Maize Stalk Lodging: Morphological Determinants of Stalk Strength

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ABSTRACT

An incomplete understanding of stalk strength and stalk lodging impedes efforts to improve maize (Zea mays L.) production. To develop a more complete understanding of stalk strength, the current study examined the effect of stalk morphology on stalk bending strength. A detailed geometric analysis was conducted on five varieties of dent corn sown at five planting densities in two replicates at each of two locations near Greenville, IA, in 2013. Stalks were imaged using high-resolution X-ray computed tomography, and morphological features of the stalk were quantified using customized computer code. After scanning, stalks were subjected to mechanical tests to determine stalk bending strength and rind penetration resistance. The section modulus of the stalk (a morphological quantity derived from engineering beam theory) was found to be highly predictive of stalk strength, and its predictions appear to be largely unaffected by common confounding factors such as hybrid and planting density. By assuming the stalk cross section to be a hollow ellipse, the section modulus of the stalk can be estimated using measurements of stalk diameter and rind thickness (which does not require computerized tomography scanning). The elliptical section modulus is highly predictive of stalk strength, does not appear to be confounded by experimental variables, and can be obtained using a pair of calipers. Thus, it demonstrates potential as a selective breeding index to improve lodging resistance. In the current study, the elliptical section modulus predicted stalk strength with four times the accuracy of rind penetration resistance (a more common method used in breeding studies).

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Abbreviations: CT, computed tomography; MOI, moment of inertia.

A incomplete understanding of stalk bending strength impedes efforts to improve maize (*Zea mays* L.) production. In particular, the problem of late-season stalk lodging (breakage of the stalk prior to harvest but after reproductive stage six) has been estimated to reduce worldwide corn yields by 5 to 20% (Flint-Garcia et al., 2003; Hu et al., 2013). Furthermore, high-yielding varieties of corn that are tolerant of overcrowding and drought stress are frequently eliminated from breeding studies due to high lodging propensity. Increasing the bending strength of plant stems is therefore important to both current production and future development. Using insights from engineering theory, the current study examined the effect of stalk morphology on stalk bending strength.

Several studies have speculated that stalk strength may be a reliable predictor of lodging propensity (Zuber and Grogan, 1961; Cloninger et al., 1970; Singh, 1970; Remison and Akinleye, 1978; Zuber and Kang, 1978; Hondroyianni et al., 2000; Ma et al., 2014). Naturally lodged corn stalks break due to excessive bending loads imposed by wind and gravity. It naturally follows that stalks with improved structural bending strength are more resistant to lodging. In addition, while both stalk bending strength and lodging resistance are affected by genetics and environment, the *relationship* between bending strength and lodging resistance should not be affected by genetics and environment (Hu et al., 2013; Brulé et al., 2016). Furthermore, a recent structural engineering analysis of mechanical stresses in the maize stalk suggests that stalk bending strength (and therefore lodging

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© Crop Science Society of America | 5585 Guilford Rd., Madison, WI 53711 USA This is an open access article distributed under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/). propensity) is highly dependent on stalk morphology (Von Forell et al., 2015).

To investigate the influence of morphology on maize stalk strength, a detailed geometric analysis was performed on five dent corn hybrids sown at five planting densities in two replicates at each of two locations. All stalks were imaged using high-resolution X-ray computed tomography (CT), and numerous morphological features of the stalk were quantified and analyzed. Morphological features examined included basic geometric measurements of cross sections (e.g., diameter and area), as well as several structural engineering measurements that may be less familiar to plant scientists (e.g., radius of gyration, slenderness, etc.). After imaging, stalks were subjected to mechanical tests to determine stalk bending strength and rind penetration resistance. Stalk morphology measurements were then compared against rind penetration measurements based on their ability to predict stalk bending strength.

MATERIALS AND METHODS

All stalks in this study were subjected to three analyses. First, a morphological analysis of each stalk was conducted via CT scanning; second, stalk bending strength was measured using a mechanical three-point bend test; and third, rind penetration resistance tests were performed on undamaged internode segments of each stalk. Statistical procedures were then used to analyze and compare results. The methodological details are provided in the paragraphs below.

Plant Materials

Stalks were sampled from two replicates of five DKC commercially available, trait-protected hybrids of dent corn (maize) seeded at planting densities of 119,000, 104,000, 89,000, 74,000, and 59,000 plants ha-1 (48,000,42,000, 36,000, 30,000, and 24,000 plants ac⁻¹). Stalks were grown at Monsanto facilities in two locations in Iowa in 2013. The first location was in northwestern Iowa and was a Gillett Grove silty clay loam (fine-silty, mixed, superactive, mesic Typic Endoaquolls); the second site was in north-central Iowa and was a Maxfield silty clay loam (fine-silty, mixed, superactive, mesic Typic Endoaquolls). Two replicates were planted per location and 10 stalks were sampled for each plot. The hybrids ranged in maturity from 94 to 110 relative maturity (RM) and were adapted and suited for the environment. They were planted timely in early spring in good field conditions and were managed for optimum yields. The previous crop was soybeans [Glycine max (L.) Merr.]. A total of 1000 stalks were used in this study (5 hybrids \times 5 densities \times 2 locations \times 2 replicates \times 10 stalks plot⁻¹). Stalks were allowed to remain in the field until full maturity (reproductive stage six) and were gathered just prior to harvest. Stalks were cut just above the ground and just above the ear internode. Stalk sections generally consisted of five to eight internodes. As in previous studies, leaves and ears were removed and the stalks were placed in forced air dryers to reduce stalk moisture to a stable level (~10-15%) to prevent fungal growth and spoilage (Robertson et al., 2014, 2016). To avoid confounding factors, only stalks found to be free of disease and pest damage were included in the study.

Morphological Analysis

Stalks were imaged using X-ray CT scanning. Scans were performed using an X5000 scanner (NorthStar Imaging, Rogers, MN). Stalks were scanned in groups of 10. Grayscale calibration of CT data was accomplished by referencing two acrylic reference objects of known density in each scan. Reconstructed three-dimensional scan images had a native size of 1564 × 1743 × 1743 voxels, providing a spatial resolution of 78 microns voxel⁻¹ and a 16-bit intensity range. This enabled identification of both rind and pith tissues, as well as individual vascular bundles (see Fig. 1).

Prior research on maize stalk failure indicated that morphologic features near the node are associated with stalk failure (Robertson et al., 2015a). The scan region for each stalk was therefore centered on the most central node of each stalk sample (see Fig. 1). The scan data for an individual stalk typically consisted of a three-dimensional data array of approximately $300 \times 300 \times 1350$ voxels. Forty-two cross sections were sampled for each stalk. Because morphology changes more rapidly near the node, a higher spatial sampling frequency was implemented near the node, as shown in Fig. 1.

Computed tomography reconstruction software (efX-ct, version 1.8, NorthStar Imaging, Rogers, MN) was used to convert three-dimensional CT data into a series of cross-sectional tif-format images. Custom computer code developed by the authors in the MATLAB environment (Mathworks, Inc., Natick, MA) was then used to extract morphological attributes from cross-sectional tif-format images. Thresholding techniques were used to obtain the exterior outline of each cross section. The cross section outline was then used to determine the major and minor diameters, geometric center, and orientation of each cross section. Perpendicular local offsets to the exterior boundary were used to determine the rind thickness. In total, over 30 morphological attributes were determined for each cross section. Table 1 lists several of these morphological attributes, as well as their abbreviations. Results pertaining to these attributes will be presented in detail. Additional results are provided in the supplemental material.

Because the maize stalk cross section is approximately elliptical, certain quantities were calculated both explicitly (based on CT data) and implicitly by assuming the stalk cross section to be a hollow ellipse. In this latter approach, analytic equations for an ellipse were used with inputs consisting of simple geometric parameters of the stalk: major radius, minor radius, and rind thickness. Such elliptical quantities could viably be obtained from stalks in the field using a pair of calipers. They are included in the current study to represent morphological quantities that could immediately be used in breeding studies (CT scanning is prohibitively expensive for use in most breeding studies). The ellipse-based quantities listed in Table 1 were calculated in this manner. It should be noted that none of the stalks tested in this study were physically hollow. However, the simplifying assumption of a hollow ellipse is typical in mechanical engineering analyses of composite structures composed of relatively weak and flexible cores (i.e., pith) surrounded by a stiff and strong shell (i.e., rind). Information on morphological features calculated using the entire cross section of the stalk is found in the supplemental material.

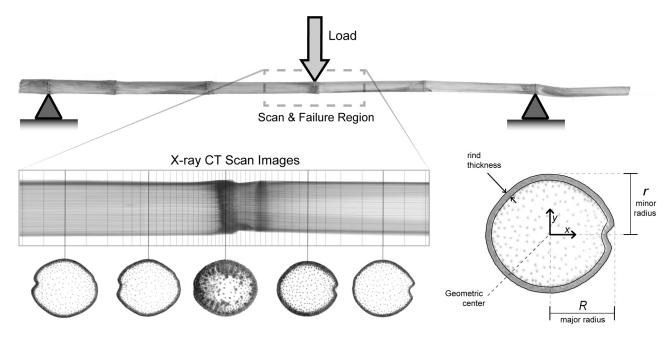


Fig. 1. Diagram depicting three-point bending test arrangement and region of computed tomography (CT) scan (top), axial, and transverse CT scan images (lower left) and an annotated cross section indicating some features identified through image processing (lower right).

One morphological feature that will be referred to often in this paper is the area moment of inertia (MOI) (Hibbeler and Fan, 2004). This quantity refers to the manner in which crosssectional material is distributed. Area is weighted by the square of its distance from one axis of a coordinate system. This quantity is also known as the second moment of area. In this study, the coordinate system was located at the geometric center of each cross section, with the x axis aligned with the major axis of the stalk (see Fig. 1). Because maize stalk failure predominantly occurs in the direction of the minor axis of the stalk (Robertson et al., 2015a) and because prior research on similar crop species suggests that the rind is the primary load bearing component of dry stalks (Maranville and Clegg, 1984), all MOI measurements in the body of this paper are based on the rind only and relate to the minor stalk diameter. Information on other MOI measurements (e.g., major axis and whole stalk) is provided in the supplemental material.

Bending Strength

Stalk bending strength is the most appropriate strength measurement to consider when assessing stalk lodging. Several methods for measuring stalk bending strength have been presented previously. In the current study, bending strength tests were performed according to the protocol outlined by Robertson et al. (2014, 2015b). This method produces the same distinctive failure pattern (a crease just above the node) as naturally lodged stalks.

Bending tests were performed using an Instron universal testing machine (Model 5965, Instron Corp., Norwood, MA,). The stalk was supported at the most basal and most apical node, while the most central node was displaced at a constant rate of 10 cm min⁻¹. A 500-N load cell was used to collect force data at a rate of 10 Hz. Force and displacement data were used to calculate the induced bending moment (M) according to the following equations (Howell, 2001)

$$M(x) = \frac{Fbx}{L}, x \le a$$

$$[1]$$

$$M(x) = \frac{Fa}{L}(L-x), x > a$$

$$[2]$$

where X is the distance along the stalk measured from the left support, a is the distance to the applied load as measured from

Table 1. The primary morphologic features presented in this study. Features prefaced by the phrase "ellipse-based" refer to features that were calculated by assuming the stalk to be a hollow ellipse. Additional features and results are available in supplemental material.

Stalk attribute	Abbreviation	Mathematical equation (where appropriate)		
Computed tomography (CT) intensity of rind	CT	_		
Major radius	R	R = (major diameter)/2		
Minor radius	r	r = (minor diameter)/2		
Rind thickness	t	-		
Cross-sectional area	A	-		
Area moment of inertia of the rind in the direction of the minor stalk diameter	MOI	∭y²dxdy		
Ellipse-based area moment of inertia of the rind in the direction of the minor stalk diameter	eMOI	$\pi/4[Rr^3 - (R-t)(r-t)^3]$		
Section modulus in the direction of the minor stalk diameter	SM	(∬y²dxdy)/r		
Ellipse-based section modulus in the direction of the minor stalk diameter	eSM	${\pi/4[Rr^3 - (R - t)(r - t)^3]}/r$		

the left support, and b is the distance to the applied load measured from the right support. L is the distance between supports (e.g., a + b) and F is the applied load. Bending strength was defined as the maximum moment supported by the stalk at the location of stalk failure.

Rind Penetration Resistance

Rind penetration resistance measurements were acquired using the universal testing machine described above. A stainless steel needle measuring 1.5 mm in diameter that tapered to a sharp point over a distance of 5 mm was used in all experiments. The needle was lowered at a constant rate of 30 mm s⁻¹ while a 50-N load cell acquired load data at a rate of 100 Hz. Each test continued until the needle had completely punctured the rind and entered the pith tissue of the middle portion of the third aboveground internode of each stalk (Gou et al., 2010). Rind penetration resistance was defined as the maximum load measured during the test.

Engineering Theory

Engineering beam theory was used to inform the analysis of maize stalk strength. The equation for a simple beam in bending (Howell, 2001) states that tissue stress (σ) depends on the applied moment (M), the area MOI, and the distance between the neutral bending axis and the point at which the stress is being measured (c) as shown here:

$$\sigma = M\left(\frac{c}{\text{MOI}}\right)$$
[3]

According to this equation, tissue stresses will be highest on the exterior surface of the structure (when c is at a maximum). Algebraically rearranging the equation to solve for bending strength by assuming the neutral bending axis lies at the centroid of the cross section gives the following:

$$M_{\rm max} = \sigma_{\rm max} \left(\frac{\rm MOI}{\rm r} \right)$$
 [4]

where $M_{\rm max}$ represents the stalk structural bending strength, $\sigma_{\rm max}$ is the ultimate tissue strength, and *r* is the minor radius of the stalk. The equation indicates that structural bending strength is dependent on both tissue strength $\sigma_{\rm max}$ and a morphological quantity known in structural engineering as the section modulus (MOI/*r*) (Beer et al., 2006). This study focuses on the influence of morphology only.

Statistics

Two types of regression analyses were employed in the current study. First, a univariate regression was conducted in which data from all hybrids, planting densities, replicates, and locations were combined and a correlation between the independent variable of interest (i.e., rind penetration resistance or a morphological feature) and the dependent variable (stalk strength) was calculated.

A second regression analysis was conducted to determine if the abovementioned regression relationships are confounded by factors such as hybrid and planting density. In other words, is the regression relationship between strength and morphology consistent across different hybrids, or different planting locations? For example, can the regression relationship obtained at one planting density be used to predict the strength of plants sown at different planting densities or different locations?

To answer this question, the data obtained in the current study was split into training datasets and validation datasets. Training datasets consisted of data acquired from a single experimental factor (e.g., hybrid 1 or planting density 1). Validation datasets consisted of all remaining data (e.g., hybrids 2–5 or planting densities 2–5). A coefficient of determination was then calculated between the training set regression line and the data of the validation set. This coefficient of determination represents the capability of each factor to predict outside its training data, and will be referred to as (R^2_{pred}) . Similarly, the coefficient of as R^2_{univ} and coefficients of determination from training datasets will be referred to as R^2_{train} . The process described above was repeated once for each factor level (i.e., once for each of five hybrid types, once for each of five planting densities, etc.).

RESULTS

The bending strength methodology used in the current study produced the same failure types and patterns observed in naturally lodged stalks. In particular, 98% of all stalks tested in this study demonstrated a creasing failure mode, and 95% of all failures occurred within 3 cm of a node. These same failure types and patterns are observed in naturally lodged stalks (Robertson et al., 2015a).

Morphological features of corn stalk measured in this study varied with regards to hybrid and planting density. At low planting densities, stalks were stronger and possessed a larger MOI than stalks at high planting densities. This trend was consistent across all hybrids. However, fewer statistical differences in rind penetration resistance measurements were observed among different planting densities and hybrids. Boxplots displaying key variables of interest (stalk bending strength, elliptical MOI, and rind penetration resistance) are shown in Fig. 2.

Univariate Regression Analysis

The correlation between cross-sectional morphology and stalk strength was found to vary spatially. This effect can be seen in Fig. 3 which displays the R^2_{univ} values of select morphological factors as a function of distance from the node. The poor correlation results near the node were related to the highly variable nature of morphological features in this region. While morphological changes near the node likely influence stalk strength (Robertson et al., 2015a), the internode region was found to be a more consistent predictor of strength. For the remainder of this paper, only R^2 values acquired from the central portion of stalk internodes are reported.

Several morphological factors were highly correlated with stalk strength. As expected, the section modulus and elliptical section modulus were the best overall predictors

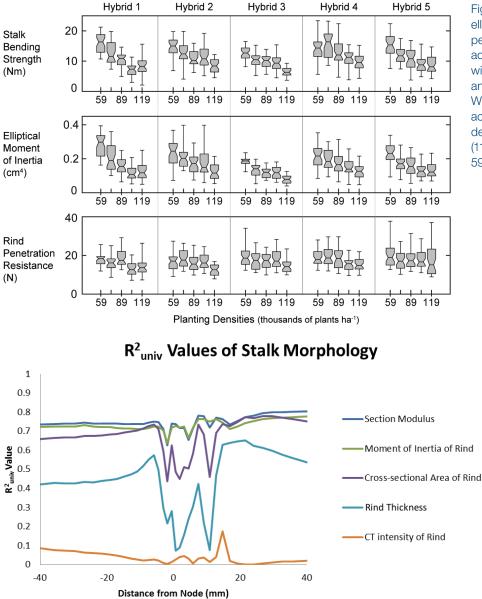


Fig. 2. Boxplots of stalk bending strength, elliptical moment of inertia, and rind penetration resistance. Plots are grouped according to hybrid and planting density, with hybrid 1 shown in the far left column and hybrid 5 shown in the far right column. Within each hybrid column, data is organized according to planting density. Five planting densities were analyzed in the current study (119,000, 104,000, 89,000, 74,000, and 59,000 plants ha⁻¹).

Fig. 3. Spatial variation of the univariate coefficient of determination (R^2_{univ}) of stalk morphology versus stalk bending strength. In general, internodal morphology was a more consistent predictor of stalk strength as compared with morphology near the node.

of stalk strength (R^2_{univ} values of 0.79 and 0.80, respectively). The CT intensity of the rind was the worst overall predictor of stalk strength ($R^2_{univ} = 0.01$). Rind penetration resistance was positively correlated with stalk strength, but the relationship was relatively weak ($R^2_{univ} = 0.18$). Figure 4 displays a bar graph of R^2_{univ} values of morphological factors and rind penetration resistance. The whiskers in the plot represent 95% confidence intervals.

Regression Analysis with Training and Validation Datasets

Coefficient of determination values for training and validation sets generally followed the same patterns shown above for univariate correlations. The rind section modulus and rind elliptical section modulus in the direction of the minor stalk axis exhibited the highest R^2_{train} and R^2_{pred} values ($R^2_{\text{train}} > 0.73$ and $R^2_{\text{pred}} > 0.76$, respectively). The average difference between R^2_{train} and R^2_{pred} for section modulus terms was <0.02, indicating that the relationship with stalk strength and section modulus is not confounded by the effects of hybrid, planting density, location, or replicate. In other words, the section modulus appears to accurately predict strength, even across hybrids and planting densities. On the other hand, rind penetration resistance was significantly affected by factors such as hybrid and planting density and had an overall R^2_{pred} value 0.09. Table 2 lists the R^2_{univ} , R^2_{train} , and R^2_{pred} values of morphological parameters and rind penetration resistance. A table with additional morphological parameters can be found in the supplemental material.

Scatterplots of stalk strength versus elliptical section modulus and stalk strength versus rind penetration resistance are shown in Fig. 5. Data in the plots are separated according to hybrid, planting density, location, and replicate. Regression lines for each hybrid, planting density, location, and replicate are presented. Regression lines for

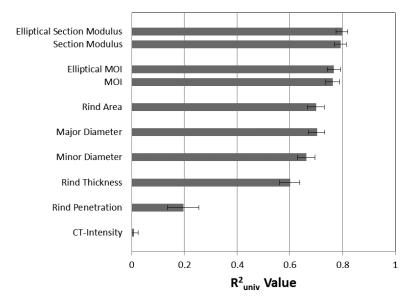


Fig. 4. Bar plot of univariate coefficient of determination values for internodal morphology versus stalk bending strength. Whiskers indicate the 95% confidence interval for each value.

rind penetration resistance are quite variable and appear to be particularly dependent on planting density. However, regression lines for the elliptical section modulus are fairly consistent across each experimental variable, indicating the ability of this quantity to consistently predict strength.

DISCUSSION

Basic physics and engineering theory state that the strength of any structure depends on both material (tissue) and geometry (morphology). A computational sensitivity analysis of maize stalk strength indicated that mechanical stresses in maize stalk are largely determined by stalk morphology, while material properties have a significantly smaller effect (Von Forell et al., 2015). In the current study, morphological features consistently exhibited a closer relationship to stalk strength than measurements related to tissue properties (i.e., CT intensity and rind penetration resistance). In particular, the section modulus predicted 70 to 80% of the variation in stalk strength, whereas measurements related to material properties (i.e.,

rind penetration resistance and CT intensity) accounted for <20% of the variation in stalk strength. In addition, a previous study indicated that flexural stiffness predicted 81% of the variation in stalk bending strength (Robertson et al., 2016) and is therefore an important trait to consider when selecting for lodging resistance. Measurements of flexural stiffness depend on both material (tissue stiffness) and geometry (cross-sectional area MOI). However, flexural stiffness is only a slightly better predictor of stalk strength than cross-sectional area MOI (i.e., morphology) alone. Taken together, these results indicate that stalk strength is determined primarily by stalk morphology.

Practical Considerations and Implications for Breeding

Previous breeding efforts to improve lodging resistance in maize have typically relied on counting the number of lodged stalks at harvest. Unfortunately this method is severely confounded by disease, pest damage, wind, rain,

						rain prou						
		R ² _{train}					R ² _{pred}					
	- 0					Overall			·		Overall	
	R ² _{univ}	Hybrid	Density	Replicate	Location	mean	Hybrid	Density	Replicate	Location	mean	
Elliptical section modulus	0.80	0.80	0.74	0.81	0.81	0.79	0.78	0.77	0.79	0.80	0.78	
Section modulus	0.79	0.80	0.73	0.81	0.80	0.78	0.77	0.76	0.79	0.80	0.78	
Rind area	0.77	0.77	0.71	0.79	0.79	0.77	0.76	0.75	0.79	0.80	0.77	
Elliptical MOI‡	0.77	0.79	0.71	0.78	0.77	0.76	0.71	0.72	0.75	0.77	0.74	
MOI	0.76	0.78	0.70	0.78	0.77	0.76	0.71	0.72	0.75	0.76	0.73	
Major diameter	0.70	0.72	0.63	0.71	0.70	0.69	0.66	0.63	0.69	0.72	0.67	
Minor diameter	0.66	0.72	0.58	0.67	0.66	0.66	0.53	0.58	0.65	0.67	0.61	
Rind thickness	0.60	0.65	0.54	0.62	0.62	0.61	0.51	0.48	0.62	0.62	0.56	
Rind penetration	0.18	0.21	0.16	0.22	0.22	0.20	0.14	-0.19	0.15	0.27	0.09	
CT intensity	0.01§	0.06§	0.03§	0.02§	0.01§	0.03	-0.13	-0.53	-0.05	-0.01	-0.18	

Table 2. Coefficient of determination values for univariate (R^2_{univ}) , training (R^2_{train}) , and predictive (R^2_{pred}) correlations.⁺

 \dagger All P-values for $R^2_{\rm train}$ and $R^2_{\rm univ}$ < 0.01 unless marked otherwise.

‡ MOI, area moment of inertia.

§ *P*-value > 0.01.

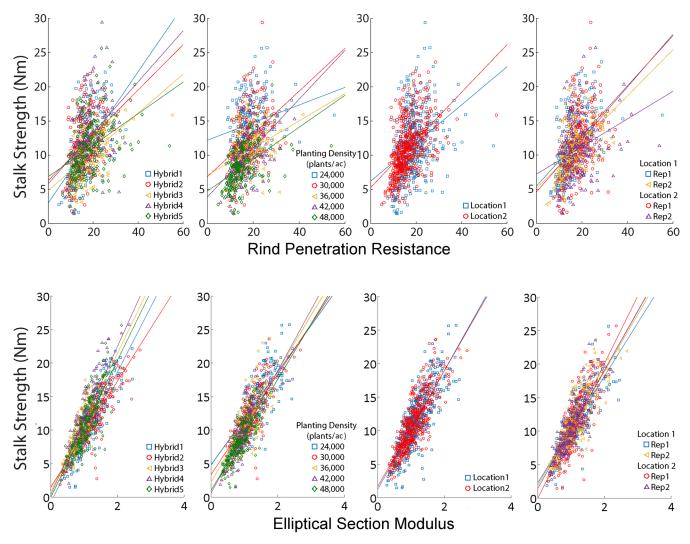


Fig. 5. Scatterplots of stalk strength versus rind penetration (top row) and elliptical section modulus (bottom row). Each individual chart shows the regression line for each dataset in the respective legend. The elliptical moment of inertia was a more consistent and accurate predictor of stalk strength as compared with rind penetration resistance.

and climate (Flint-Garcia et al., 2003). Several studies have hypothesized that rapid gains in lodging resistance could be achieved by developing a reliable measure of lodging propensity that is not confounded by lodging-related weather events, such as wind and rain storms (Cloninger et al., 1970; Hu et al., 2012).

The section modulus of corn stalk demonstrates promise as a reliable measure of lodging propensity. In particular, data from this study suggest that the relationship between section modulus and stalk strength is independent of genetic and environmental factors such as hybrid and planting density (see R^2_{pred} values in Table 2). In addition, the section modulus of maize stalk can be calculated by assuming the stalk cross section to be elliptical, thus eliminating the need for expensive CT scans. This approach requires measurement of just three quantities: major diameter, minor diameter, and rind thickness. These three quantities should be measured at the internodes, since this region is most predictive of bending strength and the geometry of the stalk is more consistent in this region (see Fig. 3). The elliptical section modulus values calculated based on internodal measurements is remarkably accurate ($R^2 = 0.996$ between elliptical section modulus and the section modulus computed directly from CT data). Furthermore, the ellipse-based approach appears to be just as highly correlated with stalk strength as the CT approach, as shown by the R^2_{univ} , R^2_{train} , and R^2_{pred} values in Table 2. Specialized tools to rapidly measure stalk section modulus in the field are currently being developed by the authors.

Several other morphological attributes of the stalk presented in Table 2 provide predictive capabilities that are appealing. For example, the major and minor radii both explain over 60% of the variation in strength. From a cost-benefit standpoint, it might seem reasonable to use one of these simpler features as a breeding index, as opposed to section modulus. While this approach (like rind penetration resistance) may provide initial success, it is incomplete. Factors such as major radius, minor radius, and rind thickness are correlated with stalk strength because they affect the section modulus of the stalk. As a consequence, breeding efforts to increase section modulus will likely provide the optimal path for improving stalk bending strength. This approach results in a more structurally efficient use of biomass and is therefore less likely to negatively affect yield. In other words, engineering theory dictates that when considering the bending strength of a structure, increasing the section modulus results in an optimal cross-sectional distribution of biomass, whereas increasing only diameter or rind thickness may result in a suboptimal cross-sectional distribution of biomass. Therefore, increasing section modulus will give a greater increase in bending strength per additional gram of stalk biomass as compared with increasing diameter or rind thickness alone.

For the stalks analyzed in this study, the greatest increase in the elliptical section modulus would be expected if the major diameter, minor diameter, and rind thicknesses were increased in ratios of approximately 1:2:23. This ratio indicates that while an increase in rind thickness will likely provide the greatest benefit, this increase should be accompanied by slight increases in the major and minor diameters. In some instances, increasing the section modulus may require increasing stalk dry matter and may therefore compete with dry matter allocation to the ear (i.e., may affect kernel number and yield potential). This effect has yet to be determined experimentally and remains the subject of future work

Limitations

As in previous studies (Robertson et al., 2014, 2015b, 2016), stalk samples used for analysis were fully mature, stalk moisture had been reduced to stable levels (10–15% w/w), and all samples were free of disease and pest damage. This study design was chosen by the authors for several reasons. Mature stalks were used in this study because the authors were primarily interested in the problem of late-season stalk lodging, which occurs after the plant has reached full maturity. Stalks were dried to prevent spoilage and eliminate the effect of confounding factors (turgor pressure, moisture content, and numerous other biological process affected by harvesting and sample-handling procedures). Diseased and pest-damaged stalked were likewise excluded to limit the number of confounding factors in the study. Turgor and moisture content affect the strength of corn stalks, but at the time of writing, the authors are not aware of any studies that have addressed these issues directly. Drying the stalks eliminated relative differences in moisture and turgor between stalk samples, thus enabling a more direct comparison between samples by isolating the influence of stalk morphology on stalk strength. The primary limitation of this study may be that the effects of moisture and turgor pressure on stalk strength were intentionally excluded from investigation to

focus on the contribution of morphology. Further research will be needed to assess the effects of moisture and turgor pressure on stalk strength. The strength values reported in this study are therefore most applicable to dry, mature stalks, a common state just before harvest.

The stalks samples in this study were acquired from commercially available hybrids and were thus fairly strong and resilient. Some previous studies have used very broad sampling designs when investigating the ability of various measurements to predict stalk strength. The inclusion of both exceptionally weak and exceptionally strong hybrids (i.e., using very broad sampling designs) can tend to inflate R^2 values. A narrower sample design was used in this study to determine the ability of morphology to predict the relative differences in lodging resistance between latestage, precommercial hybrids of dent corn.

On the Use of Engineering Equations and Theory

It should be noted that Eq. [1] and [2] are intended for use with beams that have a constant cross section and isotropic, homogenous material properties (i.e., material that is spatially uniform, in which the properties are not dependent on direction of measurement) (Howell, 2001; Beer et al., 2006). The corn stalk violates each of these assumptions because its tissue properties are complex and because both material and morphology vary spatially. In addition, when calculating the MOI and section modulus, the pith material was neglected, and for some results presented above, the stalk cross section was assumed to be an ellipse. In spite of all these assumptions, engineering theory provided valuable insights that were used to identify features of stalk morphology that are highly correlated with stalk strength. Features such as the MOI and elliptical section modulus would likely never be discovered by performing a multiple regression analysis of obvious parameters such as diameters, cross-sectional area, and rind thickness. The use of engineering mechanics to inform statistical analysis in this way can be referred to as mechanics-based regression.

CONCLUSION

The purpose of this study was to identify relationships between morphological features of corn stalk and stalk bending strength. Several geometric features were found to be related to stalk strength, with coefficient of determination (R^2) values ranging from 0.5 to 0.8. In contrast, rind penetration resistance was found to have R^2 values ranging from 0.1 to 0.3. The section modulus was found to be the strongest predictor of stalk strength, with R^2 values ranging from 0.73 to 0.80. This quantity was obtained from engineering theory and represents the contribution of morphology to stalk bending strength. These data indicate that morphology of the maize stalk accounts for ~75% of the variation in stalk strength. Cross validation confirmed that strength predictions provided by the section modulus were not significantly affected by hybrid type, planting location, or planting density. The section modulus can easily be calculated based on the major diameter, minor diameter, and rind thickness. Breeders interested in improving lodging resistance should consider breeding for increased section modulus.

Conflict of Interest

The authors declare there to be no conflict of interest.

Supplemental Material Available

Supplemental material for this article is available online.

Acknowledgments

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References

- Beer, F., E. Johnston and J. Dewolf. 2006. Mechanics of materials. McGraw-Hill, New York.
- Brulé, V., A. Rafsanjani, D. Pasini, and T.L. Western. 2016. Hierarchies of plant stiffness. Plant Sci. 250:79–96. doi:10.1016/j. plantsci.2016.06.002
- Cloninger, F., M. Zuber, H. Calvert, and P. Loesch, Jr. 1970. Methods of evaluating stalk quality in corn. Phytopathology 60:295-300. doi:10.1094/Phyto-60-295
- Flint-Garcia, S.A., C. Jampatong, L.L. Darrah, and M.D. McMullen. 2003. Quantitative trait locus analysis of stalk strength in four maize populations. Crop Sci. 43:13–22. doi:10.2135/ cropsci2003.0013
- Gou, L., J. Huang, R. Sun, Z. Ding, Z. Dong, and M. Zhao. 2010. Variation characteristic of stalk penetration strength of maize with different density-tolerance varieties. Nongye Gongcheng Xuebao 26:156–162.
- Hibbeler, R.C. and S. Fan. 2004. Statics and mechanics of materials. Prentice Hall, Upper Saddle River, NJ.
- Hondroyianni, E., D. Papakosta, A. Gagianas, and K. Tsatsarelis. 2000. Corn stalk traits related to lodging resistance in two soils of differing salinity. Maydica 45:125–133.
- Howell, L. 2001. Compliant mechanisms. John Wiley & Sons, Hoboken, NJ.

- Hu, H., W. Liu, Z. Fu, L. Homann, F. Technow, H. Wang et al. 2013. QTL mapping of stalk bending strength in a recombinant inbred line maize population. Theor. Appl. Genet. 126:2257–2266. doi:10.1007/s00122-013-2132-7
- Hu, H., Y. Meng, H. Wang, H. Liu, and S. Chen. 2012. Identifying quantitative trait loci and determining closely related stalk traits for rind penetrometer resistance in a high-oil maize population. Theor. Appl. Genet. 124:1439–1447. doi:10.1007/ s00122-012-1799-5
- Ma, D., R. Xie, X. Liu, X. Niu, P. Hou, K. Wang et al. 2014. Lodging-related stalk characteristics of maize varieties in China since the 1950s. Crop Sci. 54:2805–2814. doi:10.2135/ cropsci2014.04.0301
- Maranville, J., and M. Clegg. 1984. Morphological and physiological factors associated with stalk strength. In: G. Rosenberg, editor, Sorghum root and stalk rots: A critical review. Proceedings of the Consultative Group Discussion on Research Needs and Strategies for Control of Sorghum Root and Stalk Rot Diseases, 27 Nov.–2 Dec. 1983, Bellagio, Italy. ICRI-SAT, Patancheru, India. p. 111–118.
- Remison, S., and D. Akinleye. 1978. Relationship between lodging, morphological characters and yield of varieties of maize (*Zea mays L.*). J. Agric. Sci. 91:633–638. doi:10.1017/ S0021859600060019
- Robertson, D., S. Smith, B. Gardunia, and D. Cook. 2014. An improved method for accurate phenotyping of corn stalk strength. Crop Sci. doi:10.2135/cropsci2013.11.0794
- Robertson, D.J., M. Julias, B.W. Gardunia, T. Barten, and D.D. Cook. 2015a. Corn stalk lodging: A forensic engineering approach provides insights into failure patterns and mechanisms. Crop Sci. 55:2833–2841. doi:10.2135/cropsci2015.01.0010
- Robertson, D.J., S.Y. Lee, M. Julias, and D.D. Cook. 2016. Maize stalk lodging: Flexural stiffness predicts strength. Crop Sci. 56:1711–1718. doi:10.2135/cropsci2015.11.0665
- Robertson, D.J., S.L. Smith, and D.D. Cook. 2015b. On measuring the bending strength of septate grass stems. Am. J. Bot. 102. doi:10.3732/ajb.1400183
- Singh, T. 1970. Association between certain stalk traits related to lodging and grain yield in maize (*Zea mays* L.). Euphytica 19:394–397. doi:10.1007/BF01904220
- Von Forell, G., D. Robertson, S.Y. Lee, and D.D. Cook. 2015. Preventing lodging in bioenergy crops: A biomechanical analysis of maize stalks suggests a new approach. J. Exp. Bot. 66:4367–4371. doi:10.1093/jxb/erv108
- Zuber, M., and C. Grogan. 1961. A new technique for measuring stalk strength in corn. Crop Sci. 1:378–380. doi:10.2135/crop sci1961.0011183X000100050028x
- Zuber, M., and M. Kang. 1978. Corn lodging slowed by sturdier stalks. Crops and Soils 30:1–32.