

Article

Positive Correlation of Lodging Resistance and Soybean Yield under the Influence of Uniconazole

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Abstract: Increasing planting density is one of the most effective ways to increase soybean yield, but supra-optimum density leads to an increase in the risk of lodged soybean. In this study, two varieties were selected. Heinong84 (lodging-susceptible variety, HN84) had planting densities of 200,000 plants/hm², 300,000 plants/hm², and 400,000 plants/hm². Henong60 (lodging-resistant, HN60) had planting densities of 300,000 plants/hm², 400,000 plants/hm², and 500,000 plants/hm². When the foliar application of uniconazole (50 mg/L) occurred at the beginning of the flowering stage (R1), the plant morphology, fiber composition, and mechanical properties of soybean internodes were determined at the podding and seed filling stages, and the yield was measured at the harvest stage. The results showed that spraying uniconazole at the R1 stage changed the morphology structure of soybean plants (i.e., plant height and petiole length reduction; stem diameter and leafstalk angle increase), improved the internode quality (i.e., increased breaking force, lignin content, cellulose content, hemicellulose content, and stem dry weight per unit length), and increased the number of grains per plant at the harvest stage. Thus, it is concluded that the application of uniconazole improved the plant population structure by changing the morphology of soybean plants, which was conducive to good light transmission and ventilation, improved the internode quality and lodging resistance, and increased the yield.

Keywords: uniconazole; planting density; lodging resistance coefficient; yield



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1. Introduction

Soybean (*Glycine max* L.) is one of the most widely cultivated oil crop worldwide. Soybean is rich in oil and protein [1,2] and plays an important role in the human diet, animal feed, bio-oil production, and industrial product raw materials [3]. Increasing planting density has been considered an efficient strategy to increase crop yield [4,5]. An appropriate planting density can coordinate the relationship between individual growth and population growth [6], but as planting density increases, plant height increases [6–9], and it becomes more sensitive to lodging. Coordinating the balance between planting density and population lodging is the main way to achieve a large-scale balanced yield increase in soybean.

The quality of a soybean stem is a key indicator used to measure soybean lodging, and its morphological characteristics, physiological traits, and mechanical properties are closely related to soybean lodging resistance [10]. Related studies have shown that plant height and the length of the basal internodes are negatively correlated with lodging resistance [11,12], and stem diameter, stem wall thickness, and stem plumpness are positively correlated with lodging resistance [13,14]. In addition, the mechanical properties such as bending strength, inertia moment, elastic ratio, and flexural rigidity of the stem are also deeply studied in soybean. The mechanical properties are distributed differently along the stem. The strength of the basal internode between 1 and 5 cm is the highest, which plays an important role in

the lodging resistance of soybean [15–18]. The lodging resistance coefficient of soybean, which is mainly based on plant mechanical properties, can comprehensively reflect the lodging resistance of soybean and is significant correlated with lodging resistance [19]. The plant height, stem diameter, and internode length are the main indexes affecting the mechanical properties, and stem strength is negatively correlated with plant height and internode length, but positively correlated with stem diameter [20,21]. Stem strength is the product of the chemical and biochemical components of the stem. Cellulose and lignin are the main components of stem cell wall and the key factors used to determine stem strength. Previous studies have shown that the content of lignin and cellulose in stems is positively correlated with lodging resistance; the higher the cellulose content in the unit volume of the plant, the stronger the stem strength, though the lodging resistance is worse [22–24]. Jun et al. [25] believed that under high-density planting conditions, the accumulation rate of lignin and cellulose in the stems slowed down, which is not conducive to the formation of epidermal tissue and the epidermal puncture strength of stems, which was also the main reason for high-density planting.

Controlling plant height is an important way to enhance the lodging resistance of crops. Uniconazole is an inhibitor of gibberellin biosynthesis. Its main role is to regulate endogenous hormone levels by inhibiting kaurene oxidase (KO), increasing plant dry weight, reducing plant height [26], shortening internode length, increasing stem diameter, and enhancing lodging resistance and yield [27,28]. Spraying uniconazole on buckwheat [29] and wheat [30] could significantly reduce plant height, increase lignin content and bending strength, and improve lodging resistance. Han et al. [31] showed that uniconazole soaking treatment could regulate soybean plant shape, strengthen the photosynthetic characteristics, and increase yield. Yan et al. [28] believed that uniconazole treatment significantly inhibited the vegetative growth of intercropping soybean at the seedling stage, increased the light transmittance of soybean canopy, decreased the soybean internode length and leaf area per plant, delayed the leaf senescence at the podding stage, and was directly related to the increase in soybean yield. Wan et al. [32] showed that spraying uniconazole at the three-leaf stage of soybean could reduce the ratio of internode length to stem diameter and significantly increase petiole length, leaf length, and leaf width. In addition, uniconazole could significantly increase the chlorophyll content and Pn, Tr, and intercellular CO₂ concentration (Ci) of soybean, as well as increase the content of sucrose and starch [33,34]. Feng et al. [35] showed that uniconazole could increase the soluble sugar content, soluble protein content, superoxide dismutase, and peroxidase and catalase activities in soybean leaves under drought conditions.

Increasing planting density has become an important measure to increase soybean yield. Lodging resistance is an important index used to measure density tolerance. It is of great significance to ensure soybean population yield by screening suitable planting density, constructing reasonable population structures, and increasing soybean lodging resistance. Based on the field experiment, we hypothesized that uniconazole application at soybean R1 would (i) reduce soybean plant height and increase stem diameter and the D/H ratio; (ii) increase the content of lignin, cellulose, and hemicellulose in soybean stems; and (iii) increase the dry weight of soybean plant, dry weight per unit length of internode, and stem breaking force. The purpose of this study was to verify that uniconazole had optimization and improvement effects on plant type, lodging resistance, and the yield of two soybean plants with different lodging resistances under different planting densities, and to provide theoretical support for the scientific use of chemical regulators to construct reasonable population structures and increases in the lodging resistance and yield measures of soybean.

2. Materials and Methods

2.1. Experimental Site

The field trial was conducted at the Northeast Agricultural University Experimental Station (126°45' E, 45°42' E) in Harbin City, China, in 2021 and 2023. The experimental site is located in the middle of Songnen Plain, which belongs to the cold temperate continental

climate. The experimental field was black soil, and the contents of organic matter, available nitrogen, available phosphorus, and available potassium were 32.46 g/kg, 82.51 mg/kg, 58.20 mg/kg, and 172.20 mg/kg, respectively.

2.2. Field Experimental Design

In this experiment, Heinong84 (HN84, a tall variety, lodging-susceptible variety) and Henong60 (HN60, a dwarf variety, lodging-resistant) were selected. The experiment was conducted in a split-pot, and the planting density was the main factor. Each variety set three densities; HN84 was set at 200,000 plants/hm², 300,000 plants/hm², and 400,000 plants/hm², which were denoted as D20, D30, and D40. HN60 was set at 300,000 plants/hm², 400,000 plants/hm², and 500,000 plants/hm², which were denoted as D30, D40, and D50. The sub-factor was the foliar spraying of 50 mg/L uniconazole (S3307) and water (CK), respectively. In this experiment, the spraying day was July 13, and the amount of liquid applied was 225 L/hm². In order to promote the absorption of uniconazole by soybeans, we added the additive Tween 20 in the process of uniconazole configuration and selected a windless sunny day for foliar spraying. Plot ridge planting was adopted, with 6 ridges in each plot, 10 m ridge length, 0.65 m row spacing, and 3 repetitions, and the plots were randomly arranged.

In order to verify the uniconazole treatment, we planted the HN84 in the same plot in 2023, repeated the experimental treatment we first conducted in 2021, and investigated the yield and its components during the harvest period. The standard agronomic measures for soybean production were adopted during the growth period, including necessary chemical fertilizers, herbicides, and irrigation.

2.3. Sampling and Measurements

2.3.1. Growth and Physiological Parameter Determination

After treatment on soybean plants, 10 soybean plants were continuously sampled in the area with uniform growth in each plot, and the dry weights of the stems, leaves, and pods were measured once every 7 days 7 consecutive times.

In the podding stage and seed filling stage, 10 plants were randomly selected from each plot to measure plant height, stem diameter, petiole length, leafstalk angle, stem dry weight, and structural carbohydrate content (i.e., lignin, cellulose, and hemicellulose).

Plant height: The height of the stem cotyledon to the apical meristem was measured with a ruler.

Stem diameter: The diameter of the second internode of the soybean base was measured by a vernier caliper.

Petiole length: The length of the soybean petiole (the third trifoliolate leaf petiole downward from the apical meristem) was measured with a ruler.

Leafstalk angle: The angle between the petiole third trifoliolate leaf petiole (downward from the apical meristem) and stem was measured by a protractor.

At the end, the soybean plant stems were put into a forced-draft convection oven at 80 °C to dry to a constant weight, were weighed, and the dry weight per unit length was calculated (DWUL).

$$DWUL = \frac{\text{The weight of the stem}}{\text{The length of the stem}}$$

At the same time, three soybeans were randomly selected from each plot, and the second internode of the stem base was conserved at −80 °C in a refrigerator. The content of cellulose, hemicellulose, and lignin in soybean stems was determined by an ELISA [36].

2.3.2. Breaking Force and Stem Lodging Resistance Coefficient Determination

In the pod stage and seed filling stage, 10 plants were randomly selected from each plot, referring to three-point bending for mechanical analysis [19], the mechanical properties of soybean stem were determined, as shown in Figure 1, the distance between the two fulcrums was adjusted and fixed, and the push force on the middle position was assessed.

At this time, the distance between the action point of the thrust on the stem and the upper fulcrum is L (HN84 podding stage $L = 8$ cm, seed filling stage $L = 7$ cm; HN60 $L = 7$ cm at podding stage and $L = 8$ cm at seed filling stage).

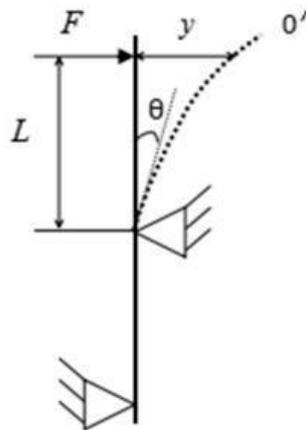


Figure 1. Assay schematic of the breaking force of soybean stem [19].

In Figure 1, when the breaking force on the stem is F , the stem bending moment is FL . The center of the plant height is the center of gravity, and the gravity moment of the plant is $1/2HMg$. The ratio of the bending moment to the gravity moment is defined as the lodging resistance coefficient (Q) and is expressed as follows.

$$Q = \frac{2FL}{MgH}$$

In the formula: H : plant height; F : breaking force; L : the distance between the upper fulcrum and the action point of the push force; and M : plant fresh weight (Table S1); $g = 9.8$ N/kg.

When the stem breaks, the angle between the tangential line of the curve of the bent stem ($0'$) and the straight line of the initially erect stem (0) is defined as the rotation angle (θ).

$$\theta \approx \frac{180}{\pi} \arctan \frac{y}{L}$$

2.3.3. Yield Determination

The yield was measured during the soybean harvest period. Two square meters with a uniform density were hand-harvested in each plot. The soybean plants in the selected area were all harvested, and the soybean yield was measured. Five soybean plants with uniform growth were selected in each plot, and each treatment entailed three repetitions. The number of internodes per plant, grain weight, grain number, and 100-grain weight were measured.

2.4. Statistical Analysis

IBM SPSS 26 (SPSS Inc., Chicago, IL, USA) statistical software was used for data management and variance analysis. Variance analysis (ANOVA) and mean values were compared by the LSD test at $p < 0.05$. Pearson's correlation coefficient was performed using Origin 2021 (OriginLab, Northampton, MA, USA) to determine the correlation between the indicators and construct figures.

3. Results

3.1. Morphological Characteristics of Soybean Plants

The plant height, stem diameter, and D/H ratio of soybean were compared between the podding stage and seed filling stage. It was indicated that there was no significant difference

in the plant height of HN84 under different planting densities, and the plant height of HN60 increased with the increase in the planting density (Figure 2). The application of S3307 significantly reduced the plant height of HN84 and HN60. The application of S3307 under D20, D30, and D40 planting densities reduced the plant height of HN84 by 8.7%, 5.8%, and 3.3%, respectively. The application of S3307 under D30, D40, and D50 planting densities reduced the plant height of HN60 by 3.8%, 4.0%, and 1.5%, respectively. Under the same planting density, the S3307 treatment increased the stem diameter of soybean, and the two varieties showed the same performance.

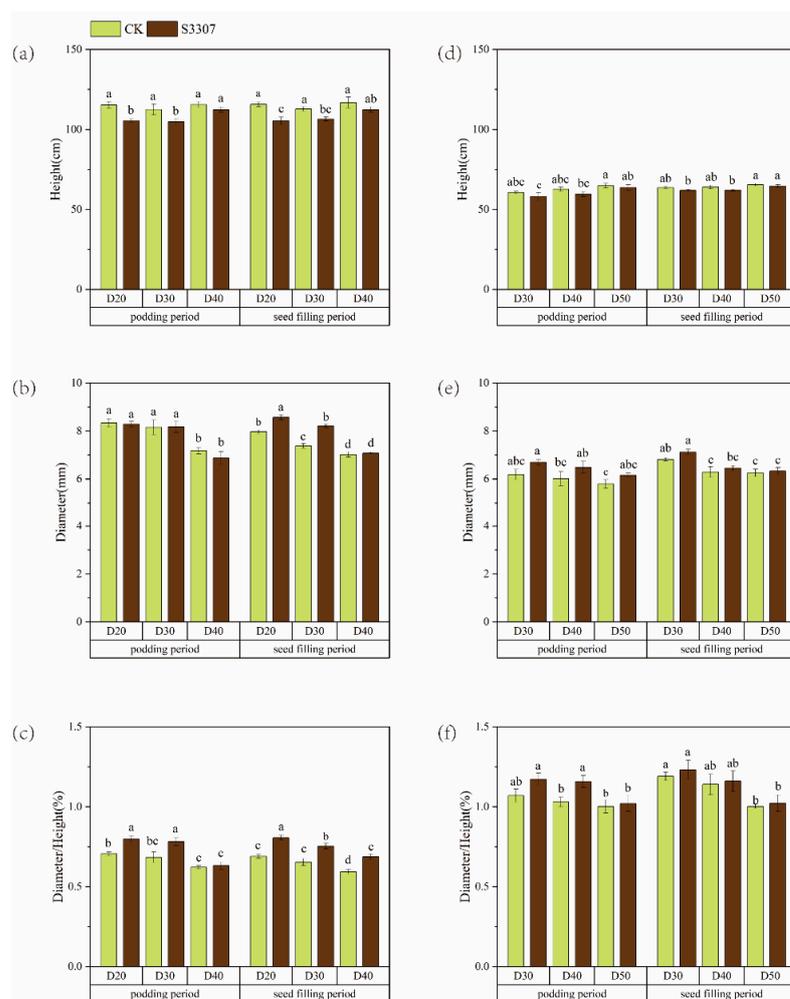


Figure 2. Effects of S3307 on plant height, stem diameter, and D/H ratio of soybean in 2021. Note: (a–c) The morphological properties of HN84 at podding stage and seed filling stage; (d–f) the morphological properties of HN60 at podding stage and seed filling stage. Comparing the same period, different letters indicate a significant difference of 5%.

The D/H ratio is an important index to estimate the lodging resistance of soybean plants [19]. It was indicated that S3307 treatment increased the D/H ratio of HN84 and HN60 under the same planting density (Figure 2c,f). The D/H ratio of HN84 under D20 density with S3307 treatment was significantly higher than that of other treatments, and the D40 density with the control was significantly lower than that of other treatments. The D/H ratio of the S3307 treatment increased under the three planting densities of HN60, but the difference between treatments was not significant. It indicated that S3307 could increase the D/H ratio of HN84 and HN60 under different planting densities and had a more significant effect on HN84.

As shown in Figure 3, S3307 significantly reduced the petiole length of HN84 at the podding stage, but it had no significant effect on the petiole length at the seed filling

stage. The petiole length of HN60 under the S3307 treatment was not significant at the podding stage, but it significantly reduced the petiole length of HN60 at the seed filling stage. The leafstalk angle was affected by the growth period. At the podding stage, the S3307 treatment significantly increased the leafstalk angle of HN84 and HN60, but there was no significant difference between the treatments at the seed filling stage.

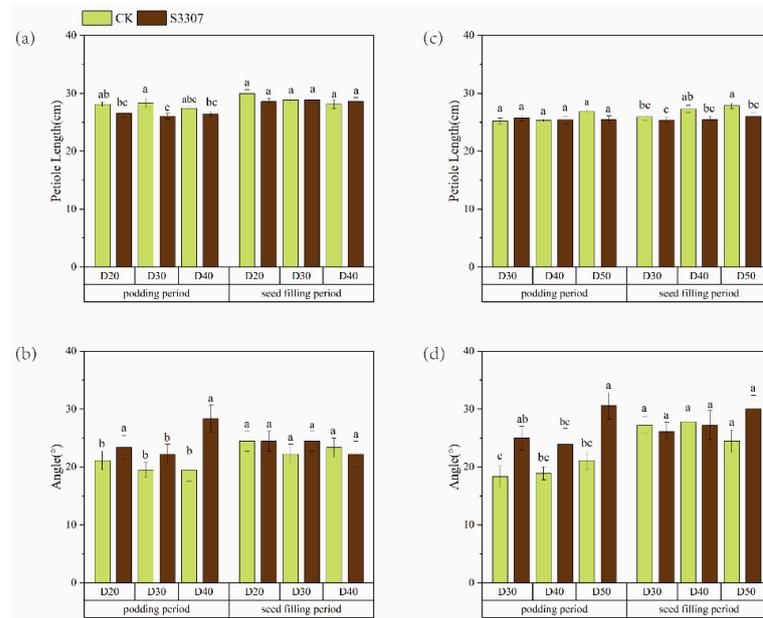


Figure 3. Effects of S3307 on petiole length and leafstalk angle of soybean plants in 2021. (a,b) HN84 and (c,d) Henong60 compared during the same period; different letters indicate a difference of 5% significant level.

3.2. Plant Dry Weight

In this study, the soybean plant population from 3 July 2021 (before treatment) to 25 September 2021 was continuously sampled to analyze the effects of S3307 on the dry matter weight of the stems, leaves, and pods of soybean plants under different density conditions, and these effects were compared (Figure 4). The results showed that the total dry matter weight of HN84 and HN60 decreased with the increase in the planting density. The S3307 treatment could significantly increase the total dry matter weight, stem dry matter weight, pod dry matter weight, and leaf dry matter weight of soybean plants.

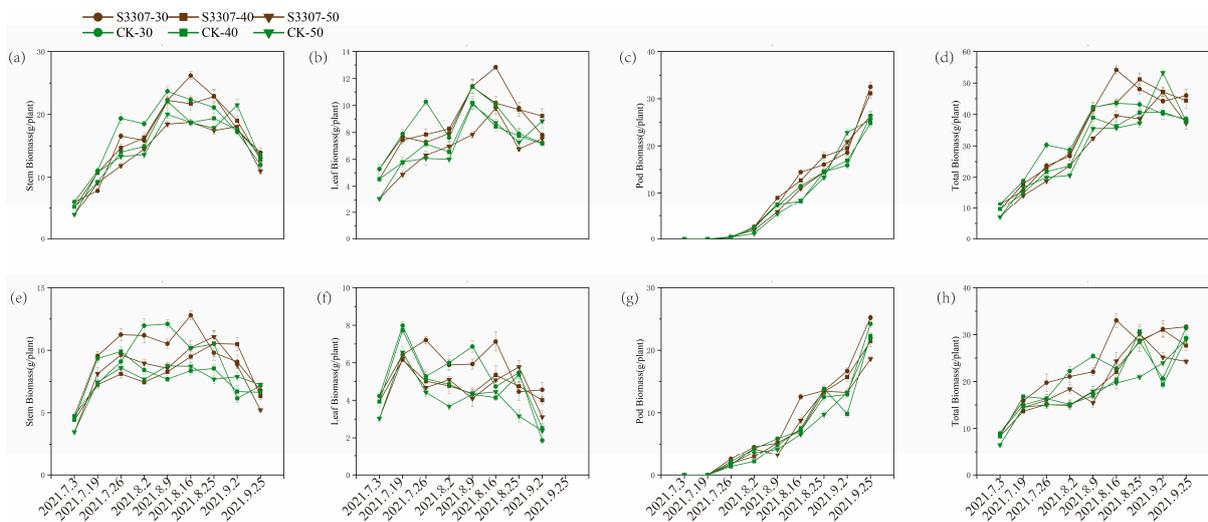


Figure 4. Effects of S3307 on dry matter weight of soybean plants in 2021. (a-d) HN84 and (e-h) HN60.

3.3. Carbohydrates Contents

For HN84, both high-density planting conditions and the S3307 treatment increased the fiber composition content in soybean stems (Figure 5a). The S3307 treatment considerably affected the contents of lignin, cellulose, and hemicellulose in soybean stems at the podding stage. Under D20, D30, and D40 with the application of S3307, lignin increased by 10.7%, 16.9%, and 8.0% (the average value of the two growth periods), cellulose increased by 2.2%, 13.5%, and 13.7% (the average value of the two growth periods), and hemicellulose increased by 19.2%, 24.3%, and 11.9% (the average value of the two growth periods). Further analysis revealed that although the content of fiber composition in the stems of HN84 was higher under high-density planting conditions, S3307 had a more significant effect on the soybean plants of D30 (optimal planting density).

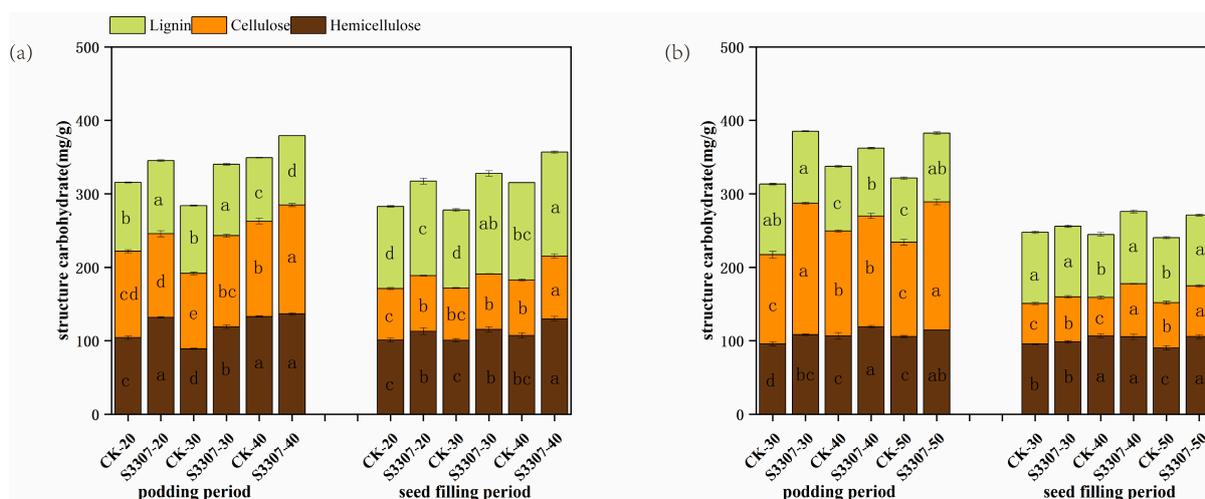


Figure 5. The content of lignin, cellulose, and hemicellulose in soybean stem with S3307 application in 2021. (a) HN84 and (b) HN60: compared at the same time period; different letters indicate a significant difference of 5%.

As shown in Figure 5b, the change in the planting density had no significant effect on the fiber composition content of HN60. S3307 significantly increased the content of lignin, cellulose, and hemicellulose of HN60 at the podding stage. However, at the seed filling stage, S3307 significantly increased the content of lignin and cellulose under D50 density, but it had no significant effect on the lignin content of the D20 treatment, and it reduced the hemicellulose content. It can be seen that compared with the dwarf variety HN60, the S3307 treatment had a more significant effect on the fiber composition content in the stem of HN84.

3.4. Breaking Force and Lodging Resistance Coefficient

In this study, the mechanical properties of soybean internodes of HN84 and HN60 at the podding stage and seed filling stage were investigated. Table 1 shows that with the increase in the planting density, the DWUL, deformation, breaking force, bending moment, gravity moment, rotation angle, and lodging resistance coefficient of HN84 present a downward trend. After the application of S3307, the DWUL, deformation, breaking force, bending moment, gravity moment, rotation angle, and lodging resistance coefficient of HN84 increased, and the lodging resistance coefficient under D20 with the S3307 treatment was significantly higher than that of other treatments.

The analysis of variance revealed that density significantly affected the DWUL, deformation, breaking force, bending moment, rotation angle, and lodging resistance coefficient of HN84 stem ($p < 0.01$) and had significant effects on gravity moment ($p < 0.05$). S3307 had significant effects on the DWUL, deformation, breaking force, bending moment, and rotation angle ($p < 0.01$) and significantly affected the lodging resistance coefficient ($p < 0.05$).

The growth period had a significant effect on the breaking force, gravity moment, rotation angle, and lodging resistance coefficient ($p < 0.01$), but it had no significant effect on the DWUL and bending moment. $D \times S$ and $S \times P$ only had a significant effect on the DWUL ($p < 0.01$), $D \times P$ had a significant effect on the DWUL and lodging resistance coefficient ($p < 0.01$), and $D \times S \times P$ was not significant on each index.

Table 1. Effects of plant density and S3307 on the quality traits of the HN84 stem in 2021.

Period	Treatment	DWUL (g/cm)	Deformation (cm)	Breaking Force (N)	Bending Moment (Nm)	Gravity Moment (Nm)	Rotation Angle (°)	Lodging Resistance Coefficient	
podding period	D20	CK	0.20 ± 0.01 ab	1.54 ± 0.05 ab	58.41 ± 5.75 b	4.67 ± 0.46 b	0.78 ± 0.01 a	10.9 ± 0.35 ab	6.02 ± 0.65 b
		S3307	0.22 ± 0 a	1.68 ± 0.05 a	70.96 ± 0.65 a	5.68 ± 0.05 a	0.74 ± 0 b	11.86 ± 0.34 a	7.68 ± 0.05 a
	D30	CK	0.20 ± 0.01 ab	1.42 ± 0.09 bc	48.33 ± 3.25 bc	3.87 ± 0.26 bc	0.76 ± 0.01 ab	10.06 ± 0.6 ab	5.09 ± 0.38 bc
		S3307	0.21 ± 0.01 a	1.5 ± 0.04 ab	50.64 ± 4.14 bc	4.05 ± 0.33 bc	0.78 ± 0.01 a	10.62 ± 0.31 bc	5.15 ± 0.4 bc
	D40	CK	0.17 ± 0.01 bc	1.24 ± 0.07 c	43 ± 1.97 c	3.44 ± 0.16 c	0.74 ± 0.01 b	8.81 ± 0.52 c	4.64 ± 0.2 c
		S3307	0.16 ± 0 c	1.3 ± 0.07 c	47.93 ± 2.12 bc	3.83 ± 0.17 bc	0.76 ± 0.01 ab	9.23 ± 0.49 c	5.05 ± 0.27 bc
seed filling period	D20	CK	0.19 ± 0 b	1.54 ± 0.02 b	63.44 ± 2.68 a	4.44 ± 0.19 a	1.09 ± 0.05 a	12.41 ± 0.19 b	4.09 ± 0.15 ab
		S3307	0.25 ± 0 a	1.72 ± 0.05 a	68.2 ± 2.75 a	4.78 ± 0.19 a	1.1 ± 0.05 a	13.8 ± 0.38 a	4.35 ± 0.19 a
	D30	CK	0.17 ± 0.01 c	1.5 ± 0.04 b	56.05 ± 1.44 bc	3.92 ± 0.1 bc	1.08 ± 0.04 a	12.09 ± 0.35 b	3.63 ± 0.07 c
		S3307	0.20 ± 0.01 b	1.5 ± 0.03 b	56.77 ± 1.56 b	3.97 ± 0.11 b	1.07 ± 0.03 a	12.09 ± 0.25 b	3.71 ± 0.14 bc
	D40	CK	0.15 ± 0 d	1.36 ± 0.05 c	50.2 ± 1.71 c	3.51 ± 0.12 bc	0.99 ± 0.01 a	10.99 ± 0.4 c	3.56 ± 0.12 c
		S3307	0.17 ± 0 c	1.48 ± 0.04 b	53.09 ± 1.4 bc	3.72 ± 0.1 bc	1.02 ± 0.02 a	11.94 ± 0.29 b	3.66 ± 0.15 bc
Analysis of variance									
	Density(D)	60.883 **	25.931 **	38.37 **	36.724 **	4.289 *	26.438 **	25.097 **	
	S3307(S)	33.879 **	9.611 **	8.464 **	8.422 **	0.13 ns	10.088 **	6.846 *	
	Period(P)	0.611 ns	5.04 *	8.646 **	2.548 ns	358.404 **	77.356 **	116.624 **	
	D × S	6.981 **	1.246 ns	1.689 ns	1.688 ns	0.518 ns	1.349 ns	2.773 ns	
	D × P	5.864 **	1.68 ns	1.27 ns	2.156 ns	2.476 ns	1.099 ns	7.019 **	
	S × P	15.283 **	0.011 ns	1.39 ns	1.754 ns	0.13 ns	0.088 ns	2.954 ns	
	D × S × P	0.475 ns	0.491 ns	0.381 ns	0.452 ns	0.623 ns	0.599 ns	1.692 ns	

Note: The values in the table are the means ± standard error ($n = 5$); different letters indicate that the difference between treatments reached significance at the level of $p < 0.05$, and the treatments are compared longitudinally. * and ** represent the significant levels of 5% and 1%, respectively, and ns indicates no significant difference.

Table 2 shows that the change in the mechanical properties of HN60 was basically the same as that of HN84, but the lodging resistance coefficient was significantly higher than that of HN84. At the podding stage, the increase in the mechanical properties of the internode under S3307 was not significant, but it revealed significant differences between the treatments at the seed filling stage.

Table 2. Effects of plant density and S3307 on the quality traits of the HN60 stem in 2021.

Period	Treatment	DWUL (g/cm)	Deformation (cm)	Breaking Force (N)	Bending Moment (Nm)	Gravity Moment (Nm)	Rotation Angle (°)	Lodging Resistance Coefficient	
podding period	D30	CK	0.22 ± 0.01 a	1.72 ± 0.07 b	29.07 ± 0.56 ab	0.12 ± 0 ab	0.21 ± 0 ab	76.44 ± 0.25 ab	9.68 ± 0.31 a
		S3307	0.18 ± 0.01 b	2.08 ± 0.05 a	31.78 ± 1.46 a	0.14 ± 0 a	0.22 ± 0 a	77.48 ± 0.57 a	10.21 ± 0.49 a
	D40	CK	0.14 ± 0.01 c	1.62 ± 0.13 b	25.82 ± 1.61 bc	0.12 ± 0.01 b	0.21 ± 0 ab	74.6 ± 1 abc	8.64 ± 0.58 a
		S3307	0.15 ± 0.02 bc	1.7 ± 0.09 b	26.55 ± 0.59 bc	0.12 ± 0.01 b	0.21 ± 0.01 ab	75.2 ± 0.31 abc	8.93 ± 0.23 a
	D50	CK	0.14 ± 0.01 c	1.24 ± 0.2 c	23.32 ± 2.12 c	0.09 ± 0.01 c	0.19 ± 0 c	72.72 ± 1.74 c	8.4 ± 0.78 a
		S3307	0.14 ± 0.01 c	1.56 ± 0.1 bc	24.26 ± 1.66 c	0.11 ± 0.01 bc	0.2 ± 0.01 bc	73.64 ± 1.07 bc	8.6 ± 0.73 a
seed filling period	D30	CK	0.17 ± 0.02 b	1.76 ± 0.02 a	37.76 ± 2.83 b	0.14 ± 0 a	0.32 ± 0.01 a	77.78 ± 0.91 b	9.45 ± 0.72 a
		S3307	0.25 ± 0.02 a	1.8 ± 0.07 a	51.65 ± 1.65 a	0.14 ± 0.01 a	0.31 ± 0 a	81.16 ± 0.28 a	9.7 ± 0.32 a
	D40	CK	0.14 ± 0.01 b	1.72 ± 0.1 a	32.07 ± 2.61 bcd	0.14 ± 0.01 a	0.33 ± 0.01 a	75.7 ± 0.96 bcd	7.72 ± 0.52 bc
		S3307	0.16 ± 0.02 b	1.74 ± 0.05 a	35.15 ± 1.54 bc	0.14 ± 0 a	0.32 ± 0.01 a	77.09 ± 0.51 bc	8.74 ± 0.33 ab
	D50	CK	0.14 ± 0.01 b	1.62 ± 0.08 a	28.23 ± 1.37 d	0.13 ± 0.01 a	0.31 ± 0 a	74.05 ± 0.7 d	7.19 ± 0.33 c
		S3307	0.15 ± 0.01 b	1.7 ± 0.03 a	30.82 ± 1.06 cd	0.14 ± 0 a	0.32 ± 0.01 a	75.39 ± 0.45 cd	7.55 ± 0.14 bc
Analysis of variance									
	Density(D)	22.166 **	10.853 **	42.366 **	9.629 **	2.682 ns	26.256 **	13.896 **	
	S3307(S)	3.66 ns	7.613 **	16.127 **	6.989 *	0.038 ns	8.91 **	2.368 ns	
	Period(P)	0.479 ns	1.658 ns	84.789 **	30.727 **	1070.104 **	14.614 **	5.625 *	
	D × S	0.171 ns	0.846 ns	4.705 *	0.902 ns	1.261 ns	0.631 ns	0.147 ns	
	D × P	0.022 ns	4.071 *	6.926 **	3.695 *	3.953 *	0.468 ns	0.626 ns	
	S × P	6.577 *	3.613 ns	6.486 *	1.636 ns	1.858 ns	1.504 ns	0.131 ns	
	D × S × P	4.598 *	0.5 ns	2.376 ns	0.611 ns	1.204 ns	0.371 ns	0.255 ns	

Note: The values in the table are the means ± standard error ($n = 5$); different letters indicate that the difference between treatments reached significance at the level of $p < 0.05$, and the treatments are compared longitudinally. * and ** represent the significant levels of 5% and 1%, respectively, and ns indicates no significant difference.

The analysis of variance revealed that density significantly affected the DWUL, deformation, breaking force, bending moment, rotation angle, and lodging resistance coefficient of HN60 ($p < 0.01$). The S3307 treatment had a significant effect on the deformation, breaking force, and rotation angle ($p < 0.01$) and had a significant effect on the bending moment ($p < 0.05$). The growth period had a significant effect on the breaking force, bending moment, gravity moment, and rotation angle ($p < 0.01$) and had a significant effect on the lodging resistance coefficient ($p < 0.05$). $D \times S$, $D \times P$, $S \times P$, and $D \times S \times P$ had no significant effect on the lodging resistance coefficient. This indicated that planting density had a significant effect on the mechanical properties of HN84 and HN60. The application of S3307 had a significant effect on the mechanical properties of HN84, but it did not have a significant effect on HN60.

3.5. Correlation Analysis on the Mechanical Properties of Soybean Plants

The correlation analysis revealed that the lodging resistance coefficient of HN84 and HN60 was significantly positively correlated with the breaking force. Under the S3307 treatment, the lignin content in the stem of HN84 was significantly positively correlated with the lodging resistance coefficient, and the cellulose content was significantly negatively correlated. However, the lignin content and hemicellulose content were significantly negatively correlated with the lodging resistance coefficient at the seed filling stage, and the DWUL had a significant positive correlation with it (Figure 6). Under the S3307 treatment, the lodging resistance coefficient of HN60 at the podding stage was significantly positively correlated with lignin content, and the lodging resistance coefficient at the seed filling stage was significantly positively correlated with the stem diameter, breaking force, and rotation angle, significantly positively correlated with D/H, significantly negatively correlated with the hemicellulose content, and significantly negatively correlated with plant height (Figure 7).

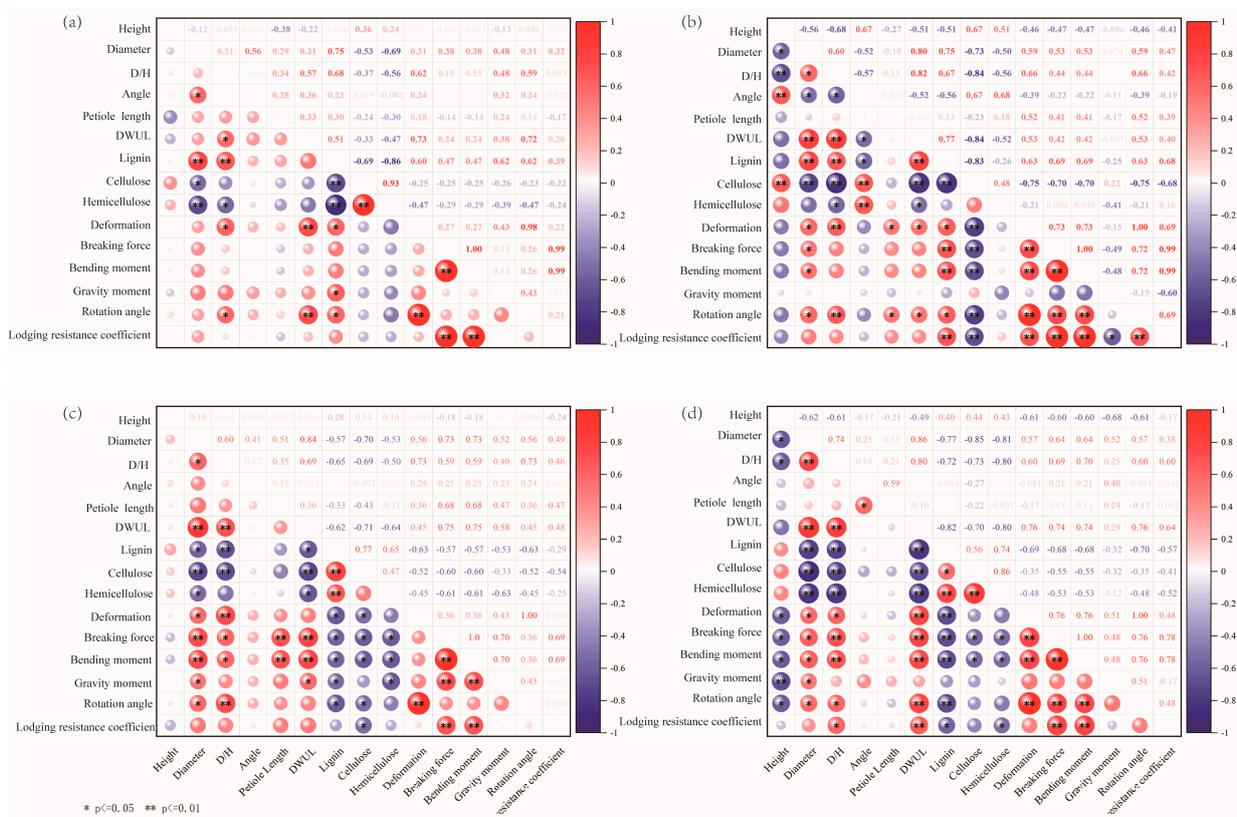


Figure 6. Correlation analysis of internode traits of HN84. (a) Control at podding stage; (b) S3307 treatment at podding stage; (c) control at seed filling stage; (d) S3307 treatment at seed filling stage. The size of the circle shows the correlation level, and the color of the circle shows positive or negative correlation; * and ** are $p \leq 0.05$ and $p \leq 0.01$, respectively.

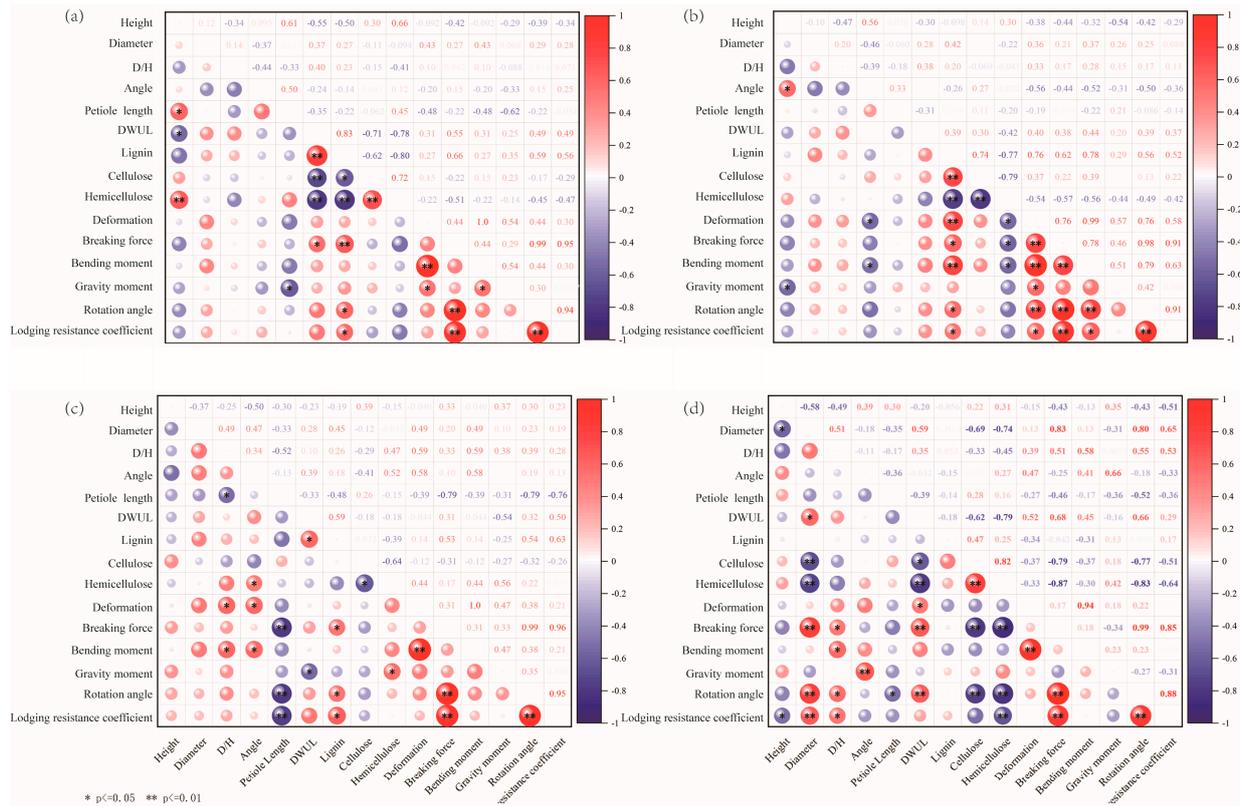


Figure 7. Correlation analysis of internode traits of HN60. (a) Control at podding stage; (b) S3307 treatment at podding stage; (c) control at seed filling stage; (d) S3307 treatment at seed filling stage. The size of the circle shows the correlation level, and the color of the circle shows positive or negative correlation; * and ** are $p \leq 0.05$ and $p \leq 0.01$, respectively.

3.6. Grain Yields and Yield Components

As shown in Table 3, under control conditions without S3307, the yield of HN84 reached the maximum at D30 (optimum density) and HN60 at D40 (optimum density). The S3307 treatment increased the soybean yield of HN84 under D20, D30, and D40 treatments by 2.5%, 8.3%, and 18.7%, respectively, and the number of grains per plant increased by 24.2%, 24.7%, and 9.8%, respectively, but had no significant effect on the 100-grain weight and the number of internodes. The analysis of variance showed that the density and S3307 treatment had a significant effect on the number of grains per plant and the yield of soybean plants ($p < 0.01$), and the density and S3307 significantly interacted, which affected the grain yield of HN84 soybean.

The S3307 treatment increased the soybean yield of HN60 under D20, D30, and D40 treatments by 14.7%, 5.5%, and 16.2%, respectively. Similar to HN84, the S3307 treatment significantly increased the number of grains per plant. The variance analysis revealed that the density and S3307 had significant effects on the grain number per plant and yield, but they had no interaction effect on the grain number per plant and soybean grain yield. Therefore, we speculated that the increase in the soybean yield under the S3307 treatment may be caused by the increase in the grain number per plant. It is worth noting that the application of S3307 seems to affect the lowest pod position of soybean. The internode of the first pod of the S3307-D20 treatment of Heinong84 and S3307-D30 treatment of Henong60 was significantly lower than that of the other treatments.

In order to verify the effect of S3307 on soybean yield, we re-measured the yield of HN84 in 2023 (Table 4). The results revealed that the S3307 treatment increased the soybean yield and grain number per plant and had a significant effect on the grain number per plant and yield of soybean plants ($p < 0.01$).

Table 3. Yield and yield components of different treatment in 2021.

Cultivar	Treatment	Pod Number per Plant	The Internode of the First Pod	Number of Internodes	Grain Number per Plant	100-Grain Weight (g)	Grain Yield (kg/hm ²)	
HN84	D20	CK	38.71 ± 0.71 bc	4.14 ± 0.26 ab	16.86 ± 0.26 a	94.29 ± 4.07 b	19.65 ± 0.5 ab	2906.00 ± 65.65 cd
		S3307	49.57 ± 1.65 a	3.71 ± 0.18 b	16.43 ± 0.37 a	117.14 ± 4.83 a	19.95 ± 0.27 ab	2981.00 ± 60.20 c
	D30	CK	36.00 ± 1.05 cd	4.14 ± 0.26 ab	17.00 ± 0.31 a	88.57 ± 2.20 b	20.42 ± 0.16 a	3076.94 ± 63.85 bc
		S3307	46.29 ± 1.96 a	4.00 ± 0.22 ab	16.71 ± 0.36 a	110.43 ± 4.33 a	20.15 ± 0.41 ab	3333.35 ± 110.60 a
	D40	CK	33.43 ± 0.84 d	4.57 ± 0.2 a	16.71 ± 0.29 a	86.86 ± 1.24 b	20.29 ± 0.10 a	2735.06 ± 60.44 d
		S3307	40.14 ± 0.91 b	4.00 ± 0.22 ab	17.14 ± 0.26 a	95.43 ± 4.47 b	19.21 ± 0.35 b	3247.88 ± 45.90 ab
	Analysis of variance							
	Density(D)		16.941 **	1.267ns	0.141 ns	7.547 **	1.621 ns	12.934 **
	S3307(S)		80.053 **	4.267 *	0.459 ns	33.402 **	1.743 ns	39.593 **
	D × S		1.560 ns	0.467 ns	1.094 ns	2.244 ns	2.201 ns	8.064 **
HN60	D30	CK	36.57 ± 1.69 cd	1.86 ± 0.14 ab	12.14 ± 0.26 a	101.00 ± 0.82 bc	15.43 ± 0.23 b	2906.00 ± 55.15 c
		S3307	43.71 ± 1.21 a	1.57 ± 0.20 b	12.29 ± 0.29 a	109.29 ± 2.63 a	16.40 ± 0.15 a	3333.35 ± 110.60 b
	D40	CK	35.43 ± 1.09 cd	2.29 ± 0.29 ab	11.86 ± 0.14 a	95.29 ± 4.33 c	16.47 ± 0.35 a	3247.88 ± 65.658 b
		S3307	41.00 ± 1.27 ab	2.14 ± 0.26 ab	11.86 ± 0.14 a	106.14 ± 1.81 ab	15.70 ± 0.36 ab	3615.33 ± 44.20 a
	D50	CK	33.86 ± 1.01 d	2.43 ± 0.30 ab	11.86 ± 0.34 a	82.14 ± 2.01 d	15.87 ± 0.25 ab	3162.41 ± 64.68 b
		S3307	38.00 ± 1.45 bc	2.14 ± 0.34 a	11.71 ± 0.18 a	99.00 ± 2.23 bc	16.26 ± 0.19 ab	3675.23 ± 50.16 a
	Analysis of variance							
	Density(D)		5.220 **	2.803 ns	1.86 ns	17.355 **	0.231 ns	21.121 **
	S3307(S)		27.774 **	1.230 ns	0.00 ns	33.588 **	0.796 ns	96.585 **
	D × S		0.660 ns	0.49 ns	0.18 ns	1.504 ns	5.551 *	0.905 ns

Note: The values in the table are the means ± standard error (*n* = 5); different letters indicate that the difference between treatments reached significance at the level of *p* < 0.05, and the treatments are compared longitudinally. ns is *p* > 0.05, * and ** are *p* ≤ 0.05 and *p* ≤ 0.01, respectively.

Table 4. Yield and yield components of different treatment in 2023.

Cultivar	Treatment	Number of Internodes	Grain Number per Plant	100-Grain Weight (g)	Grain Yield (kg/hm ²)	
HN84	D20	CK	19.25 ± 0.16 a	116.94 ± 1.33 bc	18.94 ± 0.30 a	2539.00 ± 77.96 c
		S3307	19.38 ± 0.26 a	128.13 ± 3.35 a	19.03 ± 0.26 a	2563.11 ± 38.56 c
	D30	CK	19.13 ± 0.30 a	113.94 ± 4.69 bc	19.10 ± 0.27 a	2805.26 ± 36.26 b
		S3307	19.25 ± 0.31 a	122.81 ± 4.86 ab	19.38 ± 0.25 a	2973.24 ± 69.55 a
	D40	CK	19.13 ± 0.23 a	111.00 ± 3.92 c	18.69 ± 0.32 a	2475.44 ± 25.04 c
		S3307	19.50 ± 0.19 a	114.81 ± 1.36 bc	19.09 ± 0.27 a	2576.44 ± 23.81 c
	Analysis of variance					
	Density(D)		0.170 ns	3.689 *	0.849 ns	33.128 **
	S3307(S)		1.061 ns	7.519 **	1.268 ns	5.761 *
	D × S		0.170 ns	0.563 ns	0.159 ns	1.042 ns

Note: The values in the table are the means ± standard error (*n* = 5); different letters indicate that the difference between treatments reached significance at the level of *p* < 0.05, and the treatments are compared longitudinally. ns is *p* > 0.05, * and ** are *p* ≤ 0.05 and *p* ≤ 0.01, respectively.

4. Discussion

Density planting is an important method used to increase soybean yield, but it is also used to increase the lodging rate [37]. The morphological, physiological, and mechanical properties of stems are closely related to lodging resistance. Stem length and plant height are two levers that constitute lodging moment and are the most important morphological characteristics for stem lodging [38,39]. In this study, with an increase in planting density, both varieties revealed an increase in plant height and a decrease in stem diameter and the D/H ratio, and the lodging resistance coefficient of the dwarf variety HN60 was higher, which may be caused by the smaller gravity moment [9,40].

The application of uniconazole helps to improve plant lodging resistance [27,28]; it is shown to reduce plant height and stem gravity height, shorten soybean internode length, and increase stem diameter (Figure 1, Tables 1 and 2). In addition, the S3307 treatment significantly reduced the petiole length of HN84 at the podding stage and increased the leafstalk angle between HN84 and HN60 at the podding stage (Figure 2). It was indicated that the adjustment of the S3307 treatment in terms of morphology is not limited to plant height; it also tends to have an effect on more compact plant types, which is conducive to enhancing plant lodging resistance. At the same time, the larger petiole angle made the plant obtain more light [41], which was conducive to the accumulation of dry matter and

the increase in the yield. However, the S3307 treatment had no significant effect on the petiole length and leafstalk angle of the two varieties at the seed filling stage, indicating that S3307 had timeliness in the regulation of soybean stem morphology, similar to the results of Han et al. [31].

Stem strength is the main index used to measure the lodging resistance of soybean plants [42,43]. The DWUL is positively correlated with stem strength, indicating that the increase in crop biomass is related to improvements in stem strength and lodging resistance [44]. In this study, the S3307 treatment significantly increased the dry weight of the stem, leaf, pod, and whole plant (Figure 3). The deposition of structural carbohydrates (i.e., lignin, cellulose, hemicellulose) can lead to thicker stem tissue [45], affecting the elastic modulus of the stem and thus affecting its bending strength [46,47]. Zheng et al. [10] and Hussain et al. [45] believed that the content of lignin and cellulose in basal internodes was positively correlated with the lodging resistance of stems. Yang et al. [5] believed that cellulose had a positive effect on the rigidity of maize stem and could improve the lodging resistance of maize. Hussain et al. [45] believed that the soybean stem strength was mainly determined by the content of lignin and cellulose. Compared with cellulose, the lignin content notably had an effect on stem strength. In this study, the S3307 treatment induced a significant increase in the content of the lignin, cellulose, and hemicellulose of HN84, but it had no significant effect on the content of the fiber composition of HN60 at the seed filling stage, indicating that the S3307 treatment had a more significant effect on the content of structural carbohydrates in the stems of HN84 (Figure S1). In addition, the results showed that the content of structural carbohydrates in stems was less under the optimum planting density (D30) of HN84, and the content was significantly increased under a high planting density (D40) (Figure 5a). We speculated that the increase in the structural carbohydrate content in stems only played a positive role in plant lodging resistance within a certain range. Correlation analysis showed that the content of the lignin and hemicellulose of the HN84 had a significantly negative correlation with the lodging resistance coefficient and breaking force under the S3307 treatment (Figure 6d), indicating that the increase in the structural carbohydrate content in the late growth stage was not conducive to enhancing the lodging resistance of soybean, which is different from the views of Tripathi and Sayre [48] and Hu et al. [49].

Increasing stem strength and decreasing plant height help to maintain plant morphology, increase aboveground biomass and stability [50,51], maximize resistance to lodging, and increase yield [52]. The number and length of internodes determine soybean plant height. It is generally believed that the genotype soybean varieties with a smaller plant height have higher lodging resistance [53–55], but the decrease in the number of internodes may lead to a decrease in the number of pods per plant and the number of grains per plant, thereby reducing the yield [56]. Therefore, dwarfing soybean plants is an available way to increase soybean yield, increasing lodging resistance and preserving internode number. In this study, the S3307 treatment reduced the height of soybean plants under different planting densities, increased the lodging resistance coefficient, and had a more significant effect on the lodging-resistant variety HN84. Han et al. [31] revealed that the S3307 treatment could increase the number of grains per plant and the number of pods per plant, which was one of the main factors causing yield changes, but it had no significant effect on the 100-grain weight. In this study, the S3307 treatment significantly increased the yield and grain number per plant of HN84 and HN60 (Tables 3 and 4). Correlation analysis revealed that the density and S3307 treatment had extremely significant effects on the yield and grain number per plant, but there was no interaction between them.

The lodging resistance coefficient at the podding stage was related to the yield of soybean plants (Table S2). Based on this, we established a model to explain the relationship between the indexes of soybean plants and the lodging resistance coefficient under the S3307 treatment (Figure 8). The results revealed that the S3307 treatment had a significant effect on the regulation of the morphological, physiological, and mechanical characteristics of the lodging-resistant varieties and could significantly improve their lodging resistance

coefficient. The S3307 treatment improved the lodging resistance and increased the lodging resistance coefficient by adjusting the morphology of soybean plant and the content of fiber composition in stem so as to achieve an increase in yield.

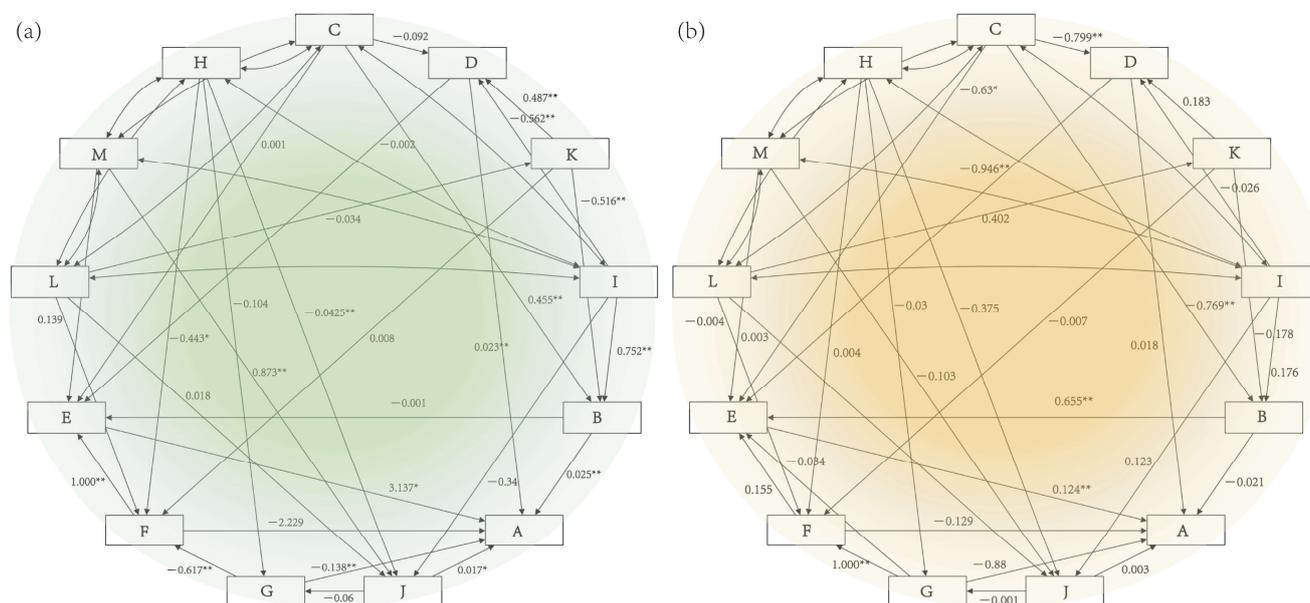


Figure 8. Path analysis of soybean internode traits and lodging resistance coefficient. (a) HN84; (b) HN60. The letter representative indicators in the figure are as follows: lodging resistance coefficient (A), lignin (B), hemicellulose (C), cellulose (D), stem breaking force (E), bending moment (F), gravity moment (G), plant height (H), stem diameter (I), D/H (J), leafstalk angle (K), petiole length (L), DWUL (M). * and ** are $p \leq 0.05$ and $p \leq 0.01$, respectively.

5. Conclusions

The application of uniconazole at the R1 stage significantly affected the lodging resistance and final yield of soybean plants. Uniconazole treatment significantly inhibited the growth of soybean plant height and petiole elongation, increased stem diameter and the D/H ratio, and increased lodging resistance by changing plant type. The uniconazole treatment significantly increased the dry matter weight of stems, pods, and leaves and promoted the accumulation of lignin, cellulose, and hemicellulose, thereby increasing the breaking force. The application of uniconazole increased the grain number per plant and ultimately increased the yield of soybean. In summary, these findings indicate that uniconazole can improve the lodging resistance and yield of the two varieties, and the effect on the high-stalk varieties is more significant.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy14040754/s1>, Figure S1: The percentage accumulation diagram of lignin, cellulose and hemicellulose content in soybean stem; Table S1: The soybean fresh weight (g); Table S2: Correlation coefficient between soybean lodging resistance coefficient and yield.

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