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QTL mapping for abiotic stress tolerance in maize: A brief review

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Abstract

In this review article, we describe various QTLs that are associated with abiotic stress tolerance in maize. As we know, as global climate is becoming unpredictable and erratic. Yield in maize is affected by abiotic stress caused by unfavourable environment. So, exploiting QTLs associated with abiotic stress is the one of the way to achieve yield increase in maize. This review tells how QTL-based approaches has helped in improving the maize crop to perform well under various kinds of abiotic stresses. Success can be achieved by the identification of large effect QTLs that are linked with abiotic stress tolerance related traits. The QTL approach therefore provides a way to investigate out the various components affecting source sink relationships of maize plants under abiotic stress.

Keywords: Maize, QTLs, abiotic, stress

Introduction

There is evidence that global mean temperatures are increasing and the climate is becoming increasingly erratic, with increased drought in some areas and more and stronger storms (IPCC 2007) [15]. The future challenges of crop production in the tropics, especially in certain arid and semi-arid areas of Africa, will be related to higher temperatures and less rainfall (Sivakumar *et al.* 2005) [49].

The increase in yield of maize many folds is probably possible through the direct or indirect exploitation of quantitative trait loci (QTLs) which control heritable variance of traits and various physiological mechanism of maize in different environment. This review probe how QTL-based approaches contribute has helped in improving the maize crop to perform well under various abiotic stresses (drought, water logging, and heat) so that it can help further breeders to release varieties in maize.

The performance of any crop under a particular environment is the resultant of the action of thousands of gene with that particular environment. Success can be achieved by the identification of large effect constitutive QTLs for abiotic stress tolerance related traits and their validation in a related mapping population. The QTL approach provides an opportunity to investigate out the genetic and physiological components affecting source sink relationships under abiotic stress (Prioul *et al.*, 1997, 1999; Miralles and Slafer, 2007; Welcker *et al.*, 2007) [35, 34, 29, 55]

QTLs for drought tolerance in maize

Among the different abiotic stresses drought is by far the most complex and devastating one globally (Pennisi, 2008) [33]. Drought at any stage of plant development affects grain production, but causes maximum damage in maize when it occurs around the time of flowering (Banziger *et al.* 2007) [2]. A commonly used secondary trait for drought tolerance in maize is the asynchrony between silk emergence and pollen shedding. Under water-limited conditions, this asynchrony, termed the anthesis-silking interval (ASI), is highly correlated with grain yield (Edmeades *et al.* 1993) [10], which has been extensively studied through linkage analysis (Ribaut 2009) [39].

A number of studies have revealed QTLs for root architecture and have investigated their effects on yield under various moisture conditions in maize (Tuberosa *et al.*, 2002, 2003; Landi *et al.*, 2007) [51, 52, 16]. In Maize, a major QTL originally reported for leaf ABA concentration (Tuberosa *et al.*, 1998) [53] whereas, later shown to affect root size and architecture (Giuliani *et al.*, 2005) [13] and grain yield (Landi *et al.*, 2007) [16]. Following its isogenization (Landi *et al.*, 2005) [17].

Biomass accumulation and the maintenance of growth under water deficit permits better light interception by leaves, leading to increase in photosynthesis side by side increasing transpiration by leaves, leading to not only increase in photosynthesis but also transpiration rate and soil water depletion. Therefore, it is an appropriate strategy for mild water deficits. The water deficit along with decline in leaf growth rate results in decreased photosynthesis and transpiration rate. With a cessation of nocturnal leaf growth occurring in a range from -0.8 to -1.6 M Pa (Welcker *et al.*, 2007) [55], a high degree of genetic variability in sensitivity has been observed in maize. QTLs of leaf growth sensitivity to water deficit largely overlapped with QTLs for leaf responses to evaporative demand were reported in three maize mapping populations, (Reymond *et al.*, 2003; Sadok *et al.*, 2007; Welcker *et al.*, 2007) [38, 46, 53]. Half of the QTLs for silk growth overlapped with those for sensitivity of leaf growth (Welcker *et al.*, 2007) [55] in one mapping population, which suggest that mechanisms favouring expansive growth affect multiple organs.

Water stress at flowering, when pollination, fertilization and grain initiation take place, has a stronger negative effect on cereal production than at other developmental stages (Saini and Westgate 2000) [47]. Maize in particular is highly susceptible to water stress at flowering (Claassen and Shaw 1970; Westgate and Boyer 1985) [8, 56], because it is an open pollinating crop, the male and female flowers of which are spatially separated on the plant. Extensive research into the tolerance of maize to drought stress at flowering identified key secondary traits of grain yield, such as the anthesis-to-silking interval (ASI), improved ear fertility, stay-green and, to a lesser extent, leaf rolling (Bruce *et al.* 2002) [6]. Drought stress limits photosynthesis and reduces the flux of assimilates to the developing ears (Schussler and Westgate 1995; Zinselmeier *et al.* 1995) [48, 58], slowing down ear and silk growth and delaying silk emergence. Since tassel growth is less affected by drought than ear growth, the characteristic widening of the ASI is observed under waterlimited conditions (Heisey and Edmeades 1999) [14]. As a consequence of the time lag between pollen release and silk emergence, pollination and kernel set are affected. Pollen viability and silk receptivity can also be reduced (Saini and Westgate 2000) [47]. Conventional selection for grain yield and secondary traits considerably improved the tolerance of maize to water-limited conditions (Campos *et al.* 2004; Monneveux *et al.* 2006; Ribaut *et al.* 2008) [7, 31, 40], but remains a slow and challenging task. The growth rate of the silks in maize differs between genotypes, resulting in differences in the relative timing of female and male flowering, which is negatively correlated with yield and increased by water deficit (Duvick, 2005) [9]. Large genetic gains produced by Phenotypic selection under well-managed stress environments for low Anthesis-Silking Interval (ASI) (Ribaut *et al.*, 2004) [41]. Five QTL alleles for short ASI introgressed through MABC were from a drought-tolerant donor to an elite line. When compared to unselected control, under severe drought, the selected lines has clearly out yielded. However, this advantage vanished when stress curtailed yield less than 40% and decreased at a lower stress intensity (Ribaut and Ragot, 2007) [42].

QTLs for waterlogging tolerance in maize

Waterlogging which results in oxygen deprivation in the rhizosphere, is a serious abiotic stress in plants (Visser *et al.* 2003) [54]. Substantial variation exists among maize genotypes

in response to waterlogging (Zaidi *et al.* 2004; Liu *et al.* 2010) [57, 20]. The degree of stress in waterlogged soils is associated with growth stage, duration of flooding, soil type, soil acidity/alkalinity, climatic factors, growth conditions and genotypes (Rathore and Warsi, 1998) [57]. In a previous study (Zaidi *et al.*, 2004) [57], the early stages of maize development were shown to be the most sensitive to waterlogging, especially from the second leaf stage (V2) to the seventh leaf stage (V7), and roots are the first to be affected under waterlogged conditions. When the waterlogging treatment was continued for 6 d, most roots except for some adventitious ones were found to be decomposing, and plants were unable to take up the required atmospheric and edaphic nutrients, resulting in leaching and denitrification as a result of nitrogen deficiency. The latter is observed as a yellowing of the older leaves. Nitrogen deficiency itself then further increases plant stress. During waterlogging, gas exchange between soil and air decreases as gas diffusion in water is decreased 104-fold (Armstrong and Drew, 2002) [1], O₂ in the soil is rapidly depleted, and the soil may become hypoxic or anoxic within a few hours (Gambrell and Patrick, 1978; Malik *et al.*, 2002) [12, 22]. The anaerobic response of maize has been extensively reviewed previously (Sachs, 1993, 1994; Sachs *et al.*, 1996; Mustroph and Albrecht, 2003) [44, 45, 43, 32].

Some recent studies have documented variation in the anaerobic response of maize to flooding (Sachs *et al.*, 1996) [43] and several morphological responses during waterlogging have been also reported (Subbaiah and Sachs, 2003) [50]. According to previous studies, the inheritance and expression of traits associated with waterlogging tolerance in maize seedlings are physiologically and genetically complex (Sachs, 1993; Liao and Lin, 2001; Subbaiah and Sachs, 2003) [44, 19, 50]. Complicated responses to waterlogging, such as anaerobic proteins synthesis, alterations of gene expression, metabolic (switch to a fermentative pathway) and structural changes (e.g. aerenchyma formation) have been observed. There appears to be inherent genetic variability in maize with regard to waterlogging tolerance (Sachs *et al.*, 1996) [43]. However, manipulating waterlogging tolerance in maize is still hampered by inadequate knowledge of the molecular and physiological basis of the process.

The waterlogging tolerant mechanism in maize comprises of a large number of many minor QTLs and only a few major QTLs ($R^2 > 10\%$ often was adopted as major QTL) (Li *et al.* 2012) [18] were associated with waterlogging tolerance for example, *Qarf7.04-5* (Mano *et al.* 2005) [24], *Qaer 1.06* (Mano and Omori 2009) [26], *Qaer 1.06-1.07* (Mano *et al.* 2012) [28] and *sdw9-1*, *rdw9-1*, *tdw9-1*, *tdw9-2*, *tdw9-3*, *sdw9-4* (Qiu *et al.* 2007) [36].

Mapping of Quantitative trait loci (QTL) has revealed a number of chromosomal regions that affect important traits, Such as root and shoot development traits (Qiu *et al.* 2007) [36], Capacity for root aerenchyma formation (Mano *et al.* 2007, 2012; Mano and Omori 2008, 2009) [27, 28, 25, 26], Adventitious root formation (Mano *et al.* 2009) [26], tolerance to toxins under reducing soil conditions and leaf injury.

In maize, adventitious (nodal) root formation (ARF) at the soil surface can provide resistance to soil flooding or waterlogging (Bird, 2000) [4]. It has also been reported that some maize lines can express ARF during flooding (Lizaso *et al.*, 2001) [21]. It has been seen that *Z. luxurians* and *Z. mays* ssp. *huehuetenangensis* exhibit a higher capacity for ARF than some maize inbreds and QTLs associated with ARF in chromosome 8 and chromosome 4.

QTLs for heat tolerance in maize

Excessive heat in maize perturbs many cellular and developmental processes which in turn directly affects grain quality and grain production by reducing fertility. (Barnabas *et al.*, 2008) [13]. Male gametophyte development seems most prone to distribution by heat as well as drought (Mamun *et al.*, 2006) [23]. It is not clear if there is any common basis of sensitivity of male reproduction to various stresses. In maize, QTLs were identified that controlled pollen heat tolerance (germinability and pollen tube growth), a factor influencing heat-induced sterility (Frova and Sari-Gorla, 1994) [11] maize is less prone to heat stress one of the reason might be maize originated in tropical regions. In maize drought and heat stress often occur simultaneously in the field, which affects crops more severely than drought or heat stress alone (Mittler 2006) [30].

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