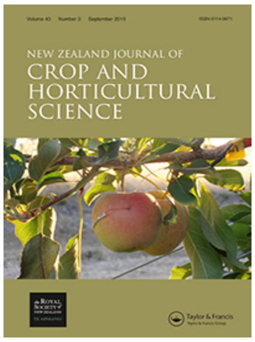

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RESEARCH ARTICLE

Photosynthetic rates and kernel-filling processes of big-spike wheat (*Triticum aestivum* L.) during the growth period

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Photosynthetic rate and the kernel-filling process are two crucial determinants of kernel yield in cereal crops. In the present study, the dynamic photosynthetic rates (P_n), kernel-filling characteristics, and kernel-filling rate and duration of five big-spike wheat lines (*Triticum aestivum*; 2005, 2026, 2037, 2038 and 2040) were compared with a control multiple-spike cultivar (Xi'nong 979) in 2010–11 and 2011–12. The 1000-kernel weight of the upper, middle and basal parts of the spike experienced a 'slow-fast-slow' pattern of growth from flowering to maturity. The big-spike lines had greater dry matter accumulations than the control cultivar 46 days after flowering, and also had higher kernel-filling rates in the basal part of the spike during the late growth period and greater kernel weights in the middle part of the spike throughout the entire kernel-filling process. The kernel-filling rates of the different parts of the spike during the three kernel-filling stages were ranked in the order of V_2 (rapidly increasing kernel-filling stage) > V_3 (slowly increasing kernel-filling stage) > V_1 (moderately increasing kernel-filling stage). The mean P_n for each of the big-spike lines was lower than that of the control cultivar. These results indicate that the plumpness, size and weight of kernels produced by the big-spike lines can likely be increased by simultaneously increasing the photosynthetic rate and the kernel-filling duration during the late kernel-filling stage.

Keywords: big-spike wheat; kernel-filling process; kernel yield; photosynthetic rate; *Triticum aestivum* L.; wheat

Introduction

In China, the primary aim of agricultural development has been to increase the yield of crops such as wheat (*Triticum aestivum* L.). The yield of wheat depends on the number of spikes per unit area, the number of kernels per spike and, in particular, the weight of kernels (Sayre et al. 1997; Brancourt-Hulmel et al. 2003). Kernel weight depends on a plant's kernel-filling rate and duration (Kim et al. 2011), which themselves depend on the level of leaf photosynthesis and the mobilisation of carbohydrates stored in the plant's stem into the growing kernels (Foulkes et al. 2007; Tambussi et al. 2007; Ehdaie et al. 2008). Previous studies have explored the relationship between source activity (i.e. leaf photosynthesis and related parameters) and the kernel-filling process or kernel yield. Murchie et al. (2009) proposed that during the kernel-filling period, the characteristic of wheat to stay green contributes to increasing its kernel yield by increasing its photosynthetic rate—in a similar way to rice (*Oryza sativa*), which improves its kernel yield by keeping its leaves green into the late growth period through delayed upper leaf senescence and rapid lower leaf senescence (Mayup et al. 2010). Wheat has also been found to terminate kernel filling and foliage senescence separately (Hossain et al.

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2011). Therefore, both kernel-filling rate and duration, and photosynthesis seem to be key factors determining yield in wheat.

In cereal crops such as wheat, the kernel-filling period is an important physiological stage in kernel formation and enrichment and is influenced by the ways in which a plant's sources, sinks and transport systems work together (Yang et al. 2008). Borrás et al. (2004) showed that wheat grain growth is limited mainly by the sink capacity of plants, although the degree of source-sink limitation varies between genotypes and environments. Therefore, it is important to study the kernel-filling characteristics in a range of cultivars to exploit their yield potentialities. In rice, it has been shown that different parts of the spike have different kernel-filling processes and thus different kernel weights, and that kernels developing from early flowers have higher weights than those developing from later flowers (Yang & Zhang 2010). However, previous studies on wheat have investigated mainly the grain-filling process on a spike basis (Blum 1998; Shah & Paulsen 2003), with little consideration for variation between different parts of the spike. Therefore, in this study, we investigated the differences in kernel-filling parameters between the different parts of the spike in wheat using five big-spike lines and their control cultivar.

The main objectives of this study were to: (1) explore the dynamic photosynthetic characteristics of big-spike wheat; (2) compare the kernel-filling parameters of big-spike wheat lines with the multiple-spike wheat cultivar; and (3) evaluate the relative contributions of kernel-filling rate and duration on kernel weight. It is hoped that the findings from this study will provide a theoretical basis for wheat breeding and improve wheat production by ensuring that hydrological and fertiliser conditions are properly regulated.

Materials and methods

Plant materials

In this study, five new high-yield, big-spike lines of partial spring wheat were used, which had been tested in the Shaanxi provincial wheat variety trial test in 2009 and the Shaanxi provincial wheat variety regional test in 2010. These lines were bred through many generations over many years, and have excellent spike characteristics and an obvious yield advantage. The winter wheat cultivar Xi'nong 979 (*Triticum aestivum* cv. Xi'nong 979) was also grown as a control cultivar; this cultivar has been planted across large areas of the Huang-Huai-Hai production region of winter wheat.

Study location

The field experiment was conducted at the Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, Shaanxi (34°16′N, 108°04′E) during the winter wheat growing seasons (October–June) of 2010–11 and 2011–12. This area is situated in the sub-humid warm temperate continental monsoon climate zone and generally has a flat topography. The soil is well-aerated Eum-Orthic Anthrosol, which is characterised by favourable permeability, very good water and nutrient-retaining capacities, and is suitable for growing a wide range of crop species. Precipitation was similar across the two growing seasons (231.1 mm and 229.8 mm, respectively), as were other climatic conditions; therefore, we chose to analyse data only from the 2011–12 season.

Experimental design

The field experiment adopted a randomised block design composed of six treatments and three replicates. Each plot was 2 × 2 m, with 10 rows (20 cm spacing) of wheat sown at 110 seeds per row. Three rows of wheat were also planted as guarding rows around the experimental farmland. Wheat was sampled from the central rows of wheat in each plot.

Field management practices matched those that are commonly used in the region. Prior to sowing each season, the experimental site was ploughed to bury weeds and pests, and chemical fertiliser (360 kg ha^{-1} N and 70 kg ha^{-1} P_2O_5)

was applied to the top 20 cm of soil. The winter wheat was planted on 10 October 2011, and the big-spike lines of 2005, 2026, 2037, 2038, 2040 and control cultivar flowered on 20 April, 18 April, 24 April, 26 April, 19 April and 17 April 2012, respectively. During the growing period, no irrigation was carried out and no fertiliser was added, and weeds were hand-hoed several times.

Plant sampling and measurement

Photosynthetic rates (P_n, μmol CO_2 m^{-2} s^{-1}) were measured between 0900 and 1100 h on clear days with a wind speed below 1 m s^{-1} during the heading, flowering, early-ripening, mid-ripening and later-ripening stages. The P_n of the fully expanded top-down penultimate and flag leaves of the lines and cultivar were measured using an LI-6400XT Portable Photosynthesis System (LI-6400, Li-Cor, USA) equipped with a 2 × 3 cm leaf chamber and integrated light source. Three randomly selected, fully expanded leaves were measured for each treatment; only intact leaves that had not suffered insect and disease attacks were measured, and the upper one-third of the leaves were chosen. During measurement, the leaf chamber temperature was kept at 25 °C; the mean CO_2 concentration was set at 382.6 ± 2.5 μL L^{-1}; the photosynthetically active radiation (PAR), generated by the LED (mixed red and blue) system, was set at 1300 μmol m^{-2} s^{-1}; the humidity was set at 53%–56%; and the gas flow rate was set at 5 mL min^{-1}. Measurements were made over 3 min until the P_n and transpiration rates stabilised.

In each plot, 200 spikes that headed and flowered on the same days were chosen and tagged, and the flowering date was defined as the time when 50% of the plants flowered (Forrest et al. 2010). Ten spikes were collected as samples approximately every 5 days from the first day after the onset of flowering. The spikes were divided into upper, middle and basal parts, which were of equal length (Dong et al. 2012). Ten of the sample spikes were used for DW (dry weight) measurement immediately after sampling by deactivating at 105 °C and then drying at 80 °C to a constant weight. Kernels from the different parts of the spike were collected separately and measured, from which 1000-kernel weights and kernel-filling rates were calculated.

Data analysis

For each plot, logistic regression analysis was carried out to investigate the relationship between the 1000-kernel dry weight (dependent variable) and the number of days since flowering (independent variable; assuming that the first flowering day was day 0). This relationship was described using the logistic equation:

$$W = W_0/(1 + Ae^{-Bt}) \qquad (1)$$

where W is the average kernel dry weight (g), t is the number of days since flowering, W_0 is the final kernel dry weight (g), A is a coefficient related to both kernel-filling rate and duration, and B is a coefficient related to kernel-filling rate (Yang et al. 2001). By using Equation 1, a series of secondary kernel-filling parameters were also obtained, including maximum kernel-filling rate (V_m), day on which the kernel-filling rate appeared to be highest (T_m), total number of kernel-filling days (T), mean kernel-filling rate (V_a), duration of the moderately increasing kernel-filling stage (T_1), duration of the rapidly increasing kernel-filling stage (T_2), duration of the slowly increasing kernel-filling stage (T_3), kernel-filling rate of the moderately increasing kernel-filling stage (V_1), kernel-filling rate of the rapidly increasing kernel-filling stage (V_2) and kernel-filling rate of the slowly increasing kernel-filling stage (V_3).

Data are presented in the form of means ± SEM (standard errors) for three replicate averages. The significance of differences between treatments ($P < 0.05$) was tested using Duncan's multiple range test in SPSS (2004, Version 13.0 SPSS Inc, USA). The parameters of kernel-filling processes were obtained using CurveExpert 1.3.

Results

Dynamic leaf photosynthetic rates

Leaf photosynthetic rates (P_n) varied markedly through the growth period for all the test materials. P_n was highest at the heading stage after the flag leaves had fully expanded and then slowly decreased from the flowering stage through the early-ripening stage to the mid-ripening stage; there was then a significant decrease at the late-ripening stage.

P_n differed significantly ($P < 0.05$) between some of the big-spike lines and the control cultivar during the early-ripening (2040 vs. control cultivar) and late-ripening stages (2026, 2038 and 2040 vs. control cultivar) (Table 1); the big-spike wheat also had lower P_n during the entire kernel-filling period, but this was not significant. These differences in P_n were most likely due to significant differences in the genotype of the two for the test materials.

Dynamic 1000-kernel weights

The 1000-kernel weights tended to increase in a 'slow-fast-slow' pattern through the growth period for all test materials (Fig. 1A–C). In the big-spike lines, the final kernel weights for the basal, middle and upper parts of the spike were 8.22, 7.14 and 7.45 g higher, respectively, than in the control, which indicated that the big-spike lines had higher photosynthetic transfer and reserve capacities, allowing them to effectively increase their kernel weights.

During the early growth stage, more nutrients were transferred into the upper and middle parts of the spike, and fewer nutrients passed into the basal parts, whereas during the late growth stage, more nutrients were transferred into the basal parts. The big-spike lines transferred nutrients into the basal parts of their spikes later than the control cultivar. Throughout the kernel-filling process, all of the middle parts of the spikes had higher biomasses, higher levels of photosynthetic production, and greater integrated utilising ability. The big-spike wheat lines transferred more photosynthetic products to each part of their spikes, probably as a result of physiological advantages.

Dynamic kernel-filling rate

During the kernel-filling process, the 1000-kernel weight tended to follow a parabolic curve (Fig. 2A–C). This, combined with the equation parameters given in Table 2, shows that the average maximum kernel-filling rate of the basal parts of the spike appeared later, which could contribute to increasing the kernel-weight during the later growth stage.

The average kernel-filling durations were ranked in the order of basal spike parts > middle spike parts > upper spike parts for the big-spike lines and basal spike part > upper spike part > middle spike part for the control cultivar during the moderately increasing kernel-filling stage. By contrast, during the rapidly and slowly increasing kernel-filling stages, the kernel-filling durations were ranked in the order of middle spike parts > upper spike parts > basal spike parts for both the big-spike lines and the control cultivar. During the slowly increasing stage, the average kernel-filling durations for the big-spike lines were longer than

Table 1 Leaf photosynthetic rates (μ mol CO_2 m^{-2} s^{-1}) of five big-spike wheat lines and one multiple-spike wheat cultivar (Xi'nong 979) during the different growth stages.

Test materials	Heading	Flowering	Early ripening	Mid ripening	Late ripening	Mean
2005	26.47 ± 2.5 a	20.50 ± 1.3 a	21.30 ± 0.3 a	18.98 ± 1.2 a	8.72 ± 1.3 ab	19.19
2026	24.67 ± 1.2 a	19.87 ± 1.6 a	19.50 ± 0.7 a	19.46 ± 0.9 a	5.58 ± 1.5 b	17.81
2037	27.87 ± 0.5 a	24.03 ± 0.6 a	20.50 ± 1.6 a	19.06 ± 0.5 a	10.29 ± 1.2 ab	20.43
2038	27.33 ± 1.2 a	22.30 ± 0.7 a	19.13 ± 2.1 abc	18.02 ± 1.2 a	6.81 ± 1.1 b	18.72
2040	26.73 ± 0.6 a	20.63 ± 0.4 a	15.57 ± 1.9 bd	16.58 ± 1.2 a	5.55 ± 2.7 b	17.01
Xi'nong 979	29.03 ± 1.1 a	21.70 ± 0.8 a	21.07 ± 1.3 a	18.86 ± 1.3 a	12.86 ± 0.8 a	20.71

Different lower case letters within a column indicate significant differences between the test materials at $P = 0.05$. Values are presented as mean ± SE ($n = 6$).

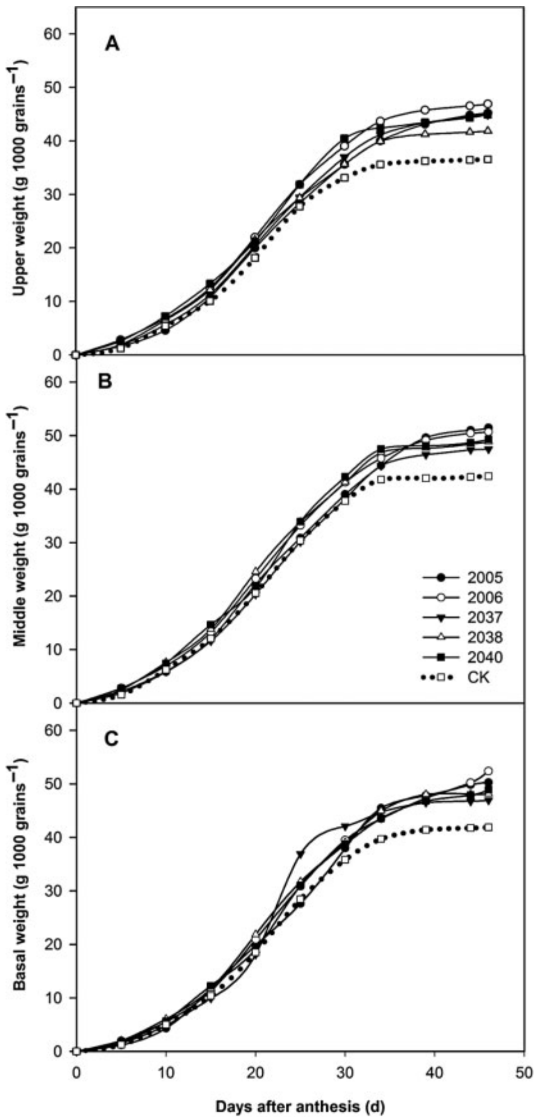

Figure 1 The 1000-kernel weights of different parts of the spike in five big-spike wheat lines and one multiple-spike cultivar (Xi'nong 979) from flowering to maturity. **A,** upper part; **B,** middle part; **C,** basal part.

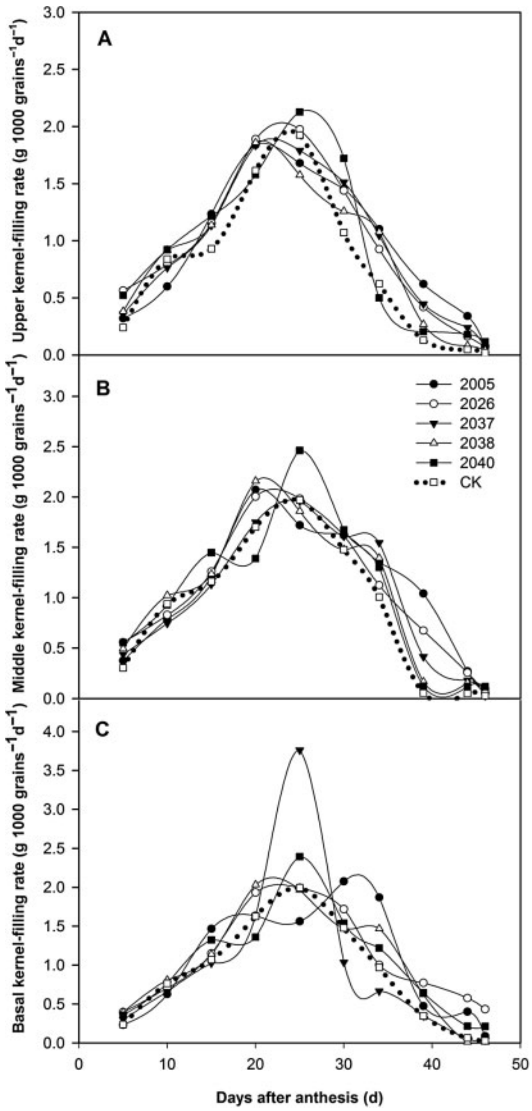

Figure 2 Kernel-filling rates of 1000-kernel weights for different parts of the spike in five big-spike wheat lines and one multiple-spike cultivar (Xi'nong 979) from flowering to maturity. **A,** upper part; **B,** middle part; **C,** basal part.

for the control cultivar, which could delay senescence during the late growth period.

The average kernel-filling rates for the big-spike lines were ranked in the order of middle spike parts > basal spike parts > upper spike parts during the moderately increasing kernel-filling stage, and basal spike parts > middle spike parts > upper spike parts during the rapidly and slowly increasing stages. By contrast, the average kernel-filling rates for the control cultivar were ranked in the order of middle spike parts > basal spike parts > upper spike parts during all three kernel-filling stages.

Table 2 Param eters of the kernel-filling logistic equations for the different parts of the spike of five big-spike wheat lines and one multiple-spike cultivar (Xi'nong 979).

		Primary parameters						Secondary parameters							
Test materials	Spike parts	r^2	W_0 (g)	A	B	T (d)	V_a (g 1000 kernels^{-1} d^{-1})	T_m (d)	T_1 (d)	T_2 (d)	T_3 (d)	V_1 (g d^{-1})	V_2 (g d^{-1})	V_3 (g d^{-1})	V_m (g d^{-1})
2005	Upper	0.9986	45.43	45.78	0.17	48.41	0.94	21.99	14.41	15.15	18.85	0.60	1.16	0.91	1.98
	Middle	0.9982	52.58	36.87	0.16	51.68	1.02	22.73	14.43	16.60	20.66	0.67	1.24	0.96	2.09
	Basal	0.9973	51.64	47.79	0.17	51.28	1.01	23.43	15.45	15.96	19.87	0.64	1.25	0.98	2.13
2026	Upper	0.9986	43.89	67.25	0.19	45.81	0.96	21.90	15.05	13.71	17.06	0.57	1.22	0.97	2.11
	Middle	0.9994	51.45	35.71	0.17	48.82	1.05	21.37	13.50	15.74	19.59	0.70	1.29	0.99	2.15
	Basal	0.9980	51.98	39.57	0.16	51.43	1.01	22.87	14.68	16.37	20.38	0.66	1.24	0.96	2.09
2037	Upper	0.9991	42.96	60.63	0.20	43.39	0.99	20.47	13.90	13.14	16.35	0.60	1.25	0.99	2.15
	Middle	0.9990	48.62	43.85	0.17	48.67	1.00	21.97	14.32	15.31	19.05	0.64	1.23	0.96	2.09
	Basal	0.9953	47.02	165.60	0.24	39.71	1.18	20.91	15.52	10.78	13.41	0.62	1.62	1.32	2.87
2038	Upper	0.9987	42.39	36.77	0.18	45.78	0.93	20.13	12.77	14.71	18.30	0.61	1.13	0.87	1.90
	Middle	0.9984	49.34	38.70	0.18	45.80	1.08	20.29	12.98	14.62	18.20	0.71	1.32	1.02	2.22
	Basal	0.9988	49.22	44.82	0.18	47.64	1.03	21.57	14.10	14.94	18.60	0.66	1.28	1.00	2.17
2040	Upper	0.9978	45.33	40.19	0.18	45.13	1.00	20.11	12.94	14.34	17.85	0.66	1.23	0.96	2.08
	Middle	0.9972	50.22	39.28	0.18	46.80	1.07	20.78	13.33	14.91	18.56	0.70	1.32	1.02	2.22
	Basal	0.9988	49.38	44.59	0.17	49.14	1.00	22.24	14.52	15.42	19.19	0.64	1.24	0.97	2.11
Xi'nong 979	Upper	0.9988	36.95	59.32	0.21	42.14	0.88	19.82	13.43	12.79	15.92	0.54	1.11	0.87	1.90
	Middle	0.9982	43.20	49.77	0.19	44.04	0.98	20.24	13.42	13.64	16.98	0.62	1.22	0.96	2.09
	Basal	0.9993	42.52	58.27	0.19	45.20	0.94	21.22	14.34	13.75	17.11	0.58	1.84	0.93	2.04

r^2 indicates the goodness of fit of the logistic equation to the kernel-filling processes of the different spike parts in the big-spike lines and the control cultivar.
The kernel-filling parameters were as follows: W_0, the final kernel dry weight; A, a constant related to both kernel-filling rate and duration; B, a constant related to kernel-filling rate; T, the total number of kernel-filling days; V_a, the mean kernel-filling rate; T_m, the day on which the kernel-filling rate appeared to be highest; T_1, the duration of the moderately increasing kernel-filling stage; T_2, the duration of the rapidly increasing kernel-filling stage; T_3, the duration of the slowly increasing kernel-filling stage; V_1, the kernel-filling rate of the moderately increasing kernel-filling stage; V_2, the kernel-filling rate of the rapidly increasing kernel-filling stage; V_3, the kernel-filling rate of the slowly increasing kernel-filling stage; V_m, the maximum kernel-filling rate (Yang et al. 2001).

Primary and secondary kernel-filling parameters of individual spikes during the kernel-filling period

The high r^2 values shown in Table 3 suggest that the logistic equation had a good fit to the kernel-filling processes of the big-spike lines and the control cultivar. Based on the two inflection points during the growth period (Fig. 1), the kernel-filling process of wheat can be divided into three kernel-filling stages: moderately, rapidly and slowly increasing stages.

The kernel-filling parameters of the big-spike lines were significantly different from those of the control cultivar. During the late-ripening stage, the 1000-kernel weights of the big-spike lines ranged from 47.56–55.42 g, which was 5.85–13.71 g higher than control cultivar. The kernel-filling durations of the big-spike lines ranged from 45.06–53.32 d, which is significantly longer than that of the control cultivar (43.4 d). The kernel-filling durations of big-spike lines were ranked in the order of T_3 (the slowly increasing kernel-filling stage) > T_2 (the rapidly increasing kernel-filling stage) > T_1 (the moderately increasing kernel-filling stage). During the moderately increasing kernel-filling stage, the kernel-filling duration of line 2005 appeared longer, while during the rapidly and slowly increasing kernel-filling stages, line 2026 had the longer duration.

The kernel weight increments during the different kernel-filling stages made up different proportions of the kernel weights for all of the test materials. The kernel weight increment made up 19.35% of the kernel weight during the moderately increasing kernel-filling stage, 59.8% during the rapidly increasing stage, and 20.85% during the slowly increasing stage. Thus, the rapidly increasing kernel-filling stage is the primary stage in the kernel-filling process.

Primary and secondary kernel-filling parameters of the different spike parts during the kernel-filling period

The 1000-kernel weights of the upper, middle and basal parts of the spike in the big-spike wheat

Table 3 Parameters of the kernel-filling logistic equation for the individual spikes of five big-spike wheat lines and one multiple-spike cultivar (Xi'nong 979).

Test materials	Primary parameters						Secondary parameters							
	r^2	W_0 (g)	A	B	T (d)	V_a (g 1000 kernels^{-1} d^{-1})	T_m (d)	T_1 (d)	T_2 (d)	T_3 (d)	V_1 (g d^{-1})	V_2 (g d^{-1})	V_3 (g d^{-1})	V_m (g d^{-1})
2005	0.9986	51.35	41.86	0.16	51.00	1.01	22.87	14.80	16.13	20.07	0.65	1.24	0.96	2.10
2026	0.9972	55.42	32.55	0.15	53.32	1.04	22.99	14.30	17.39	21.64	0.70	1.26	0.96	2.10
2037	0.9970	48.43	51.98	0.18	47.41	1.02	21.92	14.61	14.61	18.18	0.64	1.28	1.00	2.18
2038	0.9986	47.56	40.93	0.18	45.06	1.06	20.13	12.99	14.29	17.78	0.69	1.30	1.01	2.19
2040	0.9959	50.59	29.12	0.15	51.51	0.98	21.80	13.28	17.03	21.19	0.68	1.19	0.90	1.96
Xi'nong 979	0.9987	41.71	56.02	0.20	43.40	0.96	20.27	13.64	13.26	16.50	0.59	1.21	0.95	2.07

r^2 indicates the goodness of fit of the logistic equation to the kernel-filling processes in the individual spikes of the big-spike lines and the control cultivar.
See Table 2 for a definition of the kernel-filling parameters.

lines were higher than those of the control cultivar during the late-ripening stage (Table 2).

The total kernel-filling durations of the upper parts of the spike in the big-spike lines ranged from 43.39–48.41 d, with durations of 12.77–15.05 d, 13.14–15.15 d and 16.35–18.85 d during the moderately increasing, rapidly increasing and slowly increasing kernel-filling stages, respectively. The total kernel-filling durations of the middle parts of the spike in the big-spike lines ranged from 45.80–51.68 d, with durations of 12.98–14.43 d, 14.62–16.60 d and 18.20–20.66 d during the moderately increasing, rapidly increasing and slowly increasing kernel-filling stages, respectively. The total kernel-filling durations of the basal parts of the spike in the big-spike lines ranged from 39.71–51.43 d, with durations of 14.10–15.52 d, 10.78–16.37 d and 13.41–20.38 d during the moderately increasing, rapidly increasing and slowly increasing kernel-filling stages, which were -0.24–1.18 d, -2.97–2.03 d and -0.34–3.27 d higher than the control cultivar, respectively.

The kernel weight increments of the upper, middle and basal parts of the spike during the three kernel-filling stages made up different proportions of the kernel weights for all the test materials. During the moderately increasing kernel-filling stage, the kernel weight increments of the upper, middle and basal parts of the spike made up 20%, 19.75% and 19.98%, respectively, of the kernel weights in the big-spike lines, which were all lower than observed for the cultivar. However, during the rapidly increasing kernel-filling stage, the kernel weight increments of the upper, middle and basal parts of the spike in the big-spike lines were all higher than those of the control cultivar. During the slowly increasing kernel-filling stage, the kernel weight increments of the upper and middle parts of the spike made up a higher proportion of the kernel weights than the basal parts of the spike for the lines and the cultivar.

The kernel-filling parameters of wheat showed that the maximum kernel-filling rates (V_m) and average kernel-filling rates (V_a) of the big-spike lines were higher than those of the control cultivar—although the V_m and V_a were lower for the upper parts of the spike in the big-spike lines, they were higher for the middle and basal parts of the spike. The kernel-filling rates of the individual spikes and their different parts during the three kernel-filling stages were ranked in the order of $V_2 > V_3 > V_1$. Therefore, the higher average kernel-filling rates of the three spike parts of big-spike lines during the different kernel-filling stages contributed to its high yield by helping plants to obtain more nutrients during the growth period.

Discussion

To produce a high yield in crops, leaf photosynthesis needs to be able to meet the demands of the kernel-filling process (Farooq et al. 2009), as the photosynthesis of plants contributes 60% ± 100% to the final carbon content of their kernels (Serrago et al. 2013). Therefore, it is generally agreed that the photosynthetic performance of crop plants needs to be improved to increase biomass production rates (Fischer et al. 1998). In the present study, the big-spike lines of wheat had lower average photosynthetic rates (P_n) than the control cultivar (Xi'nong 979) throughout the entire kernel-filling process. This was due to the big-spike lines having larger individual plants and greater sink capacities than the multiple-spike cultivar, causing them to suffer from nutrient deficiency and thus needing to supply more photosynthetic products for their plant growth (Wang et al. 2012). The kernel yield of wheat is often limited by its sink strength rather than by assimilate availability (i.e. the 'source') (Cartelle et al. 2006; Farooq et al. 2009), with the level of sink capacity-resulted limitation depending on the environment in which the crops grow (Blade & Baker 1991). The kernel yield of a cereal stand is also a function of a number of genetically and environmentally regulated factors (Gonzalez et al. 2011), which implies that genetic variability in plant senescence and kernel-filling rates need to be exploited to help improve kernel size and plumpness. Therefore, future studies need to consider the relationship between photosynthetic rates and sink capacity in order to improve the kernel-filling rate, kernel plumpness and kernel weight of wheat crops.

Field crops initially experience slow kernel growth; this is then followed by linear kernel growth combined with fast plant growth, and finally slow kernel growth until maturity (Wei et al. 2011). In this study, the logistic curve appeared to have a good fit to the kernel-filling data for all the test materials, with increases in the kernel weights in different parts of the spike tending to follow an S-shaped curve. After flowering, the kernel-filling rate and duration are the primary factors affecting final kernel yield in wheat, within the limits set by the previous life history of a particular plant (Brdar et al. 2008). Previous studies have shown that the kernel yields of different genotypes fit a non-linear growth equation (Harris & Taylor 2013) and mainly depend on the kernel-filling rates (Borràs-Gelonch et al. 2012). The present study showed that the kernel-filling rates of the different parts of the spike were ranked in the order of $V_2 > V_3 > V_1$ for the three kernel-filling stages. This differed from the findings of Qin et al. (2013), who ranked them in the order of $V_2 > V_1 > V_3$, probably due to the difference of materials and environment in each test.

In rice, a longer kernel-filling duration contributes to improved kernel filling, thereby leading to higher yield, as long as higher mean cumulative temperatures and levels of solar radiation are provided (Yang et al. 2008). The kernel-filling durations of the different test materials in the present study affected their kernel weights in different ways. The kernel-filling durations of the individual spikes and their different parts in the big-spike lines were ranked in the order of $T_3 > T_2 > T_1$ for the three kernel-filling stages. It has previously been shown that the key to kernel weight improvement is to breed cultivars that have shorter moderately increasing kernel-filling stages, longer slowly increasing kernel-filling stages, higher kernel-filling rates and non-premature senescence during the late growth period (Wang et al. 2013). Thus, the short moderately increasing kernel-filling stage of the big-spike lines meant that they entered the rapidly increasing kernel-filling stage earlier, thus accumulating more dry matter; and the longer slowly increasing kernel-filling stage prevented premature senescence from occurring during the late growth period because the kernel-filling stages were well accorded with the kernel-filling requirements. Therefore, the kernel weights can be increased in these new lines by optimising their photosynthetic characteristics and kernel-filling characteristics in the future.

Since the inflorescences and vascular bundle systems in wheat spikes develop at different times, the upper, middle and basal parts of the spike have different kernel-filling characteristics. The present study indicated that during the early growth stage, more nutrients were transferred into the upper part of the spike and fewer nutrients into the basal part, whereas during the late growth stage, more nutrients were transferred into the basal parts and fewer nutrients into the upper parts. This contrasts with the findings of Li et al. (2013), who showed that during the early kernel formation stage, the largest amounts of nutrients were transported into the middle parts of the spike, followed by the upper parts and then the basal parts; by contrast, during the middle and late kernel-filling stages, more nutrients were transported into the middle parts, and fewer nutrients into the upper and basal parts. The average maximum kernel-filling rates of the upper parts of the spike occurred later than in the middle and basal parts, and the average kernel-filling rates of all parts of the spike in the big-spike lines were higher than in the control cultivar during each of the kernel-filling stages.

Farming practices or the application of growth regulators can enhance carbohydrate transport into the middle and especially the basal parts of the spike, which can significantly increase final kernel weights. It has been shown that under nitrogen-rich conditions, big-spike lines can take up more nitrogen than multiple-spike cultivars (Mi et al. 2002). Therefore, kernel plumpness, size and weight could be increased by simultaneously increasing the photosynthetic rate and the kernel-filling duration during the late kernel-filling stage. Future research should also investigate variation in the number of grains per spike and per spikelet between genotypes, and the contribution of leaf nitrogen concentration and leaf mass on kernel yield in wheat.

Conclusion

The big-spike lines of wheat had lower average P_n throughout the entire kernel-filling process. More nutrients were transferred into the upper parts of the spike and fewer nutrients into the basal parts during the early growth period, whereas more nutrients were transferred into the basal parts during the later growth period. The 1000-kernel weights of the middle parts of the spike were higher throughout the entire kernel-filling process and the kernel-filling rates of the different parts of the spike were ranked in the order of $V_2 > V_3 > V_1$ for the different kernel-filling stages. Further research is required to determine the optimal farming practices and chemical regulation measures for the big-spike lines to maximise the photosynthetic rate and kernel-filling duration.

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