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Full Length Article

Difference of Grain Filling Characteristics and Starch Synthesis between the Superior and Inferior spikelet of Tartary Buckwheat

Y. Zhang, X.H. Wu, X.Y. Huang, P.Y. He, Q.F. Chen and K.F. Huang*
Research Center of Buckwheat Industry Technology, Guizhou Normal University, Guiyang 550001, China
*For correspondence: hkf1979@163.com
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Abstract

In this research, Tartary buckwheat (*Fagopyrum tataricum* Gaertn) "cv Jinqiao 2" (JQ2) was used to determine the difference among grain filling characteristics, starch and starch synthesis enzyme activities, and photosynthetic characteristics between superior and inferior spikelet and to clarify the physiological mechanism of the formation of inferior spikelet of Tartary buckwheat. The initial growth power (R_0), maximum grain filling rate (G_{max}), and average grain filling rate (G_{mean}) of superior spikelet were remarkably higher than those of inferior spikelet, whereas the time required to reach the maximum grain filling rate ($T_{max.G}$) was lower than that of inferior spikelet. The contribution rate to grain weight in the middle filling stage was the largest, followed by the later filling stage and the smallest in the early filling stage of superior spikelet. The contribution rate of the middle filling stage was the largest, followed by the early filling stage, and the smallest was the late filling stage of inferior spikelet. The starch content and net photosynthetic rate of superior spikelet were higher than those of inferior spikelet. The activities of adenosine diphosphate glucose pyrophosphate and soluble starch polymerase in the superior spikelet at the early filling stage were stronger than those in the inferior spikelet but lower than those in the inferior spikelet in the middle and late filling stages. In summary, low light energy utilization and biosynthesis activity at the early filling stage are important physiological conditions for the low grain filling rate and the light grain weight of inferior spikelet.

Keywords: Tartary buckwheat; Superior and inferior spikelet; Grain filling; Starch synthesis

Introduction

Buckwheat belongs to the genus *Fagopyrum* Mill., and is an annual herbaceous plant widely distributed worldwide, mainly in Russia, China, Ukraine, France, Kazakhstan, Poland and Japan. Tartary buckwheat (*Fagopyrum tataricum* Gaertn) is a food crop of great health value and has remarkable functions of lowering blood sugar, blood pressure, blood lipid, and antitumor risk due to its rich flavonoid and D-chiral inositol contents (Steadman *et al*. 2001a; Choi *et al*. 2015; Giménez-Bastida and Zieliński 2015). However, the yield of Tartary buckwheat is currently low at approximately 1,500–2,400 kg·hm^{-2} (Song *et al*. 2014). Therefore, the production of high and stable yield of Tartary buckwheat is of great importance to develop the buckwheat industry (Huang *et al*. 2019).

The yield of crops depends on the size of grain storage and the degree of grain filling. The grain weight of cereal crops, such as rice, wheat, and corn varies greatly according to the position of grain formation on panicle. In general, the grain with good grain filling and high grain weight is called superior spikelet, whereas that with slow filling, poor filling, and low grain weight is called inferior spikelet (Mohapatra *et al*. 1993; Yang *et al*. 2000; Ali *et al.* 2010). Poor grain filling and low grain weight of inferior spikelet limit the yield potential of crops and seriously affect grain quality. Inferior spikelet needs to consume many nutrients and water during differentiation and growth. Poor filling of inferior spikelet also greatly influences the efficient use of nutrients and water in crops. Therefore, the mechanism of superior spikelet formation should be clarified for the realization of high yield and good quality of crops.

In our previous study, the grains on the upper part and main stem of buckwheat were regarded as superior spikelet, whereas those on the lower part and branches were regarded as inferior spikelet (Wang *et al*. 2016). However, the mechanism of poor filling of inferior spikelet that affects the reasonable regulation and control of buckwheat is poorly studied. We predict that grain filling characteristics and starch synthesis are important physiological conditions for the low grain filling rate and the light grain weight of inferior spikelet. Thus, Tartary buckwheat "cv. Jinqiao 2" (JQ2) was used to investigate the differences in grain filling characteristics, starch content, and enzyme activities related to starch synthesis between superior and inferior spikelet. The results have important theoretical and practical importance for defining the formation mechanism of Tartary buckwheat inferior spikelet and provide some theoretical basis for high-yield cultivation of Tartary buckwheat.

Materials and Methods

Plant materials and growth

Tartary buckwheat "cv. Jinqiao 2" (JQ2) with high yield was used. The experiment was conducted in cement pools at Huangnitang's Cultivation Experiment Station of Guizhou Normal University (Bijie City, Guizhou Province, 922 m, 27°05′ N, and 105°71′ E) on March 9, 2018 and March 1, 2019. The soil in the pool is yellow loam with 31.37 $g \cdot kg^{-1}$ soil organic matter, 1.06 $g \cdot kg^{-1}$ total nitrogen, 111 $mg \cdot kg^{-1}$ hydrolyzed nitrogen, available phosphorus, 112.72 $mg \cdot kg^{-1}$ available potassium, and 1.34 $g \cdot cm^{-3}$ soil bulk density. Furthermore, the soil pH was 5.76.

Tartary buckwheat was cultivated in cement pools with an area for each test plot measuring 2 m × 10 m × 0.3 m. The optimum application rates of nitrogenous, phosphate, and potassium fertilizers were 100 (urea), 69 (calcium superphosphate), and 5.1 $kg \cdot hm^{-2}$ (potassium chloride), respectively (Song *et al*. 2014). The three fertilizers were mixed and applied as base fertilizer at one time, and no fertilizer was applied throughout the growth period. The row spacing was 0.33 m, the sowing rate was 52.5 g per plot, and the basic seedling per plot was 900–1000 plants. Tartary buckwheat seeds were harvested on June 18, 2018 and June 12, 2019. Normal agricultural practices were implemented.

Sample preparation

At the beginning of the flowering period, approximately 1,000–1,500 flowers that bloom on the same day when Tartary buckwheat plants were marked in each pool, and the marked flowers were sampled every 7 days from flowering to maturation to determine. The superior spikelet (SS) was the grain of 1–3 nodes at the top of the main stem of Tartary buckwheat, and the inferior spikelet (IS) was the grain on the secondary branch at the base of Tartary buckwheat.

Growth and physiological determinations

Simulation of grain filling: The dried grains were weighed to calculate the average dry weight of 100 grains. Richards' equation (Richards 1959) was used to describe the grain filling of superior and inferior spikelet Zhu *et al*. (1988).

$$W = A/(1 + Be^{-Kt})^{1/N}$$

Divided grain-filling stage: The contribution rates of the grain-filling period, including the prophase of filling stage (RGC1), the middle of filling stage (RGC2), and the anaphase of filling stage (RGC3) for grain weight, were calculated as described by Yang *et al*. (2013).

$$RGC1 = W1/A \times 100\%$$
$$RGC2 = (W2 - W1)/A \times 100\%$$
$$RGC3 = (W3 - W2)/A \times 100\%$$

Starch synthase enzyme activity: The grain was ground in a mortar with 3–5 mL Tricine-NaOH (100 $mmol \cdot L^{-1}$) extract containing $MgCl_2$ (10 mmol L^{-1}), EDTA (2 $mmol \cdot L^{-1}$), 2-mercaptoethanol (50 $mmol \cdot L^{-1}$), glycerol (12%, *v*/*v*), and PVP40 (5%, *w*/*v*) at pH 8.0, and the temperature was kept at 0ºC. It was centrifuged at 15,000 ×g for 10 min (4ºC), and the supernatant (crude enzyme solution) was used for the determination of enzyme activity. Referring to Yang et al (2003), the activities of adenosine diphosphate glucose pyrophosphate (AGPase), soluble starch polymerase (SSS), and starch branching enzyme (SBE) were determined.

Photosynthetic characteristics: LI-COR-6400 portable photosynthetic meter (Li-Cor 6400 portable photosynthesis measurement system (Li-Cor, Lincoln, NE, USA) was used to determine the net photosynthetic rate, stomatal conductivity, and transpiration rate of the leaves, where the superior and inferior spikelets were located. The measurements were obtained at 10:00–11:00 in the morning, and 10 leaves were measured in each treatment.

Determination of agronomic characters and yield: Agronomic characters items were measured as described by Zhang and Lin (2007). The yield was determined at maturity and converted per ha yield.

Statistical analysis

The collected data were statistically analyzed through SPSS analysis of variance from CR design. Treatment means were compared using the least significant difference at the 5% probability level" as "Excel 2003 and SPSS 22.0" were used for processing and one-way analysis of variance was performed.

Results

Simulation of grain-filling process

A 100-grain dry weight of JQ2 increased rapidly at the early filling stage, and extent of increase decreased significantly after 28 days after anthesis (Table 1). The dry weight of 100-grain superior spikelet was significantly higher than that of inferior spikelet. The laws of change in 2018 and 2019 were similar, and the dry weight of 100-grains in each period in 2019 was lower than that in 2018 of JQ2.

The determination coefficient R^2 of each curve equation ranged from 0.9938 to 0.9972, indicating that fitting the grouting process of Tartary buckwheat with Richards's equation is feasible (Table 2). *A* value was the maximum value for 100-grain weight in theory during simulated grain filling. The *A* value of four treatments was very close to the final actual 100-grain weight, and the *A* value of superior spikelet was higher than that of inferior

Table 1: The hundred-grain weight of superior and inferior spikelet of Tartary buckwheat (g/100 grains DW)

Year	Grain position	period				
		7d	14d	21d	28d	35d
2018	SS	0.086a	0.370a	0.708a	0.877a	0.901a
	IS	0.062b	0.269b	0.513b	0.622b	0.655b
2019	SS	0.056a	0.224a	0.508a	0.686a	0.712a
	IS	0.034b	0.198b	0.437b	0.553b	0.591b

Note: $P<0.05$. The same below

Table 2: Parameters of the Richards equation for evaluating the grain-filling process of Tartary buckwheat

Year	Grain position	A	B	K	N	R^2	R_0	$T_{max.G}$/d	G_{max} (g/100·d)	G_{mean} g/100	I/%	D/d
2018	SS	0.9198	0.9920	0.1835	0.0827	0.9958	2.2174	13.5400	0.0596	0.0405	38.2594	22.7051
	IS	0.6693	1.2935	0.1431	0.0850	0.9972	1.6831	19.0275	0.0244	0.0230	38.2985	29.1456
2019	SS	0.7371	1.1364	0.1512	0.0738	0.9938	2.0483	18.0861	0.0360	0.0269	38.1052	27.4352
	IS	0.6252	1.2089	0.1231	0.1053	0.9947	1.1693	19.8284	0.0229	0.0183	38.6437	34.2045

Table 3: The divided grain-filling stage of Tartary buckwheat

Year	Grain position	Early filling stage			Middle filling stage			Later filling stage		
		Duration/d	Average rate (g/100·d)	Contribution%	Duration/d	Average rate (g/100·d)	Contribution (%)	Duration/d	Average rate (g/100·d)	Contribution (%)
2018	SS	8.0972	0.0094	8.2629	18.9828	0.0510	60.3937	38.6121	0.0142	30.2765
	IS	12.0416	0.0155	27.9057	26.0134	0.0296	61.7964	51.1765	0.0027	10.1798
2019	SS	11.5063	0.0108	16.8268	24.6659	0.0364	65.0059	48.5123	0.0055	17.8216
	IS	11.6392	0.0110	20.4556	28.0176	0.0249	65.1344	57.1934	0.0030	14.1916

spikelet. The *N* values of superior and inferior spikelet were both less than 1, and the *N* value of inferior spikelet was higher than that of superior spikelet. The initial growth power (R_0), maximum grain filling rate (G_{max}), and average grain filling rate (G_{mean}) of superior spikelet were significantly higher than those of inferior spikelet, while the time to reach the maximum grain filling rate ($T_{max.G}$) and active filling growth period (approximately 90% of total growth completed) (*D*) was lower than that of inferior spikelet. The ratio of the growth of maximum grain filling rate to final value of grain (I) for superior and inferior spikelet did not differ. The results in 2019 were similar to those in 2018, and *A* value, R_0, G_{max} and G_{mean} of 2018 were higher than those in 2019.

Divided grain-filling stage of superior and inferior spikelet

In comparison with the superior spikelet, the days of reaching the early filling stage and the average filling rate of the inferior spikelet were longer and larger (Table 3). In comparison with the superior spikelet, the time of reaching the middle filling stage and the late filling stage of the inferior spikelet was longer, but the average filling rate was smaller. The contribution rate to grain weight in the middle filling stage was the largest, followed by the later filling stage, and then the early filling stage of superior spikelet. The contribution rate of the middle filling stage was the largest, followed by the early filling stage, and then the late filling stage of inferior spikelet. There was no significant ($P>0.05$) difference in the 2018 and 2019 results.

Starch accumulation and starch synthase enzyme activity

The starch content of JQ2 increased rapidly from 7 days to 14 days, and then the extent of the increase decreased slightly from 14 days to 21 days after anthesis and almost stopped decreasing 21 days after anthesis (Table 4). The starch content of superior spikelet was higher than that of inferior spikelet. The AGPase activity in the grains of JQ2 initially increased and then decreased with the increase in growth stage. The highest AGPase activity of superior spikelet was reached on the 14th day after anthesis, while the AGPase activity of inferior spikelet reached the maximum on the 21st day after anthesis. In the early filling stage (7–14 days), the AGPase activity of superior spikelet was higher, while that of the inferior spikelet was higher in the middle and late filling stage (21–35 days). The highest SSS activity in the grains of JQ2 was reached on the 14th day after anthesis, which then decreased rapidly. Before 14 days after anthesis, the SSS activity of superior spikelet was higher than that of inferior spikelet, and became lower thereafter. The SBE activity in the grains of JQ2 initially increased and then decreased with the advancement of growth stage, reaching the maximum at 14 days after anthesis. The SBE activity of superior spikelet was higher than that of inferior spikelet. The starch content and starch synthase enzyme activity of 2018 were higher than those in 2019.

Photosynthetic characteristics

The net photosynthetic rate in the leaves of JQ2 initially increased and then decreased with the advancement of

Table 4: The starch accumulation and starch synthase activity of superior and inferior spikelet of Tartary buckwheat

Year	Item	Grain position	Period				
			7d	14d	21d	28d	35d
2018	Starch (%)	SS	27.80a	67.70a	76.34a	77.84a	79.17a
		IS	15.05b	56.79b	69.98b	72.41b	73.52b
	AGPase (U g^{-1} min^{-1})	SS	0.280a	0.493a	0.416b	0.320b	0.244b
		IS	0.181b	0.328b	0.437a	0.385a	0.294a
	SSS (U mg^{-1} min^{-1})	SS	5.560a	8.502a	4.216b	2.018b	0.870b
		IS	4.167b	7.247b	5.070a	2.864a	1.290a
	SBE (U g^{-1} min^{-1})	SS	2.099a	4.024a	3.891a	3.517a	3.054a
		IS	1.170b	2.928b	3.601b	3.275b	2.855b
2019	starch（%）	SS	26.32a	61.57a	73.81a	76.03a	78.86a
		IS	13.22b	50.38b	66.51b	70.83b	71.79b
	AGPase (U g^{-1} min^{-1})	SS	0.235a	0.417a	0.319b	0.243b	0.186b
		IS	0.136b	0.283b	0.372a	0.288a	0.210a
	SSS (U ·mg^{-1} min^{-1})	SS	3.149a	7.861a	3.582a	1.832b	0.827b
		IS	2.887b	6.394b	4.018b	2.016a	1.126a
	SBE (U ·g^{-1} min^{-1})	SS	2.023a	3.933a	3.823a	3.425a	2.869a
		IS	1.054b	2.760b	3.507b	3.081b	2.249b

Table 5: Photosynthetic characteristics of superior and inferior spikelet of Tartary buckwheat

Year	Item	Grain position	Period				
			7d	14d	21d	28d	35d
2018	Net photosynthetic rate	SS	12.891a	15.072a	9.545a	6.214a	5.150a
	(μmolCO_2/m^2/s)	IS	9.245b	13.034b	8.805a	5.629a	3.913b
	Stomatal conductivity (mmol H_2O/m^2/s)	SS	0.060a	0.071a	0.055a	0.044a	0.021a
		IS	0.051a	0.056b	0.059a	0.028b	0.018a
	transpiration rate	SS	1.869b	2.955b	1.908b	1.534b	0.732b
	(mmol H_2O/m^2/s)	IS	2.561a	3.672a	2.732a	2.651a	0.940a
2019	Net photosynthetic rate	SS	11.064a	14.885a	9.048a	5.923a	4.404a
	(μmol CO_2/m^2/s)	IS	8.728b	12.284b	8.031b	5.177a	3.267b
	Stomatal conductivity (mmol H_2O/m^2/s)	SS	0.055a	0.058a	0.054a	0.021a	0.017a
		IS	0.048a	0.049a	0.049a	0.026a	0.016a
	Transpiration rate (mmol H_2O/m^2/s)	SS	1.835a	2.501a	1.173b	1.311a	0.685a
		IS	1.957a	2.550a	2.127a	1.523a	0.693a

Table 6: Agronomic traits and yield of Tartary buckwheat

Year	Plant height (cm)	Number of main stem nodes (individual)	Number of branches of main stem (individual)	Grain number per plant (grain)	Grain weight per plant (g)	1000-grain weight(g)	Yield (kg·ha^{-1})
2018	120.92a	9.1b	8.6a	501.3a	12.63a	25.07a	2103.6a
2019	72.22b	10.3a	5.7b	474.6b	11.52b	22.10b	1858.2b

growth period and reached the maximum at 14 days after anthesis (Table 5). The net photosynthetic rate of superior spikelet was significantly higher than that of inferior spikelet. Stomatal conductivity initially increased and then decreased with the advancement of growth period. The stomatal conductivity of superior spikelet reached the maximum on the 14^{th} day after anthesis, while that of inferior spikelet reached the maximum on the 21^{st} day after anthesis. The stomatal conductivity of superior spikelet was higher than that of inferior spikelet, and their difference reached a significant level at 14 and 28 days after anthesis. The transpiration rate initially increased and then decreased with the advancement of growth period and reached its maximum at 14 days after anthesis. The transpiration rate of inferior spikelet was higher than that of superior spikelet. The net photosynthetic rate, stomatal conductivity, and transpiration rate of 2018 were higher than those in 2019.

Agronomic traits and yield

Differences were observed in the agronomic characters and yield between 2018 and 2019 (Table 6). The plant height, branch number of main stem, grain weight per plant, 1000-grain weight, and yield in 2018 were significantly higher than those in 2019, while the number of main stem nodes in 2019 was significantly higher than that in 2018.

Discussion

The Richards equation (Richards 1959) growth curve was used to fit the filling process of superior and inferior spikelet, and the fitting degree exceeded 0.9938, which indicated that the Richards growth curve could quantitatively express the continuous process of the quality change of superior and inferior spikelet. The growth curve of Richards equation presents a cluster of curves determined by the size of N value. Results showed that the *N* values of superior and inferior spikelet were less than 1, which indicated that the filling rate curve leans to the left. This further indicated that the grain filling was limited by reservoir capacity (Zhu *et al*. 1988) and that the grain filling material was more sufficient (Gu *et al*. 2001), witnessing that the grain filling material grows rapidly in the early stage of filling and then gradually weakened. Grain filling initiation potential (R_0) reflects the growth potential of ovary. The R_0 value was large, the endosperm cell division cycle was short, the division was fast, and grain filling started early. In this study, the grain filling initiation potential of superior spikelet was significantly higher than that of inferior spikelet, which indicated that the grain filling of superior spikelet starts early. The photosynthetic products were obtained first, and the maximum grain filling rate was reached in a short time after anthesis, which supports that the time for superior spikelet to reach the maximum filling rate ($T_{max.G}$) was less than that of inferior spikelet.

Grain weight is a function of filling rate and filling duration (Zhai *et al*. 2017). Some studies show that grain weight is positively correlated with filling rate (Li *et al*. 2019), but not with grouting duration, while some studies show that grain filling duration is closely related to grain weight (Lu *et al.* 2002). Results showed that the grain weight of Tartary buckwheat was affected by filling rate more than filling time, which was consistent with the results of Peng and Xiao (2012) on wheat and those of Wang *et al.* (2017). The grain weight of the Tartary buckwheat might be mainly affected by the grain filling rate, especially the grain filling rate in the middle of the grain filling, because the contribution rate of the medium term to the grain weight of grain exceeded 60%. Besides being affected by the filling rate in the middle stage of grain filling, the superior spikelet was mainly affected by the late stage of grain filling, while the inferior spikelet was affected by the filling rate in the early filling stage, that is, the rate of late grain filling has more influence on its particle weight.

Generally, the accumulation of starch in grains is the result of plant photosynthesis, and the net photosynthetic rate is the most direct manifestation of the utilization of light energy by crops (Ju *et al.* 2018; Ba *et al.* 2019). Our results showed that the photosynthetic rate of superior spikelet was higher than that of inferior spikelet, which indicates that the utilization of light energy of strong grain is better than that of inferior spikelet, which indicates that the superior spikelet has more "source", thus providing the large grain filling initiation potential of superior spikelet. The starch content in Tartary buckwheat grain is approximately 75% (Steadman *et al*. 2001b). The process of grain filling in Tartary buckwheat is the same as the process of starch accumulation. The light contract compounds of source organ are transported to the grains in the form of sucrose through phloem, and then starch is formed under the action of a series of enzymes (Nakamura and Yuki 1992; Jeng *et al*. 2003; Yang *et al*. 2003). AGPase, SSS, and SBE are the key enzymes during starch synthesis and metabolism (Fu *et al*. 2012). These enzymes play an important role in regulating the synthesis and accumulation of grain starch. Our results showed that the AGPase and SSS activities of superior spikelet in the early filling stage were higher than those in inferior spikelet, while those in the middle and late filling stages were lower than those in inferior spikelet, which is consistent with the results of Yang *et al*. (2001). Considering that the superior spikelet has a high filling rate, the low starch biosynthesis activity in the early filling stage explains the low filling rate and light grain weight of inferior spikelet (Fu *et al*. 2012).

Conclusion

The low light energy utilization and resource assimilation efficiency in the early filling stage are important physiological factors for the low grain filling rate and the light grain weight of inferior spikelet.

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