

INVITED SPECIAL PAPER

# MOLECULAR INSIGHTS INTO THE EVOLUTION OF CROP PLANTS<sup>1</sup>

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The domestication and improvement of crop plants have long fascinated evolutionary biologists, geneticists, and anthropologists. In recent years, the development of increasingly powerful molecular and statistical tools has reinvigorated this now fast-paced field of research. In this paper, we provide an overview of how such tools have been applied to the study of crop evolution. We also highlight lessons that have been learned in light of a few long-standing and interrelated hypotheses concerning the origins of crop plants and the nature of the genetic changes underlying their evolution. We conclude by discussing compelling evolutionary genomic approaches that make possible the efficient and unbiased identification of genes controlling crop-related traits and provide further insight into the actual timing of selection on particular genomic regions.

**Key words:** association mapping; crop improvement; crop origins; domestication genes; genetic architecture; genome scans; QTL mapping.

Recent advances in molecular genetics have ushered in a new and exciting age for investigating where, when, and how crop plants arose. Progress in understanding crop evolution began with morphological studies and archeological finds of early domesticates. Beginning in the mid 20<sup>th</sup> century, chromosome homology was used to investigate crop origins; later, allelic variants of enzymes (i.e., allozymes) were used to explore the origins and population genetics of crop species. The greatest technological leap for studying domestication, however, came with the development of DNA-based molecular markers beginning in the 1980s.

The development of increasingly informative molecular markers has allowed for detailed investigations of the evolution of a number of crops. Such studies have provided insight into many issues, including the identification of crop progenitors (e.g., Brubaker and Wendel, 1994; Jacobs et al., 1995; Heun et al., 1997; Matsuoka et al., 2002; Harter et al., 2004; Konishi et al., 2006; Li et al., 2006b), the localization and timing of domestication events, and the demographics of domestication (Eyre-Walker et al., 1998; Buckler et al., 2001; Liu and Burke, 2006). Moreover, with the increasing ease and decreasing cost of molecular tool development, the resources necessary for investigating the genetic underpinnings of phenotypic traits are now in place for most major crops. These advances not only allow for an investigation of the overall genetic architecture of the wild-crop transition, but also make possible the identification of genomic regions and genes that were subjected to selection during the evolution of various crops. In some cases, researchers have been able to pinpoint the exact nucleotide changes responsible for the production of key crop-related traits.

Our goal here is to review recent discoveries regarding the origin and subsequent evolution of our primary food crops. We do so against a backdrop of long-standing hypotheses as to where, how often, and how quickly domestication occurred, as well as the types of genetic changes that are involved in crop domestication and improvement. In doing so, we seek to clarify the present state of the field and highlight promising avenues for research going forward. Our review is limited to seed-propagated, annual crop species because they are the best studied examples of domestication.

## CENTERS OF DOMESTICATION AND THE ORIGIN OF CROPS

The Russian plant geneticist Nikolai Vavilov, who was the first to scientifically pursue the study of domestication origins, proposed seven primary geographic “centers of domestication” in the world, based on the regions having high crop varietal diversity (Vavilov, 1926). These were China, South Asia, Southwest Asia (i.e., the Fertile Crescent), the Mediterranean, Ethiopia, greater Mexico, and the Andes. Vavilov’s centers of domestication are a valuable first hypothesis as to where crops originated and where our sessile, agrarian cultures began. Since then, we have made great strides in pinpointing where our domesticates have arisen and from which wild species they are derived. The most conclusive evidence comes from complementary investigations of archaeobotanical records, neutral genetic variation, and domestication-related genes.

Our understanding of the number, size, and identity of the aforementioned centers of domestication has changed substantially over the last 80 yr of research. Interestingly, there is still no clear consensus as to the location and number of domestication sites (see Gepts, 2004; Smith, 2006). Since Vavilov’s time, eastern North America (Heiser, 1951; Smith, 2006), New Guinea (Denham et al., 2003), and the Amazon Basin (Olsen and Schaal, 2001) have been added as independent centers, though the last two are only known to have produced vegetatively propagated cultigens. China, the Andes, and Ethiopia are now viewed as being less localized centers than was originally

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TABLE 1. Details regarding the origin of major seed-propagated crop species and the genetic architecture of trait changes that occurred during their evolution. Note that studies of agronomic traits based on crosses between crop lines are not included here.

Species	No. of domestications	Ploidy, chromosome no.	Genetic architecture	Source
<b>Poaceae</b>				
Oats ( <i>Avena sativa</i> L.)	≥2	Allohexaploid, 2N = 42	— <sup>a</sup>	Zhou et al., 1999; Jellen and Beard, 2000
Barley ( <i>Hordeum vulgare</i> L.)	1 or 2	Diploid, 2N = 14	Likely few gene regions of large effect <sup>a</sup>	Badr et al., 2000; Komatsuda and Mano, 2002; Tanno et al., 2002; Morrell and Clegg, 2007
Paddy rice ( <i>Oryza sativa</i> L.)	2	Diploid, 2N = 24	Few gene regions of large effect	Vitte et al., 2004; Konishi et al., 2006; Li et al., 2006a, b; Londo et al., 2006
Pearl millet [ <i>Pennisetum glaucum</i> (L.) R.Br.]	Multiple	Diploid, 2N = 14	Few gene regions of large effect	Brunken et al., 1977; Poncet et al., 1998
Cereal rye ( <i>Secale cereale</i> L.)	1 or 2	Diploid, 2N = 14	— <sup>a</sup>	Khush, 1963; Sencer and Hawkes, 1980
Sorghum [ <i>Sorghum bicolor</i> (L.) Moench]	≥2	Allotetraploid, 2N = 20	Few gene regions of large effect	De Wet and Huckabay, 1967; Harlan, 1992; Paterson et al., 1995
Einkorn wheat ( <i>Triticum monococcum</i> L.)	1	Diploid, 2N = 14	Likely few gene regions of large effect <sup>a</sup>	Heun et al., 1997
Emmer, durum wheat [ <i>T. turgidum</i> L., <i>T. durum</i> L. (Desf.)]	1 or 2	Allotetraploid, 2N = 28	Few gene regions of large effect	Brown, 1999; Oezkan et al., 2002; Peng et al., 2003
Bread wheat ( <i>T. aestivum</i> L.)	1	Allohexaploid, 2N = 42	Few gene regions of large effect <sup>b</sup>	McFadden and Sears, 1946; Pestsova et al., 2006; Simons et al., 2006
Maize ( <i>Zea mays</i> L.)	1	Diploid, 2N = 20	Very few gene regions of large effect	Doebley et al., 1997; Matsuoka et al., 2002
<b>Asteraceae</b>				
Safflower ( <i>Carthamus tinctorius</i> L.)	1	Diploid, 2N = 12	—	Imrie and Knowles, 1970; Chapman and Burke, 2007
Sunflower ( <i>Helianthus annuus</i> L.)	1	Diploid, 2N = 34	Many gene regions of small to moderate effect	Burke et al., 2002; Harter et al., 2004; Burke et al., 2005; Wills and Burke, 2007
<b>Brassicaceae</b>				
Rapeseed ( <i>Brassica napus</i> L.)	—	Allotetraploid, 2N = 38	— <sup>a</sup>	U 1935 in Ladizinsky, 1985
Cole crops ( <i>B. oleracea</i> L.)	1	Diploid, 2N = 18	Likely few gene regions of large effect <sup>a</sup>	Song et al., 1990; Purugganan et al., 2000
Field mustard, turnip, bok choy ( <i>B. rapa</i> L.)	Multiple	Diploid, 2N = 20	— <sup>a</sup>	Song et al., 1990
Radish ( <i>Raphanus sativus</i> L.)	2	Diploid, 2N = 18	— <sup>a</sup>	Yamagishi and Terachi, 2003
<b>Malvaceae</b>				
Upland cotton ( <i>Gossypium hirsutum</i> L.)	1	Allotetraploid, 2N = 52	Few gene regions of large effect	Brubaker and Wendel, 1994; Udall and Wendel, 2006
<b>Cucurbitaceae</b>				
Squash ( <i>Cucurbita pepo</i> L.)	2	Diploid, 2N = 40	— <sup>a</sup>	Sanjur et al., 2002
<b>Fabaceae</b>				
Chickpea ( <i>Cicer arietinum</i> L.)	1	Diploid, 2N = 16	Likely few gene regions of large effect <sup>a</sup>	Abbo et al., 2003; Abbo et al., 2005
Soybean ( <i>Glycine max</i> L.)	1	Diploid, 2N = 40	Likely few gene regions of large effect <sup>a</sup>	Hymowitz, 1970; Keim et al., 1990; Xu et al., 2002; Carter et al., 2004
Lentil ( <i>Lens culinaris</i> L.)	1	Diploid, 2N = 14	— <sup>a</sup>	Zohary, 1989; Mayer and Soltis, 1994; Ladizinsky, 1999
Common bean ( <i>Phaseolus vulgaris</i> L.)	2	Diploid, 2N = 22	Few gene regions of large effect	Sonnante et al., 1994; Koinange et al., 1996; Chacon et al., 2005
Pea ( <i>Pisum sativum</i> L.)	1	Diploid, 2N = 14	Few unlinked genes of large effect	Zohary, 1989; Timmerman-Vaughan et al., 2005; Weeden, 2007

TABLE 1. Continued.

Species	No. of domestications	Ploidy, chromosome no.	Genetic architecture	Source
Solanaceae				
Tomato ( <i>Solanum lycopersicum</i> L.)	—	Diploid, $2N = 24$	Gene regions of both major and minor effect	Rick and Fobes, 1975; Frary et al., 2000; Nesbitt and Tanksley, 2002
Eggplant ( <i>Solanum melongena</i> L.)	—	Diploid, $2N = 24$	Few unlinked gene regions of large effect	Doganlar et al., 2002a, b

<sup>a</sup>Quantitative trait loci have only (or primarily) been characterized from crosses between crop lines and not between cultivated lines and their putative progenitors.

<sup>b</sup>Quantitative trait loci represent those from *A. tauschii* introgression lines of the D genome.

thought (DeWet and Huckabay, 1967; Gepts, 1998; Chacon et al., 2005; Londo et al., 2006; Smith, 2006), suggesting that agriculture was generally driven by human need and was achieved independently across several cultures (Brown, 1999). Only the Fertile Crescent (Salamini et al., 2002) and Southern Mexico (Smith, 2006) remain as narrowly delimited centers of origin for multiple crops. The occurrence of several domestications in close proximity to one another suggests that agricultural technology arose with and followed the resident cultures that eventually migrated away from these regions (Zohary, 1999; Smith, 2001; Willcox, 2005).

We have also learned that high varietal diversity in a particular region is not a reliable indicator of a center of domestication, as previously believed by Vavilov and his peers. Indeed, varietal diversity does not correlate well with archeological and molecular data regarding crop origins (Harlan, 1992), perhaps in part because elevated levels of diversity can result from secondary contact between crops and their wild relatives (e.g., Ellstrand et al., 1999; Hauser and Bjorn, 2001; Weissmann et al., 2005). In fact, the evolution of diverse landraces frequently involves introgression from wild relatives, as has been the case for cotton (Brubaker and Wendel, 1994), sorghum (De Wet and Huckabay, 1967; Casa et al., 2005), pea (Timmerman-Vaughan et al., 2005), and sunflower (Putt, 1997; Burke et al., 2005). Because it often occurs well outside the original site of domestication, such introgression can lead to false conclusions regarding the origin(s) of crops.

Reconstructions of domestication origins are further complicated when crops have been moved long distances very early in the domestication process. For instance, though sorghum is native to, and was almost certainly initially domesticated in sub-Saharan Africa (Harlan, 1992), its earliest crop remains are from southern Arabia (Potts, 1993) and India (Kajale, 1991). Similarly, although the prehistoric native range of wild sunflower likely extended across the northern and central Great Plains of North America (Heiser et al., 1969), the oldest remains to date of its domesticated form were found further east, in Tennessee (Crites, 1993).

#### SINGLE OR MULTIPLE DOMESTICATIONS OF CROPS?

A number of studies have recently focused on the issue of whether particular crop species were domesticated once or multiple times. Beyond providing insight into the repeatability of the domestication process, the documentation of multiple origins provides largely unexplored replication for studying the outcome of long-term selection and answering wide-reaching

questions in the field of evolutionary biology, such as whether there are multiple genetic “paths” leading to a given (domesticated) phenotype. Furthermore, accurate inferences regarding both the identity of crop progenitors and the number of times a particular crop was domesticated are key to being able to disentangle the often complex genetic consequences of domestication and crop improvement (e.g., Ballini et al., 2007).

Vavilov (1926) assumed implicitly that crop species had each been domesticated only once when he proposed his centers of domestication, and this assumption has been borne out for a number of species (Table 1). To date, maize (*Zea mays* L.) remains the strongest and best characterized example of a single domestication, which is thought to have occurred in southern Mexico more than 6300 years ago (Piperno and Flannery, 2001; Matsuoka et al., 2002). Similarly, einkorn (*Triticum monococcum* L.), the most primitive domesticated wheat, was apparently domesticated only once within its range in the northern Fertile Crescent (Heun et al., 1997). Sunflower (*Helianthus annuus* L.), based on molecular analyses and a reevaluation of archeological remains, also appears to be the product of a single domestication, most likely in east-central North America (Harter et al., 2004; Smith, 2006; Wills and Burke, 2006), though the possibility of a second origin in Tabasco, Mexico has been proposed (see Lentz et al., 2001; Tang and Knapp, 2003).

For several crop species, however, the available evidence supports multiple origins of domestication (Table 1). Most notably, at least two independent origins of paddy rice, *Oryza sativa* L., have been confirmed based on comparisons of retrotransposons and gene sequences from the *indica* and *japonica* lineages and their progenitor (Vitte et al., 2004; Londo et al., 2006). The loss of shattering in these two subspecies is furthermore conditioned by mutations in different genes (Konishi et al., 2006; Li et al., 2006b). Both phenotypic and molecular data also suggest that common bean, *Phaseolus vulgaris* L., was domesticated twice across its broad range in South and Central America (Blumler, 1992; Koinange et al., 1996; Chacon et al., 2005) and that squash, *Cucurbita pepo* L., was likely domesticated in both southern Mexico and in northeastern Mexico or southeastern North America (Sanjur et al., 2002).

Interestingly, a consensus on the number of origins has not been reached for some of our most important crop species. This is particularly true for several cereal crops of the narrowly delimited Fertile Crescent (Zohary, 1999; Abbo et al., 2001; Salamini et al., 2002; Allaby and Brown, 2003; Salamini et al., 2004; Willcox, 2005). Conclusions drawn from whole genome analyses (such as AFLP or SSR surveys) have generally suggested single origins, whereas phenotypic data and sequence analyses of

domestication-related genes often imply multiple domestications. For instance, AFLP comparisons of wild and cultivated tetraploid wheat suggest that tetraploid emmer, *Triticum turgidum* L., and durum wheat, *T. durum* L. (Desf.), arose only once (Oezkan et al., 2002). However, the discovery of two distinct, ancient allelic lineages of a glutenin gene in different cultivated emmer accessions suggests the possibility of multiple domestications (Allaby et al., 1999; Yan et al., 2003). Similarly, AFLP data point to a single origin for two-rowed barley (*Hordeum vulgare* L.) from *H. spontaneum* L. in the western Fertile Crescent (Badr et al., 2000), yet two lineages of seed-head shattering genes are fixed across East and West Asian cultivated barley lines, suggesting two origins to domestication (Takahashi and Hayashi, 1964). Even hexaploid bread wheat, *T. aestivum* L., which is the most recently derived form of wheat and generally accepted as having originated only once from a tetraploid domesticated emmer  $\times$  wild diploid goatgrass hybrid, has a glutenin protein diversity that is too great to have emerged by mutation alone since its origin ca. 9000 years ago (Allaby et al., 1999). While this pattern could have been produced by postdomestication introgression, it is also possibly due to multiple origins of domestication.

Clearly, reconstructions of crop origins are most robust when multiple independent approaches give consistent results. Phylogenetic origins extrapolated from analyses using anonymous genomic DNA markers (AFLP, RFLP, RAPD), while based on a representative sampling of the whole genome, have been criticized for being biased toward resolving monophyly (Abbo et al., 2001; Allaby and Brown, 2003; but see Salamini et al., 2004). In contrast, inferences based on only one or only a few genes can be suspect, as they reflect the evolutionary history of only a small portion of the genome (e.g., Kopp and True, 2002; Rokas et al., 2003). In fact, the validity of basing inferences on a small number of genes depends largely on the choice of genes analyzed; genes that are directly related to domestication (e.g., a seed-head shattering gene) should reflect the actual path of domestication, whereas genes related to crop improvement and/or varietal diversification may reflect postdomestication introgression from a wild relative.

#### GENETIC ARCHITECTURE AND THE TEMPO OF DOMESTICATION

In *The Genetical Theory of Natural Selection*, R. A. Fisher (1930) famously proposed that evolution in response to natural selection is a slow, gradual process. Although crop species are generally believed to have evolved more rapidly than their wild relatives, the early stages of domestication were traditionally viewed as occurring relatively slowly, proceeding over a timescale of thousands of years (Harlan, 1992). Mathematical models estimating the time required for domestication (e.g., Eyre-Walker et al., 1998; Le Thierry D'Ennequin et al., 1999) and our greater understanding of how quickly species can evolve (e.g., Rieseberg et al., 2002; Reznick and Ghalambor, 2001) now suggest that domestication can, in theory, occur within a few hundred generations. Indeed, Hillman and Davies (1990), proposed very rapid rates of crop evolution by tracking selection on wheat with repeated sickle harvesting. In contrast, recent archeological evidence from the Fertile Crescent points to a surprisingly slow rate of transition from wild to domesticated forms (e.g., Tanno and Willcox, 2006). Inconsistent harvesting practices as well as repeated restocking of seed from the wild appear to have

reduced the speed at which domestication traits such as shattering and large seed size became fixed in early cultivated plants (Balter, 2007; Fuller, 2007). Therefore, weak selection for domestication traits appears to have driven the earliest stages of crop evolution in this region. It is worth noting, however, that the discussed conclusions regarding the tempo of domestication are based on archeological finds solely from western Asia, where crops were grown in sympatry with their wild relatives. In Meso-America, where the earliest evidence of maize cultivation occurs outside the range of its progenitor and is in the form of ancient entire domesticated maize cobs (Piperno and Flannery, 2001), the available evidence suggests that domestication may have proceeded much more rapidly.

While a variety of evolutionary factors, including effective population size, the occurrence of genetic bottlenecks, the strength of selection, and rates of gene flow, can influence the ease and tempo of domestication (e.g., Hillman and Davies, 1990; Eyre-Walker et al., 1998; Le Thierry D'Ennequin et al., 1999), genetic architecture is also critical. In this context, it is worth noting that quantitative trait locus (QTL) mapping studies of domestication-related traits have shown that domestication is typically driven by changes at a small number of loci, each of relatively large effect (e.g., Doebley, 1992; Koinange et al., 1996; Cai and Morishima, 2002). This finding is consistent both with predictions that a few loci of large effect can be selected on more efficiently than a larger number of loci of small effect (Falconer and Mackay, 1996) and with the notion that some species (perhaps those with the most appropriate genetic architecture) are more easily domesticated than others (sensu Diamond, 1997). To date, sunflower stands as the only well-documented example in which domestication has proceeded by selection on a large number of loci, most of which have small to moderate phenotypic effects (Burke et al., 2002; Wills and Burke, 2007).

Linkage relationships among loci under selection may also influence the tempo of domestication. Stebbins (1971) was among the first to propose that adaptive gene clusters could be selected for and fixed in species, though chromosomal translocations, the mechanism that he envisioned for shuffling genes throughout the genome, are too infrequent to realistically produce such a pattern in crop species. Nonetheless, there is evidence that domestication-related QTL are often found in clusters within a genome (e.g., Doebley and Stec, 1991; Fulton et al., 1997; but see Doganlar et al., 2002a; Weeden, 2007). A simulation study of evolution under domestication by Le Thierry D'Ennequin et al. (1999) has further shown that suites of favorable alleles are fixed more readily in outcrossing species when the genes in question are clustered than when they are less tightly linked. The tempo of domestication was further enhanced in these simulations by reducing population size and decreasing migration rates. While this model did not consider gene flow between the neodomesticated and its progenitor and did not propose a mechanism responsible for the gene clustering (unless high levels of genetic redundancy are assumed), it clearly suggests that species with clusters of beneficial genes might be more easily and rapidly domesticated than those in which genes controlling domestication traits are more dispersed. Alternatively, some cases of apparent gene clustering may be due to pleiotropic effects of individual genes (e.g., Doganlar et al., 2002a), and thus more detailed analyses are necessary before firm conclusions can be drawn.



## THE NATURE OF DOMESTICATION GENES

Harlan et al. (1973) proposed that a distinct suite of traits—later termed the “domestication syndrome”—would likely be selected for during the initial stages of domestication. These traits are all associated with increasing ease of harvest and include reduced shattering, more determinate growth habit, greater inflorescence size, greater seed (or fruit) size, and loss of seed dormancy. In the time since Harlan first published this list, domestication genes have frequently been more loosely defined to include any gene selected on and consistently differing between a crop and its nearest wild relative (e.g., Koinange et al., 1996; Doebley et al., 2006; Weeden, 2007). Crop improvement after domestication can, however, also result in the fixation of traits that were likely not of interest to early farmers (e.g., dwarf habit). Here, we follow a strict definition of what constitutes a domestication-related trait, in line with the views of Harlan et al. (1973).

In the past, domestication-related traits were widely believed to be conditioned by recessive, loss-of-function alleles (e.g., Ladizinsky, 1985; Lester, 1989); however, the results of QTL mapping studies as well as the lessons learned from the recent cloning of a handful of domestication genes show a less consistent pattern. While nonshattering appears to be a recessive trait in a number of cereals (e.g., Takahashi and Hayashi, 1964; Harlan et al., 1973; Watanabe, 2005; Li et al., 2006b) and fruit weight is partially recessive in tomato and eggplant (Frery et al., 2000; Doganlar et al., 2002a), a number of QTL studies suggest that the genes underlying many other domestication-related traits act in a nonrecessive manner (e.g., Doebley et al., 1990, 1994; Doebley and Stec, 1991; deVicente and Tanksley, 1993; Tanksley, 1993; Burke et al., 2002; Li et al., 2006a; Wills and Burke, 2007; reviewed in Doebley et al., 2006). Similarly, the view that domestication-related traits are typically conditioned by loss-of-function alleles has been challenged. In fact, only one of seven sequenced “domestication genes” reviewed by Doebley et al. (2006) is a loss-of-function allele (loss of red pericarp in rice; Sweeney et al., 2006), though this gene may not have truly been involved in domestication; the remainder are amino acid substitutions and/or expression level differences caused by mutations in regulatory regions (Doebley et al., 2006).

Curiously, loss-of-function alleles appear to be relatively common for genes associated with crop improvement and/or varietal divergence. Based on a recent review, nine of 19 such loci harbor alleles with premature stop codons, intron splice-site defects, or other sorts of disrupted coding sequences, with the remainder evenly split between regulatory changes and amino acid substitutions (Doebley et al., 2006). Further examples include loss-of-function alleles such as those affecting flowering time (Foucher et al., 2003) and dwarf habit (Martin et al., 1997) in pea. Likewise, the transition from two-rowed to six-rowed barley is conditioned by a recessive, loss-of-function mutation (Komatsuda et al., 2007).

The foregoing conclusions must, of course, be tempered by the realization that only a relatively small number of genes underlying crop-related traits have been characterized to date. Moreover, these loci represent a nonrandom sample of genes that were targeted for cloning because they were tractable and not necessarily because they were the most important in crop evolution. As such, the lessons that we have learned thus far might prove to be somewhat biased.

## THE ONGOING SEARCH FOR GENES INVOLVED IN CROP EVOLUTION

Until relatively recently, QTL analyses were the primary means for localizing domestication- and improvement-related genes (see Paterson, 2002). Although such analyses can provide a great deal of insight into the genetic architecture of traits of interest, they are both labor-intensive and time-consuming, requiring the development and phenotypic characterization of a large, segregating population, as well as the construction of a genetic map. Moreover, QTL mapping typically provides a relatively low level of resolution, with genes being localized to intervals spanning several centimorgans; depending on the taxon being studied, such regions can encompass hundreds of genes. While a handful of QTLs have been cloned in crop plants (discussed earlier), map-based cloning can be an inefficient process and of little utility in species that are vegetatively propagated and/or have long generation times.

An alternative to family-based QTL mapping is association mapping, which involves correlating polymorphisms in candidate genes with phenotypic variation in existing, diverse populations (Buckler and Thornsberry, 2002). Not only does association mapping obviate the need to develop a mapping population via controlled crosses, but it also provides a much greater level of precision, as the resolution of any mapping approach depends on the extent of linkage disequilibrium (LD; i.e., the nonrandom association of alleles at two loci) in the focal population. In the case of family-based mapping populations, the limited opportunity for recombination during population development results in high LD over large physical distances. In contrast, the individuals that comprise a typical association mapping population are the product of many generations of historical recombination, thereby resulting in greatly reduced LD and consequently increased mapping precision. In fact, depending on the taxon under consideration, functional variation can potentially be mapped to the level of one or a few genes (e.g., Thornsberry et al., 2001; Palaisa et al., 2004; Olsen et al., 2006). The principal limitation of this approach is that it requires a priori knowledge of candidate genes and phenotypes to be tested.

A third strategy for identifying the genes underlying crop-related traits is to perform a large-scale genomic scan in a crop species and its wild progenitor to identify loci that show evidence of selection during domestication. Selective sweeps (i.e., periods of intense selection during which an allele is “swept” to fixation) are predicted to dramatically decrease genetic variation in and around the selected locus (Maynard-Smith and Haigh, 1974; but see Innan and Kim, 2004) without changing levels of diversity elsewhere in the genome. Assuming that the LD breaks down sufficiently rapidly, it should thus be possible (at least in theory) to identify narrow genomic regions that have experienced a recent selective sweep. In its purest form, this approach involves generating population genetic data for a large number of randomly selected loci, ranking the loci based on the relative change in diversity between the ancestral and derived (i.e., wild and crop) populations, and identifying those in the tail of the distribution that have a greater than expected loss of diversity (Schlötterer, 2002; Storz, 2005; Ross-Ibarra et al., 2007; Fig. 1). More recently, it has been suggested that the use of a demographic null model that is based on observed patterns of neutral genetic diversity and implicitly accounts for factors such as the occurrence of a population bottleneck during domestication (e.g., Buckler et al., 2001), will further improve

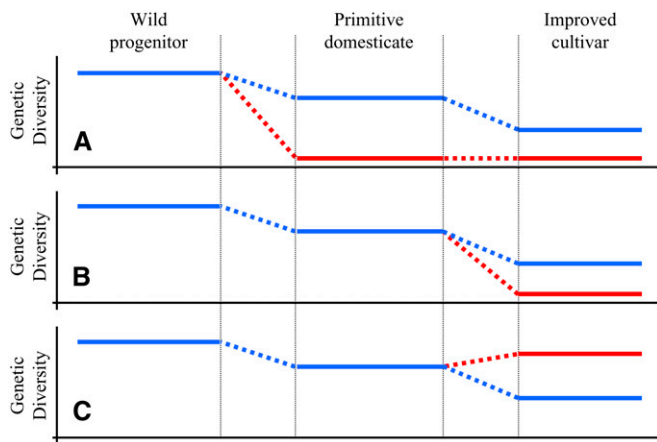


Fig. 1. Schematic representation of the predicted loss of diversity across cultivar lines during crop evolution. The blue line represents the diversity of a selectively neutral locus, and the red line shows that of a hypothetical gene under selection. Depicted are (A) the reduction in diversity of a neutral gene and of a gene that underwent selection during domestication, (B) the reduction in diversity expected for a gene that underwent strong directional selection during improvement, and the special case in which (C) gene diversity is maintained or even increases across lines due to divergent selection and the possible effects of introgression during improvement.

our ability to detect past selection (e.g., Wright et al., 2005; reviewed in Ross-Ibarra et al., 2007).

Beyond simply identifying genes that underwent selection during crop evolution, this approach (when coupled with appropriate sampling) has the potential to provide insight into the timing of selection (i.e., domestication vs. improvement). Indeed, domestication-related genes are expected to have an extreme loss of diversity in even the most primitive cultivars (Fig. 1A). In the case of improvement-related genes, however, the situation is more complex. While a strong selective sweep during improvement would result in a similar selectively induced loss of diversity across the primitive-improved transition (Fig. 1B), genes involved in the diversification of crop lineages and/or local adaptation might be expected to harbor different alleles in different lineages, thereby resulting in the retention of diversity across lines. When coupled with introgression from wild relatives, this sort of diversifying selection could even produce an increase in diversity across improved lines (Fig. 1C).

To date, genomic scans for selection have been carried out in a handful of taxa using either genotype- or sequence-based approaches. For example, an analysis of SSR diversity in sorghum (*Sorghum bicolor* L.) revealed that nearly 15% of the loci analyzed had evidence of past selection (Casa et al., 2005). A similar sequence-based analysis, however, failed to find evidence of selection, possibly due to the confounding effects of population structure, migration, and limited sampling depth (Hamblin et al., 2004, 2006). For maize, an SSR-based analysis (Vigouroux et al., 2002) and analyses of sequence variation (Tenailon et al., 2004; Wright et al., 2005; Yamasaki et al., 2005) have yielded a number of promising candidates for domestication-related genes. Interestingly, in both sorghum and maize, the loci identified as candidates for selectively important genes often mapped to regions of the genome known to harbor domestication-related QTLs (Casa et al., 2005; Wright et al., 2005).

Returning to the issue of the timing of selection, two studies have thus far used stratified sampling to investigate whether

selection occurred during the initial period of domestication or during the subsequent period of improvement. In one case, Burke et al. (2005) used an SSR-based scan of wild, primitive, and improved sunflower lines to document the likely occurrence of multiple postdomestication selective sweeps along a single linkage group, presumably due to recent selection on seed oil characters. In the other case, Yamasaki et al. (2005) performed a sequence-based analysis that allowed them to identify eight genes that had evidence of selection during maize domestication as well as 10 genes that had evidence of selection during the subsequent period of improvement.

The primary drawback of the genome scan approach is that it provides no direct information on the phenotypic effects of the genes of interest. Once identified, the effects of these genes must be investigated using a combination of bioinformatic tools, genetic map data, and reverse genetic approaches. A second concern in identifying genes under selection based on a genome scan is the possibility of false positive results. Fortunately, the combined use of multiple statistical tests can reduce the false positive rate significantly as compared to the use of only a single test (e.g., Schlötterer and Dieringer, 2004; Bonin et al., 2006). Despite these drawbacks, genome scans remain an attractive option for the identification of genes that were likely involved in crop evolution because they avoid many of the limitations of map-based cloning and also obviate the need for a priori identification of candidate genes. Going forward, technological advances in the realm of high-throughput genotyping and sequencing should greatly increase the efficiency of these sorts of investigations.

## SUMMARY

Crop evolution continues to be a fascinating area of research for anthropologists, evolutionary biologists, and crop scientists. Over the years, the development of an increasingly broad array of molecular tools has resulted in a variety of fascinating insights into the origins and subsequent evolution of our primary food crops. In particular, it has become clear that a number of crops are the product of multiple origins; that although domestication can in theory be rapid, it appears to have proceeded slowly in many cases; and that contrary to past assumptions, traits related directly to domestication are not generally conditioned by recessive loss-of-function mutations. Most recently, the development of evolutionary genomic approaches for identifying genomic regions that have undergone selection has made possible the efficient (and unbiased) identification of genes involved in crop evolution. Such approaches also have the potential to provide insight into the timing of selection (i.e., domestication vs. improvement), thereby allowing for the temporal dissection of the genetics of crop evolution. These advances have provided a great deal of insight into the genetic changes underlying the transformation of wild and sometimes weedy species into the valuable crops upon which agrarian societies have been built. Such work has also pushed crop plants toward center stage in the field of evolutionary genetics, where they serve as useful models for studying the molecular basis of adaptive trait divergence.

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