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Maize domestication: Facts and proofs

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Abstract
Maize (*Zea mays* L.; 2n = 20) is a member of the world's most successful family of agricultural crops, including wheat, rice and sugarcane. Its versatile spread across the world has its nativity to Central America. The genus *Zea* includes wild taxa known as teosinte (Zea *mays ssp. parviglumis*) and domesticated corn or maize (*Z. mays ssp. mays*). Maize domestication is one of the greatest events of artificial selection and evolution, wherein a weedy plant in Central Mexico was converted through human-mediated selection into the most productive crop in the world. In fact, the changes were so notable between modern maize's and true ancestor. From its primate form to modern cultivated maize, there were several facts and proofs to show cultivated maize were originated from teosinte about 9000 years ago. The major domestication events led to odds and ends in modern maize along with some beneficial traits useful for mankind. The present review briefly explains the domestication events and breeding aspects of maize and how selection influenced on differential traits in domesticated maize?

Keywords: Archaeological evidence, domestication, polyploidization, wild progenitors, *Zea mays*

Introduction

Zea mays (maize or corn) is the third most important food crop globally after wheat and rice in terms of production and the second most widespread genetically modified (GM) crop after soybean that is grown widely throughout the world in a range of agro-ecological environments. Most historians believe maize was domesticated in the Tehuacan Valley of Mexico. Scholars now indicate the adjacent Balsas River Valley of south-central Mexico as the center of domestication. The word maize derives from the Spanish form of the indigenous Taíno word for the plant, *mahiz*. Maize is the domesticated from teosinte, a wild grass occurring naturally in isolated patches of central Mexico.

Domestication event

Domestication event of major crops from its wild progenitors took place around the world between 4000 and 10000 years ago. The process of domestication of this crop over several thousand years has resulted in profound changes in their morphological traits giving them a very different architecture, simultaneously the modern plant breeding approaches has resulted in development of varieties or cultivars that are conform to the modern ideotypic pattern (plant type), as a result of multiple domestication events and major selection process either naturally (environment) or artificially (mankind) has made popularity among the formers to cultivate in large scale.

This multiple domestication and breeding strategies have intense effect on present day diversification with regard to both phenotype and genotype of modern crop species which we are cultivating now. Due to these two major events the cultivated crops has lost some of valuable genes from its progenitors but some have gained genes too.

Voyage of maize domestication

Maize was domesticated from teosinte (*Zea mays* ssp. *parviglumis*) in a single domestication event, approximately 9000 years ago in southern Mexico. As primitive maize and more advanced maize were spread across North and South America, it encountered new environments (e.g., humid regions with high disease pressure, dry plateaus, etc.). The first mention of the crop on the records was November 5, 1492, when Columbus reached the America mainland and his scouts brought to him the maize samples from the Island of Cuba.

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Maize adapted to these new environments in the form known as landraces that is open pollinated populations adapted to specific environments and/or human uses. Although each landrace has distinct genetic and morphological characteristics, there is often more diversity within a landrace than between landraces, indicating their broad genetic base. By the time the New World was discovered the Europeans, maize had spread from Mexico to Canada, Argentina and had become part of early American agriculture. In India, maize was introduced by Portuguese during the seventeenth century (Fig. 1). At the end of the 18th century, now its breeders time to widen high-yielding maize lines and as an efforts of breeder's art its roped to the development of 1st maize inbreds and then crossing the inbred lines to form hybrids.
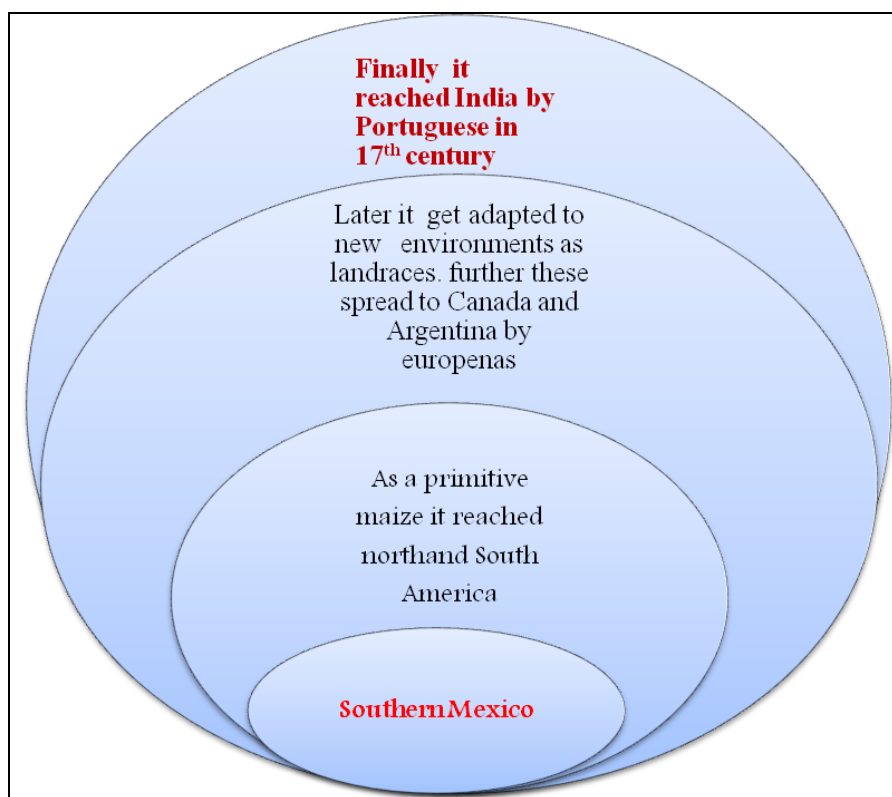

**Fig 1:** Voyage of maize during domestication phase

The germplasm pool of maize was often described in terms of teosinte, landraces, and inbred lines. The B73 maize reference genome has recently been published which is summarizing over 100 years of maize research and formally bringing maize into the genomics era. (Springer *et al*., 2009; Wagner *et al*., 2010) [3, 4] reported study on genome comparison in maize and they compared B73 and Mo17 inbred lines of maize through genome wide comparison along with the reference genome *teosinte* (ancestral maize) lines, from this conclusive evidence they reported that more than 50% of the genome has been missed from the reference genome. In future studies B73 was chosen as the reference inbred for the genome project because its importance in the history of hybrid breeding in the United States and for its role as a genetic stock. Maize's10 chromosomes are the result of multiple polyploidization events, the most recent of which was a whole genome duplication event, a common theme in plant evolution that occurred 5 to12 million years ago (Sherry, 2013) [2]. Selection at the *teosinte* glume architecture1 (tga1) locus was responsible for transforming the hard cupulate fruit case of teosinte into the uncovered grain of the maize ear, a key step in making teosinte an edible crop. The role of a fourth gene, ramosa1 in shaping maize ear morphology has also been recently identified (Wright *et al.*, 2005) [5].

The genome sequence project predicted approximately 32700 genes in B73, although the final number of genes will likely be higher, perhaps 40000 or more. Nearly 85% of the B73 genome sequence is annotated as transposable elements or what was referred to until recently as "junk DNA".

Comparisons were made for SNPs diversity between maize inbreds and teosintes in 774 genes, they found 60% of the diversity of *Zea mays ssp. parviglumis* and 80% of the diversity of the landraces (Wright *et al.*, 2005) [5].

Wild progenitors
✓ Gama grass : *Tripsacum sp (*2n=2x=36; 72),
✓ Teosinte (2n=2x=20): is the closest relative of maize and crosses readily with it.
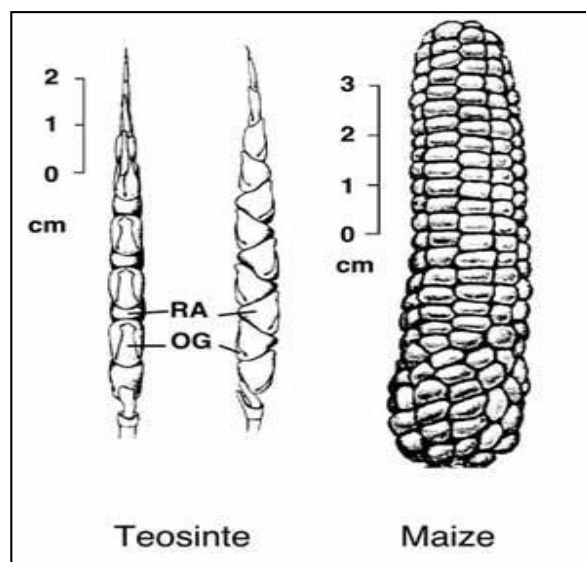
Journey of MAIZE (*Zea mays ssp. mays*) from TEOSINTE (*Zea mays ssp.* Parviglumis)

Archaeological and molecular evidence indicates that modern maize *(Zea mays ssp. mays)* was domesticated from teosinte in Southern Mexico between 6600 and 9000 years ago. Although corn (maize) officially only made the journey from the 'New-world' following Columbus discovery of the Americas, maize is found in India several hundreds of years before his time as per the archaeological evidence. Isozyme and microsatellite data pin-point the annual Balsas teosinte *(Zea mays ssp. parviglumis)* as the direct progenitor to maize. Dispersal occurred rapidly, with evidence of cultivation in South America more than 6000 years ago. Selection soon followed: favorable alleles at loci controlling plant morphology and kernel nutritional quality were fixed at least 4400 years ago and further selection by Native Americans saw maize adapt to numerous varied environments.

During domestication phase, selection was probably focused on making maize cultivatable and improving access to the seed, while during the improvement phase, selection focused on yield, grain quality, and agro-ecosystem adaptations. Maize domestication and subsequent selection events necessarily reduced genetic diversity in the maize genome when compared to its progenitor populations.

Effect of artificial selection on the genetic diversity of maize genes

Artificial selection is the process of intentional or unintentional modification of individuals in a population through human action, resulting in phenotypic evolution of plants and animals. Crop varieties consequently experienced strong selection at genes controlling agronomically important traits. Therefore genes that are identified as targets of artificial selection can be assumed to be important genetic factors controlling agronomic traits'. The artificial selection has led to decreased genetic diversity but has improved cultivated maize in many ways compared to natural corn. During earlier days corn was limited only to latin America with only few known varieties with hard kernels and less nutritional enrichment. But due to the effect of selection phase for cultivation and edible purpose has led revolution to breed an artificial corn with improved nutritive values and easy to peel kernels which can be grown extensively throughout the world. As a result of advancement in breeding strategies for improvement of maize for huge cultivation during last decade we can note that there was increase in hybrids and inbreds released with potential performance (Fig. 2) (Kennedy, 2014).
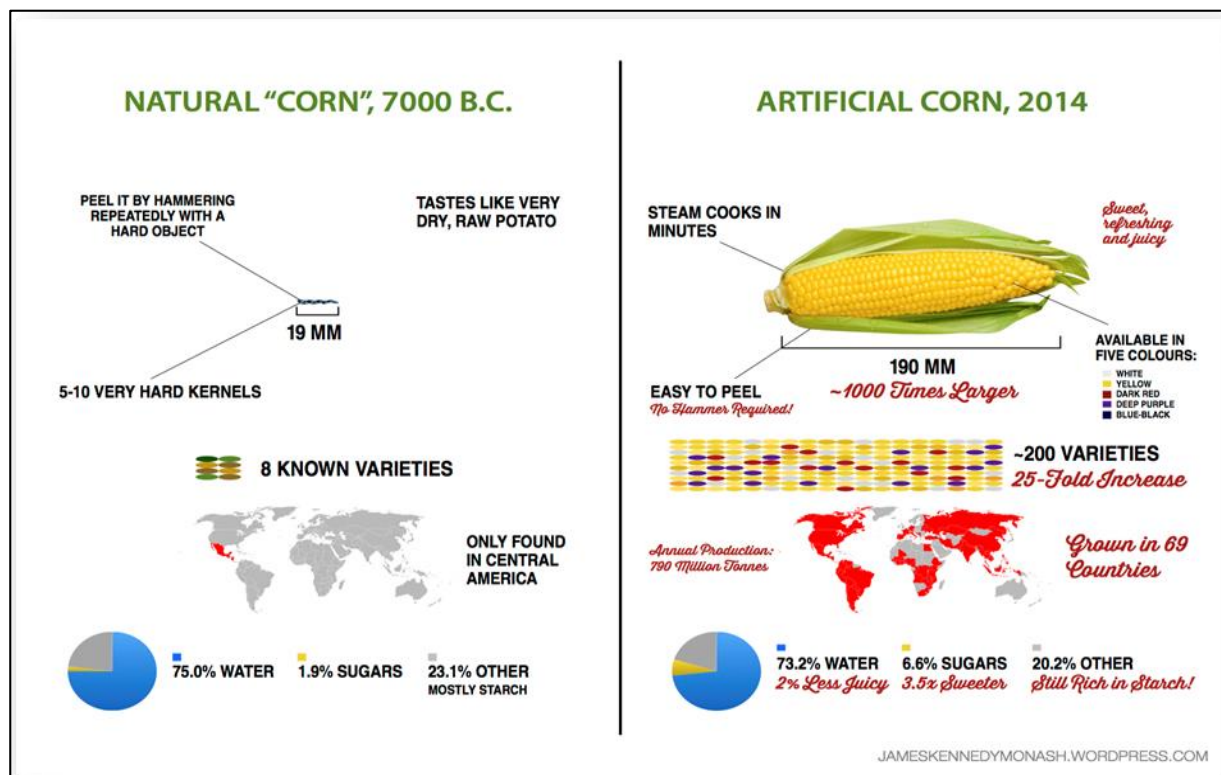
Fig 2: Difference between natural corn and artificial corn during domestication and selection phase

Artificial selection in maize can be divided into two stages: domestication and improvement (plant breeding). The coloured circles represent different alleles. The shaded areas indicate bottleneck effects placed on all genes by the processes of domestication and improvement (Fig. 3). The model assumes that there will be three types of genes; neutral (unselected) genes that show reduction of diversity by the general bottleneck effects, domestication genes in which diversity is greatly reduced by selection between the teosintes and landraces, and improvement genes in which diversity is greatly reduced by selection between the landraces and inbreds. A re-sequencing study of 774 maize genes across 14 inbred lines revealed that 2-4% of the genes examined experienced artificial selection. But vast majority of genes (96-98%) are neutral genes that were not affected by artificial selection (Wright *et al.*, 2005) [5].
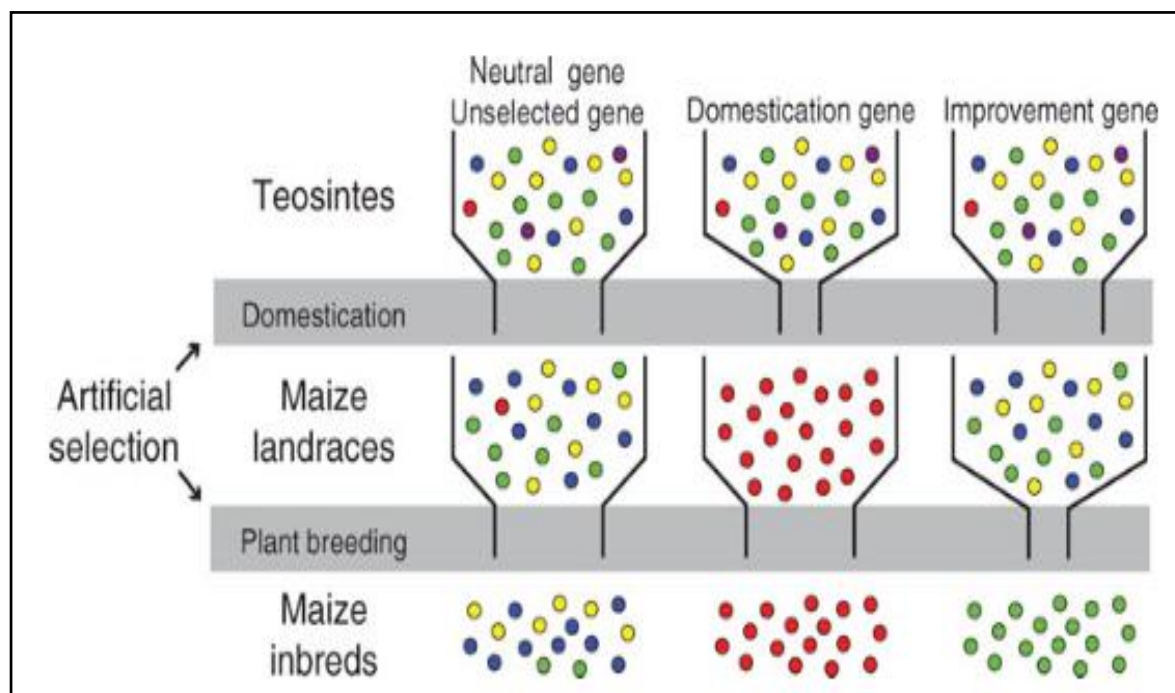

**Fig 3:** Effect of artificial selection on teosinte and maize

Effect of artificial selection during maize domestication and subsequent improvement
Evidence for selection across the genome during both domestication and improvement was evaluated in landraces versus wild relatives for domestication and in improved lines versus landraces for improvement, using the whole-genome polymorphism data generated by the large-scale re-sequencing of maize varieties. The selected genomic loci are

expected to have a much higher allele frequency in landraces than in wild relatives (for example, a selective sweep in maize domestication; locus A) or in modern cultivars than in landraces (for example, a selective sweep in maize improvement; locus B), whereas other loci are expected to be nearly neutral in different panels (for example, a random genomic region without selection; locus C).
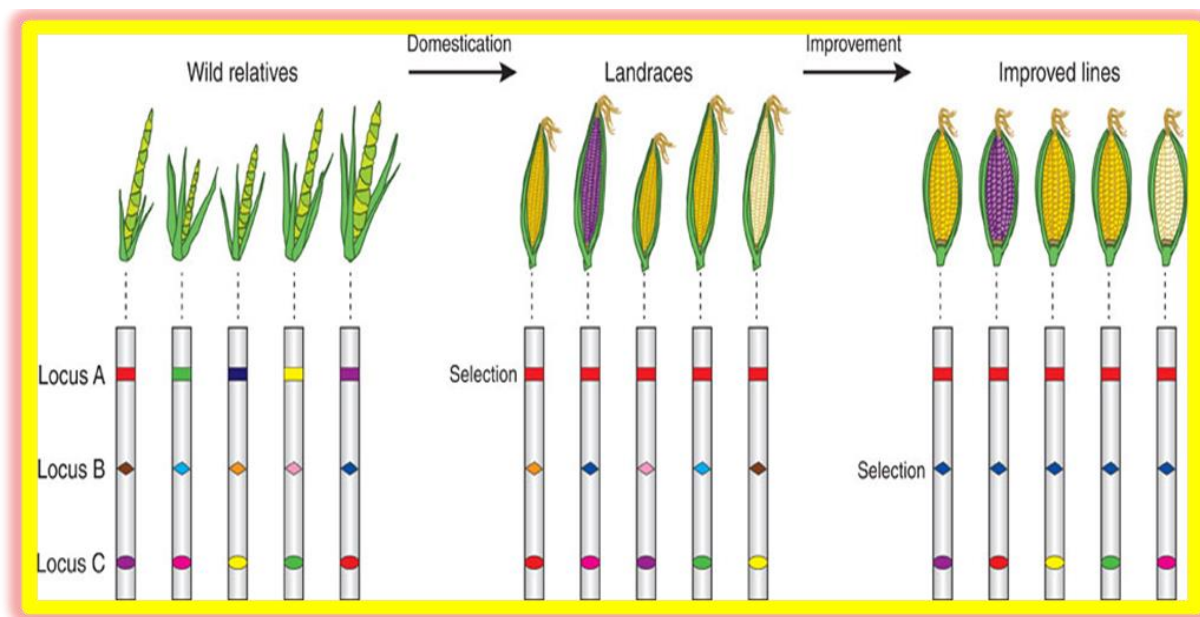
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