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Review

Utilization of wild relatives for maize (*Zea mays* L.) improvement

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Experimentally induced introgression and selection during domestication and maize (*Zea mays* L.) improvement involved selection of specific alleles at genes controlling morphological and agronomic traits, resulting in reduced genetic diversity relative to unselected genes. The plant breeder would have to extend crosses to the wild relatives to introduce novel alleles and diversify the genetic base of elite breeding materials. The use of maize wild relatives (Teosintes and *Tripsacum*) genes to improve maize performance is well established with important examples dating back more than 60 years. In fact, Teosintes and *Tripsacum* are known to possess genes conferring tolerance to several biotic and abiotic stress including chlorotic dwarf virus, downy mildew, *Fusarium, Striga hermonthica,* rootworms, drought and flooding. This review provides an overview of the application of these wild relatives and demonstrates their roles on the development of stress tolerant maize plants. It also highlights the use of Teosintes and *Tripsacum* to improve selected quantitative traits such as yield.

Key words: Maize (*Zea mays* L.), Teosintes, *Tripsacum*, stress tolerance, maize improvement.

INTRODUCTION

Maize (*Zea mays* L.) is one of the oldest domesticated plants dating back to as far as 7,000 years ago in Central Mexico by Mesoamerican natives. The crop seems to have developed as a result of gradual selection upon primitive annual teosinte (*Zea mexicana*), an ancient grass found in Mexico and Guatemala (Doebley, 1990a). Although a rapid boost in maize production has being achieved as a result of using single, double and three-way crosses, the hybrid technology has also posed a challenge on meeting the target growth in maize production due to narrowing down of genetic variability (Aditya and Jitendra, 2014). In fact, domestication has led

to a severe reduction in genetic diversity within most cultivated crops including maize when compared to their wild relatives (Olsen and Gross, 2008). To meet the challenges of the future, plant breeders will need all the genetic diversity that they can get. Some of this diversity can be found in landraces and heirloom varieties that are still being cultivated by farmers around the world. However, a much wider spectrum of diversity can be found in the genomes of crop wild relatives (Hannes et al., 2014). Wild crop relatives have been playing enormously important roles both in the depiction of plant genomes and the genetic improvement of their cultivated

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counterparts (Brar, 2005; Hajjar and Hodgkin, 2007; Pickering et al., 2006; Canci and Toker, 2009; Miller and Seiler, 2003). They have contributed immensely to resolving several fundamental questions, particularly those related to the origin, evolution, phylogenetic relationship, cytological status and inheritance of genes of an array of crop plants; provided several desirable donor genes for the genetic improvement of their domesticated counterparts; and facilitated the innovation of many novel concepts and technologies while working on them directly or while using their resources (Bai et al., 1995; Clifford, 1995; Kamala et al., 2002; Nevo et al., 2002 ; Nevo, 2004; Raskina et al., 2002, 2004; Sharma et al., 2005; Price et al., 2005, 2006; Dillon et al., 2005, 2007; Peleg et al., 2005, 2007; Petersen et., 2006; Salina et al., 2006; Matsuoka and Takumi, 2007; Bennetzen et al., 2007; Gill et al., 2007; Feldman and Kislev, 2007; Oliver et al., 2008; Loskutov, 2008; Gavrilova et al., 2008; Kuhlman et al., 2008; Xu et al., 2009; Wang et al., 2009; Ashraf et al., 2009; Nevo and Chen, 2010; Chittaranjan, 2011). For example, a wild rice (*Oryza officinalis*) has recently been used to change the time of flowering of the rice cultivar Koshihikari (*Oryza sativa*) to avoid the hottest part of the day (Ishimaru et al., 2010).

In maize, alien introgression has been accomplished for improvement of kernel composition, yield and yield related traits including kernel weight, kernel row number (KRN), kernel area and kernel length using sexual hybridization (Gallinat, 1984; William et al., 2007; Wang et al., 2008; Liu et al., 2016a, b; Karn et al., 2017). Cohen and Gallinat (1984) suggested improvement of maize inbreds with respect to quantitative traits like yield via introgression of alien chromatin segments both from teosintes (closely related species, *Zea mays spp.*) and *Tripsacum* (distantly related genus).

These wild relatives of maize have also long been recognized for their remarkable ability to withstand pests and various abiotic stresses including chlorotic dwarf virus, downy mildew, *Fusarium*, *Striga hermonthica*, rootworms, drought and flooding and thus a potentially rich source of beneficial genes (Reeves and Dockholt, 1964; De Wet, 1979; Kindiger and Beckett, 1990; Leblanc et al., 1995; Savidan et al., 1995; Berthaud et al., 1995, 1997; Masanori et al., 2005; Eubanks, 2006; Mano et al 2007; Amusan et al., 2008; Prischmann et al., 2009).

In this review, we describe the wild relatives of maize (teosintes and *Tripsacum*) and discuss the results of the introduction of genes from these alien germplasm into cultivars of maize.

CHARACTERISTICS OF WILD *ZEA* SPECIES

Maize belongs to the family Poaceae and tribe Maydeae which comprises seven genera, viz. Coix (2n = 10 or 20), Chionachne (2n = 20), Sclerachne (2n = 20), Trilobachne (2n = 20), Polytoca (2n = 20), *Zea* and *Tripsacum*

(Aditya and Jitendra, 2014). The genus *Zea* consists of four species of which only *Z. mays* L. (2n = 20) is economically important. The other *Zea* sp., referred to as teosintes, are largely wild grasses native to Mexico and Central America (Doebley, 1990b).

Teosintes

The teosintes are annual and perennial grasses native to Mexico and Central America. Most of these wild *Zea* species and subspecies are distributed across narrow ranges and can only be found in some tropical and subtropical areas of Mexico, Guatemala, Nicaragua, and Honduras (Chittaranjan, 2011; Aditya and Jitendra, 2014). Among teosintes, the nearest teosinte relative to *Zea mays* is *Zea mays* ssp. *mexicana* (Schrader) Iltis, which grows in central highlands of Mexico. It possesses the same diploid chromosome number as maize (2n = 20) and their chromosomes are known to generally pair and recombine with the chromosome of maize. The other teosintes include perennial teosintes, viz. *Zea diploperennis* (2n= 20) and *Zea perennis* (2n= 40), distributed in Jalisco, Mexico. The annual teosintes include *Zea luxurians* from southeastern Guatemala, *Zea mays* spp. *parviglumis* of southern and western Mexico and *Zea mays* spp. *huehuetenangensis* from the western highlands of Guatemala (Reeves and Mangelsdorf, 1942; Hitchcock, 1951; Iltis et al., 1979; Iltis and Doebley, 1980; Doebley, 1990b; Watson and Dallwitz, 1992; Aditya and Jitendra, 2014).

As the wild ancestor of modern maize, the plant architecture and general growth forms of teosintes are similar to maize. A typical teosinte plant usually has a main stalk that typically contains a series of nodes and elongated lateral branches at most nodes. The internodes can reach up to 20 to 30 cm in length. The ears occur in clusters of 1 to 5 (or more) at each node along the branch (Chittaranjan, 2011). The main morphological differences between teosinte and maize are their branches and inflorescences. Teosinte plants contain more branches and smaller female inflorescences than maize. For wild *Zea* species, the inflorescences can only form 5 to 10 triangular or trapezoidal black or brown seeds with a hard fruitcase. By comparison, maize usually has 100 or more naked seeds.

Tripsacum

The genus *Tripsacum* is comprised of about 12 perennial and warm season species that are mostly native to Mexico and Guatemala but are widely distributed throughout warm regions in the USA and South America, with some species present in Asia and Southeast Asia. Species of economic importance to agriculture in the

genus are *Tripsacum dactyloides* (L., 2n = 72) (Eastern gama grass), *T. laxum* Scrib and Merr (2n = 36). Other species include *T. andersonii* (2n = 64), *T. latifolium* (2n = 36), *T. lanceolatum* (2n = 72), *T. floridanum* (2n = 36) and *T. manisuroides* (2n = 72) (De Wet and Harlan, 1972; De Wet et al.,1972; De Wet et al., 1983; Talbert et al., 1990; Watson and Dallwitz, 1992; Aditya and Jitendra, 2014).

For example, De Wet et al. (1972) obtained hybrids with diploid *T. floridanum* (2n = 36), as well as both diploid and tetraploid races of *T. dactyloides*, *T. lanceolatum* and *T. pilosum*, using maize as the female parent. The reciprocal cross was also successful with both diploid and tetraploid *Tripsacum*, but only when the cytologically unreduced female gamete functioned sexually. Further repeated backcrossing with maize results in rapid elimination of *Tripsacum* chromosomes, and eventually plants with 20 *Zea* chromosomes only are obtained. The vast majority of these plants are pure maize. However, a few individuals with 2n = 20 *Zea* chromosomes have inherited from *Tripsacum* a tillering habit, flag leaf development, habit of producing several cobs on each stem, and probably several other less obvious tripsacoid characteristics (De Wet et al.,1972) .

Tripsacum has higher chromosome numbers (2n = 36; 64 or 72), than maize and hybridizes with it only under special circumstances. The genus, like maize, is monoecious but like teosinte differs from maize in having distichous spikes, solitary, sessile pistillate spikelets, and kernels enclosed in hard shells consisting of segments of the rachis and lower glumes (Mangelsdorf, 1961). However, genomic instability and sterility of hybrids between maize and *Tripsacum dactyloides* have limited direct genetic transfer of valuable traits into maize (Stalker et al., 1977; De Wet, 1979; Kindiger and Beckett, 1990). But fortunately, Eubanks (2006) reported a genetic bridge that permitted movement of *Tripsacum* genes into maize with conventional breeding methods by crossing the *Tripsacum* with *Zea diploperennis.*

PESTS AND DISEASE RESISTANCE

Plant breeders have been exploiting wild relatives for introgressing resistance against biotic stresses for over a century. Over 80% of the beneficial traits conferred by wild relatives involve pest and disease resistance (Harinder et al., 2014).

Disease resistance

Findley et al. (1982) introgressed resistance against maize chlorotic dwarf virus (MCDV) into maize from *Z. diploperennis*. The hybrid between maize and *Z. diploperennis* exhibited sterility, hence backcross generations were generated which revealed resistance to MCDV. Another teosinte was used to confer resistance to

downy mildew in maize. In fact, the introgression of resistant genes from *Z. mays* ssp. *mexicana*, *Z. diploperennis,* and *Z. perennis* into maize were carried out by Ramirez (1997) using sexual hybridization. Moreover, introgression of resistance against *Fusarium* was reported in F1 and F2 generations of crosses between maize and *Z. mays* ssp. *mexicana* (Pásztor and Borsos, 1990). Similarly, Bergquist (1979) reported introgression of resistance from distant relatives, viz. *T. dactyloides*, where sexual mating is difficult, against *Colletotrichum graminicola*, *Helminthosporium turcicum*, *H. maydis*, *Erwinia stewartii* and *Puccinia sorghi* by backcrossing into various maize genotypes. In BC5–BC10 generations, resistance to each of the pathogens appeared to be dominant; however, a gradual breakdown of qualitative traits, including resistance, occurred in later generations. Later, Bergquist (1981) successfully transferred a dominant gene *RpTd* conferring resistance against rust pathogen of corn *Puccinia sorghi*, from *T. dactyloides.* Similarly, *T. floridanum* was used to introgress resistance gene *Ht* into the genetic background of maize (Hooker and Perkins, 1980). In another study, Zhou et al. (1997) conducted the distant hybridization involving maize × teosinte *(Z. diploperennis* L.) in order to introduce novel genetic variability. They reported fourteen inbred lines resistant to diseases, insects and environmental stress after eighth-generation selfing and selection. The best crossing of these 14 lines with normal testers produced 1,000 hybrids which showed strong heterosis. On the basis of the success of maize × teosinte (*Z. diploperennis* L.) crosses for introgression of desirable traits, *Z. diploperennis* was suggested as one of the potential sources for widening germplasm pool of maize and to overcome the static situation of maize production in China. Likewise, the alloplasmic inbred lines derived from maize × *Z. diploperennis* interspecific hybrids were reported to exhibit resistance against *H. turcium* and *H. maydis* (Wei et al., 2003).

Parasitic weed resistance

The parasitic weed *Striga* (*Striga* spp.) threatens cereal grain production in tropical and subtropical regions of Africa and Asia. Striga infests 40% of the cereal-producing areas of sub-Saharan Africa (Lagoke et al., 1991). In West Africa, Striga is believed to infest over 50 million ha (Lagoke et al., 1991), and the weed continues to expand its range.

Recently, the utility of wild relatives of maize (teosintes and *Tripsacum dactyloides*) for developing genetically improved maize was well illustrated by Rich and Ejeta (2008) in terms of resistance to the 'witch weeds' (*Striga* species), which are particularly prevalent in Africa. While there appears to be paucity of *Striga* resistance genes among maize landraces in Africa, although some
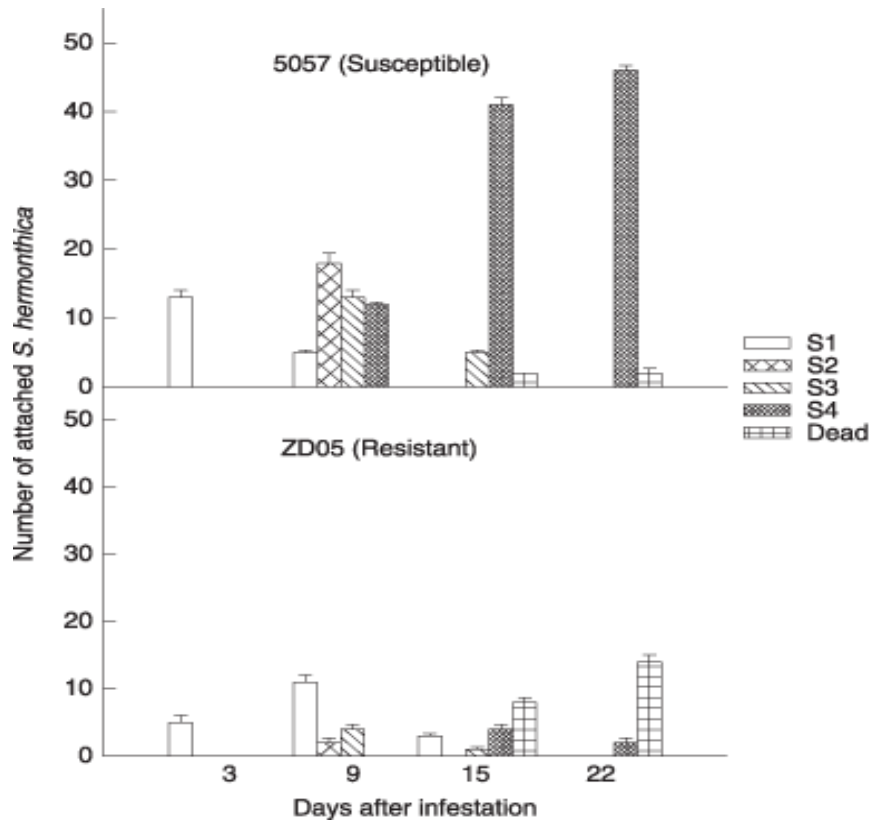
Figure 1. Development of *Striga hermonthica* on the roots of 5057 (susceptible) and ZD05 (resistant) maize genotypes at 3, 9, 15 and 22 days after infestation. Stages of development were defined as follows: S1, attached *Striga* with seed coat intact; S2, emergence of first leaf primordial; S3, attached *Striga* had three or four leaf pairs; S4, attached *Striga* having five or more leaf pairs; dead, attached *Striga* died, evident from tissue discoloration or withering (Amusan et al., 2008). Bars, +1SE.

resistance sources have been identified (Kim et al., 1999); both perennial teosintes (*Z. diploperennis*) and *T. dactyloides* showed relatively higher levels of resistance (Lane et al., 1997; Gurney et al., 2003). In addition, through a long-term breeding effort, researchers from the International Institute of Tropical Agriculture (IITA) developed a *Striga hermonthica*-resistant inbred, ZD05 (Figure 1); this inbred has in its pedigree a *Z. diploperennis* accession as well as tropical maize germplasm (Menkir et al., 2006; Amusan et al., 2008). The resistant ZD05 and the susceptible 5057 differed in root morphology. The resistant inbred had fewer, thin branched roots in the upper profile compared with the susceptible maize (Figure 2). However, further genetic studies are needed to determine the mode of inheritance as well as loci involved in the expression of this trait.

Insect resistance

Another beneficial trait conferred by wild relatives is insect-pest resistance. In fact, insect-pests cause huge yield losses by inducing direct damage to plants and by rendering the grains unfit for human and animal consumption. The major insect-pests of corn are stem and cob borers, rootworms and aphids which are generally polyphagus and damage almost all corn varieties (Aditya and Jitendra, 2014). The wild relatives of maize, viz. *Z. mays* ssp. *mexicana*, *Z. mays* ssp. *diploperennis* and *Z. mays* ssp. *perennis*, have resistance against a number of insect-pests, and these species were used to impart resistance against Asiatic corn borer (Ramirez, 1997). Pásztor and Borsos (1990) reported certain degree of resistance in the maize × *Z. mays* ssp. *mexicana* hybrids for corn borer (*Ostrinia nubilalis*). *T. dactyloides* exhibits resistance to corn rootworms via non-preferences and or antibiosis as reported by Branson (1971), Moellenbeck et al. (1995) and Eubanks (2001). Eubanks (1997, 2001, 2002) crossed *Tripsacum* with diploid perennial teosinte and produced viable recombinants that were cross-fertile with maize. This allowed the incorporation of *Tripsacum* genetic material into corn and development of experimental lines, some of which exhibited rootworm resistance, as evidenced in
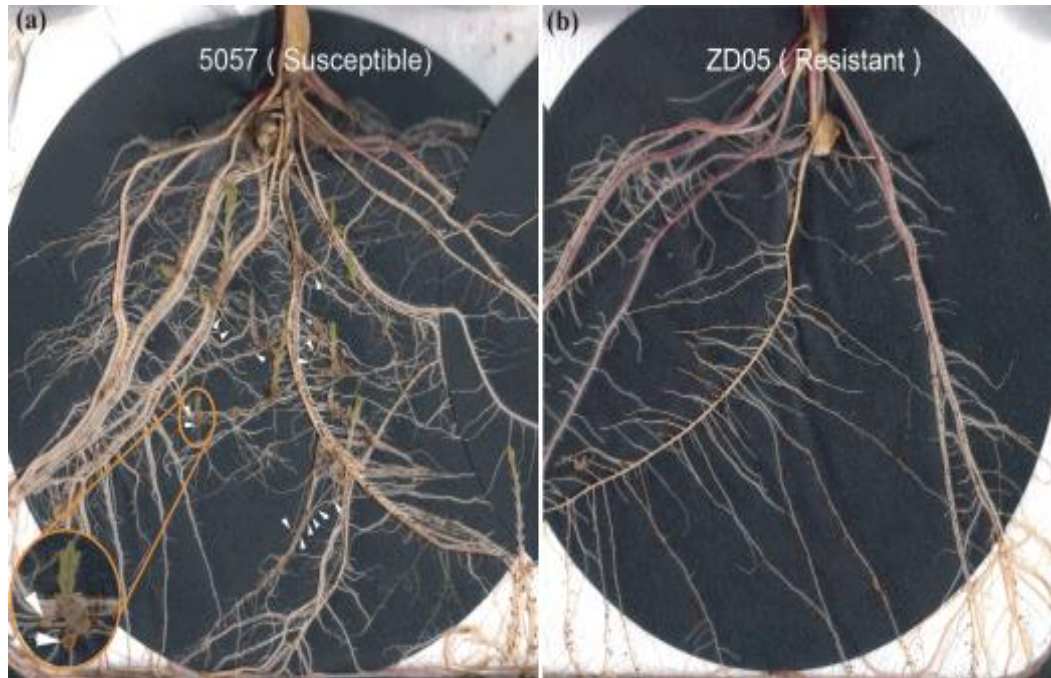
Figure 2. The root systems of 5057 (susceptible) and ZD05 (resistant) maize genotypes at 22 days after infestation with parasite *Striga hermonthica* (Amusan et al., 2008). Arrowheads, secondary haustoria.

insect bioassays and field root damage ratings (Eubanks, 2002; Eubanks, 2006). Similarly, Prischmann et al. (2009) produced *Tripsacum*-introgressed maize germplasm in breeding programmes to enhance plant resistance or tolerance to corn rootworms.

ABIOTIC STRESS RESISTANCE

Drought resistance

Drought is the most significant factor causing crop loss in hybrid maize and climate change resulting from the build-up of greenhouse gases is expected to increase its frequency and severity. The use of genetics to improve drought tolerance and provide yield stability is an important part of the solution to stabilizing global production (Sayadi et al., 2016). That is why the development of maize varieties with enhanced tolerance to drought stress and higher water use efficiency (WUE) has become a high priority goal for major breeding programs, both in the private and public sectors (Sayadi et al., 2016).

Descriptions of the anatomical and other properties of wild relatives, specially *Tripsacum* that contribute to its ability to withstand drought, come from studies of aerenchyma tissue in roots (Comis, 1997; Kemper et al., 1997), root penetration (Clark et al., 1996), and increased biomass (Risser et al., 1981). Physiological evidence

suggests that superior drought tolerance in *Tripsacum* is based on high photosynthesis and WUE in leaf gas exchange analysis (Coyne And Bradford, 1985; Kemper et al., 1997). Furthermore, in another study Eubanks (2006) observed that, even under drought stress, the *Tripsacum*-introgressed SDG cultivar outperforms the maize control. *Tripsacum*-introgression appears to confer larger, more robust root systems and overall increase in grain yield.

Tolerance to flooding

Flooding damage to maize is highly dependent on the developmental stage of the plant, the length of the flooding period and the soil-air temperatures. Maize is affected most by flooding in the early stages of growth and hence is a major concern for maize growers due to huge yield losses and limited availability of flooding-tolerant lines (Aditya and Jitendra, 2014).

Although a few maize lines were reported to form adventitious roots at the soil surface during experimental flooding conditions (Mano and Omori, 2007), teosintes obtained from regions that are known to receive frequent rainfall may provide a superior genetic resource for the development of flooding-tolerant maize. The teosintes, viz. *Z. nicaraguensis* (Bird, 2000; Iltis and Benz, 2000), *Z. luxurians* and *Z. mays* ssp. *huehuetenangensis* (Mano et al., 2005), have been observed to exhibit a higher

capacity for adventitious root formation than some maize inbreds. Z. *mays* ssp. *huehuetenangensis* seedlings were observed to exhibit a high adaptability to flooding by developing adventitious roots above the soil surface (Mano and Omori, 2007). 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. Similarly, *Z. nicaraguensis* and *Z. luxurians* were reported to develop well- formed aerenchyma in adult plants (Ray et al., 1999) hence imparting tolerance to flooding conditions.

Yield and yield related traits

Yield and yield related traits are mostly governed by polygenes, and the role of alien germplasm to improve quantitative traits is less reported. The possible reason for this is a limitation in introgressing a large number of loci responsible for expression of a quantitative trait into the target host (Dela Vina et al., 1995). However, by introgression of alien chromatin segments both from teosintes and *Tripsacum*, Cohen and Gallinat (1984) suggested improvement of maize inbreds by a significant increase of yield and combining ability. In addition, Wang et al. (2008) crossed maize with *Z. mays* ssp. *mexicana* and reported that 54.6% of the hybrids had a higher yield than the superior maize hybrid checks. They also observed that the advanced backcross generations exhibited improved characters like a large number of tillers, increased height and increased 100-kernel weight. In a recent study, Liu et al. (2016b) performed joint linkage QTL analysis on each of the kernel size traits including area, perimeter, length, and width, kernel shape traits including roundness and length/width ratio (LW), weight of 50 kernels (Wt50k) and kernel density (FFD), as well as the principal component (PC) traits, in order to identify the loci responsible for kernel trait differences between teosinte and maize. They identified 43 QTL for kernel size traits, 11 QTL for kernel shape traits, four QTL for FFD, and five QTL for Wt50k. The 63 QTL were distributed only on chromosomes 1 to 8, with no QTL on chromosomes 9 and 10. For the newly defined PC traits, PC1, PC2, and PC3, the total number of QTL detected were 15, 3 and 5, respectively. The same study revealed that maize-teosinte introgression populations provide substantial power to detect pleiotropy among overlapping QTL for multiple traits. In fact, positive pleiotropy was observed between kernel weight and kernel size traits (area, perimeter, and length) and was observed among the size traits themselves. Wt50k also had positive pleiotropy with FFD. In contrast to kernel size traits, the kernel shape traits (roundness and L/W) show negative pleiotropy with each other. In another study, Liu et al. (2016a) developed 10 NIL populations derived from geographically diverse teosinte accessions by backcrossing 10 accessions into the B73 background for

four generations before inbreeding. They identifed four QTL for KRN located on chromosomes 1, 2, 4 and 5, which accounted for 33.7% of the phenotypic variation. However, They were unable to calculate the effect of two alleles (Z029 allele for chromosome 4, and Z030 allele for chromosome 5) because of lack of introgression of those donors in the QTL region. Of the 38 remaining alleles, 27 alleles (71%) signifcantly decreased KRN, and no alleles increased KRN. For Wt50k, they identifed eight QTL for kernel weight located on chromosomes 1 (three QTL), 2, 3 (two QTL), 5, and 8, which accounted for 38.2% of the phenotypic variation. They were also unable to calculate the effect of nine alleles because of lack of introgression in the QTL region. Of the remaining 71 alleles, 30 alleles signifcantly decreased Wt50k, while one allele (Z036 allele for chromosome 2) significantly increased seed weight. More recently, a study done by Karn et al. (2017) revealed that teosinte can be exploited for the improvement of kernel composition traits in modern maize germplasm. In fact, teosintes near isogenic lines (NILs) were developed by backcrossing ten accessions of geographically diverse *Zea* mays ssp. *parviglumis* into the inbred B73 for four generations prior to inbreeding, creating a total of 961 NILs. They identified a total of eight QTL across the three traits: Two starch QTLs that explained 18% of the variation, three protein QTLs that explained 23% of the variation, and six oil QTLs which explained 45% of variation. The chromosome 1 QTL was significant for both protein and oil, and the chromosome 3 QTL was significant for all three traits. In addition, a total of 9 starch, 12 protein, and 25 oil teosinte significant alleles were identified. All the QTLs had a range of strong additive allelic effects, with the largest allelic effects for starch, protein, and oil QTLs being -2.56, 2.21 and 0.61% dry matter, respectively, and displayed both positive and negative additive allelic effects depending upon the trait.

CONCLUSION AND FUTURE PROSPECTS

The studies reported in this review described the continuing increase in the use of wild relatives for the production of new cultivars of maize. The ultimate value of these studies awaits demonstration that maize improvement can be advanced by interesting traits present in Teosintes and *Tripsacum*. It is specially the alleles of these wild relatives that need to be added into maize breeding programmes. Moreover, the *Tripsacum*-teosinte genetic bridge, which permits transfer of new genes into maize with conventional plant breeding methods, offers an exciting opportunity to overcome the *Tripsacum*-maize crossing barrier and confert new genetic diversity in maize breeding. The transfer of important traits such as resistance to chlorotic dwarf virus, downy mildew, *Fusarium, Colletotrichum graminicola*, *Helminthosporium turcicum*, *H. maydis*, *Erwinia stewarti*, *Puccinia sorghi, Striga hermonthica,* rootworms, drought

resistance, tolerance to flooding and increase of yield and combining ability described herein are just a few examples of a suite of valuable traits that could be targeted for maize improvement with these wild relatives.

Improving molecular technologies such as marker-assisted breeding, interspecific hybridization techniques and genetic knowledge will continue to increase the capacity to use the valuable traits found in maize wild relatives. In these circumstances, it becomes increasingly important to conserve a broad range of diversity of teosintes and *tripsacum* species, and their utilization must also increase in importance.

Further studies on phenotypic and genomic picture of introgression could greatly expand the understanding of particular alleles and genes' flow between maize and its wild relatives.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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