Maize grain yield enhancement in modern hybrids associated with greater stalk lodging resistance in high planting density: A case study in Northeast China

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Abstract

Lodging resistance is a critical trait in modern maize breeding. To examine maize stalk lodging and related characteristics in response to increasing planting densities in modern hybrids. A 2-year field trial was conducted from 2018-2019 with two widely grown commercial hybrids (Xy335, Fm985) and three planting densities (LD, MD, HD) of 4.5, 6.5, and 8.5×10^4 plant/ha. Results showed new hybrid Fm985 had significantly higher grain yield and lower lodging rate in HD, while there was no significance at LD and MD. Compared to Fm985, old cultivar Xy335 had a significantly higher plant height, ear and gravity height, culm length (CL) across three planting density averages, while opposite stalk bending strength (SBS), dry weight per unit length (DWPU), cross-sectional area, and the content of cellulose and lignin in basal internode. The correlation and path analysis revealed that kernels amount per ear lodging rate directly contributed to maize grain yield, while lodging-related traits of SBS, stem lignin and DWPU and indirect effect on maize grain yield, suggesting modern hybrid maize yield enhancement associated with greater stalk lodging resistance in high planting density in Northeast China.

Introduction

Maize (*Zea mays* L.), which originates from Mesoamerica and was introduced to China approximately 500 years ago¹, has become the first major cereals crop in China from 2012 and plays an important role in ensuring ever-increasing food supply¹. The Songliao Plain, located in Northeast of China (containing Jilin, Heilongjiang, Liaoning, & the eastern of Inner Mongolia of China), is one of the three world-famous Black soil areas, with arable land of 3.59×10^7 ha and maize yield of 16.54×10^7 Mg in 2019, accounting for nearly a quarter of the total national grain yield and about one-third of the national total commodity grain output in China², thus playing an important role in feeding the national food security and known as the "ballast stone" delivered by the first domestic "White Paper on Northeast Black Land (2020)", China³.

Maize is a widely grown C4 crop with a high rate of photosynthetic activity leading to high grain and biomass yield potential globally⁴. The potential grain yield of maize increased tremendously during the past several decades in China¹, and other countries such as the US^{5,6}, South Africa⁷. Numerous studies have been proved that raising planting density is the most important reason for the increase of maize production worldwide⁸⁻¹². Lu et al.,¹³ reported that maize genetic gain averaged $78.99 \text{ kg}^{-1} \text{ ha}^{-1} \text{ year}^{-1}$ from the released hybrids 1999 to 2018 in China, with 54.41 % of the total yield gain attributed to breeding. In the US, commercial grain yield increased 6-fold from about $1,300 \text{ kg ha}^{-1}$ in 1939 to $7,800 \text{ kg ha}^{-1}$ in 2005, with 50 % of the yield increase was attributed to breeding¹⁴. The increase in grain yield for modern commercial maize hybrids is mostly owed to increasing the tolerance to high planting, which is largely attributed to the genetic improvements of crop productivity and associated traits^{10,15,16}.

However, raising planting density usually deserved a high probability of stalk lodging¹⁷. Stalk lodging not only causes harvest losses by limiting maize cultivar grain yield potential¹², as well as raise harvest cost due to difficulties in harvest operations⁷. An earlier survey showed stalk lodging resulted in annual yield loss ranging by 5 % to 25 % in the USA^{18,19}, as well as 14 % and 28 % yield loss for summer maize under root and stalk lodging during the 12-leaf stage in China²⁰, and consequently resulting in billions of dollars of financial loss²¹. In northeast China, a wind-induced stalk lodging in the grain filling stage leads to a yield loss by 14.75 % to 29.68 % in 2013⁸. Therefore, it's sensible to make a balance between grain yield gain and lodging rate in raising planting density for modern hybrids.

Maize stalk lodging is a complicated phenomenon which not only influenced by many external factors^{22,23}, such as wind but also associated with the stalking strength and related traits²¹. The improved grain yield in modern hybrids may be associated with the plant architecture shaping and stem morphology and mechanics improvement related to high planting tolerance in genetic improvements. Sergio²⁴ reported that genetic gain in modern hybrids is related to increased grain number per ear, enhanced post-silking biomass accumulation, as well as enhanced biomass allocation to reproductive sinks in Argentina. In West Africa, the average rate of increase in maize grain yield was mainly associated with significant improvements in plant and ear stay green characteristic during the past 22 years¹⁰, which prolonged the grain filling duration time and directly affected maize grain yield. In the US, on-farm maize genetic yield gains of released maize hybrid during 1934 to 2004 averaged $115 \text{ kg ha}^{-1} \text{ yr}^{-1}$, and the genetic improvement in gain was attributed to the continuing phenotypic improvement²³, such as smaller tassels, more upright leaves, fewer tillers, and lower grain protein percentage, which can directly or indirectly influence the grain yield. However, which specific traits play a key role in reducing the occurrence of lodging in maize genetic improvement are still unclear.

The Songliao Plain is the main production area of spring maize, increasing maize planting density is a major approach in maize production, the average maize grain yield has been increased from 2.44 Mg ha^{-1} in 1980 to 6.87 Mg ha^{-1} in 2019. However, maize hybrid's genetics improvement and shifting play a key role in maize yield enhancement. Xy335 is a wide planted maize hybrid with high-dense, which accounts for 40 % of total maize planting area in Jilin province in 2010^{8,25,26}, and Fm985 is a local newly released typical hybrid maize has the similar growing degree-days (GDD) and plant architecture characteristics with Xy335. But it is unclear how the lodging-resistance capability and related traits respond with the increasing plant density.

Therefore, the objectives of this study were to (i) quantify how maize grain yield and stalk lodging rate respond to the raising planting density; (ii) how stalk bending strength and related characteristics changed with increased planting density; (iii) identify the main effects (direct and indirect) contributing to maize grain yield and lodging resistance in modern commercial cultivars.

Materials And Methods

2.1 Site description

The study was conducted at the Jilin Academy of Agriculture Science experiment station (Gongzhuling, Jilin province, China; 43°31'28" N, 124°48'35" E) during two successive maize growing seasons of 2018 and 2019; The site is located in the core zone of "Golden corn belt" in Songliao plain, northeast of China. This area is a classic rain-fed, long-term spring maize monoculture region with an annual rainfall was about 600 mm, the monthly temperature and precipitation during the time of the experiment were obtained from an automatic meteorological station and are given in Fig.1. The experimental field was a typical Blank Soil (Mollisols in USDA classification) with a pH of 6.89 containing 22.01 g kg⁻¹ organic matter, 1.75g kg⁻¹ total N, 17.60 g kg⁻¹ Olsen-P, 111.1 g kg⁻¹ NH₄OAc-extracted K in the 0-20 cm subsoil layer.

2.2 Experimental setup

Two typical commercial hybrid maize Xianyu335 (Xy335) and Fumin988 (Fm985), obtained from Maize Research Institute, Jilin Academy of Agricultural Science, and Jilin Fumin Seed Company Co., LTD, China, were used in the present study, respectively. Both of the two cultivars have large planting areas with more than millions of acres in this zone²⁷, and the details about the hybrids were listed in table 1.

The experimental was arranged in a randomized complete block in a split plot arrangement with three replications, where maize cultivars in main plots and planting density in sub-plots. Maize seeds were planted by using manual seeder on 5 May in both 2018 and 2019 at three planting densities of 45 000 (LD), 65 000 (MD), and 85,000 plant/ha (HD). The sub-plots were 30 m long, 6 m wide (with 10 rows spaced 60 cm apart). To create an equal and sufficient soil growth environment, corn compound fertilizer with 220 kg N ha⁻¹, 100 kg P₂O ha⁻¹ and 100 kg K₂O ha⁻¹ were applied at the sowing time according to the recommended soil nutrient management¹². Weeds in the plots were controlled using herbicides applied before emergence (atrazine and acetochlor) and at the V6 stage (Mesotrione). Pesticides were applied as needed to control insect populations during the maize growth seasons.

2.3 Determination of plant architecture and internode morphological characteristics

At 35 days after silking, five continuous plants in each plot were randomly selected to measure the plant architecture characteristics of plant height (PH), ear height (EH), and gravity height (GH). PH and EH referred to the distance from the ground to the top of the tassel, and to the node bearing the ear, respectively; GH was measured from the base to the fulcrum of the balance site (Fig. 2b), following the method of Xue et al.,²⁸.

At physiological maturity, ears were harvested from 10-m² plant samples at the center in each plot. From the harvested ears, 10 were chosen to estimate the ear characteristics included ear length, kernels amount per ear, 100-grain weight, grain moisture, then maize grain yield and yield components were calculated at a moisture content of 14 %.

2.4 Determination of stalk bending strength and internode morphology

To assess maize stalk bending strength (SBS), a self-made instrument by the combination of a digital force ergometer (YYD-2; The Zhejiang Top Instrument Co. Ltd) and a circle iron tool²⁹ was conducted at 35 days after silking^{28,29}. 5 adjacent plants in each plot were chosen, after removing the leaves and sheaths of each selected plant, the stems were cut at 0.8 m height from the soil surface, then were pulled until it was 30° from vertical (Fig. 3), the pulling force can be determined by the ergometer and SBS were calculated using the following formula:

$$SBS = \frac{\sqrt{\text{Stem length(cm)} \times \text{Ear height (cm)}}}{\text{Horizontal pulling resistance (N)}}$$

Meanwhile, the internode morphology of stem cross section area (CSA) and dry weight per unit length (DWPU) were measured following the method of Cao, et al.⁸, culm length measured using a meter ruler as shown in Fig.2 a.

2.5 Data Analysis

All data were analyzed statistically using Microsoft Excel 2016 and SPSS 24.0 software (Inc. Headquarters, Chicago, IL, USA). Fingers were generated in GraphPad Prism 9.0. Probabilities of significance were used to test the significance among treatments and their interactions, and the least significant difference (LSD) test was used to compare the means ($P < 0.05$). A structural equation model (SEM) was constructed using AMOS software (IBM SPSS AMOS 23.0) to explore the direct and indirect impacts of maize yield component, SBS, plant architecture characteristics, and lodging rate on maize grain yield, as well as stem morphology and structural carbohydrates content on SBS. This was based on a multivariate approach.

2.6 Declaration of plant materials legality

We confirm the plants and plant materials used in the present manuscript complied with the laws and regulations of the People's Republic of China.

Results And Analysis

Grain yield, yield components and lodging rate

To identify the differences in grain yield and lodging rates between two cultivars in response to increased planting density, maize grain yield, yield components, and lodging rate were investigated in both years. The ANOVA analysis showed maize grain yield was significantly ($0.01 < P < 0.05$) or high significantly ($P < 0.01$) affected by corn cultivars (C), planting density (PD), and their interaction (C×PD) in both years (Fig 4; Table 3). The grain yield of hybrid maize Fm985 was 4.76 % and 8.10 % higher than of the Xy335 in 2018 and 2019 respectively, across the average of three PD (Fig. 4). For hybrid

Fm985, the maize grain yield increased with the increase of PD, while the highest maize yield was recorded in MD for Xy335, which indicated newly released cultivar Fm985 had a high yield potential in HD.

Maize cultivar (C), planting density (PD) and year (Y) significantly affected yield components of ear number per ha and 100-grain weight, while kernel amount per ear was only significantly affected by planting density (PD) (Table 2, 4). On the whole, the modern commercial hybrid of Fm985 had a higher ear number per ha and 100-kernel weight across three PD average, and significant differences only observed at HD, while not significant at LD and MD over two hybrids. Kernel amount per ear only significantly affected by PD, whereas not cultivar and other effects.

Stalk lodging rates were significantly affected by C, PD, Y, and the interaction of PD×Y. The lodging rate of hybrid Xy335 was 5.26 folds higher than Fm985 in 2017, and 4.04 folds in 2018 across the three PD average (Fig. 4). Increased PD produced an obvious increase in maize lodging rate for both cultivars, PD increased from LD to HD, the lodging rate reached from 5.21 % to 21.71 % for Xy335 on two-year average, while from 0.41 % to 4.42 % for Fm985 reached, correspondingly. The results indicated that maize Fm985 had a higher stalk lodging resistance in the present study.

Stalk lodging related stem morphological characteristics

Maize plant architecture such as plant height (PH), ear height (EH), and gravity height (GH) was investigated, the results indicated hybrid maize Xy335 had higher PH, EH and GH across two years of investigation (Table 3). Compared with LD and MD, PH, EH and GH at HD had significantly higher values for both cultivars, while no significant differences of these plant architecture characteristics were found on PD and year, except EH.

The basal stalk morphological characteristics related to stem lodging resistance of dry weight per unit (DWPU) were significantly affected by C and PD; In LD and MD, the differences of DWPU under the same PD were not significant for both cultivars, while hybrid Fm985 had higher DWPU than Xy335 in HD in both years. Culm length (CL) and cross-sectional area (CSA) of the stem were both significantly influenced by PD, while no significant effect was observed in C, Y and other interactions (Table 4).

Stalk bending strength (SBS) and carbohydrates content of basal internode

As shown in Fig. 5, SBS was significantly reduced with the increase of PD in both cultivars in two consecutive years (Table 4). Hybrid maize Fm985 showed a relatively higher SBS at MD and HD treatments, which were 4.74 % and 21.02 % higher than Xy335 in MD and HD in 2018, as well as 8.24 % and 18.19 % higher in 2019, correspondingly.

Cellulose and lignin are the main structural substances in the crop stem. As shown in Fig. 6, significant differences in stem cellulose content (Fig. 3a, 3b) and lignin content (Fig. 3c, 3d) were observed over hybrids and PD (Table 4), the content of cellulose and lignin for Fm985 was 12.81% and 34.23% higher than Xy335 on two-year average, respectively. In addition, increased PD produced a significant decrease in cellulose content for Xy335, while the differences were not significant for Fm985, except for HD in 2018. Stem lignin content displayed a significant decrease of 17.01-29.49 % for Xy335 and 10.23-26.06 % for Fm985 as PD increased from LD to HD in 2018, as well as decrease of 18.25-38.28 % and 24.30-28.58 % in 2019, correspondingly.

Correlation analysis between lodging rate and lodging related characteristic

Correlation analysis between lodging rate and lodging related characteristics (Fig. 7) showed maize lodging rate strongly negatively correlated with SBS ($r=-0.89$, $p<0.01$), the content of stem lignin ($r=-0.87$, $p<0.01$) and cellulose ($r=-0.84$, $p<0.01$), as well as DWPU ($r=-0.75$, $0.01<p<0.05$); as well as significantly positively correlated with GH ($r=0.86$, $p<0.01$) and EH ($r=-0.89$, $p<0.01$). Moreover, SBS was highly positively correlated with DWPU ($r=0.86$, $p<0.01$) and stem lignin content ($r=0.84$, $p<0.01$), and negatively correlated with EH ($r=-0.79$, $0.01<p<0.05$) and GH ($r=-0.77$, $0.01<p<0.05$).

Path analysis

In order to further analyze the direct and indirect effects of plant architecture characteristics, stem lodging-related morphological and mechanical properties on maize lodging rate and maize grain yield, a structural equation model (SEM) approach was conducted among these characteristics. Of the considered factors, kernels amount per ear and lodging rate directly contributed to maize grain yield; maize lodging rate ($P<0.001$), which directly affected by SBS ($P<0.001$) and GH had a negative effect on 100-grain weight and kernels amount per ear, made an indirect effect to maize grain yield (Fig. 8). In addition, the content of stem lignin can directly contribute to DWPU and SBS, which are highly related to maize lodging rate also indirectly contribute to maize grain yield (Fig. 9).

Discussion

Lodging is a serious problem that constrains grain yield stability and grain quality in modern crop production^{21,8}. Stalk lodging is not only affected by cultivar genotypes, agricultural practices¹⁰, but also associated with the growth environment, mainly including wind and rainfall³⁰. The Super Typhoon Lekima with heavy rainfall occurred in mid grain-filling stage in the year 2019, thus resulting in a higher lodging rate and reduction of grain yield, compared with 2018. However, higher grain yield and lower stalk lodging rate of hybrid Fm985 were both observed in consecutive years at high planting density, which indicates the newly released maize hybrid Fm985 had a higher lodging resistance than the old cultivar of Xy335, the results are consistent with the previous studies of Liu et al.,¹⁶ and Luque et al.,²⁴ who demonstrated that the overall trend in new cultivars are toward have effective in increasing grain yield and reducing stalk lodging in Northeast China and other places.

Stalk lodging induced bending and/or breakage of stems during maize growing season generally cause damages to vascular bundles³¹, and thereby prevent water transport from root to leaves and impair assimilates phloem transportation from the mesophyll into the stalk phloem, thus may allocating more photoassimilates to leaves or stalk than the ear^{2,32}, hence affecting grain filling and decreased the kernel weight and effective ear number, that's why the decreased yield components of 100-grain weight and ear number were found in the less lodging-resistant hybrid of Xy335 in the present study.

Maize stalk lodging resistance ability is also related to many plant characteristics²¹. Increasing planting density brings about fiercer competition for solar radiation and other resources available of the individual plant, which results in the higher canopy morphology of PH, EH and GH. Our results are consistent with the previous results of Zhao et al.,³¹ who found that the PH and EH were enhanced with the planting density raised from 4.5×10^4 plant/ha under three N levels. As known, cultivars with high stalk and ear position are more susceptible to lodging due to higher plant gravity and enhanced upper fresh weight²¹. In the present study, the maize cultivar of Xy335 had a significantly higher PH, EH, as well as GH in high planting density, while not significant for hybrid Fm985, these results are in agreement with the results of higher lodging rate observed in hybrid of Fm985 in the current study, as well as the previous studies of Cao et al.,⁸ and Xue et al.,³³ who also confirmed that hybrid Xy335 is lodging-susceptible under high planting density. In addition, plant morphological characteristics have evolutionary changed with the genetic improvement during the past few decades¹⁶, the increased plant height has been demonstrated linearly positively with the maize grain yield in the US³⁴, as well as in China¹. However, no differences of grain yield were found between two hybrids in LD and MD, suggesting the improved grain yield in HD is associated with enhanced stalk lodging resistance, which contributed to small yield loss.

Numerous studies have shown that the basal part of the stalk plays an important role in maintaining lodging resistance^{21,35}. Stalk morphological characteristics of basal stem internodes length, DWPU, and CSA have a strong correlation with stem wall thickness^{17,19}, and therefore influence lodging susceptibility. Our results showed hybrid Fm985 had a higher DWPU than Xy335, while no significant differences of CL and CSA were found neither in hybrids nor planting density, indicating DWPU may mainly contribute to the higher bending strength of Fm985 under high planting density. The maize lodging resistance ability is a rather complicated phenotype, besides morphological traits of plants, the basal stem chemical composition of cellulose and lignin are also important and contribute significantly to lodging resistance¹⁹. It has been proved that culm cellulose can determine stem strength and increase stem rigidity, while lignin as a vital structural component of the secondary cell walls can provide strength to plants²⁹. Thus the culm content of cellulose and lignin played a critical role in stalk strength and rigidity of basal stem and therefore influence stalk lodging resistance. Significant differences of cellulose and lignin content were both observed over planting densities and hybrids, the hybrid maize Fm985 had higher cellulose and lignin content in the basal stem, thereby providing strong bending strength and stiffness of plant culms. Additionally, with planting density increased from LD to HD, the content of cellulose and lignin for Fm985 had a slight decrease, while opposite to Xy335. The relative higher content of cellulose and lignin in basal stem at high planting density may be associated with the improved stem bending strength and lower lodging rate in the present study.

Stalk lodging occurred mainly depends on two conditions: the strength of external loading (e.g. wind) and its duration time²¹, thus the plant lodging-resistance ability not only depends on basal stem rigidity but is also related to the tensile strength of plant³⁶. Stalk bending strength is a measure to estimate stalk mechanical strength, both related to stem rigidity and tensile strength with a plant¹⁹. Hybrid maize Fm985 showed a relatively higher stalk bending strength at MD and HD in the present study, suggesting the improved SBS of Fm985 may contribute to the enhanced lodging-resistance ability. Moreover, the correlation analysis between lodging rate and related traits also showed a significant negative effect between the SBS and maize stalk lodging rate indicating the SBS after 35 days of silking could act as an important indicator to estimate the stalk lodging resistance in maize breeding or cultivation. It has been well documented that plant SBS is highly associated with the stalk morphology and chemical characteristic of the dry weight per unit length (DWPU), basal internode length, as well as carbohydrate contents in culm^{28,29}, the correlation analysis in present study also confirmed that SBS is significantly positively related to DWPU ($r=0.86$, $P<0.01$) and stem lignin content ($r=0.84$, $P<0.01$), as well as highly negatively correlated with EH ($r=-0.79$, $0.01<P<0.05$), and GH ($r=-0.77$, $0.01<P<0.05$), these factors may coordinately play a key role in enhancing the plant stalk lodging resistance and thereby reduce the lodging rate, and contrast to maize grain yield.

Structural equation modeling (SEM) is a powerful, multivariate technique found increasingly in scientific investigations to evaluate multivariate causal relationships³⁷. In recent years, it has been widely used to estimate the direct or indirect effect on the agronomy^{27,28}. The path analysis by SEM model showed kernels amount per ear directly contributed to maize grain yield in the present study, and lodging rate directly affected by SBS and GH had a negative effect on kernels amount per ear and 100-grain weight, made an indirect effect on maize grain yield; the stem lignin content which significantly affected DWPU and SBS also directly contribute to the grain yield. These results are consistent with the previous study of Xue et al.²⁸ and Shinoto et al.²⁹, as well as in agreement with our previous study that SBS and DWPU in maize were markedly enhanced by the application of plant growth regulators (PGRs) in Northeast China⁸. In Northeast China, maize morphological traits have changed with the improved genotypes over the past few decades, the two typical hybrids were compared in two consecutive years in the present study, and more maize hybrids should be conducted to verify our results in the future.

Conclusion

Newly released maize hybrid Fm985 had a higher grain yield while lower lodging rate in high planting density, compared with Xy335 in the present study in Northeast China. The improved grain yield was significantly correlated with maize kernels amount per ear and lodging rate, which directly affected by SBS and GH, as well as indirectly by stem lignin content and DWPU, suggesting these characteristics which related to maize stalk lodging resistance in genetic improvement played a critical role in grain yield enhancement during modern commercial maize breeding.

Declarations

Declaration of Competing Interest

The authors declare that there are no declarations of interest.

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Author contributions

J. Cui wrote manuscript and contributed from beginning to the completion of the experiment. Q. Cao made study plan and designed the experiments. Z. Cui, Y. Lu, X. LV and Y. Hou collected raw data in field experiment. G. Yan was the leader of the research group, arranged the data statistically and gave final corrections.

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Tables

Hybrid	Seed Company	Year of release	Relative maturity	Density-tolerance	Endosperm type
Xy335	DuPont Pioneer	2004	125	High	Flint
Fm985	Fumin Seed Company	2015	127	High	Flint

Table 1 Characteristics of maize hybrids used in the experiments.

Year	Cultivar	Ear number per ha ($\times 10^4$)			Kernel amount per ear			100-grain weight (g)		
		LD	MD	HD	LD	MD	HD	LD	MD	HD
2018	Xy335	4.48 $\pm$ 0.02	6.12 $\pm$ 0.06	8.00 $\pm$ 0.07	567.03 $\pm$ 17.50	522.28 $\pm$ 3.79	482.16 $\pm$ 4.70	34.55 $\pm$ 0.25	32.49 $\pm$ 0.34	28.87 $\pm$ 0.24
	Fm958	4.47 $\pm$ 0.02	6.29 $\pm$ 0.06	8.23 $\pm$ 0.07	587.31 $\pm$ 8.53	522.28 $\pm$ 10.16	475.49 $\pm$ 8.95	33.38 $\pm$ 0.59	32.80 $\pm$ 0.31	32.20 $\pm$ 0.64
2019	Xy335	4.46 $\pm$ 0.02	6.20 $\pm$ 0.05	7.88 $\pm$ 0.07	568.64 $\pm$ 23.52	521.22 $\pm$ 10.52	483.23 $\pm$ 5.77	31.59 $\pm$ 0.30	29.60 $\pm$ 0.89	27.31 $\pm$ 0.60
	Fm958	4.45 $\pm$ 0.05	6.26 $\pm$ 0.05	8.25 $\pm$ 0.03	562.03 $\pm$ 11.15	522.28 $\pm$ 6.90	475.49 $\pm$ 6.65	31.40 $\pm$ 0.33	30.99 $\pm$ 0.12	29.19 $\pm$ 0.56

Table 2 Maize yield components under different treatments in 2018-2019. LD, MD, and HD represent low, medium, and high planting densities, respectively. Mean $\pm$ S.E (n=3)

Year	Cultivar	PD	Plant architecture			Stem morphological characteristics		
			PH (cm)	EH (cm)	GH (cm)	DWPU (g cm ⁻¹)	CL (cm)	CSA (cm ²)
2018	Xy335	LD	319.37±3.0	107.91±1.1	104.34±0.77	0.79±0.06	285.33±1.76	565.87±9.36
		MD	317.93±2.7	108.56±0.6	106.59±0.59	0.53±0.03	292.67±3.93	454.16±9.67
		HD	327.04±1.3	112.80±1.1	117.10±1.10	0.43±0.04	302.33±3.18	439.81±24.04
	Fm985	LD	305.64±2.9	107.79±1.4	103.20±1.17	0.73±0.04	273.33±4.25	511.66±18.09
		MD	295.34±1.5	108.62±1.3	104.85±0.45	0.65±0.02	283.00±3.78	460.54±10.75
		HD	298.55±3.2	111.26±1.1	103.51±1.66	0.59±0.02	281.00±3.53	406.46±17.13
2019	Xy335	LD	314.34±4.6	109.64±0.8	110.41±0.95	0.77±0.02	290.00±2.99	529.84±17.09
		MD	312.78±5.6	111.39±21.3	113.78±2.1	0.59±0.01	289.33±3.84	436.75±25.91
		HD	320.52±2.7	123.63±3.8	116.94±1.88	0.47±0.01	300.33±5.45	370.24±23.85
	Fm985	LD	305.32±4.1	105.31±1.66	110.84±2.54	0.75±0.11	286.00±5.29	455.13±31.36
		MD	300.92±3.3	106.35±2.11	105.20±1.96	0.60±0.02	285.00±3.21	438.64±10.89
		HD	296.04±3.3	108.65±1.57	106.95±1.61	0.56±0.01	287.67±4.70	406.08±15.24

Table 3 Plant architecture and stem morphological characteristics under different treatments.

PD, planting density; PH, plant height; EH, ear height; GH, gravity height; DWPU, dry weight per unit length; CL, culm length; CAS, stem cross-section area. Mean±S.E (n=3)

	Y	C	PD	Y×C	Y×PD	C×PD	Y×C×PD
Grain yield	ns	*	**	ns	ns	***	ns
Lodging rate	*	***	***	ns	**	ns	ns
Ear number per m ²	*	*	**	*	ns	ns	*
Kernel amount per ear	ns	ns	**	ns	ns	ns	ns
100-grain weight	**	*	**	ns	ns	**	ns
PH	ns	*	ns	ns	ns	**	ns
EH	ns	**	*	ns	ns	*	ns
GH	ns	*	ns	ns	ns	*	ns
DWPU	ns	*	***	ns	ns	ns	ns
CL	ns	ns	*	ns	ns	ns	ns
CSA	ns	ns	*	ns	ns	ns	ns
SBS	ns	**	**	ns	ns	ns	ns
Cellulose content	ns	**	*	ns	ns	**	ns
Lignin content	ns	*	*	ns	**	**	ns

Table 4 Output of three-way ANOVA on the effects of the year (Y), Cultivar (C), planting density (PD), and their interactions. PH, plant height; EH, ear height; GH, gravity height; DWPU, dry weight per unit length; CL, culm length; CAS, stem cross-section area; SBS, stem bending strength.

Figures

Figure 1

Rainfall and monthly mean temperature recorded during maize growing season (April to October) of experiment in 2018 (b) and 2019 (b)

Figure 2

Schematic diagram of the method for measuring the culm length (a) and height of the center of gravity (b) of maize plants.

Figure 3

Schematic diagram of the method for measuring the stalk bending strength of maize plants.

Figure 4

Comparison of maize grain yield, lodging rate in 2018 (a) and 2019 (b) at varied planting density. LD, MD, and HD represent low, medium, and high planting densities, respectively. Bars denote the SE of the mean ($n = 3$). ns, not significant ($P > 0.05$), ** and *** indicate differences of grain yield significant at 0.01 and 0.001 levels, # and ### indicate differences of lodging rate significant at 0.01 and 0.001 levels.

Figure 5

Stalk bending strength (SBS) under different treatments in 2018 (a) and 2019 (b); SBS were estimated by horizontal pulling resistance value; bars denote the SE of the mean ($n = 5$); *, ** and *** indicate differences significant at 0.05, 0.01 and 0.001 level; ns indicates no significant ($P > 0.05$).

Figure 6

The stem cellulose content in 2018 (a) and 2019 (b), and lignin content in 2018 (c) and 2019 (d) under different treatments. LD, MD and HD represent low, medium, and high planting densities, respectively. Bars denote the S.E of the mean ($n = 4$).

Figure 7

Correlation analysis between lodging rate and lodging related characteristics. The red and blue colors present the positive and negative correlation, respectively; * and ** indicate differences significant at 0.05 and 0.01 levels, respectively.

Figure 8

Path analysis of maize grain yield, yield component, SBS, and plant architecture characteristics.

Figure 9

Path analysis of SBS, stem morphology and structural carbohydrates content.