DOMESTICATION AND DEVELOPMENT OF PLANT CULTIVARS

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Summary

The development of plant cultivars started with plant domestication and has played the major role in agriculture toward food security. Both direct and indirect selection pressures have been exerted during the domestication process, resulting in marked differences between crops and their wild ancestors. Over thousands of years of plant domestication, an impressive wealth of diversity has accumulated in landraces. That diversity has been the starting basis for efforts in plant breeding. Plant breeding has helped secure the yield potential of landraces through the transfer of disease and pest resistances. It has also been instrumental in securing yield increases and adaptations to other photoperiod and soil conditions, much faster than traditional selections, once heritability of traits has been established. A qualitative and quantitative shift in the field of plant breeding arose in the 1960s with the advent of molecular genetics.

Molecular marker-assisted selection is accelerating the picking up of interesting variants in early segregations, and quantitative trait loci (QTL) analysis is helping to maximize quantitative traits among distant or phenotypically not attractive genotypes. The regeneration of cells *in vitro* has made possible the recovery of entire viable plants; it was the requisite for transformation. Techniques to introduce alien DNA from distant plant species but also bacteria into target crop species is progressing fast and becoming routine. These techniques are used for the introduction of resistance to pests, viruses, frost, but also for technological traits such as delayed maturity and tolerance to herbicides, or novel traits (starches, amino acids, enzymes). If technological innovations are often promising in terms of crop productivity, all consequences are not yet fully realized, nor are their implications widely discussed at the society level. On one hand, our agrobiodiversity heritage is threatened and its conservation is not yet fully secured; on the other hand, plant breeding could be applied on a much bigger scale to local or neglected crops, and to promising wild species, for economic and social development.

1. Introduction

Plant domestication—etymologically the entering of plants into the human domain—is an action or set of actions by which plants are brought into intimate association with and to the advantage of people. It can be considered historically and biologically as the first step in the development of plant cultivars. It is a process rather than a geographic location or an event within a definite timeframe or a straightforward invention by a single individual or human community. Such a process implies changes in plants in response to human needs and to changes induced by humans in the domain. Plants, at least some, adapt themselves—as they did to other environmental changes for millions of years before the appearance of humans—and thus change to better respond to human selective pressures. These pressures can be direct (and thus conscious), with the keeping of variants, for instance with bigger seeds or more tasty fruits or with grouped harvest. They can be indirect (often unconscious), with the modification of the habitat and the relationships with other biota of the ecosystem, for instance when changing crop production systems.

The diversity in human needs for food, medicine, clothing, shelter, adornment, and so on, reflecting cultural diversity, is immense, thereby creating accordingly a huge variety of selection pressures exerted on plants. Reflecting that diversity, almost any plant part has been found useful at one time or another: root (sugar beet), tuber (potato), rhizome (arrowroot), stem (palmito), bark (cinnamon), petiole (celery), leaf (lettuce), axillary bud (Brussels sprouts), inflorescence (broccoli), floral bud (caper), floral bracts (artichoke), flower (squash), stigma (saffron), infrutescence (pineapple), fruit (apple), lint (cotton), seed (bean), and seedling (green gram). It is likely that over thousands of years these plants that responded positively to specific selection pressures were the ones selected. Selection pressures have often been directed to the increase of the harvested part (showing so-called gigantism in comparison with the original part in the plant ancestor), causing a different distribution of metabolites in the plant. Selection pressures have also been directed to a grouping in time for the harvest of such parts, inducing changes in life cycles. Selection pressures are effective if applied for some time and in one direction so that variants can appear, be selected and maintained; thus the importance of sufficient duration in human cultural diversity and uniqueness as the dynamic guarantor of such selective pressures.

Ecological disturbance has long been considered as a distinctive feature of agriculture. Indeed the art of cultivating the field (*ager* in Latin) often implies a change in the natural land cover, that is a change in the floristic composition, both qualitative and quantitative, of the original vegetation. Plant species—a couple of hundred—responding to such an ecological modification are considered as weeds or ruderals, independently from their use value. Indeed, weeds are often precursors of crops (i.e. rye), but many remain as weeds. On the other hand, wild plants growing in natural habitats can be used by humans (it is the case of many medicinal plants and spices; it is also the case of many mushrooms), and are maintained there with almost no care and frequently without any genetic changes in the makeup of the species. In the case of wild plants, any human intervention starting with excessive harvest might even be detrimental. There is thus quite a large range of ecological disturbances paralleling a wide range of plant responses, from truly wild plants not tolerating human intervention, to fully cultivated plants or crops depending entirely on humans for survival, through despised, tolerated, or encouraged weeds.

The development of plant cultivars—currently the ultimate basis of almost all human food—logically begs the questions: When, where, why, and how did this process of development take place? These aspects shall be briefly considered below, focusing on three major steps: the beginnings as early plant domestication, the development of formal plant genetics as a scientific discipline applied in breeding programs, and the emergence of molecular genetic technology.

2. Early Plant Domestication

Plant domestication appears late in human development during which activities of plant gathering and hunting were long the mainstay, and extends over the past 10 000 years to 12 000 years (see *Historical Origins of Agriculture*). In the beginning, plant domestication activities contrary to (wild) plant utilization were not widespread and were rather concentrated in a few places on this planet. These places were within the range of distribution of wild plants that responded positively to human selection pressures and thus became ancestors of crops, and they were relatively suitable for agricultural development. These places were also related to human settlements (for the permanence and uniformity of selective pressures!). Increased food production through plant products made possible higher human populations, thus permitting more people to cultivate the land, thereby requiring more food! An autocatalytic process of plant domestication was thus initiated in those few places. The geographical foci of agricultural development shall be considered, and some implications shall be revisited afterward.

We owe to N.I. Vavilov the concept of centers of crop diversity. After extensive travel with his staff, he observed the wide diversity of crops and large numbers of varieties within each of them concentrated in a few rather limited areas in the tropics and subtropics. These he hypothesized were the centers of origin of cultivated plants. It is important to note that he looked at *final* products not the *original* process.

The Fertile Crescent in the Near East was long considered a cradle of agriculture, with wheat, barley, oats, peas, and fava beans being domesticated there. Changes in plants (emmer wheat, einkorn wheat, barley, lentil, and pea) appeared as early as 10 000 BP to 8 000 BP. In contrast to the New World, animals (goat, sheep, and then cattle and pig) were also domesticated together there with these plants. The domestication of plants and animals made for such nutritional advantage that plant gatherers and hunters in the area were either converted into farmers or forced to leave. Initially, this center contributed significantly to the Mediterranean and European regions, and to the Ethiopian and Indian regions of crop diversity.

Another long known cradle of agriculture has been China with rice, broomcorn millet, foxtail millet, soybean, cabbages, onions, many other vegetables, some of which have been abandoned since, and several fruit species of the peach family. It seems that farming cultures were established in China by 6000 BP, although there might be earlier records. Initially the Chinese region contributed plants to the Southeast Asian and Indian regions. The inhabitants of these regions were particularly instrumental in importing crops and developing them further, while domesticating local plants, particularly pulses (for instance mung bean, mat bean, rice bean, urd), vegetables (amaranth, eggplant), and fruits (durian, mango, orange, lemon, lime). Western Melanesia also contributed crops (e.g., bananas, sugarcane) that were developed further in Southeast Asia.

In the Americas, Mesoamerica, the Central Andes, and a vast ill-defined region extending from Amazonia to Chaco have been places of crop husbandry. While the Mesoamerican plant trilogy (maize, bean, squash) together with chili peppers quickly expanded in Central America and the Caribbean, cropping systems with many roots and tubers (potato, oca, mashua, and so on) were developed in the Central Andes. Amazonia contributed cassava, rubber, and many tropical fruits. If for human and geographic reasons a centric focus of agriculture seems justifiable for Mesoamerica, it seems less the case for South America. Authors disagree about dates, from 4000 BP to 10 000 BP, but dates may be as ancient in Mesoamerica as in the Central Andes.

Africa continues to be puzzling regarding its agricultural past. Crops such as sorghum, pearl millet, finger millet, “minor” millets, cowpea, yams, cotton, and African rice, were obviously domesticated there, more than likely in savanna-like habitats. Forest habitats contributed coffee, oil palm, cola, and many fruit and vegetable species. While archaeological evidence is scarce, apart from the Sahara and the Nile Valley, linguistic evidence points to dates before 7000 BP. No particular distinct center seems evident, although the Sahel region and Ethiopia extending to the northern part of the Rift Valley have been important zones of several domestication and crop assemblage efforts.

Additional studies of the aforementioned centers reveal indeed much complexity, right up to questioning their existence as centers. If centers exist, they would tend to have the following attributes: uniqueness, exclusivity, originality, and comprehensiveness. So, one would assume first that all cultivated crops would be included within such centers. Several crops of worldwide importance (e.g., peanut, cacao, sunflower, sorghum, and coconut) did not fall within any “center” as originally described, or the geographic area as initially thought had to be expanded accordingly. Second, centers are supposed to cover limited acreage. This is not particularly the case in the South American "center," the Mediterranean "zone," or the Sahelian "center," with each extending over thousands of square kilometers. Third, centers are supposed to have original, high concentrations of plant species, and that is the case for wild floras in several tropical areas because of the higher concentration of biota in such latitudes. However, such levels of endemism for ancestors of crop plants rarely exist.

Wild relatives of crops are rarely endemic species, but extend over large areas; indeed their ecological competitiveness makes them prone to domestication because humans during their travels often plant them in several disturbed habitats. Fourth, centers also would lead one to assume that domestication processes of all plant species have started at the same time. In almost all "centers" domestication processes seem heterogeneous, with crops well advanced and highly dependent on humans for survival, while others are still at an incipient stage.

In fact, centers become enriched with crop imports—through people—from other places. In Mesoamerica, early agriculturists combined maize—whose ancestor is probably the Mexican Balsas teosinte—with their local races of common bean and squash. In Ethiopia, barley, introduced from the Fertile Crescent, acquired unique genetic diversity through environmental and human selection pressures. In other and later cases, people quickly imported already well-domesticated crop complexes from elsewhere and advanced them further.

This seems to have been the case for pre-Columbian civilizations on the Peruvian Coast, in the Southwest US, again in Ethiopia, in Europe, Southeast Asia, India, and China. This trend accelerates further in historic post-Columbian times in Africa with New World inputs (for instance with maize, peanut, cassava, and beans), in different parts of the neotropics with Old World inputs (coffee, bananas, sugarcane, and Asian rice). It also happened in the US with Old World crops (wheat, grape, and soybean), in Brazil (wheat and soybean), and in Australia with crop inputs from many parts of the world.

So, the rigid equation of places of origin(s) of agriculture with places or centers of crop diversity may be wrong and misleading. Centers of crop diversity may be more constructs than reflections of original plant richness. Centers of crop diversity did not exist at the beginnings but were assembled, first with plants from the surroundings, later with plants from more distant areas.

At each step, plants were selected by farmers and by the environment in which they thrived, and the variants were carefully conserved by farmers and rural communities. The seed conservation technologies that they mastered were determinants for the viability of the propagules. In this regard, it is important to again mention the importance of continuity in the domestication process. A few crops have become extinct already, because people discontinued their cultivation. It seems to be the case of *Bromus mango* in Chile, *Panicum sonorum* in Mexico, *Lathyrus sativus* in Spain, *Ceratotheca sesamoides* in Cameroon, and *Setaria italica* in China. In other cases, as for marrowstem kales, fodder cabbages, and vegetable marrows in Western Europe, it is a particular group of plant cultivars that has disappeared.

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Biographical Sketches

Daniel G. Debouck graduated from the University of Gembloux, Belgium, in 1976, did postgraduate work at the same university in 1984, and worked for 17 years with the Food and Agriculture Organization and the Consultative Group on International Agricultural Research (IBPGR and CIAT). He is a germplasm conservation specialist. Areas of interest include evolution of neotropical crops and implications for conservation and sustainable use. He is the (co-)author of 54 publications, one book, and 19 book chapters.

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Luigi Guarino graduated from the University of Cambridge in 1980. He did graduate work at the same university, followed by a germplasm-collecting position for the International Board for Plant Genetic Resources in the Middle East and North Africa for five years. He has been a genetic diversity scientist for the International Plant Genetic Resources Institute in Africa and Latin America since 1992. He has edited 3 books and authored about 25 scientific papers.