

Crops and Soils Review

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Corresponding author:
A. G. McDonald;
Email: armandm@uidaho.edu

Effect of cell wall compositions on lodging resistance of cereal crops: review

E. Mengistie and A. G. McDonald 

Forest and Sustainable Products Program, Department of Forest, Rangeland and Fire Sciences, University of Idaho, Moscow, ID, USA

Abstract

Lodging is the permanent displacement of stalks due to disrupted secondary cell walls caused by external factors, plant characters and their interaction. Anatomical, morphological and compositional traits are among lodging-inducing plant traits. In comparison with morphological and anatomical features, the correlation of lodging resistance and cell wall composition is not frequently reviewed. In this review, the relation between cell wall composition and lodging resistance of cereal stalks is comprehensively reviewed based on major cell wall components (lignin, cellulose and hemicellulose) and trace minerals. From the body of literatures reviewed across all cereal crops, lignin and cellulose were found to have significant positive correlation with lodging resistance. However, the effect of structural features of cellulose and lignin on lodging resistance was not investigated in most of the studies. This review also highlights the importance of biomass recalcitrance and lodging resistance trade-offs in the spectrum of genetic cell wall modifications.

Introduction

The structural stability of stems (for small grain cereal crops), stalks (corn and sorghum) and roots of cereal crops is vital to provide mechanical support (Shah *et al.*, 2017; Ana *et al.*, 2022; Maqbool *et al.*, 2022). The structure of the crops may fail by either stem buckling of the lower internodes or failure of root–soil anchorage, respectively called stalk lodging and root lodging (Neenan and Spencer-Smith, 1975). Root lodging is caused by disturbance to the root–soil interaction and occurs when the total bending moment of a plant exceeds the strength of the root–soil interface (Berry *et al.*, 2004). Lodging is a multi-factor and complex phenomenon caused by external factors (wind speed, disease, pest damage, rain, topography, soil, etc.), plant characters (stalk morphology, anatomical traits and chemical composition) and their synergistic interactions (Stubbs *et al.*, 2020a, 2020b). The combined and/or individual factors may contribute to overall change in plant structural integrity, thus could lead to structural failure. Lodging resistance, on the other hand, is an inherent trait of the cell walls (CWs) to withstand loads exerted on the stalks (Long *et al.*, 2020). Morphological, anatomical and compositional trait-associated factors influencing stem lodging in cereals are shown in Fig. 1. Crop stems can be considered as slender cylindrical columns which are loaded by both self-weight and external loads (Huang *et al.*, 2016). Thus, for crops to be lodging-resistant, their stalks need to be not only structurally rigid enough to support their own weight but also sufficiently flexible to resist external forces (Erndwein *et al.*, 2020).

The stalks of crops perform multiple physiological functions and encompass complex structural heterogeneity resulting in mechanical response variation under different conditions (Du and Wang, 2016). Lodging in cereal crops is mainly the result of interaction between plant character and external force. External factors are uncontrollable, while plant characters (anatomical, morphological and compositional) are genetic controllable traits associated with the material properties of the plant. Furthermore, the proportionality between the mechanical strength of lower stems and the weight of the upper parts of the stem determines a plant's vulnerability to lodging. As a result, plant lodging resistance is also determined by the weight of its upper portion (upper leaves, stems and seeds) and the resistance of the lower portion (Fan *et al.*, 2018a, 2018b). Thus, the biomechanical properties of the stem in cereals play an important role for its lodging resistance.

The effect of morphological and anatomical characteristics (plant height, internode length, cross-sectional morphology and culm diameter) of crops is studied thoroughly (Fig. 1) (Kong *et al.*, 2013; Gomez *et al.*, 2017; Bayable *et al.*, 2020; Oduntan *et al.*, 2022). The current review aims to provide comprehensive insights about the role of CW composition for lodging resistance. The review first introduces general plant CW organization, function and composition from the point of view of analytical chemistry. Finally, it focuses on the correlation of CW compositions and lodging of cereal crops and provides an up-to-date survey of the role of chemical composition, and structural features to the lodging resistance.

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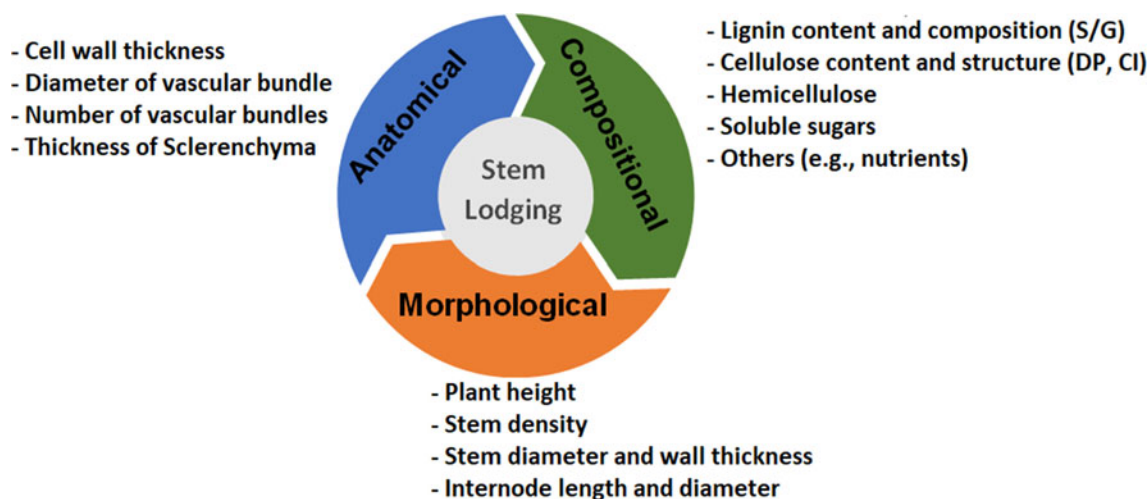


Figure 1. Lodging-inducing plant characters: anatomical, compositional and morphological traits associated with stem lodging; S/G, syringyl/guaiacyl ratio; DP, degree of polymerization; CI, crystallinity index.

Plant cell walls

The growth of plant cells requires the synthesis and deposition of dynamic structural multilayers and extracellular matrices surrounding the cell, called CWs (Sarkar *et al.*, 2009). CWs are composed of structural polymers (cellulose, hemicellulose and lignin) that are woven into an organized and highly cross-linked network allowing them to provide mechanical support (Sarkar *et al.*, 2009; Zhang *et al.*, 2021a). CWs constitute the majority of plant biomass and significantly vary in their composition and microstructure depending on the species of origin, tissue type, stage of development and environmental conditions (Pattathil *et al.*, 2015). The distinctions of CWs in physico-chemical, mechanical, rheological and ultrastructural features of CWs are largely governed by both the organization and relative proportion of the main polymeric components: cellulose, lignin and hemicelluloses (Pattathil *et al.*, 2015; Geitmann *et al.*, 2019). The CW is the main determining factor for the mechanical strength of plants (Bidhendi and Geitmann, 2016). The structural integrity of plant CWs arises from the main structural polymers (cellulose, lignin and hemicellulose) and their interactions. Non-covalent interactions such as hydrogen bonding and van der Waals forces are primarily responsible for the integrity of cellulose microfibrils and the cellulose–hemicellulose associations and networks within plant CWs (O’Sullivan, 1997). Lignin–carbohydrate complexes (LCCs) that are held together via ester and ether linkages between lignin and hemicelluloses can further strengthen wall integrity (Silveira *et al.*, 2013). The strengths of the synergistic interactions between hemicelluloses with the cellulose core and lignin are subject to significant variation (Pattathil *et al.*, 2015).

Cell wall organization

The plant CWs of structural tissue most commonly integrated with vascular bundles are organized from three compositionally and structurally distinctive layers: middle lamella (ML), primary cell walls (PCW) and secondary cell walls (SCW) (Nishitani and Demura, 2015). The cell plate formed during cell division develops into the ML – a thin layer which connects two plant cells and is mainly composed of pectins (Cosgrove, 2005) (Fig. 2c). The PCW is then deposited on each side during cell

expansion. PCW is composed of carbohydrate-based polymers such as cellulose, hemicelluloses, pectin and structural glycoproteins (Harris and Stone, 2009) and contains cellulose microfibrils with a dispersed orientation. After cessation of cell growth, the SCW is deposited inside the PCW, making the walls thicker and rigid, subsequently determining mechanical characteristics of plants. SCW are composed of cellulose, hemicellulose and lignin in varying proportions. The SCW is further organized into three layers: an outer layer (S1), middle layer (S2) and the innermost layer (S3). The S2 layer constitutes the highest proportion of the CW thickness, endowed with smaller microfibril angle (Königsberger *et al.*, 2023). The mechanical properties of a plant mainly depend on the architecture of the SCWs and structural parameters like microfibril angles (Sorieul *et al.*, 2016). Plant CW structure consisting of ML, PCW and SCW is shown in Fig. 2c.

Function

The ML and PCW play an indispensable role for cell-to-cell adhesion, cell expansion and determination of cell shape (Sorieul *et al.*, 2016). The ML glues adjacent cells together after lignification (Cosgrove, 2005). The PCW is a semi-flexible layer that needs to be not only rigid to withstand the internal and external stresses but also flexible enough to allow CW expansion during cell growth (Burgert, 2006). On the other hand, the SCW provides axial stiffness along with collapse and burst resistance. The S2 layer accounts for the majority of the CW (Gibson, 2012), thus it has a profound effect on the properties of the plant. The microfibril angle, thickness and cellulose content are important characteristics of the S2 layer (Li *et al.*, 2019). Compared to the S2 layer, the S1 and S3 layers are relatively thin but play a critical role in increasing the elastic modulus of the cell in the transverse plane (Sorieul *et al.*, 2016). The S1 layer acts as reinforcement, preventing excessive radial expansion and rotation of the cell, while the S3 layer helps to avoid sideway collapse when under hydrostatic tension forces (Sorieul *et al.*, 2016). The fibres will slightly rotate under stress because of the microfibril angle arrangement of the S2 layer. Because of the thickness, the high-volume fraction and alignment of cellulose fibrils, the mechanical properties of the

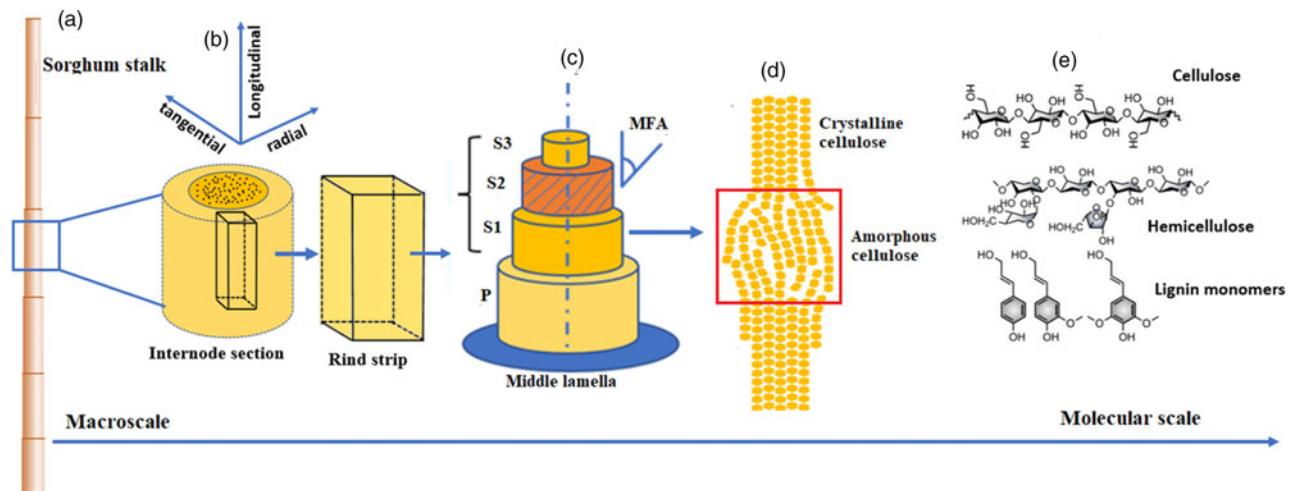


Figure 2. Conceptualization of top-down (macroscale-to-molecular scale) arrangement based on a sorghum stalk; (a) schematic depiction of stalk; (b) sections and rind strip of stalk internode; (c) depiction of plant cell wall structure consisting of primary cell wall (P), secondary cell wall layers (S1, S2 and S3) and microfibril angle (MFA); (d) representation of crystalline and amorphous cellulosic forms; (e) structures of major cell wall components.

CW in the longitudinal direction are largely dependent on the S2 layer (Gibson, 2012).

Plant cell wall and mechanical strength

Plant CWs are a complex assembly of biopolymers naturally resistant to deformations (Harris and Stone, 2009). Mechanical strength refers to the ability to withstand an applied load without failure. In line with CW composition, structural factors contributing to the mechanical strength arises from (1) lignin, cellulose and hemicelluloses contents, (2) cellulose crystallinity index (CI), degree of polymerization (DP), lignin structure and composition (e.g. S/G ratio) and (3) component interactions such as lignin-carbohydrates complexes. Physical failure mechanisms of cereal stalks at macroscale are results of nano structural and molecular phenomena (Gangwar *et al.*, 2021, 2023). Systematic conceptualization of top-down/macroscale-molecular scale arrangement based on sorghum stalks is shown in Fig. 2.

Cellulose

Cellulose is the primary structural framework of plant CWs consisting of a linear D-glucosyl repeating unit linked via β -(1,4) glycosidic bonds (Maleki *et al.*, 2016; Rongpipi *et al.*, 2019). Cellulose is the load-bearing structural component of plant CWs due to its high DP and linear orientation (Harris and Stone, 2009). Cellulose is a long-chain polysaccharide made up of 7000–15 000 D-glucose monomer units, and cellulose molecules align in a single cellulose synthase complex rosette to form an elementary fibril 3–5 nm wide (Cosgrove, 2005; Gibson, 2012). The properties of cellulose contributing to its mechanical stiffness include the degree of crystallinity, MFA and DP (Rongpipi *et al.*, 2019). Each glucose unit contains three free hydroxyl moieties that can interact with other cellulose molecules to form hydrogen bonds which play a crucial role in the aggregation of cellulose chains to form fibrils and establishes the crystalline structure of cellulose (Sorieul *et al.*, 2016). Long-chain cellulose elementary fibrils contain numerous hydrogen bonds and are difficult to deform. Cellulose elementary fibrils contain both crystalline and non-crystalline

(amorphous) regions (Fig. 2d) and are encapsulated in a lignin-hemicellulosic matrix (Lee *et al.*, 2015). CI refers to the relative proportion of crystalline to non-crystalline (amorphous) regions that influence mechanical properties such as strength and stiffness (Lee *et al.*, 2015). Cellulose molecules are aligned into microfibrils (a bundle of several elementary fibrils) of about 10–25 nm diameter within the lignin and hemicellulose matrix (Gibson, 2012). The orientation of the cellulose microfibrils in the S2 layers of the CW has a significant influence on the mechanical properties. Thus, the variation of MFA in S1, S2 and S3 layers in the CW of plants could result in anisotropy in the mechanical properties of the CW (Maleki *et al.*, 2016). The DP of cellulose is another superstructural feature affecting the stiffness (flexural modulus) of the plant CW. The cellulose DP varies between 2000 and 6000 in the PCW and about 10 000 in the SCW (Sorieul *et al.*, 2016).

Lignin

Lignin is a three-dimensional and amorphous biopolymer composed of the monolignols coniferyl, sinapyl and p-coumaryl alcohols (Frei, 2013), which are respectively polymerized to guaiacyl (G), syringyl (S) and hydroxyphenyl (H) units through a dehydrogenative polymerization reaction. The monolignols differ in their degree of methoxylation and are coupled by C–C or ether inter-unit linkages, forming arylglycerol- β -ether dimers, resinols, phenylcoumaran, spirodienone and dibenzodioxin (Del Río *et al.*, 2012; Kang *et al.*, 2019) (Fig. 3). Lignin gives structural rigidity and mechanical strength to the CWs via covalent linkage with hemicellulose, and by occupying the voids between polysaccharides (Kang *et al.*, 2019). There are van der Waal interactions between lignin and cellulose microfibrils, which creates cohesion between the lignin-hemicellulose matrix and the crystalline cellulose. The weakest interactions are found between the amorphous cellulose and the lignin-hemicellulose matrix (Sorieul *et al.*, 2016). Besides the total lignin content, its composition (S, G, H and S/G ratio) could influence the mechanical property of the CW (Ana *et al.*, 2022). The S/G ratio indicates the ratio of different monolignols present in lignin and influences the linkage distribution (β -O-4, β - β , etc.) within lignin. G-rich lignin is highly

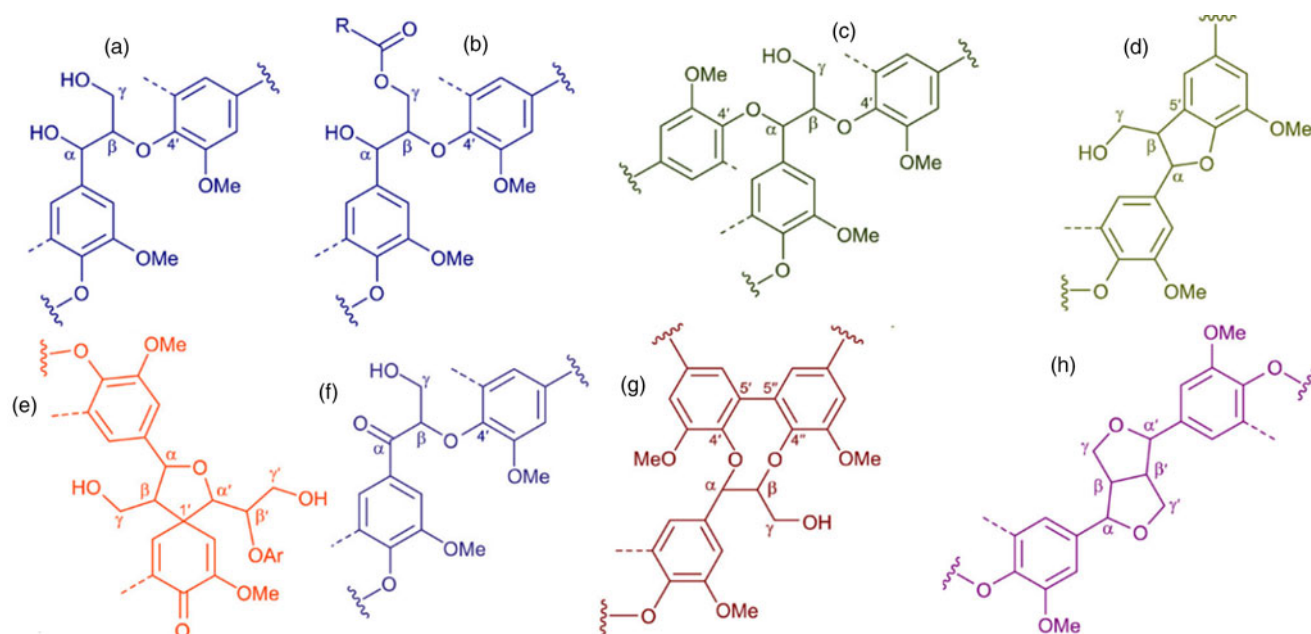


Figure 3. Lignin interunit linkages (a) β -O-4 alkyl-aryl ethers; (b) β -O-4 alkyl-aryl ethers with acylated γ -OH; (c) α,β -diaryl ethers; (d) phenylcoumarans; (e) spiro-dienones; (f) $C\alpha$ -oxidized β -O-4 structures; (g) dibenzodioxocins; (h) resinols (Del Rio *et al.*, 2012).

cross-linked due to a greater proportion of biphenyl and other carbon–carbon bonds, whereas S-rich lignin is less condensed, and linked by more labile ether bonds at the 4-hydroxyl position (Ferrer *et al.*, 2008). Furthermore, S-rich lignin is more easily depolymerized than G-rich lignin, due to the fact that an additional methoxy group at position 5 on a lignin monomer results in reduced available reactive sites ($S < G < H$) for coupling and fewer possible combinations during polymerization (Ziebell *et al.*, 2010).

Hemicelluloses

Hemicelluloses are heteropolysaccharides containing pentose (C5, xylose and arabinose), and hexose (C6, mannose, glucose and galactose) monosaccharides, uronic acids and acetyl groups (Huang *et al.*, 2021). The heterogeneous nature of hemicelluloses plays an important role for molecular interactions with cellulose microfibrils and covalent linkages with lignin (Peřkala *et al.*, 2023). Hemicelluloses are highly branched (Fig. 2e) and amorphous polysaccharides with a DP of 100–3000 (Gibson, 2012), which is lower compared to cellulose. Hemicellulose cross-links cellulose and amorphous lignin (Rongpipi *et al.*, 2019).

Interactions between polymers

The plant CW consists of a network of interlinked polymers with distinct mechanical properties. Attributed to its complex structural behaviour, the CW has been compared with a composite material formed by the combination of two or more materials with different properties without dissolving or blending each other. This emphasizes that CW polymers play different roles for the overall mechanical behaviour of the structure (Bidhendi and Geitmann, 2016). Because of the CW's intricate interwoven nature, studying the behaviour of individual polymer components may have limited predictive potential for the bio-mechanical property of the heterogeneous structure (Robertson *et al.*, 2022). Hence, cross-links and other interactions between

biopolymers are crucial for comprehensive understanding of the mechanical property of CW (McCann and Carpita, 2008). Strong interactions between the CW components may alter CW biomechanical properties. Cellulose and hemicelluloses are linked by hydrogen bonds, whereas lignin is covalently bounded to hemicelluloses in order to create the LCC (Giummarella *et al.*, 2019; Kang *et al.*, 2019). Computational CW network model study of the PCW showed that stiffness is most sensitive to the cellulose microfibril–hemicellulose interaction in which Young's (tensile) modulus increases with the interaction (Yi and Puri, 2014). Although considering the whole CW polymer network is crucial, general principles can be decoded by characterizing the properties of individual components (Bidhendi and Geitmann, 2016).

Composition and strength of cereal stems

Even though cross-sectional morphologies have been recently indicated as key determinant of stalk lodging resistance (Oduntan *et al.*, 2022; Ottesen *et al.*, 2022), the biochemical factors causing cross-sectional variation is not yet clearly understood. Thus, looking into CW composition could enlighten it. The CW structural compositions are not uniformly distributed within the CWs of cereal stalks. The structure and the quantity of these CW components vary according to species, tissues and maturity of the plant CW (Houston *et al.*, 2016). As shown in Table 1, the CW compositions of cereals stems are fundamentally different: generally consisting of 32–46% cellulose, 12–37% hemicellulose and 14–31% lignin, whereas extractives (solvent extractable components, such as lipids), ash and proteins make up the remaining fractions. Because of heterogeneity in the composition, structure and CW interaction with other external lodging-inducing factors, the response and mechanism of each crop against lodging might be different. Stems resist the forces of gravity and powerful lateral wind forces through the cumulative strength of the CW surrounding each cell.

Table 1. Summary of literature for cell wall composition and crystallinity index (CI) of some cereal crop stalks (% dry mass)

| Cereal | Cellulose | Hemicellulose | Lignin | Extractives | Ash | CI (%) | References |
|---------|-----------|---------------|-----------|-------------|------|-----------|-----------------------------------------------------------|
| Wheat | 32.0–46.4 | 18.0–29.3 | 18.0–25.1 | – | 9.7 | 43–58 | Zheng <i>et al.</i> (2018); Muhammad <i>et al.</i> (2020) |
| Rice | 37.0 | 22.7 | 13.6 | 13.1 | 19.8 | – | Raveendran <i>et al.</i> (1995) |
| Millet | 41.0 | 20.9 | 18.3 | – | 6.0 | – | Saeed <i>et al.</i> (2017) |
| Sorghum | 36.1–39.4 | 26.9–29.2 | 20.8–22.1 | 1.5–2.2 | – | 45.5 | Dong <i>et al.</i> (2019) |
| Rye | 37.9 | 36.9 | 17.6 | – | 3.0 | – | Sun <i>et al.</i> (2000) |
| Oat | 39.6 | 22.6 | 18.2 | 10.1 | 1.4 | – | Tamaki and Mazza (2010) |
| Barley | 30.0–31.0 | 27.0 | 16.0–19.0 | 13.37 | 3.9 | – | Lara-Serrano <i>et al.</i> (2019) |
| Corn | 42.4 | 11.8 | 30.62 | 8.2 | 7.0 | 57.0–65.0 | Zhao <i>et al.</i> (2013) |

The stalk mechanical properties dictate the structural stability of cereal crops to maintain the stalk in an upright position and ultimately their lodging resistance. Setting aside the CW heterogeneity, identifying the key contributing parameters for structural integrity of the stalks in cereal crops is crucial for the development of robust cultivars.

Stalk strength in cereal crops, an important agronomic trait directly related to lodging resistance, is closely associated with stalk geometry, structure and composition of the CW. In most cereal crops, stem strength is the main determinant of resistance to lodging, which is a well-known factor affecting harvesting efficiency, yield and quality. For example, in barley (Kokubo *et al.*, 1989), breaking strength of brittle stems was found to be significantly lower than non-brittle stems. The association of brittleness with lower bending strength implied that stems with lower bending strength are prone to structural failing and stalk lodging. Although lodging resistance varies among different genotypes, it is still selected primarily based on mechanical phenotyping. For instance, Chuanren *et al.* (2004) recommended selection of high-yield and lodging resistant rice species based on the ‘middle stem’ and ‘rigid stem’ traits, which are not explicitly defined in terms of composition or other parameters. The rigidity, height of plants and other anatomical and morphological features relevant to lodging are genetically controlled, thus evaluation of the complicated lodging trait should not be based on such factors alone. Knowing the role of CW composition and structural features on stalk lodging might lead to a more comprehensive understanding of the phenomena.

Stems endowed with lodging resistance and mechanically stiff character can prevent crops from breaking. There are no standardized approaches for quantitative measurement of stalk lodging resistance. Biomechanical properties such as bending (flexural) strength (Sekhon *et al.*, 2020), and rind penetration (Erndwein *et al.*, 2020) are indicators of its strength, thus can be associated with lodging resistance. But single measurement entities may not sufficiently define lodging resistance due to the complex and multivariate nature of lodging (Gangwar *et al.*, 2021, 2023). General methods to measure the biomechanical properties of stems are discussed and reviewed elsewhere (Shah *et al.*, 2017).

Macroscopic lodging mechanisms

Lodging is the state of permanent and irreversible displacement of the stems from their upright position (Pinthus, 1974). Macroscopically, stalk lodging generally arises from two distinct types of failure mechanisms: bending type and root lodging.

Bending lodging occurs when stems fail to resist bending pressure and is commonly observed in the upper internodes affected by strong winds and rain (Hirano *et al.*, 2017). Semi-dwarfism of cereals improved such lodging by lowering the ‘centre of gravity’ of the plant. Even if the introduction of the semi-dwarf trait has reduced lodging, it remains a challenge for high-yield cereals. Thus, improving lodging resistance in barley by the semi-dwarf trait alone is possible only up to a certain limit, beyond which other traits may be needed for enhancement (Hirano *et al.*, 2014). On the other hand, root lodging happens when the stem remains intact, and failure occurs at the root–soil anchorage due to the low bending moment of roots rather than the above-ground parts. In wheat, barley and oats, stem lodging is usually caused by one of the bottom two internodes buckling (Berry *et al.*, 2004), whereas in maize, it occurs primarily due to the stalk buckling below the ear and usually occurs in the middle of the third internode below the ear (Gou *et al.*, 2010; Robertson *et al.*, 2015). Stalk lodging of cereals is a severe challenge leading to significant grain yield and quality loss, as shown in Fig. 4, where corn yield decreased with an increase in stalk breakage. A study (Berry and Spink, 2012) reported in wheat that during the grain filling stage, lodging between an angle of 25 and 90° from the perpendicular could result in lodging-induced grain yield reduction of 20–61%. Annual yield losses of 5–35% in corn (Zuber and Kang, 1978) and 28–65% in barley (Berry, 2013) have been reported.

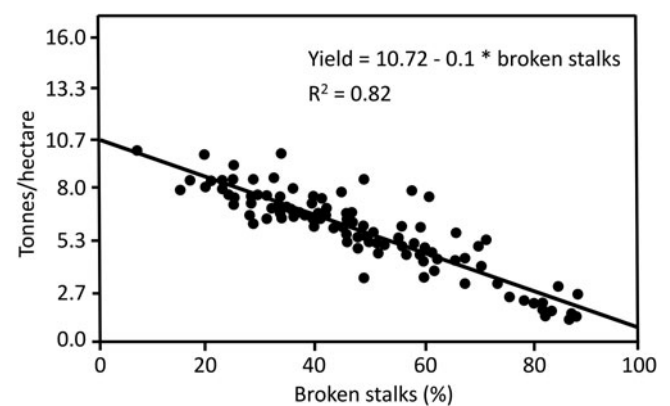


Figure 4. The effect of stalk breakage on grain yield of different corn hybrids. In 1993, stalk breakage in Nebraska ranged from 7 to 88% at 160 km/h wind speed, and grain yield was reduced 0.1 tonnes/hectare (1.5 bu/acre) for every 1% increase in stalk breakage, adapted from Elmore and Ferguson (1999).

Microscopic lodging mechanisms

Apart from the macroscopic failure mechanisms, what really happens at the microscopic scale during lodging is unknown and unexplored in cereals. The nanomechanical properties of various crop stalks (Wu *et al.*, 2010; Al-Zube *et al.*, 2018) confirm the elastic nature of stems. In general, failure of materials can be explained in terms of molecular phenomena in a stress–strain relationship. If plastic deformation causes overall structural failure, then failure leads to rupture of bonds at the molecular level. Upon loading, stresses are created and spread throughout the material, resulting in different extents of strain. The phenomena and phases of stalk lodging at the molecular and cellular level in situations below and beyond the proportionality limit of the strength of the stem remains unclear. It is unknown whether the phenomena below and above the proportionality limit of stress–strain of stems is related to the breaking, sliding and uncoiling of CW hydrogen and covalent (C–C and C–O) bonds.

Composition-lodging correlations

From a materials property perspective, the mechanical strength of materials is determined by both microstructure and chemical composition. The composition and interaction between individual biopolymers of CWs affects plant CW mechanical strength (Vogler *et al.*, 2015; Gangwar *et al.*, 2021).

Lignin for lodging resistance

The deposition of lignin significantly enhances the mechanical strength of CW (Wu *et al.*, 2017), thus has direct implication for stalk lodging resistance. There is a body of knowledge corroborating the contribution of lignin for lodging resistance. Gui *et al.* (2018) found that lodging resistance was significantly and positively correlated with lignin content in rice. Moreover, Liu *et al.* (2018) also studied 56 rice varieties with distinct CW compositions and reported that lignin was the predominant biopolymer that enhances lodging resistance. The authors also reported that lignin was directly correlated with stem CW thickness thereby improving rice lodging resistance by increasing the mechanical strength. On the other hand, a study (Heuschele *et al.*, 2020) showed no correlation between lodging and CW components at the nodes and internodes of wheat and barley.

An investigation (Muhammad *et al.*, 2020) correlated lignin content and monomer composition with the strength of wheat stems, and reported that greater strength was related to higher lignin content. Furthermore, significant variation in lignin monomer composition (H, S and G) was found between high and low strength stalks; specifically, reduction of S units by 27.6% was detected for the stronger stems. Concomitantly, H and G monomers were significantly increased respectively for the stronger stalks by 19.7 and 11.7%, causing a reduction of the S/G ratio by 16.8%. Another study by Li *et al.* (2015a, 2015b) demonstrated that lignin content positively impacted lodging resistance in rice, where the G monomer had a predominant impact on loading resistance over S and H monomers. Similarly, a study in maize (Manga-Robles *et al.*, 2021) revealed that H lignin and high ferulic acid content increased maize stalk strength and lodging resistance. The literature suggests that lodging susceptibility of stalks could be due to more than the bare content of CW polymers, rather it may also be conditioned by structural features of CWs. Although the mechanism underlying this correlation remains poorly understood and needs further elucidation, the positive

impact of G and H monomer content on lodging resistance could be associated with its inherent inter-unit linkage structures. G monomer-rich lignin is structurally more condensed than S lignin, due to a higher proportion of C–C linkages (β -5 and 5–5), which are absent in S lignin due to the unavailability and occupation of 5 position with the methoxyl (–OCH₃) group (Mottiar *et al.*, 2016). S lignin oxidizes more easily than G lignin due to the presence of more susceptible β -O-4 linkages. In contrast to this, G units can more easily polymerize than S units as it can form more diverse cross-linkages. This property might influence its role in lodging. However, in relation to lodging, further studies are required to tease out the relationship between mechanical strength, lignin monomer composition and condensed C–C lignin linkages such as β -5 and 5–5.

Ahmad *et al.* (2020) reported that elevated lignin content considerably enhanced the lodging resistance in the internodes of wheat. Activities of lignin biosynthesis enzymes such as phenylalanine ammonia-lyase (PAL), peroxidase (POD), tyrosine ammonia-lyase (TAL), 4-coumarate: CoA ligase (4CL) and cinnamyl alcohol dehydrogenase (CAD) all had a positive relationship with lignin content and lodging resistance at the basal internodes of maize (Kamran *et al.*, 2017; Ahmad *et al.*, 2018). Another study on winter wheat by Zheng *et al.* (2017) reported a positive significant correlation ($r = 0.97$) between lignin content and culm breaking strength; the high correlation could be due to test method limitation. Li *et al.* (2021) demonstrated that stalk lodging resistance, mechanical strength and lignin accumulation increased significantly with lignin synthesis-related enzyme activities (PAL, POD, 4CL and CAD). In the same report, lignin monomer composition (ratio of H, G and S) were reported to have significant contribution for lodging resistance. The enzymes PAL, TAL, CAD, POD and 4CL are key enzymes involved in the lignin biosynthesis pathway. This suggests that lignin biosynthesis enzyme activities dictate lignin content, lignin monomer composition (H, G and S ratios), lignin structure, CW strength and stalk strength which implies their contribution to enhancing the lodging resistance of stalks (Kamran *et al.*, 2018). Even though the correlation between lignin S/G ratio and stalk lodging of the cereal stalks is not extensively studied, some studies (Table 2) showed that cereal stalks with higher S/G ratio are found to be more susceptible to lodging. This could be attributed to the higher binding capacity of G (with branched structure) over S (with low DP) to cellulose.

Structural carbohydrates and lodging resistance

Cellulose content, MFA and CI are important structural parameters of fibres that can be related to the lodging property of cereal stalks. In the barley culm (live tissue), the cellulose content of a ‘non-brittle’ strain was significantly higher than that of ‘brittle’ strains (Kokubo *et al.*, 1989), suggesting the contribution of cellulose to the mechanical strength of the culm. Furthermore, the maximum bending stress, at which the culm was broken, was significantly and positively correlated with the cellulose content. A study by Tan *et al.* (2015) also supports the role of cellulose in enhancing the stem strength, where low cellulose-content barley displayed a significant reduction in stem strength. Sekhon *et al.* (2020) reported that mature maize stalk bending strength was strongly associated with lodging incidence, which implies the influence of cellulose on lodging resistance. A study of maize (at silking, grain filling and harvesting stages) also showed (Zhang *et al.*, 2019) that internode breaking resistance increases with cellulose content. Similarly, cellulose content was reported

Table 2. Summary of literature on correlation of cell wall compositions, cellulose crystallinity (CI), structural features, nutrient elements and mineral to the stalk lodging resistance of different cereal crops

| Cereal | Cultivar name | Region | Cel. | Lignin | Hemi. | TNC | CI | MFA | S/G | Others | Reference | |
|----------------------|-------------------------|-------------|----------------|---------------------|-------|------|------|------|------|---------------------------|-----------------------------------|-----------------------------------|
| Sorghum | Sorghum | US | NS | Pos. | NS | Pos. | - | - | - | - | Isbell (1992) | |
| | Bmr-12 | China | - | NS | - | - | - | - | - | - | Li <i>et al.</i> (2015a, 2015b) | |
| | BMR and others | US | - | NS | - | -- | - | - | - | - | Bean <i>et al.</i> (2013) | |
| | LR, LS | US | - | - | - | Pos. | - | - | - | Pos. (K) | Esechie <i>et al.</i> (1977) | |
| | Della, RG | US | Pos | Pos. | NS | - | - | - | - | - | Mengistie <i>et al.</i> (2022) | |
| | bm1-bm4 | US | - | Pos. | - | - | - | - | - | - | Pedersen <i>et al.</i> (2005) | |
| Oat | Brisasu and 7 others | Brazil | NS | NS | NS | - | - | - | - | - | Silveira <i>et al.</i> (2021) | |
| | LENA and others | China | Pos. | Pos. | Pos. | Pos | - | - | - | - | Zhang <i>et al.</i> (2020) | |
| | - | US | - | Pos. (on Internode) | - | - | - | - | - | - | Heuschele <i>et al.</i> (2020) | |
| Maize or corn | LI68, Q1261, others | China | NS | NS | NS | - | - | - | - | - | Guo <i>et al.</i> (2021) | |
| | Gibberella and Diplodia | US | Neg. | NS | - | - | - | - | - | Neg.(ash) | Zuber <i>et al.</i> (1957) | |
| | Exotic | Oman | - | Pos. | - | Pos. | - | - | - | NS (K) | Esechie <i>et al.</i> (2004) | |
| | ZD958 and XY335 | China | Pos. | Pos. | - | - | - | - | - | - | Yang <i>et al.</i> (2020) | |
| | - | Greek | NS | NS | NS | - | - | - | - | NS (N, K, Na) | Hondroyianni <i>et al.</i> (2000) | |
| | Dongnong 253 | China | Pos. | Pos. | Pos. | - | - | - | - | - | Fan HC <i>et al.</i> (2018b) | |
| | LR and LS | US | - | - | - | - | - | - | - | Neg. (ash & K) | Zuber and Loesch (1966) | |
| | Maize | | Pos. | Pos. | Pos. | Neg. | - | - | - | - | Wang <i>et al.</i> (2020) | |
| | B73 and 11 others | Spain | NS | Pos. (H lignin) | NS | - | - | - | - | Neg. | - | Manga-Robles <i>et al.</i> (2021) |
| | B14A/H95 and others | US | NS | NS | NS | - | - | - | - | - | - | Sekhon <i>et al.</i> (2020) |
| DH605 and XD20 | China | - | Pos. (H, G, S) | - | - | - | - | - | Neg. | Pos. (PAL, CAD, 4CL, POD) | Li <i>et al.</i> (2021) | |
| KongYu131 and others | China | NS | Pos. | NS | - | - | - | - | - | - | Liu <i>et al.</i> (2018) | |
| Rice | bp1 | | Pos. | - | Pos. | - | - | - | - | - | Zhang <i>et al.</i> (2021b) | |
| | fc17 | China | Neg. | Pos. | - | - | Neg | - | - | - | Li <i>et al.</i> (2018) | |
| | DSRAL | Philippines | - | NS | - | - | - | - | - | - | Marcelo <i>et al.</i> (2017) | |
| | Osfc16 | | Neg. | - | - | - | Neg. | - | - | - | Li <i>et al.</i> (2017) | |
| | Ben 250 and 4 others | China | - | - | - | - | - | Neg. | - | - | Huang <i>et al.</i> (2018) | |
| | S1 and Koshihikari | Japan | NS | NS | - | - | - | - | - | NS (Si), Pos. (Starch) | Ishimaru <i>et al.</i> (2007) | |
| | | China | - | NS | - | - | - | - | - | - | - | Zhao <i>et al.</i> (2019) |

| | | | | | | | | | | | | |
|--------|------------------------------------------------------|---------|------|-------------------------|------|---|------|---|------|-----------------------------|-------------------------------------|------------------------------------|
| | indica LY084 and japonica WYJ23 | | | | | | | | | | Pos. (Starch), NS (P, K), Neg. (Si) | |
| | OsSUS3 and others | China | Pos. | NS | Pos. | - | Neg. | - | - | - | | Fan <i>et al.</i> (2017) |
| Wheat | HC and WH | China | Pos. | Pos. (H, G contents) | Neg. | - | Pos. | - | Neg. | Pos. (Silica) | | Muhammad <i>et al.</i> (2020) |
| | Pastor and others | Mexico | Pos. | Pos. | - | - | - | - | - | NS(K) | | Tripathi <i>et al.</i> (2003) |
| | BN AK58 | China | - | - | - | - | Pos. | - | - | - | | Fan WX <i>et al.</i> (2012) |
| | HD-2329, Raj-4014 and C-306 | India | Pos. | Pos. | Pos. | - | - | - | - | Pos. (K, Ca, Mg, Silica) | | Bhagat <i>et al.</i> (2011) |
| | XNSX, CS | China | NS | NS | - | - | -- | - | - | - | | Kong <i>et al.</i> (2013) |
| | CK and PB | China | - | Pos. | - | - | - | - | - | Pos. (PAL, TAL, CAD, 4CL) | | Kamran <i>et al.</i> (2018) |
| | JM22 and SN16 | China | - | Pos. | - | - | - | - | - | Pos. (PAL, TAL, POD) | | Peng <i>et al.</i> (2014) |
| | Yangmai 20 | China | Pos. | Pos. | - | - | - | - | - | NS (Si), Pos. (WSC/N ratio) | | Zhang <i>et al.</i> (2017a, 2017b) |
| Millet | Yugu 18 and others | China | Pos. | NS | - | - | - | - | - | - | | Tian <i>et al.</i> (2015) |
| | FC1 (<i>Paspalum scrobiculatum</i> L.) | India | Pos. | Pos. | Pos. | - | - | - | - | - | | Sreeja <i>et al.</i> (2016) |
| Barley | Astor, Scarlett and Jaran | Croatia | - | Pos. | - | - | - | - | - | - | | Begović <i>et al.</i> (2018) |
| | Brittle (<i>Hordeum vulgare</i> L.) and non-brittle | Japan | Pos. | - | NS | - | - | - | - | - | | Kokubo <i>et al.</i> (1989) |
| | T1, S1 and others | China | - | Pos. (H, G, S contents) | - | - | - | - | - | - | | Yu <i>et al.</i> (2021) |
| | Kunlun14 and others | China | - | Pos. | - | - | - | - | - | Pos. (TAL, PAL, CAD, 4CL) | | Wang <i>et al.</i> (2019) |

The correlations are significantly positive (Pos.), significantly negative (Neg.), Not significant (NS), and uninvestigated (-) to lodging resistance.

H, G and S are respectively *p*-hydroxyphenyl, guaiacyl and syringyl.; Cel., cellulose content; Hemi., hemicellulose content; TNC, total non-structural carbohydrate; CI, crystallinity index; MFA, microfibril angle; PAL, phenylalanine ammonia-lyase; CAD, cinnamyl alcohol dehydrogenase; 4CL, 4-coumarate-CoA ligase; POD, peroxidase; TAL, tyrosine ammonia-lyase; WSC, water-soluble carbohydrate; N, nitrogen; Ca, calcium; K, potassium; Mg, magnesium; P, phosphorus; Na, sodium; Si, silicon.

to have a positive relationship with breaking strength of mature wheat stalks (Muhammad *et al.*, 2020). In contrast, the same study showed that hemicellulose content was reported to have a negative impact on the CW breaking strength. Kokubo *et al.* (1989) stressed the role of cellulose content for mechanical properties of CWs of barley stems (live tissues). However, the result failed to show if significant strength variations are associated with the structure of cellulose, such as CI and MFA, as low cellulose content in the culm might also indicate low levels of crystallinity or higher MFA.

Stalk architecture is reported to be a stronger predictor of stalk bending strength than chemical composition (Robertson *et al.*, 2022). Some results regarding the role of cellulose and hemicellulose are inconsistent and contradictory. Liu *et al.* (2018) reported that cellulose and hemicellulose contents were not correlated with lodging resistance in rice. A study (Guo *et al.*, 2021) also reported that none of the major CW structural carbohydrates (cellulose and hemicellulose) in maize has an impact on lodging. Likewise, among four genotypes of wheat studied by Kong *et al.* (2013), lodging resistance was not significantly correlated with cellulose contents in three of the cultivars, while other morphological characteristics such as stem width were reported to have significant impact on lodging. These inconsistent results might be due to the inherent genetic differences between the genotypes used in different studies.

Mutation of wild-type rice resulted in a significant reduction of cellulose DP and crystallinity, and an improved lodging resistance character (Li *et al.*, 2017). Cellulose synthesis and/or biosynthesis of glucose, the substrate for cellulose synthesis, could have been impaired during mutation. However, it is not clear how disordered orientation of cellulose fibrils improves lodging resistance, or possibly flexibility of stalks is more important than their stiffness for short stems like rice. Furthermore, the impact of crystallinity on lodging resistance is not clearly understood and extensively studied in cereal stalks. For example, research on rice (Li *et al.*, 2015a, 2015b) showed that lodging increased with the CI of cellulose fibres, but another study reported that crystallinity correlated positively with stem strength of wheat (Muhammad *et al.*, 2020). The results summarized in Table 2 show this gap. Generally, the association of mechanical strength and lodging resistance to cellulose structural features is not yet extensively elucidated and is open for further investigation.

Other contributing factors

The effect of minor chemical constituents on lodging resistance has been appraised. Esehie (1985) reported that lodging was negatively correlated with total non-structural carbohydrate (TNC), protein and potassium. However, TNC content could be an indication of the healthiness and vigour of the stalk rather than defining lodging resistance. Hasan *et al.* (1993) reported that silica content was found to be significantly higher in lodging-resistant than lodging-susceptible rice. The same study also showed that ash content was positively correlated to the lodging resistance of the rice stems. According to reports (Muhammad *et al.*, 2020), the presence of silicon has been found to improve the structural integrity of the CW matrix and strengthen the physical properties of stems, leading to a reduction in lodging. Additionally, silicon enhances the regulation of CAD, a crucial gene involved in lignin biosynthesis, resulting in an elevation of lignin content. Yet, the use of higher nitrogen fertilizer in rice and wheat significantly reduced the mechanical strength of stems and the lodging resistance by reducing lignin biosynthesis (Zhang *et al.*, 2017a, 2017b; Ahmad *et al.*, 2020). The presence

of excessive nitrogen has a substantial impact on the synthesis of H, G and S lignin monomers, as well as the overall lignin content in maize, which indicates a direct relation between nitrogen supply and the composition of lignin in crops (Li *et al.*, 2022). Higher nitrogen fertilizer decreased lignin deposition in the SCW of the sclerenchyma cells and vascular bundle cells compared to low nitrogen treatments (Zhang *et al.*, 2017a, 2017b). The rapid CW elongation due to fertilizer is believed to reduce the concentration of lignin while each cell contains the same amount. As nutrients are essential for the growth and development of plants, this finding could be an indication of how fertilizer nutrients are affecting the lignin and carbohydrate biosynthesis. Therefore, the impacts of nutrients on lodging are possibly related to their enhancement/inhibition of lignin and carbohydrate accumulation in the SCWs rather than their direct effect on lodging. In addition, the quality of stalks is also dependent on the nutrient levels and soil fertility.

The most marked and significant CW component related to lodging resistance is lignin. The results regarding the lignin content of the cereal stalks are mostly corroborating that lignin significantly enhanced lodging resistance. Especially in wheat and corn, the literature points to a significant positive correlation with lodging resistance, which is ascribed to its molecular and physiological function to stiffen the CW. The notion that cellulose content enhances lodging resistance of wheat is supported by the literature (Wang *et al.*, 2012; Kong *et al.*, 2013). Among the main CW components, the role of hemicellulose in lodging resistance remains least explored. Consequently, the correlation between hemicellulose contents and lodging resistance of stalks is still unclear as consistent correlations were not reported. Meanwhile, there are only a few trials aimed at correlating the strength of the stems with the CW composition in cereals like barley, millet and sorghum. The development of lodging-resistant cultivars requires a comprehensive understanding of the role of enzyme activities, which dictate the lignin and structural carbohydrate biosynthesis pathways. However, only a few studies related to lignin enzymatic activities are given in Table 2. The relationship of lodging with cellulose (structural features) and lignin (structural, compositional, linkage and enzymatic activities) in CWs remained unexplored. Nutrient and minerals contents in the stalk have been found to be associated with lodging resistance in certain cases; nevertheless, the results are inconsistent and sometimes even contradictory.

Huang *et al.* (2018) investigated the correlation of mechanical properties of rice stems to the cellulose MFA and found that tensile modulus and strength of rice stems decreased with an increase in MFA. Because the mechanical properties of stalks are indicators of lodging behaviour, the ultrastructural parameters of cellulose in the CW might be an important factor affecting the lodging resistance of cereal crops. However, as can be seen in Table 2, structural features of cellulose (MFA, CI) and lignin (monomer composition, polydispersity, S/G, linkages) are the least-investigated parameters affecting the mechanical strength of stalks. Thus, in connection with lodging, exploring the effect of molecular parameters of cellulose and structural features of lignin should be given attention. Practically, studying the effect of structural polymer interactions on lodging is quite challenging. However, molecular simulations and models developed for composite materials could help to reveal synergistic effects of lignin-cellulose-hemicellulose interactions.

A survey of 43 studies conducted in different regions on the relationship between lodging resistance and CW components

Table 3. Summary of investigated correlations between lodging resistance and cell wall composition across all crops in Table 2

| Relation | Cellulose (%) | Lignin (%) | Hemicellulose (%) |
|-----------------|---------------|------------|-------------------|
| Positive | 53.9 | 63.9 | 41.2 |
| Negative | 11.5 | 2.8 | 5.9 |
| Not significant | 34.6 | 33.3 | 52.9 |

Structural features microfibril angle, syringyl to guaiacyl ratio, crystallinity index and other contributing factors were not considered as these factors remain unstudied.

for different cereal crops are summarized in Table 2. The studies were selected entirely based on data availability. Regardless of the regions and crops, the significance (significantly positive, significantly negative and not significant) of CW components across all crops is summarized in Table 3. It was found that cellulose had a significant effect on lodging resistance in 53.9% of studies, no significant effect in 34.6% of studies and a negative effect in 11.5% of studies. Likewise, lignin had rates of 63.9, 33.3 and 2.8%. On the other hand, hemicellulose had 41.2, 52.9 and 5.9%, respectively, for positive, not significant and negative correlation. These studies show, in most cases, that there are correlations between CW components, mainly lignin, and lodging resistance.

Lodging and the biofuel digestibility paradigm

Agro-residues derived from cereal crop biomass are an alternative lignocellulosic feedstock for second generation biofuel production. The main digestibility impediment for cereal crop residues is the recalcitrance of CWs. Biomass recalcitrance to digestion and plant lodging are two complex traits that tightly associate with plant CW structure and morphology (Fan *et al.*, 2017). Recalcitrance of biomass in broader terms is defined as ‘*those features of biomass which disproportionately increase energy requirements in conversion processes, increase the cost and complexity of operations in the biorefinery, and/or reduce the recovery of biomass carbon into desired products*’ (McCann and Carpita, 2015). Biomass recalcitrance to enzymatic hydrolysis due to the heterogeneous and multi-scale structure of plant CWs is the major obstacle for efficient conversion of biomass to biofuels (Zoghalmi and Paës, 2019). Enhanced enzymatic digestibility on the other hand is a requirement for reducing the cost of pretreatment in biorefineries. Engineering and modifying CWs by altering its major constituents have been suggested as a strategy to overcome the enzymatic digestibility problem (Himmel *et al.*, 2007). This strategy is mainly focused on changing lignin content and structure, LCCs and cellulose-related properties. In line with this, lignin reduction and/or structural alteration have been shown to reduce biomass recalcitrance and improve CW digestibility (Li *et al.*, 2016). Furthermore, reduction of two features of cellulose (DP and crystallinity) in rice (Li *et al.*, 2017) through mutation has significantly increased enzymatic saccharification. However, a lignin- and cellulose-reduced crop will likely become susceptible to stalk lodging. Thus, the lodging-digestibility trade-off is a great challenge. As stem-based lodging is a crucial yield-limiting factor for cereal crops (Tian *et al.*, 2015), digestible stems might suffer from low yield. On the other hand, there is an increasing interest in the development of dual-purpose crops that have high grain yield with residues that are easily digestible by enzymes to biofuel (Townsend *et al.*, 2017). Crops grown for dual purpose

application should endow simultaneously high grain and stalk yields, low lodging susceptibility and high conversion efficiency (Gabbanelli *et al.*, 2021). But increased digestibility is characteristically associated with low structural strength and a tendency for lodging (Forell *et al.*, 2015), suggesting negative correlation between digestibility and lodging resistance. Thus, breeding to increase lodging resistance through greater stem/stalk stiffness could result in modified anatomical features that reduce the biomass digestibility (Townsend *et al.*, 2017). On the other hand, lignin content reduction has been strongly associated with reduction in the mechanical stiffness of crop stalks. The trade-off between lodging resistance and digestibility has been noted in the literature (Townsend *et al.*, 2017). Since susceptibility to lodging is highly related to grain yield and quality reduction (Berry *et al.*, 2004), the development of dual food-bioenergy crops with higher grain yield and digestibility remains a significant challenge.

Research and development efforts on genetic modification of CWs to reduce recalcitrance, lignin content, for optimized biofuels production, should focus on identifying key genomic factors altering the CWs without compromising strength of plant (Townsend *et al.*, 2017). Even though genetic modification of plant CWs can potentially reduce recalcitrance and enhance biomass saccharification, it could be challenging to sustain both reduced recalcitrance and enhanced lodging resistance traits at the same time (Berry *et al.*, 2004).

Summary and perspectives

The aim of this review was to evaluate the effect of CW composition on stalk lodging and highlight the key CW entities that contribute to the structural integrity of the stalk. The correlation between lodging resistance and CW composition showed inconsistencies across crops, which could be due to the inherent connections between stalk architecture, stalk chemistry and stalk strength. Lignin and cellulose were found to be the most investigated CW components. Across all the studies examined, 63.9% showed that lignin content of the cereal stalks is positively correlated with lodging resistance. On the other hand, only 53.9% of the studies reported a positive relation of cellulose with lodging resistance. The role of hemicellulose on lodging resistance remains little explored, of which 52.9% of the studies indicated no significant correlation with lodging. Studying the relation of CW chemistry with the morphological and anatomical features could increase our understanding towards lodging.

Developing lodging-resistant and high-yielding crops is challenging and therefore requires comprehensive understanding of the biochemical and physiological pathways behind the development of stronger plant phenotypes. Lodging-inducing factors (meteorological, biological, nutrient levels, morphological, anatomical, biochemical composition) and the interactions of all these factors make lodging a complex multi-scale phenomenon. Thus, lodging cannot simply be assayed by one single or few factors due to the complex and still unknown interactions between these parameters. Furthermore, the complex structure of the plant CW and the exact effects of its individual polymers on crop lodging resistance interact with plant morphology. Genetic analysis combined with compositional and environmental factors could reveal lodging traits. The material science concept ‘structure determines the properties’ can be applied to crop CWs to investigate the structure–property correlation of the stalks and develop governing models and principles. Hence for future progress, the integration and analysis of large amount of data using different machine learning algorithms

could assist in developing complex models and predicting vulnerability to lodging. Advanced imaging of CWs and understanding of structural features at the cellular level might be essential to comprehending the underlying molecular mechanisms of lodging. In addition, 'bottom-up' or 'top down' mechanisms integrated with CW structure and organization could help to enlighten the lodging phenomenon. As with other complex natural nanostructures, employing all technological advancements can be an effective way of understanding CW component interactions and their effect on lodging mechanisms.

Genetic modification of CWs has been proposed as a mechanism to improve biofuel digestibility of lignocellulosic biomasses. However, the exact effect on lodging resistance has not yet been studied. Thus, correlation of lodging resistance and biomass digestibility needs to be fully explored, otherwise it could lead to counterproductive results. In addition, the underlying mechanisms for the formation of strong CWs of cereals have not been widely studied. Although the effect of lignin content and cellulose on lodging has been extensively studied, the correlation of lodging with their structures, composition and linkages remains unexplored in the majority of the cereal crops. For example, S/G ratio, DP, CI and MFA are structural parameters that need to be investigated in parallel. The other limitation frequently observed in the literature is that identification of lodging-prone varieties relies on assessment of mechanical properties conducted in laboratories. Such assessments may not provide a clear picture, thus evaluation of lodging based on direct field observations is suggested.

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