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Unveiling the Science of Lodging in Rice (*Oryza sativa* L.)

Kalaichelvi K.[1] and Murali Sankar P.[2*]
[1]Assistant Professor (Agronomy), KVK, Vridhachalam (Tamilnadu), India.
[2]Assistant Professor (Plant Pathology), Sampoorna School of Agriculture, Chennapatna (Tamilnadu), India.
(Corresponding author: Murali Sankar P.)*
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ABSTRACT: Lodging, the irreversible displacement of the rice plant from its upright position, results in significant economic losses by drastically reducing both yield quality and quantity. This phenomenon is categorized into three types based on the point of failure: bending lodging, breaking lodging (culm failure), and root lodging (anchorage failure). Traditional varieties, which are characteristically taller, are highly susceptible to lodging. Genetic approaches primarily target reducing plant height through dwarfism genes, although only the Sd1 gene is widely integrated into breeding programs, as alternatives like RGA1 and OSH15 often carry a yield penalty. Beyond height, culm strength is the key determinant of resistance. This strength is conferred by anatomical traits, including greater culm diameter (governed by loci like one found on chromosome 1), thicker culm walls, and increased density of both sclerenchyma cells and vascular bundles. Biochemically, the cell wall is critical. While lignin is a key strengthening polymer, its content is complexly regulated; for instance, excessive nitrogen application reduces the expression of lignin synthesis genes (e.g., OSCAD2, OSCAD7, and OSCAD20), increasing susceptibility. However, studies on DEP1 mutants suggest that mechanical integrity can be maintained despite reduced lignin through the compensatory upregulation of cellulose and hemicellulose synthesis genes. This structural balance is further enhanced by physiological factors: high levels of Non-Structural Carbohydrates (NSC) in the culm during senescence (linked to the Pr15 locus) and the crucial contribution of Silicon to cell wall rigidity.

Keywords: Cellulose, Dwarfing genes, Lodging, *Oryza sativa* (L.), Silicon, Rice.

INTRODUCTION

Rice (*Oryza sativa* L.), is a fundamental food source for the population in Asia, particularly in South and Southeast Asia, where over 90% of the world's rice is both produced and consumed. It serves as a major source of livelihood for over 250 million households globally (Chen *et al*., 2024). Rice occupies a pivotal place in Indian agriculture and is estimated to provide a substantial percentage of the calorie requirement for the majority of its people. India and China dominate global rice production, together accounting for over half of the global output. Other major rice-producing countries include Bangladesh, Indonesia, Vietnam, and Thailand. The global area under rice cultivation is approximately 168 million hectares (Mha.) (Yadav and Chattopadhyay 2025). India is currently the largest producer and the largest exporter of rice in the world (surpassing China in production). Rice is the most dominant cereal crop in the country, contributing a large share around 40% of the total food grain production. For the crop year 2023-24, India's total rice production was estimated at a record 137.8 million tons from a harvested area generally around 43-44 million hectares (Mha.) (www.india.gov.in).

Lodging, the permanent displacement of the plant stem from the vertical, is a major abiotic stress that causes significant economic loss by reducing both the quality and quantity of the rice harvest (Rashid *et al*., 2022). Lodging is generally classified into two main types: stem lodging (also called culm lodging) and root lodging (Dahiya *et al*., 2018). Stem lodging can be further subdivided into culm-bending and culm-breaking types. Tall culms are highly susceptible to bending-type lodging, while root anchorage failure leads to root lodging (Oladokun, 2006). The Green Revolution achieved significant reductions in lodging through the introduction of dwarfism or semi-dwarfism, primarily by targeting genes involved in gibberellic acid (GA) metabolism, such as the *sd1* gene (Long *et al*., 2020). This genetic modification alters the plant's architecture by significantly reducing plant height and consequently lowering the center of gravity of the plant closer to the ground, which increases mechanical stability against external forces like wind and rain (Zhu *et al*., 2016). While the semi-dwarf trait is a cornerstone of lodging resistance, modern breeding efforts are also focusing on enhancing culm strength through increasing levels of cell wall polymers like lignin, which improves the mechanical strength of the basal stem (Liu *et al*., 2018).

A. Background of Crop Lodging

Lodging is caused not only by uncontrollable external factors like strong winds and climate change characterized by unexpected, unseasonal rainfall and storms but also by suboptimal agronomic practices. These practices include over-fertilization with nitrogen, which encourages excessive, weak vegetative growth; inappropriate sowing dates; and closer-than-optimal planting density (Zhang *et al*., 2014; Pan *et al*., 2019). Furthermore, crop health factors like sheath rot and soil conditions such as low soil density or excessive moisture also contribute to a plant's susceptibility. The consequences of lodging are severe: a). During grain filling, lodging impedes the transport of assimilates, water, and nutrients to the developing grains, which can cause poor grain filling, vascular disconnection, and a higher proportion of unfilled (or) empty spikelet; b). Lodging in a high-humidity environment dramatically increases the risk of the grain being infected by mould and fungi, which severely deteriorate grain quality and can, lead to premature seed sprouting in the panicle (Yang and Zhang, 2006). To develop rice varieties with better physical strength, mastering mechanical strength testing using tools like a universal testing machine is essential for accurately quantifying the bending and breaking resistance of the culms (Mullangie *et al*., 2024).

Lodging susceptibility is primarily attributed to a plant's morphological, anatomical, and biochemical constituents. Reducing plant height is a highly effective measure that improves resistance to bending-type lodging (Hirano *et al*., 2014). However, extreme reduction, known as ultra-dwarfism, often leads to reduced grain yield. Resistance to breaking-type lodging is provided by the cell wall resistance and mechanical strength of the culm. Plant height and culm diameter are the key morphological characteristics that determine lodging resistance. Morphological traits such as plant height, the strength of the basal internode, and culm diameter are interconnected (Mullangie *et al*., 2024). Although larger culms are often present in taller plants, the increased height makes them prone to lodging due to a greater leverage effect. Crucially, the pushing resistance (or anchorage strength) of the lower internode is a critical factor for overall plant stability. Lodging resistance is therefore assessed by analyzing these morphological characters and the structural chemical constituents (e.g., lignin and cellulose) of the stem (Shah *et al*., 2019).

B. Physical Characteristics

Plant height

In taller plants, the centre of gravity is usually located in the upper internodes resulted in carrying the panicle at the top.

T (torque) = $F x r x \theta$

F= Force applied

r= distance from the pivot point to the tip of the panicle

θ= the angle between the force at the lever arm

Reducing r through dwarfing can mitigate effect of bending (Fujisawa *et al*., 2022), decrease in plant height leads to lodging resistance. Traditional varieties are taller and highly prone to lodging. Lodging resistance in rice is often controlled by dwarfism genes. Key genes studied for their impact on plant height include $OsGA20ox_2$ (commonly known as Sd1; Monna *et al*., 2002; Sasaki *et al*., 2002), OSH15 and RGA1 (Fujisawa *et al*., 2022). Among these, the Sd1 gene has been the most widely integrated into rice breeding programs globally because it confers the semi-dwarf trait without significantly compromising yield. In contrast, genes like RGA1 and OSH15, while affecting height, are generally detrimental to grain yield or overall plant fitness (Fan *et al*., 2017), limiting their utility in commercial variety development.

Gene editing of the SD1 gene (which encodes Gibberellin 20-oxidase 2, a key enzyme in GA synthesis) successfully results in a desirable reduction of plant height and enhanced lodging resistance. However, a significant challenge with highly severe sd1 alleles is the potential for pleiotropic effects, which can include a reduction in seed germination rate and overall yield. Therefore, careful selection of the edited allele is necessary to ensure the reduced Gibberellin (GA) synthesis is sufficient for semi-dwarfism while not adversely affecting essential agronomic traits like germination and final yield. For example, the widely grown aromatic rice basmati has been successfully edited with optimized sd1 alleles, leading to the development of lodging-resistant basmati varieties that retain desirable grain quality (Wang *et al*., 2024).

In addition to sd1, the semi-dwarf trait can also be introduced using alleles of SLR1 (a negative regulator in the GA signaling pathway). Specific semi-dominant SLR1 mutants, such as slr1−d7 and slr1−d8, offer an alternative strategy for breeding semi-dwarf plants because they reduce plant height by making the plant less sensitive to GA, thereby improving lodging resistance (Jung *et al*., 2020).

Rice culm

Rice culm can be a hollow tube with thick or thin walls or a solid culm featuring a locus. The culm is connected to the root parenchyma. Culm diameter is a key factor for resistance to lodging (Zhao *et al*., 2021). Culm diameter found on chromosome 1 underscores its essential role in resistance to lodging. The presence of schelerenchyma cells enhanced mechanical strength. A thicker stem has shown to enhance rice production (Hirose *et al*., 2006). Furthermore, a QTL located on chromosome 6 within the marker interval (RM20547–RM20557) exhibiting an R2 value of 10.39 is associated with enhanced culm diameter, with potential candidate genes recognized as microtubule-related genes that play roles in cell expansion (LOC_0s0645900) and potassium transport (LOC_0s06g45940) (Merugumala *et al*., 2019). An increase in vascular bundles results in a greater culm diameter and thicker walls, contributing to resistance against lodging. Decreasing the medullary cavity enhances culm wall thickness, improving resistance to lodging. The gene LFY contributes to a short and sturdy culm that enhances resistance to lodging (Wang *et al*., 2017).

C. Biochemical Characteristics

Biochemical constituents can solve the breaking type lodging. Not only the biochemical constituents improve the lodging resistance this is also responsible for biomass production, bio- ethanol generation and fodder quality (Mengistie and McDonald 2024).

Lignin

Lignin is a complex aromatic polymer that primarily resides in the secondary cell wall of plants, providing structural support and rigidity. It is built from three basic monomers (not units): p-hydroxyphenyl (H), guaiacyl (G), and syringyl (S). These monomers are derived from monolignols (coumaryl, coniferyl, and sinapyl alcohols, respectively), which originate from the phenylpropanoid pathway (not the isoprenoid pathway) (Ali *et al*., 2024).

The biosynthesis of lignin is a complex process involving over 90 genes from at least 10 different families (Raes *et al*., 2003; Li *et al*., 2015; Dixon and Barros 2019). Insufficient lignin content, which provides mechanical strength, is often a major factor contributing to lodging (stem breakage or falling over) in crops like rice (Zhang *et al*., 2016). Contrary to what might be expected, increased nitrogen application has been shown to potentially decrease the expression of genes involved in lignin synthesis, which can paradoxically increase lodging susceptibility (as reduced lignin weakens the stem). However, the overall effect is complex and variety-dependent. Specific genes, such as OsCAD 2, OsCAD 7, and OsCAD 20, which are involved in lignin biosynthesis, show higher expression in lodging-resistant rice varieties compared with their susceptible counterparts, suggesting a role for robust lignification in resistance (Liu *et al*., 2018). Furthermore, studies on DEP1 mutants (a gene linked to plant architecture) in rice indicate that DEP1 plays a major role in cell wall biosynthesis. While these mutants exhibited less total lignin, they were found to be lodging-resistant, likely due to the compensatory upregulation of genes involved in the synthesis of cellulose and hemi-cellulose (Wang *et al*., 2024).

Cellulose

The main component of cell walls is cellulose, which makes up 20% to 30% of the dry weight of primary walls and 40% to 90% of secondary walls. This emphasises how important cellulose is to the mechanical strength of plants. Apart from the amount of cellulose and its percentage in the cell wall, the extent of structural Mechanical strength is also influenced by the cellulose fibres' orderliness. Since amorphous cellulose is linked to a lower lodging index and cellulose crystallinity can be measured by X-ray diffraction, culms with lower cellulose crystallinity (Crl) have higher lodging resistance (Liu Q *et al*., 2022).

More organized cellulose fibers form a stiff structure that lacks flexibility, which can lead to culm breakage when subjected to external forces, especially during intense storms. The discovery of the CESA9 mutant, which influences cellulose synthase, highlighted lower Crl and degree of polymerization, thereby increasing resistance to lodging (Li *et al.*, 2017). In another study involving the sucrose synthase (*SUS3*) gene with its transgenic promoter AtCesA8, a decrease in Crl was observed, which improved lodging resistance in rice (Fan *et al*, 2017). There is a trade-off between lignin and cellulose levels, indicating that breeding rice varieties resistant to lodging may result in lower lignin content alongside increased cellulose, or the opposite. Lv *et al*. (2024) emphasized cases in which decreased lignin results in enhanced cellulose biosynthesis and increased resistance to lodging. OsTCP19 is recognized for its ability to attach to the promoters of MYB108 and MYB103L; the first is linked to diminished lignin biosynthesis, whereas the second promotes cellulose biosynthesis, suggesting a possible route for enhancing lodging resistance in rice. SuS3 sucrose synthase gene with transgenic plant Atcesa8 exhibits lodging resistance in rice. Reduced lignin resulted in improvement in cellulose biosynthesis, indicating a potential efficiency for improving lodging resistance in rice (Fan *et al*., 2017). OSTCP19 is repressed even with an increase in lignin content; plants are susceptible to lodging. Structural order of cellulose microfibrils through X-ray diffraction is essential for detecting lodging resistance (Lv *et al*., 2024).

Non structural carbohydrates (NSCs)

During senescence, the lodging resistance is reported in the Pr15 locus due to the higher accumulation of NSCs. Pr14 produced more NSC at the basal internode to increase lodging resistance due to a higher center of gravity at the base. Varieties like leaf star, which accumulate NSCs, contribute to lodging tolerance without undergoing senescence. Even in tall varieties, Prl genes improve the NSC content, resulting in a reduction of bending-type lodging (Kashiwagi *et al*., 2006).

Silicon (Si)

The presence of Si exhibits resistant to abiotic and biotic stresses in rice. Rice accumulates Si. Si plays a pivotal role in reducing rice blast, salinity, drought and lodging. Silicon contributes to the mechanical strength and rigidity of cell wall helpful in lodging resistance (Duan *et al*., 2004).

E. Case Studies

Findings on lodging resistance

The mean annual rainfall was 1408 mm during June–September. In September, a slight shift in wind was recorded, with an average speed of 4.49 km/h in the north-east and north-west directions in the evening and morning hours, respectively, which significantly impacted the basal nodes. September onwards gradually declined in wind speed from 4.40 to 3.15 km/h was recorded. Correlation study was synchronized, both the factors, wind and rain, together made susceptibility to lodging the varieties like Benisar, Bewara, Chhota Kabari, Chhota Kabari 1, Dagad desi 2, Kakai 1, Kankeri 1, Kanji 1, Kanji, Kantabuta, Kardhana, Karahani, Kari, Karikhuji, Kohikari, and Koliya. The variety (Barhi, Benisar, Kalasu, and Kanji 1) attained more than 140 cm height, coupled with >6 leaves per plant (Chanda and Kanji 1), and had higher lodging. Lodging was also observed in leaf length >70 cm that produced more biomass in Bhaya gonad, Butabari, and Kankeri 1. Plant height showed the highest eigenvalue, and the reverse was in stem thickness; whereas number and length of leaf were almost similar and expressed greater affinity than leaf width and 1st nodal distance in lodging (Pradhan *et al*., 2024). Three centimeter (3 cm) depth of transplanting is optimal for reducing lodging damage as well as for obtaining high yield. Potassium application successfully overcame lodging incidence in all three varieties (Zhang *et al*., 2021). It was inferred that improving the breaking resistance of the basal internodes is the most effective measure to increase the lodging resistance in rice breeding processes. (Luo *et al*., 2022).

Rice breeders could set the shorter and thicker basal internode as the main selection criteria to cultivate lodging-resistant indica cultivars to ensure a high yield at a higher ambient temperature (Diaz, 2022). If the rice plant height in the booting stage exceeded 70.7 cm and nitrogen fertilizer was continuously applied, according to the predicted growing curve of plant height, the plant would be at risk of lodging. Results showed more rainfall accumulated in the later stage of rice growth accompanied by strong instantaneous gusts, the risk of lodging increased (Wu *et al*., 2022).

F. Assessment

Instruments used for estimating lodging resistance

Daiki Rika Kogyo Co., Ltd. (Tokyo, Japan) makes the DIK7400 prostrate tester, a multipurpose handheld instrument that gauges a plant's culm strength and bending resistance. It functions according to the principle of action and reaction, with the milky stage of development serving as the ideal time for measurements. When the plant reaches a 45º angle, the measurement is taken. The tester is pushed forward and positioned perpendicular to the culm (Hai *et al*., 2005). This tool is used to determine the bending resistance and strength of a group of plants in the canopy. Comprehensive analysis capabilities are offered by the plant lodging tester, another small device. By progressively adding a force on the culm until breakage occurs, this equipment can quantify the elastic modulus and create a stress-strain curve. To determine the variations in stress and strain, two points are chosen from this curve along a straight line (Duan *et al*, 2004). The high-throughput capability and versatility of UTMs in measuring different mechanical properties make them very valuable. By positioning the rice culm between two fulcrums, usually 4 or 5 cm from the center, and applying the force until the culm breaks, bending stress can then be measured using a UTM. When the culm breaks under stress, the load point is noted using the culm length ratio (cLr) and BMB are significant mathematical elements that breeders use to evaluate the mechanical characteristics of rice. The cLr is easy to phenotype and inexpensive, while BMB necessitates the employment of advanced equipment such as the UTM. Erndwein *et al*. (2020) proposed the cLr concept, which entails forming a sequence of multiple fundamental units connected to the inflorescence and evaluating the bent plant for various forms of bending and breaking lodging. This approach signifies one of the easiest and most economical mechanical assessments for determining the quality of rice culms (Hirano *et al*., 2017). A novel, affordable phenotyping index called relative culm wall thickness has recently been introduced to evaluate lodging resistance in rice, taking into account the ratio of wall thickness to the diameter of the lower internodes (Li *et al*., 2023).

CONCLUSIONS

Dwarfism genes are *RGA1* (Fujisawa *et al*., 2022), OSH15 (Niu *et al*., 2022), and *Sd1* (Monna *et al*., 2002; Sasaki *et al*., 2002). Since the genes *RGA1* and *OSH15* are detrimental to yield (Yang *et al*., 2024), the gene Sd1 alone has been integrated into breeding programs. Culm diameter, which is located in chromosome 1, highlights a crucial role in lodging resistance. Mechanical strength was increased by schelerenchyma cells. A thicker culm has proved to increase the rice yields (Hirose *et al*., 2006). Additionally, a QTL on chromosome 6 between the marker interval (RM20547–RM20557) with an R2 value of 10.39 is linked to increased culm diameter, with candidate genes identified as microtubule-related genes involved in cell expansion (LOC_0s0645900) and potassium transport (LOC_0s06g45940) (Merugumala *et al*., 2019). Increasing vascular bundles increases the culm diameter and wall thickness, leading to lodging resistance. Lower lignin may induce lodging. Increased nitrogen application reduces the expression of more genes involved in lignin synthesis, leading to lodging susceptibility. *OSCAD 2, OSCAD 7,* and *OSCAD 20* show higher expression in lodging-resistant varieties compared with their susceptibility counterparts (Liu *et al*., 2018). DEP mutants indicate *DEP 1* plays a major role in cell wall biosynthesis; they showed less lignin but were found to be resistant due to upgradation of genes involved in cellulose and hemicellulose synthesis (Wang *et al*., 2024). SuS3 sucrose synthase gene with transgenic plant Atcesa8 exhibits lodging resistance in rice. Reduced lignin resulted in improvement in cellulose biosynthesis, indicating a potential efficiency for improving lodging resistance in rice (Fan *et al*., 2017). The higher the NSCs during senescence higher the lodging resistance noted in the Pr15 locus. Silicon contributes to the mechanical strength and rigidity of the cell wall, helpful in lodging resistance (Duan *et al*., 2004).

FUTURE SCOPE

While current research has established a crucial foundation for understanding lodging mechanisms, the path to developing completely lodging-resistant, high-yield rice varieties remains unfinished. Subsequent research must focus on combining high-resolution phenotyping with sophisticated molecular and environmental modeling methods to deliver precise breeding solutions. This future scope centers on three main areas: utilizing high-throughput phenomics (HTP), involving non-invasive tools like unmanned aerial vehicles (UAVs), LiDAR, X-ray CT, and nano-indentation for quantification; advancing functional genomics through CRISPR/Cas9 deployment and pangenomics for allele discovery; and developing environment-associated 'digital twin' models integrated with microbial interventions and agronomic practices. These interconnected strategies will pave the way for accelerated rice breeding, ultimately securing sustainable food production and stability.

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