataset was from Sichuan Climate Bulletin 2021 released by Sichuan Provincial Meteorological Service, http://sc.cma.gov.cn/xwzx/202202/t20220216_4513493.html. In recent years, some studies have shown that when the temperature increases by 1°C in China during its growing period of wheat the yield decreases by 3.0% ~ 10.0% and the growth period is shortened by about 17 days (You *et al.*, 2009; Yin *et al.*, 2015). The growth and development of wheat was inseparable from water. Drought affects protein changes, osmotic adjustment, opening and closing of stomata, photosynthesis inhibition, transpiration reduction, growth inhibition and other aspects of wheat, and ultimately lead to the decrease of wheat yield (Szegeletes *et al.*, 2000; Yordanov *et al.*, 2000; Lawlor & Cornic, 2002; Zhu, 2002). However, waterlogging causes soil anoxia and severe anoxia in wheat roots, which inhibits root development and resulting in reduced yields (Armstrong, 1979; Jackson, 1984; Colmer & Voesenek, 2009). From 1961 to 2021, the annual precipitation in Sichuan Province showed a slow rising trend, with a range of 0.14 mm / decade (Fig. 1b). Wheat production requires a suitable climate, but in recent years extreme weather events have occurred frequently around the world, so the selection and improvement of wheat varieties is crucial to maintain or increase yields.

It is of significant importance to summarize the historical process of wheat breeding for guiding breeding strategies. This study evaluated the development of wheat breeding and the effect of climate on it using the data of yield of wheat in production, yield and yield composition trait of wheat regional testing, annual average temperature and annual average precipitation. These results have positive value for improving the ability of wheat to cope with climate change and continuously increasing wheat yield in Sichuan Province.

Material and Methods

In China, the first version of the Seed Law of the People's Republic of China was adopted on July 8, 2000. New wheat varieties must be approved with the provincial or national crop variety approval committees before release. To identify excellent wheat varieties, an evaluation system was established in China. First, the breeder selects some new wheat lines and submits the application for new varieties test to the provincial crop variety approval committees. Next, the seed management department organizes the test, including a 2-year regional test and a 1-year production test. Through this process, new qualified varieties can be released in the provinces where they are being tested. Finally, new varieties approved at the provincial level can submit an application for new varieties test to the national crop variety approval committees. New varieties that pass the national variety test can be released in a wider area.

In accordance with the method of registration for wheat variety Received for publication 12 May 2023 i.e., NY/T 967-2006), the recordation detail of regional testing includes the yield ability, variety characteristics, adaptability, stress resistance, use, etc. The regional test of Sichuan province was performed at 8-24 sites in the wheat ecosystems of the region where the variety was selected. A random complete block design was used for each test site with 3 replicates. The area of each plot was 13.3 m², and the distance between each plot was 0.4 m. Our data collected from the regional trial data of Sichuan province was published by Sichuan Seed Station from 1981 to 2021. To evaluate the new varieties, six traits were analyzed in the field, including YH, SNH, GNS, TGW, GD and PH. After anthesis, the representative area of 1 m² from each plot were selected for measuring the SNH. PH was measured from the ground surface to the tip of the tallest spike. The number of grains was counted for each spike to measure GNS. After drying in the air, YH was the yield per plot multiplied by 750, TGW was calculated based on 1,000 grains in each plot. The data of yield and planting area for wheat was obtained from the Statistical Bureau of Sichuan (<http://tjj.sc.gov.cn/>, accessed on 10 November 2022). The data of mean annual temperature and annual precipitation were inquired by Sichuan Climate Bulletin 2021 released by Sichuan Provincial Meteorological Service (http://sc.cma.gov.cn/xwzx/202202/t20220216_4513493.html, accessed on 10 November 2022).

Data analysis

To evaluate the rates of variation for YH, SNH, GNS, TGW, GD and PH with the year of release, regression analysis with a standard linear model was applied, and the significance of the slope of linear regression was tested using *t*-test analysis. Use 100 times the linear regression slope to represent the annual growth rate (Fischer *et al.*, 2012; Hu *et al.*, 2022). The gap between potential genetic yield and actual yield was regarded as genetic yield gap (Senapati & Semenov, 2020; Hu *et al.*, 2022). The standard deviation (SD) of YH, SNH, GNS, TGW, GD and PH of wheat variety was regarded as stability (Mohammadi & Amri, 2008). SD value was used to evaluate the phenotypic difference of the same wheat variety at different test sites. The SD values of the less stable varieties were greater. In order to analyze the effect of breeding on wheat stability, the average of SD was taken as the dependent variable and the year as the independent variable, and then univariate linear regression analysis was performed. The relationship between phenotypes and climate was analyzed using SPSS18.0 software (SPSS; <http://en.wikipedia.org/wiki/SPSS>). All graphs were drawn using Original software.

Results

The development of wheat in Sichuan province: The history of wheat breeding in Sichuan Province dates back from 1936 to 2020 (Zheng *et al.*, 2019). This study only presents data from 1952 to 2020 (Fig. 2). Both the area and yield increased first and then decreased, and the former reached a maximum of 1.87 10⁶ ha in 1998, while the latter reached a maximum of 6.87 10⁶ t in 1997. In 2020, the area and yield were 0.60 10⁶ ha hectares and 2.47 10⁶ t respectively (Fig. 2a). Fortunately, YH continues to grow from 0.82 t ha⁻¹ in 1950 to 4.13 t ha⁻¹ in 2020 (Fig. 2b). The total number of varieties released in Sichuan Province from 1984 to 2021 was 298, and the number shows an overall increasing trend year by year. Before 2002, the average number was not more than 5, but since 2002, the average number was more than 10, and the maximum number was 23 in 2020 (Fig. 2c). The yield per hectare (YH) was significantly and positively correlated with the number of varieties (Fig. 2d).

Phenotypic variation in regional test: The statistics of YH, SNH, GNS, TGW, GD and PH were shown in (Table 1). The data presented here showed that the coefficients of variation (CV) in turn were YH > GNS > TGW > SNH > PH > GD, and they are all less than 15%. The frequency distribution of YH, SNH, GNS, TGW, GD in each group was shown in (Fig. S1).

In the past four decades, yield of new wheat varieties in regional test rapidly increased with breeding progress (Fig. 3). The annual rates of increase for YH, SNH, GNS, TGW, GD and PH were 0.63% (36.60 kg ha⁻¹ yr⁻¹), 0.23% (0.79 10⁴ spikes ha⁻¹ yr⁻¹), 0.26% (0.11 yr⁻¹), 0.39% (0.19 g yr⁻¹), -0.19% (-0.34 d yr⁻¹), and -0.34% (-0.27 cm yr⁻¹) in regional experiments. Whereas the annual rates of increase in YH of actual yield for Sichuan province was 0.43% (17.90 kg ha⁻¹ yr⁻¹) from 1981 to 2020. The YH of regional test was significantly higher than that obtained by actual yield.

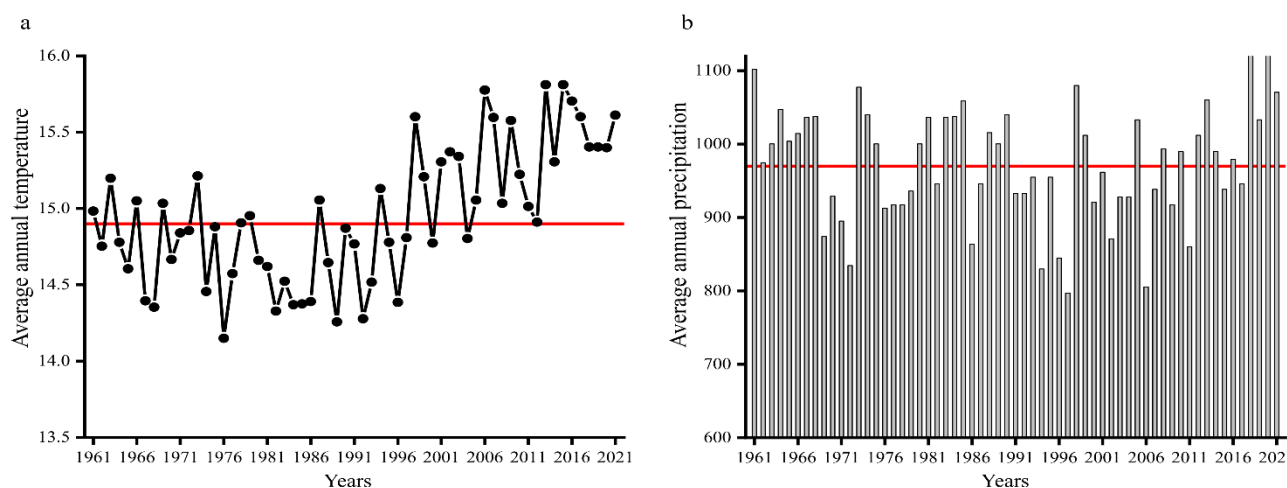


Fig. 1. The climate of Sichuan Province from 1961 to 2021. The red line is the average. a Annual average temperature variation in Sichuan. b Annual average precipitation variation in Sichuan.

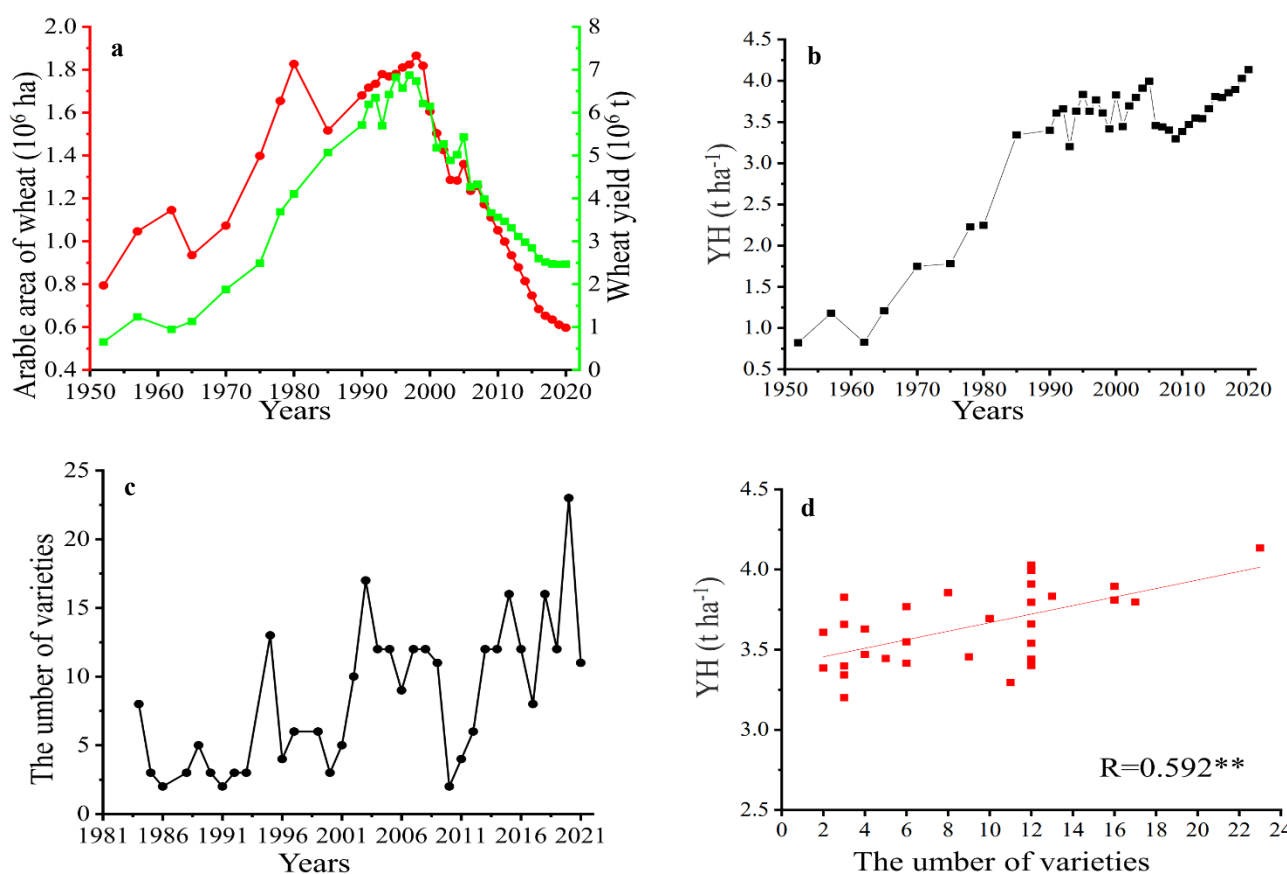


Fig. 2. The history of wheat development in Sichuan. a Development of acreage and yield from 1952 to 2020. b The yield per hectare (YH) of wheat in Sichuan from 1952 to 2020. c Number of varieties released from 1984 to 2021. d The correlation between yield per hectare (YH) and number of varieties 1984 to 2021.

Table 1. The statistics of regional test in Sichuan province.

Statistics	Number	Average	SD	Min	Max	CV (%)
YH (t ha ⁻¹)	1386	5.16	0.61	2.18	6.69	11.87
SD (10 ⁴ spikes ha ⁻¹)	1386	320.76	29.94	164.55	436.68	9.34
GNS	1386	42.29	4.71	15.24	58.00	11.13
TGW (g)	1386	44.41	4.36	29.01	59.22	9.82
GD (d)	1386	183.38	5.51	171.50	202.60	3.01
PH (cm)	1386	87.47	6.30	68.79	116.60	7.20

Note: YH for yield per hectare SNH for spikes number per hectare, GNS for grain number per spike, TGW for thousand grain weight, GD for growth duration, PH for plant height, SD for standard deviation, CV for coefficients of variation

Correlation analysis between yield and other traits:

Phenotypic correlations between the yield and yield components were evaluated using the average phenotypic values of each wheat varieties (Fig. 4). YH was positively correlated with SNH, GNS and TGW ($p < 0.01$); Significant and negative correlations were detected among YH and GD; There was no significant correlation between YH and PH.

Effects of temperature and precipitation on wheat:

The annual average temperature and its interannual variation trend and characteristics in Sichuan during 1961-2021 were shown in the figure 1a. The interannual variation trend increases gradually, with a range of about $0.15^{\circ}\text{C} / \text{decade}$, and the average temperature of 60 years was about 14.90°C . Since the 1980s, the average annual temperature has been gradually increased significantly, with an average annual increase of about $0.31^{\circ}\text{C} / \text{decade}$. The correlation between temperature and YH, SNH, GNS, TGW, GD, PH and the actual YH in Sichuan Province were shown in the figure 5. Temperature was positively correlated with YH, GNS and TGW ($p < 0.05$), and negatively correlated with GD and PH. There was no obvious correlation between temperature and actual yield. The annual average precipitation and its interannual variation trend and characteristics in Sichuan Province during 1961-2021 are shown in the figure 1b. The interannual variation trend

increased gradually, with a range of about 0.14 mm/decade , and the average annual precipitation of 60 years was about 970.00 mm . The correlation between average annual precipitation and yield and yield components was analyzed from 1981 to 2021 (Fig. 5b). Precipitation had an obvious positive correlation with GNS, a significant negative correlation with GD, and no significant correlation with the others was observed. These results indicated that the phenotype of wheat was somewhat affected by temperature and precipitation, but did not significantly change the actual yield.

Phenotypic stability: The average SD values of yield and yield components in 2021 were 1.08 t ha^{-1} for YH, $35.77 \cdot 10^4 \text{ spikes ha}^{-1}$ for SNH, 6.70 for GNS, 4.54 g for TGW, 9.04 d for GD, 5.22 cm for PH (Fig. 6). The average SD values of YH and GNS showed a slight degradation trend with the interannual slope of -0.0006 and -0.1039 , indicating that their stability was improved. On the contrary, the average SD values of GNS, TGW, GD and PH were continuously increasing with the interannual slope of 0.059 , 0.0212 , 0.0789 and 0.0012 , respectively. For the average SD values, the annual average temperature was positively correlated with GNS, TGW and GD respectively, and the annual average precipitation was dramatically and positively correlated with GNS (Fig. S2).

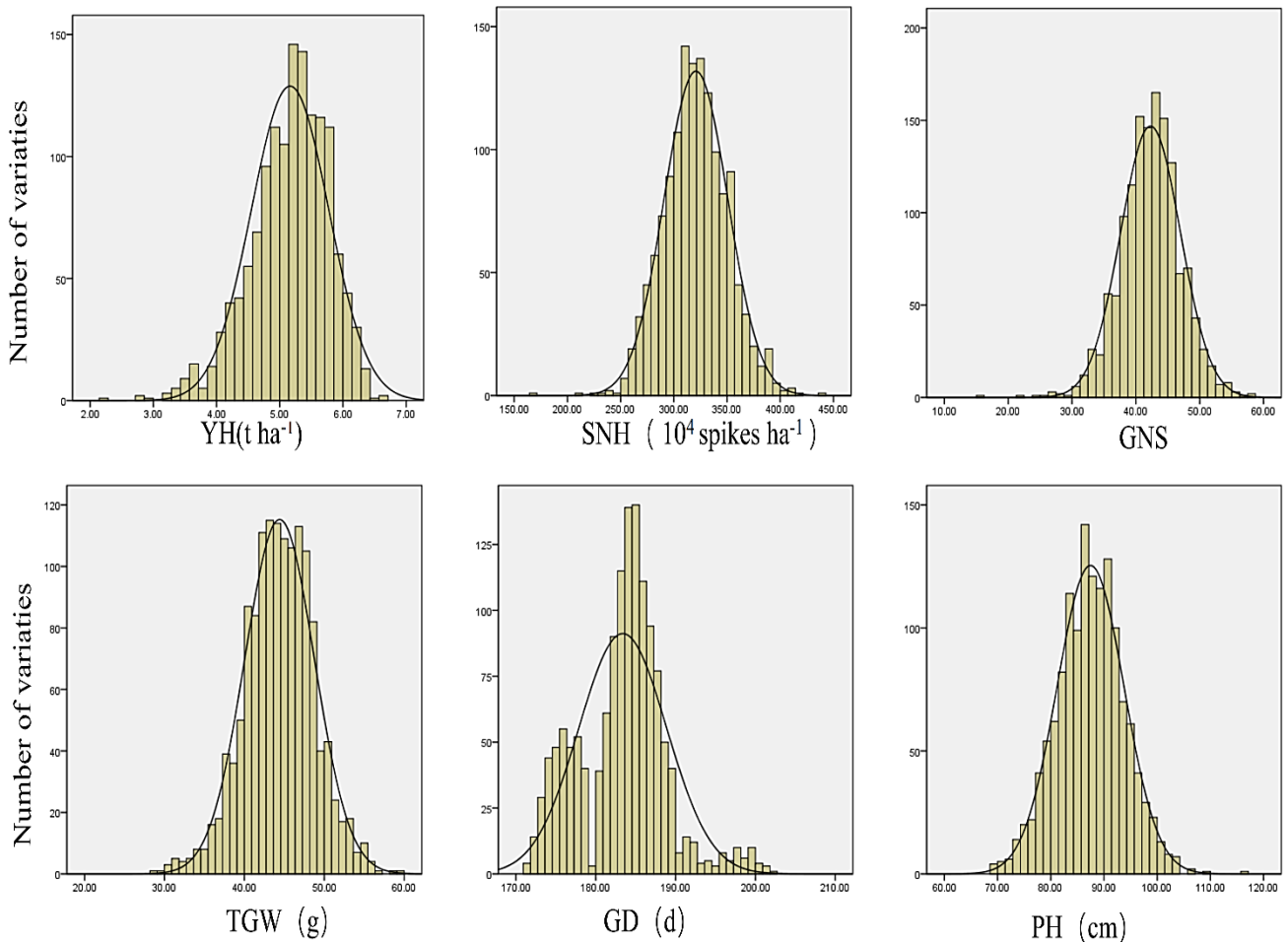


Fig. S1. Frequency distribution of yield per hectare (YH), spikes number per hectare (SNH), grain number per spike (GNS), thousand grain weight (TGW), growth duration (GD), plant height (PH).

Discussion

Optimize wheat varieties by breeding: Since 1981, the SNH, GNS and TGW of new wheat cultivars have been increasing continuously, while the GD and PH have been decreasing continuously. The yield of wheat mainly depends on three factors: SNH, GNS and TGW. The increase of SNH was the most obvious, and it was significantly and positively correlated with yield (Fig. 4). These results are similar to those of earlier studies (Wu & Zhu, 2008; Jiang *et al.*, 2019). The breakthrough of SNH, GNS and TGW was the key to wheat breeding in Sichuan. However, a significant negative correlation was detected between GD and YH (Fig. 4), which might be due to the improvement of grain filling rate in new wheat varieties (Wu *et al.*, 2014), and the shortening of growth period, which was more suitable for adjusting cultivation management to improve production efficiency (Nie *et al.*, 2019).

Wheat breeding increased diversity and productivity:

The use of new wheat varieties is one of the main factors for the increase of yield (Shi *et al.*, 2021). During 1950-1999, wheat yield and planting area of Sichuan exhibited a continuous increase, and decreased during 2000-2021, but the decline rate of wheat yield slowed down after 2015 (Fig. 2a). This was because the yield per unit area of wheat has been continuously increasing, indicating that breeding has a significant contribution to wheat production (Fig. 2b). By 2020, the wheat yield in the regional experiment was all over 5.5t ha⁻¹, but it just reached about 4 t ha⁻¹ in the actual production. The reason

for this phenomenon is that there was a big difference between the genetic yield potential and the actual yield (Hu *et al.*, 2022), which also indicated that there was still room for growth of the wheat yield in the production, which could be enhanced through improving the cultivation management. Actual production in high yield areas was at or close to 80% of China's potential production (Cassman *et al.*, 2003). When the actual yield reaches about 80% of the genetic yield potential, it becomes more difficult to increase the yield through cultivation management, and the increase of yield at this time is mainly from the increase in the genetic yield potential. (Cassman, 1999). Furthermore, the production conditions of the test site were in the upper medium level, but in the actual production there are higher or lower levels. Such as, the wheat variety "Chuanmai 104" had a maximum yield of 10,947 kg/ha, far exceeding the yield in regional trials. Since 2015, large-scale production has been increasing in Sichuan, and standardized production methods are also one of the important reasons for the increase in wheat yield.

Thus, improvements in genetic yield potential by wheat breeding will be a key component of ensuring food security and, in actual production, changing biological and abiotic conditions, such as rising temperatures and changes in the types of microbes that cause disease, will continue to reduce yields (Peng *et al.*, 2010; Espe *et al.*, 2018; Shew *et al.*, 2020; Laidig *et al.*, 2021). Therefore, it is an important measure to increase and maintain wheat yield by providing an abundant number of new wheat varieties and a suitable variety replacement rate.

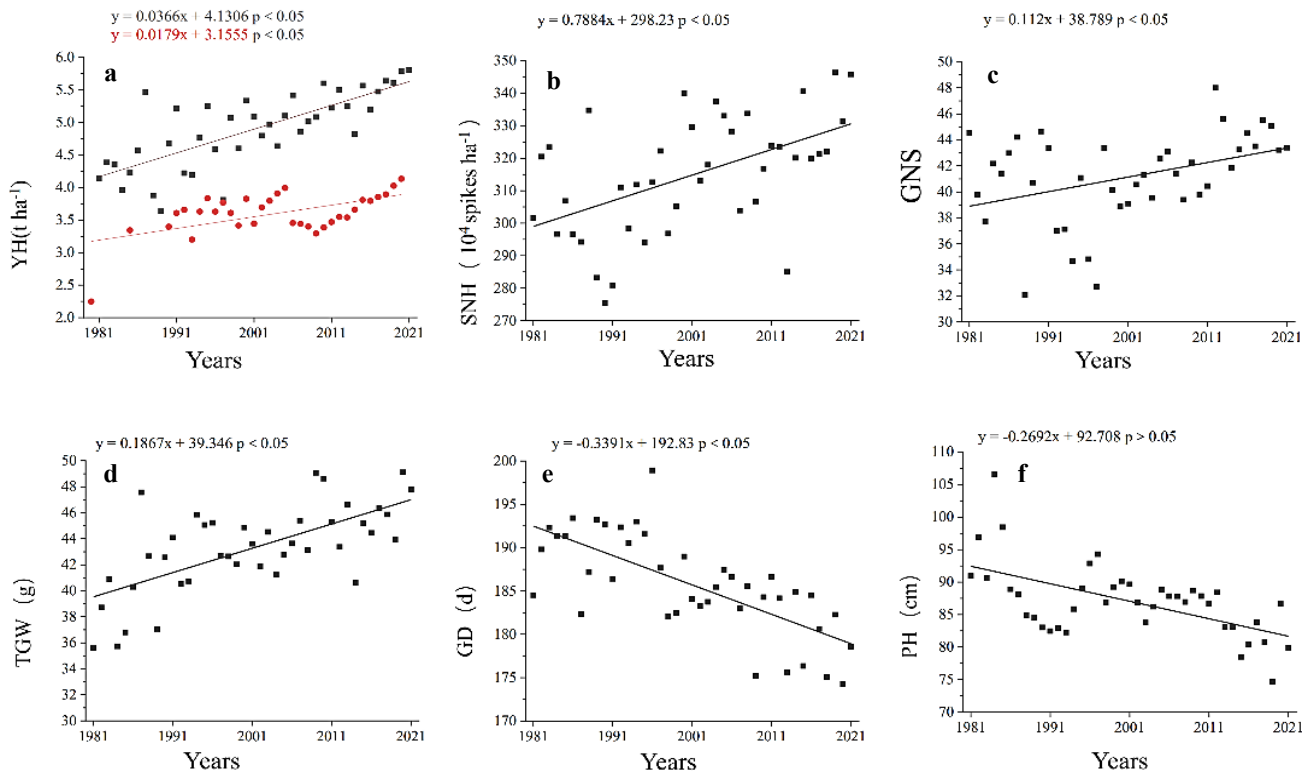


Fig. 3. The average value of yield and yield components of wheat lines in regional test from 1981–2021. **a** The yield per hectare (YH) of regional test and actual yield in Sichuan Province from 1981–2021. Black for regional test, red for actual yield in Sichuan Province. **b** The spikes number per hectare (SNH) of regional test from 1981–2021. **c** The grain number per spike (GNS) of regional test from 1981–2021. **d** The thousand grain weight (TGW) of regional test from 1981–2021. **e** The growth duration (GD) of regional test from 1981–2021. **f** The plant height (PH) of regional test from 1981–2021.

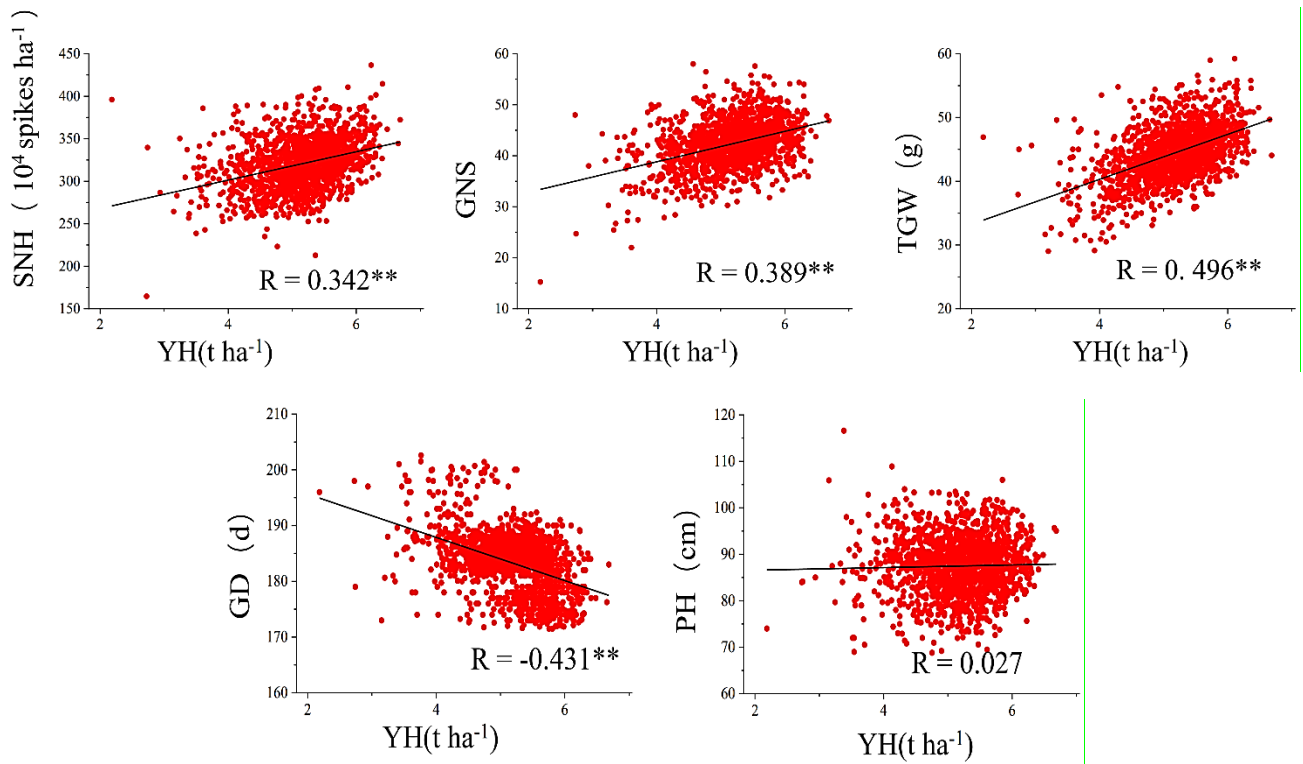


Fig. 4. The relationship between yield and yield components of wheat lines in regional test. YH for yield per hectare, SNH for spikes number per hectare, GNS for grain number per spike, TGW for thousand grain weight, GD for growth duration, PH for plant height. **Significant at $P = 0.01$. *Significant at $P = 0.05$.

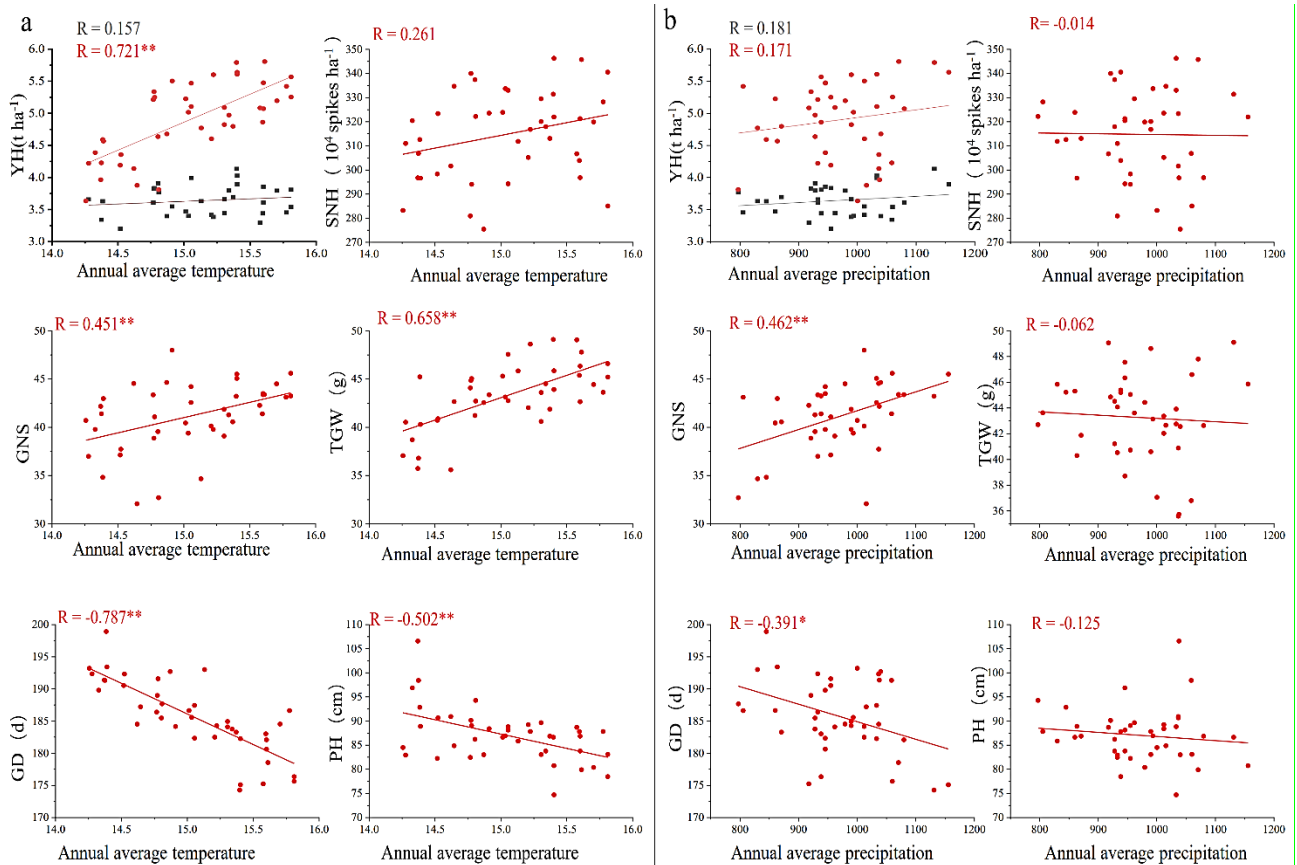


Fig. 5. The relationship between phenotype and climate in regional test. **a** The relationship between phenotype and annual average temperature. Black for regional test, red for actual yield in Sichuan Province. **b** The relationship between phenotype and annual average precipitation. YH for yield per hectare, SNH for spikes number per hectare, GNS for grain number per spike, TGW for thousand grain weight, GD for growth duration, PH for plant height.

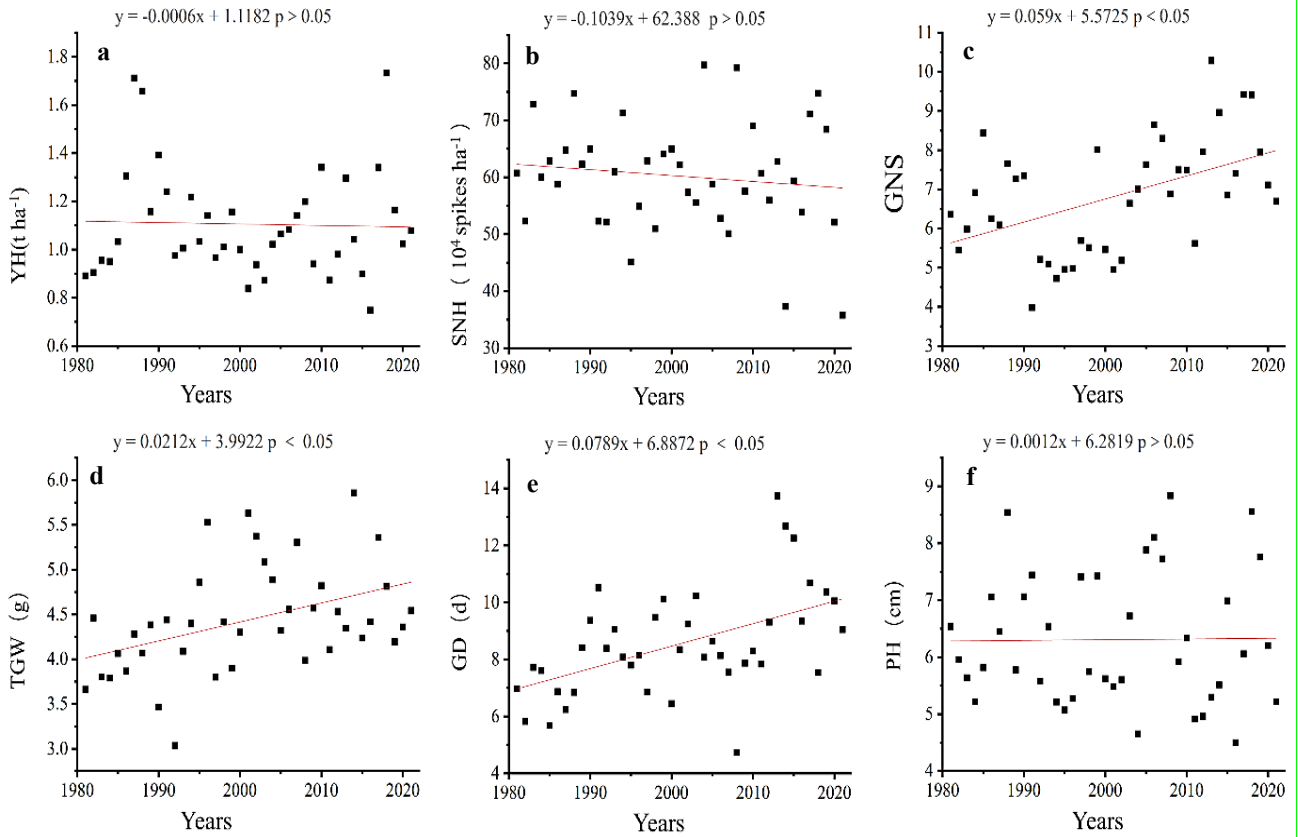


Fig. 6. The stability of yield per hectare (YH), spikes number per hectare (SNH), grain number per spike (GNS), thousand grain weight (TGW), growth duration (GD), plant height (PH) in regional test.

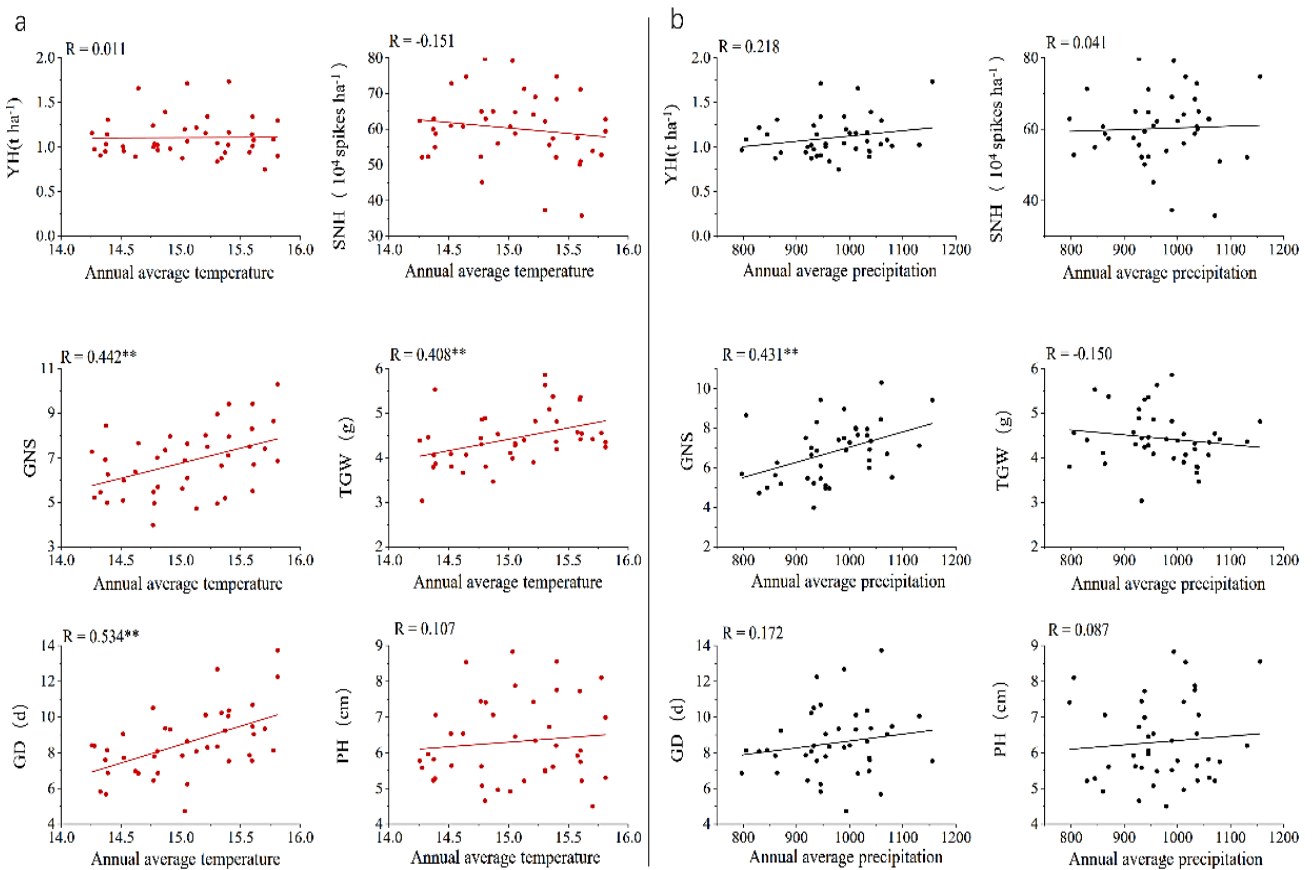


Fig. S2. The relationship between phenotype and climate in regional test. **a** The relationship between phenotype and annual average temperature. **b** The relationship between phenotype and annual average precipitation.

Improvements in genetic methods have facilitated wheat breeding: In the past 40 years, the major goal of wheat breeding in Sichuan is to increase wheat yield, which has made an important contribution to increasing yield. As previously reported, genetic improvement of wheat in the south winter wheat increased by 45 kg per year, equivalent to an increase of 0.78% per year, which was similar to our results (Hu *et al.*, 2022). Traditional breeding, such as cross, backcross and shuttle breeding, was still the foundation of wheat breeding (Baenziger & Depauw, 2009). However, traditional breeding has some drawbacks, such as low precision, high cost and slow genetic gain, which can be effectively overcome by biological breeding methods, such as marker-assisted selection, transgene and genome editing (Wallace *et al.*, 2018). With the improvement of breeding methods, the formation of new wheat varieties was more rapid. In the past five years, an average of about 12 new varieties have been released each year in Sichuan. It can be seen that the diversification of wheat varieties will contribute to the operation and stability of the food production system.

Wheat breeding changed the sensitivity of yield to climate: In the past 20 years, the temperature in Sichuan has been rising continuously (Fig. 1), which is a great challenge to the stability of wheat production. Previous studies (You *et al.*, 2009; Yin *et al.*, 2015; Liu *et al.*, 2016) had confirmed the negative impacts of rising temperatures and urgent investments in environmental adaptation strategies were needed to offset the adverse effects of changing temperatures on wheat production. In this study, the correlation between temperature and yield was not significant. The correlation between temperature and YH of actual yield was not significant, but it was significantly positive with YH of regional test (Fig. 5a). The effects of warming were offset by varieties replacement through genetic improvement and compensation by increasing atmospheric CO₂ under adequate irrigation and fertilization (Cossani & Reynolds, 2012; Zheng *et al.*, 2012; Asseng *et al.*, 2013). Moreover, breeding provides a buffer for adaptation to climate change by changing the growth period of wheat. The growth period adjustment is an effective management technique to cope with climate change adaptation, and reasonable stagger planting time can escape environmental pressure (Jagadish *et al.*, 2012; Zhao *et al.*, 2016; Hu *et al.*, 2017). In conclusion, wheat's tolerance to climate has been improved by breeding, which needs to be further improved with optimized cultivation techniques.

Conclusion

In Sichuan, wheat breeding has contributed significantly to the increase in yield. Compare to traditional varieties, modern varieties were a huge improvement in YH, SNH, GNS and TGW. The YH of wheat continued to rise despite the rising temperature, suggesting that wheat breeding could offset some of the effects of climate change. Wheat breeding in Sichuan has achieved remarkable results, but rising food demand and climate change are still potential risks, so it is necessary to continuously increase the investment in wheat breeding.

Acknowledgments

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