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REGULAR ARTICLE

Grain yield and associated photosynthesis characteristics during dryland winter wheat cultivar replacement since 1940 on the Loess Plateau as affected by seeding rate

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ABSTRACT

An experiment was conducted to verify how the grain yield and associated photosynthesis characteristics of wheat respond to seeding rate with cultivar replacement. Seven wheat cultivars released from 1940 to 2004 that were once widely grown on the Loess Plateau were grown in field experiments during the 2011-2012 growing season at the Changwu experiment station in China using three seeding rates (100, 250, and 350 seeds m^{-2}), using a randomized complete block with a split-plot design and three blocks. The grain yield increased linearly with cultivar development in all seeding rate treatments, with annual genetic gains ranging from 0.65% to 1.29%. The cultivars released after the 1980s were less sensitive to seeding rate and had better population regulation. The improvements in the harvest index and thousand grain weights of the modern cultivars were significantly and positively correlated with the grain yield. The photosynthetic rate of the flag leaf and the leaf area index at anthesis consistently increased with cultivar replacement, contributing more to the thousand-grain weight and resulting in grain yield increases. Diffuse non-interceptance at anthesis resulted in opposite, stable trends with time. One reason to adapt modern cultivars for modern cultivation is their lower sensitivity to seeding rate. Thus, larger sinks for the grains and the optimization of plant types for light interception should be given greater consideration in dryland wheat breeding on the Loess Plateau.

Keywords: Dryland wheat; Genetic gain; Seeding density; Light interception ability

INTRODUCTION

Wheat (*Triticum aestivum* L.) grain yields have doubled in the last century (Richards, 2000), with the development of genetic resources accounting for more than 40% of this increase (Brancourt-Hulmel et al., 2003). Genetic progress regarding the grain yield, agronomic traits and photosynthetic traits of wheat has been studied in many countries (e.g., in the UK (Austin et al., 1980), Mexico (Fischer and Edmeades, 2010), Canada (McCaig and DePauw, 1995), Argentina (Maydup et al., 2012), Australia (Potgieter et al., 2016), and China (Tian et al., 2011; Zheng et al., 2011). These studies suggest that cultivar replacement has increased the leaf area index and the net photosynthetic rate (per-unit leaf area) (Fischer and Edmeades, 2010; Tian et al., 2011), which are correlated with greater grain weights and harvest index (HI) values and result in genetic yield improvements (Austin et al., 1980; Perry and D'Antuono, 1989). Different results from the USA (Gent and Kiyomoto, 1985) have indicated that the photosynthetic capacity has remained stable despite cultivar replacement. Verifying the evolution of agronomic traits and the physiological basis of grain yields will assist breeders and agronomists in developing new wheat cultivars with stable and high yields.

The population size significantly influenced the yield performance of winter wheat due to changes in individual

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growth (Gooding et al., 2002) and lodging (Easson et al., 1993). No marked differences are reported among varieties regarding the responses of grain yields to variations in plant density (Arduini et al., 2006; Brian et al., 2011). However, Black and Aase (1982) reported that USSR winter wheat cultivars were more capable of maintaining a high number of kernels per spike at a high plant density than USA cultivars. According to Marshall and Ohm (1987) and Anderson and Barclay (1991), optimal plant populations change according to their variety and local conditions. In Italy, narrow row spacings of between 12 and 18 cm and seeding densities of approximately 400 seeds m^{-2} are traditionally used for wheat (Arduini et al., 2006). In contrast, densities of approximately 250 seeds m^{-2} or less are considered optimal in the USA and China (Carr et al., 2003; Fang et al., 2010). The response of grain yields to seeding rate with cultivar replacement requires further research.

At least six wheat cultivar replacements have been grown on the Loess Plateau since 1940s (Chen et al., 2003). Although increases in production slowed in the early 2000s (Zhang et al., 2009), significant genetic gains have been observed (Chen et al., 2003). According to a previous study in this region, greater wheat yields were strongly and positively correlated with increasing grain weights, which resulted from an increased filling rate (Zhang et al., 2008). The photosynthetic capacity per unit of leaf area after elongation is also an important source of this progress (Chen et al., 2012). Although different cultivars might vary differently when different seeding rates are used, it has not been considered.

Thus, seven cultivars released since 1940 were studied using different seeding rates (1) to explore the evolution of wheat grain yields and agronomic traits with their responses to seeding rate and (2) to identify the correlations between photosynthetic characteristics and yield progress under different seeding rates.

MATERIALS AND METHODS

Plant materials, growth conditions and meteorological conditions

Seven wheat cultivars released from 1940 to 2004 and once planted on the Loess Plateau (Table 1) were used. Field experiments were conducted on the Loess Plateau in Changwu (107°40' to 107°42 E, 35°12' to 35°16'N, 1200 m asl), Shaanxi Province, China, during the growing season from 2011 to 2012. The site was located in a semi-humid area of the Loess Plateau, where rain-fed cropping with one harvest per year is standard practice. The soil is a dark loessial soil locally classified as a Heilu soil. The average annual precipitation (rain and snow) in the area is 584 mm, and mainly occurs from July to September. The precipitation during the experimental year (Fig. 1) was recorded at an automated meteorological station on the site. In the experimental year, the total precipitation was 388.4 mm during the fallow period (July-September) and 278.4 mm during the growing season (September-June of the next year).

Experimental design

The experiment was conducted using a randomized complete block with a split-plot design and three blocks, and the plot size was 12 m^2 (14 rows, 4 m long and 20 cm row spacing). The main plots consisted of the different seeding rates [low: 100 seeds m^{-2}, medium: 250 seeds m^{-2} (the value adopt by the local farmers), and high: 350 seeds m^{-2}]. The subplots consisted of the seven cultivars used (Table 1). Fertilizer was applied [urea (N) 150 kg ha^{-1} and calcium superphosphate (P_2O_5) 120 kg ha^{-1}] before planting, and no additional fertilizer was applied before harvest. Fungicides and pesticides were applied in each treatment at the shooting and grain filling stages to prevent attack by diseases and pests.

Plant sampling and observations

At maturity, four central rows (1 m long) were harvested, air-dried and weighed to determine the total aboveground biomass, grain yield and grain number per m^2. Subsamples were used to record the height, grain number per spike and thousand-grain weight (TGW).

The photosynthetic traits were recorded 3 days after flowering. The photosynthetic rate (Pn) of the flag leaf was measured between 9:30 and 11:30 AM using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) in every plot. These measurements were performed approximately halfway along the length of the flag leaf, which was exposed to full sunlight. The Pn values were calculated as the sum of the mean readings for five leaves per plot. The canopy characteristics were recorded using an LAI-2200 Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE, USA) without direct sunlight. One above-canopy measurement and three below-canopy measurements at the soil surface were taken in each plot. The leaf area index (LAI), mean tilt angle (MTA) and diffuse non-interceptance (DIFN) were measured.

Statistical analyses

Analysis of variance tests were conducted using SAS V8.0 (SAS Institute, Inc., University of Texas, Arlington) and the mono factor analysis of variance method. Linear correlations between the phenotypic traits and the yield

Table 1: Representative cultivars of dryland winter wheat on the Loess Plateau from 1940 to 2004

Cultivars	Planting decade on the Loess Plateau	Year of release	Pedigree	Breeding sites	Dwarf genes
Mazha	1940s	1940	Landrace	Shaanxi Province	none
Bima1	1950s	1951	Mazha/Biyu	Shaanxi Province	none
Fengchan3	1960s	1964	Danmai 1/Xinong 6028×Bima1	Shaanxi Province	none
Hanxuan 10	1970s	1966	Nongda 16/Huabei 187	Shanxi Province	none
Xiaoyan6	1980s	1981	(ST2422×464)/Xiaoyan96	Shaanxi Province	*Rht-B1b+Rht8*
Changwu134	1990s	1997	(Changwu131×Xiaohei96) F1/Changwu131) F4/(Jinghua3/NS2761) F1	Shaanxi Province	*Rht-B1b*
Changhan58	2000s	2004	Changwu112/PH 82-2	Shaanxi Province	*Rht-B1b*

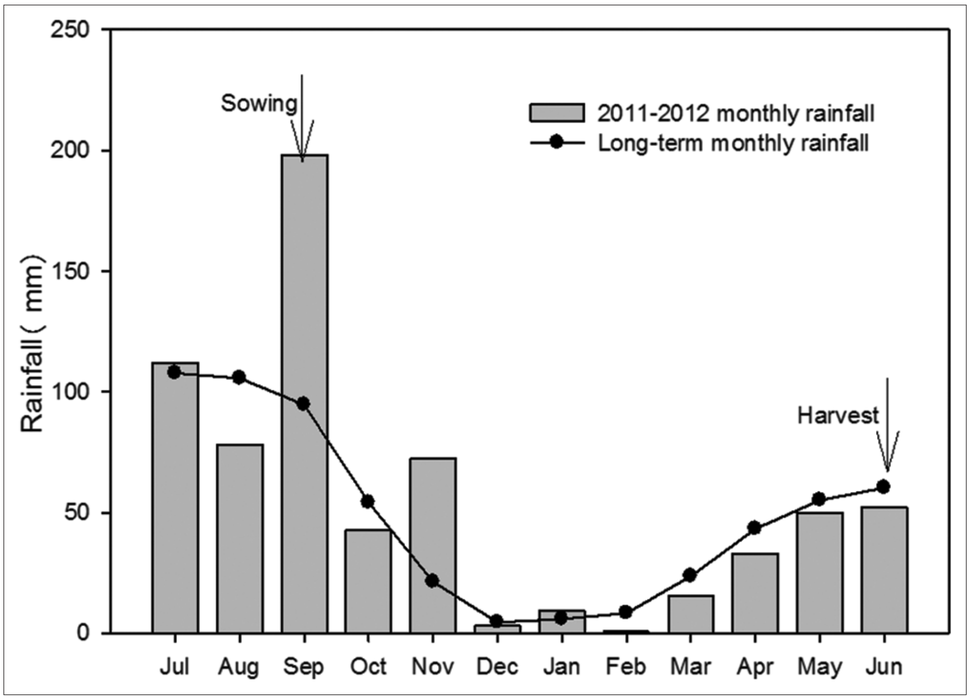

Fig 1. Monthly precipitation from July 2011 to June 2012 compared with the long-term monthly means (1956-2008) at the experimental site.

elements were determined using Pearson's test in the SPSS 19.0 software (IBM, Armonk, New York).

The absolute (1) (grain yield gains in mega-grams per hectare per year) or exponential (2) (the percentage grain yield gain per year) genetic gains of the grain yield and the related traits were modeled using the following equation:

$$yi = a + bxi + u \quad (1)$$

$$\text{or } \ln(yi) = a + bxi + u \quad (2)$$

Where *yi* is the estimated mean grain yield in each trial of cultivar i, ln(*yi*) is the natural log of *yi*, and xi is the year in which cultivar i was released. The intercepts of both equations were estimated by a, and the slope (b) was used to measure the absolute or exponential grain yield gains (percent). The residual error was estimated by u (Ortiz-Monasterio et al., 1997).

RESULTS

Genetic improvements in yield with different seeding rates

Consistent genetic gains were achieved for every seeding rate during the growing season (Table 2), with the medium rate producing the highest genetic gain (1.29%, R^2=0.81, P<0.01). The medium seeding rate (local farmers' selection) was always the best seeding rate, and only the cultivar from 2004 resulted in a greater yield as the seeding rate increased. The coefficient of variation (CV) significantly decreased with cultivar replacement.

Contributions of agronomic traits to yield and genetic improvements

The plant height at maturity decreased significantly with cultivar replacement (R^2_{Low}=0.76, P<0.05; R^2_{Medium}=0.82, P<0.01; R^2_{High}=0.84, P<0.01, respectively) in every

Table 2: Yields of the seven cultivars grown at different seeding rates

Yield (kg ha^{-1})	Low seeding rate	Medium seeding rate	High seeding rate	CV (%)
1940	4043b†	5210a	3533b	20
1951	4413b	6023a	4270b	20
1964	6590a	5593ab	4970b	14
1966	4160b	5243a	3873b	16
1981	5833b	6690a	5093b	14
1997	6860ab	7250a	6320b	7
2004	7166c	8183b	9496a	14
Genetic gain (%)	0.65	1.29	0.93	-1.15
R^2	0.79*	0.81**	0.83*	0.56*
SE	511	422	771	0.137

†Means followed by the same letters within the same column were not significantly different between the different seeding rates at P = 0.05. *Significant at P=0.05, **Significant at P=0.01

treatment (Fig. 2) because of the introduced dwarf genes (Table 1). In each seeding rate treatment, the aboveground biomass, spike number, grain number per spike and grain number per unit area were almost stable with cultivar replacement. However, the HI and TGW increased significantly (Table 3). In the supplementation treatments, the yields of the modern cultivars improved as the HI and TGW increased and were less correlated with the aboveground biomass and grain number (Table 4). However, these results were not always consistent. In the low seeding rate treatment, the aboveground biomass played an important role in the genetic gain (r=0.80, P<0.01) and in the grain number per unit area (r=0.65, P>0.05).

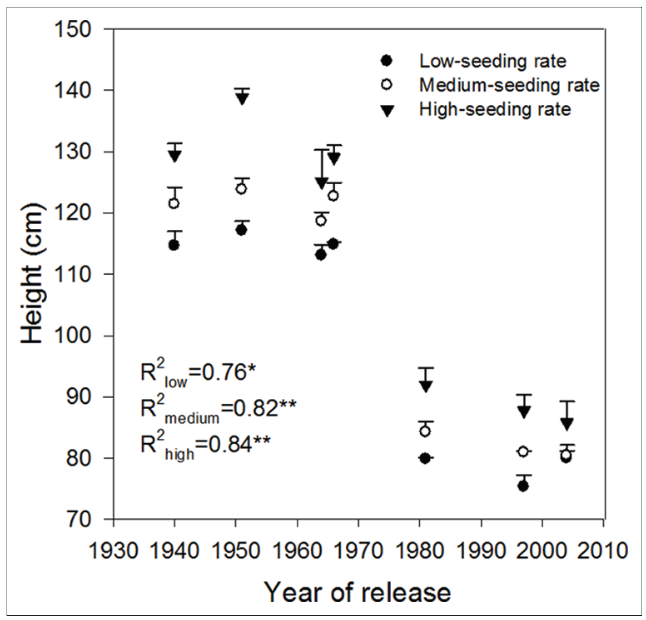

Fig 2. Plant height at maturity of the seven cultivars at different seeding rates. *Significant at P=0.05. **Significant at P=0.01.

Photosynthetic characteristic variations at anthesis and their relationship with yield improvement under different seeding rates

The Pn of the flag leaf peaked at the low seeding rate for all cultivars. However, no significant differences were observed between the medium seeding rate and the high seeding rate (Fig. 3). At the low seeding rate, the Pn of the flag leaves significantly increased with cultivar replacement (R^2=0.74, P<0.05). In contrast, this increase was small for the other seeding densities (Fig. 3a). The N contents of the flag leaves were consistent with the Pn (Fig. 3b). However, when the 1966 cultivar was excluded from the analysis, the Pn significantly increased over the decades when using medium and high seeding rates.

The canopy characteristics of all cultivars at anthesis among the different seeding rates were consistent (Fig. 4). The MTA at anthesis showed no evident difference among cultivars (Fig. 4b). However, when excluding the cultivar that was released in 1966, which had an extremely low value, positive trends in the LAI at anthesis were obvious at the medium and high seeding rates ($R^2_{\text{Medium seeding rate}}$=0.51, P>0.05; $R^2_{\text{High seeding rate}}$=0.76, P<0.05; Fig. 4a). Consequently, by excluding the extremely high value of the cultivar that was released in 1966, a significant and negative trend was observed in the DIFN with cultivar replacement at anthesis for all three seeding rates ($R^2_{\text{Low seeding rate}}$=0.89, P<0.05; $R^2_{\text{Medium seeding rate}}$=0.93, $R^2_{\text{High seeding rate}}$=0.85, P<0.01; Fig. 4c).

The yield increases of modern cultivars at all seeding rates were significantly correlated with the photosynthetic trait changes at anthesis (Table 5). Previous results indicated that these yield improvements were caused by agronomic traits, especially the thousand-grain weight and harvest index (Table 4). The Pn of the flag leaf and the LAI at anthesis had significant positive influences on the thousand grain weight and harvest index at all three densities. The DIFN at anthesis was positively correlated with the TGW and yield, especially under the high seeding rate (r_{TGW}=-0.94, P<0.01; r_{Yield}=-0.68, P>0.05).

Table 3: Yield components of the seven cultivars at different seeding rates

Year of release	Aboveground biomass (kg ha^{-1})			HI (%)			TGW (g)		
Seeding rate	Low	Medium	High	Low	Medium	High	Low	Medium	High
1940	12093	16567	13710	29.5	32.2	27	37.2	35.4	35.3
1951	13933	12733	13760	31.8	39.9	31.2	41.7	40.1	39.9
1964	13763	15527	11253	43.3	33.3	31.5	42.1	41.7	40.5
1966	12807	15443	11980	32.5	37.5	31.8	35.8	35.1	34.2
1981	13200	17577	13683	41.1	40.6	36.4	42.5	41.7	40.5
1997	15387	18340	14063	44	43.7	41.9	48.3	46.6	45.8
2004	15037	16820	18343	44.2	48.4	50.8	45.4	44.7	42.4
Genetic gain (%)	0.29	0.3	0.37	0.64	0.52	0.88	0.34	0.37	0.31
R^2	0.63*	0.35	0.32	0.71*	0.72*	0.93**	0.57*	0.63*	0.52
SE	444.7	690.4	852.5	2.5	2.1*	3.1	1.6	1.6	1.5
Year of release	Spike number per unit area (10^4 ha^{-1})			Grain number per spike			Grain number per unit area (10^4 ha^{-1})		
Seeding rate	Low	Medium	High	Low	Medium	High	Low	Medium	High
1940	450.7	739.3	686.3	37.1	31.8	27.4	16804.6	23545.3	18762.7
1951	516.7	659.3	594.3	30.5	25.9	22.2	14517.3	17133.1	13190.5
1964	539	638.7	536.3	32.1	25.8	23.4	17382.2	16411.6	12553.3
1966	576.7	742	688.3	31.8	21.8	19.5	183323	16196.8	13421.4
1981	554.7	847	753	31.3	27	29.8	18170.1	23110.4	22516.1
1997	561.7	748.3	617.3	35	24.5	26.1	19645.1	18375.4	15878.1
2004	484	604.3	726	40.4	34.8	31.6	19451.7	21069.5	22803.5
Genetic gain (%)	0.12	0.04	0.15	0.18	0.09	0.36	0.35	0.05	0.49
R^2	0.10	0.01	0.08	0.16	0.02	0.24	0.64*	0.01	0.21
SE	17.2	31.2	29.2	1.4	1.7	1.6	663.4	1186.3	1658.9

*Significant at P=0.05. **Significant at P=0.01

Table 4: Correlations between the yield and yield components at different seeding rates

Seeding rate treatments	Low seeding rate	Medium seeding rate	High seeding rate
Yield and its components	0.65	0.248	0.548
Grain number per area	0.858**	0.850*	0.666
1000-grain weight	0.804**	0.456	0.832*
Aboveground biomass	0.982**	0.933**	0.970**
Harvest index			

*Significant at P=0.05. **Significant at P=0.01

Table 5: Correlations between the yield and photosynthetic characteristics at anthesis for different seeding rates

Seeding rate	Pn£	LAI§	MTAζ	DIFNξ
Low seeding rate	0.83*	0.66	-0.17	-0.52
Yield	0.84	0.83*	0.29	-0.60
TGW	0.69	0.14	-0.33	-0.17
Grain number per area	0.80	0.79*	0.32	-0.72
Aboveground biomass	0.75	0.54	-0.26	-0.39
HI				
Medium seeding rate	0.61	0.85*	0.22	-0.83*
Yield	0.60	0.60*	0.30	-0.92**
TGW	0.63	0.40	0.54	-0.32
Grain number per area	0.38	0.55	0.03	-0.54
Aboveground biomass	0.34	0.63	0.05	-0.60
HI				
High seeding rate	0.80*	0.72	0.38	-0.68
Yield	0.86*	0.92**	0.68	-0.94**
TGW	0.53	0.39	0.33	-0.39
Grain number per area	0.69	0.40	0.31	-0.42
Aboveground biomass	0.74	0.77	0.40	-0.66
HI				

*Significant at P=0.05. **Significant at P=0.01. £Photosynthetic rate of the flag leaf. §Leaf area index. ζMean tilt angle. ξDiffuse non-interceptance

DISCUSSION

Cultivar replacement was the most important element responsible for increasing winter wheat yields, with an annual genetic gain of 0.5%-1% in China (Chen et al., 2003; Zhang et al., 2017), a bit lower than world average of 1.1% (Hall and Richards, 2013). Significant genetic gains were achieved for all of the seeding rates in our study, which was consistent with former studies in this area (Chen et al, 2012) because different cultivars showed different dry matter accumulation and yield responses to the population size (Brian et al., 2011). Thus, the effects of seeding rate should be considered in cultivar breeding and genetic progress estimates.

The cultivars produced the highest yields at a medium seeding rate (Table 2), except for the cultivar released in 2004. Gooding et al. (2002) and Fang et al. (2010), reported that the grain yield in wheat was greatest when using a seeding rate of approximately 250 seeds m^{-2}. According to Donald (1981), plants with a lower individual competitiveness result in a more established population. The yield CV of modern cultivars (Table 2) was lower than of the yield CVs of the older cultivars, indicating that the modern cultivars were much less

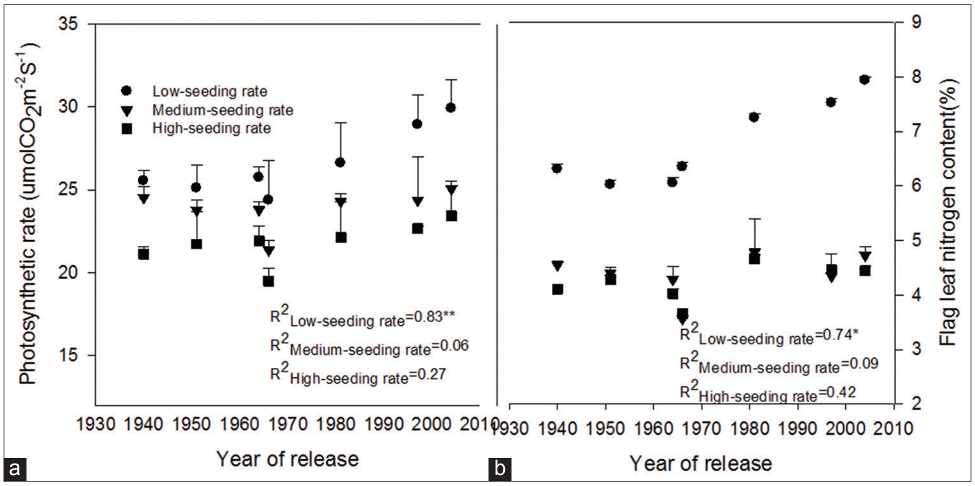

Fig 3. (a and b) Flag leaf photosynthetic rates and nitrogen contents of the seven cultivars at anthesis for different seeding rates. *Significant at P=0.05. **Significant at P=0.01.

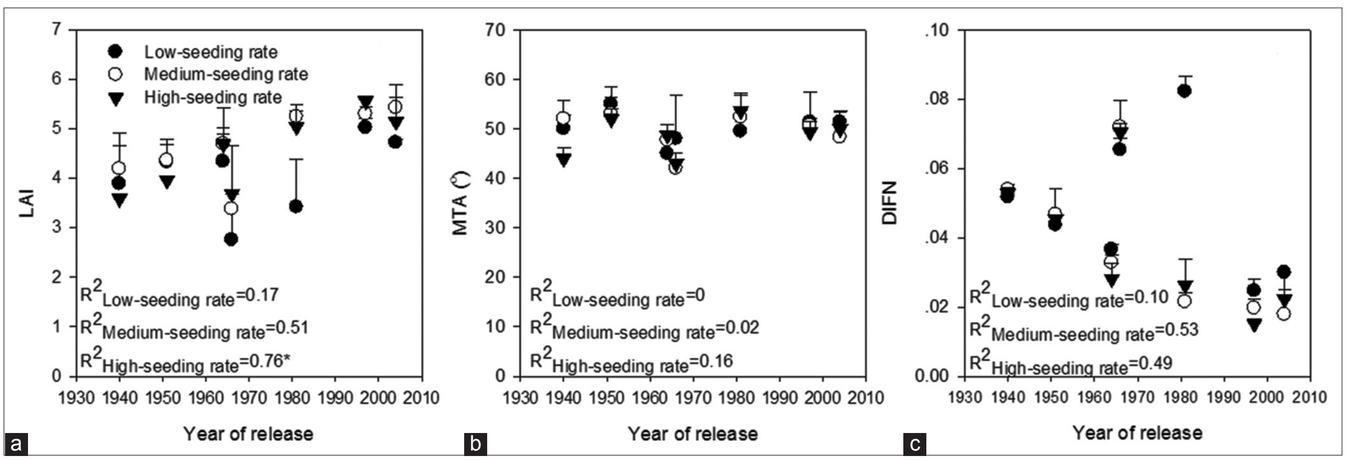

Fig 4. (a-c) Canopy characteristics (leaf area index, LAI; mean tilt angle, MTA; and diffuse non-interceptance, DIFN) of the seven cultivars at anthesis for different seeding rates. *Significant at P=0.05.

sensitive to the seeding rate. This decreased sensitivity to seeding rate is beneficial for modern planting cultivation techniques. The cultivar that was released in 2004 was not only the highest-yielding but also the most unique because it obtained the highest yield under a seeding rate of 350 seeds m^{-2} (Table 3). This result suggested the benefits of a further increase in the seeding rate for modern cultivars on the Loess Plateau.

The plant height on the Loess Plateau after the 1980s decreased to approximately 70 cm (Fig. 2), which was lower than the requirement for grain yield (Chen et al., 2003), with shorter plants affecting the population quality and reducing the grain yield. Based on the listed yield components (Table 3) and their relationships with grain yield (Table 4), the HI and TGW increases can be considered as key factors for yield improvements on the Loess Plateau, regardless of the seeding rate. The grain number per unit area showed no significant improvement for any seeding rate and contributed less to the yield production. Aisawi et al. (2015) and Donmez et al. (2001) got similar results. Brancourt-Hulmel et al. (2003) and Sayre et al. (1997), confirmed that the wheat grain yield is more strongly related to the kernel number per unit ground area than the kernel weight.

Significant increases resulting from cultivar replacement were observed in the aboveground biomass in Australia and Brazilian (Perry and D'Antuono, 1989; Beche et al., 2014), but no changes were found in England (Austin et al., 1980) or France (Brancourt-Hulmel et al., 2003). In this study, the aboveground biomass significantly increased and was only correlated with yield improvements at a low seeding rate. This result indicated that the cultivars with greater production capacities could have outstanding yields when the population size is small.

It is widely acknowledged that a large part of grain saccharides are derived from photosynthates in the leaves especially the flag leaf (Condon et al., 2004; Pierre et al., 2015). Thus, understanding changes in the photosynthetic traits of new cultivars provides important information for genetic improvement (Richards, 2000). The Pn of the flag leaves at anthesis significantly increased with cultivar replacement for each seeding rate considered in our study (Fig. 3a). In addition, the relevant contributions of the Pn to TGW and yield were positive and significant (Table 5), corresponding with the results of Reynolds et al. (2000) and Tian et al. (2011).

Canopy photosynthesis should be improved to increase cereal grain yields (Zhu et al., 2010). The LAI, MTA, and DIFN together were all effective measurements for evaluating light absorption (Lanning et al., 1997). The LAI of the modern cultivars in this study was greater than the older cultivars at the medium and high seeding rates (Fig. 4a), and the LAI at anthesis was always positively correlated with those the TGW and yield (Table 5). Wang et al. (2016) and Condon et al. (2004) also reported that rapid leaf area growth is a beneficial trait in benign environments.

Genotypes with upright leaves are considered less competitive than those with more horizontal leaf orientations (Huel and Hucl, 1996). In this study, the MTA at anthesis showed no obvious change over the decades (Fig. 4b) and was not correlation with the yield (Table 5) in any treatment. The leaf directions were nearly consistent with cultivar replacement. However, the DIFN at anthesis generally decreased with cultivar replacement at all seeding rates (Fig. 4c). These results correspond with those of Lanning et al. (1997), who considered that less light generally penetrates between the rows of taller varieties. The DIFN values obtained on the Loess Plateau were below that previously reported by Lanning et al. (1997) and Wang et al. (2009), and suggest that wheat breeding in this region could be more efficient for transmitting light. Based on the significant negative correlations between the DIFN at anthesis and the yields in every treatment (Table 5), it was concluded that the modern cultivars possessed higher LAI and lower DIFN values at anthesis, which was beneficial for light interception and use and resulted in greater TGWs and yield increases. Furthermore, the LAI values of wheat at anthesis on the Loess Plateau (Fig. 4) were just below or similar to the critical LAI value of 6 (Parry et al., 2011) and the MTA values of the cultivars were stable. Thus, it was concluded that the decrease in the DIFN at anthesis mainly resulted from the increased LAI. However, additional studies are needed.

CONCLUSIONS

Significant genetic improvements of dryland winter wheat on the Loess Plateau were achieved with 100, 250 and 350 seeds m^{-2}. Modern cultivars were less sensitive to seeding rate and were favorable for modern cultivation techniques of high population size. For further increases in grain yield, improvement in the HI and TGW would be beneficial. In addition, higher LAI and lower DIFN at anthesis are more efficient for light absorption and should be further considered.

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Author's contributions

Suiqi Zhang: Design, formulation and supervision of experiment with writing. Yingying Sun: Carried out the project and drafted the manuscript. Xiaojuan Yan and Nan Wang: Participated in data analysis. All authors read and approved the final manuscript.

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