

Crop Domestication as a Long-term Selection Experiment

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I. INTRODUCTION

In *The Origin of Species by Means of Natural Selection*, Charles Darwin (1859) devoted his first chapter to "Variation under Domestication." He expanded on this topic in *Variation of Plant and Animals under Domestication* (1868) and he became involved in pigeon breeding. The fact that

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one of the founders of evolutionary theory would pay such attention to domestication and the selection process associated with it is testimony to the exemplary value of crops and animal breeds in the study of natural selection in general. In his writings, Darwin makes several observations and raises several issues that are still relevant today, some of which have yet to be resolved. One of the benefits of considering selection under domestication was that he demonstrated that selection had heritable effects, even in the absence of any information about the histological, biochemical, and genetic foundations of heredity.

One of the major observations made by Darwin is that morphological modifications selected during domestication have been of such magnitudes that many crop plants usually cannot survive in the wild anymore without human assistance. In addition, he pointed out that selection by breeders could lead to a wide array of variation in domesticated plants and animals when compared with their wild progenitors. He also suggested that selection under human cultivation happened unconsciously or inadvertently, that is, without deliberate human action. He argued that crops are so different morphologically from their wild progenitors that humans could not have possibly identified target traits so different from those existing in the wild progenitor.

He also pondered the question as to the origin of crop plants. He was particularly interested in the number and location of domestications but stated that it would actually be very difficult to identify the centers of origin of crops. Since his time, a substantial body of information has been gathered not only on the domestication origin of crops but also on their evolution subsequent to domestication, in part through the application of a broad palette of increasingly sophisticated techniques. In addition, there have been several major contributors to the field of crop evolution studies, including A. de Candolle, who broadly laid out the types of data that can be used to trace the origin of a crop; N. Vavilov, who systematically identified the centers of domestication of crops; and J. Harlan, who also contributed to the concept of domestication centers and built close linkages between archaeology and plant science. This review will address a number of issues associated with the study of crop evolution from a long-term selection perspective.

II. THE DOMESTICATION PROCESS

Domestication is the outcome of a selection process that leads to increased adaptation of plant and animals to cultivation or rearing and utilization by humans. It is still being debated whether this selection

took place consciously by humans or if it was an inadvertent phenomenon as a by-product of human plant cultivation or animal rearing (Harlan et al. 1973; Zohary et al. 1998). Proponents of unconscious selection argue that the first farmers could not have possibly foreseen or set out to specifically select for the marked phenotypic changes that eventually arose during domestication. These changes have been so pronounced that plant taxonomists have often classified wild progenitors and domesticated descendants in different species or genera. Given these marked changes, advocates of inadvertent selection argue that early farmers could not have set out to specifically select for these changes. One could argue, however, that one need not know the end result to select intermediate steps. In a discussion of animal domestication, Zohary et al. (1998) proposed that the shift in adaptation between wild and domesticated environments was so large that cultivation or rearing would *automatically* (his italics) initiate selection for many new traits that characterize goats and sheep. He also suggested that certain traits such as the culling of young males might have been under conscious selection. This altered sex ratio in archaeological remains may be one of the earliest signs of domestication among animals.

Proponents of conscious selection argue that the first farmers were actually quite knowledgeable about their environment. They were well aware of the life cycle and some of the biological characteristics of plants and animals surrounding them well before the advent of agriculture. For example, the Cro-Magnon civilization depicted in vivid detail and color the animals that surrounded it, as can be seen in several caves in southern Europe (see the Cave of Lascaux, France: <http://www.culturefr/culture/arcnat/lascaux/en/> and the Cave of Altamira, Spain: http://www.mcu.es/nmuseos/altamira/colecl_1.html). The transition from hunting-gathering to agriculture (the Neolithic revolution) is thought to have been preceded by the so-called broad-spectrum revolution (Flannery 1969; Stiner 2001). This revolution marked a switch in subsistence patterns during the Paleolithic. From large game, hunter-gatherers turned to a more diverse diet consisting of smaller animals (Poinar et al. 2001) as well as plants, particularly grains. Evidence for this transition comes from an increase in the number of species in the diet and a greater proportional evenness among prey items, an abundance of milling tools and storage facilities, and a higher frequency of plant parts (Poinar et al. 2001; Stiner 2001). In addition to increasing the familiarity of foragers with a broader range of plants and animals, the broad-spectrum revolution also led them to develop tools and techniques that would be useful in the subsequent agricultural phase. Among these techniques are methods to detoxify plant foods (Johns and Kubo 1988). Although not

all the methods listed by these authors may have been known to hunter-gatherers, some of them were probably known, as recent studies of contemporary pre-agricultural societies indicate. Thus, the biological and technological knowledge of these societies should not be underestimated. Hillman and Davies (1990) have suggested that a combination of unconscious and conscious selection may have operated in succession, with the former operating in the early stages when the frequency of mutation(s) was too low to be noticeable.

During domestication, mutations affecting specific traits of the domestication syndrome are selected until they achieve near or full fixation. Are domesticated plants more mutable and has this mutability affected their domestication? Unfortunately, there are few studies in plants that have investigated mutation rates and the magnitudes (positive or negative) of mutations (Drake et al. 1998). Particularly, there are no studies comparing the mutation process between crops and related species. As pointed out by Hill and Mbaga (1998), mutations were not thought to play a significant role in breeding programs because of the short time span and the limited response observed in some experiments. Both empirical and theoretical analyses, however, have shown that mutations can cause a significant and continued response even in small populations (see references in Hill and Mbaga 1998). One of the best examples of continued response is the long-term selection experiment for protein and oil in maize (*Zea mays*) at the University of Illinois. It has been suggested that mutations are involved in the long-term response of the Illinois experiment but the extent is unknown (Rasmusson and Phillips 1997).

In the absence of specific values for mutation parameters, Hillman and Davies (1999) assumed a mutation rate of $\mu = 10^{-6}$. At a sowing rate of 200 spikelets/m², observed in traditional cropping systems, such a mutation would appear in a single growing season in a 1 to 2 ha area. Assuming grain needs to provide 25% of total calorie requirements, the calorie needs of humans, and incomplete absorption and digestion, Hillman and Davies (1999) estimated that areas sown for a family of five ranged between approximately 0.5 ha and 2.8 ha. (This calculation of course assumes also that early farmers derived their foods exclusively from cultivation, which is unlikely.) These are values similar to those postulated for the occurrence of a mutation in a single growing season. Mutation rates may therefore not have been a limiting factor in the progress from selection, assuming of course that these theoretical assumptions can be confirmed with empirical data.

A comparison of the morphological and physiological differences among domesticated plants has shown that a similar set of traits has been

selected during domestication. This set has been called "the domestication syndrome" (Hammer 1984; Harlan 1992). Traits included in this syndrome (see below for a more detailed discussion) include those increasing adaptation to cultivation and desirability of human consumption and use. Harlan (1992) lists some 400 cultivated plants; there are certainly more but they may be cultivated only intermittently or on a very small scale. Among these cultivated plants, the degree of domestication varies widely. Highly domesticated plants, typified by plants such as maize, rice, common bean, and peanut, have a broad range of domestication traits and express these traits at a high level. Other crops, encompassing a wide range of domestication phenotypes, can be considered to be only partially domesticated. On the one hand, a crop like canola (*Brassica rapa*, *B. napus*) is generally considered to be a highly domesticated crop. Yet, it still suffers annual seed losses of 20-50% due to silique shattering (Child et al. 1998). It can therefore be considered to be incompletely domesticated with respect to seed dispersal. Crops such as soybean and sesame also suffer from excessive shattering at maturity. On the other hand, the African oil palm has only been subjected to limited changes during domestication. Without having been planted, its distribution has increased indirectly through agricultural practices like slash and burn. The only major genetic change has been selection for a gene affecting kernel development inside fruits. Trees with thick-shelled kernels (called *durra* types) are generally tapped for palm wine and not for oil, whereas trees with thin-shelled kernels (*tenera*) or kernels without shell (*pisifera*) are preferred for oil harvest (Harlan 1992). In general, tree and forage crops are considered to be only partially domesticated.

There is also evidence of abandonment of domesticates. Both North America (currently the central and northeastern part of the United States) and northern China were once centers of crop domestication. In the North American center, a crop such as marshelder or sumpweed (*Iva annua*) was once domesticated (as evidenced by increased seed size), as were other crops such as sunflower (*Helianthus annuus*) and gourd (*Cucurbita pepo*). Marshelder, as a domesticate, has now disappeared, having been replaced by other crops, both local ones and those introduced from the Mesoamerican domestication center, including maize (Smith 1995a). In northern China, several hundred kilometers north from the Yangtze basin where rice was probably domesticated, two drought-tolerant millet species (broomcorn millet, *Panicum miliaceum*, and foxtail millet, *Setaria italica*) adapted to cultivation in regions with marginal rainfall were domesticated. With time, however, rice has increased in importance, whereas the importance of these millet species has decreased.

There are important corollaries to this definition of domestication. First, plant cultivation or animal rearing is a necessary but insufficient condition for domestication. Thus, each crop or animal breed will have been grown or reared for a generally undefined period (predomestication cultivation or rearing) during which selection operated. During this period, the definitive changes in phenotype normally associated with domestication may not have occurred. Second, certainly for plants, complete domestication leads to a lack of fitness in natural environments. Fully domesticated plants cannot survive on their own in the wild. One of the best examples of this situation is maize, where the husks surrounding the ear and the tight attachment of kernels to the cob prevent natural dispersal. In contrast, partially domesticated plants have conserved at least some ability to survive in natural environments. Examples of this situation are often fruit trees such as olive (Bronzini de Caraffa et al. 2002). This leads to the existence of feral populations that can be distinguished only with difficulty-if at all-from wild populations. Third, a mutualistic relationship exists between humans and their crop plants or animal breeds. The transition from hunting-gathering to agriculture was an experiment in cultural evolution that represented a drastic change in human societies and their environment (Richerson et al. 2001). In turn, agriculture became a necessary condition for the development of civilizations because it provided a surplus of food, which allowed specialization and diversification of crafts, trades, and other occupations (Maisels 1993). While fully domesticated plants and animal breeds (the latter to a lesser extent) cannot survive on their own, it can also be argued that humans would not be able to survive without their domesticates.

Agriculture has so far been able to keep pace with human population growth and provides sufficient food and other needs so that humans can tend to other activities (Cohen 1995; Smil 2001). This close relationship between humans and their domesticated plants and animals is precisely one of the aspects that makes the study of domestication such a fascinating area of study. Whereas humans have had a marked effect on domesticated plants and animals, the converse can also be said. Domesticated (and, in some cases, undomesticated) plants and animals have had a significant effect on human history (Crosby 1986; Viola and Margolis 1991; Hobhouse 1999). For example, exotic plants (at least to the Europeans of the 15th and 16th centuries) were one of the driving forces behind the explorations of new continents. In this respect, the discovery of the Americas by C. Columbus in 1492 was a significant date because it led to the Columbian exchange, the reciprocal exchange of crops between the Old and New Worlds.

Domestication is a continuing process. While in the strictest sense of the definition, domestication could refer only to the first stages of selection that coincided with the initiation of agriculture, selection by humans continues to this day. The advent of scientific plant and animal breeding has greatly accelerated the pace of change.

III. CENTERS OF AGRICULTURAL ORIGINS

Among technological developments and inventions, agriculture is perhaps one of the few, if not the only one, that originated independently in more than one location. Although the number and precise boundaries of the different centers of origin of agriculture remain to be determined, agriculture originated in at least six different areas of the world: Mesoamerica, the Andes of South America (including their piedmonts), Southwest Asia (the Fertile Crescent), Africa (Ethiopia and the Sahel), Southern China, and Southeast Asia (Fig. 1.1) (Hawkes 1983; Harlan 1992; Smartt and Simmonds 1995). Additional areas include eastern

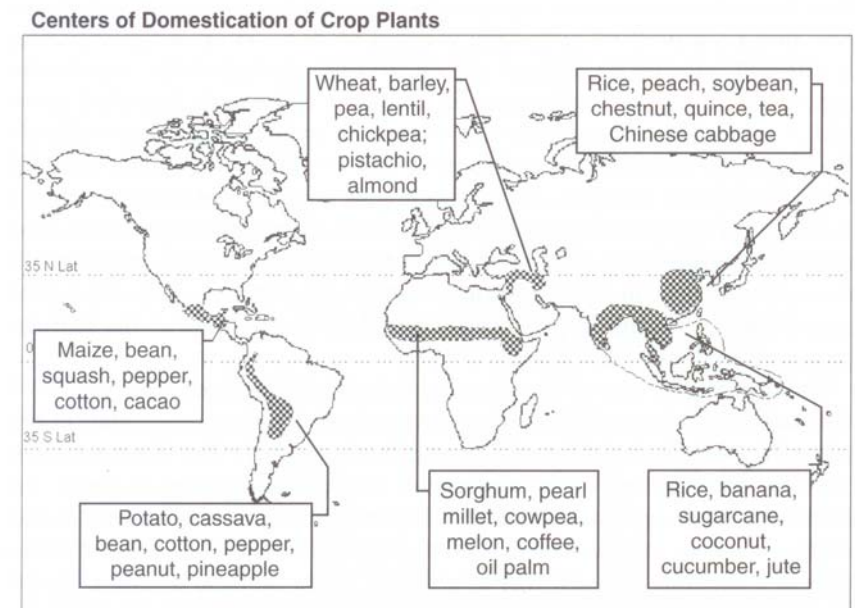


Fig. 1.1. Location of the major centers of crop domestication and some of the crops domesticated in each of them. Source: Gepts 2001.

North America, northern China, and Europe, but their impact has been much less than that of the aforementioned centers. In each of these centers, similar types of crops were domesticated. For example, in each center one or more sources of carbohydrates (cereal or root or tuber crop) and of proteins (legumes) were domesticated.

Are there commonalities between these geographically disparate regions? They are located in tropical or subtropical regions generally between 35° N. and 35° S. Lat. Their topography is generally mountainous or hilly. One can speculate that this type of environment at the time of domestication would have harbored a wider range of resources than areas that are located at higher or lower altitudes. In turn, this abundance of resources would have allowed early farmers to continue procuring food through the old methods of hunting and gathering. It would also have allowed them to more easily identify plants or animals that were predisposed to domestication.

In their natural habitat zone, Peake and Fleure (1927) proposed that the presence of a wide range of wild relatives was one of the prerequisites for a center of agricultural origin. They also suggested that an alternation of rainy and dry seasons was important and proposed that limits to migration as an alternative to agricultural intensification should exist. This could be achieved by topography or territoriality, which would prevent populations from migrating to other areas to obtain supplementary or alternative sources of food. An additional characteristic of potential centers of domestications was an absence of heavily forested areas, which would have made the conversion to agricultural lands difficult. Finally, they suggested that the existence of different groups with different traditions, cultures, and technologies would have also contributed to the development of agriculture. However, the existence of these characteristics would not per se ensure that agriculture would develop. For example, California never became a center of origin of agriculture (Bettinger 2000) although it possesses several of the distinguishing features proposed by Peake and Fleure (1927).

Elaborating on one of the characteristics of Peake and Fleure (1927), Harlan (1992) observed that most domesticated plants originated in one of two biomes, the Mediterranean and the Savannah. The Mediterranean biome is distributed on the western or southwestern edge of some continents or land masses, including the area around the Mediterranean sea, southern Africa and Australia, Chile, and California. Its main vegetation type is a shrubby or park-like grassland. Trees include conifers (cedar, pines) and evergreen broadleaf trees (such as oaks). Shrubs are often aromatic (such as rosemary, sage, and oregano). Many plants in this biome are adapted to fire. The savannah biome is also a lightly forested grass

land that merges gradually into dry deciduous forests. It is found in Africa, South America, India, and Australia. Trees include baobab and acacia. The vegetation is also adapted to fire. Both biomes are characterized by an alternation of humid and dry seasons. In the Mediterranean biomes, rains occur primarily during the colder season, whereas in the Savannah biome rains occur mainly in the warmer season. Table 1.1 lists examples of crops arranged by their biome of origin.

The existence of a marked dry season may have constituted an impetus for the transition from hunting-gathering to agriculture. In the presence of rising populations, which put more pressure on existing food resources especially during the dry season, hunter-gatherers may have planted seeds of the grain crops they were already harvesting and consuming to increase the size of the harvest. It is significant in this respect that a majority of the basic food crops domesticated in these biomes are actually annual grains. Conservation of grains is eminently feasible over a few months of dry weather and would have provided an alternative food source, especially in those years with a marked and extended dry season.

Application of molecular and biochemical markers has allowed us to further specify potential centers of domestication. In some cases, this has

Table 1.1. Examples of origin of crops in different biomes

Biome	Crop
Desert	Date palm
Mediterranean	Wheat, barley, rye, pea, lentil, chickpea, rapeseed
Savanna (and tropical deciduous forests)	Maize, rice, sorghum, cassava, sweet potato, bean, peanut, yams
Sea coasts	Coconut, cabbage, beet, cotton
Temperate prairies	Sunflower
Temperate steppes	Proso and foxtail millet, hemp, and <i>Triticum tauschii</i> (donor of the D genome of bread wheat)
Temperate forest	Apple, pear, cherry, grape, walnut
Tropical highland	Potato (and other root crops from the Andes: ullucu, mashua, oca, arracacha, achira, yacón, unchuca) and <i>arabica</i> coffee
Tropical rain forest	Sugarcane, banana and plantain, citrus, mango, cacao

provided astonishingly specific locations, assuming that alternative hypotheses that can account for the observed results can be dealt with. For example, the closest wild relative of domesticated maize is teosinte. Various types of teosinte exist, including diploid and tetraploid forms, as well as annual and perennial forms. Using isozyme data, Doebley et al. (1984) identified *Zea mays* ssp. *parviglumis* teosinte, a diploid, annual teosinte distributed principally in the states of Jalisco, Michoacán, Mexico and Guerrero, as the closest wild relative of domesticated maize. In particular, the populations from the Balsas river drainage in Guerrero appeared to be particularly close to domesticated maize. These findings have been recently confirmed based on sequence analyses of the *teosinte branched-1* (*tb1*) gene (Wang et al. 1999, 2001) and a microsatellite analysis of genetic diversity of maize germplasm (Matsuoka et al. 2002). The latter study was also able to identify two major dispersal routes for maize germplasm from the Mexican highlands, one to the north ending in the northeastern United States and the other to the south to the Andes via Central America. These dispersal data complement archaeological data that show maize was domesticated by 5,400 years before the present (in uncalibrated years) in highland Mexico (Piperno and Flannery 2001; Pope et al. 2001). However, in contrast with the Southwest Asian center of agricultural origins, there are only a few archaeological sites relevant to the study of agricultural origins in Mesoamerica. All of these centers are located outside the current distribution area of teosinte, the presumed wild progenitor of maize. Thus, the age of domestication of maize is likely to be even older than the finds of current archaeological sites. In addition, the data of Matsuoka et al. (2002) show a genetic and ecological gap between *Z. mays* ssp. *parviglumis* and the closest domesticated maize group from the Mexican highlands. Thus, further data are needed to clarify some of the details of the domestication area of maize.

Common bean (*Phaseolus vulgaris*) is also a domesticate from the Mesoamerican center, although-in contrast with maize-it has an additional major center of domestication in the southern Andes (southern Peru, Bolivia, or Argentina) and a potential minor one in Central America or Colombia (Gepts 1993, 1998). A more specific location for the Mesoamerican center was obtained by identifying those wild populations based on variation of phaseolin, the major seed storage protein type of beans. Prior studies had shown that the domesticated types from Mesoamerica carried a single phaseolin electrophoretic type (S phaseolin type), in contrast with the wild progenitor that displayed at least 15-20 types (Gepts et al. 1986). Because each electrophoretic pattern is the result of a complex series of steps at the molecular level, including

gene duplications, nucleotide divergence, and post-translational modifications, the likelihood of repeated origins of this same pattern is low. Hence, the presence of the same S phaseolin signals a common ancestry. One should therefore expect to be able to trace back the origin of this phaseolin type to a specific region in the distribution of wild beans in Mesoamerica. A caveat is possible gene flow between domesticated and wild beans. Although common bean is considered predominantly self-pollinated ($\leq 2-3\%$ outcrossing), occasionally higher levels of outcrosses have been documented (Ibarra-Perez et al. 1997). Feral populations and cases of outcrosses between wild and domesticated beans have been documented repeatedly (Debouck et al. 1993; Freyre et al. 1996; Beebe et al. 1997). To address this issue, morphological data such as seed size and growth habit were taken into consideration to disregard those wild accessions that showed signs of past hybridization with domesticated types (Vanderborgh 1983). Although one could expect-given the simple genetic control of the domestication syndrome-that some wild beans would not show any difference in spite of past hybridization, using these morphological data would have reduced the number of wild populations carrying the S phaseolin through hybridization and not common ancestry. Using this procedure, it was possible to identify a well-circumscribed area in west-central Mexico (centered around Jalisco and western Guanajuato) as the putative domestication center for common bean (Gepts 1988). It is striking that this area is located relatively close to the area proposed for the domestication of maize, although it does not match it. It remains to be determined if this lack of match truly represents a different domestication area or is an artefact due, for example, to changes in distribution of the wild relatives of common bean and maize attributable to climate changes in the last 10,000 years (Buckler et al. 1998). Even today, wild beans can be found growing on teosinte (Delgado Salinas et al. 1988). It is therefore possible that early farmers domesticated not only crops but entire cropping systems as the predominance in Latin America of the so-called milpa cropping system, which includes maize, bean, and squash, suggests. Archaeological data, however, suggests that these domestications may not have been concurrent (Kaplan and Lynch 1999).

Using AFLP analyses, Heun et al. (1997) identified a population of morphologically wild einkorn wheat that was more closely related at the DNA level to domesticated einkorn than any other wild einkorn populations. This population is located in the Karacadag mountains in southeast Turkey near major archaeological sites relevant to the study of the origins of agriculture, such as Cayönü, Cafer Höyük, and Nevalı Cori. Lev-Yadun et al. (2000) pointed out that the distribution regions of wild

relatives of several crops, including einkorn wheat, emmer wheat, barley, lentil, pea, and bitter vetch, overlap in an area encompassed by southeast Turkey, northern Syria, and northern Iraq. As for the Mesoamerican center of origin, one could suggest that cropping systems were domesticated based on pre-existing relationships in natural vegetation. However, a more definitive answer to this question is required. For several of the crops, molecular data are as yet unavailable. In the case of barley, the proposed domestication area is located to the south in the Levant (Badr et al. 2000). One can also wonder why early farmers would have domesticated not just one cereal or legume but several of them. Presumably, specific crops were domesticated because they corresponded to a specific dietary or other need. Why then domesticate more than one cereal or legume in the same locality? Perhaps these apparently similar crops did not fulfill the same function or some were saddled with major disadvantages such as low yield in the case of einkorn wheat.

Cassava (*Manihot esculentum*) is a major source of carbohydrates grown exclusively in tropical areas of Latin America, Africa, and Asia. The genus *Manihot* consists of some 100 species distributed in the Neotropics. The presumed wild progenitor of cassava is *M. esculenta* ssp. *flabellifolia* distributed only in South America (All em 1987; Allem et al. 2001). Sequence analysis of the single-copy nuclear gene glyceraldehyde 3-phosphate dehydrogenase (*G3pdh*) further focused the putative center of origin in west central Brazil (south and east of Amazon basin) and eastern Peru (Fig. 1.1) (Olsen and Schaal 1999).

In animals, considerable progress has recently also been made on determining origins of domestication of major livestock species (MacHugh and Bradley 2001). Different patterns are observed. The major pattern represents an East-West split, with domestications having taken place in the eastern and western halves of the Eurasian land mass. Examples of this pattern are cattle with domestications in the Near East and India (Loftus et al. 1994; Mannen et al. 1998; Troy et al. 2001), sheep (Wood and Phua 1996; Hiendleder et al. 1998), and pig (Watanobe et al. 1999; Giuffra et al. 2000). The goat has a major domestication in Southwest Asia, a minor one in India, and a poorly understood potential third origin in Eurasia (Luikart et al. 2001). In contrast, the horse does not have a well-defined center of origin (Vila et al. 2001). In the archaeological record, the horse appears well after other livestock species. It is possible that different agricultural societies domesticated the horse from local wild horse populations after cultural dissemination of the technology to capture, break, and train these animals had occurred.

Determining the specific geographic site of domestication is not a frivolous exercise. First, it may be important to guide archaeological

studies. For example, many if not all archaeological sites in Mesoamerica are located outside the current distribution area of wild progenitors of the main crops, maize, common bean, and squash. Guiding archaeologists to other areas such as Jalisco (for common bean) or the Balsas river basin (for maize) may in the long term be rewarded by the discovery of significant sites from the standpoint of agricultural origins in those areas (Smith 1995a). Second, identification of the immediate progenitors of a crop or breed is also important for further studies aimed at studying the effect of domestication as an evolutionary process at the genetic and physiological levels. Identifying the specific progenitor of a crop (or at least its immediate descendant) and the most primitive domesticated cultivars allows a more rigorous progenitor-descendant comparison than if the comparison was conducted between any wild and domesticated population. Knowledge of the actual progenitors is too recent for this approach to have been applied as yet. Hence, most wild-to-domesticated comparisons available may show differences that do not accurately reflect changes due only to domestication but also include changes that are due to divergence within the progenitor or domesticated descendant gene pools and are unrelated to domestication. Third, determining the specific site is also important for the management of genetic resources and their utilization in breeding programs. Utilization of wild genetic resources should focus on those accessions that are not the immediate progenitor of the crop in order to introduce novel genetic diversity into the domesticated gene pool.

In all the examples mentioned, the specificity gained by the use of molecular information is impressive. One should, however, keep in mind two important caveats. First, these molecular studies are only as good as the biological and genome samples available. It is of paramount importance to establish a sufficiently representative sample. This is not a trivial operation, because the materials either have not been collected or they are unavailable for a variety of reasons. Second, similarity between a crop and its putative wild progenitor can arise in ways other than through a progenitor-descendant relationship. Gene flow through pollen, seed, or escape from cultivation have been documented numerous times not only in outcrossing or vegetatively propagated crops, but also in predominantly selfing crops. To distinguish therefore between similarity due to a progenitor-descendant relationship or to gene flow, additional precautions ought to be taken such as using markers with a well-defined map location in relation to those of domestication genes (R. Papa and P. Gepts, unpubl. data) or analyze sequence variation at domestication loci (Wang et al. 1999, 2001) and adjacent regions to determine gene identity and recombination around the domestication loci. Until

additional studies are conducted, the specific geographic locations of domestications in the examples discussed here should be considered with caution.

IV. TIME FRAME OF DOMESTICATION

The process of domestication is but one aspect of the transition from hunting-gathering to agriculture. It is generally thought that this transition has taken several millennia (Smith 1995a). One of the milestones of this transition was the domestication of crops and animals. The point at which a crop or animal can be considered to be domesticated is somewhat speculative. As mentioned earlier, there are several traits involved in the domestication syndrome. A domesticated crop or animal usually displays several of these. Yet, the archaeological record only consists of a few types of remains, usually those that have been able to withstand decomposition. Examples of these are seeds and inflorescence axes (rachis or cobs). Cereals generally offer more clues to the status of their domestication than other crops such as legumes. In addition to an increase in seed size, which can be interpreted as a sign of domestication (see next section), a tough rachis (in contrast to a brittle rachis) and free-threshing seeds (as opposed to hulled seeds) with their characteristic morphology are also useful in this respect. For legumes, in contrast, only seed size can generally be used. Seed color and pod shape (for example, the presence of marked twisting of the pod walls) are rare additional possibilities. In light of the dearth of macroscopic traits indicating domestication, other traits have been investigated and used to document the transition from wild to domesticated types (Piperno and Pearsall 1998). These include starch grains (Piperno et al. 2000) and phytoliths or silica concretions (Zhao 1998; Piperno et al. 1999). Other features strengthening the archaeological record are the presence of a sequence within an archaeological site encompassing the transition from wild to domesticated and the number of remains.

Table 1.2 shows that the earliest finds in several domestication centers are about the same age—some 10,000 years ago. The exception is Eastern North America, where the earliest remains date from some 4,300 years ago. Although there are some differences in the actual ages of the finds among these centers of agricultural origins, it is not clear to what extent these are real or a result of insufficient sampling. With the exception of the Fertile Crescent and Eastern North America, the number of archaeological sites is quite limited. For example, Hart et al. (2002) list some 25 sites in the Eastern North America region, whereas the

Table 1.2. Time frame of domestication and early spread of agriculture

Location	Crop ^z	Age (years BP)	Source
DOMESTICATION CENTERS			
Mesoamerica	Squash	10,000	Smith 1997
	Maize	6,200	Piperno and Flannery 2001
Fertile Crescent	Einkorn wheat	9,400-9,000	Willcox 1998
	Lentil ^y	9,500-9,000	Willcox 1998
	Flax ^y	9,200-8,500	Willcox 1998
	Goat ^x	10,000	Zeder and Hesse 2000
	Pig ^x	10,000	Giuffra et al. 2000
China	Rice	9,000-8,000	Zhao 1998
Eastern United States	Squash	4,300	Asch 1995, cited by Hart et al. 2002
	Sunflower	4,300	Crites 1993
SPREAD FROM DOMESTICATION CENTERS			
Lowland	Cassava, <i>Dioscorea</i>	7,000-5,000	Piperno et al. 2000
Mesoamerica and Central America	yam, arrowroot, maize		Pope et al. 2001
Eastern North America	Maize	1,100	Smith 1989
Europe			Hart et al. 2002
	Einkorn wheat	9,000-5,000	Ammerman and Cavalli-Sforza 1984

^z Only the earliest domesticated crop remains are listed

^y Uncertainty as to the domestication status

^x Additional centers of domestication for the goat (in the Indian subcontinent) and the pig (in Eastern Asia) have been postulated

Mesoamerican center includes only five to six sites. In addition, the Mesoamerican sites, such as those in the Tehuacán and Oaxaca valleys, are located outside the current distribution area of wild progenitors of common bean, maize, and squash. It is possible that wild progenitors have retreated from these areas because of climate changes. However, the available data on past climate in the Tehuacán and Oaxaca Valleys suggest that little cultivation or domestication occurred in areas represented by the Coxcatlán (Tehuacán valley) and Guilá Naquitz (Oaxaca valley) caves (Buckler et al. 1998).

Genetic data suggest a domestication of maize in a different locale (see previous section). It is therefore possible that the presence of domesticated remains of crops such as maize represent a late introduction in these semi-arid areas, only after early farmers had mastered cultivation in these less favorable areas. Actually, recent molecular data based on microsatellites led Matsuoka et al. (2002) to suggest a domestication time for maize of 9,188 years ago (5,689-13,093 BP), surprisingly consistent with the age of squash domestication in Mesoamerica and that of domestication in other centers of agricultural origins (Table 1.2). Further archaeological sampling is therefore needed before more definitive conclusions can be drawn as to differences in timing of domestication among the different centers. As mentioned in the previous section, genetic data may guide archaeologists to areas where significant additional sites could be identified.

Determining the speed at which crops have been domesticated, that is, the period between first cultivation and fixation of domestication genes, depends primarily on the archaeological record. The ideal situation, a sequence of remains that spans the morphological evolution from the wild to the domesticated types, is rare. In many cases, one finds either type but not both in a more or less continuous situation. Nevertheless, data available from the Fertile Crescent (Willcox 1998) suggests that at least a millennium elapsed for domestication to take place. Wang et al. (1999) calculated a selection coefficient of $s = 0.04-0.08$ and a time frame of 300-1000 years for maize domestication based on sequence data for the *tb1* gene controlling branching. In einkorn wheat, field experiments to obtain realistic estimates of selection coefficients show that the most efficient cereal grain harvest system would involve sickle reaping of plant with a tough rachis. Other systems tested involved beating and uprooting. Modeling studies showed that a gene for a tough rachis could be fixed within 20-200 years (Hillman and Davies 1990). Clearly, more data are needed to document the length of the domestication process. Genetic data show that the process could have been fairly fast, with mutation and recombination rates being possible limiting factors. Nevertheless, archaeological data are also needed to document the actual time it took. It is expected that the actual time frame will be longer than the genetic time frame, because, for example, farmers may not have cultivated wild progenitors every year, given the presence of alternative resources.

Regardless of the outcome of future studies to locate additional archaeological sites, the rough similarity of domestication dates in widely different regions of the world suggests that climate change was a major factor, although not the only one, in stimulating the transition from for-

aging to farming. The period covering the last 10,000 years, also known as the Holocene, has been characterized by a generally warmer and more stable climate than the preceding Pleistocene era (Richerson et al. 2001). The latter authors have argued that the climate change, which also included a rise in CO₂ levels and increased rainfall, provided hunter-gatherers with the conditions for further intensification of food procurement, consisting of cultivation or rearing, and eventually domestication, of highly productive (but more labor-intensive) plant and animal resources.

As mentioned earlier, the period preceding the transition from hunting-gathering was also characterized by an intensification of the use of resources, the so-called broad-spectrum revolution. Agriculture can therefore be seen as an attempt some 10,000 years ago to further increase resource availability perhaps in response to ever increasing population levels or resource depletion or a combination of both. This was made possible in part by the improved climatic conditions but also because humans had reached a higher cognitive and cultural level of advancement. Richerson et al. (2001) argue that these successive bouts of intensification were driven by a competitive ratchet-like mechanism whereby each transition to more land-efficient subsistence systems both requires and allows labor intensification correlated with population growth. In turn, "early adopters" of these novel subsistence systems tended through sheer increase of their population to displace non-adopters. Displacement could take place physically by short- or long-range migration into territories occupied by non-adopters (demic diffusion). It could also take place by acculturation, whereby non-adopters eventually adopt the new life style (cultural diffusion). The two types of diffusion are extremes on a continuous scale, which includes many intermediate forms.

The speed at which agriculture was adopted was generally fast. Within the Fertile Crescent, which spans several hundreds of kilometers in both North-South and East-West directions, it is difficult to identify gradients in age of the oldest remains of crops and domesticated animals. Furthermore, Ammerman and Cavalli-Sforza (1984) suggested that the introduction in Europe of agriculture from the Fertile Crescent had an important demic component. Agricultural populations spread from the Fertile Crescent in a northwesterly direction. The process involved intermingling with preexisting hunter-gatherer populations and movement of the next generations of agriculturists further into Europe. Thus, agriculture spread over most of the European continent in a period of about 4,000 years between 9,000 and 5,000 BP at an average speed of about 1 km per year. The major gradient in contemporary human gene frequencies

has a Southeast-Northwest direction. Ammerman and Cavalli-Sforza (1984) argue that this gradient can directly be attributed to the migration associated with the introduction of agriculture into Europe.

V. THE DOMESTICATION SYNDROME

As already alluded to by Darwin (1859), the most intensively domesticated plants have lost their ability to survive on their own in the wild. In selecting plants to fulfill their needs for food, feed, and fiber, humans have—perhaps inadvertently—selected crops that, while they do extremely well in cultivated fields, are unable to grow and reproduce successfully for more than a few seasons in natural environments, away from the care of humans who provide adequate seed beds and reducing competition from weeds. What are the traits that have been modified as a result of selection under cultivation that have made crops so unadapted to the wild? As it turns out, many domesticated plants actually share several of these traits. Because of their repeated occurrence in widely different crops, these shared traits have been called the domestication syndrome (Hawkes 1983; Hammer 1984; Harlan 1992).

The two most important component characters of the domestication syndrome of seed-propagated crops are seed dispersal and dormancy. Domesticated types are characterized by lack of seed dispersal at maturity. This retention of seeds is realized in different ways depending on the crop. In cereal crops, a tough rachis prevents the disarticulation of the inflorescence and the release of seeds. Conversely, in wild graminaceous plants, an abscission layer is formed between each successive seed insertion site. At maturity, this layer causes the rachis to break and subsequently the dispersal of seeds. Seeds of domesticated plants display little or no dormancy compared to their wild progenitors, which usually have highly dormant seeds. On the one hand, dormancy prevents premature germination, which may be particularly important in unfavorable years, characterized, for example, by dry conditions unable to sustain the growth of seedlings. On the other hand, lack of seed dormancy promotes simultaneous germination and a more uniform population and, hence, harvest.

Domesticated plants generally have a more compact growth habit, with fewer and shorter branches. The most extreme case is maize. Teosinte, the wild relative of maize, has a highly branched plant growth habit, which contrasts markedly with the single stem of domesticated maize. The progenitor of some legume crops is a vine-like plant with long, twining branches (Fig. 1.2). This growth habit subsists in some



Fig. 1.2. Habitat of wild common bean (*Phaseolus vulgaris*) in Ecuador (see trifoliate leaves in the center of the photo). A viny growth habit allows plants to compete with the surrounding vegetation for light. Photo: P. Gepts.

domesticates but in greatly attenuate form as in climbing or pole varieties. These same domesticates often include bush or dwarf genotypes. The most recent stage of this trend towards a more compact growth habit is provided by the development of crop ideotypes. Donald (1968) proposed these growth habits to simultaneously increase productivity of individual plants and decrease competition among plants. A consequence of this trend is an increase in the harvest index in crops, the ratio of the harvested part (e.g., grains) to the total aboveground biomass. Whereas wild plants will typically have a harvest index of around 20-30%, contemporary advanced cultivars show a harvest index of 60% or more (Evans 1993).

The presence of toxic compounds has not been a major impediment to domestication, as evidenced by several crops that still contain these compounds, although in many cases at reduced levels. In these cases, the domestication process has included not only selection for the usual

traits of the syndrome, but also the development of a detoxification process. It is possible that in certain cases this process could have been invented prior to domestication. Food processing is known among hunters and gatherers (Johns and Kubo 1988). For example, Native Californians used to grind and wash acorn to remove tannins. Examples of crops with reduced toxicity following domestication include cassava (Wilson and Dufour 2002) and lima bean (Vanderborgh 1979).

A trait that has only recently received some attention as part of the domestication syndrome is the interaction between plant host and pathogens or other microorganisms, such as mycorrhizae and Rhizobium. A few preliminary studies have been conducted that suggest that these interactions have changed at the genetic level (Gouinguéné et al. 2001; Rosenthal and Dirzo 1997; Benrey et al. 1998; Gonzalez-Rodriguez et al. 2000; Lindig-Cisneros et al. 1997). Reciprocal selection between host and microorganism may have led to co-evolution and adaptation of the host and the micro-organism to each other. Further data are needed, however, to confirm these results.

One of the most important features of crop evolution is a change in the reproductive system of the plants involved. Usually, there is a change towards increased selfing (as in tomato or peppers; Rick 1988) or a replacement of sexual reproduction by vegetative reproduction, such as in banana/plantain (Simmonds 1966) or cassava (Elias and McKey 2000). Selfing or vegetative reproduction assures three goals. First, they would assure (re)production even under unfavorable conditions. This would be the case in particular when the crop was faced with environmental conditions unfavorable to fertilization or was disseminated into new areas without the corresponding pollinators. Second, trueness to type in the presence of outcrossing with wild relatives or other domesticated types could be maintained by farmers. Third, fruits would be more appetizing, as in the case of bananas where sterility has eliminated seeds from the fruit.

The ultimate agronomic trait, however, is yield. In addition to the harvest index already mentioned, other traits have played a role in influencing yield. Harvested organs in domesticated plants are usually much larger than those of their wild counterparts. For example, seeds of grain crops can be 5- to 10-fold larger than those of wild relatives. Because seed size is positively correlated with yield, selection for increased seed size may have led to increased yields, although yield component compensation may reduce the magnitude of this increase (Evans 1993). Heritability of seed size is usually high, thus, seed-size mediated increases in yield may have been relatively independent of environmental conditions. Other traits affecting yield are traits influencing the architecture

of the inflorescence such as reversal of sterility, which have operated in maize and barley, and increase in inflorescence size, as in maize and pearl millet (*Pennisetum glaucum*).

How then has yield fared under domestication? There are few if any historic measurements recorded of yield in wild stands, which would represent the base line for this question. Present day yield of a wild species of rice (*Oryza nivara*) in the Jeypore Tract in the state of Orissa, India, is about 1 t/ha. Stands of wild rice (*Zizania*) in North America today yield only 0.02-0.14 t/ha (Hayes et al. 1989). The wild relatives of cereals domesticated in the Fertile Crescent today yield around 0.5-0.8 t/ha (Harlan 1967; Zohary 1969). Araus et al. (2001) estimated the yield of wheat some 10,000 years ago to be around 1.5 t/ha. These numbers are similar to those deduced from cuneiform tablets, averaging about 2 t/ha around 4,400 BP (Jacobsen and Adams 1958). With time, these yields actually decreased to 1.2 t/ha by 4,100 BP and 1 t/ha by 1700 BC. Current wheat yields in the area are around 1 t/ha. This decline has been attributed to salinization of the land. This observation underscores the difficulty in distinguishing between genotypic and environmental effects in the assessment of the evolution of yield potential. In contrast, modern yields of rice are around 3,000 kg/ha in India and 6,000 kg/ha in China. Current yields of wheat are 2,000 kg/ha in Turkey, 3,000 kg/ha in Syria, and 4,000 kg/ha in the United States (FAO: <http://apps.fao.org/page/collections?subset=agriculture>). About 50% of yield increases can be attributed to genetic improvement (Fehr 1984).

Based on cob length data, Evans (1993) (his Fig. 6.7) estimated yield in maize to be around 1 t/ha some 1,000 years ago and some 0.5-0.6 t/ha around 2,000 years ago. Three thousand years ago, maize yields were approximately 0.4 t/ha. Furthermore, the initial stages of maize domestication (before 6,200 BP), which were characterized by fixation by selection of genes with major effects on the architecture of the inflorescence, may have seen initial rapid increases in seed yield. In an analysis of early (5,400 14C years) cob remains of Guilá Naquitz, Benz (2001) observed that the three samples were fixed for a tough (i.e., non-brittle) rachis and the presence of shallow fruit cupules, two domestication traits. The sample was heterogeneous, however, for the number of spikelets per cupule. Two inflorescences had one spikelet per node (and were, therefore, two-ranked), whereas the third inflorescence had two spikelets per node (and was, therefore, four-ranked). This increase in the number of seeds per inflorescence, which is positively correlated with seed yield, points to an increase in yield early on during the process of domestication. These observations suggest that the overall yield trend in maize during and after the initial domestication may have encompassed three major

phases: an initial fairly rapid increase, through conscious or inadvertent selection of major genes (see below), followed by a period of several millennia with a yield stasis or limited progress in yield potential due to inefficient farmer selection, and culminating, since the 20th century, in an era of marked progress through the application of modern plant breeding (Troyer 2000). A similar long-term trend in yield can be posited for other crops as a consequence of domestication.

Animals have also been modified considerably under domestication. The traits involved are mainly behavioral but some are also morphological (Zohary et al. 1998; Clutton-Brock 1999). For example, domesticated animals, in general and especially farm animals, are tolerant of human presence, further enhanced by imprinting of new-born animals. Human protection from predation reduced natural camouflage and allowed the appearance of contrasting color types. In addition, the size of the body, in general, and horns, in particular, and aggressive behavior have been reduced.

VI. INHERITANCE AND MOLECULAR BASIS OF THE DOMESTICATION SYNDROME

The inheritance of individual domestication traits has been based on a Mendelian approach with a segregation analysis on an individual trait basis (Ladizinsky 1985). This approach had major limitations because it was largely limited to traits with discrete segregation classes. More recently, however, the widespread availability of molecular linkage maps has allowed the conduction of genome-wide analyses based on the concept originally proposed by Sax (1923), namely to map genes for quantitative traits by establishing relationships between the continuous segregation of the quantitative trait and assess the discrete segregation of genetic markers. With this approach, one can analyze both quantitative and qualitative traits, determine the magnitude of the effect of individual genes (or at least chromosome regions), uncover the origin of the allele contributing to a trait, assess the overall proportion of phenotypic variation accounted for by the individual loci, and the linkage relationships among loci for the same or different traits. To analyze quantitative traits, replicated trials are necessary. Therefore, many studies have been performed in populations with permanent segregations such as doubled haploid or recombinant inbred populations. Disadvantages of this approach are that it tends to overestimate the effect of individual loci (called quantitative trait loci or QTLs) and that the chromosome location may be imprecise (several cMs) (Beavis 1994). Nevertheless, the chro-

mosome allocation in several instances has been sufficiently precise to initiate map-based cloning experiments, for example, *for* domestication genes (see below). In other cases, mapped QTLs *for* disease resistance were co-located with major genes *for* resistance to the same pathogen and with resistance gene analogues (Geffroy et al. 1999; Geffroy et al. 2000). Therefore, QTL analyses are powerful and sufficiently accurate analyses to analyze complex traits such as the domestication syndrome.

The inheritance of the striking differences between crops and their wild progenitors has been studied in a wide range of crops, including both outcrossing (maize, pearl millet) and selfing species (common bean, rice), using a QTL analysis approach. With the exception of sunflower, the results appear to be quite similar among these crops (Table 1.3). The average number of QTLs per trait ranged between two and five, a relatively small number, which can be attributed to limited sensitivity of the method against genes of small effect. For many traits, however, genes with major effect (R^2 or proportion of the phenotypic variation accounted for by individual genes > 25%; Burke et al. 2002) were identified, with some genes reaching $R^2 > 50\%$. The total genetic effect (i.e., sum of R^2 based on multiple regression) ranged between 40 and 50%, an underestimate given the sensitivity limits of QTL analysis. This suggests that

Table 1.3. Comparison of the inheritance of domestication syndromes in several crops^z

Crop	Mating system	Average no. QTLs or genes/trait	Average R^2 (%)	Total R^2 (%)	No. linkage groups	Source
Maize ($2n = 20$)	Outcrossing	5.3	12 (4-42)	50 (34-61)	5	Doebley et al. 1990
Pearl millet ($2n = 14$)	Outcrossing	2.2	29 (13-64)	57 (25-77)	4	Poncet et al. 1998, 2000
Common bean ($2n = 22$)	Selfing	2.2	23 (12-53)	45 (18-69)	3	Koinange et al. 1996
Rice ($2n = 24$)	Selfing	3.7	14 (7-60)	41 (16-72)	5	Xiong et al. 1999
Sunflower ($2n = 34$)	Outcrossing	4.3	12 (3-68)	NA ^y	13	Burke et al. 2002

^z Modified from Gepts 2002

^y Not available

phenotypic variation in crosses between wild progenitors and domesticated descendants is based predominantly on genetic differences rather than environmental effects. A striking observation is that some domestication genes seem to be clustered on a relatively small number of chromosomes (Fig. 1.3). In the crops mentioned, these results have also been confirmed in additional crosses involving different parents, such as in maize (Doebley and Stec 1991), pearl millet (Poncet et al. 2002), and rice (Cai and Morishima 2000; Bres-Patry et al. 2001; Cai and Morishima 2002).

The apparent exception presented by sunflower concerns two elements of this inheritance pattern (Burke et al. 2002). First, the number of genes with major effects was much smaller than in the other crops studied and, although domestication genes showed clustering, they appeared to be distributed over a larger number of chromosomes. One can speculate that the inheritance of the domestication syndrome is a reflection of the domestication process itself. For example, the presence of genes with large effects may have facilitated the rapid selection-conscious or unconscious-of traits during domestication. Conversely, the presence of these genes may signal that initial domesticates had been

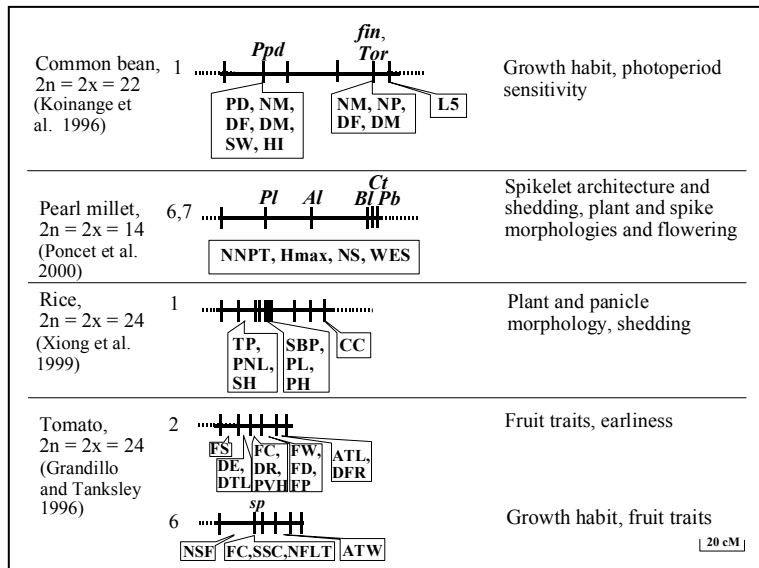


Fig. 1.3. Linkages among genes controlling the domestication syndrome in various crops.

subjected to a fairly strong selection pressure. The fact that a substantial part of the phenotypic variation can be accounted for in genetic terms suggests a relatively high broad-sense heritability that would have furthered the selection process during the early steps of domestication. Sunflower, compared to the other crops, may have undergone a slower domestication process, which did not require the presence of major genes.

Pernès (1983) suggested that linkage of domestication genes would be important in cross-pollinated crops because it would maintain the cohesion of some essential elements of the domestication syndrome when faced with repeated hybridizations of the sympatric wild progenitor. Linkage would limit recombination and aid in the recovery of domesticated types in the progeny of these crosses. This prediction was confirmed by the modeling study of Le Thierry D'Ennequin et al. (1999). They found that selection for increased fitness (increased number of domestication traits) led to selection of gametes with linked genes for domestication. The higher the outcrossing rate, the higher the proportion of parental (i.e., non-recombinant) gametes (Fig. 1.4). A similar observation was made for the migration rate. In the empirical data just reviewed, clustering, however, was observed not only in outcrossing species but also in species considered to be predominantly selfing. This suggests that these species are not as autogamous as they may seem or that they may have evolved towards autogamy as part of the domestication process. A higher level of outcrossing may have been important in the first stages of domestication to assemble the domestication syndrome. It would have been more likely that the different mutations constituting the syndrome appeared in different lineages than in the same one. Following the appearance of these mutations, they would have to be assembled into the same lineage by hybridization and recombined to achieve linkage in *cis*. Thus, linkage (but not too tight) would have facilitated the domestication process not only in outcrossing species but also in selfing ones. Linkage among domestication genes may have been made possible by clustering of genes in genomes, as shown not only by the existence of gene-rich regions in genomes (Fu et al. 2001; Weng and Lazar 2002) but also by the recent discovery of large regions (hundreds of kb) of similarly expressed but functionally unrelated genes ("expression neighborhoods" or "transcriptional territories") in the *Drosophila* genome (Spellman and Rubin 2002; Weitzmann 2002). The mechanism of the latter is not known but is likely to involve chromatin structure. The evolutionary importance may be assessed by analyzing the corresponding regions in other species. Conservation in the expression, size, and gene content of these regions would suggest a functional role.

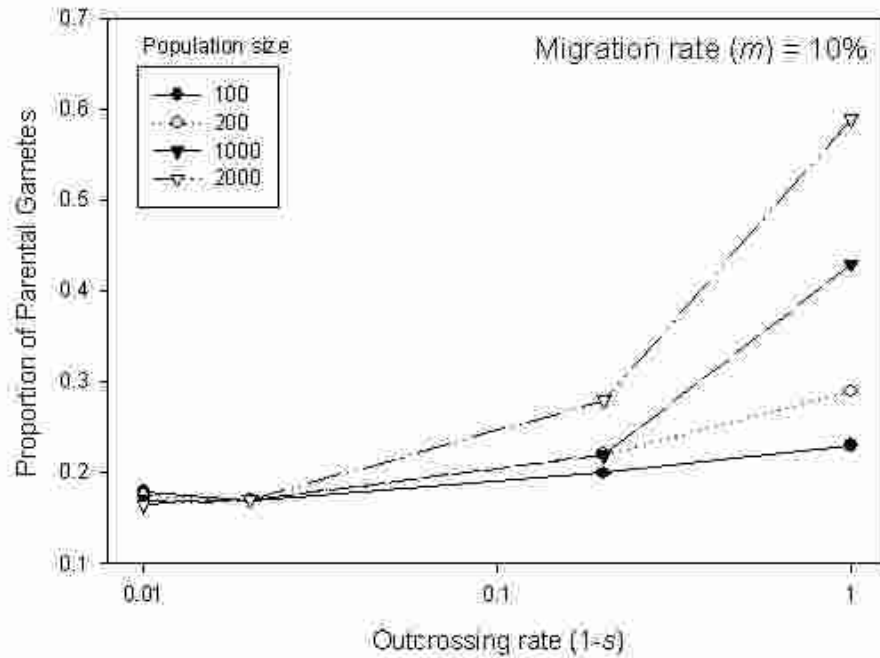


Fig. 1.4. Frequency of parental (non-recombinant) gametes as a function of outcrossing rates in domestication modeling study: linkage of domestication genes is favored in situation with high levels of outcrossing. Source: Le Thierry D'Ennequin, M., B. Toupance, T. Robert, B. Godelle, and P. Gouyon. 1999. Plant domestication: A model for studying the selection of linkage. *J. Evol. Biol.* 12:1138-1147. With permission, Blackwell and the authors.

Whether clusters of domestication genes belong to any expression neighborhood remains to be determined.

An additional consequence of hybridization is to transfer genes into different genetic backgrounds, which may allow expression of novel epistatic interactions that would only be active when different genes for domestication coexist within the same genome. An example is provided by Lukens and Doebley (1999), who backcrossed two unlinked teosinte alleles affecting plant growth habit (branching) into a domesticated maize background, either singly or in combination. The *tb1* allele had a strong additive effect on its own, but the second teosinte allele only had a phenotypic effect in the presence of the *tb1* allele. This led Lukens and Doebley (1999) to suggest that domestication involved not only selection on individual genes but gene complexes. They also observed that plants with the teosinte allele were phenotypically more plastic than their

counterparts with the maize allele. This observation may extend to other genes for domestication and is of concern for the current efforts to introduce additional genetic diversity from wild types. When attempting this, both the magnitude and the variance of the expression of the trait should be considered.

Polyploidy has affected the evolution of crops as well, although the effects may not be specific of domestication but rather reflect the high frequency of polyploidy among angiosperm species. Estimates of the frequency of polyploidy among angiosperms range from approximately 30% to 80% with a mode of 50% (Soltis and Soltis 2000). Hilu (1993) showed that the frequency of polyploids among crops is comparable to that of angiosperms in general. Furthermore, there were no differences in frequencies when considering taxonomic origin, habitat, life history (annual, perennial), and reproductive strategy. In addition to general attributes responsible for the success of polyploids (Soltis and Soltis 2000), some specific factors impinge upon the success of polyploids as crop plants. For example, polyploids have increased heterozygosity, which may in turn be associated with heterosis. The nature of this heterozygosity differs, however, between autopolyploids (arising through hybridization involving conspecific parents) and allopolyploids (arising from crosses involving species with diverged genomes). In the former, the increased heterozygosity stems from the polysomic inheritance, whereas in the latter, the heterozygosity results from the combination of different subgenomes into a single genome. The mode of origin of autopolyploids has an effect on the level of heterozygosity transferred to the progeny. In general, autopolyploids arising from the production of $2n$ gametes have higher levels of heterozygosity than those arising from chromosome doubling of the progeny. Furthermore, $2n$ gametes arising from first division restitution maintain a higher level of heterozygosity compared to those arising by second division restitution. Levels of heterozygosity have been correlated with potato tuber yield (Peloquin 1981). A second important characteristic is a widening of the ecological amplitude of species by polyploidization. Bread wheat (*Triticum aestivum*, with an AABBDD genome) is a cultigen, a plant type growing only under cultivation. It arose from the hybridization between emmer wheat, a domesticated tetraploid (*Triticum durum*, with the genome AABB), and a wild species, *Triticum tauschii*, with a DD genome. This hybridization took place when agriculture moved out of the Fertile Crescent into adjacent areas. In this particular case, emmer wheat moved out of the Fertile Crescent into the Caspian Sea region. The addition of the D genome broadened the adaptation of emmer wheat to include more continental climates than the Mediterranean climate to

which it was adapted. It now also became more adapted to regions with hotter summers and more severe winters (Sauer 1993).

Bread wheat serves to illustrate an additional feature of polyploidy, namely the opportunity for additional epistatic interactions between genomes. Seed proteins called glutenins give wheat flour a certain type of elasticity that entraps CO₂ bubbles resulting from fermentation of sugars by yeast. As a consequence, the dough rises and creates a lighter type of bread after baking. This property is unknown in the two parents of the hexaploid, suggesting that it arises from an interaction among genes of the two progenitors (Smith 1995b). An additional example is provided by cotton (Jiang et al. 1998). A QTL analysis conducted in a cross between Upland cotton (*Gossypium hirsutum*) and Pima cotton (*Gossypium barbadense*) (both species with AADD genomes) showed that most QTLs for fiber yield and quality originated in the D genome, in spite of the fact that only the A genome parent produces spinnable fiber. Interactions between the D genome fiber QTLs and genes in the A genome allowed the D genome gene to be expressed. Jiang et al. (1998) suggested that the reason that QTLs came predominantly from the D genome was due to fixation of "favorable" alleles in the A genome species. Absence of phenotypic expression of the fiber potential would have prevented the selection, and, therefore, fixation of these alleles in the D genome parent.

Several genes for domestication have now been cloned. These include the *tbi* gene in maize, which controls plant growth habit (Doebley et al. 1997; Wang et al. 1999, 2001). Specifically, it reduces the number and length of branches. The maize allele constitutes one of the exceptions to the rule that domesticated alleles are generally recessive. In this case, the dominance of the domesticated allele rests on increased levels of the message of the gene. The as yet unidentified lesion resides in the 5' upstream regulatory region of the gene. The *fw2.2* gene in tomato is a QTL that increases fruit weight by up to 30% (Frary et al. 2000). The corresponding gene is expressed early in fruit development; it is expressed at a higher level in wild, small-fruited types, than in larger, domesticated types, consistent with the dominant nature of the wild allele. Sequence comparisons show that the gene may be related to the RAX gene family, which codes for, among others, proteins controlling cell division. The gene product has a structural similarity to a human oncogene.

The *Hdl* gene in rice controls response to photoperiod and is a QTL for flowering time (Yano et al. 2000). It may be promoting flowering under short day conditions and inhibiting it under long day conditions. The levels of message are similar under long and short day conditions, suggesting that other genes are also involved in photoperiod response. The HDI

protein has two zinc finger domains and is therefore likely to be a regulatory, DNA-binding protein. The DNA sequence is similar to the flowering time gene *CONSTANS* in *Arabidopsis thaliana*. In rice, the *Hdl* gene is allelic to the *Sel* gene controlling photoperiod sensitivity. The wild allele is dominant. In *A. thaliana*, the *SHA TTERPROOF* genes (*SHP1* and *SHP2*) control fruit dehiscence (Liljegren et al. 2000). The two genes are redundant and can substitute for each other. They cause the differentiation of the dehiscence zone and the lignification of the adjacent cells. Their sequence includes a MADS box motif, suggesting that they are regulatory genes. Finally, the *CAULIFLOWER* gene in *Arabidopsis* and *BoCAL* gene in *Brassica oleracea* affect inflorescence structure and are responsible for the cauliflower and broccoli phenotypes (Purugganan et al. 2000). Sequence analysis reveals that this gene is also a MADS box gene and that the lesion resides in ex on 5 of the gene, resulting in a premature stop codon in the middle of the K domain of the MADS-box transcriptional activator. This mutation has appeared only once in *B. oleracea* and has achieved fixation in the cauliflower accessions and near-fixation in the broccoli accessions sampled. It is, however, also observed in other taxa that do not display an altered inflorescence phenotype, suggesting that the *BoCAL* gene is not sufficient to control the cauliflower phenotype.

This brief overview of the molecular basis of domestication traits confirms the predominance of recessive mutations among domestication alleles. It may be significant here that the exception so far is the *tbi* gene in maize. As maize is a highly outcrossed species, dominant mutations would be more readily selected than recessive mutations. Conversely, in selfing species recessive mutations would be more readily selected because the frequency of homozygosity is higher compared to outcrossing species. Most of the genes involved in these morphological changes are regulatory genes, whether the lesion resides in the 5' upstream regulatory genes or in the coding portion of these genes. Isolation of these domestication genes is a prerequisite to conduct molecular population genetic studies associated with the domestication process and to understand evolutionary factors that have affected the crop, including selective sweeps and gene flow processes.

VII. GENETIC BOTTLENECKS

A feature shared by nearly all, if not all, domesticated plants is a reduction in the genetic diversity during and after domestication. This genetic bottleneck has been measured with a variety of biochemical or molecular markers, including isozymes, seed proteins, RFLPs, RAPDs, AFLPs,

and more recently DNA sequences of specific genes. The magnitude of these bottlenecks depends on the type of markers. For example, chloroplast DNA restriction analyses (reviewed by Doebley 1992) show a marked decrease in genetic diversity between wild and domesticated types in widely different crops, including barley, sunflower, pea, sorghum, and maize (on average 75%). At the nucleotide sequence level, there have been fewer comprehensive studies. Only in maize have a large number of genes been studied. In that species, there has been on average a reduction in diversity of 30% compared with diversity in teosinte (White and Doebley 1999). Additional studies, reviewed by Buckler et al. (2001) suggest that other cereal species also are characterized by a genetic bottleneck of about 30% when considering nucleotide diversity.

Molecular data contrast with phenotypic data in that the latter show an increase in diversity. Darwin (1859) observed that the harvested organs of domesticated plants were more diverse than those of their wild relatives. The contrast between the two types of data can be reconciled by positing that the two traits are probably subject to different evolutionary factors. Molecular marker data are generally neutral and may be subject to genetic drift, whereas domestication traits (phenotypic data) are subject to selection. The stronger the selective advantage (in the cultivated environment), the higher the probability of survival of the domestication trait (Crow and Kimura 1970).

Caution should be exercised, however, because levels of diversity will vary substantially among genes as a function of position along chromosomes. There is a positive relationship between recombination and genetic diversity in *Drosophila* (Begun and Aquadro 1992), wheat (Dvorak et al. 1998), and tomato (Stephan and Langley 1998). In addition, population size plays a large role in determining the overall levels of genetic diversity. Superimposed on these differences attributable to genome organization and population levels are the effects of selection, particularly of selection during domestication. White and Doebley (1999) summarized studies in maize examining the genetic diversity at six loci, four of which were considered neutral (*adh1*, *adh2*, *te1*, and *gbl1*) and two that were involved in domestication (*tb1* and *c1*). In the group of four loci, diversity in the domesticated gene pool was more than half that found in teosinte (*ssp. parviglumis*). For example, when total sites are considered, variation among domesticated maize genotypes for *adh1* was 83% of that in teosinte and 60% for the *gbl1* locus. For the two domestication genes, variation contained in the domesticated gene pool was much lower. For instance, variation for *tb1* was 1-2% of that observed in teosinte.

Eyre-Walker et al. (1998) and Hilton and Gaut (1998) investigated the size and length of the genetic bottleneck that existed during maize domestication based on sequence variation and coalescent simulations for the *adh1* and *gbl1*, respectively. Both studies found that the domestication bottleneck could have been of short duration and small size. Using the combined results of both studies, the bottleneck could have had a duration of 10 generations or years and involve some 10 individuals. Considering a time frame of 2,800 years, an estimate of the duration of domestication of maize based on the archaeological record, the bottleneck would have had a size of approximately 2,900 individuals, still a remarkably small number.

Hopefully, current efforts in genomics will be applied to issues in crop evolution and will not remain confined to undomesticated model systems such as *Arabidopsis* and *Medicago truncatula*. High throughput methods can be used to evaluate sequence diversity for a larger sample of genes of known genome location in a larger number of species with contrasting life histories and domestication characteristics.

VIII. IS THERE A POTENTIAL FOR DOMESTICATION AMONG PLANT AND ANIMAL SPECIES?

There are some 250,000 angiosperm species. Of those, less than 500 have been subject to at least some attempts at domestication (Harlan 1992). Among animals, there are some 5,000 species (Myers 1999), of which less than 20 have been domesticated (Clutton-Brock 1999). Why were more species not domesticated? An admittedly incomplete list of non-mutually exclusive explanations is proposed here, which are often speculative in nature. In a general sense, for domestication to take place a number of conditions need to be satisfied from three angles: human, domesticate, and environment (Fig. 1.5). Domestication will proceed only if the conditions are satisfied in the three areas. Archaeologists study primarily the human factors and how these interact with environmental factors. Biologists focus on the plant or animal factors, although the intrinsic factors that determine whether a given plant or animal could be domesticated remain to be determined. For example, Diamond (1997) focused his analysis of domestication primarily on environmental factors influencing the various domestication areas and their subsequent influence on the development of agriculture and society.

On the plant or animal domesticate side, some species are probably more "susceptible" to domestication than others. It was F. Galton (cited

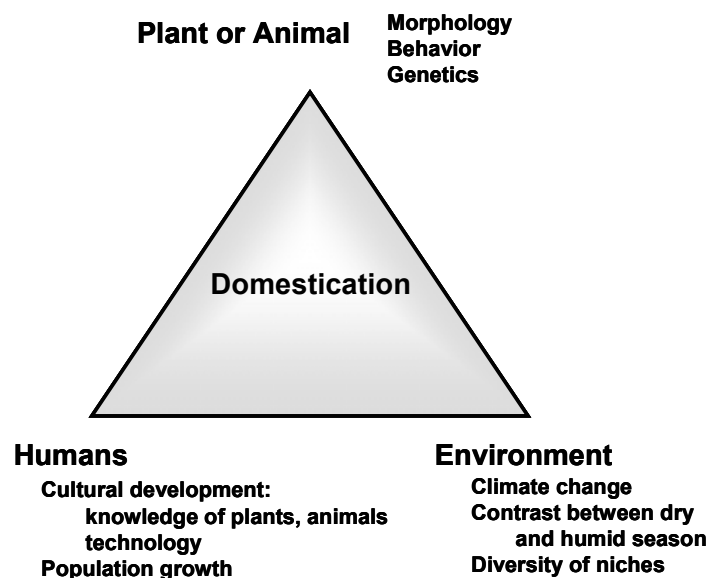


Fig. 1.5. Domestication results from the interactions of plant or animal, human and environmental factors. All three factors are required for domestication to take place.

by Clutton-Brock 1999), who in 1865 pointed out that animals should have the following characteristics (as rephrased by J. Clutton-Brock) under which they might be domesticated: (1) adaptable to different conditions, such as diet, environment, and disease pressure; (2) an inborn liking of man or at least no intense dislike or fear of humans; (3) tolerance of herding and constraint in a pen; (4) usefulness as a source of food or for other uses given the amount of effort required to rear the animals; (5) breed freely (in contrast to the difficulties encountered by zoos in maintaining some wild animal breeds or species); and (6) easy to tend by being placid, versatile in their feeding habits, and gregarious.

These characteristics in animal domestication are mainly behavioral. Although they may appear to constitute a rather unusual combination of traits that would exist only rarely among animals, which might explain the rarity of domestication, one also needs to demonstrate that other animals could not be domesticated for whatever reason. A recent study by Cameron-Beaumont et al. (2002) on potential cat domesticates is illustrative in this respect. The cat was domesticated in ancient Egypt. Some breeds of cat such as Persian and Siamese are fully domesticated,

as they satisfy the criteria of permanent isolation from the wild species and human control of breeding, territory, and food supply (Clutton-Brock 1999). Cameron-Beaumont et al. (2002) pointed out that in the cat family small felids other than the domestic cat display affiliative behavior towards human (similar to criterion 2, mentioned above). They investigated whether members of the ocelot ("small cat") lineage of the Felidae (a non-domesticated lineage) displayed affectionate behavior towards humans in captivity, such as sitting or rolling within 1 m of the keeper, head or flank rubbing, and licking of the keeper. They found that, in addition to the progenitor of the domesticated cat, other members of the Felidae displayed affiliative behavior, especially in the ocelot lineage of South America, including Geoffroy's cat (*Oncifelis geoffroyi*) and the margay (*Leopardus wiedii*). They concluded that ecological and geographical separation between humans and potential domesticates could explain why only some species were domesticated.

In plants, morphological features facilitating domestication are those listed in Section VI. What is not well known is to what extent different, non-domesticated species, especially related ones, display these traits or to what extent these traits could appear by mutation repeatedly in different species. Harlan (1967) pointed out that wild grass species show differences in threshing ratio (ratio grain over total biomass in the inflorescence, which includes rachis and glumes in addition to grain). Wild einkorn wheat had a threshing ratio of around 40%, whereas domesticated einkorn had a ratio of 70%. *Aegilops squarrosa*, which was never domesticated itself but is a putative donor of the B genome, had a threshing ratio of 10%. Clearly, wild einkorn is a better starting material for domestication than *A. squarrosa*.

There are several examples of crops where more than one species has been domesticated in a given genus, suggesting that to some extent phylogenetic relationships can help predict the domestication potential of a species. These include bean (*Phaseolus* spp.), pepper (*Capsicum* spp.), cotton (*Gossypium* spp.), and black and green grams, rice bean, and adzuki bean (*Vigna* spp.). However, there may be differences among these species in the degree of domestication. In the genus *Phaseolus*, the common bean (*P. vulgaris*) is by far the most strongly domesticated species when one considers the number of traits and the level of expression compared to its wild progenitor. In other domesticated *Phaseolus* species, some traits of the domestication syndrome, such as the determinate growth habit or stringless pods, are absent. This could mean that, for some reason, the traits were either never selected for or never appeared. Four of the five species, common bean (*P. vulgaris*), runner bean (*P. coccineus*), year bean (*P. polyanthus*, a hybrid species between the two

former species), and the tepary bean (*P. acutifolius*) belong to the same clade within the genus. The fifth species (lima bean) belongs to a very different clade of the genus. Thus, domestication potential may be unevenly distributed within the genus *Phaseolus*. A similar argument or analysis can be made for other genera or species of plants and animals.

Reproductive system and life history have influenced domestication. Generally, the earliest domesticates have been annual grain plants, with a selfing reproductive system. Maize, with its allogamous reproductive system, is a notable exception. Selfing and vegetative propagation may have been favored because they facilitate "true-to-typeness" after selection of a favored phenotype. It has been noted by Hancock (1992) that in any domestication there are several waves of domestication. The first wave included basic food crops, primarily annual grain crops. The second wave included vegetables and fruit trees. Later on, forages were domesticated. Fruit trees underwent limited domestication. Very often bud mutations were selected and propagated vegetatively. Thus, many fruit tree varieties differ little from other varieties and from their wild progenitors. It is also difficult to distinguish them from their wild progenitor. They can also naturalize easily and form feral populations that are difficult to distinguish from truly wild populations such as olive (Bronzini de Caraffa et al. 2002). Similar observations can be made to a lesser extent with forage crops.

Are there genetic characteristics that would favor domestication? As Darwin (1859, 1868) pointed out, genetic diversity has to be present or at least be generated by mutation during the time frame of the domestication phase. As mentioned earlier, there are few studies of mutation rates in plants and mammals, let alone comparisons among closely related domesticated vs. undomesticated species. Linkage of certain domestication genes may have been crucial to facilitate selection of the domestication syndrome (or certain crucial aspects of it). Thus, those species that have clustered domestication genes would have been easier to domesticate. Additional information on linkage from species that have not been domesticated would be required to help answer the question of whether linkage of certain genes is a prerequisite for domestication.

Paterson et al. (1995) observed in a series of cereals from distinct domestication centers (maize from Mesoamerica, sorghum from Africa, and rice in China) that some domestication traits appeared to be controlled by homologous genes. These observations were made possible by the existence of extensive synteny among grass species (Bennetzen and Freeling 1993). The traits investigated included seed size, seed shattering, and photoperiod response of flowering. Although there is some uncertainty as to the specific location of the genes because they were

analyzed by QTL analysis, corresponding locations occurred more often than just by chance. Overall, these results suggest that the same genes in different crops seem to be selected for in geographically widespread and independent domestication. Although these traits are complex and likely involve many genes, it appears that it is always the same set of genes that is selected. Why are these genes selected and not others? Additional information on these genes as well as other genes controlling the same trait will need to be obtained. In particular, mutagenesis and other experiments with homologous genes in related, undomesticated species will have to be conducted.

The cat example illustrates that human society needs to be present, predisposed towards domestication, and capable of taming or domesticating. These conditions were fulfilled in Ancient Egypt but not in lowland South America (although some plants such as peanut and cassava were domesticated in what is now part of the distribution area of some of the ocelot lineage felids). From crop studies, it is known that some initial domesticates have been abandoned. These include crops domesticated in the Eastern North American and Northern Chinese centers of crop domestication. The former gave rise to, among others, goosefoot (*Chenopodium bushianum*), marshelder or sumpweed (*Iva annua*), little barley (*Hordeum pusillum*), and sunflower (*Helianthus annuus*). Except for the latter, the other domesticates have become insignificant or have disappeared after domesticates (maize, squash, and beans) were introduced from the Mesoamerican center some 700-1,000 years ago. In northern China, broomcorn and foxtail millet were domesticated. Their importance diminished after introduction of rice, which had been domesticated further to the South in China as well. Thus, a number of species have been domesticated, but for reasons that are not well understood, and their cultivation was discontinued or sharply curtailed. It may be that they succumbed to the introduction of a dominant culture from elsewhere (including the crop plants associated with that culture). Or, alternatively, introduced crops had distinct agronomic or nutritional advantages over the native crops.

Finally, one has to ask how many crops can a society domesticate at once, especially of the same type (e.g., cereals or sources of carbohydrates; legumes or sources of protein). Lev-Yadun et al. (2000) suggested that domestication of the "founder crops" of the Fertile Crescent (einkorn, emmer, barley, pea, chickpea, lentil, and flax) had all taken place in a restricted area in southern Turkey. This assertion was based on genetic results for einkorn wheat (Heun et al. 1997) and Salamini et al. (2002) for emmer wheat showing close relationships between wild and domesticated types in that area (see previous discussion) as well as

an overlap in southern Turkey of the contemporary distribution of the wild relatives of the founder crops. Badr et al. (2000) have shown a domestication center for barley in the southern Levant (the western branch of the Fertile Crescent). Other areas that have remained inaccessible for political reasons remain to be explored, particularly in northern Syria and Iraq, so that they can either be identified or excluded as actual areas of domestication of these founder crops. It may well be that in a given area, only one cereal or legume would have been domesticated. Additional attempts at domestication would have been seen as too cumbersome and would not have been attempted as long as the original domesticate provided satisfactory returns. In *Phaseolus* beans, one of the centers of domestication of lima bean (*P. lunatus*) is located on the western slope of the Andes of Ecuador and northern Peru at mid to lower altitudes (Gutierrez Salgado et al. 1995). This center gave rise to the so-called "Big Lima" types of lima bean. It is remarkable, however, that at slightly higher altitudes wild populations of common bean are growing, which appear never to have been domesticated (Debouck et al. 1993; Kami et al. 1995) even though they were domesticated elsewhere. This observation suggests that in any given region only a limited number of species will be domesticated in spite of the suitability of other species. It may be that there are only a limited number of species that can be domesticated at any given time.

Thus, there are a number of reasons why so few species were domesticated. Some of these are related to intrinsic characteristics of the plants or animals. Others are related to humans and the environment in which agriculture originated. It does suggest, however, that there remain other species to be domesticated.

IX. SUMMARY

There are a number of evolutionary features under cultivation or herding by humans: (1) among major cultural developments in human evolution, agriculture is perhaps one of the only ones that independently originated multiple times in widely different areas; (2) a specific area within a broader center of domestication can now be proposed using sensitive molecular marker technology; (3) a shared feature among most domesticated plants is a marked genetic bottleneck; (4) the genetic architecture of the domestication syndrome suggests that there was no genetic impediment to a fast domestication process (less than 100-200 generations); and (5) circumstantial evidence suggests that some species may be more amenable to domestication than others. Further research is

needed, however, to fully identify the biological features that render domestication possible.

Wild-to-domesticated complexes are excellent experimental systems to investigate certain evolutionary issues. There is a known time frame extending some 10,000 years. Both the progenitors and their descendants are known. This allows the integration of evolutionary and developmental genetics and a closer look at those differences at the molecular level that are responsible for the phenotypic differences between wild and domesticated types. In the past, crop evolution has been dismissed as not typical of evolution at large, because the high level of selection pressure was thought to be unusual in natural environments. While it is true that selection in nature may operate at longer time intervals, there is now plenty of evidence that strong selection also exists in natural environments (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001). Thus, the study of evolution under plant cultivation or animal rearing has broader implications for the study of evolution in general. Its information is also useful to further develop crop or animal biodiversity, conservation, and breeding programs.

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