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Chlormequat Chloride and Uniconazole Regulate Lodging Resistance and Yield Formation of Wheat Through Different Strategies

Huimin Li, Tao Li, Wenan Weng, Gege Cui, Haipeng Zhang, Zhipeng Xing, Luping Fu, Bingliang Liu, Haiyan Wei, Hongcheng Zhang and Guangyan Li *

Jiangsu Key Laboratory of Crop Cultivation and Physiology, Jiangsu Co-Innovation Center for Modern Production Technology of Grain Crops, Research Institute of Rice Industrial Engineering Technology, Yangzhou University, Yangzhou 225009, China; dx120230130@stu.yzu.edu.cn (H.L.)
* Correspondence: gyli@yzu.edu.cn; Tel.: +86-514-8797-9528; Fax: +86-514-8797-8626

Abstract

Lodging is one of the key limiting factors in achieving high wheat yield. The application of plant growth retardants (PGRts) is regarded as an effective practice to prevent lodging. For accurate PGRt selection and the establishment of stable, high-yield production plans, it is essential to make clear the regulation strategies for lodging resistance and yield in PGRts. Field experiments were conducted at two test sites. At the initial jointing stage of wheat, Chlormequat Chloride (CCC) or Uniconazole (S_{3307}) was sprayed. Compared with the control (CK), spraying CCC or S_{3307} significantly reduced the culm lodging index (CLI) and decreased the lodging rate from 7.1% to 15.6%. CCC was more capable of adjusting plant morphology (reducing plant height and second internode length and increasing stem diameter), while S_{3307} was more effective in enhancing breaking strength. The contents of GA, IAA, and zeatin nucleoside (ZR) and the activities of lignin-related enzymes (TAL and CAD) were significantly correlated with different stem indicators and CLI. Compared with CK, the yield after spraying CCC or S_{3307} increased by 6.5% and 6.0%, respectively. CCC mainly enhanced the yield by increasing grain weight per spike and the SPAD value of leaves, while S_{3307} mainly did so by increasing the number of spikes and the effective leaf area. Moreover, carbon metabolism-related enzymes (Rubisco, SS, and SPS) were significantly positively correlated with the yield. The enzyme activity of CCC was higher at the heading stage, while that of S_{3307} was higher at the filling stage. Hence, spraying CCC or S_{3307} can significantly enhance lodging resistance and yield. The optimal PGRts should be selected based on the climate and the growth stage of the wheat.

Keywords: wheat; plant growth retardants; lodging resistance; yield

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1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most widely planted food crops in the world, and its productivity significantly affects the livelihood of farmers around the world. China is the world's largest wheat producer and consumer [1]. In 2023, the sown area of wheat in China was 2.36×10^7 ha, and the total yield was 1.37×10^{11} kg [2]. High and stable yield of wheat is very important to ensure China's food security and meet market demand. However, lodging is still an important factor limiting the high and stable yield of wheat [3]. Lodging can significantly reduce wheat yields, with yield decline ranging from 31% to 80% [4]. This phenomenon occurs in both developed and developing countries,

mainly under high-yield conditions such as in Western Europe [4]. Research shows that 90° lodging (the plant tilts 90° from the vertical direction) of wheat can reduce yield by about 61% [4,5]. In China, although modern semi-dwarf wheat varieties are used in production, lodging still occurs frequently, especially in the rice–wheat rotation areas in the middle and lower reaches of the Yangtze River, due to the insufficient drainage from the previous rice planting, which leads to high soil viscosity and poor air permeability [6]. Furthermore, high yield frequently results in heavier panicles, which raises the possibility of stem lodging due to growing yield potential [7]. For a stable and high wheat yield, preventing wheat lodging remains a significant challenge [8].

Plant growth retardants (PGRts), such as Chlormequat Chloride (CCC) and Uniconazole (S_{3307}), have been used to alleviate crop lodging for more than 40 years [9]. According to the classification of PGRts compounds, CCC belongs to quaternary ammonium compounds and S_{3307} belongs to triazole compounds [9,10]. Studies have shown that the application of CCC can reduce the plant height of wheat by 5.5 cm, increase the spike weight by 0.07 g [11], and enhance stem mechanical strength, thereby improving lodging resistance [12,13]. The second internode at the base of wheat is generally the force-bearing position for lodging. Its length, diameter, and fullness are one of the important indicators for measuring the lodging resistance of wheat stems [14]. Studies have shown that foliar application of S_{3307} can reduce the plant height and internode length of wheat by 20.2% and 26.4%, respectively, compared with the control, and increase the internode diameter by 17.8% [3,15], thereby reducing the lodging rate and lodging index [16]. The role of PGRts is not only to regulate stem development to prevent lodging but also to have a significant impact on crop morphology, photosynthetic performance, and other aspects, thereby affecting yield. Studies have shown that, in addition to inhibiting stem elongation and preventing lodging, CCC has other beneficial effects on yield formation [17]. Improving photosynthetic characteristics is a feasible method to increase wheat yield [18,19]. This improvement typically includes an increase in leaf area, net photosynthetic rate, and duration of photosynthetic activity, as well as a more balanced sink-to-source ratio [20]. Matysiak [21] demonstrated that the application of PGRts to wheat could transport more assimilates to the grains during the filling period, thereby increasing the yield. Some studies have also shown that the application of PGRts may reduce the leaf area while increasing the SPAD value at the initial filling stage [22]. At present, the specific regulatory pathways of PGRts in increasing wheat yield have not been clarified [3,23,24].

The application of PGRts mainly works by regulating the balance of endogenous hormones in plants. For example, PGRts delay stem elongation by inhibiting endogenous gibberellin (GA) synthesis [25]. Plant hormones can directly affect the appearance and morphological characteristics of wheat and can also indirectly influence the growth and development of wheat by affecting enzyme activity. Lignin-related enzymes are closely related to the lodging resistance of wheat. Studies have shown that increases in GA, auxin (IAA), and cytokinin (CTK) can promote the biosynthesis of lignin [26,27]. Lignin accumulation in wheat stems and phenylalanine ammonia-lyase (PAL), tyrosine ammonia-lyase (TAL), 4-coumarate: CoA ligase (4CL) and (hydroxy) cinnamyl alcohol dehydrogenase (CAD) activities were significantly positively correlated [28–30]. The activities of 4CL, CAD, and PAL were also negatively correlated with lodging [16]. The study by Ahmad et al. [30] indicated that after the application of S_{3307}, the activities of PAL, TAL, and CAD in wheat stems increased by 17.03%, 37.02%, and 23.40%, respectively, and the lodging rate decreased by 7.89%. After the application of PGRts, the endogenous hormone balance in wheat undergoes significant changes. However, it is currently unclear how changes in plant hormones after the application of the two PGRts affect the physiological properties of wheat and how these changes influence the lodging resistance and yield of wheat. This

study was conducted at two experimental sites in the rice–wheat rotation area in the middle and lower reaches of the Yangtze River. The purpose of the research are as follows: (1) to determine the similarities and differences between CCC and S_{3307} in terms of lodging resistance and yield formation; and (2) to clarify the different strategies of CCC and S_{3307} in terms of wheat lodging resistance and yield formation, and to lay a theoretical foundation for determining whether these two PGRts can be formulated into a new formulation.

2. Materials and Methods

2.1. Experimental Location

Field trials were conducted during the winter wheat growing season of 2023–2024 at two experimental bases of Yangzhou University (Dazhong Farm, Yancheng (33°08′ N, 120°39′ E), and Shatou Base, Yangzhou (32°18.6′ N, 119°33′ E), Jiangsu Province, China). The previous crops at both test sites were rice, and the soil type was sandy loam. The initial soil properties before the test are shown in Table 1. The Yancheng test site (YC) is located in the transition zone between the subtropical and warm temperate zones, with an average annual temperature of 14.4 °C, annual precipitation of 1040 mm, and 2078 h of sunshine. The Yangzhou test site (YZ) is situated in the subtropical monsoon humid climate, with an average annual temperature of 17.1 °C, annual precipitation of 1051.5 mm, and 2140 h of sunshine. The temperature and precipitation data for the two experimental sites during the 2023–2024 growing season are shown in Figure 1.

Table 1. Initial soil properties at two experimental sites.

Experimental Site	pH	Organic Matter (g kg^{-1})	Total N (g kg^{-1})	Available P (g kg^{-1})	Available K (g kg^{-1})
YC	7.78	23.4	1.3	47.5	192.17
YZ	7.40	22.6	1.2	33.2	125.6

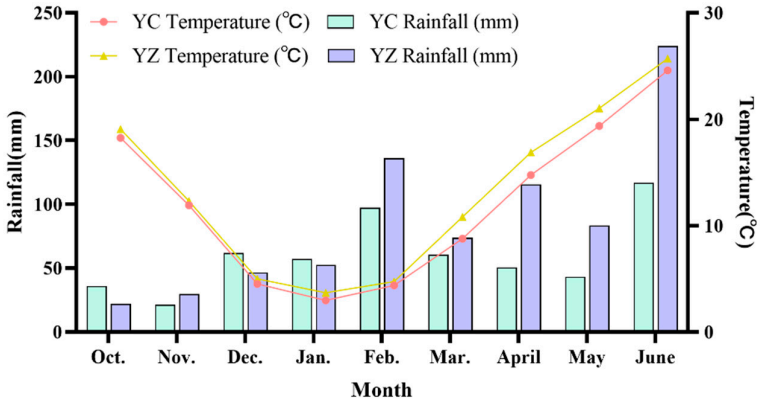


Figure 1. Mean temperature and precipitation during the 2023–2024 growing season at two experimental sites.

2.2. Experimental Design

Zhenmai 15, a wheat variety commonly cultivated in Jiangsu Province, China, was selected for this study. YC was sown on 28 October 2023, with a seeding rate of 150 kg ha^{-1} and harvested on 7 June 2024, with a plot size of 42 m^2 (12 m × 3.5 m); YZ was sown on 20 November 2023, with a seeding rate of 300 kg ha^{-1} (because the sowing time of YZ was 23 days later than that of YC, in order to increase the germination rate and keep the number of basic seedlings at both locations the same, the sowing amount was increased) and harvested on 28 May 2024, with a plot size of 48 m^2 (15 m × 3.2 m). The row spacing was 20 cm. A randomized complete block design with three replicates was

used at both experimental sites. N, P_2O_5, and K_2O fertilizer were applied at 300 kg ha^{-1}, 120 kg ha^{-1}, and 120 kg ha^{-1}, respectively. N fertilizer was applied according to the ratio of base/tillering/jointing 4:3:3, and P_2O_5 and K_2O were applied once as a basal application.

CCC is a 50% aqueous solution, and S_{3307} is a 10% aqueous suspension concentrate. The dosage was determined based on the recommended dosage of the product and the actual usage amount by farmers, in order to reflect the actual decision-making situation faced by farmers when choosing between these two products. The effective contents of 3.75 kg a.i. ha^{-1} and 0.075 kg a.i. ha^{-1}, respectively, were sprayed, and the water volume was 750 L ha^{-1}. Foliar spraying was conducted at the beginning of the jointing stage (seven-leaf stage). YC and YZ were sprayed on 3 March 2024 and 20 March 2024, respectively. The other treatments followed standard cultivation and management practices for high-yield wheat in Jiangsu Province.

2.3. Sampling and Measurements

2.3.1. Grain Yield and Yield Components

At the maturity stage, 1 m regions exhibiting similar growth trends were selected to assess the number of spikes, and 20 wheat spikes were randomly selected to determine the number of grains per spike. Subsequently, 1 m^2 areas were randomly selected for harvesting to measure the yield. The grain was threshed, air-dried, and weighed. The grain moisture content was measured, and the grain yield and 1000-grain weight were adjusted to a 13% moisture content.

2.3.2. Plant Type Characteristics

At the heading, filling, and maturity stages, 30 individual stems were randomly selected from each treatment, and plant height was measured. The midpoint of the second internode was used to record the stem diameter.

2.3.3. Breaking Strength, Culm Lodging Index, and Lodging Rate

Twenty days after the heading stage, 30 individual stems were randomly selected from each treatment, and the breaking strength (BS) of the second internode, the height of the center of gravity (CGH), and the fresh weight of the above-ground part (AFW) were measured. BS was measured using a stalk strength tester (Zhejiang Top Instrument Co., Ltd., Hangzhou, China). The second internode sample, with the stem sheath removed, was placed in the groove of the support pillars, with a 5 cm distance between the pillars. The tester was positioned perpendicular to the center of the stem, which was gradually bent, and the BS was recorded when the internode reached its breaking point. BS was expressed in Newtons (*N*). CLI was calculated using the following formula: CLI = AFW × CGH/BS [16].

The lodging stage was recorded, and the lodging area (LA) was measured when lodging occurred in each plot. Lodging rate (%) = total LA/total area of the plot (TA) × 100 [15]. Ten lodging plants were randomly selected four days before harvest for lodging level measurement. Lodging levels were divided into five levels: the lodging degree score is 0 when the angle is 76–90°, 1 when it is 61–75°, 2 when it is 46–60°, 3 when it is 31–45°, 4 when it is 16–30°, and 5 when it is 0–15° [16].

2.3.4. Dry Matter Accumulation

Thirty stems were continuously sampled at the heading stage, 20 days after anthesis, and at the maturity stage, and the samples were divided into leaves, stems, and spikes. After being blanched at 105 °C for 1 h, the samples were dried at 80 °C until they reached the set weight and then weighed.

2.3.5. Leaf Area Index and Effective Leaf Area

The leaf area index (LAI) was determined by the SS1 Sunscan instrument (Delta-T Devices, Cambridge, UK) during the heading stage. Thirty stems were continuously sampled during the heading stage and filling stages. The top three leaves were regarded as effective leaves [31], and the length and maximum width of each leaf were measured in sequence with a ruler. The calculation formula for the effective leaf area was as follows: Leaf area (cm^2) = 0.75 × length × width.

2.3.6. SPAD Value

During the heading stage and 20 days after anthesis, 30 flag leaves were selected from each treatment group, and chlorophyll content was determined using the SPAD-502 chlorophyll meter (Konica Miolta, Tokyo, Japan).

2.3.7. Endogenous Hormone Content

At the jointing stage, ten independent culms were randomly harvested, immediately snap-frozen in liquid nitrogen, and ground to a fine powder. Aliquots of 100 mg FW were weighed into 2 mL safe-lock tubes and extracted with 1 mL of ice-cold MeOH/i-PrOH/HOAc (20:79:1, *v*/*v*/*v*) containing a cocktail of stable-isotope-labeled internal standards (IS): 10 ng each of d5-trans-zeatin (d5-tZ), 13C6-indole-3-acetic acid (13C6-IAA), d2-GA3, and d4-castasterone (d4-CS). After 30 min of sonication at 4 °C, the slurry was kept at −20 °C for 16 h, vortexed, and centrifuged (12,000× *g*, 10 min, 4 °C). The supernatant was decanted, and the pellet re-extracted with 0.5 mL of the same solvent for 2 h; the combined extract was dried under a gentle N_2 stream and reconstituted in 1 mL 0.1% formic acid (FA).

Clean-up was performed on an Oasis® MCX 96-well µElution plate (Waters, Milford, MA, USA) preconditioned with 1 mL of MeOH and 1 mL of H_2O. After sample loading, the sorbent was washed with 1 mL of H_2O and 1 mL of 5% NH_4OH in MeOH; hormones were eluted with 2 × 0.3 mL of 5% NH_4OH in MeOH. The eluate was evaporated to dryness, redissolved in 100 µL of 0.1% FA/ACN (90:10, *v*/*v*), filtered through a 0.22-µm PVDF membrane, and transferred to amber glass vials.

Chromatographic separation was achieved on an Acquity UPLC I-Class system (Waters) equipped with an Acquity BEH C18 column (2.1 × 100 mm, 1.7 µm) thermostated at 40 °C. The mobile phases were (A) 0.05% FA in H_2O and (B) 0.05% FA in ACN, delivered at 0.3 mL min^{-1} under the following gradient: 0–1 min 5% B, 1–6 min linear to 40% B, 6–7 min to 100% B (held 2 min), return to 5% B, and re-equilibration for 2 min. Injection volume was 5 µL.

Mass spectrometric detection was carried out on a QTRAP 5500 triple-quadrupole/linear ion-trap hybrid instrument (SCIEX, Framingham, MA, USA) operated in scheduled multiple-reaction monitoring (sMRM) mode with positive/negative electrospray switching. Source parameters were as follows: curtain gas 35 psi, ion-spray voltage +4500/−4500 V, temperature 600 °C, nebulizer gas 55 psi, and heater gas 55 psi. Two transitions per analyte and one per IS were monitored (dwell time 20 ms); the most intense transition was used for quantification and the second for confirmation (ion ratio tolerance ±20%). Calibration curves (0.05–200 ng mL^{-1}) were constructed by plotting the analyte/IS peak-area ratio versus concentration; all correlation coefficients (r2) exceeded 0.995. Limits of detection (LOD, S/N = 3) and quantification (LOQ, S/N = 10) ranged from 0.01 to 0.05 ng g^{-1} FW and 0.03 to 0.15 ng g^{-1} FW, respectively. Recovery rates assessed by spiking blank cucumber tissues at three levels (0.5, 5, and 50 ng g^{-1}) were 87–104% with relative standard deviations (RSDs) < 8%. Each biological replicate was analyzed in triplicate, and the results were expressed as ng g^{-1} FW.

Method validation was fully compliant with recent phytohormone profiling protocols [32–34].

2.3.8. The Activity of Lignin-Related Enzymes

Seven days after spraying and at the heading stage, 10 single stems were randomly selected, quickly frozen in liquid nitrogen, and then stored at −80 °C in a refrigerator for low-temperature preservation to determine the activity of lignin-related enzymes.

The 4CL enzyme activity was modified according to Knobloch and Hahlbrock [35]. In an ice-cold mortar containing 10 mL of buffer (50 mmol L^{-1} Tris–HCl buffer, pH 8.8, 14 mmol L^{-1} 2-mercaptoethanol, 30% (v/v) glycerin, and 0.2 g PVP), 5 g of culm samples were homogenized with a pestle. For 15 min at 4 °C, the homogenate was centrifuged at 10,000× g. After mixing 3 mL of reaction mixture (5 mol L^{-1} coumalic acid, 50 mol L^{-1} ATP, 1 mol L^{-1} CoA-SH, and 15 mol L^{-1} $MgSO_4 \cdot 7H_2O$) with 0.4 mL of supernatant, the mixture was incubated at 40 °C in a water bath. After ten minutes, a spectrophotometer (UV-5800PC, Shanghai Metash Instruments Co., Ltd., Shanghai, China) was used to measure the absorbance at A333. One unit of enzyme activity (U) was defined as a change of 0.01 in absorbance per h.

The PAL enzyme activity was assayed according to Wang et al. [16]. The reaction mixture consisted of 0.2 mL of supernatant, 1 mL of 20 mmol L^{-1} 1-phenylalanine, and 2.8 mL of 100 mmol L^{-1} sodium borate buffer (pH 8.8). A UV spectrophotometer was used to measure the absorbance at 290 nm.

The TAL enzyme activity was determined according to Ahmad et al. [30]. The reaction mixture consisted of 0.2 mL of supernatant, 2.8 mL of 0.1 mol L^{-1} borate buffer (pH 8.8), and 2 mL of 0.02 mol L^{-1} L-tyrosine. A UV spectrophotometer was used to measure the absorbance at 315 nm.

The CAD enzyme activity was assayed according to Wang et al. [16]. The reaction mixture consisted of 1 mL of supernatant, 1 mL of 0.5 mol L^{-1} phosphate buffer, 1 mL of 2 mol L^{-1} NADP, and 1 mL of trans-cinnamic acid. A UV spectrophotometer was used to measure the absorbance at 340 nm.

2.3.9. The Activity of Carbon Metabolism-Related Enzymes

During the heading stage and filling stages, 10 single stems were randomly selected, quickly frozen in liquid nitrogen, and then stored in a −80 °C refrigerator at low temperatures for determination.

Rubisco carboxylase activity was determined according to the method of Parry et al. [36]. Rubisco activity was measured by rapidly grinding frozen leaf disks in liquid nitrogen to a fine powder, then followed by 2 mL of ice-cold extraction buffer that contained 50 mM Bicine, pH 8.0, 20 mM magnesium chloride ($MgCl_2$), 2 mM phenylmetylsulfonyl fluoride, 50 mM 2-mercaptoethanol, and 30 mg polyvinylpolypyrrolidone. The extract was centrifuged for at 10,000× g at 4 °C.

The activities of SPS and SS were determined according to Pavlinova et al. [37]. An incubation mixture (0.2 mL), comprising 8 mM UDPG, 8 mM fructose-6-phosphate, 15 mM $MgCl_2$, 40 mM Hepes NaOH (pH 7.5), and 0.1 mL of the enzyme preparation, was used to measure SPS activity. No UDPG was present in the control sample. The reaction mixture was incubated for ten minutes at 30 °C. To halt the reaction, the tubes were submerged in a bath of boiling water for 1 min. Once the sample had cooled, 1 mL of 0.5 N NaOH was added, and the volume was adjusted to 1 mL. To break down the extra fructose-6 phosphate that was not used in the reaction, the sample was then placed in a boiling water bath for ten minutes. Based on the amount of sucrose produced (in the resorcin reaction), enzyme activity was calculated. In the SS activity synthesis assays, 8 mM fructose was added to the incubation medium in place of fructose-6-phosphate. When resorcin was added, the amount of sucrose produced was measured.

2.4. Statistical Analysis

Analysis of variance (ANOVA) was performed with SPSS 19.0. Prior to ANOVA, data were examined for normality with the Shapiro–Wilk test and for homogeneity of variances (homoscedasticity) with Levene's test. When either assumption was violated, data were log-transformed and re-checked; if assumptions still failed, the non-parametric Kruskal–Wallis test was used instead of ANOVA. Additivity of main effects was verified by the Tukey test for non-additivity. Regression analysis was conducted in SigmaPlot 14.0 (Systat Software Inc., San Jose, CA, USA). Treatment means were compared with the least significant difference (LSD) test at $p < 0.05$ only after ANOVA assumptions were satisfied.

3. Results

3.1. Stem Agronomic Traits and Lodging Resistance

The application of PGRts significantly reduced the plant height of wheat. In YC, the plant heights treated with CCC and S_{3307} were significantly reduced by 9.05% (7.13 cm) and 4.4% (3.4 cm), respectively, compared with CK. In YZ, compared with CK, the plant height treated with CCC and S_{3307} was significantly reduced by 6.3% (4.8 cm) and 3.5% (2.7 cm), respectively. In addition, the plant height treated with CCC was significantly lower than that treated with S_{3307}. The stem diameter treated with CCC was significantly greater than that of CK, with increases of 8.1% (0.4 mm) and 11.4% (0.5 mm) observed in YC and YZ, respectively. The stem diameter treated with S_{3307} was significantly larger than that of CK, increasing by 5.5% (0.3 mm) and 9.4% (0.4 mm) in YC and YZ, respectively (Table 2).

Table 2. Effects of CCC and S_{3307} on plant height and internode characteristics of wheat.

Experimental Site	Treatment	PH (cm)	SD (mm)	1st IL (cm)	2nd IL (cm)	3rd IL (cm)	4th IL (cm)	5th IL (cm)
YC	CCC	71.7 c	5.5 a	6.8 a	12.3 b	19.1 b	14.6 b	10.5 b
	S_{3307}	75.4 b	5.3 a	7.0 a	13.5 a	20.0 a	14.6 b	10.9 b
	CK	78.8 a	5.1 b	7.0 a	143 a	20.7 a	15.7 a	12.4 a
YZ	CCC	71.4 c	5.1 a	6.4 b	13.5 b	19.2 b	15.4 b	8.7 a
	S_{3307}	73.5 b	5.0 a	5.9 c	13.1 c	20.3 a	16.5 a	9.2 a
	CK	76.2 a	4.6 b	7.3 a	15.0 a	19.8 ab	16.0 ab	9.9 a

Average value of three growth stages; Abbreviations: IL: internode length, PH: plant height, and SD: stem diameter. Values within a column followed by different letters are significantly different at $p = 0.05$.

After the application of CCC, the second internode could be shortened in both YC and YZ, with a significant reduction of 14.0% and 9.6%, respectively, compared to CK. In YC, the length of the first internode under CCC treatment was shortened by 2.7% compared with CK, and the lengths of the third, fourth, and fifth internodes were significantly shortened by 8.0%, 7.1%, and 15.1%, respectively, compared with CK. In YZ, compared with CK, the application of CCC significantly reduced the length of the first internode by 19.78%, and the third, fourth, and fifth internodes were 3.0%, 3.4%, and 11.5% shorter than CK, respectively (Table 2). After the application of S_{3307}, the second internode could be shortened in both YC and YZ, with a significant reduction of 5.6% and 12.7%, respectively, compared to CK. In YC, the S_{3307} treatment significantly reduced the lengths of the fourth and fifth internodes by 6.9% and 12.1%, respectively, compared to CK. The application of S_{3307} in YZ significantly reduced the lengths of the first and second internodes, by 18.5% and 12.7%, respectively, compared to CK (Table 2). The application of S_{3307} in both places had no significant impact on the length of the third internode compared with CK.

Application of CCC or S_{3307} increased stem BS and decreased CLI, with S_{3307} having a more significant effect on lodging resistance (Figure 2). The BS treated with CCC increased significantly by 39.9% (YC) and 43.1% (YZ) compared with CK, while the CLI decreased significantly by 37.2% (YC) and 21.7% (YZ) compared with CK. In contrast, the BS treated

with S_{3307} was significantly higher than that of CK by 67.0% (YC) and 45.3% (YZ), and the CLI was significantly reduced by 49.3% (YC) and 31.4% (YZ).

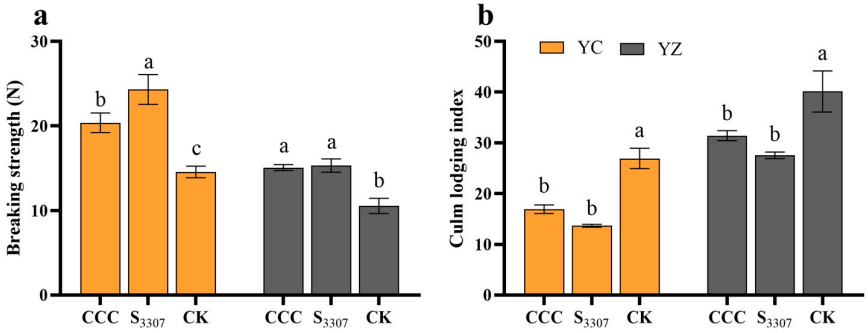


Figure 2. Effect of CCC and S_{3307} on breaking strength (**a**) and culm lodging index(**b**) of wheat. Values within a column followed by different letters are significantly different at $p = 0.05$.

As shown in Table 3, no lodging occurred in wheat treated with CCC or S_{3307} at the two test sites, while CK showed varying degrees of lodging. Among them, in YC, CK treatment experienced level 3 lodging during the anthesis period, with a lodging rate of 7.1%. In YZ, the CK treatment during the filling period experienced level 2 of lodging, with a lodging rate of 15.6%. The average lodging rate was reduced by 11.4% through PGRts treatment.

Table 3. Effect of CCC and S_{3307} on lodging stage, lodging degree, and lodging rate (%) of wheat.

Experiment Site	Treatment	Lodging Stage	Lodging Level	Lodging Rate (%)
YC	CCC	-	0 b	0 b
	S_{3307}	-	0 b	0 b
	CK	Filling stage	3 a	7.1 a
YZ	CCC	-	0 b	0 b
	S_{3307}	-	0 b	0 b
	CK	Anthesis stage	2 a	15.6 a

Values within a column followed by different letters are significantly different at $p = 0.05$.

3.2. Yield

As shown in Table 4, the number of spikes treated with CCC in YC and YZ increased by 5.8% and 3.7%, respectively, compared with CK, while the number of grains per spike decreased by 4.51% and 7.54%, respectively; the 1000-grain weight increased by 6.5% and 8.6%, respectively; and the yield increased by 6.0% and 7.0%, respectively. The number of spikes treated with S_{3307} increased by 10.7% and 11.3%, respectively, in YC and YZ compared with CK, while there was no significant difference in the number of grains per spike and 1000-grain weight, and the yields increased by 5.9% and 6.2%, respectively. In contrast, the number of spikes of S_{3307} increased by 4.6% (YC) and 7.4% (YZ), respectively, compared with CCC, the number of grains per spike increased by 4.3% (YC) and 2.0% (YZ), respectively; the 1000-grain weight decreased by 8.0% (YC) and 8.8% (YZ), respectively; and the yield decreased by 0.1% (YC) and 0.7% (YZ), respectively. The above results indicate that CCC and S_{3307} have different regulatory pathways for yield. Although both regulators can increase the number of spikes and reduce the number of grains per spike, CCC may increase yield by achieving a higher 1000-grain weight, while S_{3307} often achieves high yield by obtaining a larger population number of spikes to compensate for the reduction in the number of grains per spike.

Table 4. Effect of CCC and S_{3307} on wheat yield.

Experimental Site	Treatments	Spikes per hectare ($\times 10^4$)	Grain Number Per Spike	1000-Grain Weight (g)	Crop Yield (kg ha^{-1})
YC	CCC	453.3 b	41.5 b	50.6 a	7693.2 a
	S_{3307}	474.3 a	43.3 a	46.5 b	7682.8 a
	CK	428.3 c	43.4 a	47.5 b	7258.4 b
YZ	CCC	353.1 b	38.5 b	50.4 a	7299.4 a
	S_{3307}	379.2 a	39.3 ab	46.0 b	7247.5 a
	CK	340.6 b	41.7 a	46.4 b	6824.5 b

Values within a column followed by different letters are significantly different at $p = 0.05$.

3.3. Dry Matter Accumulation Pre-Anthesis and Post-Anthesis

Compared with CK, CCC treatment in both experimental fields could significantly increase the dry matter accumulation of wheat after anthesis, and the S_{3307} treatment significantly increased the dry matter accumulation of wheat before anthesis (Figure 3). Among the pre-anthesis dry matter treated with CCC, the proportion of spikes was the highest, and that of leaves was the lowest. Among the post-anthesis dry matter treated with CCC, the proportion of spikes was the lowest, and that of stems was the highest. Among the pre-anthesis dry matter treated with S_{3307}, the proportion of spikes was the lowest, and that of stems was the highest. In the post-anthesis dry matter treated with S_{3307}, the proportion of spikes and leaves was the highest, while that of stems was the lowest (Figure 3). It is indicated that spraying PGRts can increase the accumulation of dry matter in wheat. Meanwhile, CCC can promote the growth and development of pre-anthesis spikes and post-anthesis stems, and S_{3307} can also promote the growth and development of pre-anthesis stems and post-anthesis spikes.

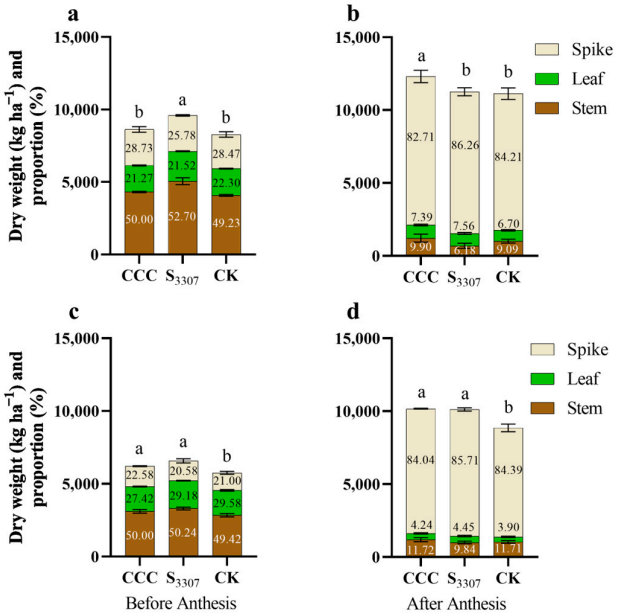


Figure 3. Effects of CCC and S_{3307} on dry weight of wheat in YC (**a**,**b**) and YZ (**c**,**d**) ((**a**,**c**) represents the accumulation of dry matter from sowing to anthesis stage, which is referred to as pre-anthesis; (**b**,**d**) represent the accumulation of dry matter from anthesis stage to maturity stage, which is referred to as post-anthesis). Values within a column followed by different letters are significantly different at $p = 0.05$.

As shown in Figure 4, after the application of PGRts, the dry weight of the first and second internodes of wheat during the filling period increased to varying degrees, while that of the fourth and fifth internodes decreased. The CCC treatment in YC and YZ significantly increased the dry weight of the second internode compared with CK, by

7.9% and 18.9%, respectively. The dry weight of the third internode was not significantly different from that of CK. The dry weight of the fourth internode decreased significantly by 10.2% and 16.8%, respectively, and that of the fifth internode decreased significantly by 25.5% and 15.0%, respectively. In addition, in YC, CCC treatment significantly increased the dry weight of the first internode by 9.8% compared with CK. In YZ, the dry weight of the first internode under CCC treatment was not significantly different from CK, increasing by 3.1% compared with CK. The S_{3307} treatment in YC and YZ significantly increased the dry weight of the first internode compared with CK, increasing by 22.1% and 18.6%, respectively. The dry weight of the third internode showed no significant difference from CK, while the dry weight of the fourth internode decreased significantly by 18.9% and 14.5%, respectively. Furthermore, in YC, the dry weight of the second internode was not significantly different from that of CK, increasing by 4.6% compared with CK. The dry weight of the fifth internode was significantly reduced by 40.5% compared with CK. In YZ, S_{3307} treatment significantly increased the second internode dry weight by 17.1% compared to CK, while the fifth internode dry weight showed no significant difference from CK, decreasing by 6.0% compared to CK.

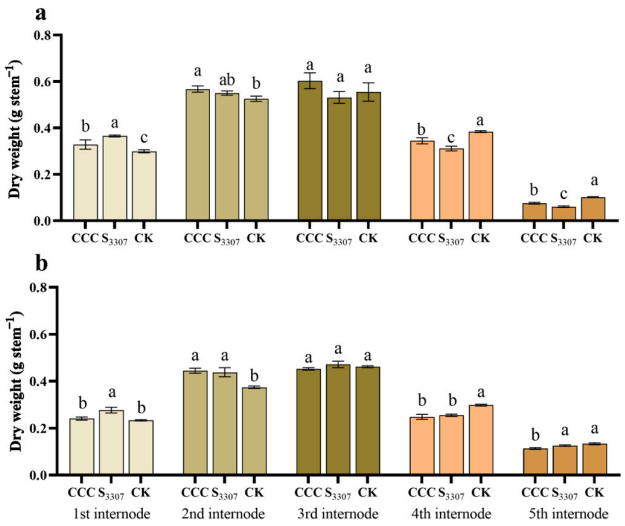


Figure 4. Effects of CCC and S_{3307} on the internode dry weight of wheat at filling stage in YC (**a**) and YZ (**b**). Values within a column followed by different letters are significantly different at $p = 0.05$.

3.4. LAI, Effective Leaf Area and SPAD

The results of the experiments at the two sites indicated that spraying PGRts could increase the LAI of wheat at the heading stage. Among them, the LAI of the S_{3307} treatment was significantly higher than that of CK, increasing by 6.1% (YC) and 13.4% (YZ), respectively. There was no significant difference between the CCC treatment and CK, which increased by 1.8% (YC) and 9.4% (YZ), respectively (Figure 5). The effective leaf area of individual plants during the heading stage treated with CCC was not significantly different from that treated with CK. S_{3307} was significantly higher than CK, increasing by 5.2% (YC) and 7.5% (YZ), respectively (Figure 5). In conclusion, the LAI after CCC treatment was slightly higher than that of CK, and the change in the effective leaf area of individual plants was not significant. Spraying S_{3307} significantly increased the LAI and the effective leaf area per plant, thereby enhancing the photosynthetic area of wheat.

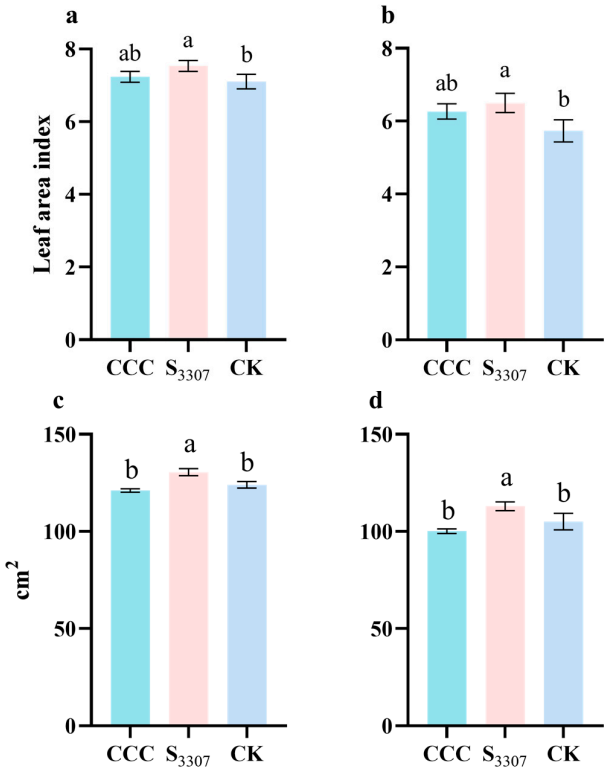


Figure 5. Effect of CCC and S_{3307} on leaf area index and efficient leaf area in heading stage in YC (**a**,**c**) and YZ (**b**,**d**). Values within a column followed by different letters are significantly different at $p = 0.05$.

The SPAD values of flag leaves at the heading stage and 20 days after anthesis after CCC treatment were significantly higher than those of CK. Among them, the heading stage was 12.1% (YC) and 20.8% (YZ) higher than CK, respectively, and the values 20 days after anthesis were 4.0% (YC) and 6.6% (YZ) higher than CK, respectively (Figure 6). The SPAD values of flag leaves treated with S_{3307} were significantly increased by 5.5% (YC) and 7.8% (YZ), respectively, compared with CK at the heading stage, and by 3.8% (YC) and 3.2% (YZ), respectively, 20 days after anthesis (Figure 6). These results indicate that the application of both types of PGRts can increase the SPAD values of flag leaves during the heading and filling stages, thereby enhancing photosynthetic production capacity.

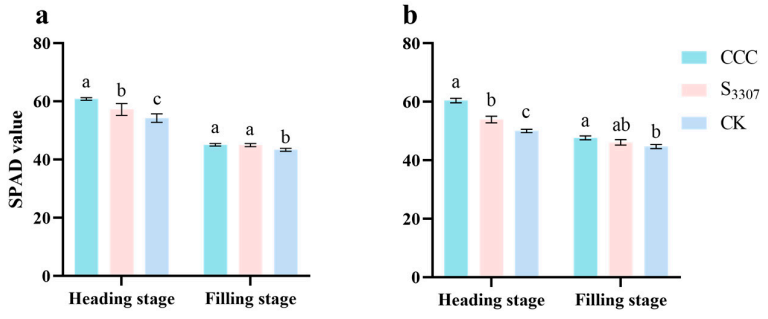


Figure 6. Effects of CCC and S_{3307} on SPAD values in different stages in YC (**a**) and YZ (**b**). Values within a column followed by different letters are significantly different at $p = 0.05$.

3.5. Stem Plant Hormones

As shown in Figure 7, seven days after spraying CCC (jointing stage), the contents of GA and ZR in wheat stems were significantly reduced by 12.2% and 24.5%, respectively, compared with CK, while the content of IAA was significantly increased by 7.6%, and there was no significant difference in the content of BR compared with CK. Seven days

after the application of S_{3307}, the contents of GA, ZR, and BR were significantly reduced by 23.0%, 28.1%, and 22.5%, respectively, compared with CK, while the content of IAA was significantly increased by 20.4%. In comparison, the reduction in GA and BR contents of stems by S_{3307} treatment was significantly greater than those by CCC treatment, while the increase in IAA content was higher than that by CCC treatment.

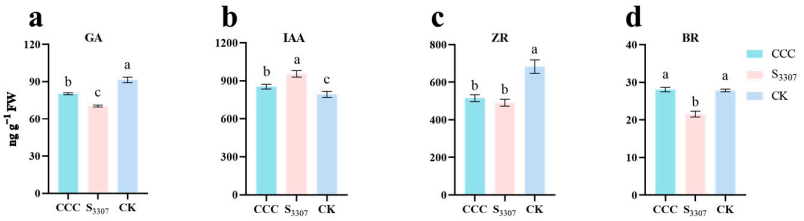


Figure 7. Effect of CCC and S_{3307} on plant hormones of the wheat jointing stage. (**a**) GA; (**b**) IAA; (**c**) ZR; (**d**) BR. Values within a column followed by different letters are significantly different at $p = 0.05$.

3.6. Stem Lignin-Related Enzymes

Seven days after the application of CCC, the activities of 4CL, TAL, and CAD were significantly reduced by 19.1%, 2.8%, and 10.4%, respectively, compared with CK. The activities of these enzymes recovered at the heading stage and were significantly higher than those of CK, increasing by 18.1%, 30.6%, and 21.7%, respectively. Seven days after the application of CCC, the PAL activity was significantly increased by 80.1% compared with CK, while the PAL activity at the heading stage was significantly decreased by 29.1% compared with CK. Seven days after the application of S_{3307}, the activities of 4CL, PAL, TAL, and CAD were significantly higher than those of CK by 26.1%, 36.4%, 24.5%, and 8.3%, respectively. At the heading stage, the activities of 4CL, TAL, and CAD were still significantly higher than those of CK by 38.2%, 33.9%, and 26.9%, respectively, while there was no significant difference in PAL activity compared with CK (Figure 8). Except that the PAL activity at seven days after application of CCC was higher than that of S_{3307}, the activities of other lignin-related enzymes in S_{3307} treatment were significantly higher than those in the CCC treatment.

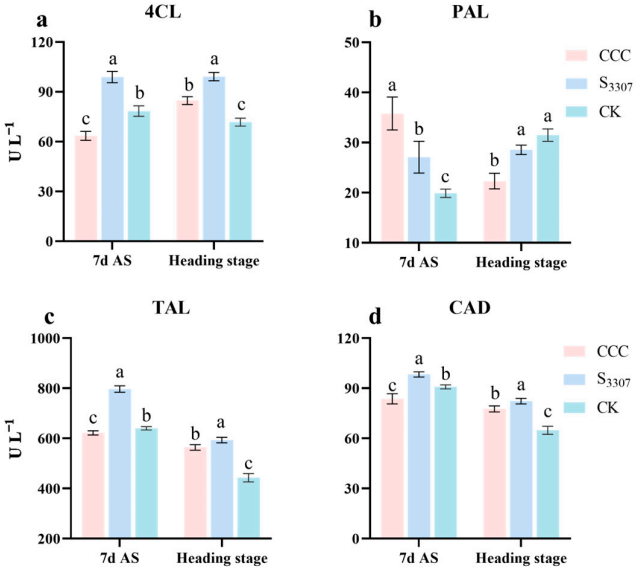


Figure 8. Effect of CCC and S_{3307} on lignin-related enzymes of wheat. (**a**) 4CL; (**b**) PAL; (**c**) TAL; (**d**) CAD. Values within a column followed by different letters are significantly different at $p = 0.05$.

3.7. Leaf Carbon Metabolism-Related Enzymes

As can be seen from Figure 9, spraying CCC or S_{3307} can significantly increase the activity of carbon metabolism-related enzymes in leaves during both the heading stage and filling stages. The activity of carbon metabolism-related enzymes treated with CK increased with the growth period. The activities of Rubisco and SS in CCC treatment were the highest at the heading stage, significantly higher than those under S_{3307} treatment, increasing by 8.9% and 21.9%, respectively. They were significantly higher than CK treatment, increasing by 30.41% and 43.84%, respectively. At the heading stage, SPS activity in the CCC treatment was significantly 60.5% higher than that of CK, but the difference was not significant compared with S_{3307}. The activities of Rubisco, SS, and SPS treated with S_{3307} were the highest during the filling stage, which were significantly higher than those treated with CCC (25.1%, 12.1%, and 19.0%, respectively), and they were significantly higher than CK by 53.3%, 46.4%, and 41.1%, respectively. Compared with the two types of PGRts, the CCC treatment significantly increased the activity of enzymes related to leaf carbon metabolism during the heading stage, whereas the S_{3307} treatment significantly increased the activity of enzymes related to leaf carbon metabolism during the filling stage, which was consistent with the trend of dry matter accumulation in the spike before and after anthesis.

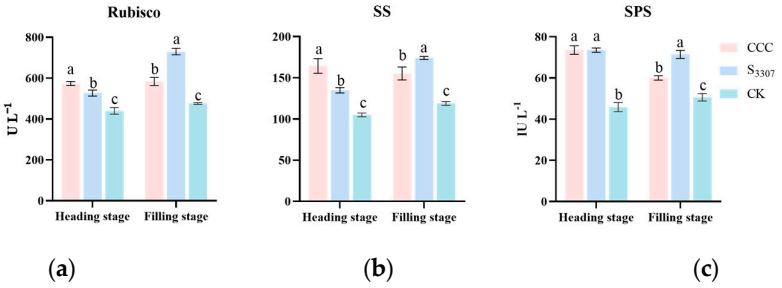


Figure 9. Effect of CCC and S_{3307} on carbon metabolism-related enzymes of wheat. (**a**) Rubisco; (**b**) SS; (**c**) SPS. Values within a column followed by different letters are significantly different at $p = 0.05$.

3.8. Correlation Between Lodging Resistance Indexes and Correlation Between Yield and Material Production

As shown in Figure 10, almost all stem and spike indicators during the filling period are significantly correlated with CLI. Among them, BS, stem diameter, the dry weights of the first, second, third, and fourth internodes, and the activities of TAL and CAD enzymes at the heading stage were significantly negatively correlated with CLI, while the lengths of the second and fourth internodes, the dry weight of the fifth internode, spike dry weight, and the contents of GA, IAA, and ZR were significantly positively correlated with CLI. Interestingly, there is no significant correlation between plant height and CLI.

The yield was significantly positively correlated with the SPAD value, dry leaf weight, and LAI at the heading stage, and significantly positively correlated with the SPAD value, dry leaf weight at the filling stage, and the activities of Rubisco enzyme, SPS enzyme, and SS enzyme. However, the correlation with the effective leaf area at both stages was not significant. The photosynthetic indicators of the two growth stages basically showed a significant positive correlation (Figure 11).

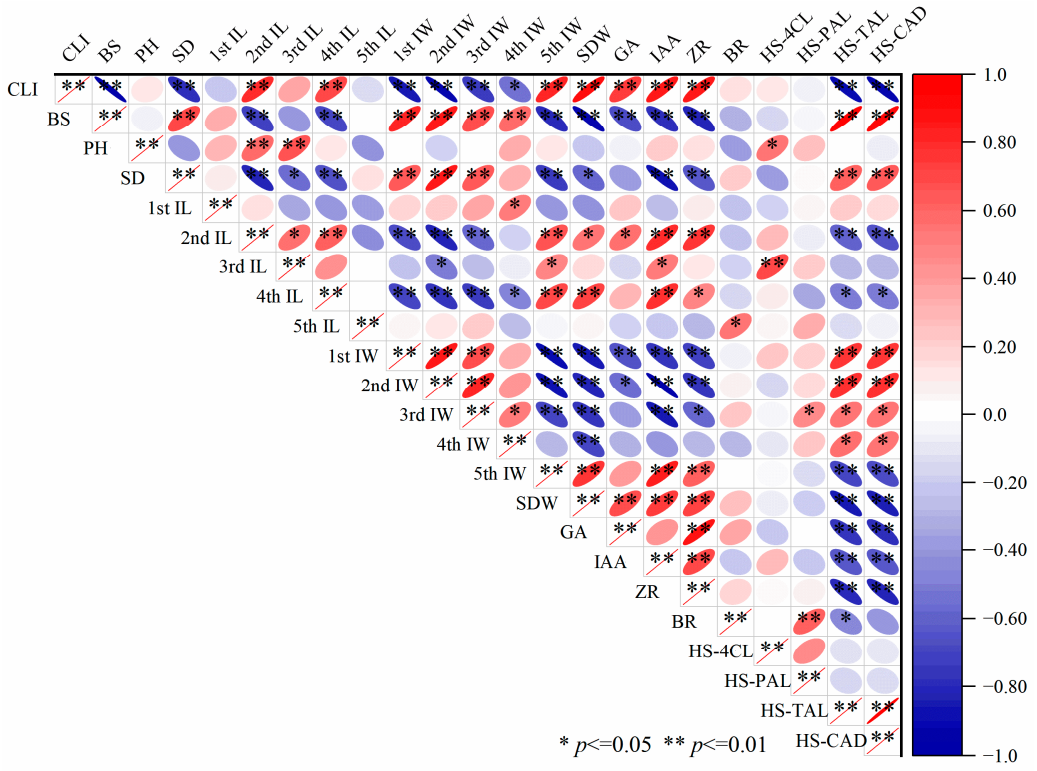


Figure 10. Relationship between stalk indexes, spike indexes, and culm lodging indexes in wheat filling stage. Abbreviations: IW: internode dry weight and SDW: spike dry weight. Significance of correlation: * $p \leq 0.05$; ** $p \leq 0.01$.

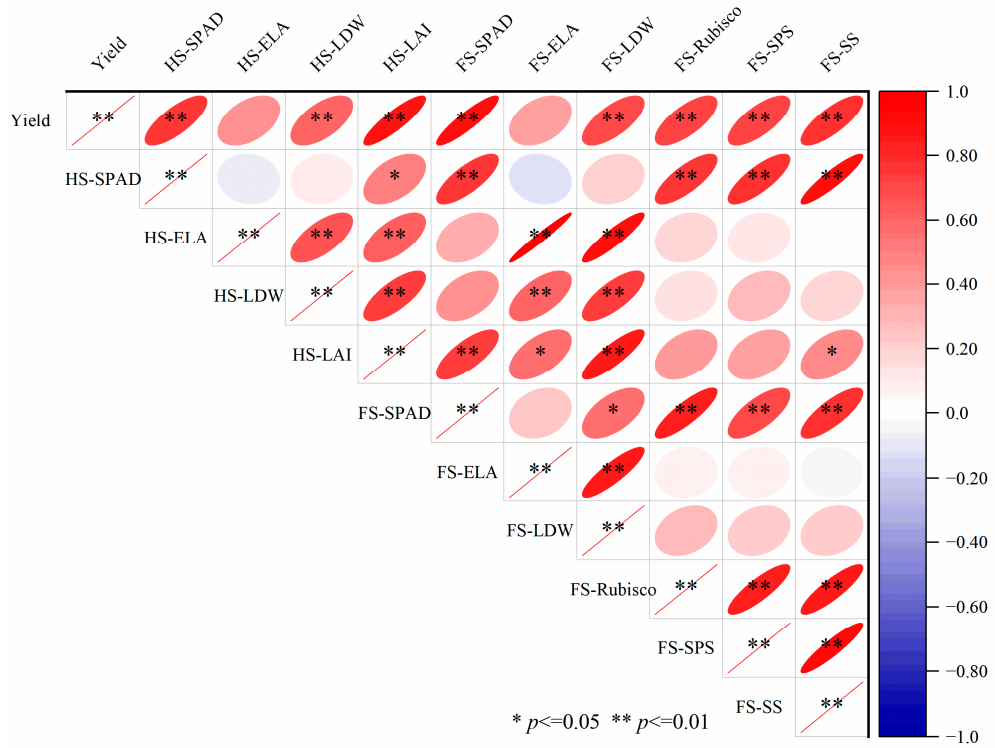


Figure 11. Relationship between photosynthetic indexes and yield in heading and filling stages. Abbreviations: ELA: efficient leaf area and LDW: leaf dry weight. Significance of correlation: * $p \leq 0.05$; ** $p \leq 0.01$.

4. Discussion

4.1. Effects and Differences in CCC and S_{3307} on the Stem Morphology and Lodging Resistance

The application of PGRts, such as paclobutrazol, S_{3307}, CCC, etc., to improve internode morphology and enhance stem strength has been widely used in wheat lodging resistance [30,38,39]. It is generally believed that the second internode at the base is the main site where wheat plants fall over due to stress. Therefore, most anti-lodging measures mainly focus on improving the second internode. Previous studies suggest that PGRts such as CCC or S_{3307} can both reduce the length of the second internode and increase stem thickness to improve plant type and enhance lodging resistance, but there are differences in their effects [3,11,15,16,39]. In this study, CCC was superior to S_{3307} in terms of plant height reduction and inhibition of internode elongation, while S_{3307} was better than CCC in improving stem strength. The plant height of wheat treated with CCC or S_{3307} was significantly reduced by 6.3–9.1% and 3.5–4.4%, respectively, compared with CK, and the stem diameter was significantly increased by 8.1–11.4% and 5.5–9.4%, respectively, compared with CK. The length of the second internode was significantly shortened by 9.6–11.0% and 5.6–12.7%, respectively, compared with CK (Table 2). These morphological improvements are conducive to increasing stem strength and reducing the CGH, enabling wheat to resist stronger lodging stress, and the average lodging rate of wheat decreased by 11.4% (Table 3). Meanwhile, the BS of wheat stems treated with CCC or S_{3307} increased significantly by 39.9–43.1% and 45.3–67.0%, respectively, compared with CK, while the CLI decreased significantly by 21.7–37.2% and 31.4–49.3%, respectively, compared with CK (Figure 2). It can be seen that S_{3307} has a better effect on enhancing stem strength and reducing lodging index. There is no significant correlation between plant height and CLI (Figure 10). Some studies have shown that plant height is a key factor affecting lodging because it affects the bending stress of the stem [40,41]. On the contrary, other studies have shown that plant height is not the main factor affecting lodging. Stem wall thickness and stem thickness are traits that affect lodging sensitivity more significantly [42,43]. The inconsistent findings regarding plant height's role in lodging highlight that lodging resistance is a complex trait determined by the interplay of multiple morphological and anatomical factors, rather than being governed by a single parameter. In our study, the superior lodging resistance achieved by S_{3307}, despite its lesser effect on height reduction compared to CCC, underscores that enhancements in stem strength, driven by anatomical improvements, can be more critical than merely shortening the plant.

PGRts mainly achieve stem elongation inhibition by inhibiting the GA synthesis pathway. GA is involved in physiological processes such as stem elongation and young spike development [44,45]. Mutations in key genes in GA biosynthesis or signaling pathways can alter changes such as plant height and spike traits [46]. The results of this study indicate that spraying CCC or S_{3307} at the seven-leaf stage can significantly reduce the GA content in the stems of wheat during the jointing stage (Figure 7). For wheat, the differentiation of young panicle is synchronized with the height of stem elongation. The reduction in GA in the stems after PGRts treatment undoubtedly has a negative impact on young spike development, thereby leading to a decrease in the number of grains per spike (Table 4). The reduction in GA and BR contents of stems by S_{3307} treatment was significantly greater than that by CCC treatment, while the increase in IAA content was higher than that by CCC treatment (Figure 7). This is because CCC and S_{3307} mainly inhibit GA biosynthesis to delay wheat growth and enhance lodging resistance, but their specific mechanisms are different. CCC inhibits the cyclization step of GA synthesis by targeting *ent*-Kaurene synthesis [47], while S_{3307} inhibits the oxidation step of GA synthesis by blocking the synthesis of P450, ultimately preventing the conversion of *ent*-Kaurene to *ent*-Kaurenoic acid [48]. Since the synthesis of BR also requires P450 [49,50], spraying S_{3307} will also

cause a decrease in the amount of BR synthesis in wheat stems. The content of IAA in the stems treated with S_{3307} increased significantly, which could promote the growth and differentiation of stems, corresponding to a greater number of spikes and higher accumulation of dry matter in the stems before anthesis (Figure 3, Table 4). The application of PGRts undoubtedly has adverse effects on the development of young spikes and the final number of grains per spike. However, the differences in the number of grains per spike between CCC and S_{3307} are significant, which may be the result of the combined regulation of endogenous hormones such as IAA, GA, and BR. Studies have shown that PGRts can also stimulate lignin synthesis to increase stem thickness and strength [16,38,51,52]. PAL, TAL, 4CL, and CAD jointly affect the synthesis of H-lignin, G-lignin, and S-lignin [53]. Studies have shown that seven days after the application of CCC, PAL activity in stems increased, while the activities of TAL, 4CL, and CAD decreased. The activities of TAL, 4CL, and CAD then increased during the heading stage, promoting lignin synthesis. After the application of S_{3307}, the activities of PAL, TAL, 4CL, and CAD all increased at both seven days after application and at the heading stage (Figure 8). Relevant analysis indicated that the activities of lignin-related enzymes (PAL, TAL, 4CL, and CAD) were positively correlated with lignin content [16,30,51,52]. This indicates that the higher the activity of these enzymes, the more lignin accumulates, increasing stem fullness and dry weight, and thus increasing stem strength [53]. Our results indicated that the activities of TAL and CAD were significantly negatively correlated with CLI (Figure 10). Similarly, Wang et al. [16] and Kamran et al. [51,52] also found that the activities of lignin-related enzymes (PAL, 4CL, and CAD) were negatively correlated with CLI. This might explain why the lodging resistance treated with S_{3307} is better than that treated with CCC. The distinct hormonal profiles induced by CCC and S_{3307} provide a physiological basis for their differential effects on agronomic traits. The more substantial reduction in GA and BR by S_{3307}, coupled with a greater increase in IAA, likely redirects assimilates towards strengthening stem structures and promoting tillering, partially compensating for the negative impact on grain number per spike through an increase in effective panicles.

4.2. Effects of CCC and S_{3307} on Wheat Yield and the Differences in Yield-Increase Approaches

In addition to reducing the risk of lodging, the use of PGRts such as CCC or S_{3307} can significantly increase wheat yield [15,24,30,54]. Studies have shown that the increase in wheat yield after spraying CCC is mainly attributed to the increase in the number of grains per spike [55] and the average grain weight [56]. Appropriate application of S_{3307} can significantly increase the 1000-grain weight of wheat by 1.3 g and the yield by 11.2% [15]. The research results of Zhang et al. [3] indicated that S_{3307} could increase the number of tillers per plant but significantly reduce the number of small flowers per panicle (8.9 less than CK), thereby lowering the number of grains per spike. Our research results also indicate that the application of CCC or S_{3307} significantly increases wheat yield (Table 4), but there are differences in the ways they increase yield. The application of CCC can increase the number of spikes and 1000-grain weight but reduces the number of grains per spike. S_{3307} mainly increases yield by increasing the number of spikes, and the differences in 1000-grain weight and the number of grains per spike compared with CK are not significant (Table 4).

Existing studies have shown that flag leaf area, SPAD value, and net photosynthetic rate are significantly positively correlated with yield [20], and thereby affect total biomass accumulation [18,19]. Furthermore, it has been determined that the SPAD value at the heading stage can be used as a reliable predictor of the final wheat yield [57]. Our research results show that wheat yield is significantly positively correlated with the SPAD value, leaf dry weight, and LAI at the heading stage, as well as the SPAD value and leaf dry

weight at the filling stage (Figure 11). Studies have shown that the application of CCC can significantly increase the surface area of wheat flag leaves and delay leaf senescence [56], but CCC and S_{3307} may also reduce the total surface area of leaves [58] or the area of flag leaves [3]. This study found that both CCC and S_{3307} treatments could significantly increase the SPAD value and LAI of wheat at the heading stage (Figures 5 and 6), while the effective leaf area of wheat treated with CCC was significantly smaller than that treated with S_{3307} and slightly lower than that of CK (Figure 5). Stahli et al. [53] also reported that CCC increased the chlorophyll content in the flag leaves of the main stem, possibly due to the enhancement of the protein–chlorophyll complex, the increase in chlorophyll content, and the decrease in the activity of chlorophyll-degrading enzymes. The pre-anthesis dry matter accumulation and total dry matter accumulation of CCC and S_{3307} were significantly higher than those of CK, and the proportion of pre-anthesis stem dry weight was significantly higher than that of CK, among which the proportion of post-anthesis spike dry weight of S_{3307} was the highest (Figure 3). It can be inferred that after S_{3307} treatment, more pre-anthesis photosynthetic products were allocated to the growth and development of leaves and stems, while the significantly increased LAI and effective leaf area promoted the accumulation and output of post-anthesis photosynthesis, thereby promoting the weight of spikes (Figure 3). In addition, spraying CCC or S_{3307} can significantly enhance the activities of three key photosynthetic carbon metabolism-related enzymes, namely Rubisco, SS, and SPS, during the heading and filling stages (Figure 9), and the activities of these three carbon metabolism-related enzymes during the filling stage are significantly positively correlated with the yield (Figure 11). In comparison, S_{3307} maintains the photosynthetic physiological activity of wheat leaves for a longer period because the carbon metabolism-related enzyme activity of S_{3307} is higher during the filling stage. In conclusion, the application of PGRts can increase the LAI and SPAD values during the heading stage, enhance the activity of carbon metabolism-related enzymes during the filling stage to promote dry matter accumulation, and CCC can further increase the SPAD value of flag leaves and delay leaf senescence to maintain the active period of photosynthetic organs. S_{3307} mainly increases production through higher LAI, effective leaf area, and higher activity of carbon metabolism-related enzymes.

5. Conclusions

The application of CCC or S_{3307} can effectively reduce the plant height and enhance lodging resistance. CCC is more effective than S_{3307} in reducing plant height and inhibiting internode elongation, while S_{3307} is better than CCC in improving stem strength. The reduction in GA and BR content in the stem by S_{3307} is significantly greater than that by CCC, and the increase in IAA content is higher than that by CCC. The activities of lignin-related enzymes in the S_{3307} were consistently higher than those in the CK. The application of CCC or S_{3307} can increase the LAI and SPAD value at the heading stage, enhance the activity of carbon metabolism-related enzymes, and thereby increase yield. CCC can more effectively increase the SPAD value of flag leaves after flowering, increase the number of spikes and 1000-grain weight; in contrast, S_{3307} mainly increases yield through higher LAI, more effective leaf area, and a greater number of spikes. Strategically, CCC is the preferred option when the primary risk is excessive stature, whereas S_{3307} is the better agronomic choice where stem strength and photosynthetically active leaf area are limiting factors. Therefore, the optimal PGR should be selected based on local environmental conditions and the growth and development characteristics of wheat.

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Zhang): Investigation, Data Curation, and Conceptualization. Z.X.: Data Curation, Resources, and Conceptualization. L.F.: Investigation, Resources, and Conceptualization. B.L.: Writing—Review and Editing, Resources, and Software. H.W.: Writing—Review and Editing, Resources, and Conceptualization. H.Z. (Hongcheng Zhang): Writing—Review and Editing, Writing—Original Draft, Supervision, Resources, and Conceptualization. G.L.: Writing—Original Draft, Writing—Review and Editing, Formal Analysis, Resources, and Conceptualization. All authors have read and agreed to the published version of the manuscript.

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References

1. Yu, Y.; Yang, X.; Guan, Z.; Zhang, Q.; Li, X.; Gul, C.; Xia, X. The impacts of temperature averages, variabilities and extremes on China's winter wheat yield and its changing rate. *Environ. Res. Commun.* **2023**, *5*, 071002. [CrossRef]
2. National Bureau of Statistics of China. Available online: https://www.stats.gov.cn/sj/ndsj/ (accessed on 11 March 2025).
3. Zhang, G.P.; Chen, J.X.; Bull, D.A. The effects of timing of N application and plant growth regulators on morphogenesis and yield formation in wheat. *Plant Growth Regul.* **2001**, *35*, 239–245. [CrossRef]
4. Acreche, M.M.; Slafer, G.A. Lodging yield penalties as affected by breeding in Mediterranean wheats. *Field Crops Res.* **2011**, *122*, 40–48. [CrossRef]
5. Berry, P.M.; Spink, J. Predicting yield losses caused by lodging in wheat. *Field Crops Res.* **2012**, *137*, 19–26. [CrossRef]
6. Jin, Z.; Mu, Y.; Li, Y.; Nie, L. Effect of different rice planting methods on the water, energy and carbon footprints of subsequent wheat. *Front. Sustain. Food Syst.* **2023**, *7*, 1173916. [CrossRef]
7. Berry, P.M. Lodging Resistance in Cereals. In *Crop Science*; Encyclopedia of sustainability science and technology series; Springer: Berlin/Heidelberg, Germany, 2019. [CrossRef]
8. Mangin, A.; Brule-Babel, A.; Flaten, D.; Wiersma, J.; Lawley, Y. Canopy management: The balance between lodging risk and nitrogen use for spring wheat production in the Canadian Prairies. *Can. J. Plant Sci.* **2022**, *102*, 984–1000. [CrossRef]
9. Li, H.M.; Cui, G.G.; Li, G.Y.; Lu, H.; Wei, H.Y.; Zhang, H.P.; Zhang, H.C. Assessing the efficacy and residual impact of plant growth retardants on crop lodging and overgrowth: A review. *Eur. J. Agron.* **2024**, *159*, 127276. [CrossRef]
10. Zheng, R.; Yan, W.; Xia, Y. Highly water-dispersible hydroxyl functionalized covalent organic frameworks as matrix for enhanced MALDI-TOF MS identification and quantification of quaternary ammonium salts in water and fruits. *Anal. Chim. Acta* **2022**, *1227*, 340269. [CrossRef]
11. Khan, H.; Parkash, O.; Mamrutha, H.M.; Bairwa, R.K.; Mishra, C.N.; Kumar, R.; Jasrotia, P.; Kumar, S.; Krishnappa, G.; Ahlawat, O.P.; et al. Foliar application of chlormequat chloride improves lodging resistance and grain yield in bread wheat. *Plant Physiol. Rep.* **2025**, *30*, 199–205. [CrossRef]
12. Gebre, E.; Schluter, U.; Hedden, P.; Kunert, K. Gibberellin biosynthesis inhibitors help control plant height for improving lodging resistance in *E. tef (Eragrostis tef)*. *J. Crop Improv.* **2012**, *26*, 375–388. [CrossRef]
13. Miranzadeh, H.; Emam, Y.; Seyyed, H.; Zare, S. Productivity and radiation use efficiency of four dryland wheat cultivars under different levels of nitrogen and chlormequat chloride. *J. Agric. Sci. Technol.* **2011**, *13*, 339–351.
14. Yang, M.; Chen, S.; Chao, K.; Ji, C.; Shi, Y. Effects of nano silicon fertilizer on the lodging resistance characteristics of wheat basal second stem node. *BMC Plant Biol.* **2024**, *24*, 54. [CrossRef] [PubMed]
15. Ahmad, I.; Kamran, M.; Guo, Z.; Meng, X.; Ali, S.; Zhang, P.; Liu, T.; Cai, T.; Han, Q. Effects of uniconazole or ethephon foliar application on culm mechanical strength and lignin metabolism, and their relationship with lodging resistance in winter wheat. *Crop Pasture Sci.* **2020**, *71*, 12–22. [CrossRef]
16. Wang, C.; Hu, D.; Liu, X.; She, H.; Ruan, R.; Yang, H.; Yi, Z.; Wu, D. Effects of uniconazole on the lignin metabolism and lodging resistance of culm in common buckwheat (*Fagopyrum esculentum* M.). *Field Crops Res.* **2015**, *180*, 46–53. [CrossRef]
17. Mathews, P.R.; Caldicott, J.J.B. The effects of chlormequat chloride formulated with choline chloride on the height and yield of winter wheat. *Ann. Appl. Biol.* **1981**, *97*, 227–236. [CrossRef]
18. Foulkes, M.J.; Slafer, G.A.; Davies, W.J.; Berry, P.M.; Sylvester-Bradley, R.; Martre, P.; Calderini, D.F.; Griffiths, S.; Reynolds, M.P. Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *J. Exp. Bot.* **2011**, *62*, 469–486. [CrossRef]

19. Fischer, R.A. Wheat physiology: A review of recent developments. *Crop Pasture Sci.* **2011**, *62*, 95–114. [CrossRef]
20. Tian, Z.; Jing, Q.; Dai, T.; Jiang, D.; Cao, W. Effects of genetic improvements on grain yield and agronomic traits of winter wheat in the Yangtze River Basin of China. *Field Crops Res.* **2011**, *124*, 417–425. [CrossRef]
21. Matysiak, K. Influence of trinexapac-ethyl on growth and development of winter wheat. *J. Plant Prot. Res.* **2006**, *46*, 133–143.
22. Espindula, M.C.; Rocha, V.S.; Rezende Fontes, P.C.; Correa Da Silva, R.C.; De Souza, L.T. Effect of nitrogen and trinexapac-Ethyl rates on the SPAD index of wheat Leaves. *J. Plant Nutr.* **2009**, *32*, 1956–1964. [CrossRef]
23. Shekoofa, A.; Emam, Y. Effects of nitrogen fertilization and plant growth regulators (PGRs) on yield of wheat (*Triticum aestivum* L.) cv. Shiraz. *J. Agric. Sci. Technol.* **2008**, *10*, 101–108.
24. Chhokar, R.S.; Kumar, N.; Gill, S.C.; Tripathi, S.C.; Singh, G. Enhancing wheat productivity through genotypes and growth regulators application under higher fertility conditions in sub-humid climate. *Int. J. Plant Prod.* **2024**, *18*, 85–95. [CrossRef]
25. Schluttenhofer, C.M.; Massa, G.D.; Mitchell, C.A. Use of uniconazole to control plant height for an industrial/pharmaceutical maize platform. *Ind. Crops Prod.* **2011**, *33*, 720–726. [CrossRef]
26. Gutierrez, J.; Lopez Nunez-Flores, M.J.; Gomez-Ros, L.V.; Novo Uzal, E.; Esteban Carrasco, A.; Diaz, J.; Sottomayor, M.; Cuello, J.; Ros Barcelo, A. Hormonal regulation of the basic peroxidase isoenzyme from *Zinnia elegans*. *Planta* **2009**, *230*, 767–778. [CrossRef] [PubMed]
27. Li, Y.; Xi, K.; Liu, X.; Han, S.; Han, X.; Li, G.; Yang, L.; Ma, D.; Fang, Z.; Gong, S.; et al. Silica nanoparticles promote wheat growth by mediating hormones and sugar metabolism. *J. Nanobiotechnol.* **2023**, *21*, 2. [CrossRef] [PubMed]
28. Khan, W.; Prithiviraj, B.; Smith, D.L. Chitosan and chitin oligomers increase phenylalanine ammonia-lyase and tyrosine ammonia-lyase activities in soybean leaves. *J. Plant Physiol.* **2003**, *160*, 859–863. [CrossRef] [PubMed]
29. Nguyen, T.N.; Son, S.; Jordan, M.C.; Levin, D.B.; Ayele, B.T. Lignin biosynthesis in wheat (*Triticum aestivum* L.): Its response to waterlogging and association with hormonal levels. *BMC Plant Biol.* **2016**, *16*, 28. [CrossRef]
30. Ahmad, I.; Meng, X.; Kamran, M.; Ali, S.; Ahmad, S.; Liu, T.; Cai, T.; Han, Q.F. Effects of uniconazole with or without micronutrient on the lignin biosynthesis, lodging resistance, and winter wheat production in semiarid regions. *J. Integr. Agric.* **2020**, *19*, 62–77. [CrossRef]
31. Jesus, W.C., Jr.; Vale, F.X.R.; Coelho, R.R.; Paul, P.A.; Hau, B.; Bergamin, A. Relationships between angular leaf spot, healthy leaf area, effective leaf area and yield of *Phaseolus vulgaris*. *Eur. J. Plant Pathol.* **2003**, *109*, 625–632. [CrossRef]
32. Dobrev, P.I.; Kamínek, M. Fast and efficient separation of cytokinins from auxin and abscisic acid and their purification using mixed-mode solid-phase extraction. *J. Chromatogr. A* **2002**, *950*, 21–29. [CrossRef]
33. Liu, J.F.; Ding, J.; Yuan, B.F.; Feng, Y.Q. Magnetic solid phase extraction coupled with in situ derivatization for the highly sensitive determination of acidic phytohormones in rice leaves by UPLC-MS/MS. *Analyst* **2014**, *139*, 5605–5613. [CrossRef] [PubMed]
34. Pan, X.; Welti, R.; Wang, X. Quantitative analysis of major plant hormones in crude plant extracts by high-performance liquid chromatography-mass spectrometry. *Nat. Protoc.* **2010**, *5*, 986–992. [CrossRef] [PubMed]
35. Knobloch, K.H.; Hahlbrock, K. Isoenzymes of p-coumarate: CoA ligase from cell suspension cultures of Glycine max. *Eur. J. Biochem.* **1975**, *52*, 311–320. [CrossRef] [PubMed]
36. Parry, M.a.J.; Andralojc, P.J.; Parmar, S.; Keys, A.J.; Habash, D.; Paul, M.J.; Alred, R.; Quick, W.P.; Servaites, J.C. Regulation of Rubisco by inhibitors in the light. *Plant Cell Environ.* **1997**, *20*, 528–534. [CrossRef]
37. Pavlinova, O.A.; Balakhontsev, E.N.; Prasolova, M.F.; Turkina, M.V. Sucrose-phosphate synthase, sucrose synthase, and invertase in sugar beet leaves. *Russ. J. Plant Physiol.* **2002**, *49*, 68–73. [CrossRef]
38. Peng, D.; Chen, X.; Yin, Y.; Lu, K.; Yang, W.; Tang, Y.; Wang, Z. Lodging resistance of winter wheat (*Triticum aestivum* L.): Lignin accumulation and its related enzymes activities due to the application of paclobutrazol or gibberellin acid. *Field Crops Res.* **2014**, *157*, 1–7. [CrossRef]
39. Ghuman, L.; Ram, H. Enhancing wheat (*Triticum aestivum* L.) grain yield and quality by managing lodging with growth regulators under different nutrition levels. *J. Plant Nutr.* **2021**, *44*, 1916–1929. [CrossRef]
40. Zheng, M.; Chen, J.; Shi, Y.; Li, Y.; Yin, Y.; Yang, D.; Luo, Y.; Pang, D.; Xu, X.; Li, W.; et al. Manipulation of lignin metabolism by plant densities and its relationship with lodging resistance in wheat. *Sci. Rep.* **2017**, *7*, 41805. [CrossRef]
41. Stubbs, C.J.; Kunduru, B.; Bokros, N.; Verges, V.; Porter, J.; Cook, D.D.; Debolt, S.; Mcmahan, C.; Sekhon, R.S.; Robertson, D.J. Moving toward short stature maize: The effect of plant height on maize stalk lodging resistance. *Field Crops Res.* **2023**, *300*, 109008. [CrossRef]
42. Ma, Q.H.; Xu, Y.; Lin, Z.B.; He, P. Cloning of *cDNA* encoding COMT from wheat which is differentially expressed in lodging-sensitive and -resistant cultivars. *J. Exp. Bot.* **2002**, *53*, 2281–2282. [CrossRef]
43. Berry, P.M.; Spink, J.H.; Gay, A.P.; Craigon, J. A comparison of root and stem lodging risks among winter wheat cultivars. *J. Agric. Sci.* **2003**, *141*, 191–202. [CrossRef]
44. Zhang, Y.; Ni, Z.; Yao, Y.; Nie, X.; Sun, Q. Gibberellins and heterosis of plant height in wheat (*Triticum aestivum* L.). *BMC Genet.* **2007**, *8*, 40. [CrossRef] [PubMed]

45. Acheampong, A.K.; Hu, J.; Rotman, A.; Zheng, C.; Halaly, T.; Takebayashi, Y.; Jikumaru, Y.; Kamiya, Y.; Lichter, A.; Sun, T.P.; et al. Functional characterization and developmental expression profiling of gibberellin signalling components in *Vitis vinifera*. *J. Exp. Bot.* **2015**, *66*, 1463–1476. [CrossRef] [PubMed]
46. Ordonio, R.L.; Ito, Y.; Hatakeyama, A.; Ohmae-Shinohara, K.; Kasuga, S.; Tokunaga, T.; Mizuno, H.; Kitano, H.; Matsuoka, M.; Sazuka, T. Gibberellin deficiency pleiotropically induces culm bending in sorghum: An insight into sorghum semi-dwarf breeding. *Sci. Rep.* **2014**, *4*, 5287. [CrossRef] [PubMed]
47. Rademacher, W. Growth retardants: Effects on gibberellin biosynthesis and other metabolic pathways. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **2000**, *51*, 501–531. [CrossRef]
48. Orozco-Melendez, L.R.; Hernandez-Rodriguez, O.A.; Cruz-Alvarez, O.; Robles-Hernandez, L.; Avila-Quezada, G.D.; Chavez, E.S.; Porras-Flores, D.A.; Ojeda-Barrios, D.L. Paclobutrazol and its use in fruit production: A review. *Phyton-Int. J. Exp. Bot.* **2022**, *91*, 1–12. [CrossRef]
49. Fujioka, S.; Yokota, T. Biosynthesis and metabolism of brassinosteroids. *Annu Rev. Plant Biol.* **2003**, *54*, 137–164. [CrossRef]
50. Clouse, S.D. Brassinosteroids. *Arab. Book.* **2011**, *9*, e0151. [CrossRef]
51. Kamran, M.; Ahmad, I.; Wang, H.; Wu, X.; Xu, J.; Liu, T.; Ding, R.; Han, Q. Mepiquat chloride application increases lodging resistance of maize by enhancing stem physical strength and lignin biosynthesis. *Field Crops Res.* **2018**, *224*, 148–159. [CrossRef]
52. Kamran, M.; Cui, W.; Ahmad, I.; Meng, X.; Zhang, X.; Su, W.; Chen, J.; Ahmad, S.; Fahad, S.; Han, Q.; et al. Effect of paclobutrazol, a potential growth regulator on stalk mechanical strength, lignin accumulation and its relation with lodging resistance of maize. *Plant Growth Regul.* **2018**, *84*, 317–332. [CrossRef]
53. Zhang, S.; Yang, J.; Li, H.; Chiang, V.L.; Fu, Y. Cooperative regulation of flavonoid and lignin biosynthesis in plants. *Crit. Rev. Plant Sci.* **2021**, *40*, 109–126. [CrossRef]
54. Han, H.; Yang, W. Influence of uniconazole and plant density on nitrogen content and grain quality in winter wheat in South China. *Plant Soil Environ.* **2009**, *55*, 159–166. [CrossRef]
55. Ramburan, S.; Greenfield, P.L. The effects of chlormequat chloride and ethephon on agronomic and quality characteristics of South African irrigated wheat. *S. Afr. J. Plant Soil.* **2007**, *24*, 106–113. [CrossRef]
56. Stahli, D.; Perrissin-Fabert, D.; Blouet, A.; Guckert, A. Contribution of the wheat (*Triticum aestivum* L.) flag leaf to grain yield in response to plant growth regulators. *Plant Growth Regul.* **1995**, *16*, 293–297. [CrossRef]
57. Monostori, I.; Arendas, T.; Hoffman, B.; Galiba, G.; Gierczik, K.; Szira, F.; Vagujfalvi, A. Relationship between SPAD value and grain yield can be affected by cultivar, environment and soil nitrogen content in wheat. *Euphytica* **2016**, *211*, 103–112. [CrossRef]
58. Bode, J.; Wild, A. The influence of (2-Chloroethyl)trimethylammoniumchloride (CCC) on growth and photosynthetic metabolism of young wheat plants (*Triticum aestivum* L.). *J. Plant Physiol.* **1984**, *116*, 435–446. [CrossRef]

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