

BREEDING AND GENETICS

Changes in the Lint Yield and Associated Traits of Upland Cotton in China Since 1950

Pengfei Dang, Yajun Li, Xuan Pu, Hongyi Xing, and Xiaoliang Qin*

ABSTRACT

This study reviewed data from 1950 to 2014 on 1,257 upland cotton (*Gossypium hirsutum* L.) cultivars from three agroecological regions in China: Yellow River Valley, Yangtze River Valley, and Northwest Inland. The main aim was to establish future breeding and cultivation strategies. Lint yields significantly increased linearly in the three regions over time. Yield improvement in the new cultivars was due to: the decrease in planting density and increase in lint percentage and single boll mass in Yellow River Valley, the decrease in planting density and increase in lint percentage and bolls per plant in Yangtze River Valley, and the increase in planting density and lint percentage and decrease in bolls per plant in Northwest Inland. Planting density had significant effects on bolls per plant, single boll weight, lint percentage, growing period, and plant height in the three ecological regions. Our results suggest that different regions require different breeding strategies, and the evaluation of the genetic improvement process of cotton should not ignore the effects of planting density.

Cotton is an economically important crop worldwide and has been planted in China for at least 2,000 years. Upland cotton (*Gossypium hirsutum* L.) was introduced as late as 1892 (Feng, 1935) and accounts for 99% of today's cotton production in China (Kong et al., 2000). Progress in cultivation techniques and conventional and transgenic breeding, such as the use of transgenic *Bacillus thuringiensis* cotton (Huang et al., 2002), has promoted cotton cultivation in China. These improvements have led to increased production from 44.4 million tons in 1949 to 630 million tons in 2013 (Fig. 1). China has been the highest worldwide producer since 2012 (FAO website, <http://www.fao.org/faostat/en/#home>). Cotton yield improvements have increased the average yield from

0.16 t ha⁻¹ in 1949 to 1.45 t ha⁻¹ in 2013 (Fig. 1). Since 2007, the area under cotton cultivation has decreased (Fig. 1); however, rapid development of the textile industry in China has increased the demand for cotton to sustain industry growth (Ministry of Agriculture of the People's Republic of China, 2008).

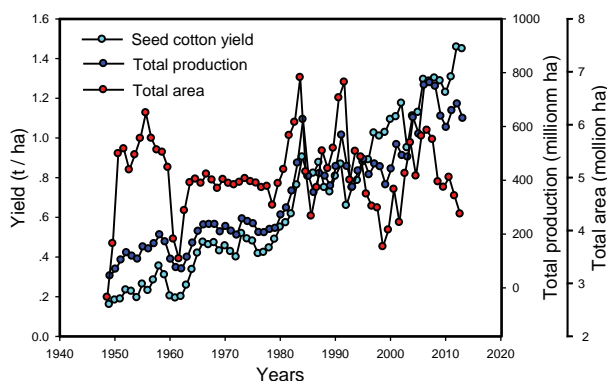


Figure 1. Average cotton lint yield, total area, and total production in China from 1949 to 2014. Data provided by the Ministry of Agriculture of China (average cotton yields per area in 2014 are not included; <http://zdscxx.moa.gov.cn:8080/nyb/pc/index.jsp>).

Previous research has highlighted prime agronomic characteristics such as lint percentage, single boll weight, bolls per unit area, and boll number per plant, associated with the future progress of cultivars (Bayles et al., 2005; Campbell et al., 2011; Fok, 1998; Schwartz and Smith, 2008; Zhang et al., 2005). Studies conducted to date on genetic improvement have showed that improvements in lint yield in new cultivars mainly have been due to the increase in lint percentage and boll number per plant (Kong et al., 2000; Li et al., 2001; Schwartz and Smith, 2008; Zhang et al., 2003). In the U.S., data obtained from annual yield trials revealed that lint yield and lint percentage in Acala cotton have increased steadily since the 1930s, whereas boll size and seed index has gradually decreased since the 1960s (Zhang et al., 2005). In China, the average genetic gain from 1950 to 1995 was 3.384 kg ha⁻¹ yr⁻¹ and mainly was due to the increase in lint percentage and boll number per plant (Li et al., 2001). In the Yellow River Valley, lint yield increased by 8.00 kg ha⁻¹ yr⁻¹ from 1950 to 1994 with 30% of the total yield gain attributed to breeding (Kong et al., 2000). In the Yangtze River Valley, the average rate of genetic gain was 6.50 kg ha⁻¹ yr⁻¹ (Zhang et al., 2003).

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In the 1940s, based on climate adaptability and cotton production area, China was divided into three cotton regions: Yellow River Valley, Yangtze River Valley, and Southwest China (Feng, 1948). In the 1950s, cotton production expanded into five regions: Yellow River Valley, Yangtze River Valley, South China, North China, and Northwest Inland (Huang and Cui 2002). At present, cotton is planted only in the regions of the Yellow River Valley, Yangtze River Valley, and Northwest Inland (Du and Liu, 2008), which accounted for 99.85% of cotton production in China from 2005 to 2007 (Ministry of Agriculture of the People's Republic of China, 2008; Fig. 2).

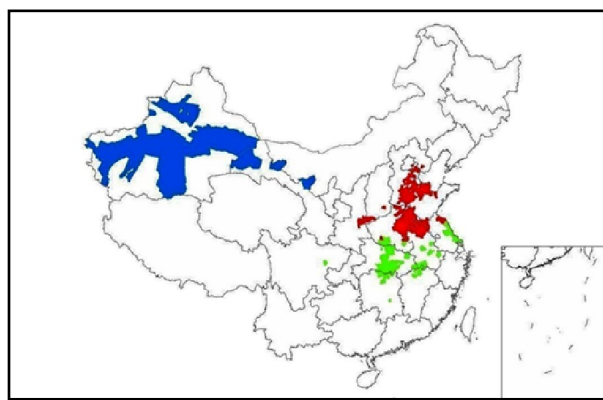


Figure 2. Three distinct agroecological production zones for cotton in China: Yellow River Valley (red), Yangtze River Valley (green), and Northwest Inland (blue) (Ministry of Agriculture of the People's Republic of China, 2008).

A common cropping system in Yellow River Valley is relay intercropping spring cotton with winter wheat. The annual frost-free period in this region ranges from 180 to 230 days, the accumulated temperature $\geq 10\text{ }^{\circ}\text{C}$ (when air temperature is higher than $10\text{ }^{\circ}\text{C}$) ranges from 4,000 to 4,600 $^{\circ}\text{C d}$, annual sunshine hours range from 2,200 to 2,900 hours, and annual rainfall ranges from 500 to 1,000 mm. Wheat–cotton and rape–cotton double cropping systems occur in more than 90% of Yangtze River Valley. The annual frost-free period in this region ranges from 240 to 300 days, the accumulated temperature $\geq 10\text{ }^{\circ}\text{C}$ ranges from 4,600 to 6,000 $^{\circ}\text{C d}$, annual sunshine ranges from 1,700 to 2,400 hours, and annual rainfall ranges from 800 to 1,600 mm. A single crop per year is usually grown in Northwest Inland, where most of the cotton is planted in April and is called “spring cotton”. The annual frost-free period in Northwest Inland ranges from 155 to 230 days, the accumulated temperature $\geq 10\text{ }^{\circ}\text{C}$ ranges from 3,100 to 5,500 $^{\circ}\text{C d}$, annual sunshine ranges from 2,700 to 3,300 hours, and annual rainfall is < 200 mm. Irrigation is available in this region (Ministry of Agriculture of the People's Republic of China, 2008).

Genetic improvement in cotton can be evaluated by testing historically important cultivars using the latest agronomic techniques. Such testing has been done for the cultivars released from various breeding programs and/or regions (CAAS, 1981; Evans and Fischer, 1999; Jiang et al., 2000; Kong et al., 2000; Liu, 2004; Schwartz and Smith; 2008, Tursunjan et al., 2012; Zhang et al., 2003). However, the increase of lint yield in China has not been due to breeding efforts only but also to changes in cultivation technologies, such as fertilization (Dong, 2007) and expert use of plant growth regulators (Mao, 2007; Mao et al., 2002). Changes in cultivation technologies can result in older cultivars responding differently under modern agronomic practices. It can offer an important reference value for breeding by analyzing the historical area test data to determine the succession process of a character (Jiang et al., 1999; Roth et al., 2014; Tang et al., 2011a,b; Wei et al., 2003), which can supplement the existing genetic improvement research.

In this study, we reviewed data from 1,257 upland cotton cultivars grown in three agroecological regions from 1950 to 2014 to determine the trends in lint yield, agronomic traits, and planting densities over the years; determine the effects of planting density on agronomic traits; and explore future breeding and cultivation strategies.

MATERIALS AND METHODS

Data from 1,257 upland cotton cultivars were collected from *Chinese Cotton Cultivars* (CAAS 1981), *Flora of Cotton Cultivars in China* (Du and Liu, 2008), and from regional variety test trials organized by the Department of Agriculture Seed Management Station, Ministry of Agriculture of the People's Republic of China. Important cultivars, such as those released by the province and the Department of Agriculture Seed Management Station (cultivars registered by the Ministry of Agriculture in China), were selected. Trials usually were conducted under middle fertility land for growing conditions and managed in accordance with local farming practices in each region.

For each variety, average values for the growing period, plant height, boll number per plant, single boll weight, lint percentage, lint yield, and planting density were taken from regional test data. All the agronomic characters in each production zone were divided into seven groups representing different decades: 1950s, 1960s, 1970s, 1980s, 1990s, 2000s, and 2010s. Percentage gain in yield between decades was calculated by dividing the difference between

the yield in the first and last decades by the yield in the first decade. Regression analysis using a standard linear model identified the rates of change in the traits. Bolls per plant had few data points in the Yellow River Valley and Northwest Inland before 1990, and in the Yangtze River Valley before 1980. To prevent being affected by outliers, we performed two regressions: including outlier data points (y_1) and excluding outliers (y_2), respectively. Data points in the regression graphs represent mean values from multiple locations and years for each variety using:

$$y_i = a + bx_i,$$

where y_i is mean value of traits, x_i is the year in which variety i was released, a is the intercept of both equations, and b is the absolute slope.

The phenotypic relationships among lint yield and agronomic characters were determined using a Pearson correlation analysis. We used Gen Stat (VSN International Ltd.) to fit multiple regression models and summarized the results in ANOVA to explain how agronomic traits affected the changes in lint yield with the year of release.

RESULTS

Lint Yield and Related Agronomic Traits. Lint yield in the three agroecological regions increased significantly linearly over time (Fig. 3a-c). Planting density in the Yellow and Yangtze River valleys decreased over time, whereas density in Northwest Inland increased linearly (Fig. 4a-c). Boll number per plant in the Yellow and Yangtze River valleys increased linearly but decreased in Northwest Inland from the 1950s to the 2010s ($p < 0.01$, Fig. 4e-g), boll number per plant also decreased but not significantly from 1990s to 2010s in Northwest Inland. In the Yellow and Yangtze River valleys, single boll weight increased linearly ($p < 0.001$), whereas no significant change was observed in Northwest Inland (Fig. 5a-c). Lint percentage increased linearly over time in all three regions ($p < 0.01$, Fig. 5e-g). In the Yellow and Yangtze River valleys, plant height also increased linearly but showed a linear decline in the Northwest Inland region ($p < 0.01$, Fig. 6a-c). The growing period in the Yellow River Valley and Northwest Inland declined linearly ($p < 0.01$), whereas it increased in Yangtze River Valley ($p < 0.05$, Fig. 6e-g).

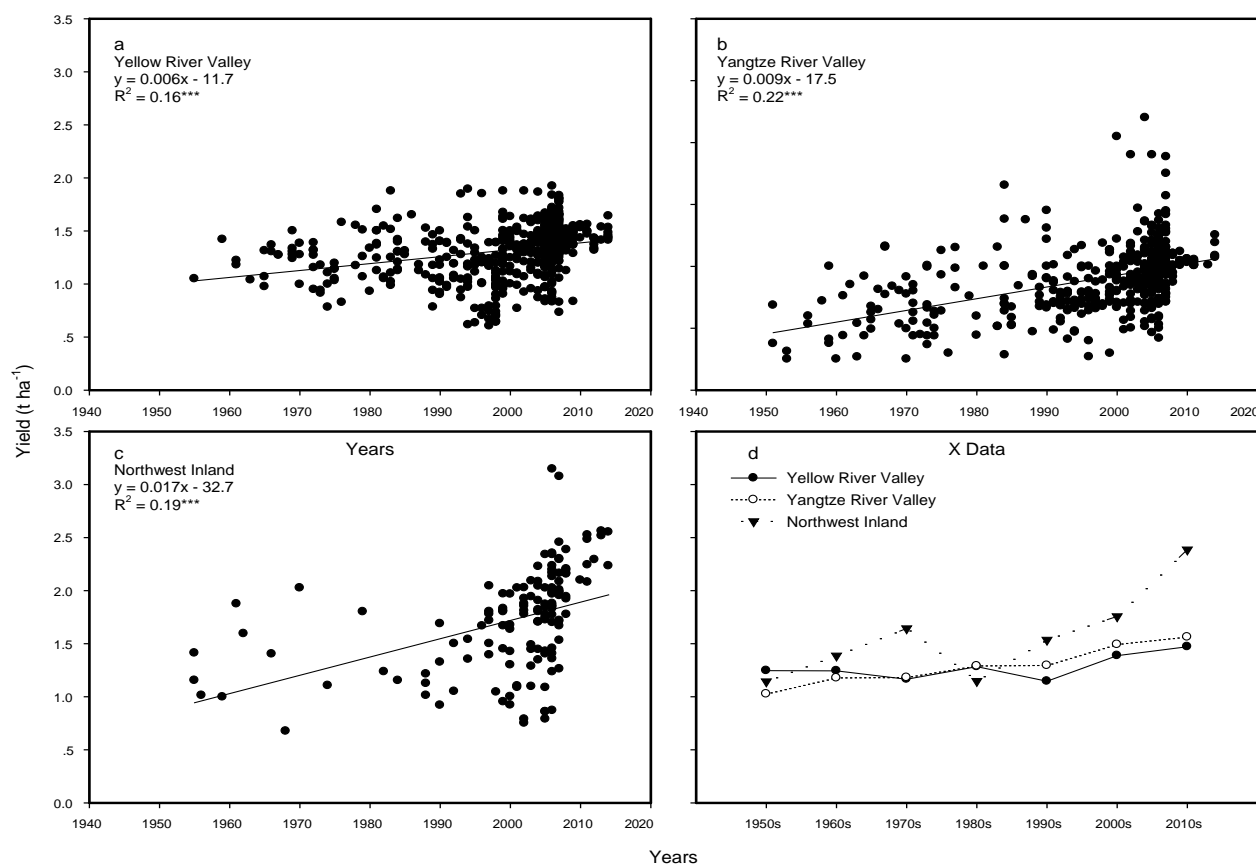


Figure 3. The change of yield (a–d) with year of release in the Yellow River Valley (a), Yangtze River Valley (b), and Northwest Inland (c), along with mean values for the different years (d). *** = significant correlation at 0.001 level.

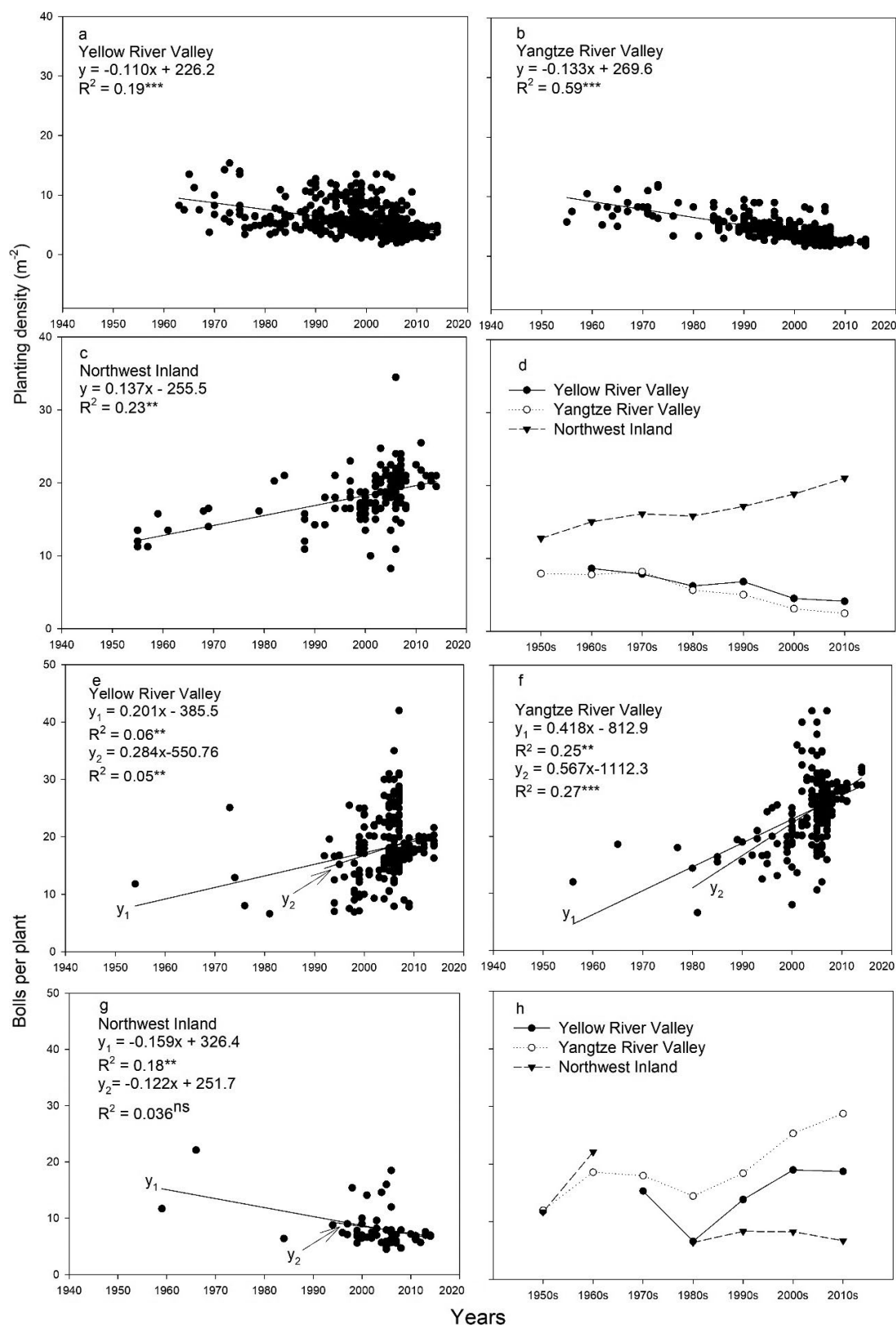


Figure 4. The change of planting density (a–d) and number of bolls per plant (e–h) with the year of release in Yellow River Valley (a, e), Yangtze River Valley (b, f), and Northwest Inland (e, g), along with mean values for different years (d, h). ** = significant correlation at 0.01 level. *** = correlation significant at the 0.001 level. ns = no significant correlation. y_1 are regressions including all points, y_2 are regressions excluding points before 1990 in the Yellow River Valley and Northwest Inland, and before 1980 in the Yangtze River Valley.

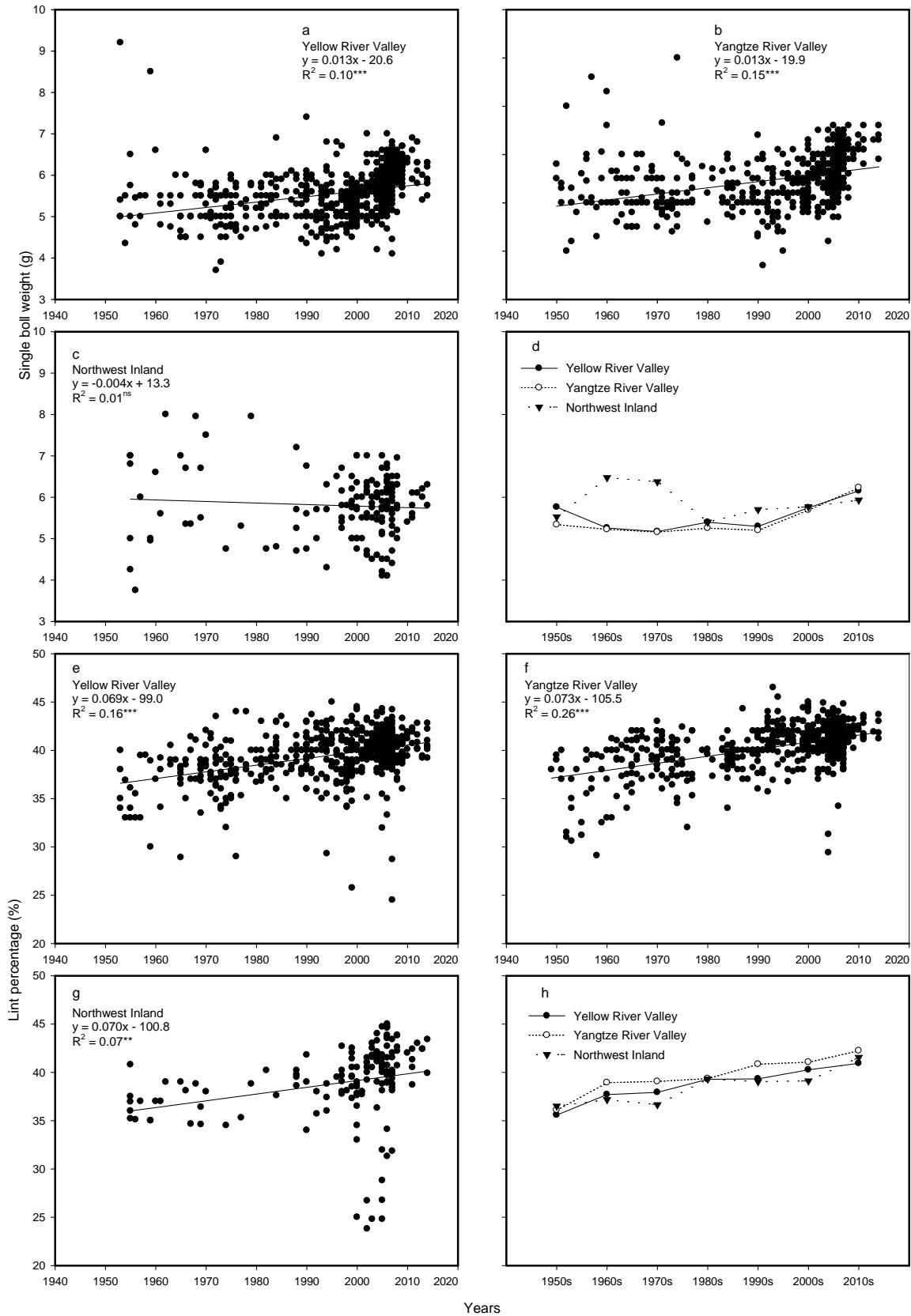


Figure 5. The change of single boll weight (a–d) and lint percentage (e–h) with year of release in Yellow River Valley (a, e), Yangtze River Valley (b, f) and Northwest Inland (e, g), along with the mean values for different years (d, h). ** = significant correlation at 0.01 level. *** = significant correlation at 0.001 level.

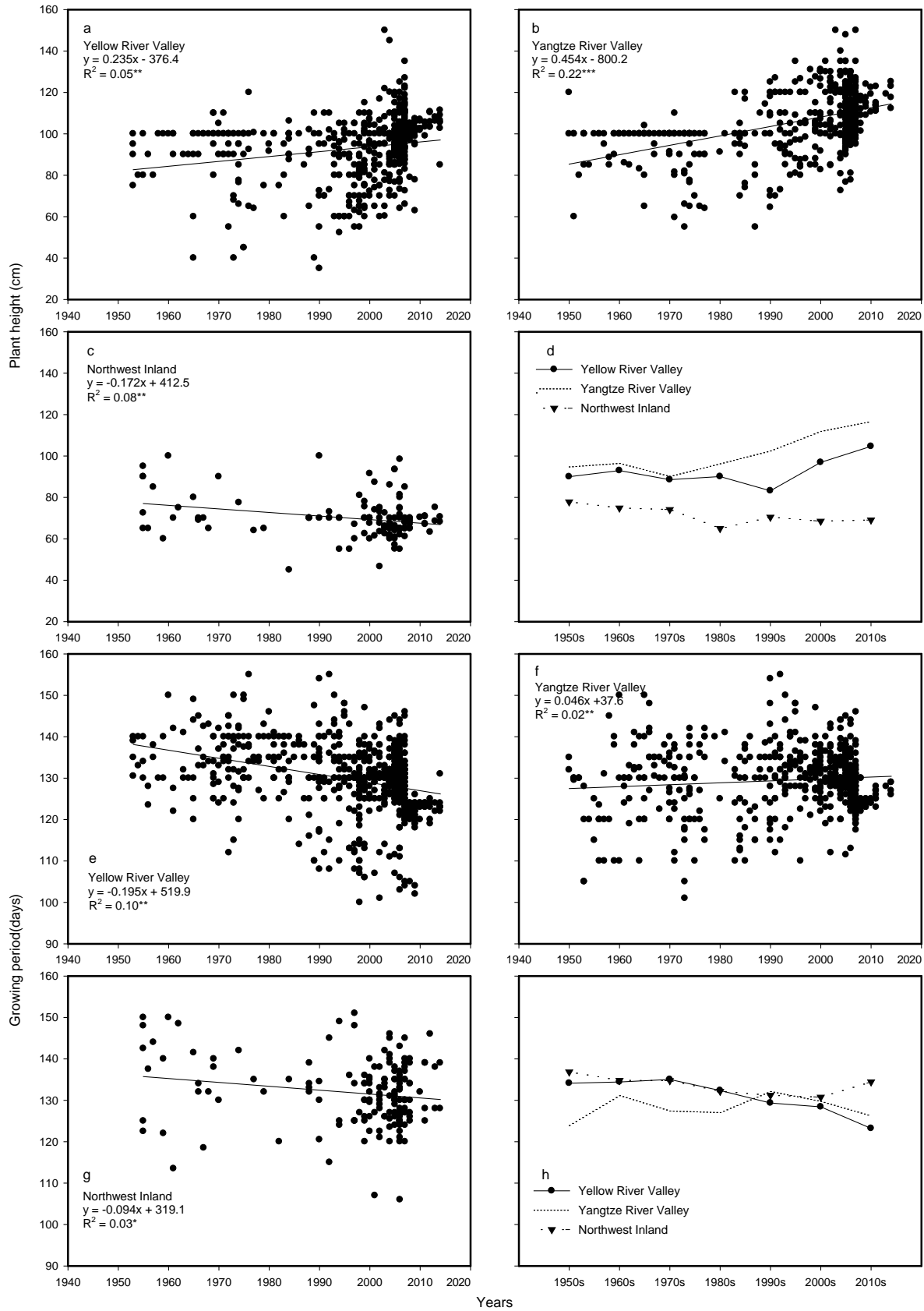


Figure 6. The change of plant height (a–d) and growing period (e–h) with the year of release in Yellow River Valley (a, e), Yangtze River Valley (b, f), and Northwest Inland (e, g), along with mean values for different years (d, h). * = significant correlation at 0.05 level. ** = significant correlation at 0.01 level. *** = significant correlation at 0.001 level.

Since the 1990s, Northwest Inland had the highest lint yield, whereas the yield was lowest in Yellow River Valley (Fig. 3d). From the 1950s to the 2010s, the planting density was highest in Northwest Inland (Fig. 4d). From the 1990s to 2010s, boll number per plant was highest in Yellow River Valley and lowest in Northwest Inland (Fig. 4h). Single boll weight in Yellow and Yangtze River valleys increased since 1990, but no significant changes were observed in Northwest Inland (Fig. 5d). From the 1990s to 2010s, lint percentage was highest in the Yangtze River Valley (Fig. 5h). From the 1950s to 2010s, the Yangtze River Valley had the tallest plants, whereas Northwest Inland had the shortest (Fig. 6d). In the 2010s, Northwest Inland had the longest growing period and Yellow River Valley had the shortest (Fig. 6h).

Correlation Between Lint Yield and Related Agronomic Traits. In the Yellow River Valley, lint yield had positive relationships ($p < 0.05$) with growth period, plant height, boll number per plant, single boll mass, and lint percentage, and was negatively ($p < 0.01$) related to the planting density (Table 1). In Yangtze River Valley, lint yield had positive relationships ($p < 0.01$) with plant height, boll number per plant, single boll weight, and lint percentage, and was negatively ($p < 0.05$) related to the planting density and growth period (Table 1). In Northwest Inland, lint yield had positive relationships ($p < 0.01$) with planting density and single boll weight lint percentage and was negatively ($p < 0.01$) correlated to the boll number per plant (Table 1). The largest component

accounting for the largest proportion of the variation in lint yield was plant density in the Yellow and Yangtze River valleys and single boll weight in Northwest Inland (Table 2).

Correlation Between Planting Density and Related Agronomic Traits. Planting density had negative effects ($p < 0.01$) on bolls per plant, lint percentage, and plant height in the three agroecological regions. Planting density negatively ($p < 0.01$) correlated with single boll weight in Yellow and Yangtze River valleys but had no such correlation in Northwest Inland (Table 3).

DISCUSSION

Yield Progress in Different Agroecological Regions. The average annual lint yield in China increased from 3.38 to 8.16 kg ha⁻¹ from 1950 to the 1990s (Kong et al., 2000; Li et al., 2001; Liu, 2004; Tursunjan et al., 2012; Zhang et al., 2003). Similar trends were observed in this study (Fig. 3a-c) with lint yields increasing significantly in the three agroecological regions from 1950 to 2014, with the highest rate of increase observed in Northwest Inland. The increase in average annual lint yield in the Yellow River Valley, the Yangtze River Valley, and Northwest Inland were 3.76, 8.94, and 20.71 kg ha⁻¹ yr⁻¹, respectively (Fig. 3). The rates of increase in the Yangtze River Valley and Northwest Inland were higher than those reported elsewhere (Kong et al., 2000; Liu, 2004; Tursunjan et al., 2012; Zhang et al., 2003).

Table 1. Pearson correlation coefficients between lint yield and agronomic traits in three regions

	Planting density	Bolls per plant	Single boll weight	Lint percentage	Growing period	Plant height
Yellow River Valley						
Correlation	-0.54**	0.50**	0.38**	0.47**	0.10*	0.54**
N	440	231	506	503	511	419
Yangtze River Valley						
Correlation	-0.44**	0.41**	0.28**	0.43**	-0.10*	0.42**
N	358	187	431	430	435	350
Northwest Inland						
Correlation	0.36**	-0.36**	0.35**	0.66**	0.15	-0.13
N	117	57	136	129	140	114

*Significant at the 0.05 level of probability.

**Significant at the 0.01 level of probability.

Table 2. ANOVA table showing the effects of planting density, bolls per plant, single boll weight, lint percentage, growing period, and plant height on lint yield

	SS	F	P
Yellow River Valley			
Planting density	3273451	157.24	< 0.001
Bolls per plant	8539	0.41	0.523
Single boll weight	332175	15.96	< 0.001
Lint percentage	654016	31.41	< 0.001
Growing period	26942	1.29	0.257
Plant height	151248	7.27	0.008
Residuals	4267818		
Yangtze River Valley			
Planting density	803564	36.10	< 0.001
Bolls per plant	345817	15.53	< 0.001
Single boll weight	22617	1.02	< 0.001
Lint percentage	458925	20.62	< 0.001
Growing period	209934	9.43	0.003
Plant height	232517	10.45	0.001
Residuals	3606284		
Northwest Inland			
Planting density	1328241	15.06	< 0.001
Bolls per plant	579661	6.57	0.016
Single boll weight	4014633	45.52	< 0.001
Lint percentage	347410	3.93	0.056
Growing period	629593	7.14	0.012
Plant height	2144180	24.31	< 0.001
Residuals	2645714		

Table 3. Pearson correlation coefficients between planting density and agronomic traits in the three regions

	Bolls per plant	Single boll weight	Lint percentage	Growing period	Plant height
Yellow River Valley					
Correlation	-0.662**	-0.340**	-0.345**	-0.198**	-0.790**
Yangtze River Valley					
Correlation	-0.598**	-0.405**	-0.294**	-0.045	-0.587**
Northwest Inland					
Correlation	-0.537**	0.045	-0.273**	-0.069	-0.374**

**Significant at the 0.01 level of probability.

Changes in Associated Agronomic Traits with Lint Yield. An increase in boll number per plant is an important component for increasing lint yield (Li et al., 2001; Rauf et al., 2004). The number of bolls per plant was positively correlated with the yield in all the three agroecological regions (Table 1). In the Yellow and Yangtze River valleys, boll number per plant significantly increased linearly from 1950 to 2014 (Fig. 4e, f), accounting for 6% of the change in lint yield in the Yangtze River Valley and 5% in the Yellow River Valley (Table 2); similar trends were

observed in previous studies (Kong et al., 2000, Liu, 2004, Zhang et al., 2003). However, in Northwest Inland, the average number of bolls per plant decreased (Fig. 4g), which was contrary to that reported earlier (Liu, 2004; Tursunjan et al., 2012). The boll number per plant increased by up to 27% from 1953 to 2000 in the more recent cultivars compared to the earlier cultivars in Xinjiang (Tursunjan et al., 2012). The reason for this could be the increasing trend noted in planting density on Northwest Inland, which had a negative effect on boll number per plant (Table 3).

Some studies have shown that genetic gain in cotton cultivars is attributed to larger bolls (Bayles et al., 2005). Our results showed that single boll weight in the Yellow and Yangtze River valleys increased significantly linearly (Fig. 5a, b), accounting for a 4% change in the lint yield (Table 2). This trend differed from previous reports where boll weight did not significantly change from 1950 to 1994 in the Yellow River Valley (Kong et al., 2000; Wei et al., 2003) or from 1950 to 1995 in the Yangtze River Valley (Zhang et al., 2003), whereas the boll size in Acala 1517 cultivars has decreased gradually since the 1960s in the U.S. (Zhang et al., 2005). The reason for this could be the decreasing trend noted in planting density in the Yellow and Yangtze River valleys, which had a negative effect on single boll weight (Table 3). Furthermore, single boll weight did not significantly change in the Northwest Inland (Fig. 5c); this result also differed from a previous report where single boll weight in southern Xinjiang increased from 1953 to 1994 (Tursunjan et al., 2012).

Lint percentage has steadily increased in the U.S. since the 1930s (Campbell et al., 2011; Zhang et al., 2005) and China from the 1950s (Li et al., 2001; Liu, 2004; Tursunjan et al., 2012). In this study, lint percentage was positively correlated with yield in the three regions (Table 1), accounting for an 8% change in lint yield in the Yellow and Yangtze River valleys and 5% change in Northwest Inland (Table 2). Lint percentage increased significantly in the three agroecological regions (Fig. 5e-g), which was consistent with previous reports (Li et al., 2001; Liu, 2004; Tursunjan et al., 2012).

Changes in plant height varied among the three agroecological regions. In the Yellow River Valley, plant height increased linearly (Fig. 6a), unlike the reported downward trend based on historical data from 1956 to 1996 (data from 1966 to 1972 was missing) (Jiang et al., 2000). In the Yangtze River Valley, plant height increased, whereas it decreased in Northwest Inland (Fig. 6b, c), as observed in previous studies. Plant height also increased in cotton cultivars from 1950 to 1990 in the Hubei province (a province in Yangtze River Valley) (Zhang et al., 2003) and decreased from 1953 to 1994 in southern Xinjiang (Tursunjan et al., 2012). Different trends of plant height between the regions could be due to differences in dimethyl piperidinium chloride practices since the 1980s or 1990s when these chemicals were introduced (Mao et al., 2013). The plant height of different planting areas also is affected by planting density (Table

3), the Yangtze River Basin has the highest plant height but the lowest plant density, plant height in the Northwest inland is the lowest but the plant density is highest of the three agroecological regions, these results suggest that lower plant height is beneficial to alleviate the lodging risk under high density.

From the 1950s to 1990s, the growing period of short-season cotton declined by nearly 10 d with increases in yield (Yu and Fan, 2003). In the Yellow River Valley, the growing period significantly declined linearly (Fig. 6e), which was consistent with the results of other studies; Jiang et al. (2000) reported the growing period was 3 to 5 d shorter in this region since the 1950s. In the Northwest Inland, the growing period declined significantly (Fig. 6g), which contradicted an increase over the years reported by Tursunjan et al. (2012) and Wang et al. (2008). The observed decrease likely was due to cultivation changes involving film mulching in northwest since the 1980s; this technology is widely used by farmers and breeders now and can shorten the growth period (Mao, 2007). In contrast to the other two regions, the growing period increased significantly linearly in the Yangtze River Valley (Fig. 6f). This was because of the cultivation changes involving seedling transplantation in Yangtze River Valley since the 1980s; this technology, widely used by farmers and breeders now, can lengthen the growth period (CAAS, 1981; Mao, 2007).

Changes in Planting Density. Many studies have focused on identifying the optimum planting density to increase the commercial yield (Feng et al., 2014; Wang et al., 2011; Zhang et al., 2004) without considering any changes that have occurred in planting density over time. We observed different trends with planting densities in the three agroecological regions from the 1950s to 2010s. The planting density in the Yellow and Yangtze River valleys decreased significantly (Fig. 4a, b) and was negatively correlated with lint yield (Table 1), which accounted for a 38% and 14% change in lint yield, respectively, in the two regions (Table 2). This was consistent with the planting density determined from the historical data in Henan Province that density decreased from 1978 to 2007 (Tang et al., 2011a). During urbanization in the Yellow and Yangtze River valleys, young migrant farmers gradually left the countryside to work in the cities, reducing the surplus rural labor force; on the other hand, high labor input, as a result of precise management and the use of transplanting or hybrids (expensive seeds) reduced the planting density to counter the deficit in labor force (Tang et al., 2011b).

In contrast, planting density in Northwest Inland increased (Fig. 4c) and was positively correlated with lint yield (Table 1). The planting density increased to a high level because of the expert use of plant growth regulators, such as mepiquat chloride (Mao, 2007; Mao et al., 2002) as well as an increase in highly mechanized harvesting in Xinjiang (a province in Northwest Inland) in recent years (Zhang et al., 2012), which accounted for an 11% change in lint yield (Table 2). Because sowing and harvesting of cotton in the Yellow and Yangtze River valleys is done by hand at small production scales, cotton production suffered due to a labor shortage that seriously hindered cotton sowing in these areas; therefore, improved planting densities are needed along with improved mechanization for increasing the production.

Breeding Strategies. Lint yield of upland cotton was determined by its component traits, namely boll number per area, boll weight, and lint percentage (Wu et al., 2004). The improvements in lint yield in new cultivars are considered mainly to be due to the increase in lint percentage and boll number per plant (Kong et al., 2000; Li et al., 2001; Schwartz and Smith, 2008; Zhang et al., 2003). In this study, the three agroecological regions in China presented different breeding paths with yield improvements in new cultivars due to reduced planting densities and increased lint percentage and single boll weights in Yellow River Valley; reduced planting densities and increased lint percentage and bolls per plant in Yangtze River Valley; and increased planting densities, insignificant changes in single boll weight, and fewer bolls per plant in Northwest Inland (Table 2). Thus, our results highlight the importance of the differences in ecological regions that should be considered for future breeding strategies. Planting density and bolls per plant were highly correlated in three agroecological regions (Table 3); bolls per unit area (plant density \times bolls per plant) is a more meaningful yield component and should be give more attention in future (Campbell et al., 2011).

Furthermore, it should be noted that the 35% increase in cotton yield in China is attributed to the change in cultivation technology (Mao, 2007). Since 1950, many breakthrough cotton cultivation techniques, such as chemical control techniques, film mulching, and seedling transplantation (Mao, 2007), have been developed and applied and have positively impacted cotton yield component traits. The changes in cotton yield cannot be attributed only to cotton breeding but is also affected by cultivation

techniques (Liu et al., 2013; Mao, 2007; Mao et al., 2002). In this study, the planting densities changed in the three agroecological regions since 1950, significantly affecting the plant height, boll number per plant, and single boll weight (Table. 3). If changes in planting technology are ignored, available information regarding genetic improvement using the latest agronomic techniques could mislead breeders.

CONCLUSION

Lint yield significantly increased linearly in the three agroecological regions of China as a response to changes in different yield components. Yield improvements in the new cultivars were associated with: decrease in planting density and increase in lint percentage and single boll mass in the Yellow River Valley; decrease in planting density and increase in lint percentage and bolls per plant in the Yangtze River Valley; and the increase in planting density and lint percentage and the decrease in bolls per plant in Northwest Inland. The change in planting density over time differed among the three ecological regions, and planting density had significant effects on the agronomic traits. Thus, our results highlight the importance of differences in ecological regions and the effects of plant density on the genetic improvement that should be considered for future breeding strategies.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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