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Changes in the yield and associated photosynthetic traits of dry-land winter wheat (*Triticum aestivum* L.) from the 1940s to the 2010s in Shaanxi Province of China

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ABSTRACT

Eight dry-land winter wheat cultivars (*Triticum aestivum* L.), representative of those widely cultivated from the 1940s to the 2010s in Shaanxi Province of China, were grown in plots that could be sheltered from rain. The plots were subjected to irrigation and drought treatments to identify the agronomic and photosynthetic traits associated with yield progress. Plant height at maturity decreased from 140.7 cm to 79.5 cm from the earliest to the most recent studied cultivar. The yield increased significantly with an annual genetic gain of 0.48% and was consistently and positively associated with the grain weight and harvest index. Modern cultivars were more sensitive to drought stress, and no obvious increase in harvest index was found to indicate possible limitations on further yield increase after the 1980s. The mean tilt angle was similar among all of the cultivars. A trend over time towards a high photosynthetic rate of flag leaf and leaf area index at the heading stage was observed. Both trends were significantly related to a yield increase. The post-anthesis photosynthetic traits showed no trend with cultivar replacement or obvious stable relationship with yield. A future challenge for wheat breeding in this region is to increase the genetic gain in grain yield under water deficits, likely through increases in the grain weight and harvest index as well as an improvement of the photosynthetic rate before and after anthesis.

1. Introduction

A genetic improvement in wheat yield has been reported throughout the world (Austin et al., 1980; Brancourt-Hulmel et al., 2003; McCaig and DePauw, 1995; Maydup et al., 2012; Perry and D'Antuono, 1989), and China is included in this trend (Zhang et al., 2010; Zheng et al., 2011; Zhou et al., 2007). In these studies, no changes resulting from cultivar replacement were observed in aboveground biomass (Austin et al., 1980; Brancourt-Hulmel et al., 2003), although there were a few exceptions (Perry and D'Antuono, 1989). Several studies confirmed that an increased harvest index (HI) with decreased height resulted from increased grain weight and grain numbers per unit area (Austin et al., 1980; Brancourt-Hulmel et al., 2003; Zheng et al., 2011). These observed morphological changes directly gave rise to the yield increase.

Photosynthesis plays a pivotal role in grain yield; approximately 60% of grain saccharides are derived from photosynthates in the flag leaf (Thorne, 1974). Thus, understanding changes in the photosynthetic traits of new cultivars provide important information for genetic improvement (Austin et al., 1989). An enhanced grain yield of wheat has consistently been associated with changes in photosynthetic characteristics such as stomatal conductance, photosynthetic rate (Pn) increase and canopy temperature depression (Reynolds et al., 2000). Several studies reported that modern cultivars possess an increased Pn and stomatal conductance in the flag leaf (Fischer et al., 1998; Reynolds et al., 2000; Tian et al., 2011), especially after anthesis (Zheng et al., 2011), although other studies have presented contradictory results (López-Castañeda et al., 1996; Richards, 2000). Extended leaf area was verified with cultivar replacement (Tian et al., 2011), and extended green leaf area duration (Evans, 1993) with cultivar replacement has been verified. However, most previous studies were conducted under favorable soil moisture conditions. Plants exposed to drought showed decrease in the photosynthesis rate and stomatal conductance as well as a concomitant increase in the intercellular CO_2 concentration (Siddique et al., 1999). Gent and Kiyomoto (1985) reported that

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inter-specific differences in grain yield are not necessarily related to differences in leaf photosynthesis. Wada et al. (1994) found a positive correlation between leaf photosynthesis and grain yield only in a non-irrigated treatment. Because there are significant differences in cultivation practices and environmental conditions between wheat-growing regions, the responses of cultivars released at different times and in different areas may vary significantly. It is therefore necessary to validate the association between physiological selection criteria and yield potential before cultivars are used in wheat breeding programs in northwest China.

Shaanxi Province, situated in a semi-humid to semi-arid transitional area, is the most important wheat-producing region in northwestern China (Fan, 2007), with more than 4 million tons harvested from approximately 1.6 million ha of farmland every year (Li and Ren, 2009). Winter wheat is the major crop in this region. At least six wheat cultivar replacements have been recorded in this province since the 1940s; higher-yielding cultivars with shorter heights and stronger disease and lodging resistance were planted (Zhuang, 2003). According to a study by Chen et al. (2012) in Shaanxi Province, an increased yield of wheat was strongly and positively related to the photosynthetic capacity per unit of leaf area after elongation. However, no studies have examined whether and how canopy characteristics play a role in cultivar replacement. Zhang and Song (1994) suggested that the yield of winter wheat in Shaanxi Province increased by 740 kg ha^{-1} from the 1940s to the 1990s, mainly due to an enhanced spike number per unit area. However, Zhang et al. (2008) found that the grain-yield increase was primarily due to increased grain weight. All of the aforementioned studies were conducted under a single water treatment regime in a single year; however, water shortage is a consistent phenomenon in this region, especially after anthesis, and the climate varies widely between years (Zhang et al., 2013). As a result, the findings of previous research may not be representative of the actual conditions.

In this study, field experiments with two different water treatments were conducted in three successive years using eight cultivars developed between 1940 and 2010 to (1) explore the evolution of grain yield characteristics and main agronomic traits and their responses to water treatment and to (2) identify the correlation between photosynthetic characteristics and yield progress.

2. Materials and methods

2.1. Plant material and trial configurations

Eight cultivars formerly or currently planted in Shaanxi Province were selected (Table 1). Field experiments were conducted in Yangling, Shaanxi Province, in northwest China (34°16′56.24″N, 108°4′27.95″E; 460 m above sea level) over the winter–spring growing season (October–June of the following year between 2010 and 2013). Seeds of the experimental cultivars were planted in the field on October 7, 2010; October 10, 2011; and October 12, 2012. The field had been used for grain production for at least 20 years with similar cultural practices before initiation of this study. The soil consists of Earth-cumuli-Orthic Anthrosols with a deep profile and is considered suitable for crop production. Mung beans were planted during the fallow period of each year, and irrigation was provided to regulate the soil water and fertilization. In the 2 m soil profile, the average field capacity was 28% (q/v). The soil nutrient stations before the three seasons were almost stable, and the average nutrient content levels were as follows: organic matter, 19.10 g kg^{-1}; total nitrogen, 0.93 g kg^{-1}; alkali-hydrolyzable nitrogen, 65.01 mg kg^{-1}; total phosphorus, 0.88 g kg^{-1}; rapidly available phosphorus, 17.90 g kg^{-1}; and available potassium, 163.63 g kg^{-1}. A base fertilizer was applied [urea (*N*) 150 kg ha^{-1} and calcium superphosphate (P_2O_5), 120 kg ha^{-1}] prior to planting, and no top-dressing was applied before harvest.

Two water treatments were implemented, one with normal rainfall and two irrigation events (irrigation, Ir) and another treatment with no rainfall after the recovering stage (drought, D). Two irrigation events (70 mm each irrigation) were provided for the Ir treatment at the tillering stage (before the wintering stage) and at the elongation stage to ensure the achievement of a high yield potential. The exception was during the elongation stage of 2011–2012, when 80 mm of water was provided due to the dry weather. As the harvest dates differed among the study seasons due to the influence of irrigation and precipitation, the cultivars in the drought treatment were harvested between May 26 and June 2 of the three seasons, whereas the date of harvest for the irrigation treatment was delayed to June 1–June 5.

The cultivars were planted manually in plots (2.2 × 3.3 m^2 per plot; 11 rows, 20 cm apart; plant spacing of 2 cm). Plots were arranged in randomized blocks with three replicates. Fungicides and pesticides were applied at shooting and grain filling to prevent attack by diseases and pests. Due to the greater height of the low-yield cultivars (Mazha, Bima1), which makes them prone to falling, bamboo poles (50–200 cm long) were used to prevent lodging so that the ultimate yield potential could be reached.

2.2. Plant sampling and determination

Photosynthetic traits were recorded in both the 2010–2011 and 2011–2012 seasons. The Pn of flag leaf was measured between 9:30 and 11:30 AM using an Li6400 portable photosynthesis system (LI-COR, USA) in all plots at heading and at 3 days and 20 days after anthesis. The Pn values of flag leaves were calculated as the mean readings for five leaves per plot at all three stages. All measurements were performed on the middle portions of the flag leaf exposed to full sunlight, approximately halfway along the length of the leaf.

Canopy characteristics were recorded in both the 2010–2011 and 2011–2012 seasons. The leaf area index (LAI) and mean tilt angle (MTA) of whole canopy were measured using an LAI-2200 Plant Canopy Analyzer (LI-COR, USA) at heading and 3 days after anthesis.

At maturity in all three seasons, four central rows (1 m long) were harvested, counted, and weighed to determine the grain number per square meter, total above-ground biomass dry weight, grain yield and HI. Subsamples were used to record the grain number per spike and grain weight. In addition, samples were taken in each plot at flowering in 2011–2012 to determine the aboveground biomass.

2.3. Statistical analyses

The significance of cultivar effects was determined using an analysis of variance. Correlations between phenotypic traits and yield elements were determined using Pearson's test. SPSS 19.0 software was used to perform the analyses.

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 grain yield and related traits were modeled using the following equation:

$$y_i = a + bx_i + u \qquad (1)$$

or

$$\ln(y_i) = a + bx_i + u \qquad (2)$$

where y_i is the estimated mean grain yield in each trial of cultivar *i*, $\ln(y_i)$ is the natural logarithm of y_i, and x_i is the year in which cultivar *i* was released. The intercept of both equations was estimated

Table 1
Representative cultivars of dry-land winter wheat in Shaanxi Province during the period of 1940–2010.

Cultivars	Planting decade in Shaanxi	Pedigree	Dwarf genes	Breeding sites
Mazha	1940s	Local cultivar in Shaanxi Province	None	Shaanxi Province
Bima1	1950s	Mazha/Biyu	None	Shaanxi Province
Fengchan3	1960s	Danmai1/Xinong 6028 × Bima1	None	Shaanxi Province
Taishan1	1970s	54405(Bima4 × Zaoshu1)/Ourou	*RhtD1b*	Shandong Province
Xiaoyan6	1980s	(ST2422 × 464)/Xiaoyan96	*Rht-B1b + Rht8*	Shaanxi Province
Jinmai33	1990s	Pingyang79391((Naixue × 5017)036 × 76-1256)/Pingyang76262	None	Shanxi Province
Changwu134	2000s	(Changwu131 × Xiaohei96)F1/Changwu131)F4/(Jinghua3/NS2761)F1	*Rht-B1b*	Shaanxi Province
Changhan58	2010s	Changwu112/PH82-2	*Rht-B1b*	Shaanxi Province

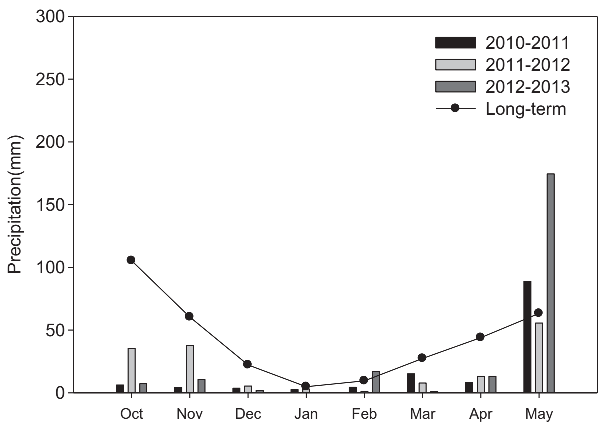

Fig. 1. Precipitation during the experimental period (October–May of following year) compared with the long-term means (1956–2005) at the experimental site.

by *a*, while the slope *b* measured absolute or exponential grain yield gains; the latter was converted to a percentage. The residual error was estimated by *u* (Ortiz-Monasterio et al., 1997).

The degree to which yield was affected by the drought treatment was calculated with the following equation:

SSI(stress susceptibility index) = $(1-y_D/y_{Ir})/(1-\bar{y}_D/\bar{y}_{Ir})$ (Fischer and Maurer, 1978),

where y_D is the yield of the cultivar under drought, y_{Ir} is the yield of the cultivar under irrigation, $\bar{y}_D$ and $\bar{y}_{Ir}$ are the mean yields of all cultivars under the drought and irrigation conditions, respectively, and $(1-\bar{y}_D/\bar{y}_{Ir})$ is the water intensity.

3. Results

3.1. Precipitation conditions during growing seasons

The total precipitation during the growing seasons of all three years was not very stable (Fig. 1), and each growing season's total precipitation was less than the long-term average precipitation. However, the use of irrigation ensured that the wheat in the irrigation treatment was free from drought stress. Although the yields achieved in the three trial seasons were not completely consistent, the trends were almost exactly the same (Table 2); therefore, the overall trait means from the three seasons for both water treatments were analyzed (except for photosynthetic traits that were available only for 2010–2011 and 2011–2012). The rainfall during the experimental period (October–May of the following year) occurred primarily from July to September of each year, which might have led to a delayed water deficit in the drought treatment.

3.2. Genetic improvement in grain yield

The overall mean yield of the trial was 4919 kg ha^{-1}, with yields ranging from 3781 kg ha^{-1} for cultivars released in the 1940s to 5630 kg ha^{-1} for cultivars released in the 1990s (Table 2). The yields under the D treatment of cultivars released after 2000 were not as high as that those of cultivars released in the 1990s. Increases in grain yield were observed when all eight cultivars released in different years were planted in the same habitat, although the overall mean annual genetic gain ($R^2=0.707$, $P<0.01$) was not as large as in the historical record (i.e., greater than 1%, Zhuang, 2003). The mean annual genetic gain in yield over the three seasons under the Ir treatment ($R^2=0.723$, $P<0.01$) was significantly greater than in the D treatment ($R^2=0.449$, $P>0.05$). During the growing season of 2012–2013 in particular, the annual genetic gain of yield under the D treatment was less than 0.3% ($R^2=0.148$, $P>0.05$), and the SSI showed an increase from the 1940s to the 2010s ($R^2=0.185$, $P>0.05$), especially if it was calculated without the abnormal value for the 1990s ($GN_{SSI}=1.31\%$, $R^2=0.538$, $P>0.05$).

3.3. Agronomic traits and their associations with grain yield

The spike number per unit area and grain number per spike are two subcomponents of the grain number per unit area. The annual genetic gain in the spike number per unit area was negative ($R^2=0$, $P>0.05$), meaning that the spike number per unit area was approximately stable and the change was not significant (Table 3). In contrast, the annual genetic gain in the grain number per spike showed only a slight increase of 0.19% ($R^2=0.126$, $P>0.05$). Therefore, no meaningful change in the grain number per unit area was observed in either the Ir or D treatments between the 1940s and the 2010s. The thousand-grain weight (TGW) was significantly increased with cultivar replacement and ranged from 32.1 g for the 1940s to 38.6 g for the 2000s, and the mean annual genetic gain was significant with cultivar replacement ($R^2=0.607$, $P<0.05$).

No significant genetic gain in the aboveground biomass was observed for either treatment, although there was a significant genetic gain in the HI (Table 3). The aboveground biomass dry weight at maturity showed a slight increase in both the D ($R^2=0.011$, $P>0.05$) and Ir ($R^2=0.002$, $P>0.05$) treatments. The mean HI increased significantly ($R^2=0.674$, $P<0.05$) between the 1940s and the 1970s, ranging from 29.4% to 41.7%, and it was almost stable after the 1970s. Therefore, the significant increase in the grain yield achieved between the 1940s and the 2010s was largely due to the significant and strong increase in the HI. Similarly, because the increases in both the grain density and above ground biomass were not significant, the significant increase in the HI was largely due to the significant increase in the TGW.

Overall, the decrease in plant height with cultivar replacement was significant between the 1940s and the 2010s (Fig. 2). The negative correlations between planting years and plant heights at maturity were all significant. The plant heights of cultivars planted before the 1970s were greater than 100 cm. All cultivars planted after the 1970s were 75–95 cm tall except for Jinmai33, which was planted in the 1990s.

The grain yield was determined by multiple factors, and associations among grain yield and other agronomic traits are shown in Table 4. The correlation trends under the Ir treatment and the

Table 2
Yield of eight cultivars under irrigation (Ir) and drought (D) treatments during 2010–2011, 2011–2012 and 2012–2013.

Decade	Yield ($kg\,ha^{-1}$)								Overall mean	SSI
	2010–2011		2011–2012		2012–2013		Treatment mean			
	Ir	D	Ir	D	Ir	D	Ir	D		
1940s	3820b	3720a	4633b	4229c	3383b	2900a	3945b[a]	3616a	3781b	0.36
1950s	4637ab	3480a	5954ab	5362bc	4775ab	3133a	5122ab	3992a	4557ab	0.95
1960s	4540ab	3670a	5937ab	5250bc	5267ab	2938a	5248ab	3953a	4600ab	1.06
1970s	4703ab	3717a	4554a	6683ab	6046a	2888a	5101ab	3817a	4459ab	1.08
1980s	5860ab	3893a	7354a	6270ab	6721a	3571a	6645a	4578a	5612a	1.33
1990s	6010a	4133a	6295ab	7112a	5429a	4800a	5911a	5348a	5630a	0.41
2000s	5457a	4063a	7350a	6204ab	6063a	3163a	6290a	4477a	5383ab	1.23
2010s	5267a	3810a	7504a	6116ab	6096a	3183a	6289a	4370a	5329ab	1.31
SE	262	76	415	326	366	225	313	195	236	0.0013
Genetic gains (%)	0.49	0.16	0.55	0.5	0.66	0.28	0.58	0.36	0.48	0.92
R^2	0.608*	0.483	0.696**	0.518*	0.560*	0.148	0.723**	0.449	0.707**	0.185

[a] Means followed by the same letter within a column were not significantly different at $P = 0.05$.
* Significant at $P = 0.05$.
** Significant at $P = 0.01$.

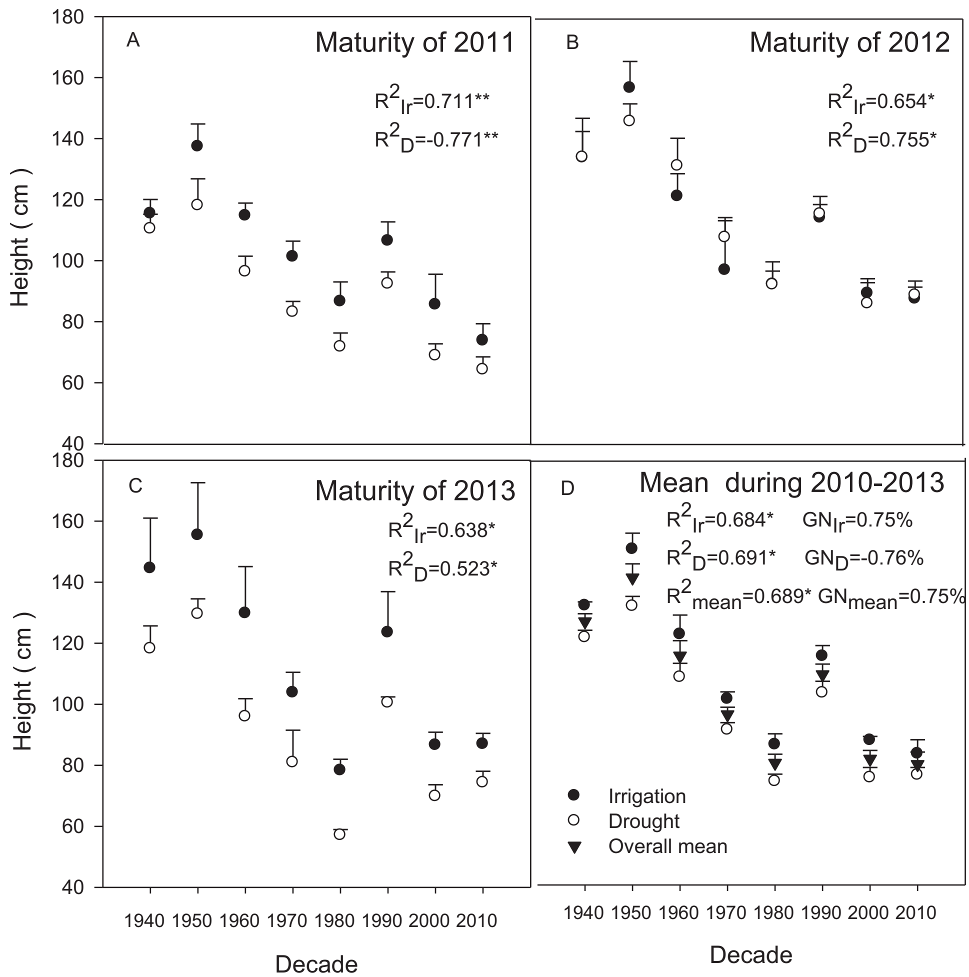

Fig. 2. Height of eight cultivars under the irrigation (close circles), drought (open circles) treatments and overall mean (close triangles) during 2010–2011, 2011–2012 and 2012–2013.* Significant at $P = 0.05$;** significant at $P = 0.01$. GN indicates the annual genetic gain; Ir indicates the irrigation treatment; D indicates the drought treatment.

D treatment were similar. The overall mean grain yield was significantly positively associated with the TGW ($r = 0.764$, $P < 0.05$) and HI ($r = 0.877$, $P < 0.01$), negatively associated with the plant height ($r = -0.699$, $P > 0.05$), and positively associated with the grain number per unit area ($r = 0.604$, $P > 0.05$) and aboveground biomass dry weight at maturity ($r = 0.315$, $P > 0.05$). The TGW was consistently and positively associated with various traits including the dry weight of aboveground biomass at maturity and the HI. These associations further indicate the important contributions of the TGW to yield performance, which is in agreement with the previous conclusion that the significantly increased grain yield largely resulted from the increased TGW. The correlation between grain number per area and yield under the D treatment was more significant than in the Ir treatment, whereas the correlation between the HI and

Table 3
Average yield components of eight cultivars under irrigation (Ir) and drought (D) treatments during 2010–2011, 2011–2012 and 2012–2013.

Decade	Yield components																	
	Spike number per unit area (10^6 ha^{-1})			Grain number per spike (spike^{-1})			Grain number per unit area (10^6 ha^{-1})			TGW (g)			Aboveground biomass (kg ha^{-1})			HI (%)		
	Ir	D	Mean	Ir	D	Mean	Ir	D	Mean	Ir	D	Mean	Ir	D	Mean	Ir	D	Mean
1940s	4.83b[a]	4.65ab	4.74bc	42.5ab	34.8b	38.6b	231.5ab	172.5a	202a	32.2b	32a	32.1b	17548a	11578a	14563a	26.5b	32.4a	29.4c
1950s	5.43b	4.92ab	5.18bc	35.5b	34.1b	34.8bc	183b	168.1a	175.5a	36.3ab	32.7a	34.5ab	16119a	12728a	14424a	32.3ab	32.3a	32.3bc
1960s	5.96ab	5.48ab	5.72b	35.5b	31b	33.2bc	219.9ab	191.9a	205.9a	39a	33.9a	36.5ab	16945a	12345a	14645a	31.8ab	32.7a	32.3bc
1970s	6.2ab	5.83ab	6.01ab	36b	29.3b	32.7bc	235.9ab	175.3a	205.6a	35.4ab	34.2a	34.8ab	16348a	11748a	14048a	35.8ab	36.6a	36.2abc
1980s	6.03ab	5.17ab	5.6bc	41.1ab	34.1b	37.6b	267.7ab	175.4a	221.6a	37.7ab	32.8a	35.3ab	16434a	12333a	14384a	44.2a	39.1a	41.7a
1990s	7.7a	6.7a	7.2a	30.4b	27.9b	29.2c	275.8a	191.8a	233.8a	37.2ab	36.8a	37a	16670a	14807a	15738a	36.9ab	36.7a	36.8abc
2000s	5.6b	4.61ab	5.11bc	39.4ab	33.8b	36.6bc	240.5ab	159.7a	200.1a	39.9a	37.3a	38.6a	16812a	11592a	14202a	38.6ab	39.4a	39ab
2010s	4.68b	3.96b	4.32c	51.8a	44.7a	48.3a	243.2ab	198.3a	220.8a	37.5ab	35.1a	36.3ab	17071a	11811a	14441a	38.7ab	38.2a	38.4ab
SE	0.3	0.3	0.3	2.3	1.8	2	10	5	6	0.8	0.7	0.7	161	378	182	1.9	1.1	1.5
Genetic gains (%)	0.08	−0.11	−0.01	0.19	0.18	0.19	0.3	0.09	0.21	0.17	0.18	0.18	−0.03	0.03	0.01	0.5	0.3	0.4
R^2	0.219	0	0	0.116	0.131	0.126	0.335	0.092	0.343	0.408	0.618*	0.607*	0	0.011	0.009	0.581*	0.762**	0.674*

[a] Means followed by the same letter within a column were not significantly different at $P = 0.05$.
* Significant at $P = 0.05$.
** Significant at $P = 0.01$.

Table 4
Correlation between yield and yield components under irrigation and drought treatments during 2010–2011, 2011–2012 and 2012–2013.

Correlation coefficient	Irrigation					Drought					Overall				
	Grain number per area	Thousand grain weight	Aboveground biomass	Harvest index	Height	Grain density	Thousand grain weight	Aboveground biomass	Harvest index	Height	Grain density	Thousand grain weight	Aboveground biomass	Harvest index	Height
Yield	0.521	0.784*	−0.348	0.946**	−0.747*	0.299	0.679	0.754*	0.581	−0.392	0.604	0.764*	0.315	0.877*	−0.669
Grain number per area		0.157	0.178	0.591	−0.671		0.124	0.386	−0.022	−0.092		0.308	0.548	0.537	−0.582
Grain weight			−0.3	0.613	−0.467			0.324	0.599	−0.493			0.168	0.605	−0.549
Aboveground biomass				−0.446	−0.064				−0.046	0.248				−0.092	0.256
Harvest index					−0.795*					−0.943*					−0.881*

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

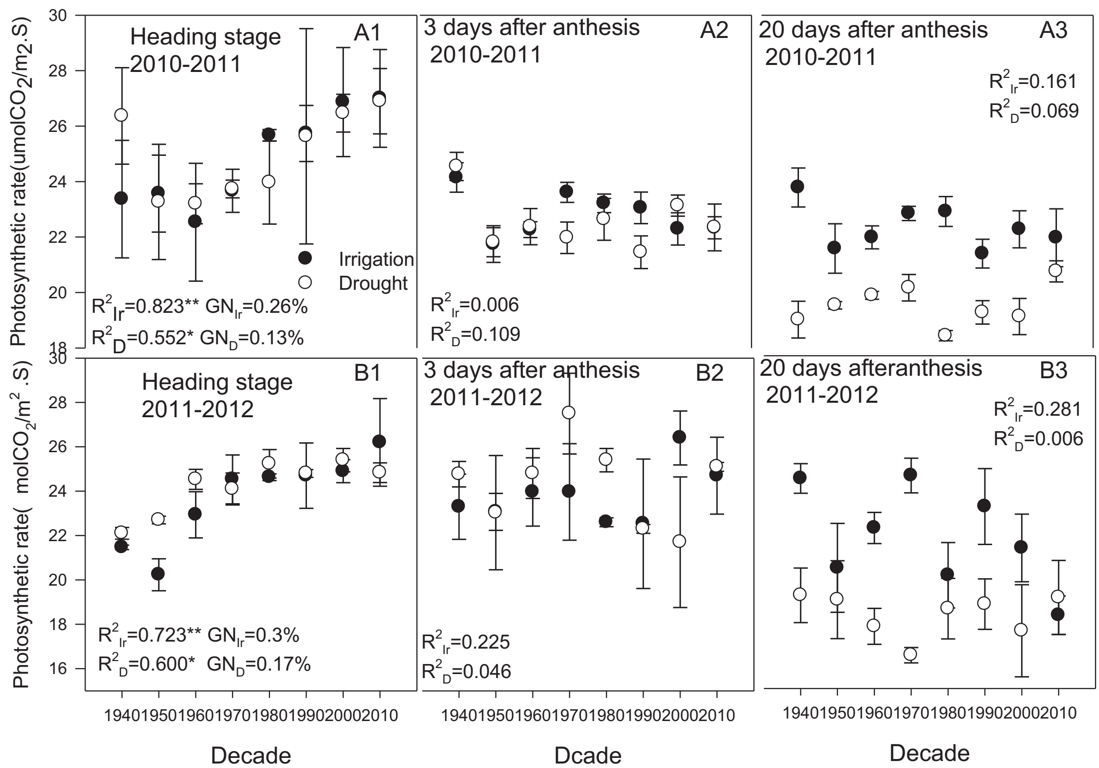

Fig. 3. Photosynthetic rate of flag leaf measured under irrigation (close circles) and drought (open circles) treatments during 2010–2011 and 2011–2012.* Significant at $P = 0.05$;** significant at $P = 0.01$; GN indicates the genetic gains; Ir indicates the irrigation treatment; D indicates the drought treatment.

yield was more significant under the Ir treatment, indicating that dry matter accumulation was different under different moisture conditions.

3.4. Changes in photosynthetic traits and their associations with grain yield

Changes in the Pn of flag leaves at heading, 3 days and 20 days after anthesis are shown in Fig. 3. The Pn of flag leaves did not consistently increase at different developmental stages with cultivar replacement between the 1940s and the 2010s. The net Pn values under both the irrigated and drought treatments significantly increased at heading during 2010–2011 and 2011–2012 (Fig. 3A, B1). However, the Pn values at 3 days (Fig. 3A, B2) and 20 days after anthesis did not increase significantly and even slightly decreased with cultivar replacement (Fig. 3A3, B3), especially in the Ir treatment at 20 days after anthesis ($R^2_{2010-2012}$ = 0.161, $R^2_{2010-2012}$ = 0.185, $P > 0.05$). Pn differences between the Ir and D treatments increased with increase in the growth period, resulting from an increase in the difference in moisture content. The previous analysis of the yield components indicated that significant genetic improvement in grain yield was directly attributable to the increased TGW and HI. Both in the Ir and in the D treatments, TGW was positively associated with the Pn of the flag leaves at the heading stage ($r_{2010-2012}$ = 0.608, $r_{2011-2012}$ = 0.685, $P > 0.05$) but was not greatly affected by the Pn after anthesis, as was also the case with HI.

MTA as a key factor for wheat to intercept light showed no obvious change with decades in either treatment during 2010–2011 and 2011–2012 (Fig. 4), indicating that the plant types of modern cultivars in Shaanxi Province did not show significant improvement in this parameter. The same results as those found for the Pn of flag leaves in this region were observed for the LAI (Fig. 5, Table 5). The LAI of modern cultivars after 1980s at the heading stage tended to be greater than that of the older cultivars under both irrigation and drought during the two growing seasons (Fig. 5A1, B1) and was positively correlated with the HI and yield (Table 5). At the flowering stage, however, although differences were found among cultivars, neither an obvious trend over time nor a relationship with yield was found (Fig. 5A2, B2, Table 5). In the D treatment, the influence of LAI on TGW was weaker than in the irrigation treatment (Table 5).

Modern cultivars (planted after the 1990s) showed greater accumulation of aboveground biomass at flowering than older cultivars (Fig. 6). Moreover, Pn of flag leaves and LAI at the heading stage had a significant impact on this parameter, especially Pn under the D treatment ($r = 0.841$, $P < 0.01$).

4. Discussion

4.1. Genetic gains of dry-land wheat yield from 1940s to 2010s in Shaanxi Province

Winter wheat yields have made great progress in China due to the expansion of planting areas, improvements in cultural techniques and other elements (Zhuang, 2003). Breeding improvements and the replacement of cultivars are the most important elements (Zhuang, 2003). This study found an annual genetic gain of 0.48% or 22.87 kg ha^{-1} ($R^2 = 0.707$, $P < 0.01$) in Shaanxi Province between the 1940s and the 2010s (Table 2). This value is much less than that found by previous studies in China (Zhuang, 2003; Xiao et al., 2012) and other countries (Calderini et al., 1995). This result indicates that the genetic gain in yield of dry-land wheat in China has not reached that observed in wheat planted in irrigated farmland (Yasir et al., 2013; Zheng et al., 2011; Zhou et al., 2007), consistent with the previous results for the region (Zhang and Song, 1994; Zhang et al., 2008). In addition, the annual genetic gain under the drought treatment was only 0.36%, which was significantly less

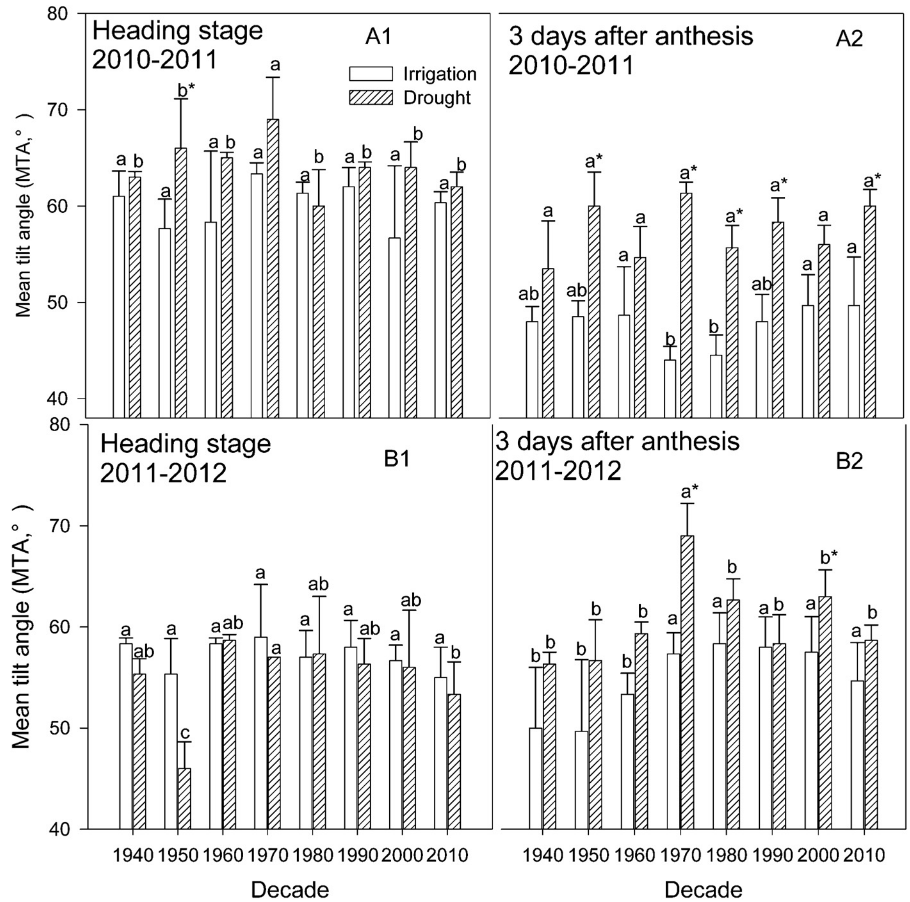

Fig. 4. Mean tilt angle measured under irrigation (blank bars) and drought (slash bars) treatments during 2010–2011 and 2011–2012. The data represent means ± SE and $N = 3$. The different lowercase letters above the bars denote significant differences for different cultivars under the same water treatment ($P = 0.05$); * significant differences in the same cultivar under different water treatments ($P = 0.05$).

Table 5
Correlations between the photosynthetic rate of flag leaf (Pn), leaf area index (LAI) and yield during 2010–2011 and 2011–2012.

		Yield and yield components	Pn[a] at heading stage	Pn at 3 days after anthesis	Pn 20 days after anthesis	LAI[b] at heading stage	LAI at 3 days after anthesis
Growing season during 2010–2011	Ir	Yield	0.740*	−0.197	−0.469	0.798*	0.306
		HI	0.694	0.25	0.087	0.789*	0.331
		TGW	0.608	−0.421	−0.419	0.552	0.684
	D	Yield	0.568	−0.033	−0.319	0.435	0.693
		HI	0.602	0.129	0.135	0.324	0.067
		TGW	0.592	−0.035	0.559	0	−0.013
Growing season during 2011–2012	Ir	Yield	0.762*	0.413	-0.555	0.814*	0.154
		HI	0.738*	0.366	−0.435	0.690	0.036
		TGW	0.685	0.415	−0.421	0.466	0.236
	D	Yield	0.829*	−0.046	−0.378	0.801*	−0.159
		HI	0.772*	−0.072	−0.517	0.610	−0.332
		TGW	0.596	0.570	−0.223	0.494	0.161

[a] Pn indicates the photosynthetic rate of flag leaves.
[b] LAI indicates the leaf area index.
* Significant at P = 0.05.

than that in the irrigation treatment (0.58%), and the SSI increased significantly over time (Table 2), indicating that the yield of modern cultivars are more sensitive to water deficits, in contrast to previous conclusions for Shaanxi (Chen et al., 2012). Fischer and Maurer (1978) explained that genotypes with an SSI of less than a unit are drought resistant because their yield reduction under drought is smaller than the mean yield reduction of all genotypes. A much greater improvement in both yield and drought resistance must be achieved for dry-land winter wheat yield in this region due to the highly drought-prone climate.

4.2. Associations between grain yield and other agronomic traits for dry-land wheat from the 1940s to the 2010s in Shaanxi Province

A significant genetic improvement in grain yield has always been attributed to an increased grain number, improvements in the TGW and HI and a reduced plant height (Aisawi et al., 2010; Donmez et al., 2001). Recent studies have shown that the grain yield in wheat has a stronger relationship with the kernel number per unit ground area than with the kernel weight (Brancourt-Hulmel

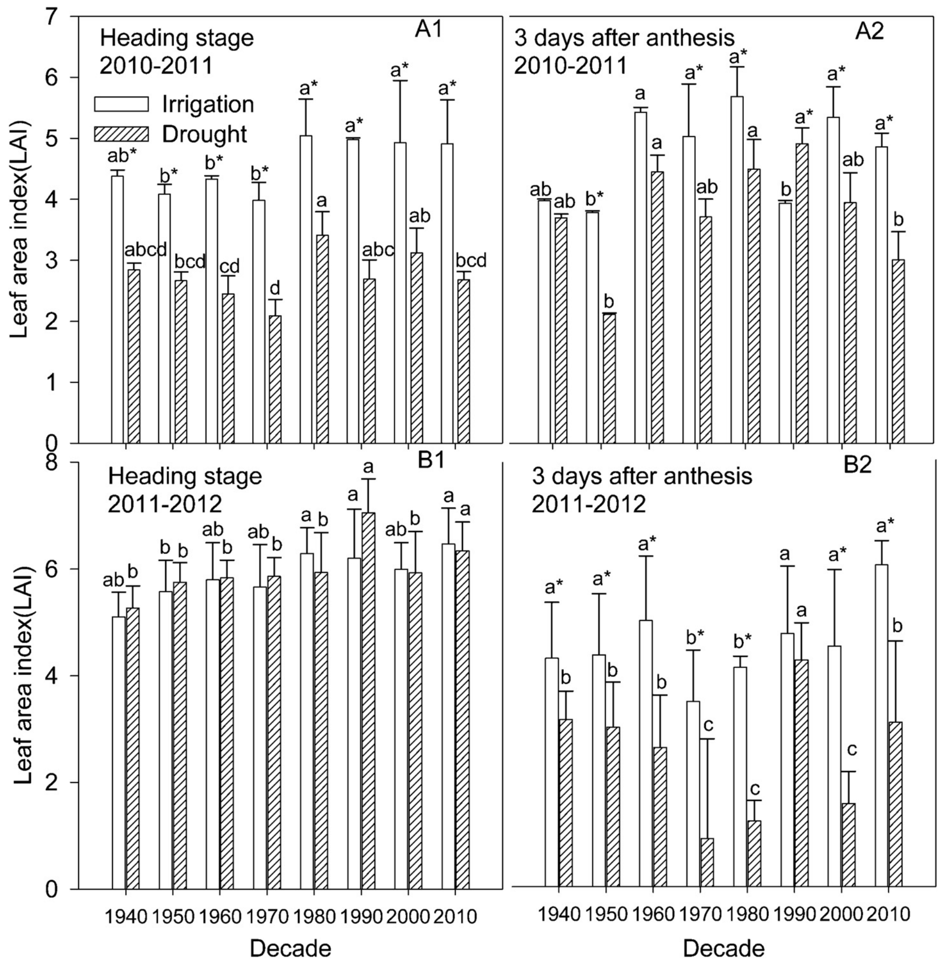

Fig. 5. Leaf area index measured under irrigation (blank bars) and drought (slash bars) treatments during 2010–2011 and 2011–2012. The data represent means ± SE and $N = 3$. The different lowercase letters above the bars denote significant differences for different cultivars under the same water treatment ($P = 0.05$); * significant differences for the same cultivar under different water treatments ($P = 0.05$).

et al., 2003; Sayre et al., 1997). Our study showed that a significant genetic improvement in the grain yield from the 1940s to the 2010s in Shaanxi Province was largely due to both the TGW and grain number per area (Table 3). This change in grain number per area was largely the result of an increase in the grain number per spike rather than the spike number, indicating that to avoid individual competition (Evans, 1993), breeders paid more attention to increasing the grain number than the tiller number when seeking to increase yield. Furthermore, the influence of the TGW on the grain yield was more important in the D treatment than in the Ir treatment due to a restriction of the tillers by water deficit (Naruoka et al., 2011). Therefore, further increases in the grain number per spike and TGW are considered the most likely way to improve the yield potential in the future.

Lodging has been a major limiting factor for wheat yield improvement (Peng et al., 2014). Short plant cultivars have lodging resistance as well as increased HIs and yield resulting from shortened internode distances (Austin et al., 1980). Plant height has been reduced through breeding (Canevara et al., 1994; McCaig and DePauw, 1995) with the introduction of dwarf (Rht2 and Rht1) or semi-dwarf genes. This study confirmed that the height at maturity of winter wheat in Shaanxi Province decreased markedly from 140.7 to 79.5 cm with the introduction of dwarf genes in wheat breeding. (Fig. 2). According to Richards (1992), the height necessary for high yields ranges from 70 to 100 cm, whereas cultivars with heights greater than 100 cm are prone to lodging (Richards, 1992). Based on the experience of Chinese wheat breeders, it is generally believed that the optimum plant height under irrigated conditions is approximately 80 cm (Zhuang, 2003). The cultivar of the 1990s achieved the highest yield and lowest SSI in the drought treatment in three successive seasons (Table 2), with the greatest height found for the cultivars from the 1970s to the 2010s (Fig. 2). Such findings are extremely rare (Austin et al., 1980; Zhuang, 2003). Cultivars with greater height might be useful in exploring breeding materials for drought resistance due to their high tiller number.

The wheat HI has a 60% ceiling (Austin et al., 1980), and comparisons of genetic progress of the HI in wheat indicate systematic increases over time with values reaching approximately 50% (Brancourt-Hulmel et al., 2003; Sayre et al., 1997). Despite the significant increase in the HI (Table 3) and positive correlation with yield (Table 4) since the 1940s, the highest HI for the cultivars planted in Shaanxi Province was only approximately 40% (Table 3), which was far below the reported value in North China (Zheng et al., 2011) and other countries (Foulkes et al., 2007; Reynolds et al., 1999). In addition, the HI has been nearly stable after the 1980s, without any obvious change. This finding might explain the limited production obtained from modern cultivars (Table 3). This low observed HI was most likely the result of the accumulation of a large proportion of carbohydrates in root tissues as an adaptation for drought resistance (Ma et al., 2008). Accordingly, there are potential opportunities for further improvement of the HI in Shaanxi Province.

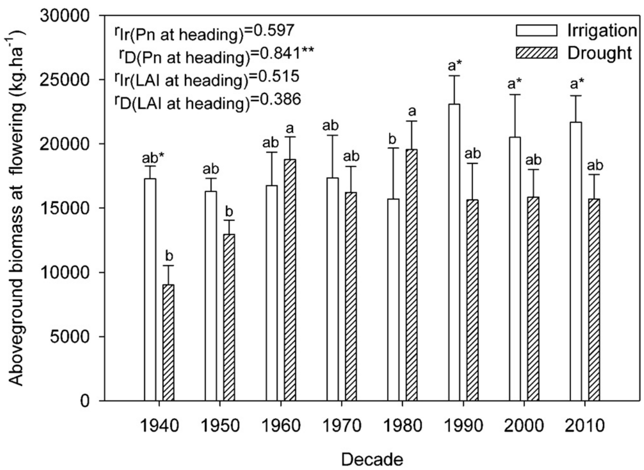

Fig. 6. Aboveground biomass at flowering and its relationship with Photosynthetic rate of flag leaf (Pn) and leaf area index (LAI) at heading stage under irrigation (blank bars) and drought (slash bars) treatments during 2011-2012. The data represent means ± SE and $N = 3$. The different lowercase letters above the bars denote significant differences for different cultivars under the same water treatment ($P = 0.05$); * significant differences in the same cultivar under different water treatments ($P = 0.05$); Ir indicates the irrigation treatment; D indicates the drought treatment.

4.3. Changes in photosynthetic traits and their associations with grain yield from the 1940s to the 2010s in Shaanxi Province

Photosynthetic capacity is important for the growth of crop plants (Parry et al., 2011). The Pn per unit of leaf area remains virtually unchanged (López-Castañeda et al., 1996; Richards, 2000), although it has been reported to increase with cultivar replacement (Fischer et al., 1998). The LAI and MTA are regarded as elements of the canopy light capture (Parry et al., 2011). In general, genotypes with upright leaves are less competitive than those having a more horizontal leaf orientation (Huel and Hucl, 1996). Many studies have described increases in the leaf area during the genetic improvement of cultivars (López-Castañeda et al., 1996; Richards, 2000; Tian et al., 2011). A leaf area index of 6 may be required to achieve 85% radiation interception, meaning that increasing the leaf area beyond a certain point will not greatly improve light interception (Parry et al., 2011). However, rapid leaf area growth is a beneficial trait in benign environments (Condon et al., 2004), whereas the same strategy could be disadvantageous in water-limited environments (Parry et al., 2005). Thus, genotypes with substantially greater leaf area expansion rates and LAI would be more prone to drought, especially after anthesis (Austin et al., 1980).

In this study, the Pn of the flag leaf at the heading stage was significantly increased (Fig. 3) and closely and positively associated with the grain yield from the 1940s through the 2010s (Table 5). However, no consistent change in the Pn or correlation between the yield and photosynthetic traits after anthesis was observed with cultivar replacement (Fig. 3, Table 5). It can be concluded that during wheat cultivar replacement in Shaanxi Province, the post-anthesis Pn had less of an effect on the grain yield accumulation compared to the Pn prior to anthesis. This conclusion is very different from the findings of previous reports (Fischer et al., 1998; Reynolds et al., 2000; Shimshi and Ephrat, 1975), suggesting that delayed senescence of the flag leaf is a valuable trait for increasing photosynthesis over the entire life cycle of modern wheat. However, the result does not mean that the post-anthesis period is less important than pre-anthesis in determining yields of dry-land wheat; as stem transport and ear photosynthesis are understood to have a greater contribution in modern cultivars than in older ones (Pheloung and Siddique, 1991; Maydup et al., 2012).

Our results regarding the LAIs and MTAs did not coincide exactly with those of previous reports (Richards, 2000; Tian et al., 2011) (Figs. 4 and 5). Modern cultivars with high yields consistently had higher LAIs at the heading stage (Fig. 5A1, B1), and the yield and HI showed positive correlations with the LAI at this stage (Table 5). However, this advantage decreased after anthesis (Fig. 5A2, B2), and the correlation of LAI after anthesis with yield and yield components was not obvious (Table 5). The MTA showed no consistent trend over time, meaning that the light interception ability of the modern cultivars does not vary substantially from that of the older cultivars despite the decrease in internodal distance (Fig. 4). The result suggests that in the modern dry-land wheat cultivars, high LAIs prior to anthesis tended to result in the accumulation of more photosynthetic product (Fig. 6); after anthesis, low LAIs can allow the plant to avoid the risk of excessive vegetative growth. This result is consistent with results reported in a previous study (Austin et al., 1980). In conclusion, high LAIs prior to anthesis and low LAIs after anthesis could be selection criteria for improving grain yield in the future. Canopy photosynthesis should be improved to increase the yield of cereals (Zhu et al., 2010). Furthermore, increases in the Pn and leaf area both before and after anthesis present potential modes for increasing dry-land wheat yield in Shaanxi Province.

5. Conclusions

Wheat production faces great challenges in China, particularly in arid and semi-arid areas, including Shaanxi Province, due to water shortages. This study suggests that the increases in TGW and HI accompanying the decrease in height over time have significantly improved the yield in Shaanxi. Modern cultivars were found to be more sensitive to drought, and genetic differences in the HI could be pivotal to continue improving the yield of dry-land wheat. Increases in the Pn and LAI at the heading stage may be productive because they could result in increased dry matter accumulation to improve TGW. Increased LAIs after anthesis might lead to an accumulation of a large proportion of aboveground biomass for reducing drought resistance, resulting in decreased grain yield.

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