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Ecological approaches to crop domestication

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Introduction: the scope of this essay

Understanding evolutionary adaptation of crop plants requires understanding the ecology of their wild ancestors¹ and the selective pressures that cultivators exerted when they began manipulating plants and shaping agricultural environments. For most crops, especially the diverse clonally propagated ones, we have only a broad-brush picture of the evolutionary ecology of domestication. Detailed investigations of crop wild relatives are rare, as are studies that take into account the full complexity of cultivated environments, from altered ecosystem processes and selective mechanisms to biotic interactions of crop plants with parasites and mutualists. The most important mutualists are the cultivators themselves, and an important part of the biotic environment of crop plants—what happens inside farmers' heads—has sometimes been neglected. Ecology—the interactions among cultivators, plants, and environments—has shaped the process of domestication. It continues to provide insights into ongoing processes of domestication today, in settings as diverse as landrace populations and biotechnology laboratories, and can inform strategies for managing the biodiversity of crop plants and their wild relatives.

In this essay, we develop major themes in the evolutionary ecology of domestication. We show that evolution under domestication can contribute important insights into general questions in evolutionary ecology. We argue that much is to be gained from a broadening of domestication studies beyond their current focus on evolution in cereals and grain legumes, to encompass the great diversity of plants

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¹Evolutionary biologists avoid referring to any extant taxon as an "ancestor" of another extant taxon, preferring formulations such as "closest wild relative". However, the recency of crop domestication makes it often possible to identify the wild ancestral taxon or taxa (if not the common ancestral populations), justifying our use of the shortcut term "wild ancestor" here.

that cultivators have manipulated over the past 10 000 years, in what is the world's longest-running selection experiment (Gepts, 2004).

The essay is organized in four sections. First, we describe how domestication studies have served as a window into evolutionary processes and analyze the crucial role of ecology in this exploration. We discuss the ecological context in which domestication took place, showing that understanding the evolution of domesticated plants depends on understanding how humans domesticate environments. In the second section, which comprises the bulk of the manuscript, we focus on a large group of plants that have been particularly neglected in domestication studies: clonally propagated crops. We show that the principal reasons for our poor understanding of their evolution under domestication are our fragmentary knowledge of the biology and ecology of their wild relatives, preventing an appreciation of trait evolution, and a poor understanding of the reproductive ecology of the domesticates themselves, clouding our notions of how evolution in their populations might proceed. We illustrate these points with three crops, manioc, guinea yams, and bananas. These cases exemplify the great diversity of ecologies represented among the wild relatives of clonally propagated domesticated plants, the corresponding diversity of traits that have evolved under domestication, and the selective mechanisms responsible for trait evolution. In two short final sections, we discuss promising directions in crop ecology. We first show that domestication studies offer underexploited opportunities as tractable models for attacking some fundamental questions in evolutionary ecology, such as ecological speciation and evolution in (partly) clonal populations, and then discuss new applications of ecology in crop improvement and management strategies.

Domestication studies as a window into evolutionary processes

Ever since Darwin, domesticated plants have served as models for studying many questions of broad interest in evolutionary biology (Gepts, 2004). Their rapid evolution, and the fact that their wild ancestors usually still exist and often can still be crossed with them (Ellstrand *et al.*, 1999), facilitate comparative and experimental studies of evolution. However, the analysis of evolution under domestication appears to have captivated geneticists more than it has ecologists. Indeed, domesticated plants offer choice material for questions at the frontiers of evolutionary genetics, such as the genetic basis of traits, the evolution of development, and the architecture of genomes (Ross-Ibarra *et al.*, 2007). In contrast, evolutionary ecologists have shown much less interest in domestication as a model, possibly because selective pressures imposed by farmers and by agricultural environments seemed to them to be straightforward and easily understood. Most of the seminal insights we have gained into the ecology of crop domestication have been contributed not by “card-carrying” evolutionary ecologists, but by agronomists (Harlan, 1992), agricultural botanists and plant ecologists (Hillman & Davies, 1990) and geographers (Blumler, 1996). A very broad approach to ecology is required to fill important gaps in our understanding of the ecological aspects of domestication.

The importance of ecology in domestication studies

Ecology has a role to play in many aspects of domestication studies. First, it helps explain why some plants possess traits that made them easier to domesticate than others, and why such plants were more likely to be found in some regions than in others (Diamond, 2002; Gepts, 2008). Ecology

is also crucial to explanations of the evolutionary processes acting during domestication. In wild plants intensively harvested and managed by people, much artificial selection can take place before 'cultivation'. Analysis of such incipient domestication ('*in situ* domestication' [Casas *et al.*, 2007]) depends on a fine understanding of the plant in relation to its environment. Ecology also has shaped the traits of wild relatives and how they evolve under domestication, as examples presented here will develop in detail. Finally, ecology may constrain how rapidly domestication occurs. In one well-known case, the evolution of wheat, models based on knowledge of the genetic basis of traits associated with the domestication syndrome such as non-shattering panicles, and on the frequency of non-shattering mutants in wild populations, suggested that this and other domesticated traits should have evolved rapidly, over a few generations (Hillman & Davies, 1990). Archaeological evidence, however, showed that the transition to domestication took over a thousand years (Tanno & Willcox, 2006). Investigation of cultural behavior and how it affects domesticated environments is helping to resolve this paradox. Hillman & Davies (1990) based their selection coefficients on harvesting by sickles or uprooting. However, with harvesting techniques and field-tenure practices likely employed by many early farmers, and with their continued forced reliance on gathering wild seeds when crops failed, self-sown seeds (from shattering panicles harvested by beating or stripping) in soil seed banks may have continued to contribute to harvests—and to the genetic composition of crop populations—for many generations, slowing the evolution of this domesticated trait (Tanno & Willcox, 2006). Interestingly, another domesticated trait, evolution of large grain, began earlier than loss of seed dispersal and was completed in only a few centuries (Fuller, 2007). This could be explained by selection imposed by tillage, large seeds germinating more successfully than small ones when buried deeply (Harlan *et al.*, 1973; Fuller, 2007).

Domestication of plants, domestication of environments

People began domesticating environments long before they began cultivating plants (Yen, 1989), but cultivation led to environmental changes even greater than those that preceded it. Agricultural environments often present strong ecological contrasts with the environments in which the wild progenitors of crop plants grow (Denison *et al.*, 2003). Farmers endeavour to grow their crops in the resource-richest habitats available, to supply their crops with limiting resources, such as water, nitrogen, or mineral nutrients, and to protect their crops from herbivores and pathogens and from disturbances such as fire. One way of achieving these goals is by managing crop phenology (Bunting, 1973). Farmers can synchronize planting and harvest time in ways that satiate predators of sprouting plants or seeds (Lansing & Miller, 2005). They can also time agricultural cycles to adapt to seasonally changing environmental constraints. Domesticated plants thus often begin their life not only in highly favorable microsites but also—due to a combination of reduced dormancy of domesticates and farmer choice of when to plant—at times when risk of fire, drought or other stresses is minimal. Farmers also choose resource-rich environments and modify them to make them even richer. The extent to which farmers modify habitats is often truly astounding. Taking advantage of the nutrient-retaining capacities of charcoal, pre-Columbian farmers in Amazonia created *terra preta* soils whose nutrient status greatly surpasses anything seen in the region's zonal soils, highly weathered, acid and nutrient-poor oxisols and ultisols (Glaser & Woods, 2004).

Changes produced by domestication of the environment condition trait evolution in domesticated

plants. Theory developed for wild plants, and well supported by data, emphasizes trade-offs between traits that confer rapid growth and those that confer tolerance to stresses associated with nutrient scarcity (Reich *et al.*, 2003). Selection on plants living in resource-rich environments favors traits augmenting the plant's ability to acquire resources, whereas in resource-poor environments selection favors traits allowing the plant to conserve hard-earned resources. Following the same reasoning, the environmental changes associated with domestication should favour resource-acquisition strategies, compared to resource-conservation strategies of wild relatives. Much of the increased yield observed under domestication and crop improvement can indeed be ascribed to evolution driven by such trade-offs (Denison *et al.*, 2003), and as will be developed here, such a shift in strategy appears to be one of the dominant themes of the evolutionary ecology of domestication.

Some crops are more 'resource-conserving' than others. Manioc (*Manihot esculenta* Crantz) is prized for its ability to produce viable yields even under marginal conditions of water and nutrient availability. In resource-poor environments, maintaining yield requires resource-conserving traits, and some of these, such as chemical defense, have been retained, and possibly even enhanced (McKey & Beckerman, 1993), during domestication of manioc. Different varieties of crop plants may also occupy different positions along the resource conservation/acquisition continuum. In manioc, 'sweet' varieties with non-toxic roots may have higher yields than bitter varieties in rich soils, or if herbivores and pathogens are absent, while 'bitter' varieties with toxic roots give higher yields than sweet varieties in poor soils (McKey & Beckerman, 1993; Wilson, 2008), especially if potential enemies are abundant. Ecological strategies show variation even among bitter manioc varieties: '*fraca*' varieties characterized by rapid production are adapted to richer alluvial and *terra preta* soils, while '*forte*' varieties, slower to produce but more resistant, are adapted to the poorest soils (Fraser & Clement, 2008). Finally, in some regions, such as the semi-arid Sahel region of Africa, resource availability to crops varies dramatically among years. In at least two crops of this region, pearl millet (*Pennisetum glaucum* [L.] R. Br.) and sorghum (*Sorghum bicolor* [L.] Moench), continued gene flow with wild relatives (Mariac *et al.*, 2006; Barnaud *et al.*, 2009) generates variation that may help farmers adapt to such unpredictability. According to a hypothesis first proposed by Pernès (1986), genes from wild relatives may contribute to the rustic (resource-conserving) varieties that are the best yielders in bad years. Introgression from wild relatives has similarly been implicated in aiding local adaptation as crops expand their areas of domestication, in sunflower (Heiser Jr, 1965) and in common bean (Beebe *et al.*, 2000; Chacón *et al.*, 2005). These examples could be particularly instructive in the search for plant breeding strategies to adapt to climate change (Jones *et al.*, 1997).

Defense is a component of ecological strategies whose evolution under domestication merits particular attention. Ecological shifts to resource-richer environments are predicted to lead to relaxed selection for chemical and physical defenses and the plant's investment in them could be reallocated to increase yield (Rosenthal & Dirzo, 1997). Furthermore, humans select against toxic or digestion-inhibiting compounds in parts of plants they consume. Variation in the ease with which toxin-free plants can be selected is thought (Diamond, 2002) to help explain why some plants could be domesticated (*e.g.*, almonds, in which cyanogenesis has a simple genetic basis) and others could not (*e.g.*, oaks, in which the polygenic inheritance of tannins makes it impossible to select tannin-free acorns). However, the balance of selection pressures could well favor the maintenance of defenses in many agricultural environments. First, resource availability varies even within agricultural

environments. It is interesting that two crops which have maintained conspicuous defenses—manioc, which is cyanogenic, and grasspea (*Lathyrus sativus* L.), which contains neurotoxins—are both considered as being particularly adapted to marginal conditions where few other crops can produce viable yields (McKey & Beckerman, 1993; Vaz Patto *et al.*, 2006). Second, while greater resource availability in agricultural environments often does favor relaxed defenses, their species diversity is also usually lower than in the environments of their wild relatives, making them more apparent to herbivores and weakening other mechanisms of associative resistance, such as indirect defense provided by assemblages of natural enemies of herbivores, assemblages supported by the diverse resources of species-rich plant communities. Maintaining chemical defenses could be particularly important in herbivore- and pathogen-rich tropical agroecosystems, in extensive systems such as long-fallow swidden cultivation where crops are far from villages (where human presence dissuades some vertebrate herbivores), and in crops where edible organs such as leaves or tubers are potentially available to herbivores for long periods of their development. Synchronously ripening grain crops can be more easily protected from birds and other pests when most vulnerable, at maturity. Faced by such selective pressures, farmers have often retained varieties that contain anti-nutritional substances, adopting processing techniques that enable them to detoxify these built-in pesticides. Bitter manioc (McKey & Beckerman, 1993; Wilson & Dufour, 2002), grasspea (Butler *et al.*, 1999), and tannin-rich red sorghum are the best-known examples, but others are known among both tuber and grain crops (Johns & Kubo, 1988).

Integrating clonally propagated crop plants into domestication studies

The evolutionary ecology of clonally propagated crop plants is in general poorly understood. This is a huge gap in knowledge, because they include a large number of economically important plants. For example, nine of the world's 24 top crops in terms of tonnage harvested (Myers, 1985) are clonally propagated: potato, sweet potato, manioc, grapes, sugarcane, bananas, oranges, apples and yams. Collectively, clonally propagated crops represent tremendous phyletic, morphological and ecological diversity. Even considering only a small number of globally or regionally important crops, they represent a host of families of both monocots (Araceae, Dioscoreaceae, Musaceae, Poaceae, Zingiberaceae, and others) and dicots (Euphorbiaceae, Moraceae, Oxalidaceae, Piperaceae, Solanaceae, and many others) and diverse life forms including herbs, shrubs, trees and vines. Direct human selection has acted on a great diversity of plant structures that are either consumed (roots, tubers, stems, leaves, fruits and even seeds) or used to propagate the plant (rhizomes, stolons, corms, stems, underground and aerial tubers). Indirect selection has undoubtedly acted on many other structures.

Why is the evolutionary biology of these crops so poorly explored? We believe there are two main reasons. First, our poor knowledge of the biology and ecology of their closest wild relatives prevents an appreciation of what traits have evolved. Part of the problem is their very diversity. Our ideas about evolution under domestication are primarily based on studies of seed-propagated crops belonging to only two plant families, Poaceae and Fabaceae, in which domestication has been characterized by widespread parallel evolution of similar traits, the classical features of the “domestication syndrome” such as the loss of mechanisms of seed dispersal and seed dormancy, and the reduction of branching.

The obvious parallel and convergent evolution of crops in these families has stimulated comparative approaches that have led to many exciting discoveries about the genetic basis of traits (Doebley, 2004; Ross-Ibarra *et al.*, 2007). In contrast, the taxonomically and morphologically diverse clonally propagated crops do not seem to be characterized by any readily identifiable common domestication syndrome. As a group the wild relatives of these crops have very diverse ecologies and often quite unusual growth strategies, which have not always been appreciated by agronomists. This overwhelming diversity, and the lack of appreciation of complexity in the ecology of wild relatives, have hindered our ability to identify traits that have evolved under domestication, to understand why they have evolved, and to study their genetic basis.

Second, an incomplete understanding of the reproductive ecology of the crops themselves has clouded our ideas about how evolution in their populations might proceed. In an update of a classical 1984 essay comparing the reproductive systems of seed-propagated and clonal crops, Zohary (2004) stated that “in terms of selection, domestication of clonally propagated crops is largely a single step operation. With the exception of rare somatic mutations, selection is completed once a given clone is picked up.” He added that clonal crops “frequently underwent only a few recombination-and-selection cycles” and that “in terms of basic ecological adaptations they remained relatively close to their wild progenitors”. Referring to bananas (*Musa* spp.), Heslop-Harrison & Schwarzacher (2007) wrote: “Most of the cultivars are wild collections made by farmers of spontaneously occurring mutants with parthenocarpic fruit production, which were brought into cultivation and then multiplied and distributed by vegetative propagation.” Similarly, in a popular article about the same crop, one reads that “hunter-gatherers must have discovered rare mutant plants that produced seedless, edible fruits” (Pearce, 2003). In our experience, the notion that clonal crops were “instantly domesticated” by the capture and clonal multiplication of mutant wild individuals is widely held. Many students have probably thought that studying such a simple event—as opposed to a process of some complexity—was not very exciting and offered little basis for a career. We take issue with the notion of “instant domestication” on two points. First, we believe such notions ascribe too much importance to recurring mutations and too little importance to recombination of previously existing alleles (see Pickersgill [2007] for a general discussion of this question in domestication studies). Second, generalizations about the paucity of recombination-and-selection cycles in clonal crops (Zohary, 2004) are based primarily on studies of Mediterranean fruit trees. They appear less applicable to a large number of tropical clonal crops. In several such crops it has been demonstrated that reproductive systems are not strictly clonal, as usually thought, but mix clonal and sexual reproduction, so that populations have undergone repeated recombination-and-selection cycles, permitting the accumulation of domesticated traits often strikingly different from those of their closest wild relatives.

Reproductive systems and the evolutionary ecology of clonally propagated crop plants

Why have farmers chosen to propagate some plants clonally and others by seeds? Zohary (2004) pointed out that, in contrast to most seed-propagated crops, which are mainly autogamous (maize, pearl millet and rye are conspicuous exceptions), clonally propagated crops are primarily outcrossers. Such plants do not breed true to type; clonal propagation enabled farmers to selectively multiply favorable new phenotypes. Alternative ways to achieve the same result would be to select for increased

selfing ability (Gepts, 2004), or for tighter linkage of domesticated traits (le Thierry d'Ennequin *et al.*, 1999). Clonal propagation also has other agronomic advantages, such as the more rapid growth and greater survivorship conferred by the larger propagules associated with this mode of reproduction.

Many clonally propagated crops appear to have reduced fertility (Zohary, 2004). It is sometimes unclear whether it is the plant's ability to reproduce sexually that has been diminished, or only the opportunity to do so, because of harvesting before flowering (Hather, 1996) or other causes, such as mate limitation (see the banana case below). Still, reduction of sexual fertility is often considered a general evolutionary trend in these plants (Zohary, 2004), and sexual fertility has been completely lost in some crops (*e.g.*, kava, *Piper methysticum* G. Forst. [Lebot *et al.*, 1992]).

A selective pressure often proposed to account for reduction or loss of fertility is a trade-off between yield and the production of flowers and fruits. Plants that invest less in sexual reproduction may have increased yield of the plant part that is consumed, and farmer selection for high-yielding plants may automatically select for reduced production of flowers and fruits, unless these are the parts consumed, as in bananas and some varieties of taro. In what could be a frequent scenario, interspecific hybridization could produce plants that exhibit both heterosis and sterility, each contributing to increased yield.

While virtual loss of sexual fertility characterizes some domesticates, such as kava and most varieties of banana, it is far from being a universal trait of clonally propagated crop plants. Many retain a capacity for sexual reproduction that is far from "residual", and as we show below, sexual reproduction plays an important role in the evolution of populations of these crops that are managed dynamically by farmers today. It continues to be important because cultivators are interested in its products and carefully observe plants originating from sex, incorporating some of these volunteer plants from seed as new clones.

What we know about trait evolution under domestication of these plants strongly suggests that sex and recombination also played a crucial role in their initial domestication. Where detailed studies have been conducted, as in manioc (see below), it is clear that domesticates of these plants differ in numerous genetically independent traits from their wild relatives. These differences have evolved over no more than the past 10 000 years (Gepts, 2004). Such rapid evolution is difficult to square with limitations to evolution in purely clonal populations (Barton & Charlesworth, 1998). Where somatic mutations are the only source of new genetic variation, deleterious mutations accumulate, reducing performance (and thereby fitness, if farmers prefer high-performing plants). Favorable mutations are rarer. By creating a great diversity of genotypes, recombination allows selective elimination of those with large numbers of deleterious mutations, and conservation of those that unite several favorable mutations, so that they cooperate within lineages rather than compete among lineages, increasing the rate of adaptive evolution. It is difficult to envisage how numerous genetically independent traits could be assembled in the absence of such recombination-and-selection cycles.

Sexual reproduction in these crops is integrated into a mixed clonal/sexual reproductive system, in which clonal propagation maintains favorable phenotypes at high frequency and recombination generates a diversity of genotypes, a few of which are highly selectively incorporated as new clones. Such a system combines the advantages of each reproductive pathway (maintenance of agronomic performance in a population dominated by selected clones, maintenance of adaptive potential by sex) while minimizing their respective disadvantages.

As we will show, in such mixed clonal/sexual systems, how and when selection acts, and what traits are affected by it, all depend on the ecology of the crop being considered and how it is managed by people. The ecological and morphological diversity of clonally propagated crops, and the diverse ends to which they are manipulated by cultivators, mean that the results of evolution, in terms of the kinds of traits that are modified, and how they are modified, show much greater diversity among clonal crops than among seed-propagated crops. We will illustrate this with three cases. We will first summarize findings for the best-studied case, that of manioc, and then present information on two less-studied cases, the guinea yam of Africa (*Dioscorea cayennensis*/*D. rotundata* species complex) and the banana. These three plants contrast strongly in growth form and ecologically important traits of their wild relatives, and in the traits selection has favored under domestication.

The evolutionary ecology of manioc

Manioc is the clonally propagated crop whose evolutionary ecology has been most thoroughly investigated, largely in studies conducted by our group at Montpellier. The account given here draws heavily on a recent review of this work (Rival & McKey, 2008). We first summarize the biology of the crop's closest wild relatives, showing how it has conditioned the ecology of the crop under traditional cultivation systems. Following this, we describe the patterns in the genetic diversity of landraces that initially suggested the importance of continuing recombination-and-selection cycles in the domestication of this plant. We then describe the functioning of the crop's mixed clonal/sexual reproductive system, better understood for manioc than for any other crop. Finally, we show how the selection pressures documented in contemporary crop populations can account for the evolution of the plant's traits during initial domestication.

Traits of the closest wild relative and the domestication syndrome. Manioc's closest wild relative, *M. esculenta* subsp. *flabellifolia* (Olsen & Schaal, 1999), is a plant of forest/savanna ecotones distributed around the drier seasonal rim of Amazonia. Among its adaptations to these environments are tuberous roots, underground reserves that enable rapid regrowth after fire or other disturbances. This closest wild relative of manioc also shows plasticity in growth form. A much-branched shrub in open environments, it persists as a scandent vine as vegetation closes during succession. The plant also possesses several adaptations allowing rapid regeneration from a soil bank of dormant seeds following a new disturbance. Its two-stage seed dispersal system features ballistic autochory (explosively dehiscent capsules) followed by myrmecochory: each seed bears an elaiosome (a food body rich in lipids and other nutrients) that attracts ants (Elias & McKey, 2000). Ants carry diaspores to nests, where the elaiosome is fed to brood. Seeds are then discarded in a refuse pile near the nest, where they become buried at varying depths in the soil. Thus protected, they can lie dormant for years (seeds from which the elaiosome has been removed are perfectly capable of germinating [Pujol *et al.*, 2002]). Seeds of manioc's wild relatives use soil temperature as a germination cue. At temperatures typical of vegetation-shaded soils in the lowland tropics (25°C) they remain dormant, but when soil temperatures of 35°C or more signal that vegetation cover has been removed by a disturbance, they germinate if ample water is available (Pujol *et al.*, 2002). These features of seed and seedling biology have been inherited largely intact by domesticated manioc.

Other traits of the domesticate, however, have diverged from the wild relatives. These include

of course traits directly selected by humans, such as the size and production of tuberous roots and traits facilitating clonal propagation via stem cuttings. For example, reduction in the extent of branching results in thicker stems, producing clonal propagules with more reserves and less subject to desiccation (Jennings, 1995; Schaal *et al.*, 2006). (Owing to a peculiarity of manioc's architecture, it also incidentally reduces the number of inflorescences the plant produces [Elias *et al.*, 2007].) However, the domesticate has also diverged from the wild relative in traits only indirectly selected: leaf tannin content has undergone reduction (Mondolot *et al.*, 2008) and several leaf traits have led to higher mass-based photosynthetic rates in domesticated manioc (Pujol *et al.*, 2008). Finally, and most curiously, domesticated manioc and its wild ancestor differ in seedling morphology (Pujol *et al.*, 2005b). Domestication of this crop by Amerindians over the last 10 000 years thus involved the assembly of a large number of independent traits, not something that would be easily accomplished under purely clonal evolution.

The nature of landraces and landrace diversity in a clonally propagated crop. A brief walk in a manioc plantation of Amerindian cultivators in Amazonia raises further questions about the origin of diversity in this “clonally” propagated crop. The number of different named categories, *i.e.*, landraces (varieties as they are named and recognized by cultivators), present in the fields of a single village can surpass 100 (Boster, 1983; Duputié *et al.*, 2009). Common-garden experiments show that despite environmental effects on traits, these different landraces are also phenotypically distinct, each possessing particular combinations of independent traits, such as the extent of branching, the form of roots and their composition (starch content, toxicity [“sweet” vs. “bitter”]) and the color of different organs (Elias *et al.*, 2001a). The structure of trait variation indicates not diversification within purely clonal lineages, but frequent recombination. Genetic analysis confirms this impression. Phenotypic diversity is underlain by great genetic diversity, and landraces are genetically differentiated. Most strikingly, most landraces do not correspond to a single clone. Although one or two clones may be numerically predominant, a landrace is usually constituted of groups of genotypes that are derived from distinct recombination events but share similar phenotypes (Elias *et al.*, 2000a, 2001b). Sex thus appears to continue to play an important role in the structure of diversity. Furthermore, because farmers plant numerous distinct landraces in a single field (Elias *et al.*, 2000b; Duputié *et al.*, 2009), there is enormous scope for continued recombination.

How sex enters the game. Like most other clonally propagated crop plants, manioc is primarily outcrossing (David *et al.*, 2007), although self-compatible, and the benefit of clonal propagation is seen in the genotypic composition of the predominant clones. Their high heterozygosity for neutral microsatellite markers—typical both of Amazonian (Elias *et al.*, 2004) and African (Fregene *et al.*, 2003) landraces—indicates genome-wide heterozygosity, signalling their origin from matings between unrelated plants and thus their relative freedom from inbreeding depression. Clonal multiplication enabled these “elite” clones to reach their high frequency. However, the rapid evolutionary divergence of manioc from its wild relative is difficult to reconcile with evolution in a purely clonal reproductive system. The diversity of traits that evolved during the domestication of manioc suggests the action of repeated cycles of recombination (necessary to generate variation) and selection (to fix certain traits and maintain agronomic performance).

Sex gets into the system by the interaction between the biology of manioc and the actions of cultivators. The field-fallow cycles of swidden agriculture nicely take advantage of the reproductive traits manioc inherited from its wild ancestor. Seeds, dispersed by ants, are buried and remain dormant in the shaded soils throughout the fallow period. When a new field is opened, volunteer seedlings from this seed bank emerge in large numbers, their emergence coinciding with the period when cultivators plant stem cuttings (Elias *et al.*, 2000b). Volunteer seedlings are closely observed by cultivators, who allow them to grow. Those that survive to maturity are harvested and their roots processed. Farmers evaluate them and multiply some of them as new clones. Rarely, plants from seed are judged sufficiently novel to be multiplied as a new named variety. Much more frequently, they are incorporated into the stock of clones of a named variety they resemble, explaining the polyclonal nature of these varieties (Elias *et al.*, 2000b). As in many other crops, cultivators increase the diversity of material upon which recombination and selection can act by the frequent and widespread exchange of cultivars, both directly via exchange of stem cuttings in social networks (for an example see Elias *et al.*, 2000b) as well as indirectly via soil seed banks (Pujol *et al.*, 2007).

Mixing clonal propagation and sex is not as straightforward as it may at first seem. Two problems may arise: population structures created by clonal propagation may lead to frequent inbreeding; and crossing of highly differentiated clones may break up favorable trait combinations conserved in distinct landraces. Because the aim of clonal propagation is to multiply selected genotypes to high frequencies, many plants in a field are likely to be clonemates. Furthermore, in at least the three Amerindian groups we have studied (Makushi [Carib linguistic family] in Guyana, Palikur [Arawakan] and Wayãpi [Tupi-Guaraní] in French Guiana), cultivators tend to plant cuttings in monovarietal patches, so that a plant's neighbors are frequently clonemates. This clumping of clonemates affects the population's mating system. Because pollinators transport pollen mostly between neighboring plants, many seeds are the result of highly inbred matings. At the same time, cultivators usually plant several highly differentiated varieties in each field, and pollen transfer between them produces highly outcrossed offspring. The overall result of the peculiar spatial genetic structure of these polyvarietal populations is a quite unusual mating structure, with great variance in the extent of inbreeding. Given this diversity, it is clear that incorporation of plants from seeds as new clones must be highly selective if agronomic quality and favorable trait combinations are both to be maintained.

Detailed field studies in Palikur farms have shown that volunteer plants from seeds are subjected to high mortality, that this mortality is selective, and that while at least four different selective mechanisms operate at different times in the field cycle, they all have similar consequences for phenotypes and genotypes: selection favours plants that grow rapidly, and these are the most outcrossed individuals. One stage of selective mortality occurs when farmers manually weed their fields several months after planting. Those plants that are removed are smaller (size is a good indicator of vigor because seedlings in a field are a single even-aged cohort) and more inbred than those that survive (Pujol *et al.*, 2005a). Another stage of selective mortality is caused by intraspecific competition, mostly in the first year of growth. Competition is severe because ant-mediated seed dispersal generates clusters of seedlings. In these clusters, individuals with an initial size advantage win. They are also the most outbred (Pujol & McKey, 2006). The third stage of selection occurs at harvest time, when farmers select large, vigorous plants for propagation. The fourth stage of selection was studied not among the Palikur but among the Wayãpi. Plants from seed selected for clonal

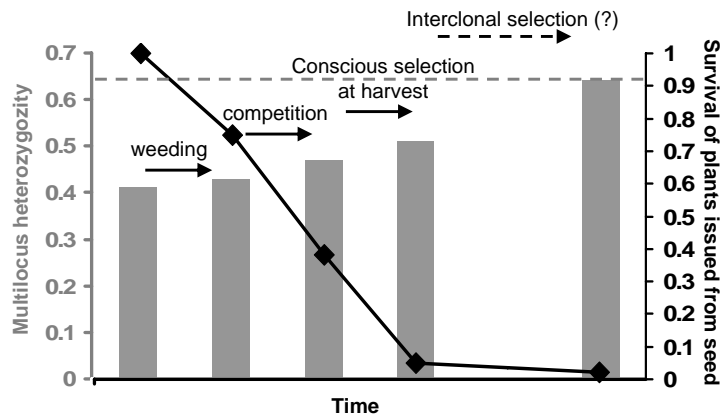


Figure 1: Stages in the selective incorporation, as new clones, of volunteer plants of manioc issued from seeds in fields of Amerindian cultivators. Seedlings appear in newly cleared fields, then steadily decrease in number until the field is harvested (black line; black legend on right-hand vertical axis indicates proportional decline relative to initial density, set as 1). Arrows indicate causes of mortality. Selective mortality of inbred seedlings occurs in four stages. First, some are removed by farmers during manual weeding. Others die from "natural" causes, mainly intraspecific competition. At harvest, most are discarded. Finally, new clones that are incorporated undergo a trial period of several years, during which many probably disappear via interclonal selection (see Duputié *et al.* [2009] for discussion). At all four stages, inbred individuals are selected against, as shown by the increase in multi-locus heterozygosity of surviving individuals over time (grey bars; grey legend on left-hand vertical axis), until they eventually reach the average level of landraces (grey dashed line). Figures for survival and multi-locus heterozygosity are from Pujol *et al.* (2005a), Pujol & McKey (2006) and Duputié *et al.* (2009).

propagation undergo a trial period, during which they are multiplied and managed separately from established clones of the same landrace. Clones under trial are more inbred than established clones (Duputié *et al.*, 2009). From a strong heterozygote deficit at the beginning of the cycle, testifying to a globally inbred mating system, seedlings that survive these different selective processes progressively come to resemble established clones in their high heterozygosity and vigor (Figure 1). The highly selective incorporation of products of sex injects genetic diversity, and thereby adaptive potential, while maintaining the population's agronomic performance.

How do cultivators deal with the other problem that arises in the mixing of clonal propagation and sex, the breakup of favorable trait combinations when highly differentiated landraces cross? Duputié *et al.* (2009) found that Wayãpi farmers selected not only against the most inbred plants but also against the most outbred. This result was attributed to ideotypic selection against 'off-type' plants resulting from intervarietal crosses.

Studying the functioning of mixed clonal/sexual systems in contemporary fields of Amerindian cultivators opens a window into evolutionary dynamics throughout domestication. The picture that emerges from our studies—strong selection favoring rapidly growing plants—fits quite well with theory predicting that selection in agricultural environments should favor a move from the resource-conservation end of the allocation spectrum to a strategy emphasizing resource acquisition. The same selective forces that have favored outbred plants appear to have also driven selection for other traits leading to increased growth rates, such as leaf traits leading to increased mass-based photosynthetic rates (Pujol *et al.*, 2008) and reduced foliar tannin levels (Mondolot *et al.*, 2008).

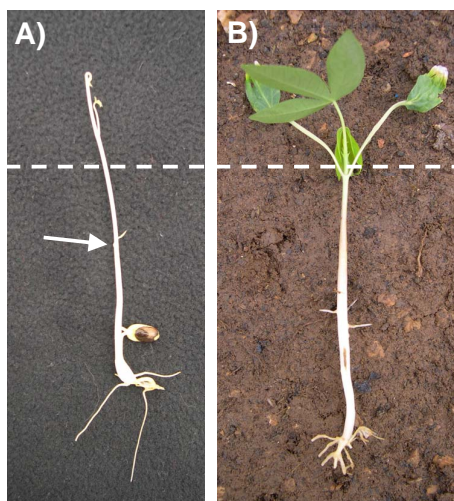


Figure 2: Morphology and germination strategies of seedlings of manioc's closest wild relatives (A) and of manioc itself (B). The dashed line indicates the level of the soil. Pictures were taken about eight days after seed germination. Underground reserves in storage cotyledons and in the swollen hypocotyl, and axillary meristems (arrow) on the underground part of the epicotyl, enable the seedlings of the wild relative to resprout if its aboveground parts are destroyed by drought, herbivores, pathogens or fire. However, initial growth rate is slow, because photosynthetic surfaces (the first true leaves) are only slowly put in place. In contrast, the green, foliaceous cotyledons of seedlings of domesticated manioc quickly fuel more rapid initial growth, but the plant cannot resprout if its aerial parts are destroyed (*unpubl. data*).

An unexpected feature of the domestication syndrome. These forces also appear to be responsible for the most striking and surprising evolutionary change of manioc under domestication, the divergence from its wild relatives in seedling morphology and germination type (Pujol *et al.*, 2005b). Seeds of manioc's closest wild relatives are characterized by hypogeal germination (Figure 2a). The hypocotyl does not elongate during germination, so that cotyledons remain buried in the soil. Enclosed in the testa, they serve as stored reserves. The epicotyl grows to the surface. The seedling's first photosynthetic organs are its first true leaves. In contrast, seeds of domesticated manioc exhibit epigeal germination (Figure 2b). The hypocotyl elongates, elevating the cotyledons above the soil surface. The cotyledons emerge from the testa and expand into foliaceous photosynthetic organs. This difference is truly remarkable. In forest trees, seedling functional morphology is evolutionarily highly conserved, often being invariant within a genus (Garwood, 1996). In contrast, comparison of manioc and its closest wild relatives indicate that the domesticate has evolved a radically different germination type in less than 10 000 years. This evolutionary change is all the more surprising in that it has occurred in a clonally propagated crop plant in which sexual reproduction has until recently been thought to play an insignificant role.

However, this transformation can be explained by the selective pressures we now know to be operating in Amerindian manioc farms. Based on what is known about the strategies of forest trees (Kitajima & Fenner, 2000), the seedlings of the wild relative should be much more tolerant of stresses such as drought, fire or herbivory to above-ground parts, for if these are destroyed the seedling has reserves (storage cotyledons) and meristems (axillary to cataphylls at nodes on the underground portion of the epicotyl) that permit resprouting. However, the seedling's tolerance to stress comes

at the cost of a reduction in growth rate: its initial photosynthetic surface, the tiny first true leaf, is much smaller than if the cotyledons had served as photosynthetic rather than storage organs. The strategy of manioc's wild relatives emphasizes resource conservation. In contrast, the seedling of domesticated manioc should be intolerant of loss of its above-ground parts, for it has neither reserves nor meristems to resprout. On the other hand, its photosynthetic cotyledons confer rapid growth. The strategy of domesticated manioc thus emphasizes resource acquisition. Competition, ultimately mediated by human selection, appears to have outweighed potential hazards to seedlings. Although spectacular and surprising, the transformation of seedling morphology during domestication of manioc can be understood as one more trait that increases the growth rate of volunteer plants from seed, and the probability they will attract the attention of farmers and become established clones (Pujol *et al.*, 2005a).

One further aspect of the evolution of seedling morphology in manioc is noteworthy. The depth at which seeds are buried in soil is variable. They may sometimes be so close to the surface that cotyledons are exposed to light during germination. When this happens, seedlings of the wild relative adopt a morphology somewhat different than that described above. While the behaviour of the hypocotyl is unchanged, the cotyledons emerge from the testa and become foliaceous (see Figure 1d in Pujol *et al.* [2005b]). This plasticity enables the plant to use its cotyledons for photosynthesis when their location at the soil surface precludes their serving as protected underground reserves. This plasticity probably facilitated the transformation to true epigeal germination in domesticated manioc. Interestingly, plasticity in this trait was apparently lost during domestication: the cotyledons of domesticated manioc seeds emerge and expand into foliaceous organs even under conditions of total darkness.

To summarize, our results show that the domestication of manioc involved divergence from the wild ancestor in numerous independent traits. Domestication was not a one-step event but a process of adaptation, and the assembly of so many traits must have required numerous recombination-and-selection cycles. Natural and unconscious selection played an important role, as shown particularly by the evolutionary transformation of seedlings, although farmers do not directly manipulate any facet of the plant's sexual reproduction. The process of domestication continues, and studying the dynamics of contemporary landrace populations gives clues about evolutionary mechanisms and selective pressures acting during initial domestication.

Evolutionary biology of domestication of the guinea yam

The ongoing domestication of yam in West Africa. The literature on domestication of the guinea yam (*Dioscorea cayennensis*/*D. rotundata* species complex) emphasizes a curious phenomenon termed "ennoblement". Farmers are reported to transplant into their fields "wild" yams found in secondary forest (Chikwendu & Okezie, 1989; Dumont & Vernier, 2000). Clonal derivatives of these plants are initially characterized by wild traits. Their tubers bear large, long thorns, are highly fibrous, and are irregular in shape, often long, branched, and deeply buried. Once plants are placed in cultivated environments and carefully managed, these and other wild traits disappear over several clonal generations (Chikwendu & Okezie, 1989). Various techniques are employed. For example, some farmers place obstacles such as pottery fragments beneath the sett. Thus constrained, the plant produces a short, squat, shallow tuber that is much more easily harvested. After a few clonal

generations of such treatment, the plant produces such tubers without requiring manipulation. The nature of this process, which seems to achieve “domestication” with little or no genetic change, has remained somewhat mysterious. Somatic mutations and epigenetic effects have been invoked to explain the process (see Tostain *et al.*, 2003), but we know of no evidence favoring this hypothesis. Recent work by Nora Scarcelli and colleagues (Scarcelli *et al.*, 2006b,a) has begun to shed light on the problem. Using diagnostic molecular markers, they found that although most of these “wild” yams were referable to the wild parent (*D. abyssinica* in savanna environments, *D. praehensilis* in forest environments; the two are likely conspecific ecotypes), some were wild x domesticated hybrids. Other accessions, which had successfully undergone ennoblement (termed “pre-domesticated” accessions by these authors), included not only hybrids but also recombinant domesticated genotypes. The work of Scarcelli and colleagues suggests that domestication, as in all other crop plants, did indeed involve genetic change, and that this process is ongoing. Furthermore, a plausible interpretation of the genetic difference between “wild” and “pre-domesticated” accessions is that individuals of hybrid and domesticated genotypes are more easily ennobled. In fact, attempted “ennoblement” is not always successful. Farmers consider some individuals as non-domesticable, judging that others are exploitable immediately and others only after several years of “ennoblement” (Chair *et al.*, 2005). “Ennoblement”, sometimes abusively equated with “domestication”, may simply be the expression of extraordinary phenotypic plasticity in the domesticate, at least in the populations managed in this way by farmers. In fact, plasticity may be one of the traits most favored by selection.

A reproductive ecology presenting strong contrasts with that of manioc. In the context of this essay, the principal lesson to be drawn from this example is the great contrast in the ecology of sexual reproduction between the yam case and that of manioc in fields of Amazonian Amerindians. Despite the irregularity of flowering of domesticated guinea yam compared to wild relatives and the greater frequency of male clones (Hamon & Toure, 1990), many cultivated varieties of this crop do produce seeds (Hamon & Toure, 1990; Dumont & Vernier, 2000; Scarcelli *et al.*, 2006b). Although much less is known about sexual reproduction and its frequency in yams, as in the manioc case some African cultivators regularly incorporate yam plants from seed as new clones (Scarcelli *et al.*, 2006b,a). However, the ecology of seeds and seedlings is very different in these two plants, leading to fundamental differences in the process of their incorporation and in the kinds of traits favoured by selection. The principal contrast in their ecology is that while plants from seed of manioc pass their entire life, from seedling to mature plant, in cultivated fields, plants from seeds of yam pass their early life in secondary forest, and are later transplanted into field environments. This should select for great phenotypic plasticity.

How can this difference between the two crops in life cycles of plants from seeds be explained? Seeds of *Dioscorea* are very small. Lacking dormancy, they germinate rapidly. Survival and growth of seedlings is highly dependent on light availability. The winged seeds are very light, and many are dispersed to secondary forest near cultivated fields. Because it takes several years for seedlings to develop to a size that would attract the attention of farmers, even those that fall into cultivated fields will probably not be targets for incorporation until long after the field has been left to fallow. Thus, in marked contrast to manioc, plants originated from seed are likely to spend the first years of their lives not in field environments but in secondary forest. Plants found by farmers and transplanted into fields have thus survived for several years in secondary forest. Once in the new field environment, a very

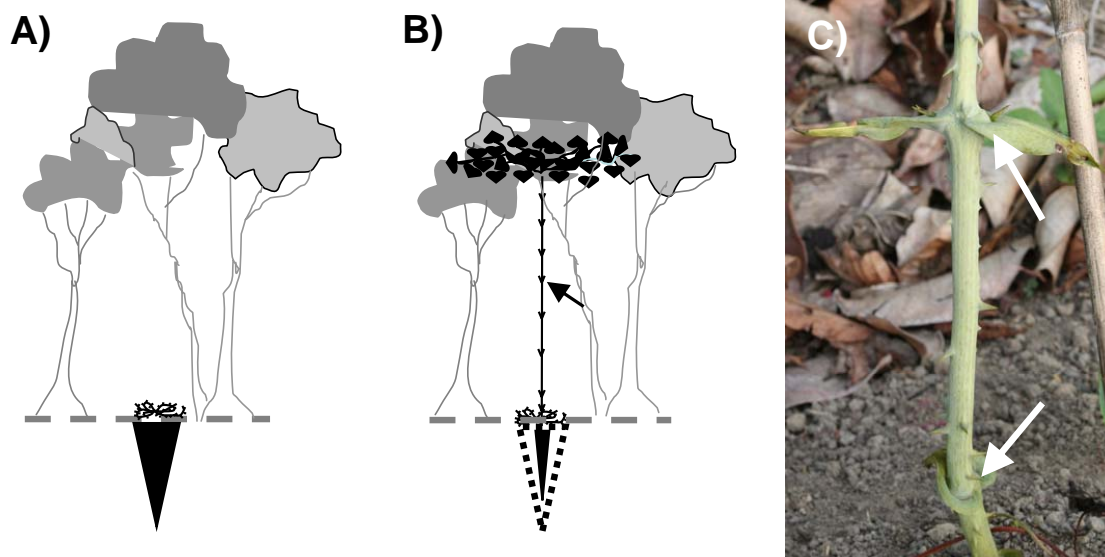


Figure 3: Growth strategy of *Dioscorea praehensilis*, a wild ancestor of the guinea yam, as studied in forests of southeastern Cameroon (Di Giusto, 2002). The plant is a geophyte, i.e., the aerial apparatus dies to the ground each year, during the dry season (A). Its life cycle features an annually repeated struggle, using reserves stored in the underground tuber, to reach the forest canopy and by its photosynthesis during the rainy season (B) replenish the tuber reserves that will enable the plant to make the same trip the following year. While traversing the forest understory, the plant bears no true leaves, only cataphylls, indicated by arrows in (B) and (C). Axillary meristems are associated with each pair of cataphylls.

different set of requirements is imposed on the plant. To satisfy the exigencies of farmers and thereby be incorporated and multiplied as new clones, they must produce large, shallow tubers that are easily harvestable. This life cycle, encompassing very different ecologies at different stages, appears to have maintained great phenotypic plasticity in a number of traits. Thus, depending on the reproductive ecology of the crop in question, domestication may result in either reduction of plasticity, as in the branching architecture of maize (Lukens & Doebley, 1999) and the seedling morphology of manioc, or in its maintenance or even enhancement, as in the guinea yam. The ecological context in which traits of the domesticate are expressed appears to determine whether plasticity is adaptive or not.

Ecology and the domestication syndrome. What traits have evolved under domestication of this plant? Answering this question requires understanding the adaptations of the plant's closest wild relatives. One of these, the forest yam *D. praehensilis*, is characterized by one of the strangest ecologies we have encountered among wild relatives of crop plants, an evolutionary ecologist's dream but an agronomist's nightmare. Like many other yams of the section *Enantiophyllum*, *D. praehensilis* has a very unusual growth strategy (Figure 3). A geophytic vine of seasonal humid forests, the central feature in its life cycle is an annually repeated race to the forest canopy, fuelled by reserves stored in an underground tuber (Di Giusto *et al.*, 2001). Upon reaching the canopy, which may be at 30 m or higher, its aerial apparatus has a single season of photosynthesis to restock the reserves for next year's trip. After this single season of growth (about six months), the aerial apparatus dies to the ground. The tuber remains quiescent during the dry season, its reserves protected by their deep burial and by the presence of a "crown of thorns"—densely branched spiny roots—in superficial soil

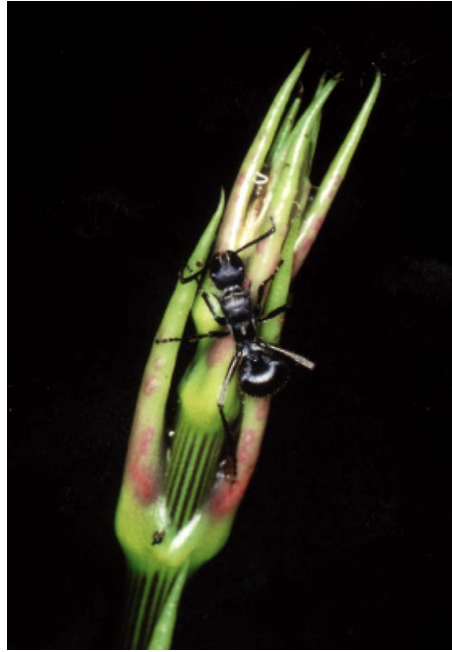


Figure 4: An ant (*Polyrhachis* sp.) at extrafloral nectaries (darker-colored areas) on cataphylls of an apical meristem of *Dioscorea praeheasilis* in a forest in southeastern Cameroon. Protection conferred by constant ant patrolling of the apical meristem during its long trip to the canopy is essential to the plant's success. Photograph courtesy of Bruno DiGiusto.

layers above the tuber. Just before the beginning of the rainy season, the race to the canopy begins anew. This heliophile cannot conduct net positive photosynthesis in the shaded understory, and how much the shoot system can produce in its single season of growth depends on how rapidly it reaches the canopy. Its morphology is thus adapted to maximize the rate of vertical growth. In the shaded understory, the plant does not branch: a single apical meristem assures stem height extension rates of up to 30 cm or more each day (Di Giusto, 2002). Nor does the plant produce true foliage leaves at this growth stage. At each node are two opposite cataphylls (scale leaves), with associated axillary meristems that remain dormant as long as the apical meristem is active. While this morphology allows rapid height extension, it has a conspicuous weak point: if the tender apical meristem, continuously present through this critical growth phase, is attacked by herbivores, this delays the shoot's arrival to the canopy. Field experiments conducted by Bruno Di Giusto (2002) showed that loss of the apical meristem leads to a delay of from 10 to up to 45 days in reaching the canopy, depending on when during its climb the apical meristem is attacked. One reason for the long delay is that, like other monocots, yams lack secondary growth. The small axillary meristem that takes over must first undergo establishment growth (Tomlinson, 1987) to reach its definitive, unchanging primary diameter, which must be large enough to produce stems capable of supporting the plant's entire crop of leaves throughout the growth season. As expected from its important contribution to plant fitness, the apical meristem is provided with chemical defenses (saponins) against herbivores (Di Giusto *et al.*, 2001). Nevertheless, meristems are attacked by herbivores, favoring the evolution of additional defenses. Here is where the significance of cataphylls is seen. Although morphologically reduced, they have a crucial function, because when young each bears numerous extrafloral nectaries that secrete sugar- and amino acid-rich nectar throughout the day and night, attracting ants to the apical

meristem (Figure 4). Their presence dissuades most herbivores. However, one specialist herbivore, the chrysomelid beetle *Lilioceris latipennis* Clark, not only tolerates the plant's chemical defenses, but also turns them against ants: larvae cover their body with a "fecal shield" containing slightly altered plant saponins. Although ants attack adult *Lilioceris*, reducing oviposition on the plant, and can kill early-instar *Lilioceris* larvae, if larvae escape long enough to reach a critical minimum size, they can no longer be killed or dislodged by ants. Constant patrolling is thus required for effective protection. The fate of apical meristems, and thus of the plant, depends on the balance of interactions between the plant, its herbivores, and ants.

From this ecologically complex starting material, what traits have evolved under domestication? This question is currently unanswerable, for two reasons. First, equating "ennoblement" with "domestication" has generated confusion, at least in our minds, about whether traits have been lost or whether their expression is conditioned by complex patterns of phenotypic plasticity. Several traits of the wild relative should be strongly counter-selected in domesticated environments. These include traits that make the tuber more difficult to harvest, such as deep burial and the "crown of thorns". The long phase of stem elongation without foliage leaves is no longer adaptive in cultivated environments, as it would reduce (or at least delay) production. However, these traits would continue to be adaptive in wild environments, where volunteer plants from seed spend the first years of their lives. Variation in these traits persists among cultivated varieties, particularly where farmers still practice dynamic management featuring the incorporation of volunteer plants from seed (Chikwendu & Okezie, 1989). To what extent this variation reflects genetic diversity, or phenotypic plasticity, is quite unclear. Second, because agronomists have generally not appreciated the complex ecology of the wild relative, many ecologically important traits have largely escaped their attention. For example, we have uncovered no mention of the functional roles of cataphylls, only the observation that the number of cataphylls is reduced in domesticated yams (Chikwendu & Okezie, 1989). Yams of the section *Enantiophyllum* thus present a number of intriguing traits that should be under divergent selective pressures in wild and domesticated environments, but whether they have evolved under domestication has been little explored, largely owing to our poor understanding of the ecological context of domestication.

Bananas: processes of domestication in a crop characterized by almost purely clonal reproduction today

The two previous examples illustrate the ecological diversity of clonally propagated crops. Their complex and strongly contrasting life forms and life cycles have led to great differences in the process of incorporation of volunteer plants from seed, and in the kinds of traits that selection favors under domestication. The third example, banana, is a crop in which many contemporary populations have virtually lost the capacity for sexual reproduction. Owing to our familiarity with the seedless fruits of today's widespread varieties, bananas and plantains exemplify the popular notion (e.g., Pearce, 2003) of crops evolving under purely clonal reproduction since their initial domestication. If such were the case, somatoclonal variation would be the main source of diversity. At local or regional scales, this may be true. East and West Africa each have distinctive banana types consisting of a cluster of local landraces which appear to have resulted from evolution under virtually purely clonal reproduction (De Langhe & de Maret, 1999; Pickersgill, 1998). Whether there were one or more introductions

of the crop into Africa, and when, are still controversial (Kennedy, in press). However, the almost exclusive predominance of clonal reproduction in many contemporary banana populations has tended to obscure our understanding of the crop's early evolution. As pointed out by Jean Kennedy (in press; Kennedy & Clarke, 2004), most accounts of banana evolution under domestication give very little insight into the crucial early stages of human intervention. Mixed clonal/sexual reproduction played a key role in the origin and early diversification of the crop, and mixed clonal/sexual systems still operate in some domesticated banana populations today.

Wild *Musa* species are light-loving giant herbs that colonise disturbed sites in forest, such as landslides and treefalls (Simmonds, 1962). Seed dispersal by frugivorous vertebrates is an important part of this ecological strategy. Whereas selection under domestication favored the evolution of seedless fruit (independently in two different sections of the genus), this was a complex process, not an event (Simmonds, 1962). Sexual fertility was progressively reduced, but probably remained sufficiently high, over a long enough period of time, for recombination to assemble important domesticated traits. As pointed out by De Langhe & de Maret (1999), "both semi-wild [*i.e.*, by seed] and vegetative propagation may have co-existed for a considerable time." Why did seedlessness take so long to evolve? First, selection against seediness may have been weaker than our current fixation on the edible fruit of this crop would lead us to suppose. Kennedy (in press; Kennedy & Clarke, 2004) has emphasized the diversity of uses of different organs of the banana plant by many of its contemporary cultivators. Immature seedy fruits, corms, stems and inflorescences are eaten; fibres of leaves and stems are used to make textiles. Edible fruits are not always the most important product of the plant, and this situation is likely to have been more frequent in the past. Secondly, seedlessness is frequently revealed to be due not to one trait but to a combination of traits—parthenocarpy and sterility (male, female or both)—which themselves have been assembled by recombination. Parthenocarpy involves mechanisms at least partly independent of the loss of fertility (Simmonds, 1962). Many so-called 'archaic' edible banana varieties are in effect only *facultatively* parthenocarpic, as emphasized by Kennedy (in press). Capable of producing fleshy, seedless fruit in the absence of suitable pollen, they can also produce seeded fruit if they are fertilized. In populations including such varieties, even the occasional incorporation of volunteer plants from seed could have a huge impact on the genotypic diversity of clones. In evolutionary terms, a little sex goes a long way (Halkett *et al.*, 2005).

Observations among contemporary cultivators of facultatively parthenocarpic landraces give tantalizing clues into the ecology that may have characterized banana populations during much of their evolutionary history under domestication (Kennedy & Clarke, 2004; and J. Kennedy, *pers. comm.*²). In Milne Bay Province, Papua New Guinea, village elders express annoyance when favorite old-fashioned varieties produce increasingly seedy fruits. Worried that they would break their few remaining teeth (meaning that they would no longer be able to chew betel nut), the elders' crescendo of complaints eventually persuade the village's young men to search out and cut down, in forest fallow fringing their gardens, the wild *Musa* they perceived as being the source of the viable pollen. Such anecdotes suggest that the evolutionary ecology of banana is every bit as rich and as full of surprises as that of crops such as manioc and yams.

Ironically, the most extravagant events of outcrossed sex in bananas may have also sealed the end of recombination as a source of diversity in the crop. The seeds produced by facultatively parthenocarpic

²February 2009, Jean Kennedy, Department of Archaeology and Natural History, Research School of Pacific and Asian Studies, Australian National University.

varieties when they are pollinated include diploid, triploid and tetraploid interspecific hybrids. As in a number of clonally propagated crops, polyploidization through interspecific hybridization probably led not only to heterosis but also accelerated the suppression of fertility. Productive, sterile, seedless varieties, favored by multiple selective forces, put most populations of this crop onto the road of purely clonal evolution.

As publicized in a popular article (Pearce, 2003), bananas appear to illustrate one of the predicted consequences of the loss of sex: the loss of evolutionary potential and thereby of the capacity to adapt to new pressures, particularly biotic pressures such as pathogens. Commercial banana production, based on a small group of clones with very little genetic diversity, has from the start depended on heavy application of agrochemicals, which may account for 30% of the production costs, and diseases are also responsible for steady yield declines in smallholder systems (Heslop-Harrison & Schwarzacher, 2007). In terms of its evolutionary dynamics, the relationship between humans and bananas recalls the argument of Law (1988) that nurture of an asexual symbiont by the host can favor asexuality, or at least can allow asexual lineages to persist, in the face of Red Queen challenges. In the coevolutionary race between banana's human symbionts and its pathogens, increasingly sophisticated intervention may be necessary to save the crop from extinction (Pearce, 2003).

Domesticated plants as models in evolutionary ecology

We argue that integrating ecology—and in particular that of clonally propagated crops—into domestication studies can lead to fundamentally new insights. To a degree, each clonally propagated crop has its own domestication syndrome. These plants can thus provide model systems for studying a different, and collectively much larger, set of ecologically important traits than the seed-propagated crops on which most evolutionary research has focused so far (Doebley, 2004; Ross-Ibarra *et al.*, 2007). The three crops presented in this chapter include only a small fraction of the plants, structures and characters that have evolved under domestication, but they illustrate evolution in a great range of traits. They show the interest of these plants for studying the evolution of phenotypic plasticity and investigating the genetic basis of complex ontogenies. It is certain that in-depth study of a wider selection of crops would multiply the opportunities. The literature suggests that many other clonal crops have evolved under mixed clonal/sexual systems similar to those explored in the examples presented here. These include potato (Johns & Keen, 1986), taro (Caillon *et al.*, 2006), ensete (Shigeta, 1996) and sweet potato (Yen, 1974).

Seed-propagated crops and clonally propagated crops can thus each make unique and complementary contributions to evolutionary studies. Comparative studies of parallel and convergent evolution in cereals and grain legumes will continue to provide detailed information about the genetic and developmental basis of a few well-studied traits, whereas clonal crops, once we know enough about their ecology to intelligently use the genetic tools available for them, could provide good material for studying a host of other traits.

Clonally propagated crops could also add new twists to themes already explored in seed-propagated crops, such as the evolutionary role of gene flow between crops and wild relatives (Duputié *et al.*, 2007). Crop-wild hybridization is often approached as a problem in managing the consequences of gene flow so as to conserve genetic resources and prevent the evolution of invasive weeds (Ellstrand *et al.*, 1999), but its study can also give insights into fundamental questions about speciation (Ladizinsky,

1998). Ecological speciation plays an important role in the generation of biodiversity, but “the threads connecting genes and selection are still few” (Schluter, 2009). Crop plants and their wild relatives could provide model systems for studying links between adaptive divergence and reproductive isolation. Whether one approaches the problem from an applied or fundamental standpoint, a potentially important difference between seed-propagated and clonally propagated crops needs to be taken into account. In the former, selection pressures on seed dispersal and seed dormancy are strongly divergent between crops and their wild relatives. Depending on the environment(s) in which hybrids live, this could impose biological barriers to their viability at very early stages of ontogeny. Although these and other barriers to hybridization are far from impermeable, they act as a selective filter channelling introgression (e.g., Papa *et al.*, 2005). In contrast, in clonally propagated crops, selection under domestication has not acted to reduce seed dispersal and dormancy. To the extent that volunteer plants from seed are important contributors to the crop’s genetic constitution, selection has acted instead to *maintain* traits essential to the plant’s sexual reproductive ecology, as in manioc and guinea yams. Crop/wild hybridization may thus face fewer biological barriers at crucial early stages of plant development than in many seed-propagated crops. However, the case of manioc shows that selection on volunteer plants from seed can lead to divergences in traits affecting sexual reproductive ecology (Pujol *et al.*, 2005b), albeit very different from those involved in the classical ‘domestication syndrome’.

Their unusual reproductive systems could make clonal crops tractable models for exploring open questions about evolutionary dynamics in mixed clonal/sexual strategies (Halkett *et al.*, 2005). Finally, those crops whose populations have undergone strictly clonal evolution for a long time, such as many bananas, could offer rare opportunities to examine genomic evolution in the absence of recombination (Judson & Normark, 1996). For example, how rapidly do meiotic genes become non-functional (Schurko & Logsdon, 2008)? Plants such as cardoon (*Cynara cardunculus* L., Asteraceae) could be particularly interesting models in this regard. Leafy cardoon and artichoke were both domesticated from the same wild ancestor, the former propagated from seed as an annual, the latter vegetatively as perennial clones (Sonnante *et al.*, 2007). Comparative studies could give data on the effect of clonal propagation on genetic structure and genome evolution.

Ecology and crop improvement and management strategies today

Ecology must also make essential contributions to crop improvement today. Major challenges must be faced. What kinds of crop plants, and agroecosystems, can we devise that will ensure food security for growing populations while maintaining ecosystem services and biodiversity (Siedow, 2001)? How can our crops and agricultural environments adapt to climate change (Smit & Skinner, 2002)? A solid understanding of crop ecology is crucial to these endeavors. Domestication and “improvement” may have bred out traits that would be useful in tomorrow’s crop environments. Crop roots and their interactions with environment are a particularly neglected facet of the ecology of domestication. Waines & Ehdaie (2007) point out that domestication over the past 10 000 years has largely proceeded with observation and direct selection of mostly above-ground organs, unless roots were used as food and selected for directly. Below-ground organs, up to half of the plant or more, were neglected. For example, high yield in the ‘green revolution’ dwarf wheats of the 1970’s entailed not only the well-known reduction in above-ground vegetative parts, but also—as an unconsciously selected pleiotropic

effect—the dwarfing of root systems as well. It should be possible to increase yield, particularly under future conditions of increased drought stress but even in irrigated/fertilized conditions, by selecting specifically for larger root systems. Similarly, plant breeding, largely targeting performance in nutrient-rich environments, has led to the reduced efficiency of root-symbiotic mutualisms (Kiers *et al.*, 2007), which could be key allies of farmers in future environments. Another group of neglected friends are the wild relatives of crop plants, potential sources of many genes useful in agriculturally marginal environments (Heywood *et al.*, 2007). But for wild relatives of many crops, unlocking their potential depends on better knowledge of their ecology, including the range of environments they inhabit (Jones *et al.*, 1997) and their own response to climate change (Jarvis *et al.*, 2008).

Responses to global change of farmers and of crops may both be complex, and their interactions even more so. As soils become degraded and droughts become more frequent with climate change, farmers in some areas, *e.g.*, southeastern Africa, shift from more demanding plants to manioc, because of its ability to yield even under marginal conditions. Insufficiently familiar with detoxification techniques, these new farmers of manioc are frequently affected by konzo and other diseases associated with chronic toxicity when this crop is improperly prepared (Nhassico *et al.*, 2008). This problem could be aggravated by the plant's response to global change: under increased atmospheric CO₂ concentrations, manioc produces smaller roots with increased cyanogen content (Gleadow *et al.*, 2008). Thus several factors may combine to produce a significant public health problem. Engineering cyanogens out of manioc is a frequently proposed solution (Siritunga & Sayre, 2003), but it ignores the considerable evidence that the agronomic advantages of manioc in part result from its having a built-in pesticide (McKey & Beckerman, 1993; Wilson & Dufour, 2002). Such complexity shows that adapting crops and their environments to climate change will require all our ingenuity.

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