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Review

Genetic management of drought in tef: Current status and future research directions

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Tef is the principal source of staple food supporting some 50 million people in Ethiopia. The crop is increasingly receiving global interest for its nutritional advantages because it is rich in nutrients and is gluten free. The yields of this crop are much lower compared to other cereal crops due to production constraints such as lodging, drought, pre- and post-harvest losses and poor agronomic management. Drought alone typically causes yield losses of 40% in tef. Consequently, developing drought tolerant varieties is of an overriding consideration to enhance productivity, especially in tef growing areas affected by drought. Success of breeding for drought tolerance depends on accumulation of additive genes for drought tolerance, accurate control of the stress environment and the use of high throughput selection methods to maximize selection gains. The review was aimed at providing perspectives on the current status and future research directions on the genetic management of drought tolerance in tef in order to reduce losses incurred due to moisture stress.

Key words: Drought, Ethiopia, gene action, gluten free, single seed decent, tef

INTRODUCTION

Tef [*Eragrostis tef* (Zucc.) trotter] is an allotetraploid (2n=4x=40), small cereal grain crop that belongs to the family Poacea, sub-family Eragrostoideae, tribe Eragrostidae and genus *Eragrostis* (Ketema, 1997). Tef is a staple food supporting some 50 million people in Ethiopia. Ethiopia is the center of diversity and origin of tef (Vavilov, 1951). Currently, the crop is increasingly receiving global attention for its nutritional advantages because it is rich in nutrients and is gluten free. It contains 11% protein, 80% complex carbohydrates, 3% fat (Piccinin, 2002). Tef has become globally known and various products are available in Europe and North America as health foods especially for persons with gluten intolerance (Saturni *et al*., 2010). Recently, limited levels of tef cultivation have started in the USA, the Netherlands and Israel. Tef straw is also a valuable source of livestock feed. In South Africa, India, Pakistan, Uganda, Kenya and Mozambique tef is mainly grown as a forage or pasture crop (Assefa *et al*., 2011). Interestingly, unlike other cereals, tef is little affected

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by field and storage pests and diseases (Ketema, 1997).

Tef grows under a wide range of ecological conditions from sea level to 2800 meter above sea level (m.a.s.l). It performs best at an altitudinal ranges of 1800 to 2100 m.a.s.l. The rainfall requirement of the crop varies from 450 to 550 mm. Tef requires temperatures of 10 to 27^{o}C and flowers best under 12 hour day length (Ketema, 1997).

Among the cultivated food crops grown in Ethiopia, tef ranks first, with an estimated production area of 2,730,272.95 ha and a mean productivity of 1.38 t ha^{-1} (CSA, 2013). Tef has the genetic potential to yield up to 6 t ha^{-1} (Ketema, 1993). The low productivity of tef in Ethiopia is mainly attributed to its susceptibility to lodging, its small seed size, poor pre- and post-harvest agronomic management practices, and moisture stresses (Ketema, 1997). Yield losses are estimated to reach up to 40% during severe moisture stress (Ayele, 1993). Further, yield reduction of up to 77% has been reported to have occurred as a result of drought at the anthesis stage of tef (Takele, 2001).

Most resource constrained farmers in sub-Saharan Africa including those in Ethiopia, face food insecurity due to regular droughts that are often exacerbated by climate change. In Ethiopia, agricultural activities and crop productivity are influenced by a wide range of environmental variables including; altitude, soil conditions, rainfall and temperature (Kassahun, 2013). As a coping strategy to deal with the risk of drought, smallholder farmers cultivate various crops and landrace varieties with different maturity periods. Due to its versatile environmental adaptation, tef grows in high rainfall as well as in drought-prone agro-ecologies. The crop yields relatively well in seasons with good rainfall, but also provides limited yields during drought periods, without a complete crop failure as would occur with other cereal crops such maize and sorghum.

Drought tolerance is a complex quantitative trait controlled by many genes and affected by the environment and genotype by environment interactions (Xoconostle-Cazares *et al*., 2010). Breeding for drought tolerance depends on the accumulation of additive genes, a controlled stress screening environment and high throughput selection methods to maximize selection gains (Blum, 2011). This review summarizes the literature on the genetic management of drought in tef. It highlights yield losses and the implication of drought, mechanisms of drought tolerance, important traits to be considered in tef breeding, gene action and selection methods for developing drought tolerant varieties. The aim of the review is to provide perspectives on current status and future research directions of the genetic management of drought in tef for reducing losses incurred by moisture stress. Literature from related cereal crops is adapted wherever necessary because of the scarcity of literature that deals specifically with breeding tef for drought tolerance.

DROUGHT AND YIELD LOSS IN TEF PRODUCTION

Drought is one of the main challenges facing world agriculture, but its effects may vary from region to region. Ethiopia is one of the sub-Saharan African countries facing recurrent droughts leading to low crop productivity or crop failure and food insufficiency (Deressa and Hassan, 2009). Declining levels and high variability of rainfall is among the main causes for low crop productivity in different parts of Ethiopia (Tilahun, 2006). Farming systems study at Adda District in Ethiopia indicated that poor rainfall distribution was among the major tef production constraints accounting to yield losses. A grain yield reduction of 1.0 t ha^{-1} was reported in tef due to 25% soil moisture deficit at the mid growth stage. Studied on effect of drought is so limited, which needs further investigation to come up with the solution.

BREEDING FOR DROUGHT TOLERANCE

Mechanisms of Drought Tolerance

Plants respond to drought with different mechanisms such as drought escape, dehydration avoidance and dehydration tolerance (Blum, 2011; Shashidhar *et al*., 2013). Drought escape is a mechanism in which plants mature early before drought occurs. This mechanism is advantageous in environments with frequent terminal drought stress (Tuberosa, 2012). Dehydration avoidance can be defined as the plant's ability to retain a relatively higher level of hydration under stress conditions. It is a mechanism where plants maintain their water potential through controlling the stomata opening and developing a deep and prolific root system (Mitra, 2001). Dehydration tolerance describes the ability of plants to continue metabolizing at low leaf water potential and to maintain growth despite dehydration of the tissue, or to recover after release from stress conditions.

Traits for Selection to Drought Tolerance

Phenological and morphological traits of drought tolerance

Among the different morphological traits, early crop establishment and vigor, early flowering and maturity, leaf rolling and a deep and extensive root system are the most commonly evaluated ones for selection of drought tolerant genotypes. In a dry climate, vigrous growht and efficient utilization of plant growth resources are deserable crop traits for good yield performance (Lidon and Cebola, 2012). Early and vigorously developed leaf biomass of a genotype enables storage of water that can be used in later growth stages when soil moisture is less available. This reduces the inhibition of stomata conductance (Monneveux *et al*., 2012).

Flowering and maturity period are two easily measured traits to be considered in screening trials. In optimum environments, the numbers of days to flowering and maturity have a positive correlation with yield while under moisture stress the correlation is negative. Therefore, selection should be targeted for early flowering and maturity genotypes (Kilic and Yagbasanlar, 2010; Blum, 2011). Plasticity of these traits enables the crop plants to have wide adaptation to environmental fluctuation by adjusting their growth duration to the specific environmental situation (De Rouw and Winkel, 1998). Moisture stress during the grain filling stage is a critical period which leads to significant yield loss in tef (Tsegay *et al*., 2012), indicating the importnace of selection for early flowering and maturity. Drought tolerance study on recombinant inbred lines (RIL) of tef along with varieties Key Murri, Cross-37 (a widely grown drought tolerant improved variety) and *Eragrostis pilosa* showed that, some of the RIL populations, Cross-37 and *Eragrostis Pilosa* were all early maturing genotypes that could escape late season drought events and yielded better under these conditions than the other varieties (Admas and Belay, 2011).

Leaf rolling is a dehydration avoidance mechanism. It assists in the reduction of transpiration water loss and often occurs if the plant leaf water potential is reduced (Kadioglu *et al*., 2012). This trait is also easily measured and can be evaluated in large number of genotypes grown under moisture stress. Another morphological trait that mitigates drought events is deep and extensive root system that enables crop genotypes to exploit moisture from deeper soil layers. Breeding and selection for root characteristics can, therefore, provide an indirect selection for drought tolerance in crop plants (Chloupek *et al*., 2010). Drought tolerant tef genotypes showed longer root (Ayele *et al*., 2001; Degu *et al*., 2008) indicating the importance of this trait for drought tolerance selection. However this trait is difficult and costly to evaluation (Babu, 2010). Consequently it is desirable to look for other traits that are correlated with root architecture to undertake indirect selection, especially when screening large number of genotypes.

Physiological traits correlated with drought tolerance

Physiological traits such as chlorophyll content, stomata conductance, canopy temperature and osmotic adjustment are among the important parameters found to be well-correlated with yield performance of genotypes under stressed environmental conditions. Crop growth is dependent on photo-assimilates of the whole plant, and proper functioning of photosynthetic pathways depends on continued transpiration and gas exchange through opened stomata (Arve *et al*., 2011). In tef, a 95% reduction of stomatal conductance was reported, when plots were watered at 25% field capacity (severe moisture stress level) (Mengistu, 2009). This reflects the sensitivity of stomata openings in tef to moisture stress that has adverse effects on yield through reduced rates of photosynthesis.

Plants keep their leaves at an optimum temperature through transpiration. Under moisture stress they avoid loss of water by closing their stomata, which leads to increased leaf temperatures. High temperatures impact on enzyme efficiencies in the leaves (Gonzalez-Dug *et al*., 2006). Drought susceptible genotypes that showed greater yield losses under drought tended to have warmer canopies. Lower canopy temperature of plants can be useful as an indicator of drought tolerance and its measurement is recommended at the vegetative growth stages (Monneveux *et al.*, 2012).

Osmotic adjustment is a process that lowers osmotic potential and increases leaf water potential due to the accumulation of soluble compounds in plant cells. This enables maintenance of cell turgor, improved soil water extraction and enhanced water use efficiency. The accumulation of organic compounds such as proline provides stabilization and protection of cell membrane systems (Zivcak *et al*., 2009). High osmotic adjustment enabled tef genotypes to delay wilting and hence retain higher leaf water content (Ayele *et al*., 2001; Degu *et al*., 2008).

Genetic Diversity and Environment in Breeding for Drought Tolerance

Breeding for drought tolerance largely depends on the existence of genetic diversity within the target and related crop species. The initial population for screening must be large and diverse enough to ensure that adequate genetic variability is represented to achieve strong selection response (Fischer *et al*., 2003). Selected cultivars, landraces, wild species, mutants and transgenic plants are some of source of variability in breeding for drought tolerance. Crossing of locally adapted varieties with improved varieties is recommended in developing drought tolerant varieties (Fischer *et al*., 2003). Often, the local varieties are a good source of genes for drought tolerance whereas the improved varieties are mostly known for their high yield (Shashidhar *et al.*, 2013). Tef productivity study under terminal drought in northern Ethiopia showed that, under severe moisture stress, the local tef varieties; Abat-Nech, Kobo and the widely grown drought tolerant improved variety DZ-Cr-37 had comparative grain yields of 1.43, 1.42 and 1.48 $t.ha^{-1}$ respectively. In contrast, the improved varieties namely; DZ-Cr-358, Dz-01-1281, DZ-01-1681 and DZ-01-99 yielded 0.93, 1.33, 0.60 and 0.31 $t.ha^{-1}$ respectively, indicting the sensitivity of the improved varieties to terminal drought stress (Mengistu and Mekonnen, 2011).

High throughput phenotyping for drought tolerance requires adequate control of the stress environment. Among other factors, site homogeneity and controlled drought conditions are two major factors. The site should be uniform in topography, soil fertility status, previous season cropping, and moisture status (Blum, 2011). For a managed drought tolerance study, different methods can be employed to control unwanted rainfall such as the use of dry season environment, delayed planting, rain-out shelters and greenhouses (Blum, 2011). In using delayed planting, it is important to know the planting time of the area at which the trial is to be conducted and the likelihood of unwanted rainfall to avoid its confounding effect on deliberate moisture stress. In semi-arid environments where the rainfall is erratic and unpredictable, it is difficult to conduct drought tolerance studies using delayed planting. Rain-out shelters offer the possibility of investigating the adaptive response of crops to a desired level of drought stress through avoiding the unpredictable rainfall events. An off-season study of drought tolerance is a common approach in the semi-arid tropics (Blum, 2011). But during the off-season the climatic conditions may be different from the main season; so it is important to understand the off-season conditions of the location where the trial is to be conducted. Greenhouse pot experiments are also an option to study drought tolerance in an artificial environment. This is mostly used in studying root characteristics of crop plants under drought condition. It is easy to manage the stress conditions but the greenhouse soil and environmental conditions will be different from that occur in the field.

Gene Action of Drought Tolerance

Drought tolerance is a complex trait, in which its expression depends on the action and interaction of different genes, and the environment, which control morphological, physiological and biochemical characters. The success of any breeding program for developing drought-tolerant varieties depends on precise estimates of genetic variance components of the traits of interest that mainly consist of additive, dominant and epistasis genetic effects (Nouri *et al*., 2011).

In wheat, Chowdhry *et al*. (1999) reported flag leaf area and spike length being controlled by over-dominance gene action while number of fertile tillers per plant, 100-grain weight and grain yield showed partial dominance gene action when genotypes were tested under drought stress. Farshadfar *et al*. (2011) studied the inheritance of drought tolerance in bread wheat (*Triticum aestivum* L.) and reported that additive and non-additive gene actions were responsible for controlling all agronomic and physiological traits. There is no information on gene action and inheritance about tef under stress condition. While under non-stressed condition, Tefera and Peat (1997) reported dominance gene action for grain yield and panicle weight and large portion of additive gene action controlled plant height, panicle length, days to heading and days to maturity. Similarly, Tefera (2002) reported largely additive gene effects controlling plant height, kernels per spikelet, primary panicle branches, panicle weight and spikelet's per panicle, while there was small additive effect for grain yield. The author emphasized the importance of selecting for additive gene effects when selecting for drought tolerance in tef.

Selection of Drought Tolerant Genotypes Using Single Seed Descent

Single seed descent (SSD) is one of the most important selection methods for complex quantitative traits such as drought tolerance. It is a procedure of advancing early segregating generation through a single seed derived from each plant of diverse crosses. In this method, selection of progenies and families starts at the F_6 or F_7 generations, enabling the accumulation additive genetic variance effects. At the F_2 generation, only half of the additive genetic variance is present and could not guarantee high selection response. From the F_8 onwards, multi-location preliminary and national variety trials can be conducted as per national testing requirements (Acquaah, 2007). This procedure was developed with an aim of advancing large numbers of F_2 plants from diverse cross combinations to yield trials to assess their potential for producing lines with a full spectrum of desirable characteristics. In self-pollinated crops such as tef, additive genetic variance along with additive x additive gene action can be exploited through the use of SSD selection method. To exploit the total additive genetic variance, continuous selfing is required to attain homozygosity. Other selection methods such as pedigree selection or pure line selection begin at earlier generations leading to a loss of additive genetic variance. The SSD method has been used by various researchers to fix additive genetic variance (Sleper and Poehlman, 2006).

Lalic *et al*. (2003) compared barley genotypes developed by pedigree and SSD methods. The authors reported that genotypes developed through SSD selection showed superior grain yield performance to the genotypes developed through the pedigree method. Knott and Kumar (1975) also reported the advantages of SSD methods for developing superior yielding wheat gentoypes and reduced the cost of handling segregating generations relative to the pedigree selection method. Tefera and Peat (1997) and Tefera (2002) proposed leaving selection of tef segregants to advanced generations to increase homozygosity to enable the exploitation of additive gene action for quantitiative traits such as yield and drought tolerance.

Pre-breeding and Breeding of Drought Tolerant Tef in Ethiopia

There is limited information on the genetic basis of drought tolerance in the Ethiopian tef landraces, cultivars and breeding lines despite the significance of the crop and occurrence of frequent droughts in the country. Understanding the present information on genetic management of drought tolerance in related cereal crops should aid in the identification of an appropriate breeding strategy. This will enable tef breeders to routinely introduce candidate genes into drought susceptible breeding lines for cultivar release. These genes should be introgressed into the widely used tef cultivars as a means to increase drought tolerance.

Given the need to breed tef for drought tolerance and other relevant agronomic traits, the Institute of Biodiversity Conservation of Ethiopia and the Ethiopian Tef Breeding Project based at Debre-Zeit have collected a wide genetic pool of tef germplasm. These genetic resources can be explored to combat drought by searching for novel drought tolerant genes aimed at developing germplasm with drought tolerance. Phenotypic field selection can be complemented with genomic techniques to identify and diagnose effective drought tolerant genes. Marker-assisted selection (MAS) has been proven to be a powerful tool to aid in the development of cultivars with drought tolerance in other crops such as wheat, rice and pearl millet (Jongdee *et al.*, 2006; El Ameen, 2013).

There is a need to develop and identify diagnostic molecular markers that are linked to effective drought tolerance genes in tef for routine applications of MAS in breeding programs. The markers linked to drought tolerance genes could be used to predict the presence of specific genes and might help in the transfer several genes in to adapted materials. Presently, low cost and next-generation sequencing platforms are becoming available. Consequently, more diagnostic markers may be made available for high-throughput screenings and application of MAS in tef breeding for drought tolerance. To date, there is no research on gene cloning in tef aimed to incorporate drought tolerant genes into suitable genetic backgrounds. Tef breeders should consider using the doubled haploid (DH) breeding technique, which has the potential to reduce the number of selfing generations required for maximium homozygosity and release of new varieties (Gugsa and Kumlehn, 2009; Tadesse *et al*., 2013). Overall, pre-breeding and breeding efforts should be strengthened to develop drought tolerant cultivars in Ethiopia. With advancements in high throughput technology and MAS, tef breeding programs can integrate new sources of drought tolerance into the existing gene pool to sustainably manage drought in water limited agro-ecologies.

CONCLUSIONS

Tef is an important staple food grain crop in Ethiopia, and it is internationally gaining popularity as a health food. Despite its great economic and nutritional importance, the current tef yield is low, about 1.38 t ha^{-1} (CSA, 2013). The major constraints are lodging, small seed size, moisture stress and poor pre- and post-harvest managements. Breeding drought tolerant tef varieties would provide a genetic management approach to enhance and sustain tef productivity, especially in the drought-prone regions.
Breeding for drought tolerance remains the most feasible and economical approach to drought management. Tef breeders need to continuously search new sources and introgress these genes into susceptible cultivars. Germplasm screening using both phenotypic and genotypic data is important to identify drought resilient breeding lines. Furthermore, the national breeding project should strengthen capacity development efforts for effective breeding for drought tolerance in the country. The need for international collaborative initiatives needs to be emphasized to adapt new and advanced technology. This imitative will assist in the release and promotion of new cultivars with drought tolerance genes aligned with rapid seed multiplication systems and institutional coordination. There is a need for an intensive study and understanding of the genetics and variability of drought tolerance which will require research funds to be allocated to breed better tef cultivars.

Thus far, research activities on breeding tef for drought tolerance are limited. In light of this limitation, the present paper highlighted important outlooks on the current status and future research directions on the genetic management of drought in tef for reducing losses incurred due to low moisture stress.

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