



Tansley review

The evolutionary ecology of clonally propagated domesticated plants

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Summary

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While seed-propagated crops have contributed many evolutionary insights, evolutionary biologists have often neglected clonally propagated crops. We argue that widespread notions about their evolution under domestication are oversimplified, and that they offer rich material for evolutionary studies. The diversity of their wild ancestors, the diverse ecologies of the crop populations themselves, and the intricate mix of selection pressures, acting not only on the parts harvested but also on the parts used by humans to make clonal propagules, result in complex and diverse evolutionary trajectories under domestication. We examine why farmers propagate some plants clonally, and discuss the evolutionary dynamics of sexual reproduction in clonal crops. We explore how their mixed clonal/sexual reproductive systems function, based on the sole example studied in detail, cassava (*Manihot esculenta*). Biotechnology is now expanding the number of clonal crops, continuing the 10 000-yr-old trend to increase crop yields by propagating elite genotypes. In an era of rapid global change, it is more important than ever to understand how the adaptive potential of clonal crops can be maintained. A key component of strategies for preserving this adaptive potential is the maintenance of mixed clonal/sexual systems, which can be achieved by encouraging and valuing farmer knowledge about the sexual reproductive biology of their clonal crops.

I. Domesticated plants as model systems in evolutionary biology: bringing clonally propagated crops into the fold

1. Domesticated plants as model systems

Domesticated plants and animals have long fascinated evolutionary biologists, and have been used as models for testing evolutionary hypotheses inspired by studies of wild species. The insights provided by domesticated plants have come primarily from the study of seed-propagated crops, mostly those belonging to two families, Poaceae and Fabaceae (for recent examples see Gepts, 2004; Purugganan & Fuller, 2009; Glémin & Bataillon, 2009). However, a large number of crop plants are vegetatively (clonally) propagated. These are much more diverse in phylogenetic, morphological and ecological terms (Supporting Information Table S1) than seed-propagated crops, and with advances in biotechnology their number is increasing. Despite this diversity – or perhaps because of it – clonally propagated crops have collectively contributed much less to the literature of evolutionary biology than have seed-propagated crops (McKey *et al.*, in press). The purpose of this review is to redress this neglect. Because of space restrictions, we consider clonally propagated food crops only. We first compare the advantages and disadvantages of clonal and sexual propagation, to understand why farmers chose to propagate some plants clonally and others sexually. We then discuss the evolutionary dynamics of sex in crops that farmers chose to propagate clonally. Many of these crops have retained sexual fertility, and are characterized by mixed clonal/sexual reproductive systems. We discuss how these systems function, and how farmers take advantage of them and maintain them.

In seed-propagated crops, the domestication syndrome often involves the loss of seed dispersal and of dormancy mechanisms (Harlan *et al.*, 1973). In clonally propagated crops, the reduction of sexual fertility and adaptations facilitating clonal propagation have been emphasized (Zohary, 2004). We argue that the domestication syndromes of clonally propagated crops encompass a much broader range of adaptations, whose recognition has been hampered by the diversity of these plants, and by the diverse evolutionary trajectories they followed during domestication.

The many gaps in our knowledge will be filled only if evolutionary biologists pay more attention to these plants. Having testable general hypotheses about their evolution under domestication could help bring this about. In this review, we propose a set of general hypotheses about the evolutionary ecology of clonal crops. These hypotheses, grounded in evolutionary theory, are suggested by our own findings on one of the most thoroughly studied clonal crops, cassava (*Manihot esculenta*). Necessarily speculative, they are offered in the belief that this speculation is well

founded, and in the hope that they will stimulate the research we need to go forward.

2. The great diversity of clonally propagated crops

Clonally propagated food crops encompass a huge range of phylogenetic, morphological and ecological diversity (Table S1). Belonging to at least 34 families, they include herbs, shrubs, trees and vines. Their wild relatives are correspondingly diverse in their ecology, morphology and life form. Different parts of these plants have been selected to provide food: roots, tubers and other underground or above-ground specialized storage organs, stems, leaves, fruits and even seeds. Diverse parts, which may or not be the same as the consumed parts, have also been shaped to provide clonal propagules: stems, tubers, rhizomes, bulbs and corms, among others. This diversity of human-exerted selective pressures means that domestication encompasses an enormous range of adaptive scenarios. Not surprisingly, each of these plants displays an idiosyncratic domestication syndrome (McKey *et al.*, in press). Clonally propagated crops can thus provide model systems for studying a different, and collectively much larger, set of ecologically important traits from those of the seed-propagated crops on which most evolutionary research has focused so far.

Today, biotechnology – we focus here on engineering of transgenic plants – is adding to the number of clonally propagated crops, as the genetically engineered introduction of apomixis promises to extend clonal propagation to many seed crops (Spillane *et al.*, 2004). Gaining insights into the sustainable management of these new crops, through understanding the evolutionary ecology of domestication under clonal propagation, is thus more important than ever before. One aim of this review is to contribute to this objective.

II. Advantages and disadvantages of clonal propagation

1. Why propagate a crop clonally?

Fixation of agronomically valuable genotypes While sexually propagated crops are often selfing annuals (with the conspicuous exceptions of the outcrossing maize (*Zea mays* L.), rye (*Secale cereale* L.) and pearl millet (*Pennisetum glaucum* L.)), most clonally propagated crops are perennial woody outcrossers (Zohary, 1984, 2004; Table S1). Some of them, such as cassava, or taro (*Colocasia esculenta* (L.) Schott) and other aroids (*Alocasia* and *Xanthosoma* spp.), are only preferential outcrossers (David *et al.*, 2007; Ivančić & Lebot, 2000), but others are self-incompatible (e.g. sweet potato (*Ipomoea batatas*); Nishiyama *et al.*, 1975) or dioecious (e.g. yams (*Dioscorea* spp.); Engels & Rao, 1995). These plants therefore do not breed true to type, but clonal propagation ensures that favourable genotypes are passed

on to the next crop generation. Clonal propagation in these outcrossing plants helps to preserve very heterozygous genotypes that show hybrid vigour (Balloux *et al.*, 2003; Dobzhansky, 1952; Glémin *et al.*, 2006). Cassava (Elias *et al.*, 2004; Fregene *et al.*, 2003) and hops (*Humulus lupulus*; Jakše *et al.*, 2001) are among the many crops in which clones have been shown to be highly heterozygous, at least for neutral loci.

Prevention of sexual reproduction in these crops also avoids biparental inbreeding and the resulting inbreeding depression, which is often considerable in outcrossers (Husband & Schemske, 1996), and has been documented in several clonally propagated crops, including potato (*Solanum tuberosum*; Simmonds, 1997) and cassava (Pujol & McKey, 2006). Inbreeding depression is an important consideration because clonal multiplication – the purpose of which is to multiply some genotypes to high frequencies – increases the likelihood of biparentally inbred crosses.

Clonal propagation also ensures that very specific chemical composition can be preserved, which is a very important feature in crops such as hops or grapevines (*Vitis vinifera*).

Finally, favourable mutations can easily be identified in the field, and quickly propagated. Somatic mutations can arise in a given meristem, and may confer a direct selective advantage or a novel phenotype that the farmers may find worth keeping. For example, 70 yr ago, more than 1600 spontaneous bud mutations had already been recorded and propagated in *Citrus* (Shamel & Pomeroy, 1936).

Control of wild-to-crop gene flow Most clonal crops that have retained sexual fertility can easily cross with wild relatives. Clonal propagation ensures that the deleterious effects of this gene flow will be reduced, as farmers control the introduction of genes from wild populations. Gene flow in the other direction is a different matter, and will be treated in section VII. African yam farmers, for example, readily incorporate carefully selected crop–wild hybrids, or even wild plants, in their collection of clones (Scarcelli *et al.*, 2006). By contrast, in seed-propagated plants, the domesticated or hybrid status of seeds or seedlings often becomes evident only long after planting and germination, particularly when weeds, including the crop's wild relatives, mimic the crops (Barrett, 1983), thus limiting farmers' ability to control gene flow. Even some mostly selfing seed-propagated crops, such as sorghum (*Sorghum bicolor* [L.] Moench) (Barnaud *et al.*, 2009), form hybrid swarms with their wild relatives, and introgressed plants can become invasive or lower the agronomic quality of the crop (Bartsch *et al.*, 2003; Ellstrand & Schierenbeck, 2000).

Ease of propagation Finally, clonal propagation may simply have been the easiest way to multiply these plants. The wild relatives of many of them possess tubers or stolons, and clonal growth is a regular feature of their biology (e.g.

strawberry (*Fragaria* spp.), wild cherry (*Prunus avium*; Stoeckel *et al.*, 2006), and many monocotyledonous tropical crops (Hather, 1996)).

However, wild relatives of other clonally propagated crops show little or no inclination towards clonal propagation. In slow-growing species, most notably trees (e.g. olive (*Olea europaea*)), clonal propagation often ensures faster initial growth and higher survival rate than propagation from seeds. For other plants, clonal propagation may ensure higher yield. In cassava, for example, plants from true seedlings often have only one tuberous root, while stem cuttings produce one or more tuberous roots from meristems at each node of the stem cutting buried in the soil. In yet other cases, the choice of clonal propagation probably results from short lifespan and lack of dormancy of seeds. Seeds of *Piper nigrum* (pepper) can only live for a week (Zeven, 1976). Finally, some plants have lost sexual fertility during the process of domestication, making clonal propagation now obligatory. Sometimes, sterile and fertile varieties coexist (e.g. in grapevine and citrus; Table S1). In banana (*Musa* spp.), most 'modern' varieties have almost completely lost the capacity for sexual reproduction, probably as a consequence of counter-selection against hard seeds (Kennedy, 2008) and of their hybrid origin, which causes meiotic irregularities in a number of cultivars (Grivet *et al.*, 2004). Even in banana, however, both clonal propagation and sexual propagation still occur at a non-negligible rate in some 'semi-domesticated' cultivated varieties (De Langhe *et al.*, 2009; Kennedy, 2008).

2. Why not propagate a crop clonally?

A number of pitfalls are associated with the benefits noted above.

Loss of some components of diversity The most conspicuous cost of clonality is precisely the absence of sexual recombination under exclusive clonality. In selecting propagules for the next crop generation, farmers choose not to propagate all clones at the same rate, and in the long term, some clones are inevitably lost. Even though many phenotypically diverse cultivars are propagated, not all components of diversity are valued. The genetic diversity of clonally propagated crops is therefore bound to erode, if no mechanism generates new diversity. Genetic diversity sometimes leads to higher yields (Crutsinger *et al.*, 2008; Reusch *et al.*, 2005; Zhu *et al.*, 2000), although not always (Ronsheim & Anderson, 2001). In 'modern' agriculture, low-diversity field populations are often part of a system including higher diversity populations in plant breeding stations. Overall genetic diversity may be the key to sustainable high yields.

Apart from considerations of short-term productivity and yield, there is general agreement that genetic diversity is

necessary to help maintain the evolutionary potential of crop populations (Lebot, 1992), notably when they are faced with pathogens (Gibson *et al.*, 2000; Strange & Scott, 2005). Maintaining a genetically heterogeneous crop does not ensure high yields, but it minimizes the variance of yield (Chapin *et al.*, 2000; Hajjar *et al.*, 2008). Some ecologically relevant phenotypic variation can be achieved through the fixation of somatic mutations or through epigenetic variation (see section III); however, it is unlikely to counteract the erosion of genetic diversity under exclusively clonal propagation.

Deleterious mutations Vegetatively propagated populations are, in addition, more prone to accumulate deleterious mutations than are sexual populations. Indeed, deleterious mutations arise much more frequently than do beneficial mutations, because there are many more ways to destroy a function than to improve it (Fisher, 1930). Selection subsequent to recombination can help purge the mutational load, while combining advantageous mutations. When there is no recombination, the mutational load increases. This phenomenon, known as Muller's ratchet (Muller, 1932, 1964), or its newer formulation (Kondrashov, 1988), is often advocated to explain the persistence of sex. The accumulation of mutations in a purely clonal line ultimately leads to lowered fitness, associated with lower agronomic performance. Improved mechanisms of DNA repair, notably through gene conversion, have sometimes been proposed to explain why some organisms have apparently evolved without sex for millions of years (Schön & Martens, 2003). However, it is unlikely that such mechanisms could have evolved in clonally propagated crops, which have a very recent evolutionary history. Another mechanism that could help get rid of some deleterious mutations is diplontic selection (section III).

Greater competition between use of plant parts as propagules and their use as food In many clonal crops, the part of the plant used to make propagules is also the part eaten by humans. Of course, this is also true of most seed-propagated crops. However, the large size of most clonal propagules means that a much larger proportion of the harvest is diverted from food use. About 10% of the world's potato crop is thus diverted from food use (Spillane *et al.*, 2004). By contrast, in seed-propagated crops such as quinoa (*Chenopodium quinoa* Willd.), only 0.3% of the crop must be reserved for seed (Parlevliet, 2007).

Pathogen accumulation Last, but not least, vegetative propagation is often associated with the spread of systemic pathogens, some of them with disastrous consequences for yield. Clonal propagules can bear viruses, bacterial pathogens, fungi or other parasites (Lozano & Nolt, 1989), and healthy plants can be infected if the same tool is used for pre-

paring all propagules. The older a clone, the more pathogens it is likely to bear. Pathogen accumulation can be compared to a very fast version of Muller's ratchet, and is also countered by sexuality (more precisely, by reproduction through true seeds), although not for the same reasons. Indeed, surfaces of seeds (in contrast to clonal propagules) are often quite clean, and seed storage conditions usually reduce the risk of further infection. In addition, most systemic pathogens are not transmitted through seeds. For example, cassava mosaic viruses, which cause much damage to this crop in Africa, do not cross the placenta (Legg, 1999). However, passage through seeds does not eliminate all pathogens: the potato spindle tuber viroid, for example, is transmitted to the plant's sexual progeny (Simmonds, 1997).

The advantages and disadvantages of clonal propagation help explain why farmers chose to propagate some plants clonally and others by seed, and how clonal propagation influenced evolution under domestication. Understanding the evolutionary dynamics of clonal crops also requires taking into account sources of heritable variation that may be particularly important under clonal propagation.

III. Evolution in clonal populations: somatic mutations and epigenetic traits as sources of heritable variation

1. Sex and clonality: challenges to classical theory and their relevance to clonally propagated crops

Some recent work has challenged the classical view of the advantages of sexual reproduction, and the disadvantages of pure clonality (presented in the previous section). The bdelloid rotifers have apparently refrained from sex for millions of years, which makes them 'asexual scandals' (Judson & Normark, 1996): lineages can persist and diversify through purely clonal evolution. Evolution under strict clonality is more dynamic than is usually thought: somatic mutations are so frequent that strict genetic identity of 'clonemates' is vanishingly improbable (Lushai & Loxdale, 2002). Clonally propagated domesticated plants are cited as examples of the power of somatic mutations to provide genetic variation that contributes to adaptive evolution (Whitham & Slobodchikoff, 1981). What are the implications of these studies for understanding the evolutionary ecology of clonally propagated crops?

In modular organisms such as plants, soma and germline are not separated: gametes bear the somatic mutations of the cell lineage from which they are descended. The evolutionary consequences have only recently been formalized in mathematical population genetic models (Orive, 2001; Otto & Hastings, 1998; Pineda-Krch & Lehtilä, 2002). First, as mutations accumulate over time and different branches inherit different mutations, the growing plant can become a genetic mosaic (Gill *et al.*, 1995), and the plant's

clonal descendants can thus be genetically heterogeneous. Secondly, competition within meristems between cell lineages differing in somatic mutations can lead to diplontic selection (also termed clonal selection or developmental selection): a cell lineage bearing a mutation conferring an advantage in terms of cell proliferation can replace other lineages. Selection at the cellular level is expected to be often concordant with selection at the individual level (Otto & Hastings, 1998). Diplontic selection could thus be a powerful force purging deleterious mutations, helping to explain how long-lived organisms avoid the accumulation of mutational load (Orive, 2001), and allowing the individual to selectively accumulate favourable new alleles, without the break-up of existing adaptive traits by recombination (Otto & Hastings, 1998). The individual itself evolves over its lifetime. Unequal growth rates among branches differing in somatic mutations can contribute to intra-individual evolution. Thirdly, the continual filtering of mutations during vegetative growth means that those that occur in gametes, when they are produced, are not a random set but are biased towards favourable mutations. Models suggest that somatic mutations inherited by gametes could be a source of genetic variation quantitatively comparable to mutations occurring directly during meiosis (Orive, 2001).

Somatic mutations could be an important source of genetic variation in clonally propagated plants, with diplontic selection accelerating the accumulation of favourable alleles in clonal lineages. However, taking these considerations into account in no way undermines conclusions about the evolutionary advantages of sex in these plants: only recombination can create populations in which many favourable mutations can cooperate in the same individuals, rather than compete among lineages (Gerrish & Lenski, 1998).

Empirical study of diplontic selection has hardly begun. The only reasonably well-documented examples we have found, for any plants, concern cultivars with variegated leaves, known in a great diversity of ornamental plants. These plants are chimeras, bearing both chlorophyllous and achlorophyllous cell lineages. The latter are eliminated by diplontic selection when human selection no longer maintains the variegated condition (Klekowski, 2003). Given the paucity of studies of other traits, the evolutionary role of diplontic selection is uncertain. For example, how efficiently it purges deleterious mutations is unclear. Many deleterious mutations are recessive, and would presumably be invisible to diplontic selection, except in cell lineages homozygous for them. Arguments about the importance of inbreeding depression in clonally propagated crops (section II) would thus seem to retain their full force.

Numerous other questions about diplontic selection await exploration. Clonally propagated crops appear to be choice model species for studying the role of diplontic selection in the evolution of modular organisms. Known

chimeric cultivars, such as those documented for grapevine (Franks *et al.*, 2002), offer one starting point.

2. Transgenerational epigenetic inheritance as a source of heritable phenotypic variation in clonally propagated crops

Epigenetic inheritance is 'the inheritance of developmental variations that do not stem from differences in the sequence of DNA or from persistent inducing signals in the present environment' (Jablonka & Raz, 2009). Whether transgenerational inheritance to *meiotic* descendants through sexual reproduction is frequent and important is still debated, although many cases have been documented in animals, micro-organisms and plants (Jablonka & Raz, 2009). By contrast, transgenerational inheritance by *mitotic* descendants is not at all controversial. In clonally propagated plants, especially those with infrequent sex, it could be a significant source of heritable phenotypic variation.

The best information on this poorly explored aspect of the biology of clonal crops comes from trees, where epigenetic inheritance across clonal generations creates management problems. In some species (e.g. Norfolk Island pine (*Araucaria heterophylla*)), cuttings from orthotropic (vertical) or plagiotropic (horizontal) axes inherit the growth trait of the axis from which they were prepared. This is known as topophysis (Robbins, 1964). The effects of the age and of the environment of the part used for cutting are dubbed 'cyclophysis' and 'periphysis', respectively (Klaehn, 1963). While these are distinguished by foresters as three different effects, it is sometimes difficult to separate them.

These phenomena are very poorly explored in clonal crops, where there is great scope for many different kinds of 'maternal' effects. The 'seed' is chosen by the cultivator: its size, age and position on the parent plant can all vary, and affect the phenotype of the clonal descendant. Only some of these phenotypic variants are likely to be stable across many clonal generations (see discussion in Elias *et al.*, 2007). Sorting out heritable epigenetic traits from transient 'maternal' effects, on the one hand, and from somatic mutations, on the other, will not be easy. Heritable epigenetic variation has been shown to occur in a phenotypically diverse collection of plantain accessions, which showed hardly any polymorphism for amplified fragment length polymorphism (AFLP) markers and microsatellite loci, but varied in patterns of cytosine methylation (Noyer *et al.*, 2005). This phenomenon could also help to account for the apparent genetic homogeneity of phenotypically diverse taro accessions from Polynesian islands (Meilleur, 1998). Transgenerational epigenetic variation can also lead to deleterious phenotypes. In oil palm (*Elaeis guineensis*), some artificially produced somatic embryos show feminized male flowers with more or less reduced fertility (Rival *et al.*, 2008).

IV. Evolutionary dynamics of sex in clonally propagated crop plants

In all clonally propagated crops – including those in which clonal reproduction already featured prominently in the biology of wild ancestors, and those that have lost sexuality and are propagated exclusively clonally today – sexual reproduction has played a major role in evolution under domestication (Pickersgill, 2007). The widespread notion of ‘single-step domestication’ of these crops by capture and multiplication of mutant clones is, we believe, untenable (McKey *et al.*, in press). Once farmers began to propagate a crop clonally, however, the selective pressures acting on sex were altered. In flowering plants, sexual reproductive traits can evolve relatively quickly in response to a change in ecology or population genetic structure (Ashman, 2006; Harder & Johnson, 2009). Fields of clonally propagated crops can be seen as a natural laboratory in which to study the rapid evolution of sexual traits.

Interestingly, breeders have frequently and intensively used sexual reproduction in the genetic improvement of clonally propagated crops. From this work we know some of the evolutionary pressures acting on the evolution of sex in these plants. However, understanding this depends on combining data on plant reproductive systems with what little information exists on the ecology and genetics of field populations in ‘traditional’ settings, where the practices of cultivation still resemble in important ways those that have held for thousands of years.

1. Trade-offs between flowering/fruitletting and yield, and the counter-selection of sex

Sex may have an allocation cost. If genotypes with reduced investment in flowers and fruits allocate more resources to other functions (Eckert, 2002; López-Almansa *et al.*, 2003; Obeso, 2002), this may result in increased yield. Farmer selection of higher-yielding genotypes could thus drive the reduction of sexual fertility. This appears to have occurred in potato (Simmonds, 1997), Jerusalem artichoke (*Helianthus tuberosus*; Kays & Nottingham, 2008), and yams (Abraham

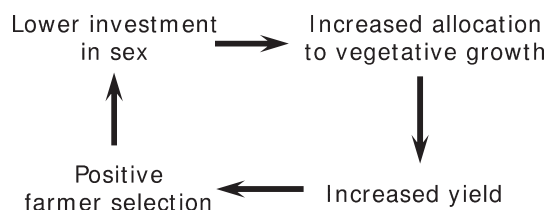


Fig. 1 Reduced sexuality mediated by a yield–sex trade-off. If lower investment in flowering and fruitletting leads to increased yield of harvested parts, farmer selection for higher yield could drive the reduction, or even loss, of sexual fertility.

& Gopinathan Nair, 1991; Abraham *et al.*, 1986; Segnou *et al.*, 1992). Selectively multiplied by farmers, sterile and high-yielding clones may then spread rapidly (Fig. 1).

In plants grown for their fruits, selection may more easily lead to reduced investment in male function, as postulated for domesticated plants in general (Waller, 1988) and as suggested by cytoplasmic male sterility in several clonally propagated fruit trees (e.g. Besnard *et al.*, 2000; Thompson *et al.*, 1976; Yaegaki *et al.*, 2003; Yamamoto *et al.*, 1997), although alternative explanations exist for the latter phenomenon.

2. Clonal/sexual fecundity trade-offs

Particularly complex trade-offs between sexual and clonal reproduction may occur in some plants. In cassava, for example, the plant’s architecture mediates a trade-off between sexual fecundity and ‘clonal fecundity’: the stem system is comprised of a series of terminally flowering modules. Branching occurs when the apical meristem of the module differentiates into an inflorescence (Médard, 1973). Cassava’s wild ancestor branches, and thus flowers, frequently. In obedience to Corner’s rules (Corner, 1949), its many-branched stems have thin primary diameters and bear small leaves. Domesticated cassava, however, has been selected for enlarged meristems, large leaves, and thick stems that produce reserve-rich stem cuttings resistant to desiccation, and consequently has reduced numbers of branches and of flowers. Human selection for increased ‘clonal fecundity’ led to architectural changes that resulted in reduced sexual fecundity.

3. Changes in population genetic structure

Clonal propagation modifies the genetic structure of populations. This has important, but variable, consequences for the evolution of sex in wild clonal plants (Eckert, 2002) and in clonally propagated crops.

Inbreeding depression Clonal propagation interacts with the highly allogamous mating systems that characterize most of these plants and their wild ancestors (see Table S1). Because clonal propagation raises a few genotypes to very high frequencies in populations of these crops, a large proportion of pollen transfers are likely to occur between clonemates. The frequency of such crosses might even be amplified when clonemates are planted in spatial aggregates, a pattern commonly encountered in ‘traditional’ farming systems (McKey *et al.*, in press). Rates of inbreeding will therefore increase in self-compatible preferential outcrossers and may lead to a greater impact of inbreeding depression in plants generated by sex (Pujol & McKey, 2006; Pujol *et al.*, 2005a). If inbred seedlings are frequent, their poor or unpredictable performance may lead farmers to rely

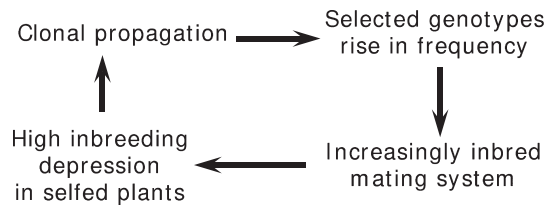


Fig. 2 Reduced sexuality through increased inbreeding depression in preferential outcrossers. Low or unpredictable performance of plants issued from sexual reproduction can lead farmers to rely increasingly on clonal propagation, increasing the opportunity for accumulation of mutations that reduce sexual fertility.

increasingly on clonal propagation. The diminishing role of sex in the plant's life cycle could then facilitate the accumulation of mutations reducing sexual fertility (Fig. 2).

Mate limitation in self-incompatible or dioecious crops In obligate outcrossers, multiplication of selected clones to high frequencies should lead to diminished mate availability, which is exacerbated when farmers plant their crops in monoclonal patches, or when one sex is preferentially multiplied. Mate limitation will be especially pronounced if reduced genotypic diversity leads to local fixation of incompatibility alleles. If this occurs, even potentially highly fertile genotypes are effectively sterile; if these are selected for, the resulting reduction in the number of sexually produced offspring may lead farmers to rely increasingly on clonal propagation (Fig. 3). Thus, as in wild clonal plants, 'ecological sterility' (Eckert, 2002). Alternatively, plants could evolve increased self-compatibility in response to mate limitation, as in potato (Hosaka & Hanneman, 1998). Local fixation can also be countered by widespread exchange of clonal propagules in social networks extending over large regions (Emperaire *et al.*, 1998).

In dioecious plants, mate limitation may interact with gender-dependent cost of sex. In most dioecious plants, the costs of flowering in males are lower than the cost of flowering and fruiting in females (Obeso, 2002). Other things being equal, this could lead to higher yield in male clones,

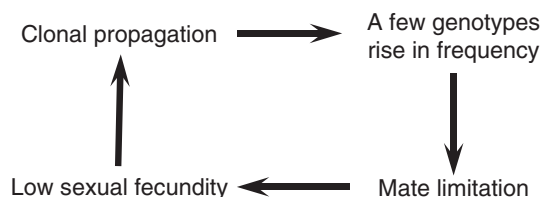


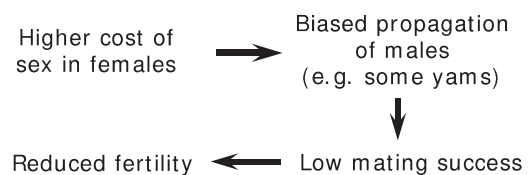
Fig. 3 Reduced sexuality through mate limitation in obligate outcrossers. In these plants, clonal propagation can lead to increased mate limitation and thereby to decreased fecundity, leading farmers to rely increasingly on clonal propagules. This 'ecological sterility' increases the opportunity for accumulation of mutations leading to genetic sterility.

which might explain why male clones are predominant in most yam species (Hahn, 1995; Lebot, 2009; see Fig. 4a).

In dioecious plants cultivated for their fruits (including the domesticated fig *Ficus carica*, which is anatomically gynodioecious but functionally dioecious; Kjellberg *et al.*, 1987), biased propagation of females could quickly lead to severe mate limitation. Human selection can lead to parthenocarpy (fruit development without fertilization), as in some domesticated figs (Zohary & Spiegel-Roy, 1975; Fig. 4b). In grapevine, another mechanism has allowed bypassing of mate limitation. This crop's ancestor is dioecious, and obviously, only females are of agronomic interest. In addition, the crop is planted in monovarietal fields. Cultivated grapevine still forms berries thanks to the evolution under domestication of hermaphroditism, self-compatibility, and sometimes also parthenocarpy (Zohary & Spiegel-Roy, 1975; Fig. 4b). In yet other plants, such as hops, sex reversal is sometimes observed in fields. Even though reversal most often transforms male plants into female plants (Bressman, 1934), reversals in the other direction also occur (Schaffner, 1923; USDA, ARS, National Genetic Resources Program, 2009), and this could be a mechanism that helps bypass mate limitation, given the number of females present in the fields.

However, selection for clonal propagation has not always modified sexual fertility or mating systems. In the dioecious

(a) Plants not grown for fruits



(b) Plants grown for their fruits

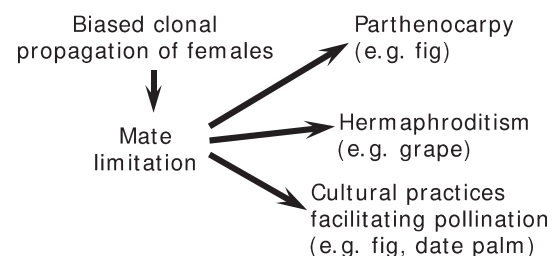


Fig. 4 Effects of clonal propagation on the reproductive biology of dioecious plants. (a) In those grown for parts other than fruit, higher allocation cost of sex in females could lead to biased clonal propagation of males, as may have occurred in some yam species. Reduced male mating success can then facilitate evolution of sterility. (b) In plants grown for their fruits, mate limitation resulting from clonal propagation can lead to the evolution of parthenocarpy (as in some figs) or of hermaphroditism (as in grapevine). It can also lead to the development of cultural practices to counter mate limitation, as in figs and date palms.

date palm (*Phoenix dactylifera*), some cultivars have evolved parthenocarpy, but because parthenocarpic fruits are smaller and grow more slowly than those of artificially pollinated plants, the cultural practice of laborious hand-pollination has been conserved (Wrigley, 1995; Fig. 4b). Similarly, the higher quality of naturally pollinated figs has led to maintenance of the ancient practice of caprification, in which branches of male figs bearing the tree's specific pollinators are gathered and placed in female trees bearing receptive figs (Zohary & Spiegel-Roy, 1975).

Conscious counter-selection of sex Parthenocarpy has also evolved in pineapple (*Ananas comosus*) and bananas, albeit for different reasons from those outlined in the cases above: both produce very hard seeds that make seeded fruits inedible, or at least much less desirable. Selection for seedless clones has triggered not only parthenocarpy, but also the virtual loss of sexual fertility in banana (Kennedy, 2008) and, in pineapples, the evolution of self-incompatibility. In this latter crop, facultative parthenocarpy, self-incompatibility, and the planting of the crop in monoclonal fields together ensure that no seed is produced (Coppens d'Eckenbrugge & Leal, 2003).

Reduced fertility through hybrid origin or polyploidization Interspecific hybrids may grow more rapidly (and, in domesticated plants, have higher yields) than parental species, and any or all of several factors may contribute to this: hybrid vigour (Dobzhansky, 1952), polyploid vigour (Lippman & Zamir, 2007), and sterility (for example, by lowering the plant's allocation to sex, thereby freeing resources for yield; Obeso, 2002). Sterile clones could evolve and spread very rapidly by this means. Allopolyploidization may have led to the reduced sexual fertility of sugarcane (*Saccharum officinarum*), and a trade-off between flowering and the sugar content of stems probably favoured sterile hybrid clones (Grivet *et al.*, 2004; Fig. 5). In wild plants, increase in vigour or fitness of hybrids is often a

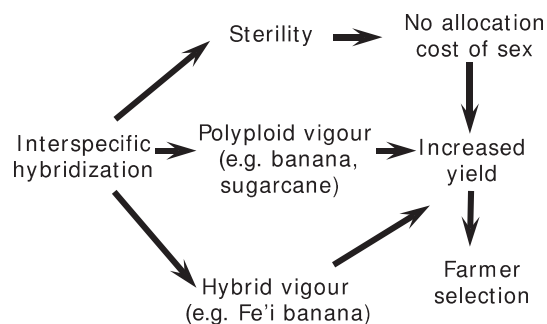


Fig. 5 Interspecific hybridization and polyploidy can lead simultaneously to hybrid vigour, polyploid vigour and genetic sterility. These can singly or in combination lead to increased yield, encouraging rapid adoption and diffusion of these plants by farmers.

short-lived phenomenon, breaking down in F_2 and successive generations (Burke & Arnold, 2001). This phenomenon is circumvented when farmers clonally propagate vigorous hybrid clones.

Enjoying the benefits of clonal propagation, while avoiding its costs, is made possible by introducing a dose of sexual recombination into a predominantly clonal propagation system. This is often, however, easier to state than to put into practice.

V. Mixed clonal/sexual systems: how do they work?

1. Clonal and sexual reproduction interact to shape evolutionary dynamics

As in wild 'clonal' plants (Eckert, 2002; Gabrielsen & Brochmann, 1998; Mock *et al.*, 2008), the frequency of sexual reproduction and its impact on patterns of genetic diversity in clonally propagated crops have often been underestimated (McKey *et al.*, in press). Whether sex is still important in crop populations today depends largely on whether farmers incorporate sexual progeny into their stocks of vegetative propagules. This practice is common in many 'traditional' farming systems (which we may define as those in which farmers produce their own 'seed' for the next generation), and has probably been continuous from the origin of domestication up to the present time. In such crops, a mixed clonal/sexual reproductive system persists and the crop population consists of two interlinked compartments: clonally propagated plants and sexually produced plants. In the long run, farmer management of these two compartments shapes the evolutionary processes presented above. Examining the genetic and ecological dynamics of mixed clonal/sexual systems at small scales of space and time gives insight into these long-term processes.

Sex is incorporated into the cultivation cycle when farmers decide to propagate clonally 'volunteer' (spontaneous) plants, issued from sexual reproduction, that appear in their fields, in fallows, or in secondary forests. Farmers observe young seedlings and may decide to spare them from weeding, and in some cases (e.g. cassava seedlings in Vanuatu; D. McKey, pers. obs.) they actively transplant seedlings to locations where they can grow better or simply be more conveniently observed. Farmers can thus select, and then multiply clonally, advantageous variants resulting from recombination, and benefit from the advantages of each reproductive system while minimizing their disadvantages.

Although the mating system of most clonally propagated crops is documented, their sexual reproductive ecologies are poorly known. We know that in aibika (*Abelmoschus manihot*), ensete (*Ensete ventricosum*), potato, sweet potato, taro, guinea yam (*Dioscorea rotundata*) and cassava, farmers in traditional systems incorporate plants originating from

seeds into the stock of clones (McKey *et al.*, in press). However, we know next to nothing about the ecology and genetics of this process. What insects pollinate these plants, and what mating systems result from the interaction of their behaviour, farmers' planting practices, and the plant's reproductive traits? How diverse is the compartment of volunteer seedlings, and what selective forces act on it? How and when do farmers decide what plants to incorporate? How, and how far, are seeds dispersed, and can they remain dormant in the soil? We usually have no answers to these questions, but they are crucial, and the answers certainly vary among crops (McKey *et al.*, in press).

2. A well-studied example: cassava

In only one clonally propagated crop, cassava, has reproductive ecology been studied in some detail. The results of this work, carried out in fields of Amerindian farmers in Amazonia, have been synthesized and discussed elsewhere (McKey *et al.*, in press; Rival & McKey, 2008), and will be only briefly summarized here. This crop, whose starch-rich tuberous roots provide the staple food for more than 600 million people throughout the tropics, is propagated by stem cuttings. Most varieties of cassava have retained sexual fertility, with farmers regularly incorporating 'volunteer' plants from seeds into the stock of clonal landraces (Elias *et al.*, 2000, 2001b).

Fig. 6(a) describes the mixed clonal/sexual reproductive system of cassava in Amerindian fields. Sexual reproduction

begins when insects (mostly stingless bees; D. McKey, pers. obs.) pollinate the plant's flowers. While unisexual flowers and protogynous inflorescences limit self-pollination in this self-compatible preferential outcrosser, they do not exclude it. When the fruit matures, it dries and dehisces explosively, scattering seeds on the ground up to several metres from the mother plant. Ants then play a crucial role in the plant's reproductive ecology: attracted by the seed's caruncle, ants transport and bury seeds in their nest or in refuse heaps nearby (Elias & McKey, 2000). Thus is formed a soil seed bank, in which seeds can remain dormant for up to dozens of years. Dormancy is physiological and based on thermal cues. Seeds remain dormant if vegetation cover maintains soil temperatures around 25°C (as during fallow periods), and germinate if the vegetation cover is removed by a disturbance, such as field clearing and burning, that heats the soil. Cassava's dormancy system was inherited from its wild ancestors, which are adapted to periodic disturbances, often fire, in forest-savannah ecotone habitats (Pujol *et al.*, 2002). Seedlings thus emerge when a farmer opens a new field by clearing and burning an old fallow and plants stem cuttings. Young plants in the field are a mixture of planted clones and recombinant genotypes issued from sexual reproduction. Amerindian farmers can easily distinguish plants derived from seed from those derived from stem cuttings (e.g. by the shorter basal internodes of the former), even when plants become very large. Farmers observe volunteer plants with interest, spare them when weeding and allow them to grow. Those that survive to harvest time are

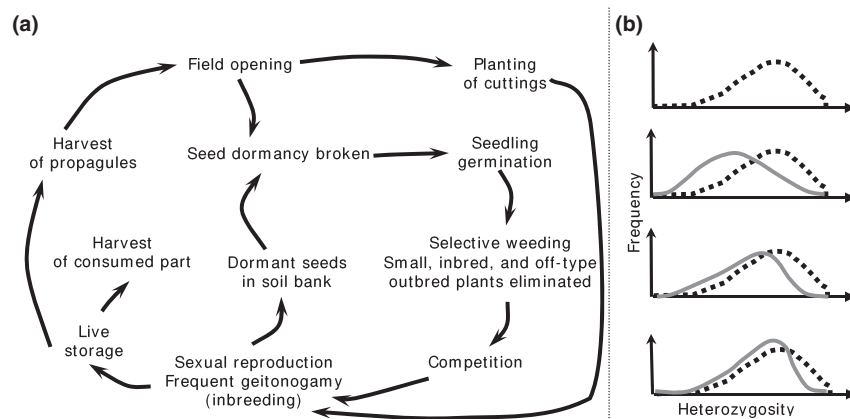


Fig. 6 Life cycles of clonal crops under mixed clonal/sexual reproduction. The case of cassava is exemplified here. (a) Cultivation cycle of cassava begins with the opening of a new field, which triggers seedling germination at about the time that clonal propagules are planted. Seedlings endure several steps of natural and artificial selection, and reach sexual maturity at the same time as the plants issued from cuttings. Sexual reproduction takes place freely and results in the formation of a bank of dormant seeds, which will germinate at the beginning of the next cycle (which may be decades later). Farmers then harvest the tuberous roots and make stem cuttings for further propagation in a different field, and the frequency of each clone will be different in the next crop generation. Plants issued from sex that attract the interest of farmers may also be selected for propagation. (b) Evidence of seedling selection during the cultivation cycle. The first graph shows the schematic distribution of multilocus heterozygosity in established clones (dashed black line). Subsequent graphs show multilocus heterozygosity in established clones and in seedlings (grey line) at germination, after weeding and after mortality resulting from competition among seedlings. Throughout the cycle, both very inbred and very outbred seedlings are selected against, and the multilocus heterozygosity of the seedling compartment tends towards that of the compartment of established clones.

examined, and some are incorporated into the stock of clonal propagules, each usually being assigned by the farmer to the landrace it most resembles (Duputié *et al.*, 2009; Elias *et al.*, 2001a). Each landrace is thus a diverse assemblage of multiple clones sharing phenotypic characteristics.

Long-established clones are highly heterozygous, while plants originating from seeds are characterized by high variance in the degree of inbreeding (Pujol *et al.*, 2005a; Fig. 6b). Indeed, landraces are planted in monovarietal patches: intra-patch crosses are highly inbred, while inter-patch crosses are outbred. Both natural and artificial selection favour outcrossed, highly heterozygous volunteer plants, which are larger than inbred ones. During weeding, early in the cultivation cycle, farmers unconsciously remove small volunteers, which are too small to be distinguished amidst other adventitious plants (Pujol *et al.*, 2005a). Later in the cultivation cycle, intraspecific competition among volunteers is the major source of mortality, striking smaller volunteers (Pujol & McKey, 2006; Fig. 6b). Finally, at harvest time farmers select from among surviving volunteers those that display interesting agronomic qualities, and prepare from them stem cuttings that will serve as propagules for the next generation. Throughout the cultivation cycle, the decreasing number of survivors are increasingly outbred, coming to resemble established clones in this respect (McKey *et al.*, in press; Fig. 6b). Of course, in the approximate process of natural and artificial selection, some favourable genotypes are eliminated and some less favourable genotypes survive, as a result of chance and environment-related variation. Selection during the first cycles of clonal multiplication should weed out new recombinant clones whose incorporation was a result more of chance than of a favourable genotype (Duputié *et al.*, 2009).

By allowing (and contributing to) selection against inbred volunteers, farmers solve one of the major problems associated with sexual recombination in this clonally propagated crop. Because volunteer plants constitute only a small fraction of all the plants in the field, and because farmers invest no time in managing them, the high selective mortality in this compartment imposes a negligible cost to the farmer. With the problem of inbreeding depression thus cheaply solved, and the diversity-generating advantage of sex fully exploited by selective incorporation of new variants, sexuality of the crop continues to provide advantages to farmers. The importance of sex in the crop's life cycle is shown by the fact that seedling morphology has evolved under domestication, allowing faster initial growth of the seedlings (Pujol *et al.*, 2005a,b).

Amerindian cassava fields in some ways resemble breeding programmes that use backcrosses to selectively add new favourable genes to already 'elite' genotypes (Cooper *et al.*, 2001). These farms thus combine two functions – production today and the generation of new genotypes that will ensure continued adaptation and production tomorrow –

that are usually performed by separate populations (in fields and in breeding stations, respectively) in 'modern' agriculture.

Cassava is so far the only clonal crop for which we have much information on how mixed clonal/sexual systems work. Scattered information from other crops suggests that many of the features discussed above may be quite general, but that there is also interesting variation among crops (McKey *et al.*, in press). For example, in guinea yam the great difference in the environments experienced by established clones (farms) and by volunteer seedlings (secondary forest of old fallows nearby) could have a profound impact on many traits, among them the overarching trait of phenotypic plasticity, which must be considerable if a single genotype is to survive such divergent environments at different stages of its life cycle (McKey *et al.*, in press). Differences in techniques of clonal propagation also lead to variation in how mixed clonal/sexual systems function. In the many fruit-bearing trees and vines propagated clonally by grafting, populations may include nongrafted plants (often 'wild' or feral plants from seed), some of which are used as rootstocks for the clonally propagated landraces (Janick, 2005). Intrapopulation genetic diversity might thus present very different patterns between rootstock and graft compartments. Such possibilities, and their potential consequences for population functioning, appear not to have been investigated. However, as early as Roman times there are records of specific easily rooted apple (*Malus pumila*) rootstock landraces, clonally propagated like the fruit-bearing landraces (Janick, 2005). 'Modern' cropping systems routinely employ improved rootstock cultivars, distinct from fruit cultivars, in crops such as grapevine and apple.

Given such diversity in the functioning of mixed clonal/sexual systems across different crops, their comparative study offers rich scope for advancing our understanding of evolutionary dynamics under domestication.

VI. Domestication syndromes in clonally propagated crops

Domestication syndromes in these crops have been poorly understood. Selection has obviously acted to increase yield and to facilitate propagation, as in seed-propagated plants. Some traits of the classical domestication syndrome apply only to seed-propagated crops; but others, such as reduced branching (Lukens & Doebley, 1999), also characterize some clonal crops, even though the selective pressures leading to them appear to be different, as illustrated by the case of cassava (section V). Finally, perhaps the most frequently cited feature of domestication syndromes in these crops, reduction of sexual fertility, turns out to be much more complex than often recognized (section IV).

Why has it been so difficult to identify a 'domestication syndrome' in clonal crops? One explanation holds that

domestication of these plants was a simple, almost instantaneous process – the capture and multiplication of genotypes with desirable traits – and that domesticated populations have had too few recombination-and-selection cycles to have accumulated numerous differences from their wild ancestors (Zohary, 2004). According to the alternative hypothesis we propose, mixed clonal/sexual systems have generated ample opportunity for the accumulation of domesticated traits. Furthermore, evolution under domestication has been a more diverse set of processes than in seed-propagated crops, resulting in a confusing diversity of domestication syndromes.

As in seed-propagated crops, selection has often favoured reduced chemical or mechanical defences (Chikwendu & Okezie, 1989; Ivančić & Lebot, 2000; Mondolot *et al.*, 2008; Ross-Ibarra & Molina-Cruz, 2002). However, selection has also favoured increased production of high-quality propagules, often supplied by a different part of the plant. Selection has also acted on these plants' sexual traits, as clonal propagation has modified fertility, mating systems and the genetic structure of populations, and as farmers have favoured fast-growing volunteers (Pujol *et al.*, 2005a,b). Populations of most clonal crops consist of two compartments, established clones and sexually produced volunteers, which experience different selective environments. Interactions between traits are thus much more complex than in seed-propagated crops and selection often acts in conflicting directions.

VII. The future of clonally propagated domesticated plants

1. Biotechnology and the expanded scope of clonal propagation in agriculture

The evolutionary dynamics of crop populations have long been driven by compromise between maximizing yield (under a given set of conditions) and minimizing the risk of crop failure (when conditions change). Some strategies emphasize risk minimizing. For example, subsistence farmers with little access to the inputs necessary to maximize yield (the best soils, fertilizer, pesticides and technology) often find it more important to avoid crop failure. Maintaining genetic diversity in their crop populations may contribute to this goal.

However, diversity has its disadvantages. Over the last 10 000 yr, humans have domesticated landscapes and have used inbreeding, backcrossing, and vegetative propagation to fix desired traits in their crop populations. Over the past two centuries, marine macroalgae have been added to the panoply of clonally propagated crops (Guillemin *et al.*, 2008). Today, the creation of transgenic plants is an extension of the same approach (Salick, 1995), albeit one that opens unprecedented possibilities in terms of the scale of its

impact, both on agroecosystems and on nontargeted 'wild' nature (Andow & Zwahlen, 2006). Most of these new extensions of domestication expand the realm of clonal propagation at the expense of sexual reproduction. Clonal propagation thus is becoming an increasingly important theme in the evolutionary biology of domestication.

One major development is the domestication of timber trees. The sexual reproductive biology of long-lived, late-reproducing perennial plants presents particularly strong obstacles to the fixation of domesticated traits (Johannessen, 1966). Vegetative propagation and selection for early-bearing individuals have sped up breeding cycles (Zohary & Spiegel-Roy, 1975). While many fruit trees have been domesticated, tree species used for wood and paper have been subject to little genetic modification. Today there is a perceived need to accelerate their domestication through biotechnology. Current proposals envisage engineering sterility into timber trees, thereby shifting resources previously allocated to sex to increased vegetative growth, and at the same time stopping any gene flow to wild populations (Campbell *et al.*, 2003).

A second major development is the genetically engineered introduction of apomixis (Spillane *et al.*, 2004). Hybrid seeds hold desirable gene combinations. Because seeds produced by open pollination in farmers' fields are genetically heterogeneous, farmers who choose to use hybrid seeds must purchase them anew each year. In contrast, farmers can produce apomictic seeds with desired trait combinations themselves. The gain in production and the reduction in cost to farmers could be considerable. If the genetically engineered introduction of apomixis progresses as expected, a large number of seed-propagated crops could become clonally propagated, thus entering the realm of the evolutionary dynamics outlined in this review. Because apomixis is usually facultative (Spillane *et al.*, 2004), some sexual seeds may still be produced, and mixed clonal/sexual systems like those discussed here could become prominent features in the evolutionary ecology of these new clonal crops. Apomixis could also confer advantages to crops that are already clonally propagated, by combining the advantages of clonal propagation with the pathogen-cleansing effects of passage through seed (Spillane *et al.*, 2004). These advances may, however, imply loss of diversity and of adaptive potential.

2. Crop-to-wild gene flow in clonally propagated plants: integrated management of genetically modified crops and wild populations.

Where clonally propagated crops have maintained their sexual fertility, their wild relatives should be no less subject to gene flow from crop populations than those of seed-propagated crops (e.g. Duputié *et al.*, 2007). Some traits may even make gene flow easier. First, these crops and their wild relatives are mostly outbreeders. Secondly, post-zygotic barriers

to hybridization at early stages of development may be weaker than in domesticated cereals and pulses. In the latter, selection on seed dispersal and dormancy has produced adaptations strongly divergent from those of their wild relatives. Hybrid seedlings may be maladapted to both wild and domesticated environments, creating a biological barrier at a crucial early stage of plant development. By contrast, in sexually fertile clonally propagated crops, selection on volunteer plants from seeds has maintained adaptations similar to those of the wild ancestor, and hybrid seedlings may suffer little reduction in fitness in wild environments (McKey *et al.*, in press). Gene flow may thus be an important problem in the integrated management of crop and wild populations in centres of diversity of wild relatives (Halsey *et al.*, 2008; Scurrah *et al.*, 2008). Incorporating male sterility into genetically modified plants has been advocated as a way to limit crop-to-wild gene flow in potato (Celis *et al.*, 2004).

3. Maintaining the adaptive potential of clonal crops under global change

Biotechnology should result in increased yields, but will yields be stable if conditions change? Under the rapid environmental, social, economic and cultural changes the planet is now experiencing, it is more important than ever to find ways to manage crop evolution so that yields will continue to be high in tomorrow's environments. Maintaining the adaptive potential of crop plants is an essential ingredient in the management mix. As outlined in this review, clonally propagated crop plants face particular problems in this regard. Will these crops be able to maintain their capacity to generate diversity? We have seen that the reduction in clonal diversity can trigger feedback processes leading to the reduction, or even loss, of sex. To the extent that developments in biotechnology accelerate the replacement of diversity by a few 'elite' clones, they contribute to this reduction of adaptive potential.

Perhaps the most fragile component of systems maintaining the evolutionary potential of clonally propagated crops is the local knowledge of 'traditional' farmers about the sexual reproductive biology of these crops. Several factors endanger this knowledge. For instance, farmers' specialized knowledge about volunteer seedlings may not travel along with the plant, when the plant is introduced into new continents. Some African farmers of sweet potato, a plant introduced from tropical America, know nothing about volunteer seedlings, and their failure to exploit them raises doubt about the stability of sweet potato yields (Gibson *et al.*, 2000). Knowledge present can also be eroded, if its transmission and diffusion are not encouraged. By encounters with 'modernity', young farmers may come to associate traditional knowledge with 'backward' tendencies and may thus not be receptive to its transmission. Whatever the traits that are engineered into plants, whatever technical solutions

are proposed, it seems crucial that any innovation proffered be accompanied by a willingness to understand, to recognize and to foster the knowledge of local farmers about volunteer seedlings and their interest as a source of diversity. Integrating this knowledge into farmer-participatory breeding approaches (Morris & Bellon, 2004) could provide plant scientists with a powerful tool in helping local communities seeking to adapt their farming systems to environmental and societal changes. Breeding programmes that incorporate true seeds, such as those that exist for potato (Simmonds, 1997) and for cassava (Ceballos *et al.*, 2004), are particularly promising avenues for linking technological innovation with local farmer knowledge to produce farming systems that increase yields while maintaining the adaptive potential of crop populations.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 A nonexhaustive list of clonally propagated crop plants, giving information pertinent to their evolutionary ecology and indicating gaps to be filled by future research.

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