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Wild Progenitor and Landraces Led Genetic Gain in the Modern-Day Maize (*Zea mays* L.)

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Abstract

Maize (*Zea mays ssp. mays*) originated from Mexico and Central America and grew worldwide for food, feed and industrial products components. It possesses ten chromosomes with a genome size of 2.3 gigabases. Teosinte (*Z. mays ssp. parviglumis*) is the probable progenitor of the modern-day maize. The maize domestication favored standing gain of function and regulatory variations acquired the convergent phenotypes. The genomic loci *teosinte branched 1 (tb1)* and *teosinte glume architecture 1 (tga1)* played a central role in transforming teosinte to modern-day maize. Under domestication and crop improvement, only 2% (~1200) genes were undergone selection, out of ~60000 genes. Around ~98% of the genes have not experienced selection; there is enormous variation present in the diverse inbred lines that can be potentially utilized to identify QTLs and crop improvement through plant breeding. The genomic resources of wild relatives and landraces harbor the unexplored genes/alleles for biotic/abiotic tolerance, productivity and nutritional quality. The human-made evolution led to the transformation of wild relatives/landraces to the modern-day maize. This chapter summarized the maize's wild relatives/landraces and the genetic gain over time in biotic/abiotic, productivity, and nutritional quality traits.

Keywords: maize, teosinte, landrace, domestication, *Zea mays*

1. Introduction

Maize (*Zea mays ssp. mays*) is a member of the Maydaceae tribe of the Poaceae family, originated in Mexico and Central America. Maize with somatic chromosome $2n = 20$, 2.3 gigabase of genome size and more than 60000 genes [1]. After Columbus entered the New World and introduced maize to Europe, it gradually spread worldwide [2]. Its production exceeds wheat (*Triticum aestivum*) and rice (*Oryza sativa*) nowadays (<http://www.fao.org>). It has emerged as a crop of global importance due to its use as human food, livestock feed and various industrial products. A significant portion of maize production is utilized as animal consumption as it serves as important source of calories and protein in the developing countries [3]. A debate emerged at the beginning of the last century concerning the origin of maize. Maize ought to be derived from the cross between a close relative of maize and *Tripsacum* or the oldest wild maize is the progenitor of maize [4]. Subsequent archeological and genetical evidences indicated that teosinte

(*Z. mays* ssp. *parviglumis*) is the only ancestor of maize and is widely accepted [5, 6]. The discrepancy between teosinte and modern day maize were found around the Balsas River in southwestern Mexico around 9000 years ago [7].

The ancestor teosinte originated from Mexico, the selection by Native Americans for improved plant types and seed types become corn. According to modern breeding, different generations of selection turned teosinte into landraces and ultimately to the modern-day maize. The modern day maize differs from teosinte in the key traits; for example, teosinte is characterized by multi-branched, tiny reproductive parts and two rows of seed. In comparison, the modern-day maize possesses 20–22 kernel rows. The reproductive separation is not complete in primitive strains. The modern-day maize reproductive separation is complete, i.e., ear and tassels, taller plant height, erect stature, more light interception and more photosynthesis [4]. Domestication leads to the evolution of wild progenitor species to early domesticated landraces and ultimately to modern cultivars. The loss of genetic diversity often accompanies domestication. Typically landraces are heterogeneous (non-uniform) and, therefore, a good source of genetic diversity. Landraces are usually less diverse than wild relatives but more diverse than modern-day cultivars [8].

Typically, domesticated plant species' wild relatives do not have all the desirable characteristics for normal agricultural production and use. Only a small portion of the genome's selection and the key genes/QTLs/transcription factors involved under domestication have been identified and cloned [1]. In transforming teosinte into modern maize, genetic loci such as *teosinte branched 1 (tb1)* and *teosinte glume architecture 1 (tga1)* has played a pivotal role [9, 10]. The loci involved in transforming plant architecture and morphology were shown to have a pleiotropic effect on other traits. This lead to the development of convergent phenotype of the modern-day maize. Maize later spread from the centre of origin to various parts of the globe, including America, Europe, Africa and Asia. Genetic resources, especially wild relatives and landraces, harbor novel alleles/genes to impart resistance/tolerance to various biotic/abiotic stresses and boost productivity and nutrition quality. Teosintes and *Tripsacum* are native to Mexico and Central America among wild families, while in Southeast Asia, *Coix*, *Chionachne*, *Sclerachne*, *Trilobachne* and *Polytoxa* originated. Landrace accessions with unexplored alleles/genes function as important donors with substantial characteristics.

This chapter summarizes the early crop domestication process from thousands of years ago to modern-day plant breeders' success in plant improvement. Understanding the domestication of crops and plant breeding provides a background for the importance, significance and usage of wild relatives of crops maintained either in situ or in gene banks. The importance of landrace accessions and wild relatives of maize in supplying useful genes for different essential traits has been addressed.

2. Evolution of maize

Maize (*Zea mays* ssp. *mays*, Taino: mahiz, Spanish: maíz), also known as corn (North American English), is a cereal grain that was first domesticated by indigenous people around 10,000 years ago in southern Mexico. The ancient farmers from Mexico took the initiative to domesticate the maize by only looking at their kernels. They observed that all plants are not the same; some kernels look better, taste better or easier to grind. They saved the kernels based on the beneficial characteristics and used them to plant in the next season for their harvest. This forms artificial selection or selective breeding. Over time, with more rows of kernels, maize cobs grew bigger, gradually taking the form of modern maize. The identity

of maize's progenitor or wild ancestor remained a mystery for a while compared to other crops. Although there are apparent wild relatives of other grains such as wheat and rice, there is no wild plant that looks like maize, with smooth, starchy kernels arranged along the cob. To explain the origin of maize, various researchers explained several theories/hypotheses: tripartite hypothesis, catastrophic theory of sexual transmutation, *Tripsacum-Zea diploperennis* hypothesis, and teosinte hypothesis were discussed and discussed in depth by various scientists.

The tripartite hypothesis stated that the progenitor of maize was the extinct popcorn. The crosses between corn and related genera *Tripsacum* lead to teosinte formation, with further crosses giving rise to the diversity of maize we observe today [11]. Among the theories, the teosinte hypothesis is the most accepted one. Teosinte does not look much like maize, particularly when its kernels are compared to maize kernels. But at the DNA level, the two are surprisingly alike. Both possess the same number of chromosomes and similar gene arrangements. The hybrids between teosinte and maize are fertile and can reproduce naturally. Beadle [4, 12, 13] was one of the first scientists to establish the close relationship between maize and teosinte. He proposed that ancient people cultivated teosinte for food. During the cultivation of teosinte, mutations arose and being selected by the people. A set of five major mutations transformed teosinte into maize. Beadle [4] has studied the advanced generations of teosinte × maize derived hybrids. In the F₂ population of 5000 plants, the frequency of parental types was 1 in 500 plants. He concluded that 5 major loci/genes are responsible for maize domestication based on simple Mendelian genetics. Later five major quantitative trait loci (QTLs) and QTLs with minor effect for the key traits differ for maize and teosinte [9]. Wright et al. [14] reported 2–4% of genes had been selected during evolution/domestication by investigating around 774 genes. Out of a total of 3900–42000 protein-coding genes, only 800–1700 (2–4%) protein-coding genes underwent selection during the process of domestication. With the advent of next-generation sequencing (NGS) techniques, Hoffard et al. [15] identified 484 domesticated loci, of which 107 loci were further selected during improvement. The evidence mentioned above suggests that only a small portion of the genome was selected during maize domestication and improvement.

Genetic studies have provided firm evidence that maize was domesticated from Balsas teosinte (*Zea mays* subspecies *parviglumis*). This wild relative is endemic to the mid-to lowland regions of southwestern Mexico. Thus, genetic data point to the primary diffusion of domesticated maize from the highlands rather than from the region of initial domestication. The gene flow between maize and its wild relatives meaningfully impacts geographic origins [16].

3. Genes selected under domestication

Selection during evolution, whether natural or artificial, acts through the phenotype. For multifaceted phenotypes such as plant and inflorescence architecture, the underlying genetic architecture comprises a complex network of interacting genes rather than single genes that act independently to determine the trait. As such, selection acts on entire gene networks [17]. A set of genes/loci were selected during domestication knowingly or unknowingly by farmers then breeders. The earlier selection mainly focused on plant morphology, ear size, seed type and single stalk etc., for transforming its wild progenitor to the modern-day maize. Only a few genes, i.e., 2% genes (1200 genes) of the 60000 genes of maize, have been selected during the process of domestication. Those genes that have experienced artificial selection have greatly reduced genetic diversity in modern germplasm. Therefore

cannot contribute to the variation for agronomically important traits. Artificial selection has impacted maize diversity during its domestication from teosinte (*Zea mays ssp. parvoglumis*) to landraces and plant breeding from landraces to modern inbred lines. Artificial selection has impacted protein, oil, starch and amino acid content.

Maize domestication started around 10000 years ago. Early farmers selected and planted seeds from plants with beneficial traits while eliminating the undesirable ones. As a result of good alleles, i.e., alleles of genes controlling the favored traits, the frequency has been increased within the population. At the same time, bad/deleterious alleles frequency decreased. Such selection is made possible due to the tremendous availability of natural genetic variability in the teosintes. Over time, with current agricultural practices, certain combinations of genes have been selected. This includes major and minor gene mutations distinguishing from wild ancestors. That's why only few genes are responsible for the transformation. Beadle and Doebly revealed that only five genes might be responsible for the dramatic morphological changes. The "one gene-one trait" model for such genes is still questionable. Although a small number of genes has striking effects, on-ear and plant morphology resulted in the maize evolution. However, the vast majority of genes have an only a modest effect. Thousand of genes were likely necessary to contribute to the transformation like, increase in the size of the ear, adapting maize to the modern agricultural practices and an increase in the maize kernel's nutrient status.

3.1 Traits modified under domestication

3.1.1 Glume

Teosinte was characterized by hard glumes, the seed, which were passed through the digestive tract of the ruminants and not get digested. This ultimately serves as propagating material for the next generation under natural conditions. The locus *tga1*, *teosinte glume architecture* leads to a decrease in the size of glumes (**Figure 1**). It encodes the squamosa-promoter binding protein (SBP) transcription factor. This QTL has been mapped on chromosome 4 [18] and cloned [19]. Interestingly, in the *tga1* promoter region, *tga1* is regulated by *tb1* via direct binding of *tb1* to two GGNCCC motifs [20].

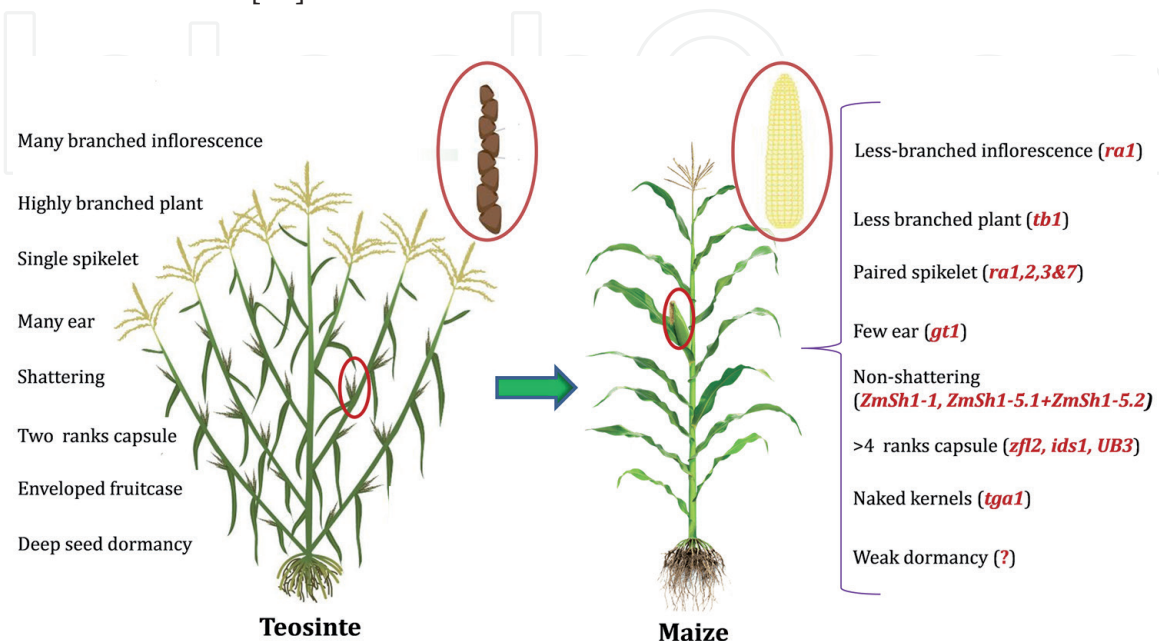


Figure 1. Morphological changes during maize domestication and the underlying key genes.

3.1.2 Plant architecture

The loci teosinte branched 1 (*tb1*) responsible for the transformation from many tillers, many inflorescence to the single stalk with single inflorescence in the modern day maize. Concentrating the energy resources in a single ear and stalk made it possible to increase the ear size. The *tb1* encodes the TCP family transcription factor, i.e., *TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL NUCLEAR ANTIGEN FACTOR*, which is mapped for apical dominance and inflorescence development [10]. The *tb1* was mapped by transposon tagging, which leads to the inhibition of axillary bud formation and transformation to female inflorescence [21, 22]. The causal variant of this phenotype was transposable element (TE) in the upstream of *tb1* suggests the role of long range chromatin insertions in the maize domestication [23]. The ortholog *tb1* locus also has been reported in the other crops suggesting its conserved nature in other plant species. In rice *OsTB1* with negative regulation [24], *BRC1* in *Arabidopsis thaliana* [25], *HvTB1* for higher tiller number in barley [26]; *TaTB1* along with *FLOWERING LOCUS T1* regulates inflorescence architecture in wheat [27]. These conserved loci of *tb1* explained the evidence for its role during domestication.

3.1.3 Others

QTLs at genes responsible for shattering vs. solid cobs, single vs. paired spikelets and distichous (two rank ear) vs. polystichous (> four ranks ear). The gene *Zea mays* *floricaula leafy2* (*zfl2*) primarily regulates the teosinte ear's two ranks [9, 28]. Sweet maize and popcorn retain tillering growth habit during maize diversification. However, the underlying molecular genetic mechanism remains unknown. The retention of maize tillering is controlled by a major quantitative trait locus (QTL), *tin1*, which encodes a C2H2-zinc-finger transcription factor that acts independently of *tb1*. *tin1* is involved in multiple pathways, directly represses two tiller-related genes, *gt1* and *Laba1/An-2*, and interacts with three TOPLESS proteins to regulate the tiller buds' outgrowth. Therefore maize *tin1*, derived from a standing variation in wild progenitor teosinte population, determines tillering retention during maize diversification [29].

Characterization of variations in the Four-row Wax landrace of China reported kernel row number (KRN) related genes and KRN QTL regions revealed potential causal mutations in *fea2*, *td1*, *kn1*, and *te1* [30].

3.1.4 Starch

In the initial phase of domestication, the focus was mainly on the plant shape and ear morphology. Many additional traits were acts as the targets from recent years. Grain yield, ear size (increased from 2 cm to 30 cm), quality and starch. Starch is the major byproduct of maize, constitutes ~73% of kernels' total weight. The three loci, i.e., *Su1*, *bt2* and *ae2*, are targets of selection during maize domestication and improvement. *Tassel*, *seed2* and *dwarf8* as the targets of selection based on a screen of genes on chromosome1 [31, 32].

3.2 QTLs beyond the domesticated genes

Various QTLs were reported beyond the domesticated genes/loci affecting the morphological traits (Table 1). Around 314 QTLs were identified for 22 morphological traits involved in domestication and improvement [34]. Out of 314 QTLs, only 14 QTLs explained phenotypic variation >10 percent, affecting the

SN.	Trait	Gene/QTLs	Chromosome	Phenotype	Reference
1.	Plant architecture	<i>teosinte branched1 (tb1)</i> , <i>grassy tillers 1 (gt1)</i>	1	Number of basal branches or tillers, Limited number of large ears	[28, 33]
2.	Glume hardness	<i>teosinte glume architecture1 (tga1)</i>	4	Inhibits secondary sexual traits in the female flower, preventing glumes from hardening	[9, 28, 34]
3.	Paired and single spikelets of maize	<i>ramosa1</i> , <i>ramosa2</i> , <i>ramosa3</i> , <i>ramosa7</i>	7 3	High number of kernels in each row of the ear of modern maize parents	[35, 36]
4.	Distichous and polystichous ear	<i>Zea floricaula leafy2 (zfl2)</i> , <i>Zea floricaula leafy1 (zfl1)</i>	2 10	Multiple ear ranks along the inflorescence meristem	[9, 28, 34]
5.	Disarticulating rachides and non-disarticulating rachises	<i>ZmSh1-1</i> , <i>ZmSh1-5.1 + ZmSh1-5.2</i> , <i>Zga1</i>	1 5	Shattering, ear size	[33, 37-39]

Table 1.
QTLs/gene their chromosome location and phenotype.

morphological traits. Further research leads to the cloning of some of these QTLs, enabling identifying differences in the morphological traits between maize and teosinte. Plant architecture *grassy tillers1 (gt1)* encodes the Homeodomain leucine zipper transcription factor [40]. Plant architecture is impacted by the enhanced expression of BTB/POZ ankyrin repeat protein and Homeodomain leucine zipper transcription factor encoded by *tru1* and *grassy tillers1 (gt1)*, respectively [33, 41]. The increased expression of transcription factors encoded by *gt1 (grassy tillers1)* and *tru1 (tassels replace upper ears1)* encodes Homeodomain leucine zipper transcription factor BTB/POZ ankyrin repeat protein [33, 40, 41]. *Tassels replace the upper ears1 (tru1)* confers a sexual conversion of the terminal lateral inflorescence in teosinte to ear (pistillate) in maize from tassel (staminate). Other genes for seed filling *ZmSWEET4c* [42], *UB3*, *ids1/Ts6* for kernel row number [43], shattering *ZmSh1-1*, *ZmSh1-5.1 + ZmSh1-5.2* [37] and for inflorescence architecture *ra1* [44], were cloned, key domesticated genes of maize. Most of these domesticated genes were the transcription factors that were unregulated during domestication. A maize-teosinte-derived BC₂S₃ population, the QTLs *UPA1 (Upright Plant Architecture1)* and *UPA2*, which confer on upright plant architecture, were identified. The teosinte allele at *UPA2*, which reduces leaf angle, was lost during maize domestication [45]. More compact plants and improved yields under high planting densities could be developed by incorporating this allele into modern maize hybrids [45, 46].

4. Pleiotropic gene interactions during maize domestication and improvement

Pleiotropy generally describes the effect of an allele of a gene for producing an unrelated phenotype. It affects the path of evolution as it facilitates if a directional selection of a phenotype affects other beneficial phenotypes' fitness or restricts if the allele has the deleterious effect on another phenotype. Generally, the developmental traits reveal pleiotropy by explaining the association among flowering time in male and female flowers [47], ear and tassel developmental traits [48], leaf length and flower length [49]. Apart from these, QTLs responsible for tassel and ear development are also responsible for flowering time [50].

Understanding pleiotropy and the association between phenotypes will help to explain the selection outcome constraints. For example, the maize allele at *zfl2* is responsible for spiral ear phyllotaxy that increases the kernel number and is involved in other traits like early flowering [51]. So in a well-adapted environment stabilizing selection for flowering might limit directional selection for kernel number. Therefore such pleiotropy may limit domestication alleles when selection disallows variation.

Various researchers have reported that domestication alleles were pleiotropic [11, 12, 52, 53]. The *teosinte branched1* (*tb1*) is pleiotropic across many traits; apical dominance, growth of leaves on the lateral branches, length of lateral branches, ear and root architecture [54]. *tb1*, as a transcription factor, binds to many locations in the genome. It directly regulates *gt1* by binding to its promoter. Still, it directly affects the cell cycle by suppressing many cell cycle genes (*proliferating cell nuclear antigen2* (*pcna2*) and *minichromosome maintenance2/prolifera* (*mcm2/prl*) [20]. *zga1* is a MADS-box transcription factor associated with ear size and has a pleiotropic effect on flowering time [33]. *tga1*, a glume architecture allele shown to have pleiotropic effect on lateral branch length, ear phyllotaxy and ear disarticulation [55].

5. Effect of maize domestication on genetic diversity (Domestication Bottleneck)

Both domestication and artificial selection during crop improvement led to selecting only desirable/beneficial traits, resulting in the reduced genetic diversity of the unselected genes. During the process of domestication, nearly all crop species experience “Domestication Syndrome” or “Domestication Bottleneck” [22, 56]. These effects happen in two stages; i) initial bottleneck effect, when a subset of crop wild species population brought under cultivation and ii) subsequent reduction in the genetic diversity through selective breeding for the desirable traits during crop improvement is improvement bottleneck. Among crop species, maize experiences a relatively mild genetic bottleneck, as domesticated maize retains around ~81% of the genetic diversity of teosinte [15]. Approximately 2–4% of genes were the target during the initial domestication and crop improvement stage [14, 15]. It is established that genetic diversity generally declines with the domestication of teosinte to the landraces. Subsequently, modern plant breeding reduces the genetic diversity of modern-day maize inbred lines relative to the landraces (**Figure 2**). Therefore such genes strongly influenced by domestication or improvement are enriched in modern improved varieties in the subset of genes that show low nucleotide diversity [14]. Yamasaki et al. [57] proposed a model containing three types of genes: ‘neutral genes that demonstrate diversity reduction by general bottleneck effects, domestication genes in which diversity by selection between the teosintes and landraces is significantly reduced, and improvement genes in which diversity by selection between landraces and inbreds is significantly reduced (**Figure 2**).’

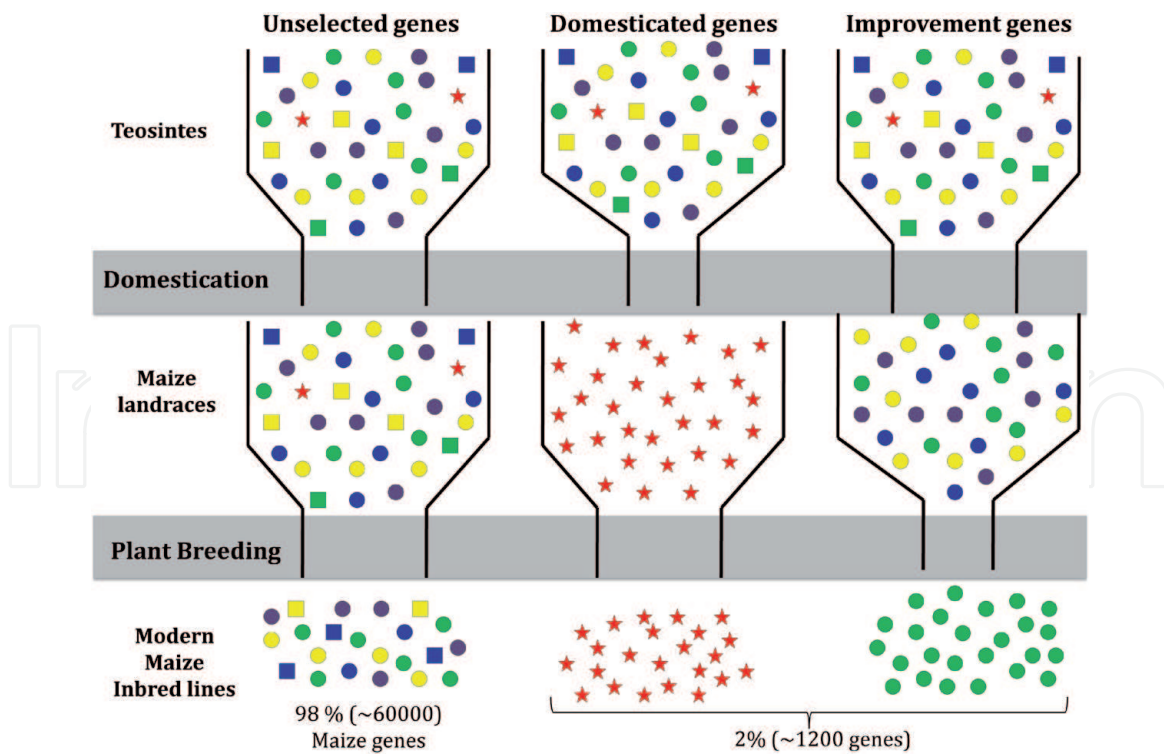


Figure 2.

Domestication and plant breeding effects on genetic diversity of maize genes [redrawn from Yamasaki et al. [57]]: Shapes with different color represents different genes and shaded area depicts the bottleneck effect.

The genes that experienced artificial selection during domestication and crop improvement have significantly reduced genetic diversity in the modern germplasm and cannot contribute to the agro morphological traits. Therefore the selected genes are difficult to identify in the genetic screens and may not be useful in traditional breeding programmes. If we need to utilize the selected genes fully, the new variation must be reintroduced from teosintes. Additionally, for the 98% of genes, which do not experience selection during domestication and crop improvement, there are huge genetic variations in the diverse inbred lines that could be utilized by identifying the genetic loci/QTLs and improvement through plant breeding.

6. Wild relatives of maize

Wild relatives of crops are the species of wild plants that are genetically linked to cultivated crops. Unattended by humans, they continue to grow in the wild, developing traits that farmers and breeders can cross with domesticated crops to produce new varieties, such as drought tolerance or pest resistance. The *Zea* genus of grass consists of seven genera with different chromosome numbers divided into two groups: viz. old-world and new world groups. *Chionachne*, *Coix*, *Polytoca*, *Sclerachne* and *Trilobachne* originated in Southeast Asia and belonged to the old-world group. The new world group consists of *Zea* and *Tripsacum* and originated in Mexico and Central America. *Zea mays ssp. mays* is the only species of economic importance and other species referred to as teosintes.

7. Landraces of maize

A landrace is defined as 'dynamic population(s) of a cultivated plant that has a historical origin, distinct identity, and lacks formal crop improvement and often

being genetically diverse, locally adapted, and associated with traditional farming systems' [58]. Compared to other crops, maize has tremendous genetic diversity, which offers potential for crop improvement for biotic/abiotic stresses, nutritional quality and grain yield. In landraces, the diversity/genetic variations lie within-population rather than among populations. Worldwide, the landraces have been characterized both morphologically and molecularly. The genetic variability present in the available landraces has been utilized to improve agro morphological traits, biotic/abiotic stresses and specialty traits. In crop centers of origin and diversity, often biotic and abiotic conditions vary across the landscape, creating the possibility of local adaptation of crops. Local landraces perform better than non-local ones under local conditions. Some of the examples of their utilization are given below:

7.1 Agromorphological traits

The conservation of landraces is fundamental to safeguarding crop diversity, food security, and sustainable production. 'Jala' is a particular maize landrace from the region in and around the Jala Valley of Mexico that produces the largest ear and tallest plant of all maize landraces in the world. Changing socio-economic and environmental conditions in the Jala Valley could lead to the genetic erosion of the ancestral 'Jala' landrace, leading to global consequences [59]. In southwest China, Four-row Wax landrace, with four rows of kernels on the cob.

7.2 Tolerance to abiotic stresses

Maize landrace accessions constitute an invaluable gene pool of unexplored alleles that can be harnessed to mitigate the challenges of the narrowing genetic base, declined genetic gains, and reduced resilience to abiotic stress in modern varieties developed from repeated recycling of few superior breeding lines. Some landraces of Mexico origin that imparts abiotic stress tolerance are Bolita, Breve de Padilla, Conica, Conica Nortena, Chalqueno × Ancho de Tehuacan cross (alkalinity tolerant), La Posta Sequia, Nal Tel, Oloton (acid soil tolerant) and Tuxpeno (drought tolerant) [60]. At CIMMYT, the production of inbred lines, drought-tolerant population-1 (DTP-1) and drought-tolerant population-2 (DTP-2) is exploited for imparting drought tolerance. Some of the inbred lines derived from 'La Posta Sequia' were reported to have drought and heat tolerance [61]. Maize landraces L25, L14, L1, and L3, are reported as the most valuable source of drought tolerance [62]. A higher transcript accumulation in shoot tissues of *ZmATG* genes reported in landrace 'Argentino Amarelo' under the osmotic stress conditions compared to landrace 'Taquarão' [63]. Nelimor et al. [64] identified extra-early maize landraces that express tolerance to drought and heat stress. Root system architecture plays a crucial role in water and nutrient acquisition in maize. *ZmCKX5* (cytokinin oxidase/dehydrogenase) was resequenced in maize landraces and revealed its importance in developing the maize root system [65].

7.3 Resistance to biotic stresses

Maize crops encounter a lot of diseases due to their wide distribution. Among fungal diseases, Turicum leaf blight (TLB) and Maydis leaf blight (MLB) results in the decline in maize production throughout the world. A subpopulation Tuxpeno Crema derived from the landrace Tuxpeno known to possess resistance to the foliar diseases [66]. Palomero Toluqueno, a landrace of popcorn reported to have resistance to the maize weevil [67], few Carrebian landraces possess resistance to larger grain borer [68]. Two Kenyan maize landraces (Jowi and Nyamula) and one Latin

American landrace (Cuba 91) shown a lower number of eggs and egg batches deposition of *C. partellus* due to production of herbivore-induced plant volatiles (HIPVs) [69, 70]. The fall armyworm *Spodoptera frugiperda* J. E. Smith (Lepidoptera: Noctuidae) is one of the most damaging maize production pests in tropical areas. The maize landraces 'Chimbo' and 'Elotillo' had the lowest leaf damage, calculated by the area under the severity progress curve [71]. The maize landrace 'Pérola' from Brazil showed resistance to fall armyworm in the winter and summer seasons [72].

7.4 Enhancement of specialty traits

A northeastern Indian landrace, 'Murlimakkai,' was utilized to develop Baby Corn composite VL Baby Corn [60]. Several landraces, viz., Azul, Bolita, Tlacoya, Pepitilla and Oaxaqueno, were very popular and utilized for tortilla quality. Mexican popcorn landrace 'Palomero,' utilized to understand the landrace structure and improvement in the popping quality. Landraces had significantly higher values than checks for oil content, oleic acid, MUFA and tocopherol contents. Genetic analyses suggest that the kernel quality traits could be successfully manipulated using the investigated plant material [73].

7.5 Unlocking the genetic variability present in the landraces

Using landraces for broadening the genetic base of elite maize germplasm is hampered by heterogeneity and high genetic load. Production of DH line libraries can help to overcome these problems. Landraces of maize (*Zea mays* L.) represent a vast reservoir of genetic diversity untapped by breeders. Genetic heterogeneity and a high genetic load hamper their use in hybrid breeding. Production of doubled haploid line libraries (DHL) by the in vivo haploid induction method promises to overcome these problems. Böhm et al. [74] developed doubled haploid lines from European flint landraces and reported considerable breeding progress. This reveals that there is tremendous potential of landraces for broadening the narrow genetic base of elite germplasm. DH technology's use demonstrated broadening the flint heterotic pool's narrow genetic base [75]. Altogether, the DH technology also provides new opportunities for characterizing and utilizing the genetic diversity present in gene bank accessions of maize [76].

8. Conclusions

The domestication and crop improvement processes lead to converting teosinte into landraces and subsequently to the modern-day maize inbred. During domestication, based on genetic evidence, it is clear that selection was mainly focused on five genes. This leads to the change in the architecture and morphology of teosinte into maize. Maize has evolved distinct genetic solution towards domestication: domestication of maize has involved distinct genetic and regulatory networks have been used to acquire convergent phenotypes. During domestication and artificial selection, only a small part of the genome underwent selection, which ultimately led to the modern-day maize. So, wild relatives and landraces encompassing the unselected genes possess enormous potential as the donor for beneficial genes/alleles. The derived inbred lines from such material could not be directly utilized in the breeding programme. They must be utilized as a donor for the specific traits, i.e., tolerance to biotic/abiotic stresses and nutritional quality traits. The utilization of wild relatives and landraces in the breeding programmes is not that easy; utilization of bridging species and embryo rescue provides the solution to this problem.

The pre-breeding programme helps to utilize wild relatives and landraces to enrich the ongoing crop improvement programmes. The availability of the genome sequence of 'B 73' and 'Palmoreo' landrace and strong pre-breeding programme can potentially enhance unexplored germplasm in the maize breeding programme.

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