PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol 12(2): 1-10
https://doi.org/10.14719/pst.6613

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REVIEW ARTICLE

Genomic changes during crop domestication: structural and functional perspectives

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OPEN ACCESS

ARTICLE HISTORY
Received: 09 December 2024
Accepted: 28 February 2025
Available online
Version 1.0 : 05 March 2025
Version 2.0 : 11 April 2025

Check for updates

Additional information
Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

CITE THIS ARTICLE
Lakshmidevamma TN, Rajeshwari R, Masuthi D, Suwetha S, Sangeetha M, Dhandapani M. Genomic changes during crop domestication: structural and functional perspectives. Plant Science Today. 2025; 12(2): 1-10. https://doi.org/10.14719/pst.6613

Abstract

Domestication of crop species occurred through the processes of natural selection followed by human intervention which further diversified the crop species and contributed to the accelerated crop cultivation from the ancient civilizations across the world. Based on the soil and climatic factors, crops were domesticated primarily for food purposes in different regions of the world which now recognized as the centres of origin. The genetic diversity patterns of genomes of crop plants have provided a detailed understanding of domestication processes. Elucidation of structural and functional perspectives of genomic changes during crop domestication covering strategies, current status and future perspectives are discussed in this article. Domestication of crop phenotypes is influenced by both pre-existing variations in the progenitor species as well as novel mutations. Genes responsible for the domestication syndrome in different crops have been dissected through several QTL and GWAS studies. The intergenerational selection of plant traits promotes improved acclimatization and adaptation to agricultural management strategies. Only a small number of genes are involved in crop domestication, despite the lengthy process, some of these genes are conserved across species. De novo wild species domestication as well as targeted re-domestication are both possible. Modern genetic tools can be effectively utilized for the modifications of targeted genes. In the era of global climatic change patterns, the potential of super domesticating wild crop species will play a major role in adaptation processes, which in turn would safeguard food security effectively through sustainable approaches.

Keywords

adaptation; food security; GWAS; mutations; QTL; variations

Introduction

Crop domestication is the consequence of multigenerational selection and reselection of plant traits resulting in phenotypic and genetic changes. Most of the economically important crop plants like wheat, barley and lentils were domesticated nearly 10000-12000 years ago (1, 2). The crops with easy harvesting tendencies and flavour were selected by the prehistoric humans, which led to the accumulation of beneficial traits contributing alleles. Domestication is often regarded as the foundation for the transition from a hunter- gatherer lifestyle to organized farming. As human societies evolved, so

did plants. The process of cultivation increased association between humans and the plants resulting in several dynamic evolutionary processes leading to many morphological and physiological changes. These changes were so significant that many crop plants diverged from respective wild progenitors and in extreme cases, which refer to drastically changed phenotypes of crop plants such non shattering types from shattering types need human intervention for perpetuation manual seed harvest, field preparation, sowing and other cultural operations for crop growth and development (1-5). Elucidation of genetic architecture and understanding the molecular basis of morphological changes which determined domestication and diversification are the major areas of genetical and genomic studies. The present day crop plants evolved over several thousand years due to both intentional and unintentional human selection, changing wild ancestors into desirable crop plants.

Domestication has been widely recognized as an evolutionary process. Charles Darwin highlighted in his most famous book that the solid directional and diversifying as well as purifying selection during crop domestication serve as a basic tool for deciphering the process of evolution because in crop plants, both antecedent and descendants are available for comparison (6). Domestication studies explained its role in human evolution and the structural and functional changes between wild and domesticated traits associated with plant development, reproduction and adaptation. The stable supply of food for early human settlement was attributed by the following the adaptive changes in crop plants viz., non-shattering, loss of dormancy, reduced branching, increased tillering, photo insensivity, reduced toxic compounds, increased fruit size and increased grain size. These changes helped the human beings to co evolve with crop plants with the start of civilization (7). The Advent of the genomics era has greatly facilitated comparative studies, providing new insights into domestication. Elucidating the domestication process has been a multidisciplinary approach and the analysis of genomic changes and the molecular basis of domestication traits has been a major focus of current research. Progress in ethnobotany and advancement in high throughput next-generation sequencing (NGS) are important tools to reveal the pattern of genome wide changes associated crop domestication and breeding. In recent years, the progress in genomic resources resulted in genome-wide sequencing of several wild relatives and modern cultivars (8, 9). High throughput parallel genotyping and sequencing technologies are deciphering quantitative insights into the patterns of domestication, structure of gene pools, geographic origin of domestication, crop plant admixtures, extent of introgression shape (change in divergence pattern due to natural selection) and size of genetic bottlenecks (reduced population size of domesticated lines from the base wild progenitor lines) during domestication (10). Currently, the enhanced research on domestication-related traits in various crops through molecular genetic studies is leading to a better understanding of genomic changes contributing for phenotypic differences, which also provide for de novo domestication of new genes and new crops for the future (11).

Whether a particular crop species was domesticated only once or several times has been the focus of many studies providing an overview on the spatial and temporal distribution of domestication, repeatability of the process and multiple origins of the phenotypes. Nikolai Vavilov, who studied the domestication origins and by considering high crop diversity suggested seven primary centres of domestication (12). The best characterized example of a single domestication event is maize (*Zea mays* L.), which originated in southern Mexico about 6300 years ago (13). Similarly, based on archaeological remains and molecular analyses, sunflower (*Helianthus annuus* L.) was determined to have been domesticated once, in east-central North America (14). Likewise, the most primitive wheat i.e., einkorn wheat (*Triticum monococcum* L.), had also single domesticated event in the northern Fertile Crescent (15). However, available evidence based on gene sequences from the *japonica* and *indica* lineages and retrotransposons documents multiple origins for, rice, *Oryza sativa* L., with a minimum of two independent origins (16). Similarly, mutations in several genes resulted to the loss of seed shattering in both *indica* and *japonica* subspecies (17). Furthermore, the common bean, *Phaseolus vulgaris* L. analysed using phenotypic and molecular data also revealed two domestication events in South and Central America (18).

Evolutionary Path of Domestication and Diversification

Domestication refers to the initial divergence of crops from the wild species, accompanied by a decrease in plant fitness in the wild while increasing fitness under human cultivation. In contrast, diversification is the process of subsequent development of new crop varieties, improving yield, quality or adaptation through natural crossing and selection. Hence the diversification phase is also referred as the improvement phase. This path of becoming cultivated crop species from wild ancestor is a highly complex multi-staged process (2).

Stage 1: As cultivation is established, new crop is selected for in an agricultural ecosystem resulting in the initiation of domestication.

Stage 2: This stage starts with the in situ amplification of crop plants with desirable phenotypes as well as favourable alleles contributing for yield increase.

Stage 3: Traits that persist permanently within a crop species are considered domestication features i.e., pod corn was evolved for ceremonies by Native Americans; popcorn selected in Peru; Italian red sweet corn and dent corn preferred by Native Americans.

Stage 4: Comprises of intentional targeted breeding for high yield, uniformity, ease of farming and quality.

Domestication and Diversification of Traits

Traits selected throughout domestication and post-domestication stages vary depending on the species, the type and number of domestication events and other factors, different traits may be chosen throughout these stages. Traits that persist permanently within a crop species are considered domestication features. Traits are the variation in domesticated genotypes as a result of crops adapting to specific uses, preferences and geographical growing

conditions. According to a study, "domestication syndrome is a unique set of characteristics that emerge during domestication and differentiate crops from their wild predecessors" (19). The most predominant characteristics of domestication include: decreased branching with strong growth on the primary stem (erect plant habit); decreased seed dormancy; decreased seed dispersal (shattering); determined growth; uniform seed maturation and blooming (lack of sensitivity to photoperiod); more resources were devoted to the parts of the plant that were harvested (fruits, seeds, roots and stems); reduced morphological and chemical defences (spines, indigestible secondary chemicals); a reduction in the bitterness of edible structures (20).

It is thought that characteristics of the domestication syndrome, such as changes in seed dormancy, seed distribution and resistance to herbivores, are detrimental to wild plants. Recessive alleles that are obscured by the heterozygous background of many wild populations frequently regulate these traits.

Diversification traits vary widely among different populations or cultivars, which are often region specific, target trait oriented, like Adaptation to specific climates - photoperiod sensitivity; Seed starch composition - *WAXY* in multiple species and maize *sugary1* (*su1*); Fruit morphology- *SUN*, tomato *FW2.2* and *OVATE*; fruit pigmentation- *Brassica rapa TT8* and the grape myb-related transcription factor namely *MYBA1* and *MYBA2*; Specific cultural practices and preferential traits like dwarfism (*O. sativa sd1*), sticky or aromatic grains in rice, fragrance (rice *BADH*2), pod corn (*MADS19* (*m19*) and popcorn in maize (2).

Microbiome Mediated Adaptive Processes

Tall *indica* rice genotypes have nutrients mobilizing abilities through inherent association of microbes on various levels for nitrogen, phosphorus, potassium, zinc and iron. Tall *indica* rice varieties have stronger microbiome association than modern high yielding semi dwarf varieties. Genotype specific microbiome scrutiny followed by colonization and strong association due to genetic compatibility lead to increased fitness through association of microbes. Interaction of microbiome in rice roots induce expression of biochemical root exudates which are involved in release of insoluble nutrients viz., low molecular weight organic acids and bio chelating agents (phyto siderophores) involved in accumulations. Associative symbiotic bacterial species like *Azospirillum* fix the atmospheric nitrogen into amino acids and it is being incorporated into structural and functional proteins.

Root exudates which include amines, vitamins, antioxidants and flavanoids involved in colonization and multiplication in rhizosphere and endophytic levels. these adaptive mechanisms of tall indica varieties utilize unavailable forms of nutrients (N, P, K, Zn and Fe). Semi dwarf modern rice varieties are having inefficient root exudation traits which limit them to use the soil and atmospheric unavailable forms of nutrients. Zinc uptake, translocation, accumulation is mediated by specific microbiome present in the seed endophytic regions (21). Organic acids composition, proton effluxes and root length were genotypic specific in rice genotypes differing in zinc accumulation efficiencies. It was attributed by the specific microbiome present in the root endophytic regions (22). Genotypes and microbiome were coevolved and it was attributed by the adaptive fitness of the genotype supported by the functional roles of microbiome.

Novel Variation versus Pre-Existing Variation

Domestication of crop phenotypes were influenced by both pre-existing variations and novel mutations in the ancestral species. The absence of alleles governing protective seed shells or interfering with seed shattering in wild species indicates novel genetic variation (23, 24). Surprisingly, very low frequencies of alleles linked to higher apical dominance in maize or higher fruit size in tomatoes were found in the wild relatives. Domestication and diversification can further lead to population expansion through the introduction of new alleles into a population, even while genetic diversity is reduced. It is possible to preserve newly created alleles during the domestication and breeding processes, in addition to pyramiding pre-existing alleles in the wild progenitors. Functionally beneficial alleles that were once rare in the ancestral population have been accumulated through recombination and selection to become frequent in advanced breeding varieties such as the alleles of *fw2.2, tga1* and *sh4*. Natural hybridizations between weedy, wild and domestic populations introduced newer allelic combinations which resulted in improved fitness, tolerance to biotic and abiotic stresses as well as improvement in yield. Natural crossing of wild progenitors with domesticated ones created newer populations with extended phenotypes of adaptive fitness and other important agronomic traits simultaneously domesticating wild progenitor and improving the domesticated lines through recombination of new genes. It resulted in new domesticated species, sub species and genotypes. Hybridizations is the foremost driving element in crop domestication (3). Domestication over time entailed picking out the best desired alleles from existing allelic variation in ancestors as well as selecting new mutations for numerous traits. From the specific sites of domestication, crop species have expanded and dispersed to varied geographical areas.

A specific domestication allele's origin and range can be inferred from the geographic distribution of its ancestral types and diversity. For instance, Southeast Asia is home to the original haplotype of the rice glutinous allele, suggesting that region is where it originated. The origin and dissemination of alleles were systematically shown in maize. The assembly and dissemination of alleles, also the fixing of mutations with their accompanying phenotypes, have all been documented in maize based on archaeological evidence and ancient DNA samples. Research on 8700-year-old maize cobs from southern Mexico showed that samples taken 1500 years later had a mutation in *teosinte glume architecture1* (*tga1*) that uncovered the grains and prevented the grains from breaking off the cob. Additionally, *prolamin-box binding factor* (*pbf*) and *teosinte branched1* (*tb1*) domestication alleles were chosen for in northeastern Mexico (25, 26). After an additional of 2500 years, while the trait *sugary1* (*su1*) was fixed in North America. Approximately 6200

years ago, when maize was introduced to Peru, the genes that cause polystichy, a form of multiple-ranked maize ear distinct from teosinte's two-ranked inflorescence had already been chosen, preserving the popcorn phenotype (27).

Effect of Genetic Bottleneck and Selective Sweeps

The genetic diversity patterns present in the genomes of crop plants reveal the signatures of the agricultural practices. The most common pattern during crop domestication is a significant reduction in genetic diversity, owing to the use of a small number of progenitor species plants by the early farmers. During the domestication process, only the best plants' seeds were used to create the next generation, as a consequence, this winnowing greatly reduced the genetic diversity across the genome which altered the population structure (28, 29). During the domestication processes, when a small number of wild species become the crop founders, genetic drift will act on the traits of positive selection and reduce genetic diversity across the genome. Crop genomes were significantly altered by selection throughout domestication and breeding processes, substantially reducing genetic diversity. In contrast, genes influencing desirable phenotypes underwent a drastic loss of diversity because plants with desired alleles produced the most progeny to each of the next generation and other alleles were eliminated from the population, i.e., selection is expected to differentially reduce diversity at the specific genes. For neutral genes, the loss in diversity is a function of the population size and duration of genetic bottleneck.

Dissecting the genomic localized genetic bottlenecks can help identify the precise genes or mutations underlying characteristics associated with domestication. A molecular signature of selection is produced when a favoured allele selected or fixed to high frequency, eliminating much of the long-standing genetic variation within and surrounding the targeted gene from the population. Only desirable haplotypes are retained around specific genes after domestication, resulting in a very low genetic diversity, which can help to identify selective sweeps. The amount of selection operating throughout the genome, or the selective sweep, can be ascertained by examining nucleotide polymorphism in the upstream and downstream from genes connected to domestication by using several crop accessions. *Teosinte branched 1* (*tb1*) gene nucleotide polymorphism was analysed in a range of maize accessions and it was discovered that human selection was acting on the gene's regulatory region rather than the protein-coding region. Based on a comparison of the extent of genetic diversity present in their wild ancestors, estimates of the severity of the genetic bottleneck of domestication varied widely: from roughly 80% in maize to 40-50% in sunflower and as low as 10 -20% in rice (30-32).

Advances in Elucidation of Domestication and Diversification Genes

Crop plant origins and domestication have been well studied using recent tools of molecular genetics. Morphological research and archaeological discoveries of early domesticates marked a turning point in our understanding of crop evolution. Chromosome homology was utilized to look into the origins of crops starting in the middle of the 20th century; subsequently, allelic variations of enzymes were employed. The creation of useful molecular markers has made it possible to conduct in-depth analyses of the evolution of several crops and the majority of major crops now have the resources needed to look into the genetic basis of phenotypic traits due to the ease and decreasing cost of developing molecular tools. These developments enable the identification of genomic regions and genes that were subjected to selection during the evolution of distinct crops, in addition to facilitating the analysis of the genetic architecture of the wild-crop transition. Certain nucleotide alterations that produce important crop-related traits have been identified (2). Domestication and adoption genes have been identified using 2 methods, along the phenotype-genotype hierarchy. Top-down approach: starting with a known targeted phenotype, genetic techniques such as QTL and linkage disequilibrium (LD) mapping are used to identify candidate genes, or causal genomic areas. Bottom-up approach: Using classic molecular approaches to derive from gene to phenotype, population genetic methods are employed to find the signal of adaptation in a set of genes, based on Darwin's theory of domestication. Next, reverse genetics and common bioinformatics techniques are used to link certain genes to a phenotype. By comparing different genetic traits between 2 populations, selection sweeps can be discovered when population data of both present domesticated lines and wild ancestors are available. Selective sweeps known from genomic scanning need to be validated by other methods.

Several domestication genes have been identified as a result of recent advancements with the use of cutting-edge molecular technologies. The techniques used to identify causative mutations that result in domestication or diversification traits include: 1. Quantitative trait locus (QTL) mapping and association mapping. 2. Genome-wide association studies. 3. Genetic population screening to look for indications of selection. 4. Whole-genome resequencing investigations and candidate gene methodologies.

Quantitative Trait Locus (QTL) Mapping

Most evolutionarily significant traits are quantitative in nature. Phenotypic variation results from multiple QTL, the environment and interactions between genes and the environment (33). A QTL is the genomic region associated with phenotypic variation, which may be attributed to few genes on the same or different chromosomes. QTL mapping is the first and most powerful approach for dissecting the genetic basis of a quantitative trait and has led to major successes in identifying and cloning genes underlying domestication and diversification traits. Several studies in maize, rice and beans have specified the control of few major genes on many domestication traits (34, 35).

The majority of evolutionarily significant traits are quantitative in nature. Multiple QTLs, the environment and interactions between genes and the environment result in phenotypic diversity (33). QTL analysis of fruit mass in a domesticated tomato and wild hybrid in the themed- 1980s, localized six QTLs and mapped the area that included the main QTL fruitweight2.2 (fw2.2) (36). Differences in plant

architecture and yield between maize and its wild predecessor, teosinte, were mapped. Major genes governing phenotypic differences between maize and teosinte, such as *teosinte branched1* (*tb1*) and *teosinte glume architecture* (*tga*), which lead to differences in inflorescence architecture, were isolated through subsequent mapping and mutation investigations (37).

The genes *Btr1* and *Btr2*, which regulate grain dispersal, were discovered and cloned using QTL mapping on 3 populations derived from crossings between cultivated barley and its wild ancestor (38). Non-brittle rachis was caused by 1-bp and 11-bp deletions in *Btr1* and *Btr2*, respectively, in domesticated barley. The key alleles that were favoured throughout domestication were identified through analysis of shattering and blooming time in a foxtail millet mapping population (39). Complex rice QTLs that shatter seeds were spread across multiple chromosomes. In rice, the QTL *OsqSH1* was located on to chromosome 1 identified chromosomal 4 as the location of *SH4* (17, 31). The non-shattering *SH4* allele was fixed in *O. sativa* ssp. *indica* and *O. sativa* ssp. japonica in a different molecular cloning investigation (38). The *YABBY* transcription factor was found to be encoded by the locus Sh1 on chromosome 1 in sorghum, through QTL analysis and positional cloning (40). The three mutations created non-shattering domesticated sorghum. Many studies have also demonstrated that the same genomic regions influence numerous important domestication traits, indicating the action of pleiotropy or tight linkage among various loci. For a few features in different crops, the number of genes or QTLs controlling the traits of the domestication syndrome is clarified.

a) ***Plant and Inflorescence Architecture*:** Rice *SD1* coding culm length (a determinant of plant height), rice *TAC*1 governing erect plant growth in *japonica* varieties, rice *PROG1* and maize *tb1*, which control variations in shoot architecture, barley *Vrs 1* encoding 2-rowed versus 6-rowed inflorescence architecture

b) ***Yield*:** Rice *Ghd7*, which controls plant height, heading date and grain number; rice *OsSPL16* (*GW8*), which govern grain size and shape; rice *GW2*, grain width and weight; rice qSW5 - grain width; tomato fasciated, which govern locule number (a factor in fruit size); rice GS5, which encode rice grain size. Selection for fw2.2, lcn2.1, fw3.2 and other QTGs led to increase in fruit size in modern tomato 10 times more size compared with the cherry tomato (41).

c) ***Pigmentation***: Rice *Phr1*, encode differences between *indica* and *japonica* varieties for grain discoloration in storage; rice *Bh4* for rice hull color variation and sorghum *Tannin1* that regulate grain pigmentation.

d) ***Phenotypes Targeted to Enhance Ease of Planting and Harvesting***: Barley *Nud* regulates free-threshing or "naked" (hulless) varieties; rice *Sdr4*, regulates seed dormancy; sorghum *Sh1*, regulates loss of seed shattering and rice *Qsh 1*, controls seed shattering.

The underlying QTLs for domestication traits have been mapped (Table 1). Following the identification of QTL regions, the underlying genes are functionally characterized, fine-mapped and cloned (23, 36).

Association Mapping

Association mapping, which links molecular variation in candidate genes with phenotypic variation in existing, diverse populations reflecting many generations of historical recombination is an alternative to family-based QTL mapping.

Table 1. Genes underlying domestication and diversification traits with the causative change

Genes	Crop	Molecular and phenotypic function	Causative change
		Genes governing domestication traits	
tga1	Maize	Transcriptional regulator (SBP); seed casing	Amino acid change
tb1	Maize	Transcriptional regulator (TCP); plant and inflorescence structure	Regulatory change
qSH1	Rice	Transcriptional regulator (homeodomain); abscission layer formation, shattering	Regulatory change
sh4	Rice	Transcriptional regulator (Myb3); shattering, abscission layer formation,	Regulatory/amino acid change
Rc	Rice	Transcriptional regulator (bHLH); seed color	Disrupted coding sequence
Vrs1	Barley	Inflorescence structure Premature stop	Amino acid change
fw2.2	Tomato	Cell signaling, fruit weight	Regulatory change
Q	Wheat	Transcriptional regulator (*AP2*); inflorescence structure	Regulatory/amino acid change
		Genes controlling diversification traits	
Genes	**Crop**	**Molecular and phenotypic function**	**Causative change**
sh2	Maize	pyrophosphorylase; supersweet sweet corn	Transposon insertion
c1 *r1*	Maize	Transcriptional regulator (MYB); kernel color and Transcriptional regulator (bHLH); kernel color	Regulatory change
su1	Maize	isoamylase; sweet corn gene	Amino acid change
ovate	Tomato	fruit shape	Early stop codon
brix9-2-5	Tomato	Invertase; fruit soluble solid content	Amino acid change
R	Pea	Starch branching enzyme; seed sugar content	Transposon insertion
hd1	Rice	Transcriptional regulator (zinc finger); flowering time	Disrupted coding sequence
ehd1	Rice	B-type response regulator; flowering time	Amino acid change
waxy	Rice	Starch synthase; sticky grains	Intron splicing defect
vrn1	Wheat	Transcriptional regulator (MADS); vernalization	Regulatory change
rht	Wheat	Transcriptional regulator (SH2); plant height	Early stop codon
vrn2	Wheat	Transcriptional regulator (ZCCT); vernalization	Amino acid change

The non-random association of alleles between loci, or Linkage Disequilibrium, is significantly lower in these populations than it is in the family-based mapping populations. The main benefit of LD mapping is that it can be based on population samples; crossings and the generation of a large number of progeny are not required. Based on the considerable correlations between domesticated features and sequence variation, the investigation of structural and functional aspects of domestication has been greatly aided by genome-wide association studies (GWAS) and linkage disequilibrium mapping (LD). For GWAS, unrelated individuals with ancient LD are included in natural genetic diversity association panels. Compared to a QTL population, the phenotypic of interest might be linked to a considerably smaller chromosomal region, which could theoretically result in higher mapping resolution. LD mapping studies are very powerful when the causative mutation is genotyped. If the causative mutation is not genotyped, it is still possible to identify association via markers that are in LD with the causative mutation. The principal limitation of this approach is that it requires a priori knowledge of candidate genes and phenotypes to be tested. However, the extent of LD can vary dramatically among plant species, among genomic regions and among population samples.

The cloning of domesticated genes and understand the molecular underpinnings of changes related to domestication has been made possible by fine mapping of genes. Nine domestication traits in maize had QTLs ranging from 6 to 26 (28), while 13 domestication traits in rice were linked to 76 QTLs (42). Loci controlling photoperiod response and flowering time diversification characters in the Poaceae family have identified four hotspot genomic regions and 25 QTLs in maize (14) and 16 in foxtail millet (43). Using 267 accessions and 2 million single nucleotide polymorphisms on cotton variables linked to fiber quality, 19 relationship signals were found using GWAS (44). For seven watermelon fruit quality traits, 43 QTLs were found (45). An ortholog of the maize domestication gene *tb1*, *INTERMEDIUM-C*, has been identified by a GWAS analysis in barley as a modifier gene in the transition between 2 and 6 rowed barley cultivars. The primary shattering gene that separates cultivated and wild rice is *sh4* and the *qSH1* gene regulates the variation in shattering intensity between some *indica* and *japonica* rice varieties. One amino acid change reduces shattering in *sh4*, a transcription regulator. Non shattering of grains in *japonica* sup species was the major domestication event which increased the yield of rice tremendously and became the staple food crop of southern Chinese, Korean and Japanese regions. Sequence analysis of *sh4* has identified a single base-pair mutation in both the *indica* and *japonica* rice varieties that causes non-shattering (38). A single nucleotide in the *qSH1* gene's regulatory region causes the changed degree of seed shattering. While *qSH1* controls the creation of the abscission-layer, *sh4* initiates the abscission process.

Since unrelated individuals might accumulate many genetic recombination events since their last divergence, GWAS directly links genomic regions to domesticated phenotypes and helps the interpretation of domestication mechanisms at the molecular level with high mapping resolution. However, GWAS is dependent on the target crop diversity panel, which is typically expensive to collect and maintain. Creating a diversity panel strong enough for GWAS analysis with a minimum population structure is a very challenging task. When uncommon variants in a study panel represent the causative mutations, GWAS power may also be low (46).

Genome Re-sequencing and Screening for Selection Signatures

A potentially effective method for locating genes associated to domestication is genome-wide screening for selection signatures in crop species with well-characterized reference genomes. Only a fraction of the population's standing variation will carry the alleles under positive selection; as a result, only those alleles and alleles of genes in close linkage will be retained. This is due to selection winnowing in genomic regions surrounding genes regulating targeted phenotypes. The roles of particular genes and mutations in domestication-related phenotypes can be evaluated by using comparative expression analysis and functional tests. Genome re-sequencing or SNP genotyping in a diverse population sample can be used to identify specific genomic regions that bear signatures of domestication-related selection. WGRS in Soybean highlighted the molecular imprints of the effects of artificial selection (genetic bottlenecks) during domestication and current improvement of soybean (47). About 5000 years ago, *Glycine soja*, the wild progenitor of soybeans, was domesticated. Although their genomes are largely comparable in size and content, cultivated and wild soybeans differ significantly in terms of morphology. The small, black seeds of the wild soybean accessions (*G. soja*) grow prostrate manner like weeds. Smaller plants with poor vegetative growth and a tendency toward minor prostration are produced by the domesticated landraces. Modern breeding techniques have produced elite cultivars with compact, erect stem architecture, low branching, high harvest indices and high seed yields. Sequencing of soybean accessions followed by analysis revealed the presence of 5102244 SNPs which comprise of 701 to 792 small InDels (<5 bp) which are used as reliable markers for mapping of genes. It was found that 6.177 large deletions existed in the genome (>200 bp with a mean length of 3615 bp). The validation of 106 SNPs which were randomly selected from the genes was done using Sanger method. In land races of soybean, it was identified that totally 1661945 SNPs were not polymorphic. Of these SNPs, 4.0% (66637) were non-synonymous sites and 5.7% (94793) were found in the CDS sections of genic sequences. A decrease in genetic diversity from wild soybeans to landraces of 31% and 26% respectively was observed (47).

Likewise, comparison of sequences of 446 wild and 1083 cultivated rice accessions revealed the origin of *O. sativa* ssp. *japonica* in the middle of the Pearl River region in Southern China which was domesticated from *O. rufipogon* population. 55 selective sweeps and the selection signatures were identified. They accounted for 5.1% of the genome regions (21.9 Mb) (48). Based on WGRS 75 wild, landrace and improved maize lines, identified genes were identified with strong selection signatures (49). Genome-wide variation studied for 352 wild and domesticated cotton accessions revealed domestication sweeps across 74 Mb of the ‘A’ sub genome and spanning 104 Mb of the ‘D’ sub genome and

found asymmetric sub genome domestication for directional selection of long fibers (46).

Structural and Functional Perspectives of Crop Domestication

Numerous investigations have highlighted the molecular roles of genes involved in domestication and diversification and a number of functionally diverse loci have been identified. When about 60 genes associated in domestication or diversification were studied (35), approximately 37 genes (~62%) encoded transcription factors, 3 additional genes encoded transcription co-regulators, 14 genes encoded enzymes and 6 genes coded for transporter proteins and ubiquitin ligase. Numerous functionally significant mutations that are susceptible to selection pressures were found; the most common types were missense, cis-regulatory, nonsense, premature truncation and other structural alterations that modify protein function. Additionally, the genome structural variation resulting from these mutations was examined and their roles in the development of domesticated features was analysed revealing the Coding sequence substitutions, SNPs, Indels, copy number variation, transposon activation leading to novel gene structures and expression patterns, gene duplication and polyploidy and chromosomal rearrangements (50-52). Mutations in regulatory genes, like transcription factors, regulating phenotypic changes during domestication were deciphered (20). The aforementioned genes are subject to causal mutations that mostly result in missense, nonsense, premature truncations, cis-regulatory and other mutations that cause null function. Out of the 60 genes that were examined, 35 of them had at least one causative SNP, 23 of them had indels and 9 of them had a transposable element among the mutations generated. Larger sequence mutations are less common in genomic changes than single nucleotides and small indels. Mobile elements or transposable elements contribute to genome evolution through exon switching, insertion mutagenesis, homologous and non-homologous recombination. Transposon activity is thought to be a rich source of phenotypic variation that was either directly or indirectly selected for during domestication, either by mutagenesis or through their influence on gene expression. The most famous domestication gene in maize, *tb1*, has been shown to be caused by a transposon-mediated insertion (53).

TE Responsible for Domestication Characteristics

The teosinte branched1 (*tb1*) gene encodes a transcriptional regulator from the TCP family that functions as a repressor of organ growth, playing a crucial role in apical dominance. This gene consequently suppresses branch expansion, which in turn promotes apical dominance. Branching is more strongly repressed when the maize allele of *tb1* is expressed than when the teosinte allele is expressed (26). The transition from the highly branched wild teosinte plant to the single-stemmed maize phenotype is controlled largely by increased expression of *tb1*, which encodes a transcriptional regulator that represses growth and thought to be a key contributing QTL for apical dominance. A *Hopscotch* retroelement (*retrotransposon of Zea mays*) insertion in the *tb1 cis* regulatory region accounts for the increased *tb1* expression. A regulatory element, or "control region," that modifies this expression differential is situated between 58.7 and 69.5 kb upstream of the *tb1* ORF (2). Similarly, the insertion of a *MuDR*-like TE in the promoter sequence of maize results in the tunicate (pod corn); *Gret1* gypsy-type retrotransposons in the promoter of *VvMybA1*, a transcription factor directing anthocyanin synthesis, result in white berries in grapes. The high genetic diversity found in the domesticated genome of grape is thought to be a result of the accumulation of these repetitive elements, as revealed from genome-wide surveys of class II transposons and miniature inverted-repeat transposable elements (MITEs) (54).

Gene and Genome Duplications in Domestication

Plant genomes have a high degree of duplication and almost all genes are members of multigene families, with different copies (paralogs) connected to each other by both more recent and older duplication events. These duplications arise from polyploidy, or whole-genome doubling, as well as more localized or tandem gene duplications. They have contributed to crop diversification and function by increasing allelic diversity, providing environmental buffering, allowing for dosage fine-tuning that can lead to novel phenotypic variation and allelic complementation. Certain crop traits, such as free threshing in hexaploid wheat, are believed to have originated through polyploidy. The *Q* locus in wheat, which gives hexaploid wheat free threshing and linked to other significant domestication and improvement traits like plant height, inflorescence architecture and blooming time was studied (55). The *Q* gene, which codes for a transcription factor belonging to the *AP2* family, underwent a sequence of events during the divergence of diploid and polyploid wheat. These events included duplication and the subsequent loss of distinct paralogs at the diploid level, resulting in the loss of one gene in diploids with an A genome and the loss of the other gene in diploids with B and D genomes. The *Q* phenotype was produced by a single valine-to-isoleucine amino acid replacement in the A homeolog, which occurred after polyploid formation and the reunion of these now-divergent paralogs into a shared nucleus. B-genome gene regulates homeolog expression and the D-genome homeolog responsible for the pleiotropic aspects of the free-threshing mutant phenotype. Novel genomic changes, asymmetric sub-genome selections reported in diverse polyploidy crops, such as rapeseed, cotton, including grape and potato when compared with diploids has been indicated (44, 54, 55).

The Comparative Genetics of Domestication-Maize versus Rice

Parallel selection across taxa has acted on comparable gene sets and pathways throughout domestication. In rice, maize, common beans, soybeans, cucumbers and other crops, genome-wide selection screens have been used to uncover parallel genetic changes across species that have led to phenotypic shifts associated with domestication, such as morphological changes that have resulted in less seed dispersal, less seed dormancy, less branching or tillering, more synchronized seed maturation, larger grains and more inflorescences than their wild counterparts. Using the whole genomes of 58 maize and 16 teosinte individuals, Nucleotide polymorphism in maize (7, 53) and found 1200 areas (or 2-4% of genes) covering 1766 genes with low diversity indicating the domestication events as natural selection in positive direction. A further study in rice revealed the entire genomes of 1083 and 446 cultivated and wild rice individuals found that 2547 genes were subjected to positive selection in 55 areas. Of these, 969 of the 1766 maize genes had an ortholog

to a rice gene and 1526 of these had an ortholog in maize (53, 56).

Orthologues of Domestication Genes and Their Action

Plant transcriptional regulators involved in domestication are all members of distinct families (25). Gene organization within a family of transcriptional regulators may be sufficiently preserved to allow comparisons between taxonomically very distantly related species as well as genera within the same plant family. Thus, *Q* in wheat is identical to *APETALA2* (*AP2*) of Arabidopsis and *monoculm1* in maize is similar to *LATERAL SUPPRESSOR* from *Arabidopsis thaliana* and tomato. Q is currently the sole *AP2*-like gene linked to domestication, despite the fact that *AP2*-like genes appear to play a variety of roles in plant growth. The *qSH1*, one of the rice genes influencing shattering, is an orthologue of *Arabidopsis*' *REPLUMLESS* (*RPL*) gene (17). The differences in the transcriptional control of *RPL* and q*SH1* may account for the difference in the formation of an abscission layer between the pedicel and spikelet, which is affected by *qSH1* but not by *REPLUMLESS* in the fruit wall. Similar to maize tb1, rice also has an orthologue called *OsTB1*, which influences lateral branching (57). Due to *OsTB1* overexpression, transgenic rice with an increased dosage of *OsTB1* produced significantly fewer tillers than usual. The region where fine culm1 (fc1), a known mutant with increased tiller production, mapped to is identical to *OsTB1*, indicating that fc1 is an allele of *OsTB1* (58). The predicted polypeptide product of *fc1*'s sequencing revealed an early stop codon due to a loss, which prevented the domain associated with the transcriptional regulators *tb1* belongs to from binding DNA (59).

Conclusion

In modern breeding programmes, the practice of transferring genes from wild relatives is a continuous process. Detailed and conclusive evolutionary research would provide better understanding of the domestication process as well as helpful gene information for future breeding. The development of novel genes and crops from wild progenitors through *de novo* domestication processes offers greater adaptability in the era of global climate change and it will safeguard the food security in near future.

Acknowledgements

TNL and MD wish to acknowledge their respective Institutions viz., College of Horticulture, Bangalore 560065 and Tamil Nadu Rice Research Institute, Aduthurai 612101 for logistical and financial support during preparation of this manuscript.

Authors' contributions

TNL and MD have conceptualized the draft. TNL reviewed the literature, drafted manuscript. MD finalized the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used the Grammarly tool in order to improve language and readability of the content. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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