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Research Paper

Maize lodging resistance: Stalk architecture is a stronger predictor of stalk bending strength than chemical composition

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The chemical composition of grain stalks has been extensively studied and has long been assumed to have a major influence on stalk lodging. However, much less attention has been given to the influence of stalk architecture (i.e. physical features of anatomy and morphology). We show in this study that stalk architecture is far more influential on stalk bending strength (a common measure of lodging resistance) than chemical composition. This insight was obtained through the novel combination of structural engineering principles and a plant-by-plant experimental design using two major grain species (maize and sorghum). Lodging resistance was quantified using stalk bending strength which provides plant-specific data while also removing dependence on weather events. Stalk anatomy and morphology as and chemical composition of the stalk were also measured for each specimen in this study. Statistical results indicate that (a) the quantification of stem architecture via engineering beam theory is four times more predictive of stalk bending strength than composition, and (b) stalk architecture and chemical composition are interrelated. These results explain why previous studies attempting to link chemistry and lodging have been inconsistent. Furthermore, these results indicate that future studies aimed at studying lodging must not overlook the dominant influence of stalk architecture.

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Nomenclature

Term/Abbreviation	*Definition (units)*
architecture	internal or external features of physical anatomy and morphology such as major diameter, minor diameter, rind thickness, cross-sectional area, etc.
a	the distance to the applied load from the left support (m)
AD_ICP	acid detergent insoluble crude protein (%)
ADF	acid detergent fiber (%)
Adj_CP	Crude protein, corrected for insoluble crude protein (%)
Area (pith)	The transverse cross-sectional area of the pith tissue (m^2)
Area (rind)	The transverse cross-sectional area of the rind tissue (m^2)
Area (total)	The transverse cross-sectional area of entire stalk (total area = rind area + pith area) (m^2)
Ash	Inorganic mineral elements (%)
Ca	Calcium (%)
Cellulose	Self-explanatory (%)
Cl	Chlorine (%)
Crude_protein	Crude protein (%)
EE_Fat	Ether extract crude fat content (%)
EI	Flexural stiffness (or flexural rigidity) – an engineering quantity representing the resistance of a structure to bending deformation (Nm^2)
F	Force applied in a bending test (N)
Hemicellulose	Self-explanatory (%)
K	Potassium (%)
L	Length of the measured portion of the stalk, total distance between supports, i.e., $L = a+b$ (m)
LD_Internode	The linear density (mass per unit length) of a 5 cm internodal section (g/m)
LD_Node	The linear density (mass per unit length) of a 5 cm section centered on the node (g/m)
LD_Overall	The linear density (mass per unit length) of the tested stalk segment (including both nodes and internodes) (g/m)
Lignin	Self-explanatory (%)
M(x)	Moment as a function of x (Nm)
MajDiam	The major diameter - the largest transverse width of the stalk (m)
Mg	Magnesium (%)
MinDiam	The minor diameter – the smallest transverse width of the stalk (m)
Moment of Inertia (hollow, a)	The second moment of area of bending about the minor diameter with the pith tissue neglected (m^4)
Moment of Inertia (hollow, b)	The second moment of area of bending about the major diameter with the pith tissue neglected (m^4)
Moment of Inertia (solid, a)	The second moment of area of bending about the minor diameter – assuming a solid cross-section (m^4)
Moment of Inertia (solid, b)	The second moment of area of bending about the major diameter – assuming a solid cross-section (m^4)
Na	Sodium (%)
NDF	Neutral detergent fiber (%)
NFC	Non-fibrous carbohydrates (%)
P	Phosphorus (%)
φ (phi)	The slope of the force/deformation curve obtained from the bending test data (N/m)
Planting Density	The number of plants per area (m^{-2})
PRE	Proportional reduction of error (unitless)
Rind Thick	The thickness of the rind tissue (m)
S	Sulfur (%)
SM	Section modulus: The moment of inertia about the major diameter divided by the minor diameter (m^3)
SSE	Sum squared error (units depend upon context)
Type (bio/grain)	Categorical variable used for sorghum only: bioenergy sorghum or grain sorghum
Variety	Categorical variable indicating the type of maize or sorghum
WSC_Sugar	Water soluble carbohydrates (%)
x	axial distance along the stalk as measured from the left support point (m)

1. Introduction

Stalk lodging (breakage of the stem or stalk below the grain head or ear) is a multi-billion-dollar problem that has proved recalcitrant to numerous research efforts. In the United States farmers lose almost $3.8 billion per year in lost yield due to maize stalk lodging (Duvick, 2005). Similar losses are observed in China and India and it is estimated that global yields in cereal crops are reduced by 5% annually due to stalk lodging (Duvick, 2005). Furthermore, lodging destroys canopy structure reduces photosynthesis and grain quality and increases harvest cost (Pinthus, 1974; Berry & Spink, 2012; Wu & Ma, 2016). Lodging is also a major obstacle to development of modern, high yielding hybrids capable of growing under higher planting densities (Robertson et al., 2017). Lodging resistance is a remarkably difficult phenotype to quantify. Natural lodging rates are often used to quantify lodging resistance, but natural lodging has two significant drawbacks. First and foremost, natural lodging is strongly influenced by weather and climate (Cloninger et al., 1970; Dodd, 1980; Flint-Garcia et al., 2003; Berry et al., 2003). Because of this, lodging rates are only predictive in relatively large studies conducted over multiple years and locations. Second, the lodging rate provides only a single data point for each observed plot. This obscures meaningful stalk-level variation that could provide valuable insights on the fundamental mechanisms of lodging.

Stalk bending strength is also used to quantify lodging resistance. Stalk bending strength has been used to assess lodging resistance in multiple crops, including wheat, maize, and buckwheat (Crook & Ennos, 1994, 1995; Zhang et al., 2018; Xiang et al., 2019; Yang et al., 2020). Bending strength directly quantifies the amount of force required to break a stalk (Sekhon et al., 2020). In field studies, maize stalk bending strength has been shown to be correlated with natural lodging rates (Sekhon et al., 2020; Shi et al., 2016). Stalk bending strength provides two important advantages. First, this metric is not confounded by weather like lodging rate. Second, this approach allows lodging resistance to be quantified at the level of individual plants, thus allowing a level of resolution which is not possible when using the lodging rate.

A stalk ultimately lodges (i.e. breaks) when applied loads (including self-weight and wind) induce a bending moment that exceeds the stalk bending strength (Zuber & Grogan, 1961; Cloninger, 1970; Singh, 1970; Remison & Akinleye, 1978; Zuber & Kang, 1978; Hondroyianni et al., 2000; Ma et al., 2014; Stubbs, Baban, Robertson, Al-Zube, & Cook, 2018, 2020a). It has long been assumed that stalk chemistry is a strong determinant of stalk bending strength (Phillips et al., 1931). This notion has been supported by studies focused on mutations and/or hormone treatments that affect cellulose or lignin biosynthesis (e.g., Ching et al., 2006; Appenzeller et al. 2004). However, the idea that chemistry is strongly linked to stalk strength has been called into question by recent investigations of stalk lodging that have utilized a structural engineering perspective. Engineering theory and empirical data both indicate that stalk bending strength is determined primarily by stalk anatomy and morphology (Forell et al., 2015; Robertson et al., 2017; Stubbs, Seegmiller, et al., 2020). Thus, composition may have a weaker influence on stalk bending strength than currently thought.

The purpose of this study was to determine the relative influence of stalk composition and stalk architecture (i.e. physical geometry) on stalk bending strength. Two major grain species were utilized, maize and sorghum. The maize samples consisted of elite commercial hybrids (narrow genotypic background) while the sorghum samples were selected from a wide range of public sorghum varieties. The study is unique in three respects. First, structural engineering quantities were used to quantify stalk architecture. Second, the relative influence of stalk chemistry and architecture were determined on a plant-by-plant basis (as opposed to averaging across plots or varieties). Third, previous studies have focused on strength-morphology or strength–chemistry relationships. However, in this study all three aspects were measured. This approach allowed us to quantify the relative strength of all three relationship pairs: strength/architecture, strength/chemistry, and chemistry/architecture.

2. Methods

While lodging may occur above the soil level (stalk lodging), or below the soil level (root lodging, Stubbs et al., 2019), this study focuses only on stalk lodging. Disease and pest damage can affect stalk lodging, but neither of these factors represent inherent properties of the stalk itself. Because the purpose of this study was to differentiate the influence of chemical composition and stalk architecture on stalk strength, the confounding factors of disease and pest damage were excluded from this study. Biotic pressure from either diseases or pests increases the propensity for plants to lodge, but this is because biotic pressure changes the structural integrity of stalk architecture not because these events dramatically alter plant composition.

All stalks included in the study (both maize and sorghum) were subject to three types of measurements. First the physical geometry (i.e., stalk architecture) of each stalk was quantified. Second, the bending strength of each stalk was measured. Finally, stalks compositional analysis was performed on each stalk. Stalks were individually labeled to enable stalk by stalk comparisons (i.e. pairwise analysis) and to prevent dilution of statistical power by sample averaging. The maize and sorghum samples were selected to provide two different perspectives on this issue. Maize samples possessed limited genetic diversity, but were replicated across planting density environments whereas the sorghum incorporated vast genetic diversity but was not replicated across environments. As will be shown, the effect of architecture on stalk bending strength is strong enough that its influence was clearly evident in both experimental designs.

2.1. *Specimens*

The maize stalks used in this study have been described previously (Robertson et al., 2017) and are therefore described here only briefly. Maize stalk specimens were sampled from 5 hybrids grown at 5 planting densities across 3 locations in central Iowa. A total of 1000 stalks were sampled. Two types of sorghum were tested: grain and bioenergy sorghum, with 24 accessions of each type used in this study. The 24 lines were selected from the Sorghum Association Panel (SAP) (Casa et al., 2008) and Sorghum Bioenergy Association Panel (BAP) (Brenton et al., 2016). Accessions from each grouping were chosen from the five major sorghum varieties (i.e. bicolor, kafir, guinea, durra, and caudatum), and therefore represent the broader sorghum genus. Sorghum hybrids were grown in Florence, South Carolina, at the Clemson University Pee Dee Research and Education Center in 2013 and 2014, seeded in 76 cm rows at a planting density of approximately 96,000 plants/ha in loamy sand soil on May 16, 2013 and May 6, 2014, and were irrigated at the time of planting and on an as-needed basis. Each plot was harvested at physiological maturity of the genotype, with the exception of genotypes that did not flower, which were harvested as a single time point. At the time of harvest, ten plants from each plot were cut at the base of the stalk and their panicles were removed. Diseased and pest-damaged stalks were removed from the study, resulting in a total of 423 sorghum stalks.

2.2. *Bending strength measurements: maize & sorghum*

Since lodging is confounded by weather and disease (Cloninger et al., 1970; Dodd, 1980; Flint-Garcia et al., 2003; Robertson, Julias, et al., 2015), laboratory measurements of stalk bending strength were used to quantify lodging resistance. The relationship between bending strength and lodging resistance has been established in two previous field studies (Sekhon et al., 2020; Shi et al., 2016).

While many stalk bending strength approaches have been proposed, the long-span bending test protocol (Fig. 1, see Robertson et al., 2014; 2015a) provides several distinct advantages. First, this three-point bending test avoids the problematic aspects of short-span tests, which produce artificially low values of stalk bending strength (Robertson et al., 2014; 2015a). Second, this is the only method which replicates the failure patterns observed in naturally lodged plants (Robertson, Julias, et al., 2015). Finally, this test produces high-precision data with minimal experimental error (Al-Zube et al., 2018). All bending tests were therefore performed using the long-span three-point bending protocol (Robertson et al., 2014; 2015a).

An Instron universal testing machine (Model 5965, Instron Corp., Norwood, MA) was used to displace the center most node of each sample at a rate of 10 cm/min while samples were supported at their most basal and apical nodes. Stalks were displaced until failure and force-displacement data was acquired at a rate of 10 Hz. Bending strength was determined by calculating the maximum moment supported by the stalk at the location of stalk failure. Equation (1) (Howell, 2001) was used to calculate the bending moment at failure:

$$M(x) = \begin{cases} \dfrac{Fbx}{L} & x < a \\ \dfrac{Fa(L-x)}{L} & x > a \end{cases} \tag{1}$$

where 'a' is the distance to the applied load from the left support, 'b' is the distance to the applied load from the right support, 'L' is the total distance between supports ($a+b$), 'F' is the applied load and 'x' is the distance along the stalk measured from the left support.

Test and loading configuration data were used to compute the flexural stiffness (EI) of each stalk using the equation shown below:

$$EI = \varphi \frac{a^2 b^2}{L} \tag{2}$$

where φ represents the slope of the force/deformation curve obtained from the bending test data. The use of beam modeling equations such as these have been show in several recent studies to be appropriate for the modeling of maize stalks (Robertson et al., 2017, 2016; Stubbs, Baban, Robertson, Al-Zube, & Cook, 2018).

2.3. Architectural measurements: maize

Anatomical and morphological analysis of maize stalks was accomplished through high-resolution X-ray computed tomography (CT) scanning (X5000, NorthStar Imaging, Rogers MN) as described in (Robertson et al., 2017, Stubbs, et al, 2020, see also Fig. 1). The scan region was centered on the internode immediately apical of the most central node of each sample (i.e., the same internode that would break during subsequent 3-point bending experiments). Reconstruction software (efX0ct version 1.8, NorthStar Imaging, Rogers, MN) converted the three dimensional CT scan data to a cross-sectional, two dimensional TIF image with a spatial resolution of 78 μm/pixel. Custom image analysis code developed in the MATLAB environment (Mathworks Inc., Natick, MA) extracted anatomical attributes from each image as described in (Robertson et al., 2017). The architectural attributes utilized in the current study included major diameter; minor diameter; rind thickness; rind area; pith area; total

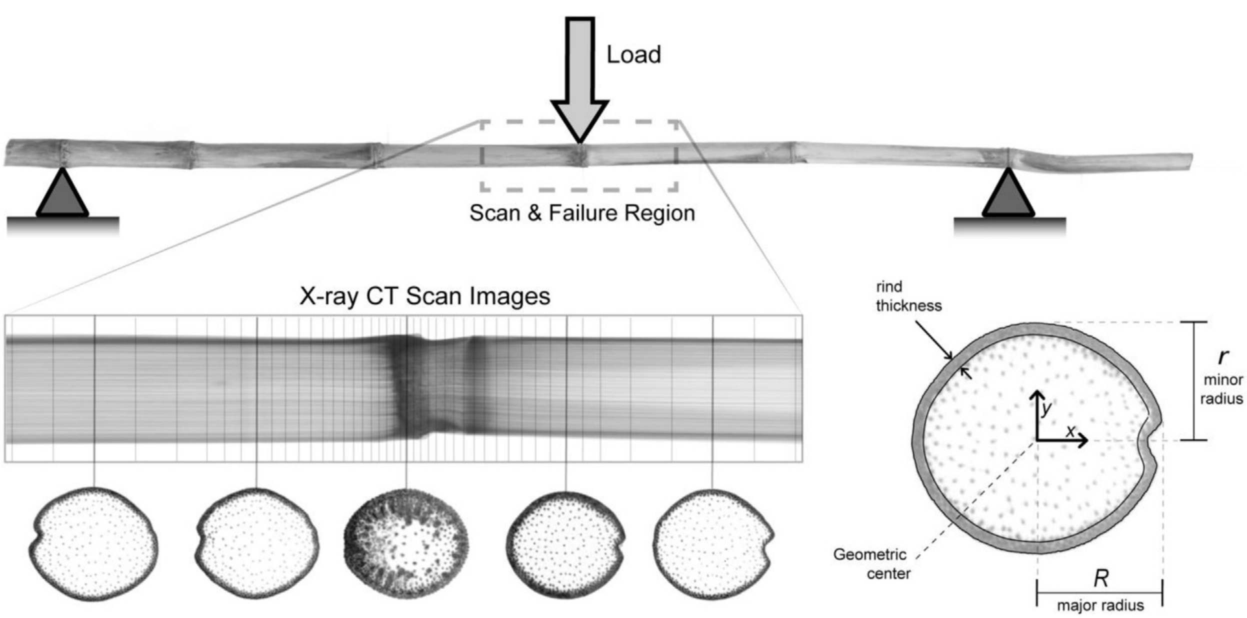

Fig. 1 – Illustration showing the long-span three-point bending test loading configuration as well as CT scan region and representative stalk cross-sections. Image reproduced from Robertson et al., 2017.

cross-sectional area; moments of inertia in for both major and minor axes; and section modulus.

2.4. Architectural measurements: sorghum

Morphological measurements of sorghum were obtained manually using digital calipers. The major diameter of each sample was determined by slowly rotating the stalk within the jaws of the caliper to determine the maximum possible diameter measurement. Minor diameters were acquired in like manner with the minimum possible diameter being recorded. Measurements of rind thickness were not acquired as the stalks exhibited a solid cross-section at the locations of stalk failure. All measurements were acquired at the location along the stalk where stalk failure was observed to occur during the 3-point bending test.

2.5. Compositional analysis: maize & sorghum

Dried samples were analyzed in accordance with previous studies (Brenton et al., 2016; Brenton et al., 2020). Samples were analyzed with a Perten DA7250 near-infrared spectroscopy (NIR) instrument for compositional data, including NDF, NFC, acid detergent fiber (ADF), and lignin. Lignin and ADF wet chemistry data were generated using the Association of Official Agricultural Chemists protocol 973.18. NDF and NFC data were generated using AOAC protocol 2002.04. The wet chemistry samples were selected based on phenotypic and spectra diversity. All compositional data are presented as a percentage of dry matter (DM).

2.6. Statistical analysis

Statistical analysis proceeded in stages. Stage 1 consisted of univariate correlation and analysis between each continuous measurement and stalk bending strength. In Stage 2, the influence of each factor was assessed in the context of multiple linear regression models. The influence of each factor was quantified using the proportional reduction of error (PRE) (Lewis-Beck et al., 2003; Kviz, 981). This is done by creating two models. The first model contained a certain number of predictors and the second included these same predictors, plus one additional predictor. The influence of the added parameter was calculated as the percentage change in SSE (sum squared error) between the two models:

$$PRE = (SSE_1 - SSE_2) / SSE_1 \tag{3}$$

One challenge in quantifying the influence of each factor was the fact that many of the measurements collected in this study were closely related to each other. There are two reasons for this: conceptual multicollinearity and empirical multicollinearity. Conceptual multicollinearity refers to a situation where several factors are known to be related to each other through their conceptual definitions. Two examples are provided to illustrate this issue. First, the total area of the stalk was calculated from measurements of major and minor diameter values. Hence, total area will always be closely related to each of the two diameter measurements. Second, acid detergent fiber (ADF) is composed primarily of cellulose and lignin, hence, ADF will always be closely related to both of these factors. Empirical multicollinearity refers to collinearity that is present in the data, through any number of unknown relationships. Regardless of the reason, multicollinearity causes problems in both model building and interpreting results (Kutner et al., 2005).

Multicollinearity was handled using two strategies. First, none of the multiple regression models contained factors known to share conceptual multicollinearity. Empirical multicollinearity is more difficult to justify. One approach is to compute the variance inflation factor, and remove variables until the variance inflation factor is reduced below some threshold. However, this approach is problematic because some level of subjective judgement is required by the model builder, and this judgement invariably affects the results. For example, in sorghum hemicellulose and water soluble carbohydrates were found to have a correlation coefficient of −0.84. In such cases, which variable should be removed from a multivariate analysis? Since the research connecting chemical composition to bending strength is incomplete, any decision to remove a variable may bias the results in unknown ways.

The problem of subjective decisions was avoided in this study by creating a design matrix representing all possible models. The PRE was then calculated for each factor within each model. This approach required the creation of over one million models and the use of parallel computing resources. The results of all these models were tabulated and compiled to provide a distribution of possible PRE values for each factor. This approach is both comprehensive and unbiased, since it does not rely upon any human judgement.

3. Results

3.1. Univariate correlation analysis

Univariate correlation analysis was performed between bending strength and each type of measurement described above (see Fig. 2). The results indicated that the strongest predictor of stalk bending strength for both maize and sorghum was flexural stiffness ($R^2 > 0.8$) for both species. For maize, the R^2 value for all architectural measurements exceeded 0.5. Primary, secondary, and tertiary architectural measurements exhibited average R^2 values of 0.66, 0.70, and 0.78, respectively. For sorghum, these same values were 0.44, 0.38, and 0.32. The discrepancy between values for maize and sorghum is addressed in the discussion section.

In both species, univariate correlation values between chemistry and bending strength were found to be significantly lower than for those related to architecture. The highest R^2 value between chemistry factors and bending strength was observed for sorghum: lignin vs. bending strength R^2 of 0.26. However, all other R^2 values between bending strength and primary chemistry were below 0.05. For maize, the highest R^2 value between bending strength and primary chemistry was 0.11 (AD_ICP). The higher correlation between lignin and stalk strength in sorghum is due to the fact that the sorghum varieties in this study represented a wider variation in lignin content and genotypic diversity than the maize varieties. This effect is also visible when

Category and Measurement	Maize Median R^2	Maize Indiv. R^2	Sorghum Median R^2	Sorghum Indiv. R^2
Beam Theory				
Flexural Stiffness	0.81	0.81	0.83	0.83
Tertiary Architecture				
Section Modulus	0.79	0.80	0.75	0.80
Moment of Inertia		0.79		0.73
Moment of inertia		0.78		0.71
Secondary Architecture				
Area (rind)	0.70	0.76	0.82	-
Area (pith)		0.61		-
Area (total)		0.70		0.82
Primary Architecture				
Major Diameter	0.66	0.70	0.69	0.75
Minor Diameter		0.66		0.63
Rind Thickness		0.53		-
Linear Density				
LD_Node	0.59	0.60	0.58	0.54
LD_Overall		0.59		0.55
LD_InterNode		0.54		0.43
Experimental Design				
Variety	0.15	0.05	0.37	0.56
Planting Density		0.26		-
Type (bio/grain)		-		0.18
Primary Chemistry				
Lignin	0.05	0.05	0.01	0.26
Cellulose		0.09		0.04
AD_ICP		0.11		0.01
Hemicellulose		0.10		0.01
WSC_Sugar		0.02		0.01
Adj_CP		0.00		0.03
Starch		0.01		0.01
Secondary Chemistry				
ADF	0.08	0.09	0.04	0.08
NDF		0.12		0.03
NFC		0.11		0.00
Ash		0.06		0.02
Crude_protein		0.00		0.04
EE_Fat		0.00		0.04
Micronutrients				
Mg	0.01	0.11	0.03	0.07
Ca		0.00		0.10
Na		0.06		0.03
P		0.01		0.05
K		0.01		0.01
S		0.02		0.00
Cl		0.01		0.00

Fig. 2 – Quantities and graphical representation of univariate correlation values between bending strength and predictors variables. Variables are grouped by conceptual categories.

comparing the influence of variety on strength. In sorghum, the variety/strength R^2 value was 0.56, while in maize it was 0.05.

Correlation values between secondary chemistry and bending strength were likewise low, with all R^2 values less than 0.13. Micronutrients also exhibited low predictive power, with all R^2 values below 0.12. R^2 values for all tertiary chemical factors were at or below 0.15.

Linear density and CT scan data was collected only for maize specimens. Linear density measurements (mass per unit length) were more highly correlated with bending strength than any chemistry factors. The R^2 values between linear density and maize bending strength ranged from 0.54 to 0.60. However, CT scan intensity, which is related to tissue density (mass per unit volume) exhibited relatively low R^2 values (less than 0.07).

3.2. *Multivariate analysis*

As described in the methods section, the proportional reduction in error (PRE) was used to assess the predictive influence of each factor through the use multiple linear regression models. For each species, several hundred thousand multiple regression models were created, spanning the entire range of possible models that could be created while avoiding conceptual multicollinearity and any bias caused by human judgement or empirical multicollinearity.

Results of the proportional reduction of error approach demonstrated that architectural features were by far the most predictive factors (see Fig. 3). For sorghum, the flexural stiffness and major diameter had median PRE values of 0.79 and 0.43, respectively. In contrast, median sorghum PRE values for primary chemistry ranged from 0.003 (starch) to 0.0069 (lignin). Median sorghum PRE values for micronutrients ranged from 0.002 (Na) to 0.014 (Cl). Finally, median sorghum PRE values for secondary chemistry factors ranged from 0.0008 (EE fat) to 0.034 (ash).

Maize PRE values were similar to those observed in sorghum. The median maize section modulus was 0.62. The highest medial PRE value for maize from within the primary chemistry group was 0.012 (AD_ICP). The highest PRE value within the micronutrient group was 0.01 (S). Cellulose, lignin, and hemicellulose each had median PRE values below 0.005.

3.3. *Relationships between chemistry and architecture*

The relationships between chemical composition and architecture were investigated to understand the relationships between these parameters. In general, chemistry was found to be equally predictive of both strength and architecture. Univariate correlations between compositional factors and architectural factors were computed and compared to univariate correlations between composition and strength. Because multiple geometric parameters were measured, these correlation values are shown as boxplots in Fig. 4 while correlation values between composition and strength are shown as black circles. Figure 4 shows that the composition/strength and composition/architecture results are themselves highly correlated, with R^2 values of 0.89 and 0.82 for maize and sorghum, respectively. Multivariate analyses of composition/strength and composition/architecture produced results that were consistent with Fig. 4. This suggests that chemical composition varies simultaneously with both architecture and strength.

4. Discussion

The results above shed new light on previous studies relating composition to stalk bending strength and by extension, lodging resistance. For example, two prior studies have found that linear density was a strong predictor of stalk strength (Appenzeller et al., 2004; Gomez et al., 2018). In summarizing their findings, Appenzeller et al. Stated. “Cellulose in a unit length of the stalk below the ear node in maize is the main determinant of mechanical strength” and suggested that increasing cellulose concentration would improve the mechanical strength of maize stalks. Density per unit length is a metric that includes *both* compositional and architectural features. Our experimental design separated these factors to reveal that architecture is a much more influential determinant of stalk strength than chemical composition.

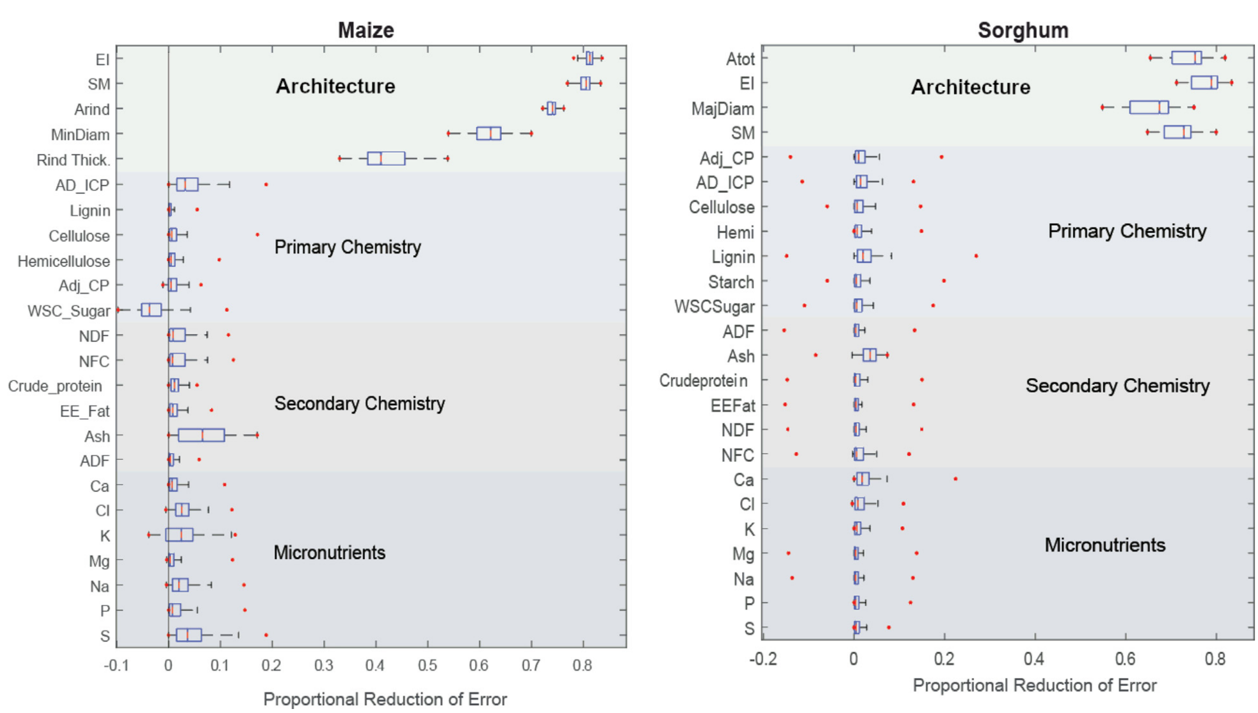

Fig. 3 – The distributions of proportional reduction of error results for sorghum and maize for various predictors. and bending strength. Factors are grouped by category. Definitions of terms are available in the supplementary information that accompanies this paper.

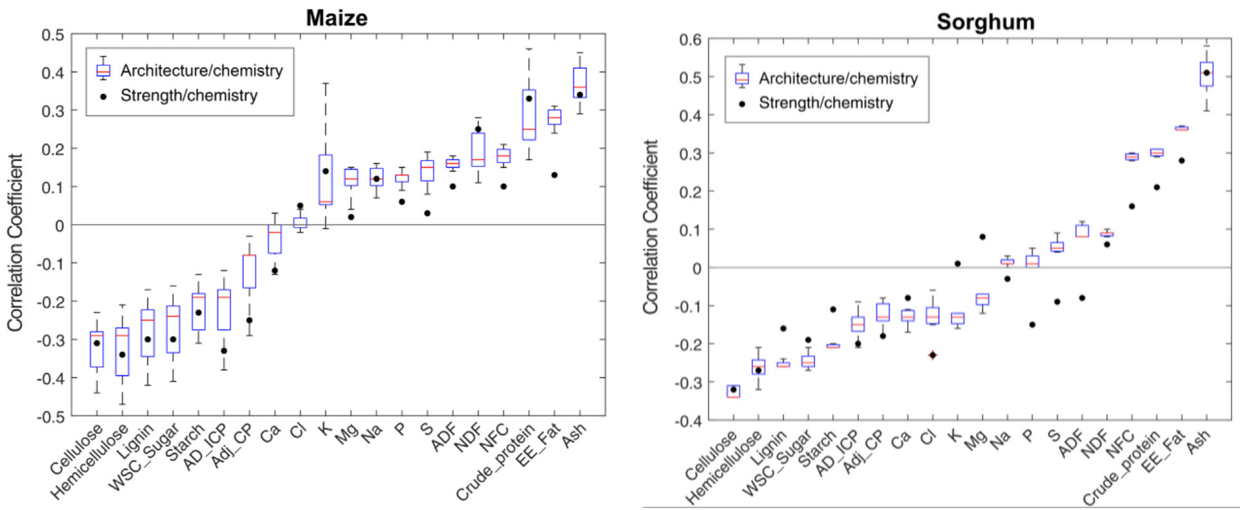

Fig. 4 – Charts showing correlation coefficient values between architectural factors and stalk chemistry (boxes), and between stalk chemistry and stalk bending strength (black dots).

Ching et al. reported that reduced stalk strength in maize was caused by a mutation which interferes with the deposition of cellulose (Ching et al., 2006). That study also reported that linear density was significantly affected by the brittle stalk mutation. Micrographs in that study clearly showed changes to the cell wall architecture. These results further reinforce the idea that composition and architecture are closely linked, and that both factors influence stalk and tissue strength. Additionally, microscopy has shown that (a) multiple cell types are present in a cross-section (Hunter & Dalbey, 1937) and (b) chemical composition is not uniformly distributed in cross-sections of stalks (Zhang et al., 2013, 2019). Although composition is generally thought to be closely related to stalk strength, a careful review of the literature reveals that the evidence is not at all clear on this point (Pederson et al., 2005; Sattler et al., 2010). Some studies show composition-strength effects while others show no effect and still others show an opposite effect (see Sattler et al., 2010). A reduction in lignin via mutation is generally thought to reduce overall quality, but Pedersen et al. have identified several studies in which this is not the case (Pedersen et al., 2005). These authors noted that the behavior of mutated varieties are highly dependent upon environmental and background genetics. Perhaps one reason for these mixed results and prevailing perceptions is that the scientific community has previously lacked an explanation for these mixed results.

Maize and sorghum stalks can be accurately modeled using engineering beam theory (Robertson et al., 2015; 2017; Stubbs, Baban, Robertson, Al-Zube, & Cook, 2018). Engineering beam theory derives from Newton's Laws of Motion and is used extensively in civil and mechanical engineering. When longitudinal strain levels in a beam are small (less than 5% strain), the maximum stress within a beam under bending is governed exclusively by the section modulus, which is a purely geometric quantity. Thus, from an engineering perspective, the most effective way for a plant to reduce stress is to increase the section modulus. And the most effective way to increase section modulus is to increase diameter in the direction of bending. Because stress is closely related to ultimate strength, the most cost-effective ways to predict bending strength of maize and sorghum stems is to measure the section modulus (Robertson et al., 2017). Alternatively, the flexural stiffness (EI) is closely related to both strength and stalk stiffness, and is more easily measured than section modulus (Robertson et al., 2016, 2017; Erndwein et al., 2020).

Engineering theory is able to explain why quantities such as section modulus, rind thickness, and area are strong predictors of stalk strength. The first reason is that the rind is the primary load-bearing tissue of the stalk (Niklas, 1991; Al-Zube et al., 2017, 2018; Ottesen et al., 2022). The second reason is that each of these factors are closely interrelated. Figure 2 lists artchitectural factors as primary (major diameter, minor diameter, and rind thickness) because these factors define the cross-sectional geometry using units of length. Secondary factors (areas of rind, pith, and tissue) have units of m^2 and are formed from primary factors. Tertiary factors consist have units of m^4 (various moments of inertia), or units of m^3 (section modulus). Secondary and tertiary features can be calculated from the primary architectural features (Robertson et al., 2017; Ottesen et al., 2022), but vary in their predictive power. For linearly elastic materials, mechanical stresses developed during bending are entirely dependent upon architecture (Stubbs, Baban, Robertson, Al-Zube, & Cook, 2018). Of course, tissue strength also influences stalk strength, but the results of this and other studies indicate that shape has a larger influence on stalk strength than tissue strength (Forell et al., 2015; Stubbs et al., 2022).

Results from this study are also supported by findings in the field of wood science. In wood, material properties are primarily determined not by chemistry, but by microscale morphology (i.e., cell wall organization and especially the orientation of the microfibril angle (Cave & Walker, 1994; Evans & Elic, 2001; Gherardi Hein & Tarcísio Lima, 2012; Via et al., 2009). However, the relatively weak link between chemistry and mechanical properties of wood was surprising to wood scientists. As John Ralph has written, "*It was eye-*

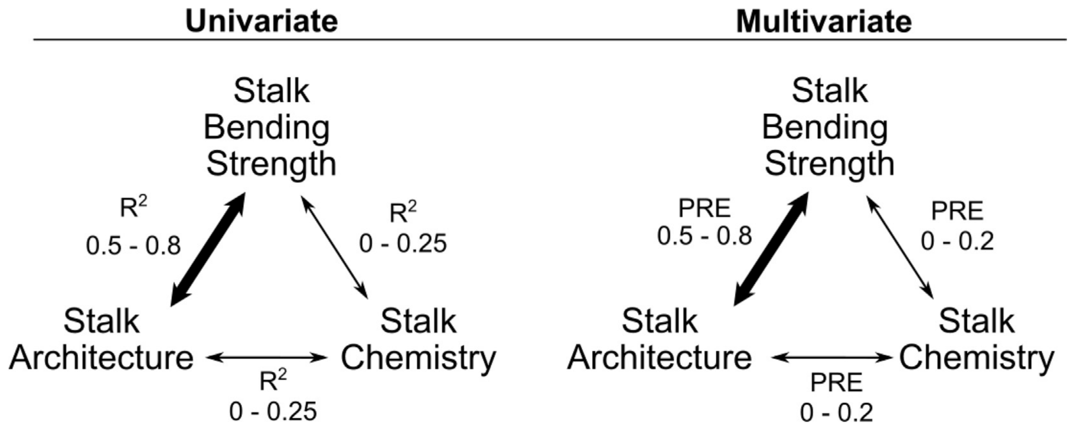

Fig. 5 – Relationship strengths reported in this study. Arrow width is proportional to the strength of each relationship.

opening to learn that wood properties might in fact be relatively independent of the nature of the lignin. They appear to be driven by the cellulose fibers and, importantly, by microfibril angle. It is conceivable that the changes made to the lignin, dramatic though they are, may not have much of an impact. One can't help but feel that the reason exact lignin structure is of little concern to the plant is that the plant really only needs this polymer to have certain properties, properties within a range that can be met by lignins with considerably varying compositions and structure" (Ralph, 2007).

Finally, our results and the broader literature suggest that chemical composition and physical stalk architecture are not independent variables, but rather are interrelated. Figure 5 provides a visual representation of these relationships, where the thickness of each line is proportional to the strength of the relationships.

As shown in Fig. 5, stalk bending strength is strongly related to stalk architecture, and weakly related to stalk chemistry. Stalk chemistry was found to have similar relationships with both bending strength and architecture. This finding explains results such as those reported by Ahmad et al., 2018, in which homonal treatments influenced *both* stalk chemistry and stalk architecture. Mutations or interventions that influence chemistry may have a deleterious effect on stalk bending strength because they simultaneously alter stalk chemical composition and stalk architecture simultaneously. In fact, changes in stalk architecture may be an adaptive response of plants that possess unusually low levels of cellulose and/or lignin. It has been suggested that intentional changes to stalk architecture via breeding could be an effective means of improving stalk strength (Forrell et al., 2015), though this would be more difficult if architecture and chemistry are closely linked. More research is needed to determine the degree of causality that is embedded in the correlational relationships reported in this study.

5. Conclusion

This study demonstrates that stalk architecture is a much stronger predictor of stalk bending strength than chemical composition. While composition alone explained a minority of the total variation in bending strength, stalk architecture alone was able to explain more than 75% of the total variation in bending strength. This insight is consistent with findings in the field of wood science research where it has long been understood that the macroscale properties are dependent upon both architecture and chemical composition.

This study highlights the importance of including architectural measurements in future studies and in carefully separating the effects of composition and architecture. Given the strong influence of stalk architecture, future studies aimed at relating chemistry and strength will be improved by controlling for the influence of architecture. This approach will provide a clearer, more complete understanding of the complex relationships between chemistry, stalk architecture, and stalk bending strength. In addition, a realization of the influence of stalk architecture may allow breeders to effectively and independently select for these traits, which could have numerous benefits on productivity, metabolism, and ultimately yield.

Authors' contributions

All authors were fully involved in the study and preparation of the manuscript. The material within has not been and will not be submitted for publication elsewhere.

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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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.biosystemseng.2022.04.010.

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