

Article

Plant Growth Regulators Enhance Wheat Yield Under Shading Conditions by Optimizing Stem Sugar Metabolism and Lodging Resistance

Yongqiang Zhang ^{1,2}, Jingcan Zhang ³, Chuanxin Chen ¹, Shihui Nie ¹, Juan Li ¹, Yuting Hou ¹, Jiantao Ma ¹, Liusheng Duan ², Qijiang Xu ¹ and Junjie Lei ^{1,*}

¹ Crop Research Institute, Xinjiang Academy of Agricultural Sciences/Key Laboratory of Desert-Oasis Crop Physiology, Ecology and Cultivation, Ministry of Agriculture and Rural Affairs, Urumqi 830091, China; zyq988@yeah.net (Y.Z.); lixp618@163.com (C.C.); nieshihui@hotmail.com (S.N.); l_juan@yeah.net (J.L.); 18160501359@163.com (Y.H.); mjt0323@163.com (J.M.); 18234874770@163.com (Q.X.)

² College of Agronomy, China Agricultural University, Beijing 100193, China; dls@bua.edu.cn

³ College of Agronomy, Xinjiang Agricultural University, Urumqi 830052, China; myjc0120@163.com

* Correspondence: leijunjie@sohu.com

Abstract

Shading in agroforestry systems reduces light availability and increases the risk of lodging, limiting wheat (*Triticum aestivum* L.) yield. A two-year field experiment was conducted to assess the effects of chlormequat chloride (CCC) on wheat stem morphology, carbohydrate metabolism, lignin biosynthesis, lodging resistance, and yield under four shading intensities (S0: natural light; S1: 10% → 25% shading; S2: 20% → 50% shading; S3: 30% → 75% shading) from jointing to maturity stage. Shading resulted in taller plants with increased center of gravity, thinner stems, and reduced lignin, cellulose, and soluble sugar content, weakening stem-breaking strength and reducing yield. CCC application decreased internode length, increased stem solidity, and enhanced lignin and cellulose accumulation, as well as lignin biosynthesis enzyme activity. These changes improved stem-breaking strength and lodging resistance. Moreover, CCC significantly increased wheat yield by 2.7% to 23.3% ($p < 0.05$) depending on the shading intensity, and there was a significant interaction between shading intensity and CCC application on wheat grain yield ($p < 0.05$). The results demonstrate that CCC application can mitigate shading-induced yield loss by enhancing lodging resistance and improving stem integrity under the artificial-shading conditions evaluated in this study. Its effectiveness in actual agroforestry systems requires further field validation.

Keywords: *Triticum aestivum*; shading; chlormequat chloride (CCC); stem morphology; lodging resistance; lignin biosynthesis; carbohydrate metabolism

Academic Editor: Hongkun Yang

Received: 6 July 2026

Revised: 20 July 2026

Accepted: 22 July 2026

Published: 26 July 2026

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1. Introduction

Wheat (*Triticum aestivum* L.) is one of the world's most important staple crops, serving as the primary food source for over one-third of the global population. As the physiological foundation of wheat growth, photosynthesis plays a pivotal role in regulating both its morphological development and overall productivity [1]. Alley cropping agroforestry systems—where trees are planted in rows within croplands or pastures—have gained widespread adoption globally, with particularly extensive implementation in

southern Xinjiang, northwestern China [2]. However, as trees mature and their canopies expand, they create pronounced spatial and temporal heterogeneity in understory light availability [3]. The resulting competition for light can restrict crop growth and substantially reduce the yield of associated understory crops [4].

Insufficient light exposure induces substantial alterations in the internal structure of wheat culms, characterized by increased plant height and center of gravity, accompanied by reductions in stem diameter, wall thickness, and tissue solidity. These morphological changes collectively diminish culm mechanical strength and thereby elevate the risk of lodging. The culm plays a critical role in nutrient translocation, storage, and mechanical support. Previous studies have demonstrated that traits such as plant height, internode length, stem diameter, wall thickness, and culm solidity are closely associated with lodging resistance [5]. Lodging remains one of the principal constraints on wheat yield, grain quality, and harvest efficiency, with culm resistance significantly influenced by the degree of shading [6]. It has been shown that under shaded conditions, the accumulation of photosynthetic assimilates is markedly reduced, leading to diminished culm solidity at basal internodes, thinner stems and walls, and consequently, a significant decline in both bending strength and culm lodging resistance index.

Wheat stems represent a natural organic polymer primarily composed of lignin and cellulose. As a critical structural component, lignin accumulates within the cell wall and substantially enhances stem rigidity, compressive strength, and mechanical support [7]. The lignin content in stems is closely associated with lodging resistance; in grasses, approximately 20% of the secondary cell wall is constituted by lignin [8]. Empirical evidence suggests that enhancing the activity of lignin biosynthetic enzymes promotes lignin deposition in the stem, thereby reinforcing mechanical strength and reducing the risk of lodging [9]. Moreover, the application of gibberellin (GA) inhibitors has been shown to effectively restrict stem elongation, resulting in increased stem solidity, diameter, and wall thickness. These morphological changes collectively contribute to improved stem strength and significantly enhanced lodging resistance [10]. CCC is a classic gibberellin (GA) synthesis inhibitor, which inhibits the key enzyme in the GA synthesis pathway (ent-kaurene oxidase), reduces the endogenous GA content of wheat, delays cell elongation in stem internodes, suppresses vegetative growth, and promotes the accumulation of photosynthetic assimilates in reproductive organs and stem structural components [11]. CCC functions by delaying cell elongation, suppressing vegetative growth, promoting reproductive development, increasing stem robustness, and shortening internode length, ultimately leading to reduced plant height. Recent studies have demonstrated that foliar application of plant growth regulators can significantly reduce the plant height, thereby enhancing their resistance to lodging [11]. It has been observed that the application of plant growth regulators enhances the activity of key enzymes involved in lignin biosynthesis, such as phenylalanine ammonia-lyase (PAL) and tyrosine ammonia-lyase (TAL), thereby increasing the lignin content in the internodes [12]. These biochemical alterations enhance the mechanical properties of wheat stems, thereby increasing their resistance to bending and breakage under environmental stresses such as strong winds or heavy rainfall [13]. Zhang et al. further reported that CCC application at the stem elongation stage markedly reduced both plant height and the height of the plant's center of gravity, with a more pronounced effect compared to applications during the green-up or jointing stages [14].

Although the independent effects of shading on wheat lodging and yield and of chlormequat chloride (CCC) on plant height and stem-breaking strength have been well documented, two important questions remain unresolved. First, it is unclear whether the effectiveness of CCC is maintained, enhanced, or diminished as shading progressively intensifies during wheat development. Second, few studies have simultaneously examined how CCC-induced changes in basal-internode morphology are coordinated with

soluble and structural carbohydrates, lignin-biosynthesis-related enzyme activities, stem mechanical performance, and yield formation under low-light stress. This knowledge gap limits our understanding of whether CCC merely shortens plants or produces a broader, shading-dependent coordination of structural, biochemical, and agronomic responses. Therefore, a two-year split-plot field experiment with four stage-dependent artificial-shading regimes was conducted to quantify the shading $\times$ CCC interaction. The unique contribution of this study is the integrated evaluation of basal-internode morphology, carbohydrate accumulation, lignin-biosynthesis-related enzyme activities, lodging resistance, yield components, and grain yield across a progressively intensified shading gradient. Specifically, we aimed to determine whether the agronomic response to CCC depended on shading severity and to identify the measured traits associated with the maintenance of stem-breaking strength and grain yield.

2. Materials and Methods

2.1. Experimental Site

The experiment was conducted over two consecutive winter wheat growing seasons (2020–2022) in the 9th village of Bosikaimu Township, Zepu County, Kashgar region, Xinjiang (77°16' E, 38°10' N). The study area is located at an elevation of 1266 m, with an annual mean temperature of 11.6 °C, an average annual precipitation of 54.8 mm, and a growing degree-days (≥ 0 °C) accumulation of 4183 °C. The region receives an annual solar radiation of 5300–6200 MJ·m⁻², with a total annual sunshine duration of approximately 2900 h. The average frost-free period is 212 days, and the annual potential evapotranspiration reaches 2079 mm, classifying it as a typical arid climate zone. The soil texture is sandy loam, and the initial soil nutrient content at depths of 0–20 cm and 20–40 cm is detailed in Table 1.

Table 1. Soil basic property information of the experimental site.

Soil Depth	Organic Matter (g·kg ⁻¹)	Total Nitrogen (g·kg ⁻¹)	Total Phosphorus (g·kg ⁻¹)	Total Potassium (g·kg ⁻¹)	Alkaline Hydrolyzed Nitrogen (mg·kg ⁻¹)	Available Phosphorus (mg·kg ⁻¹)	Available Potassium (mg·kg ⁻¹)	pH
0–20 cm	13.61	0.74	0.95	19.18	45.29	17.37	110.57	8.47
20–40 cm	13.18	0.53	0.91	19.54	38.27	10.48	98.78	8.81

2.2. Experimental Design

A split-plot experimental design was implemented under field conditions with drip irrigation. The main plots corresponded to different shading treatments, simulated using black nylon mesh (composed of nylon-66 synthetic fibers) with customized light transmittance levels, fabricated by the Junmin Screen Factory in Luqiao, Taizhou. Shading was applied from the jointing to the maturity stage of winter wheat. Based on the phenological stages of the fruit trees and the growth periods of wheat, four variable shading treatments were set: S0: Natural light (NL); S1: 10% shading from jointing to 25% shading at heading; S2: 20% to 50% shading; S3: 30% to 75% shading. Subplots were assigned to different application rates of chlormequat chloride (CCC) (Guoguang, Sichuan Guoguang Agrochemical Co., Ltd., Chengdu, China), with two levels: a water-only control (CK), and CCC applied at 4500 mL·hm⁻² during the erecting stage and 3000 mL·hm⁻² during the jointing stage (ST), each diluted in 300 L·hm⁻² of water. The stage-specific CCC application rates were selected according to local agronomic recommendations for winter wheat production in southern Xinjiang. The two rates represented sequential applications within the same ST treatment rather than two independent CCC-rate treatments. A total of eight

treatment combinations were established, each replicated three times. The plot size was 12 m² (3 m × 4 m), with 0.5 m buffer zones between adjacent plots. The winter wheat cultivar used was ‘Xindong 60’, sown at a rate of 270 kg·hm⁻² with a row spacing of 20 cm. All other agronomic practices were uniformly applied across treatments.

2.3. Plant Sampling and Measurements

Morphological traits of the basal internodes: At maturity, ten representative wheat plants were randomly sampled from each plot. The length and diameter of the second basal internode were measured using a ruler and a digital caliper with a precision of 0.01 mm. The dry weight of the internode was then determined using an analytical balance with an accuracy of 0.1 mg. Stem filling degree (FD) was calculated as the ratio of stem dry weight to stem length, using the following equation [15]:

$$FD = \frac{\text{Stem dry weight (mg)}}{\text{Stem length (cm)}}$$

Plant Architectural Characteristics: At the flowering stage of winter wheat, plant height (PH) and center of gravity height (CGH) were measured using a ruler. Plant height was defined as the vertical distance from the stem base to the tip of the spike, while center of gravity height was measured as the distance from the stem base to the balance point of the stem.

Breaking strength and culm lodging resistance index (CLRI): At the flowering stage of winter wheat, stem-breaking strength was measured for different treatments. The plants were fixed at the base, and the YYD-1 stem strength tester (Top Instrument Co., Ltd., Zhejiang, China) was used to apply force vertically at the mid-point of the internode. The maximum reading on the force gauge at the moment of stem fracture was recorded as the stem’s breaking strength.

$$CLRI = \frac{\text{Breaking strength of basal second internodes}}{\text{Height of plant gravity center}}$$

Biochemical Composition of the Stem: At the flowering stage, the samples were taken from plants with uniform growth in each measurement and stored at −80 °C. At the flowering stage, ten uniformly growing single-stem wheat plants were selected from each plot. The second basal internode was excised, and the leaf sheath was removed. Samples were immediately snap-frozen in liquid nitrogen for 15 min and then stored at −80 °C until analysis. The contents of lignin, cellulose, glucose, sucrose, and fructose were determined using commercial assay kits provided by Shanghai Enzyme-linked Biotechnology Co., Ltd.

Lignin Biosynthesis Enzyme Activities: At the flowering stage, samples were collected for the determination of key enzyme activities involved in lignin biosynthesis. Ten single-stem wheat plants with uniform growth were selected from each plot, and the second basal internodes were excised after removing the leaf sheaths. Samples were immediately frozen in liquid nitrogen for 15 min and then stored at −80 °C until analysis. The activities of phenylalanine ammonia-lyase (PAL), tyrosine ammonia-lyase (TAL), cinnamyl alcohol dehydrogenase (CAD), 4-coumarate:CoA ligase (4CL), and cinnamate 4-hydroxylase (C4H) were determined using commercial assay kits provided by Shanghai Enzyme-linked Biotechnology Co., Ltd. (Shanghai, China), following the manufacturer’s instructions. All kits were validated (coefficient of variation <5%), with three technical replicates per sample; measurement accuracy was 0.01 U·g⁻¹ FW for PAL/TAL/C4H, 0.001 U·mg⁻¹ FW for 4CL, and 1 U·g⁻¹ FW for CAD. Enzyme activity was expressed in terms of the amount of product formed per unit time and tissue mass (e.g., U·g⁻¹ FW).

Grain Yield and Yield Components: At maturity, two representative wheat sample segments (1 m × 2 rows) were selected from each plot for indoor yield component analysis, including measurements of effective spike number, grains per spike, and thousand-grain

weight (TGW). A harvest area of 4 m² (2 m × 2 m) per plot was used to determine actual grain yield.

2.4. Statistical Analysis

Data were analyzed separately for each sampling date and growing season using split-plot ANOVA in SPSS 18.0; no combined analysis across growing seasons was performed. Shading and CCC were treated as the main-plot and subplot factors, respectively, with block and block × shading as random effects. Residual normality and homogeneity of variance were assessed using the Shapiro–Wilk and Levene’s tests. When the omnibus F-test was significant, Fisher’s protected LSD test was used for pairwise comparisons at $p < 0.05$. Plot means were treated as biological replicates ($n = 3$). Pearson correlations were calculated using the two-year means of the eight treatment combinations ($n = 8$), without treating plant or technical subsamples as independent observations. Correlation analysis, PCA, and graphing were performed using Origin 2021.

3. Results

3.1. Plant Height, Center of Gravity Height and Single Plant Biomass

Plant height, center of gravity height, and individual plant biomass were significantly affected by varying shading treatments and CCC application rates across two growing seasons (Figure 1). No significant differences in PH or CGH were observed between the two growing seasons. Compared with the S0 condition, ST treatments resulted in increases of 1.40~5.87% in plant height and 4.33~18.27% in CGH. In contrast, relative to the CK, ST treatment significantly reduced PH and CGH by 2.20~4.52% and 1.51~6.29%, respectively ($p < 0.05$). The suppressive effect of ST on both PH and CGH generally intensified with increasing shading intensity. Under increasing levels of shading, the individual aboveground biomass of wheat declined progressively. Foliar application of CCC partially mitigated this reduction by enhancing individual plant biomass to varying degrees under different shading conditions. The promotive effect of CCC on biomass accumulation exhibited a non-linear trend, decreasing initially and then increasing as shading intensity rose.

3.2. Morphological and Mechanical Traits of the Second Basal Internode and Culm Lodging Resistance Index

Second-basal-internode length, diameter, and structural solidity were influenced by varying shading intensities and CCC application rates across both growing seasons (Figure 2). Compared to the 2020~2021 growing season, the 2021~2022 season exhibited increased second-basal-internode length and diameter, accompanied by a reduction in stem solidity. Internode length demonstrated a consistent increase with escalating shading intensity, while CCC application significantly reduced internode length in both seasons. Under different shading conditions, CCC shortened the second basal internode by 15.40~20.38% relative to the CK ($p < 0.05$). Conversely, internode diameter showed a decreasing trend as shading intensity increased. Notably, under ST treatment, internodes were shorter and thicker, with enhanced stem solidity. As a consequence, both stem-breaking strength and culm lodging resistance index were elevated under ST treatment (Figure 3). However, increasing shading levels led to a gradual decline in stem mechanical strength and lodging resistance. In general, both stem-breaking strength and culm lodging resistance index were higher in the 2021~2022 season than in 2020~2021. Across both growing seasons, the positive regulatory effect of CCC on stem-breaking strength tended to diminish with increasing shading intensity.

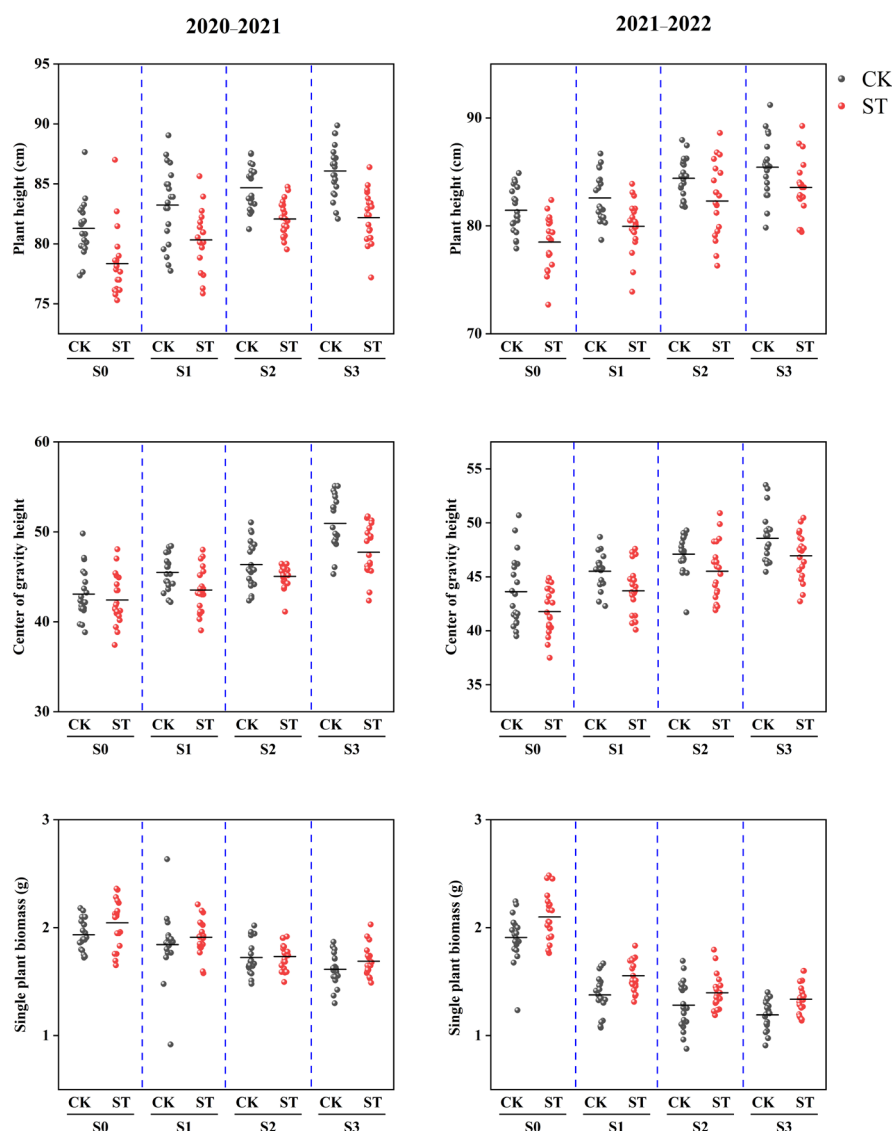


Figure 1. The effects of shading treatments and chlormequat chloride rates on plant height, center of gravity height and single plant biomass. S0, Natural light; S1, 10% shading from jointing to 25% shading at heading; S2, 20% to 50% shading; S3, 30% to 75% shading. CK, water control; ST, CCC applied at $4500 \text{ mL} \cdot \text{hm}^{-2}$ during the erecting stage and $3000 \text{ mL} \cdot \text{hm}^{-2}$ during the jointing stage. Each point represents a measurement from one individual plant. For each treatment in each growing season, 10 plants were measured in each of three independent replicate plots, resulting in 30 plotted observations per treatment. The horizontal line represents the mean of the 30 individual measurements. For statistical analysis, the mean of the 10 plants within each plot was treated as one biological replicate ($n = 3$).

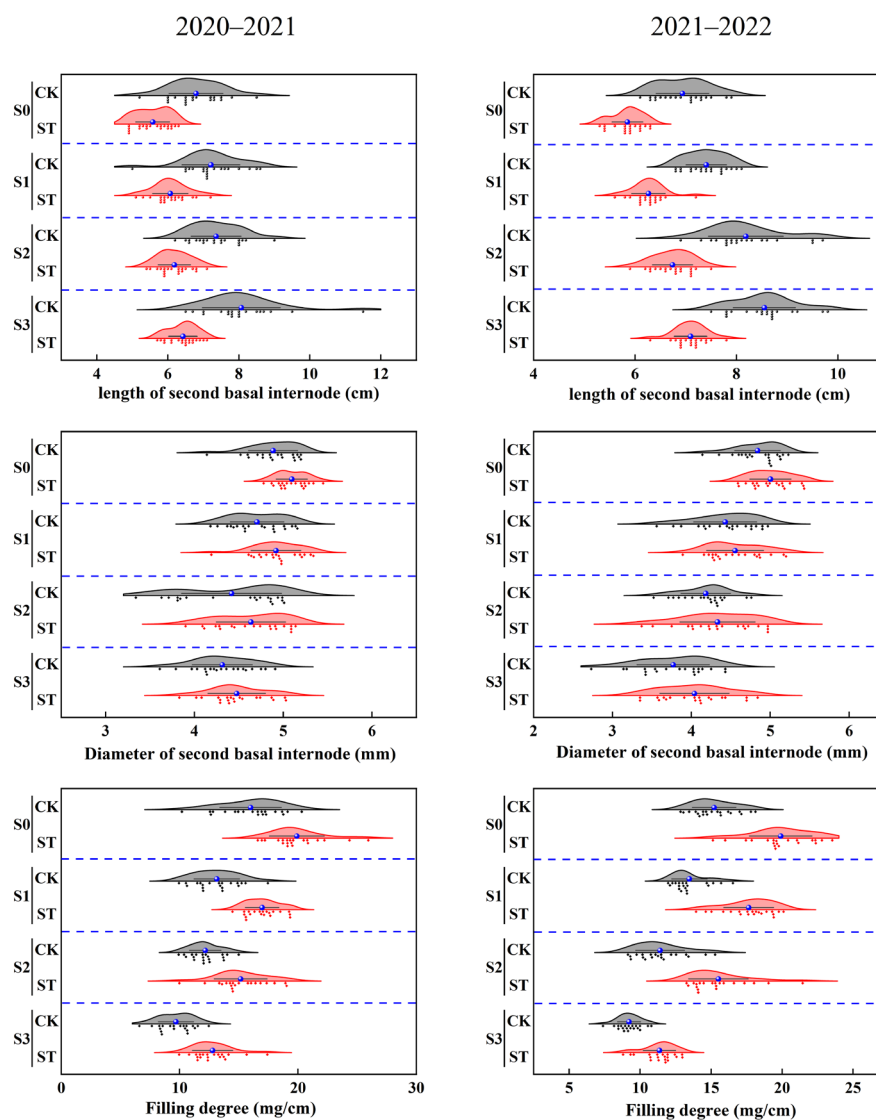


Figure 2. The effects of shading treatments and chlormequat chloride rates on the length, diameter and filling degree of the second basal internode, with individual data points overlaid to illustrate variation within each group. S0, Natural light; S1, 10% shading from jointing to 25% shading at heading; S2, 20% to 50% shading; S3, 30% to 75% shading. CK, water control; ST, CCC applied at 4500 mL·hm⁻² during the erecting stage and 3000 mL·hm⁻² during the jointing stage. Each short vertical point represents a measurement from one individual plant. For each treatment in each growing season, 10 plants were measured in each of three independent replicate plots, resulting in 30 plotted observations per treatment. The width of each violin represents the kernel density distribution of the 30 individual measurements, and the blue dot indicates their mean. For statistical analysis, the mean of the 10 plants within each plot was treated as one biological replicate ($n = 3$).

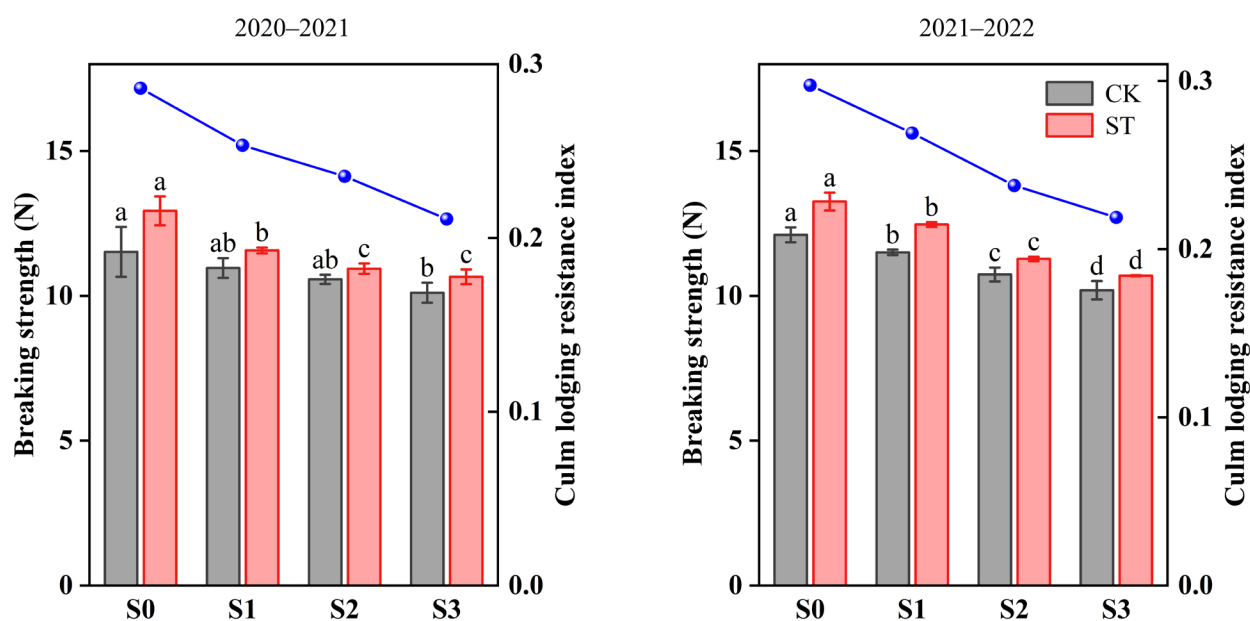


Figure 3. The effects of shading treatments and chlormequat chloride rates on breaking strength and culm lodging resistance index in the 2020–2021 and 2021–2022 growing seasons. Values are presented as means $\pm$ SD of three independent plot replicates ($n = 3$). S0, Natural light; S1, 10% shading from jointing to 25% shading at heading; S2, 20% to 50% shading; S3, 30% to 75% shading. CK, water control; ST, CCC applied at 4500 mL·hm⁻² during the erecting stage and 3000 mL·hm⁻² during the jointing stage. The bar plot represents the breaking strength (left Y-axis) and the line plot represents the culm lodging resistance index (right Y-axis). The bar chart shows the breaking strength for each treatment group, with error bars indicating the standard deviation. The blue data points represent the mean culm lodging resistance index of wheat under different shading treatments. Lowercase letters indicate significant differences at $p \leq 0.05$ (LSD test).

3.3. Contents of Lignin, Cellulose, and Soluble Sugars

Stem carbohydrate content in wheat exhibited a declining trend with increasing shading intensity, whereas foliar application of CCC significantly promoted carbohydrate accumulation in the stem (Figure 4). This trend was consistent across both the 2020–2021 and 2021–2022 growing seasons. Compared with the natural light (S0) treatment, various levels of shading led to reductions in both lignin and cellulose contents within the stem. In contrast, relative to the control (CK), CCC application (ST) resulted in an average increase of 8.55% in lignin content and 7.25% in cellulose content across different shading conditions ($p < 0.05$). Although soluble sugar content declined progressively with increasing shading intensity, the magnitude of this reduction varied considerably among different sugar types, indicating differential sensitivity to light availability. Across both growing seasons, increasing shading progressively reduced lignin, cellulose, and soluble sugar contents. CCC partially alleviated these reductions under all shading treatments, although the magnitude of its effect varied among shading intensities and carbohydrate components.

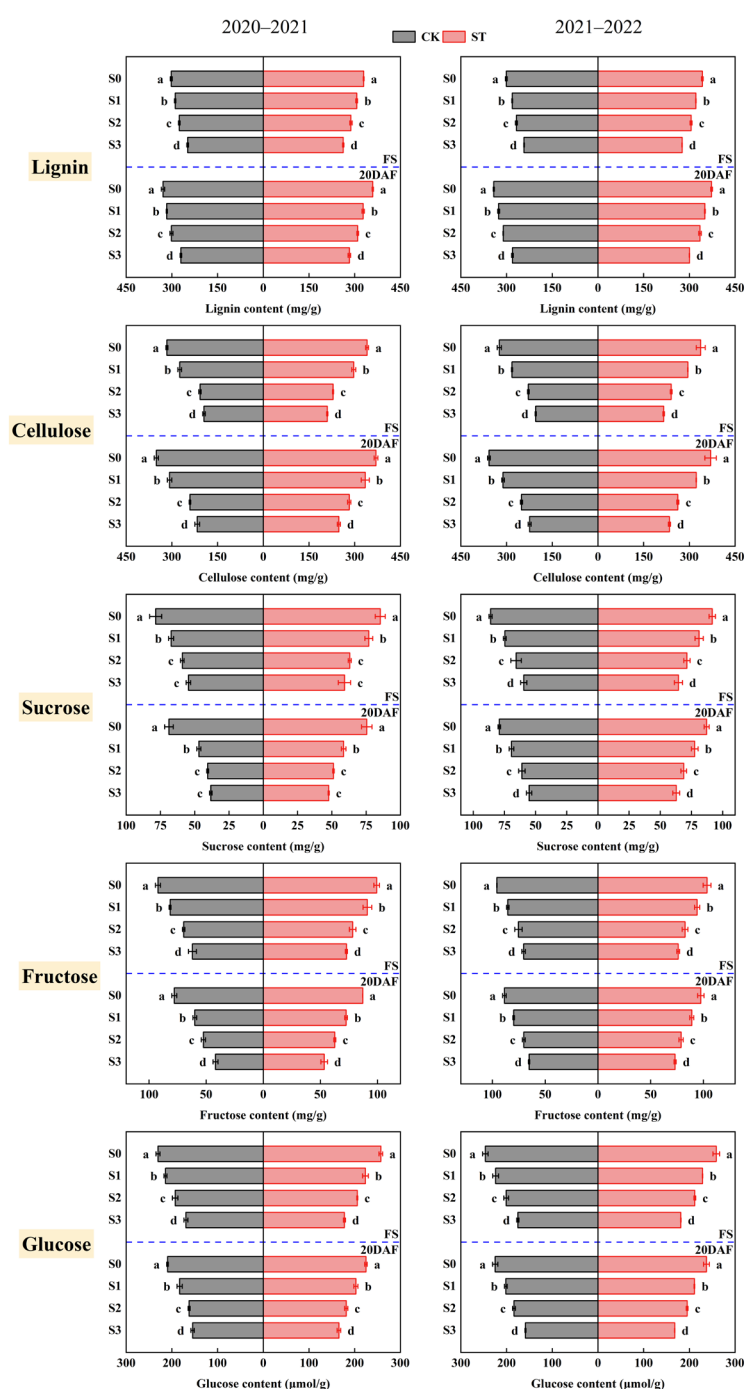


Figure 4. The effects of shading treatments and chlormequat chloride rates on lignin, cellulose, sucrose, fructose and glucose content at the flowering stage and 20 days after flowering in the 2020–2021 and 2021–2022 growing seasons. Values are presented as means $\pm$ SD of three independent plot replicates ($n = 3$). S0, Natural light; S1, 10% shading from jointing to 25% shading at heading; S2, 20% to 50% shading; S3, 30% to 75% shading. CK, water control; ST, CCC applied at 4500 mL·hm^{−2} during the erecting stage and 3000 mL·hm^{−2} during the jointing stage. The vertical bars represent the standard error of the mean ($n = 3$). The lowercase letters indicate significant differences at $p \leq 0.05$ (LSD test).

3.4. Activities of Lignin-Biosynthesis-Related Enzymes

The activities of enzymes related to lignin biosynthesis were affected by shading treatments and CCC application during both growth seasons (Table 2). The interactions between shading treatments and CCC application on PAL, TAL and CAD content at the flowering and 20-days-after-flowering stages during 2020–2021 and on PAL, TAL and C4H content at the flowering stage and on CAD and C4H content at the 20-days-after-flowering stage during 2021–2022 were all significant. The activities of enzymes related to lignin biosynthesis were lower in 2020–2021 and higher in 2021–2022. The PAL and C4H content at the flowering stage were lower compared with the 20-days-after-flowering stage, and the TAL, 4CL and CAD content at the flowering stage were higher compared with the 20-days-after-flowering stage. Compared with the CK, CCC application increased the activity of enzymes related to lignin biosynthesis. The mean data for the two years indicated that ST treatments improved PAL, TAL, 4CL, CAD and C4H content by 11.65, 8.69, 21.67, 9.83 and 19.26% respectively.

Table 2. Effects of shading treatments and chlormequat chloride rates on phenylalanine ammonia-lyase (PAL, U·g⁻¹ FW), tyrosine ammonia-lyase (TAL, U·g⁻¹ FW), 4-Coumarate-CoA Ligase (4CL, U·g⁻¹ FW), Cinnamaldehyde Dehydrogenase (CAD, U·g⁻¹ FW) and cinnamate 4-hydroxylase (C4H, U·g⁻¹ FW) at flowering stage and 20 days after flowering of wheat in 2020–2021 and 2021–2022 growing seasons.

Year	Shading Treatment	Chlormequat Chloride Rate	PAL(U·g ⁻¹ FW)		TAL(U·g ⁻¹ FW)		4CL(U·mg ⁻¹ FW)		CAD(U·g ⁻¹ FW)		C4H(U·g ⁻¹ FW)	
			FS	20DAF	FS	20DAF	FS	20DAF	FS	20DAF	FS	20DAF
2020–2021	S0	CK	57.13 b	62.40 b	56.20 b	51.60 b	5.87 b	5.43 c	1207.00 b	1094.00 b		
	S0	ST	64.10 a	70.13 a	60.27 a	54.83 a	6.90 a	6.33 a	1294.67 a	1170.67 a		
	S1	CK	51.33 c	55.60 c	52.90 c	48.87 c	5.07 c	4.77 d	1086.33 d	984.33 d		
	S1	ST	57.63 b	61.73 b	55.53 b	51.47 b	6.10 b	5.80 b	1111.33 c	1038.00 c		
	S2	CK	42.10 e	44.57 e	48.00 d	45.40 e	4.10 d	3.80 f	896.67 f	821.00 f		
	S2	ST	47.73 d	50.37 d	52.37 c	47.20 d	5.10 c	4.77 d	999.67 e	919.00 e		
	S3	CK	36.30 g	39.57 g	40.37 e	38.73 f	3.07 e	3.00 g	811.33 g	745.33 g		
	S3	ST	39.56 f	42.30 f	47.40 d	44.47 e	4.13 d	4.21 e	904.00 f	823.00 f		
	Average											
	S0		60.61 a	66.27 a	58.23 a	53.22 a	6.38 a	5.88 a	1250.83 a	1132.33 a		
	S1		54.48 ab	58.67 ab	54.22 a	50.17 a	5.58 ab	5.28 ab	1098.83 ab	1011.17 ab		
	S2		44.92 bc	47.47 bc	50.18 ab	46.30 ab	4.60 ab	4.28 ab	948.17 bc	870.00 bc		
	S3		37.93 c	40.93 c	43.88 b	41.60 b	3.60 b	3.60 b	857.67 c	784.17 c		
	CK		46.72 b	50.53 b	49.37 b	46.15 b	4.53 b	4.25 b	1000.33 b	911.17 b		
	ST		52.26 a	56.13 a	53.89 a	49.49 a	5.56 a	5.28 a	1077.42 a	987.67 a		
	ANOVA											
	S		**	**	**	**	**	**	**	**		
	C		**	**	**	**	**	**	**	**		
	S × C		*	*	*	**	ns	ns	**	**		
2021–2022	S0	CK	61.67 b	64.47 b	58.93 b	54.80 c	6.23 c	6.07 b	1225.33 b	1078.33 b	229.00 c	238.33 c
	S0	ST	68.57 a	72.33 a	61.47 a	59.97 a	7.77 a	6.63 a	1307.33 a	1221.33 a	269.00 a	310.67 a
	S1	CK	55.20 c	58.50 c	55.47 c	51.53 d	5.50 d	5.33 c	1102.00 d	949.00 c	202.67 d	222.33 d
	S1	ST	61.83 b	66.40 b	59.73 ab	56.63 b	6.57 b	5.90 b	1195.00 c	1088.00 b	237.00 b	270.67 b
	S2	CK	45.77 e	49.07 e	52.97 d	47.83 e	4.33 f	3.77 e	927.33 f	818.33 e	166.67 f	187.00 e
	S2	ST	51.23 d	55.73 d	54.77 c	51.37 d	5.47 d	4.67 d	1042.33 e	943.00 c	193.00 e	221.00 d
	S3	CK	39.93 g	41.60 g	45.77 e	42.40 f	3.70 g	3.20 f	846.67 g	742.00 f	130.67 h	149.33 g
	S3	ST	43.03 f	46.40 f	51.43 d	47.53 e	4.93 e	3.83 e	924.67 f	847.00 d	151.00 g	169.33 f
	Average											
	S0		65.12 a	68.40 a	60.20 a	57.38 a	7.00 a	6.35 a	1266.33 a	1149.83 a	249.00 a	274.50 a
	S1		58.52 ab	62.45 ab	57.60 a	54.08 ab	6.03 ab	5.62 a	1148.50 ab	1018.50 ab	219.83 ab	246.50 ab
	S2		48.50 bc	52.40 bc	53.87 ab	49.60 ab	4.90 ab	4.22 b	984.83 bc	880.67 b	179.83 bc	204.00 ab
	S3		41.48 c	44.00 c	48.60 b	44.97 b	4.32 b	3.52 b	885.67 c	794.50 b	140.83 c	159.33 b
	CK		50.64 b	53.41 b	53.28 b	49.14 b	4.94 b	4.59 b	1025.33 b	896.92 b	182.25 b	199.25 b
	ST		56.17 a	60.22 a	56.85 a	53.88 a	6.18 a	5.26 a	1117.33 a	1024.83 a	212.50 a	242.92 a
	ANOVA											
	S		**	**	**	**	**	**	**	**	**	**

C	**	**	**	**	**	**	**	**	**	**
S × C	*	ns	*	ns	ns	ns	ns	**	**	**

S0, Natural light; S1, 10% shading from jointing to 25% shading at heading; S2, 20% to 50% shading; S3, 30% to 75% shading. CK, water control; ST, CCC applied at 4500 mL·hm⁻² during the erecting stage and 3000 mL·hm⁻² during the jointing stage. Values are means of three replications, and different lowercase letters within a column indicate significant different at $p \leq 0.05$ (LSD test). ANOVA indicates analysis of variance; * and ** indicate the 5 and 1% probability levels, respectively; ns indicates non-significance.

3.5. Grain Yield and Yield Attributes

The shading treatment and CCC application significantly affected spike number, number of grains per spike, thousand-grain weight and grain yield during the 2020–2021 and 2021–2022 growing seasons (Table 3). The interactions between shading treatments and CCC application on number of grains per spike, thousand-grain weight and grain yield during 2020–2022 were all significant. The spike number, number of grains per spike and grain yield were higher in 2020–2021 and lower in 2021–2022. The ST treatment significantly improved spike number, number of grains per spike, thousand-grain weight and grain yield. The spike number, number of grains per spike, and thousand-grain weight all exhibited a declining trend with increasing shading intensity. The grain yield reached its minimum under the S75 shading level. The mean data for the two years showed that treatments S0ST, S1ST, S2ST and S3ST improved spike number (by 1.13, 1.58, 0.58 and 1.51%, respectively), number of grains per spike (by 4.94, 8.99, 7.05 and 9.14%, respectively), thousand-grain weight (by 2.48, 1.52, 5.95 and 9.41%, respectively), and grain yield (by 3.35, 10.03, 17.48 and 16.68%, respectively) compared with the S0CK, S1CK, S2CK and S3CK treatments.

Table 3. Effects of shading treatments and chlormequat chloride rates on spike number (SN, 10⁴ hm⁻²), number of grains per spike (NGS), thousand-grain weight (TGW, g) and grain weight (GY, kg hm⁻²) in 2020–2021 and 2021–2022 growing seasons.

Year	Shading Treatment	Chlormequat Chloride Rate	SN (10 ⁴ hm ⁻²)	NGS	TGW (g)	GY (kg hm ⁻²)
2020–2021	S0	CK	649.92 ab	43.20 b	40.12 b	8328.72 b
	S0	ST	651.11 a	44.53 a	40.96 a	8552.90 a
	S1	CK	632.11 c	33.28 d	34.80 c	5450.80 d
	S1	ST	636.86 bc	35.53 c	35.10 c	5840.90 c
	S2	CK	609.21 d	28.44 f	30.88 e	4009.51 f
	S2	ST	613.70 d	30.08 e	32.29 d	4549.72 e
	S3	CK	579.70 e	21.12 h	27.46 g	2557.42 h
	S3	ST	584.96 e	22.39 g	29.16 f	2814.76 g
	Average					
	S0		650.51 a	43.86 a	40.54 a	8440.81 a
	S1		634.49 b	34.41 b	34.95 b	5645.85 b
	S2		611.46 c	29.26 c	31.59 c	4279.62 c
	S3		582.33 d	21.76 d	28.31 d	2686.09 d
	CK		617.74 b	31.51 b	33.32 b	5086.61 b
	ST		621.66 a	33.13 a	34.38 a	5439.57 a
	ANOVA					
	S		**	**	**	**
	C		ns	**	**	**
	S × C		ns	*	**	*
2021–2022	S0	CK	642.77 b	42.14 b	41.57 b	8328.64 b
	S0	ST	656.11 a	45.01 a	42.76 a	8661.88 a

S1	CK	624.23 c	32.72 d	35.85 d	5452.03 d
S1	ST	639.25 b	36.39 c	36.63 c	6155.79 c
S2	CK	593.25 d	27.81 f	30.44 f	3770.41 f
S2	ST	595.75 d	30.13 e	32.67 e	4580.58 e
S3	CK	557.25 e	20.23 h	26.69 g	2299.66 h
S3	ST	569.02 e	22.71 g	30.06 f	2835.31 g
Average					
S0		649.44 a	43.58 a	42.17 a	8495.26 a
S1		631.74 a	34.56 b	36.24 b	5803.91 b
S2		594.50 b	28.97 b	31.56 c	4175.50 c
S3		563.14 c	21.47 c	28.38 c	2567.49 d
CK		604.38 b	30.73 b	33.64 b	4962.69 b
ST		615.03 a	33.56 a	35.53 a	5558.39 a
ANOVA					
S		**	**	**	**
C		**	**	**	**
S × C		ns	*	**	**

S0, Natural light; S1, 10% shading from jointing to 25% shading at heading; S2, 20% to 50% shading; S3, 30% to 75% shading. CK, water control; ST, CCC applied at 4500 mL·hm⁻² during the erecting stage and 3000 mL·hm⁻² during the jointing stage. Values are means of three replications, and different lowercase letters within a column indicate significant difference at $p \leq 0.05$ (LSD test). ANOVA indicates analysis of variance; * and ** indicate the 5 and 1% probability levels, respectively; ns indicates non-significance.

3.6. Correlation Analysis

Correlation analysis revealed that the length of the second basal internode, stem filling degree, stem-breaking strength, spike number, grains per spike, thousand-grain weight, and grain yield were significantly and positively correlated with the contents of lignin, cellulose, sucrose, fructose, and glucose, as well as with the activities of lignin-biosynthesis-related enzymes, including PAL, TAL, 4CL, CAD, and C4H (Figure 5). Wheat yield exhibited a significant negative correlation with plant height ($r = -0.86$, $p < 0.01$) and center of gravity height ($r = -0.98$, $p < 0.01$), whereas it was positively and significantly correlated with individual plant biomass ($r = 0.98$, $p < 0.01$), the diameter of the second basal internode ($r = 1.00$, $p < 0.01$), filling degree ($r = 0.93$, $p < 0.01$), breaking resistance ($r = 0.95$, $p < 0.01$), and culm lodging resistance index ($r = 0.98$, $p < 0.01$). Subsequent analyses evaluated the trade-off relationships between stem carbohydrate content and enzymatic activities under shading stress and CCC application, and their associations with stem morphological traits and yield components. The results revealed that the length of the second basal internode, stem filling degree, stem-breaking strength, number of spikes per plant, grains per spike, thousand-kernel weight, and overall grain yield were all significantly and positively correlated with both metabolites (lignin, cellulose, sucrose, fructose, and glucose) and the activities of lignin-biosynthesis-related enzymes (PAL, TAL, 4CL, CAD, and C4H). Moreover, plant center of gravity height and single plant biomass were also significantly and positively correlated with metabolites including lignin, cellulose, sucrose, fructose, and glucose.

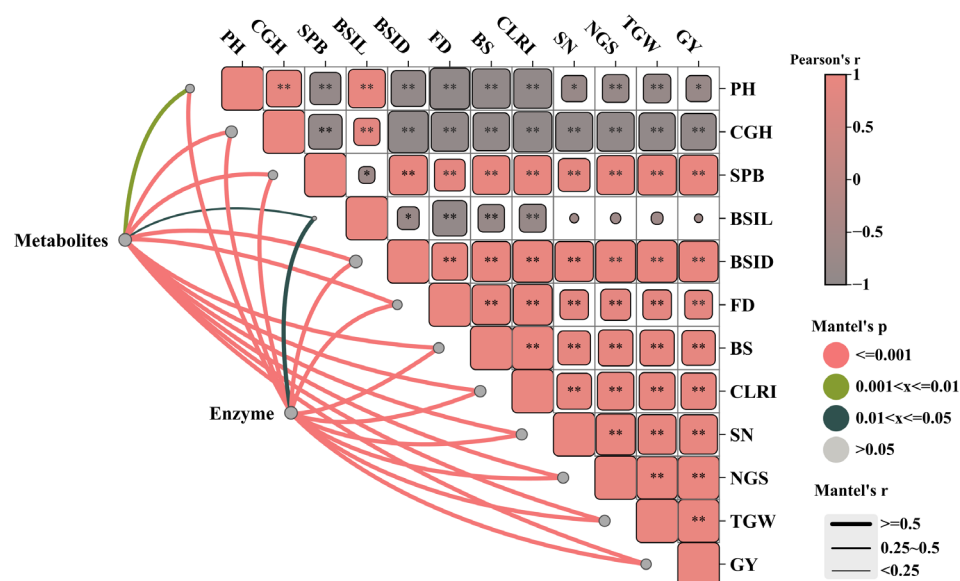


Figure 5. The relationship between stem metabolic products, lignin-related enzyme activity, stem traits, and yield. Each circle represents the Mantel correlation between a pair of variables. The circle color denotes the Pearson correlation coefficient (r), with blue shades indicating positive correlations and brown shades indicating negative correlations. Circle size and edge color indicate the statistical significance of the Mantel test: red ($p \leq 0.001$), green ($0.001 < p \leq 0.01$), blue ($0.01 < p \leq 0.05$), and gray ($p > 0.05$). Line thickness reflects the strength of correlation: thick lines ($r > 0.5$), medium ($0.25 < r \leq 0.5$), and thin lines ($r \leq 0.25$). The figure illustrates the overall pairwise correlations between metabolites and enzymes across multiple samples. Pearson's correlation coefficients were calculated using the two-year mean values of the eight treatment combinations ($n = 8$). The three independent plot replicates were averaged before calculating the treatment means. * indicates $p < 0.05$, and ** indicates $p < 0.01$.

4. Discussion

4.1. Morphological and Mechanical Improvements of Stems Under PGR Application

Under shading conditions, wheat plants exhibit pronounced stem elongation, an elevated center of gravity, and a reduction in mechanical strength, thereby increasing their susceptibility to lodging (Figures 1 and 3). In the present study, CCC application significantly reduced plant height and center of gravity height while increasing the diameter of the second basal internode and stem dry biomass (Figures 1 and 2). These morphological changes improved plant gravitational distribution, shortened the effective lodging lever arm, and enhanced stem mechanical stability. The exogenous application of plant growth regulators (PGRs) in cereal crops has been demonstrated to effectively reduce lodging by modulating plant architecture and enhancing stem strength [16,17]. Studies have demonstrated that plant growth regulators significantly reduce wheat plant height, with a 4~48% decrease observed in the length of the second basal internode [18]. The application of different concentrations of chlormequat chloride has also been found to reduce plant height and center of gravity height, thereby improving lodging resistance and contributing to stable growth and yield formation in wheat [19].

CCC is generally recognized as a gibberellin-biosynthesis inhibitor that restricts excessive internode elongation. Consistent with this physiological role, the reductions in plant height and center of gravity height and the increases in basal-internode diameter and solidity observed in the present study suggest that CCC improved lodging resistance primarily by optimizing stem morphology. Stem-breaking strength declined markedly under shading conditions, whereas CCC application effectively alleviated this adverse

effect (Figure 3). Peng et al. also reported that increased stem diameter and wall thickness can enhance the bending strength and lodging resistance of wheat [20]. Similar effects have also been observed by Ali et al., who demonstrated that the application of plant growth regulators can effectively modulate stem development [21]. These findings support the view that CCC-induced changes in stem morphology contributed substantially to the maintenance of mechanical strength under shading conditions.

In addition to its effects on stem morphology, CCC application increased the activities of lignin-biosynthesis-related enzymes, including PAL, TAL, 4CL, CAD, and C4H, and promoted the accumulation of lignin, cellulose, and soluble sugars in the stem. Greater deposition of lignin and cellulose may reinforce secondary cell walls and improve the structural integrity of the basal internodes, thereby increasing stem-breaking strength and the culm lodging resistance index. Soluble sugars may also provide carbon substrates for the synthesis of structural carbohydrates, although this relationship requires further direct verification. Collectively, the coordinated improvements in stem morphology, structural carbohydrate accumulation, and mechanical strength reduced lodging susceptibility under shading conditions and may have contributed to the maintenance of yield components and grain yield. Therefore, the judicious application of plant growth regulators represents an effective agronomic strategy for enhancing crop resilience and stabilizing yield under unfavorable growing conditions [16].

4.2. Biochemical Enhancement of Stem Tissue Composition

This study demonstrates that the accumulation of lignin, cellulose, and soluble sugars in wheat stems is significantly influenced by shading intensity and CCC (chlormequat chloride) application. As shading levels increased, the overall content of structural and non-structural carbohydrates in stems exhibited a declining trend. However, CCC treatment markedly enhanced the levels of lignin and cellulose across all shading conditions and promoted the accumulation of certain soluble sugars (Figure 4). Previous studies have reported that lignin content in wheat stems decreases under shaded conditions, leading to reduced stem-breaking strength [22]. This reduction may result from the limited supply of photosynthetic assimilates and metabolic energy available for secondary cell-wall biosynthesis under low-light conditions [23]. In contrast, CCC increased lignin and cellulose contents by 8.55% and 7.25%, respectively, consistent with previous findings [24].

CCC application enhanced the activities of PAL, TAL, 4CL, CAD, and C4H, indicating an overall stimulation of lignin biosynthesis. PAL and TAL generate the initial phenylpropanoid precursors, while C4H directs cinnamic acid into downstream phenylpropanoid metabolism. Subsequently, 4CL activates hydroxycinnamic acids, and CAD catalyzes the final reduction step in monolignol formation, producing precursors of H-, G-, and S-type lignin units [25]. Therefore, the coordinated increases in these enzyme activities suggest that CCC promoted lignin accumulation by enhancing multiple successive steps of phenylpropanoid and monolignol biosynthesis.

Lignin biosynthesis is metabolically demanding because the 4CL reaction requires ATP, while C4H- and CAD-associated reactions depend directly or indirectly on reducing equivalents [26]. CCC inhibits gibberellin biosynthesis and restricts internode elongation, which may reduce the resource demand for cell expansion and favor the allocation of assimilates to secondary cell-wall formation [27]. The CCC-induced accumulation of soluble sugars observed in this study may also provide respiratory substrates for ATP production and reducing-equivalent regeneration. This resource-reallocation effect may partially explain the maintenance of lignin-related enzyme activities under shading. However, ATP, NAD (P)H, gene expression, and protein abundance were not directly measured; therefore, this explanation should be regarded as a physiologically plausible mechanism rather than direct evidence.

Interannual differences in enzyme activities may be associated with variations in temperature, precipitation, and soil moisture. During the jointing-to-flowering period, the average temperature in 2021–2022 was 1.2 °C higher and precipitation was 18.5 mm greater, which may have contributed to differences in enzyme activity and carbohydrate accumulation between the two growing seasons.

4.3. Yield Benefits Associated with Improved Stem Traits

This study investigated the effects of CCC application on wheat yield under varying shading conditions. The results revealed that CCC significantly influenced key yield components, including the number of spikes, grains per spike, thousand-grain weight, and overall grain yield. With increasing shading intensity, the yield components were markedly compromised, as evidenced by reductions in spike number, grains per spike, and thousand-grain weight to varying extents (Table 3). This finding is consistent with previous studies, which have established light as a critical environmental factor limiting crop yield formation [28,29]. Li et al. demonstrated that under shading conditions, reduced light intensity markedly impaired the photosynthetic efficiency and ultimately diminished the yield of wheat [19]. Insufficient photosynthetically active radiation directly impairs the carbon assimilation process, thereby restricting wheat grain development and yield formation [30]. Shading limits yield via four pathways: (1) disruption of the source–sink relationship, whereby reduced light interception and Rubisco activity weaken photosynthetic source capacity, restrict soluble sugar accumulation in the stem as a temporary sink, and subsequently reduce carbohydrate remobilization to grains as the final sink; (2) altered assimilate partitioning, with a greater relative proportion retained in vegetative organs and less allocated to developing grains, thereby weakening stem structural reinforcement and limiting grain filling; and (3) abnormal reproductive development (delayed heading/flowering, shortened filling period, fewer fertile florets) [19]. It is noteworthy that the exogenous application of CCC has, to some extent, mitigated the adverse effects of shading on wheat yield and its contributing factors. Compared to the CK, CCC application under both natural light and various shading treatments significantly enhanced the number of effective spikes, grain number per spike, thousand-grain weight, and yield. Notably, the effects were more pronounced under moderate to severe shading conditions. For instance, under S2 and S3 shading conditions, the wheat yields treated with CCC showed increases of up to 21.49% and 23.29%, respectively. These results indicate that CCC partially alleviated the reductions in wheat yield and its components under the artificial-shading conditions evaluated in this study. Previous studies have suggested that CCC may influence yield formation by restricting excessive stem elongation and modifying plant architecture, while changes in photosynthetic performance, assimilate partitioning, and endogenous hormone regulation may also be involved. However, these physiological processes were not directly evaluated in the present study and therefore require further experimental verification. Previous studies in wheat have shown that CCC can improve lodging resistance and yield-related traits by restricting stem elongation and regulating yield components [31]. However, its ability to mitigate yield losses across different shading intensities, particularly under low-light conditions representative of agroforestry systems, remains insufficiently understood.

Shading is the primary stress factor leading to wheat yield loss in agroforestry systems. Shading first reduces the photosynthetic efficiency of wheat, leading to a decrease in photosynthetic carbon assimilation. On the one hand, the insufficient carbon source leads to an insufficient supply of stem development material, resulting in the excessive elongation of internodes, thin stem diameter, low solidity, and a decrease in plant morphological stability; on the other hand, it reduces the activity of lignin-biosynthesis-related enzymes, inhibits the synthesis of lignin and cellulose, and decreases the content of

soluble sugars, leading to the weakening of stem mechanical strength. The combined effect of morphological and biochemical changes leads to the significant decrease in culm lodging resistance index, and the increase in lodging risk leads to the loss of wheat yield. In addition, shading also directly affects the grain development of wheat by reducing the transport of photosynthetic assimilates to grains, which further reduces the yield components.

4.4. Study Limitations

This study used black nylon mesh to simulate reduced light intensity and therefore did not reproduce changes in light quality (e.g., the red/far-red ratio), root and nutrient competition, microclimatic variation, or allelochemical effects (e.g., walnut juglone) typical of natural agroforestry systems. In addition, year-specific meteorological conditions were not continuously recorded; therefore, the environmental causes of the observed interannual variation could not be determined. The experiment was conducted at a single site in southern Xinjiang using one cultivar ('Xindong 60'), and the effects of CCC require further validation across different ecological regions and cultivars. Additional gradient experiments are also needed to optimize CCC dosage and application timing under different shading intensities.

5. Conclusions

Under varying shading conditions, CCC application significantly influenced the morphological characteristics, mechanical strength, structural and non-structural carbohydrates, lignin-biosynthesis-related enzyme activity, and yield composition of wheat stems. Compared with the control, foliar application of CCC markedly improved the stem morphology, mechanical strength, concentrations of both structural and non-structural carbohydrates, and the activity of lignin-related enzymes, thus enhancing the culm lodging resistance index and increasing wheat yield. Shading considerably reduced both the yield and its contributing factors in winter wheat, while CCC treatment significantly increased actual yield and theoretical yield, with the increment being more pronounced under higher shading intensities.

Author Contributions: Y.Z.: Conceptualization, supervision, and writing—review and editing. J.Z.: Writing—original draft preparation. C.C.: Formal analysis and investigation. S.N.: Validation and methodology. J.L. (Juan Li): Methodology and visualization. Y.H.: Visualization. J.M.: Visualization. L.D.: Supervision. Q.X.: Supervision and funding acquisition. J.L. (Junjie Lei): Supervision and funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the Xinjiang Uygur Autonomous Region "Tianshan Talents" Training Program (2023TSYCLJ0009, 2023TSYCCX0013), the National Wheat Industry Technology System (CARS-03-88), the Xinjiang Uyghur Autonomous Region Wheat Industry Technology System Project (XJARS-01-06, XJARS-01-19), and the Project of Fund for Stable Support to Agricultural Sci-Tech Renovation(xjnkywdzc-2025002-01).

Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding author(s).

Conflicts of Interest: On behalf of all authors, the corresponding author states that there is no conflict of interest.

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