Effects of Nitrogen Application and Post-Anthesis Soil Relative Water Content on Nitrogen Uptake, Translocation, and Distribution During Grain Filling in Black-Grained Wheat (Postprint)

Authors: Wang Mei, Zhao Guangcai, Shi Shubing, Xuhong Chang, Wang Demei, Yang Yushuang, Guo Mingming, Qi Zhen, Wang Yu, Liu Xiaocheng

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Abstract

Black-grained wheat 'Luozhen No. 1' was used as the experimental material in pot experiments under a shed to investigate the effects of different nitrogen application rates and post-anthesis soil relative water content on plant nitrogen absorption, translocation, and distribution, as well as on grain protein and its component contents. The results showed that under the same nitrogen application rate, grain nitrogen content and protein accumulation in black wheat decreased with intensifying water stress. Changes in various protein component contents differed among nitrogen application rates: under low nitrogen [N1, 150 kg(N) · hm−2] conditions, albumin, globulin, and gliadin contents increased with intensifying water stress, while under high nitrogen [N3, 300 kg(N) · hm−3] conditions, albumin and globulin contents increased, whereas gliadin content decreased. 相同水分胁 嗞 辔霤睬 嗞狁辔 睬 辔 睬絃晌 辔榊睬 睕 睬 晌捣睕 睬悇晌蒝晻⊠晌镨晻 晌囯睕밈睥⊠睕髧晻釆睥 睕齭晻⊠睳⊠晻좋睥 睳 ⊲ 晻舜睥裓睰⊠睥뿔 睳 畄 睥睵睳滴畄⊠睳뙨睰 翻 † 睳フ睰啤翻龠睰굉畄젠畱 睰 畄肵畱麟畄⊠翻깃晌 F 畄 翻 晌翻畱

Full Text

Effect of Nitrogen Fertilization and Soil Relative Water Content After Anthesis on Nitrogen Absorption, Translocation, and Distribution in Black Wheat During Grain Filling

WANG Mei[1,2], **ZHAO Guangcai**[1], SHI Shubing[2], **CHANG Xuhong**[1], **WANG Demei**[1], **YANG Yushuang**[1], **GUO Mingming**[3], **QI Zhen**[1], **WANG Yu**[1], **LIU Xiaocheng**[2]

[1]Institute of Crop Science, Chinese Academy of Agricultural Sciences/Key Laboratory of Crop Physiology and Ecology, Ministry of Agriculture, Beijing 100081, China; [2]College of Agronomy, Xinjiang Agricultural University, Urumqi 830052, China; [3]Lianyungang Institute of Agricultural Science of Xuhuai Area/Lianyungang Academy of Agricultural Sciences, Lianyungang 222006, China

Abstract

Using the black wheat variety 'Luozhen 1'as experimental material, a pot experiment under rainproof shelter was conducted to investigate the effects of different nitrogen application rates and post-anthesis soil relative water content on nitrogen absorption, translocation, distribution, and grain protein and its component contents in 'Luozhen 1' . The results showed that under the same nitrogen rate, grain nitrogen content and protein accumulation decreased with intensifying water stress. Changes in protein component contents varied with nitrogen application rate: under low nitrogen [N1, 150 kg(N) · hm^{-2}], albumin, globulin, and prolamin contents increased with water stress, whereas under high nitrogen [N3, 300 kg(N) · hm^{-2}], albumin and globulin contents increased but prolamin content decreased. Under water stress conditions (soil relative water content of 55%–65%, W2; and 35%–45%, W3), grain nitrogen content and protein accumulation increased with nitrogen rate, while the proportion of grain nitrogen to total nitrogen at maturity decreased. However, under adequate water supply (soil relative water content of 75%–85%, W1), the medium nitrogen treatment [N2, 240 kg(N) · hm^{-2}] achieved the highest grain protein accumulation, with maximum nitrogen translocation amount and efficiency from vegetative organs to grain and relatively high contribution rates. Under W1, albumin, globulin, and prolamin contents increased with nitrogen rate, while glutenin peaked at N2. Under W2 and W3 conditions, all protein component contents were highest at N2. In conclusion, nitrogen rate and post-anthesis soil relative water content significantly affected nitrogen metabolism in black wheat. Both excessive and insufficient nitrogen application, as well as water stress, were detrimental to efficient nitrogen metabolism. Considering all factors, the combination of adequate water supply (W1) and medium nitrogen level (N2) provided optimal regulation of nitrogen absorption, translocation, and distribution in black wheat.

Keywords: Black wheat; Nitrogen fertilization rate; Soil relative water content; Nitrogen metabolism; Protein components

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Nitrogen metabolism is one of the most fundamental metabolic processes in plants, and this holds true for wheat (*Triticum aestivum*) as well. Nitrogen metabolism significantly influences both yield formation and quality improvement in wheat. In addition to genetic characteristics of varieties, cultivation practices represent crucial factors affecting wheat nitrogen metabolism [1–5]. Xu et al. [6] demonstrated that improving soil moisture conditions could promote nitrogen translocation from vegetative organs to grains after anthesis, increasing both total nitrogen yield and biological yield while enhancing the proportion of fertilizer nitrogen absorbed by various organs. Ma et al. [7] reported that under the same nitrogen level, either excessively high or low post-anthesis soil relative water content was unfavorable for free amino acid synthesis in leaves, affecting their translocation to grains and consequently hindering grain protein accumulation. Under identical soil water conditions, grain protein content and accumulation increased with nitrogen rate, though the increment diminished when nitrogen application became excessive. Ma et al. [8] found that appropriate nitrogen application or adequate irrigation under nitrogen-fertilized conditions facilitated nitrogen translocation from vegetative organs to grains. Meanwhile, nitrogen rate and soil relative water content also affected grain protein components [9–12].

Black wheat 'Luozhen 1' is a type of colored wheat that has attracted considerable research attention due to its high protein and amino acid content, along with various essential trace elements such as Fe, Zn, and Se [13–14], offering high nutritional value and development potential [15]. Although colored wheat possesses high nutritional value, its yield remains relatively low, primarily attributable to poor photosynthetic capacity and matter translocation ability during critical yield formation stages [16]. However, previous studies on the effects of nitrogen rate and post-anthesis soil relative water content on nitrogen metabolism processes and grain protein component contents in colored wheat are scarce. Therefore, this experiment selected black wheat 'Luozhen 1' as material to investigate the effects of nitrogen rate and post-anthesis soil relative water content on nitrogen absorption, translocation, and distribution, aiming to provide theoretical and technical references for improving matter translocation capacity during critical yield formation stages and achieving high-yield, high-quality cultivation of black wheat.

1.1 Experimental Site Conditions

The experiment was conducted during 2014–2015 under a rainproof shelter at the Institute of Crop Science, Chinese Academy of Agricultural Sciences. The experimental soil was loam with the following nutrient contents: organic matter 9.84 $g \cdot kg^{-1}$, total nitrogen 0.58 $g \cdot kg^{-1}$, alkaline hydrolysis nitrogen 91.91 mg·

kg^{-1}, available phosphorus 21.55 $mg \cdot kg^{-1}$, available potassium 146 $mg \cdot kg^{-1}$, and pH 7.86.

1.2 Experimental Design and Treatments

The experimental material was black wheat 'Luozhen 1' . A two-factor randomized block design was employed with nitrogen application rate (N) and post-anthesis water control (W). Three water gradients were established: (1) Adequate water supply throughout the growth period (W1), with soil relative water content at 75%–85% of field capacity; (2) Moderate water stress (W2), with water management identical to W1 before anthesis but soil relative water content at 55%–65% of field capacity from anthesis to harvest; and (3) Severe water stress (W3), with water management identical to W1 before anthesis but soil relative water content at 35%–45% of field capacity from anthesis to harvest. During the water treatment period, pots were weighed daily and water was supplemented according to the control standards [17]. Three nitrogen rates were applied: low nitrogen (N1) at 150 $kg \cdot hm^{-2}$ pure nitrogen, medium nitrogen (N2) at 240 $kg \cdot hm^{-2}$, and high nitrogen (N3) at 330 $kg \cdot hm^{-2}$. Urea (46% N) was applied at a basal fertilizer to jointing fertilizer ratio of 5:5.

The pot experiment was conducted under a rainproof shelter using soil as the substrate. Pots were 26 cm in diameter with a surface area of 0.053 m^2, containing 21 kg of dry soil per pot. Fifteen plants were grown per pot and thinned to the desired density at the five-leaf stage.

1.3.1 Determination of Nitrogen Content in Various Organs

Sampling began at anthesis (the day water treatments commenced and before water application) and continued every 7 days thereafter. Three replicates per treatment (nine plants total) were sampled and separated into stems, leaves, and spikes. At maturity, samples were separated into stems, leaves, glumes + rachises, and grains. Samples were immediately brought indoors, placed in an oven at 105°C for 30 minutes to deactivate enzymes, then dried at 80°C to constant weight for dry weight measurement. Grains were ground using an FS-II laboratory cyclone mill, while other organs were ground using a high-speed mill. Ground samples [grains $(0.100\$\pm0.005)g, otherorgans(0.200\pm\$0.005)$ g] were digested with 6 mL concentrated sulfuric acid and a catalyst (a 10:1 mixture of potassium sulfate and copper sulfate) at 420°C on a digestion block until completely digested. Nitrogen content was determined using a K1302 Kjeldahl nitrogen analyzer from Shanghai Sheng Sheng Company.

Grain protein content (%) = Grain nitrogen content (%) × 5.7 (1)

1.3.2 Determination of Grain Protein Components

At maturity, grains were sampled from three replicates per treatment (one pot per replicate). Grains were removed, deactivated at 105°C for 30 minutes, dried

at 80°C to constant weight, and ground using an FS-II laboratory cyclone mill for protein component extraction and determination.

Protein components were extracted sequentially using a continuous extraction method. Ground grain samples (0.5 g, weighed with 0.001 g precision) were placed in 10 mL centrifuge tubes and extracted in the order of albumin, globulin, prolamin, and glutenin using distilled water, 2% sodium chloride solution, 70% ethanol solution, and 0.5% potassium hydroxide solution, respectively. The extraction procedure involved adding 5 mL of extraction solution, stirring with a glass rod until completely broken down, shaking on a vibrator (30 minutes for the first extraction, 20 minutes for subsequent extractions), timing with a timer, then centrifuging at 4,000 rpm for 5 minutes. The supernatant was transferred to a stoppered glass tube for storage, and the procedure was repeated three additional times. The four extracts were combined and mixed thoroughly for measurement. For determination, 5 mL of each component extract was taken and analyzed using the method described in Section 1.3.1.

1.3.3 Calculation Methods for Nitrogen-Related Indices

Nitrogen accumulation amount in various organs ($mg \cdot plant^{-1}$) = Nitrogen content ($mg \cdot g^{-1}$) × Dry matter weight of each organ ($mg \cdot plant^{-1}$) (2)

Nitrogen accumulation amount in vegetative organs at anthesis ($mg \cdot plant^{-1}$) = Sum of nitrogen accumulation in stems, leaves, and spikes at anthesis ($mg \cdot plant^{-1}$) (3)

Nitrogen translocation amount from pre-anthesis storage ($mg \cdot plant^{-1}$) = Nitrogen accumulation per plant at anthesis − Nitrogen accumulation in non-grain parts (stems, leaves, rachises + glumes) at maturity (4)

Nitrogen translocation efficiency from pre-anthesis storage = (Nitrogen translocation amount from pre-anthesis storage / Nitrogen accumulation per plant at anthesis) × 100% (5)

Contribution proportion of pre-anthesis accumulated nitrogen to grains = (Nitrogen translocation amount from pre-anthesis storage / Total nitrogen amount in grains at maturity) × 100% (6)

Nitrogen accumulation amount in grains at maturity ($mg \cdot plant^{-1}$) = Grain nitrogen content at maturity × Grain weight at maturity ($mg \cdot plant^{-1}$) (7)

Nitrogen accumulation amount in vegetative organs at maturity ($mg \cdot plant^{-1}$) = Sum of nitrogen accumulation in stems, leaves, and spikes at maturity ($mg \cdot plant^{-1}$) (8)

1.4 Data Processing

Data processing and analysis were performed using Microsoft Excel 2013 and DPS 15.10 statistical analysis software. Multiple comparisons were conducted using the LSR method.

2.1 Effects of Nitrogen Rate and Post-Anthesis Soil Relative Water Content on Grain Protein Accumulation in Black Wheat After Anthesis

As shown in Table 1 , grain protein accumulation in all treatments continuously increased with growth progression, reaching maximum values at 35 days after anthesis, though differences existed among treatments. Under the same nitrogen rate, grain protein accumulation increased with intensifying water stress from 7 to 21 days after anthesis; however, after 28 days post-anthesis, grain protein accumulation decreased with water stress, with significant differences observed. Under the same irrigation level, N2 and N3 treatments showed greater grain protein accumulation than N1 at 7–14 days after anthesis, though differences were not significant. At 21 days after anthesis, under W1 and W2 irrigation, N1 and N3 treatments had higher protein accumulation than N2, while under W3, protein accumulation increased with nitrogen rate but differences were not significant. At 28 days after anthesis, under W1, protein accumulation followed the pattern N2 > N1 > N3, whereas under W2 and W3, the pattern was N1 N3 > N2, with no significant differences among treatments. At 35 days after anthesis, under W1, protein accumulation remained N2 > N1 > N3, while under W2 and W3, grain protein accumulation significantly increased with nitrogen rate. These results indicate that during late grain filling, increasing nitrogen rate significantly enhanced grain protein accumulation under moderate and severe water stress conditions, whereas adequate water supply combined with medium nitrogen rate effectively improved protein accumulation, with both low and high nitrogen rates being detrimental to grain protein accumulation.

2.2 Effects of Nitrogen Rate and Post-Anthesis Soil Relative Water Content on Nitrogen Accumulation in Various Organs at Maturity

Nitrogen rate and post-anthesis soil relative water content significantly affected nitrogen accumulation in grains and vegetative organs of black wheat at maturity (Table 2). Regarding grains, post-anthesis soil relative water content significantly influenced nitrogen accumulation under the same nitrogen level, with nitrogen accumulation decreasing as water stress intensified (W1 > W2 > W3). The proportion of grain nitrogen to total plant nitrogen showed the same trend. Under the same soil relative water content, grain nitrogen accumulation increased with nitrogen rate, while its proportion of total plant nitrogen decreased, indicating that increased nitrogen application enhanced grain nitrogen accumulation but excessive nitrogen was unfavorable for nitrogen translocation to grains. Regarding vegetative organs at maturity, nitrogen accumulation in stems and sheaths decreased with intensifying water stress under the same nitrogen rate, while nitrogen accumulation in leaves and glumes + rachises increased, as did their proportions of total nitrogen, suggesting that water stress hindered nitrogen translocation from vegetative organs to grains. Under the same soil relative water content, nitrogen accumulation in all vegetative organs increased with nitrogen rate, as did their proportions of total nitrogen, indicating that

excessive nitrogen application increased nitrogen accumulation in vegetative organs rather than promoting its translocation to grains.

2.3 Effects of Nitrogen Rate and Post-Anthesis Soil Relative Water Content on Translocation of Pre-Anthesis Stored Nitrogen to Grains

As shown in Table 3 , both nitrogen rate and post-anthesis soil relative water content significantly regulated nitrogen translocation from vegetative organs to grains in black wheat. Grain nitrogen was derived 68.6%-89.3% from translocation of pre-anthesis stored nitrogen in vegetative organs. Nitrogen translocation amount and efficiency from vegetative organs to grains reached maximum values under the W1 irrigation and N2 nitrogen treatments, with relatively high contribution proportions to grains, indicating that the W1N2 water-nitrogen combination was most favorable for translocation of stored nitrogen to grains. The contribution proportion of translocated nitrogen to grains reached its maximum under the W3N3 combination, suggesting that under severe water stress, high nitrogen application ensured greater translocation of vegetative organ nitrogen to grains; however, due to relatively low total nitrogen accumulation in vegetative organs under severe water stress, translocation amount and efficiency were lower than under adequate water supply and moderate water stress treatments.

Comparing among the same nitrogen treatments, when nitrogen rate was N1, nitrogen translocation amount and efficiency from vegetative organs increased initially then decreased with intensifying water stress (W2 > W1 > W3), indicating that moderate water stress favored translocation of stored nitrogen to grains when nitrogen application was low. At N2 and N3 nitrogen rates, both translocation amount and efficiency decreased continuously with intensifying water stress (W1 > W2 > W3). Under the same soil relative water content, translocation amount, efficiency, and contribution proportion to grains all showed a trend of increasing then decreasing with nitrogen rate, with W2 > W3 > W1, demonstrating that increased nitrogen application significantly enhanced translocation capacity of stored nitrogen to grains, but excessive nitrogen was similarly unfavorable for this translocation.

2.4 Effects of Nitrogen Rate and Post-Anthesis Soil Relative Water Content on Grain Protein and Component Contents and Proportions

As shown in Table 4 , nitrogen rate and post-anthesis soil relative water content significantly affected total protein content in black wheat grains. Under the same water treatment, total protein content increased significantly with nitrogen rate. Under low nitrogen conditions, water stress treatments showed significantly higher total protein content than adequate water supply treatments. Under medium nitrogen conditions, water stress treatments had lower total protein content than adequate water supply treatments, though differences were not significant. Under high nitrogen conditions, total protein content showed an initial increase then decrease with intensifying water stress.

Nitrogen rate and post-anthesis soil relative water content significantly affected protein component contents (Table 4). Post-anthesis soil relative water content significantly affected albumin and globulin contents but had no significant effect on prolamin and glutenin contents. Nitrogen rate significantly affected all protein components except prolamin. Under the same nitrogen level, post-anthesis soil relative water content significantly affected albumin, globulin, and prolamin contents, which increased with water stress at N1 and N2 nitrogen rates. At N3, albumin and globulin contents increased with water stress while prolamin content decreased. Post-anthesis soil relative water content had some influence on glutenin content, but differences among treatments were not significant. Under the same water control condition, different nitrogen rates significantly affected protein component contents. Under adequate water supply (W1), albumin, globulin, and prolamin contents increased with nitrogen rate, while glutenin peaked at N2. Under water stress conditions (W2, W3), all protein component contents were highest at medium nitrogen rate N2, indicating that both excessive and insufficient nitrogen rates were unfavorable for increasing protein component contents under water stress conditions.

Analysis of Table 5 shows that the interaction of nitrogen and post-anthesis water control affected the proportions of protein components in total protein. Post-anthesis soil relative water content significantly affected the proportions of globulin, glutenin, and storage proteins, while nitrogen rate significantly affected the proportions of globulin, prolamin, and glutenin.

3.1 Effects of Nitrogen Rate and Post-Anthesis Soil Relative Water Content on Nitrogen Accumulation, Translocation, and Distribution in Black Wheat

Nitrogen rate and post-anthesis soil relative water content regulate post-anthesis nitrogen accumulation and distribution in wheat, with significant interaction effects between the two factors. Previous studies [18] have shown that increased grain protein content primarily depends on enhanced nitrogen accumulation capacity in grains and increased contribution of vegetative organ nitrogen accumulation to grains. Zheng et al. [19] reported that nitrogen rate and irrigation amount significantly affected wheat grain protein content, while drought stress could affect fertilizer efficiency, which could only be realized under reasonable water supply conditions [20]. Duan et al. [21] found that within the nitrogen application range of 0–150 $kg \cdot hm^{-2}$, increasing nitrogen rate significantly improved plant nitrogen accumulation at various growth stages, grain nitrogen accumulation at maturity, post-anthesis nitrogen absorption rate, and nitrogen translocation amount from pre-anthesis vegetative organs; however, when nitrogen rate exceeded 150 $kg \cdot hm^{-2}$, further increases did not promote these indices and instead reduced grain nitrogen accumulation and distribution proportion at maturity. Ma et al. [8] noted that under zero nitrogen application, the contribution proportion of vegetative organ nitrogen translocation to grains showed an initial increase then decrease with irrigation amount, whereas under nitrogen

application conditions, this contribution proportion increased with irrigation amount, and the contribution proportion of stored nitrogen from vegetative organs to grains also increased with nitrogen rate under various water treatments, demonstrating that reasonable water and fertilizer conditions could enhance the contribution proportion of stored nitrogen to grains.

Our results indicated that during late grain filling, increasing nitrogen rate significantly improved grain protein accumulation under moderate (W2) and severe (W3) water stress conditions, whereas adequate water supply (W1) combined with medium nitrogen rate effectively increased protein accumulation, with both low and high nitrogen rates being detrimental to grain protein accumulation. Under the same nitrogen treatment, water stress reduced grain protein accumulation, possibly because water stress affected nitrogen translocation from vegetative organs to grains, thereby reducing the grain' s own nitrogen accumulation capacity [18].

After anthesis, nitrogen in wheat vegetative organs continuously translocates and distributes, primarily transporting to grains. Over 60% of grain nitrogen originates from re-translocation of nitrogen accumulated in vegetative organs before anthesis [22–23]. Under water stress conditions, the translocation amount and efficiency of nitrogen stored in vegetative organs before anthesis decrease, reducing grain nitrogen accumulation and yield [24]; improved soil moisture conditions promote nitrogen transfer from vegetative organs to grains, increasing total nitrogen yield [25]. Our results showed that increased nitrogen application enhanced grain nitrogen accumulation in black wheat, but excessive nitrogen was unfavorable for nitrogen translocation to grains. Under the same nitrogen level, nitrogen accumulation in stems and sheaths at maturity decreased with intensifying water stress, while nitrogen accumulation in leaves and glumes + rachises increased, as did their proportions of total nitrogen. This occurred because water stress caused premature senescence in black wheat plants, reducing nitrogen translocation amount and efficiency from vegetative organs and causing nitrogen loss. Under the same water control condition, nitrogen accumulation in all vegetative organs increased with nitrogen rate, as did their proportions of total nitrogen. In summary, water stress hindered translocation of stored nitrogen from vegetative organs to grains, while increased nitrogen application significantly enhanced this translocation capacity, though excessive nitrogen was similarly unfavorable.

3.2 Effects of Nitrogen Rate and Post-Anthesis Soil Relative Water Content on Grain Protein and Component Contents in Black Wheat

Previous studies have extensively investigated the effects of nitrogen rate and soil relative water content on wheat grain protein and component contents, though findings have been inconsistent. Zhao et al. [26–27] reported that nitrogen application significantly increased grain protein and component contents, with all component contents increasing with nitrogen rate. Shi et al. [28] suggested that responses of protein component contents to nitrogen rate differed

among varieties, showing that grain protein and component contents in strong-gluten wheat 'Jimai 20' and medium-gluten wheat 'Taishan 23' initially increased then decreased with nitrogen rate, whereas weak-gluten wheat 'Ningmai 9' showed significant increases in all protein components with nitrogen rate. Zhao et al. [29–31] proposed that different protein components responded inconsistently to nitrogen rate changes. Previous research on the effects of different water treatments and water-nitrogen interactions on grain protein and component contents [12,25,32–35] has yielded varying results, indicating that grain protein and component contents have different sensitivities to water and nitrogen, with variations existing among varieties.

Our results showed that total grain protein content in black wheat increased with nitrogen rate under the same water treatment, but decreased with intensifying water stress when nitrogen rate was high. Under the same nitrogen level, water control significantly affected albumin, globulin, and prolamin contents but had no significant effect on glutenin. Under the same water control condition, nitrogen rate significantly affected component contents. Under adequate water supply (W1), albumin, globulin, and prolamin contents increased with nitrogen rate, while glutenin peaked at N2. Under water stress conditions (W2, W3), all protein component contents were highest at medium nitrogen rate N2, indicating that both excessive and insufficient nitrogen rates were unfavorable for improving protein component contents under water stress. The interaction of nitrogen and post-anthesis water control had no significant effect on the proportions of protein components in total protein.

Similar to common wheat, nitrogen rate, post-anthesis soil relative water content, and their interaction affect nitrogen accumulation, translocation, distribution, and protein component contents in black wheat 'Luozhen 1'. Low nitrogen rate combined with water stress could appropriately increase total grain protein content, whereas moderate or high nitrogen rates with water stress hindered total protein content increase. Under our experimental conditions, adequate water supply (W1) and medium nitrogen level (N2) effectively regulated nitrogen metabolism processes in black wheat. Therefore, considering all factors, the optimal water-nitrogen combination was W1N2. Since this experiment used pot cultivation, root absorption and utilization of deep soil water differed from field conditions; thus, further verification through field experiments is required for broader application of these results.

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Note: Figure translations are in progress. See original paper for figures.