

Genomics and Crop Domestication

Subjects: Agriculture, Dairy & Animal Science

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Most domesticated crop species share common traits such as increased yield and seed size and decreased dormancy and seed shattering. Though crop domestication is long and slow, only a few genes are involved in it, and some of them are conserved in various species. Hence, both targeted re-domestication and *de novo* wild species domestication are feasible. In these processes, targeted genes are identified, introgressed, or modified to produce new cultivars. Unlocking the potential of wild crop species domestication will improve global food security and help realize certain sustainable development goals of the United Nations such as zero poverty (No. 1) and zero hunger (No. 2). Targeted domestication, crop improvement, and mass crop cultivation are generally cost-effective approaches towards these objectives.

Keywords: crop ; genomics approaches ; domestication ; application ; Gene editing

1. Overview

Crop domestication occurred ~10,000–12,000 years ago when humans shifted from a hunter–gatherer to an agrarian society. Crops were domesticated by selecting the traits in wild plant species that were suitable for human use. Research is crucial to elucidate the mechanisms and processes involved in modern crop improvement and breeding. Recent advances in genomics have revolutionized our understanding of crop domestication. In this review, we summarized cutting-edge crop domestication research by presenting its (1) methodologies, (2) current status, (3) applications, and (4) perspectives. Advanced genomics approaches have clarified crop domestication processes and mechanisms, and supported crop improvement.

2. Crops

Crops played a major role in human cultural evolution by causing a shift from a nomadic to a sedentary society. Hence, crops are suitable as evolutionary models illuminating genetic variation and selection. Crop domestication is a major agricultural advance ensuring food security for human society. Domestication is the result of phenotypic and genetic changes mediated by breeding. It involves multigenerational selection of plant traits favoring enhanced adaptation and acclimatization to farming management practices. Approximately 12,000 years ago, most economically important crops were domesticated [1][2]. Our ancestors instinctively selected crops that were easy to harvest and those with improved yield and flavor. These simple selection strategies helped pyramid important alleles and recombinants and resulted in naturally transformed plants with beneficial traits facilitating cultivation, breeding, storage, trade, and dissemination.

Of the ~5500 food crops worldwide, 15 contribute to ~70% of the total calories consumed by humans. Rice, wheat, and maize account for >50% of the calorie demand [3]. Up to 7000 known plant species are semi-cultivated or orphan crops [4]. These natural plant resources comprise a valuable pool of genetic material that could enable future crop breeding, increase food diversity, and respond to the new challenges of global climate change and population expansion [5]. The domestication of orphan and underutilized crop plants via recently developed biotechnologies such as genome-editing and genome-enabled approaches is highly promising in crop development for smart agriculture.

Most domesticated crop species share common traits such as increased yield and seed size and decreased dormancy and seed shattering. Though crop domestication is long and slow, only a few genes are involved in it, and some of them are conserved in various species [2][6][7][8][9][10]. Hence, both targeted re-domestication and *de novo* wild species domestication are feasible. In these processes, targeted genes are identified, introgressed, or modified to produce new cultivars. Unlocking the potential of wild crop species domestication will improve global food security and help realize certain sustainable development goals of the United Nations such as zero poverty (No. 1) and zero hunger (No. 2). Targeted domestication, crop improvement, and mass crop cultivation are generally cost-effective approaches towards these objectives. A concerted effort under the joint leadership of the Food and Agriculture Organization (FAO), Consultative Groups of International Agricultural Research Institutions, National Agricultural Research Institutions, and

various governments is required for the research, popularization, and large-scale utilization of undomesticated crops with potential.

3. Population Genomics

Population genetics and genomics have revealed that crops passed through four major stages during their evolution from wild progenitors to modern domesticated species [2]. These include (1) the onset of domestication when only one or a few wild progenitors with traits favored by humans were selected; (2) in situ propagation of selected wild progenitors to increase desirable alleles; (3) the spread and adaptation of cultivated populations to new environments; and (4) deliberate plant breeding to improve agronomic traits. During domestication, only a few individuals with traits serving human interests were selected from the wild progenitor population. Genetic drift caused by the founder effect and by selection reduced genetic diversity in domesticated crops. Genetic drift was assessed by comparing the genomes of domesticated crops and their wild relatives [11]. Advances in sequencing technologies and reduction of their costs have supported the publication of numerous high-quality studies on crop domestication using population genomics methods (Table 1). Huang et al. [12] compared the genome sequences of 446 wild and 1083 cultivated rice accessions. They found that *O. sativa japonica* originated in the middle of the Pearl River region in Southern China and was domesticated from a specific *O. rufipogon* population. There were 55 selective sweeps, and the genome signatures for selection during domestication were identified. They accounted for 5.1% of the genome regions (21.9 Mb) [12]. Hufford et al. [13] identified a few genes with strong selection in domesticated maize based on whole-genome resequencing of 75 wild, landrace, and improved maize lines. The authors also demonstrated that post-domestication diversity may have been recovered through introgression from wild relatives.

Table 1. The application of population genomics to crop domestication.

Crop	Population Type	Population Size	Key Statistic	Discovery	Ref.
Rice	Ancestral progenitor; cultivated indica and japonica varieties	1529	Sequence diversity (π) population-differentiation (F_{ST}), cross-population extended haplotype homozygosity (XP-EHH)	Identify 55 domestication sweeps, and reveal the domestication and development of cultivated rice	[12]
Maize	Wild, landraces and improved maize lines	75	π , ρ , F_{ST} , Tajima's D, normalized Fay and Wu's H, and a composite likelihood approach (XP-CLR)	Evidence of recovery of diversity after domestication, and stronger selection for domestication than improvement	[13]
Maize	Ancient samples, modern maize landraces, and teosintes	134	Mutation load, D-statistics, and f3 and f4 statistic	Reveal domestication center and human-mediated spread of maize	[14]
Wheat	Ancient and modern domestic emmer	64	Haplotype structure	Uncover the history and diversity of emmer wheat	[15]
Cotton	Wild and domesticated cotton accessions	352	π , F_{ST} , and XP-CLR	Identify 93 domestication sweeps	[16]

Advances in genetics, archeology, and their interdisciplinary areas have contributed to the clarification of crop domestication. Analyses of modern and ancient DNA have uncovered details about human and animal history. However, few studies have reported on the history of crop domestication, as there has been insufficient archeological evidence or DNA for genetic analysis [17]. Kistler et al. [14] sequenced 40 indigenous maize landraces and nine archeological samples from South America and compared them against 85 published maize genomes. The ancestral South American maize population was brought from its domestication center in Mexico before its domesticated traits were established. Multiple subsequent dispersal events led to maize diversity and biogeography. Scott et al. [15] prepared whole-genome sequences of a museum specimen of Egyptian emmer wheat chaff and demonstrated that ancient Egyptian emmers already shared a common origin with modern domesticated emmer even before the crop was introduced to Egypt. The foregoing results furnished evidence for early southeastern wheat dispersal and gene flow from wild to ancient Egyptian emmer.

Wang et al. [16] used a genome-wide variation map for 352 wild and domesticated cotton accessions. They scanned domestication sweeps covering 74 Mb of the 'A' subgenome and 104 Mb of the 'D' subgenome and found asymmetric subgenome domestication for directional selection of long fibers. Hufford et al. [13] conducted population genomic studies

and discovered that 7.6% of all maize genomic regions were under selection during domestication. However, population genomics has certain drawbacks. First, genomic signals caused by domestication or improvement might be confused because genetic diversity is reduced in both cases. Second, certain crops have undergone multiple independent domestications wherein different genomic region layers may have been selected at different times. Hence, mixtures of samples from various domestication processes could obscure signals targeted for selection. Third, introgression may bilaterally occur between wild and domesticated crops and weaken signals identified through population genomics. Fourth, certain genomic signatures identified under domestication are not directly related to any agronomic traits, and their molecular mechanisms remain unclear. Hence, they must be validated by genome-wide association studies (GWAS), quantitative trait locus (QTL) mapping, map-based cloning, and functional targeted gene analyses.

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