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ABSTRACT

Stalk lodging in maize causes yield and quality losses worldwide. This could potentially be prevented through breeding and improved crop management. Breeding efforts and management optimization are however, hampered by the lack of an internode growth model and an indicator for stalk lodging resistance. With this study, we aim to contribute to a solution for this problem. We report on the results of a two-year field study in which we measured and analyzed plant traits assumed to be related to stalk lodging resistance, in five cultivars. These traits include plant and basal internode morphology, dry matter constituents accumulation, and mechanical strength of basal internode. Results from a logistic regression analysis indicate that, the stalk lodging incidence was significantly affected by the development process of the basal internode. The rapid accumulation duration of lignin, internode plumpness and cellulose were found to be the most important contributors to mechanical strength of basal internode. The correlation between Rind penetration strength (PS) and stalk lodging rate was found to be higher than the correlation between bending strength (BS) and the stalk lodging rate. In addition, PS was found to be more stable than BS over development stages and years. Dry matter constituents accumulation in the basal internode, especially lignin accumulation, were found to be the dominant process determining the mechanical strength of the basal internode. Breeding and crop management strategies aiming to prolong the duration of rapid lignin and dry matter accumulation in the basal internode may thus significantly contribute to improved lodging resistance in future maize cultivars.

1. Introduction

Maize (*Zea mays* L.) is one of the world's most important grain crops. High productivity is required to meet rising demands for food, feed, and biofuel (Wen et al., 2019). Maize stalk lodging is a critical problem in modern maize production. It causes annual yield losses of up to 75 % (Shu-Yan et al., 2015), lowers grain quality (Dahiya et al., 2018), and raises harvest and drying costs (Jun et al., 2018). Furthermore, the frequency of weather events including extreme wind speeds, one of the primary causes of stalk lodging (Zhang et al., 2021), is increasing. A better understanding of the processes influencing maize stalk lodging is crucial for reducing the vulnerability of maize production to extreme weather conditions e.g. through genetic improvement and/or crop management optimization.

Maize lodging can be divided into root and stalk lodging. Root lodging occurs when plants lean more than a certain degree (30° or 45°) from a vertical position. Stalk lodging includes three types: snap-, split- and crease lodging. Of these, snap lodging is responsible for most yield

Abbreviations: BS, Stalk bending strength (N); CC, Cellulose content (mg/cm); ER, Ear ratio (%); IP, Internode plumpness (mg/cm); IL, Internode length (cm); IS, Internode cross-sectional area (mm^2); LC, Lignin content (mg/cm); NSC, Non-Structural carbohydrate; PS, Rind penetration strength (N/mm^2); R1, Silking; R2, Blister; R3, Milk; R4, Dough; R6, Physiological maturity; SLR, Stalk lodging rate (%); V6, The six-leaf stage of maize..

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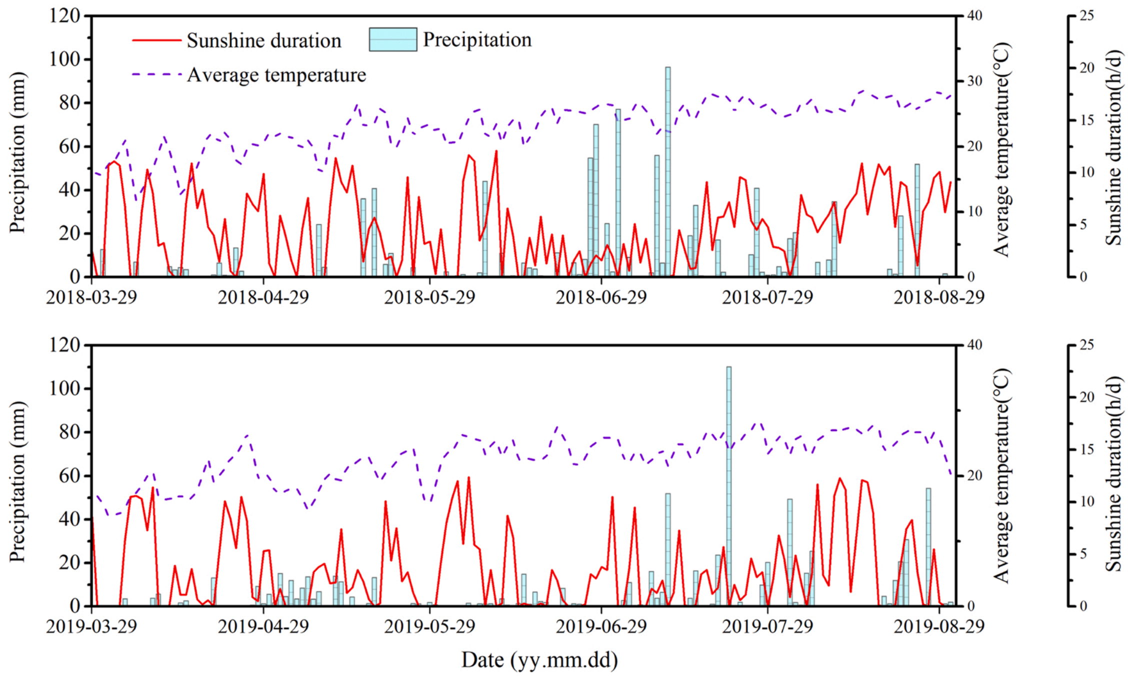

Fig. 1. Daily temperature (in ℃), daily precipitation (in mm), and sunshine duration (h/d) during the 2018 and 2019 growing seasons.

losses (Robertson et al., 2015). Stalk lodging may occur in basal internodes 2–7 but mainly occurs in internodes 2–5 (Xue et al., 2020c). Actual maize stalk lodging however mostly depends on lodging resistance, crop management and the wind forces the crop is subjected to.

Studies have shown that the maize lodging resistance is highly correlated with a number of specific plant morphological characteristics such as the anatomical structure of the basal internode, the structure and composition of the cell wall, the accumulation of structural and non-structural substances, and the mechanical strength of the stalk (XUE et al., 2017; Xue and Shun-Li, 2021). Changes in the internode cross-sectional area (IS) were found to be more than 10 times more sensitive to maximum stress levels tolerated than changes in the material qualities (biomass component) of the maize internode (Von Forell et al., 2015). The section modulus of the stalk was highly predictive of stalk strength. In addition, its predictive power appears to be largely unaffected by common confounding factors such as cultivar and planting density (Robertson et al., 2017). The variation of tensile properties found can be largely attributed to differences in the ratio of the area of the vascular bundle sheath and fiber cell wall thickness. Gradient distribution of bundle stiffness, which is found along the radial and axial directions of the stem, increases the stiffness of the basal stem and is a key component of maize lodging resistance (Huang et al., 2016). The key indicators affecting the maize lodging resistance were different in various growth stages. At R1, plant height had a positive effect on stalk breaking force, implying that taller plants have a higher breaking force. At R3, the coefficient of ear height and the dry weight per unit length of basal internodes were key indicators of stalk lodging resistance. At R6, the key indicators were the coefficient of the center of gravity height and plant fresh weight. After R6, the key indicator was the coefficient of the center of gravity height (Wang et al., 2020a, 2020b).

Bending tests are among the fastest and most replicable measurement to determine maize lodging resistance (Al-Zube et al., 2018). The failure patterns of "node-loaded stalks" are more similar to naturally occurring failure patterns than crush tests, rind penetrometry and four-point bending (Robertson et al., 2014). Sekhon et al. (2020) used a joint analysis to demonstrate that, among the phenotypes considered, the stalk bending strength measured by DARLING(a new platform) is the strongest predictor for the naturally occurring stalk lodging incidence in maize, followed by the rind penetrometer resistance and cellulose content. However, the integrated puncture score (IPS) was able to differentiate between the strongest and weakest cultivars in the elite cultivar data set whereas the traditional rind penetration method was not (Stubbs et al., 2020). There is little correlation between rind penetration strength and natural wind-induced lodging (Robertson et al., 2015). Meanwhile, approximately 63 % of the breaking force was explained by the average dry weight per unit length (DWUL) of the basal three internodes, ear height, and fresh weight of the basal three internodes at silking. At 35 days after silking, approximately 88 % of the difference in breaking force was explained by the plant height, ear ratio, crush strength (CS) of the fourth internode, average DWUL, and fresh weight per unit volume (FWUV) of the basal three internodes (Xue et al., 2020a).

Additionally, most of the stalk traits related to lodging resistance studied by predecessors are in a certain stage from R1 to R6. However, these traits in the basal internodes gradually develop after V6. The growth process and parameters will also affect the final level of the internode traits. Xue Jun et al. studied the growth dynamics of the third internode at different densities within 41 days after the V6. The results showed that decrease plant densities can increase lodging resistance under high plant density, can reduce the rate of rapid internode elongation, and can increase the rate of rapid cellulose and lignin accumulation (Xue et al., 2016). However, in this study the growth dynamics and lodging resistance of the remaining internodes was not analyzed. Internode elongation (Xue et al., 2020b), dry matter accumulation, and internode mechanical strength from V12 to R6 were also studied (Kamran et al., 2017) but there is still a lack of systematic research on the quantitative relationship between basal internode growth parameters and lodging resistance. The relationship between key growth parameters and indicators which can affect the crucial internode characteristics of maize lodging resistance are still unclear. Determination of these parameters / indicators is critical in timely taking field management measures to regulate plant growth and the formation of internode traits, enhance maize lodging resistance, and simplify the test indicators in relevant field experiment research.

There are many indicators related to maize stalk lodging. So far, there is inconsistency in the correlation and importance of each indicator and lodging resistance. The key indicators that determines stalk lodging resistance is still unknown. Based on the above, we hypothesized that the growth dynamics of maize basal internodes affect lodging resistance by affecting its fully-developed basal internode traits, directly. In this study, we selected 5 cultivars representing a wide range of morphological characteristics and lodging resistances to carry out two field trials in growth season 2018 and 2019. The morphological characteristics, dry matter constituents accumulation, and mechanical strength of each basal internode were measured over time from V6 to R6. The main objectives of this study were to (1) establish the growth model of each basal internode, and identify important growth parameters contributing to morphological characteristics, dry matter constituents accumulation, and mechanical strength of each basal internode; (2) to clarify the relationship between the mechanical strength of the basal internode and its main growth parameters; (3) to explore the key indicators affecting the mechanical strength of basal internodes. Findings from our study will provide an improved theoretical basis for breeding highly lodging resistant varieties and help to establish crop management measures reducing lodging, and thus enhance maize production.

2. Materials and methods

2.1. Location and maize cultivars

Both field experiments were conducted at the Wenjiang Experimental Farm, Sichuan Agricultural University, China (30°68'N, 103°85'E, and 539 m elevation) during the 2018 and 2019 maize growing seasons. The region was classified as "humid subtropical with a monsoon climate". The soil was a sandy loam with a bulk density of 1.12 g/cm^3 in the top 20 cm and 1.45 g/cm^3 at the other two depths examined (20–40 and 40–60 cm). Soil analysis in 2018 and 2019 at 0–20 cm depth gave the following characteristics: 28.28 g/kg organic matter, 1.9 g/kg total nitrogen, 122.96 mg/kg available nitrogen, 69.18 mg/kg available phosphorus, 57.45 mg/kg available potassium, and a pH of 7.8. The main meteorological conditions during the experiment were given in Fig. 1.

Four maize cultivars (ZH505, ZH6, XY1171 and YHD6) with a wide range of lodging resistance and large differences in the morphological characteristics were planted in 2018. Based on the results for 2018, four widely planted maize cultivars (ZH505, RB9, XY1171 and YHD6) with diverse lodging resistance were planted in 2019.

2.2. Experimental design and management

The four cultivars per trial were grown in a randomized complete block design with three replications in 2018 and 2019 growing seasons. In each replication, each cultivar was planted in plots (plot length, 13 m; plot width 3.2 m; plot area, 41.6 m^2) with a row length of 13 m and row-to-row distance of 0.8 m (plant spacing, 23.8 cm; sowing depth, 5 cm) at a planting density of 52500 plant ha^{-1}. To prevent any edge effect on the cultivars planted on the outer sides of the experimental plot, non-experimental maize cultivars (i.e. border) were planted on all two sides of the experimental plot.

The sowing date was 2018-03-29 and 2019-03-30. For each experiment, 600 kg/ha compound NPK (15:15:15) mineral fertilizer was added at the sowing and an additional 90 kg/ha nitrogen was applied after 30 days of emergence. Standard agronomic practices were followed for crop management.

2.3. Sampling strategy for internodes morphology and mechanical strength

Maize plants were randomly selected for sampling after every 7days from V6 to R1 (sampling days alter to after 15 d per time from R2 to R6). The first elongated internode was 2 cm long. The maize plants were cut at ground level, and the position of each elongated internode above the soil surface was measured on each stalk. For each cultivar, measurements were taken six times (6 plants per plot × 3 replications). Rind puncture tests were performed on the same set of plants that were tested in bending. Samples for morphology, carbohydrate accumulation, and metabolic data were acquired from the same plants that were subjected to bending tests and rind puncture tests.

The length of each internode (1st to 7th) was measured from the adjacent nodes. The minor diameter and major diameter were measured with a Vernier caliper at the midpoint of the internode at its narrowest and widest side cross section. The internode cross-sectional area was calculated through the following equation:

$$IS = \pi \times \tfrac{1}{2} a \times \tfrac{1}{2} b$$

Where *IS* was the internode cross-sectional area in mm^2, *a* and *b* were the major diameter and minor diameter in mm, respectively.

After measuring internode morphology, we determined the Rind Penetrating strength (PS) and Bending strength (BS) of the third, fifth and seventh elongated internode above the soil by using an AWOS-SL04 stalk strength tester (Xue et al., 2020a) according to the methods of Xue et al. During PS measurements, the stalk was held firmly and the needle shaped probe (1 cm long, 1 mm^2 cross-sectional area) was slowly thrust perpendicularly into the stalk until the stop bar touched the stalk. Before measuring BS, the plates were adjusted to a 10 cm interval. Next, a "U"-shaped probe was vertically aligned to the internode and slowly pressed downwards until the internode was broken. The maximum value of the force applied was the BS. The values of PS and BS (unit = N) were displayed on the screen of the tester. All measurements were taken at the middle of each internode at its widest side. The measurements were performed by the same person to minimize the experimental errors.

Before the stalk lodging rate (Ahmad et al., 2018) and grain yield were measured, the plant height and ear height of 20 plants in each plot were measured at physiological maturity. Plant height (from the ground to the top of the tassel) and ear height (from the ground to the node bearing the ear) were measured by using a ruler. The ear height coefficient was calculated through the following equation:

$$\text{Ear ratio } (\%) = \text{Ear height/Plant height} \times 100\ \%$$

2.4. Internode plumpness

The 3rd, 5th, and 7th internodes were cut from the nodes after measuring the mechanical strength. Internode dry mass was weighed after drying them at 105 °C (2 h) and 80 °C (70 h) to get constant weight. The internode Plumpness (Ahmad et al., 2021) was determined according to the following equation:

$$\text{Internode plumpness (mg/cm)} = \text{Internode dry mass/Internode length}$$

2.5. Structural carbohydrate contents

The 3rd, 5th, and 7th internodes were cut from the 0.5 cm top and bottom of internodes after measuring the internode Plumpness. The samples were subsequently dried at 80 ℃ in a forced air dryer to attain constant weight after determination of the dry mass. Dried internodes were then milled by using a laboratory grinder, sieved (0.5 mm), and the flour obtained was stored in plastic bags in a desiccator at 4 ℃ until further analysis. The cellulose content was measured by the anthrone colorimetric method (Zhang, 2020), and the lignin content was measured by the modified Sancho semi-quantitative method (Moreira-Vilar et al., 2014; Sancho et al., 1996; Yang Dong-dong, 2006).

We related the internode length, the internode cross-sectional area, internode plumpness, PS, BS, and structural carbohydrate contents to the time (days after V6) during 2018 and 2019. The Logistic equation was as follows:

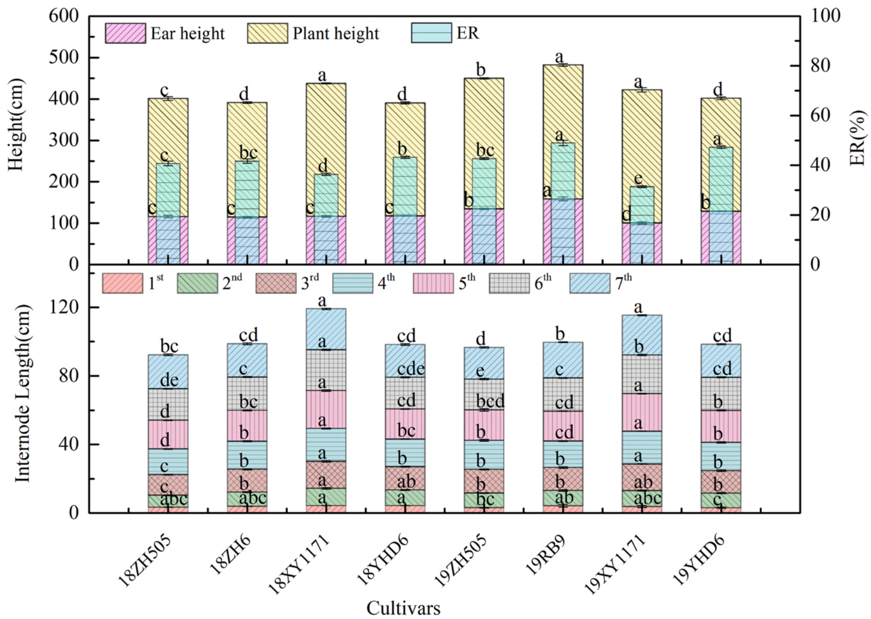

Fig. 2. Differences in plant height and basal internode length of five maize cultivars tested in 2018 and 2019. Plant height and ear height were measured at R6, internode length was the average of the last 3 measurements. Ear ratio (ER) was Ear height/Plant height× 100. 1st, 2nd, 3rd, 4th, 5th, 6th, 7th represent the respective above ground internodes. 18ZH505, 18ZH6, 18XY1171 etc. represent the cultivar names preceded by the year of cultivation. Different lowercase letters indicate significant differences at the 0.05 level.

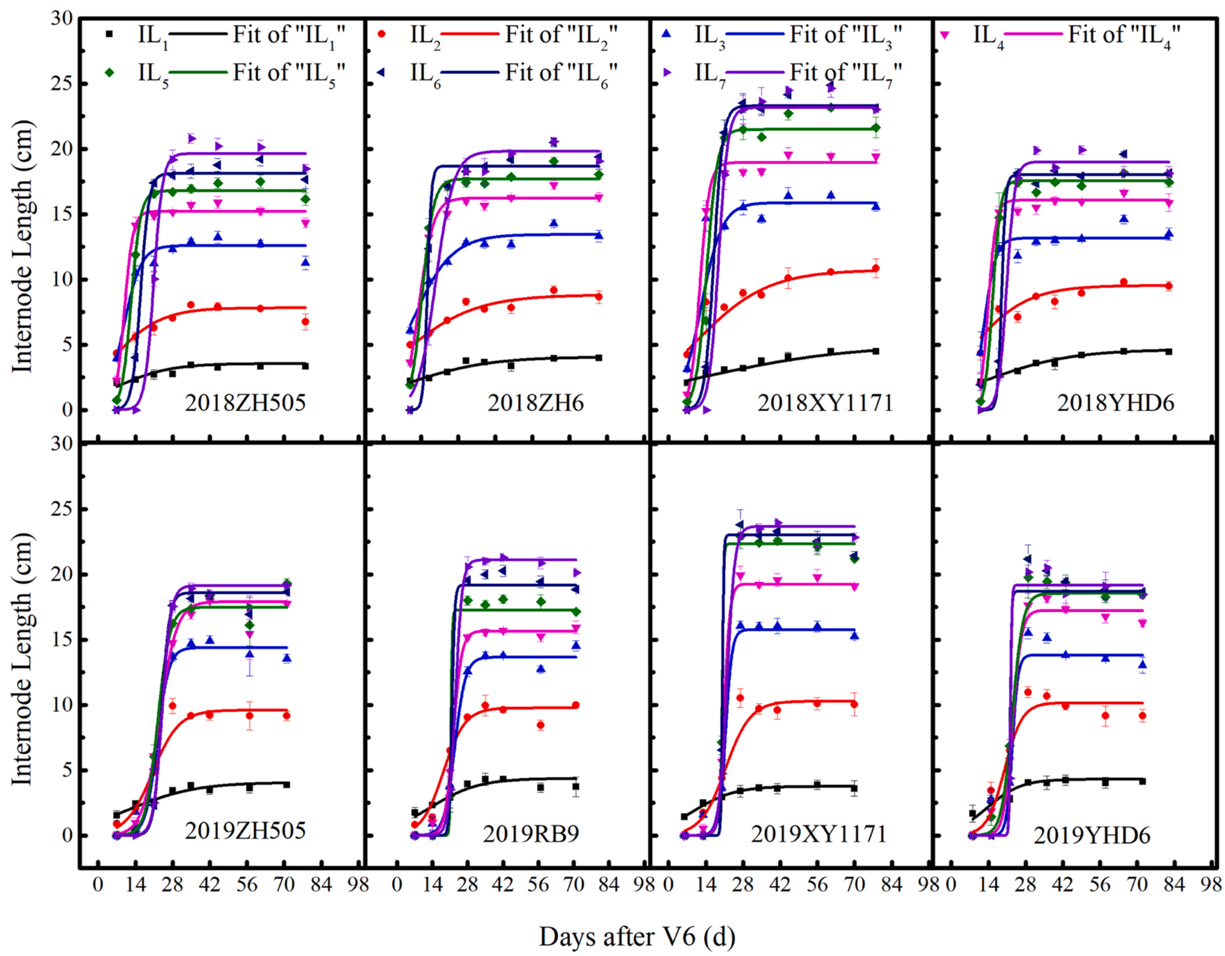

Fig. 3. Dynamics of maize basal internode length development of five cultivars in 2018–2019. IL_1, IL_2, IL_3, IL_4, IL_5, IL_6, IL_7 represent the internode length of the respective above ground internodes. 2018ZH505, 2018ZH6, 2018XY1171 etc. represent the cultivar names preceded by the year of cultivation. V6 indicates the six-leaf stage of maize.

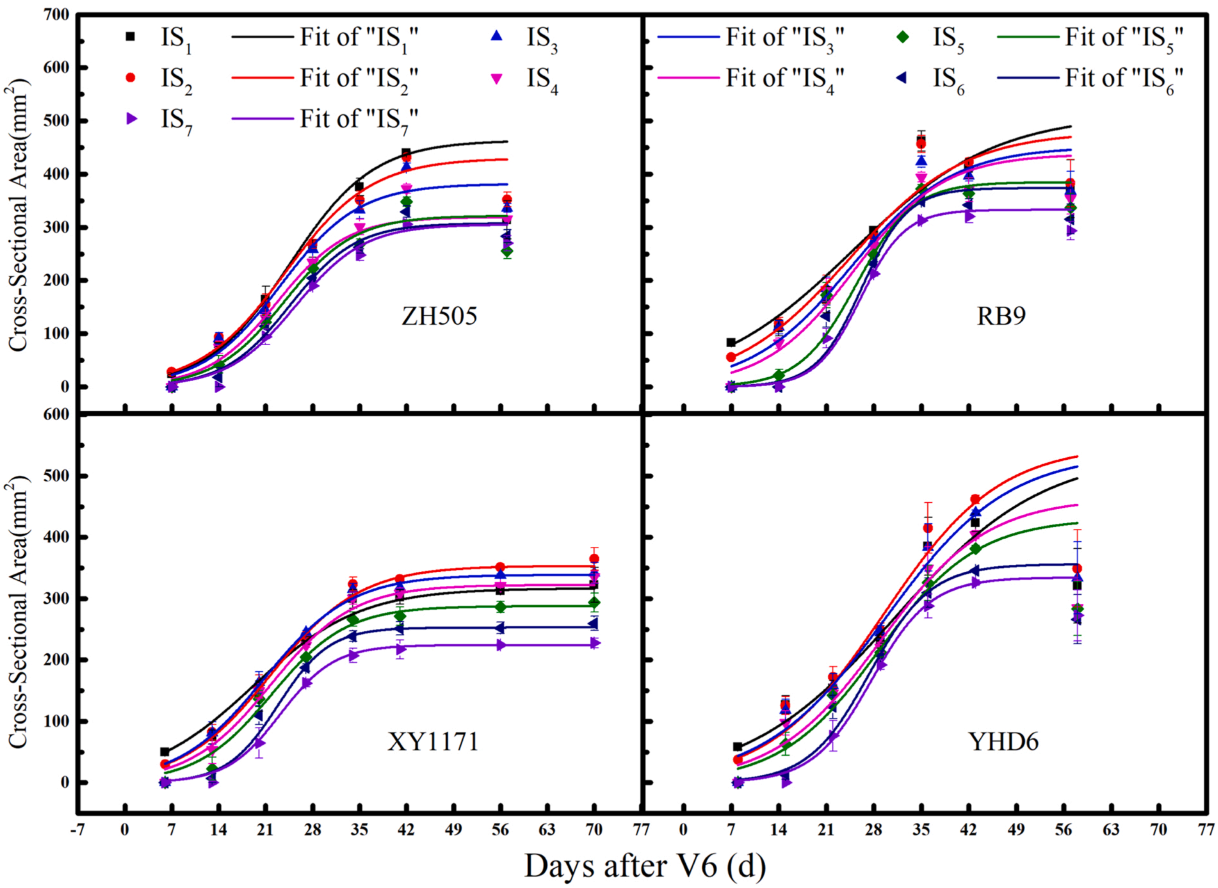

Fig. 4. Dynamics of basal internode Cross-sectional areas development of four cultivars in 2019. IS_1, IS_2, IS_3, IS_4, IS_5, IS_6, IS_7 represent the respective above ground internode Cross-sectional areas. V6 indicates the six-leaf stage of maize.

$$y = a/(1 + be^{-kt}) \quad (1)$$

Where t was the number of days after V6, y was either the internode length (IL), internode cross-sectional area (IS), internode plumpness, PS, BS, and structural carbohydrate contents, and a was the maximum theoretical value of internode traits. The parameters b and k were constants related with environmental conditions of the field. Using the equations given below, the initiation (t_1) and termination (t_2) times of rapid internode development, the duration of these periods (T), the time to reach the maximum development rate (T_{max}), the maximum rates of rapid internode development (V_{max}) and average development rate (V_t) were calculated.

$$t_1 = -\frac{1}{k}\ln\frac{2+\sqrt{3}}{b} \quad (2)$$

$$t_2 = -\frac{1}{k}\ln\frac{2-\sqrt{3}}{b} \quad (3)$$

$$V_{max}=(a*k)/4 \quad (4)$$

$$T=t_2-t_1 \quad (5)$$

$$V_t = \frac{y2-y1}{T} \quad (6)$$

$$T_{max} = \ln b / k \quad (7)$$

2.6. Statistics

Statistical analysis was conducted by using Statistical Analysis System (SAS) 9.4. Means were tested by performing the least significant difference tests at the $P < 0.05$ level (LSD 0.05). Origin 9.0 was used for data display and logistic regression analysis. Pooled data was expressed as mean ± standard error (S.E.).

Correlation, regression, and pathway analysis were calculated to determine the relationship between the development parameters of internode length, the internode cross-sectional area, internode plumpness, PS, BS, and structural carbohydrate contents, respectively. The contribution rate (C) of each index (parameters) was calculated according to the Pearson Correlations (R) and the Standardized Coefficients (Daoxu, 2006).

3. Results

3.1. Variation in plant morphology parameters

There were significant differences in the plant height, ear height, and basal internode length between the five maize cultivars studied (Figs. 2–4). XY1171 gave the highest plants with the longest basal internode length, lowest ear height, smallest ear ratio and internode cross-sectional area. RB9 plants were similar in height to XY1171 plants in 2019, but had higher ear height and ear ratio than XY1171. YHD6 plants had the highest stem diameter and ear ratio. The L/S ratio (internode length/cross-sectional area) of XY1171 was the largest, followed by ZH505 and YHD6, and the smallest was RB9.

The final length of the internodes in each maize cultivar (the average of the last 3 measurements) showed a gradual increase with the rise of

Table 1
Growth parameters of internode length (IL) and cross-sectional area (IS) of maize in 2018–2019. 1st, 2nd, 3rd, 4th, 5th, 6th, 7th represent the respective above ground internodes. a is the maximum theoretical value of internode length (cm) and cross-sectional area (mm^2), t_1 and t_2 are the initiation and termination times of rapid elongation and thickening(d), respectively. T is the duration of rapid elongation and thickening (d), V_{max} is the maximum elongation rate ($cm\ d^{-1}$) and thickening rate ($mm^2\ d^{-1}$), V_t is the average elongation rate ($cm\ d^{-1}$) and thickening rate ($mm^2\ d^{-1}$), T_{max} is the time reached Vmax after V6(d). Different letters to the right of the value indicate significant differences at $p < 0.05$ as determined by the LSD test in different cultivars in the two years.

Traits	internode	a	t_1	t_2	T	V_{max}	V_t	T_{max}
IL	1st	4.21 ± 0.16 f	3.22 ± 3.22c	28.54 ± 3.47a	34.56 ± 6.44a	0.10 ± 0.01d	0.07 ± 0.01d	11.26 ± 0.91d
	2nd	9.58 ± 0.32e	14.37 ± 4.18ab	24.32 ± 1.31ab	20.89 ± 3.88b	0.40 ± 0.08d	0.12 ± 0.02 cd	13.87 ± 2.41 cd
	3rd	14.09 ± 0.42d	12.90 ± 2.90b	20.63 ± 1.64b	7.73 ± 1.92c	1.70 ± 0.36 cd	0.34 ± 0.07bcd	16.77 ± 2.15bc
	4th	17.06 ± 0.54c	14.80 ± 1.97ab	19.79 ± 2.04b	5.00 ± 0.65c	2.51 ± 0.33bcd	0.41 ± 0.05bcd	17.30 ± 1.98abc
	5th	18.64 ± 0.74bc	15.99 ± 1.63ab	20.02 ± 1.42b	4.04 ± 0.76c	6.35 ± 2.64ab	0.93 ± 0.37ab	18.00 ± 1.48abc
	6th	19.69 ± 0.77ab	18.37 ± 1.16ab	20.79 ± 0.97b	2.42 ± 0.54c	8.61 ± 2.45a	1.22 ± 0.32a	19.58 ± 1.04ab
	7th	20.59 ± 0.66a	19.33 ± 0.89a	23.63 ± 0.55ab	4.30 ± 0.79c	4.92 ± 1.85abc	0.69 ± 0.28abc	21.48 ± 0.62a
IS	1st	435.02 ± 29.25a	15.14 ± 1.33c	34.51 ± 1.95a	19.38 ± 2.04a	15.54 ± 1.46a	0.11 ± 0.01d	24.83 ± 1.32a
	2nd	438.69 ± 23.58a	15.68 ± 1.00c	33.78 ± 1.24a	18.10 ± 1.04a	16.19 ± 0.97a	0.11 ± 0.01d	24.73 ± 1.00a
	3rd	412.62 ± 23.51a	15.61 ± 1.12c	33.13 ± 1.44a	17.52 ± 1.12a	15.75 ± 0.96a	0.11 ± 0.01d	24.37 ± 1.16a
	4th	379.10 ± 19.66ab	16.59 ± 1.04bc	32.83 ± 1.19a	16.24 ± 0.89ab	15.55 ± 0.85a	0.12 ± 0.01 cd	24.71 ± 1.02a
	5th	347.88 ± 18.46bc	18.01 ± 0.95abc	31.86 ± 1.18a	13.84 ± 0.87bc	16.91 ± 1.25a	0.14 ± 0.01bc	24.93 ± 0.98a
	6th	320.20 ± 16.91bc	19.31 ± 0.78ab	31.26 ± 0.89a	11.96 ± 0.78c	18.08 ± 1.50a	0.16 ± 0.01ab	25.29 ± 0.74a
	7th	295.31 ± 16.44c	20.57 ± 0.75a	31.52 ± 0.83a	10.95 ± 0.70c	18.12 ± 1.31a	0.18 ± 0.01a	26.04 ± 0.71a

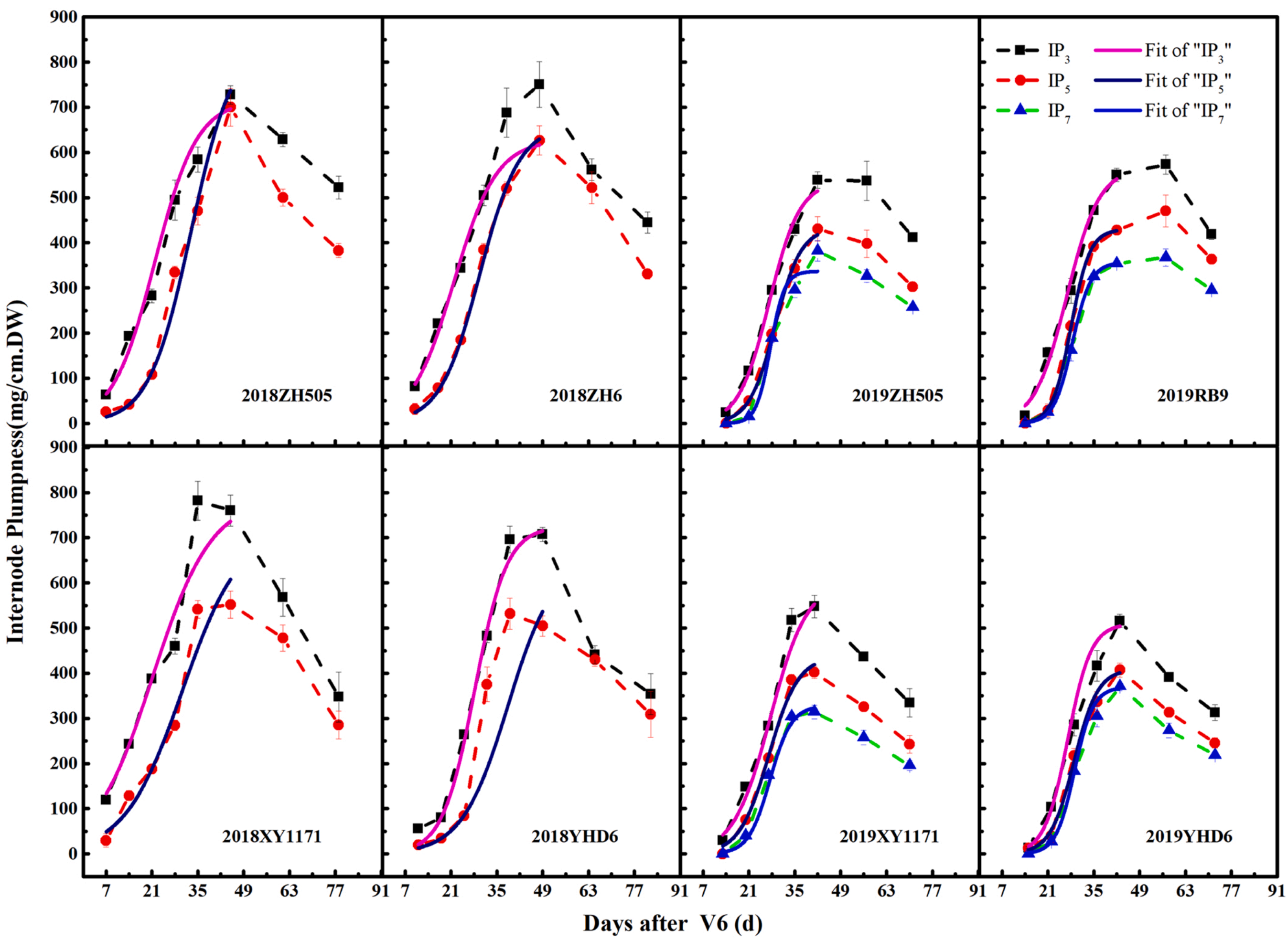

Fig. 5. Dynamics of basal internode plumpness development of five cultivars in 2018–2019. IP_3, IP_5, IP_7 represent the internode plumpness of third, fifth, seventh internode above the ground, respectively. 2018ZH505, 2018ZH6, 2018XY1171 etc. represent the cultivar names preceded by the year of cultivation. V6 indicates the six-leaf stage of maize.

internode position (Fig. 4). There was a linear relationship between internodes morphology (internode length (y_{IL}) and cross-sectional area (y_{IS})) and internodes position (x) based on the average of the five cultivars in two years. The regression equations were $y_{IL}= 3.5986 + 2.7579x$ (R^2 =0.8805 **) and $y_{IS}= 415.3698–18.5183x$ (R^2 =0.8882 **), respectively. With the internode position rising by 1, the average length of the internode increased by 2.76 mm, and the internode cross-sectional area decreased by 18.52 mm^2.

Table 2
Growth parameters of basal internode IP, LC and CC in 2018–2019. IP is the internode plumpness (dry weight per unit length), LC is the lignin content per unit length, CC is the cellulose content per unit length. 3rd, 5th, 7th represent the third, fifth, seventh internode above the ground, respectively. a is the maximum theoretical value of IP, LC and CC (mg cm^{-1}), t_1 and t_2 are the initiation and termination times of rapid accumulation of IP, LC and CC (d), respectively. T is the duration of rapid accumulation of IP, LC and CC (d), V_{max} is the maximum accumulation rate of IP, LC and CC (mg cm^{-1} d^{-1}), V_t is the average accumulation rate of IP, LC and CC (mg cm^{-1} d^{-1}), T_{max} is the time reached V_{max} of IP, LC and CC after V6(d). Different letters to the right of the value indicate significant differences at $p < 0.05$ as determined by the LSD test in different cultivars in the two years.

Traits	Internode	a	t_1	t_2	T	V_{max}	V_t	T_{max}
IP	3rd	633.87 ± 35.22a	17.71 ± 1.73b	32.71 ± 0.61b	15.00 ± 1.53a	28.89 ± 1.85a	0.13 ± 0.01b	25.21 ± 1.05b
	5th	574.53 ± 59.37a	23.40 ± 1.08a	37.65 ± 1.96a	14.24 ± 1.89a	27.72 ± 1.95a	0.15 ± 0.02b	30.52 ± 1.27a
	7th	347.86 ± 8.63b	24.48 ± 0.45a	31.76 ± 0.48b	7.28 ± 0.57b	32.18 ± 2.69a	0.26 ± 0.02a	28.12 ± 0.37a
LC	3rd	25.07 ± 1.97a	22.07 ± 1.17b	35.76 ± 0.94a	13.69 ± 0.74a	1.21 ± 0.07a	1.21 ± 0.07a	28.92 ± 0.99a
	5th	16.20 ± 1.32b	24.86 ± 0.76a	35.61 ± 0.87a	10.75 ± 0.63b	1.02 ± 0.10a	1.02 ± 0.10a	30.23 ± 0.76a
	7th	13.06 ± 1.06b	26.43 ± 0.78a	34.60 ± 1.11a	8.17 ± 0.67c	1.05 ± 0.02a	1.05 ± 0.02a	30.52 ± 0.90a
CC	3rd	180.56 ± 10.35a	21.34 ± 1.31b	33.53 ± 0.71ab	12.19 ± 1.01a	9.99 ± 0.64a	0.16 ± 0.01b	27.44 ± 0.92b
	5th	125.37 ± 10.61b	24.78 ± 0.85a	35.53 ± 0.88a	10.75 ± 0.95a	8.09 ± 0.89a	0.19 ± 0.02b	30.16 ± 0.72a
	7th	93.64 ± 9.45c	26.06 ± 0.70a	32.50 ± 0.76b	6.44 ± 0.53b	9.62 ± 0.81a	0.30 ± 0.02a	29.28 ± 0.68ab

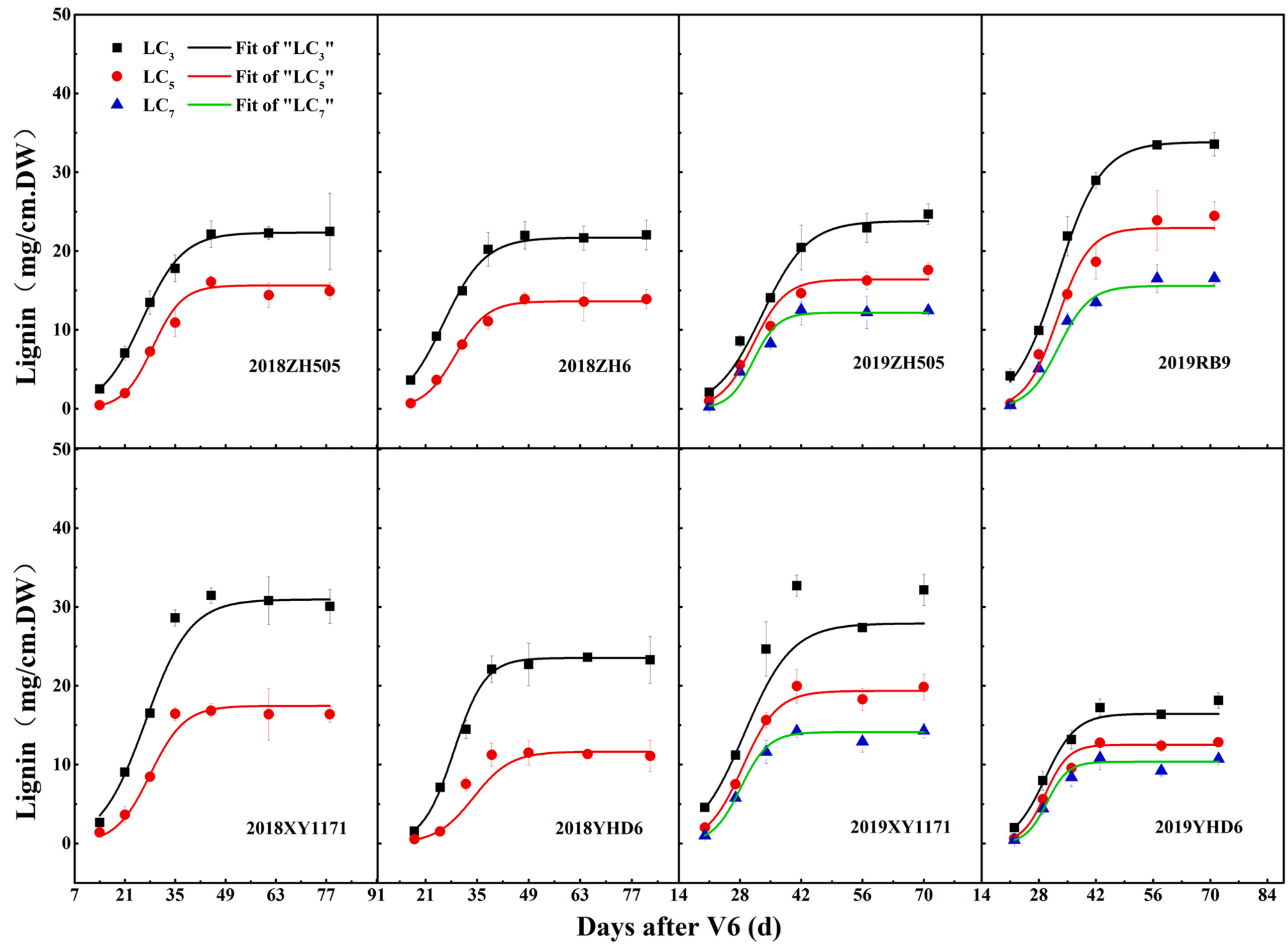

Fig. 6. Dynamics of lignin accumulation per unit length in basal internodes of five cultivars in 2018–2019. LC_3, LC_5, LC_7 represent the lignin content of third, fifth, seventh internode above the ground, respectively. 2018ZH505, 2018ZH6, 2018XY1171 etc. represent the cultivar names preceded by the year of cultivation. V6 indicates the six-leaf stage of maize.

3.2. Morphological development of basal internodes

The development of the length and cross-sectional area of each basal internode of the 5 cultivars was conformed to the Logistic model. All the fitting equations attained higher significant levels ($R^2_{IL} = 0.7743^{**} \sim 0.9969^{**}$ and $R^2_{IS} = 0.5701^{**} \sim 0.9967^{**}$). The IL and IS of each basal internode began to develop in turn from the day after V6 (Figs. 3 and 4, and Table 1). The initiation and termination times of rapid development of the IL and IS were also followed one by one from bottom to top. From the initiation time of 1st to the termination time of the 7th internode, the duration of the rapid development of length lasted for about 20 days, and for the internode cross-sectional area, it was lasted for about 16 days. The overall performance of the same internode was to first elongate and then gradually thicken.

With the rise of internodal position, the initiation time (t1) of the IL and IS for each basal internode in the rapid development stage was

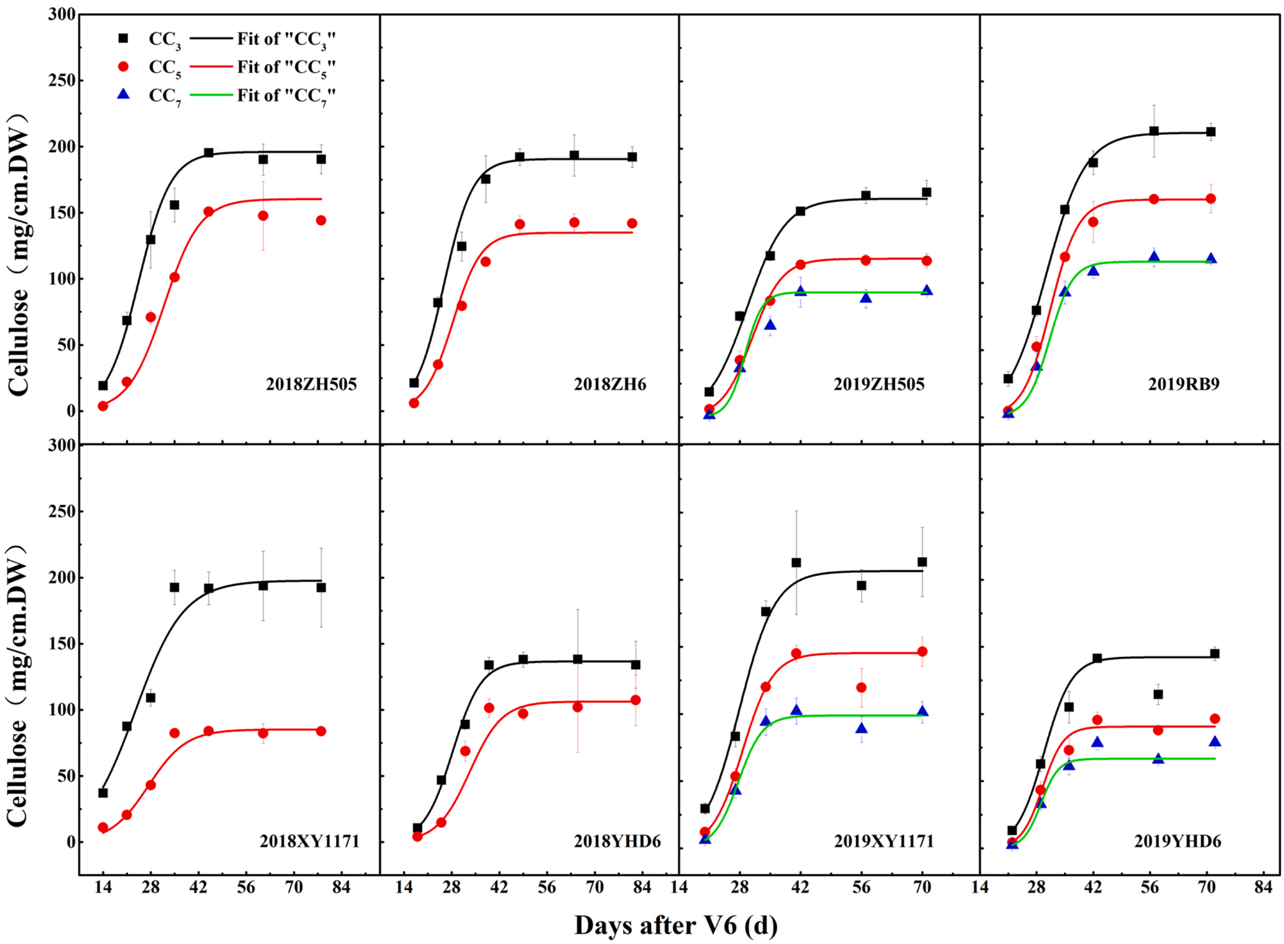

Fig. 7. Dynamics of cellulose accumulation per unit length in basal internodes of five cultivars in 2018–2019. CC_3, CC_5, CC_7 represent the cellulose content of third, fifth, seventh internode above the ground, respectively. 2018ZH505, 2018ZH6, 2018XY1171 etc. represent the cultivar names preceded by the year of cultivation. V6 indicates the six-leaf stage of maize.

delayed; but the development rate was accelerated, and the duration of the rapid development (T) was shortened. Regression analysis showed that with the internode rise by 1, the initiation time of rapid development of the IL and IS was delayed by 1.94d and 0.99d, respectively, and the average rate of rapid development of the IL and IS was increased by 0.10 cm/d and 0.012 mm^2/d, respectively.

3.3. Dynamics of dry matter constituents accumulation in basal internodes

Due to 190.5 h more sunshine from April to August, the basal internode plumpness (IP) in 2018 were higher than those in 2019 (Fig. 1). IP showed a trend of first increasing and then decreasing with the development of the internodes (Fig. 5). About 10 days after silking, IP increased to the maximum, and then decreased gradually. IP was decreased with the rise of the internode position.

The IP development of each internode followed the logistic model during the period from V6 to 10 days after silking (Fig. 5, $R^2 = 0.7512^{**} \sim 0.9999^{**}$). The relevant growth parameters were shown in Table 2.

After V6, the accumulation of lignin and cellulose per unit length of internodes was increased gradually and then tended to be stable. The accumulation dynamic of lignin and cellulose also followed the logistic model ($R^2_{LC} = 0.8547^{**} \sim 0.9972^{**}$, $R^2_{CC} = 0.9163^{**} \sim 0.9988^{**}$). The effect of internode position, cultivar, and year in the accumulation of lignin and cellulose was significant (Figs. 6 and 7). With the rise of the internode position, the accumulation of lignin and cellulose per unit length was decreased in the later stage of development. Overall, the accumulation of lignin and cellulose per unit length of RB9 was highest, followed by XY1171 while YHD6 was the lowest.

3.4. Variation of mechanical strength in basal internodes

There were significant effects of cultivar, year and internode position on rind penetration strength (PS) and stalk bending strength (BS) (Figs. 8 and 9). With the rise of the internode position, the mechanical strength of basal internodes decreased, especially the BS. To compare the mechanical strength of five tested cultivars, RB9 was the highest both in PS and BS. YHD6 was lower than the others, especially in its PS. The PS of XY1171 was higher, but the BS was lower, especially in 2019. The PS and BS in 2018 were comparatively higher than in 2019, especially the BS.

The development of PS at the basal internode followed the logistic growth curve ($R^2 = 0.8559^{**} \sim 0.9969^{**}$, Fig. 8) from V6 to physiological maturity (R6). The dynamic process of BS formation was the same as IP. The development of BS at the basal internode can be considered as a logistic model ($R^2 = 0.5535^{**} \sim 0.9921^{**}$, Fig. 9) from the 7 days after V6 to the 10 days after silking.(Table 3).

3.5. Relationship between basal internode traits and growth parameters

The morphological characteristics, dry matter constituents accumulation, and mechanical strength of the basal internode were highly

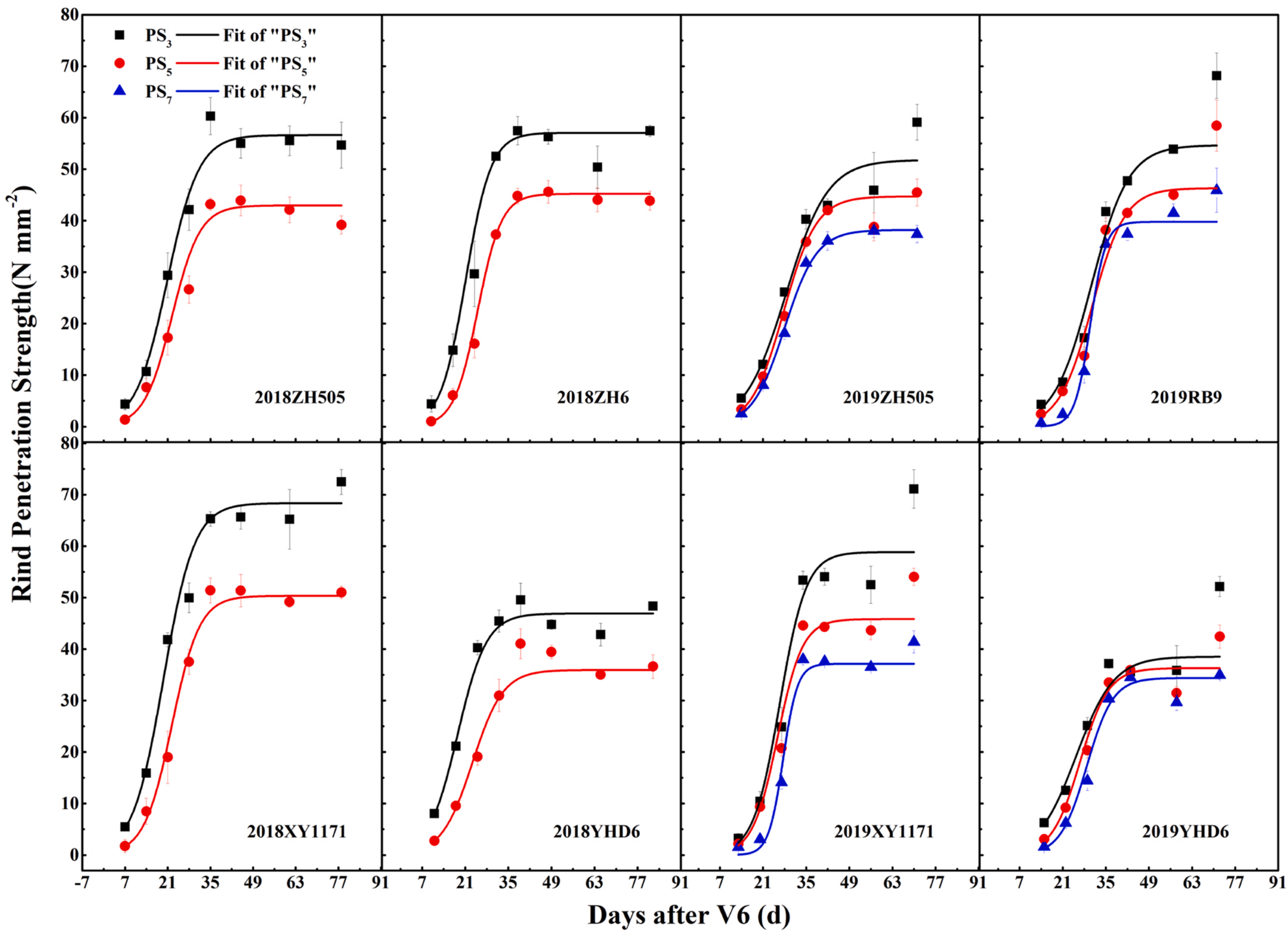

Fig. 8. Dynamics of Rind penetration strength formation in basal internodes of five cultivars in 2018–2019. PS_3, PS_5, PS_7 represent the penetration strength of third, fifth, seventh internode above the ground, respectively. 2018ZH505, 2018ZH6, 2018XY1171 etc. represent the cultivar names preceded by the year of cultivation. V6 indicates the six-leaf stage of maize.

correlated with their duration and average rate of the rapid development (Table 4). Most of the correlation coefficients attained a significant, some even highly significant levels. Further analysis showed that the duration of rapid development was the highest contributor to the internode length, cross-sectional area, IP, and lignin content per unit length, but the average rate of rapid development was the highest contributor to PS, BS, and cellulose content per unit length.

3.6. Stalk lodging rate (SLR) and grain yield

In this field experiment, the stalk lodging mainly occurred from the blister stage (R2) to the physiological maturity stage (R6). Due to more heavy rain during this period, the stem lodging rate in 2018 were higher than that in 2019 (Fig. 1). There were significant differences in the stalk lodging rate of the five cultivars (Table 5). To compare the grain yield and stalk lodging rates of the five cultivars, ZH505 had the highest yield and SLR, followed by YHD6. The resistance against stalk lodging in RB9 was the highest, but the grain yield was lower. The lower lodging resistance was an important factor affecting the yield potential of high-yield cultivars such as ZH505, YHD6 and XY1171. Correlation analysis showed that there was a significantly negative correlation between SLR and PS. The correlation coefficient was −0.731*. This indicates that enhancing the mechanical strength of maize basal internodes could improve lodging resistance.

3.7. Relationships between the mechanical strength of basal internodes, morphological characteristics, dry matter constituents accumulation

Correlation analysis showed that the mechanical strength of the basal internode was significantly correlated with the morphological characteristics (IL and IS) and dry matter constituents accumulation (IP, lignin, and cellulose content) from the V6 to R6 (Table 6). The correlation coefficient of dry matter constituents accumulation reached a highly significant level, especially. Further analysis showed that IP was the highest contributor to the BS during the whole growth stage. IP also was the highest contributor to the PS from V6 to silking (R1). But the lignin content became the highest contributor to the PS after the silking and during the whole growth stage. Meanwhile, lignin content was main contributor to the PS and BS formation before silking. The cellulose content also contributed in PS after the silking and during the whole growth stage. But the contribution rate was far less than the lignin content.

Further analysis found that the mechanical strength of maize basal internodes was not only correlated with its morphological characteristics and dry matter constituents accumulation (Table 7) but also in correlation with its growth parameters. Among all growth parameters, the duration of the rapid accumulation of lignin content was the highest contributor to the PS and BS during the whole growth stage, while the duration of the rapid accumulation of IP was the second-highest contributor to the BS formation. The average rate of the rapid accumulation of IP and the duration of the rapid accumulation of cellulose

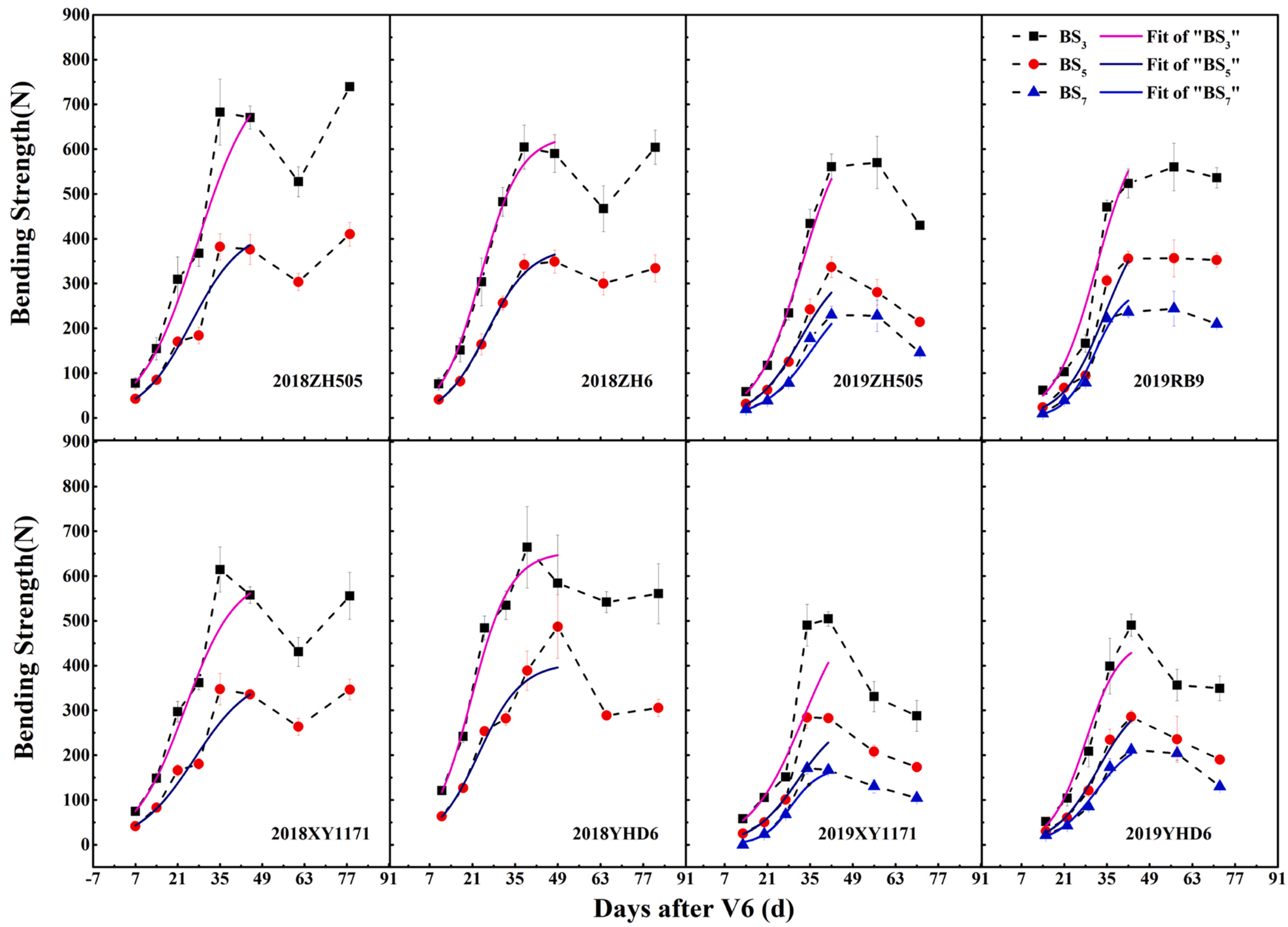

Fig. 9. Dynamics of Stalk bending strength formation at the basal internodes of five cultivars in 2018–2019. BS_3, BS_5, BS_7 represent the bending strength of third, fifth, seventh internode above the ground, respectively. 2018ZH505, 2018ZH6, 2018XY1171 etc. represent the cultivar names preceded by the year of cultivation. V6 indicates the six-leaf stage of maize.

Table 3
Growth parameters of basal internode mechanical strength in 2018–2019. PS is Rind penetration strength, BS is Stalk bending strength. 3rd, 5th, 7th represent the third, fifth, seventh internode above the ground, respectively. a is the maximum theoretical value of PS and BS (N), t_1 and t_2 are the initiation and termination times of rapid formation of PS and BS (d), respectively. T is the duration of rapid formation of PS and BS (d), V_{max} is the maximum formation rate of PS and BS (N d^{-1}), V_t is the average formation rate of PS and BS (N d^{-1}), T_{max} is the time reached V_{max} of PS and BS after V6(d). Different letters to the right of the value indicate significant differences at $p < 0.05$ as determined by the LSD test in different cultivars in the two years.

Traits	Internode	a	t_1	t_2	T	V_{max}	V_t	T_{max}
PS	3rd	54.11 ± 3.11a	16.89 ± 1.32b	30.81 ± 1.86a	13.92 ± 0.88a	2.66 ± 0.26a	0.14 ± 0.01b	28.56 ± 1.55a
	5th	43.46 ± 1.76b	19.33 ± 0.90b	31.61 ± 1.13a	12.27 ± 0.50a	2.36 ± 0.15a	0.15 ± 0.01b	25.47 ± 0.99ab
	7th	37.39 ± 1.05b	23.82 ± 1.08a	33.29 ± 0.89a	9.47 ± 1.71b	2.94 ± 0.55a	0.22 ± 0.04a	23.85 ± 0.50b
BS	3rd	630.86 ± 32.95a	17.64 ± 1.56b	37.29 ± 1.88a	19.65 ± 1.21a	21.45 ± 1.17a	0.10 ± 0.01b	27.47 ± 1.61b
	5th	379.66 ± 19.56b	18.70 ± 1.62b	38.81 ± 1.35a	20.11 ± 0.81a	12.56 ± 0.81b	0.09 ± 0.00b	28.76 ± 1.43ab
	7th	250.24 ± 27.39c	23.69 ± 0.61a	39.61 ± 2.13a	15.92 ± 1.79b	10.56 ± 1.26b	0.12 ± 0.01a	31.65 ± 1.29a

content was the second-highest contributors to PS formation before silking and the whole growth stage. The average rate of the rapid thickening was the highest contributor to mechanical strength before silking.

4. Discussion

4.1. Growth model of basal internodes

The maize stalk above the ground was composed of nodes and internodes, supporting the plant, connecting leaves and ears, and transporting nutrition. Its development not only affects the yield production but also related with the lodging resistance, especially for the basal internodes of maize, so agronomists are very concerned about maize stalk development. The development of basal internodes was gradually formed one by one from bottom to top after V6, and there were certain overlapping stages between adjacent nodes (Fig. 10). The regression analysis showed that initiation times of rapid elongation and thickening were delayed 2.1 d and 0.93 d, respectively, with the rise of 1 internode. As far as morphological characteristics were concerned, the results of previous studies about elongation and thickening were inconsistent, such as elongation first and then thickening (Zhang et al., 2020), thickening first and then elongation (Xue et al., 2016; Zhang et al., 2019) and development simultaneously (Jung and Casler, 2006). Our study

Table 4
Correlation and contribution rate of basal internode traits and their growth parameters in 2018–2019. R, C, IL, IS, IP, LC, CC, PS and BS are Pearson correlations coefficient, contribution rate, internode length, cross-sectional area, internode plumpness, lignin and cellulose content per unit length, rind penetration strength and stalk bending strength, respectively. T is the duration of rapid elongation, thickening, accumulation or formation (d); V_t is the average rate of elongation (cm d^{-1}), thickening (mm^2 d^{-1}), accumulation (mg cm^{-1} d^{-1}), or formation (N mm^{-2} d^{-1}); V_{max} is the maximum rate of elongation (cm d^{-1}), thickening (mm^2 d^{-1}), accumulation (mg cm^{-1} d^{-1}), or formation (N mm^{-2} d^{-1}). T_{max} is the time reached the V_{max} of IL, IS, IP, LC, CC, PS and BS after V6 (d). ** mean Correlation is significant at the 0.01 level (2-tailed). * mean Correlation is significant at the 0.05 level (2-tailed).

	R				C (%)	
	T	T_{max}	V_t	V_{max}	T	V_t
IL	-0.762**	0.589**	0.487**	0.518**	85.32	14.68
IS	0.706**	0.504**	-0.668**	0.092	84.11	15.89
IP	0.870**	-0.011	-0.868**	-0.303	51.22	48.78
LC	0.742**	-0.133	-0.710**	0.702**	84.17	15.83
CC	0.573**	-0.349	-0.642**	0.474*	13.58	86.42
PS	0.252	-0.411	-0.279	0.380	19.90	80.10
BS	0.396	-0.304	-0.417	0.889**	14.16	85.84

Table 5
Grain yield and stalk lodging rate in two years.

Cultivars	2018		2019	
	Grain yield (10^4 kg/ha)	Stalk lodging rate (%)	Grain yield (10^4 kg/ha)	Stalk lodging rate (%)
ZH505	1.291 ± 0.029a	18.7 ± 1.2a	1.181 ± 0.246a	15.5 ± 2.7a
XY1171	1.312 ± 0.066a	9.3 ± 1.8b	1.097 ± 0.576ab	2.7 ± 1.2bc
YHD6	1.263 ± 0.033a	14.5 ± 1.5a	1.180 ± 0.547a	9.1 ± 2.7ab
ZH6	1.109 ± 0.067b	6.8 ± 1.5b	/	/
RB9	/	/	0.961 ± 0.437b	1.7 ± 0.8c

Different letters to the right of the value indicate significant differences at $p < 0.05$ as determined by the LSD test.

showed that the basal internode length first entered into rapid elongation, followed by internode cross-sectional area, then the accumulation of photosynthetic products in it. Finally, the biosynthesis of structural carbohydrates (lignin and cellulose) occurred and get rapidly accumulated. The mechanical strength of basal internodes increased after the rapid elongation and thickening. Although there were significant differences in the initiation and the termination times of each trait, the duration of the rapid development was not completed independently and there was some overlapping growth period. Not only the initiation and termination times of rapid elongation were the earliest, but also the average rate of rapid elongation was the fastest, and the duration of rapid elongation was also shortest. Compared with internode elongation, the average rate of rapid thickening was slower, so the duration of rapid thickening was longer. The average rate of rapid PS formation was faster than BS, and the duration of rapid PS formation was shorter than BS. The development rate of each trait was accelerated, and the duration of rapid development of each trait was shortened with the internode position rising from bottom to top. Based on the average of each trait from 5 cultivars, the internode position rises by 1, the duration of rapid growth of IS, IP, LC, CC, PS, and BS were shortened by 1.41d, 1.92d, 1.38d, 1.44d, 1.11d, and 1.05d, respectively.

Stalk lodging was possible for all the basal internodes. Most stalk lodging (75 %) occurred between the 3rd to 5th internodes (Xue et al., 2020b). The rapid growth stage of these three internodes was about 12d-35d after V6. From 12 days after V6 to 5 days after silking, that was a critical period for the morphological formation, dry matter constituents accumulation, and mechanical strength formation of the 3rd to 5th internodes. Considering the fertilizer application, water management, chemical regulation, and other management measures that were not regulating the development of internode immediately. Therefore, the implementation time of the management strategies to regulate the growth of these internodes for improving its lodging resistance should be earlier.

4.2. Crucial factors affecting stalk lodging

The mechanical strength of the basal internode is a critical indicator to measure the lodging resistance of maize stalks, and the stalk lodging rate is significantly negatively correlated with the mechanical strength (Kamran et al., 2017). The indicators which are commonly used to measure the mechanical strength of maize stalks include stalk pushing or pulling bending strength (Sekhon et al., 2020), rind penetration strength, stalk bending strength, and crushing strength (Wang et al., 2020a, 2020b). Some researchers believed that stalk bending strength was the best evaluation indicator (Al-Zube et al., 2018; Sekhon et al., 2020), and some researchers considered both stalks bending strength and rind penetration strength, as the best evaluation indicators for stalk lodging (Robertson et al., 2016). Our study showed that the stalk lodging was significantly negatively correlated with the PS, but not significantly correlated with the BS. Such as both the BS and stalk breaking rates of ZH505 were all high in two years. The PS was significantly positively correlated with the thickness of the internode cortex and mechanical tissue, the number and area of vascular bundles, and the content of structural carbohydrates (such as lignin and cellulose) (Xue et al., 2016). Excluding these traits, the BS was also correlated with the dry matter constituents accumulation of the pith (for example non-structural carbohydrate content(NSC)) (Yang et al., 2020). However, some NSC that was stored in internodes and leaves, needed to be transported into the ear during the late growth stage, which lead to a decrease in IP and a reduction of BS (Wu et al., 2019). Therefore, the growth curve of BS at

Table 6
Correlation coefficient and contribution rate of basal internode mechanical strength with its morphological characteristics and dry matter constituents accumulation in 2018–2019. IL, IS, IP, LC and CC are internode length, cross-sectional area, internode plumpness, lignin and cellulose content per unit length, respectively. PS0 and BS0 are the measured rind penetration and stalk bending strengths before silking, PS2 and BS2 are the measured rind penetration and stalk bending strengths after silking (including the silking), PSm and BSm are the measured rind penetration and stalk bending strengths during the whole growth stages, and other indicators are the measured values of corresponding internodes at corresponding periods. R and C are Pearson correlations coefficient and contribution rate. ** mean correlation is significant at the 0.01 level (2-tailed). * mean correlation is significant at the 0.05 level (2-tailed).

Factors	N	R					C (%)				
		IL	IS	IP	LC	CC	IL	IS	IP	LC	CC
PS0	60	0.486**	0.707**	0.926**	0.892**	0.896**	3.02	9.23	49.54	30.80	7.41
BS0	60	0.243	0.583**	0.839**	0.800**	0.799**	2.47	9.07	43.58	29.30	15.59
PS2	68	-0.412**	0.195	0.406**	0.810**	0.763**	10.43	0.72	8.84	52.03	27.98
BS2	68	-0.814**	0.615**	0.748**	0.594**	0.678**	34.43	11.99	23.31	17.11	13.16
PSm	128	0.373**	0.734**	0.809**	0.911**	0.913**	5.64	2.48	21.92	41.24	28.72
BSm	128	0.022	0.740**	0.851**	0.781**	0.812**	0.60	16.46	56.21	24.67	2.06

Table 7
Correlation coefficients and contribution rates of basal internode mechanical strength and internode growth parameters of each traits in 2018–2019. PS0 and BS0 are the average measured rind penetration and stalk bending strengths before silking, PS2 and BS2 are the average measured rind penetration and stalk bending strengths after silking (including the silking), PSm and BSm are the average measured rind penetration and stalk bending strengths during the whole growth stages. R is the correlation coefficient and C is the contribution rate. ILT, IST, IPT, LCT and CCT are the duration of rapid elongation, thickening or accumulation of IL, IP, LC and CC. ILV_t, ISV_t, IPV_t, LCV_t and CCV_t are the average rate of elongation, thickening or accumulation of IL, IP, LC and CC. ** mean correlation is significant at the 0.01 level (2-tailed). * mean correlation is significant at the 0.05 level (2-tailed).

	Factors	ILT	ILV_t	IST	ISV_t	IPT	IPV_t	LCT	LCV_t	CCT	CCV_t
R	PS0	0.567**	-0.293	0.531*	-0.613**	0.466*	-0.511*	0.646**	-0.568**	0.519*	-0.512*
	BS0	0.508*	-0.367	0.468*	-0.548*	0.422	-0.556*	0.675**	-0.644**	0.511*	-0.590**
	PS2	0.497*	-0.249	0.384	-0.452*	0.630**	-0.613**	0.882**	-0.835**	0.747**	-0.718**
	BS2	0.590**	-0.412	0.43	-0.521*	0.532*	-0.620**	0.808**	-0.771**	0.664**	-0.698**
	PSm	0.600**	-0.321	0.449*	-0.541*	0.679**	-0.671**	0.869**	-0.807**	0.756**	-0.723**
	BSm	0.594**	-0.417	0.437	-0.532*	0.537*	-0.634**	0.788**	-0.751**	0.645**	-0.689**
C	PS0	9.87	1.66	6.21	18.58	9.97	0.57	25.85	14.42	5.81	7.07
	BS0	4.53	1.25	8.92	16.43	17.98	10.23	19.98	7.90	2.99	9.79
	PS2	3.98	2.85	0.40	3.83	0.33	18.88	48.01	0.38	16.05	5.28
	BS2	5.35	0.92	7.47	11.53	16.40	0.65	23.86	12.04	9.84	11.95
	PSm	8.95	3.00	2.72	10.04	1.52	12.45	36.16	4.90	14.81	5.44
	BSm	5.93	1.00	7.93	12.75	17.34	4.24	21.85	10.04	8.30	10.62

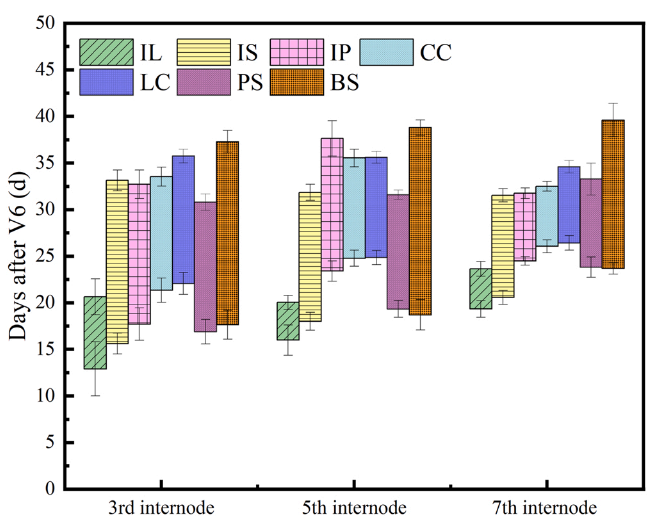

Fig. 10. The duration of rapid development of internode morphology, dry matter constituents accumulation and mechanical strength. 3rd, 5th, 7th represent the third, fifth, seventh internode of maize stalk from bottom to top, respectively. IL and IS represent internode length and cross-sectional area. IP, CC, LC, PS and BS represent internode plumpness, cellulose content, lignin content, rind penetration strength and stalk bending strength, respectively. V6 indicates the six-leaf stage of maize.

the basal internodes was increased first and then decreased after silking (Fig. 9). The BS showed greater instability, while the PS was relatively more stable after silking. There were no significant differences among the averages of PS at different measurement stages after silking. But there were significant differences, in the variation scale, between the two indicators for two years. To compare the averages of 3rd and 5th internodes for the three same cultivars that were measured after two years of silking, the BS in 2018 was 40.0 % higher than that in 2019, while the PS was only 9.1 % higher. It showed that the PS was more stable and reliable to evaluate the mechanical strength of the stalk in maize.

The mechanical strength is significantly correlated with the morphological characteristics, anatomical structure, IP, the structural and non-structural carbohydrate content of basal internodes (Xue et al., 2020b, 2016). Our study showed that the mechanical strength of the basal internodes was highly significantly correlated with substances (IP, LC, and CC) accumulation during the whole growth stage, while the IP was the highest contributor to the BS and the LC was the highest contributor to the PS during the whole growth stage (Table 6). Increasing the substances accumulation in the basal internodes, especially the LC, could significantly increase their mechanical strength and lodging resistance. Based on the two years field experiment, the basal internodes of YHD6 and ZH505 were neither the longest nor the thinnest, but the lodging rate was still higher because of the lower substances accumulation. Although the basal internodes of XY1171 were longest and thinnest, the lodging rate was still lower due to the higher lignin content. It indicates that enhancing the substances (especially the LC) accumulation ability in the basal internodes was more important than improving its morphological characteristics to increase the lodging resistance in maize. The breeders should focus on increasing the substances accumulation of basal internodes first, followed by improving morphological characteristics.

Carbohydrates that are abundantly present in the basal internodes of maize include structural (cellulose, hemicellulose, and lignin) and non-structural carbohydrates (Desta et al., 2016). Most of the researchers agreed that both LC and CC are the crucial indicators for the mechanical strength of basal internodes (Wang et al., 2020a, 2020b; Xue et al., 2016; Yang et al., 2020). However, this study found that although the PS and BS were highly significantly positively correlated with LC and CC, the correlation coefficient of CC was even higher than LC, but the contribution rate of LC to PS and BS were higher than CC during the whole growth stage. It showed that the LC is more critical than CC for the mechanical strength of basal internodes. This result may be correlated with the variation of the molecular structure and distribution of lignin and cellulose in the cell wall. Cellulose is a macromolecular polymer with a complex molecular structure and large intramolecular and intermolecular porosity, while lignin monomer is a small molecule with smaller intramolecular and intermolecular porosity (Ding et al., 2014). The lignin molecules are cross-linked with polysaccharide molecules such as cellulose and hemicellulose in the cell wall, which increases the mechanical strength of plant cells and tissues (Ding et al., 2014; Vanholme et al., 2019). Meanwhile, cellulose is mainly distributed in the cell wall, while lignin accumulates both in the xylem of vascular bundles and the cell wall (Ding et al., 2012).

4.3. Relationship between mechanical strength and growth parameters of basal internodes

The characteristics of each basal internode are formed gradually, and the development process affects its lodging resistance by determining the maturity traits directly. Xue, et al. demonstrated that high plant density decreased the duration of internode thickening and dry matter accumulation, as well as the rates of cellulose and lignin accumulation, which caused the diameter and DWUL to decline, that was adverse for the formation of cortex tissue and PS (Xue et al., 2016). This study showed that the duration and the average rate of rapid development were significantly correlated with IL, IS, IP, LC, CC, PS, and BS. Especially, the duration of rapid development was the highest contributor to IL, IS, IP, and LC. The average rate of rapid development was the highest contributor to CC, PS, and BS.

The mechanical strength of basal internodes was not only correlated with full-development basal internode traits but also correlated with their development process and parameters (Table 7), in which it was positively related to the duration of its rapid growth period and negatively related to the growth rate of its rapid growth period. The duration of rapid accumulation of lignin was the highest contributor to PS and BS during the whole growth stage, followed by the duration of rapid accumulation of IP and CC. Regression analysis showed that the average PS increase 1.39 N and 2.82 N during the S_0 (V6 to R1) and S_2 (R1 to R6), respectively, with the duration of rapid lignin accumulation increased by 1d. At the same time, the BS increased 21.0 N and 44.3 N during the S_0 and S_2, respectively. Breeders should increase the duration of rapid lignin accumulation by gene editing and other techniques to increase the lignin content of the basal internode which in turn increased its PS and stalk lodging resistance, while the agronomists could do that by fertilizer and water management, chemical regulation, etc.

In maize production, the mechanical kernel harvesting is usually carried out 2–5 weeks after physiological maturity (R6). The harvesting efficiency is significantly influenced by the change in mechanical strength of basal internodes after R6. Therefore, further research work can be carried out to improve the efficiency of mechanical kernel harvesting by focusing on the change pattern and regulation mechanism of maize stalk characteristics after physiological maturity.

5. Conclusion

The growth of each basal internode traits (IL, IS, IP, LC, CC, PS, and BS) in maize all conformed to the Logistic model. The duration and average rate of the rapid growth were significantly positively and negatively correlated with the mechanical strength of basal internode, respectively. The duration of rapid lignin accumulation was the highest contributor to mechanical strength, followed by IP and CC. The correlation coefficient of PS between stalk lodging rates was higher than BS. Meanwhile, the PS was more stable than BS both in variation measurement stages and years. The substances (IP, LC and CC) accumulation of basal internode was more important than the formation of morphological characteristics for enhancing mechanical strength. It should be an important strategy for both breeders and agronomists to prolong the rapid accumulation duration of the substances, especially the lignin content, could increase the mechanical strength of basal internodes and improve stalk lodging resistance.

CRediT authorship contribution statement

Zhan Xiaoxu: Conceptualization, Methodology, Investigation, Data curation, Writing – original draft preparation and Editing. **Liu Qinlin:** Visualization, Investigation. **Liu Yaqi:** Visualization, Investigation. **Xu Juzhen:** Visualization, Investigation. **Ou Qian:** Visualization, Investigation. **Chen Liang:** Visualization, Investigation. **Geert Kessel:** Supervision, Writing- Reviewing and Editing. **Corné Kempenaar:** Supervision, Writing - reviewing and editing. **Kong Fanlei:** Funding acquisition, Writing - reviewing & editing. **Lan Tianqiong:** Writing - reviewing & editing. **Yuan Jichao:** Conceptualization, Methodology, Supervision, Funding acquisition, Writing - reviewing & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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