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Moving toward short stature maize: The effect of plant height on maize stalk lodging resistance

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ABSTRACT

Background: Stalk lodging is the structural failure of crops due to external loading such as wind. Short-stature (i.e., dwarf) varieties of wheat and rice have shown promise in reducing lodging rates. However, similar dwarfing in large gains like maize and sorghum has typically been accompanied by undesirable commercial characteristics, including significantly decreased grain yields. The purpose of this paper is to quantify the relationship between lodging resistance and plant height in maize to better understand the potential impact of short-stature varieties of maize on lodging resistance.

Results: Results from both the engineering analysis and the experimental field study indicate a nearly 1:1 relationship between plant height and plant lodging resistance. These data support the validity of the engineering analysis and suggest that there exists a nearly linear relationship between crop lodging incidence and plant height.

Conclusions: Plant height has a direct and quantifiable impact on crop lodging resistance as it influences the bending stresses experienced in the plant stem. This study presents the engineering analysis, supported by field experiments, that explains the cause of this nearly linear 1:1 relationship.

1. Introduction

Stalk lodging occurs when crop stems experience a critical structural failure. Although the global community has been working to resolve the problem of stalk lodging for over a century, breeding for stalk lodging resistance, particularly in cereal grains, remains challenging. These challenges are due to the complex biomechanical nature of stalk failure as well as the presence of continuously varying agronomic and environmental factors such as drought (Bänziger, 2000; Efeoğlu et al., 2009), nutrient deficiencies (Arnold et al., 1974; Bänziger, 2000), disease and insect pressure (Anderson and White, 1994; Hooker, 1956; Horrocks et al., 1972). These issues confound the study of the complex stalk lodging phenotype (Berry et al., 2004; Flint-Garcia et al., 2003; Guo et al., 2021; Robertson et al., 2014). However, it is generally accepted that reducing plant and ear height will improve stalk lodging resistance by reducing the mechanical moment arm of the stalk, thereby lowering the mechanical bending stress experienced by stalks during wind storms.

The benefits of reducing plant height have been extensively observed for small grains like wheat and rice (Berry et al., 2004). In both crops, improvements in grain yield were the direct result of the integration of dwarfing and semi-dwarfing genes into new, elite commercial hybrids following the green revolution (Khush, 2001). Hybrids carrying these genes – now known to interfere with the action or production of gibberellin (GA) phytohormones – display significantly reduced plant heights and improved stalk lodging resistance and allow a larger proportion of photosynthate assimilates to be transferred to crop grains rather than excess structural straw materials (Hedden, 2003).

However, the introgression of dwarfing genes regulating GA

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production or response in large grains like maize and sorghum has typically been accompanied by undesirable commercial characteristics, including significantly decreased grain yields (Cassady, 1965; Duvick, 2015; Graham and Lessman, 1966; Milach and Federizzi, 2001). This phenomenon has limited the study and commercial utility of this otherwise morphologically and architecturally critical trait (Khush, 2001). In fact, historical increases in maize yields have stemmed primarily from improvements in new germplasms' ability to tolerate higher planting densities and increase yield per plant (Assefa et al., 2018). Recently, however, the GA-insensitive Brachytic2 (br2) maize mutants have been characterized (Multani et al., 2003). These mutants display more compact stalk internodes, reducing total plant height by up to 50% without negatively affecting grain yields (Multani et al., 2003; Xing et al., 2015). Major seed companies are now beginning to introduce the first "short stature" maize varieties.

While previous studies have shown significant correlations and genetic linkage between plant heights and stalk lodging resistance, no prior studies have quantified the extent to which reductions in plant height reduce incidents of stalk lodging (Flint-Garcia et al., 2003; Gomez et al., 2020; Peiffer et al., 2014). With the recent development and release of short-stature maize commercial hybrids, a new avenue of yield improvements – analogous to those experienced by wheat and rice during the green revolution of the 1950 s – appears to be on the horizon. The purpose of this study is thus to evaluate the relationship between lodging resistance and plant height in maize. Such quantification will enable better forecasting of how the problem of stalk lodging in maize may be impacted by short-stature maize hybrids. In addition, it will enhance in-field phenotyping methods used to investigate stalk lodging resistance.

In-field phenotyping for stalk bending strength is commonly used to gain meaningful insights into the mechanical underpinnings of stalk lodging events (D. Cook et al., 2019; Erndwein et al., 2020; Robertson et al., 2021a, 2021a, 2022a, 2016, 2015b). Stalk bending strength is a material property that quantifies the magnitude of mechanical stress a stalk can withstand before permanent failure or lodging (Sekhon et al., 2020; Stubbs et al., 2019). The authors have regularly used the *Device for Assessing Resistance to Lodging in Grains* (DARLING) over the past six years to acquire reliable measurements of stalk bending strength and flexural rigidity of field-grown plants (D. Cook et al., 2019a; Cook et al., 2019b). When used in the field, the DARLING device induces mechanical bending stresses in the stalk analogous to those caused by heavy wind and rain storms and, therefore, produces failure types and patterns in the tested stalks that replicate natural lodging events (Robertson et al., 2015a). However, neither the DARLING device nor devices developed by other groups (e.g., Jo Heuschele et al., 2019) properly account for or quantify the confounding effect of plant height on stalk lodging resistance (Stubbs et al., 2020b). Thus, even though the competitive ability of a plant to thrive and produce is highly dependent on height (Stubbs et al., 2020c, 2020b), no formal engineering analysis quantifying stalk lodging resistance as a function of plant height currently exists that has been validated by field experiments (Weiher et al., 1999). Therefore, the current study presents an analytical engineering analysis of the effects of plant height on stalk lodging resistance based on a multi-environment experimental field trial in maize. This study will enable future research programs to better forecast and understand the potential advantages of new short-stature maize hybrids. It will also allow future phenotyping studies focused on characterizing stalk bending strength to more accurately predict the lodging resistance of hybrids with varying bending strengths and plant heights. Box 1.

2. Materials and methods

A two-pronged approach was undertaken to quantify the effects of plant height on crop lodging resistance. First, a structural engineering analysis was conducted to determine the primary effects of plant height on lodging resistance. This analysis was purely theoretical in nature and was based on well-established engineering equations and physical phenomena. This analysis is akin to the process used by engineers to

Box 1
Definitions of Key Terms Related to Crop Lodging.

Lodging Resistance	A conceptual, holistic assessment of the ability of a genotype to withstand external forces (wind and gravity) and biotic factors (insects, disease, etc.) that contribute to lodging. This term refers to the overall behavior of a particular variety or genotype.
Bending Moment	In the most basic sense, a bending moment causes bending deformations and is generated by applying a force to a structure at a given distance away from a point of reference. Bending moments have units of force x length.
Maximum Bending Moment or Failure Moment	The maximum bending moment that can be supported by a stalk or the root-soil complex before failure occurs (i.e., before the stalk lodges)
Bending Stress	Bending moments induce mechanical bending stresses in structural elements. Bending stress can be calculated usingEq. 2. Bending stress can be thought of as a "normalized bending moment" that accounts for the distribution of structural material within a stalk. For example, if two stalks were subjected to the same bending moment, then a stalk with a bigger diameter and larger rind thickness would experience lower bending stresses as compared to a stalk with a smaller diameter and thinner rind. Bending stress has units of force / area.
Structural Bending Strength	The maximum bending moment a stalk or the root-soil complex can withstand before permanent deformation (failure).
Ultimate Bending Strength	The maximum amount of bending stress a stalk can resist before permanent failure
Flexural Rigidity	A measure of a stalk's ability to resist bending deformation (sometimes referred to as bending stiffness). Higher flexural rigidity indicates a higher magnitude of force is required to bend a stalk a certain distance.
Drag Force	The external load placed on a plant due to wind
Plant Height	The vertical distance from the base of the stalk at the ground to the tip of the tassel following reproductive maturity
Ear Height	The vertical distance from the base of the stalk at the ground to the node supporting the primary ear on a stalk of maize

design structural members such as bridges and buildings. It is important to note that this analysis was conducted to determine the primary and not secondary or tertiary effects of plant height. In other words, this analysis did not consider that plant height may affect disease resistance or pest pressure, which in turn could affect lodging resistance.

Second, in addition to the engineering analysis, a large experimental field study was conducted. In this study, several hybrid varieties of maize underwent extensive field testing to characterize several phenotypes of interest, including stalk bending strength, plant height, and historical lodging rates. A statistical analysis was then conducted to determine the effect of plant height on the historical lodging rates of these varieties.

2.1. Engineering stress analysis of the effect of plant height

A chain is only as strong as the weakest link. Likewise, the lodging resistance of a plant is ultimately determined by the weakest link in the plant. Two structural links of interest to the current study include stalk lodging (breakage of the stalk/stem) and root lodging (failure of the root system). The overall lodging resistance of a plant is determined by the weaker of these two links (i.e., the stalk or the root system).

Stalk lodging resistance is ultimately determined by two key factors: (1) the ultimate bending strength of the stalk and (2) the bending moment applied to the stalk by external forces. If the applied moment induces bending stresses that exceed the ultimate bending strength of the stalk, then the stalk will break. Likewise, root lodging resistance is determined by two key factors: (1) the structural bending strength of the root-soil complex and (2) the bending moment applied to the root-soil complex. If the applied bending moment exceeds the structural bending strength of the root-soil complex, then root lodging will occur.

Plant height does not directly affect the strength of stalks or root-soil complexes and instead modifies how externally applied loads get distributed throughout the plant. This alters the bending moments at the root-soil complex and the bending stresses experienced by the stalk. Thus, plant height directly alters the bending moments that the plant experiences but does not directly affect the ultimate bending strength of the stalk or the structural bending strength of the root-soil complex. A visual description of the relationship between stalk lodging resistance, bending strength and plant height can be seen in Fig. 1.

The engineering concept of a safety factor (SF) can be used to mathematically quantify lodging resistance. An SF expresses how much stronger a structure is than it needs to be for an intended load. In other words, the safety factor of a structure is the ratio of the structure's strength to actual applied loads.

$$SF = \text{Strength} / \text{Applied Loads} \tag{1}$$

For safety factors > 1, the reliability of the structure will increase as the SF increases in size.

It follows that lodging resistance will proportionally increase or

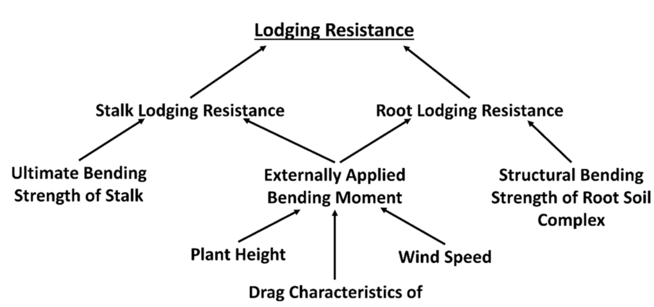

Fig. 1. Visual depiction of principle relationships that exist between lodging resistance, plant height and strength. Arrows indicate dependencies. For example, Stalk Lodging Resistance is dependent upon the Ultimate Bending Strength of the Stalk and the Externally Applied Bending Moment.

decrease as the SF of a plant increases or decreases. The engineering analyses presented in the following sections estimate the effect of plant height on the SF as a way of determining the effect of plant height on lodging resistance.

In engineering analyses, it is common practice to start with basic models, which include several simplifying assumptions. Complexity is then added to the basic model as simplifying assumptions are removed. Following this approach, we first created a basic model to analyze the effect of plant height on bending stresses in the stalk and bending moments in the root-soil complex. All the models presented below are basic and include several simplifying assumptions. These simple models (as opposed to overly complex models) are more intuitive and more easily shared and understood by researchers from multiple disciplines.

2.1.1. Single point load model

The first engineering model we considered approximated the maize stalk as a simple cantilever beam supported on one end, with a point force applied to the free end. Previous studies have demonstrated that while field crops experience a number of complex loading conditions that vary in both time and space, the assumption of a single force applied at the ear is a useful assumption that can be used to produce insights into crop lodging (Speck, 2003; Stubbs et al., 2020c). For example, field phenotyping experiments used to characterize the ultimate / structural bending strength of maize stalks typically apply a single force near the ear (D. D. Cook et al., 2019; Erndwein et al., 2020). These tests produce the same failure types and patterns observed in naturally lodged plants (Cook et al., 2019b). For a cantilever beam with force applied at the free end, the bending stress can be calculated as

$$\sigma = \frac{M}{\varsigma} \tag{2}$$

$$M = F(h - z) \tag{3}$$

where **σ** is bending stress, $\boldsymbol{M}$ is the applied bending moment, $\boldsymbol{z}$ is the length along the stalk measured from the base, $\boldsymbol{h}$ is plant height, and **ς** is the section modulus of the stalk. Section modulus, a geometric feature used to describe the cross-section of a stalk (Robertson et al., 2017; Stubbs et al., 2018, 2020a, 2020c), is a mathematical combination of rind thickness and diameter. The bending moment $\boldsymbol{M}$ is equal to the applied force $\boldsymbol{F}$ multiplied by the distance from the point force to the location of interest (Eq. #2). In other words, the moment increases from the most apical section of the stalk to the most basal section of the stalk, as shown in Fig. 2. The bending moment applied to the root-soil complex ($\boldsymbol{z} = 0$) is equal to the applied load $\boldsymbol{F}$ multiplied by the length of the beam (i.e., plant height) $\boldsymbol{h}$.

To quantify the effect of changes in plant height on bending moments $\boldsymbol{M}$**,** we introduce a linear scaling factor, $\boldsymbol{c}$. Assuming the height of a nominal plant is $\boldsymbol{h}$, then the height of a scaled plant is $\boldsymbol{c}\cdot\boldsymbol{h}$. Observation of Eq.#1 and Eq. #2 illustrates that if the force $\boldsymbol{F}$ is held constant, then scaling the height of a nominal plant by a factor $\boldsymbol{c}$ will proportionally reduce the bending moment applied to the root-soil complex and the bending stress experienced by the stalk by $\boldsymbol{c}$. Stated more explicitly, using the subscript ***nom*** to represent the nominal plant and the subscript ***sc*** to represent the scaled plant:

$$M_{nom} = F(h - z), M_{sc} = F(c\cdot h - c\cdot z)\text{therefore}M_{sc} = c\cdot M_{nom} \tag{4}$$

and

$$\sigma_{nom} = \frac{M}{\varsigma}, \sigma_{sc} = \frac{c\cdot M}{\varsigma}\text{therefore}\sigma_{sc} = c\cdot\sigma_{nom} \tag{5}$$

Combining the above results, we see that for the single point load model

$$SF_{sc} = \frac{SF_{nom}}{c} \tag{6}$$

In other words, when $\boldsymbol{c} = 0.9$ (10% reduction in height), the bending

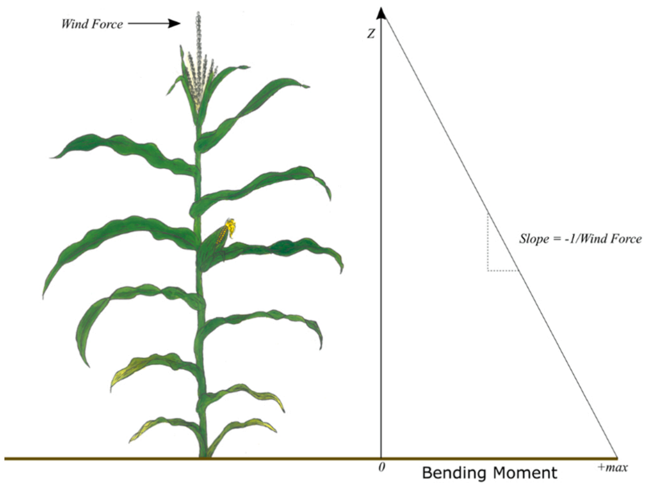

Fig. 2. The effect of wind loading on a maize stalk can be roughly approximated (i.e., modeled) by considering the maize stalk to be a cantilever beam with a single point load applied to the top of the plant (left). This loading condition produces a mechanical bending moment that linearly increases from 0 at the top of the plant (i.e., the free end of the cantilever beam) to a maximum at the base of the plant (i.e., fixed end of the cantilever beam) as shown in the bending moment diagram (right).

stress throughout the stalk and the bending moment applied to the root-soil complex is reduced by 10%, and the SF against lodging is increased by a factor of $1/\boldsymbol{c}$ (i.e., SF of the scaled plant is 1.11 times greater than the SF of the nominal plant).

Next, we can consider if a decrease in plant height will affect the external drag force $\boldsymbol{F}$ that is applied to the stalk by the wind. Calculating the exact forces applied to a plant by the wind is very complex and involves fluid-structure interactions and turbulence effects that vary in both space and time. However, it is common practice to obtain a first-order approximation of time-averaged wind forces using the drag force equation:

$$F = 0.5 \cdot C_d \cdot A \cdot \rho \cdot v^2 \tag{7}$$

where $\boldsymbol{C_d}$ is the characteristic drag coefficient, $\boldsymbol{A}$ is the frontal area, ρ is the air density, and $\boldsymbol{v}$ is the velocity of the air (Niklas and Spatz, 2012). It should be noted that this equation does not account for structural deformations of the stalk or leaves. The characteristic drag coefficient $\boldsymbol{C_d}$, is typically determined experimentally using a wind tunnel and is an aggregate of many complex factors such as shape, surface roughness, and Reynolds number. The drag coefficient, air velocity, and air density are each independent of plant height. However, plant height is expected to alter the frontal area $\boldsymbol{A}$ of the plant. Short stature maize varieties typically possess the same number of leaves and internodes as taller varieties, but their internodes are shorter. Thus short-stature varieties nominally possess the same leaf area but a reduced stalk area. Therefore, the frontal area $\boldsymbol{A}$ would decrease slightly as plant height $\boldsymbol{h}$ is decreased, thereby reducing the externally applied drag force $\boldsymbol{F}$. Mathematically, we can represent the relationship between plant height and the externally applied bending moment as follows:

$$M_{sc} = [c^a \cdot F] \cdot [(c \cdot h - c \cdot z)] \tag{8}$$

Where $\boldsymbol{a}$ is a positive constant near zero. The terms in the first set of square brackets scale the applied drag force, and the terms in the second set of square brackets scale the moment arm. Simplifying the above equation and calculating the safety factor against lodging reveals:

$$SF_{sc} = \frac{SF_{nom}}{c^\alpha} \tag{9}$$

Where $\boldsymbol{\alpha} = \boldsymbol{a} + \boldsymbol{1}$ and $\boldsymbol{\alpha}$ is, therefore, a constant slightly larger than 1. For example, if we assume the leaves make up approximately 90% of the frontal area $\boldsymbol{A}$ of the plant while the stalk makes up 10% of the frontal area $\boldsymbol{A}$, then $\boldsymbol{\alpha} \approx 1.1$.

Finally, decreasing plant height decreases ear height which in turn lowers bending stresses induced in the stalk and the bending moments induced in the root-soil complex due to the weight of the ear. However, a previous study done in our lab showed that for maize, the effect of the ear weight on the bending moments and bending stresses is negligible when compared to the bending moments induced by the wind that causes lodging (Stubbs et al., 2020b). We will, therefore, not consider the effects of reductions in ear height in this manuscript.

In summary, the point force model presented above predicts that for a given wind speed, plant height and bending stress are positively correlated. Moreover, the relationship between plant height and bending stress (or bending moment applied to the root-soil interface) is expected to be a nearly 1-to-1 relationship. When ignoring changes in drag force due to changes in plant height, the model predicts the safety factor against lodging will change by a factor of $\frac{1}{c}$. When accounting for a reduction in drag force due to changes in plant height, the model predicts the safety factor against lodging will change by a factor of $\frac{1}{c^\alpha}$ where $\boldsymbol{\alpha}$ is slightly larger than unity.

2.1.2. Multiple point load and distributed load model

The second, more complex engineering model approximated the plant as a cantilever beam with multiple discrete and distributed forces applied along the length of the stalk. In reality, the wind creates a distributed load profile on maize stalks that changes in time and space. The ever-changing shape of the distributed load is determined by complex fluid-structure interactions between the crop canopy, the surrounding air, and the individual plant of interest. Because these interactions are extremely complex, the shape of the resulting distributed load is not well understood (Burgess et al., 2016). During windstorms, downdrafts, updrafts, and constantly changing wind directions further complicate an understanding of airflow within crop canopies. However, a mathematical analysis of the *effects* of a generalized distributed load profile can provide insights regarding the impact of changes in plant height on stalk lodging resistance regardless of the exact distributed load profile.

In creating this model, we first assume that the drag force imparted to the leaves by the wind is propagated into the stem at distinct points, namely at the attachment point of the leaf to the stalk or stem. Second, we assume that the stem itself is loaded by the wind and that the wind creates a distributed load profile on the stem. We also assume that all loads applied to the stem and leaves are positive (left-to-right) and that the loads are quasi-static (i.e., averaged over time).

2.2. Accounting for the drag force on leaves

To account for the drag force imparted on the leaves, we assume that a series of loads $\boldsymbol{F_n}$, each at height $\boldsymbol{z_n}$, of unknown magnitude are applied to the maize stalk at distinct points via the attachment of the leaves to the stem (Fig. 3).

From basic engineering mechanics, we find the bending moment $M(z)$ exerted at the base of the plant is given by:

$$M(z_0) = \sum_{n: z_0 < z_n} F_n (z_n - z_0) \tag{10}$$

where the sum includes only the forces above the location of interest ($\mathbf{z} < \mathbf{z_n}$). Next, we assume that a change in plant height does not alter the load magnitudes but does affect the height ($\boldsymbol{z_n}$) at which each load is applied. In particular, we assume that the height at which each load is applied $\boldsymbol{z_n}$ scales with the overall height of the plant. For example, if the plant height is decreased by 10%, then the vertical location $\boldsymbol{z_n}$ of each corresponding load $\boldsymbol{F_n}$ will be lowered by 10%. Mathematically, this can be accomplished by using the linear scaling factor $\boldsymbol{c}$ we introduced in

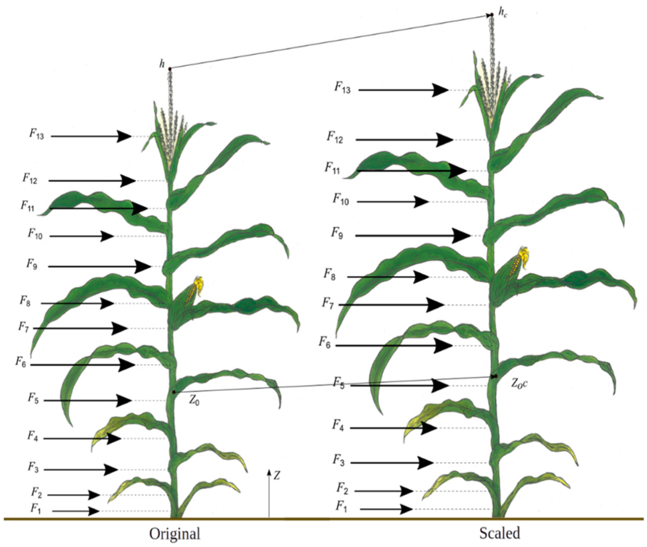

Fig. 3. A more accurate method of accounting for the wind loading on a maize stalk considers the stalk as a cantilever beam subjected to multiple point loads $\mathbf{F_i(z)}$ instead of a single point load. This model assumes that drag forces on the leaves are propagated to the stalk at the leaf attachment points. The right-hand section of the figure shows a scaled version of the same stalk with the same loads.

Section 2.1. Each point on the nominal stalk is scaled linearly as $c\cdot z_n$. The resulting bending moment equation for the scaled stalk is:

$$M_{sc}(z_0c) = \sum_{n:z_0<z_n} F_n(z_nc - z_0c) \tag{11}$$

As c is simply a constant scalar, we can remove it from the summation and simply scale the resulting sum by the value c to obtain the new bending moment. Thus, the relationship between bending moments induced by leaf drag in the nominal plant and the scaled plant can be stated simply as:

$$M_{sc}(z_0c) = c\quad M(z_0) \tag{12}$$

Which is to say that the change in bending moment resulting from leaf loading has a 1:1 positive correlation with the change in plant height.

2.3. Accounting for drag forces on the stalk

To account for the drag force imparted on the stalk by the wind, we assume that an *unknown* distributed load $f(z)$ is applied to the maize stalk. We also assume that scaling the stalk in the vertical direction will proportionally scale the loading profile in the vertical direction, as shown in Fig. 4 below.

This wind-loading profile induces bending moments along the length of the stalk: $M(z_0)$, where z_0 is the location of interest on the stalk. From basic engineering mechanics, the expressions for $M(z)$ is:

$$M(z_0) = \int_{z_0}^{h} f(z)(z - z_o)dz \tag{13}$$

Here, $M(z_0)$ represents the bending moment induced at the point z_0 by the unknown distributed wind force profile $f(z)$. The symbol h represents the height of the stalk.

As mentioned above, we assume that a change in plant height does not change the essential shape of the wind loading function $f(z)$. In other words, increasing the height of the plant stretches both the stalk morphology and the corresponding wind-loading function. Mathematically, this can be accomplished by defining a linear scaling factor, c, as was done previously. Each point on the nominal stalk is scaled as $z_{sc} = z_{nom}\cdot c$. The loading function $f(z)$ is scaled as $f(z/c)$. After scaling both the plant and the distributed load profile induced by the wind by a factor c, the expressions for bending moments at any location along the stalk are given as:

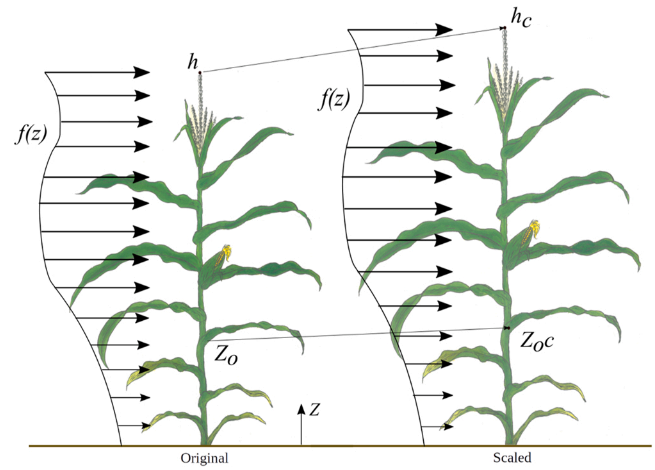

Fig. 4. A diagram of a maize stalk subjected to a continuous wind loading function, **f(z)** instead of discrete point loads (left). The scaled diagram shows the same stalk and wind loading function but stretched in the z-direction (right).

$$M_{sc}(z_0c) = \int_{z_0c}^{hc} f\left(\frac{z}{c}\right)(z - z_oc)dz \tag{14}$$

where the subscript "*sc*" refers to "scaled". Note that both the loading functions and the limits of integration have been scaled, but z_o still refers to the physiological point of interest, which will experience different bending moment loadings in the nominal and scaled scenarios.

We can quantify the differences in bending moments between nominal and scaled situations by applying the fundamental theorem of calculus to Eq. 14, where **F(z)** represents the anti-derivative of $f(z)$, and **G(z)** represents the anti-derivative of $f(z)z$.

$$M(z_0) = [G(h) - G(z_0)] - z_0[F(h) - F(z_0)] \tag{15}$$

The chain rule can then be used to verify the following for the scaled functions:

$$\frac{d}{dz}\left[cF\left(\frac{z}{c}\right)\right] = f\left(\frac{z}{c}\right) \tag{16}$$

$$\frac{d}{dz}\left[cG\left(\frac{z}{c}\right)\frac{z}{c}\right] = f\left(\frac{z}{c}\right)\frac{z}{c} \tag{17}$$

Finally, the results of the previous equations can be used to write the values of the scaled bending moments in terms of the original functions:

$$\begin{aligned} M_{sc}(z_0c) &= \int_{z_0c}^{hc} f\left(\frac{z}{c}\right)(z - z_0c)dz = c\int_{z_0c}^{hc} f\left(\frac{z}{c}\right)\frac{z}{c}dz - z_0c\int_{z_0c}^{hc} f\left(\frac{z}{c}\right)dz \\ &= c^2\left[G\left(\frac{hc}{c}\right) - G\left(\frac{z_0c}{c}\right)\right] - c^2z_0\left[F\left(\frac{hc}{c}\right) - F\left(\frac{z_0c}{c}\right)\right] \\ &= c^2[G(h) - G(z_0) - z_0(F(h) - F(z_0))] = c^2M(z_0) \end{aligned} \tag{18}$$

These results can be summarized as follows:

$$M_{sc}(z_0c) = c^2M(z_0) \tag{19}$$

Eq. 19 states the bending moment due to wind loading of the stalk (not including drag forces imparted on the leaves) in a scaled plant is equal to the bending moment present in the unscaled plant multiplied by the square of the scale factor. For moderate changes in height ($0.85 < c < 1.15$), this corresponds roughly to a 1:2 effect ratio. For example, a

10% decrease in stalk height (c = 0.9) will decrease bending moments in the stalk by approximately 19% ($0.9^2 = 0.81$). We now proceed to combine this result for the drag force imparted on the stalk with the previously derived result for the drag force imparted on the leaves.

2.4. Combining leaf loading and stalk loading

Combining the results of the previous two subsections, we can relate the change in plant height by a factor of $\boldsymbol{c}$ with the change in the total bending moment in the stalk due to both leaf loading and stalk loading:

$$M_{sc}(z_0c) = \mu \bullet c \bullet M_{leaves}(z_0) + \rho \bullet c^2 \bullet M_{stalk}(z_0) \tag{20}$$

$$SF_{sc} = \frac{SF_{nom}}{\mu \bullet c + \rho \bullet c^2} \tag{21}$$

Where $\boldsymbol{\mu} + \boldsymbol{\rho} = 1$ such that $\boldsymbol{\mu}$ represents the relative contribution of drag forces exerted on the leaves to the total bending moment and $\boldsymbol{\rho}$ represents the relative contribution of drag forces exerted on the stalk to the total bending moment. This demonstrates that bending moments induced by drag forces on the leaf scale linearly with height while bending moments induced by drag forces on the stem scale quadratically with height. As mentioned previously, we expect that the majority of drag force will be imparted to the leaves, thus $\boldsymbol{\mu} > > \boldsymbol{\rho}$. The primary advantage of this more complex analysis is that no simplifying assumptions regarding the shape or magnitude of the wind velocity profile nor the resulting distributed load profile applied to the stalk and leaves were made. The results of this analysis confirm the results of the first, more simplified analysis. Namely, altering plant height can have a profound effect on the bending stress experienced by the stalk and the bending moments experienced by the root-soil complex. This more complex analysis indicates that the safety factor against lodging will scale by a factor of $\frac{1}{\mu c + \rho c^2}$, whereas the previous more basic analysis indicated the safety factor against lodging would scale by a factor of $\frac{1}{c^\alpha}$. While the form of the two proposed factors are different, they can both effectively capture the same behavior over a reasonable range of values. For example, when $0.5 < \boldsymbol{c} < 2$, $1 > \boldsymbol{\alpha} > 2$, $1 > \boldsymbol{\mu} > > \boldsymbol{\rho} > 0$), there is less than 1% difference between the two proposed factors. Therefore, in the experimental analyses (explained further below), we assumed the form of the safety factor against lodging was

$$Lodging \quad Reistance = Strength \quad \frac{1}{c^\alpha} \tag{22}$$

We expect that the optimal value for $\boldsymbol{\alpha}$ should be somewhere between 1.0 (linear, loading is dominated by wind interacting with leaves) and 2.0 (quadratic, loading is dominated by wind interacting with the stalk). A value of 1.1 would suggest that the leaves play a much larger role than the stem, while a value of 1.9 would suggest the opposite. Based on other engineering structures which possess fairly rigid cylinders with connected flags (similar to a fairly rigid stalk with connected leaves) we expect to find a value closer to 1, indicating that the leaves are the dominant factor.

2.5. Experimental methods for determining the effect of plant height on lodging resistance

2.5.1. Plant materials

Forty-eight maize hybrids were evaluated to understand the effect of plant height on stalk lodging resistance. These hybrids were derived from publicly available inbred lines and chosen to form a representative sample of the North American maize genetic diversity (Sekhon et al., 2020). These hybrids were evaluated by the Genome to Fields (G2F) initiative (www.genomes2fields.org), a multi-institutional public collaborative (McFarland et al., 2020), over multiple locations in North America with the help from respective local G2F collaborators.

2.5.2. Measured phenotypes

Several phenotypes related to lodging resistance were measured in this study. In particular, plant height, ear height, and the incidence of naturally occurring lodging in the test hybrids (lodging rate) for four years (2014–2017) were obtained from the G2F initiative. Over these four years, the hybrids were nominally evaluated in 110 distinct environments spanning 43 geographical locations covering 20 states across the United States and one province in Canada. At each location, hybrids were grown in a randomized complete block design with two replications. The stalk lodging data for the test hybrids was not available for all environments included in the study. Details of the experiments, locations, and the methodology for recording data on different traits are available through the G2F website (https://www.genomes2fields.org/about/project-overview/#standards-and-methods). Phenotyping data can be downloaded directly from the website and includes factors such as yield, plant height, lodging percentage etc. The details of weather data at the test locations are also available through the G2F website (https://www.genomes2fields.org/resources/).

Two additional phenotypes related to lodging resistance were measured in three unique environments. The phenotypes included the maximum bending moment each plant could resist before lodging (i.e., bending strength) measured by DARLING (Cook et al., 2019b) and the plant height. A detailed description of the DARLING and the type of data it collects is described in (Cook et al., 2019a; Cook et al., 2019b). Briefly, the DARLING consists of a vertical arm with an attached force sensor and a hinged footplate. A user aligns the force sensor mounted on the vertical arm with the center of the internode beneath the ear of the plant to be tested and places the footplate flush with the base of the stalk. The user then steps on the footplate and pushes the device forward. The device pivots at the intersection of the vertical arm and footplate and pushes the stalk over. During the test, the device continuously measures the applied force and deflected angle of the plant. At the end of the test, the load applied to the stalk, the height at which the load was applied, and the deflected angle of the stalk are recorded, and the sensors are reset for the next measurement. The point force the DARLING applies to the stalk induces a bending moment distribution in the stalk similar to the bending moment distribution created by wind loading and creates a failure pattern that is consistent with natural lodging (Robertson et al., 2015; Cook et al., 2019b). In other words, the DARLING device enables researchers to approximate wind forces applied to plants and provides a continuous quantitative output of stalk bending strength. Other methods of evaluating stalk lodging resistance are typically binary (lodged vs not lodged) and can be significantly confounded by weather events (Hondroyianni et al., 2000; Robertson et al., 2016; Sekhon et al., 2020; Thompson, 1972). The DARLING methodology has been used in several other studies to quantify stalk bending strength and lodging resistance (Erndwein et al., 2020; Hostetler et al., 2022; Reneau et al., 2020; Sekhon et al., 2020; Stubbs et al., 2022).

In 2017, 48 hybrids were planted at the Clemson University Simpson Research and Education Center (Pendelton, South Carolina). In 2018, 28 of the 48 hybrids were evaluated at the Clemson University Calhoun Field Laboratory (Clemson, SC) and the Clemson University Pee Dee Research and Education Center (Florence, SC). Plants were grown in a Random Complete Block Design with two replications. Two-row plots were planted for each hybrid/replicate with a row length of 4.57 m and row-to-row distance of 0.76 m (plot length, 4.57 m; plot width, 1.52 m; plot area, 6.95 m^2) at a planting density of 70,000 plants ha^{-1}. Non-experimental maze hybrids were planted on all four sides of the experimental plot to prevent edge effects. Standard agronomic practices were followed for crop management. Further details regarding soil type, fertilizer application, and other crop management practices can be found in a previous publication (Sekhon et al., 2020). DARLING data were collected at physiological maturity when all the hybrids were either at or past 40 days after anthesis. DARLING data were collected on 10 randomly chosen competitive plants in each plot. Nominally, 60 total measurements were acquired for each hybrid (10 plants per plot x 2 replications x 3 locations). However, some plots lacked 10 competitive plants and, therefore, the total number of plants evaluated for each hybrid varied.

In summary, bending strength measurements were acquired for 10 plants x 2 replications x 3 environments = nominally 60 bending strength measurements per hybrid. Height measurements and lodging incidence were nominally acquired for 2 replications of each hybrid in 110 environments. However, several environments were excluded due to missing data. Therefore, plant height and lodging incidence data included in our analysis comprised 2 replications of 48 hybrids in 93 environments which spanned 41 geographical locations and 4 years (2014, 2015, 2016, and 2017). These hybrids were chosen to form a representative sample of the North American maize genetic diversity.

2.5.3. Statistical analysis of the effect of plant height on lodging resistance

As mentioned previously, the lodging resistance of a plant is dependent upon the bending strength of the plant and the loads to which the plant is subjected (Fig. 1). While plant height does not directly alter the bending strength of a plant, it does alter the bending loads (i.e., bending moments and bending stresses) experienced by the plant. Therefore, in the experimental field portion of this study, we measured plant height, bending strength, and lodging rate and then used a generalized mixed effects model to relate lodging rate with plant height given bending strength. The available lodging rate and plant height data were collected in 93 environments which spanned 41 unique geographical locations and 4 years (2014, 2015, 2016, and 2017). Note lodging data was not available for every location-year combination. To account for the heterogeneity that exists across the various environments, we make use of random effects in our model formulation. This is common practice in agricultural research; e.g., see (Ball et al., 2006; Loyce et al., 2008; Sahai and Ojeda, 2005). Let N_{ij} denote the number of plants of the ith variety that were present in the jth environment, and let Y_{ij} denote the number of those plants that were lodged. The previously presented engineering models indicate that lodging resistance (i.e., the safety factor) is a function of both plant height and bending strength. Engineering analysis suggests the general form of this function can be given as $SF_{ij}(\alpha) = s_{ij}\cdot h_{ij}^{\alpha}$, where s_{ij} is stalk bending strength, h_{ij} is plant height, and $\alpha < -1$. A few comments are warranted. First, the proposed function $SF_{ij}(\alpha)$ is an engineering inspired aggregation of bending strength and plant height. Second, the proposed function represents a continuum of potential values which is governed by the unknown value of α; i.e., every value of α provides a different measure by uniquely combining stalk bending strength and plant height. Third, a primary focus of this analysis is aimed at revealing, in a data-driven manner, the value of α that is most reasonable with respect to explaining lodging resistance as measured by historical lodging rates. The engineering analysis presented previously suggests that $\boldsymbol{\alpha}$ should be in the vicinity of -1.1. However, in the statistical analysis that follows $\boldsymbol{\alpha}$ was allowed to take on any value. To this end, we posit the following mixed effects binomial regression model:

$$\Pr(Y_{ij} = y_{ij}) = \binom{N_{ij}}{Y_{ij}} \pi_{ij}^{Y_{ij}} (1 - \pi_{ij})^{N_{ij}} \tag{23}$$

where $g^{-1}(\pi_{ij}) = \beta_0 + \beta_1 f_{ij}(\alpha) + \gamma_j$. In the expression above, $\binom{N}{Y}$ is the binomial coefficient, π_{ij} is the probability that a plant of the ith variety would lodge in the jth environment, $g()$ is the logistic link function, β_0 is the usual intercept, β_1 is a regression coefficient describing the effect of the proposed function on the propensity of lodging, and γ_j is a random effect associated with the jth environment. As is the usual convention, we assume that the random effects independently obey a normal distribution with mean zero and variance σ^2; i.e., $\gamma_j \sim N(0, \sigma^2)$. Thus, the observed data likelihood can be expressed as

$$L(\beta_0, \beta_1, \alpha, \sigma^2) = \prod_{j=1}^{J} \int_{-\infty}^{\infty} \binom{N_{ij}}{Y_{ij}} \pi_{ij}^{Y_{ij}} (1 - \pi_{ij})^{N_{ij}} f(\gamma_j | 0, \sigma^2) d\gamma_j \tag{24}$$

where $f(|0, \sigma^2)$ is the density function of a normal random variable with mean 0 and variance σ^2. By maximizing $L(\beta_0, \beta_1, \alpha, \sigma^2)$ with respect to the unknown parameters (namely; β_0, β_1, α, and σ^2) we obtain their maximum likelihood estimates (MLEs). To accomplish this task, we approach this problem from a profile likelihood-based perspective; i.e., for a fixed value of α we first identify

$$\widehat{\beta}_0(\alpha), \widehat{\beta}_1(\alpha), \widehat{\sigma}^2(\alpha) = argmax_{\beta_0, \beta_1, \sigma^2} \log\{L(\beta_0, \beta_1, \alpha, \sigma^2)\} \tag{25}$$

That is, $\widehat{\beta}_0(\alpha)$, $\widehat{\beta}_1(\alpha)$, and $\widehat{\sigma}^2(\alpha)$ are the MLEs of β_0, β_1, and σ^2, respectively, for a fixed value of α. These can be found directly using the *glmer* function in the R package *lme4*. The second step then identifies the MLE of α as

$$\widehat{\alpha} = argmax_{\beta_0, \beta_1, \sigma^2} \log\{L(\widehat{\beta}_0(\alpha), \widehat{\beta}_1(\alpha), \alpha, \widehat{\sigma}^2(\alpha))\} \tag{26}$$

Given the unidimensional nature of this step, it is easy to identify $\widehat{\alpha}$ via a grid search. The completion of this step also reveals the MLEs of β_0, β_1, and σ^2 as $\widehat{\beta}_0(\widehat{\alpha})$, $\widehat{\beta}_1(\widehat{\alpha})$, and $\widehat{\sigma}^2(\widehat{\alpha})$, respectively.

Note stalk bending strength and plant height were not measured on the same plants that lodging rate data was collected for in the G2F study. Rather, bending strength and plant height phenotypes were measured in a smaller study conducted in three environments across two years (2017 and 2018). The data from the smaller study was used to impute these measures for the plants in the G2F study. The imputed values were stratified by genotype and represent the average of the observed values. For example, s_{ij} is imputed as the average strength measured on the ith variety in the smaller study. This approach was also taken in (Sekhon et al., 2020).

2.6. Experimental methods for determining the effect of genetic and environmental factors on stalk lodging

To examine the role of genetic and environmental factors on stalk lodging incidence, we analyzed the experimental field data using a linear mixed model. This was accomplished using the *lme4* package in R. The posited model partitions sources of variation as follows:

$$Y_{ij} = \mu + \alpha_i + \beta_j + \delta_{ij} + \varepsilon_{ij}$$

where Y_{ij} denotes the logit transformed Firth corrected (Firth, 1993) proportion of stalks of the ith genotype that lodged in the jth environment, μ is the intercept parameter, α_i is a genotype (hybrid) specific random effect, β_j is an environment specific random effect, δ_{ij} is a genotype by environment (G×E) interaction also treated as a random effect, and ε_{ij} is the usual error term.

3. Results

3.1. Engineering stress analysis

Results from both engineering stress analyses indicate that as plant height is reduced, lodging resistance is increased. The simpler single point load model predicts that for a given wind speed, bending stresses and plant height are positively correlated and the relationship between plant height and bending stress is a nearly 1-to-1 relationship. More specifically, this model predicts that scaling plant height by a factor of $\boldsymbol{c}$, will change the safety factor against lodging by $1/\mathbf{c}^{\boldsymbol{\alpha}}$ where $\boldsymbol{\alpha}$ is slightly larger than unity.

The more complex engineering stress analysis, which included multiple point loads and distributed loads, also indicated the relationship between plant height and plant lodging resistance is expected to be in the vicinity of a 1-to-1 relationship. More specifically, this more complex model predicts that the safety factor against lodging is equal to $\frac{1}{\mu c+\rho c^2}$ (see Eq. 21). While this safety factor is more complex than the safety factor derived using the single point load model, both proposed forms for the safety factor capture the same behavior.

Considering both of the engineering stress analyses presented above and using our best engineering judgment to make reasonable assumptions, we believe that if 90% of the drag force is imparted to the leaves and 10% is imparted to the stalk directly, then the safety factor against stalk lodging will equal the strength of the stalk times $\boldsymbol{c}^{-1.1}$, where $\boldsymbol{c}$ is the scaling factor. It should be noted that some standard simplifying assumptions were made when conducting both of these engineering analyses. Therefore, a comprehensive experimental field study and statistical analysis was also conducted to determine the effect of plant height on lodging resistance. Results from the experimental field study are presented below.

3.2. Statistical analyses of experimental field data to determine the effect of plant height on lodging resistance

Plant height, bending strength, and lodging rate were each measured experimentally and then analyzed using a generalized linear mixed effects model to determine the effects of plant height on lodging rate given bending strength. Lodging rate and plant height data for the 48 hybrids were collected in 93 environments, which spanned 41 unique geographical locations. The bending strength measurements on these hybrids were acquired in three environments. Table 1 displays all 48 hybrids included in the study, the number of unique environments in which stalk lodging incidence and plant height data were collected, and the number of stalks evaluated for bending strength for each hybrid / environment.

Lodging resistance (i.e., the safety factor) is a function of both plant height and bending strength. The general form of the safety factor against lodging can be given as $SF = Strength{\cdot}Height^{\alpha}$. We used experi-

Table 1
Hybrids and environments evaluated for stalk lodging associated traits.

#	Hybrid	Natural stalk lodging incidence and plant height # of unique plots evaluated				Stalk Strength # of stalks evaluated		
		G2F_2014	G2F_2015	G2F_2016	G2F_2017	CUS_2017	CUC_2018	CUP_2018
1	B14A/H95	16	18	19	26	16	17	14
2	B14A/MO17	5	5	20	28	3	19	11
3	B14A/OH43	16	18	22	26	17	18	17
4	B73/MO17	21	18	20	25	12	18	3
5	B73/PHM49	20	18	21	28	16	18	20
6	CG44/CGR01	9	9	20	26	7	NA	NA
7	F42/H95	16	3	20	26	15	NA	NA
8	F42/MO17	16	18	21	26	9	16	10
9	F42/OH43	15	18	20	26	13	NA	NA
10	LH216/LH195	3	4	19	26	13	12	10
11	PHN11_PHW65_0323/LH195	5	18	19	26	13	14	8
12	LH74/PHN82	21	18	20	28	13	15	10
13	PHG39/TX205	17	6	20	26	11	NA	NA
14	PHW52/PHN82	20	18	21	29	9	8	6
15	PHW52/PHM49	20	18	20	28	10	6	5
16	WF9/H95	18	18	19	26	4	12	14
17	2369/PHZ51	NA	18	3	15	8	18	16
18	B97/PHB47	NA	18	20	26	8	19	7
19	CG60/LH162	NA	18	14	26	7	19	9
20	LH212HT/LH195	NA	18	18	26	14	16	10
21	LH195/PHZ51	NA	18	16	24	12	18	13
22	LH195/LH82	NA	4	21	29	8	18	17
23	LH198/PHZ51	NA	14	21	27	10	NA	NA
24	PHN11_OH43_0001/PHB47	NA	10	19	26	17	10	4
25	PHN11_PHG47_0251/PHB47	NA	9	20	26	8	8	2
26	PHP02/PHB47	NA	18	19	27	9	18	12
27	TX204/PHB47	NA	7	5	15	5	NA	NA
28	W37A/PHB47	NA	12	21	25	5	4	5
29	PHB47/PHZ51	NA	18	21	26	14	20	11
30	PHG80/PHZ51	NA	18	19	28	6	15	7
31	PHV63/PHZ51	NA	4	5	10	14	NA	NA
32	A679/3IIH6	NA	NA	12	20	8	18	19
33	B73/3IIH6	NA	NA	13	21	7	20	14
34	B73/TX777	NA	NA	11	6	15	NA	NA
35	CGR03/CG108	NA	NA	16	26	8	11	5
36	LH195/LH123HT	NA	NA	15	25	17	NA	NA
37	PHG29/PHG47	NA	NA	20	27	16	14	1
38	PHHB9/PHZ51	NA	NA	5	10	15	NA	NA
39	PHHB9/LH123HT	NA	NA	5	10	18	NA	NA
40	PHP38/LH123HT	NA	NA	6	10	11	NA	NA
41	PHP38/LH210	NA	NA	6	10	3	NA	NA
42	PHV63/LH123HT	NA	NA	5	10	16	NA	NA
43	PHV63/PHN47	NA	NA	6	10	17	NA	NA
44	PHW52/PHZ51	NA	NA	14	22	11	NA	NA
45	PHW52/Q381	NA	NA	16	22	5	NA	NA
46	2369/PHN82	NA	NA	NA	28	13	NA	NA
47	PHP02/PHG47	NA	NA	NA	26	9	NA	NA
48	VA35-B15/LH195	NA	NA	NA	23	5	NA	NA

NA - Not evaluated or data not available; G2F - Genomes to Fields initiative; CUS - Clemson University Simpson Small Ruminant Research and Education Center; CUC - Clemson University Calhoun Field Laboratory; CUP - Clemson University Pee Dee Research and Education Center mental field data to reveal in a data-driven manner, the value of **α** that best explains lodging incidence. To accomplish this, maximum likelihood techniques were utilized with the optimization over **α** being facilitated via a grid search. Fig. 5, provides a depiction of the grid search. In particular, the value of the objective function (i.e., $\log\{L(\widehat{\beta}_0(\alpha), \widehat{\beta}_1(\alpha), \alpha, \widehat{\sigma}^2(\alpha))\}$) at each considered value of **α** is shown. The red line highlights the point at which the objective function is maximized and corresponds to a value of − 1.14. Bootstrapping was implemented to generate estimates of the standard error and 95% confidence intervals. The standard error was 0.15, and the 95% bootstrap confidence interval for α is (−1.43,−0.87). These results indicate that the experimentally observed variation in lodging incidence of the 48 hybrids is best explained by the quantity: strength x height$^{-1.14}$. Table 2 summarizes the regression coefficient estimates at $\widehat{\alpha} = -1.14$. From these results, we find a strong association between the proposed function and stalk lodging incidence. In particular, we estimate that the log-odds of lodging decrease by 0.268 (p-value<2e-16) for every unit increase in the proposed function.

3.3. The effect of genetic and environmental factors on stalk lodging

The lodging incidence data showed sizable variation among hybrids and environments (Fig. 6); therefore, these data were analyzed to determine the effect of genetics and environment on lodging incidence (as described in the methods Section 2.3). The analysis included 48 genotypes and 93 unique environments, revealing highly significant ($P < 0.001$) variance components for genotype, environment, and G×E interaction. These three components were able to explain about 58% of phenotypic variation observed for stalk lodging incidence, and among different components evaluated, environment accounted for the largest proportion of variance observed for stalk lodging incidence, followed by G×E interaction, and genotype (Table 3).

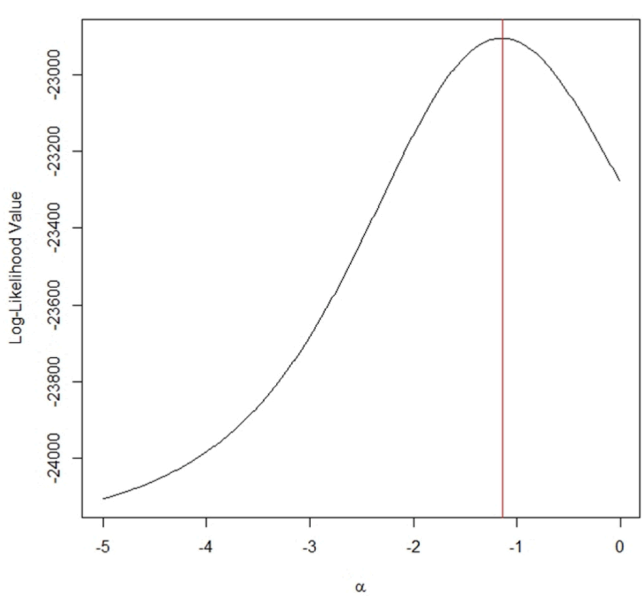

Fig. 5. Estimating the relationship between lodging propensity and plant height. The safety factor against lodging (i.e., the lodging propensity of a given hybrid) can be related to bending strength and height as follows: Safety Factor = Strength x Height$^{\alpha}$. Engineering analyses suggest the value of **α** is close to − 1.1 We empirically determined via a mixed effects model the value of **α** using lodging incidence data, bending strength data, and plant height data collected as part of a large multi-year field experiment. Results of this empirical data analysis are shown in the graph above as log-likelihood value vs **α** for the experimental field data. The optimal value of **α** that best explains lodging incidence given bending strength and plant height is − 1.14 (indicated by the red line).

Table 2
Summary of regression coefficient estimates obtained from the empirical analysis that related the proposed safety factor (SF = strength x height$^{\alpha}$) to stalk lodging incidence. These analyses were conducted with **α** = − 1.14.

	Estimate	Std. Error	P-value
β_0	-2.148	0.202	< 2.2e-16
β_1	-0.268	0.005	< 2.2e-16

4. Discussion

The lack of a holistic, quantitative phenotype or breeding index for lodging resistance has limited our understanding of the genetic underpinning of this economically important trait. Several quantitative metrics have been proposed that include rind penetration resistance, bending strength, bending stiffness, diameter, and rind thickness. However, none of these metrics properly account for the effect of plant height, which is known to be one of the primary determinants of crop standability. Results from this study can be used to properly account for the effect of plant height on stalk lodging resistance when measuring bending strength. These results should be used in future phenotyping studies seeking to discover the genetic underpinning of lodging resistance.

Results from the engineering stress analysis and the experimental field study both indicate a nearly 1-to-1 relationship between plant height and lodging resistance. It should be noted that the engineering analysis was conducted before the results of the experimental field study were known. That is to say that the engineering analysis was conducted independently and was truly a predictive analysis of the field test results. The strong agreement between engineering theory and experimental field trials confirms basic human intuition that reducing plant height will reduce the incidence of lodging. Moreover, these analyses quantify the nature of the relationship between plant height and lodging propensity. Specifically, the lodging resistance of a scaled plant is equal to the lodging resistance of a nominal plant multiplied by $\boldsymbol{c}^{-1.14}$. Therefore, doubling the height of a plant ($\boldsymbol{c} = 2$) will reduce its lodging resistance by $2^{-1.14}$ times that of the nominal plant (i.e., $SF_{sc} = 0.45 \cdot SF_{Nom}$). Note that for simplicity, the nominal plant can be assumed to have a height of one. The scaling factor $\boldsymbol{c}$ for any given plant in a study would then be equal to the height of that plant. This enables the definition of a simple lodging resistance index that can be used in future phenotyping studies:

$$lodging \quad resistance \quad index = strength \bullet height^{-1.14} \tag{27}$$

Lodging is a complex multiscale phenomenon that varies in both time and space. Numerous intermediate component phenotypes at multiple temporal and spatial scales ultimately determine the lodging resistance. Therefore, plant height is but one of many anatomical determinants of lodging propensity. For example, numerous studies have demonstrated that cross-sectional morphology (e.g., diameter and rind thickness) has a large impact on mechanical bending stresses and lodging resistance (Oduntan et al., 2022; Seegmiller et al., 2020; Stubbs et al., 2022; Von Forell et al., 2015). In addition, the clasping leaf sheath has recently been shown to significantly impact the bending strength of grain crops (Kempe et al., 2013; Robertson et al., 2021b). Furthermore, the chemical composition of stalks (Ahmad et al., 2018; Kamran et al., 2018; Robertson et al., 2022b), mechanical properties such as the modulus of elasticity, rind penetration resistance (Al-Zube et al., 2017, 2018; Cook et al., 2020; Kumar et al., 2021; Stucker et al., 2021), and cellular organization (Sayad et al., 2023) have been studied in relation to stalk lodging. The engineering stress analysis presented in this work did not directly consider these other factors or that modifying plant height may modify cross-sectional morphology, for example. However, all these factors were at play in the experimental field study conducted as part of this work. The strong agreement between engineering theory and field trials, which included the effects of other deterministic

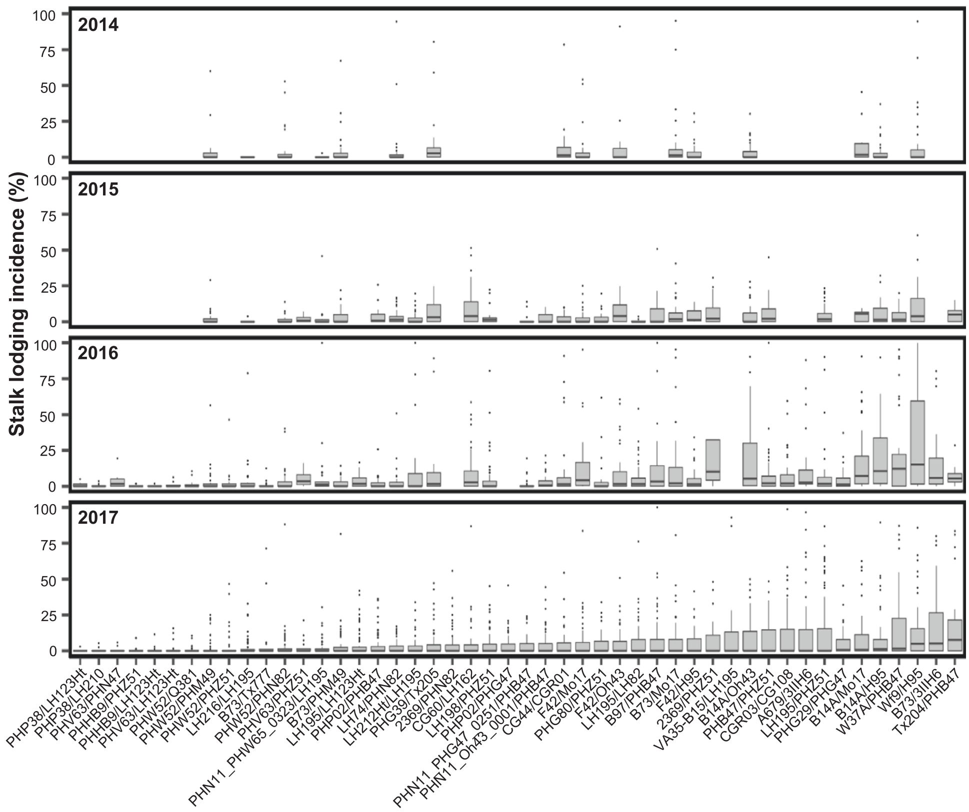

Fig. 6. Distribution of stalk lodging incidence among 48 hybrids grown in the different environments included in this study. The hybrids are arranged in increasing order of the median stalk lodging incidence for the year 2017. Within each box plot, the horizontal line denotes the median, and the lower and upper end of the boxes correspond to the 25th and 75th percentiles of the observed data, respectively. The tips of whiskers at the lower and upper end of the boxes represent the 10th and the 90th percentiles of the observed data, respectively, and the dots indicate outliers.

Table 3
Partitioning of variance for stalk lodging incidence.

Genetic Variance		Environmental Variance		Genotype × Environment Variance	
% of V_P	p-value	% of V_P	p-value	% of V_P	p-value
5.69	* **	34.73	* **	8.90	* **

* ** indicate $P < 0.001$; % of V_P indicates total phenotypic variance.

phenotypes, suggests that plant height is a primary determinant of stalk lodging resistance. This observation also illustrates the importance of understanding the hierarchical nature of lodging resistance. Many of the phenotypes that have been studied in relation to lodging resistance can be thought of as intermediate or lower-level phenotypes. In other words, rind penetration resistance, diameter, rind thickness, cellular organization, the leaf sheath, chemical composition, etc., are determinants of stalk strength which is, in turn, a determinant of lodging resistance. Thus, by measuring stalk strength directly the effect of these lower-level phenotypes can be accounted for even though they are not explicitly measured.

This study clearly indicates that the newly released short-stature hybrids are a promising approach to reduce lodging. However, this study did not investigate how plant height may affect other important phenotypes of interest (e.g., yield, light interception, pest resistance, disease resistance etc.). Future studies investigating these relationships are warranted. The authors are particularly interested in knowing how lower-level, intermediate phenotypes (such as cross-sectional morphology) may be affected by the genetic modifications that induce reduced plant height. For example, if short-stature hybrids exhibit reduced diameters and rind thicknesses, then they will likely have lower bending strengths which could negate the effect of reduced plant height. The authors are not aware of any published studies investigating this topic.

When analyzing the experimental field data via a linear mixed model to determine the effects of genetics and environment on lodging incidence, we found a highly significant genetic variance component. This underscores the value of pursuing genetic improvement of stalk lodging related traits (e.g., reduced plant height, improved cross-sectional geometry) for improving the stalk lodging resistance of maize. As expected for a complex trait, we also found that natural stalk lodging incidence is highly influenced by the environment and G×E interaction. However, it is important to note that natural stalk lodging incidence, the phenotype used for the analysis provided here, is confounded by numerous factors, including disease and pest incidence, soil fertility, wind speed, and other weather conditions at the locations used for evaluation (Flint-Garcia et al., 2003; Hondroyianni et al., 2000; Hu et al., 2012; Robertson et al., 2016; Thompson, 1972). Therefore, careful multi-environment evaluations combined with robust phenotyping approaches should be used to make decisions during artificial selection for stalk lodging resistance (Cook et al., 2019b; Sekhon et al., 2020).

4.1. Limitations

Both engineering models presented in the methods section have certain limitations. For example, neither approach accounts for stalk deformation, stalk flexibility, or unanticipated changes in wind loading that might result from reduced plant heights. An increase in plant height would increase the overall spacing between leaves, likely increasing the wind velocity within the canopy and, thereby, increasing wind loading. Similarly, decreasing plant height would be expected to make the canopy denser, thus decreasing wind speed and the overall wind loading. We also expect plant height to impact plant-to-plant interactions within the canopy. As plant height increases, the stalks will deflect further into the wind and be supported by contacting neighboring plants (Bebee et al., 2021). Further research is needed to elucidate these effects more specifically. It is interesting to note that while the engineering analyses did not explicitly account for these effects, they closely predicted the outcome of the field study in which all these factors were at play. There are two potential explanations for this observation. The first is that the influence of these other factors on lodging resistance is minimal. The other potential explanation is that these factors are significant but that they tend to cancel each other out. In other words, some have a positive effect on lodging resistance, and some have nearly equal and opposite negative effects on lodging resistance.

This study was focused on dent maize germplasm. Other crop species that suffer from the problem of lodging can exhibit unique phenomena that were not accounted for in this study. For example, the height of the center of gravity of maize plants was not considered in this study because in maize, the bending moments and forces induced by self-weight are much smaller than bending moments and forces induced by the wind (Stubbs et al., 2020b). However, in small grains like wheat and barley, plant weight and the height of the center of gravity can significantly impact lodging resistance. The ratio of the weight of a plant to its flexural stiffness is a key factor in determining the relative contribution of external forces (wind) and body forces (plant weight) to stalk lodging. In general, plant weight has a negligible effect on stiff and strong stems like bamboo and maize but becomes more influential in smaller stemmed species like rice and wheat. The topic of plant weight was comprehensively investigated in (Stubbs et al., 2020b), and methods of accounting for plant weight in small grains are presented therein. Additionally, differences in canopy structure and tillering can vary significantly between crop species, and some of these differences significantly impact lodging. For example, in wheat, primary stems and tillers are in close contact with one another, and the most basal leaves often become intertwined, thus forming a type of self-supporting net that mechanically connects the plants. A similar phenomenon can be seen in maize, but it is far less relevant as the strength of maize stalks is much higher than the strength of intertwined maize leaves. Because of such interspecies differences, results from this study should not be directly extrapolated to other crop species.

The primary conclusion of this study is that reducing plant height in maize will reduce lodging incidence. However, one must ultimately consider the overall breeding objectives of a program before selecting for reduced plant height. For example, in grain production, it would be beneficial to breed for reduced plant height as this will limit the wind force imparted on the plant and therefore reduce the likelihood of lodging. However, for silage breeding, reduced height may translate into less total biomass. In addition, one must consider harvesting equipment. In grain production the ear must be high enough off the ground to enable automated harvesting by a combine. It is also important to recognize that plant height is a complex plant trait, and selective breeding for reduced plant height could potentially induce unpredictable changes in other important phenotypes of interest.

5. Conclusion

Growers and producers have battled with the problem of crop lodging in maize for over 100 years. Significant advances in crop science and genetics have increased yields and produced plants that are more tolerant of biotic and abiotic stresses. However, the problem of crop lodging persists. As we constantly seek to increase yields, there is a concomitant need to ensure that plants can mechanically support the additional stresses induced by heavier grain heads and extreme weather events. Plant height has a direct, measurable impact on crop lodging resistance as it modulates the bending stresses plants are subjected to during windstorms. This study has demonstrated a nearly linear 1-to-1 relationship between crop lodging incidence and plant height. Future studies can use Eq. 27 to properly account for the effect of plant height on lodging resistance when acquiring measurements of stalk bending strength. Using this equation in combination with in-vivo measurements of stalk bending strength (e.g., DARLING measurements) can be a more efficient, precise, and economically viable route to quantifying lodging resistance as compared to collecting lodging incidence data in multiple environments/years. For example, it was recently shown that DARLING measurements acquired in three environments could accurately predict historical lodging incidence data collected in over 100 environments (Sekhon et al., 2020).

The primary conclusion of this study is that reducing plant height will reduce lodging in maize by reducing the magnitude of bending moments imparted on the plant by the wind. The recent introduction of commercial "short stature" maize varieties, which exhibit reduced plant height, represents a promising approach to mitigate the problem of crop lodging in the future. Nonetheless, additional studies investigating the relationships between plant height and other anatomical and biological determinants of bending strength and crop lodging resistance should be conducted in the future.

CRediT authorship contribution statement

Christopher J Stubbs: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition. **Bharath Kunduru:** Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – review & editing, Visualization. **Norbert Bokros:** Investigation, Writing – original draft, Writing – review & editing. **Virginia Verges:** Investigation, Writing – original draft, Writing – review & editing. **Jordan Porter:** Formal analysis**. Douglas D. Cook:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Seth DeBolt:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Christopher McMahan:** Methodology, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition. **Rajandeep S. Sekhon:** Methodology, Validation, Investigation, Resources, Data curation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Daniel J. Robertson:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

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.

Data Availability

Data will be made available on request.

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