Low contribution of photosynthesis and water-use efficiency to improvement of grain yield in Chinese wheat

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Abstract

The contribution of photosynthesis to yield improvement is important to know in order to determine future breeding strategies. The objectives of this study were to determine the contribution of photosynthesis and water-use efficiency (WUE) to grain yield improvement of facultative wheat (*Triticum aestivum* L.) cultivars on the Loess Plateau of China released between 1937 and 2004. The grain yield has increased nearly sevenfold during this period. Surprisingly, these increases were not correlated with the rate of photosynthesis per unit of leaf area when the cultivars were planted and managed in the same environment. The increases were also not correlated with transpiration rate, stomatal conductance, or WUE, except at the jointing stage. The total increase in photosynthesis may be due to enlargement of photosynthetic area and photosynthesis duration. The grain yield was positively correlated with the number of grains per unit of area ($r = 0.855$, $P<0.05$), harvest index (HI) ($r = 0.885$, $P<0.01$), and thousand-grain mass ($r = 0.879$, $P<0.01$). The increase in grain yield was limited by the grain number and the grain size (sink-limited) and the yield improvement was attributed to a rise in HI over the last 70 years in a highland agricultural system in China.

Additional key words: agronomic traits; flag leaf; grain number per area unit; highland agricultural system; jointing stage; rate of photosynthesis per leaf area unit; stomatal conductance; thousand-grain mass; transpiration rate; water-use efficiency; winter wheat.

Introduction

The average global grain yield of wheat (*Triticum aestivum L.*), maize, and rice more than doubled from 1940 to 1980 (Slafer 1994), coincidentally with important advances in our understanding of photosynthesis. A further increase in the production of biomass is likely by enhanced photosynthesis and with the maintenance of sink capacity. Agronomic, physiological, and botanical traits have been identified; it could potentially affect the wheat yield, including a kernel number, stomatal conductance, plant height, and duration of flag leaf area. While the enhancement of leaf P_N has paralleled the genetic improvement of wheat (Puckridge 1971, Peng *et al.* 1991, Jiang *et al.* 2000), some negative associations between photosynthesis and the grain yield have been reported (Evans 1993, Moll *et al.* 1994, Reynolds *et al.* 2000, Richards 2000). These studies focused on the relative influence of sink and source limitations on the wheat yield, *i.e.*, limitation by the grain number and mass or by photosynthate production. Richards (2000) suggested that photosynthate production in wheat and maize was not limiting, except for a period just before anthesis, and that crops possess a reserve capacity for photosynthesis under favourable conditions. Nevertheless, changes in photosynthetic parameters, such as P_N and g_s, can improve a yield potential (Puckridge 1971, Peng *et al.* 1991, Jiang *et al.* 2000). These findings were considered breakthroughs for overcoming a yield barrier. The relationship between P_N and the grain yield has continuously improved in recent years, but the debate continues (Frederick 1997, Richards 2000, Jiang *et al.* 2000, 2003).

A deficiency of rain for the growth of crops (*e.g.*,

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maize and soybean) frequently occurs on the Loess Plateau of China. The semidwarf wheat shows a strong adaption to dry environment and it contributes to the significant increase in wheat yields after the 1980s. In this study, we examined the relationships between the grain yield and leaf photosynthetic traits throughout the growth of semidwarf wheat. We examined these relationships more thoroughly in eight Chinese wheat cultivars developed during the period of 1937–2004 grown under the same environment.

Materials and methods

Site description: The field experiment was carried out at the Agro-ecological Experimental Station of the Chinese Academy of Sciences, Changwu county (35.12°N, 107.40°E, *ca*. 1,200 m a.s.l.), Shaanxi Province. The climate is warm and semiarid with mean daily air temperatures of 9.2 ± 2.3°C. Annual precipitation from 1990 to 2008 averaged 578 ± 69 mm, 55% of which occurred from July to September (Table 1). The soils are Cumuli-Ustic Isohumosols of the Chinese soil taxonomy (Gong *et al.* 2007) containing 11.6 g(organic C) kg^{-1}, 0.8 g(total N) kg^{-1}, 52.3 mg(available N) kg^{-1}, 0.7 g(total P) kg^{-1}, and 11.1 mg(available P) kg^{-1}.

Experimental design and management: Wheat had been grown at the site since September 2004. Samples were collected and measured from September 2007 to June 2008 and from September 2008 to June 2009. The plants received the same amounts of fertilisers [150 kg(N) ha^{-1} and 75 kg(P$_2$O$_5$) ha^{-1}], equivalent to the amounts used by local farmers. Our experiment included eight cultivars of winter wheat. These cultivars were the principal cultivars developed from 1937 to 2004. Most of the cultivars show similar developmental times (Table 2). The experiments were set in a randomised block design with three replicates; each replicate had eight rows of 7 m in length with 0.20 m between rows. Weeds were removed by hand in all treatments. Fungicides and pesticides were applied at jointing and grain filling stages to prevent diseases and pests. Wooden supports were constructed for the older cultivars, which are taller and tend to lodge. However, strong winds on the Loess Plateau continued to lodge these cultivars; it prevented them from attaining their yield potential.

Table 1. Meteorological conditions during the growing season. Maximum and minimum temperature are monthly averages. Precipitation is monthly totals.

Month	2007–2008				2008–2009			
	Maximum temperature [°C]	Minimum temperature [°C]	Average temperature [°C]	Precipitation [mm]	Maximum temperature [°C]	Minimum temperature [°C]	Average temperature [°C]	Precipitation [mm]
September	26.0	4.2	15.4	102.1	20.5	7.3	15.2	104.8
October	18.8	–4.5	9.1	73.8	15.0	5.8	10.3	46.2
November	19.5	–9.2	5.5	1.7	7.3	–2.7	2.2	9.2
December	8.3	–16.2	–1.3	7.7	5.6	–10.7	–1.4	0.0
January	1.1	–13.6	–7.0	16.8	2.5	–11.7	–3.3	0.0
February	4.0	–11.4	–4.1	11.0	6.7	–0.5	2.3	17.2
March	13.3	3.8	8.9	13.6	16.3	0.1	6.6	22.0
April	17.6	4.4	11.7	21.6	19.7	3.8	13.3	15.6
May	21.7	12.0	17.5	7.2	19.4	12.3	15.3	59.4
June	25.3	15.0	20.1	83.4	26.6	17.8	21.9	14.4
Total				338.9				288.8

Table 2. Representative cultivars of winter wheat released during a period of 1937-2004, with year of release, height, stem type, and date of flowering.

Cultivar	Year of release	Stem type	Height [cm]	Flowering date (May)
Wuzhi	1937	Tall	98.87	16
Hongtu	1939	Tall	101.07	15
Bima 1	1951	Tall	96.19	15
Zhengzhou 24	1965	Tall	94.17	15
Fengchan 3	1979	Tall	92.96	17
Changwu 131	1984	Semidwarfing	77.04	15
Changwu 134	1997	Semidwarfing	71.82	15
Changhan 58	2004	Semidwarfing	3.33	16

Wheat cultivars: We used eight wheat cultivars: Wuzhi, Hongtu, Bima 1, Zhengzhou 24, Fengchan 3, Changwu 131, Changwu 134, and Changhan 58. Wuzhi and Hongtu were launched before 1940 and were planted on more than 40% of the cultivated land on the Loess Plateau. However, their stems are tall, thus the plants got stuck in yields over 750 kg ha^{-1}. Bima 1 was bred in 1948 to resist lodging and disease. Bima 1 exhibited the yield 15–20% higher than the other cultivars at that time. Fengchan 3 was bred in 1964 and was planted on more than 2 million ha until 1976. Zhengzhou 24 was the first high-yield, drought-tolerant cultivar in the Henan Province. Changwu 131 and 134 were bred in 1984; the stems were short and highly resistant to stripe rust, powdery mildew, and lodging. Changhan 58 was authorised by the National Crop Variety Identification Committee of China in 2004. Plant height was 75–80 cm, the thousand-grain mass was 40.8 g, and yields were as high as 9,750 kg ha^{-1}.

Sampling and analytical procedures: The photosynthetic characteristics of the flag leaves were measured at the jointing, flowering, and grain filling stages with a *CID-340* portable photosynthetic apparatus (*CID Bio-Science*, Camas, USA). An intact, disease-free flag leaf was selected at each stage and its net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) were measured from 09:30 to 11:00. These measurements were used to calculate WUE (P_N/E). The measurements were taken at the atmospheric CO_2 concentration of 360–400 µmol m^{-2} s^{-1} and the flow rate of 400 mL min^{-1}. The instrument was equipped with an artificial light source. The light intensity was adjusted to 1,000–1,200 µmol(photon) m^{-2} s^{-1}, and the relative humidity was adjusted to 60–80%. The temperature was not controlled but was automatically recorded according to the ambient environment. We measured photosynthesis as soon as possible to minimize the influence of temperature.

The crops were sown *ca*. 25 September and harvested *ca*. 30 June every year. The crops were harvested at maturity at a ground level, and their aboveground biomasses and grain yields were measured after drying to a constant mass. The yield and biomass of each cultivar were calculated from the central four rows of each plot. HI was calculated as (grain mass)/(aboveground biomass). The grain number per unit of area and the thousand-grain mass were recorded for ten uniform plants. Spikes per ha were calculated from the counts of a half of each plot.

Statistical analysis: To determine the effect of photosynthesis on the yield, we examined the relationships between the yield and photosynthetic traits at the different growth stages of winter-wheat. We also examined the relationships between the photosynthetic traits and yield traits. These relationships were established by correlation regression analysis. Linear regressions between photosynthetic, yield traits, and the yield were established by least squares. Analysis of variance and regression were performed using *JMP 10.0* (*SAS Institute, Inc.,* Cary, NC, USA). Means were compared using *Fisher*'s protected least significant difference (*LSD*) tests. Differences were considered significant at *P*<0.05.

Results

P_N: The P_N of the flag leaves was higher at the flowering stage in the cultivars released between 1943 and 2004 (Fig. 1*B*), but the quadratic term for this relationship was not significant at this stage. Various cultivars showed the increased P_N at the jointing stage (Fig. 1*A*), ranging from 9.19 µmol m^{-2} s^{-1} for Wuzhi (released in 1937) to 13.35 µmol m^{-2} s^{-1} for Changhan 58 (released in 2004). A chronological trend was highly significant, whereby P_N increased by 0.051 µmol m^{-2} s^{-1} a^{-1}. The increase continued to the grain filling stage in all cultivars except Changhan 58 (2004) (Fig. 1*C*). The overall mean P_N increased by 12% from the jointing to the grain filling stage. The P_N was 56% higher in Changhan 58 (2004) than that of Wuzhi (1943), but the P_N of Zhenzhou 24 (the final tall wheat cultivar planted in this region and released in 1963), was higher than those of the other cultivars except Changhan 58 (2004).

E: The changes in E at the jointing stage were similar to the changes in P_N (Fig. 1*D*). A highly significant chronological trend was observed whereby E increased at 0.015 mmol m^{-2} s^{-1} a^{-1}. The E increased sharply at the flowering stage in the tall cultivars released before the 1980s, but did not change significantly in the semidwarf cultivars (Fig. 1*E*), so that the E did not consistently vary by the year of cultivar release. The E gradually increased after flowering, reaching a maximum at the grain filling stage (Fig. 1*F*). The average E of all cultivars increased by 94% from jointing to grain filling, and some cultivars released between 1937 and 2004, such as Hongtu (1939) and Changhan 58 (2004), exhibited rapid increases.

g_s: A decrease in g_s at the jointing stage was clearly observed in the cultivars from later release dates (Fig. 2*A*). The g_s of most cultivars was always lower at flowering and grain filling than that at the previous stage (Fig. 2*B, C*). The g_s increased at the grain filling stage in the cultivars released after the 1980s, especially, in Changwu 131 (1989) and Changwu 134 (1997). Compared to the tall cultivars, the average increase in g_s of the semidwarf cultivars was as large as 58% over the last 60 years, *i.e.*, from 123 to 194 mmol m^{-2} s^{-1}.
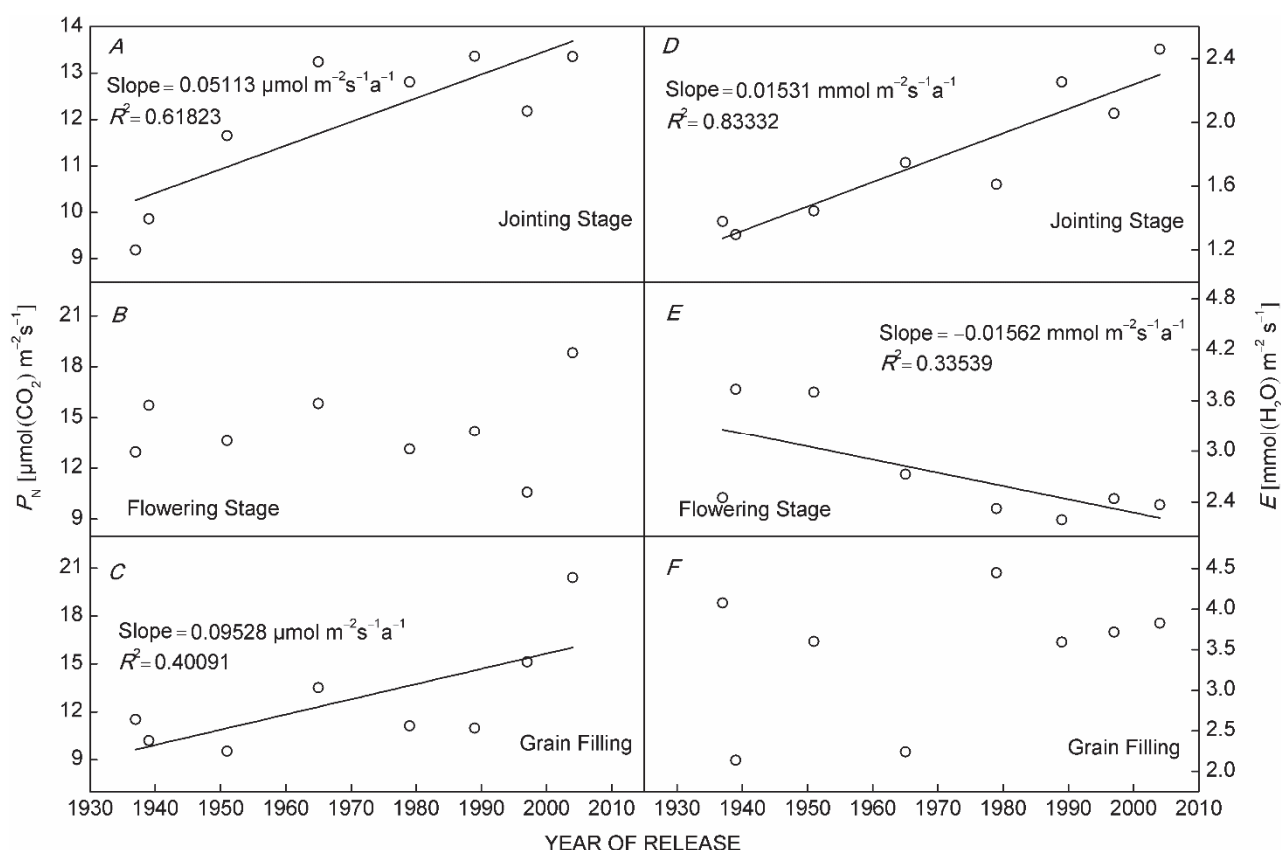
Fig. 1. Developmental stage-dependent changes in leaf net photosynthetic (P_N) and transpiration (E) rates of winter wheat cultivars released during 1937–2004 ($P<0.05$). $A – P_N$ at the jointing stage; $B – P_N$ at the flowering stage; $C – P_N$ at the grain filling; $D – E$ at the jointing stage; $E – E$ at the flowering stage; $F – E$ at the grain filling stage. Each point is a mean of 12 observations with 6 observations measured in 2008 and others in 2009.

WUE: The WUE of the flag leaf at the jointing stage decreased by 0.002% per year throughout the development of the newer cultivars (Fig. 2D), especially in those released after the 1980s, ranging from 55 to 74%. The WUE in the semidwarf cultivars remained roughly constant over the three growing seasons of the study period, but gradually decreased after jointing in the cultivars released before the 1980s, reaching a minimum at the grain filling stage (Fig. 2E, F). The changes in the WUE at the flowering and grain filling stages did not follow any obvious regular patterns throughout the development of the newer cultivars.

Grain yield and other agronomic traits: The grain yield increased significantly (from 2.62 to 4.19 t ha^{-1}) with a slope of 0.02 t ha^{-1} a^{-1}, when all cultivars released in different years were planted under the same conditions (Fig. 3C). The grain yield of the older cultivars increased about four-fold under favourable conditions, indicating that improvements in growing conditions contributed to much of the increase in the grain yield. The yields, however, were still more than 40% lower than those of the modern cultivars. The grain number per unit of area and the thousand-grain mass, which are two major determinants of the wheat yield, increased significantly by plant breeding in the last 60 years (Fig. 3A,B). The grain number per unit of area increased from 29.27 to 32.07 grains per spike, with a rate of 0.05 grains per spike a^{-1} and the thousand-grain mass increased from 29.01 to 44.05 g, at a rate of 0.28 g a^{-1}. The number of spikes per ha (Fig. 3D), another major determinant of the wheat yield, however, decreased at a rate of 0.03 million plants a^{-1}. Most of the increase in the yield was achieved by an increase in HI (Fig. 3F); it is surprising that increases in above-ground biomass were not observed (Fig. 3E) as in other studies (Austin *et al.* 1989).

Correlations between photosynthesis, yield traits and grain yield: A significant change in genetic gains for the wheat yield associated with the changes in E and g_s were observed in flag leaves only at the jointing stage (Table 3). P_N, E, and WUE were weakly correlated with the grain yield. The g_s was negatively correlated. The grain yield was generally positively correlated with the mean thousand-grain mass, the grain number per unit of area, and HI (Table 4). The spike number per ha, however, was negatively correlated with the grain number per unit of area, the thousand-grain mass,
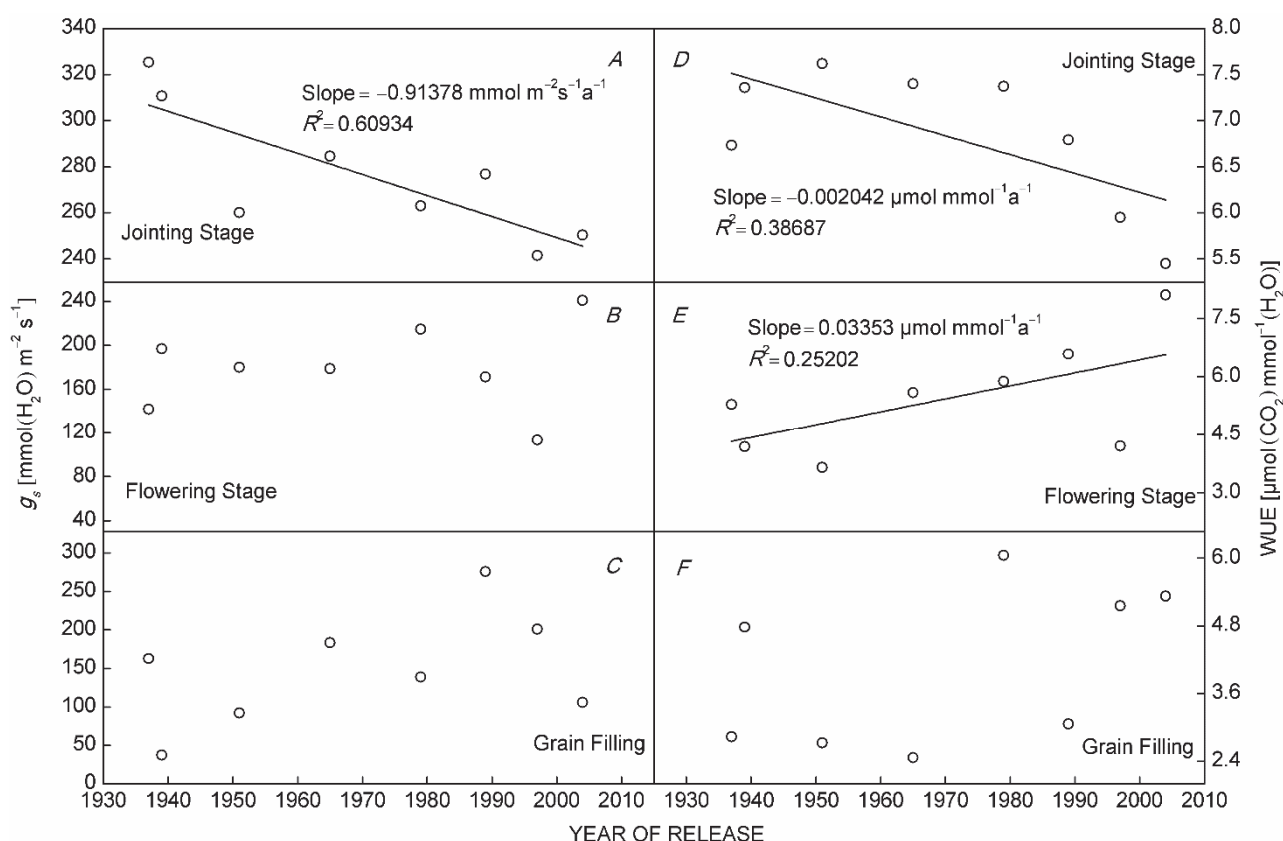
Fig. 2. Developmental-stage changes in leaf stomatal conductance (g_s) and water-use efficiency (WUE) of winter wheat cultivars released 1937–2004 ($P<0.05$). A – g_s at jointing stage; B – g_s at flowering stage; C – g_s at grain filling; D – WUE at jointing stage; E – WUE at flowering stage; F – WUE at grain filling. Each point is a mean of 12 observations which 6 observations measured in 2008 and others in 2009.

and HI. Harvest index was consistently and positively associated with various traits, such as P_N, the grain number per unit of area, and thousand-grain mass.

Photosynthetic traits differed significantly between the first (2007–2008) and the second (2008–2009) runs of the experiment (Table 5). Leaf P_N, E, g_s, and WUE decreased in the second-year experiment. Among the eight cultivars evaluated in the study, the semidwarf cultivars had a significantly higher P_N and WUE than that of the tall cultivars; E and g_s did not differ significantly between these two groups of cultivars. The cultivar, year, and the interaction for photosynthetic traits also did not produce any significant difference in the yield.

Discussion

In this experiment, none of the correlations between the four photosynthetic variables and the wheat yield were significant under favourable conditions ($P>0.05$), except for E and g_s at the jointing stage. Our results showed that the grain yield significantly increased with HI, but was not affected by P_N, suggesting that higher P_N does not necessarily lead to the higher grain yield. This result was consistent with the findings of Evans (1993). The increase in the grain yield was limited by the grain number and grain size (sink-limited) rather than by photosynthate production (source-limited), in agreement with the findings by Richards (2000). The absence of any relationship between leaf P_N and the enhancement of the grain yield was not due to the lack of genetic variation in photosynthesis. Although P_N was positively associated with HI, the factors related to HI are more closely associated with the yield than the factors related to photosynthesis in the selection process for increased yields, yet the former one is genetically more variable and shows higher heritability. The lack of correlation between genetic changes in P_N and the yield increase suggests that either leaf photosynthesis does not limit the grain yield and wheat may have an adequate photosynthetic capacity or that other factors are limiting. The determinants of sink strength should be a target for increasing the yield rather than selection for P_N in this semiarid rainfed agricultural region.
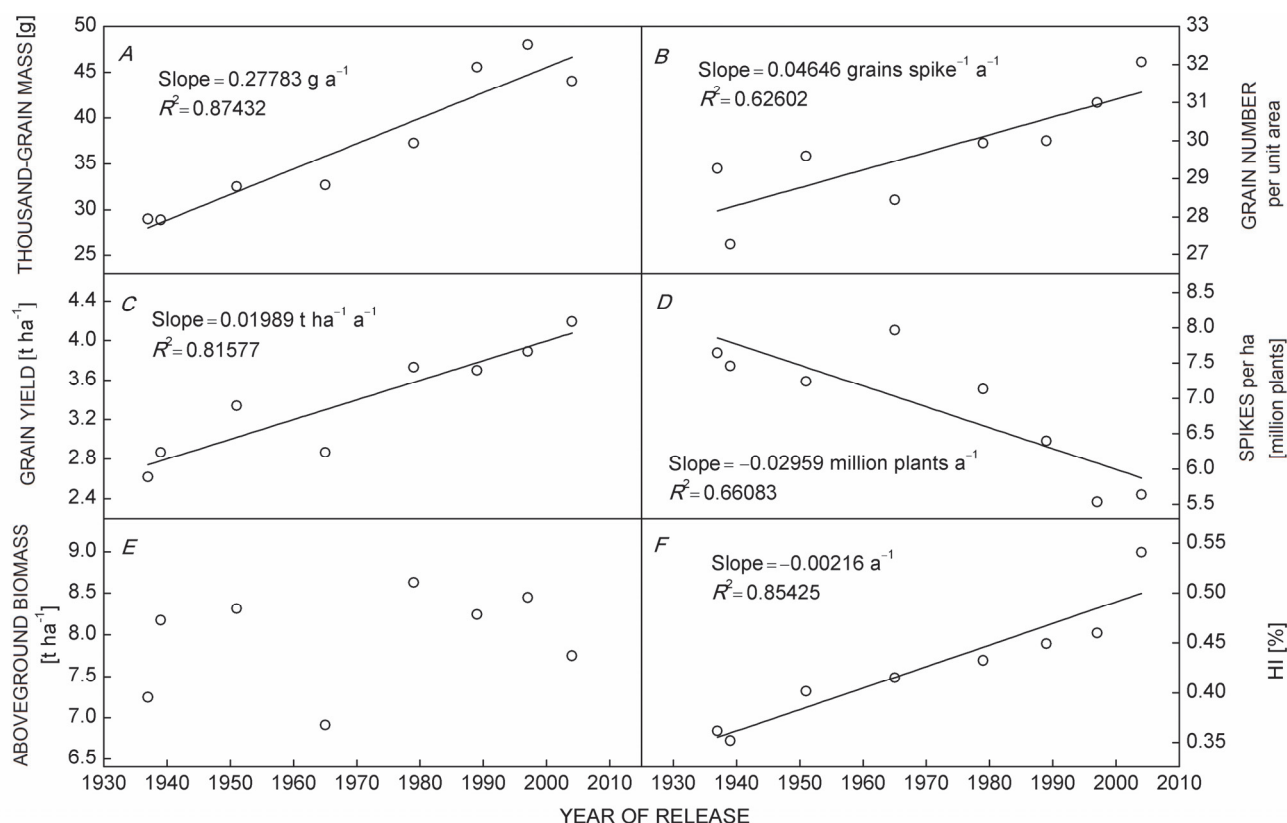
Fig. 3. Changes in thousand-grain mass (*A*), grain number per unit of area (*B*), grain yield (*C*), spikes per ha (*D*), aboveground biomass (*E*), and harvest index (HI) (*F*) of winter wheat cultivars released during 1937–2004 ($P<0.05$). Each point is a mean of six observations (three observations measured in each crop season), but Fig. 3*B* is a mean of 20 observations (10 observations measured in each crop season).

Table 3. Correlation coefficients between photosynthetic traits and the grain yield at different growth stages of winter wheat cultivars released during 1937–2004. P_N – net photosynthetic rate; E – transpiration rate; g_s – stomatal conductance; WUE – water-use efficiency. * – significant at $P=0.05$; ** – significant at $P=0.01$.

Variable	Jointing stage	Flowering stage	Grain filling	Mean
P_N	0.703	0.088	0.586	0.484
E	0.799*	−0.446	0.499	0.380
g_s	−0.879*	0.288	0.205	−0.061
WUE	−0.622	0.483	0.605	0.571

Table 4. Correlation coefficients between photosynthetic and yield traits and the grain yield during 2007–2008 and 2008–2009. P_N – net photosynthetic rate; E – transpiration rate; g_s – stomatal conductance; WUE – water-use efficiency; SN – spike number per ha; GN – grain number per unit of area; TGM – thousand-grain mass; ABG – aboveground biomass; HI – harvest index. .* – significant at $P=0.05$; ** – significant at $P=0.01$.

Variable	P_N	E	g_s	WUE	SN	GN	TGM	AGB	HI
Grain yield	0.568	0.677	0.014	0.575	−0.883**	0.855*	0.879**	0.564	0.885**
P_N		0.115	0.143	0.556	−0.493	0.579	0.464	−0.267	0.846**
E			−0.216	0.218	−0.595	0.759*	0.447	0.568	0.473
g_s				0.209	0.061	0.069	0.252	−0.302	0.182
WUE					−0.333	0.382	0.342	0.266	0.545
SN						−0.840**	−0.909**	−0.462	−0.795*
GN							0.793*	0.233	0.877**
TGM								0.411	0.822*
ABG									0.117

Table 5. Correlation coefficients bewtween yield and photosynthetic traits of the various cultivars during 2007–2008 and 2008–2009. No significant difference was found between year × photosynthetic traits, cultivar × photosynthetic traits, year × cultivar × photosynthetic traits and yield. P_N – net photosynthetic rate; E – transpiration rate; g_s – stomatal conductance; WUE – water-use efficiency.

Variable	P_N	E	g_s	WUE
Year				
2007-2008	16.58[a]	3.04[a]	241.15[a]	6.55[a]
2008-2009	10.33[b]	2.30[b]	135.53[b]	4.81[b]
Cultivar				
Wuzhi	11.21[b]	2.64[a]	179.08[a]	4.95[b]
Hongtu	13.03[ab]	2.48[a]	185.51[a]	5.90[b]
Bima 1	11.60[b]	2.92[a]	146.64[a]	4.67[ab]
Zhengzhou 24	15.12[ab]	2.31[a]	188.02[a]	5.16[ab]
Fengchan 3	12.35[b]	2.79[a]	207.71[a]	6.66[a]
Changwu 131	13.77[ab]	2.51[a]	223.81[a]	6.04[ab]
Changwu 134	13.05[ab]	2.86[a]	176.96[a]	5.76[ab]
Changhan 58	17.52[a]	2.89[a]	199.00[a]	6.29[ab]
Interaction	F value			
Year	0.635	0.911	0.995	0.679
Cultivar	0.480	0.226	0.697	0.468
Year × cultivar	0.480	0.478	0.506	0.535

In addition, variations in leaf E for wheat occured due to differences in g_s (Condon et al. 1990, Martin et al. 1994, Morgan and LeCain 1991). In our study, the semidwarf cultivars had generally the higher g_s at the grain filling stage (Fig. 2C), resulting in higher transpiration (Fig. 1F) relative to the tall cultivars. The extent to which variation in conductance affects E is dependent on boundary-layer conductance in the field (Condon et al. 1990, Jarvis 1986), but the higher g_s might enhance transpiration per unit of leaf area in the present study. This enhanced transpiration might increase the photosynthetic capacity as it was observed in the semidwarf cultivars at grain filling. However, the highly significant chronological trend of release dates was observed, whereby the E increased at the jointing stage (Fig. 1D). Conversely, WUE declined with the release date at the same stage, and this stage was affected mostly by the accumulation of dry matter under water deficit. Breeding, though, increased the yield. Leaf WUE may have no effect on yield; WUE was not significantly correlated with the yield.

Genetic changes in P_N, E, g_s, and WUE did not accompanied the yield increases. We tried to deduce the physiological mechanisms of leaf photosynthesis during the development of the newer cultivars from three aspects.

First, increase in P_N in individual leaves does not necessarily accompany increase in the grain yield. Cao (1998) suggested that measurements of P_N should be restricted to certain periods or times of day. The total increase in photosynthesis is the result of enlargement in leaf area, daily duration of photosynthesis, or duration of leaf area rather than the increase in leaf P_N (Crosbie et al. 1978, Evans 1993, Richards 2000). Crop physiologists have demonstrated an association between breeding for the yield and the variables of gas exchange in leaves, particularly for increased photosynthetic activity (Evans 1993, Austin 1994). The formula for the grain yield = [(photosynthetic area × photosynthetic capacity × photosynthetic time) − consumption] × economic coefficient, (where consumption is mainly the consumption by respiration, and the economic coefficient is the ratio of grain mass to total dry mass) can adequately describe the relationship between the wheat grain yield and photosynthesis. Photosynthetic capacity, though, had no significant effect on the yield, which was more likely dependent on photosynthetic area and photosynthesis duration. Our results may reflect the long days and high light intensities of this highland agricultural system on the Loess Plateau. We did not measure the photosynthetic area and photosynthesis duration, but it should be also tested.

Second, wheat plants may not need genetically improved photosynthesis. An analysis of growth in transgenic tobacco plants with antisense *rbcS* (to decrease Rubisco) demonstrated the buffering capacity of processes important for photosynthesis. The Rubisco content decreased to about one half that of the wild-type before the rate of photosynthesis began to decline, when the nitrogen supply was adequate (Quick et al. 1991). Even when the rate of photosynthesis declines in transgenic tobacco plants, growth may not necessarily decline, because the specific leaf area can increase and can partly compensate for the decreased rate of photosynthesis (Fichtner et al. 1993), although this effect may vary with light intensity (Stitt et al. 1991). It is important to consider whether selection for high rates of leaf photosynthesis could be effective. Crops may possess reserve capacities for photosynthesis, as suggested by their responses to favourable conditions and photosynthetic responses to altered sources and sinks (Richards 2000). The management practices might be a substitute for genetic changes in photosynthesis. Enhanced fertilisation with nitrogen may be a quick and relatively inexpensive substitute for genetic increases in total photosynthesis. If breeding trials are conducted under favourable nutrient conditions, as they usually are, then the selection pressure for increased photosynthesis may be low, because the favourable nutrient status of the soil is producing a higher rate of photosynthesis. However, is difficult to distinguish between the effects of genetic increases in photosynthetic duration and those due to better nutrition, genetic resistance to foliar diseases, genotypic differences in nitrogen allocation to seeds, or increased demand for photosynthates due to sink strength. The relationship between single-leaf photosynthesis and the grain yield is very complicated and many uncertainties are continually demonstrated.

Third, the improvement in HI mediated by two heritable traits, such as height and flowering time, proved to be simpler than photosynthesis. Cultivars with dwarfing genes reduce lodging, thus allowing more fertilizers to be used by plants under adequate rainfall or suitable irrigation system. Higher inputs of fertilizers and proper irrigation definitely result in substantially greater crop yields. In addition, the increase of HI in wheat can be maintained with dwarfing genes without compensation of aboveground biomass, thereby resulting in greater yields. Appropriate flowering time has been the single most important factor to maximize the yield and adaptation in dry environments (Richards, 1991). In the further northern wheat belt, where there is no frost risk, autumn sown crops reach anthesis during middle of the winter, which is essential for obtaining the highest wheat yields (Woodruff 1983). Later it was found that the yield declines 1.2% per day during the anthesis period, provided that the preanthesis growth was accurate. Cultivars can be more appropriately developed by the photoperiodic delay of floral initation.

In conclusion, changes in leaf photosynthesis had no significant effect on the yield during the last 70 years in this highland agricultural system on the Loess Plateau, despite some genetic variation in photosynthetic ability. The enhancement of the grain yield in the wheat cultivars was associated with the increases in the grain number per unit of area, thousand-grain mass, and HI.

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