

## Article

# Synergistic Ability and Effect of Leaf Color and Leaf Thickness to Improve the Photosynthetic Performance of Wheat

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**Abstract:** Leaf traits are important factors affecting the photosynthetic capacity of crops. In Bainong 4199 (BN4199) and Aikang 58 (AK58) wheat, the role of leaf color and leaf thickness in improving wheat photosynthetic performance and its influence on material accumulation and yield were studied in the field environment. Compared with AK58, BN4199 has a deeper leaf color and thicker leaves. Further study on photosynthetic physiological characteristics showed that the photosynthetic capacity of BN4199 with deep color and thick leaves was higher than that of AK58 at flowering stage, 7 days after flowering, 15 days after flowering, and 20 days after flowering regardless of low light in the morning and evening or light at noon. During the flowering stage, the light saturation point and compensation point were 1% higher and 15.23% lower, respectively, in BN4199 than AK58. According to the diurnal variation in chlorophyll content in different growth stages, BN4199 was generally higher than AK58, and the chlorophyll content was the highest at each time point 7 days after flowering. The chlorophyll content was highest at each time point 7 days after flowering. Chlorophyll fluorescence parameters and light reflectance analyses indicated that BN4199 has significantly higher photosynthetic electron transport and population light energy absorption and utilization capacity than AK58. The 2-year field yields indicated significantly higher material accumulation in BN4199 than AK58. In summary, thick leaves with deep color were resistant to both strong light and weak light, thus, markedly increasing photosynthetic efficiency. Improvement in leaf color and leaf thickness might serve as an important index to enhance the photosynthetic performance of wheat, and achieve improvement and breeding of wheat with high light efficiency.

**Keywords:** wheat; leaf color; leaf thickness; photosynthetic characteristics; material accumulation and transport; yield



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## 1. Introduction

Wheat (*Triticum aestivum* L.) is an important cereal crop worldwide [1,2]. Because wheat is a staple food for approximately 35% of the world's population [3,4], estimates suggest that wheat production must increase by 60% by 2050 to feed nearly 9 billion people worldwide [5]. Therefore, increasing wheat yield remains an important goal for global wheat breeders. However, the narrow genetic base, severe homogenization, extreme weather, cultivation techniques, and other factors aggravate the instability of wheat production systems and consequently hinder improvements in wheat yield. The frequent

occurrence of extreme weather caused by global climate change poses a major threat to crop production [6,7], by severely affecting the growth, development, and yield of major crops such as wheat, corn, and rice, thus posing major challenges in global agricultural production [8]. For wheat with a long growth cycle and demanding growth environment, abiotic stress alters the water state of the leaves, destroys photosynthetic pigments, decreases photosynthetic performance, leads to growth retardation and physiological abnormalities, and ultimately decreases yield [9–11].

China is among the largest wheat producers worldwide. To breed breakthrough wheat varieties, more germplasm resources must be created and used to increase wheat yield. Photosynthesis runs through the whole life activity and is the basis of material formation and accumulation [12,13]. In variety replacement, improvement in wheat photosynthetic capacity is closely associated with improvement in wheat traits and increased yield; consequently, enhancing the photosynthesis of C3 crops has been identified as an important method to increase crop yield [14]. Photosynthesis duration and ability within a day have become key factors in increasing grain yield during wheat's limited lifespan [15]. Because the harvest index of wheat varieties is currently close to the limit, improving the ability of plants to absorb and use light energy will be important to achieving future breakthroughs in the yield potential of wheat. However, the problems of limiting light energy utilization, such as excessive light intensity and insufficient light caused by rainy, cloudy, or hazy weather, have become the main ecological factors affecting the post-flowering production of winter wheat in the Huanghuai wheat growing region in China [16–18]. Many studies have shown that excessive light exposure increases the accumulation of ROS and oxidative damage in plant chloroplasts [19,20] and photo inhibition decreases photosynthetic efficiency by approximately 10% in the absence of other stresses [21]. The weak light environment has multiple effects on the chlorophyll content of plant leaves [22], by directly affecting the photosynthetic characteristics of leaves [23], thus, decreasing the leaf photosynthetic rate and increasing photochemical efficiency [24], and further affecting the grouting rate and dry matter accumulation and distribution, decreasing the plant biomass and relative growth rate, and ultimately affecting grain yield [25–27]. Even slow adjustment of wheat leaves in terms of shading and continuous conversion of sunlight has the potential to lead to an assimilation loss of 21% [28]. Therefore, investigating how to cope with environmental fluctuations and improve the photosynthetic capacity of wheat has become a research hotspot. However, most research by breeders and geneticists aiming to increase wheat yield has focused on molecular biology and genetic diversity [29–31], whereas limited research has been aimed at improving the physiological traits of wheat to increase individual plant yield. Studies have shown that the thicker the rice leaves are, the more favorable it is for the upright leaf, and the higher the number of grains per spike and grain weight per spike [32]. Based on the study of barley leaf morphology, it was concluded that there was a significant positive correlation between flag leaf thickness and grain size [33]. The *Amaranthus tricolor* genotype has excellent color properties, and the color properties obtained in the study are helpful for pharmacologists [34]. Rich in anthocyanins and food pigments, purple leaf mustard provides an ideal material for studying the gene regulatory network and molecular mechanism of anthocyanin biosynthesis [35]. The ability to enhance photosynthesis by exploring resources, and improving leaf color and leaf thickness traits in wheat, would provide new ways to increase yield, address stress resistance, and explore important agronomic traits in a changing climate [36].

Many relevant studies have been performed in artificial facilities under steady state conditions [28], which cannot fully reflect the response process of leaf photosynthetic efficiency to changes in sunlight intensity under natural light in the field. This study investigated the leaf traits of wheat, and the changes in photosynthetic characteristics

and yield characteristics at various growth stages in the late growth period under field conditions, to better reflect the changes in leaf color and thickness on light energy absorption and utilization ability under natural conditions. Thus, this study was aimed at providing a theoretical basis for the physiological breeding of wheat with high light efficiency, by addressing the following objectives: (i) to explore the roles of leaf color and thickness in the ability to absorb and use light energy; (ii) to examine whether these characteristics might synergistically enhance the photosynthetic capacity of wheat; and (iii) to provide new ideas for high-efficiency wheat breeding.

## 2. Materials and Methods

### 2.1. Experimental Site

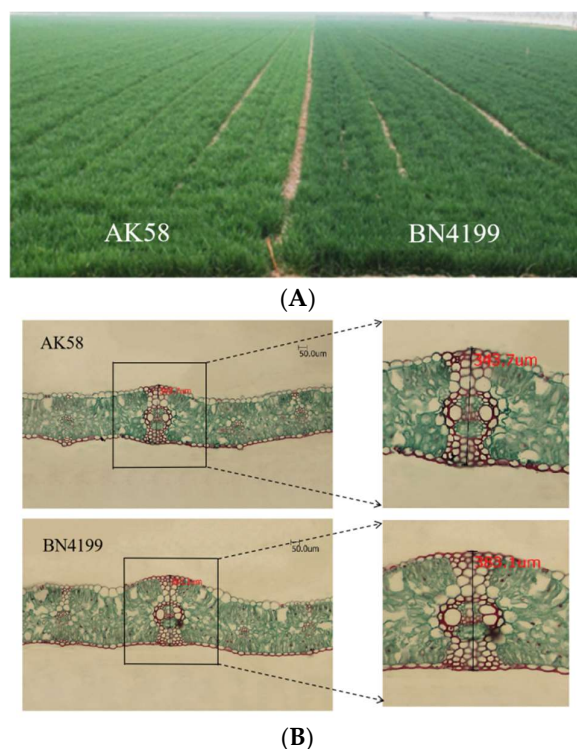
This study was conducted at the wheat experimental base of Henan University of Science and Technology (113.54 N, 35.18 E) in 2022–2023. Located at the center of the North China Plain, the site has a warm temperate continental climate, flat terrain, sufficient sunlight, abundant rainfall, good irrigation and drainage conditions, and an average rainfall in the wheat growing season of 200 mm. The soil in the experimental field was medium soil. Before wheat sowing, the 0–20 cm soil layer of yellow brown soil had an organic matter content of 12 g/kg<sup>-1</sup>, a total nitrogen content of 0.9 g/kg<sup>-1</sup>, an available phosphorus content of 9.8 mg/kg<sup>-1</sup>, and an available potassium content of 100 mg/kg<sup>-1</sup>. The previous crop in the experimental field was corn (*Zea mays*), and the straw was crushed and returned to the field.

### 2.2. Experimental Design

This study examined two wheat varieties: BN4199, with deep leaf color and thick leaves, and AK58, with lighter and thinner leaves, as shown in Figure 1A,B. Both varieties were from the Wheat Research Center of Henan University of Science and Technology. A split zone experimental design was used, with a plot area of 24 m<sup>2</sup> (3 m × 8 m), row spacing of 23 cm, and seedling density of 270 plants. Pure nitrogen was applied at a rate of 180 kg/hm<sup>2</sup> throughout the entire growth period, with a ratio of N, P<sub>2</sub>O<sub>5</sub>, and K<sub>2</sub>O of 15:20:15 in Jinzhengda compound fertilizer (Jinan, China). The fertilizer was divided into two stages: sowing base application and jointing topdressing, with a base topdressing ratio of 7:3. Topdressing was combined with irrigation during the early jointing stage. During the entire growth period, watering was performed four times, as wintering water, jointing water, flowering water, and grouting water. Other field management measures followed local cultivation techniques for high winter wheat yield. The experiment was conducted annually during the flowering stage, 7 days after flowering, 15 days after flowering, and 20 days after flowering of wheat. A digital illuminance meter (VICTOR 1010D, Shenzhen Yisheng Shengli Technology Co., Ltd., Shenzhen, China) was used to measure the light intensity at 8:00, 10:00, 12:00, 14:00, 16:00, and 18:00 in fine weather conditions, and the average was determined. The specific light intensity by time is shown in Table 1.

**Table 1.** Treatment table for testing different light conditions.

	Light Intensity (μmol m <sup>-2</sup> s <sup>-1</sup> )					
	8:00	10:00	12:00	14:00	16:00	18:00
flowering stage	600	900	1200	1000	750	400
10 days after flowering	700	950	1300	1100	800	450
15 days after flowering	700	900	1300	1200	800	500
20 days after flowering	800	1000	1400	1200	1000	600



**Figure 1.** (A) Comparison of leaf color differences between BN4199 and AK58 in the field environment. (B) Cell architecture plots of BN4199 and AK 58 leaves, used to reflect the blade thickness.

### 2.3. Measurement Index and Method

#### 2.3.1. Leaf Thickness Measurement

Paraffin section method: Live sampling of wheat was carried out in the field environment, and the samples were put into the FAA fixed liquid prepared in advance. The material was vacuumed during fixation, and the vacuuming time was about 15 min. After vacuuming, the fixed liquid was changed, and then stored in 70% ethanol (4 °C). Finally, sectioning, wax dissolution, embedding, staining, and microscopic observation were performed.

#### 2.3.2. Net Photosynthetic Rate Determination

The Li-6400 XT portable photosynthetic measurement system was used (LI-COR, Inc., Lincoln, NE, USA). Three plants were randomly selected from each treatment group. The net photosynthetic rate ( $P_n$ ) of flag leaves was measured at 08:00, 10:00, 12:00, 14:00, 16:00, and 18:00 on sunny days at the flowering stage, 7 d after flowering, 15 d after flowering, and 20 d after flowering. The  $\text{CO}_2$  concentration in the leaf chamber was measured as  $350 \pm 10 \mu\text{L}\cdot\text{L}^{-1}$ , and the illumination intensity of the built-in red and blue light source was set to  $1000 \pm 50 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

#### 2.3.3. Measurement of Light Saturation Point and Light Compensation Point

We set 12 photosynthetically active radiation intensity gradients: 1800, 1500, 1200, 1000, 800, 600, 400, 200, 150, 100, 50, and  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The photosynthetic response curve was measured with a programmable open gas exchange portable system (LI-6400, LI-COR, Inc., Beijing, China). The light response curve was fitted at a  $\text{CO}_2$  concentration of  $400 \mu\text{mol mol}^{-1}$  with light curve 2 in the photosynthetic workbench program. With a previously described method [37], the light response curve model of wheat leaves was fitted.

A digital illuminance meter (VICTOR 1010D, Shenzhen Yisheng Shengli Technology Co., Ltd., Shenzhen, China) was used to measure the light intensity at 8:00, 10:00, 12:00,

14:00, 16:00, and 18:00 in fine weather conditions, and the average was determined. The specific light intensity by time is shown in Table 1.

#### 2.3.4. Measurement of Light Reflectivity

With a HandHeld 2 portable spectrometer (ASD Inc., Beijing, China), we measured the light reflectance at 30 cm above the canopy of the population at 12:00 noon on clear and windless days at the flowering stage, 7 days after flowering, 15 days after flowering, and 20 days after flowering, in three replicates.

#### 2.3.5. Determination of Chlorophyll Content

The photosynthetic pigments of wheat were determined with reference to the method [22]. A 1:1 mixture of acetone and ethanol was used to extract chlorophyll content, and 3 plants were randomly selected from each treatment group. A mature, functional leaf was cut from each seedling. A total of 0.2 g of fresh leaves per sample were weighed using an analytical balance, cut, and dipped into 25.0 mL of 95% ethanol plastic tubing. Determination and calculation were performed by ultraviolet spectrophotometer (UV-2600, Shimadzu, Japan). “The following formulas are used to calculate Chl a, Chl B, Chl a + b”.

$$\begin{aligned} \text{Chla} &= (12.7D_{663 \text{ nm}} - 2.69D_{645 \text{ nm}}) \times V / (1000 \times m) \\ \text{Chlb} &= (22.9D_{645 \text{ nm}} - 4.68D_{663 \text{ nm}}) \times V / (1000 \times m) \\ \text{Chl(a + b)} &= (20.21D_{645 \text{ nm}} + 8.02D_{663 \text{ nm}}) \times V / (1000 \times m) \end{aligned}$$

In the formula, D<sub>663 nm</sub> and D<sub>665 nm</sub> are the absorbance values at 663 and 665 nm, respectively, where V is the volume of liquid to be measured (mL) and m is the fresh mass of the leaves.

#### 2.3.6. Chlorophyll Fluorescence Parameters

The photochemical efficiency (F<sub>v</sub>/F<sub>m</sub>) and other chlorophyll fluorescence parameters of PSII were determined by PAM-2500 (Walz Ger, Effeltrich, Germany) portable fluorescence meter produced. Flag leaves and ear were clamped and bagged for 20 min to avoid light leakage. Three samples of each variety were determined. The results were expressed as mean ± standard error.

#### 2.3.7. Material Accumulation

Wheat plants with consistent growth and anthesis on the same day were selected and tagged in each plot. At flowering stage and maturity stage, a representative sample of 3 × 30 cm was taken from the experimental plot and brought back to the laboratory. The samples were degreened for 15 min at 105 °C, dried to constant weight at 80 °C, and weighed. The calculations were based on the following equations:

$$\text{Pre-anthesis translocation amount (kg/hm}^2\text{)} = \text{dry weight of vegetative organs at anthesis} - \text{dry weight of vegetative organs at maturity.}$$

$$\text{Pre-flowering storage transport rate (kg/hm}^2\text{)} = \text{dry weight at flowering stage} - \text{dry weight at maturity stage} / \text{dry weight at flowering stage} \times 100.$$

$$\text{Contribution of pre-anthesis translocation to grains (\%)} = \text{translocation of dry matter in pre-anthesis vegetative organs} / \text{dry weight of grains at maturity} \times 100.$$

### 2.3.8. Production Testing and Seed Testing

After wheat ripening, 1.5 m<sup>2</sup> sample points were selected from each plot, and the wheat was manually harvested and threshed, air-dried, and weighed, and the yield was measured. The experiments were repeated three times. Simultaneously, 1 m double-row samples were selected in each cell with uniform growth to investigate the number of spikes, panicle number, kernel number per spike, and mass of thousand grains.

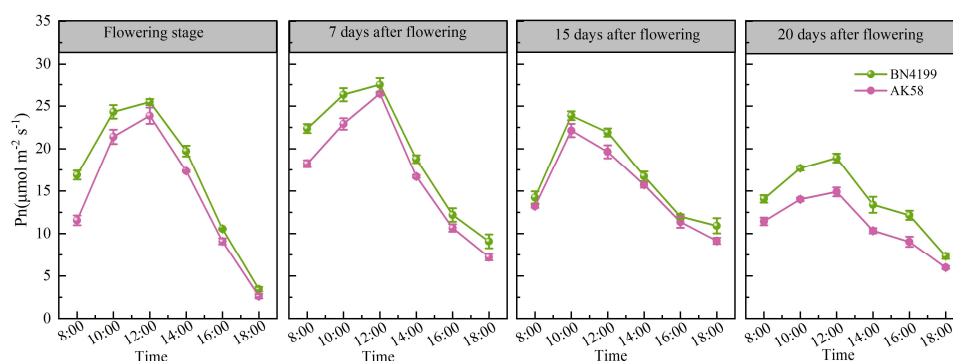
### 2.4. Data Analysis

Microsoft Excel 2007 (Microsoft Corporation, Microsoft Way, Redmond, WA, USA) and Origin 2021 (Northampton, MA, USA) were used to process and analyze tabular data and generate charts. The least significant difference method was used for multiple comparisons to determine statistical significance ( $p < 0.05$ ). The statistical analysis software SPSS (version 13.0, SPSS Inc., Chicago, IL, USA) was used to conduct analysis of variance and comprehensive data analyses.

## 3. Results

### 3.1. Daily Variations in Photosynthetic Rate

During the four growth periods, the diurnal variation in photosynthetic rate in flag leaves of wheat generally first increased and then decreased, as seen in Figure 2. The photosynthetic rate of flag leaves of wheat was highest at 12:00. On the basis of data in Table 1, the daily variation in photosynthetic rate was found to be directly proportional to light intensity radiation within a day, showing a trend of first increasing, peaking at 12:00, and then decreasing. Comparison of varieties under weak light radiation in the morning and evening, or strong light radiation at noon, indicated that the photosynthetic rate of BN4199 was significantly higher than that of AK58 at all growth stages. At 8:00, 12:00, and 16:00 during the flowering period, 7 days after flowering, 15 days after flowering, and 20 days after flowering, BN4199 was 31.56%, 6.28%, and 13.84% higher than AK58, and 18.46%, 3.82%, and 11.96%, 7.23%, 10.41%, and 5.33%, and 18.75%, 21.21%, and 25.66% higher, respectively. From the comparison of photosynthetic rate changes in various growth stages, the photosynthetic rate was the highest 7 days after anthesis.

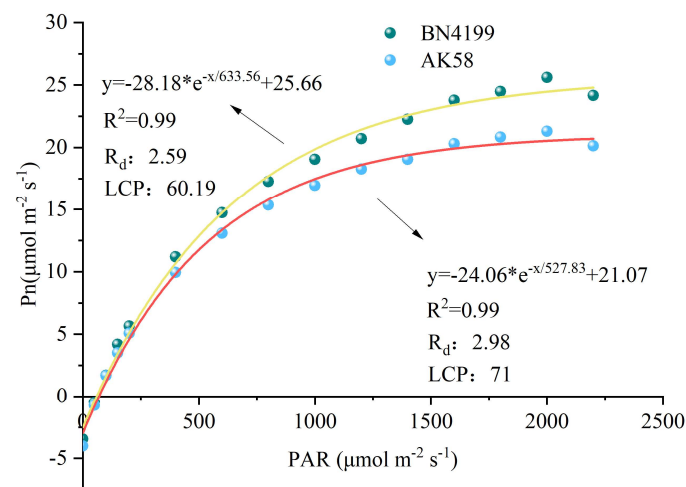


**Figure 2.** Diurnal changes in the photosynthetic rates of flag leaves of wheat at various growth stages. In the figure, the wheat growth stages are flowering stage, 7 days after anthesis, 15 days after anthesis, and 20 days after anthesis. The times of day are 8:00, 10:00, 12:00, 14:00, 16:00, and 18:00. The error bars indicate standard error here and below.

### 3.2. Light Saturation Point and Light Compensation Point

The light saturation point, light compensation point, dark respiration rate ( $R_d$ ), and determination coefficient ( $R^2$ ) of the wheat varieties were studied at the flowering stage to quantitatively and accurately analyze the response of wheat photosynthesis to various light intensities. As shown in Figure 3, after the light intensity exceeded the light compensation

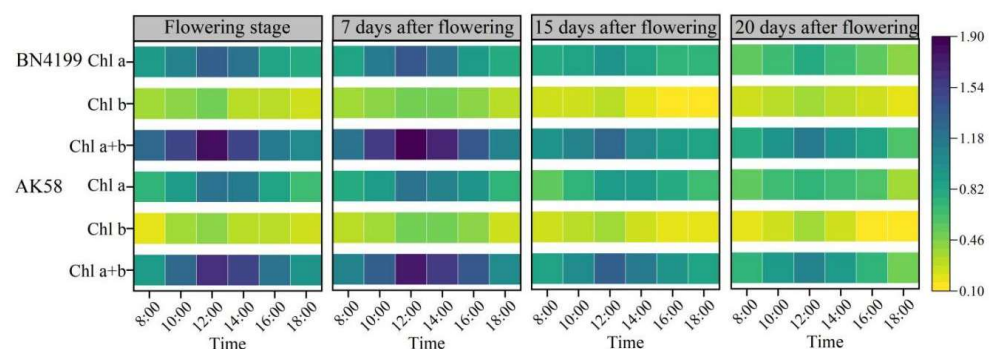
point, within a certain range of light intensity, the photosynthetic rates of BN4199 and AK58 both increased with increasing light intensity. However, the photosynthetic rate of BN4199 was greater than that of AK58 under the different light conditions. When the light intensity increased to  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ , the photosynthetic rate of AK58 stopped increasing and reached saturation; when the light intensity increased to  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ , the photosynthetic rate of BN4199 gradually stabilized and reached saturation. The light saturation point of BN4199 was 1.0% higher than that of AK58. When the light intensity is 0, plants generally begin to consume the oxygen and organic matter generated by photosynthesis and enter respiratory mode. As indicated in the figure, the light compensation point of BN4199 was  $60.19 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and that of AK58 was  $71 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The light compensation point of BN4199 was 15.23% lower than that of AK58, and its respiratory rate was significantly lower than that of AK58. As indicated in Figure 3, BN4199 had characteristics of a high light saturation point and low light compensation point.



**Figure 3.** Changes in the light response curve of wheat leaves at flowering stage. Light saturation point (LPS), compensation point (LCP), dark respiration rate (Rd), and determination coefficient ( $R^2$ ).

### 3.3. Chlorophyll Content

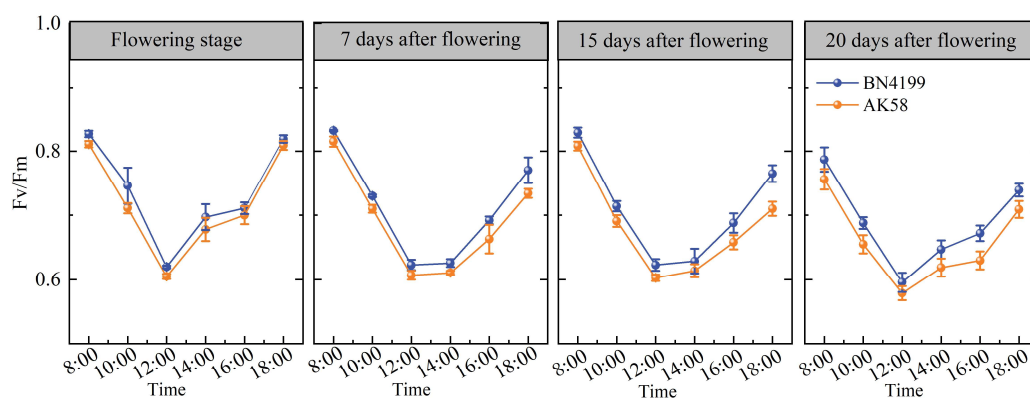
The photosynthetic pigment content of wheat also differed with varying light intensity. As shown in Figure 4, the content of chlorophyll a, chlorophyll b, and chlorophyll (a + b) in flag leaves at various growth stages increased with increasing light intensity, peaked at 12:00, and then began to decline, thus showing a trend of first rising and then decreasing throughout the day. The content of Chl a, Chl b, and Chl (a + b) in BN4199 at various growth stages was higher than that in AK58. At 8:00, 12:00, and 18:00 7 days after flowering, the content of Chl a, Chl b, and Chl (a + b) in BN4199 was higher than that in AK58 by 2.63%, 9.83%, and 4.48%, 22.54%, 4.02%, and 11.37%, and 8.93%, 8.23%, and 6.41%.



**Figure 4.** Diurnal changes in photosynthetic pigments in flag leaves of wheat in various growth periods. Chl a (chlorophyll a), Chl b (chlorophyll b), Chl a + b (chlorophyll a + b).

### 3.4. Chlorophyll Fluorescence

Chlorophyll fluorescence is an important parameter reflecting the electron transfer speed in plant photosynthesis. The intensity of light is an important factor affecting the chlorophyll fluorescence parameters (Fv/Fm) in wheat. As shown in Figure 5, under various light intensities, significant differences were observed in the Fv/Fm variation trends in wheat flag leaves at various growth stages. Comparison of growth stages indicated that the highest Fv/Fm value was observed 7 days after flowering, whereas the lowest Fv/Fm value was observed 20 days after flowering. Compared with the daily variation in each growth period, the daily variation trend of Fv/Fm showed a trend of first decreasing and then increasing with the change in light intensity from strong to weak in a day. The lowest value was observed at noon, when the light intensity was highest, and the highest value was observed when the light intensity was lower in the morning and evening. Although differences in Fv/Fm changes all were observed among various growth stages, BN4199 showed higher Fv/Fm values than AK58 in all four growth stages. At 8:00, 12:00, and 18:00 on the 7th day after flowering, the values for BN4199 were 2.1%, 2.7%, and 4.24% higher, respectively, than those for AK58.

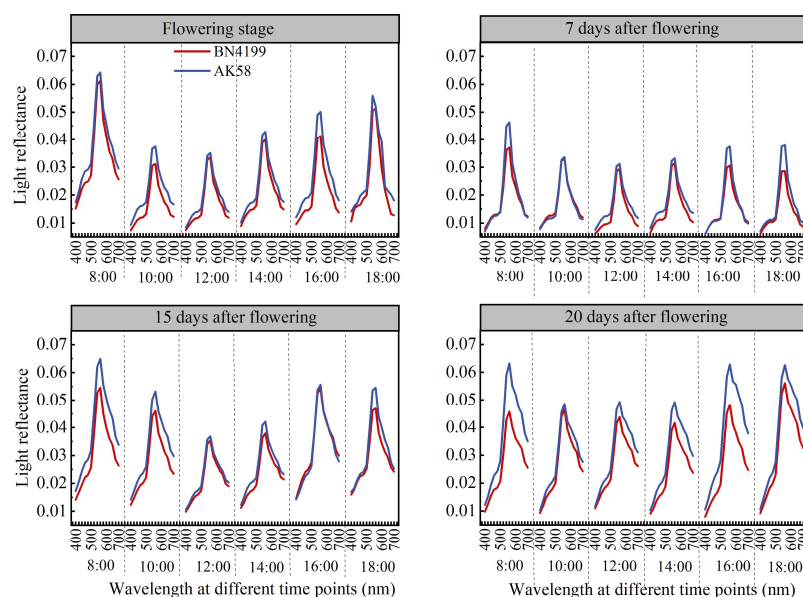


**Figure 5.** Diurnal changes in Fv/Fm in flag leaves of wheat in various growth periods. The error bars indicate standard error.

### 3.5. Characteristics of Light Absorption Capacity in Wheat Population

Canopy light reflectance indicates the absorption and utilization of solar energy in wheat, and is affected by multiple factors. As shown in Figure 6, the optical reflectance of blue-violet light with a wavelength of 400 nm to 700 nm under visible light varied greatly from the flowering stage to the 20th day after flowering. The optical reflectance was relatively low from the 7th to the 15th days after flowering, and relatively high from the 20th day after flowering. The daily variations in different growth stages revealed different light intensity and light reflectance values. As can be seen from Figure 6, from 8:00 to 18:00 in a day, the light reflectivity changes with the change in light intensity. The stronger the light intensity is, the lower the light reflectivity is. Among them, the light intensity is highest at 12:00, and the light reflectivity is lowest at this time. The light intensity is shown in Table 1. This is closely related to the leaf color and leaf thickness of wheat; the deeper the leaf color and the thicker the leaf, the stronger the light absorption ability, and the lower the light emissivity. The different characteristics of varieties included varying light reflectance. In the wavelength ranges of 400–500 nm blue purple light and 600–700 nm red light, the reflectance of the BN4199 population was significantly lower than that of the AK58 population at various growth stages under various light intensities, thus indicating BN4199's strong light absorption ability.





**Figure 6.** Diurnal variation in light reflectance of the wheat population in various growth periods. The error bars indicate standard error.

### 3.6. Dry Matter Accumulation and Yield

As shown in Table 2, we observed significant differences between varieties. BN4199 showed a significantly higher material transshipment volume, transfer efficiency, and contribution rate than AK58. During 2021–2022, the material transshipment volume, transfer efficiency, and contribution rate of BN4199 were 30.74%, 16.51%, and 29.27% higher, respectively, than those of AK58, and these differences were significant. During 2022–2023, the transshipment volume, transfer efficiency, and contribution rate of BN4199 were 18.49%, 10.07%, and 0.13% higher, respectively, than those of AK58, and these differences were significant.

**Table 2.** Dry matter redistribution before flowering, and contribution rate of the wheat population to grain yield in 2 years.

	Variety	Dry Matter Weight at Flowering Stage	Dry Matter Weight at Maturity	Transshipment Volume (kg hm <sup>-2</sup> )	Transfer Efficiency (%)	Contribution Rate (%)
2021–2022	BN4199	11,511.92 a	8890.23 a	2621.69 a	22.71 ab	31.84 a
	AK58	9515.09 b	7699.19 ab	1815.90 b	18.96 b	22.52 b
2022–2023	BN4199	10,798.54 ab	8062.35 ab	2736.20 a	25.41 a	31.24 ab
	AK58	9778.10 b	7547.80 b	2230.30 ab	22.85 ab	31.20 ab

Different lowercase letters show there were significant differences among different varieties in different years ( $p < 0.05$ ).

On the basis of the 2-year yield and three yield change factors (Table 3), the yield per hectare of BN4199 was 7% higher in the first year, and 6.2% higher in the second year, than that of AK58, and the differences between years were significant ( $p < 0.05$ ). This finding was essentially consistent with the changes in above-ground dry matter accumulation (Table 2). The results of the three yield factors are shown in Table 3. BN4199 also showed strong advantages in its significantly higher numbers of spikes, grains per spike, and 1000-grain weight than those of AK58.

**Table 3.** Characteristics of wheat yield and three related factors in 2 years.

Year	Variety	Spike Numbers (/10 <sup>4</sup> /hm <sup>-2</sup> )	Grain Number per Spike	1000-Grain Weight/g	Yield/(kg·hm <sup>-2</sup> )
2021–2022	BN4199	602.9	47.3	42.7	9284
	AK58	628.99	45.2	41.39	8634.5
2022–2023	BN4199	795.76	45.2	42.98	11,200
	AK58	710.15	45.8	41.55	10,511

There were significant differences among different varieties in different years ( $p < 0.05$ ).

#### 4. Discussion

Photosynthesis, the cornerstone of plant development, coordinates the conversion of light energy into chemical energy, thus providing energy for various life support processes in plants [38]. Photosynthesis is also a physiological process sensitive to environmental factors, and light intensity is a major factor affecting photosynthesis. Light intensity either too high or too low decreases the photosynthetic efficiency and affects normal growth in plants. However, more than 80% of wheat grain yield is derived from photosynthetic products after flowering [39]. Therefore, studies aimed at improving photosynthetic efficiency through high-efficiency breeding may aid in increasing wheat yield and quality [40]. Many methods exist to study high-efficiency wheat breeding by improving photosynthetic efficiency, yet many areas remain to be explored to enhance wheat's photosynthetic efficiency by improving its photosynthetic characteristics. Through this study, we found that the deeper the leaf color and the thicker the leaf, the better the strong light and weak light resistance; this property is a good regulation of wheat photosynthesis performance, with a higher substance accumulation. Leaf color and leaf thickness may be one of the important research directions to improve the photosynthetic efficiency of wheat. In the breeding process, the advantages of deep leaf color and thick leaves of wheat can be amplified. This provides a theoretical basis for high light efficiency breeding.

Light is a crucial environmental factor for plant survival and growth [41]. Photosynthesis is responsible for more than 90% of crop biomass production, and increasing photosynthetic efficiency at the leaf level might increase overall crop productivity [42]. According to the study results, BN4199 and AK58 varied by growth period or daily: the photosynthetic rates of both varieties changed with the intensity of light, thus indicating mutual positive effects between the photosynthetic rate and light intensity; that is, within the range of the light saturation point, the photosynthetic rate increased with increasing light intensity. This finding is essentially consistent with previous research results [22,43]. However, our study indicated that the photosynthetic capacities of BN4199 and AK58 significantly differed. Compared with AK58, BN4199 had a higher photosynthetic rate under various light intensity environments at various growth stages. Moreover, BN4199 had a higher light saturation point and a lower light compensation point than AK58. These differences might be associated with the leaf color and leaf thickness characteristics of BN4199: deep leaf color and leaf thickness were associated with greater light energy absorption and photosynthetic rate.

Photosynthesis in plants relies on photosynthetic phosphorylation reactions by photosynthetic pigments to absorb the energy of sunlight, thereby driving photosynthetic reactions. Chlorophyll, the most important pigment in photosynthesis, plays important roles in light energy absorption and transmission [44]. Under exposure to various natural factors, the chlorophyll content adjusts in a timely manner to adapt to the environment and enable plants to capture as much light energy as possible. Studies have shown that, under low light intensity environmental conditions, the chlorophyll content of *Angelica* seedlings increases to capture more light energy and improve photosynthetic efficiency [45].

Bertamini [46] found that the chlorophyll a/b ratio of plants decreases in deep shaded environments, thereby increasing utilization of blue violet light as an adaptation to shaded environments. The content of pigment in leaves has been shown to reflect the photosynthetic capacity of plants, and changes in chlorophyll content are an important indicator of plants' photosynthetic characteristics [47]. The results of this study demonstrated that, to adapt to various growth periods and the changes in light intensity from strong to weak in a day, the chlorophyll content first increased and then decreased to adapt to the influence of solar radiation intensity. However, different varieties have different characteristics and marked differences in adaptation. We observed that BN4199, with deep leaf color and thick leaves, had higher chlorophyll content than AK58 during various growth periods and diurnal time points; moreover, its adaptability to various light intensities was stronger. This adaptation process was reflected in the close relationship between chlorophyll content and leaf color and thickness: the deeper the leaf color and the thicker the leaf, the higher the chlorophyll content, the greater the photosynthesis, and the better the adaptability to various light intensities.

The chlorophyll fluorescence parameter ( $F_v/F_m$ ) is an important index for measuring the speed of electron transfer in plant photosynthesis. Under normal conditions, the  $F_v/F_m$  of plants is generally 0.75–0.85 [48]. This parameter is positively correlated with photosynthesis and the chlorophyll content of plants [49]. Our findings indicated that during the period from flowering to 20 days after flowering,  $F_v/F_m$  generally showed an increasing trend with increasing grouting rate and light intensity, and its change trends mirrored those of the photosynthetic rate and chlorophyll content, in agreement with results reported by Lee [49]. Light reflectance is an index indicating the light energy absorption and utilization capacity of the canopy of a plant population [50]. In general, the stronger the light intensity, the faster the grouting rate, whereas the lower the light reflectance, the stronger the light energy absorption and utilization capacity. Therefore, in this study, the reflectance in each growth stage showed a high-low-high trend with changes in light intensity. This index is the main measure of the photosynthetic intensity of plants and the light energy utilization capacity of wheat varieties. The  $F_v/F_m$  of BN4199, which has deep leaf color and thick leaves, was significantly higher than that of AK58 at various growth stages and under various light intensities; moreover, its population light reflectance was in the range of 400–500 nm blue light and 600–700 nm red light. BN4199 was significantly lower than AK58 in various growth stages and under various light conditions. These results indicated that the photosynthetic electron transport and population light energy absorption and utilization capacity of BN4199 were significantly higher than those of AK58, and BN4199 had better photosynthetic characteristics. The importance of leaf color and thickness in light absorption capacity was again verified by the results of chlorophyll fluorescence parameters and light reflectance.

Dry matter formation and accumulation is the final result of wheat photosynthesis, and wheat yield depends primarily on pre-flowering dry matter transport and post-flowering accumulation of photosynthetic products, among which 60–80% of wheat yield comes from the accumulation of photosynthetic products in flag leaves after flowering [51,52]. However, the characteristics of crops differ, including their material transshipment volume, transfer efficiency, and contribution rate. The photosynthetic productivity of crops and the transport capacity of photosynthetic compounds to vegetative organs differ [53]. Our 2-year research experiments indicated that the yield of BN4199 was significantly higher than that of AK58 in both years. This finding might be closely associated with the deeper and thicker leaves of BN4199, which enhanced its material accumulation, transport, and contribution ability before and after flowering. Therefore, improving leaf color and leaf thickness characteristics

was found to synergistically improve the photosynthetic performance and yield potential of wheat.

## 5. Conclusions

Photosynthesis is an important basis for material accumulation, and the yield of wheat is closely associated with its photosynthetic performance. In this study, deep colored, thicker leaves were associated with higher chlorophyll content, faster photosynthetic electron transfer, greater photosynthetic capacity, higher material accumulation, and a significantly enhanced yield advantage, compared to wheat with lighter colored, thinner leaves. These results indicated that the deepening of wheat leaf color and thickening of wheat leaves effectively improved the ability to tolerate and adapt to strong light, and to use weak light, thus jointly improving wheat photosynthetic performance and promoting increasing biomass. Therefore, improving the leaf color and leaf thickness characteristics of wheat is conducive to improving photosynthetic performance, thus providing a theoretical basis for high light efficiency wheat breeding in the future. If the characteristics of dark wheat leaf color, low light compensation point, low light resistance, thick wheat leaves, high photosynthetic saturation point, and strong light resistance are combined in the breeding process, wheat varieties that can make full use of various light conditions and adapt to different environments might be cultivated, thereby increasing grain yield. In this study, only the physiological characteristics were studied; therefore, the related molecular mechanisms remain to be further explored.

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