

## Quantitative trait loci and the study of plant domestication

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### Abstract

Plant domestication ranks as one of the most important developments in human history, giving human populations the potential to harness unprecedented quantities of the earth's resources. But domestication has also played a more subtle historical role as the foundation of the modern study of evolution and adaptation. Until recently, however, researchers interested in domestication were limited to studying phenotypic changes or the genetics of simple Mendelian traits, when often the characters of most interest – fruit size, yield, height, flowering time, etc. – are quantitative in nature. The goals of this paper are to review some of the recent work on the quantitative genetics of plant domestication, identify some of the common trends found in this literature, and offer some novel interpretations of the data that is currently available.

*Abbreviations:* DRT – domestication related trait; QTL – quantitative trait locus.

### Introduction

Plant domestication ranks as one of the most important developments in human history, giving human populations the potential to harness unprecedented quantities of the earth's resources. But domestication has also played a more subtle historical role as the foundation of the modern study of evolution and adaptation. Darwin explicitly identified domestication as the basis for his ideas of natural selection and evolution (Darwin, 1899), and many of his ideas about how natural selection might function are based on keen observations of the human-mediated selection of domesticated plants and animals. In fact, Darwin had good reason to look to domestication for an understanding of adaptation in nature. Unlike most natural cases of adaptation, studies of plant domestication have the potential to identify what selection pressures populations have responded to and infer how selection may have acted. Moreover, it has often been possible to pinpoint the

geographic and phylogenetic origin of domesticates, thus allowing direct comparisons of descendants with their (usually extant) ancestors.

With only rare exceptions (e.g. Anderson et al., 1991; Dudley & Lambert, 1992; Cowie & Jones, 1998; Visser et al., 1998; Grant & Grant, 2002), studies of adaptation are restricted by the inability to observe selection in action over a meaningful period of time; the resulting changes are frequently the only clues biologists have with which to infer the processes involved in adaptation. Though focusing on domesticates alleviates many of the difficulties inherent in the study of adaptation, until recently researchers interested in domestication were limited to studying phenotypic changes or the genetics of simple Mendelian traits, when often the characters of most interest – fruit size, yield, height, flowering time, etc. – are quantitative in nature.

The last 15 years, however, have seen an outpouring of data on the genetic basis of quantitative traits. Dozens, if not hundreds, of articles have investigated the number, location,

and effects of the chromosomal regions responsible for the phenotypic variation observed among organisms in the natural world. Whether for expediency or scientific curiosity, much of this research has focused on quantitative variation in crop plants, and a number of studies have specifically investigated traits thought to have been important in domestication. Two recent reviews highlight several of the major patterns that have emerged from the growing body of quantitative mapping studies in domesticated plants (Paterson, 2002; Frary & Doganlar, 2003) including the number, effect, and distribution of the quantitative trait loci (QTL) underlying domestication related traits (DRT), as well as similarities across species in the QTL involved in the domestication process. In the last two years, however, several new studies have helped to flesh out the patterns recognized by these reviews. These data reinforce many of the conclusions of earlier reviewers, but also allow us to extrapolate beyond the patterns recognized by those authors.

I will begin with a brief discussion of the major patterns present in QTL mapping studies of domesticated plants. Many of these trends have been recognized previously (Paterson, 2002; Frary & Doganlar, 2003), and I will instead focus on extending the analysis of these trends, adding information from the recent literature and suggesting some novel interpretations of the data currently available.

## Major patterns

### *Distribution of QTL*

Perhaps the most widely cited pattern to emerge from QTL mapping studies in domesticated plants has been the clustering of QTL. Most mapping studies have found that QTL are not randomly or even uniformly distributed throughout the genome, but occur in apparently linked clusters in certain regions of the chromosome (Cai & Morishima, 2002; Paterson, 2002). The few studies that fail to find extensive clustering (e.g. Hashizume, Shimamoto & Hirai, 2003) tend to suffer from methodological problems that severely constrain the power of these studies to detect QTL. In spite of the strong empirical support for this pattern, its genetic basis (i.e. tight physical linkage or pleiotropic

effects) and its significance in terms of adaptation remain open to debate.

### *Size and number of QTL*

To many biologists, one of the most surprising finds of QTL studies has been the number of loci controlling many quantitative traits. QTL analysis allows the determination of a lower bound on the number of genes that control a given trait. And while classical quantitative genetic theory attributes continuous variation in nature to the small, additive effects of a nearly infinite number of genes, many studies of traits associated with domestication have found that much of the phenotypic variation can be explained by a few loci of relatively large effect. Though methodological problems – marker density, sample size, crossing scheme, etc. – can cloud the interpretation of these data (Beavis, 1994; Mauricio, 2001), the claim that most DRT are controlled by few loci of large effect seems to hold true for many studies across a variety of taxa. Counterexamples (Burke et al., 2002) do exist however, and the reasons for differences in effect size across studies or taxa are not completely clear. One difficulty in comparing QTL across studies has been the definition of ‘major effect,’ since transgressive variation among the progeny can decouple absolute morphological change from percent of phenotypic variance explained by a QTL.

### *QTL homology*

The central theme of Frary and Doganlar’s (2003) review is the similarity of QTL location and identity across taxa. Extensive synteny among QTL of major effect for DRT has been well established in the grass family (Paterson et al., 1995), and recent work has extended these findings to the Solanaceae, revealing similarities in QTL number and location across several genera of the family (Doganlar et al., 2002, Frary et al., 2003b). This similarity of genic and phenotypic character variation across a wide array of taxa seems to corroborate Vavilov’s (1922) ‘law of homologous series in variation,’ – the assertion that character variation found in one taxa should exist in related or similar taxa.