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The effects of post-anthesis shading on starch granule size distribution and viscosity parameters in waxy and non-waxy soft wheat

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Abstract: To clarify the effects of post-anthesis low light on grain yield and starch quality of waxy and non-waxy soft wheat, a field experiment was conducted from 2023 to 2025. Two wheat cultivars, Jinuo 2 (waxy soft wheat) and Quanmai 725 (non-waxy soft wheat), were employed as test materials, and four shading treatments (no shading, 10% shading, 20% shading, and 30% shading) were applied after anthesis. The regulatory effects of different shading intensities on wheat yield, grain quality, starch granule size distribution and starch viscosity properties were systematically analysed. The results showed that post-anthesis low light stress significantly reduced the grain number per spike, 1 000-grain weight and grain yield, while increasing the protein content, wet gluten content and sedimentation value of wheat grains. Under low light stress, the volume and surface area proportions of A-type starch granules increased, while those of B-type starch granules decreased. Under the same shading condition, Jinuo 2 exhibited a higher proportion of B-type starch granules and a lower proportion of A-type starch granules than Quanmai 725. With increasing shading intensity, the peak, trough and final viscosities, as well as the breakdown and setback values, of grain starch decreased continuously, and all viscosity parameters of Quanmai 725 were significantly higher than those of Jinuo 2. Furthermore, post-anthesis low light reduced the onset, peak and conclusion gelatinisation temperatures and increased gelatinisation enthalpy. Quanmai 725 had higher gelatinisation temperatures, whereas Jinuo 2 possessed higher gelatinisation enthalpy. Correlation analysis indicated that the volume distribution of B-type starch granules (≤ 10 μm) was significantly positively correlated with starch viscosity parameters, while A-type starch granules (> 10 μm) showed a significant negative correlation. In conclusion, post-anthesis low light reduces the yield and the proportion of B-type starch granules, increases the proportion of A-type starch granules, decreases starch pasting viscosity and elevates gelatinisation enthalpy in both soft wheat cultivars. Compared with Quanmai 725, Jinuo 2 is more sensitive to post-anthesis low light stress in terms of starch granule distribution characteristics.

Keywords: brewing wheat; photosynthesis; sunshine; climate change; stress-resistant cultivation; thermal properties

Light is a critical climatic factor regulating wheat growth and development by dominating photosynthesis and dry matter accumulation (Wu et al. 2019). In recent years, global climate change has reduced sunshine duration and solar radiation, especially in the Yangtze-Huaihe River region, the major soft-

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wheat-producing area in China (Wang et al. 2012, Han 2021, Li et al. 2021, Luo et al. 2023). The regional decline in light has become a key environmental factor limiting wheat yield and quality.

Grain filling is the critical stage for photosynthate accumulation and starch quality formation, and light conditions strongly affect starch synthesis, granule development and processing quality of wheat (Cai 2008, Chen et al. 2024a, Yang et al. 2024). Brewing wheat is a special soft wheat for Chinese Baijiu and starter preparation, characterised by low protein content, low kernel vitreousness and hardness, low amylose and high amylopectin content. Starch accounts for about 65% of wheat grain dry weight, serving as the primary storage substance and a core determinant of yield and processing quality (Rahman et al. 1995, Cai et al. 2021).

Wheat endosperm starch granules are classified into A-type (> 10 μm) and B-type (≤ 10 μm) according to particle size (Li et al. 2016). Their structure and distribution greatly affect wheat milling quality and the quality of processed products such as noodles, bread and Baijiu (Park et al. 2009). B-type starch granules are smaller in size but greater in quantity and specific surface area, capable of binding more proteins and lipids, whereas A-type starch granules show the opposite characteristics (Šebečić 1995a, Soh et al. 2006). Such differences directly determine the physicochemical properties of starch, including gelatinisation, thermodynamic characteristics and pasting viscosity.

Starch physicochemical properties, such as peak viscosity, breakdown value and gelatinisation enthalpy, are closely related to food processing quality (Šebečić and Šebečić 1995b, Primo et al. 2007, Chen et al. 2023) and are controlled by both genotype and cultivation environment. Under climate change, wheat often suffers from high temperatures, drought and overcast, rainy, low-light stress, severely limiting the yield and quality of soft wheat. Waxy soft wheat is featured with homozygous deletion of Wx-A1b, Wx-B1b and Wx-D1b, with grain amylose content less than 2% (Zhou et al. 2022, Liu et al. 2023, Shang et al. 2023, Liang et al. 2024). There are obvious differences in starch granule distribution, viscosity parameters and processing quality between waxy and non-waxy soft wheat (Cui et al. 2020). Most previous studies mainly focused on conventional wheat and weak-gluten wheat under low light. However, the coordinated variation of starch granule distribution, viscosity and thermodynamic characteristics in brewing soft wheat under post-anthesis low light, as well as cultivar differences in stress tolerance, remains unclear. Given the light limitation in the Yangtze-Huaihe River basin and insufficient research on waxy brewing soft wheat, this experiment selected Jinuo 2 (waxy soft wheat) and Quanmai 725 (non-waxy soft wheat) to explore the effects of post-anthesis low light on starch granule distribution and viscosity parameters. The results can provide a theoretical reference for stress-resistant cultivation of waxy and non-waxy brewing wheat in light-limited regions.

MATERIAL AND METHODS

Experimental design. The experiment was carried out at the experimental farm of Anhui Science and Technology University (Fengyang, Anhui) over two consecutive wheat-growing seasons (2023–2024 and 2024–2025). The field was previously planted with maize. The topsoil has a clay loam texture and is classified as Cambisol according to the FAO World Reference Base for Soil Resources (WRB). The topsoil properties were as follows: organic carbon (OC) 16.6 g/kg, alkaline hydrolysable nitrogen 72.8 mg/kg, available phosphorus (P) 17.5 mg/kg, and available potassium (K) 96.0 mg/kg. Two wheat cultivars, Jinuo 2 (JN2) and Quanmai 725 (QM725), were used in this study. The sowing density was 1.8×10^6 plants/ha. Each plot was 3 m × 3 m (9 m^2) with a row spacing of 0.25 m, and the experiment was arranged in a randomised complete block design with three replications. During the grain-filling stage (7–35 days after anthesis), four gradient shading treatments were established using white shade nets: no shading (CK); 10% shading (S1); 20% shading (S2), and 30% shading (S3). The nets were suspended 80 cm above the wheat canopy to ensure good ventilation within the canopy. During 7–35 days post-anthesis, actual shading intensity and shading rate were continuously monitored using automatic photosynthetically active radiation (PAR) recorders and regular manual measurements, with PAR as the primary indicator. All light sensors were calibrated before shading treatment. Loggers captured PAR data every 5 min throughout the grain-filling period, and shading rates were calculated by comparing PAR values from shaded plots with those from the unshaded control. Manual spot surveys were implemented every three days from 9:00 to 17:00 for cross-checking. Calibration inspections were carried out on day 7, day 21 and day 35 to fix net gaps and exclude light leakage. The averaged canopy PAR

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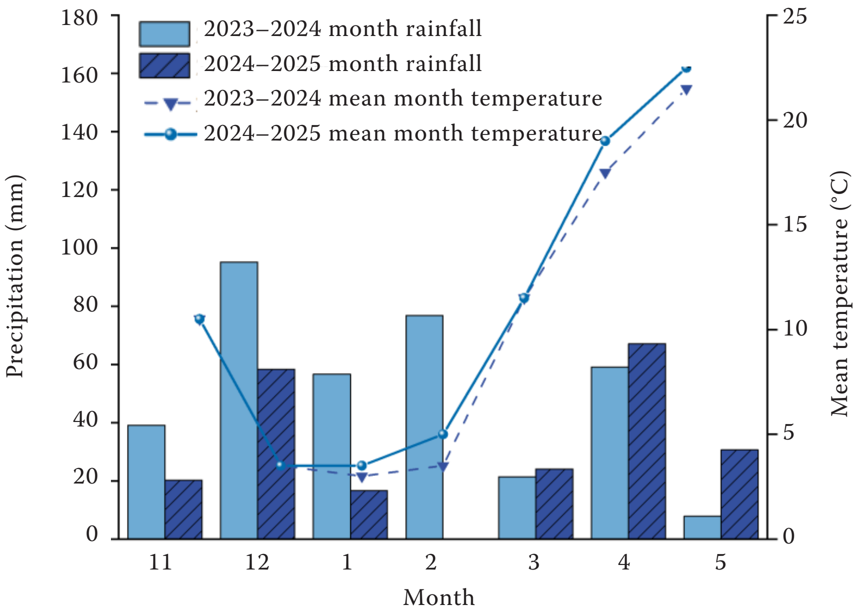

Figure 1. Monthly rainfall and mean temperature during the 2023–2024 and 2024–2025 experimental periods

data in Table 1 proved stable shading gradients, and canopy temperature, humidity and CO_2 concentration did not differ significantly among treatments. Fertiliser application rates were 180 kg N/ha, 39.30 kg P/ha, and 37.34 kg K/ha. All phosphorus and potassium fertilisers were applied as basal fertiliser. Nitrogen fertiliser was split-applied at a basal-to-topdressing ratio of 7:3, with topdressing conducted at the jointing stage. Other field management practices followed local conventional high-yield wheat cultivation standards. Wheat was sown on October 31, 2023 and November 1, 2024, and harvested on May 28, 2024 and May 21, 2025. Microclimate data of the wheat canopy for both growing seasons are presented in Table 1.

Measurement items and methods

Grain hardness measurement. Grain hardness was determined in accordance with the Chinese National Standard GB/T 21304-2007, "Wheat Hardness Determination – Hardness Index Method". The hardness of wheat samples was measured immediately after temperature treatment using the hardness index.

Yield and its components measurement. At maturity, 1 m^2 of uniformly growing wheat plants was selected from each plot to count the number of effective spikes. Thirty wheat plants were randomly selected at maturity to investigate the number of grains per spike. After maturity, 1 m^2 of wheat was harvested from each plot to measure yield. The sam-

Table 1. Effects of low light during the grain filling stage on the field microclimate

Year	Treatment	Light intensity (μmol/m^2/s)	Air temperature (°C)	Humidity (%)	CO_2 concentration (μmol/mol)
2023–2024	CK	1 645.00 ± 402.00^a	26.42 ± 2.25^a	41.61 ± 4.89^a	441.73 ± 0.77^a
	S1	1 260.63 ± 508.63^b	27.01 ± 2.35^a	41.52 ± 4.05^a	443.00 ± 1.79^a
	S2	1 156.50 ± 480.25^c	27.20 ± 2.64^a	41.77 ± 5.2^a	445.50 ± 4.37^a
	S3	816.00 ± 345.38^d	27.13 ± 2.93^a	41.29 ± 5.07^a	444.67 ± 4.84^a
2024–2025	CK	1 183.00 ± 533.25^a	26.49 ± 2.11^a	37.39 ± 4.76^a	442.83 ± 1.47^a
	S1	1 040.13 ± 510.63^b	26.53 ± 2.39^a	37.88 ± 5.12^a	443.00 ± 1.79^a
	S2	874.75 ± 450.13^c	27.08 ± 2.58^a	37.91 ± 3.54^a	443.33 ± 3.98^a
	S3	602.25 ± 312.13^d	27.16 ± 2.98^a	38.01 ± 2.65^a	444.50 ± 1.52^a

The data in the table are mean values from the weak light post-anthesis experiment (1–7 days after shading) during the 2023–2025 growing season. CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading

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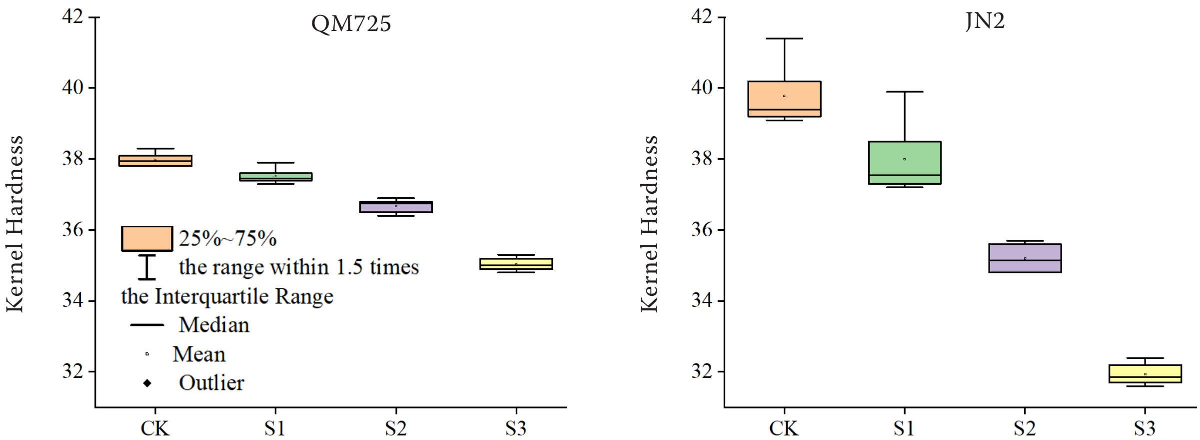

Figure 2. Effects of post-anthesis shading on grain hardness in waxy and non-waxy wheat. The data are the average values of two experimental growing seasons. QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading

ples were threshed manually, and the 1 000-grain weight was measured.

Grain quality measurement. Sun-dried grains were stored in a cold storage room for three months.

Table 2. Effects of post-anthesis low light stress on wheat yield and yield components

Year (Y)	Cultivar (C)	Treatment (T)	Spike number (× 10^4/ha)	Grain number per spike	1 000-grain weight (g)	Yield (kg/ha)
2023–2024	QM725	CK	584.00 ± 91.48	46.53 ± 3.75	43.34 ± 0.72	9 684.44 ± 73.43
		S1	580.00 ± 17.44	42.53 ± 3.75	42.32 ± 1.38	8 404.44 ± 301.21
		S2	560.00 ± 44.54	38.33 ± 2.10	41.67 ± 0.77	8 017.78 ± 126.02
		S3	553.33 ± 92.98	32.27 ± 6.77	37.03 ± 3.26	7 795.56 ± 420.44
	JN2	CK	564.00 ± 54.11	49.07 ± 0.83	42.43 ± 0.09	9 391.11 ± 655.55
		S1	549.33 ± 70.24	42.33 ± 1.86	40.39 ± 0.13	8 035.56 ± 106.94
		S2	541.33 ± 30.02	39.07 ± 0.64	40.30 ± 0.12	7 537.78 ± 146.87
		S3	552.00 ± 80.89	38.47 ± 0.90	36.36 ± 4.26	6 840.00 ± 214.58
2024–2025	QM725	CK	545.33 ± 44.60	44.53 ± 2.02	39.52 ± 1.70	7 648.00 ± 104.92
		S1	588.00 ± 22.27	40.33 ± 0.76	38.91 ± 1.45	7 226.67 ± 281.86
		S2	584.00 ± 46.13	38.73 ± 2.93	36.18 ± 0.97	6 778.67 ± 75.61
		S3	570.67 ± 6.11	37.67 ± 0.61	34.56 ± 2.49	6 048.00 ± 257.50
	JN2	CK	562.67 ± 70.47	47.33 ± 7.94	42.39 ± 2.10	7 418.67 ± 166.53
		S1	549.33 ± 40.46	44.33 ± 1.81	40.39 ± 1.38	6 992.00 ± 80.00
		S2	546.67 ± 33.31	41.47 ± 2.25	38.43 ± 0.45	6 469.33 ± 176.97
		S3	544.00 ± 35.55	37.53 ± 0.90	36.86 ± 1.54	5 802.67 ± 314.49
F-value		Y	0.00	0.20	18.23**	220.64**
		C	1.67	6.93**	1.07	20.14**
		T	0.13	25.02**	25.19**	119.00**
		Y × C	0.01	0.00	12.51**	7.34**
		Y × T	0.23	1.03	1.38	7.96**
		C × T	0.24	0.12	0.30	1.01
		Y × C × T	0.22	1.64	0.03	1.15

QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading; ***P* < 0.01

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Grain bulk density, protein content, wet gluten content, and sedimentation value were determined using a DA7200 near-infrared analyser (Perten Company, Hägersten, Sweden).

Starch extraction and analysis. Starch was extracted from wheat grains with slight modifications, following the method reported by Wu et al. (2020). In brief, 3 g of wheat grains were weighed and soaked in 25 mL of distilled water for 24 h. After being thoroughly milled, the mixture was filtered through a 200-mesh sieve and centrifuged at 3 000 r/min for 10 min, and the supernatant was discarded. Then, 25 mL of 2 mol/L NaCl solution was added, and the mixture was vortexed and homogenised before centrifugation under the same conditions; this step was repeated three times. Following the same procedure, 25 mL of 0.2% NaOH solution, 25 mL of 2% SDS solution, and 25 mL of distilled water were added sequentially. Each mixture was vortexed, centrifuged at 3 000 r/min, and the supernatant was removed. Finally, 10 mL of acetone was added, and the air-dried precipitate was obtained as purified starch, which was stored at –18 °C for subsequent analysis. The volume, surface area, and number distributions of starch granules were determined using an LS13320 laser diffraction particle size analyser (Beckman Coulter, Brea, USA).

Starch granule size distribution and viscosity parameter measurement. Wheat grains were milled into flour using a Laboratory Mill 3100 (Perten Instruments AB, Hägersten, Sweden). All RVA measurements were based on a 14% moisture basis, with dry-matter correction. A 3 g flour sample was weighed into an aluminium canister, mixed with 25 mL of distilled water, and tested using a Starchmaster-2 rapid visco analyser (RVA, Newport, Australia). The standard RVA procedure included holding at 50 °C for 1 min, heating to 95 °C, maintaining at 95 °C, cooling to 50 °C, and holding at 50 °C. The

Table 3. Effects of post-anthesis low light treatment on grain protein content, wet gluten content and sedimentation value of wheat

Year (Y)	Cultivar (C)	Treatment (T)	Protein (%)	Wet gluten (%)	Zeleny sedimentation value (mL)
2023–2024	QM725	CK	14.73 ± 0.15	30.73 ± 0.51	35.43 ± 1.90
		S1	15.07 ± 0.15	31.77 ± 0.85	40.17 ± 1.58
		S2	15.20 ± 0.17	32.13 ± 0.67	40.80 ± 0.56
		S3	15.57 ± 0.15	32.57 ± 0.29	42.27 ± 1.20
	JN2	CK	14.43 ± 0.15	30.40 ± 0.26	35.50 ± 0.85
		S1	14.70 ± 0.17	30.73 ± 0.47	36.60 ± 2.52
		S2	14.93 ± 0.15	31.27 ± 0.38	39.33 ± 1.27
		S3	15.40 ± 0.10	32.47 ± 0.25	42.03 ± 0.91
2024–2025	QM725	CK	14.99 ± 0.21	35.37 ± 0.47	42.73 ± 1.76
		S1	15.29 ± 0.15	36.00 ± 0.36	43.67 ± 1.14
		S2	15.32 ± 0.17	36.13 ± 0.38	44.43 ± 1.08
		S3	15.82 ± 0.50	37.23 ± 1.15	49.27 ± 4.20
	JN2	CK	15.30 ± 0.10	31.90 ± 0.35	30.10 ± 0.61
		S1	15.43 ± 0.06	32.43 ± 0.06	30.37 ± 0.57
		S2	15.57 ± 0.29	32.80 ± 0.69	31.57 ± 2.37
		S3	16.17 ± 0.12	34.63 ± 0.61	37.93 ± 1.93
F-value		Y	72.77**	399.85**	0.27
		C	0.01	156.79**	196.38**
		T	42.42**	34.06**	35.59**
		Y × C	22.80**	75.73**	129.50**
		Y × T	0.47	0.79	3.04*
		C × T	0.53	1.79	1.38
		Y × C × T	0.05	0.27	0.38

QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading; $^{**}P < 0.01$

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stirring speed was 960 rpm for the first 10 s and 160 rpm thereafter. Each treatment was performed in three biological replicates to determine peak, trough, and final viscosities, breakdown, and setback.

Determination of starch thermodynamic properties. Starch thermodynamic properties were determined using a DSC-3 differential scanning calorimeter (Mettler-Toledo, Greifensee, Switzerland) according to the method described by Yu et al. (2012). Scanning was performed from 20 °C to 100 °C at a heating rate of 10 °C/min, and the heat flow changes were recorded.

Data analysis

Data were organised using Microsoft Excel 2021 (Hangzhou, China), and ANOVA was conducted *via* DPS 7.0 (Redmond, USA).

For all traits measured across two growing seasons (Tables 2–7), three-way analysis of variance was performed with year, cultivar and shading treatment as fixed factors, including all two-way and three-way interactive effects. Only cultivar and shading treatment were included in the two-way ANOVA for starch thermal properties in Table 8. The DSC measurement was completed within a single growing season, and year-related interactions exerted no significant influence on starch thermal characteristics. Excluding the year factor improved the statistical power to detect cultivar and shading effects as well as their interaction. Duncan's multiple range test was used for mean separation at $P < 0.05$

RESULTS

The effect of post-anthesis low light on wheat grain hardness. From the box plots in Figure 2, compared with the control, post-anthesis low light significantly reduced kernel hardness. Moreover, the magnitude of the reduction increased as light intensity

Table 4. Effects of post-anthesis low light on volume distribution of wheat starch granules

Year (Y)	Cultivar (C)	Treatment (T)	Diameter of starch granule (%)					
			0.1~2.8 μm	2.8~10 μm	≤ 10 μm	~10 μm	10~22 μm	> 22 μm
2023–2024	QM725	CK	9.23 ± 0.98	22.64 ± 2.39	31.87 ± 3.34	68.13 ± 3.34	37.17 ± 0.36	30.96 ± 3.65
		S1	8.55 ± 0.39	19.84 ± 0.66	28.39 ± 0.91	71.61 ± 0.91	38.59 ± 0.49	33.02 ± 0.61
		S2	7.88 ± 0.74	16.59 ± 2.88	24.47 ± 3.62	75.53 ± 3.62	39.67 ± 1.55	35.86 ± 2.09
		S3	6.53 ± 1.03	13.74 ± 0.59	20.27 ± 1.12	79.73 ± 1.12	42.15 ± 0.33	37.58 ± 0.91
	JN2	CK	13.15 ± 0.51	24.37 ± 1.16	37.52 ± 1.49	62.48 ± 1.49	35.24 ± 1.38	27.24 ± 2.45
		S1	11.50 ± 0.25	18.91 ± 1.56	30.41 ± 1.32	69.59 ± 1.32	36.93 ± 0.86	32.66 ± 2.10
		S2	10.47 ± 0.14	16.34 ± 0.91	26.81 ± 0.86	73.19 ± 0.86	38.12 ± 0.64	35.07 ± 1.50
		S3	8.04 ± 0.08	14.24 ± 0.22	22.28 ± 0.29	77.72 ± 0.29	41.23 ± 0.35	36.49 ± 0.60
2024-2025	QM725	CK	8.27 ± 0.77	20.12 ± 0.20	28.39 ± 0.91	71.61 ± 0.91	38.60 ± 0.49	33.02 ± 0.61
		S1	7.88 ± 0.74	16.92 ± 2.46	24.80 ± 3.19	75.20 ± 3.35	39.34 ± 1.09	35.86 ± 2.09
		S2	6.70 ± 0.86	14.31 ± 0.27	21.01 ± 1.05	78.99 ± 1.05	41.43 ± 0.80	37.56 ± 0.87
		S3	5.49 ± 0.66	13.97 ± 2.56	19.46 ± 2.51	80.54 ± 2.51	42.76 ± 0.99	37.78 ± 1.55
	JN2	CK	13.97 ± 0.74	25.62 ± 0.55	39.59 ± 1.20	60.41 ± 1.20	32.47 ± 1.22	27.94 ± 0.16
		S1	12.31 ± 0.23	22.03 ± 1.34	34.34 ± 1.42	65.66 ± 1.42	35.11 ± 1.05	30.55 ± 0.48
		S2	10.28 ± 0.48	21.02 ± 0.51	31.30 ± 0.97	68.70 ± 0.97	37.82 ± 0.25	30.88 ± 0.84
		S3	7.93 ± 0.61	19.66 ± 0.36	27.59 ± 0.95	72.41 ± 0.95	38.90 ± 0.39	33.50 ± 0.57
F-value		Y	2.73	4.40*	1.05	3.83*	1.75	0.27
		C	314.28**	52.17**	139.05**	110.22**	139.02**	63.51**
		T	86.99**	65.69**	87.89**	77.41**	83.92**	43.35**
		Y × C	11.42**	43.48**	39.07**	26.16**	33.69**	20.15**
		Y × T	0.94	3.27*	1.36	2.25	2.05	2.42
		C × T	9.61**	0.61	1.74	2.67	2.11	0.88
		Y × C × T	0.28	0.66	0.27	0.44	0.81	1.37

QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading; $^{*}P < 0.05$; $^{**}P < 0.01$

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decreased. Between the two wheat cultivars, JN2 was more severely affected under low-light treatments.

Effect of post-anthesis low light on wheat yield. As shown in Table 2, post-anthesis weak light had no significant effect on spikes per hectare of wheat, but significantly reduced grains per spike, 1 000-grain weight, and grain yield, with consistent trends across the two years. Compared with the control, the two-year average reductions in grains per spike, 1 000-grain weight, and grain yield under S1–S3 treatments were greater for Jinuo 2 than for Quanmai 725. Thus, post-anthesis weak light decreased yield components and grain yield, with Jinuo 2 being more sensitive to weak light stress.

Effect of post-anthesis low light on wheat quality. As shown in Table 3, post-anthesis weak light treatment exerted significant effects on protein content, wet gluten content and sedimentation value of wheat. Compared with the control, post-anthesis low light significantly increased protein content, wet gluten content and sedimentation value in both Jinuo 2 and Quanmai 725 and consistent trends were observed over the two years. In the 2023–2024 growing season, under post-anthesis low light treatments, the protein content of Quanmai 725 increased by 2.31, 3.19 and 5.70% compared with the control, accompanied by increases in wet gluten content and sedimentation value. For Jinuo 2, protein content increased by 1.87, 3.46, and 6.72%; wet gluten content increased by 1.09, 2.86, and 6.81%; and sedimentation value increased by 3.10, 10.79, and 18.39%, respectively. Jinuo 2 showed the same variation trends as Quanmai 725 in protein content, wet gluten content and sedimentation value. In the 2024–2025 growing season, under post-anthesis low light treatments, the protein content of Quanmai 725 increased by 2.00, 2.20 and 5.54% relative to the control, wet gluten content increased by 1.78, 2.15 and

Table 5. Effects of post-anthesis low light on surface area distribution of wheat starch granules

Year (Y)	Cultivar (C)	Treatment (T)	Diameter of starch granule (%)					
			0.1–2.8 μm	2.8–10 μm	≤ 10 μm	≈10 μm	10–22 μm	> 22 μm
2023–2024	QM725	CK	48.78 ± 1.41	26.33 ± 0.69	75.10 ± 1.30	24.90 ± 1.30	16.64 ± 0.50	8.25 ± 1.73
		S1	45.61 ± 4.58	24.71 ± 0.13	70.32 ± 4.46	29.68 ± 4.46	18.73 ± 2.64	10.95 ± 1.84
		S2	44.86 ± 3.36	23.63 ± 0.65	68.49 ± 3.97	31.51 ± 3.97	19.93 ± 2.86	11.58 ± 1.43
		S3	39.46 ± 1.12	22.29 ± 1.82	61.75 ± 0.78	38.25 ± 0.78	25.51 ± 0.87	12.74 ± 1.62
	JN2	CK	53.84 ± 1.15	26.93 ± 2.74	80.77 ± 3.74	19.23 ± 3.74	13.62 ± 2.16	5.61 ± 1.68
		S1	53.09 ± 1.11	22.99 ± 2.27	76.08 ± 3.33	23.92 ± 3.33	15.90 ± 1.76	8.02 ± 1.60
		S2	50.77 ± 4.05	20.97 ± 6.06	71.74 ± 9.91	28.26 ± 9.91	19.15 ± 6.39	9.11 ± 3.57
		S3	48.72 ± 0.30	18.47 ± 0.12	67.19 ± 0.39	32.81 ± 0.39	20.80 ± 0.28	12.01 ± 0.13
2024–2025	QM725	CK	41.31 ± 0.82	32.95 ± 0.69	74.27 ± 1.30	25.73 ± 1.30	15.71 ± 0.50	10.02 ± 1.73
		S1	39.83 ± 0.65	28.64 ± 0.13	68.47 ± 4.46	31.53 ± 4.46	19.11 ± 2.64	12.42 ± 1.84
		S2	38.86 ± 0.93	26.34 ± 0.65	65.20 ± 3.97	34.80 ± 3.97	21.24 ± 2.86	13.56 ± 1.43
		S3	37.68 ± 0.84	24.28 ± 1.82	61.96 ± 0.78	38.04 ± 0.78	22.58 ± 0.87	15.46 ± 1.62
	JN2	CK	47.79 ± 0.39	28.64 ± 2.74	76.43 ± 3.74	23.57 ± 3.74	15.88 ± 2.16	7.69 ± 1.68
		S1	46.21 ± 0.66	26.26 ± 2.27	72.47 ± 3.33	27.53 ± 3.33	16.99 ± 1.76	10.54 ± 1.60
		S2	42.42 ± 0.81	24.24 ± 6.06	66.66 ± 9.91	33.34 ± 9.91	19.11 ± 6.39	14.23 ± 3.57
		S3	40.75 ± 0.24	22.57 ± 0.12	63.33 ± 0.39	36.67 ± 0.39	21.44 ± 0.28	15.23 ± 0.13
F-value		Y	121.53**	32.36**	7.82**	7.82**	0.12	24.01**
		C	107.15**	13.91**	12.90**	12.90**	10.14**	8.66**
		T	22.35**	22.85**	30.18**	30.18**	21.86**	22.74**
		Y × C	3.25	0.35	1.88	1.88	1.38	1.38
		Y × T	0.77	0.21	0.24	0.24	0.49	0.55
		C × T	0.64	0.11	0.27	0.27	0.33	0.93
		Y × C × T	1.93	1.54	0.09	0.09	0.78	0.37

QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading; $^{**}P < 0.01$

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Table 6. Effects of post-anthesis low light on the number distribution of wheat starch granules

Year (Y)	Cultivar (C)	Treatment (T)	Diameter of starch granule (%)					
			0.1–2.8 μm	2.8–10 μm	≤10 μm	< 10 μm	10–22 μm	> 22 μm
2023–2024	QM725	CK	95.51 ± 0.28	4.06 ± 0.24	99.57 ± 0.05	0.43 ± 0.05	0.37 ± 0.04	0.06 ± 0.01
		S1	96.85 ± 1.52	2.92 ± 1.39	99.77 ± 0.13	0.23 ± 0.13	0.20 ± 0.12	0.03 ± 0.02
		S2	97.13 ± 1.29	2.59 ± 1.20	99.72 ± 0.11	0.28 ± 0.11	0.24 ± 0.10	0.04 ± 0.02
		S3	97.70 ± 0.03	2.15 ± 0.04	99.85 ± 0.02	0.15 ± 0.02	0.13 ± 0.01	0.02 ± 0.01
	JN2	CK	97.50 ± 0.13	2.37 ± 0.15	99.87 ± 0.02	0.13 ± 0.02	0.12 ± 0.02	0.01 ± 0.01
		S1	97.49 ± 0.04	2.27 ± 0.04	99.76 ± 0.00	0.24 ± 0.00	0.2 ± 0.00	0.04 ± 0.00
		S2	97.33 ± 0.62	2.42 ± 0.45	99.75 ± 0.18	0.25 ± 0.18	0.21 ± 0.16	0.04 ± 0.03
		S3	97.05 ± 0.09	2.77 ± 0.11	99.82 ± 0.02	0.18 ± 0.02	0.15 ± 0.02	0.03 ± 0.01
2024–2025	QM725	CK	96.32 ± 0.42	3.15 ± 0.25	99.47 ± 0.17	0.53 ± 0.17	0.42 ± 0.13	0.11 ± 0.04
		S1	96.80 ± 0.55	2.97 ± 0.53	99.77 ± 0.05	0.23 ± 0.05	0.19 ± 0.04	0.04 ± 0.01
		S2	97.03 ± 0.35	2.71 ± 0.48	99.74 ± 0.14	0.26 ± 0.14	0.22 ± 0.12	0.04 ± 0.02
		S3	96.65 ± 0.49	2.91 ± 0.47	99.55 ± 0.06	0.45 ± 0.06	0.37 ± 0.04	0.08 ± 0.02
	JN2	CK	97.47 ± 0.12	2.12 ± 0.14	99.59 ± 0.19	0.41 ± 0.19	0.34 ± 0.14	0.07 ± 0.05
		S1	95.87 ± 1.29	3.81 ± 1.23	99.68 ± 0.11	0.32 ± 0.11	0.28 ± 0.08	0.04 ± 0.02
		S2	97.37 ± 0.18	2.26 ± 0.18	99.63 ± 0.02	0.37 ± 0.02	0.32 ± 0.02	0.05 ± 0.01
		S3	96.91 ± 0.76	2.80 ± 0.69	99.72 ± 0.07	0.28 ± 0.07	0.24 ± 0.06	0.04 ± 0.02
F-value		(Y	1.72	0.62	15.03**	15.03**	14.25*	16.29**
		C	3.40	3.03	2.39	2.39	1.88	4.63*
		T	1.51	1.54	3.15*	3.15*	3.18*	2.75
		Y × C	0.70	0.58	0.75	0.75	1.61	0.65
		Y × T	1.85	2.43	1.99	1.99	1.68	3.79*
		C × T	4.11**	3.73*	4.05**	4.05**	4.15**	3.24*
		Y × C × T	1.79	1.71	1.91	1.91	2.25	0.70

QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading; *$P < 0.05$; **$P < 0.01$

5.26%, and sedimentation value increased by 2.20, 3.98 and 15.30%, respectively. For Jinuo 2, protein content increased by 0.85, 1.76 and 5.69%, and wet gluten content increased by 1.66, 2.82 and 8.56%, respectively. It can be seen that post-anthesis low light treatment resulted in changes in wheat quality traits.

Effects of post-anthesis low light stress on wheat starch granule distribution. As shown in Tables 4–6, post-anthesis low-light treatment significantly affected the volume and surface area distributions of wheat starch granules but had no significant effect on their number distribution. Compared with the control, post-anthesis low light decreased the volume and surface area proportions of B-type starch granules (≤ 10 μm) in both Jinuo 2 and Quanmai 725, while increasing the volume and surface area proportions of A-type starch granules (> 10 μm). With reduced light intensity, the percentage volume and percentage surface area of B-type starch granules decreased, whereas those of A-type starch granules increased. These results indicate that post-anthesis low light is unfavourable to the formation and development of B-type starch granules in wheat grains. Further analysis revealed that the volume and surface area distribution proportions of B-type starch granules in Jinuo 2 were higher than those in Quanmai 725, while the proportions of A-type starch granules were lower.

Effects of post-anthesis low light on viscosity parameters of wheat grains. As shown in Table 7, post-anthesis low-light treatment had significant effects on peak, trough and final viscosities, as well as the breakdown and setback values of wheat grains. Compared with the control, post-anthesis low light significantly decreased all viscosity parameters in both Jinuo 2 and Quanmai 725. With the reduction in light intensity, peak viscosity, trough viscosity, final viscosity, breakdown value and setback value all exhibited a decreasing trend. These results indi-

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Table 7. Effects of post-anthesis low light treatment on wheat viscosity parameters

Year (Y)	Cultivar (C)	Treatment (T)	Peak viscosity (cP)	Trough viscosity (cP)	Final viscosity (cP)	Breakdown (cP)	Setback (cP)
2023–2024	QM725	CK	1 492.33 ± 134.20	1 116.67 ± 104.29	2 110.67 ± 193.40	994.00 ± 89.20	375.67 ± 30.24
		S1	1 312.33 ± 204.37	1 000.67 ± 141.35	1 869.33 ± 214.19	868.67 ± 73.36	311.67 ± 63.32
		S2	1 292.00 ± 25.51	990.67 ± 24.34	1 816.67 ± 14.50	826.00 ± 10.44	301.33 ± 3.51
		S3	1 043.00 ± 77.09	819.33 ± 44.75	1 545.67 ± 46.88	726.33 ± 7.64	223.67 ± 40.25
	JN2	CK	989.33 ± 68.49	676.67 ± 39.80	1 011.67 ± 74.63	335.00 ± 35.68	312.67 ± 32.59
		S1	918.00 ± 26.51	657.67 ± 15.53	980.33 ± 31.13	322.67 ± 16.04	260.33 ± 12.50
		S2	767.33 ± 15.14	560.00 ± 16.52	835.67 ± 30.11	275.67 ± 14.05	207.33 ± 1.53
		S3	673.67 ± 78.50	494.33 ± 80.48	715.67 ± 120.95	221.33 ± 41.86	179.33 ± 2.08
2024-2025	QM725	CK	1 372.33 ± 125.30	929.00 ± 52.94	1 674.67 ± 144.33	745.67 ± 101.91	443.33 ± 76.66
		S1	1 284.00 ± 116.25	916.67 ± 67.68	1 563.00 ± 50.69	646.33 ± 38.68	367.33 ± 49.22
		S2	1 194.33 ± 309.65	835.67 ± 180.51	1 474.00 ± 254.38	638.33 ± 74.07	358.67 ± 129.15
		S3	1 130.33 ± 80.56	775.00 ± 74.28	1 409.67 ± 95.02	634.67 ± 23.03	355.33 ± 33.50
	JN2	CK	1 260.33 ± 86.03	494.33 ± 74.27	677.00 ± 109.06	182.67 ± 36.35	766.00 ± 28.16
		S1	1 195.33 ± 136.77	490.33 ± 51.05	658.67 ± 60.29	168.33 ± 18.50	705.00 ± 92.00
		S2	967.67 ± 338.19	417.67 ± 122.15	561.67 ± 160.73	144.00 ± 38.57	550.00 ± 216.11
		S3	894.33 ± 220.27	354.00 ± 81.71	492.33 ± 87.96	138.33 ± 6.43	540.33 ± 139.18
F-value		Y	5.02*	31.38**	64.95**	123.85**	101.22**
		C	46.06**	270.36**	653.21**	1411.53**	16.98**
		T	10.84**	11.85**	14.38**	15.67**	7.73**
		Y × C	9.73*	0.67	0.05	4.01*	45.93**
		Y × T	0.26	0.63	1.35	3.15*	0.32
		C × T	0.37	0.39	1.11	3.12*	0.92
		Y × C × T	0.35	0.34	0.33	0.41	0.68

QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading; $^{*}P < 0.05$; $^{**}P < 0.01$

Table 8. Effects of post-anthesis low light on starch thermodynamic properties of wheat grains

Cultivar (C)	Treatment (T)	Gelatinisation enthalpy (J/g)	Onset temperature (°C)	Peak temperature (°C)	End temperature (°C)
QM725	CK	9.05 ± 0.02^{e}	65.91 ± 0.11^{a}	74.27 ± 0.53^{a}	75.42 ± 0.10^{a}
	S1	9.68 ± 0.35^{cd}	63.47 ± 0.69^{b}	70.5 ± 0.63^{c}	73.09 ± 0.35^{ab}
	S2	9.87 ± 0.22^{cd}	61.18 ± 0.49^{cde}	66.12 ± 0.77^{d}	69.37 ± 0.86^{c}
	S3	10.22 ± 0.53^{bc}	60.96 ± 0.59^{de}	64.75 ± 0.74^{e}	69.26 ± 0.86^{c}
JN2	CK	9.63 ± 0.51^{d}	65.36 ± 1.78^{a}	72.15 ± 0.05^{b}	72.55 ± 0.60^{b}
	S1	10.02 ± 0.10^{cd}	62.86 ± 0.04^{bc}	70.22 ± 1.01^{c}	70.85 ± 1.15^{bc}
	S2	10.75 ± 0.67^{b}	61.61 ± 1.2^{cd}	66.24 ± 0.52^{d}	69.51 ± 0.61^{c}
	S3	11.76 ± 0.11^{a}	59.52 ± 3.64^{e}	62.99 ± 0.09^{f}	68.71 ± 3.97^{c}
F-value	C	40.18**	1.86	17.45**	4.86
	T	28.30**	34.83**	298.72**	13.90**
	C × T	3.95*	0.92	5.10**	1.27

QM725 – Quanmai 725; JN2 – Jinuo 2; CK – control; S1 – 10% shading; S2 – 20% shading; S3 – 30% shading; $^{*}P < 0.05$; $^{**}P < 0.01$

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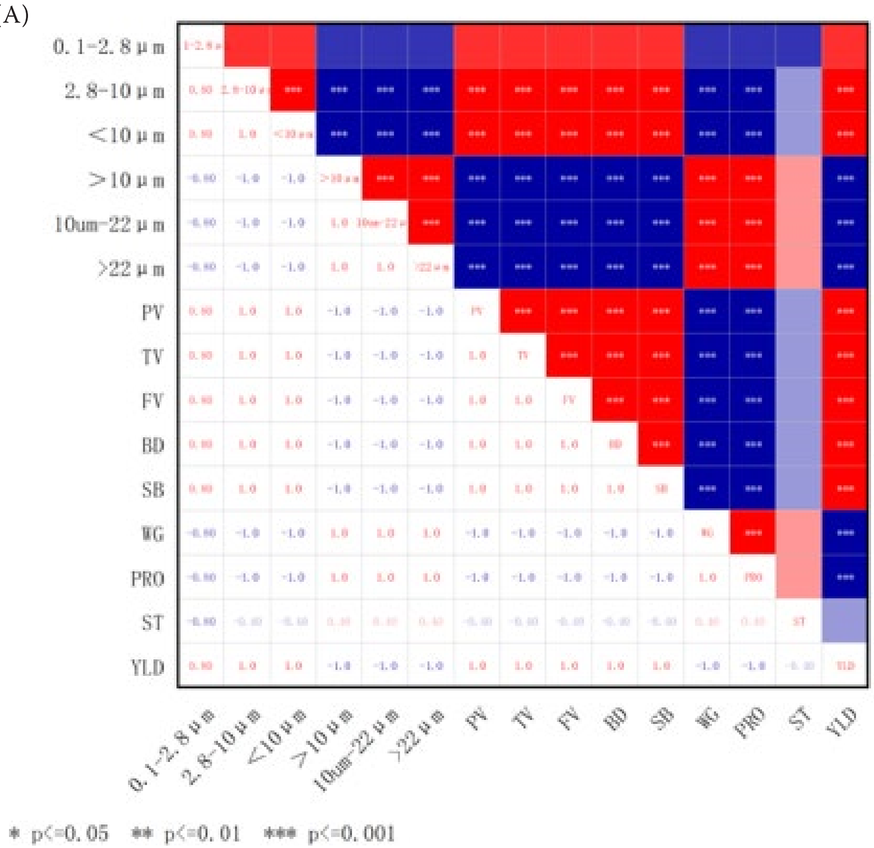
(A)



(B)

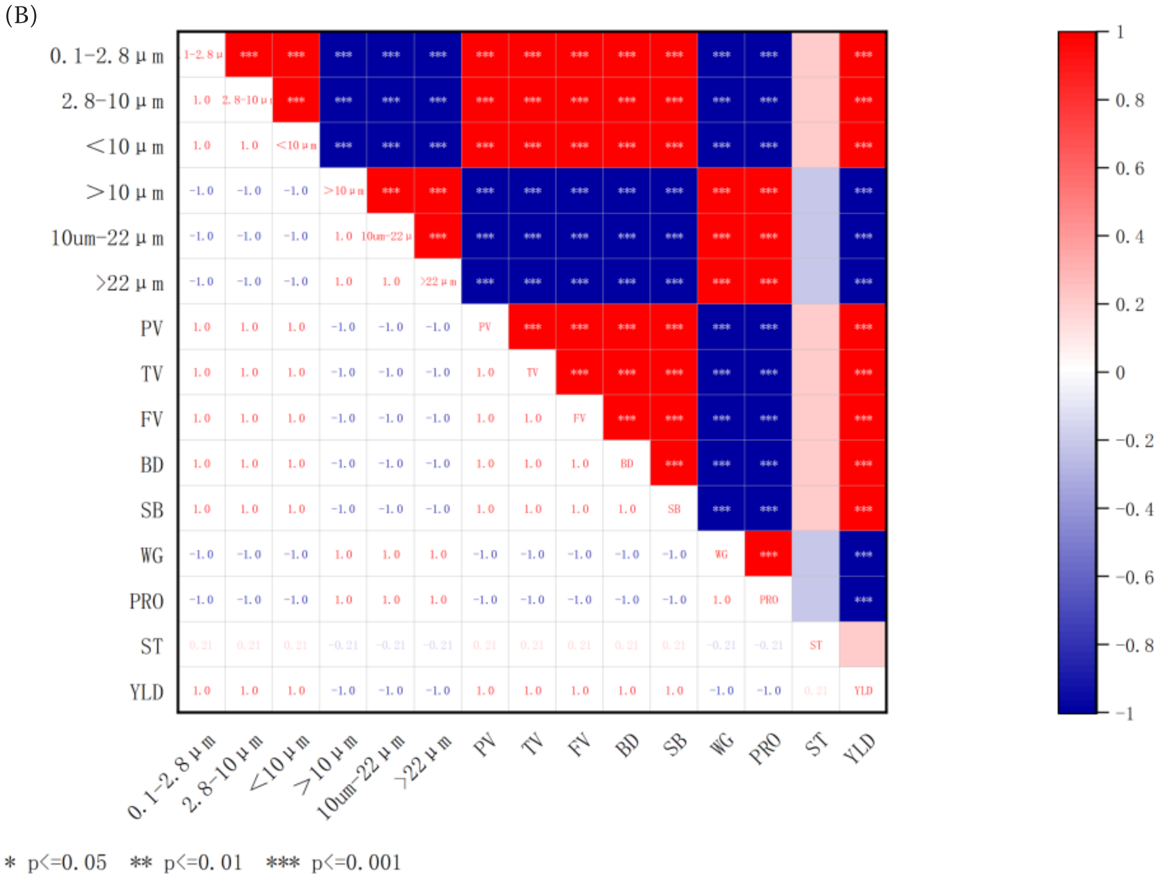


Figure 3. Correlation between the volume of starch granules, viscosity parameters, etc., of (A) Quanmai725 and (B) Jinuo 2. PV – peak viscosity; TV – trough viscosity; FV – final viscosity; BD – breakdown; SB – setback; WG – wet gluten; PRO – protein; ST – starch; YLD – yield

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cate that post-anthesis low light is not conducive to improving viscosity parameters such as peak, trough and final viscosity in wheat grains. Further comparison between Jinuo 2 and Quanmai 725 revealed that Jinuo 2 had lower trough viscosity, final viscosity and setback value. Peak viscosity, trough viscosity, final viscosity and setback value of Quanmai 725 were all higher than those of Jinuo 2.

Effects of post-anthesis low light on starch thermodynamic properties. As shown in Table 8, post-anthesis low light decreased the onset, peak, and conclusion temperatures of wheat starch and increased gelatinisation enthalpy in both cultivars. These changes became more pronounced as light intensity decreased. Across treatments, Quanmai 725 had higher characteristic temperatures, while Jinuo 2 had higher gelatinisation enthalpy.

Correlation analysis between starch granule types and quality parameters. Correlation analysis results, as illustrated in Figure 3, indicate that for both wheat cultivars, the volume fraction of B-type starch granules (≤ 10 μm) showed a remarkable posi-

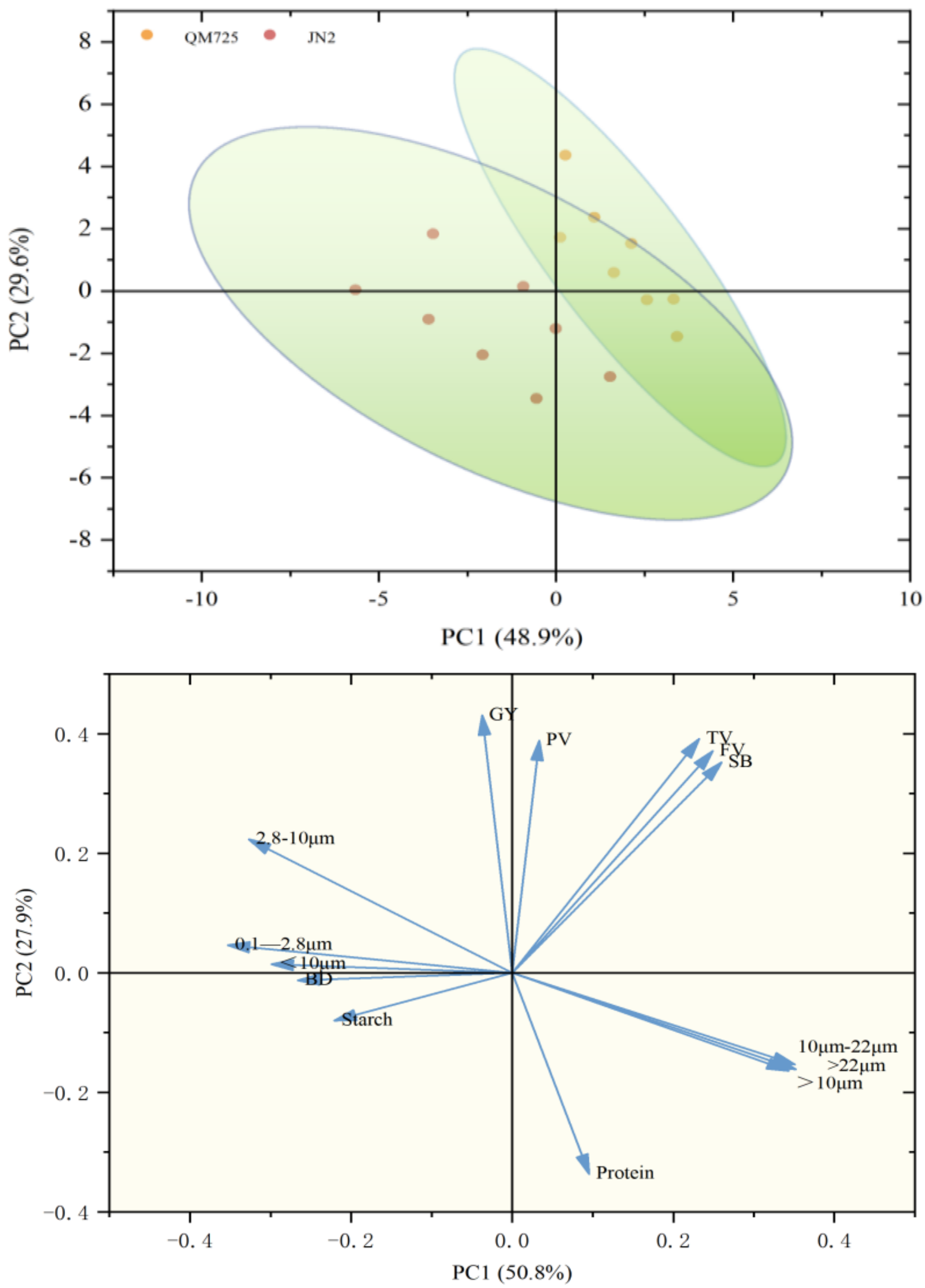

Figure 4. Principal component analysis (PCA) biplot of starch quality indicators in two wheat varieties under post-anthesis low light stress. Arrows represent the loading vectors of each indicator on the principal components. E-R – 0.1–2.8 μm; R – 2.8–10 μm; K – ≈10 μm; N – ≈10 μm; M – 10–22 μm; L – >22 μm; E – PV (peak viscosity); G – FV (final viscosity); O – TV (trough viscosity); H – ST (pasting temperature); J – BD (breakdown); P – protein; Q – starch; S – GY (grain yield)

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tive correlation with peak viscosity, trough viscosity, final viscosity, breakdown, and setback. Conversely, it showed a notable negative correlation with the same viscosity metrics for A-type starch granules (> 10 μm). Among B-type starch granules (≤ 10 μm), viscosity parameters such as peak viscosity exhibited a highly significant positive correlation with the volume fraction of starch granules in the 0.1–2.8 μm size range. Under low-light conditions, considerable variation in starch quality parameters was observed between the two wheat varieties, Quanmai 725 and Jinuo 2, indicating that the composition of starch granules plays a vital role in determining quality traits under shading stress.

Principal component analysis of starch granule types and quality parameters. As can be seen from the sample score plot, Quanmai 725 (orange) is distributed toward the first quadrant and shows a strong correlation with the index of A-type starch granules (> 10 μm). Jinuo 2 (red) is distributed toward the second quadrant and exhibits a strong correlation with B-type starch granules (< 10 μm) and viscosity parameters (PV, FV). These observations are consistent with the conclusion that the proportion of A-type starch granules increased. In contrast, the proportion of B-type starch granules decreased under low light stress, and Jinuo 2 had a higher proportion of B-type starch granules. Further verification from the loading plot reveals that indicators of B-type starch granules are significantly and positively correlated with viscosity parameters, with starch granules ranging from 0.1 to 2.8 μm showing an extremely significant positive correlation. In contrast, the indicators of A-type starch granules are significantly negatively correlated with viscosity parameters. This explains the phenomenon that viscosity parameters decreased with the decline in the proportion of B-type starch granules under low light stress and also confirms the varietal characteristic that waxy wheat (Jinuo 2) inherently possesses lower viscosity parameters.

DISCUSSION

Light intensity is a key factor affecting wheat grain yield. Long-term insufficient sunshine restricts grain filling and declines yield and grain quality. The late growth stage of wheat in the Jianghuai region is often accompanied by rainy, dim weather, and insufficient light has become a major limiting factor for high-yield, high-quality wheat production in this region. Low light stress notably decreases wheat grain plumpness, 1 000-grain weight and grain number per spike (Yang et al. 2019). Reduced light intensity decreases the 1 000-grain weight of waxy and non-waxy wheat, raises abortive spikelet quantity, and leads to variety-dependent yield decline (Liu et al. 2015). In this study, post-anthesis low light significantly reduced grain number per spike, 1 000-grain weight and grain yield of Jinuo 2 and Quanmai 725, while effective spike number per unit area remained stable. Jinuo 2 showed more obvious yield reduction, proving it was more susceptible to weak light stress.

Wheat protein and starch contents are jointly regulated by genetic and environmental factors, among which environmental conditions play a vital role. Waterlogging stress decreases wheat wet gluten and protein contents and increases starch content (Chen et al. 2024b). Reduced topdressing nitrogen combined with increased planting density lowers wheat wet gluten content, protein content and sedimentation value (Zhou et al. 2025). Low-light treatment increased the three quality indices for both tested wheat varieties, and the values for Quanmai 725 were higher than those for Jinuo 2. This phenomenon was closely related to changes in carbon and nitrogen allocation. Weak light inhibits photosynthate accumulation, limits the starch-synthesis carbon source, and relatively elevates grain protein content.

Starch particle size distribution determines wheat starch quality and is affected by genotype and environment, and environmental influence is stronger during grain filling. High temperature primarily alters the volume and surface area distribution of starch granules, and B-type starch granules are more sensitive to high temperatures (Lu 2013). Late sowing reduces the proportion of A-type starch granules and increases that of B-type starch granules (Yong et al. 2024). Low light changes starch granule distribution and reduces B-type starch granule quantity (Li et al. 2009). Post-anthesis shading obviously changed the structure of wheat starch granules, lowered the volume and surface area proportion of B-type starch granules, and increased those of A-type starch granules. Large starch granules can differentiate into small ones, and the growth of small starch granules requires sufficient nutrients. Continuous shading during grain filling results in an insufficient supply of photosynthates, and assimilates are preferentially allocated to the development of large A-type starch granules, thereby restricting the growth of small starch granules. Shading exerted little influence on the quantities of the two types of starch granules because there were sufficient

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initial small starch granules. Differences in low-light sensitivity, photosynthate accumulation and amylose content led to differences in starch granule composition between the two wheat cultivars.

Starch viscosity characteristics are important indices of starch quality and are easily affected by the growth environment (Yan et al.2019), including light conditions. Grain-filling stage shading reduces wheat's peak, trough and final viscosities (Yuan et al. 2020). Rational nitrogen application adjusts starch granule composition and improves starch viscosity and processing quality (Li et al. 2024). The viscosity characteristics of waxy wheat decreased gradually with increasing degree of shading (Liu et al. 2017). This study obtained different results, showing that low light significantly reduced various viscosity indices of Jinuo 2, and Quanmai 725 had higher viscosity and setback value. The inconsistent results were attributed to different shading measures, light intensity and test cultivars. Waxy wheat always has a lower setback value and a lower trough viscosity under natural and weak-light conditions (Wen et al. 2021).

Thermodynamic properties are important physicochemical indicators for evaluating the uniformity of starch composition and thermal stability in wheat grains, reflecting starch thermal stability, homogeneity of granule composition and retrogradation tendency (Sing et al. 2003). Under post-anthesis low-light conditions, the gelatinisation temperatures (onset, peak and conclusion) of both waxy and non-waxy wheat decreased significantly as light intensity decreased. The present study demonstrated that the gelatinisation temperatures of both waxy and non-waxy wheat decreased with decreasing light intensity, while the gelatinisation enthalpy of both cultivars increased. Quanmai 725 had higher gelatinisation temperatures than Jinuo 2, whereas Jinuo 2 exhibited higher gelatinisation enthalpy than Quanmai 725.

Under post-anthesis weak light stress, the 1 000-grain weight, grain number per spike, and yield of waxy soft wheat Jinuo 2 and non-waxy soft wheat Quanmai 725 were reduced. Both Jinuo 2 and Quanmai 725 exhibited an increased proportion of A-type starch granules and a decreased proportion of B-type starch granules. With decreasing light intensity, the peak, trough, and final viscosities, setback, and breakdown of Jinuo 2 and Quanmai 725 grains decreased significantly; the peak viscosity of Quanmai 725 was higher than that of Jinuo 2. Post-anthesis low light reduced the proportion of B-type starch granules and increased the proportion of A-type starch granules in both wheats, thereby reducing their viscosity parameters, decreasing gelatinisation temperature, and increasing gelatinisation enthalpy, ultimately altering the processing quality and thermodynamic properties of starch.

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