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NEWS AND VIEWS

PERSPECTIVE

Insights on the evolution of a vegetatively propagated crop species

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Abstract

The opportunity for gene flow between a vegetatively propagated crop and its wild relatives is expected to be much lower than for seed-propagated crops, since sexual reproduction in the crop occurs only infrequently. A study by Duputié and colleagues now demonstrates evidence of sexual reproduction between a vegetatively propagated crop and a closely related wild congener. Working in French Guiana, these workers have documented a hybrid zone arising from introgression between cassava (*Manihot esculenta* ssp. *esculenta*, Euphorbiaceae), which is propagated by stem cuttings, and wild *Manihot* populations growing in close proximity. Patterns of heterozygosity suggest that there are little–to–no barriers to reproduction between the crop and these wild populations. Previous work by these researchers has documented the importance of occasional sexual reproduction for the development of cassava varieties in traditional Amerindian farming systems. Taken together with their previous work, these new findings suggest that gene flow between wild *Manihot* populations and cassava plants could potentially play a much greater role in the crop's evolution than previously thought.

Studies of crop domestication have provided important insights into the genetic underpinnings of basic micro-evolutionary processes. The vast majority of crop species are propagated by seed, where sexual recombination can potentially occur with every growing season. For such species, selection and recombination can interact to efficiently generate a rapid evolutionary response to human selective pressures. Seed-propagated crops are also under strong stabilizing selection for the maintenance of fertility through sexual reproduction; this selection acts to maintain the potential for bidirectional gene flow between crops and their wild relatives and suggests that wild-crop introgression may be an important component of the domestication process in seed-propagated species.

In vegetatively propagated crop species, where reproduction and sexual recombination are decoupled, the evolutionary dynamics governing both selection and gene flow can differ fundamentally from that of seed-propagated crops. Opportunities for sexual recombination are greatly reduced, since propagation by farmers does not require seed production. Moreover, since the fitness of a crop cultivar is no longer tied to its ability to reproduce sexually, selection for agronomically favourable traits (e.g. increased tubers, ease of vegetative propagation) may be associated with relaxed selection or trade-offs for the maintenance of sexual reproduction. Indeed, many vegetatively propagated crops show disruption of flowering and fruiting mechanisms as well as unbalanced chromosomal arrangements (Zohary 2004). This relaxed selection for sexual reproduction will act to decrease opportunities for crossing among crop varieties as well as opportunities for gene flow between the crop and its wild relatives.

The vegetatively propagated crop cassava (*Manihot esculenta* ssp. *esculenta*) has, until recently, been thought to fit the picture of a nonsexually reproducing crop species, with few opportunities for sexual recombination in agricultural fields, and little or no potential for gene flow with wild relatives. Cassava (also known as manioc, tapioca, and yuca) is a perennial shrub cultivated throughout the humid tropics for its starchy root (Fig. 1). A native of the Neotropics, it is the staple crop for over 600 million of the world's poorest people and the third most important calorie source in the tropics (FAO 2002). Cassava is propagated

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Fig. 1 Cassava (*Manihot esculenta* ssp. *esculenta*, Euphorbiaceae). Photo credit: K.M. Olsen.

by stem cuttings, so that a field planted with a given variety comprises multiple clonal replicates of the same genotype. Selection for vegetative propagation in cassava has led to increased resource allocation to stems and roots relative to its wild progenitor (*Manihot esculenta* ssp. *flabellifolia*). This increased resource allocation is achieved in part through a thickening of stems and a decrease in the degree of branching in the plant. Since cassava only flowers following branching, the crop thus shows greatly decreased rates of sexual reproduction compared to its wild relatives.

The recent work of McKey and colleagues, including that by Duputié *et al*. (2007) in this issue, has challenged the longstanding view that sexual reproduction has played a minimal role in cassava's evolution. By conducting ethnobotanical and population genetic analyses of Amerindian traditional farmers in French Guiana, these workers have documented that farmers actively incorporate volunteer seedlings from cassava fields if they show promising agronomic traits (Elias *et al*. 2001; Pujol *et al*. 2005). If such practices are common in other areas of traditional cassava farming, then sexual reproduction could have played a much greater role in cassava's evolution than previously thought.

The current study by Duputié *et al*. further extends evidence for a significant role of sexual reproduction in cassava's evolution. In this study, genetic and morphological data are presented that suggest intercrossing of cultivated cassava plants and proximal populations of their wild relatives in French Guiana. The resulting hybrids are apparently fertile, and they show higher levels of heterozygosity than either crop varieties or wild populations; they may also show evidence of heterosis in vegetative traits. Thus, in regions of the Neotropics where cassava's wild relatives occur, traditional farming practices (i.e. those that exploit volunteer cassava seedlings) could potentially be actively promoting sexual reproduction and gene flow between wild and cultivated plants.

Cassava appears to have been domesticated from southern Amazonian *M. esculenta* ssp. *flabellifolia* populations (Olsen & Schaal 1999; Léotard 2003; Olsen 2004), and the crop likely became widespread throughout the Neotropics by several thousand years ago (e.g. Piperno *et al*. 2000). It is thus interesting to note that in the current study by Duputié *et al*., cassava varieties and the neighbouring wild populations remain genetically distinct outside of the obvious hybrid zones. This suggests that, despite the potential for many generations of crossing between cassava and neighbouring wild populations, genetic introgression between the crop and wild populations has not played a major role in the crop's evolution. Corroborating evidence for this conclusion is provided by the work of Léotard & McKey (2004), who examined *G3pdh* haplotype variation in a large sample of French Guianan cassava landraces, as well as cassava varieties worldwide; they found that the genetic diversity of all cassava varieties is primarily a subset of that found in southern Amazonian *Manihot* populations.

Wild species of *Manihot* are widely distributed from the southwestern USA into Argentina, and all species in the genus have been proposed to be interfertile (Jennings 1995). While current data do not indicate a major role for wild-to-crop gene flow in the evolution of cassava, the findings of Duputié and coworkers suggest that introgression from wild *Manihot* populations into cassava fields is possible in the Neotropics. This process could potentially enhance the genetic diversity of geographically localized crop landraces and increase their adaptedness to local environmental conditions. Recent genome-wide assessments of simple sequence repeat (SSR) diversity in a worldwide sample of cassava landraces have revealed some instances of regionally elevated genetic diversity (e.g. Guatemalan landraces examined by Fregene *et al*. 2003). It will be interesting to see whether additional analyses of genetic diversity in cassava and its wild relatives can reveal further evidence for wild-crop gene flow. It will also be interesting to see the role that such gene flow may have played in the evolution of other vegetatively propagated crop species.

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