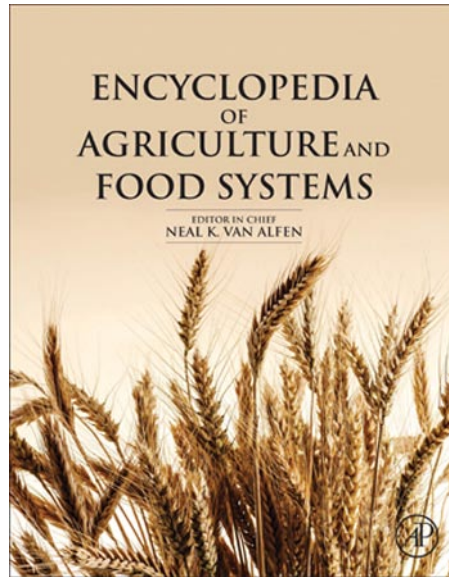


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Gepts P. Domestication of Plants. In: Neal Van Alfen, editor-in-chief. *Encyclopedia of Agriculture and Food Systems*, Vol. 2, San Diego: Elsevier; 2014. pp. 474-486.

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Domestication of Plants

P Gepts, University of California, Davis, CA, USA

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Glossary

Archaeobotany The identification and analysis of botanical remains found in archeological investigations. The remains can be subdivided into macroremains (identifiable to the naked eye) and microremains (require the use of a microscope). Among macroremains are seeds and pods. Microremains include pollen grains and subcellular structures like starch grains and phytoliths (silica deposit inside plant cells). The shape of microremains can be diagnostic of the identity of the plant material. The conservation of archaeobotanical remains can be favored by certain environmental conditions (like dryness or excess water).

Centers of agricultural origins Agriculture started in multiple locations in the world some 10 000 years ago. These locations (where crop domestications took place) are distributed in some 10 areas generally between 30° northern latitude and southern latitude. They tend to occur in areas with higher levels of biodiversity.

Domestication Evolutionary process driven by natural and human (whether conscious or unconscious) selection applied to wild plants or animals and leading to adaptation to cultivation and consumption or utilization. Domestication can be complete, whereby organisms become entirely dependent on humans for their continued existence or can be partial or incipient, whereby they still reproduce independently of human intervention.

Domestication syndrome A set of morphological, biochemical, and physiological traits that distinguishes domesticated plants or animals from their wild progenitor. These traits depend on the life history (annual vs. perennial) and reproductive system (outcrossing, selfing, and vegetative reproduction). Traits affected include dispersal of

propagules (e.g., seed shattering and pod dehiscence), seed dormancy, growth habit, diversity of harvested parts (size, shape, and color), flowering response to environmental cues (temperature and day length), organoleptic qualities (taste, texture, and toxicity), and any other traits affecting harvested product use (e.g., fiber quality).

Molecular markers Markers are traits with a simple inheritance (like Mendel's characters). Molecular markers are based directly or indirectly on deoxyribonucleic acid (DNA) sequence variation. Indirect molecular markers are proteins, such as isozymes (enzymes of the basic metabolism, which can be distinguished by their electric charge) and seed proteins (which can be distinguished by their size). Direct molecular markers include RFLP, RAPD, AFLP, etc. markers (which can be distinguished by the DNA fragment sizes). Increasingly, the actual DNA sequence is used to distinguish among individuals and trace back their ancestry.

Quantitative trait loci Locus controlling a quantitative trait that differs from a Mendelian trait (or marker locus: see Molecular marker) in that it does not exhibit clear-cut segregation classes because the trait is controlled by more than one gene or is subject to environmental effects or a combination of the two. These are often measured traits (e.g., yield and seed weight) or counts (number of seeds or days to flowering). Because of the lack of segregation classes, the inheritance is analyzed by correlating markers with the expression of the trait in segregation populations resulting from the cross between two contrasting parents.

Taphonomy The science of fossilization. It studies the factors that favor or hinder the formation of fossils.

Introduction

The evolutionary lineage leading to the modern human species (*Homo sapiens*) has been marked by several key inventions, such as the development of increasingly sophisticated tools (Stout, 2011), the mastery of fire (Alperson-Afil and Goren-Inbar, 2010; Berna *et al.*, 2012; Twomey, 2013), the acquisition of writing (Houston, 2004), and the current digital revolution. Among these inventions is agriculture or the transition from hunting-gathering (HG) to the cultivation of crops and tending of animals. This transition initiated a change that cannot be overestimated in all aspects of life on the earth, including the biological and physical environment and, obviously, also the way of life of humans. It is, therefore, not surprising that this transition has been called the Neolithic Revolution.

The signs of the changes brought about by the momentous introduction of agriculture are numerous. For example, many

famous 'natural' landscapes on the earth are actually agricultural landscapes: the rice terraces of Yunnan in China, the rolling, cypress-studded lands of Tuscany in Italy, and the big-sky, luminous plains of the Palouse in Northwest United States. Thirty-eight percent of total land area is now devoted to agriculture, making it currently the single most important land use. For example, forests (most of which are subjected to some type of anthropic exploitation) only account for 30% of the land area (FAO, Land use database).

Among the changes that were more or less concurrent with the origination of agriculture were sedentism (as opposed to nomadism) and the appearance of villages and ultimately cities, the introduction of ceramics, the transformation of more egalitarian societies into more hierarchical ones, a stronger division of labor by the addition of nonfood production related occupations, and, later on, the introduction of writing. The actual sequence and order of these technologies is still being disputed and may diverge in different regions where

agriculture was initiated. Ultimately, the transition from HG to agriculture was a precursor and a necessary condition for the eventual appearance of civilizations. The sequence of events subsequent to the initial transition to agriculture is beyond the scope of this article but is the subject of intensive, long-term studies (e.g., Maisels, 1993; Price and Bar-Yosef, 2010; Kuzmin *et al.*, 2011). As stated by Diamond (1997), "plant and animal domestication meant much more food and hence much denser populations. The resulting food surpluses ... were a prerequisite for the development of settled, politically centralized, socially stratified, economically complex, technologically innovative societies."

Agriculture has been for some time and is still the main source of food, fiber, and feed for humanity. So far, it has been able to keep up with the tremendous growth in population. It has been estimated that the total human population at the time of the Neolithic Revolution was approximately 6 million people (Livi-Bacci, 2012), which now amounts to 7 billion (World Population Clock, US Census Bureau), with a nearly certain prospect of a further increase of 2 billion by 2050 (United Nations, Department of Economic and Social Affairs). The current hunger episodes are not due to insufficient production but other factors affecting food security (FAO, The State of Food Insecurity). Nevertheless, the dominance of agriculture as a human activity has come at an ecological price, which includes habitat destruction, reduction in biodiversity both of natural and agricultural ecosystems, widespread contamination with chemicals of agricultural origins, such as fertilizers and pesticides, and a significant part of the emissions of greenhouse gases.

It is in this broader context that domestication of crop plants (and farm animals) has operated, not only as a component of the adaptive process to which cultivation (or captive rearing) has subjected them by humans but also more broadly as part of the Neolithic Revolution that included the transition from HG to agriculture.

The Concept of Domestication and the Domestication Syndrome

Domestication is, in essence, an evolutionary process of selection for adaptation to changed environmental conditions, as plants are not only consumed but also actively cultivated. Cultivation is a necessary condition for domestication to take place. The selective forces that act on plant populations in the original natural environments are to a great extent different from those in the subsequent cultivated environments. In natural environments, strong intra- and interspecific competition exists among plants for light, water, and soil nutrients. In contrast, agroecosystems are characterized by less competition, even in well-known, diverse arrangements like agroforestry (Leakey, 1998; Perfecto and Vandermeer, 2010) and gardens (e.g., Ban and Coomes, 2004; Buchmann, 2009). This reduced competition is then converted into higher productivity for harvested organs (e.g., grain, leaves, roots, etc.) through modified partitioning of photosynthates and a higher harvest index (ratio of harvested biomass to total biomass).

A second major difference between natural and cultivated environments is the need for developing a more efficient

production system, in terms of biomass per unit of surface and time. The overall goal has been to increase the harvested biomass although decreasing the total effort necessary to harvest this biomass. Hence, several traits have been selected to achieve this goal. These traits include: (1) loss of seed dormancy, which led to more uniform stands at planting; (2) a more compact growth habit, with reduced branching and shorter branches, which reduces intraspecific competition and makes harvest more synchronous; (3) a tendency for reproduction to evolve from outcrossing to inbreeding to vegetative propagation, which makes reproduction less dependent on abiotic and biotic factors; and (4) reduced or loss of seed shattering, which limits grain losses at harvest.

Third, humans also exert an important selective role not only as farmers but also as consumers of their production, irrespective of whether it is for food, feed, or fiber. A key aspect here is the attraction of humans for novelties, such as new seed and fruit colors or shapes, which has led to the striking morphological diversity in some crops, such as developmental differences in cabbages (*Brassica* spp.: red cabbage, Brussels sprouts, cauliflower, etc.); seed color, size, and shapes in certain legumes (*Phaseolus* sp. and *Vigna* sp.); and fruit size, shape, texture, and color in the Rosaceae (e.g., apple: *Malus* sp.; pear: *Pyrus* sp.; and cherry and plum: *Prunus* sp.). Generally, domestication has led to an increase in the size of the harvested organs, irrespective of whether they are roots, leaves, fruits, or grains. Increases in size can sometimes be remarkable as they can reach a 10x–20x difference between wild and domesticated types. Plants generally contain toxic substances that fulfill several functions like protection against diseases or pests. During domestication, the concentration of these compounds has generally decreased in all or at least part of the domesticated gene pool, as shown, for example, by the reduction in cyanogenic glucosides in cassava (Bradbury *et al.*, 2013) or lima bean (Vanderborght, 1979).

The existence of these sets of correlated traits that are characteristic of domesticated plants and show some degree of consistency among different, even unrelated, crops led Hammer (1984) to call them 'domestication syndromes.' Such syndromes are generally applicable to more strongly domesticated plants; however, there are sometimes important differences among crop plants, depending on their life history and reproductive mode (Harlan *et al.*, 1973; Smartt, 1990; Ladizinsky, 1998; Hancock, 2004; McKey *et al.*, 2010, 2012). Perennial plants, such as fruit and nut trees or vines, often show more limited differences between wild and domesticated types because of their extended juvenile phase, long life cycle, high gene flow levels, and potential for vegetative reproduction (Miller and Gross, 2011). For example, the main domestication trait in grape vine is the evolution from a diecious (separate male and female individuals) reproduction to an autogamous reproduction, made possible by hermaphroditic flowers (with both male and female reproductive organs). This change is controlled by a single locus (Battilana *et al.*, 2013). Thus, in general the domestication syndrome of perennial crops consists of fewer differences between wild progenitor and domesticated descendant (Pickersgill, 2007). The expression of constituent traits is also often limited. For a given crop, there may be different domestication syndromes, depending on the local production circumstances. For example,

one could envision a different domestication syndrome for maize grown for grain (as is currently the case) or for its vegetative matter as feedstock for biofuels. The latter could involve a more branched plant type that increases the production of stems and leaves rather than grain. Meyer *et al.* (2012) provided an extensive overview of the broad range of traits characterizing domesticated plants. Dempewolf *et al.* (2008) provided a discussion on the level of domestication.

Finally, the constituent traits of the domestication syndrome are often deleterious in the wild. For example, more compact growth habits and loss of spontaneous seed shattering reduce the fitness in natural environments because they limit competitiveness with the surrounding vegetation and reproductive ability, respectively. Although they are selected against in the wild, the opposite is true in agricultural environments.

Where Did Domestications Take Place?

The domestication of crops, as an invention, is embedded in the origins of agriculture. The transition from HG to agriculture has taken place in multiple regions of the earth, remarkably at about the same time approximately 12 000–10 000 years ago in the aftermath of the last (Wurm) ice age. The actual causes for this transition are poorly understood and therefore both the location and timing of the transitions can only be investigated empirically using a combination of information from different fields, each with their strengths and weaknesses.

The main fields contributing knowledge about the origins of agriculture have traditionally been archeology, biology, linguistics, and history as proposed by de Candolle (1882) in the nineteenth century. Since then, a broad range of scientific fields have been applied to solve the puzzle of agricultural origins. Archaeobotany seeks to describe archeological remains of crop plants and their wild progenitors from Neolithic sites. Of particular interest is the transition in the archeological record from cultivation of wild plants (predomestication cultivation) to the cultivation of actual domesticates. Some key traits have been identified, mainly pertaining to seed shattering in cereals, such as wheat and barley (Hillman and Davies, 1990; Tanno and Willcox, 2006; Fuller and Allaby, 2009). An additional advantage of archeobotanical remains is that they can be dated by ^{14}C accelerator mass spectrometry, which allows direct dating of the remains rather than indirect stratigraphic dating previously practiced with ^{14}C dating (Smith, 1989, 1997; Kaplan and Lynch, 1999; Benz, 2001; Pinhasi *et al.*, 2005). A disadvantage of archeobotanical approaches is that they are limited to the available archeological sites, which may not be representative of the geographic distribution of early agriculture and in many regions are limited in number.

Genetic evidence is based primarily on the study of contemporary wild and domesticated populations of plants. An important element is to determine the identity of the wild ancestor of each crop. This has been accomplished for most crops, first through artificial hybridizations that determine the viability and fertility of progenies between crops and putative wild ancestors (Harlan and de Wet, 1971). Because

domestication took place only 10 000–12 000 years ago at most, there has been limited differentiation between a crop plant and its wild ancestor, one expects normal viability and fertility in their cross in most cases, with the exception of polyploid series, such as wheat. In the latter crops, crosses involving different ploidy levels usually do not yield viable or fertile progenies in spite of the close genetic relationship expected from ancestor–descendant relationship.

Additional analyses involving molecular markers can then refine the identity of the crop ancestor. All molecular markers are ultimately based on deoxyribonucleic acid (DNA) sequences, irrespective of whether they are proteins, such as enzymes (allozymes) and seed storage proteins, or DNA sequences themselves. Because of advances in DNA sequencing technologies, plant populations are increasingly being characterized by sequencing directly (genotyping by sequencing) (Doebley, 1992; Gepts, 1993; Burke *et al.*, 2007; Gross and Olsen, 2010; Olsen and Wendel, 2013). These analyses, akin to paternity tests, reveal a minimum number of domestications and in some cases also a more defined putative region of domestication within the overall distribution area of the wild ancestral form. Recent examples of this capability include the identification of putative domestication areas for crops in the Mesoamerican center of agricultural origins, such as maize (*Zea mays*; Matsuoka *et al.*, 2002), common bean (*Phaseolus vulgaris*; Kwak *et al.*, 2009), and pepper (*Capsicum annum*; Loaiza-Figueroa *et al.*, 1989), in different areas of the Mexican territory. This polycentric process of assembly of cropping systems in the Mesoamerican center is mirrored in other centers of agricultural origins like Southwest Asia ('Fertile Crescent') and China (Fuller *et al.*, 2012; Riehl *et al.*, 2013; Cohen, 2011; d'Alpoim Guedes, 2011).

Two potential confounding factors operate when attempting to determine an area of domestication. First, gene flow both within the domesticated types and between domesticated and wild types can obscure the local relatedness relationships. For example, maize (*Z. mays* var. *mays*) was domesticated from lowland teosinte (*Z. mays* var. *parviglumis*), but the close relationship between domesticated maize and highland teosinte (*Z. mays* var. *mexicana*) is due to gene flow (van Heerwaarden *et al.*, 2011). Common bean, a predominantly self-pollinated species, nevertheless shows evidence of low but detectable levels of gene flow between wild and domesticated types (Papa and Gepts, 2003; Papa *et al.*, 2005, 2007; Payró de la Cruz *et al.*, 2005; Zizumbo-Villarreal *et al.*, 2005).

Second, there is possibility that the distribution of the wild relative has changed since the initial domestication process. Contemporary wild progenitors are the immediate descendants of the wild types that were domesticated and genetically closest to the original types that were domesticated. They are, therefore, the plant material of choice when studying domestication (Ross-Ibarra *et al.*, 2007). Existing climate models combined with species distribution models may be used to retrospectively estimate the original distribution of the putative ancestral type.

Occasionally, genetic analyses target ancient DNA contained in archeobotanical remains (Jaenicke-Després *et al.*, 2003; Roullier *et al.*, 2013). Although these experiments represent a laboratory tour de force to obtain data from degraded

DNA, their scope is generally limited, however, by the small sample size of the analyses so far, thus limiting the inferences that can be made. Linguistic analyses also contribute to the determination of the area of domestication. The existence of words designating a crop, its product, or tools related to the crop, in native languages provide an additional indication of the importance of the crop. More recently, paleobiolinguistics has reconstructed words in precursors of modern languages (protolanguages), dated them based on lexical similarity, and located the homeland center based on lexical diversity (e.g., common bean, Brown, 2006; cassava, Brown *et al.*, 2013b; and pepper, Brown *et al.*, 2013a). A question associated with the linguistic approach – and other approaches as well – is the antiquity of the evidence it can uncover.

Based on these analyses, Figure 1 shows a sample of crop domestication origins. Several of these centers of origin are fairly well circumscribed, such as the Mesoamerican, Southwest Asian, and Chinese centers. Others cover a much broader territory, such as the South American, African, and Southeast Asian centers. In all cases, however, recent archeobotanical and genetic data suggest that individual crops were domesticated in different areas within each of these centers (Fuller *et al.*, 2012; Riehl *et al.*, 2013; Cohen, 2011; d'Alpoim Guedes, 2011; Clement *et al.*, 2010; Piperno and Pearsall, 1998; Piperno, 2011). For example, maize and common bean were

domesticated in different watersheds in western Mexico but were eventually united postdomestication into the milpa ('three sisters') cropping system with squash (Matsuoka *et al.*, 2002; Kwak *et al.*, 2009; Zizumbo-Villareal and Colunga GarcíaMarín, 2010; Zizumbo-Villarreal *et al.*, 2012). Einkorn, durum, and bread wheat were domesticated in different areas of the Fertile Crescent or adjacent regions (Riehl *et al.*, 2013, Willcox, 2013). Barley was domesticated not only in the Fertile Crescent but also further east in Central Asia (Morrell and Clegg, 2007) and Tibet (Dai *et al.*, 2012). In China, there may be at least two domestication areas (Bettinger *et al.*, 2010; Cohen, 2011), one primarily in the Yellow River basin, where millets (broomcorn millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*)) were domesticated, and the Yangtze River basin, where Asian rice (*Oryza sativa*) was domesticated.

This geographic analysis can be complemented with an ecological analysis through the identification of the major biomes in which crops originated (Harlan, 1992). A biome is a major terrestrial environment characterized by its overall climate (mainly temperature and rainfall), vegetation, and fauna. Some 10 biomes have been described, including tundra, taiga (evergreen coniferous forest), temperate deciduous forest, grasslands (prairie or steppe), deserts, Mediterranean or chaparral, tropical savanna, tropical deciduous forest, and tropical evergreen forest. For each of these biomes, one can

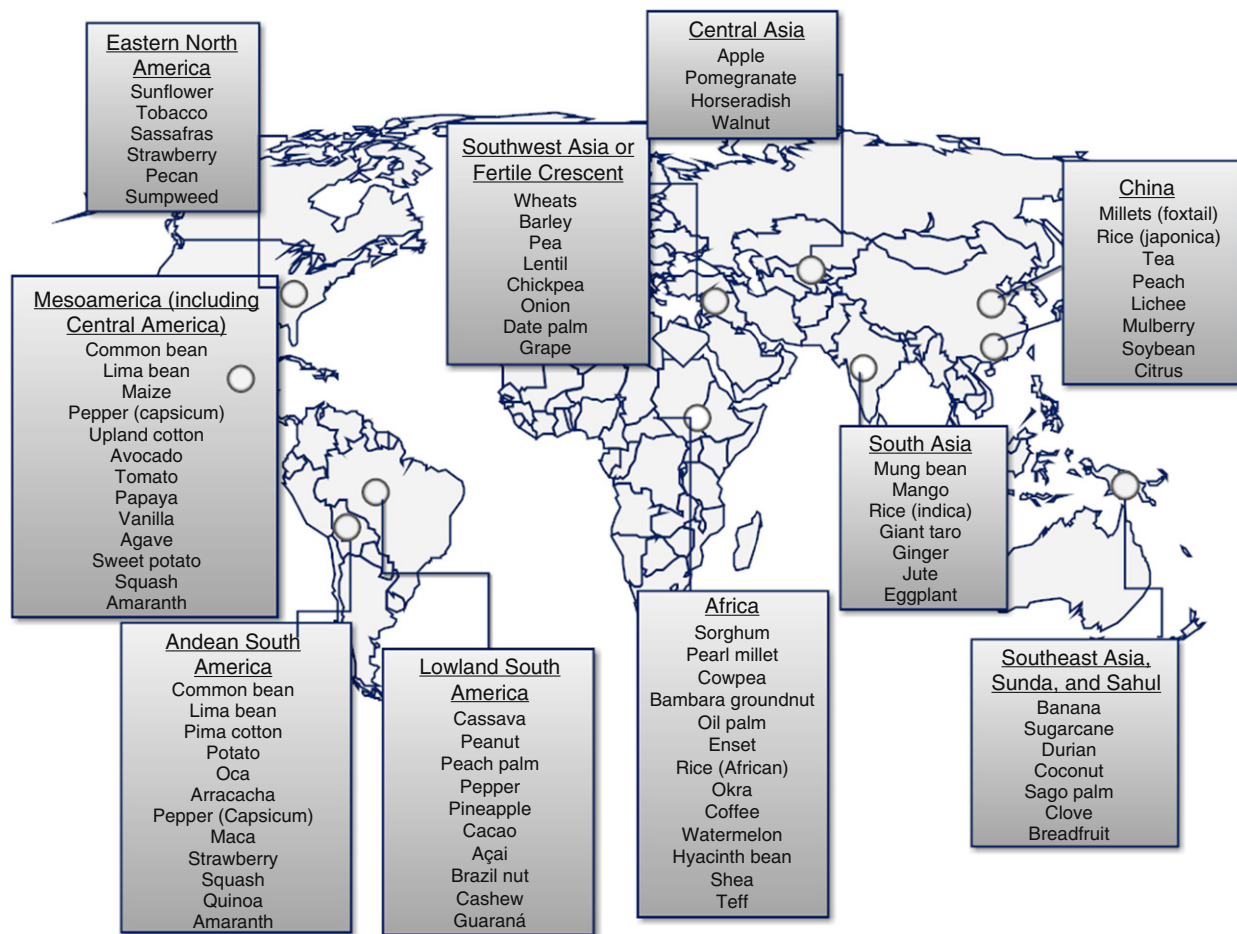


Figure 1 Selected centers of agricultural origins and their respective crops.

then assess to what extent they have played a role in the origins of agriculture and crop domestication. Such an analysis reveals that several crops originated in two biomes, the Mediterranean and tropical savanna biomes. Among crops domesticated in the Mediterranean biome are those from the Fertile Crescent, such as wheat, barley, lentil, chickpea, and pea. Crops domesticated in the savanna biome (and adjacent dry tropical forest) include crops such as maize, common bean, rice, cassava, and peanut. These two biomes share the characteristic of a long dry season, whether during the summer for the former or the winter for the latter (monsoon-type of climate). The dry season may have been an impetus toward cultivation because of the increased need to develop a store of food, irrespective of whether they are grain or roots.

Domestications are not exclusive to the Mediterranean or tropical dry savanna and forest biomes. Other environments have contributed crops as well, such as highland environments (e.g., coffee in the Ethiopian plateau; several root crops, including potato in the Andes Mountains). Coastal areas have contributed coconut, beets and more recently sugarbeets, and cotton. Temperate forest may have contributed fruits and nuts, such as apples, pear, cherry, and walnut. Tropical rain forests were most likely the home of sugarcane, banana and plantain, mango, and cacao.

Centers of domestication tend to occur in areas of higher biodiversity or biodiversity hotspots (Gepts, 2008). Thus, actual or prospective farmers have been opportunistic in recognizing potential crop plants by domesticating them from local biodiversity, wherever they were located. In this regard, it is perhaps not surprising that certain species or groups of related species have been domesticated multiple times. For example, there are five domesticated *Phaseolus* bean species, two of which – common bean and lima bean (*Phaseolus lunatus*) – have been domesticated twice, in Mesoamerica and in the Andes (Gepts, 1998; Serrano-Serrano *et al.*, 2012; Andueza-Noh *et al.*, 2013). Three other domesticated *Phaseolus* species – runner bean (*Phaseolus coccineus*), year bean (*Phaseolus dumosus*), and tepary bean (*Phaseolus acutifolius*) – were domesticated in ecologically different environment (Freytag and Debouck, 2002), reflecting a possible choice on the part of farmers to select different domesticates rather than adapt a single domesticate to a broad range of environments. Other examples are *Capsicum* species (five species domesticated in different areas of Mexico, Central America, and South America; Pickersgill, 2007), cotton (four species domesticated, two in the Old World and two in the New World; Wendel *et al.*, 2009), and wheat (three species domesticated in and around the Fertile Crescent; Willcox, 2013).

When and How Quickly Did Domestication Take Place?

One of the remarkable observations concerning the origins of agriculture is that most origins trace back to a similar period, approximately 11 500–8 000 BP (Price and Bar-Yosef, 2011 and other articles in the same special issue). This period coincides with the end of the last Ice Age. This may suggest that climate change may have played a role in the transition from HG to agriculture, either because the warming temperatures

may have been more favorable for cultivation or may have increased the length of dry seasons. In addition, a climatic singularity may have played a role. It has also been suggested that there was an increase in CO₂, which may have stimulated plant growth around that time (Sage, 1995), or that the climatic conditions became more stable thereby facilitating selection for adaptation during the domestication process (Richerson *et al.*, 2001). However, alternative explanations can be offered. For example, the different groups of humans initiating the practice of agriculture did so because they had reached similar levels of cultural development, including knowledge of food plants and their respective harvest and processing methods. An additional feature of this transition is that climate change did not proceed linearly toward a warmer and drier state. Following an initial, brief warming after the last age, there was a reversion – the Younger Dryas – when cold and dry conditions returned from the preceding warmer/wetter Bølling–Allerød interstadial between the Pleistocene and Holocene eras. The Younger Dryas lasted approximately from 13 000 to 11 500 BP years (Balter, 2010). It is thought to have been one of the factors leading hunter-gatherers to start cultivating plants, not only in the Fertile Crescent (but for opinions to the contrary, see, e.g., Willcox *et al.*, 2008), but also to varying degrees in other areas involved in the origins of agriculture (Bar-Yosef, 2011).

Although there is some variation in the earliest dates for each of the centers of origin, there is also great variation in the abundance of archeological sites among centers. The Fertile Crescent is generally considered to be the most intensively studied center of agricultural origins. One is more likely to find older when the number of sites increases. Another factor influencing the antiquity of archeobotanical remains is the nature of the remains. Macroremains (e.g., whole seeds) are generally less likely to survive undamaged for a long time. Hence, they will generally be younger than microremains (e.g., phytoliths or starch grains). For example, the oldest remains for common bean and maize are starch grains (Piperno and Dillehay, 2008; Piperno *et al.*, 2009). Thus, when comparing the domestication age of different crops, the type of remain and the taphonomic parameters that affect their survival should be taken into account (Allison and Bottjer, 2011).

The duration of the process of domestication has only recently drawn attention, in part because of the recent discovery of sites that harbor a mix of wild and presumably domesticated remains, principally in the Fertile Crescent and China (Fuller *et al.*, 2009, 2012). Two traits have been studied principally: seed shattering (in cereals only) and seed size (in cereals and other crops). Seed shattering in cereals takes place because of the presence of a brittle inflorescence axis (also called rachis). A brittle rachis can be recognized because of the smooth break area where the seed developed on the rachis, in contrast with the rough breakage area caused by mechanical threshing to release seeds from the nonbrittle rachis. Because of the qualitative nature of the trait (presence or absence of abscission scar) and the clear segregation classes, there are no environmental effects on the trait and therefore limited ambiguities in determining the domesticated status of the remains (aside from potential developmental differences). Thus, this anatomical diagnostic trait makes it possible to follow the progress toward full domestication (~100% of remains in the

domesticated category) in any given archeological site. For seed weight, one or more of the dimensions of the seed are measured. Based on observations on contemporary wild and domesticated seeds, one can determine a threshold beyond which a seed can be considered domesticated as opposed to a wild-type seed. A complicating factor here is that seed size is influenced by environmental conditions (Johannsen, 1909; Harper *et al.*, 1970; Motto *et al.*, 1978). An increase in seed size can, therefore, not be considered automatically as a result of an ongoing domestication process (i.e., a genetic change due to selection) but could also represent an improvement in growing conditions. For example, reduced population densities in wild stands (because of previous harvests) may lead to larger seeds, as does cultivation, even in the absence of selection during domestication. An increase in seed size can potentially be taken as evidence for domestication, but only with the necessary caution.

Several approaches have been followed to estimate the duration of domestication. Empirical approaches involving harvesting of contemporary wild populations of cereals – einkorn wheat (*Triticum monococcum*), emmer wheat (*Triticum dicoccum*), and barley (*Hordeum vulgare*) – as well as mathematical modeling of the frequency of mutant (nonshattering) alleles have shown that with the appropriate harvest method (e.g., use of sickles) could proceed quickly (from 20–30 to 300 generations) (Hillman and Davies, 1990). Factors considered in the modeling experiments were the level of selection intensity and self-pollination, with stronger selection and higher inbreeding levels accelerating the pace of domestication. Thus, it would appear on the face of these experiments that there would be no genetic impediments to a rapid domestication once mutations were present in the wild populations.

Molecular analysis of DNA sequence variation has also provided estimates of the length of the domestication bottleneck. In maize, when taking a domestication duration of at most 2800 years (Eyre-Walker *et al.*, 1998), the bottleneck size was estimated at 3500 individuals.

In soybean, a domestication bottleneck of 3000 year was posited for a founding population of 6000 individuals (Guo *et al.*, 2010), whereas in rice the founding population was only 1500 for a similar duration (Zhu *et al.*, 2007). These estimates are ambiguous, however, because the bottleneck severity depends on both population size and duration of the bottleneck. Thus, estimates of the duration of the bottleneck are dependent on the size of the population of the wild progenitor during the domestication process, which is essentially unknown.

One should also take into account several considerations that can slow down the speed of domestication. First, the source of variation for domestication alleles may determine how quickly domestication could proceed, namely, whether variation originated in existing variation in the wild progenitor populations ('standing variation') or if it originated in *de novo* mutations. Standing variation may have led to faster domestication than reliance on *de novo* mutations; however, it remains to be determined how strong a barrier the appearance of mutations would be, given the large population sizes observed for some wild relatives. Observations in a wide range of organisms and traits have shown that selection for adaptation relies on both standing variation and *de novo* mutations

(Durand *et al.*, 2010; Peter *et al.*, 2012; Fu and Akey, 2013; Studer *et al.*, 2011). Second, the modeling experiments assume constant, nonzero selection levels in each generation, which may not have been the case, given that at least in its initial phase, agricultural production may have been a supplementary source of food rather than a mainstay. In some years, there may not have been any cultivation at all and therefore no selection leading potentially to domestication. Third, domestication in most cases is based on multiple traits, which have to be recombined into a single evolutionary lineage. Even if selection for individual domestication traits was taking place in different lineages, ultimately these individual traits needed to be combined through outcrossing among lineages and recombination in the progenies. Aside from the likely chance encounter of lineages, outcrossing (especially in autogamous species) and the concomitant recombination will almost certainly have slowed down, although not prevented the domestication process. Fourth, hybridizations between the wild ancestor and the incipient domestication, a likely occurrence if the two types were sympatric, would have also slowed down domestication by diluting the frequency of domestication alleles and decreasing the expression of the traits they control, given their generally recessive nature (Ladizinsky, 1985).

These considerations, as well as archeobotanical observations, have led to the current proposal that domestication was a drawn-out process taking place over several millennia, generally approximately 2000–3000 years (Allaby *et al.*, 2008; Fuller *et al.*, 2012). This proposal is based on several observations. There is a relationship between the frequency of domesticated phenotypes (e.g., seed size and nonbrittleness) and their age over several sites in the Fertile Crescent and China (Fuller, 2007): the younger the site, the higher the frequency of domesticated archeobotanical remains. Concomitantly, there is an increase in the frequency of seeds of the so-called arable weeds that accompany crop cultivation (Colledge and Conolly, 2010). Finally, the amounts of stored grains also increased around this time and have been deemed to be too large to originate in mere gatherings of wild seeds.

In turn, these new arguments need to be considered with caution. The development of a timeline for domestication based on different archeological sites (e.g., Tanno and Willcox, 2006) introduces a confounding factor, namely, the differential rate of spread or adoption of agriculture. Thus, differences in the percentage of domesticated remains among locations may not reflect the degree of advancement of the domestication process but rather the differential spread or the earlier or later adoption of cultivation of plants. In addition, the presence of weeds may not necessarily indicate the presence of cultivation. The main characteristic of these weeds is their adaptation to disturbed conditions and their ability to colonize these environments. Although plowed fields are disturbed environments, they are not the only anthropogenic environments. Terrains with intensely harvested wild populations or the surroundings of villages could also be a source of arable weed seeds. Thus, the mere presence of these plants does not necessarily indicate cultivation and may lead to an overestimate of the duration of the domestication process. Large amounts of grains in storage likewise is not indicative of harvest from cultivated plots. Several experiments or observations on the production of wild stands of plants, whether

annuals or perennials, suggest high levels of productivity in natural stand of crop wild relatives (CWR) (Harlan, 1967; Hillman and Davies, 1990). The proposed extended pre-domestication cultivation also needs to be reconciled with a potential push-pull situation related to the cultivation and harvest of wild plants. Cultivation of a wild plant that is unadapted to cultural practices, including planting and harvesting, may not lead to expected yields needed to complement harvests from wild plant gathering. Abbo *et al.* (2011, 2013) showed how harvests of wild pea are very variable and low across location and years, making cultivation for a substantial number of years less likely unless key mutations would be present in these populations to increase yield, such as mutations for reduced seed dormancy after planting and limited pod dehiscence at maturity. However, once this type of mutation is present, domestication could proceed more rapidly as suggested by Tzarfati *et al.* (2013), who showed how the nonbrittleness and free-threshing mutations in emmer wheat (*Triticum turgidum*) reduced threshing time by 30% and 85%, respectively, thus providing an incentive for cultivation of these variants. An important limiting factor may, therefore, be the frequency of mutations pertaining to domestication syndrome traits in wild progenitor populations, combined with gene flow and recombination rates of these different mutations into a single evolutionary lineage.

Overall, the actual duration of the domestication process is still a controversial topic. Although it is probably longer than what the analysis of individual traits suggests, claims for a long pre-domestication cultivation phase need to be examined with caution and the actual length should be determined more precisely.

A Common Feature among Domestications: Reduction of Genetic Diversity at the Genome Level

A general feature of domestication is the reduction of genetic diversity in the domesticated gene pool compared with the gene pool of the wild progenitor. The amount of reduction depends on the species, its reproductive system, and the molecular marker system used. In general, outcrossing species show a smaller reduction compared with selfing species (e.g., maize: 83% nucleotide diversity retained in domesticated gene pool, Hufford *et al.*, 2012, 2013; rice: 60–65%, Caicedo *et al.*, 2007, or 35%, Zhu *et al.*, 2007; common bean: ~40% each in Andean and Mesoamerican domestications, Bitocchi *et al.*, 2013; soybean: ~60%, Lam *et al.*, 2010). Vegetatively propagated crops also tend to maintain high levels of genetic diversity as illustrated by grape and apple (95% retention of diversity, Myles *et al.*, 2011; Cornille *et al.*, 2013). Techniques of propagation of specific phenotypic variants, such as grafting or cuttings, as well as the role of major genes in the genetic control of individual traits, and the presence of a juvenility period and the long production period in vine or tree crops could have strongly reduced genetic diversity. Nevertheless, gene flow from local wild populations, small-scale propagation, local adaptation to environmental conditions, and consumer preferences could act to maintain high levels of diversity (Cornille *et al.*, 2013).

Domestication has also affected multilocus association as measured by linkage disequilibrium (LD), the nonrandom association of gametes. The nonrandomness can arise from close linkage, in which case LD can be used to map loci controlling phenotypic traits. LD, however, is also induced by other factors, such as population structure induced by geographic isolation, genetic bottlenecks, and reduced recombination. For example, in common bean, which consists of two geographically separated taxa (Andean vs. Mesoamerican), there is much higher LD in a sample including the two taxa (95% of locus pairs in LD) than in separate Andean and Mesoamerican samples (~70%; Kwak and Gepts, 2009). In general, LD increases as a consequence of domestication (e.g., maize: Wright *et al.*, 2005; Hufford *et al.*, 2012; rice: Zhu *et al.*, 2007; soybean: Hyten *et al.*, 2007; sunflower: Kolkman *et al.*, 2007; common bean: Kwak and Gepts, 2009; Rossi *et al.*, 2009; foxtail millet: Wang *et al.*, 2010).

The Genetic and Molecular Basis of the Domestication Syndrome

Although crops and their wild progenitors belong to the same biological species and their divergence was initiated only some 10 000 years ago, they generally show marked morphological and physiological differentiation as a result of the selection for adaptation to human cultivation and consumption for food and nonfood uses. The genetic basis for this profound change resulting in crop plants as are known today has only relatively recently been elucidated. Initially, genetic analyses were conducted on individual traits. The general conclusion was twofold, namely, that most domesticated traits were controlled by recessive alleles at one or two genes, suggesting loss of function mutations (Ladizinsky, 1985). Such studies were generally limited, however, by the lack of information on the location of these genes within plant genomes and their potential linkage. The ability to develop linkage maps with molecular markers of sufficient density and distribution in the crop genome, together with the development of segregating populations resulting from crosses between carefully selected wild and domesticated genotypes, remedied this situation and provided a more complete picture (including linkage information) on the inheritance of the domestication syndrome.

Results from these analyses have led to a series of general conclusions about the architecture of the genetic control of the domestication syndromes across a broad range of crops, mostly annual, herbaceous plants (Gepts, 2004). A first conclusion is that often major, Mendelian genes or quantitative trait loci (QTLs) control individual traits, in addition to genes or QTLs of smaller effect. This observation confirms the single-trait analyses. Second, the phenotypic variation is often mainly due to genetic rather than environmental effects, suggesting high heritability. The first two observations suggest a simple genetic control, which would have facilitated and speeded up selection during the first stages of domestication. Third, in many crops, a subset of the genes controlling the domestication syndrome are linked, at least loosely, on a limited number of chromosomes. The latter situation may have been an advantage in situation where hybridizations take place, either between wild and domesticated types or among

incipient domesticates in the early phases of domestication when lineages with different elements of the domestication syndrome were recombined. Linkage made recovery of parts of the hybridization syndrome easier, although not preventing assembly of the domestication syndrome because of repulsion linkage.

With the availability of very large numbers of markers, such as microsatellite or simple-sequence repeats, genome-wide association studies (GWAS) have been made possible among nonpedigreed individuals. In contrast with QTL analyses, which are conducted in the segregating progeny of crosses between parents, GWAS are conducted among individuals of a species, which are presumed to be unrelated. After removing the potentially confounding effect of population structure, which could lead to false positives, any association between marker and a phenotypic trait could be attributed to linkage. In this way, the different genes controlling the domestication syndrome can be placed on the crop linkage map. An example of this approach is provided by association of certain genes, such as the photoreceptor gene *PHYC* and flowering time in pearl millet and changes in frequency of alleles at this locus in a 27-year period corresponding to aridity in Western Africa (Saïdou *et al.*, 2009; Vigouroux *et al.*, 2011). Another example is the identification of the *INTERMEDIUM-C* gene responsible for the 6-rowed variants in barley (*H. vulgare*) (Ramsay *et al.*, 2011).

The introduction of next-generation sequencing has made sequencing more efficient and cheaper. Hence, sequencing of multiple genotypes has also been made possible, allowing sequence comparisons on a genome-wide basis and a larger sample of genotypes. Comparisons between wild and domesticated types identify potential genome regions that have been targets of selection during the domestication process. An interesting feature of this approach is that it does not require prior knowledge or assumptions about traits under selection. In contrast with QTL and GWAS approaches, which require phenotypic variation (top-down approaches; Ross-Ibarra *et al.*, 2007), the resequencing approach is a bottom-up approach that relies on molecular population genetic arguments, such as allele frequencies differences. For example, a sharp reduction in nucleotide variation in certain areas of the genome in domesticated types compared with wild types suggests selection on phenotypes controlled by one or more genes in this region (also known as a selective sweep). Genetic drift associated with domestication would lower genetic diversity across the entire genome during and after domestication, whereas selection will be confined to those regions of the genome that contain traits under selection. The size of the region is negatively correlated with the level of recombination but positively correlated with the selection intensity. An example of this approach is the identification of a selective sweep around the waxy (*wx*) locus in rice. The *wx* locus is involved in starch metabolism in rice grains; in particular, it is responsible for the stickiness of rice grains and was selected during or after domestication in *japonica* rice (Olsen *et al.*, 2006).

In sunflower, a genome-wide study identified 36 genes showing evidence of selection during and after domestication (Chapman *et al.*, 2008). Many of the genes involved were involved in amino acid metabolism and protein catabolism (as in maize; Wright *et al.*, 2005) and were located in the same

regions as previously identified QTLs for the sunflower domestication syndrome. The timing of selection could be presumably narrowed down to the initial domestication process per se or the subsequent improvement stage by distinguishing within the domesticated group between the so-called primitive (or landrace) varieties and varieties improved by selective breeding. Hufford *et al.* (2012) conducted a genome-wide resequencing in wild, landrace, and improved maize entries. Among their findings were the existence of stronger selection during the actual domestication phase than in the subsequent improvement phase. An additional observation is the existence of potential introgression from a wild relative (*Z. mays* var. *mexicana*), which is not the progenitor of maize but contributed nevertheless alleles that are potentially instrumental in adaptation to higher altitudes (van Heerwaarden *et al.*, 2011). Furthermore, several regions were identified that showed evidence of selective sweeps, representing some 1–2% of the maize gene set. Some of these genes map near QTLs that had been identified previously. As a note of caution, the separation between domestication and improvement genes may not always be clear-cut, and in some cases, such as color or shape, variants may involve arbitrary decisions as to the timing of the appearance of these variants. In addition, some domestication genes (identified as such by their absence in the wild progenitor gene pool) are not distributed across the entire domestication gene pool but characterize only a subset of the gene pool, suggesting that there is no clear dichotomy between these two classes of genes.

Concurrent with these studies, many genes controlling important domestication traits, whether they are considered domestication or improvement traits, have been isolated using map-based cloning of QTLs or a candidate gene approach, based on sequence information of genes controlling similar phenotypes in other species (Paterson *et al.*, 1995; Lenser and Theyßen, 2013). Doebley *et al.* (2006), Gross and Olsen (2010), and Olsen and Wendel (2013) presented recent overviews of genes that have been isolated. The majority of these genes are transcriptional regulators, such as the *tb1* gene in maize (conditioning the single-stem, nonbranched plant type of domesticated maize; Wang *et al.*, 1999); however, a significant proportion codes for structural genes like enzymes, such as the waxy locus (not only in rice but also in broomcorn millet and maize) and the *BADH2* gene (for rice fragrance). The types of mutations involved are diverse and include nucleotide substitutions (leading to premature stop codons or amino acid substitutions), insertions or deletions (indels), transposon insertions, or *cis*-regulatory changes (the latter outside the gene, such as is the case for the *tb1* locus controlled by an enhancer-like transposon insertion some 65 kbp upstream of the gene). In most cases, a single causative mutation can be identified. An exception to this pattern is the *PvTFL1y* gene, which is responsible for the determinate growth pattern in common bean, in which a retrotransposon insertion, synonymous substitutions, nonsynonymous substitutions, indels, a putative intron-splicing failure, and a deletion of the entire locus, all lead to loss of function, consistent with the recessive nature of the determinate phenotype (Repinski *et al.*, 2012; Kwak *et al.*, 2012). This observation suggests that the determinate trait has been selected multiple times, underscoring the importance of earliness and compact growth habit in crop cultivation.

In general, therefore, the extensive sequence data available from wild and domesticated types of major crop plants and related genetic and genomic approaches have provided a trove of information about several important features of the domestication process, including the genetic structure of the domesticated gene pool in relation to its progenitor gene pool, the effect of domestication on genetic diversity, evidence for selection, and the nature of the genes underlying domestication phenotypes.

Implications of Domestication Studies for Crop Improvement, Distributed Breeding, Redomestication, and Neodomestication

Although domestication analyses are integral part of broader studies on the origins of agriculture, results of these have important practical applications in three major areas. First, they provide essential information for conservation of genetic resources. In most, if not all, crops, improved cultivars contain less diversity than landraces (varieties selected and grown by farmers in a subsistence agriculture context) and markedly less than wild progenitors and other wild relatives because of the genetic bottleneck and selective effect that have operated during domestication and dissemination and improvement subsequent to domestication. It is hard to overestimate the importance of the diversity contained in landraces and CWR for continued improvement of crops. Yet, this diversity is also being severely threatened by a number of interconnected factors, such as habitat destruction and climate change. Both *in situ* (in farmers' fields and natural vegetation) and *ex situ* (in gene banks, botanical gardens, and other collections) approaches are being used to conserve this diversity (Gepts, 2006), but a more intensive characterization is urgently needed, at the molecular (McCouch *et al.*, 2013) and phenotypic (Furbank and Tester, 2011; Andrade-Sánchez *et al.*, 2013) levels. More basic research on plant function, especially gene interactions as well as gene-environment interactions (e.g., Mochida and Shinozaki, 2011), are required to increase the use of this genetic diversity. An additional finding – the existence of selective sweeps – has also profound impacts on breeding, because it suggests that, in addition to beneficial effects, some genes may have been introduced that have deleterious effects but are in coupling phase with the introgressed beneficial genes, a possible explanation for linkage drag. Identification of these deleterious genes and recombinants between them and beneficial genes would represent a significant progress in the introgression of genetic diversity of the exotic germplasm represented by landraces and CWR.

Domestication is not just a process that occurred at the transition from HG to agriculture. To the extent that this process involves an active and conscious selection process, it has also been operative in subsequent phases of crop evolution during the different dissemination steps to other growing regions, especially those outside the centers of origin. Current breeding efforts aiming to produce improved cultivars through selective breeding can also be construed as a step in the domestication process. During these different domestication steps, farmers have played a significant role in

maintaining existing but also selecting new diversity appearing in their fields, leading to domesticated gene pools with high levels of phenotypic diversity up until the nineteenth century and beginning of the twentieth century (e.g., von Martens, 1860; Tracy, 1907; Freeman, 1912; Hedrick, 1931). Although genetic diversity in domesticated gene pools has decreased in the latter part of the twentieth century and early twenty-first century, farmers continue to play an important role in maintaining crop genetic diversity (e.g., beans: Payró de la Cruz *et al.*, 2005; Zizumbo-Villarreal *et al.*, 2005; Worthington *et al.*, 2012; cassava: Elias *et al.*, 2001; Pujol *et al.*, 2005; pearl millet: Couturon *et al.*, 2003; Lakis *et al.*, 2011; and sorghum: Alvarez *et al.*, 2005; Barnaud *et al.*, 2008) through their knowledge of adaptation to local conditions and consumer preferences. Through their seed systems, farmers can control levels of genetic diversity, the genetic composition of their fields, and in- and outflows of diversity in their fields, including wild relatives and improved varieties.

It is this ability of farmers to recognize useful genetic variation and to assemble their own seed stock as part of the capital of their farms (Soleri *et al.*, 2002) that has led to successful efforts of participatory breeding generally involving farmers and villages in subsistence agriculture settings (e.g., maize: Smith *et al.*, 2001; barley: Ceccarelli *et al.*, 2000, 2003; common bean: Asfaw *et al.*, 2012; and agroforestry: Leakey, 2012). These participatory activities are particularly significant because they lead to a decentralized or distributed type of breeding in contrast with the current prevalent model, which is primarily centralized in public agricultural experiment stations or seed companies. Distributed breeding (by analogy with computing) may give a boost to genetic improvement by addressing local needs of farmers dictated by the needs of local adaptation and consumer preferences for individual crops. As proposed by Leakey and Asaah (2013), domestication has more than production benefits; it can have social, economic, and environmental benefits when it is applied to the entire spectrum of plants. This process includes not only continued domestication of existing crops but also incipient domestication of locally adapted, underutilized, and often perennial tree crops (for agroforestry purposes). In turn, these improved crops can play diverse roles, for example, in mitigating environmental degradation, creating new income opportunities, and promoting local employment and commerce related to food and tree products (Leakey and Asaah, 2013). This local focus of plant domestication may get a further boost in the response to climate change. The inherent uncertainty associated with climate change (e.g., Thornton *et al.*, 2009) will make it difficult to institute breeding programs with broad adaptation. Hence, to make agroecosystems more resilient, the response should be local and should combine a broad variety of responses, genetic and nongenetic, as proposed by Kiers *et al.* (2008) and Clough *et al.* (2011).

Finally, domestication is and will be playing a role in redomestication and neodomestication of plants. For example, some crops may be repurposed for an entirely different objective than the one they were first domesticated for. Maize was initially a food crop before it became an important feed crop and was also used for industrial purposes. Using maize as a feedstock for alcohol fuel production should decrease the emphasis on seed production but increase the emphasis on

vegetative matter (stems and leaves) production, essentially leading to maize varieties with reduced seed harvest index, reversing the millennia-long trend toward a higher seed harvest index. It has often been observed that domesticated plants constitute a very small fraction (<0.01%) of the total number of plant species (approximately 300 000 species; Mora *et al.*, 2011). Even if not all of plant species can be domesticated (for a variety of reasons), it seems likely that additional species can be domesticated to satisfy the needs of humanity. The experience acquired with domestication of existing crops should help one conduct deliberate and conscious neodomestication of additional plants; conversely, one does not know why so few plants have been domesticated so far. The concept of domestication potential needs to be explored further to assess which plants could be domesticated with greater ease. Further basic research in plant domestication is, therefore, needed to better understand the domestication process and the process of transition from HG to agriculture in general. These studies, although ostensibly turned toward the past, have an important practical role in the future of humanity and its well-being.

See also: Agroforestry: Complex Multistrata Agriculture. Agroforestry: Participatory Domestication of Trees. Biodiversity: Conserving Biodiversity in Agroecosystems. Breeding: Plants, Modern. Climate Change: Agricultural Mitigation. Climate Change and Plant Disease. Climate Change: Cropping System Changes and Adaptations. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Cloning: Plants – Micropropagation/Tissue Culture. Domestication of Animals. Food Security, Market Processes, and the Role of Government Policy. Food Security: Yield Gap. From Foraging to Agriculture. Genebanks: Past, Present, and Optimistic Future. Genomics: Plant Genetic Improvement. Intellectual Property in Agriculture. Plant Cloning: Macropropagation

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