

FROM FOREST TO FIELD: PERENNIAL FRUIT CROP DOMESTICATION¹

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- *Premise of the study:* Archaeological and genetic analyses of seed-propagated annual crops have greatly advanced our understanding of plant domestication and evolution. Comparatively little is known about perennial plant domestication, a relevant topic for understanding how genes and genomes evolve in long-lived species, and how perennials respond to selection pressures operating on a relatively short time scale. Here, we focus on long-lived perennial crops (mainly trees and other woody plants) grown for their fruits.
- *Key results:* We reviewed (1) the basic biology of long-lived perennials, setting the stage for perennial domestication by considering how these species evolve in nature; (2) the suite of morphological features associated with perennial fruit crops undergoing domestication; (3) the origins and evolution of domesticated perennials grown for their fruits; and (4) the genetic basis of domestication in perennial fruit crops.
- *Conclusions:* Long-lived perennials have lengthy juvenile phases, extensive outcrossing, widespread hybridization, and limited population structure. Under domestication, these features, combined with clonal propagation, multiple origins, and ongoing crop–wild gene flow, contribute to mild domestication bottlenecks in perennial fruit crops. Morphological changes under domestication have many parallels to annual crops, but with key differences for mating system evolution and mode of reproduction. Quantitative trait loci associated with domestication traits in perennials are mainly of minor effect and may not be stable across years. Future studies that take advantage of genomic approaches and consider demographic history will elucidate the genetics of agriculturally and ecologically important traits in perennial fruit crops and their wild relatives.

Key words: artificial selection; clonal propagation; crop evolution; domestication; genetic bottleneck; perennial plants.

For over 150 years, evolutionary biologists have used domestication as a way to study selection under controlled conditions (Darwin, 1859, 1899; de Candolle, 1886); accordingly, domesticated systems have occupied a critical role in the development and testing of evolutionary theory (Ross-Ibarra et al., 2007; Pickersgill, 2009; Purugganan and Fuller, 2009). Recent archaeological, genetic, and genomic analyses of annual crops, such as maize (*Zea mays* L.), rice (*Oryza sativa* L.), sunflower (*Helianthus annuus* L.), tomato (*Solanum lycopersicum* L.), and wheat (*Triticum* L. spp.), have greatly advanced our understanding of plant domestication (Doebley et al., 2006; Zeder et al., 2006; Bai and Lindhout, 2007; Burke et al., 2007; Burger et al., 2008; Glémin and Bataillon, 2009). However, comparatively little is known about the way in which perennial plants respond to artificial selection (Zohary and Spiegel-Roy, 1975; Zohary, 2004; Clement et al., 2010; McKey et al., 2010), a relevant topic for understanding how genes and genomes evolve in long-lived species, and how perennial populations respond to other selection pressures operating on a relatively short time scale, such as contemporary climate change (Hamrick, 2004; Reusch and Wood, 2007).

Plant domestication is an evolutionary process operating under the influence of human activities (Harlan, 1992). Over time,

artificial selection causes cultivated populations to diverge morphologically and genetically from their wild progenitors (Clement, 1999; Emswiller, 2006; Pickersgill, 2007). The domestication process produces a continuum of plant populations, ranging from exploited wild plants to incipient domesticates to cultivated populations that cannot survive without human intervention (Clement, 1999; Pickersgill, 2007; Clement et al., 2010). Here, we consider cultivated plant species that are evolving in response to artificial selection pressures to be undergoing domestication. This inclusive approach requires that cultivated populations exhibiting any morphological or genetic divergence from their wild ancestors be treated as part of the domestication continuum.

Perennial species include herbaceous plants as well as woody shrubs and trees that live for more than 2 years. They are generally divided into two groups: short-lived perennials, which live for 3–5 years, and long-lived perennials, which live for more than 5 years. In addition to living longer than annual plants, the reproductive biology of perennials differs from that of annuals in that many perennials have long juvenile phases, are obligate outcrossers, experience high rates of intra- and interspecific gene flow, and frequently reproduce both sexually and asexually (Petit and Hampe, 2006; Savolainen et al., 2007; Smith and Donoghue, 2008; Vallejo-Marín et al., 2010). Under domestication, perennial plants are often propagated clonally, which, in addition to long juvenile phases, further decreases the number of sexual cycles separating domesticated individuals from their wild progenitors (Zohary and Spiegel-Roy, 1975; McKey et al., 2010, in press). On the basis of life history characteristics and mode of reproduction, slow rates of evolution in perennial crops might be expected (Zeder et al., 2006; Olsen and Schaal, 2007;

¹Manuscript received 22 December 2010; revision accepted 31 May 2011.

The authors thank G. K. Croft, J. H. Knouft, D. M. Spooner, J. L. Strasburg, members of the Miller laboratory group, and two anonymous reviewers for valuable comments on previous versions of the manuscript.

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Pickersgill, 2007); however, numerous perennial crops exhibit substantial morphological and genetic divergence from their wild progenitors.

Domesticated perennials are an important component of agricultural economies around the globe (Schreckenberget al., 2006). Perennial crops produce an abundance of useful products including fleshy roots and other belowground materials (e.g., cassava, *Manihot esculenta* Crantz; horseradish, *Armoracia rusticana* G. Gaertn., B. Mey. & Scherb.; potato, *Solanum tuberosum* L.; oca, *Oxalis tuberosa* Molina), woody stems [e.g., *Populus* L. spp.; Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco], fleshy fruits [e.g., apples, *Malus* × *domestica* Borkh.; avocados, *Persea americana* Mill.; sweet cherries, *Prunus avium* L.; oranges, *Citrus sinensis* (L.) Osbeck], and dry fruits [e.g., almonds, *Prunus dulcis* (Mill.) D. A. Webb; pecans, *Carya illinoensis* (Wangenh.) K. Koch; walnuts, *Juglans regia* L.], and interest in perennial grains is on the rise (Glover et al., 2010). How perennial species respond to artificial selection depends in part on the lifespan of the individual (short-lived or long-lived perennial) and whether the target of selection is a vegetative part of the plant (root, underground stem, above-ground stem, leaf base, fleshy leaf) or reproductive component (fruit, seed).

The majority of domesticated perennials are long-lived, woody species cultivated for their edible fruits (Van Tassel et al., 2010). Botanically, a fruit is a mature ovary; here, the term “fruit crops” refers to cultivated plant species in which some component of the fruit is used by humans (e.g., mature ovary, seed, additional flower parts attached to the mature ovary). Long-lived, perennial fruit crops were domesticated in all major agricultural centers including eastern Asia (*Citrus* L.), Mesoamerica [avocado; papaya, *Carica papaya* L.; white sapote, *Casimiroa edulis* La Llave], the Near East (date palm, *Phoenix dactylifera* L.; fig, *Ficus carica* L.; grape, *Vitis vinifera* L.; olive, *Olea europaea* L. subsp. *europaea*; pistachio, *Pistacia vera* L.; pomegranate, *Punica granatum* L.), South America (*Annona* L. spp.; cashew, *Anacardium occidentale* L.; guava, *Psidium guajava* L.), and western Asia [almond; apple; peach, *Prunus persica* (L.) Batsch; pear, *Pyrus communis* L.]. Some fruit crops were domesticated from perennial wild progenitors but are grown primarily as annuals (e.g., chile, *Capsicum* L. spp.; eggplant, *Solanum melongena* L.; and tomato (Janick and Paull, 2008). Because these crops are functionally annuals and share several similarities with domesticated annuals, they will not be treated as perennial fruit crops here.

This review focuses on long-lived perennials, primarily trees and a few woody vines and shrubs, that are cultivated for their edible reproductive structures. Historically, perennial plants were considered intractable systems for studying evolution due to long generation times and low rates of selfing. However, emerging technologies (e.g., transcriptome sequencing) and analytical techniques (e.g., association mapping), in conjunction with mature breeding collections housed in common gardens, are now facilitating detailed evolutionary analyses in perennial species. These advances, along with a steadily increasing body of literature dealing with previously ignored domesticated species mean that perennial fruit crops present excellent study systems to investigate the tempo and mode of evolutionary processes in species that live for multiple years. Do perennial fruit crops evolve under artificial selection just like annuals, only more slowly? What are the hallmarks of domestication in perennial plants? In this review, we (1) revisit the basic biology of natural tree populations and set the stage for perennial do-

mestication by considering what is known about how trees evolve under natural selection pressures, (2) define the suite of morphological features commonly associated with the evolution of perennial fruit crops under domestication, (3) summarize present understanding of the origins and evolution of domesticated perennials grown for their fruits, and (4) describe the genetic basis of domestication in perennial fruit crops.

EVOLUTIONARY PROCESSES IN NATURAL TREE POPULATIONS

Although many important advances in evolutionary biology were made first in crops and later tested in wild populations, it appears that the opposite may be true for long-lived perennials, where recent progress has occurred primarily in natural (undomesticated) tree populations. At neutral or nearly neutral genetic loci (see Van Oosterhout et al., 2004), natural populations of long-lived species exhibit high levels of within population variation and weak population structure (Loveless and Hamrick, 1984; Hamrick et al., 1992; Duminil et al., 2007, 2009). Despite this, these populations appear locally adapted, with multiple loci of small effect underlying adaptive traits (Petit and Hampe, 2006). Below, we provide a brief summary of recent evolutionary analyses of natural tree populations and discuss their relevance for understanding human-mediated evolutionary processes in long-lived species.

On the basis of neutral marker data for natural populations, limited population structure is correlated with lifespan: annuals are more structured than short-lived perennials, which are more structured than long-lived perennials. Other factors correlated with population structure include breeding system, floral morphology, mode of reproduction, mechanisms of pollination and seed dispersal, successional stage, and geographic range, among others (Loveless and Hamrick, 1984; Hamrick and Godt, 1990). Differences in lifespan may account for variable degrees of population structure exhibited by annual and perennial species, and mutation rates likely play a role as well. Although long-lived perennial plants accumulate more somatic mutations than annuals (Klekowski, 1997), annual plants exhibit 2.7–10 times the mutation rates observed in perennials (Savolainen and Pyhäjärvi, 2007; Smith and Donoghue, 2008). Another important aspect of long-lived perennials is the extended juvenile phase; this prolonged nonreproductive period may dilute or minimize the impact of founder effects because until trees reach maturity, newly established populations will grow only through the arrival of new migrants (Austerlitz et al., 2000).

It is possible that patterns of limited population structure in perennials might not reflect lifespan alone, but also variables that are strongly correlated with perenniality, primarily mating system (e.g., outcrossing) and sexual type (e.g., unisexual flowers, monoecious, gynodioecious, dioecious taxa; Duminil et al., 2007, 2009). In perennial species, benefits of reproductive assurance gained through selfing appear to be outweighed by the cumulative, deleterious effects of inbreeding that may accrue over the life of the organism (Barrett, 1998; Petit and Hampe, 2006). Accordingly, long-lived species are generally outcrossers, a system maintained through the physical and temporal separation of the sexes via (hetero)dichogamy, dioecy, or self-incompatibility (Barrett, 1998; Renner, 2001; Vamossi et al., 2003; Ward et al., 2005; Petit and Hampe, 2006; Scofield and Schultz, 2006). Although many annual crops were domesticated from self-compatible wild ancestors, including barley (*Hordeum vulgare* L.),

chickpea (*Cicer arietinum* L.), eggplant, lentils (*Lens culinaris* Medik.), maize, pea (*Pisum sativum* L.), chile (*Capsium annuum* L.), tomatoes, and wheat (Zohary and Hopf, 2000; Bai and Lindhout, 2007; Janick and Paull, 2008), it appears relatively few perennial crops were derived from selfing wild populations (see *A domestication syndrome for perennial fruit crops* later).

The same mechanisms that allow perennial plants to avoid selfing also facilitate extensive intra- and interspecific gene flow in trees across short and long distances, and one consequence of this is that interspecific hybridization is fairly common in trees (e.g., Hamrick et al., 1992; Ellstrand et al., 1996; Petit et al., 2003; Latouche-Hallé et al., 2004; Dutech et al., 2005; Ward et al., 2005; Gerard et al., 2006; Hardy et al., 2006; Curtu et al., 2007; Dick et al., 2007; Ahmed et al., 2009; Du et al., 2009; LePais et al., 2009; Ashley, 2010). Interspecific hybridization in natural tree populations has implications for species coherence and adaptive evolution in the wild and can also play a role in the process of plant domestication. The importance of hybridization in domesticated species was noted by Stebbins (1950, p. 292), particularly in clonally propagated domesticates, where “any single valuable hybrid individual, once obtained, can immediately become the progenitor of a new variety and can be perpetuated indefinitely.” Indeed, it appears hybridization has been a potent force in the evolution of domesticated perennials (see *Hybridization in domesticated perennial fruit crop lineages* later).

Despite low levels of among-population structure based on neutral markers, common garden analyses of populations originating from geographically distinct areas indicate that natural tree populations are locally adapted (Howe et al., 2003; reviewed in González-Martínez et al., 2006b; Neale, 2007; Neale and Ingvarsson, 2008; Neale and Kremer, 2011). Current understanding of the genetic basis of adaptation in long-lived populations is based largely on temperate forest trees that have been evolving in response to selection pressures such as disease, drought, and cold; examples include *Picea* A. Dietr. (Namroud et al., 2008), *Pinus* L. (Savolainen et al., 2004; González-Martínez et al., 2006a; Notivol et al., 2007; Palmé et al., 2008; Wachowiak et al., 2009), *Populus* L. (Chen et al., 2002; Jansson and Douglas, 2007; Rae et al., 2007), and *Pseudotsuga* Carrière (Palmé et al., 2008; Eckert et al., 2009a, b). Quantitative trait locus (QTL) analyses and association studies have demonstrated that these traits are generally associated with variation at multiple loci of small effect (Jermstad et al., 2001a, b, 2003; Howe et al., 2003; Wheeler et al., 2005; González-Martínez et al., 2006a; Heuertz et al., 2006; Rae et al., 2007; Neale, 2007; Eckert et al., 2009a, b, 2010). In contrast, recent studies characterizing the genetic basis of domestication traits (traits that evolved under cultivation in response to artificial selection) in annual crops demonstrate that many domestication traits are the result few loci of large effects (Gepts, 2004; Purugganan and Fuller, 2009). Similar studies in long-lived crops indicate that some traits parallel natural tree populations in genetic architecture, while others more closely resemble the genetic architecture detected in annual crops (see *Genetic basis of perennial fruit crop domestication* later).

A DOMESTICATION SYNDROME FOR LONG-LIVED, PERENNIAL FRUIT CROPS

The evolution of plant morphology in response to human selection pressure is the foundation upon which agriculture is

built. Plant domestication has resulted in a suite of morphological changes in cultivated populations relative to their wild progenitors called a “domestication syndrome” (Harlan et al., 1973; Harlan, 1992; Zohary and Hopf, 2000; Careau et al., 2010). A large body of work quantifying morphological differences between cultivated annuals and their wild progenitors has accumulated. Recent studies have described aspects of the domestication history of individual perennial crops, and a few studies have considered general patterns associated with evolutionary processes in these long-lived crop species (Zohary and Spiegel-Roy, 1975; Zohary 2004; McKey et al., 2010, in press). Using analyses of annual crops as a basis of comparison, we describe the evolution of reproductive and vegetative traits in perennial fruit crops under domestication (Table 1).

Evolution of reproductive traits—Two of the primary differences between annual and perennial crops are breeding system and mode of reproduction (Zohary and Spiegel-Roy, 1975; Zohary 2004; McKey et al., 2010). In terms of breeding system, natural populations of annual and perennial crop relatives differ with regards to self-compatibility and dioecy. As noted already, many cereals and pulses were domesticated from self-compatible, wild progenitors, but self-compatible, wild ancestors of perennial crops are less common (Zohary and Hopf, 2000). Dioecy, however, is weakly correlated with woody growth and fleshy fruit production (Muenchow, 1987; Renner and Ricklefs, 1995; Vamasi et al., 2003); consequently, several dioecious perennials have been domesticated while few (if any) dioecious annuals have been selectively cultivated for food. Under domestication, the breeding systems of dioecious perennials have evolved to gynodioecy, andromonoecy, or hermaphroditism (e.g., papaya, grape, carob [*Ceratonia siliqua* L.]). On the other hand, annual and perennial crops are similar in that many were domesticated from allogamous wild populations, which, under domestication, have switched to an autogamous breeding system; for example, the annual crops rice and faba bean (*Vicia faba* L.), and the perennial crops almond, grape, and plum (*Prunus domestica* L.; Table 1).

The vast majority of annual crops are grown from seed. In contrast, more than 75% of perennial fruit crops are clonally propagated (Table 2). This is not necessarily the case for perennial species that are grown as annuals; those grown for their belowground vegetative components are generally clonally propagated (e.g., horseradish, oca, potato), and those grown for their fruits (e.g., tomato, chile, eggplant) are grown from seed. Long juvenile phases in perennial species place severe limits on traditional breeding efforts because farmers are required to wait multiple years (in some cases, decades) before fruits can be evaluated, selected, and cultivated. Early farmers sidestepped challenges associated with juvenile phase length by adopting clonal propagation, the primary form of reproduction in perennial fruit crops and a key component of the domestication syndrome in long-lived plants (Zohary and Spiegel-Roy, 1975). The shift from sexual to clonal reproduction allowed for the faithful reproduction of individuals with superior features by eliminating uncertainty associated with sexual reproduction (Bhojwani and Razdan, 1996). Clonal reproduction can result in rapid rates of change in domesticated systems because individuals with favored traits, once identified, can be reproduced exactly and extensively. The shift from sexual to clonal reproduction has also led to concomitant changes in reproductive biology (discussed below), some of which are the most striking changes associated with perennial fruit crop domestication (Zohary and Spiegel-Roy, 1975; McKey et al., 2010; Table 1).

TABLE 1. Morphological traits associated with domesticated annual and perennial crops. Vegetative and reproductive traits are classified into two character states: the ancestral state, which is found in the wild relatives of the crop, and the derived state, the state exhibited by the domesticated populations. Examples and citations are listed for each trait when available, but are not meant to represent an exhaustive list in every case.

Category	Trait	Wild (ancestral) state	Domesticated (derived) state	Examples in annuals	Examples in perennials
Reproductive	Breeding system ^{a, b}	Allogamous	Autogamous	Rice (Oka and Morishima 1967, 1971); faba bean (Zohary and Hopf, 2000)	Almond (López et al., 2006; Sánchez-Pérez et al., 2007); grape (Zohary and Hopf, 2000); papaya (Janick and Paull, 2008); plum (Zohary and Hopf, 2000)
	Mode of reproduction	Dioecious Sexual	Gynodioecious, andromonoecious, hermaphroditic Asexual via parthenocarpy		Black pepper (Zeven, 1974); grape, carob (Zohary and Hopf, 2000) Banana (Heslop-Harrison and Schwarzacher, 2007); fig (Kislev et al., 2006a); jocote (Juliano, 1932); pistachio (Polito, 1999); pears (Zohary and Hopf, 2000) <i>Citrus</i> spp. (Moore, 2001; Rao et al., 2008) ~75% of cultivated perennials; see Table 2
	Inflorescence ^c	Sexual Sexual Sterile flowers	Asexual via nucellar embryony Asexual via propagation by humans (e.g., grafting, layering, cuttings) Sterile flowers become fertile	Cereals (Harlan, 1992; Zohary and Hopf, 2000) Wheat, barley, rice (Zohary and Hopf, 2000) Cereals, sunflowers, pulses (Zohary and Hopf, 2000) Sunflower, corn, sorghum, millet (Harlan, 1992); tomato (Bai and Lindhout, 2007) Flax (Zohary and Hopf, 2000)	
	Seeds ^c	Few Shattering Smaller size Lower seed set	Many Nonshattering Larger size Higher seed set		
		More toxic	Less toxic	<i>Cucurbita</i> * spp. (Janick and Paull, 2008) Flax (Zohary and Hopf, 2000); sunflower (Putt, 1997) Pulses (Zohary and Hopf, 2000); rice (Cai and Morishima, 2000) Chickpeas (Zohary and Hopf, 2000); tomato (Bai and Lindhout 2007); chile peppers (Pickersgill, 1997) Pulses (Zohary and Hopf, 2000); tomato (Bai and Lindhout, 2007)	Almond (Lyle, 2006; Sánchez-Pérez et al., 2010) Clove (Wit, 1976) Polaskia (Otero-Arnaiz et al., 2003) Apples (Lyle, 2006); jocote (Miller, 2008)
	Fruit ^{a, c}	Low oil content High dormancy Relatively homogeneous fruit Smaller size Low oil content Dehiscent Thick	High oil content Low dormancy Increased variation in color, size, and shape Larger size High oil content Indehiscent Thin		Olive, date, grape, pomegranate, apples, plums (Zohary and Hopf 2000) Olives (Zohary and Hopf 2000) Kapok (Dick et al., 2007) Pecan, almond (Browicz and Zohary 1996)
	Shell thickness				

TABLE 1. Continued.

Category	Trait	Wild (ancestral) state	Domesticated (derived) state	Examples in annuals	Examples in perennials
Vegetative	Defensive structures ^a	Spines	No spines	Eggplant (Weese and Bols, 2010)	Olive, plum (Zohary and Hopf 2000); kapok (Dick et al., 2007)
	Growth form	Perennial Indeterminate growth Large	Grown as annuals Determinate growth Dwarf	Tomato, chile peppers, eggplant (Janick and Paull, 2008) Cereals, sunflowers (Zohary and Hopf, 2000); soybean (Tian et al., 2010)	Avocado (Lahav and Lavi, 2002); castor (Singh, 1976); coconut (Janick and Paull, 2008); papaya (Niklas and Marler, 2007); apple, cherry, peach, pear, plum, citrus (Tukey 1964) Kiwi (Atkinson et al., 1997); breadfruit (Zerega et al., 2004); sour cherry (Tavaud et al., 2004)
	Ploidy level	Diploid	Polyploid	Wheat (Zohary and Hopf, 2000); peanut (Kochert et al., 1996)	

^a Described by Hancock (2004)

^b Described by Zohary and Spiegel-Roy (1975) and Zohary (2004).

^c Described by Harlan (1992)

When one or just a few clones (cultivars) are planted across a geographic region, clonal propagation can result in mate limitation (McKey et al., 2010). In nature, tree populations are almost exclusively outcrossers (see previous section); mate limitation resulting from clonal propagation in agricultural environments has resulted in the evolution of alternative strategies to ensure fruit production. For example, clonally propagated perennials undergoing domestication have shifted from unisexual flowers to bisexual flowers (e.g., carob, grape) and from dioecy to monoecy (e.g., black pepper [*Piper nigrum* L.]). Papaya includes dioecious, gynodioecious, and andromonoecious cultivars, but it is unclear if variation in reproductive biology evolved as a result of human selection or if it was present in the wild ancestors (Storey, 1976a; Niklas and Marler, 2007). Some cultivated perennials have evolved from producing fruit through sexual reproduction in the wild to parthenocarpic fruit production in cultivation (e.g., banana [*Musa* L. spp.], fig, jocote [*Spondias purpurea* L.], pear, pistachio). Other perennial species have evolved self-compatibility under domestication (e.g., almond, grape, plum; Table 2). Domesticated perennials and their wild relatives provide outstanding model systems for understanding the evolution of plant mating systems when clonal reproduction is common (Vallejo-Marín et al., 2010), although to date few comparative analyses have been conducted (Otero-Arnaiz et al., 2003).

In addition to changes in breeding system and mode of reproduction, the domestication of perennials has resulted in changes in inflorescence, seed, and fruit characteristics (Table 1). In many ways, evolutionary changes in domesticated perennials mirror features that have evolved during the domestication of annual crops (Harlan et al., 1973; Zeven and deWet, 1982; Hammer, 1984; Harlan, 1992; Hancock, 2004; Glémin and Bataillon, 2009; Purugganan and Fuller, 2009). For example, relative to their wild progenitors, both annuals and perennials have less toxic seeds with higher oil content and lower rates of dormancy. In addition, domesticated annuals and perennials exhibit larger fruits that are more variable in color, taste, and other traits related to human preferences (Table 1).

Despite these similarities, some morphological features traditionally associated with the domestication syndrome of annual plants either do not occur in perennials or have not (to our knowledge) been recorded for perennials (Table 1). For example, the number of inflorescences in annual crops is greater in cultivated populations than in wild, and under domestication, sterile flowers found in wild populations have become fertile. Further, the inflorescences of many domesticated annuals remain intact, while those of their wild ancestors shatter when ripe. Although plausible, it is unclear whether similar changes have occurred in domesticated perennials. Conversely, some perennial crops have reproductive features that are not found in annual crops; notably, domesticated perennials have higher oil content in nonseed parts of the fruit and thinner shells than do their wild progenitors.

Evolution of vegetative traits—Although the primary focus of selection in fruit crops has been reproductive structures, changes in vegetative traits have occurred during the domestication process as well (Table 1). Like some annual crops, domesticated perennials exhibit a reduction in their defensive structures relative to their wild progenitors. A common vegetative feature of domesticated perennials is dwarfism, which has been documented in avocado (*Persea americana* Mill.), castor (*Ricinus communis* L.), coconut (*Cocos nucifera* L.), and numerous Rosaceae crops;

TABLE 2. Some domesticated perennial fruit crops, their putative regions of origin(s), hybridization history, breeding systems in wild and cultivated populations (where known), method(s) of propagation (clonal, seed), and ploidy level. For breeding systems, the breeding system(s) found in nature is listed; if variations in breeding system have been identified in cultivated populations, those are listed in parentheses following the natural breeding system of each species. For propagation method, both clonal and seed propagation methods are listed. Methods of clonal reproduction includes air layering, cuttings, grafting, or nucellar embryony. Seed production can result from cross-fertilization or self-fertilization. The most commonly used method of propagation is listed first; less common methods follow in parentheses. In cases where there are multiple methods of propagation but none predominates, the methods of propagation are listed alphabetically. Here, cultivars are abbreviated as "cvs."

Species (Family)	Common name	Region of origin (no. of origins)	No. of origins	Hybridization, origin, ongoing gene flow with relatives	Breeding system (breeding system in cultivated pops., if different from native pops.)	Propagation: primary (secondary)	Ploidy of cultivated pops.	References
<i>Actinidia delictosa</i> (A. Chev.) C. F. Liang & A. R. Ferguson (Actinidiaceae)	Kiwifruit	China	1	Allopolyploid origin, <i>A. chinensis</i> Planch. <i>A. chinensis</i> X?	Dioecious	Clonal: rooted cuttings, grafting; (seed)	6n = 164	Atkinson et al., 1997; Lyle, 2006
<i>Anacardium occidentale</i> L. (Anacardiaceae)	Cashew	Central Brazil	?	?	Andromonoecious	Clonal: grafting, cutting; (seed)	2n = 24, 30, 40, 42	Mitchell, 1987; Janick and Paull, 2008; S. Pell and J. Mitchell, personal communication
<i>Annona cherimola</i> Miller (Annonaceae)	Custard apple, cherimoya	South America (Peru, Ecuador)	?	Hybridizes with <i>A. squamosa</i> L.	Bisexual flowers; flowers dichogamous, generally self-incompatible	Seed: outcrossed; (clonal propagation difficult)	?	Perfecti and Pascual, 2004; Lyle, 2006; Janick and Paull, 2008
<i>Annona squamosa</i> L. × <i>A. cherimola</i> Miller (Annonaceae)	Atemoya	South America	?	Hybrid origin	Bisexual; self-compatible	Clonal: cuttings, grafting; (seed)	?	Lyle, 2006
<i>Artocarpus heterophyllus</i> Lam. (Moraceae)	Jackfruit	Western Ghats, India	?	Cvs. have been crossed with <i>A. integer</i> Merr.	Monoecious	Seed: outcrossed; (clonal: rooted or grafted cuttings)	2n = 2x = 56	Lyle, 2006; N. Zerega, personal communication
<i>Artocarpus</i> spp. (<i>A. altilis</i> (Parkinson) Fosberg) and <i>A. altilis</i> × <i>A. mariannensis</i> Trécul (Moraceae)	Breadfruit	Melanesia/Polynesia; Micronesia	At least 2	<i>A. altilis</i> : domesticated from <i>A. camansi</i> Blanco, hybridized with <i>A. mariannensis</i> in Micronesia	Monoecious (parthenocarpic cvs.)	Seed: outcrossed; (clonal: rooted or grafted cuttings, or air layering)	2n = 3x = ~84; 2n = 2x = 56	Zerega et al., 2004, 2006; N. Zerega, personal communication
<i>Asimina triloba</i> (L.) Dunal (Annonaceae)	Pawpaw	North America	?	?	Bisexual flowers, strongly protogynous, self-compatible (self-compatible cvs.)	Clonal: budding, grafting; (seed)	?	Lyle, 2006; Janick and Paull, 2008
<i>Averrhoa carambola</i> L. (Oxalidaceae)	Starfruit, Carambola	Southeast Asia	?	?	Bisexual, heterostylous	Clonal: grafting; (seed, outcrossed)	2n = 22 or 24	Lyle, 2006; Janick and Paull, 2008
<i>Carica papaya</i> L. (Carcaceae)	Papaya	Eastern Central American lowlands	?	?	Bisexual (self-compatible); dioecious (parthenocarp); or monoecious with bisexual flowers	Seed: outcrossed; (clonal: rooted cuttings)	2n = 2x = 18	Storey, 1976a; Lyle, 2006; Janick and Paull, 2008; Ming et al., 2008
<i>Carya illinoensis</i> (Wangenh.) K. Koch. (Juglandaceae)	Pecan	North America	Multiple	Hybridizes with <i>C. aquatica</i> (F. Michx.) Nutt., <i>C. cordiformis</i> (Wangenh.) K. Koch, and <i>C. laciniata</i> (F. Michx.) Loudon	Monoecious, heterodichogamous; generally self-incompatible	Clonal: grafting, cuttings; (seed: outcrossed)	2n = 2x = 32	Manos and Stone, 2001; Grauke et al., 2011
<i>Casimiroa edulis</i> La Llave (Rutaceae)	White Sapote	Mesoamerica	?	?	Bisexual, sometimes functionally unisexual, self-incompatible (some self-compatible cvs.)	Seed; (clonal: grafting onto three-year old seedlings)		Lyle, 2006; Janick and Paull, 2008

TABLE 2. Continued.

Species (Family)	Common name	Region of origin (no. of origins)	No. of origins	Hybridization, origin, ongoing gene flow with relatives	Breeding system (breeding system in cultivated pops., if different from native pops.)	Propagation: primary (secondary)	Ploidy of cultivated pops.	References
<i>Castanea sativa</i> Mill. (Fagaceae)	European Chestnut	Northeast Turkey and Caucases?	?	Hybridize readily	Monoecious, dichogamous	Seed; (clonal: grafting)	$2n = 2x = 24$	Mattioni et al., 2008; Conedera et al., 2004; Lang et al., 2007; Ivanova and Vladimirov, 2007
<i>Ceratonia siliqua</i> L. (Fabaceae)	Carob	Middle East	?	?	Dioecious (bisexual cvs.)	Clonal: scion grafting, budding, or cuttings; (seed: outcrossed)	?	Zohary and Hopf, 2000; Lyle 2006; Janick and Paull, 2008
<i>Citrus aurantiifolia</i> (Christm.) Swingle	Mexican lime	?	?	Hybrid origin: <i>C. medica</i> L. × <i>C. grandis</i> (L.) Osbeck × <i>Microcitrus</i> Swingle spp.	Bisexual, self-compatible (nucellar embryony and polyembryony)	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Lyle, 2006; Janick and Paull, 2008
<i>Citrus aurantium</i> L. (Rutaceae)	Sour oranges	?	?	Hybrid origin: <i>C. reticulata</i> Blanco × <i>C. grandis</i>	Apomixis	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Janick and Paull, 2008
<i>Citrus clementina</i> Hort. Ex Tan (Rutaceae)	Clementine	Algerian orphanage	1	Product of uncontrolled, unknown cross		Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Bretó et al., 2001; Janick and Paull, 2008
<i>Citrus grandis</i> (L.) Osbeck (Rutaceae)	Pummelo	Southeast Asia	?	Hybridizes regularly with congeners	Monoembryonic; outcrossing, some selfing clones	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Janick and Paull, 2008
<i>Citrus limon</i> (L.) Osbeck (Rutaceae)	Lemon, lime	Southeast Asia	?	Hybrid origin: <i>C. medica</i> × <i>C. grandis</i> × <i>Microcitrus</i> spp.?	Bisexual (self-compatible)	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Lyle, 2006; Janick and Paull, 2008
<i>Citrus medica</i> L. (Rutaceae)	Citron	?	?	Hybridizes readily; parent of <i>C. aurantiifolia</i> and <i>C. limon</i> (L.) Osbeck	Bisexual, some andromonoecious	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Lyle, 2006; Janick and Paull, 2008
<i>Citrus paradisi</i> Macfad. (Rutaceae)	Grapefruit	Southeast Asia or West Indies	?	Hybrid origin: <i>C. sinensis</i> (L.) Osbeck × <i>C. grandis</i>	Bisexual, self-compatible	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Lyle, 2006; Janick and Paull, 2008
<i>Citrus reticulata</i> Blanco (Rutaceae)	Mandarin orange	Asia	?	Hybridizes readily; parent of <i>C. aurantium</i> L., <i>C. sinensis</i>	Bisexual (self-compatible); monoembryonic and polyembryonic clones; parthenocarpic clones	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Lyle, 2006; Janick and Paull, 2008

TABLE 2. Continued.

Species (Family)	Common name	Region of origin (no. of origins)	No. of origins	Hybridization, origin, ongoing gene flow with relatives	Breeding system (breeding system in cultivated pops., if different from native pops.)	Propagation: primary (secondary)	Ploidy of cultivated pops.	References
<i>Citrus sinensis</i> Osbeck (Rutaceae)	Sweet orange (common/blond, acidless, blood, navel)	?	?	Hybrid origin: <i>C. reticulata</i> × <i>C. grandis</i>	Bisexual, self-compatible; nucellar embryony	Clonal: budding, layering, grafting, top-working; (seed: cross-pollinated, nucellar embryony)	?	Moore, 2001; Janick and Paull, 2008
<i>Cocos nucifera</i> L. (Arecaceae)	Coconut	Pacific Ocean Basin, Indian Ocean Basin	2	None known	Monoecious, outcrossing (selfing)	Seed	$2n = 2x = 32$	Whitehead, 1976; Gunn, 2004; K. Olsen, personal communication
<i>Coffea arabica</i> L. (Rubiaceae)	Coffee	Ethiopia	?	Hybrid origin from <i>C. canephora</i> Pierre ex A. Froehner and <i>C. eugenioides</i> S. Moore	Bisexual flowers, self-compatible	Seed; (clonal: cuttings, grafting)	Allotetraploid; $2n = 4x = 44$	Ferwerda, 1976; Anthony et al., 2002; Maurin et al., 2007
<i>Corylus avellana</i> L. (Betulaceae)	Hazelnut	Mediterranean, Turkey, Iran	3	In native populations, with <i>C. colurna</i> L. and <i>C. maxima</i> Mill.	Monoecious, heterodichogamous; generally self-incompatible (some self-compatible cvs.)	Clonal: rhizomes, layering, or grafting; (seed: outcrossed primarily)	$2n = 22$	Pomper et al., 1998; Palmé and Vendramin, 2002; Persson et al., 2004; Lyle, 2006; Boccecci and Botta, 2009
<i>Diospyros digyna</i> Jacq. (Ebenaceae)	Black sapote	Mesoamerica	?	?	Bisexual flowers, male flowers; (parthenocarpic fruit development)	Seed; (clonal: grafting) ?	?	Lyle, 2006
<i>Diospyros kaki</i> Thunb. (Ebenaceae)	Persimmon	China	?	?	Monoecious, dioecious, polygamomonocious (hermaphroditic flowers, parthenocarpic fruit production)	Clonal: grafting; (seed) $2n = 6x = 90$	$2n = 6x = 90$	Tamura et al., 1998; Lyle, 2006; Janick and Paull, 2008
<i>Diospyros virginiana</i> L. (Ebenaceae)	North American Persimmon	North America	?	?	Dioecious	Clonal: cuttings or suckers	$2n = 6x = 90$	Lyle, 2006
<i>Elaeis guineensis</i> Jacq. (Arecaceae)	Oil palm	West Africa	1	Interspecific hybridization for crop improvement	Monoecious	Seed: outcrossed	$2n = 2x = 32$	Hardon, 1976
<i>Ficus carica</i> (Moraceae)	Fig	Middle East, Lower Jordan Valley	1	Hybridization with wild ancestors in the Mediterranean region	Gynodioecious; parthenocarpic fruit development in native and cultivated populations	Clonal: cuttings or grafting; (seed)	$2n = 2x = 26$	Storey, 1976b; Zohary and Hopf, 2000; Kislev et al., 2006a; Lyle, 2006
<i>Juglans regia</i> L. (Juglandaceae)	Walnut	Southwest Asia	?	Interspecific hybridization with <i>J. sigillata</i> Dode	Monoecious, dichogamous	Seed: outcrossed; (clonal: grafting)	$2n = 2x = 32$	Zohary and Hopf, 2000; Manos and Stone 2001; Gunn et al., 2010
<i>Leucaena</i> spp. Benth. (Fabaceae)		Mesoamerica	Multiple origins of <i>L. leucocephala</i> (Lam.) de Wit.	Several cultivated allopolyploid species	Bisexual	Seed	Variable	Zaraté, 2005; Hughes et al., 2007; C. Romero-Hernandez, personal communication
<i>Litchi chinensis</i> Sonn. (Sapindaceae)	Lychee	Southern China	?	?	Monoecious, dichogamous	Seed: outcrossed; (clonal: layering)	?	Lyle, 2006

TABLE 2. Continued.

Species (Family)	Common name	Region of origin (no. of origins)	No. of origins	Hybridization, origin, ongoing gene flow with relatives	Breeding system (breeding system in cultivated pops., if different from native pops.)	Propagation: primary (secondary)	Ploidy of cultivated pops.	References
<i>Malus × domestica</i> Borkh. (Rosaceae)	Apple	Central Asia	Unknown	Ongoing with <i>M. sylvestris</i> Mill. and other <i>Malus</i> species	Bisexual flowers, self-incompatible	Clonal: grafting since 3800 BC; (seed: outcrossed)	$2n = 2x = 34$; some $3x$ cvs.	Watkins, 1976a; Harris et al., 2002; Coart et al., 2006; Kron and Husband, 2009
<i>Mangifera indica</i> L. (Anacardiaceae)	Mango	Northeastern India	?	?	Andromonoecious; self-incompatible; monoembryonic and polyembryonic	Seed: nucellar embryony; (clonal: grafting)	$2n = 2x = 40$	Singh, 1976; Mukherjee, 1997; Iyer and Degani, 1997; Janick and Paul, 2008
<i>Manilkara zapota</i> (L.) P. Royen (Sapotaceae)	Sapodilla, Chicozapote	Mesoamerica	?	?	Bisexual flowers, self-incompatible	Clonal: layering or grafting; seed: outcrossing	?	Lyle, 2006; Janick and Paul, 2008
<i>Musa</i> L. spp. (Musaceae)	Banana	Southeast Asia (Malay Penn.)	Multiple	Hybrid origin: <i>M. acuminata</i> Coll. × <i>M. balbisiana</i> Colla	Monoecious; (sterile, fruit production via parthenocarpy)	Clonal: corm cuttings	Wild species $2n = 2x = 22$; most cvs. $2n = 3x = 33$	Simmonds, 1976; Heslop-Harrison and Schwarzscher, 2007
<i>Olea europaea</i> L. subsp. <i>europaea</i> var. <i>europaea</i> (Oleaceae)	Olive	Near East, western Mediterranean Basin	≥2	Hybridization with wild olives (oleasters)	Andromonoecious, self-compatible or self-incompatible	Clonal: cuttings or grafting	$2n = 2x = 46$	Besnard and Bervillé, 2000; Baldoni et al., 2006; Breton et al., 2006
<i>Persea americana</i> Mill. (Lauraceae)	Avocado	Mesoamerica	?	Hybridization with <i>P. schiedeana</i> Nees. and <i>P. parviflora</i> Spreng.	Bisexual flowers; heterodichogamous	Clonal: grafting; (seed: outcrossed)	$2n = 2x = 24$	Lahav and Lavi, 2002; Lyle, 2006
<i>Phoenix dactylifera</i> L. (Arecaceae)	Date palm	Northern Africa?	?	Ongoing with <i>P. canariensis</i> Hort. Ex Chabaud, <i>P. reclinata</i> Jacq., <i>P. sylvestris</i> (L.) Roxb. ?	Dioecious; (hermaphroditic flowers)	Clonal: suckers (seed: outcrossed)	$2n = 2x = 36$	Zohary and Hopf, 2000; Chao and Krueger, 2007; González-Pérez et al., 2004
<i>Pistacia vera</i> L. (Anacardiaceae)	Pistachio	South Central Asia	?	?	Dioecious (parthenocarpic fruit development)	Clonal: grafting; (seed: outcrossed)	$2n = 2x = 30$	Golan-Goldhirsh et al., 2004; Yi et al., 2008; Shanjani et al., 2009
<i>Polaskia chichipe</i> (Rol.-Goss.) Backeb. (Cactaceae)	Chichipe	Mesoamerica		With wild <i>P. chichipe</i> populations	Bisexual, outcrossing (self-compatible)	Clonal: planted branches; seed		Otero-Arnaiz et al., 2003, 2005a, b
<i>Prunus armeniaca</i> L. (Rosaceae)	Apricot	Northeastern China	2 (western China, western Asia)	?	Bisexual flowers, self-compatible or self-incompatible	Clonal: grafting (seed: selfed or outcrossed)	$2n = 16$	Darwin, 1899; Watkins, 1976b; Singh, 2003; Zhebentyayeva et al., 2003; Maghuly et al., 2005; Khadari et al., 2006; Lyle, 2006; He et al., 2007;
<i>Prunus avium</i> (L.) L. (Rosaceae)	Sweet Cherry	Europe, northern Africa	?	No	Bisexual flowers, self-incompatible	Clonal: grafting onto wild rootstocks; (seed: outcrossed)	$2n = 2x = 16$	Watkins, 1976b; Tavaud et al., 2004; Cottrell et al., 2009
<i>Prunus cerasus</i> L. (Rosaceae)	Sour cherry	Eurasia	?	No	Bisexual flowers, self-incompatible (self-compatible)	Clonal: grafting; (seed: outcrossed)	$2n = 4x = 32$	Watkins, 1976b; Tavaud et al., 2004; Lyle, 2006

TABLE 2. Continued.

Species (Family)	Common name	Region of origin (no. of origins)	No. of origins	Hybridization, origin, ongoing gene flow with relatives	Breeding system (breeding system in cultivated pops., if different from native pops.)	Propagation: primary (secondary)	Ploidy of cultivated pops.	References
<i>Prunus domestica</i> L. (Rosaceae)	European plum	Eurasia	?	All plums are interfertile and are used in common breeding programs	Bisexual flowers, self-compatible and self-incompatible	Clonal: grafting; (seed) selfed, outcrossed	$2n = 6x = 48$	Watkins, 1976b; Singh, 2003; Lyle, 2006; Janick and Paull, 2008
<i>Prunus dulcis</i> (Mill.) D. A. Webb (Rosaceae)	Almond	Eastern Mediterranean	?	Interfertile with <i>P. argentea</i> (Lam.) Rehder; <i>P. bucharica</i> Hand.-Mazz.; <i>P. mira</i> Koehne, <i>P. persica</i> , <i>P. scoparia</i> Schneider, and <i>P. webbii</i> Vierh.	Bisexual flowers; self-incompatible (some self-compatible cvs.)	Clonal: grafting; (seed) outcrossed or selfed	?	Watkins, 1976b; Gradziel et al., 2000; López et al., 2006; Ladizinsky, 1999; Browicz and Zohary, 1996
<i>Prunus persica</i> (L.) Batsch (Rosaceae)	Peach	Central Asia?	?	Hybridizes with species in subgenus <i>Amygdalus</i>	Bisexual flowers, mostly self-compatible (pollen-sterile cvs.)	Clonal: grafting; (seed) outcrossed or selfed	$2n = 16$	Watkins, 1976b; Tao et al., 2007; Abbott et al., 2008
<i>Prunus persica</i> var. <i>nucipersica</i> (Suckow) Dippel (Rosaceae)	Nectarine	China, western Asia	2	Hybridizes with species in subgenus <i>Amygdalus</i>	Bisexual flowers, mostly self-compatible	Clonal: grafting; (seed) self- or cross pollinated	$2n = 16?$	Watkins, 1976b; Lyle, 2006; Tao et al., 2007
<i>Psidium guajava</i> L. (Myrtaceae)	Guava	Mesoamerica, South America	?	?	Bisexual, some self- and cross-incompatible, some self-compatible	Clonal: grafting; (seed) (variable)	?	Lyle, 2006; Janick and Paull, 2008
<i>Punica granatum</i> L. (Punicaceae)	Pomegranate	Middle East	?	?	Bisexual flowers, self-fertile (some parthenocarpic cvs.)	Clonal: cuttings; (seed)	$2n = 2x = 16$, 18	Lyle, 2006; Sheikh, 2006
<i>Pyrus communis</i> L. (Rosaceae)	Pear	Western Asia	2	Ongoing with several congeners (<i>P. pyraeaster</i> (L.) Du Roi, <i>P. caucasica</i> Fed.)	Bisexual flowers, mostly self-incompatible	Clonal: grafting; (seed)	$2n = 2x = 34$; some $3x$ cvs.	Watkins, 1976a; Zohary and Hopf, 2000
<i>Ribes</i> L. spp. (Grossulariaceae)	Currants	Different species domesticated in different areas	8 cultivated species in 2 groups (red, black currants)	Extensive interspecific hybridization for crop improvement	Bisexual flowers, self-compatible or self-incompatible populations	Clonal: cuttings; (seed)	$2n = 2x = 16$	Keep, 1976
<i>Rubus idaeus</i> L. (Rosaceae)	Red raspberry	Northern Europe/Asia (1), North America (2)	3	Extensive interspecific hybridization for crop improvement	Outcrossing (self-compatible cvs.)	Clonal: cuttings; (seed)	Variable	Jennings, 1976; Lyle, 2006
<i>Rubus</i> L. spp. (Rosaceae)	Blackberry	Europe/Asia, Eastern North America, Western North America	3	Extensive interspecific hybridization for crop improvement	Bisexual, self-incompatible (some self-compatible cvs.)	Clonal: cuttings; (seed)	Variable	Jennings, 1976; Lyle, 2006
<i>Spondias purpurea</i> L. (Anacardiaceae)	Jocote, purple mombin, hogplum	Mesoamerica	At least 2	Ongoing hybridization with <i>S. mombin</i> L.	Dioecious (parthenocarpic fruit production)	Clonal: cuttings	$2n = 15$	Miller and Schaal, 2005, 2006
<i>Theobroma cacao</i> L. (Sterculiaceae)	Cacao, chocolate	Mesoamerica, Northern South America?	One	No	Bisexual flowers; self-incompatible near center of origin, self-compatible away from origin	Clonal in commercial cultivation; seed	$2n = 2x = 20$	Cope, 1976; Motamayor et al., 2002, 2003
<i>Vitis vinifera</i> L. subsp. <i>vinifera</i> (Vitaceae)	Grape	Near East between Black Sea and Caspian Sea	One	Extensive interspecific hybridization for crop improvement	Dioecious in the wild (bisexual, self-compatible flowers in cultivation)	Clonal: cuttings or grafting; (seed)	$2n = 2x = 38$	Mullins et al., 1992; Arroyo-García et al., 2006; This et al., 2006; Myles et al., 2011

this is similar in some ways to determinant growth, which has accompanied the domestication of many annuals. Finally, polyploid crops have evolved from diploid progenitors in both annual and perennial plant species.

ORIGINS AND EVOLUTION OF PERENNIAL FRUIT CROPS

Understanding the ways in which tree populations respond to artificial selection may shed light on how long-lived species evolve in response to short-term evolutionary pressures in general. Slow rates of evolution under domestication are expected in perennial crops relative to annuals due to fewer sexual cycles per unit time, the result of long juvenile phases and clonal propagation (Zeder et al., 2006). Relative rates of evolution of annual fruit crops vs. perennial fruit crops are difficult to characterize; however, it is clear that some perennial fruit crops have been responding to artificial selection pressures for as long as annuals (e.g., fig; Kislev et al., 2006a, but see Lev-Yadun et al., 2006 and Kislev et al., 2006b), and in many aspects, they have evolved under domestication in comparable ways (see discussion above; Table 1). In this section, we examine the effect of domestication on genetic variation in cultivated populations. We quantify domestication bottlenecks in perennial crops by comparing levels of genetic variation in cultivated and wild populations. We then consider how changes in reproductive biology, evolutionary history of cultivated populations, and hybridization influence the extent of genetic variation housed in cultivated populations of perennial fruit crops.

Domestication bottlenecks in perennial fruit crops—Current research on domestication bottlenecks conducted in annual fruit crops suggests that only a subset of the total number of individuals in a wild species is initially brought into cultivation (Doebley et al., 2006). This limited sampling results in a genetic bottleneck (a reduction in genetic variation across the genome, including neutral variation) in cultivated populations relative to their wild progenitors (Olsen and Gross, 2008). Over time, the genetic base of cultivated populations narrows as superior individuals are selectively propagated, to the point where as a group, elite cultivars can be genetically depauperate (e.g., Yamasaki et al., 2005; Hyten et al., 2006). Genetic bottlenecks in annual fruit crops result in cultivated populations that retain an average of 59.9% (ranging from 5.5 to 119.5%) of the neutral variation found in wild populations (Table 3).

Do perennial fruit crops exhibit the same type of genetic bottleneck observed in annual plants? Comparative analyses of perennial fruit crops and their wild progenitors demonstrate that cultivated perennial fruit crops retain an average of 94.8% of the neutral variation found in wild populations. Data derived from codominant markers (allozymes, microsatellites) reveal that cultivated perennial populations retain at least 64.8% and up to 126.9% of the variation found in wild populations [pecan: Rüter et al., 1999; *Inga edulis* Mart.: Hollingsworth et al., 2005; red guaje, *Leucaena esculenta* (Moc. & Sessé ex DC.) Benth.: Zárate et al., 2005; apple: Coart et al., 2003; olive: Lumaret et al., 2004; *Polaskia chichipe* (Gosselin) Backeb.: Otero-Arnaiz et al., 2005a; sweet cherry: Mariette et al., 2010; grape: Aradhya et al., 2003]. Similarly, in studies using dominant marker data (AFLPs, ISSRs) cultivated perennials retained at least 62.5% and at most 117.8% of the variation found in wild populations (chestnut, *Castanea sativa* Mill.: Mattioni et al.,

2008; apple: Coart et al., 2003; pistachio: Shanjani et al., 2009; jocote: Miller and Schaal, 2006). In summary, these studies show that perennial fruit crops maintain a greater proportion of total genetic variation in cultivation than annual crops (Table 3; Fig. 1). In the cases of some more recently domesticated perennial fruit crops, the reduction in genetic variation is likely due to selective propagation of some individuals in a cultivated setting, rather than to many generations of selective breeding that could more appropriately be termed a “domestication bottleneck”. The conclusions are similar, however, if we restrict our survey to the older perennial fruit crops such as apple, olive, grapevine, and pistachio—these crops have retained an average of 94.6% of the genetic diversity present in their wild relatives (Coart et al., 2003; Lumaret et al., 2004; Aradhya et al., 2003; Shanjani et al., 2009).

In some cases, elevated levels of genetic variation were recorded for crops relative to their wild ancestors. This may be an artifact of insufficient sampling of wild populations, or it may reflect loss of wild plants following the establishment of cultivated populations due to habitat destruction or extinction for other reasons. Another possible explanation is that cultivated populations represent the descendants of controlled crosses between geographically and genetically distinct individuals, which may have yielded new variants carrying novel combinations of alleles not found in the wild. Similar patterns have been observed in introduced lizard populations where genetic variation exceeds variability observed in native (source) populations (Kolbe et al., 2004). Alternatively (or in addition), somatic mutations in clonally propagated cultivars may contribute to elevated levels of genetic variation in cultivated perennial fruit crops relative to their wild progenitors.

Note that comparisons between perennial and annual fruit crop domestication bottlenecks are complicated by the fact that most data for annual crop domestication bottlenecks comes from cereals [barley; maize; pearl millet, *Pennisetum glaucum* (L.) R. Br.; rice; sorghum, *Sorghum bicolor* (L.) Moench; wheat]. Additional information comes from *Phaseolus* L. species, soybean (*Glycine soja* Siebold & Zucc.), sunflower, and chile (Table 3). While it would be interesting to compare studies of long-lived, perennial fruit crops with domestication bottlenecks in more equivalent annual domesticates [e.g., eggplant, melon (*Cucumis melo* L.), squash (*Cucurbita pepo* L.), tomato], comparable studies quantifying reductions in diversity associated with domestication are not, to our knowledge, available in the literature. The apparent lack of information results in some cases from ambiguity concerning the identity of the wild progenitors of the cultivated populations or because the wild ancestors were only recently identified. For some species, population genetics analyses have not yet been completed—this is true in cucumber (*Cucumis sativus* L.; Sebastian et al., 2010), eggplant (Weese and Bohs, 2010; Tümbilen et al., 2011), melon (Luan et al., 2008; Sebastian et al., 2010), tomato (Bai and Lindhout, 2007; Peralta and Spooner, 2007; Labate et al., 2009; but see Nesbitt and Tanksley, 2002 for a candidate locus analysis), and squashes, pumpkins, and gourds (Sanjurjo et al., 2002; Paris et al., 2003; Sikdar et al., 2010). Comparative analyses of genetic variation housed in cultivated populations of these species and their wild progenitors represent promising areas of future research.

Overall, even with the aforementioned caveats, perennial crops retain a greater proportion of the genetic variation present in their wild progenitors than annual crops (Table 3, Fig. 1). A number of factors likely contribute to differences in the width

TABLE 3. Genetic bottlenecks resulting from domestication in annual and perennial fruit crops. When diversity measures for both landrace and elite domesticated (Dom.) varieties were reported, we included only the landrace value, to more accurately represent the initial domestication event. For consistency, we used θ_{land} or H_e in our calculations whenever they were reported in the paper and otherwise used whatever measure of diversity was available in the paper. When species names are followed by a geographic designation (e.g., “Andean”), the values are representative of one of multiple domestication events.

Common name	Wild species	Wild diversity	Domesticated species	Dom. diversity	Measure	% Retained	Reference
Annual fruit crops							
Barley	<i>Hordeum vulgare</i> L. subsp. <i>spontaneum</i> (K. Koch) Asch. & Graebn.	0.0144	<i>Hordeum vulgare</i> L. subsp. <i>vulgare</i> landrace	0.0050	θ_{land}	34.9	Caldwell et al., 2006
Bean (common bean)	<i>Phaseolus vulgaris</i> L. Andean	0.530	<i>Phaseolus vulgaris</i> Andean	0.480	H_e SSRs	90.6	Kwak and Gepts, 2009
Bean (common bean)	<i>Phaseolus vulgaris</i> L. Andean	0.100	<i>Phaseolus vulgaris</i> Andean	0.050	H_e AFLPs	50.0	Papa and Gepts, 2003
Bean (common bean)	<i>Phaseolus vulgaris</i> Mesoamerica	0.570	<i>Phaseolus vulgaris</i> Mesoamerica	0.510	H_e SSRs	89.5	Kwak and Gepts, 2009
Bean (common bean)	<i>Phaseolus vulgaris</i> Mesoamerica	0.240	<i>Phaseolus vulgaris</i> Mesoamerica	0.150	H_e AFLPs	62.5	Papa and Gepts, 2003
Bean (common bean)	<i>Phaseolus vulgaris</i> Mexico	0.220	<i>Phaseolus vulgaris</i> Mexico	0.140	H_e AFLPs	63.6	Papa and Gepts, 2003
Bean (lima bean)	<i>Phaseolus lunatus</i> L. var. <i>silvester</i> Baudet	0.0069	<i>Phaseolus lunatus</i> var. <i>lunatus</i> Andean	0.0029	π_{land}	41.5	Motta-Aldana et al., 2010
Bean (lima bean)	<i>Phaseolus lunatus</i> var. <i>silvester</i> Mesoamerican	0.0028	<i>Phaseolus lunatus</i> var. <i>lunatus</i> Mesoamerican	0.0014	π_{land}	52.4	Motta-Aldana et al., 2010
Bean (scarlet runner bean)	<i>Phaseolus coccineus</i> L.	0.500	<i>Phaseolus coccineus</i>	0.550	H_e SSRs	110.0	Spataro et al., 2011
Chile	<i>Capsicum annuum</i> L. var. <i>glabriusculum</i> (Dunal) Heiser & Pickersgill	0.0026	<i>Capsicum annuum</i> var. <i>annuum</i>	0.0023	π_{land}	91.0	Aguilar-Meléndez et al., 2009
Chile	<i>Capsicum annuum</i> var. <i>glabriusculum</i>	0.165	<i>Capsicum annuum</i> var. <i>annuum</i>	0.131	H_T RAPDs	79.4	Oyama et al., 2006
Maize	<i>Zea mays</i> subsp. <i>parviglumis</i> H. H. Iltis & Doebley	0.0211	<i>Zea mays</i> L. subsp. <i>mays</i>	0.0131	π_{divent}	62.0	Tenaillon et al., 2004
Maize	<i>Zea mays</i> subsp. <i>parviglumis</i>	0.0109	<i>Zea mays</i> subsp. <i>mays</i>	0.0063	θ_{land}	57.5	Wright et al., 2005
Pearl millet	<i>Pennisetum glaucum</i> R. Br. subsp. <i>monodii</i>	0.0036	<i>Pennisetum glaucum</i>	0.0024	θ_{land}	66.7	Gaut and Clegg, 1993
Rice (African)	<i>Oryza barthii</i> A. Chev.	0.0021	<i>Oryza glaberrima</i> Steud.	0.0005	θ_{land}	23.8	Li et al., 2011
Rice (Asian)	<i>Oryza rufipogon</i> Griff	0.0037	<i>Oryza sativa</i> L.	0.0021	θ_{land}	57.0	Caicedo et al., 2007
Rice (Asian)	<i>Oryza rufipogon</i>	0.0037	<i>Oryza sativa</i> subsp. <i>indica</i> S. Kato	0.0016	θ_{land}	42.7	Caicedo et al., 2007
Rice (Asian)	<i>Oryza rufipogon</i>	0.0082	<i>Oryza sativa</i> subsp. <i>indica</i>	0.0020	θ_{land}	24.5	Zhu et al., 2007
Rice (Asian)	<i>Oryza rufipogon</i>	0.0037	<i>Oryza sativa</i> subsp. <i>japonica</i> S. Kato	0.0012	θ_{land}	33.2	Caicedo et al., 2007
Rice (Asian)	<i>Oryza rufipogon</i>	0.0082	<i>Oryza sativa</i> subsp. <i>japonica</i>	0.0010	θ_{land}	12.3	Zhu et al., 2007
Sorghum	<i>Sorghum bicolor</i> (L.) Moench subsp. <i>verticilliflorum</i> (Steud.) de Wet ex Wiersma & J. Dahlb.	0.590	<i>Sorghum bicolor</i> subsp. <i>bicolor</i> (all landraces)	0.510	H_e SSRs	86.4	Casa et al., 2005
Soybean	<i>Glycine soja</i> Siebold & Zucc.	0.0024	<i>Glycine max</i> (L.) Merr. landrace	0.0012	θ_{land}	48.9	Hyten et al., 2006
Soybean	<i>Glycine soja</i>	0.3090	<i>Glycine max</i> landrace	0.3440	π_{land}	111.3	Li et al., 2010
Soybean	<i>Glycine soja</i>	0.871	<i>Glycine max</i> landrace	0.682	H_e SSRs	78.3	Li et al., 2010
Sunflower	<i>Helianthus annuus</i> L.	0.0144	<i>Helianthus annuus</i>	0.0072	θ_{land}	50.0	Liu and Burke, 2006
Sunflower	<i>Helianthus annuus</i>	0.817	<i>Helianthus annuus</i> landrace	0.638	H_e SSRs	78.1	Tang and Knapp, 2003
Sunflower	<i>Helianthus annuus</i>	0.0128	<i>Helianthus annuus</i> elite	0.0094	θ_{land}	73.4	Kolkman et al., 2007
Wheat (bread wheat)	<i>Triticum turgidum</i> subsp. <i>tauschii</i>	0.0211	<i>Triticum turgidum</i> subsp. <i>aestivum</i> (D genome)	0.0012	θ_{land}	5.5	Caldwell et al., 2004
Wheat (einkorn wheat)	<i>Triticum monococcum</i> subsp. <i>boeoticum</i> (Boiss.) C. Yen	0.0035	<i>Triticum monococcum</i> L. subsp. <i>monococcum</i>	0.0025	θ_{land}	71.0	Kilian et al., 2007
Wheat (einkorn wheat)	<i>Triticum monococcum</i> subsp. <i>boeoticum</i> (race β)	0.0021	<i>Triticum monococcum</i> subsp. <i>monococcum</i>	0.0025	θ_{land}	119.5	Kilian et al., 2007
Wheat (emmer wheat)	<i>Triticum turgidum</i> subsp. <i>dicoccoides</i> (Körn.) Thell.	0.0035	<i>Triticum turgidum</i> subsp. <i>dicoccum</i>	0.0013	θ_{land}	35.5	Haudry et al., 2007
Wheat (emmer wheat)	<i>Triticum turgidum</i> subsp. <i>dicoccoides</i>	0.0035	<i>Triticum turgidum</i> subsp. <i>durum</i>	0.0005	θ_{land}	14.8	Haudry et al., 2007
Annual mean							
							59.9
Perennial fruit crops							
Pecan	<i>Carya illinoensis</i> (Wangerh.) K. Koch.	0.167	<i>Carya illinoensis</i>	0.153	H_e allozymes	91.6	Rüter et al., 1999
Red guaje	<i>Leucaena esculenta</i> (Moc. & Sessé ex DC.) Benth.	0.264	<i>Leucaena esculenta</i>	0.335	H_e allozymes	126.9	Zárate et al., 2005
Apple	<i>Malus sylvestris</i> Mill.	0.721	<i>Malus \timesdomestica</i> Borkh.	0.775	H_e SSRs	107.5	Coart et al., 2003
Apple	<i>Malus sylvestris</i>	0.225	<i>Malus \timesdomestica</i>	0.265	H_e AFLPs	117.8	Coart et al., 2003
Olive	<i>Olea europaea</i> L. subsp. <i>europaea</i> var. <i>sylvestris</i>	0.449	<i>Olea europaea</i> L. subsp. <i>europaea</i> var. <i>europaea</i> Eastern	0.291	H_e allozymes	64.8	Lumaret et al., 2004

TABLE 3. Continued.

Common name	Wild species	Wild diversity	Domesticated species	Dom. diversity	Measure	% Retained	Reference
Olive	<i>Olea europaea</i> subsp. <i>europaea</i> var. <i>sylvestris</i>	0.449	<i>Olea europaea</i> subsp. <i>europaea</i> var. <i>europaea</i> Western	0.323	H_i , allozymes	71.9	Lumaret et al., 2004
Columnar cactus	<i>Polaskia chichipe</i> (Gosselin) Backeb.	0.683	<i>Polaskia chichipe</i>	0.660	H_e SSRs	96.6	Otero-Araiz et al., 2005b
Grape	<i>Vitis vinifera</i> L. subsp. <i>sylvestris</i>	0.682	<i>Vitis vinifera</i>	0.814	H_e SSRs	119.4	Aradhya et al., 2003
Chestnut	<i>Castanea sativa</i> Mill.	0.223	<i>Castanea sativa</i>	0.140	H ISSRs	62.5	Mattioni et al., 2008
Pistachio	<i>Pistacia vera</i> L.	0.220	<i>Pistacia vera</i> Iran	0.190	H AFLPs	86.4	Shanjani et al., 2009
Jocote	<i>Spondias purpurea</i> L.	0.187	<i>Spondias purpurea</i>	0.169	H AFLPs	90.7	Miller and Schaal, 2006
	<i>Inga edulis</i> Mart.	0.657	<i>Inga edulis</i>	0.673	H_e SSRs	102.4	Hollingsworth et al., 2005
Sweet cherry	<i>Prunus avium</i> L.	0.680	<i>Prunus avium</i>	0.640	H_e SSRs	94.1	Mariette et al., 2010
				Perennial mean		94.8	

of the genetic bottleneck accompanying annual and perennial domestication. For example, a principal difference between domesticated annual and domesticated perennial fruit crops is juvenile phase length. Differences in juvenile phase length mean that over similar time periods, domesticated perennials have fewer sexual cycles on which selection can act relative to annuals. Three additional factors likely play critical roles in shaping the amount and structure of neutral genetic variation in cultivated tree populations: (1) mating system and mode of reproduction, (2) geographic origins of cultivated individuals, and (3) intra- and interspecific hybridization. Recent studies addressing these topics in domesticated systems provide insights into their impact on neutral genetic variation, as discussed below.

Mating system and mode of reproduction—Mating system and mode of reproduction have been identified as primary determinants shaping the amount and structure of genetic variation in natural tree populations (Loveless and Hamrick, 1984; Hamrick and Godt, 1990; Hamrick et al., 1992; Duminil et al., 2007, 2009). Perennial fruit crops and the natural populations from which they were derived represent nearly the entire range of plant reproductive systems and include species with bisexual flowers, unisexual flowers, or a combination of the two (e.g., cashew, citron: *Citrus medica* L.; black sapote, *Diospyros digyna* Jacq.; mango, *Mangifera indica* L.). Species with bisexual flowers include plants that are self-compatible [e.g., atemoya, *Anona squamosa* L. × *A. cherimola* Miller; white sapote; lime, *Citrus aurantiifolia* (Christm.) Swingle; coffee, *Coffea arabica* L.; plum; peach; pomegranate; cacao, *Theobroma cacao* L.; grape], self-incompatible (e.g., custard apple: *Annona cherimola* Miller; apple, olive, sweet cherry, almond, pear), dichogamous [e.g., paw paw, *Asimina triloba* (L.) Dunal], heterodichogamous (avocado), or heterostylous (carambola: *Averrhoa carambola* L.). Other domesticated perennials grown for their fruits have unisexual flowers and are monoecious (e.g., breadfruit/jackfruit: *Artocarpus* J. R. Forst. & G. Forst. spp.; pecan, chestnut, coconut, hazelnut: *Corylus avellana* L., oil palm: *Elais guineensis* Jacq., fig, lychee: *Litchi chinensis* Sonn., banana, pistachio), or dioecious (e.g., carob, date palm, grape, jocote, persimmon: *Diospyros* L. spp.). More examples of each reproductive system are listed in Table 2. In addition, perennial fruit crops exhibit a range of pollination syndromes, including pollination by insects, birds, bats, and wind.

Mating system and pollination syndrome are important determinants of variation in natural populations; in cultivated populations, mode of reproduction also plays a critical role. Annual crops are mainly grown from seed; however, only a fraction of perennial fruit crops are primarily seed-propagated (e.g., black sapote, oil palm, *Leucaena* Benth., walnut; Table 2). Approximately 75% of domesticated trees are propagated primarily clonally through cuttings, layering, grafting, or nucellar embryony (seeds are genetically identical to the parent; Table 2).

Clonal propagation restricts the number of sexual cycles separating domesticated populations from their wild ancestors (Zohary and Spiegel-Roy, 1975; Zohary and Hopf, 2000; McKey et al., 2010). In the simplest domestication scenario, seeds or cuttings of one or a few individuals are taken from wild populations and transferred to a cultivated habitat, where they are maintained through clonal propagation. In this case, selection has occurred only once on a single sexual cycle, effectively isolating a favored variant that will increase in frequency with clonal reproduction. Many perennial species are highly heterozygous (Petit and Hampe, 2006); clonal propagation functions to maintain

Variation retained in domesticated populations

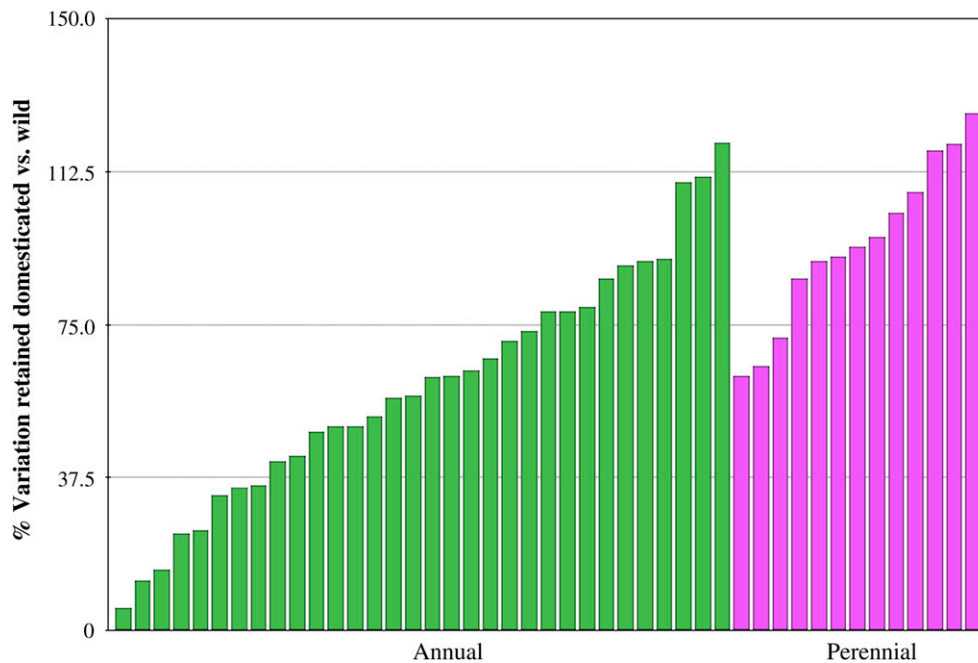


Fig. 1. Percentage of variation retained in domesticated annual and perennial fruit crop populations compared to their wild relatives (c.f. Table 3).

heterozygosity at the individual level (Zohary and Spiegel-Roy, 1975), but promotes genetic homogeneity at the population level.

In a more realistic scenario, domestication of perennials appears to have been a spatially and temporally dynamic process, where seeds and/or cuttings are removed from geographically distinct wild populations over the course of many hundreds or thousands of years. Once in cultivated settings, these individuals contribute to the domesticated pool either through directed breeding efforts characteristic of modern agriculture, or through inadvertent gene flow with other cultivated individuals. Cultivated individuals are still highly heterozygous under this scenario, but in this case clonal reproduction results in cultivated populations that are genetically heterogeneous because clones represent a broader sample of variation than is found in any one natural population (Fig. 2).

Evolutionary origins of domesticated tree populations—The geographic origins of crop plants have fascinated botanists for over a century (e.g., de Candolle, 1886; Harlan, 1971; Smith, 1995). Vavilov (1992) identified seven global centers of domestication where crop populations originated from native plant species, based on the geographic distributions of extant crops. Subsequent studies used archaeological and genetic data to pinpoint from five to 24 regions of origin (e.g., Gepts, 2004; Purugganan and Fuller, 2009). Early studies suggested that crops evolved once from native populations growing in a single geographic region (Vavilov, 1992), and several seed-propagated, annual crops conform to this expectation, including maize (Matsuoka et al., 2002), einkorn wheat (*Triticum monococcum* L.; Heun et al., 1997), soybean (Li et al., 2010), sunflower (Harter et al., 2004), and upland cotton (*Gossypium hirsutum* L.; Brubaker and Wendel, 1994). However, in a recent review

of crop evolution, roughly half of the 22 annual fruit crops for which geographical/genetic origins had been explicitly studied had either confirmed or potential multiple origins (see Table 1 of Burger et al., 2008). Examples of such crops include barley (Willcox, 2005; Fuller, 2007; Morrell and Clegg, 2007), Asian rice (Londo et al., 2006), common bean (Gepts et al., 1986; Sonnante et al., 1994; Chacón et al., 2005), and potentially one of the species of domesticated chile (Aguilar-Meléndez et al., 2009). The number of crops with multiple origins would be larger when considering multiple domestication events that occur within the same genus but result in different domesticated species; examples of these include the two species of domesticated cotton (*Gossypium hirsutum* and *G. barbadense* L.; Brubaker and Wendel, 1994; Westengen et al., 2005), domesticated Asian and African rice (*Oryza sativa* and *O. glaberrima* Steud.; Semon et al., 2005; Londo et al., 2006), multiple domesticated species of chiles (*Capsicum*; Pickersgill, 1997), chenopods (*Chenopodium* L.; Ruas et al., 1999; Smith, 2006), squashes and gourds (*Cucurbita* L.; Decker-Walters et al., 2002; Sanjur et al., 2002), and beans (*Phaseolus* L.; Gutiérrez Salgado et al., 1995; Chacón et al., 2005). Overall, our current understanding of annual crop domestication indicates that multiple origins are at least as likely as single origins.

The apparent number of domestication events has been addressed as part of a larger debate about the tempo of domestication (Tanno and Willcox, 2006; Allaby et al., 2008; Olsen and Gross, 2008; Ross-Ibarra and Gaut, 2008; Honne and Heun, 2009; Purugganan and Fuller, 2011). The rapid-transition model of domestication posits that domestication happens quickly and that most crop populations consist of individuals derived from one or two narrow geographic ranges. In contrast, the protracted model of domestication suggests that domestication takes place over an extended timeframe and that cultivated populations

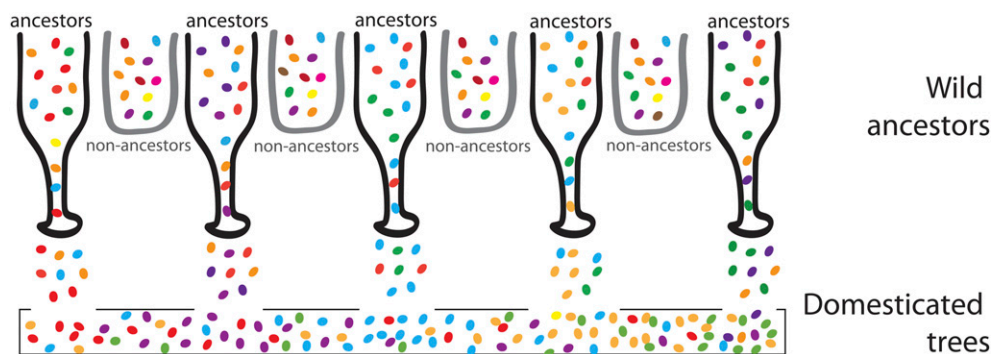


Fig. 2. Origin and evolution of perennial fruit crops. All crops are derived from native plant populations; consequently, “crop species” generally include two types of populations: 1) domesticated populations, trees that are evolving under artificial selection, and 2) native populations, the wild ancestors of the cultivated populations. Within native populations, some populations are the direct ancestors of cultivated populations (“ancestors”) and others did not contribute directly to the cultivated pools (“non-ancestors”). Recent molecular studies indicate that domesticated populations of perennial fruit crops maintain a large portion of the total genetic variation of the species. The broad genetic bottleneck that accompanied the domestication of many perennial fruit crops is likely the result of a combination of factors, including: a) relatively few sexual cycles separate domesticated populations from their wild progenitors; b) multiple geographically and genetically distinct ancestral populations; c) hybridization (including hybrid origin of cultivated species, human-mediated gene flow, and accidental gene flow with native populations (both ancestors and nonancestors) and sympatric congeners (not shown)).

consist of individuals from diverse geographic origins that undergo significant gene flow during the domestication process. Understanding the geographic origins of perennial fruit crops may shed light on the early stages of domestication because fewer sexual cycles have occurred between domesticated perennials and their wild progenitors than in annual crops.

The geographic origins of perennial fruit crops have been examined by numerous authors (de Candolle, 1886; MacNeish, 1992; Zohary and Hopf 2000). In a trend that matches or exceeds what is seen in annual crops, it appears that domesticated fruit tree populations often have diffuse origins, with cultivated populations consisting of individuals derived from multiple, geographically distinct areas (Fig. 2). For 18 species with available data (not including the multiple species of currants [*Ribes* L. spp.] or blackberries [*Rubus* L. spp.]), only five perennial fruit crops have been confirmed as having a single origin, while 12 have multiple origins (Table 2). There are six genera with multiple domesticates (*Annona*, *Artocarpus*, *Citrus*, *Diospyros*, *Prunus*, and *Rubus*), some with more than five domesticated species. One example of a perennial fruit crop with multiple origins is the olive, one of the oldest and most well-studied domesticated tree lineages. Wild olive trees are native to the Mediterranean Basin (Zohary and Spiegel-Roy, 1975; Terral et al., 2004), but pinpointing the precise geographic origins of cultivated populations has proven difficult. Some researchers have suggested a western Mediterranean origin (Terral et al., 2004); and that olives in the eastern Mediterranean represent feral forms (Bronzini de Caraffa et al., 2002). Native olive (oleaster) populations exhibit substantial geographic differentiation between the western and eastern parts of their range (Besnard and Bervillé, 2000; Besnard et al., 2002; Bronzini de Caraffa et al., 2002; Lumaret et al., 2004; Terral et al., 2004; Breton et al., 2006). Molecular genetic data have provided evidence for at least two geographic origins of cultivated olives, one from each of these general areas (western and eastern Mediterranean regions; Besnard and Bervillé, 2000), and one study identified seven geographic origins (Breton et al., 2006).

Although most commercially viable fruit trees were domesticated thousands of years ago, making many aspects of the process opaque, there are species that have been brought into

cultivation more recently. Pecan, for example, is a recently domesticated tree with a well-documented history that offers an opportunity to consider evolutionary processes during the early stages of tree domestication. Pecan is native to the river floodplains of the central United States, with isolated populations found in northeastern and central Mexico (Stone, 1997; Sparks, 2005). This species has been domesticated over the last 150 years (Manaster, 2008), and breeding records indicate that cultivated pecan populations were derived from numerous, geographically distinct ancestral populations, as well as from seedlings resulting from accidental and intentional crosses between cultivars and native or cultivated individuals. Pecan clones and seeds were transported widely; transplants have exchanged genes serendipitously with other cultivars and with sympatric native populations (L. Grauke, U. S. Department of Agriculture, personal observation). On occasion, resulting offspring were incorporated into cultivated populations as seedling selections. In addition, cultivars from different geographic regions were crossed as part of controlled breeding programs. Over this short time span, active breeding has led to domesticated individuals with larger fruits and a greater percentage of kernels relative to wild populations (Rice, 2005). Despite morphological differences, comparative analyses of allozyme variation in cultivated and native populations failed to detect reductions in variation associated with a domestication bottleneck (Rüter et al., 1999). Recently domesticated perennials like pecan offer ideal study systems for understanding the early stages of domestication.

Hybridization in perennial fruit crop lineages—Hybridization has long been recognized as an important force in domestication (Darwin, 1899; Stebbins, 1950). Extensive human-mediated gene flow related to breeding efforts sparked a reconsideration of the meaning of species boundaries in crop systems (Harlan and deWet, 1971). At the time, the dominant species concept was based on the idea that geographic isolation led to reproductive isolation, which resulted in speciation (Mayr, 1940). Observing that cultivated populations often have the capacity to exchange genes with related species, and that the product of those crosses often yielded fertile offspring, Harlan and deWet

(1971) proposed the gene pool system. This system describes pools of genes available to crops, regardless of taxonomic boundaries, and includes (1a) cultivated (domesticated) populations, (1b) ancestral (undomesticated) pool from which the domesticated populations were derived, and (2) related but distinct species capable of exchanging genes with cultivated populations. Recent molecular analyses shed light on the extent of hybridization among gene pools of domesticated perennial crops cultivated for their fruits, including (1) hybrid origins of perennial fruit crops, (2) deliberate, human-mediated gene flow between perennial fruit crops and their wild relatives, and (3) accidental gene flow between perennial fruit crops and their wild relatives.

Hybrid origins of perennial fruit crops—Clonal reproduction of many perennial fruit crops makes it possible to permanently capture hybrid genotypes, even F_1 hybrids, and any associated traits, such as lack of seeds (in sterile hybrids) or general hybrid vigor (Stebbins, 1950). Many prominent fruit crops are the result of interspecific hybridization events (sometimes with associated genome doubling) and reproduce or are propagated through clonal mechanisms, especially in *Citrus* (Moore, 2001). Other permanent interspecific hybrids include *Annona squamosa* \times *A. cherimola*, *Artocarpus altilis* (Parkinson) Fosberg \times *A. mariannensis* Trécul, and the many banana cultivars resulting from crosses between *Musa acuminata* Colla and *M. balbisiana* Colla (Lyle, 2006; Zerega et al., 2006; Heslop-Harrison and Schwarzacher, 2007). The role of early-generation hybrids is quite different in annual crops; while F_1 hybrids play a very important role in modern breeding and production practices (e.g., hybrid maize; Troyer, 1999), they must be recreated every year rather than being maintained and propagated over time as is possible for perennial crops.

Some domesticated perennials that result from hybridization form independent lineages capable of sexual reproduction rather than persisting solely through clonal reproduction (although on a practical level they may be propagated in a variety of ways); these hybrid lineages are the result of polyploid or homoploid hybrid speciation events like those observed in natural populations (Rieseberg 1997; Soltis and Soltis 1999). One example of the hybrid origin of a fruit tree is in the genus *Leucaena*, for which sympatric cultivation of previously allopatric species resulted in multiple formations of the allotetraploid *L. leucocephala* (Lam.) de Wit, now the most widely cultivated species in the genus (Hughes et al., 2007). In this way, hybrid origins of perennial crops are similar to those of annual crops, where allopolyploidy is also an important mechanism for the origin of new domesticates; the most familiar examples are the polyploid wheat series (allotetraploid *Triticum turgidum* L. and allohexaploid *T. aestivum* L.) as well as the domesticated peanut (*Arachis hypogaea* L.), a tetraploid resulting from hybridization between wild diploid species (Kochert et al., 1996).

Deliberate, human-mediated gene flow between perennial fruit crops and their wild relatives—The potential contribution of wild relatives for crop improvement has long been recognized and today forms an important component of breeding and conservation programs for most cultivated species (Darwin, 1899; Kovach and McCouch, 2008). Using wild species in a breeding program requires that the undesirable traits of wild species be separated from the desirable ones in order for them to be used; this is usually accomplished via marker-assisted selection (MAS) (Gygax et al., 2004; Patocchi et al., 2009). For

the most part, crosses between domesticated perennials and their wild relatives have been used to identify genes contributing to resistance to abiotic stress, fungal and bacterial diseases, or pests such as nematodes and insects (Dirlewanger et al., 1996; Luby et al., 2001; Foulongne et al., 2003; Bus et al., 2005).

Although most crop progenitors are, indeed, inferior to cultivars for agronomic traits, QTL mapping in annual crops has revealed the existence of cryptic variation for domestication traits in wild progenitors, i.e., alleles in wild species that can have a positive effect on agronomic traits in crops (Weller et al., 1988; Xiao et al., 1996; Tanksley and McCouch, 1997; Jiang et al., 1998; Burke et al., 2002). This same pattern has also been observed in an advanced backcross between peach and its wild relative *Prunus davidiana* (Carrière) Franch., with several QTLs in the wild species contributing favorably to peach fruit size and sugar concentration (Quilot et al., 2004). Thus, it is possible that MAS could be applied to exploit cryptic variation to improve fruit crops in the future. Other uses of hybrids include the deliberate production of sterile hybrids, such as the intergeneric hybrids between *Vitis* and the North American genus *Muscadinia* (Planch.) Small, which have been used as rootstocks (Mullins et al., 1992). While these sterile hybrids do not contribute to long-term gene flow, they do represent a unique genotypic class made available through hybridization.

Accidental gene flow between perennial fruit crops and their wild relatives—Unintentional gene flow between cultivated populations and their wild relatives is common (Ellstrand et al., 1999) and occurs both in regions where cultivated and wild species overlap naturally and where domesticated species have been brought into contact with previously allopatric relatives. Numerous studies have documented crop-wild gene flow in seed-propagated annuals such as beet (*Beta vulgaris* L.), common bean, radish (*Raphanus sativus* L.), and sunflower (Beebe et al., 1997; Linder et al., 1998; Snow et al., 2001; Viard et al., 2004) and in the clonally propagated belowground crops cassava and potato (Duputié et al., 2007; Scurrah et al., 2008). Interspecific gene flow between cultivated populations and wild relatives has also been observed in perennial food plants. In a study of two cultivated walnut species growing in sympatry in several small villages in Yunnan, China, genetic variation derived from microsatellite data were consistent with interspecific hybridization between domesticated *Juglans regia* L. and native *J. sigillata* Dode (Gunn et al., 2010). Similar patterns have been identified among species of cultivated and wild hazelnut (*Corylus avellana* and *C. maxima* Mill.; Palmé and Vendramin, 2002) as well as cultivated and wild date palm (*P. dactylifera* and *P. canariensis* Hort. Ex Chabaud; González-Pérez et al., 2004). In a different approach, Kron and Husband (2009) showed that interspecific pollination was occurring at a high rate between wild *Malus coronaria* (L.) Mill. and the introduced domesticated apple, although no living hybrids were detected.

In contrast to these examples of interspecific hybridization, we know relatively little about hybridization between perennial fruit crops and their direct wild progenitors. Undoubtedly, this is due in part to the relatively small reductions in genetic variation associated with perennial crop domestication, which makes the task of distinguishing shared ancestral variation from recent hybridization even more difficult than in traditional domestication study systems. Molecular evidence for crop-wild hybridization has now been presented for two iconic Mediterranean crops, grape and olive (Breton et al., 2006; Lopes et al., 2009).

In the case of grape, genetic evidence indicates gene flow from the cultivated species to wild populations and also reveals that several cultivars display a high percentage of wild ancestry (Di Vecchi-Staraz et al., 2009; Lopes et al., 2009; Myles et al., 2011). This latter finding emphasizes the role that wild progenitors have played in the development of new varieties of domesticated crops. In these cases, although the hybridization event itself is unlikely to be human-mediated, the selection and maintenance of admixed lines is the product of human choice (Jarvis and Hodgkin, 1999), and so the process is more controlled than is the case for gene flow from the crop into the wild. The possibility for hybridization between feral (*Olea europaea* L. subsp. *europaea*) and wild olives [*Olea europaea* subsp. *cuspidata* (Wall ex. G. Don) Cif.], both invasive in eastern Australia, has recently been documented (Besnard et al., 2007). Although this information is based on a limited data set, it raises the intriguing possibility that crop–wild hybridization may play a role in generating weedy trees, similar to what has been shown for conspecific crop weeds in annual species (Barnaud et al., 2009; Gross and Olsen, 2009).

In the New World, gene flow between traditional and modern cultivars has been documented in avocado (Birnbaum et al., 2003). This study suggested a low rate of gene flow from modern to traditional types of avocado (<20% of seedlings had a modern or “grafted” parent)—a hopeful outcome for the prospect of preserving traditional and wild diversity in the presence of improved cultivars, at least in this species. Although certainly possible, we know of no documented cases of gene flow from cultivated accessions to wild avocados or from wild avocados into modern (or traditional) cultivars. Future studies emphasizing population-level sampling of both domesticated species and their wild relatives will shed light on the extent to which genes move between wild and domesticated perennial crops.

GENETIC BASIS OF PERENNIAL FRUIT CROP DOMESTICATION

What is the genetic basis of perennial fruit crop domestication? The answer to this question is likely to be complex in perennial crops, due to the diversity of modes of propagation for different species. For example, we might expect that the domestication genetics of outcrossing, seed-propagated fruit trees will resemble the patterns seen in outcrossing, seed-propagated annual plants, i.e., genes of large effect with regulatory changes dominating (Doebly et al., 2006; Gross and Olsen 2010). The predictions for clonally propagated crops are less clear. Under the simplest scenario, a favorable mutation of major effect could be preserved through continuous clonal propagation, but realistic domestication scenarios are likely to be more complex (see previous section *Mating system and mode of reproduction*). It is also unclear how easily favorable traits could spread through domesticated populations with little sexual reproduction; this spread of domestication genes through a species is a hallmark of annual crop domestication genetics (e.g., Sweeney et al., 2007). Our understanding of perennial crop domestication genetics is still nascent, but recent advances promise interesting results.

Genetic mapping—QTL mapping has served as a major avenue for understanding the genetic basis of domestication in plants. QTL mapping requires the generation of a recombinant

hybrid population between two genetically and phenotypically divergent parents; in the case of plant domestication, the relevant cross would be between individuals from domesticated plants and their closest wild relatives or potentially between a landrace and an elite cultivar. While not precise, QTL mapping allows the detection of genomic regions associated with domestication traits and can answer the question of whether changes under domestication are due to many changes of small effect or a few changes of large effect. This approach has been applied extensively to annual crops and has shown that many domestication traits seem to be caused by relatively few changes of large effect (i.e., the traits are controlled by QTLs that contribute a minimum of 20% of the phenotypic variance in the mapping population; reviewed in Burger et al., 2008).

Neither the development nor the maintenance of a mapping population are trivial undertakings for a long-lived organism, but QTL studies have been conducted in many fruit tree genera, including *Castanea* (Casasoli et al., 2004), *Citrus* (García et al., 2000), *Coffea* (Amidou et al., 2007), *Cocos* (Baudouin et al., 2006), *Malus* (Kenis et al., 2008), *Prunus* (Quilot et al., 2004; Zhang et al., 2010), *Persea* (Sharon et al., 1998), *Theobroma* (Crouzillat et al., 1996; Crouzillat et al., 2000), and *Vitis* (Cabezas et al., 2006). Because the goal of most of these studies has been crop improvement, crosses have mainly been within the domesticated species (e.g., apple cultivars Telamon × Braeburn; Kenis et al., 2008), but also include some wide crosses between two domesticated species (e.g., almond × peach; Illa et al., 2010) or between a domesticated species and a wild species that is not a progenitor of the crop [e.g., *Citrus limon* (L.) Osbeck × *Poncirus trifoliata* (L.) Raf.; García et al., 2000]. These crosses do not lend themselves easily to answering questions about domestication genetics, but some conclusions can be drawn from them. One clear pattern is the instability of the majority of QTLs across years, which requires measurement of the traits of interest across multiple seasons (e.g., Sharon et al., 1998; García et al., 2000; Casasoli et al., 2004; Quilot et al., 2004; Cabezas et al., 2006; Kenis et al., 2008; Zhang et al., 2010). One extreme example of this pattern is from a 15-yr mapping project in cacao, where only two of 10 QTLs contributing to yield were detected in more than 3 years (Crouzillat et al., 2000). The other pattern seems to be that, while QTLs that explain over 20% of the phenotypic variation have been documented, the majority of the QTLs detected have a smaller effect. Whether this is due to the nature of these crosses (i.e., two apple cultivars might not harbor highly divergent alleles for fruit size) or due to a real difference in the nature of tree domestication compared to annual plant domestication remains to be seen. Overall, in spite of their limited utility for answering questions about domestication, these existing studies show that QTL mapping is a viable approach to understanding the genetic basis of traits of interest in perennial crops.

To our knowledge, there are very few QTL mapping studies that involve a cross between a cultivated tree and a wild relative or a cross between a classical and modern cultivar. The studies involving crop × wild crosses were both conducted in *Prunus*, one utilizing an F₁ cross in sweet cherry (Zhang et al., 2010) and one utilizing a BC₂ cross in peach (*P. persica* × *P. davidiana*; Quilot et al., 2004). Interestingly, the BC₂ cross was originally developed for the evaluation of disease resistance characters, and only later co-opted for the evaluation of fruit traits, suggesting that mapping-ready populations might exist for other crops as well. The results were strikingly different: the majority of QTLs detected in the cherry study were of major

effect, while the majority detected in the peach study were of minor effect. The cross between a classical and modern cultivar was conducted in grape and was specifically aimed at identifying the genetic basis of seedlessness (Cabezas et al., 2006). This study was similar to the cherry study in that it identified many QTLs of major effect, potentially an example of the identification and preservation of a major mutation in a clonal crop, but this observation should be tempered by the fact that only three traits were measured.

Admixture mapping is another approach to mapping the loci underlying traits of interest, with the major difference being that admixture mapping takes advantage of a naturally occurring recombinant population (Buerkle and Lexer, 2008). An admixed population could be an interspecific hybrid zone or a more subtle mixture of genetically differentiated populations within the same species. This technique has been applied in cacao, using cultivated varieties that are admixtures of the Criollo and Forastero cacao cultivars, that are estimated to have undergone about six or seven generations of recombination (Marcano et al., 2007, 2009). Admixture mapping in this system recovered many QTLs that were documented in artificial mapping populations, indicating its reliability. This technique has not yet been applied to answer questions about domestication genetics in perennial fruit crops, but it would be a very powerful technique if the appropriate crop \times wild admixed populations exist.

Domestication genes—QTL and admixture mapping studies are often seen as the first steps toward map-based (or positional) cloning, and the majority of domestication genes examined in annual plants have been cloned using this technique (Doebley et al., 2006). However, map-based cloning requires large populations (>1000) to narrow the region of interest to a reasonable size, which is not a viable possibility in many perennials (González-Martínez et al., 2006b). Instead, candidate genes, either those cloned in other species or those predicted to control relevant traits based on nucleotide sequence, may be called on to play an important role in understanding the genetic basis of domestication. For example, a study of candidate genes for anthocyanin production using functional and population genetics led to the discovery that the clustered genes *VvMYBA1* and *VvMYBA2* are inactivated, via a variety of mechanisms, in white grapes (Kobayashi et al., 2004; Walker et al., 2006, 2007; Yakushiji et al., 2006; Azuma et al., 2009; Pelsy, 2010). Similarly, *MdMADS2.1* (similar to the *Arabidopsis* gene *FRUITFULL*) is associated with apple fruit firmness within domesticated apples (Cevik et al., 2010); this type of analysis could be extended to elucidate the differences between wild and domesticated apples as well.

It is possible that perennial fruit crops will mainly skip the laborious map-based cloning phase of identifying domestication genes. Genome sequencing projects for fruit trees are increasing in number (e.g., Velasco et al., 2010), and publically available candidate gene maps (e.g., Illa et al., 2010) will also provide resources for linking genes to phenotypes, especially in combination with genome-wide scans for selection and association mapping techniques similar to those used in forest trees. These candidate gene approaches are necessary, but will likely face some stumbling blocks, as the domestication genes sequenced to date have generally proven to be uniquely important in each species (Gross and Olsen, 2010).

Conclusions—Perennial crops are attracting increasing attention as important components of sustainable agriculture, offering promising options for food sources while lowering

environmental impacts. Long-lived perennials share several features that distinguish them from annual plants and influence the way in which they evolve in nature and under domestication, including long juvenile phases, mechanisms to avoid selfing, high rates of inter- and intraspecific hybridization, extensive population genetic variation, and limited population structure. Perennial fruit crops have been domesticated in every major agricultural center and, in some ways have responded to artificial selection just like annuals (e.g., novel fruit features, larger fruit size, indehiscent fruit, larger seeds that are less toxic, fewer defensive structures). However, unlike annuals, perennial fruit crops are often clonally propagated, which has resulted in concomitant changes in reproductive biology. Domestication of perennial fruit crops is characterized by a relatively broad genetic bottleneck resulting from a combination of factors including mating system, mode of reproduction, multiple geographic origins of cultivated populations, and hybridization. Studies of the genetic basis of domestication traits in perennial fruit crops are in their infancy, but indicate that QTL underlying traits of interest can be of major or minor effect, and may not be stable across years. Future studies that take advantage of developing genomic approaches and consider demographic history (e.g., Siol et al., 2010) will shed light on the genetic basis of agriculturally and ecologically important traits in perennial fruit crops and their wild relatives.

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