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RESEARCH ARTICLE

Photosynthetic characteristics and nitrogen distribution of large-spike wheat in Northwest China

WANG Li-fang, CHEN Juan, SHANGGUAN Zhou-ping

State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling 712100, P.R.China

Abstract

The leaf photosynthesis and nitrogen (N) translocation in three large-spike lines and control cultivar (Xi'nong 979) of winter wheat (*Triticum aestivum* L.) were studied in 2010–2011 and 2011–2012. The objectives of this study were to investigate the differences in the physiological characteristics of large-spike lines and control cultivar and identify the limiting factors that play a role in improving the yield of breeding materials. The average yield, grain number per spike, kernel weight per spike, and 1 000-kernel weight of the large-spike lines were 16.0, 26.8, 42.6, and 15.4%, respectively, significantly higher than those of control. The average photosynthetic rates (P_n) were not significant between the large-spike lines and control cultivar during the active growth period. The average PSII maximum energy conversion efficiency (F_v/F_m), PSII actual quantum efficiency (Φ_{PSII}), photochemical quenching coefficient (q_P), PSII reaction center activity (F_v'/F_m') and water-use efficiency (WUE) of the large-spike lines were 1.0, 5.1, 3.6, 0.8, and 43.4%, respectively, higher than those of the control during the active growth stages. The N distribution proportions in different tissues were ranked in the order of grains>culms+sheathes>rachis+glumes>flag leaves>penultimate leaves>remain leaves. This study suggested that utilization of the large-spike wheat might be a promising approach to obtain higher grain yield in Northwest China.

Keywords: wheat, nitrogen distribution, large-spike lines, photosynthetic characteristics, yield

1. Introduction

Food demand has increased dramatically due to the increasing population (Rosegrant and Agcaoili 2010). The total yield potential of wheat can be greatly increased by improving the yields of individual plants, which is an important approach to ensure high food yield and quality (Reynolds and Borlaug 2006). Because large-spike wheat was characterized by big large spike, high grains per plant and high yield potentials, its varieties are more attractive and are given more attention in wheat production and breeding practices under the circumstances of everlasting arable land reduction and stable food demand increase (Gaju *et al*. 2014).

Wheat varieties with high yield potentials can be achieved by delaying leaf senescence, enhancing nutrient assimilate accumulation (Maydup *et al*. 2010). There have been contradictory conclusions regarding the function of the rate of photosynthesis in determining the crop yield in many studies (Richards 2000; Ehdaie *et al*. 2008; Sun *et al*. 2014). Wheat can accumulate considerable amounts of carbohydrates and

nitrogenous compounds in the vegetative organs before anthesis (Plaut *et al*. 2004; Chen *et al*. 2012; Wang *et al*. 2014) and can reallocate the accumulated carbon and nutrients among different tissues during the grain-filling period (Arndt and Wanek 2002; Fernández-García *et al*. 2014). Wilhelm *et al*. (2002) reported that the N concentrations of the culm sheathes and internodes increased with the increasing culm order in contrast to individual culms, but the nitrogen distributions among the different tissues of the large-spike wheat varieties still remain unknown. Qiu *et al*. (2008) revealed that the grain yield, dry matter, photosynthetic characteristics and water-use efficiency (WUE) of winter wheat depend on the soil water in northern China. The optimal agronomic trait compositions of wheat have been reported under some experimental conditions (Peltonen *et al*. 2011; Tian *et al*. 2011); however, the study of photosynthesis, nitrogen translocation and yield formation for large-spike wheat is still far from being completely understood. The objectives of this study were to explore differences in the photosynthetic characteristics and nitrogen distributions of large-spike wheat lines in yield formation and to provide a theoretical basis for further determining the production potential of large-spike wheat lines.

2. Results

2.1. Grain yield

The grain number per spike, kernel weight per spike and 1 000-grain weight of the three large-spike lines were significantly ($P<0.05$) higher than those of the control cultivar (Table 1). The yields of three large-spike wheat lines were also 16.5, 9.8 and 14.7%, respectively, higher than those of the control cultivar. However, the spike numbers per hectare of the large-spike lines were significantly lower than those of Xi'nong 979. These results indicate that the future yield may be improved by increasing the spike number of the large-spike lines.

2.2. Net photosynthetic rates and WUE

The P_n of wheat tended to first increase and then decrease during the growing period (Fig. 1-A), and the average P_n during heading stage and WUE during five stages of the large-spike lines was higher than that of Xi'nong 979 (Fig. 1). The line 2040 had a higher WUE than that of the other lines during the heading, flowering, pre-ripening, and mid-ripening stages, the differences between large-spike lines and Xi'nong 979 most likely resulted from genetic characters or genotype-environment interactions.

2.3. Chlorophyll fluorescence parameters

The high-energy capture efficiencies in the PSII reaction center (Fig. 2-A) showed that the wheat did not suffer from environment stress during the active growth period. The average F_v/F_m of the large-spike lines was higher than that of the Xi'nong 979, and the average F_v/F_m of the lines and cultivar during active growth stages was ranked in the order of 2040>2038>2037>Xi'nong 979, indicating that the energy-capturing transforming capacities and the quantum efficiencies of the large-spike lines were higher than those of Xi'nong 979. The Φ_{PSII} of wheat tended to first decrease from the jointing to the heading stages, then increase from the heading to the pre-ripening stage and finally decrease from the pre- to the mid-ripening stages (Fig. 2-B). The average Φ_{PSII} during active growth stages was ranked in the order of 2037>2038>2040>Xi'nong 979. The wheat varied tendency of q_P was similar to the Φ_{PSII} (Fig. 2-C). The average q_P during active growth stages was ranked in the order of 2037>2038>2040>Xi'nong 979. The average F_v'/F_m' during active growth stages was ranked in the order of 2037>2038>Xi'nong 979>2040 (Fig. 2-D).

2.4. Nitrogen distribution proportion and translocation characteristics

Table 2 demonstrated that the grains had the highest N distribution proportion, and the remaining leaves showed the lowest N distribution proportion. The flag leaves, penultimate leaves and rachis+glumes of line 2037 had the highest N distribution proportions, while the remain leaves and culms+ sheath of line 2040 had the highest N distribution proportion, indicating that the N accumulations of the above-

Table 1 Yield and its four primary components of the three large-spike lines and the multiple-spike cultivar Xi'nong 979 (control, CK) during the maturity stage of 20 individual plants

Lines or cultivars	Spike number (×10⁴ ha⁻¹)	Grain number per spike	Kernel weight per spike (g)	1 000-grain weight (g)	Yield (kg ha⁻¹)
CK	704.1±32.0 a	42.0±1.8 b	1.8±0.1 c	41.0±0.6 b	9 651.7±560.4 a
2037	475.9±17.7 b	51.0±2.2 a	2.3±0.1 b	47.1±1.7 a	11 566.3±581.6 a
2038	480.7±89.8 b	56.3±1.8 a	2.7±0.1 a	46.2±1.3 a	10 697.6±2 113.7 a
2040	532.7±53.1 ab	52.4±1.7 a	2.7±0.1 a	48.7±0.7 a	11 313.1±1 206.6 a

Different lower case letters in the same column indicate significant differences among the different lines and cultivar at *P*=0.05 (by Duncan's test). The values are presented as means±SE (*n*=3). The same as below.
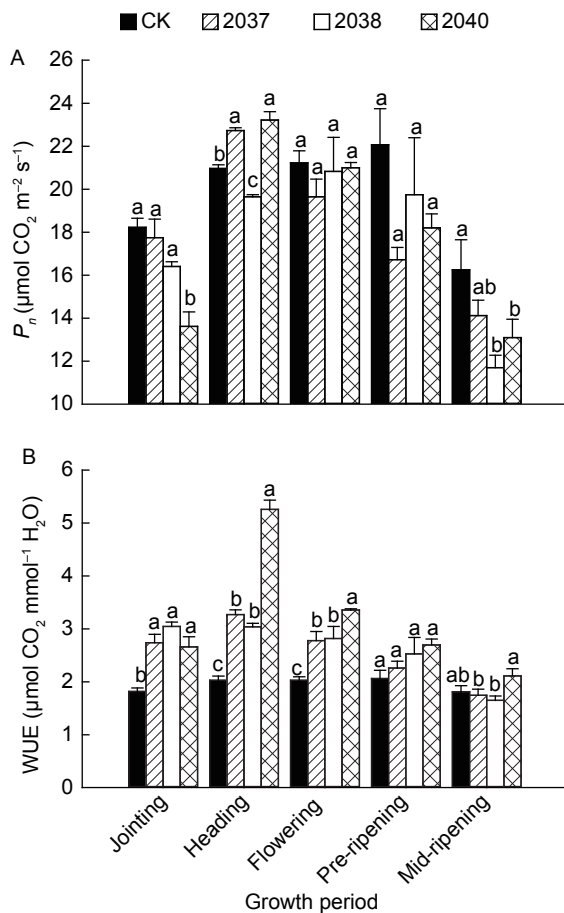
Fig. 1 Photosynthetic rates (P_n) and leaf real-time water-use efficiencies (WUE) of the large-spike lines and Xi'nong 979 (CK) during the growth period. Values followed by the same letter within a row indicate no significant difference at 0.05 level. The error bars represent SE for the observations. The same as below.

ground plant tissues most likely played an important role in their N distribution proportion, and the difference came from their genetic characteristics.

The N accumulation in the vegetative organs of the three large-spike lines was significantly higher than that of Xi'nong 979 during the maturity stage (Table 3). The N accumulation of the mature grains, N translocation and contribution proportion of the large-spike lines were higher than those of Xi'nong 979, but this difference was not significant.

3. Discussion

3.1. Yield formation characteristics of the large-spike wheat

The large-spike lines are interesting and unique breeding materials that have been bred through many generations

and have distinct panicle characteristics in terms of the grain number per spike, kernel weight per spike, 1 000-grain weight, and yield, but the spike numbers per hectare of large-spike lines were significantly lower than those of CK. Our results agreed with those of Jiang *et al*. (2000), Sui *et al*. (2010) and Lu *et al*. (2015), who reported the primary difference between the large-spike and multiple-spike cultivars. The large-spike lines maintained a higher production by strengthening their plant straws so that they appeared larger and had a smaller plant population than Xi'nong 979, and the yield potentials of the large-spike lines would be achieved by coordinating the main yield components.

3.2. Dynamic changes of photosynthetic characteristics in large-spike wheat yield formation

Leaf photosynthesis is directly proportional to the grain yield and is influenced by soil moisture (Khamssi and Najaphy 2012). Shangguan *et al*. (2000) reported that the P_n of high-N plants was enhanced compared to that of low-N plants while well watered. This study demonstrated that the average P_n of the large-spike lines was higher during the heading stage than that of Xi'nong 979. These results suggest that the heterogeneity of the P_n of a plant mainly depends on the intrinsic genetic characteristics. This study also indicated that the average fluorescence parameters of the large-spike lines, except for the F_v'/F_m' of line 2040, were significantly higher than those of Xi'nong 979 during active growth stages, suggesting that the large-spike lines had higher photochemical reaction efficiencies and patulous degrees in the PSII reaction center than those of Xi'nong 979. In addition, the primary electron acceptor of PSII (Q_A) of the large-spike lines was more oxidized despite the average lower photosynthetic rates than CK; thus, these lines could use more energy during photochemical electron transfer and had higher light-capturing capacities than Xi'nong 979, which agreed with the results of Sui *et al*. (2010) and Jiang *et al*. (2000).

Water is the limiting factor for rain-fed wheat yields which has a long history in northwest of China. For the large-spike wheat, high chlorophyll fluorescence contributed to the vegetative growth and then laid the foundation for the reproductive growth. One reason of high chlorophyll fluorescence and low photosynthetic rates for large-spike wheat may be related to the genetic traits and environmental factors, and the photosynthesis may decrease under water stress conditions (Chen *et al*. 2011), only when photosynthesis is inhibited, the fluorescence will increase (Horton *et al*. 1994); another reason for the result may be the large individual characteristics and storage capacity of the large-spike wheat, most of the photosynthetic products made by the leaves were used to supply the grains and self-growth, this
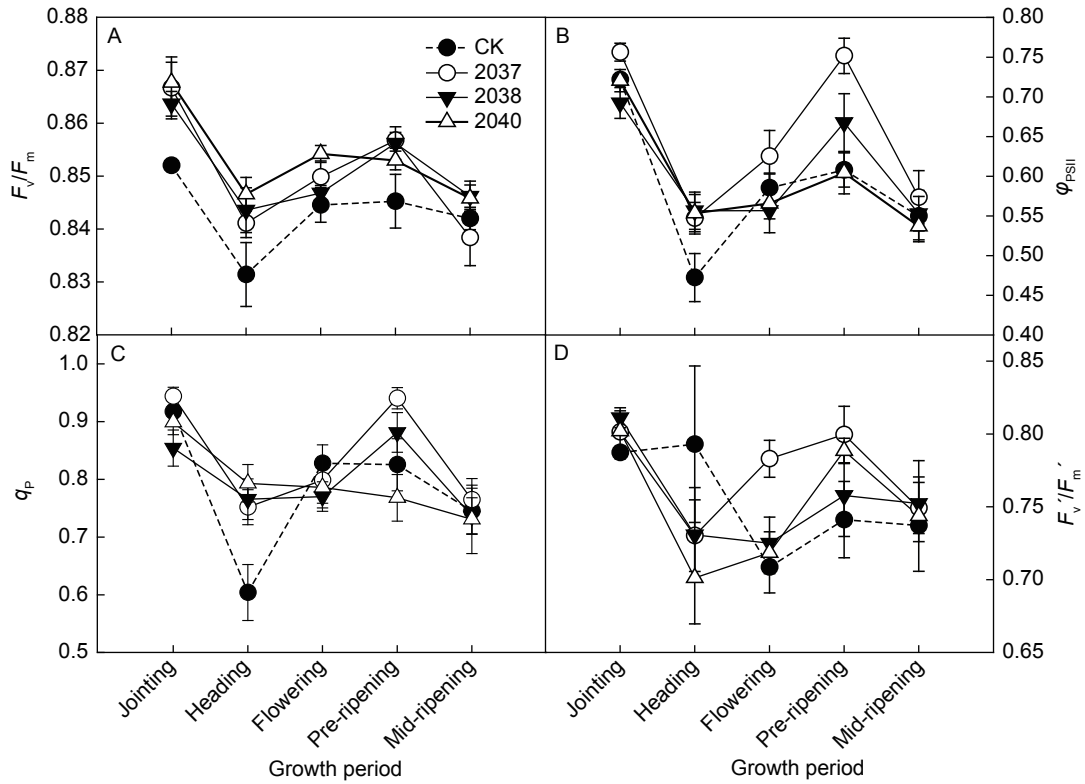
Fig. 2 PSII maximum energy conversion efficiency (F_v/F_m), PSII actual quantum efficiency (Φ_{PSII}), photochemical quenching coefficient (q_P) and PSII reaction center activity (F_v'/F_m') of large-spike lines and Xi'nong 979 during the the growth period.

Table 2 Nitrogen distribution proportions of six different tissues of the three large-spike lines and cultivar Xi'nong 979 (CK) during the maturity stage

Items	Lines or cultivars	Flag leaf	Penultimate leaf	Remain leaves	Culms+ Sheath	Rachis+ Glumes	Grain
Nitrogen distribution proportion (%)	CK	2.1±0.2 a	1.7±0.2 ab	1.1±0.1 b	9.3±0.5 b	5.7±0.5 a	80.8±0.5 a
	2037	2.9±0.2 a	2.3±0.4 a	1.5±0.2 b	11.0±0.6 ab	6.4±0.6 a	76.8±1.7 b
	2038	2.7±0.3 a	2.0±0.1 ab	2.0±0.3 a	11.9±0.3 a	4.6±0.1 a	77.6±1.1 ab
	2040	2.2±0.2 a	1.5±0.1 b	2.1±0.1 a	12.1±1.4 a	5.4±0.4 a	78.0±0.6 ab
Total nitrogen (g kg⁻¹)	CK	10.8±2.4 a	8.8±1.6 b	9.5±1.2 b	5.2±0.4 a	6.0±0.5 a	21.0±0.9 c
	2037	11.5±0.8 a	12.6±1.7 a	12.6±1.0 a	5.0±0.4 a	6.1±1.0 a	24.5±0.4 b
	2038	11.7±0.4 a	12.1±0.9 a	13.5±1.5 a	5.5±0.6 a	5.4±0.2 a	24.5±0.2 b
	2040	10.8±1.2 a	9.4±0.2 b	12.6±0.7 a	5.4±0.4 a	5.7±0.7 a	25.9±0.1 a
Dry matter (kg ha⁻¹)	CK	577.1±49.2 b	568.8±42.9 b	329.9±84.0 b	4775.7±247.7 b	2704.1±208.7 b	9651.7±560.4 a
	2037	910.3±43.6 a	669.7±43.0 a	444.4±138.5 ab	7511.1±446.2 a	3865.1±280.4 a	11566.3±581.6 a
	2038	926.5±133.7 a	670.4±40.4 a	594.9±210.4 ab	7996.9±977.8 a	3396.2±227.7 a	10697.6±2113.7 a
	2040	778.0±73.9 a	603.8±22.0 ab	634.4±68.5 a	7847.2±633.8 a	3614.0±358.7 a	11313.1±1206.6 a

Table 3 Nitrogen translocation characteristics from the vegetative tissues to the grain of the three large-spike lines and cultivar Xi'nong 979 (CK) after anthesis

Lines or cultivars	Nitrogen accumulation of the vegetative organs (kg ha⁻¹)		Nitrogen accumulation of the mature grains (kg ha⁻¹)	Nitrogen translocation (kg ha⁻¹)	Translocation efficiency (%)	Contribution proportion (%)
	Flowering	Maturity				
CK	236.7±17.2 a	63.1±3.5 b	266.3±21.0 a	173.5±15.5 a	73.2±1.8 a	66.0±7.6 a
2037	288.3±27.9 a	85.0±2.2 a	283.2±18.2 a	203.3±25.7 a	70.2±2.2 a	73.6±14.2 a
2038	295.6±38.9 a	89.8±7.6 a	309.0±12.6 a	205.9±31.8 a	69.1±2.1 a	66.6±9.9 a
2040	283.8±37.4 a	84.7±5.8 a	300.0±11.9 a	199.2±43.2 a	68.3±7.0 a	67.7±16.7 a

would cause the low photosynthetic rates due to the nutritional deficiency, future research should also investigate the accumulation and translocation of assimilation substance in large-spike wheat. The average WUE of the large-spike lines was higher than that of Xi'nong 979 during the five growth stages. Therefore, the further yield breakthrough of the large-spike wheat lines would be achieved by creating ideal wheat plant appearance and improving the P_n (Parry et al. 2011; Reynolds et al. 2012).

3.3. Nitrogen translocation characteristics among different organs of large-spike wheat

There is a strong positive correlation between the leaf photosynthetic capacity and the N content (Shangguan et al. 2000; Holaday et al. 2015). Arduini et al. (2006) suggested that the N accumulation in different tissues was ranked in the order of grains>spikes>leaves>culms during the mature stage, this study indicated that the N distribution proportions of the grains were the highest, followed by those of its culms+sheathes, rachis+glumes, flag leaves, penultimate leaves and remain leaves. The grains of the cereals were the most active sinks of N assimilation after anthesis, and the leaf was the primary source organ of N (Ntanos and Kontroubas 2002; Fageria and Knupp 2013). The remobilized N of wheat before anthesis was important for the yield due to the activity of proteases, which degrade proteins to amino acids that are transported from the leaves to the grains (Masoni et al. 2008; Cui et al. 2011; Ye et al. 2011). This study showed that the N accumulation of the vegetative tissues of the large-spike lines was significantly higher than that of Xi'nong 979 during the maturity stage. The grain N accumulation during the maturity stage, N translocation and contribution proportion of the large-spike lines were also higher than those of Xi'nong 979, but this difference was not significant. Many experiments under different management measures have reported that modest soil droughts were likely to increase the translocation ratio and contribution of N that was pre-stored into various vegetative tissues to the grains (Yang et al. 2000; Ma et al. 2015). The wheat yield is most likely related to the N concentrations of the grains, and N uptake is associated with the genotypes and farming practices; therefore, it is imperative to determine how to improve the N translocation efficiencies of large-spike lines by regulating their water and fertilization so that these lines can make full use of the residual N in their culms and other vegetative tissues.

Improving the grain yield (sink) is the main goal in wheat production, and photosynthesis (source) provides the basic matter and energy for the grain yield (Ferrante et al. 2012). The large-spike lines had a higher N accumulation in the vegetative organs; therefore, improving the translocation efficiency (flow) and P_n will improve production and maintain the sink-flow-source balance. The large-spike lines demonstrate a yield potential for quality breeding and can be used to select parent lines from different groups to create a higher degree of heterosis and promote further breeding progress.

4. Conclusion

This study investigated the dynamics of net photosynthetic rates change and nitrogen allocation and distribution among different tissues of large-spike lines and a multiple-spike cultivar of wheat. This study concluded that the yield, grain number per spike, kernel weight per spike, and 1 000-grain weight of three large-spike lines were significantly higher than those of the control cultivar. The average photosynthetic rates of the large-spike lines were lower than were those of the control cultivar during the different growth stages, while the average WUE and average fluorescence parameters of the three large-spike lines were higher than were those of the control cultivar. The nitrogen accumulation of the grains during the maturity stage, nitrogen translocation and contribution proportion of the large-spike lines were also higher than those of the control cultivar. In the context of increasing cereal production and quality based on the food demand, the results of this study are helpful for improving agricultural management practices and for further improving the cereal yield.

5. Materials and methods

5.1. Plant materials

Three new large-spike wheat lines were tested in the Shaanxi Provincial Wheat Variety Trial Test in 2009 and the Shaanxi Provincial Wheat Variety Regional Test in 2010 and were bred using different materials through many generations. The length of growing season of CK, 2037, 2038 and 2040 were 242, 245, 246, and 246 d, respectively. The other details are shown in Table 4.

5.2. Experimental design and crop management

The field experiments were conducted in Sufang Town, Wugong City, Shaanxi Province, northwestern China (34°17′N and 108°04′E), during the growing seasons of winter wheat (October–June) in 2010–2011 and 2011–2012. This location has a sub-humid warm temperate continental monsoon climate with an annual average temperature of 13.2°C and an annual rainfall of 630 mm, the soil type was loess soil and which was considered suitable for crop production. There were similar precipitation (231.1 mm, 229.8 mm) trends and other climate conditions during two wheat growing

Table 4 Main spike traits and other traits of the three large-spike wheat lines and one multiple-spike wheat cultivar Xi'nong 979 (CK)[1]

Lines or cultivar	Heading date	Spike number (×10^4 ha^{-1})	Grain number per spike	Kernel weight per spike (g)	Plant height (cm)	Maximum number of tillers (×10^4 ha^{-1})	Average number of ears per plant	Length of last internode (cm)	Yield (kg ha^{-1})	Other traits
CK	25 April	654–763	30–51	1.1–2.3	56–72	2572.5	2.26	19.7–26.4	8659.3–10598.9	Compact plant type, widely adopted in the Huang-Huai-Hai
2037	28 April	455–511	38–68	1.3–3.6	72–85	2062.2	1.12	17.3–28.3	10830.8–12714.4	Good disease resistance
2038	28 April	331–642	45–74	1.7–3.5	72–84	2183.1	1.15	21.0–27.5	7700.6–14778.2	Good light transmittance, shorter awn
2040	27 April	446–629	30–62	1.5–3.4	78–90	2101.1	1.21	17.8–29.8	8960.4–12954.7	Green leaves and culms when the grains were mature

[1] –, ranges of the traits and yields of the three large-spike lines and the multiple-spike cultivar; the variation ranges of grain parameters were summarized in different soil fertilities and experimental sites.

seasons in 2010–2011 and 2011–2012. The field experiment adopted a randomized block design composed of four treatments and three replicates. Each plot size was 2 m×2 m with 11 rows (18 cm apart) of wheat sown at 140 seeds per row. Every year, the same quantity chemical fertilizer (375 kg ha^{-1} CO(NH$_2$)$_2$, 525 kg ha^{-1} (NH$_4$)$_2$HPO$_4$ and 112.5 kg ha^{-1} K$_2$SO$_4$) was applied to the top 20 cm before planting. Experiment site was ploughed to bury weeds and pest before sowing, and weeds were hand-hoed several times during the growing period. The field managements were done as commonly practice.

5.3. Plant sampling and analysis

The P_n and transpiration rate (T_r) of the leaves were measured using a Li-6400XT Portable Photosynthesis System (Li-Cor, Inc., Lincoln, Nebraska, USA) between 09:00 and 11:00 a.m. on clear days with a wind speed of less than 1 m s^{-1} during the growth stage. During the measurement, the main stem leaves *in vivo* (fully expanded penultimate leaves or flag leaves) for the P_n measurement should be intacted without suffering insect and disease attacks and their upper one-third served as the location for measure-

ment. While in operation, the system had a leaf chamber temperature of 25°C, a mean CO$_2$ concentration of (382.6±2.5) μmol mol^{-1}, a photosynthetic active radiation (PAR) of 1 300 μmol m^{-2} s^{-1}, and a humidity of 53–56%, the P_n was measured over 3 min until the P_n stabilized, and for each plot, three randomly selected and fully expanded leaves were measured. The leaf real-time WUE was calculated using the formula of WUE=P_n/T_r (Medrano *et al.* 2015).

The chlorophyll fluorescence of the fully expanded penultimate leaves or flag leaves *in vivo* was measured using a pulse modulation fluorescence meter (FMS 2.02, *Hansatech*, King's Lynn, UK) on the adaxial leaf surface. The measurements were made between 9:00 and 11:30 a.m. local time on clear days. The leaves were enclosed in a small black plastic clamp and were dark-adapted for 30 min. The leaves were initially exposed to the weak modulated measuring beam (<1 μmol m^{-2} s^{-1}) to estimate the F_o, followed by exposure to a saturating white light (14 000 μmol m^{-2} s^{-1}) to measure the F_m. 30 s after the saturation pulse, continuous actinic light (100 μmol m^{-2} s^{-1}) was applied to measure the steady-state fluorescence yield F_s. $F_m´$ was measured for each pulse. The minimal Chl fluorescence during the light-adapted state ($F_o´$) was determined by irradiating the leaf for 3 s with far red radiation. Following each saturation pulse, $F_v/F_m=(F_m-F_o)/F_m$, $\Phi_{PSII}=(F_m´-F_s)/F_m´$, $q_P=(F_m´-F_s)/(F_m´-F_o´)$ and $F_v´/F_m´=(F_m´-F_o´)/F_m´$ were determined according to Shangguan *et al.* (2000).

The content of total nitrogen of wheat flag leaf, penultimate leaf, other leaves, culms+sheath, rachis+glumes (other parts of the spike after removing the grains) and kernels were analyzed using the standard Kjeldahl method (Kjeltec 2300 Analyzer Unit, Foss, Sweden). According to Dordas and Sioulas (2009), the different parameters were calculated as follows:

Distribution proportion=N accumulation of plant parts/Plant total N content

N translocation=N accumulation during the flowering stage–N accumulation during the maturity stage (excluding the grain nitrogen accumulation)

N translocation efficiency (%)=N translocation/N accumulation during the flowering stage×100

Contribution proportion (%)=N translocation/Grain N accumulation during the maturity stage×100

During the maturity stage, 20 single stems of wheat were collected in each plot and the yield components parameters were measured.

5.4. Statistical analysis

There were consistent change characteristics between 2010–2011 and 2011–2012 during wheat growing years, so we chose to analyze the data only from the 2011–2012

season. The data in the tables are the average value of three replicates in the form of means±SE (standard error). The significant differences (P<0.05) were tested by SPSS ver. 13.0 (SPSS Inc., Chicago, IL, USA), and the differences among the treatments were tested by Duncan's multiple range test.

Acknowledgements

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