Quantitative Trait Locus Analyses of the Domestication Syndrome and Domestication Process

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INTRODUCTION

Domestication of many of today's main food crops occurred approximately 10,000 years ago with the beginning of agriculture. It has lead to the selection by farmers of a wide range of morphological and physiological traits that distinguish domesticated crops from their wild ancestors. These characteristics are collectively referred to as the domestication syndrome and include changes in plant architecture (e.g., apical dominance in maize), gigantism in the consumed portion of the plant (e.g., fruit size in tomato and eggplant), and reduced seed dispersal (i.e., nonshattering or nondehiscence, as in the common bean, sunflower, and cereals). Many investigations based on multidisciplinary approaches—such as genetic, archaeological, and phytogeographical analyses—have succeeded in identifying progenitor species and centers of domestication. However, the genetic and molecular bases of morphological evolution in plants under domestication are largely unknown.

Advances in genome mapping, which have resulted in high-density molecular-marker linkage maps in most crops, have provided tools for dissecting the genetic basis underlying complex traits into their individual components, i.e., their quantitative trait locus (QTL). This method relies on the frequent ability to cross the crop and its wild progenitor. It enables the characterization of genetic differences in terms of the number and chromosomal location of the genes as well as quantitative estimates of the kind and amount of genetic effects associated with individual loci. Recent studies have analyzed the genetics of the domestication syndrome of crops belonging to diverse families.

GENETIC BASIS AND ORGANIZATION OF THE DOMESTICATION SYNDROME

Many quantitative genetic analyses have focused on individual traits that are related to domestication but comprehensive analyses of the inheritance of the domestication syndrome[1] as a whole are scarce.

Major vs. Minor Genes

Research has revealed that numerous traits that distinguish crop plants from their wild relatives are often controlled by a relatively small number of loci with effects of unequal magnitude.

Many qualitative traits are controlled by one Mendelian locus such as seed shattering in sorghum[2] and pearl millet.[3] But even the traits that are usually considered as exhibiting quantitative inheritance involve few QTLs of large effect plus others of more modest effect. The genetic study of an F_2 population derived from a cross of maize (*Zea mays* ssp. *mays*) and its wild progenitor, teosinte (*Z. mays* ssp. *parviglumis*),[4] revealed that the domestication traits are controlled primarily by five chromosomal segments (Table 1). One of the major QTLs, *tb1* (*teosinte branched 1*), conditions the dramatic alteration in plant architecture from a multistemmed, branched plant to the single-stemmed plant most people are familiar with. Similarly, in common bean, seed dispersal (pod dehiscence), seed dormancy, and photoperiod sensitivity are all determined by a few loci with effects of large magnitude.[5] In eggplant, most of the dramatic phenotypic differences in fruit weight, shape, color, and plant prickliness that distinguish domesticated eggplant,

Table 1   Genomic regions showing QTL clustering for domestication traits

Crop	Biology	Mapping cross (domesticated × wild forms)	Cluster	Attribute of the corresponding traits
Maize[4]	Outcrossing, $2n = 4x = 20$	F$_2$: *Zea mays* ssp. mays × *Z. mays* ssp. parviglumis	Chr 1	Shattering (ear disarticulation), growth habit, branching pattern (*tb1*), ear and spikelet architecture
			Chr 2S	Number of rows of cupules
			Chr 3L	Growth habit, ear architecture
			Chr 4S	Glume hardness (*tga1*)
			Chr 5	Ear architecture
Common bean[5]	Self-pollinated, $2n = 2x = 22$	F$_2$: *Phaseolus vulgaris* cultivated form × *P. v.* wild form	LG D1	Growth habit and phenology
			LG D2	Seed dispersal (pod dehiscence) and dormancy
			LG D7	Pod length and size
Rice[7]	Self-pollinated, $2n = 2x = 24$	F$_2$: *Oryza sativa* × *O. rufipogon*	Chr 1	Growth habit (tillering & height), shattering, panicle architecture
			Chr 3	Shattering, panicle architecture, earliness
			Chr 6	Shattering, panicle architecture, earliness
			Chr 7	Panicle architecture
			Chr 8	Growth habit (height), earliness, shattering
Pearl millet[3]	Outcrossing, $2n = 2x = 14$	F$_2$: *Pennisetum glaucum* ssp. glaucum × *P. glaucum* ssp. monodii	LG 6	Shattering, spikelet architecture, spike weight, growth habit
			LG 7	Spikelet architecture, spike size, growth habit and phenology
Sunflower[8]	Outcrossing, $2n = 2x = 34$	F$_3$: *Helianthus annus* var *macrocarpus* × *H. a.* var *annus*	LG 17	Shattering, apical dominance, achene weight, earliness
			LG 09	Achene size and weight, growth habit, head size
			LG 06	Growth habit, achene size and weight, earliness, head size
Eggplant[6]	Self-compatible, $2n = 2x = 24$	F$_2$: *Solanum melongena* × *S. linnaenum*		No obvious colocalization

Solanum melongena, from its wild relative, *S. linnaeanum*, could be attributed to six loci with major effects.[6] On this basis, early domestication is most likely to have been a process involving major genes, while subsequent changes may have occurred by the accumulation of minor mutations. Some domestication traits result from the loss of wild-type function and are associated with recessive mutations. However, mutations altering gene regulation are also reported (discussed later).

Clustered Distribution of QTLs

Another interesting feature of the inheritance of domestication traits in crop plants is that the loci for such traits are frequently clustered in a few chromosomal regions (Table 1). This pattern of genetic correlations across traits due to linkage has been documented in some cases of domestications (Table 1). For example, in common bean[5] and maize,[4] QTLs underlying domestication traits are largely restricted to three and five genomic regions, respectively. In pearl millet, two regions of the genome control most of the key morphological differences of the spike and spikelet, including seed shattering.[3] Each of the segments identified has an effect on related but also unrelated traits, suggesting that they could carry either a single mutation with pleiotropic effects or several mutations in linked genes. Linkage among domestication QTL is predicted to evolve under strong selection, especially in allogamous species. Eggplant is a predominantly self-pollinated crop and does not provide strong evidence for the colocalization of domestication syndrome traits.[6]

Table 2 Domestication-related loci with putative conservation across the fabaceae,[9,10] poaceae,[2] and solanaceae[6] families[a]

Fabaceae — Corresponding genomic region: Seed weight

Family	Center of origin	Crop	Seed weight
Fabaceae	African	Cowpea (*Vigna unguiculata*)	LG vii
	African	Mung bean (*Vigna radiata*)	LG 2
	Chinese	Soybean (*Glycine max*)	LG M
	Near Eastern	Pea (*Pisum sativum*)	LG III

Poaceae — Corresponding genomic region

Family	Center of origin	Crop	Seed dispersal (shattering) LGC	Seed mass LGA	Seed mass LGC	Seed mass LGF	Seed mass LGB	Seed mass LGE	Short-day flowering LGD
Poaceae	African	Sorghum (*Sorghum bicolor*)	chr. 5/chr. 1						chr. 9
	Mesoamerican	Maize (*Zea mays*)		chr. 1	chr. 1	chr. 4	chr. 7	chr. 9	chr. 10
	Chinese	Rice (*Oryza sativa*)	chr. 9	chr. 1	chr. 10	chr. 2	chr. 3	chr. 3	chr. 6

Solanaceae — Corresponding genomic region

Family	Center of origin	Crop	Fruit weight LGC	Fruit weight LG9	Fruit weight LGA	Fruit shape LGC	Fruit shape LGF	Fruit shape LGB
Solanaceae	Southeast Asian	Eggplant (*Solanum melongena*)	LG2 (fw2.1)	LG9 (fw9.1)	LG11 (fw11.1)	LG2 (fl2.1)	LG4 (ovs4.1)	LG7 (fs7.1)
	Mesoamerican	Tomato (*Solanum Lycopersicon*)	LG2 (fw2.2)	LG9 (fw9.2)	LG11 (fw11.1)	LG2 (ovate)	LG10 (fs10.1)	LG7 (fs7.b)
	Mesoamerican	Pepper (*Capsicum* spp.)	LG2 (fw2.1)				LG10 (fs10.1)	

[a]LG: linkage groups; ch: chromosome.

INDEPENDENT SELECTION OF ORTHOLOGOUS REGIONS UNDER DOMESTICATION?

Comparative genetic mapping provides insights into the evolution of genome organization within the species investigated. A framework of common markers provides a basis for evaluating the correspondence between the locations of genes that confer common phenotypes. Many investigations have highlighted the preservation of the basic gene order, especially across grass species. Because similar traits have been selected during the domestication of crops belonging to the same family (e.g., Poaceae or Solanaceae), a common set of loci may also have been selected under domestication. The initial report of orthologous QTL noted that a genomic region that had the greatest effect on seed weight in mung bean and cowpea spanned the same restricted fragment length polymorphism (RFLP) markers in the same linkage order in both species. Later works showed that pea and soybean also contained this conserved genomic region (Table 2). Another study[2] described the comparative molecular analysis of QTLs associated with domestication of three crops, *Sorghum*, *Oryza*, and *Zea*, each on a different continent. Correspondence was evaluated among QTLs involved in sensitivity to photoperiod, shattering, and increased seed size. Genes/QTLs were found to correspond far more often than would be expected to occur by chance, suggesting that orthologous genes (i.e., homologous genes that trace back to a common ancestral gene as a result of speciation, so that the history of the genes reflects the history of the species) may be involved in the evolution of these phenotypes. In similar manner, comparison of the genomic locations of the eggplant fruit weight, fruit shape, and color QTL with the positions of similar loci in tomato, potato, and pepper revealed that 40% of the different loci have putative orthologous counterparts in at least one of these other crop species.[6]

Overall, the results suggest that domestication within each family has been driven by mutations in a very limited number of homologous loci that have been conserved throughout the evolution of the different species. Correspondence in location of QTLs in different taxa does not prove identity between the underlying genes, but it does suggest the identity of some of them.

FROM MORPHOLOGY EVOLUTION TO MOLECULAR EVOLUTION

Plant domestication offers a powerful system for studying the genetic and developmental basis of morphological evolution. Cloning the genes that largely control the differences between wild and domesticated plants provides the opportunity to examine the effects of selection on domestication genes at molecular and physiological levels, identify characters that are relevant for future crop improvement, and infer the history of domestication. The discovery of loci such as *tb1*[11] in maize or *fw2.2*[12] in tomato represented cases in which the evolution of better adapted phenotype was largely governed by a single locus, and the genes underlying each locus were subsequently identified and analyzed.

In tomato, a QTL, *fw2.2* changes fruit weight by up to 30% and appears to have been responsible for a key transition during tomato domestication. By applying a map-based approach, the gene responsible for the QTL was identified: *ORFX*.[12] This gene has a sequence suggesting structural similarity to the human oncogene c-H-ras p21. Alterations in fruit size, imparted by *fw2.2* alleles, are most likely due to changes in upstream regulatory sequences rather than in the sequence and structure of the encoded protein. The large- and small-fruited alleles differ in the timing of *fw2.2* transcription (heterochronic allelic variation) by approximately 1 week and in total transcript level.[13] Moreover, these differences are associated with concomitant changes in mitotic activity and are sufficient to cause a major change in final fruit mass. The large-fruit allele of *fw2.2* arose in wild populations long before being fixed in most domesticated tomatoes.[14] However, despite the fact that this allele was likely a target of selection during domestication, it has not evolved at distinguishably different rates in domesticated and wild tomatoes.

The most thoroughly analyzed domestication gene is *teosinte branched 1* (*tb1*) in maize. It was shown to correspond to a QTL involved in apical dominance. During
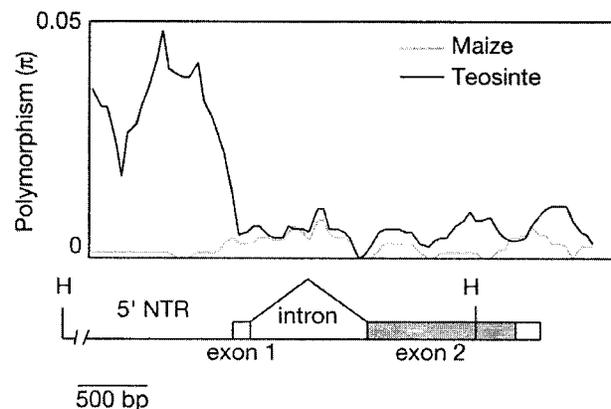

Fig. 1 Predicted structure of *teosinte branched1* (*tb1*) and analysis of polymorphism (π) in maize and teosinte. (From Ref. 11.)

development, *tb1* acts as a repressor of axillary branch growth in those organs in which its RNA messenger accumulates. The difference in mRNA accumulation in between maize and teosinte alleles suggests that the evolutionary switch involved changes in the regulatory regions of *tb1*. Indeed, population–genetic analysis of nucleotid e polymorphism in *tb1* from a diverse sample of maize and teosinte indicates that a strong selective sweep has occurred during domestication in the 5′ NTR region of the gene but not in its coding region (Fig. 1).[11] It was also inferred that the process of domestication could have taken at least several hundred years to bring the maize allele of *tb1* to fixation.

CONCLUSION

The archaeological record indicates that the domestication process of a crop, once initiated, may have been rapid, possibly encompassing only the few hundred years needed to fix relevant alleles of key genes and of their modifiers. A better understanding of the genetic differences between wild plants and domesticated crops adds important facets to the continuing debate on the origin of agriculture and the societies to which it gave rise.[15] The study of crop domestication is also an opportunity for scientists who seek to understand the genetic basis of plant growth and development. The molecular dissection of complex traits through breeding approaches, coupled with the parallel analysis of gene expression, promises to add much to our understanding of the relationships between molecular polymorphism and phenotypic diversity and the genetic basis and evolutionary dynamics of adaptation.

ARTICLES OF FURTHER INTEREST

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