

Breeding strategies for improving growth and yield under waterlogging conditions in maize: A review

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Abstract

Waterlogging, caused by flooding, excessive rains and poor drainage is a serious abiotic stress determining crop productivity worldwide. Maize (*Zea mays* L) is a basic food grain in many areas and several cultures and is cultivated under much diverse agro-climatic zones extending from subtropical to cooler temperate regions. Therefore, the crop remains open to varied types of biotic as well as abiotic stresses. Among various abiotic stresses, waterlogging is one of the most important constraints for maize production and productivity. Breeding for improved waterlogging tolerance includes modification of plant morphology, use of tolerant secondary traits and development of resistant varieties through conventional breeding and biotechnological approaches. A successful programme in conventional breeding should involve the integration of several criteria into one selection index and also successful breeding programmes for improved tolerance to submergence stress frequently combine two or more breeding strategies. Marker assisted selection (MAS) is an effective approach to identify genomic regions of crops under stress and construction of molecular linkage maps enable carry out pyramiding of desirable traits to improve submergence tolerance through MAS.

Keywords: waterlogging, anaerobic conditions, submergence tolerance, conventional and molecular strategies, maize

Introduction

Maize (*Zea mays* L) occupies a prestigious place in the world agriculture. It is a miracle crop in view of its widespread usage as food and non food items. The humble kernel of corn finds its way into our life as edible and inedible products, including rubber, plastics, fuel, clothing, food additives, adjuncts and literally thousands of other forms. Maize can be grown over a diverse environmental and geographic range. Changing climate has resulted in increase of abiotic stresses which limit the crop yields worldwide (Gosal et al, 2009; Wani and Gosal, 2010; 2011; Sanghera et al, 2011; Wani et al, 2013; Wani and Sah, 2014). The crop grown in tropics during summer-rainy season occasionally face extreme climatic conditions and various biotic/abiotic pressures that severely limit crop growth and development and eventually the yield potential. Among the abiotic stresses, Excess Soil Moisture (ESM), caused by flooding, water logging or high water table or heavy soil texture is one of the most important constraints for maize production and productivity in Asian region. It has been calculated that approximately 16% of the fertile areas of the world are affected by soil waterlogging (Ahsan et al, 2007). In South Asia alone, more than 15 per cent of total maize growing area is affected by flooding and water logging problem (Rathore et al, 1998). In India, waterlogging is the second most serious con-

straint for crop production after drought, where about 8.5 million hectare of arable land is in the grip of this problem. Maize is highly sensitive to waterlogging and submergence during germination and seedling stages and leads to poor seedling establishment, stunted growth, and delayed development (Campbell et al, 2015). Out of total 9.4 million hectare area of maize, about 2.5 million hectare is affected by excess soil moisture problem that causes an average 25-30 per cent loss of national maize production almost every year (Anonymous, 2014). In India, the season in which the crop is grown (June-October) is characterized by erratic rainfall, hence it is difficult to avoid excess moisture at one or the other stages of crop growth. In case of June planting it may coincide with flowering which may interfere with the normal pollination behaviour and seed setting (Savita et al, 2004). The maize crop suffers badly whenever it encounters temporary ESM condition during the monsoon season or grown in poorly drained converted paddy fields after a rainy season rice crop, a practice more common in Thailand, Japan and East China (Shimizu, 1992). The effects of ESM are highly unpredictable and the intensity of stress may also vary from location to location and year to year. Maize plants are injured more and greater yield losses occur when flooded at early stages. Further, maize plants have no ventilating system for transport of oxygen between upper

organs and roots.

Maize cultivars with increased resistance to ESM conditions are particularly important for cultivation in marginal and sub-marginal environments. Plant growth in the field is not affected immediately after the flooding virtually, despite the speed with which the soil is saturated, but the after effects result in substantial reduction in the final yield (Wenkert et al, 1981). Several important factors including germplasm choice, selection environment, stress levels and breeding methodology are required to be considered before attempting to improve the germplasm for the targeted ESM stress. In this review, we will elaborate the mechanism involved in waterlogging tolerance and discuss the application of conventional and modern breeding approaches for development of waterlogging tolerance in maize.

Mechanism of Waterlogging Tolerance

Depletion of oxygen is a key feature of waterlogging, because the diffusion of oxygen in water is slower than that in air. The imbalance between slow diffusion and rapid consumption of oxygen in plant roots drastically reduces the oxygen supply (Erdmann et al, 1986), which is vital to the survival of plant roots. Some plant species can withstand waterlogging condition because of the presence of various mechanisms such as increased availability of soluble sugar, aerenchyma formation, greater activity of glycolytic pathway and fermentation enzymes and involvement of antioxidant defense mechanism to cope with the oxidative stress induced by waterlogging. It has been reported that ethylene plays an important role in change of mechanisms of plants in deficiency of oxygen as it induces the genes of enzymes associated with aerenchyma formation, glycolysis and fermentation pathway (Alamgir and Uddin, 2011). The mechanism is discussed under following heads:

Hypoxia and Anoxia

Waterlogging and submergence lead to reduced gas exchange between the plant tissue and atmosphere, because gasses particularly oxygen diffuses 10000 times more slowly in water than in air (Armstrong, 1979). This leads to hypoxia and anoxic conditions around the roots of plant which are major determinants of the adverse effects of flooding. Hypoxia (reduction of oxygen below optimum level) occurs during partial submergence of plant due to short-term flooding, while anoxia (complete absence of oxygen) occurs during long-term flooding. In case of hypoxia the root goes under water and the shoots remain in the atmosphere and in anoxia condition the plant remains completely in water. Microbial flora of the soil are disturbed by anoxia which works in favour of anaerobic microorganisms which works as alternatives for electron acceptors to oxygen and in such conditions, reduced and phyto-toxic forms of mineral ions gets accumulated and there are very few number of plants which naturally adapted to grow under such

soil conditions (Ponnamperuma, 1972).

Ethylene Production and Flooding

Plants differ widely in their capacity to adapt to oxygen deficiency (Colmer, 2003). Usually, the roots of plants are not suddenly exposed to anaerobic conditions, but under most circumstances, a gradual transition from normoxia to hypoxia to anoxia provides an opportunity for acclimation before conditions become lethal (Drew, 1997; Mustroph and Albrecht, 2003). Three different mechanisms are known for sensing hypoxia or anoxia: haemoglobin gene expression linked to increased activity of alcohol dehydrogenase (ADH) (Silva-Cardenas et al, 2003), changes in the concentration of cytosolic Ca^{2+} (Drew, 1997) and ethylene (Colmar, 2003; Evans, 2003; Voesenek et al, 2006). Mostly sensing occurs under hypoxic conditions when roots cannot obtain enough oxygen for respiration. Under such conditions the roots react with fermentative processes where ethanol and lactic acid are formed (Sorrell, 1999). Accumulation of lactic acid causes cytoplasmic acidosis which inhibits lactic dehydrogenase (LDH). As a consequence, fermentation is switched to production of ethanol rather than to lactate (Armstrong and Drew, 2002). In hypoxic roots, the synthesis of ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) is stimulated. ACC is then transported to the shoot where its oxidative conversion to ethylene takes place.

Ethylene and aerenchyma formation

The soft tissues with continuous gas filled channels or much enlarged gas spaces to render low-resistance internal pathways for the movement of O_2 from the shoots to the roots are called Aerenchyma (Armstrong and Webb, 1985). The aerenchyma are formed either as part of normal development or in response to stress (e.g. hypoxia, nutrient deficiency) by two known mechanisms: lysigeny and schizogeny (Evans, 2003; Visser and Voesenek, 2004). *Lysigenous aerenchyma* is formed through cell lysis (death) (Haque et al, 2010), while *schizogenous aerenchyma* is formed by the separation of cells from each other, often accompanied by cell divisions and normal expansion (Jackson and Armstrong, 1999; Colmer et al, 2004). Under submerged conditions, ethylene production is accelerated which in turn stimulates aerenchyma formation in adventitious roots and induces the growth of the roots (Jackson, 1989). In maize roots (*Zea mays*), aerenchyma are formed by the death of cells in the mid cortex zone behind the root apex which is initiated by ethylene. Lysigeny subsequently spreads radially and longitudinally to form gas spaces separated by radial bridges of living cells linking the stele and epidermis (Gunawardena et al, 2001a; 2001b; Bouranis et al, 2003). An ethylene-induced enhancement of root formation was found in maize (Gunawardena et al, 2001a). Bragina et al (2003) reported that with the augmentation of ethylene concentration, the hydrolytic enzymes including cellulose, xylanase and pectinase are activated in

maize adventitious roots under partial flooding. The activation of cell wall loosening/degradation related enzymes are an important event in aerenchyma formation. Aerenchyma tissue in roots allows the roots to respire aerobically, to form small zone of oxygenated soil around the roots and to maintain growth under hypoxic conditions and thus prevent the influx of potentially toxic soil components such as nitrates and sulphides of Fe, Cu, and Mn (Colmer, 2003).

Ethylene accumulation and adventitious roots formation

Ethylene production is a typical response in waterlogged plants (Bailey-Serres and Voeselek, 2008). Submergence dependent ethylene accumulation plays an important role in adventitious root emergence by favoring cell-wall loosening through regulation of apoplastic pH or up-regulation of expansin genes, which promote cell-wall disassembly (Steffens and Sauter, 2009; Zhaohui et al, 2009). Cell-wall loosening would reduce the mechanical resistance of stem tissues and facilitate new root emergence. Jackson (1985) suggested that, in flooded plants, only the outgrowth of preformed primordia might be stimulated by ethylene, whereas de novo root formation needs other stimuli. He also found that application of 5 $\mu\text{l l}^{-1}$ ethylene promoted adventitious root formation in maize as well. The development of adventitious roots replaces the old root systems and because of their position close to the water surface they have more access to oxygen than the old root system. Large air space between these roots enables diffusion of gas between roots and shoots. In rice the development of these roots is initiated by the death of nodal epidermal cell covering the tip of primordia which occurred as a result of flood-induced ethylene development (Jackson and Drew, 1984).

Conventional Breeding for Water logging Tolerance

Maize crop is generally grown during the kharif season in all parts of the world and during the moonsoons, the crop faces a variety of biotic and abiotic stresses that limit yield potential. Among various abiotic stresses, water-logging is one of the most important constraints for maize production in Asia and many other parts of the world. It has been estimated that over 18% of the total maize growing areas in South and Southeast Asia alone, the crop is affected by floods and water-logging problems (Zaidi et al, 2009). Unlike rice plants, maize plants have no naturally occurring air spaces in their roots. Therefore, due to gradual decline in oxygen, plant roots suffers from hypoxia (low oxygen) followed by anoxia (no oxygen) (Dennis et al, 2000) and root rot diseases which causes reduction of growth and loss of yield (Schmitthenner, 1995), also includes nitrogen deficiency of plant (Fausey et al, 1985) or nutrient imbalance (Thomson, et al, 1989). The stress damage varies significantly with the developmental stage of

the crop. Studies have shown that maize is comparatively more susceptible to water-logging from the early seedling stage to the tasseling stage (Mukhtar et al, 1990; Zaidi et al, 2004). Increase in the development of brace root in tolerant genotypes under water logged conditions was identified as one of the stress-adaptive traits in maize (Subbaiah and Sach, 2003; Mano et al, 2005; Zaidi et al, 2007) and significant decrease in leaf chlorophyll contents was identified as one of the first stress symptoms (Zaidi and Singh, 2001; Zhou et al, 2004).

Harlan (1976) reported that wild species provide good genetic resources for introducing superior levels of biotic or abiotic stress tolerance. Some of the Teosintes obtained from Mexico, Guatemala, Honduras, and Nicaragua may provide a superior genetic resource for the development of flooding tolerant maize as these regions are known to receive frequent rainfall. An accession of *Z. nicaraguensis* (teosinte) had shown adaptation to the northwest coastal plain of Nicaragua and is known to tolerate frequent flooding during a 6-month rainy season. Some of the superior features of teosinte as a potential germplasm resource for the breeding of maize are adventitious root formation at the soil surface during flooding and formation of root aerenchyma (Bird, 2000; Iltis and Benz, 2000). Mano et al (2005a) observed adventitious roots formation at the soil surface during experimental flooding conditions of some flooding tolerant maize lines. They further observed that teosinte *Z. luxurians* and *Z. mays ssp. huehuetenangensis* exhibit a higher capacity for adventitious root formation than some maize inbreds. As a consequence, the adventitious roots of this teosinte can obtain oxygen and this characteristic may play an important role in its adaptation to flooding conditions.

An experiment was conducted to assess the effects of excess soil moisture (ESM) stress on maize extent of genetic variability and morpho-physiological / metabolic basis of stress tolerance by Zaidi et al (2003). The results revealed that ESM stress severely affected growth, biochemical composition and metabolic activities, both at early stage and knee-high stage of the crop. Genotypes with early adventitious rooting, partial stomatal closure, < 5.0 days anthesis-silking interval, increased root NAD⁺-alcohol dehydrogenase activity and high starch accumulation in stem tissues showed good tolerance to ESM stress. Most of these morpho-physiological traits associated with ESM tolerance were common in both pre-existing and induced (pre-hypoxia / anoxia) tolerance, however, hypoxia / anoxia pre-treatment enhances tolerance to waterlogging conditions. They concluded that ESM tolerance was mainly based on the stress avoidance mechanism by anaerobic metabolic and alternative arrangement like brace root development will be effective to avoid anoxia condition.

An attempt was made by Zaidi et al (2004) to identify the most susceptible/critical crop stages of maize

for excess moisture stress, and to develop a screening technique and selection strategies for identification of germplasm tolerant to excess moisture stress. Among the four crop stages viz., early seedling, knee-high, tasseling and milk stage, early seedling was found to be highly susceptible, followed by knee high stage. A screening technique (cup method) was found to be an efficient technique for large-scale screening of maize genotypes against excess soil moisture stress. The genetics of physiological traits viz., ability to grow adventitious/brace roots, capacity to form root aerenchyma and tolerance to toxins (e.g., Fe^{2+} , H_2S) under reduced soil conditions will certainly aid in manipulation of waterlogging tolerance in the maize breeding programs (Mano and Omori, 2007). Waterlogging tolerance is a polygenic trait in many crop species including maize and thereby, both additive and non-additive effects are important in the inheritance of flooding tolerance in maize. Transgressive segregation has been observed for grain yield in F_2 population involving waterlogging tolerant and sensitive genotypes and thereby indicating the possibility of favorable alleles coming from both the parental lines (Anjos e Silva et al, 2007).

Zaidi et al (2007a) attempted to assess the stress-adaptive physiological changes associated with EM-induced anoxia stress, and to establish mechanism of EM-tolerance in tropical / sub-tropical elite maize inbred lines with known reaction to EM-stress. They exposed the germplasm to excessive moisture stress at knee-high stage and observed that excessive moisture induces change in root geotropism (surface rooting) and increased brace roots development. Both these traits were stress-responsive, however, the later one was found to be a stress-adaptive trait resulting in improved stress tolerance. Furthermore, anatomical studies showed drastic changes in cortical region of root tissues in tolerant genotypes in terms of development of large aerenchymatous spaces and in case of stress-induced metabolic adjustments, increased NAD^+ -alcohol dehydrogenase (ADH) activity was seen in all genotypes though, the enzyme activity was slightly higher in tolerant genotypes, however, the product of ADH-activity (ethanol) was relatively much higher in root and leaf tissues of susceptible genotypes. These results suggest that mechanism of EM-tolerance in maize germplasm involves morphological and anatomical adaptation through development of brace roots and aerenchyma formation. Setter and Waters (2003) also reported the benefits of stress-adaptive traits for waterlogging, including stress-induced early brace root development, increases in aerenchyma and root porosity, root suberisation, ethanolic fermentation, carbohydrate reserves, tolerance to post anoxic shock and recovery mechanisms. The overall impact of EM-stress on various morphological, physiological and biochemical traits was finally expressed on grain yield and it was noticed that the susceptible group of genotypes

faced severe yield penalty which was followed by moderately tolerant entries, however, the tolerant genotypes were able to maintain the grain yield and faced comparatively least penalty by virtue of possessing stress-adaptive traits and functions.

An experiment to assess the response of maize genotypes to excess soil moisture at different stages of life cycle revealed that there was significant and detrimental effect of ESM on maize seedlings in the earlier stages (Lone and Warsi, 2009). Out of 15 genotypes (parents and their crosses made in half diallel fashion), susceptible genotypes performed poorly and did not reach two leaf stage or even germinated, whereas the genotypes that performed well at seedling stage proved promising also in the adult stages in terms of their yielding ability. In normal cup screening trial all the genotypes performed normally. Flooding at knee height stage resulted in immediate wilting of plants, while in case of tolerant genotypes there was profuse appearance of adventitious roots on even up to five nodes in some cases. Anthesis Silking Interval (ASI) got widened even more than eight days, plant height and ear height was severely affected and physiological traits also got affected due to flooding. In general, drastic reduction in most of the genotypes was observed but some genotypes viz., Pop 3121 and Pop 3118 showed fairly better yields under waterlogged conditions. Such genotypes could be selected for their use in hybridization programme to develop maize line with waterlogging tolerance and high yielding ability.

In order to investigate the suitable selection criteria of waterflooding tolerant genotypes, most susceptible stage and the best continuous treatment time to waterlogging, Liu et al (2010) used 20 common maize inbred lines to successive artificial waterflooding at seedling stage and used waterlogging tolerance coefficient (WTC) to screen waterflooding tolerant genotypes. In addition, peroxidase (POD) activities and malondialdehyde (MDA) contents were measured for 6 of 20 lines. They reported that the second leaf stage was the most susceptible stage, and 6 days after waterflooding was the best continuous treatment time. Dry weight (DW) of both shoots and roots of all lines were significantly reduced at 6 day time-point of waterlogging, compared to control. POD activities and MDA contents were also negatively and significantly correlated. They suggested that WTC of shoot dry weight can be used for practical screening as a suitable index and leaf chlorosis, MDA content and POD activities could also be used as reference index for material screening.

The genetic inheritance of water-logging tolerance is pre-requisite for developing tolerant varieties suitable for growing in water-logging prone environments and in view of this, an experiment was conducted by Zaidi et al (2010) in which inbred lines were selected for diallel and $L \times T$ studies and reported highly significant genotypic variability under water-logging stress

for all traits, including grain yield. Furthermore, they reported that stress resulted in a significant increase in ASI in all genotypes, however, inbred lines showed relatively more susceptibility to water-logging stress than their hybrid progenies which suggested the contribution of heterosis in stress tolerance (Dass et al, 1997). The grain yield under water-logging stress exhibited lack of complete dominance in the F_1 progenies and both GCA and SCA effects were significant, but the GCA effect was comparatively stronger than SCA which indicates that water-logging tolerance in maize is governed by an additive-dominance genetic model. Means of secondary traits viz., ASI, nodes with brace roots and chlorophyll contents indicated a strong relationship with grain yield which suggests that both additive and non-additive gene actions are important for water-logging tolerance in maize. Therefore, reciprocal recurrent selection under managed water-logging stress conditions may be an effective approach to increase the level of tolerance to water-logging in maize and could be used in developing water-logging tolerant synthetic varieties and hybrids.

The effect of pre-germination anaerobic stress due to excessive soil moisture showed that pre-germination anaerobic conditions are highly detrimental for maize seed germination and emergence (Zaidi et al, 2012). It was noticed that at 36 hr of stress exposure, > 50% genotypes showed significant decrease in germination and at 72 hr, except five tolerant entries, the germination of most of the genotypes was significantly reduced and seed emergence was delayed by more than 5 days. RILs-TC (recombinant inbred line test crosses) progenies showed comparatively better performance than DTM-panel (drought tolerant maize association mapping panel), which may be due to the fact that RILs were derived from a population with a female parent highly tolerant to vegetative stage waterlogging stress. Furthermore, significant genotypic variability was observed which was clearly expressed at 72 hr of exposure to stress and such variability could be exploited using managed stress screening for developing maize with an enhanced level of pre-germination anaerobic stress tolerance. Therefore, selection for per cent germination along with time taken in emergence under anaerobic conditions will help in identifying potential maize germplasm suitable for breeding pre-germination anaerobic stress tolerant cultivars for early stage waterlogging prone maize growing areas.

The contributions of genetic and environmental factors to several seedling traits observed under waterlogged and control conditions were determined by best linear unbiased predictors for each trait in the $F_{2:3}$ families (Osman et al, 2013). The values of plant height, root length, root dry weight, shoot dry weight, total dry weight under waterlogging stress were significantly lower than those for controls. Root dry weight and shoot dry weight under water-

logging stress showed nearly normal distribution at the threshold of $P < 0.01$, while other traits in the $F_{2:3}$ families fitted a normal distribution model ($P > 0.05$) suggesting that these traits were quantitative.

In a combining ability study of 8x8 diallel cross of waterlogged tolerant maize, the parental lines, E-31 and E-79 were found to be the best general combiners for yield and other desirable traits viz., waterlogging tolerance and the cross combinations, E 31 x E 40, E 31 x E 64, E 31 x E 79, E 38 x E 40, E 58 x E 79, E 63 x E 79, E 64 x E 79 showed significant and positive sca effects Amin et al (2014). These parental lines and cross combinations could be used for commercial hybrid variety development with desirable traits under water logged conditions.

Molecular Breeding for Water logging Tolerance

In the last two decades molecular markers have proved to be useful for genome characterization and breeding. DNA fingerprinting has become a practical tool for plant genotyping while DNA markers can be used to screen large numbers of entries for a particular trait with improved efficiency and effectiveness, thus assisting the conventional breeding process. In maize various major genes responsible for waterlogging tolerance have been identified and it is now possible to concentrate on modification or use of those genes to develop new waterlogging tolerant varieties. The introgression of major genes to specific varieties by marker assisted backcrossing (MAB) for various land types and choice of the farmer and addition of new varieties through genetic engineering became possible.

In a crossing programme of maize B64 x teosinte *Z. mays ssp. huehuetenangensis*, QTL's for adventitious root formation were identified on chromosome 4 and 8 under waterlogged conditions in which the favorable alleles were contributed by teosinte (Mano et al, 2005a), while in F_2 population under same conditions, QTL's controlling adventitious root formation were identified on chromosomes 4, 5, and 8 (Mano et al, 2005b). In an another population derived from a cross between maize B64 x teosinte (*Zea mays ssp. nicaraguensis*) three QTL's on chromosomes 1, 5, and 8 were identified to form aerenchyma in the cortex of adventitious roots, that together explained approximately 45% of phenotypic variance for aerenchyma under non-flooding and drained water conditions (Mano et al, 2006; 2007). Such a character may increase flooding tolerance as a plant that possesses aerenchyma channels when not flooded, may be able to adapt more rapidly to flooding conditions when they occur. Under well-aerated and drained conditions, Ray et al (1999) reported aerenchyma formation in adult plants of *Z. luxurians* and at seedling stage. Similarly, Mano et al (2006a) reported clear aerenchyma development in some accessions of *Z. nicaraguensis* and *Z. luxurians*. In a similar study in-

volving teosinte (*Zea mays ssp. luxurians*) different set of QTL's for constitutive aerenchyma formation were identified and thereby indicating the possibility of pyramiding multiple genomic regions from the different ssp. of teosinte into cultivated maize (Mano et al, 2008).

QTL's for flooding tolerance in submerged conditions in a population of 178 F₂ plants derived from a cross of inbred lines F1649 (tolerant) and H84 (sensitive) were identified by Mano et al (2006b). Flooding tolerance evaluated by leaf injury in 0.2% starch solution revealed wide variation in the F₂ population. Further, they screened 15 of the 178 F₂ plants from both the extremes ('tolerant' and 'sensitive' plants) with 64 AFLP primer combinations linked to flooding tolerance genes and found 11 AFLP markers associated with flooding tolerance in which 10 co-segregated and were assigned to chromosome 1. Six SSR primer pairs around these markers were used to construct a linkage map. Composite interval mapping analysis revealed that a single QTL for degree of leaf injury was located on chromosome 1 (bin 1.03-4). Another QTL for flooding tolerance, evaluated as dry matter production under flooding with 0.2% starch, was located at the same position. They suggested that by transferring flooding tolerance genes from F1649 to elite maize inbred lines, the productivity under submerged conditions can be increased. Wide variation for the capacity to form root aerenchyma and the ability to form surface roots was observed from segregating populations (F₂, BC₂F₁, and BC₃F₁) derived from a single F₁ plant of a cross between Mi29 (a maize inbred line) and *Z. nicaraguensis* (nica-S2) by Mano and Omori (2007). They suggested that introgression lines (IL's) originating from this F₁ plant would be useful for identifying QTL's controlling traits related to flooding tolerance. Furthermore, they reported several QTL's controlling traits related to low-oxygen stress in *Z. nicaraguensis*, such as the capacity to form constitutive root aerenchyma and the ability to form aboveground adventitious roots during flooding.

An F₂ population consisting of 288 F_{2:3} lines was created by Qiu et al (2007) from a cross between two maize genotypes, 'HZ32' (waterlogging-tolerant) and 'K12' (waterlogging-sensitive) in order to identify waterlogging tolerance at seedling stage. One hundred seventeen SSR markers with average space of 11.5cM were used for the preparation of F₂ population genotyping which was a base-map of 1,710.5cM length. Two experiments viz., Exp. 1 and Exp. 2 were conducted during 2004 and 2005 in which QTL associated with root length, root dry weight, plant height, shoot dry weight, total dry weight, and waterlogging tolerance coefficient were identified via composite interval mapping (CIM) under waterlogging and control conditions, respectively. In Exp.1 25 and in Exp.2 34 QTL's were identified where the effects of discovered QTL's were moderate with a range of 3.9% – 37.3% and some major QTL's were identified in two chromo-

somes 4 and 9 in both the experiments which were associated with shoot dry weight, root dry weight, total dry weight, plant height and their waterlogging tolerance coefficient. Chromosome 1, 2, 3, 6, 7, and 10 were also identified as secondary QTL's associated with tolerance. They suggested that these QTL's found in the study may provide useful information for marker-assisted selection (MAS) and further genetic studies on maize waterlogging tolerance. Zou et al (2010) studied gene expression profiling at four time points (12 h, 16 h, 20 h, and 24 h) after waterlogging treatment using tolerant inbred line HZ32 to know the response of maize seedlings to waterlogging at the late stage and suggested that waterlogging affected a broad spectrum of functional categories. At the late stage of waterlogging, amino acid metabolism plays an important role related to protein degradation, carbon metabolism, regulation of cytoplasmic pH and breakdown of carbon skeletons for the supply of energy. The new genes related to signal transduction identified in their study might perform key roles in regulating the response to waterlogging at the late stage.

Pei et al (2011) determined genetic relationship of a newly discovered teosinte from Nicaragua, *Zea nicaraguensis* with waterlogging tolerance through randomly amplified polymorphic DNA (RAPD) markers and the internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA using 14 accessions from *Zea* species. RAPD analysis showed 5,303 fragments by 136 random decamer primers, of which 84.86% bands were polymorphic. RAPD-based UPGMA analysis demonstrated that the genus *Zea* can be divided into section *Luxuriantes* including *Zea diploperennis*, *Zea luxurians*, *Zea perennis*, and *Zea nicaraguensis*, and section *Zea* including *Zea mays ssp. mexicana*, *Zea mays ssp. parviglumis*, *Zea mays ssp. huehuetenangensis* and *Zea mays ssp. mays*. Further, internal transcribed spacer (ITS) sequence analysis showed the lengths of the entire ITS region of the 14 taxa in *Zea* varied from 597 to 605 bp. Based on these results they suggested that *Zea nicaraguensis* is more closely related to *Zea luxurians* than the other teosintes and cultivated maize, which should be regarded as a section *Luxuriantes* species. Xiling et al (2011) studied the *prolyl 4-hydroxylase* genes to alternative splicing in roots of maize seedlings under waterlogging and reported nine *zmp4H* genes in maize among which five were alternatively spliced into at least 19 transcripts. Different alternative splicing (AS) events were revealed in different inbred lines, even for the same gene, possibly because of organ and developmental specificities or different stresses. Reverse transcription-PCR (RT-PCR) indicated that *zmp4H* genes displayed different expression patterns under waterlogging. The diverse transcripts generated from AS were expressed at different levels, suggesting that *zmp4H* genes were under specific control by post-transcriptional regulation under waterlogging

stress in the line HZ32 and thereby, indicating that alternative splicing (AS) might have an important role in the regulation of the expression profile of this gene family under waterlogging stress.

Abiko et al (2012) compared the formation of aerenchyma, radial oxygen loss (ROL) barrier induction and depositions of suberin and lignin in the roots of *Z. nicaraguensis* and maize (inbred line Mi29) grown in aerated or stagnant deoxygenated nutrient solution and reported that growth of maize was more adversely affected by low oxygen in the root zone (waterlogged soil or stagnant deoxygenated nutrient solution) compared with *Z. nicaraguensis*. In stagnant deoxygenated solution, *Z. nicaraguensis* was superior to maize in transporting oxygen from shoot base to root tip due to formation of larger aerenchyma and a stronger barrier to ROL in adventitious roots. They suggested that ROL barrier, in addition to aerenchyma, would contribute to the waterlogging tolerance of *Z. nicaraguensis*. MicroRNAs are known to be involved in growth, development and various biotic and abiotic stresses. In this context, Zhijie et al (2012) studied to characterize the involvement of these miRNAs and their targets in response to short-term hypoxia conditions through a quantitative real time PCR (qRT-PCR) assay to quantify the expression of the 24 candidate mature miRNA signatures (22 known and 2 novel mature miRNAs, representing 66 miRNA loci) and their 92 predicted targets in three inbred *Zea mays* lines (waterlogging tolerant HZ32, mid-tolerant B73, and sensitive Mo17). Based on their studies, they observed some microRNA's viz., miR159, miR164, miR167, miR393, miR408, and miR528 as key regulators in the post-transcriptional regulatory mechanisms under short-term waterlogging conditions in three inbred lines. Furthermore, they used computational approaches to predict the stress and development related cis-regulatory elements on the promoters of these miRNAs in these three inbred lines and suggested that the miRNAs are active participants in the signal transduction at the early stage of hypoxia conditions via a gene regulatory network and crosstalk occurs between different biochemical pathways.

Almeida et al (2013; 2014) performed meta QTL analyses across three tropical populations of maize for grain yield, anthesis to silking interval and other secondary traits, in which a hotspot QTL region on chromosome 3 (~170 – 214 Mb) was identified that contained an important candidate gene, *zmm16* (MADS box domain transcription factor), which is associated with reproductive organ development in maize (Setter et al, 2011). Mano and Omori (2013) produced a series of 45 introgression lines (ILs) from single F₁ plant obtained from a cross between maize Mi29 and *Z. nicaraguensis* which was backcrossed to Mi29 three times, self-pollinated four times and genotyped using simple sequence repeat markers in order to evaluate IL's for flooding tolerance at the seedling

stage under reducing soil conditions. Among these IL's 5 flooding-tolerant lines were identified by evaluating leaf injury in which line IL#18, containing a *Z. nicaraguensis* chromosome segment on the long arm of chromosome 4, showed the greatest tolerance to flooding, suggesting the presence of a major quantitative trait locus (QTL) in that region and such flooding-tolerant genotype may be useful for development of flooding-tolerant maize lines. Quantitative trait loci (QTL) associated with plant height, root length, root dry weight, shoot dry weight and total dry weight were identified via conditional analysis in a mixed linear model and inclusive composite interval mapping method at three respective periods viz., 0 - 3 days, 3 - 6 days, and 6 - 9 days under waterlogging and control conditions by Osman et al (2013). A total of 13, 19, and 23 QTL were detected at 0 - 3 days, 3 - 6 days, and 6 - 9 days of waterlogging, respectively, which individually explained 4.14% – 18.88% of the phenotypic variation. Six QTL (ph6-1, r11-2, sdw4-1, sdw7-1, tdw4-1, and tdw7-1) were identified at two consistent stages of seedling development, while the remaining QTL were detected at only one stage which suggested that expression of most QTL was influenced by the developmental status. The role of these corresponding genes in waterlogging tolerance was further identified through mapping of Expressed Sequence Tags markers and microRNAs in which seven candidate genes were observed to co-localize with the identified QTL on chromosomes 1, 4, 6, 7, and 9 and thereby indicating that these candidate genes are important for waterlogging tolerance.

Zhang et al (2013) investigated the response of maize seedling (144 maize inbred lines) to waterlogging in a genome-wide association study under normal and waterlogged conditions using 45,868 SNPs and revealed that four strong peak signals were significantly associated with the waterlogging response on chromosomes 5, 6, and 9. SNP4784, SNP200, SNP298, and SNP6314 showed significant association with corresponding traits under waterlogging and explained 14.99% – 19.36%, 15.75% – 17.64%, 16.08%, and 15.44% of the phenotypic variation, respectively. Further, the analysis of candidate genes in the delimited interval of 112 – 160 Mb on chromosome 5 revealed a *cysteine protease* gene (*ccp1*), which was previously demonstrated to be associated with anoxia-induced root tip death in maize (Subbaiah et al, 1999). These results will help to elucidate the genetic basis of differential responses and tolerance to waterlogging stress among maize inbred lines and provides novel loci for improvement of waterlogging tolerance of maize inbred lines using marker-assisted selection. Genetic variation in a population of recombinant inbred lines (RILs) (crossing of waterlogging tolerant line (CAWL-46-3-1) to an elite but sensitive line (CML311-2-1-3)) exhibited significant range of variation for grain yield (GY) under waterlogging conditions along with a number of other secondary traits

viz., brace roots (BR), chlorophyll content (SPAD), and % stem and root lodging (S&RL) (Zaidi et al, 2015). Significant positive correlation of GY with BR and SPAD and negative correlation with S&RL indicated the potential use of these secondary traits in selection indices under waterlogged conditions. QTL mapping revealed five QTL on chromosomes 1, 3, 5, 7, and 10, which explained 30% of phenotypic variance for GY under waterlogged conditions and 13 QTL's were identified for various secondary traits associated with waterlogging tolerance, each individually explaining 3 to 14% of phenotypic variance. The favorable alleles at QTL on chromosomes 1, 3, and 5 were contributed by the waterlogging tolerant parent, while the susceptible parent donated the favorable alleles at the rest of the two loci, furthermore, the favorable allele at QTL on chromosome 7 was contributed by the waterlogging susceptible parent (CML311). Recently, a major QTL named Subtol6 was mapped to chromosome 6 that explains 22% of the phenotypic variation within the RIL population (Campbell et al, 2015). In this study two candidate genes (HEMOGLOBIN2 and RAV1) were found underlying Subtol6 based on contrasting expression patterns observed in B73 and Mo18W. Therefore such studies may be useful sources of submergence tolerance in maize caused by frequent rainfall predicted by changing climate especially during early stages of growth.

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