# NEWS AND COMMENTARY

Genetic variation and domestication in grapevines

# On the identification of human selected loci in grapevines

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The domestication of crop plants from wild progenitor populations and improvement through crop breeding was a key event in the advancement of human civilization. The identification of the genes responsible for agronomically important traits can now give insights into plant phenotypic evolution. The articles published in this issue by Fournier-Level et al. (2010) and Pelsy (2010) on grapevines both contribute towards this general aim.

Most selected traits exhibit complex patterns of inheritance, and are influenced by both genetic and environmental factors (see review by Kalisz and Kramer, 2008). Not surprisingly, the identification of genes responsible for important traits has so far been achieved mainly by the use of laborious and time-consuming forward genetic approaches coupled with quantitative trait analyses. Examples of the traits (and their genetic basis) studied so far include inflorescence morphology in Brassica oleracea (BoCAL), fruit size in Lycopersicon esculentum (fw2.2), plant stature and yield in Triticum species (Rht-B1 and Rht-D1), kernel biochemistry (Rht-B1 and Rht-D1), grain filling (GIF1) and grain size in Oryza sativa (qSW5 locus), as well as apical dominance (tb1) and endosperm colour in Zea mays (Y1 locus; see Table 1 in Doebley et al., 2006, and references therein).

In maize, 2–4% of all genes may have experienced artificial selection (Wright et al., 2005). Nevertheless, these types of inferences may be hampered by the details of the domestication and post-domestication selection process. Domestication leads to the genome-wide reduction of genetic diversity in crops relative to their wild progenitors due to genetic drift in the form of 'domestication bottlenecks' (see Figure 2 in Olsen and Gross, 2008). The diversity reduction can represent up to 70% of the neutral genetic diversity present in the wild ancestors (Buckler et al., 2001; Gepts, 2004). Depending on the domestication model employed, further loss of genetic diversity may occur for many generations after the domestication process started. In the classic model of domestication, one bottleneck occurs in the initial stages of domestication; this is followed by a wide dissemination of the crop due to cultivation, and therefore, the population size becomes large enough such that any subsequent drift effects are minimal (see Olsen and Gross, 2008). In the protracted model, however, genetic drift operates not only during the initial domestication bottleneck but also for many subsequent generations, as it is assumed that the population size of the domesticated crops remains small for many generations (Allaby et al., 2008). Multiple 'domestication bottlenecks' may eliminate much of the genetic evidence required to distinguish between a single and multiple domestications. Therefore, to fully understand crop domestication, both genetic and archaeological data may be needed (Olsen and Gross, 2008). Evidence for multiregional domestication is available (Brown et al., 2009).

Post-domestication selection for the agronomic traits that distinguish crops from their ancestors may lead to further reductions in genetic diversity around the selected genes, but the strength of this effect depends on the initial frequency of the selected allele (Innan and Kim, 2004). If the selected allele is rare, selection mimics the effect of a more severe bottleneck by removing most of the genetic variation from the target locus as well as from the surrounding region through the effect of genetic hitchhiking (Galtier et al., 2000). If the selected allele is frequent, then it is likely that it occurs in the context of many different haplotypes in the population. If this is the case, the reduction in diversity levels around the selected gene may not be as evident (Innan and Kim, 2004). Therefore, to have a clear understanding of the impact of selection on genetic diversity around the selected genes, factors such as the local recombination rate, population size, population structure and breeding systems need to be considered. For instance, in Solanum lycopersicum, extensive introgression (from natural hybridization with S. pimpinellifolium, as well as from crosses with S. pimpinellifolium and additional wild relatives as an attempt to improve crops) and frequent bottlenecks need to be considered in order to be able to understand the genetic basis of domestication and selection in this species (Labate et al., 2009). When considering crops such as grapevines, making predictions becomes even harder. Grapevine varieties are likely to be arrays of clones descended by vegetative propagation from a single selected vine originally grown from a single seedling, and thus, the within-variety genetic diversity should be very low. Nonetheless, there are many different clones of the same variety; this is due to somatic mutations that go to high frequency by massive vegetative propagation through cuttings. Grape, as the oldest major crop, has an enormous population size planted over multiple locations. This, coupled with the role of germinal and somatic mutations, as well as hybridization with wild close relatives, means that the between-varieties diversity is very high (for a review see Pelsy, 2010, in this issue).

Despite the difficulties mentioned above, genes responsible for agronomically important traits have been identified in grapes. For instance, most of the variation in grape colour is explained by genetic variation at a single gene cluster of three MYB-type transcription factor genes called VvMybA1, VvMybA2 and VvMybA3 (see Fournier-Level et al., 2010, and references therein, in this issue). In the case of VvMybA1, silencing of the gene is due to the insertion of a gipsy-like retrotransposon (Gret1), whereas a single nucleotide polymorphism (K980) in the VvMybA2 coding sequence leads to protein truncation, and thus, to a non-functional protein. The manner in which these mutations emerged and affected genetic diversity at the neighbouring sites, and how they affected the structuring of the genetic diversity of cultivated grapevines, has been addressed recently by Fournier-Level et al. (2010). These analyses may lead to the development of better models for the detection of selected loci in grapevines. The Vitis vinifera genome sequence is now available. The use of resequencing techniques, large grapevine variety collections and better models for the detection of selected loci means that it may now be possible to identify most selected loci in grapevine varieties, to test hypotheses about the

evolution of grape traits and get a much better understanding of plant phenotypic evolution.

## Conflict of interest

The authors declare no conflict of interest.

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## Editor's suggested reading

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