

Review Article

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Domestication in Plants: A Key to Unexplored Variability

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ABSTRACT

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Domestication is the process in which plants are genetically modified over time by humans for traits that are more advantageous or desirable for humans. A set of morphological, biochemical, and physiological traits that distinguishes domesticated plants from their wild progenitor is known as domestication syndrome. Reduction/loss of means of dispersal reduction/loss of dormancy, compact growth habit, earliness, gigantism, photoperiod insensitivity, reduction/loss of toxic substances is the major elements of domestication syndrome. Studying the crop domestication in detail will help us to uncover the hidden variability in crop wild relatives and can help in further crop improvement and thereby ensure the food security.

Introduction

The nomadic man tried hard to survive. He wandered all around to get the food. He hunted and collected the food. In that journey he began to keep some animals and plants with him. There arise the era of domestication. Domestication literally means bringing under human management; it may be of plant or animal. This phenomenon later lead to agriculture changed the human life. The nomadic man started settlements eventually leading to civilizations. Plant domestication plays a major role in agriculture sector. What actually the

domestication done with the plant is genetic modification for a character which is advantageous or desirable for human use. In short they became the pets of the humans. As a result of domestication, a new plant form arise which will easily meet out the human needs.

Where and how did it happen?

Several crops are having different areas of distribution. The diversity includes its various forma and the crop relatives. Centers of diversity, place where more diversity was found for a particular crop species and that

particular crop is believed to be originated from that particular place. So, this originated place is believed to be domesticated place of the corresponding crop (Gepts, 2014). So there are different centers of origin and diversity for every crop. The domestication is not a rapid process. It happened knowingly or unknowingly by the action of our ancestors. The basis of domestication is the selection. Two key terms behind domestication is 'Unconscious selection' and 'Conscious selection'. Unconscious selection means the work is not intentionally done which implies that domestication happens in nature i.e., selection of most valued one is not done with the thought of altering the breed. Conscious selection means domestication is done with intention. But, many of the changes due to domestication are arisen from unconscious selection (Zohary, 2004).

Domestication process

The domestication process requires three major factors: Plant/animal, Human, and Environment. The humans and the environment influence the plants or animals and lead to the formation of their domesticated forms (Gepts, 2014). The process of domestication can be broadly divided into three stages. *Viz.*, 1. Hunting – Gathering stage, 2. Pre domestication cultivation, 3. Emergence of true agriculture.

In the first phase, the people started to search for food and led a nomadic life. They mostly hunted the food required for them. After that they began to settle down which makes them gatherers. The settled man went out to gather food. They started collecting the seeds or the propagules of the plants of their interest. They started growing them near their settlements. Thus the wild plants that they used for food became the pets. They took care of their pets and harvested and regrew them. There began the agriculture. The selected the type of plants

as per their needs. These selections later lead to the evolutionary changes in the plants. The plant evolved themselves as desirable pets for the humans and develops some characters which differentiate them from their wild forms called as 'domestication syndrome'.

Domestication syndromes

The alteration in the genetic component of the plants that created the new cultivated types is called as the plant domestication. The domestication lead to the increase of those traits that is favorable to humans. The most of the domesticated plants completely depend on the humans even for their survival and propagation. For example the crops like maize and cauliflower are such highly modified crops. While some of the crops like carrot, lettuce etc. were modestly modified when compared to their wild forms. A common set of traits in the domesticated plants that differentiate themselves from the wild progenitor is called as domestication syndrome. In general, the grain crops will have larger grains, higher grain weight, higher grain yield etc. while the fruit crops have larger and more number of fruits.

There are several traits which constitute to the major domestication syndrome traits. The larger fruits or grains is a major one in all food crops as the human always selected for the increased yield. As the agriculture crops should have a determinate growth to harvest them at a single stretch, it is also one of the evolved trait during domestication. An increase in apical dominance was there which lead to the strong central stem in the cultivated forms. Some of the plants reduced the number of fruits by increasing the weight. As the human cultivation doesn't involves any natural way of seed dispersal, the trait was eliminated from the cultivated forms. Some physiological traits also took place. The dormancy is one of the important trait that is

lost during the domestication. In many of the crops there was a bitter substance in the skin like that in cucurbit crops. But the level of the bitter substance is very less in cultivated forms when compared with the wild progenitors. The changes in photoperiod insensitivity and synchronized flowering are also involved in the process.

Elements of domestication syndrome

Though there are several common traits those evolved during the domestication, some of them revolutionized the whole agriculture. There are some major traits that are characteristics of domesticated plants.

They are Loss of brittle rachis, Loss of dormancy, Compact growth habit, Earliness, Gigantism (in case of polyploidy evolution), Photoperiod insensitivity, Loss of toxic substances, which creates major disadvantage in case of defense mechanism but increases the value of edibility (Gepts, 2014).

Genes controlling domestication syndrome

Teosinte branched1 (tb1)

Teosinte branched1 (tb1) gene was one of the major gene or QTL reported which is related to the domestication of maize. This gene controls the lateral branching in maize. This differentiates maize from its progenitor teosinte due to the action of this gene controlling the apical dominance (Doebly *et al.*, 1997; Doebly, 2004). The teosinte plants are highly branched while the maize plant have single stalk due to this gene which is a member of transcriptional regulators of cell cycles (Cubas *et al.*, 1999; Kosugi and Ohashi, 2002). *tb1* is the repressor of cell cycle genes for axillary meristem outgrowth and elongation (Li *et al.*, 2005). The expression studies indicate the higher expression of *tb1* in maize (Doebly *et al.*, 1997; Wang *et al.*, 1999).

Fruitweight2.2 (fw2.2)

Fruitweight2.2 (fw2.2) is a major QTL controlling fruit weight in tomato (Frary *et al.*, 2000). The exact function of this QTL is unknown but it is supposed to a negative regulator of cell division. The human selection caused a lower expression in fruit development causing higher fruit weight compared to wild progenitor (Cong *et al.*, 2002).

The large- and small-fruited alleles have no differences in protein sequence, supporting the model that changes in gene regulation underlie the evolution of tomato fruit size as controlled by *fw2.2* (Nesbitt and Tanksley, 2002).

Teosinte glume architecture1 (tga1)

Teosinte glume architecture1 (tga1) was identified as a QTL controlling the formation of the casing that surrounds the kernels of the maize ancestor, teosinte (Wang *et al.*, 2005). *tga1* belongs to the family of transcriptional regulators (Cardon *et al.*, 1999).

Consistent with this hypothesis, *tga1* has phenotypic effects on diverse traits including cell lignification, silica deposition in cells, three-dimensional organ growth, and organ size (Dorweiler and Doebley, 1997).

Q gene

Q is a major gene responsible for wheat domestication which affect the shattering of spike, tenacity and compact spike in cultivated forms (Simons *et al.*, 2006). Recently, *Q* is a member of the AP2 family of plant-specific transcriptional regulators. This gene family regulates traits related to inflorescence structure and flowering. The cultivated (*Q*) allele is expressed at a higher level than the wild (*q*) allele.

Shattering 4 (sh4)

shattering4 (*sh4*) is a major QTL controlling shattering in rice which is mutated to lose shattering in cultivated rice (Li *et al.*, 2006). Using transformation, Li *et al.*, (2006) were able to confirm that a single amino change in the predicted DNA binding domain converts plants from shattering to non-shattering. A decrease in expression of the cultivated allele as compared to the wild allele may also be important.

qSH1

qSH1 is another major QTL controlling shattering in rice that has recently been cloned and shown to encode a homeobox containing transcription factor (Konishi *et al.*, 2006). Grain number differences between rice varieties are controlled by *grain number1* (*gn1*), which encodes an oxidase/dehydrogenase that degrades the plant hormone cytokinin (Ashikari *et al.*, 2005).

Impact on genetic diversity a genetic sweep

As we all know, selection causes changes in allelic frequency of a population. As a result, the variation found in a population will dramatically get decrease due to fixation of some alleles in a population. The causes of decrease in genetic diversity will be of two factors. They are Bottle neck effect and Selective sweep. According to bottle neck effect, initially, the population has enormous alleles with all at equal frequency. After domestication the new population will not have all the allele. It will have the selected allele at different level of frequency which causes reduction in genetic frequency. (Doebley *et al.*, 2006)

The neutral gene represents the presence of all type of alleles in a population. During domestication some favorable alleles alone

fixed in a population and diversity gets reduced. But, in case of selected gene in a population only one type of alleles will be fixed during domestication, the resultant population will have high homogeneity. Selective sweep refers variation in nucleotide level will get reduced or eliminated. i.e., under natural condition, sudden increase in the frequency of a new beneficial mutation will be there. Before selection the population has different types of alleles. But after selection the frequency of some allele will get increased which reduces the genetic diversity (Ibarra *et al.*, 2007). Ultimately, these two factor causes reduction in genetic diversity which is considered as a major impact of domestication.

Super domestication

The process that leads to domesticate with dramatically increased yield that could not be selected in natural environments without new technologies. The array of genome manipulations that have been developed, mainly enable barriers to gene exchange to be overcome and have leads to super-domesticates with dramatically increased yields, resistances to biotic and abiotic stresses, new characters for the marketplace, Hybrid rice can be considered as super domesticate. Conversion of a crop from C3 to C4 photosynthesis would certainly be a super domesticate (Vaughan *et al.*, 2007).

Food security

Although the population-wide genomic consequences of domestication offer several predictions for levels of the genetic diversity in crops, our understanding of how this diversity corresponds to nutritional aspects of crops is not well understood. Many studies have found that modern cultivars have lower levels of key micronutrients and vitamins. Selection for palatability and increased yield

at domestication and during post-domestication divergence exacerbated the low nutrient levels of many crops, although relatively little work has examined this question. Lack of diversity in modern germplasm may further limit our capacity to breed for higher nutrient levels, although little effort has gone into this beyond a handful of staple crops. This is an area where an understanding of domestication across many crop taxa may provide the necessary insight for breeding more nutritious crops in a rapidly changing world (Smykal *et al.*, 2018).

In conclusion, the crop wild relatives are as important as the cultivated crops in terms of variability. The progress in understanding crop domestication will help the crop scientists to uncover the unexplored variability. So in this age of climate instabilities, this variability can be utilized for sustainable crop production or food security.

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