Contribution of ear photosynthesis to grain yield under rainfed and irrigation conditions for winter wheat cultivars released in the past 30 years in North China Plain

WANG Yun-qi, XI Wen-xing, WANG Zhi-min, WANG Bin, XU Xue-xin, HAN Mei-kun, ZHOU Shun-li, ZHANG Ying-hua

College of Agronomy and Biotechnology, China Agricultural University, Beijing 100193, P.R.China

Abstract
To understand the contribution of ear photosynthesis to grain yield and its response to water supply in the improvement of winter wheat, 15 cultivars released from 1980 to 2012 in North China Plain (NCP) were planted under rainfed and irrigated conditions from 2011 to 2013, and the ear photosynthesis was tested by ear shading. During the past 30 years, grain yield significantly increased, the flag leaf area slightly increased under irrigated condition but decreased significantly under rainfed condition, the ratio of grain weight:leaf area significantly increased, and the contribution of ear photosynthesis to grain yield changed from 33.6 to 64.5% and from 32.2 to 57.2% under rainfed and irrigated conditions, respectively. Grain yield, yield components, and ratio of grain weight:leaf area were positively related with contribution of ear photosynthesis. The increase in grain yield in winter wheat was related with improvement in ear photosynthesis contribution in NCP, especially under rainfed condition.

Keywords: wheat, ear photosynthesis, grain yield, improvement of cultivars

1. Introduction
Wheat is the third leading crop in China after rice and maize (Zheng et al. 2011). The rising Chinese population and the rapid growth of the economy have resulted in an increasing demand for wheat (Triticum aestivum L.) in the following decades (Zhou et al. 2013). The planting area in China is shrinking (Zhang et al. 2008; Zhou et al. 2013; Xue et al. 2014). Therefore, it is necessary to further increase yield per unit area of wheat. Water shortage is a serious issue threatening the sustainable development of agriculture in North China Plain (NCP) (Zheng et al. 2014). The rainfall during winter wheat growth can only meet 25–40% of requirement, leading to a deficit for 200–300 mm water in the northern part of the NCP (Liu et al. 2001; Zhang et al. 2006; Liu et al. 2013), due to the summer monsoon climate and climate change (Piao et al. 2010). Hence, an irrigation of more than 400 mm water was applied, carried out 3–4 times per season, achieving high grain yield of wheat (Zhang et al. 2003). However, overdraft of groundwater has resulted in a rapid decline in the groundwater table, threatening sustainable agricultural development in this region (Wang et al. 2002; Kendy et al. 2003, 2004; Foster et al. 2004). Consequently, it was imperative to adopt water-saving ag-

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rice to achieve the largest possible increase in water use efficiency (WUE) of crops (Wang et al. 2002), keeping yield of winter wheat. Researchers at China Agricultural University have developed a water-saving farming system at the Wupiao Experimental Station, Hebei, China (Li and Zhou 2000). In this system, we found that high yields can be achieved under reduced irrigation (e.g., two times irrigations instead of four times irrigations) and higher seeding rates (>600 plant m⁻²) (Zhang et al. 2011). With the further decrease in irrigated water resource in future, wheat production may be transformed to rainfed planting in NCP.

Wheat leaves, especially flag leaf, are important photosynthetic assimilation organs during jointing stage and anthesis. But the ear assumes a greater role than flag leaves in supplying assimilates to the grain when drought stress develops (Evans et al. 1972; Johnson and Moss 1976; Blum 1985). Chlorophyll contents of non-leaf organs, such as ear, stem and leaf sheath, slowly decrease, and these organs still exhibit a certain degree of photosynthesis in the late grain filling (Lu and Lu 2004). Wheat spike possesses several advantages, which include vast space for receiving light and CO₂, strong ability of osmotic adjustment, greater surface area than flag leaf (Blum 1985), a higher relative water content (Tambussi et al. 2005), and maintenance of a relatively high photosynthetic rate under drought conditions (Tambussi et al. 2007). Whole-organ photosynthesis was much higher in the ear than in the flag leaf in well-watered conditions, and as water stress developed, photosynthesis decreased less in the ear than in the flag leaf (Abbad et al. 2004). In addition, higher WUE of ear parts than that of the flag leaf is suggested by their lower Δ¹³C (Tambussi et al. 2007). Genotypic variation in ear morphology is linked to differences in photosynthetic potential to influence grain yield in winter wheat (Rebetzke et al. 2016).

The relative contribution of ear photosynthesis to grain yield was more important under abiotic stress (Abbad et al. 2004; Tambussi et al. 2007; Zhang et al. 2013). It may be an important index for cultivar selection in rainfed wheat production. Jiang et al. (2003) reported that the wheat production in North China increased significantly in recent 50 years. However, ear as an important organ of grain yield formation, the change of contribution of ear photosynthesis to grain yield during the improvement of winter wheat cultivars is still unclear in China. The response of ear photosynthesis contribution to water supply need to be further studied.

Consequently, the objectives of the paper are to (i) examine the contribution of ear photosynthesis to grain yield and the flag leaf characters of wheat cultivars widely cultivated in China from 1980 to the 2012; (ii) clarify the difference in ear photosynthesis contribution and flag leaf characters between the rainfed and irrigated conditions.

2. Materials and methods

2.1. Experimental field and meteorological conditions

The field experiments were conducted from 2011 to 2013 at Wupiao Experiment Station of China Agricultural University (37°41’N, 116°37’E, 18 m above sea level), Hebei Province, China. Total annual sunshine hours is 2724.8 h, with an average temperature of 12.9°C. Average frost free growing days are 201 days with annual total precipitation amounts of 562 mm. The precipitation is mainly distributed from June to August.

Soil was clayloam with an average bulk density of 1.5 g cm⁻³ in the upper 100 cm layer. The topsoil (0–20 cm) had a pH of 7.8 (Zhao et al. 2015). This field had 11.2 g kg⁻¹ organic matter, 0.8 g kg⁻¹ total N, 18.2 mg kg⁻¹ available P, and 76.8 mg kg⁻¹ K at 0–40 cm soil layer. The underground water level was 6–9 m (Zhang et al. 2011). There was 640 mm maximum water storage, 420 mm available water storage, a soil moisture at the maximum field capacity of 21.7% and a wilting coefficient of 7.6% in the upper 200 cm soil layer (Zhang et al. 2011). Climatic data and changes of soil water content during the two growing seasons of the experiment were given in Figs. 1 and 2.

2.2. Plant materials and experimental design

Fifteen winter wheat cultivars widely cultivated in NCP from 1980 to 2012 were used in this work. They were Fengkang 13 (released in 1980), Fengkang 8 (1983), Jing 411 (1991), Hennong 341 (1998), Jinan 17 (1999), Han 6172 (2001), Shimai 8 (2001), Weimai 8 (2003), Kemai 1 (2003), Henggui 35 (2004), Jimai 22 (2006), Nongda 211 (2007), Liangxing 66

Fig. 1 Monthly rainfall distribution (bar) and mean temperature (line) during winter wheat growing stage in 2011–2012 and 2012–2013.
experiments received 225 kg N ha\(^{-1}\) each cultivar) were arranged in randomized blocks. All a row space of 15 cm. The plots (10 m\(^{\times}\)6 m per plot for seeding, before each irrigation application and at harvest. Soil water content (%) was determined gravimetrically at 2.3. Data acquisition and October 10, 2012 with a density of 450 plants m\(^{-2}\) and Seeds of the 15 cultivars were planted on October 10, 2011 condition (75 mm at jointing stage and 75 mm at anthesis). rainfed condition (without irrigated in spring) and irrigated experiment was designed as a split-plot experiment with (2008), Heng 4399 (2008), Nongda 399 (2012). No fertilizer was applied during growth. Near anthesis (as ammonium monoacid phosphate), 150 kg K ha\(^{-1}\) (as potassium sulfate), and 75.0 mm irrigation before sow- ing. No fertilizer was applied during growth. Near anthesis (GS65, Zadoks \textit{et al.} 1974), 30 primary culms flowering on the same day with similar plant height and ear length in the four central rows of all the plots were tagged for observation and measurement. In order to estimate the contribution of ear photosynthesis to grain yield, 10 spikes from the tagged culms in each plot were kept dark by covering with aluminum foil with 1 mm-diameter holes (at least 15 mm apart, representing about 0.3% of the covered area) from day 7 after 50% of anthesis to physiological maturity, preventing accumulation of ethylene and water vapor, according to the method of Araus \textit{et al.} (1993).

2.3. Data acquisition

Soil water content (%) was determined gravimetrically at seeding, before each irrigation application and at harvest. Soil samples were taken from 0 to 200 cm in layer segments of 20 cm by using a ground auger, and dried at 105°C to constant weight.

Plant height, the length, width, area and dry matter of flag leaf and the SPAD chlorophyll readings (SPAD-502, Minolta Co. Ltd., Osaka, Japan) in flag leaf were measured at anthesis in 2013. At maturity, winter wheat was harvested from 4 m\(^{\times}\)1.5 m in each plot with one replicate of 1.5 m\(^{2}\) to determine grain yield, and 10 intact and shaded ears from each plot were harvested, counted and weighed to determine grain weight per ear, grain number per ear and individual grain weight in 2012 and 2013. The contribution of ear photosynthesis to grain yield, the ratio of grain weight:leaf area, and specific leaf weight of flag leaf were calculated as the equations below:

Ear contribution to grain yield (%)=\(\frac{\text{GW of non-shaded ear}}{\text{GW of shaded ear}}\)×100

\text{Ratio of grain weight:leaf area of flag leaf (mg cm}^{-2}\text{)=\frac{\text{Grain weight per ear}}{\text{Flag leaf area per culm}}\text{)}

\text{Specific leaf weight of flag leaf (mg cm}^{-2}\text{)=\frac{\text{Dry matter of flag leaf}}{\text{Flag leaf area per culm}}}\text{)}

2.4. Data analysis

The statistical analysis was performed with the SAS software package (SAS 2002). Figs. in the paper were finished by Sigmaplot12.0. The effects of year (Y), irrigation (I), cultivars (C) and their interactions (Y\(\times\)I, Y\(\times\)C, I\(\times\)C, Y\(\times\)I\(\times\)C) were analyzed by analysis of variance (GLM) (SAS 2002). Correlation analysis was finished by PROC CORR proce-
3. Results

3.1. Grain yield, yield components and contribution of ear photosynthesis to grain yield

In this study, grain yield showed a zigzag growth under rainfed and irrigated conditions (Fig. 3). In cultivar released in 1980, grain yield was 4 649.9–4 868.3 and 4 965.5–5 571.6 kg ha⁻¹ under rainfed and irrigated conditions, whilst in cultivar released in 2012 they were 8 972.2–9 744.1 and 10 643.2–11 806.2 kg ha⁻¹, respectively (Fig. 3). Grain yield was significantly and positively correlated with the year of cultivar release (Fig. 3). Grain weight per ear was improved from 979.8–1 002.6 and 1 016.3–1 094.1 mg ear⁻¹ in cultivar released in 1980 to 1484.8–1648.2 and 1 667.8–1 827.8 mg ear⁻¹ in cultivar released in 2012 under rainfed and irrigated conditions, respectively (Fig. 4-A). Grain weight per ear was significantly and positively correlated with the year of cultivars release under rainfed (P<0.0001) and irrigated (P<0.0001) conditions, and it was higher in irrigated condition than in rainfed condition (Fig. 4-A). There was also a linear increase in grain number per ear and individual grain weight from old to modern cultivars, and the grain number per ear was higher in irrigated condition than in rainfed condition, individual grain weight was higher in rainfed condition than in irrigated condition (Fig. 4-B and C). For an example, the grain number per ear of Nongda 399 (released in 2012) was 18.2–27.2% and 22.5–44.4% higher than those of Fengkang 13 (released in 1980) under rainfed and irrigated conditions, respectively. Similarly, the individual grain weight of Nongda 399 increased by 25.3–32.2% and 24.5–24.6% as compared with Fengkang 13 under rainfed and irrigated conditions, respectively.

The contribution of ear photosynthesis to grain yield was significantly and positively correlated with the year of cultivar release (rainfed: R²=0.65, P<0.0001; irrigated: R²=0.54, P<0.0001), and it was higher in irrigated condition than in rainfed condition (Fig. 4-D). For an example, the contribution of ear photosynthesis to grain yield of Nongda 399 increased by 26.6–38.2% and 21.0–26.5% under rainfed and irrigated condition, respectively, compared to Fengkang 13. In addition, the gap for the ear photosynthesis contribution between rainfed and irrigated conditions increased from old to modern cultivars (Fig. 4-D).

The cultivar, irrigation and their interaction significantly affected grain yield, grain weight per ear, grain number per ear, individual grain weight, and the contribution of ear photosynthesis to grain yield (Table 1). It was recorded that grain yield, grain weight per ear, grain number per ear, and individual grain weight was significantly and positively correlated with contribution of ear photosynthesis to grain yield (Table 2). These results indicated that the improvement of grain yield in modern winter cultivar is due to greater grain number per ear, higher individual grain weight and more contribution of ear photosynthesis to grain yield.

3.2. Main morphological traits of flag leaf, ratio of grain weight:leaf area and plant height

The flag leaf (FL) was the functional leaf of winter wheat. The FL length, width, area, and dry matter under irrigated condition were always higher than those under rainfed condition (Fig. 5-A–D). The FL length was dropped from 18.7 cm of Fengkang 13 (released in 1980) to 14.1 cm of Nongda 399 (released in 2012) under rainfed condition, and it was significantly negatively correlated with year of cultivars release (R²=0.69, P<0.0001), whereas there was no significant change under irrigated condition for the cultivars in the past 30 years (Fig. 5-A). The gap of FL length between rainfed and irrigated conditions became large from old to modern cultivars (Fig. 5-A). There was little change of FL weight in the past 30 years under both conditions (Fig. 5-B). The change trend of FL area was similar to FL length from 1980 to 2012 (Fig. 5-C), the phenomenon was accounted for a decrease of FL length (Fig. 5-A). There was a significant (R²=0.38, P<0.05) increase in the dry matter of FL from old to modern cultivars under irrigated condition, while no significant change occurred under rainfed condition (Fig. 5-D). It was higher under irrigated condition than under rainfed condition, and the gap between rainfed and irrigated condition became larger from old to modern cultivars (Fig. 5-D). The irrigation, cultivar and its interaction significantly (P<0.0001) affected the length, width, area and dry matter of flag leaf (Table 3). These results indicated that the leaf of modern cultivars was more sensitive to drought, and easy to become smaller under drought stress.

The specific leaf weight of FL was higher under rainfed condition than under irrigated condition for the cultivars released in 1980–2012 (Fig. 5-E). It was increased from 3.7 mg cm⁻² in 1980 to 5.0 mg cm⁻² in 2012 and from 4.0 mg cm⁻² in 1980 to 4.3 mg cm⁻² in 2012 under rainfed and irrigated condition, respectively (Fig. 5-E). It was significantly (rainfed, R²=0.30, P<0.05; irrigated, R²=0.32, P<0.05) and positively correlated with year of cultivars release (Fig. 5-E), because the FL area dropped and its dry matter changed little (Fig. 5-C and D). The FLSPAD value was higher under rainfed condition than under irrigated condition for the cultivars released in 1980–2012 (Fig. 5-F). It was increased from 52.8 in 1980 to 59.4 in 2012 and from 52.7 in 1980 to 58.0 in 2012 under rainfed and irrigated conditions, respectively (Fig. 5-F). It was significantly (rainfed, R²=0.72, P<0.0001; irrigated, R²=0.56, P<0.01) and positively correlated with...
Fig. 3 Gain yield of the 15 cultivars under rainfed and irrigated conditions during 2011–2012 (A) and 2012–2013 (B). Each point represents mean ± SE of four replicates for each cultivar. * and ** indicate significances at $P<0.05$ and $P<0.01$, respectively. The same as below.

Fig. 4 Gain weight per ear (A), grain number per ear (B), individual grain weight (C), and contribution of ear photosynthesis to grain yield (D) of the 15 cultivars under rainfed and irrigated conditions during 2011–2012 and 2012–2013. Each point represents the mean of four replicates for each cultivar. *** and **** indicate significances at $P<0.001$ and $P<0.0001$, respectively. The same as below.
year of cultivars release (Fig. 5-F). The irrigation, cultivar and its interaction significantly ($P<0.0001$) affected the specific leaf weight and SPAD value of FL (Table 3).

In order to analyze the relation between flag leaf (FL) and grain yield, the ratio of grain weight to FL area (it represents the grain yield per flag leaf area) was calculated (Fig. 6-A). The irrigation, cultivar and its interaction significantly ($P<0.0001$) affected the ratio of grain weight:leaf area (Table 3). It was increased from 45.9 mg cm$^{-2}$ in 1980 to 88.7 cm in 2012 and from 125.6 cm in 1980 to 38.4 cm in 2012 under rainfed and irrigated conditions, respectively. The correlation between flag leaf length and year of cultivar release was significant ($P<0.05$) and negative (Fig. 6-B).

### 4. Discussion

In present study, the contribution of ear photosynthesis to grain yield increased with the year of cultivar release (Fig. 4-D), and grain yield, grain number, grain weight were significantly and positively correlated with the contribution of ear photosynthesis under rainfed condition (Table 2). These results indicated that the ear photosynthesis played more important role in modern winter wheat cultivars especially under rainfed condition. An important contribution of wheat ear photosynthesis to grain yield was observed in some other studies, it was apparently more significant under water deficit (Abbad et al. 2004; Reynolds et al. 2005; Maydup et al. 2010). Araus et al. (1993) reported that the contribution of ear photosynthesis to grain yield was 59.0%, and Jia et al. (2015) found it was 25.1% in his study, while the present study showed that the contribution of ear photosynthesis to grain yield was 33.6–64.5% and 32.0–53.2% under rainfed and irrigated conditions, respectively. The estimated contribution of ear photosynthesis to grain yield differed depending on the experimental approach used (Maydup et al. 2010). Additionally, the timing of covering
Fig. 5 Flag leaf length (A), flag leaf width (B), flag leaf area (C), dry matter of flag leaf per culm (D), specific leaf weight of flag leaf (E), and flag leaf SPAD value (F) of the 15 cultivars at anthesis under rainfed and irrigated conditions in 2012–2013.

Table 3 P-values from ANOVA testing effect of irrigation (I), cultivar (C) and their interaction on FLL, FLW, FLA, FLDM, FLSPAD, PH, and GLR in winter wheat in 2012–2013

<table>
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<th>Factors</th>
<th>FLL</th>
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<th>FLA</th>
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<th>PH</th>
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<tr>
<td>I</td>
<td>22 106.10****</td>
<td>1 159.18****</td>
<td>33 071.20****</td>
<td>25 246.40****</td>
<td>119.70****</td>
<td>32 078.10****</td>
<td>4 074.88****</td>
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<tr>
<td>C</td>
<td>286.90****</td>
<td>193.92****</td>
<td>313.58****</td>
<td>586.23****</td>
<td>79.75****</td>
<td>2 091.43****</td>
<td>1 543.93****</td>
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<tr>
<td>IxC</td>
<td>240.60****</td>
<td>23.43****</td>
<td>322.49****</td>
<td>230.93****</td>
<td>12.88****</td>
<td>5 916.55****</td>
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Fig. 6 Ratio of grain weight:leaf area (A) and plant height (B) of the 15 cultivars under rainfed and irrigated conditions during 2012–2013.
ear might affect the contribution of ear photosynthesis to grain yield, and the action of shaded ear may change canopy structure and influence leaf photosynthesis, which also affect the contribution of ear photosynthesis to grain yield. Zhang et al. (2014) found that spike shading increased the photosynthetic rate ($P_r$) of flag leaf in source limited cultivar, but had no significant effect on sink limited cultivar. Meanwhile, Maydup et al. (2012) also reported that contribution of wheat ear photosynthesis to grain filling increased in modern durum wheat under favorable environment condition. In fact, there were significant ($P<0.0001$) effects of cultivar, irrigation and irrigation×cultivar on contribution of ear photosynthesis to gain yield in wheat (Table 1). Additionally, there might be tiller numbers and spike density effects on ear weight and contribution of ear photosynthesis to grain yield. It had been reported that increasing seeding rate increased the contribution of ear photosynthesis to grain yield due to high spike density resulting in high ear photosynthesis in population (Zhang et al. 2013).

The increase in ear contribution under rainfed condition was related with the decrease in flag leaf area (Table 2). Under rainfed condition, flag leaf width had no significant change, whereas flag leaf length reduced significantly, resulting in the marked fall in flag leaf area with the year of cultivar release (Fig. 5-A–C). These results indicated that the flag leaf of modern cultivars was more sensitive to drought, and easy to become smaller than old cultivar under drought stress. Our previous research also showed that the area of top three leaf blades decreased and the proportion of green non-leaf organ area to the total green area at anthesis increased with the decreasing of water supply (Zhang et al. 2011). It can be seen from these discussions that flag leaf was more sensitive to water stress than ear. So, the improvement of cultivars in the future should decrease the sensitivity of leaf to water stress by selecting short and thick leaf on one hand, on the other hand increase the ear contribution further by improving the tolerance to high density.

The specific leaf weight, flag leaf SPAD value and the ratio of grain weight:leaf area were significantly and positively correlated with the year of cultivars release under rainfed and irrigated conditions (Fig. 5-E, F and 5-A), and the flag leaf dry matter and SPAD value at anthesis were positively correlated with grain yield and ear contribution (Table 2). In other studies, Vos and Bom (1993) found the SPAD values correlated well with both chlorophyll concentration and N concentration in potato leaves, and potato yield was significantly correlated with SPAD value (Zheng et al. 2015). These indicated that modern cultivar had higher productivity, compared to old cultivars.

The plant height was significantly and negatively correlated with the year of cultivar release and grain yield (Fig. 6-B, Table 2). It can be seen that the decrement of height has played a significant role in genetic improvement of wheat yield. In several regions of the world (Ganeva et al. 2005; Zhang et al. 2006; Sun et al. 2014), this reduction was largely explained by the introduction of Rht alleles from the Norin 10 and other Japanese cultivars. Butler et al. (2005) thought that the reduction of plant height and the concomitant loss of stem biomass could impose penalties on grain filling, mainly under stress conditions, such as drought or heat stress, and semi-dwarf alleles seem to have neutral (or in some cases, even negative) effects on yield in low yielding (i.e., stressful) environments (Mathews et al. 2006; Chapman et al. 2007). It might be seen from above discussions that a decrease in plant height reduced the biomass partition to stem and enhanced the contribution of ear photosynthesis, because dry matter translocation from the stem showed the opposite pattern to the contribution of ear photosynthesis (Maydup et al. 2010), which resulted in the increase in the partition to grain and the harvest index. But Maydup et al. (2012) found there was no consistent relationship between stem weight of the near-isogenic lines and their respective contributions of ear photosynthesis, suggesting that other factors are involved in the increase of ear contribution. So the relationship between yield and plant height should be studied in future. Anyway, under rainfed condition, with the year of cultivar release, the flag leaf area and plant height decreased, the SPAD of flag leaf, the ear contribution, and the ratio of grain weight:leaf area increased, finally the grain yield was ensured.

Some research showed that increasing planting density under rainfed condition reduced soil water loss, and enhanced WUE (Woodruff et al. 2002; Querejeta et al. 2008). Under decreasing irrigated and increasing seeding rates condition, higher light transmission ratio in the canopy after anthesis was achieved with smaller size and high quality top leaf blades, higher ratio of grain:leaf and larger proportion of green non-leaf area, which lead to higher canopy photosynthetic rate and WUE after anthesis, it also increased the water soluble carbohydrates accumulation and remobilization, remobilization efficiency, and contribution to grain yield in non-leaf organs (Zhang et al. 2011, 2013). Therefore, it is possible to ensure high grain yield under rainfed condition by selecting the cultivars with shorter stems, the more erect, short, narrow, thick, and dark green leaves (Tsunoda 1959), because these characters can improve stem lodging resistance, enhance photosynthetic ability of population, and amplify plant density further, thus increasing ear contribution under high seeding rate.

5. Conclusion

Grain yield, grain weight per ear, grain number per ear, the specific leaf weight, ratio of grain weight:leaf area, SPAD
value of flag leaf and the contribution of ear photosynthesis to grain yield showed a linear increase with the year of cultivar release in NCP under rainfed and irrigated conditions. Compared to irrigated condition, the plant height, the length, width, area, and dry matter of flag leaf decreased, while the individual grain weight, the ratio of grain weight/leaf area, SPAD value of flag leaf and the contribution of ear photosynthesis to grain yield increased under rainfed condition. The ear contribution and flag leaf SPAD value were significantly and positively correlated with grain yield and yield components. Ear photosynthesis contribution can be regarded as an important index for cultivar selection especially in rainfed wheat production.

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