A Review on Overcoming Dual Challenges for Maize Cropping under High Plant Density: Stalk Lodging and Kernel Abortion

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A REVIEW ON OVERCOMING DUAL CHALLENGES FOR MAIZE CROPPING UNDER HIGH PLANT DENSITY: STALK LODGING AND KERNEL ABORTION

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ABSTRACT

Increased optimal plant density is necessary in ensuring future food security by increasing crop productivity. However, maintaining relatively high plant density has to overcome two challenges i.e. kernel abortion and stalk lodging. The response of maize to increased plant density and the effects of increased plant density on maize productivity were discussed in this research. Increased plant density induces increased plant height, causes low photosynthetic capacity, limits the carbohydrate supply and increases kernel abortion. Also, increased plant density incurs a high risk of stalk lodging due to increased ear height and diminished stem diameter associated with reduced vascular bundles that provide, mechanical force. This review proposes a potential capacity of sucrose storage in stalk for tackling kernel abortion and stalk lodging. The mechanisms of boosting stem sugar storage with more efficient unloading, transporting, and storage in internodes are discussed.

Keywords: Interplant competition, morphology, kernel abortion, stalk lodging resistance, sugar metabolism.

Abbreviations: Plant population density (PPD); Leaf area index (LAI); Leaf elongation rate (LER); Quantitative trait locus (QTL); Canopy photosynthetic capacity (CAP); Rind puncture resistance (RPR); Pith puncture resistance (PPR); Pith parenchyma inter-lumen thickness (PPIT); Non-structural carbohydrates (NSC).

Constraints of Maize Cropping under High Plant Density

A high plant population is an effective agronomic management strategy for increasing yield (Tokatilids et al., 2011; Xu et al., 2017; Zheng et al., 2017; Sher et al., 2017, 2018, 2019) and to combat the future food and dietary necessities of increasing population of the world

(Gao et al., 2010). The practice increases plant height through the greater interlength and smaller diameter (Esechie, 1985; Wang et al., 2011), thus causing stalk lodging (Acreche et al., 2011; Berry et al., 2012).

High plant populations reduce grain yield by effecting the number of kernels and kernel weight in maize crop (Maddonni and Otegui, 2006; Tiening et al., 2017; XUE et al., 2017). The kernel number is a key component to determine the grain yield potential when abiotic stress occurs (Abhinanden et al., 2018). Loss of kernel number cannot be compensated even if grain filling is with plenty of resource supply (Westgate and Boyer 1985). High plant density will thus reduce grain yield potential due to increased kernel abortion. Kernel abortion can cause 95 % of the variation in final kernel numbers and reduced yield (Edreira et al., 2011). The quantity of kernels in each row is reduced as the plant density increases to −10 % (Testa et al., 2015). High plant density is reported to reduce biomass and harvest index, increase kernel abortion, delay reproductive processes, and affect plant grain yield (Maddonni and Otegui, 2006; Borras et al., 2007; Gobeze, et al., 2012; Novacek, 2013; Yue et al., 2018).

At high plant density, lodging is a major limitation in corn yield loss (Sher et al., 2018) as shown in Figure 1. Stalk lodging is defined by Arnold and Josephson (1975) as the breaking of the stalk between the soil level and the major ear insertion node, which is caused by a complex interaction and combination of variables. Previous research has found that lodging is more severe in large plant populations, although the majority of investigations on the crop lodging response to density have produced mixed results (Zhang et al., 2017). According to, a large plant population reduces stalk crushing strength, dry weight per unit length, and internode diameter (Joe et al., 2007). Other studies (Yao et al., 2013) and Feng et al., 2014)) discovered that as planting density increased, the length of the basal internode increased and the internode diameter decreased, as well as the mechanical tissue thicknesses of the mechanical cell layers decreasing and lodging percentage increasing. Furthermore, high planting density restricted sunlight reaching lower plant leaves and decrease fertiliser availability, boosts competitive ability, resulting in weak stalks and negative root impacts, and eventually leading to stalk lodging. The crop's proclivity to lodge causes major harvesting issues, with annual yield losses ranging from 5 to 40 % (Ransom, 2005; Nielsen, 2006; Sui-Kwong et al., 2011). Stalk lodging is responsible for an even higher percentage of yield loss. For example, stalk lodging could cause 60-75 % of maize to be destroyed (Van Dyk, 2001; Sher et al., 2018).

Figure 1: Stalk lodging by wind in maize crop.

Physiological Mechanism in Regulating Stalk Lodging under High Plant Density

i.   *Morphological Mechanism in Regulating Lodging*

Plant morphology plays an important role in light interception by plant canopy and provide sources for assimilate partitioning, for example leaf angle and direction are very important morphological parameters to intercept light by canopy (Tollenaar, 2007; Lee and Hammer et al., 2009). Plant height, diameter and length of the basal internode, rind thickness, and weight of a 5 cm basal section are all morphological characteristics that are linked to stalk lodging (Esechie, 1985). It has often been observed that maize plants height increased by increasing plant population due to mutual shading, but some varieties are resistant to this characteristic (Yokozawa and Hara, 1995; Dong et al., 2006; Wang et al., 2011). The utilization of high plant densities in maize is hampered by stalk lodging, which is one of the most important restrictions (Argenta et al., 2001). Huang et al., (2008) suggested that when planting density was increased above sensitive density turning level, stem bending strength and crushing resistance decreased, but lodging rate increased. As a result, many high-yielding hybrids are discarded throughout development due to stalk lodging. Plant density effect on morphological characteristics of maize crop is presented in Table 1.

ii.   *Anatomical Mechanism Regulating Lodging*

Plants rely on anatomical characteristics to give cells shape, strength, and structure, to glue cells together, and to give stiffness to the entire plant, and the composition of anatomical features varies greatly from one cell to the next and from one species to the next (Brett et al 1996; Hazen et al., 2003). The thickness of the parenchyma layer increases stem standability and reduces the likelihood of local buckling and collapse (Dunn and Briggs, 1989; Niklas, 1991; Spats et al., 1993; Li, et al., 2003).

Table 1: Plant density effect on morphological characteristics of Maize crop.

Trait	Correlation with plant density	References
Plant height	Negative	Verma et al., (2005); Zeid et al,. (2011); Kashiwagi et al,. (2005); Yao et al., (2011)
Lamina length	Positive for lower Phytomers and negative for upper Phytomers	Song et al., 2016, Sher et al., 2016; 2018
Lamina width	Negative for all Phytomers	Song et al., 2016, Sher et al., 2016; 2018
Sheath length	Positive for lower Phytomers and negative for upper Phytomers	Song et al., 2016, Sher et al., 2016; 2018
Internode length	Not consistent	Song et al., 2016, Sher et al., 2016; 2018
Internode diameter	Negative for all Phytomers	Song et al., 2016, Sher et al., 2016; 2018

The parenchyma can absorb the effects of external forces including light, wind, and rain without heating or mechanical harm (Kokubo et al., 1989). High plant density reduces the vigour of the cells in the vascular bundles in the stalk and causes stalk lodging by increasing competition for light, nutrients, and water. This also affects carbohydrates between (source) and (sink) within the plant, reducing the vigour of the cells in the vascular bundles in the stalk and causing stalk lodging (Nielsen, 2006). There is a substantial negative link between rind penetrometer resistance (RPR) and ear height (EH), whereas a high plant population increased ear height and stalks with smaller diameters, which led to higher lodging potential (Stanger and Lauer, 2007; Novacek et al, 2013). Furthermore, increased plant density reduced peel thickness and strength, as measured by rind penetrometer resistance (Dodd, 1977; Stanger and Lauer, 2007). The diameter of the stem and the thickness of the stem wall are also crucial lodging factors. Plant density reduces stem diameter and length, increasing the risk of stalk lodging. Anatomical, physical and mechanical traits correlation with plant density is presented in table 2. Flow chart showing the mechanism of plants grown under high plant density is represented in Figure 2.

iii.   *Mechanical Force Regulating Lodging*

Quantitative trait loci (QTL) determine mechanical strength, which is influenced by growth regulators, fertiliser, and plant density (Slavodar et al., 2013; Okuno et al., 2014; Zhang et al., 2014; Kuai et al., 2015; Xiao et al., 2015; Yano et al., 2015). Mechanical traumas cause the plant to behave in a specific way.

Table 2: Anatomical, physical and mechanical traits Correlation with plant density.

| Trait	Correlation with plant density	References
Physical strength	Negative	(Nielsen, 2006)
Vigour of the cells in the vascular bundles	Negative	(Nielsen, 2006)
Ear height	Positive	Stanger and Lauer, 2007; Novacek et al, 2013
Rind thickness	Negative	Stanger and Lauer, 2007; Novacek et al, 2013
Rind strength	Negative	Stanger and Lauer, 2007; Novacek et al, 2013
Rind penetrometer resistance	Negative	Stanger and Lauer, 2007; Novacek et al, 2013; Dodd 1977
Pith parenchyma interlumen thickness	Negative	Santiago et al., 2003
Mechanical tensile strength	Negative	Xue-qian et al., 2013
Stem breaking strength	Negative	Zheng et al., 2017
Lignin Accumulation	Negative	Zheng et al., 2017
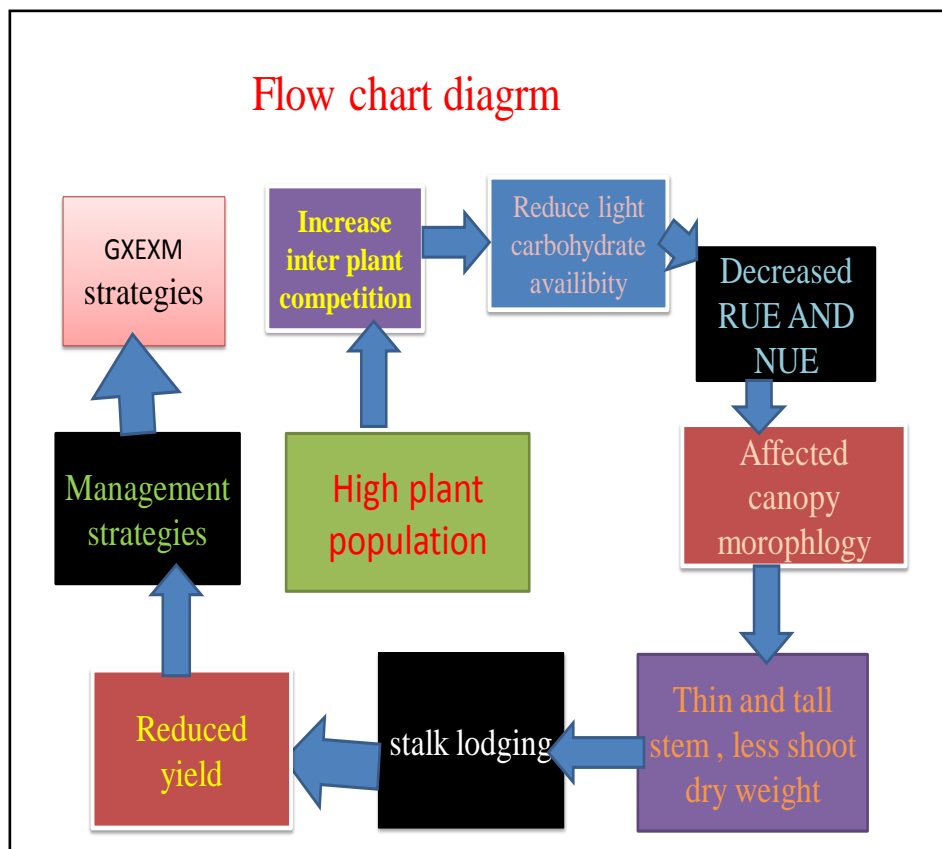
Figure 2: Flow chart mechanism of plants grown under high plant density.

According to an electron microscope investigation, mechanical injuries lead the xylem to thicken (Frankenstein et al., 2006). The plant cell wall provides mechanical support to cells, tissues, and the entire plant body (Keegstra et al., 2010). According to study, stalk lodging, rind thickness, and crushing strength of the second internode above ground in maize crops all have a negative relationship (Zuber and Grogan, 1996; Thompson, 1963). Plant density increased, resulting in smaller and weaker diameter stalks susceptible to disease and strong winds (Wilcoxson and Covey., 1963). Scientists have also shown (Stanger and Lauer, 2007) that as plant density grew, rind strength fell as rind penetrometer resistance reduced. The mechanical tensile strength of maize stems reduced as plant density rose, resulting in lodging, which has a detrimental impact on the crop's yield and quality (Xue-Qian et al., 2013).

iv.   *Chemical Basis Regulating Lodging*

Matile, (1976) reported that a decrease in stalk protein and sugar levels induces pith tissue senescence and increased stalk lodging. By affecting the source-sink ratio, higher plant density affects the vigour of vascular bundles and may lower the synthesis of total nonstructural glucose, protein, and potassium in the stalk, causing stalk lodging. The percentages of total nonstructural carbohydrate, protein, and potassium in the stalks were found to be adversely linked with lodging (Esechie, 1985). Nitrogen is one of the most important nutrients for plants, and it helps with protein storage and distribution in maize seed. However, too much nitrogen can promote stalk lodging (Hashemidezfouli and Herbert., 1992; Casta et al., 2002). Plant height and gravity centre height were greatly enhanced with a higher volume of N fertilizer, but culm wall thickness, diameter, and culm and leaf sheath plumpness status of basal internodes were reduced, resulting in stalk lodging in rice (Wei et al. 2008; Yang et al., 2009; Zhang et al., 2010; Wang et al., 2012; Zhang et al., 2013)

Physiological Mechanism in Regulating Kernel Abortion under High Plant Density

High plant population is one of the best agronomic practises for maximising crop yields (Yang et al., 2004), because it allows plants to better utilise sun energy (Tokatlidis, 2004; Jin et al., 2012). High plant density, on the other hand, reduces per-plant crop growth rates and increases intra-plant competition for assimilates, resulting in greater kernel abortion due to a decrease in carbon and nitrogen delivery to the ear (Edmeades, 2000; Yan et al., 2010). As a result, lowering N uptake will increase N remobilization from leaves and stems, which could account for one of the major components of seed N. Due to the extended pollen-to-silking gap, higher planting densities reduced grain production and may cause kernel abortion (Tokatlidis and Koutroubas, 2004). As a result, any abiotic stress, such as a high plant population or drought, can increase competition for light or cause defoliation, which delays silking and causes ear tip abortion, resulting in full barrenness. The top canopy's

leaves provide greater shade to the middle and lower canopy, especially when the plant density is high. The number of ovules per plant will be greater than the number of kernels at physiological maturity, however kernel quantity influences grain yield when different pressures occur around the silking stage, which is the important time for kernel set. The reduction in the quantity of kernels per ear could be owing to fewer flower initials being created prior to flowering, or to poor pollination caused by tasseling and silking desynchronization, resulting in kernel abortion after fertilisation (Hashemi-Dezfouli and Herbert, 1992). High plant density led to an increase in ASI, which was accompanied by increased interplant variability in this parameter, as well as a reduction in the number of grains produced per tassel (Uribelarrea, 2002). High planting densities, as a result of extending the tasseling to silking interval and a lack of kernel filling, have been reported to reduce the amount of fully developed florets, which is more determinant to crop production.

Leaf and Canopy Photosynthetic Capacity Regulating Kernel Abortion

Light intake via the canopy is critical for plants to retain high photosynthetic capability, and competition for light can occur even before canopy shadowing from surrounding plants occurs (Sattin et al., 1994). At high plant populations, the canopy begins to self-shade, reducing light penetration and canopy photosynthetic assimilates (Sinclair, 1998; Stewart et al., 2003; Hammer et al., 2009). Kernel number at maturity is linked to canopy photosynthesis during the crucial phase of kernel set, and the effects of stress on kernel number can be stated in terms of stress on canopy photosynthesis. Plant density effects canopy photosynthesis, which normally drops in response to high plant density. It influences the source-sink ratio by affecting total light intercepted by the plants (Yang et al., 2010). This has an impact on the final quantity of kernels and their properties, as well as the possibility of kernel abortion (Wei et al., 2011).

Sugar and Hormone Regulating Kernel Abortion

Sucrose is a sugar that serves as a source of Carbon precursors for the formation of starch and as a source of energy. Sucrose import is thought to be regulated by a turgor pressure gradient between source and sink tissues (Zinselmeier et al., 1995), which is caused by sucrose-metabolizing enzymes such soluble and insoluble inverts, sucrose synthesis, and growth hormone like auxin (Roitsch et al., 1995; Smith and Samach, 2013). Kernel abortion in maize could be triggered by a hormonal signal as a result of increased interplant competition, lower water, nutrient, and solar radiation, and the production of the growth hormone Abscisic Acid (ABA) as a result of less water available to roots and xylem tissues. Furthermore, Blum, (2011); and Albacete et al., (2014) claimed that Abscisic Acid is a "stress hormone" because it was created in plants exposed to abiotic stresses such as salinity, heat, and drought, and it caused cellular dehydration. This cellular dehydration lowered stomatal

conductivity, affecting photosynthesis and biomass production, as well as possibly causing kernel abortion. Aborted kernels contain higher ABA and lower IAA concentrations after kernel abortion than non-aborted kernels. After the process had begun, abscisic acid enhanced kernel abortion (Reed and Singletary, 1988; McLaughlin et al., 2004).

Overcoming Dual Challenges by Stem Sugar Metabolism

i. *Stem Sugar for Structural Tissue to Overcome Lodging*

Stalk lodging constituted a key stumbling block in maize yield development at high planting populations, resulting in annual yield losses of 5 to 25 % (Nielsen, 2006) and 40 % (Ransom, 2005). Stem stand ability is critical for reducing stalk lodging, and maize hybrids with high stem carbohydrate contents have higher stem stand ability. Is there a connection between stem sugars and lodge resistance? One theory is that a high sucrose content necessitates more water entering the parenchyma cell, which will increase cell turgor pressure and stiffen the cells, all of which will fight lodging. The second option is that the active transport carbohydrate remobilization will maintain the cells alive due to a high sugar percentage in the internode (Campbell, 1963). The 'functional stay green' trait, which reduces senescence due to high plant density, boosts photosynthetic capacity, and promotes stem stand ability, requires stem sugar build up (Thomas and Howarth, 2000). When it comes to lodging (high density, low carbohydrate supply from leaves, but high storage), one option is to use stem: non-structural carbon (NSCs) in maize to prevent stalk lodging. The presence of NSC reserves in maize stems can be utilised to counteract the negative effects of stalking in maize (Shiferaw et al., 2011).

Anatomical, metabolic, and morphological features linked to lodge resistance in cereals could be exploited to breed for lodging resistance (Pinthus, 1974; Zuber et al., 1999). Lignin, total non-structural carbohydrates, potassium, nitrogen, and salt are all biochemical markers that could be exploited to breed lodging resistance in maize (Esechie et al., 1985). Lignin is a complex aromatic polymer found in the secondary cell walls of all vascular plants. It is strongly cross-linked with other cell wall components and is known as the "cellular glue," providing strength and stiffness to plant tissues and fibres. (Rubin, 2008; Sarkar et al., 2009; Bonawitz and Chapple, 2010). It also protects plants from abiotic and biotic stressors, as well as providing stability to xylem vessels for efficient water transfer (Voelker et al., 2011). A high lignin content in the culm could improve the mechanical intensity of the culm, which would boost the culm's lodging resistance (Baucher et al., 1998; Loor et al., 2013). Lignin makes up the majority of "lignocellulosic" plant components, together with the carbohydrate polymers cellulose and hemicellulose. As a result, lignin is responsible for a significant fraction of the total organic carbon in the biosphere, second only to cellulose (Bonawitz and Chapple, 2010; Zhao and Dixon 2011). For example, lignin in crops effected

by abiotic stresses can be seen in two ways: (i) reduced lignin biosynthesis directly effects the lignin content of cereals (Magalhaes et al., 2010; Wang and Frei, 2011) and (ii) lignification of crop tissues affects plant fitness and may increases tolerance to stalk lodging (Casler et al., 2002; Pedersen et al., 2005). As a result, a high lignin concentration in the culm could improve the mechanical intensity of the culm, increasing the culm's lodging resistance (Baucher et al., 1998; Loor et al., 2013). Furthermore, new uses in the manufacture of cellulosic ethanol and biopolymers can improve stalk strength-related features such as cell wall composition and biosynthesis (Bosch et al., 2011). On lodging-resistant plants, a non-structural carbohydrate (NSC) probably gives some resistance to pith tissue senescence and reduced stalk rot. The rind Penetrometer resistance (RPR) method was created to test stalk strength in an efficient and non-destructive manner (Abedon et al., 1999).

By changing the morphological and chemical compositions of cereal crops, sulphur (S), nitrogen (N), and potash (K) can be employed to improve lodging resistance. Previous study has shown that increasing the number of chosen cells increases the strength of the culm and the breaking resistance (Singh et al. 2005). The mechanical strength and stem bending resistance of plant parts are also improved by silica deposits. Stem stability and lodging resistance are affected by a sufficient supply of Si (Idris et al. 1975; Fallah 2012). Furthermore, by decreasing the shadowing effect on lower sections of the plant, the Si improves canopy properties such as leaf angle and keeps it erect to harvest more light. The information on the importance of lignin in improving lodging resistance mechanism and how some nutrients help to improve lignin metabolism is given in Table 3.

ii. QTL-Based Improvement for Lodging Resistance in Maize Crop

According to preliminary research, QTL genetic traits represented a thorough investigation of the genetic links between morphological, anatomical, and chemical factors for lodging traits. According to Zhu et al., (2006), there are 21 QTL in rice and 6 QTL in wheat related to plant height. In addition, a high number of QTLs for biochemical features in maize, such as lignin (22), cellulose (11), hemicellulose (7), and starch contents (2), were found, all of which had a substantial impact on lodging index (Santiago et al. 2016). Furthermore, locating distinct QTLs will be easier using a marker-assisted strategy. Table 4 shows the number of QTLs for lodging resistance in maize that has been reported.

iii. Stem Sugar Metabolism Contributes to Overcome Kernel Abortion

Kernel abortion is mostly caused by a lack of carbohydrate supply (sink–source connection), hence a high stem sugar can continue to give sugar to the kernel. One theory about the origins of Corn soluble sugars in the stems is that decent, the predecessor of maize, was initially grown for stem sugar (Willaman et al., 1924; Singleton, 1948; Smalley and Blake, 2003).

Table 3: Lignin role in lodging resistance.

Lignin function	References
Lignin deposition in cell wall increases mechanical strength of stalks which helps to improve lodging.	Tripathi et al., 2003
Paclobutrazol decreased the internode length of wheat, enhanced the lateral growth and increased lignin deposition and activities of lignin biosynthesis Enzymes and thickness of internode, which also helps the wheat lodging resistance.	Peng et al., 2014
Plant population affected the morphological characteristics of wheat which influenced lignin biosynthesis of the stem and thus enhance the mechanical strength of the stem and decreases chance of lodging.	Zheng et al., 2017
Lignin biosynthesis enzymes (PAL, 4CL, CAD and POD) increased the lodging resistance according to the analysis of lignin metabolism related indexes in Fagopyrum esculentum Moench varieties with a different lodging tolerance.	Hu et al., 2017
Silicon improves lignin accumulation and increased the strength of the stalk by enhancing the lodging resistance.	Dorairaj et al., 2017
Over dose of nitrogen application reduces lodging resistance by reducing lignin biosynthesis in buckwheat, rapeseed and japonica rice.	Jie et al., 2016; Zhang et al., 2017 and Wang et al., 2015

Table 4: Number of QTLs identified for lodging resistance in maize.

Trait	No. of QTLS	Population type	Reference
Lignin Contents and Structure	22	131 RILs from (F288 × F271)	Tanaka et al,. (2003)
Starch content	2	163 RILs from (WM13 × Rio) I	Ishimaru et al., (2008)
Lignin and its contents	24	163 RILs from (WM13 × Rio) I	Ishimaru et al., (2008)
Cellulose	11	163 RILs from (WM13 × Rio) I	Ishimaru et al., (2008)
Hemicellulose	7	163 RILs from (WM13 × Rio) I	Ishimaru et al., (2008)
Rind penetrometer resistance	35	Four populations	Kong et al., (2013)

Due to the focus on basic features such as boosting yield by lowering kernel abortion, lodging resistance, drought tolerance, and nutritional content, maize stem sugar has received little attention in recent decades. Corn kernel development is divided into a series of strictly controlled, overlapping stages. Increased plant population limits photosynthesis, primarily due to shade and reduced chlorophyll availability to leaves, resulting in kernel abortion. (Rajcan, and Tollenaar, 1999; Yan et al., 2010); Thin maize stems promote stem NSC remobilization, which reduces kernel abortion and seed setting (Ruan et al., 2010). Both the embryo and the endosperm rely on photosynthate from source leaves after multiple fertilisations, which are delivered through the maternal pedicel area of the growing kernel and ends at the terminal phloem cells (Bate et al., 2004). Finally, it is obvious that sustaining the sucrose supply and converting it to hexoses is critical for male fertility, kernel abortion reduction, and seed and fruit set. Figure 3 showed very comprehensive information about physiological mechanism for regulation of lodging and to address this problem.
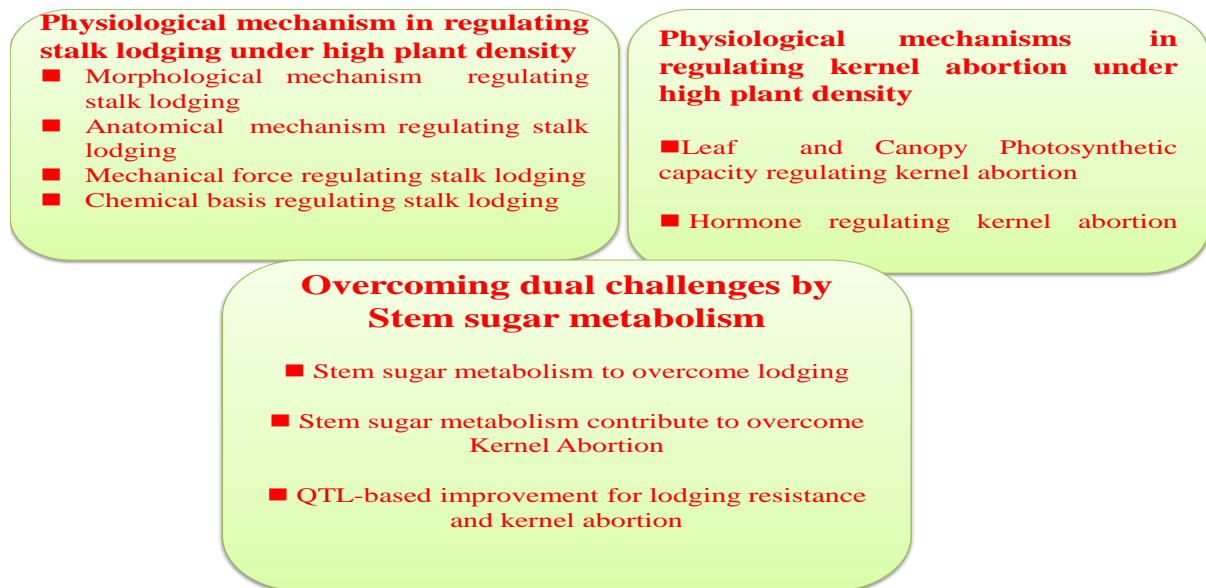
Physiological mechanism in regulating stalk lodging under high plant density
- Morphological mechanism regulating stalk lodging
- Anatomical mechanism regulating stalk lodging
- Mechanical force regulating stalk lodging
- Chemical basis regulating stalk lodging

Physiological mechanisms in regulating kernel abortion under high plant density
- Leaf and Canopy Photosynthetic capacity regulating kernel abortion
- Hormone regulating kernel abortion

Overcoming dual challenges by Stem sugar metabolism
- Stem sugar metabolism to overcome lodging
- Stem sugar metabolism contribute to overcome Kernel Abortion
- QTL-based improvement for lodging resistance and kernel abortion

Figure 3: Overcoming dual challenges by stem sugar metabolism.

Conclusion

While improved yields are significant, high density planting can also lead to increased competition for resources, morphological changes in the plant, and kernel abortion and lodging. Abortion, lodging, and lower yield have a significant impact on plant assimilate transport and photosynthetic activity. Sugar is the best strategy to solve these issues by targeting the stems. Scientists should look at how roots, root bleeding, sheath, and stem anatomy respond to high plant density in order to prevent lodging and boost output in the future. Future research on lodging and kernel abortion should look at the molecular and biochemical aspects of root, internode, sheath, and stem anatomy.

CONFLICT OF INTEREST

Authors have no conflict of interest.

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