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Review paper

Improvement of *Eragrostis tef* for lodging resistance

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Tef is largely grown in Ethiopia and plays a vital role in food security. However, its production and productivity are adversely affected by various factors; among these lodging is the major one. It affects yield and deteriorates the quality of grain and straw. The risk of lodging is determined by environmental factors, inputs, plant architecture, and stem composition. The strength of the culm internode is enhanced by nutrients like silicon, potassium, and phosphorus. However, the high nitrogen application makes the low strength of the base and increases the upper vegetative parts resulting in high lodging. Besides, chemical compositions like lignin, cellulose, hemicellulose, and carbohydrates have a positive effect on stem strength and helpful in improving lodging. Moreover, comprehensive investigations that combine conventional and molecular breeding and study on tef anatomical, morphological and chemical compositions are useful to improve tef lodging resistance.

Key words: *tef lodging, stem strength, biochemical, silicon, nutrients*

INTRODUCTION

Tef, *Eragrostis tef* (Zucc.) Trotter is endemic to Ethiopia and its cultivation is ancient in Ethiopian highlands (Reda, 2015). It plays a crucial role in food and nutritional security and income generation for smallholder farmers in Ethiopia (Cannarozzi et al., 2018). It serves as a staple food crop for about 50 million Ethiopian people (Reda, 2015) and contains good protein, essential amino acids (Gebru et al., 2019), and minerals as compared to other cereal crops such as wheat, barley, maize, rice and sorghum (Bultosa et al., 2002). Tef is free from gluten and could be beneficial for gluten-sensitive people (Spaenij-Dekking et al., 2005). Both its grain and straw (nutritious and more palatable for livestock) have good price in the market and sources of income for farmers (Alemayehu, 2001; Cannarozzi et al., 2018). Tef was covered over three million hectares of land and over five million tons of grain produced annually in Ethiopia (CSA, 2019) which is accounted 30% of the cereal crops grown in the country (Kebede et al., 2020). However, the productivity was estimated to 1.6 tons ha^{-1} (CSA, 2019), which is low as compared to its genetic potential of 4.5 tons ha^{-1} (Assefa et al., 2011). Several factors contribute to the low yield of tef in Ethiopia. Out of these factors, lodging is a common phenomenon and causes 35% yield reduction (Ben-Zeev et al., 2020). It is an abnormal condition induced by internal and external factors or the interaction between the two which results in the permanent displacement of the aerial parts from their upright position (Seyfu, 1983; Van Delden et al., 2010; Plaza-Wüthrich et al., 2016). Thus, this paper assessed the overall effects of lodging, the research progress and limitation, and the role of nutrients and stem biochemical molecules on lodging by focusing on the small cereal, tef crop.

Types of lodging

Stem lodging and root lodging are the most commonly known types of lodging in cereal crops (Berry et al., 2004). Whereas, transient and permanent lodging are the commonly known types of lodging in tef (Seyfu, 1983). Transient lodging occurs as a result of heavy wind and rain in which the crop can recover when it occurs before heading (Seyfu, 1983). It mainly occurs at the early (seedling) growth stage and not as much economically important. However, permanent lodging is a serious lodging that occurs after heading in which the crop may not recover itself (Seyfu, 1983). The damage due to permanent lodging is of considerable economic importance. Permanent lodging is further categorized as breaking, bending, and root lodging (Seyfu, 1983). Bending lodging refers to the condition where the plant loses elasticity, bends without breakage, and is permanently displaced from the upright position while the roots are securely fixed in the soil. It is the most spreading and economically important lodging in tef. Whereas breaking lodging is a condition where the stem breaks while the roots securely fixed with the soil. However, root lodging refers to the condition where the whole plant is permanently displaced from the upright position due to uprooting while the culm remains straight and intact (Seyfu, 1983, 1993). Root lodging occurs near the plants' maturity and is not of immediate economic importance (Seyfu, 1983).

Factors causing tef lodging

Tef lodging can be caused by environmental factors, agricultural inputs, and crop factors (Wang et al., 2015, Ben-Zeev et al., 2020, Ayalew et al., 2020). Wind, rain, dew, light, and temperature are the major environmental factors that predominantly affect the lodging of tef (Van Delden et al., 2010; Shu-Yan et al., 2015; Dahiya et al., 2018; Feng et al., 2019; Khobra et al., 2019; Ben-Zeev et al., 2020). Plant stalk strength is not enhanced by the conditions of frequent rainfall, low radiation, and high temperature. But high radiation and low temperature are suitable for accumulation of dry matter and can increase the strength of stalk (Xue et al., 2017). The plant anatomical and morphological characters along with the chemical composition of the stem markedly affects lodging (Shah et al., 2019; Bayable et al., 2020; Ben-Zeev et al., 2020). Tef is very susceptible to lodging because of its tall, thin and weak stems that are easily displaced when high wind and/or rain occurred (Cannarozzi et al., 2018). The stem strength is very important to reduce the effects of lodging. It is primarily dependent on the exertion of external forces and internal capability (chemical composition and dry matter allocation) (Shah et al., 2019).

Chemical molecules such as lignin, carbohydrates, silicon, cellulose contents are also enhanced the culm strength of cereals (Khobra et al., 2019). The agronomic factors like sowing date and time, seed rate, fertilizer rate, and types, irrigation method, and amount also strongly influence lodging (Wu-Jun et al., 2014; Wang et al., 2015; Wu and Ma, 2016; Shah et al., 2019). Tef lodging is significantly increased by the high seed rate (Ben-Zeev et al., 2020). The high plant density causes weak, thin, and narrow culm stem which resulting in high lodging in wheat (Berry et al., 2004; Zheng et al., 2017), rice, maize (Sher et al., 2018; Xue et al., 2017), sorghum and tef (Ben-Zeev et al., 2020). This might be due to competition for light and photosynthesis assimilation which ultimately decreases dry matter accumulation of the lower internode (Shah et al., 2016). Similarly, Zheng et al. (2017) reported that the quality of culm internode diameter is increased by decreasing plant population density. Early sowing increasing stem elongation and tillers with thin and narrow stem diameter resulting in higher bending lodging (Shah et al., 2016). The irrigation method is also affects lodging in cereals (Pinera-Chavez et al., 2016).

Furthermore, various reports indicated that some plant nutrients such as silicon, potassium and phosphorus enhanced the stem strength and contributed to the lodging resistance (Epstein, 1999; Feng, 2004; Zaman et al., 2015; Kubar et al., 2018; Fallah, 2012; Demiss et al., 2020; Ayalew et al., 2020). But the high nitrogen fertilizer application further aggravated lodging by increasing the vegetative growth (the upper canopy) (Wu-Jun et al., 2014; Pan et al., 2019). The higher upper canopy reduces light transmission and dry matter that can inhibit the lower basal internode strength (Pan et al., 2019).

The effects of lodging

Lodging significantly reduces the yield and quality of tef seed. Seyfu (1983) reported that lodging can cause 17-23 % yield reduction of tef. Most recently, Ben-Zeev et al. (2020) reported that tef yield losses by lodging were estimated at 30-35%. Yield penalty due to lodging in other cereals is reported by various researchers (Table 1). Setter et al. (1997) reported for every 2% of lodging, 1% of grain yield reduction in rice. The magnitude of yield reduction by lodging depends on the time when lodging occurs and different yield related traits to lodging (Tian et al., 2018). For instance, Li et al. (2015) reported maize stalk lodging when occurred at twelve leaves and grain filling stage the yield reduction estimated to 28% and 45-48%, respectively. Lodged tef especially at maturity, the panicle becomes in contact with soil and starting seeds sprouting on the panicle as it gets some moisture (Figure 1). This situation severely affects the production and even maybe resulting in a total loss of yield.

Thus, late sowing by considering the outlet of rainfall may minimize this problem especially for the area of long rainfall duration occurs. Lodging interferes with the translocation of nutrients and disturbs the photosynthesis parts by insufficient light utilization which leads to the poor grain filling and yield reduction (Seyfu, 1983; Setter et al., 1997). Besides, lodging is not only affecting yield but also potentially deteriorating the quality of tef straw. Once the lodging occurred, the straw contact with soil and not desirable for livestock feeding. In addition, the lodging problem makes difficult harvesting by hand and mechanical harvesting near impossible, still no proper harvesting machine has been developed for tef mainly due to lodging.

Figure 1. The tef culm bending (a) and panicle emerged (b) on severely lodged tef due to prolonged rainfall at maturity.

Table 1. Lodging induced yield penalty in few cereals

	Yield penalty (%)	References
Wheat	Up to 61	Acreche and Slafer, 2011
	Up to 54	Berry and Spink, 2012
	8–34	Berry et al., 2004
	7-35	Fischer and Stapper, 1987
Tef	30-35	Ben-Zeev et al., 2020
	17-23	Seyfu, 1983
Rice	Up to 50	Setter et al., 1997
	1% yield reduction in every 2% lodging increase	Setter et al., 1997
Barley	30-35 in Iraq	Bhiah et al., 2010
	12-66	Tandon et al., 1973
	40	Rajkumara, 2008
Maize	5-25 in USA, 15-28 in Japan	Xue et al., 2017
	30-38 root and 45-48 stalk lodging when occurred during the grain-filling stage	Li et al., 2015
	5-20	Larsson et al., 2017
	5-40	Xue et al., 2017
	5-50	Xue et al., 2020
Oats	35-40	Pendleton, 1954

Progress made to improve tef lodging

Some research progresses were made to overcome the lodging problem in tef. The lack of genetic variability and the unfavorable association between lodging resistance traits are the two big challenges faced by the breeders (Assefa et al., 2011). Yield promoting traits such as panicle length, panicle weight, panicle yield, panicle form, and peduncle length are unfavorably associated with lodging tolerance in tef (Yu et al., 2007). The short stature, thick and robust stem traits are helpful in developing tef lodging tolerant variety. Genetic variability is the fundamental basis of plant breeding and indigenous germplasms are one of the most important sources of variability in tef. Although tef germplasms have been collected, characterized and used, there isn't enough variability in the available germplasms to provide lodging resistance characteristics (Assefa et al., 2011). So the mutation breeding was utilized to generate variability, especially for lodging traits. To develop semi-dwarf and lodging resistance tef plant, scientists demonstrated the high throughput techniques like Targeting Induced Local Lesions IN Genomes (TILLING) and modified method known as Eco-tilling (Assefa et al., 2011; Esfeld et al., 2011; Zhu et al., 2012). By implementing TILLING method, over 5000 mutagenized tef populations were screened for semi-dwarf phenotypes and as a result, two genes of interest have been cloned so far from tef (Assefa et al., 2011; Esfeld et al., 2011). The first two semi-dwarf lodging tolerant tef lines known as *kegne* and *kinde* were also developed from ethyl methanesulphonate (EMS) mutagenized populations (Jöst et al., 2015; Cannarozzi et al., 2018). *Kegne* is semi-dwarf and lodging tolerant tef line developed by a mutation in the *α-Tubulin* gene *EtTUA1* (Jöst et al., 2015). *Kinde* is a promising line characterized by lodging tolerant, semi-dwarf, larger leaf size, increased tillers and deep green, but its yield was not high as improved cultivars such as *Quncho* (Jifar et al., 2017). Thus, many crosses were done between mutant line and other tef cultivars for introgression of the gene of interest through conventional breeding at Debre Zeit Agricultural Research Centre (DZARC) in Ethiopia. Then one variety, *Tesfa* (crossing of *kinde* with *Kay Murri*) was released with desirable traits such as high yield, non-shattering type, thick and strong culm and compact panicle form (Kebede et al., 2018; Cannarozzi et al., 2018).

Traits useful for lodging tolerance in tef

Plant height, culm traits, panicle length, panicle weight, and peduncle length traits are the most lodging determinant traits in tef. The main stem of a tef plant is consists of internodes, peduncle, and panicle length, which altogether account for total plant height. Plant height is the main target for the improvement of lodging resistance and it shows a moderate to strong correlation with the lodging index (Girma, 2019). In tef, lodging index strongly and positively correlated with panicle length (0.81), plant height (0.8), peduncle length (0.71), length of third (0.73), and fourth internodes (0.72), and also moderately correlated with length of first and second basal culm internodes (0.65, 0.68) suggests that these traits could be useful indicators of lodging resistance (Girma, 2019). Panicle length is strongly corrected with grain yield and lodging index, and thus, the shortening of the panicle length may be reducing lodging however, it potentially decreases the grain yield. Panicle angle, panicle weight, and forms also the most contributor traits to lodging resistance (Blösch et al., 2020). The peduncle length account for 59% of plant height (Ben-Zeev et al., 2020) and very important as it is strongly and positively correlated with lodging index (Girma, 2019), that breeder should consider the shortening of peduncle length and the lower internodes length rather than panicle length could increase the lodging resistance without the much reduction of yield in tef. Further shortening plant height to improve lodging could affect the efficiency of photosynthesis which may also affect yield (Khobra et al., 2019). Even sometimes the dwarf phenotype that has thin and weak culms is extremely susceptible to lodging. Negative genetic correlation between lodging controlling traits, combined with the lack of genetic variability in tef germplasm for lodging tolerance, has resulted in the persistence of lodging difficulties in tef (Assefa et al., 2011).

There are contradicts among the scientists on the economic importance of root lodging. Seyfu (1983) noted that root lodging is not economically important on tef, whereas, Van Delden et al. (2010) reported as tef is more susceptible to root lodging. Ben-Zeev et al. (2020) reported root morphological traits such as crown diameter, crown root number, and crown root diameter were correlated with lodging index and most critical traits related to root lodging. Further they stated that the root parameters which are related to lodging index could be important to improve tef lodging. Besides these, the stem diameter and internode thickness (are related to the stem strength which play an important role in the lodging resistance. Therefore, to improving lodging resistance in tef, the focus should be given to the chemical compositions (lignin, silica pectin, cellulose, hemicellulose, and carbohydrate contents) from which the strong stem is formed.

Lodging and culm chemical composition relationship

The lignin, cellulose, and carbohydrates present in the culm influences its thickness and provides the strength of plant stem against lodging (Khobra et al., 2019). The higher concentration of lignin and cellulose contents in the cell wall enhance the resistivity of the stem to lodging in wheat (Peng et al., 2014; Zheng et al., 2017; Hyles et al., 2017), rice (Zhang et al., 2017b), barley (Kokubo et al., 1989) and maize (Lan et al., 2016). Silicon primarily found in the cell wall may increase the hardness, toughness, and elasticity of the stem which contribute to lodging resistance if found in abundant (Zhang et al., 2017a). Zhang et al. (2017a) also reported the basal internodes index, such as stem thickness, filling degree, lignin content, cellulose content, and carbohydrate were positively and significantly correlated with the culm lodging-resistant index of winter wheat. Shah et al. (2019) reported that the enzymes involved in the lignin accumulation may improve lodging in wheat. The structural and non-structural carbohydrate contents also affect the stem lodging resistivity in rice (Zhanga et al., 2017). A large accumulation of dry matter in the basal internodes led to an increased stubble size and culm strength (Wu-Jun et al., 2014). The lower basal culm internode plays an important role in the resistance to lodging by providing a lever to keep the plant upright (Zhang et al., 2017a). Lignin is a major biopolymer component of the cell walls in the plant, and lignin synthesis is related to growth and provides mechanical strength to plant (Bainsla et al., 2018). The starch accumulation in lower internodes partly responsible for the increase in lodging resistance in rice by increasing the physical strength of culms and leaf sheaths.

Lodging and some plant nutrients relationship

Plant nutrients influence the chemical composition and dry matter accumulation in plant parts. Some nutrients relatively relieve the lodging problem while some are may aggravate the risk of lodging. The imbalanced use of fertilizer may weaken the stem strength making it more susceptible to lodging. The most predominantly used plant element is nitrogen, phosphorus, potassium, and silicon which plays a superior role in plant growth and also influences the lodging. The effects of the major nutrients on plant growth and lodging are discussed in the following.

1. Silicon

Silicon is found abundantly in the Earth's crust (Savant et al., 1999), although it is not essential, beneficial plant nutrient which can improve biotic and abiotic stress resilience of the crop (Ayalew et al., 2020). Several reports indicated that the main functions of silicon are improving the growth, biomass, yield, and quality of crops (Liang et al., 2015). It is also important for the leaves' erectness. Most of the authors' noted that silicon is most important and responsible for the strength of plant stem resulting in lodging resistance. Silicon increases the mass and volume of the root which is important to the total and adsorbing surface. It is also responsible for the stability of stem for most cereal crops (Fallah, 2012). The silicon in the basal internodes is responsible for the rigidity of the culm which is helpful for the strength of the stem resulting in the resistance to lodging (Wu and Ma, 2016). A sufficient supply of silicon enhanced the deposition of silica gel in the forms of solid amorphous silica (SiO_2 in H_2O) in the cell wall and the reinforcement of wall provided by "opal phytoliths" serve to stiffen the stem and leaves of cereals (Epstein, 1999; Fallah, 2012). In rice, the degree of lodging is positively correlated to culm and basal internode length whereas negatively correlated with culm strength. The culm basal breaking strength and stiffness are important for lodging resistance in rice (Jun et al. 2017). So the thickness of a culm wall and vascular bundle becomes larger as silica was applied and this deposited silica in the plant section contributed to the mechanical strength of the culm (Feng, 2004). Dakora and Nelwamondo, (2003) reported that silicon nutrition increases the mechanical strength of cowpea stems. Ayalew et al. (2020) reported that the tef yield increased by 100% at the application of 3.0mM Si and shoot biomass increased by 45% at 5mM Si supply.

Interestingly, the use of Si has the potential to significantly increase tef productivity, which is expected to double the yield potential (Ayalew et al., 2020). However, unlike rice and wheat, Si did not appear to have enhanced its lodging tolerance (Ayalew et al., 2020). They did not take into account the effect of silicon on the strength characteristics of the stem, such as silica deposition in basal internodes, stubble thickness, and length concerning lodging resistance. Therefore, further research is required by considering the morphological, anatomical, and biochemical traits associated with the lodging resistance traits to clearly understand whether silicon enhancing lodging tolerance or not in tef.

2. Nitrogen

Nitrogen is the most essential and abundant nutrient in plant parts. It is responsible for the dark green color of the vegetative parts, over all vegetative growth (stem elongation, branches, tillers, leaf size and number) and yield formation of the plant. The main role of nitrogen is, as a part of the chlorophyll which is the most essential constituent of all proteins and the green color of plant parts which increases the efficiency of the photosynthesis system by increasing the light track. As nitrogen is a key element for plant growth, the increased nitrogen fertilizer application can cause lodging and then yield reduction in cereal crops (Wu-Jun et al., 2014; Wang et al., 2015; Zhang et al., 2017b). A high level of nitrogen increases stem height which make plant stem susceptible to lodging (Crook and Ennos, 1995). The stem strength gradually decrease in increasing the nitrogen which significantly reduces the lodging resistance (Zhang et al., 2017a). Crook and Ennos (1995) reported that high levels (240 kg ha^{-1}) of N application in wheat, the root and stem lodging increased by 17% and 20% respectively as compared to the application of 160 kg ha^{-1} N. The thickness of the stem substantially reduced by high amount of ammonium (NH^{+}_4) fertilizer and other nitrogen containing inorganic fertilizer which is potentially alters the physical strength of wheat stem (Kong et al., 2014; Wang et al., 2015; Shah et al., 2019). Tef lodging is exacerbated by nitrogenous fertilizer (Seyfu, 1993). The application of high (69 kg N ha^{-1}) nitrogen causes 66.67% lodging index which leads to a great yield losses in tef (Tesfaye et al. (2020). Most studies have been conducted to recommend the optimal rate of nitrogen fertilizer for tef, but have not considered the direct impacts of nitrogen fertilizer on lodging. Therefore, the research focus should be on the relationship between nitrogen fertilizer and the physical strength of the stem of tef is useful to set the optimal recommendation.

3. Phosphorus

Phosphorus is also one of the most essential plant nutrients next to nitrogen. It is often the nutrient limiting for crop production in tropical soils (Mamo et al., 2002). It is involved in the process of energy transformations, protein synthesis, genetic inheritance, and cell division (Gebreslassie and Demoz, 2016). It is an "immobile nutrient", which has a relatively short range of movement in the soil over time (Malhotra et al., 2018). Phosphorus plays a major role in root growth and increases resistance to abiotic stress. Many aspects of plant physiology including root growth, and photosynthesis processes are enhanced by sufficient phosphorus fertilization (Malhotra et al., 2018). It is important for seedling germination, and vigorous plant growth (Rose et al., 2013). Phosphorus relatively improved lodging resistance in oat (Casserly, 1957). Cereals straw strength is increased by application of phosphorus. However there is no comprehensive study that indicates the relation between tef lodging and phosphorus application. Therefore, further researches are necessary to exploit the role of phosphorus nutrient on tef lodging, whether it increases or decreases the risk of lodging.

4. Potassium

Next to nitrogen and phosphorus potassium is also the most essential macronutrient for plants which is abundantly available in the soil (Roy et al., 2006). Potassium plays a key role in enzyme activation, charge balance, and osmotic regulation, transpiration and regulating the stomata opening in plants (Roy et al., 2006). The higher K^+ content in the plant tissues effectively regulates many physiological and biochemical processes. Potassium imparts resistance to lodging by increasing the rind thickness and crushing strength (Rajkumara, 2008). Potassium fertilizer improved plant parameters such as basal internode length, cellulose content, stem fiber contents, and silicon contents which contribute to stem strength against lodging and other environmental stresses (Zaman et al., 2015). Application of K significantly increases yield and most of the growth traits in wheat and accumulation of other nutrients in yield and straw (Kubar et al., 2018). Application of K also increases the root growth and the base of the stem can improve the incidence of lodging in rice (Bhiah et al., 2010). The stem strength is related to the potassium content of the lower parts of the plant culm. Proper potassium application increases the lignification of sclerenchyma cells and vascular bundles which is important to the stem strength (Zaman et al., 2015). The potassium deficiency increases the risk of lodging in barley (Mäkelä et al., 2012). It also significantly increases plant height, panicle length, and biomass in tef (Mulugeta et al., 2019). The application 60-90 kg K_2O ha^{-1} is considered as the optimum rate for the tef. Besides, tef root establishments have been improved with the K application (Gebrehawariyat et al., 2018) which is useful to improve tef root lodging. Further work should be needed to understand the physiological and biochemical mechanisms contributing to tef stem strength when K fertilization applied.

Future prospects

Tef is an important crop that plays a crucial role in the food security of Ethiopia. It is primarily used as a staple food for almost all Ethiopian people. However, its production and productivity are limiting by several factors. Among these factors, lodging is one of the major bottlenecks in the tef production and also challenging in the tef improvement program. Several attempts have been made so far to overcome the problem of lodging, however, a tangible solution has not been developed. Still, the problem of lodging persisted and the highest tef yield potential is not yet attained. Tef has a thin and weak stem which makes it very susceptible to lodging so that the study on the traits directly and indirectly associated with stem thinness and weakness is useful as they are the driving force to lodging. Strengthening the previous investigations with some systematic modification is necessary. Recently, high throughput techniques have been implemented to obtain semi-dwarf tef and such techniques should be further involved in the stem strength of tef stem. The identification and use of the gene responsible for the stem thickness stem strength, root system, and spread are also useful for the improvement of tef lodging and need further investigation. The physical strength of culm is based on the chemical composition such as lignin, cellulose silicon, carbohydrate, and dry matter content which enhance the lodging resistance in various cereals. Similarly, nutrients like silicon, potassium, and phosphorus can enhance the stem strength of rice, wheat, maize, barley, and oats. Also, the enzymatic and hormonal activities play a great role in the accumulation of chemical molecules in the plant stem. However, such studies are limited on tef and further investigations are highly necessary for these areas for the improvement of lodging.

CONCLUSION

Lodging has a great treat through limiting the production potential of the crops. Understanding the lodging mechanisms enables the development of a comprehensive and realistic model of tef lodging. Plant characters like plant height, stem thickness, culm strengths, and the spread and depth of root plate relatively determine lodging risk in tef. The chemical compositions of the stem and the minerals applied have potentially altered the strength of the stem. Finally, tef lodging needs the highest priority since it imposes substantial yield loss. Thus, the integrated research approach that may combine anatomical, biochemical, morphological, and genetic studies is important to strengthen the understanding of factors that controlling the lodging and fastening the improvement of tef lodging.

AUTHOR CONTRIBUTIONS

Misgana Merga; conceptualization, information search and wrote the manuscript. Nagassa Dachassa; revised the draft of the manuscript.

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