

Lodging stress in cereal—effects and management: an overview

Adnan Noor Shah¹ · Mohsin Tanveer¹ · Atique ur Rehman² · Shakeel Ahmad Anjum³ · Javaid Iqbal⁴ · Riaz Ahmad³

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Abstract Uncertainty in climatic and weather conditions may result in lodging. Lodging is a most chronic constraint, which is causing tremendous yield reduction in crop plants; therefore, better understanding to control lodging-induced adversities or to enhance lodging resistance in cereals is imperative. In this review, we presented a contemporary synthesis of the existing data regarding the effects of lodging on growth and yield of cereals. Moreover, we highlighted key factors which trigger the detrimental effects of lodging in cereals. Numerous morphological, anatomical, and biochemical traits in plants that can influence lodging risk have also been discussed. These traits showed significant correlation with lodging resistance in cereals. At end, we tried to link our hypothetical concepts with previous evidences and provided a comprehensive summary of all the possible management approaches that can be used to further control lodging effects on cereals. The selection of a management option though is based on cereal type and genotype; nonetheless, different agronomic approaches including seeding rate, sowing time, tillage system, crop rotation, and fertilizer application help in reducing lodging risk in cereals.

Keywords Agronomic management · Cereals · Lodging · QTL · Yield

Introduction

Lodging is one of major problem in cereal production that causes remarkable loss in crop yield (Campbell and Casady 1969; Berry 2013). This problem causes tremendous reduction in grain yield and thus limits crop productivity either by interfering assimilation of dry matter or by impeding crop harvesting (Berry and Spink 2012). Lodging is defined as a process which induced displacement of shoots from their vertical standpoint. This results in leaning or completely horizontal lying of plants on ground (Jedel and Helm 1991; Rutto et al. 2013). Lodging is of two types: stem lodging and root lodging. Stem lodging is associated with buckling of stem on the ground when wind force strongly pushes stem to ground, whereas root lodging is termed as when root fails to maintain strong soil contact or has poor anchorage in soil (Berry et al. 2003). Root lodging becomes more severe in poorly drained soils and results in permanent displacement of cereals stem (Berry et al. 2004). Bending and/or breakage of stems due to lodging damages vascular bundles and resultantly causes problems in mechanical harvesting of the crop (Wang et al. 2006). Further, yield loss due to lodging depends on the duration and time of lodging. Lang et al. (2012) reported that in rice, lodging stress at grain filling stage resulted in 2.66 to 2.71% yield loss. They further observed that this decline was associated with reduction in seed setting rate and 1000-grain weight due to lodging. Similar results have also been observed in maize, where a reduction of 25% in grain yield was observed due to lodging (Sui-Kwong et al. 2011).

Lodging reduces grain yield and quality; however, its severity depends on many plant characteristics and environmental factors as well. Different plant characteristics govern plant

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✉ Mohsin Tanveer
Mohsin_1728@webmail.hzau.edu.cn

¹ College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, Hubei 430070, China

² Department of Agronomy, Bahauddin Zakariya University, Multan, Pakistan

³ Department of Agronomy, University of Agriculture, Faisalabad, Pakistan

⁴ Ghazi University, Dera Ghazi Khan, Punjab 32200, Pakistan

stature and architecture and contribute in improving lodging resistance (Berry et al. 2004). Plant height is one of most important morphological traits that plays a significant role in determining whether plant will be lodged or not (Wang et al. 2012). Nonetheless, some researchers reported that plant height is not primary factor for lodging; stem diameter and stem wall thickness also contribute in determining the susceptibility of plant towards lodging (Ma et al. 2002; Islam et al. 2007). Zuber et al. (1999) found that higher stem dry weight, stem diameter, and stem wall thickness increased bending strength. Furthermore, the rigidity of basal stems primarily depends on carbohydrate components such as soluble sugars, starch, cellulose, and lignin in stem. Generally, lignin or cellulose determines the physical strength because lower lignin or cellulose contents cause the culm to be vulnerable (Kokubo et al. 1989; Ookawa and Ishihara 1992). Significant positive correlation was found among panicle neck diameter, whole area of xylem, and cross-sectional area of neck (Xu et al. 2000).

Chemical composition such as cellulose, hemicellulose, carbohydrates, and lignin and silicon contents of stem also played a significant role in stem strength and rigidity of basal stem and thus affects lodging in cereals (Kong et al. 2013). Lignin is a vital structural component of secondary cell wall that not only is related to growth of plant but also provides strength to plants (Ma and Yamaji 2006). In wheat, a significant correlation was observed between stem strength and lignin contents in stem and found that the lower is the lignin accumulation, the higher will be the vulnerability towards lodging (Peng et al. 2014). This study further suggested that cultivars with higher lignin accumulation can further be used for breeding in order to develop lodging resistance cultivars. Furthermore, Berry et al. (2003) substantiated that lignin and hemicellulose contents together increased the stem strength and thus increase lodging resistant, while significant reduction in the accumulation of these chemicals resulted in higher lodging index. Cellulose also has a qualitative effect on stem strength and increases stem rigidity (Reddy and Yang 2005). In rice, higher accumulation of cellulose resulted in higher lodging resistance because of better stem strength against pushing force of wind (Yang et al. 2001). Moreover, in addition to cellulose, a greater accumulation of starch increases the bending strength and stiffness of culms (Kashiwagi et al. 2006). Similarly, silicon is another important structural component, also associated with physical strength of culms in cereals (Ma and Yamaji 2006). Some anatomical features of plants also contribute in lodging resistance. The number of larger and smaller vascular bundles was also found to affect the lodging susceptibility in wheat (Khanna 1991; Berry 2013). Furthermore, wider layer of sclerenchyma tissues, containing greater amount of cellulose and lignin, also reduced the risks of lodging incidence than cultivars with thin-layered mechanical tissues (Kong et al. 2013). All these plant characteristics contribute towards lodging; therefore, this article is

drafted to review recent knowledge about plant characteristics that are important in improving lodging resistance in cereals (Fig. 1). Further agronomic management approaches to reduce lodging in cereals have also been discussed in this paper.

Growth and yield response under lodging stress

Yield reduction in different cereals is reported by number of studies and physiological bases of yield reduction due to lodging (Table 1). Lodging can occur at any growth stage; however, lodging at reproductive stage, e.g., at anthesis or during grain filling stage, results in tremendous yield reduction, while less reduction has been reported when lodging occurs at early reproductive or vegetative growth stage (Piñera-Chavez et al. 2016). In wheat, yield reduction of different levels has been observed when lodging was imposed at ear emergence (31%), milking stage (25%), soft dough stage (20%), and hard dough stage (12%) (Weibel and Pendleton 1964). Crops which lodge before anthesis often have smaller yield losses than crops that lodge soon after anthesis (Fischer and Stapper 1987). This can be related to the bending of upper first or first two internodes to partially bending position. Further, lodging at early development stage has less influence on yield reduction as compared to late development stage (Berry et al. 2004). This could be because of the reason that at the early development stage, bent stem can be re-erected, while during the anthesis or grain filling stage, stem cannot be re-erected after lodging, thus resulting in higher yield loss (Berry et al. 2000). In a study, it was found that root lodging reduced soluble solids and juice brix value by 32% (Fedenko et al. 2015). A number of mechanisms could be related to lodging-induced effects on yield reduction such as reduced mineral translocation, and carbon assimilation during grain filling enhanced respiration and chlorosis, loss of chlorophyll contents due to shade effects, and greater susceptibility to pests and diseases (Foulkes et al. 2011). The most likely mechanism appears to be associated with reduced carbon assimilation (Zhu et al. 2006). A number of studies (Table 1) showed that lodging reduces cereal yield to different magnitudes, and such variation in yield reduction was due to experiment conditions, lodging magnitude, genotypic difference, and methods of yield loss estimation. The angle of lodging also influences the extent of yield reduction. Less yield reduction has been reported when angle of lodging was less than 90° (Berry et al. 2000). Further, in wheat, barley, and oat, lodging at 45° causes yield reduction ranged one fourth to one half of total yield loss incurred from lodging at 80° (Berry et al. 2004).

Grain quality can also be degraded due to lodging by affecting grain size and grain specific weight (Lang et al. 2012). Lodging causes bending of cereals to ground, which results in the higher susceptibility of grain to fungal attack (Foulkes et al. 2011). Hirano et al. (1970) also noted lodging-induced

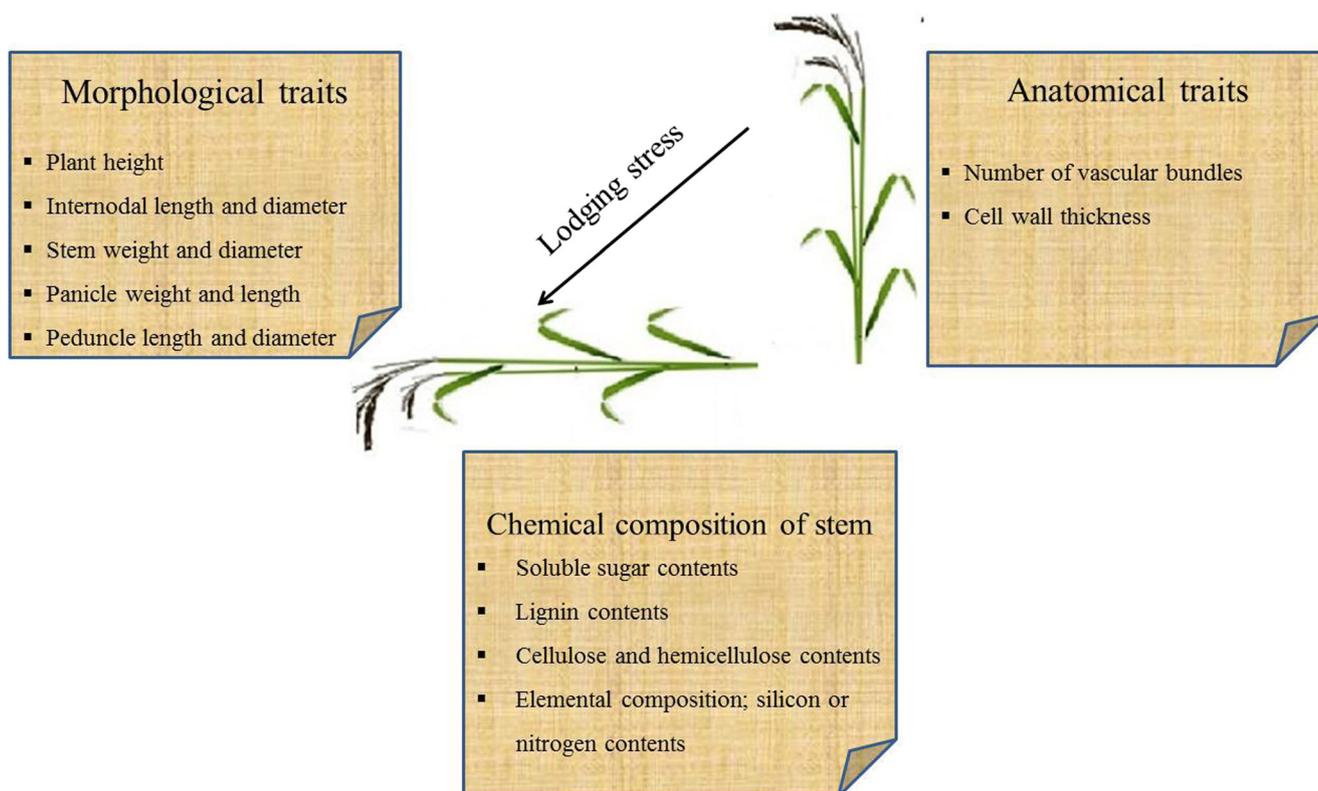


Fig. 1 Summary of different plant characteristics which are important in affecting lodging risk in cereals

reduction in milling quality in bread wheat, while in barley malting, value of barley grain was significantly affected by lodging. On other hand, Lang et al. (2012) observed a non-significant effect on brown rice rate but found a significant reduction in milling quality of rice. They also found that the earlier the lodging occurred, the higher the chalky grain rate and chalkiness degree. In another study, lower protein contents were found in rice grain due to lodging and suggested to be associated with accumulating speed of amyllum might be faster than that of protein (Zhang et al. 2002). It was further substantiated that with delay in lodging, amylose contents were decreased (Zhong and Cheng 2003), while peak viscosity, hot paste viscosity, and final viscosity were increased. Lodging results in the bending to cereal plants to ground surface; thus,

humic conditions around lodged plants increase the susceptibility of fungal attack. Nakajima et al. (2008) found a positive interaction between lodging and mycotoxin levels and observed only a fragmentary observation that when lodging occurred, deoxynivalenol production was very high irrespective of any fungicide treatment. This has been reported in wheat, oat, and barley with different fungal infections (González-Curbelo et al. 2012). Nakajima et al. (2008) examined deoxynivalenol and nivalenol contamination infected with the *Fusarium graminearum* in wheat, rice, and barley and found that these contamination indicators were higher in lodged plants as compared to non-lodged plants. Thus, lodging reduces the cereal grain yield and quality to greater extent.

Table 1 Reduction in the yield of cereal(s) due to lodging stress

Crop(s)	Yield losses (%)	Reference(s)
Wheat	12–80	Stapper and Fischer (1990); Mulder (1954); Acreche and Slafer (2011); Vera et al. (2012)
Rice	4.9–83.9	Briggs (1990); Pinthus (1973)
Barley	4–65	Jedel and Helm (1991); Sameri et al. (2009)
Oats	Up to 37–40	Pendleton (1954); Mulder (1954); Rajkumara (2008)
Maize	5–20	Flint-Garcia et al. (2003)

Plant traits and their role in lodging resistance

Plant height and internodal length Total plant height of a rice plant is an aggregate of panicle length and length of all the internodes above ground, called as components of plant height that determines the resistibility of plant against lodging (Berry et al. 2004; Kong et al. 2013). Cultivars with long plant height could be more susceptible to lodging, while those with shorter height plants sustained against lodging stress (Li et al. 2011). Okuno et al. (2014) concluded that the decrease in plant height resulted in higher resistance to lodging due to lower center of gravity and reduced upper fresh weight, which subsequently

minimize the risks of lodging. A number of studies found positive correlations between plant height, number of internodes, and internodal length and lodging index, which concluded that these traits are a significant plant character that influences the susceptibility of plant towards lodging (Table 2). Sarker and Shamsuddin (2007) indicated a negative correlation between the length of the first internode and the lodging sensitivity, which further suggested that longer internodes at base resulted in higher lodging index. They further reported that the internodal breaking strength and stem wall

thickness have a significant but negative correlation with lodging index. Some other studies also substantiated a positive effect of shorter internodes towards lodging resistance, especially the basal internode above the ground (Table 2).

Recent development of semi dwarf rice cultivar by the introduction of sd-1 gene resulted in improved lodging resistance (Spielmeyer et al. 2002). Reducing plant height with the sd-1 gene has decreased the effects of the upper part of the plant on the lower part, thereby improving resistance to lodging (Spielmeyer et al. 2002). On other hand, reduction in plant

Table 2 Plant characteristics correlated with lodging resistance in cereals

Trait (s)	Correlation with lodging resistance	Reference(s)
A. Morphological		
Plant height/culm length	Negatively	Verma et al. (2005); Zeid et al. (2011); Kashiwagi et al. (2005); Yao et al. (2011)
Basal internodal length	Negatively	Huang et al. (2006); Kelbert et al. (2004); Sameri et al. (2009)
Stem diameter/culm diameter and stem weight	Positively	Kashiwagi et al. (2008); Wang et al. (2006); Kaack et al. (2003)
Internodal diameter	Positively	Zuber et al. (1999); Peng et al. (2014); Islam et al. (2007); Yao et al. (2011)
Stem/internode wall thickness	Positively	Tripathi et al. (2003); Wang et al. (2006); Peng et al. (2014); Hai et al. (2005); Chuanren et al. (2004); Yao et al. (2011)
Panicle/ear/spike (weight or size and type)	Negatively	Zuber et al. (1999); Baker et al. (1998); Tripathi et al. (2003); Ma and Yamaji (2006)
Peduncle diameter		Tripathi et al. (2003)
Peduncle length	Negatively	Zeid et al. (2011); Yao et al. (2011)
Stem weight per unit length	Positively (increase pushing resistance)	Kashiwagi et al. (2008); Yao et al. (2011); Kong et al. (2013)
B. Anatomical features		
Number of vascular bundles larger or smaller	Positively	Ishimaru et al. (2008); Chuanren et al. (2004)
Mechanical tissues	Positively	Ishimaru et al. (2008); Dunn and Briggs (1989); Kong et al. (2013)
C. Biochemical features		
Lignin contents	Positively	Okuno et al. (2014); Tanaka et al. (2003); Kong et al. (2013); Ma and Yamaji (2006); Jones et al. (2001)
Cellulose contents and hemicellulose	Positively	Jones et al. (2001); Tanaka et al. (2003); Kong et al. (2013); Ookawa and Ishihara (1992)
Sugar contents (carbohydrates)	Positively	Kashiwagi and Ishimaru (2004)
Starch contents	Positively (increases the bending strength and stiffness of culms)	Kashiwagi and Ishimaru (2004); Kashiwagi et al. (2006); Ishimaru et al. (2008)
Si content in stem	Positively (increase physical stem strength)	Zhang et al. (2010); Fallah (2008); Mobasser et al. (2008); Ma and Yamaji (2006).

height was not a suitable option, as recent studies suggested that shorter plants (short culm length) may result in reduced canopy photosynthesis and biomass production and therefore affects grain yield (Stewart et al. 2003; Islam et al. 2007). It was, however, noted that optimum plant height for maximum photosynthetic capacity within a vegetative canopy could be a productive strategy to minimize lodging, with concomitant sustaining of grain yield (Flintham et al. 1997). Additionally, some studies indicated that Baviacora 92 is a wheat cultivar with single dwarfing gene and is much taller than many other cultivars with two dwarfing genes and yet lodges less (Sayre et al. 1997). In barley, it was found that cultivars with shorter stature showed less lodging as compared to long statured barley cultivars; therefore, short culm barley produced higher grain yield (Tamm 2003).

Culm diameter, stem wall thickness, and panicle weight

Culm diameter and stem wall thickness determine the stem breaking strength of stem. Stem diameter is usually higher at basal part of stem and declines towards the upper part of plant (Li et al. 2011). It has been reported that the more is the culm diameter and the higher is the stem wall thickness, the less will be the lodging susceptibility (Islam et al. 2007). Stem diameter and stem strength are highly associated with leaf sheath length, length of last internode from ground, and cross-sectional area of stem (Berry et al. 2004). These factors contribute significantly in reducing lodging-induced stem buckling. Chang (1964) observed that leaf sheaths contribute 30 to 60% in breaking strength of stem. Zuber et al. (1999) substantiated that stem diameter and length of internodes were directly correlated with lodging resistance. They further reported that thicker and heavier culms resulted in better lodging resistance (Zuber et al. 1999). Ookawa and Ishihara (1992) further observed that presence of leaf sheath covering doubled breaking strength while along with leaf sheath larger cross-sectional area of basal internode increased the breaking strength by threefold. Culm thickness was also found to be positively correlated with pushing resistance observed in the culm of rice plants (Terashima and Ogata 1994); however, a negative correlation of stem diameter with lodging resistance was observed in barley and oat (Dunn and Briggs 1989). Nonetheless, numerous studies showed a positive correlation between stem diameter and lodging resistance (Kashiwagi and Ishimaru 2004; Sarker and Shamsuddin 2007). Recent work has reported that increasing stem diameter and thickening of stem wall could be crucial features, which result in reducing lodging and improving lodging resistance (Xiao et al. 2002; Dong et al. 2003). Therefore, it is suggested that the selection for lodging-resistant cultivars should emphasize larger stem diameter and wall thickness of basal internodes (Tripathi et al. 2003). Culm wall thickness of the second basal internode resulted from the contribution of both additive and non-additive gene effects with a potential for transgressive

segregation in the F2 generation (Wang et al. 1998). Culm diameter of the second basal internode may result from additive and dominant genes, and the degree of dominance is of partial dominance (Cui et al. 2002).

Generally, it is believed that cereal plants with large panicle or spike size and higher panicle weight and number of grains per panicle/spike may be lodged easily as compared to otherwise. Heavier panicles may increase the bending moment of the basal internodes due to slender and longer top internodes (Ma et al. 2002). Lodging sensitivity is reduced by short panicle neck with lowered center of gravity, hence resulting in panicle erectness (Berry et al. 2004). Plants with erect and semi erect panicles, as well as short panicles, resist lodging more efficiently than the cultivars with curved panicle types (Xu et al. 2000). Lowering position of panicle, increased diameter, and smaller angle of neck-panicle also reduce the lodging susceptibility (Xu et al. 2000). Though, positive correlation of neck-panicle width with number of neck-panicle vascular bundles was observed (Xu et al. 2000), neck-panicle angle less than 40° is regarded as erect-type panicle (Yan et al. 2007). Lodging sensitivity is reduced by short panicle neck with lowered center of gravity, hence resulting in panicle erectness (Alizadeh et al. 2011).

Beside numerous morphological traits of plants, some important biochemical characters such as cellulose, hemicellulose, lignin, and soluble sugar contents are also important and contribute significantly in lodging resistance. Additionally, stem physical strength also depends on its chemical and biochemical components. The accretion of cellulose, hemicellulose, and lignin improves culm wall thickening and flexibility enhancement. Generally, stem physical strength depends on cellulose, and lignin contents and plant stems with lower lignin or cellulose contents resulted in brittleness of culm (Jones et al. 2001; Tanaka et al. 2003). Li et al. (2009) found that secondary cell wall thickness and culm strength in a rice mutant (*brittle culm1*) were explained by the higher accumulation of lignin, cellulose, and hemicellulose. Cellulose also has qualitative characteristics that relate to the strength of cellulose fibers, such as crystallinity (Reddy and Yang 2005). Further, expression analysis of COMT gene in wheat culm revealed that this gene is involved in lignin biosynthesis and higher lignin accumulation was observed in the developing stem during lodging (Ma et al. 2002). Lignin is an integral constituent that is important for plant health and function (Chen et al. 2011). The lignification in cell wall can increase cell wall stability and can improve physical strength of stem (Chen et al. 2011). Zhang et al. (2010) found that Si application can significantly increase the lignin contents in sclerenchyma cells and enhance cellulose contents and thus reduce lodging index in rice.

Starch and soluble sugars are non-constituent component in culm that play a considerable role in physical strength of culm (Arai-Sanoh et al. 2011). During comparing different maize varieties, Wang and Hu (1991) found that lodging

resistance corn varieties were due to higher accumulation of carbohydrates and lignin in stem as compared to lodging-susceptible varieties. Nonetheless, a non-significant relation was also observed between starch contents in stem and lodging resistance (Zhang et al. 2009). In rice, higher accumulation of carbohydrate contents in culm resulted in reduced lodging index (Yang et al. 2001), and this higher accumulation of carbohydrates increased stiffness and bending strength of rice culm (Kashiwagi et al. 2006). Ishimaru et al. (2001) referred that rice plants with high starch content in culms were more easily restored to a normal growth condition when culms were curved by strong winds. Kashiwagi and Ishimaru (2004) have shown that locus for pushing resistance in the lower part of the rice plant (*prl5*) increases the weight of the lower stem due to higher carbohydrate contents at maturity and consequently improved lodging resistance. Conclusively, different plant traits play a different role in controlling lodging risk in cereals. These traits should be considered in future research to develop lodging-resistant varieties.

Agronomic management of lodging stress in cereals

Sowing time and seeding rate Different agronomic approaches such as sowing time and plant population have very significant influence on lodging intensity in cereals (Berry 2013). Delayed sowing results in reduced lodging index; for instance, in wheat, it has been found that delayed sowing of wheat resulted in reduced lodging (Webster and Jackson 1993). Further, lodging index of barley plants was reduced to a significant level due to delayed sowing (Pinthus 1973). Berry et al. (2000) found that lodging index of wheat can be increased if sown 6 weeks earlier, and this was because of a significant increase in base bending moment of the shoot (30% higher) and declined stem strength (50%). Earlier sowing also resulted in higher tillering in wheat (Baloch et al. 2010), rice, oat (Jehangir et al. 2013), and barley (Huang et al. 2011). Nonetheless, earlier sowing may result in longer internodes with thin stem wall and shorter stem diameter due to higher tillering resulting in higher base bending moment. Stapper and Fischer (1990) reported that longer stems gave rise to higher bending movement. Additionally, higher number of tillers per unit area also causes weak and narrow culm stem with thinner cell wall. The mechanism behind this suggested that this might be due to a higher number of tiller per unit area competing for light, and photosynthetic assimilates during early shoot growth, which ultimately decreases the dry matter accumulation per unit length of the lower internodes (Baker et al. 1998; Berry et al. 2000). Although early sowing resulted in better stand establishment due to better anchorage in soil, stems that become weak associated with shading effect, triggered by the low ratio of red light to far-red light in the denser canopy of the early sown crops, may play a part.

Besides sowing time, seeding rate and sowing depth also influence the susceptibility of cereal plant towards lodging. Easson et al. (1993) found that increasing seed rate per unit area resulted in higher lodging index. This was because of attainment of less fresh weight and internodes with smaller diameters by lodged plants. Further, Berry et al. (2000) found that reducing plant population of wheat per unit area caused a large reduction in the lodging risk of wheat. Berry et al. (2000) found that there was 50% higher anchorage and 15% higher base stem strength of the population of 200 plants m^{-2} as compared to 400 plants m^{-2} . This was associated with better stem development and strong cell wall of stem. The anchorage of plants in soil depends on numerous plant morphological characteristics of roots such as number of roots per plant, root thickness, root width, and rooting depth. Sparsely populated plants have higher number of tillers with up to three crown roots, which helped to anchor in soil properly. Therefore, it should be of no surprise that establishing fewer plants results in plants with more crown roots. Thicker and stronger roots may be caused by the absence of a strong shade avoidance response by the plant, which stimulates a greater proportion of assimilate to be partitioned to the roots. The explanation for stronger stems on sparsely populated plants is thought to be the same as for the effect of delayed sowing discussed previously. Conclusively, sowing time and plant population played a crucial role in lodging of cereal; therefore, this should be considered while studying further aspects of lodging in cereals.

Tillage system and irrigation methods and mixed crop cultivation

Other agronomic practices also have influence on lodging index in cereals. Though limited information is available, we found very useful information from previous findings. Berry et al. (2000) found that minimum number of cultivation for seed bed preparation reduced lodging significantly in higher proportion as compared to traditional methods of cultivation. This section also investigates whether tillage caused lodging directly or indirectly. Direct effect of tillage could be associated with reducing the soil strength by continuous and intensive soil stirring and pulverizing; however, indirect effects could be related to reduced root and shoot growth in response to poor soil physical properties or formation of compacted soil (Hemmat and Taki 2003). Although direct seeding in soil increases soil strength, magnitude of increase varies and also depends on soil type; e.g., Schjønning and Rasmussen (2000) reported that direct seeding/drilling increased the shear strength of the top 8-cm silt loam soil at plant emergence by 18 to 49%, but only small increases were observed on sandy soils. Continuous tillage results in less surface roughness and leads to reduced depression storage capacity and surface

ponding, associated with increase in soil surface area for evaporation, while minimum retains a layer of stubbles on soil surface acting as mulch, thus preventing evaporation losses and conserving moisture in soil. This resultantly reduced the lodging by providing better root anchorage. Crook and Ennos (1995) also found that compaction of seed beds did not affect the length, number, and bending strength of crown roots belonging to wheat. Soil compaction may reduce the plant height, stem diameter, and plant anchorage as a result of reduced nutrient uptake and less porosity (Canbolat et al. 2006). Furthermore, it also features a declined length in primary and lateral roots, leaf area, absorption of nutrients, and grain crop yield (Zhao et al. 2007). It therefore seems likely that observations for direct drilling or minimal cultivations to reduce lodging are mainly caused directly by increased soil strength resulting from greater bulk density. The common observations for high bulk density to impede root extension and increase root thickness (Wilson et al. 1977; Materechera et al. 1991) appear to be restricted to sections of the cereal root system that play a little part in anchorage, namely, the seminal roots or the distal sections of the crown roots. Additionally, Berry et al. (2000) substantiated that soil rolling is another important approach that can reduce the risk of lodging. They further found that in spring, soil rolling resulted in 25% increased shear strength of top soil (5 cm), which remained until harvest and reduced lodging.

Irrigation methods also influence the lodging in cereals. For instance, sprinkler irrigation can promote lodging if applied at early vegetative stage. A preliminary study by Robins and Domingo (1962) reported that applying water by sprinkler irrigation promoted lodging when applied at early vegetative growth stage with higher plants, and they also suggested that irrigation by sprinkler irrigation should be withheld until plant reached the booting stage. As at this stage, roots can be fully grown and can provide better anchorage. Further, flood irrigation can make the soil soft enough that roots reduce their anchorage in soil. Thus, excessive wind speed may insert high pressure and cause lodging in cereals.

Mixed cultivation of cereals with other crops can be a useful approach to reduce lodging potential. The blending of different crops results in reducing the effect of wind to avoid lodging. Larkin et al. (2012) found that there was 30–50% reduction in lodging of barley when sown mixed with wheat. The benefit of such blend can be attributed to the support provided by secondary crop and also to synergistic effect of varieties different in growth habit, canopy architecture, and maturity time. Such practices can only be practiced possibly in feed grain field or to avoid lodging index of susceptible forage cereals. This practice may not give satisfactory result if employed in area where cereals are grown for grains instead of forage purpose. Crop rotation can also reduce lodging in cereals indirectly. Numerous studies reported the benefits of crop rotation on soil health, crop growth, soil productivity, and environmental sustainability

(Larkin et al. 2012). It is well documented that crop rotation reduced disease incidence; e.g., a close sequence of wheat and other cereals on which the disease can survive will promote its incidence (Palti 1981). Green manuring and under plowing of the stubble have been reported to reduce eyespot-induced lodging (Watson et al. 2002). Likewise, improving soil fertility due to the inclusion of leguminous crops in crop rotation increases the availability of numerous nutrients particularly nitrogen (Bagayoko et al. 2000). Thus, lodging of barley was found to be more frequent and severe following root crops, alfalfa, or well-fertilized grass than after a grain crop (Widdowson and Penny 1970).

Plant nutrition and application of growth regulators chemicals

Application of nitrogen and plant growth regulators also found to be effective in reducing lodging index of cereals; however, their concentration is of concern. Higher dose of N increased the vegetative growth, which resulted in higher lodging index and caused a significant increase in different morphological characters of plants that contribute towards lodging. However, more pronounced effects of N are well observed in shoot growth as compared to root growth and consequently increased shoot to root ratio; thus, it is highly susceptible to lodging. It is well documented that N fertilizer application at higher dose increased plant height and gravity center height while reduced culm diameter associated with reduced culm wall thickness, thus resulting in higher lodging index in rice plants (Yang et al. 2009). Furthermore, N also influences the development of basal internode by increasing upper plant canopy development and thus reduces light interception and absorption. Higher development of upper canopy reduced basal internode development, and less light interception resulted in the occurrence of eyespot disease, which also resulted in lodging (Wei et al. 2008). Elongation of the lower internodes was entirely due to shading, whereas reductions in stem diameter, wall width, and lignification resulted from a combination of shading and a direct nitrogen effect. Zhang et al. (2014) found that the lodging index of rice was increased from 62.7 to 91.5% with increasing N from 0 to 300 kg N per hectare. They found higher lodging index in this cultivar was because of higher plant height, dry matter of upper three leaves, and fresh weight and dry weight per unit length of culm in response to higher N application. Likewise, according to Huo et al. (2003), excessive N application increased plant height resulting in higher lodging index. In wheat, higher N reduced physical strength of culm because of reduced culm diameter, culm wall thickness, lignin content, cellulose content, and C/N ratio of basal culm (Wang et al. 2012). Excessive amount of N always reduced breaking strength due to reduced culm dry weight, culm strength, leaf sheath

in basal internodes, culm wall thickness, and culm diameter in rice (Zhang et al. 2014), wheat (Berry et al. 2000), barley Tamm (2003), and oats and rye (Mulder 1954). In another experiment, reduced breaking strength and higher lodging index in wheat under higher N were associated with a tremendous increase in the length of the first and second basal internodes and reduced cell wall cellulose contents and lignin contents in culm (Wei et al. 2008).

In addition to N amount, timing of N application also influences lodging index of cereals. For instance, a significant increase in lodging index was observed in wheat when N was applied before the onset of culm elongation (Baker et al. 1998) while no significant effect after anthesis (Webster and Jackson 1993). In oat, it was found that N application before stem elongation led to reduced lodging as compared to application after stem elongation (Berry et al. 2000). Berry et al. (2000) showed that high levels of residual nitrogen reduced the strength of the stem wall material, but only for early sown crops. These findings were supported by Crook and Ennos (1995) who showed that a component of material strength, Young's modulus, was also reduced by more fertilizer in spring. The cause of these effects may be due to that higher N reduced lignin contents in sclerenchyma tissue with concomitant decline in sclerenchyma cell wall thickness. In another earlier published article, it was documented that although N-deficient plants had thin stem wall and thin basal internodes, these plants were found with the lowest lodging risk as compared to adequately supplied N plants (Mulder 1954). The author also showed that in oat, higher N application limits the development of crown roots and these roots showed no lignin accumulation under epidermis cells. Thus, higher N besides increasing above ground plant growth also shortens root penetration and reduces plant anchorage in soil. This suggested that N is very important in determining the lodging risk of plants and proper management should be instigated while applying N in lodging-prone areas.

Though phosphorus (P) and potassium (K) have less pronounced effect, they contribute towards lodging resistance to some extent. Similarly, the deficiency of phosphorus (P) causes a reduction of culm wall thickness and physical strength, but adequate P fertilization causes lodging as a result of the increased weight and density of the plants (Mulder 1954). An increased application of P has been reported to increase lodging in wheat and in oat (Mulder 1954). Further, Mulder (1954) also found that P did not increase lodging in wheat on P-deficient soil and compared to oat. P reduces culm breaking strength and stronger roots and thus decreases lodging; nonetheless, P in excessive amount decreased stem strength by increasing length and diameter of internodes at the base of wheat plants. Additionally, P also interferes with N contents and thus also influences lodging in cereals. Mulder (1954) found that P excessiveness resulted in higher N contents and reduced lignin contents in wheat culm with concomitant reduction in ratio of

mechanical tissues to proteinaceous ones. This therefore suggested that P played a significant role in lodging and proper management can avoid lodging in cereals. Potassium (K) deficiency causes a reduction of length, diameter, and wall thickness of culms, and plants show more brittle culms than under adequate K fertilization, but in a number of cases, adequate K fertilization causes more lodging than K deficiency (Mulder 1954). Zhang et al. (2010) found a significant and positive correlation between total K contents in culm and physical strength, which clearly indicated the role of K in plant physical strength. Bhiah et al. (2010) found K application significantly reduced lodging index in rice. They also found that rice plant that received less amount of K exhibited poor root proliferation and thin cell walls as compared to rice plants supplied by sufficient amount of K. This is because K can promote lignification in thick-walled cells and thicken collenchyma cells and improve keratinocyte growth and increase cellulose content (Zhang et al. 2010). Similarly, a study also showed that inadequacy of K in soil resulted in reduced stem strength and diameter decreased tiller number and plant height and growth, and thus increased lodging (Crook and Ennos 1995). However, application of K or P in higher amount has no further effects on lodging either increase or decrease. For instance, Mulder (1954) observed that in plants in K-deficient soil that received K at 100 kg K ha^{-1} , lodging was reduced and extra application of 200 kg K ha^{-1} showed no further effects regarding lodging. In another study, no consistent reduction in lodging was observed in oat after application of K to plots, which had already been supplied with adequate K (Berry et al. 2004). Pinthus (1973) reported that applying K in excess amount increased stem wall thickness and strength. This therefore looks likely that excessive K application on K-deficient soils will decrease lodging index and lodging risk.

Silicon (Si) is an important trace element that plays a crucial role in array of plant processes and contributes in plant structural composition at cellular level. Si contents can be accumulated up to 10% in shoot on dry weight basis in rice (Savant et al. 1997). Rice accumulated Si in the form of silicic acid or amorphous silica in very specialized cells in cell wall (Kaufman et al. 1969; Neethirajan et al. 2009). Recently, it has been found in rice that Si also is bound to wall matrix molecules of plant parts especially culm and this may enhance the stability and integrity of cell walls (He et al. 2013). Si deposition in cereals in the form silica gel may stiffen the culms and leaves. This is further supported by He et al. (2015) who observed that in the presence of Si, Young's modulus of the cell wall was much higher as compared to rice plants that received no Si, and the difference became small after removal of pectin and hemicelluloses. This has clearly explicated the role of Si in protecting the cereal plants as a mechanical barrier by hardening the cell walls (Hattori et al. 2003).

Si, being an important biological element, not only increases plant physical strength but also plays an important role

in numerous physiological function, thus increasing the ability of plant to resist against lodging. In sorghum, Hattori et al. (2005) found that Si significantly increased plant dry matter and nutrient assimilation rate and photosynthesis rate, thus resulting in decreased lodging index.

Si in the presence of other nutrients such N or K also improves lodging resistance by contributing in a number of anatomical structures and chemical compositions of cereals. It was reported that even at higher N level, Si imparted more strength to culm and increased the breaking force by increasing the number of silicated cells and Si content in stalks even at higher levels of nitrogen (Singh et al. 2005). Silica deposited in these plant sections also contributes to an increase in the mechanical strength of a culm. A sufficient supply of Si has an effect on haulm stability and lodging susceptibility (Idris et al. 1975). An adequate availability of Si in soil has positive effects on the culm stability and decreases the lodging risk for rice plants (Fallah 2012). Additionally, Si also improves leaf angle and makes it more erect to harvest more light and to reduce shading effect on lowering leaves. Kim et al. (2002) found that Si accretion in rice increased the thickness of epidermal cell wall. Si increases culm strength by increasing lignification and silicification in cells and cellulose contents, thickening of collenchyma cells, and improving keratinocyte growth (Zhang et al. 2010). Liang et al. (1993) reported that after application of silicon fertilizer in rice, the culm diameter was bigger, mechanical strength was increased, and the lodging resistance was improved. This can be inferred that Si is an important element in order to improve lodging resistance. It enhances mechanical strength of culm by strengthening and thickening numerous anatomical structures in culm and leaves of cereals. Therefore, there is a great significance for applying Si fertilizer to improve lodging resistance.

Plant growth regulators

Plant growth regulators are chemically synthetic compounds that are used to reduce plant height and other lodging-associated plant traits. These regulators reduced cell division and also cell elongation particularly in culms of cereals. Further, the magnitude and nature of lodging can be modified by applying growth regulators or inhibitors. These plant growth regulators are classified on the basis of their specific function. Some regulators are employed to inhibit gibberellic acid biosynthesis pathway, while some are applied to produce more ethylene. Ethephon is the most commonly used ethylene-releasing compound used on cereals (Rademacher 2000). Chlormequat chloride, mepiquat chloride, and trinexapac-ethyl block gibberellic acid biosynthesis and thus help in controlling lodging in cereals. Herbert (1982) showed that applying chlormequat and choline chloride to winter

wheat at the beginning of stem extension could reduce the percentage area lodged from about 73 to less than 8%. Application of growth inhibitors, like ethephon (2-chloroethylphosphonic acid) or chlormequat chloride (CCC), was reported to be useful in decreasing plant height and subsequently reducing lodging (Crook and Ennos 1995). However, in another study, it was observed that ethephon did not provide complete lodging control but increased grain yields by 5–21% depending upon the genotype and lodging severity (Webster and Jackson 1993). Further, Nafziger et al. (1986) found 6% wheat grain yield increment due to the application of ethephon (0.56 kg ha^{-1}). Ethephon is suggested to be involved in thickening the stem, which ultimately controlled the lodging. Recently, Tripathi et al. (2003) examined ethephon application and lodging index in spring wheat and found that ethephon application increased stem wall thickness of first, second, and third internodes by 4.3, 6.3, and 8.1%, respectively, as compared to control.

Uniconazole is another plant growth retardant that can inhibit stem and coleoptile elongation and thus can decrease plant height. Uniconazole obstructs brassinosteroid and gibberellin biosynthesis by attaching to cytochrome P450 monooxygenase (Asahina et al. 2002). Further, Sellmer et al. (2001) found that uniconazole plays a significant role in increasing basal diameter and reducing plant height and thus can reduce lodging. In maize, uniconazole reduced the plant height by decreasing endogenous gibberellin, which reduced cell length, even number of nodes was not reduced (Schlutenhofer et al. 2011). In common buckwheat, similar results have also been observed and reported that uniconazole reduced the plant height, culm fresh weight, lodging percentage, and lodging index (Wang et al. 2015).

Paclobutrazol and chlormequat are another growth regulators that can be used to avoid plant lodging. Peng et al. (2014) found that treatment with paclobutrazol considerably reduced plant height and also the length of second basal internode. Moreover, they also found that paclobutrazol reduced lodging index by increasing the number of plant traits that play an important role in lodging avoidance. A significant increase in culm diameter, culm wall thickness, and lignin accumulation in the second internode was also observed due to application of paclobutrazol (Peng et al. 2014). Likewise, chlormequat also reduces the material strength of culm and Young's modulus of wheat (Crook and Ennos 1995; Berry et al. 2000). In winter barley, combined application of chlormequat and ethephon significantly reduced the lodging index. On the other hand, Olumekun (1996) found that chlormequat applied to winter wheat had no effect on the content of cellulose, hemicellulose, and lignin in the stem base, while Toyota et al. (2010) found that chlormequat application significantly shortened the spike (4.5%), culm (12.6%), and spike plus culm length (11.9%) compared with the controls. Toyota et al. (2010) reported improvement of

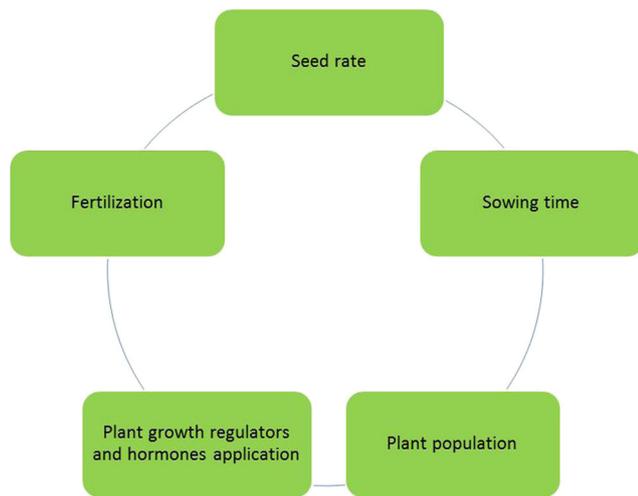


Fig. 2 Summary of agronomy practices that affect lodging in cereals

light interception by chlormequat application due to short, erect leaves.

Clark and Fedak (1977) found that chlormequat application reduced the plant height of barley, wheat, and oat by 2.4–17.8, 3.3–14.5, and 26.2–34.4%; however, the rate of reduction was cultivar specific. The mechanism behind this was suggested by Linser (1968), who reported that chlormequat inhibits biosynthesis of gibberellic acid in plants, thus responsible for increases in culm length during the time of shoot extension. Chlormequat applications therefore appear to cause the temporary cessation or general decline of gibberellic acid synthesis rather than the synthesis of a metabolite preventing stem elongation. He also found that once the chlormequat concentration within a plant reached a certain dilution, at some interval following treatment, the synthesis of gibberellic acid was enhanced and internode elongation resumed so that final plant height was either less than or exceeded that of the untreated control. Based on the previous findings, it can be suggested

that application of these growth retarders significantly changed the risk of lodging, not only by reducing plant height but also by increasing the physical strength of culm in cereals. A summary of agronomic approaches that can influence lodging resistance in cereal is presented in Fig. 2.

Crop genetic improvement approaches to avoid lodging in cereals

The introduction and identification of genes important to improve lodging resistance are needed to sustain cereal productivity in lodging-prone areas. Recent progress in the field of genomics and biotechnology, coupled with conventional breeding approaches, has the potential to find novel genes that can improve the physical strength of cereal plants to resist against lodging without sacrificing grain yield. Moreover, marker-assisted and quantitative trait loci (QTL)-based genetic improvement may also be helpful for cost-effective cereal production in lodging-affected areas. This section concludes and highlights different approaches to improve lodging resistance in cereals.

Selection and screening approach

Mass screening of genotypes is often used to identify lodging-resistant germplasm for breeding programs to develop better-performing genotypes against lodging. Quick screenings for lodging resistance based on morphological and anatomical features of plants are often deemed valuable. While comparing different cultivars of barley, Tamm (2003) found that barley cultivar with shorter stature showed less lodging as compared to long statured barley cultivars; therefore, short culm barley produced higher grain yield. Clark and Fedak

Table 3 Potential traits for screening cereals against lodging

Trait (s)	Correlation with lodging resistance	Reference(s)
Plant height/culm length	Negatively	Sayre et al. (1997)
Basal internodal length	Negatively	Yao et al. (2011)
Internodal diameter	Positively	Islam et al. (2007)
Stem/internode wall thickness	Positively	Tripathi et al. (2003)
Stem weight per unit length	Positively (increase pushing Resistance)	Wu et al. (2012)
Number of vascular bundles big or smaller	Positively	Chuanren et al. (2004)
Mechanical tissues	Positively	Kong et al. (2013)
Lignin contents	Positively	Okuno et al. (2014)
Cellulose contents and hemicellulose	Positively	Jones et al. (2001)
Silicon content in stem	Positively (increase physical stem strength)	Zhang et al. (2010)

Table 4 Number of QTLs identified for lodging resistance in cereals

Crop	Trait name	No. of QTLs	Chr no.	Population type	Reference
Rice	CWT and IL (1st and 2nd)	17	–	292 RILs	Zhu et al. (2006)
	PH	21	–		
	PR	2	5	–	Ishimaru et al. (2008)
	CL	6	1, 3, 6, 12	187 BC ₁ F ₃	
	IL	17	1, 3, 4, 5, 6, 8, 10, 11, 12		
	CWT	1	1	CSSLs from cross	
	CD	1	6	Habataki × Sasanishik	
	SD	6	1, 3, 6, 7, 8, 12	98 BILs (F ₇) from	Kashiwagi and
	LR	3	5, 6	Nipponbare × Kasalath	Ishimaru (2004)
	PR (lower part)	5	4, 5, 6, 11, 12		
	VB	9	1, 4, 5, 6, 11, 12	65 RILs from (Asominori × IR24)	
Lignin contents and structure	16	–	202 BILs cross XB//XB/DWR	Jones et al. (2001); Okuno et al. (2014)	
Wheat	Lodging-related traits	6	1B, 1D, 2B, 2D, 4B, 4D, 6D, 7D	96 doubled haploid lines from (Milan × Catbird)	Verma et al. (2005)
	LR	9	–	RILs from (Forno × Oberkulmer)	Keller et al. (1999)
	PH	4	4B, 4D, 2D	DH population form (Fukuho-komugi × Oligoculm)	
	PH	6	4B, 4D, 2D, 5B, 7A, 7B	DH population (RL4452 × AC domain)	
	LI	3	4B, 4D, 3D		
	Stem strength	2	3A, 3B	113 DH population from	Hai et al. (2005)
	PD	2	1A, 2D	(CA9613 × H1488)	
	SD and CWT	2	3B, 2D,		
	Solid stemmed	1	3B	F ₂ population.	Kong et al. (2013)
	lodging score	3	1B, 4AL, 5A.	132 F ₁₂ RILs from (Ning 7840 × US soft red Clark)	
Maize	Lignin Contents and Structure	22	–	131 RILs from (F288 × F271)	Tanaka et al. (2003)
	Starch content	2	–	163 RILs from (WM13 × Rio)	Ishimaru et al. (2008)
	Lignin and its contents	24			
	Cellulose	11			
	Hemicellulose contents	7			
Rind penetrometer resistance	35	–	Four populations	Kong et al. (2013)	
Barley	Culm strength	20	–	246 F ₂ from (ZQ320 × 1277)	Peng et al. (2014)
	CD	6	4H, 5H, 6H, 7H		
	CWT	11	All except for 6H		
	IL(1st)	3	2H, 5H, 6H		
	IL(5th)	2	4H, 5H.		
	IL and PH	1	2H, 7H, 7H, 2H, 3H,		
	PLW	2	2H		
	Sp L	2	2H, 7H	DH population (122 lines) from (Huaai 11 × Huadamaï 6)	
	CL	4	2H, 3H, 6H, 7H		
	IL (1st–5th)	14	2H, 3H, 6H, 5H, 7H		
CL	5	2HL, 3HL, 5HL, 7HS, 7HL	99 F ₁₃ RILs from Azumamugi × Kanto Nakate Gold	Samari et al. (2009)	

(1977) found that rate of lodging index was cultivar specific in barley, wheat, and oat. They also found that different cultivars showed different characteristics, and cultivars with our desired

characteristics can be used for further breeding. In another study, Kong et al. (2013) compared the morphological, anatomical, and chemical features of four different

genotypes of wheat and found a significant variation in these traits among these genotypes. They found that genotypes showed better lodging resistance due to higher pith size, transverse sections of solid stemmed, widths of stem walls, contents of cellulose and lignin, and area of the mechanical tissue. Zuber et al. (1999) observed that 49.7% of the variation in lodging in wheat was due to variation in stem weight. Khanna (1991) found that reduction in the stem lodging of wheat, oat, rye, and triticale was proportional to the vascular bundles. Tripathi et al. (2003) compared the first, second, and third internodes and peduncle stem walls of different genotypes of wheat and found that genotypes showed better lodging because of larger stem diameter and wall thickness of basal internodes and fewer tillers per unit area with heavy spikes. Therefore, these kinds of traits should be used to screen lodging-resistant genotypes. In conclusion, selection and mass screening of different cereal genotypes for lodging resistance may be done on the basis of morphological, anatomical, and chemical features. Further, traits used for screening and selection for lodging resistance should be (1) rapid, easy, and stable to measure; (2) strongly heritable; and (3) strongly correlated with lodging resistance. Potential traits for lodging resistance have been provided in Table 3, which can be used for the selection of lodging resistance genotypes.

QTL-based improvement for lodging resistance

QTL-based analysis can divulge the genetic basis of relationships among traits and allows a comprehensive investigation of the genetic relationships among morphological, anatomical, and chemical traits. Comparisons between QTLs for lodging and other traits have been made in several cereals, which revealed significant information regarding those traits and lodging resistance (Table 4). In barley, Ali et al. (2013) found one QTL for plant height and grain yield and reduces lodging index. In wheat, Keller et al. (1999) found seven QTLs that interact with the QTLs of different morphological traits such as plant height, culm stiffness and thickness, leaf growth, and leaf width. Many QTLs have been identified which are positively correlated with lodging index. In rice, 1 QTL for culm diameter, 1 for culm wall thickness, and 16 for lignin have been identified which are positively correlated with lodging (Kashiwagi and Ishimaru 2004); however, traits of their QTLs, which are negatively correlated, have also been reported. For instance, 21 QTLs for plant height in rice and 6 QTLs in wheat have been identified (Zhu et al. 2006). Several QTLs for chemical features such as lignin (22), cellulose (11), hemicellulose (7), and starch contents (2) have also been reported in maize, which significantly affected lodging index (Santiago et al. 2016). Santiago et al. (2016) found QTLs of different traits on different chromosomes while studying 246 F₂ from population of barley (ZQ320 × 1277). They noted 20 QTLs

for culm strength, 6 QTLs for culm diameter, and 11 QTLs for culm wall thickness which were positively correlated with lodging index while 3 QTLs for intermodal length of first internode, 2 QTLs for intermodal length of the fifth internode, and 1 QTL for plant height, which were negatively correlated with lodging index. In wheat, major QTLs for number of vascular bundles were reported on the long arm of 1A, 2D, 5D, and 7D chromosomes (Huang et al. 2006). QTL-based genetic improvement combined with conventional breeding is highly valuable in finding important genes to improve lodging resistance in cereals. Further marker-assisted approach could be more beneficial in finding different QTLs.

Conclusion

Until now, many lines of research have been done on lodging resistance in cereals. This has enabled to understand lodging mechanism in cereals and to develop models of lodging mechanism which could be used to identify the critical plant characters, quantify the effects of factors on lodging, and elucidate the mechanisms by which these effects are caused. Interestingly, we found that many of these effects were related to not only reducing plant height but also increasing physical strength of stem and also nutrient contents (particularly Si) in culm of cereals. Additionally, magnitude of stem strength changed with change in any management option. This means that certain types of management would be expected to reduce one type of lodging more than the other. Various agronomic practices also affect lodging in cereals and proper management, while using these practices can reduce lodging to a greater extent in cereals. We reviewed different morphological and chemical characteristics of plants that affect lodging in cereals. Plant height is not only a primary plant trait, but traits like stem wall thickness and intermodal length also contribute towards lodging resistance in cereals. Cellulose, hemicellulose, and lignin and carbohydrate contents improve the physical strength of plant and thus contribute significantly in lodging resistance. Further, this review revealed that there is a noticeable genotypic variation in different plant characteristics that determine the lodging-induced damages in cereals. For this, abrupt assessment techniques must be developed. These may be via the identification of genetic markers or through the development of novel instrumentation for rapidly measuring stem and anchorage strength. Different agronomic approaches such as tillage system, sowing time, seeding rate, nutrient application, and plant growth regulator/retarder can also reduce lodging risk, and thus, further research should investigate the effect of existing PGRs on stem and anchorage strength as well as focusing on discovering new growth-regulating chemicals that strengthen these traits and site-specific crop husbandry practices.

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