ORIGINS OF PLANT AGRICULTURE AND MAJOR CROP PLANTS

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Summary

Agriculture is one of the most momentous inventions of humanity. It generated a surplus of food as a consequence of which a sizable fraction of societies were able to engage in economic activities other than agriculture. Thus, agriculture is considered to have been a prerequisite for the development of many civilizations throughout the world. It originated independently and at similar times (around 10 000 years ago) in different areas on several continents, notably Mesoamerica and South America, the Near East, the Sahel and Ethiopia, China, and Southeast Asia. Selection resulting from the cultivation and harvesting of plants by humans induced genetic modifications in these plants resulting in their domestication. In contrast to their wild progenitors, crop plants are unable to disperse their seeds and lack seed dormancy. They also have smaller plants but larger harvested organs (fruits, seeds, leaves) and contain lower amounts of toxic compounds. Flowering time is also less susceptible to environmental influences, mainly day-length. Following their domestication crop plants were widely dispersed across the globe, chiefly after the conquest of the Americas by the Europeans from 1492 on (the "Columbian exchange"). As a consequence of this dispersal, the assemblage of crops in any agricultural region is actually an assemblage originating throughout the world. During their evolution under cultivation, plants have been subjected to three reductions in genetic diversity. Therefore, wild progenitors and primitive cultivars in the areas of origin are a source of additional genetic diversity to further improve elite cultivars of our major crop plants.

1. Introduction

In the evolution of humankind, agriculture is a fairly recent activity, having originated some 10 000 years ago after the last glaciation, more or less simultaneously in a limited

number of regions of the world, principally the Near East or southwest Asia, east Asia, Africa, Mesoamerica, and South America. In contrast to other, more recent technological advances, agriculture was invented multiple times and independently in these different regions. From the limited number of hearths of invention, agriculture spread relatively quickly over the entire world and is now practiced on the five major continents.

Prior to agriculture, food acquisition by humans depended on hunting game animals and gathering wild plants. The importance of the transition from hunter-gatherer to agricultural societies cannot be overstated. This transition, often referred to as the Neolithic revolution, saw the appearance of a sedentary lifestyle in villages, the domestication of our major crops and farm animals, and the development of ceramics and grain storage technologies. Although these individual technologies did not all appear concurrently with domestication of plants and animals, and some actually prepared domestication, there is no doubt that the introduction of agriculture led to a much-changed world.

First and foremost, because agriculture led to a surplus of food, a significant proportion of societies could devote its energies to activities other than food acquisition, including commerce, administration, and warfare. Egalitarian societies evolved into hierarchical, centralized societies. Thus, agriculture is widely considered to be a prerequisite of the subsequent development of civilizations. Indeed, one of the definitions of civilization is precisely a society that relies on agriculture for its food procurement. Striking examples of this feature are the development of the Mesopotamian civilizations such as Sumer, Ur, and Babylon and the Mesoamerican civilizations such as the Olmecs, Mayas, and Aztecs. These civilizations would not have been possible without the existence of a more or less reliable system of food supply provided by agriculture. Differences in the degree of success and hegemony among these civilizations and the ones derived from them have been related to the domestication of cereals and farm animals.

The reliance of major civilizations on agriculture and particularly specific crops for their development is mirrored by the reliance of our major crops on humankind for their continued survival. As will be explained below, fully domesticated crops have lost their means to disperse seeds. In addition, these crops have often lost seed dormancy, the requirement for vernalization, and photoperiod sensitivity—three mechanisms assuring they will grow and mature during the favorable part of the year (either the warm or the wet season). In the absence of human intervention, crops would therefore not survive in the long term. This mutual dependence of humankind and domesticated plants represents a striking example of a symbiosis or mutually beneficial relationship. It would be impossible to feed the six billion inhabitants of this planet without this relationship.

Agriculture has had other major consequences. The sedentary lifestyle and the higher labor requirements of agricultural practices have led to an increase in population growth. After having reached the carrying capacity in the centers of origin, the excess population overflowed into neighboring areas leading to a dispersal of agriculture by demic rather than cultural diffusion. Accompanying this dispersal was a diffusion of some (but not all) of the major human language families. For example, from the Near

Eastern center of agricultural origin, the Indo-European, Turkic, Elamo-Dravidian, and Afro-Asiatic (particularly Semitic) families were dispersed. From the Chinese center, the Sino-Tibetan, Austroasiatic, Austronesian-Tai, and Hmong-Mien families were dispersed.

The success of agriculture was generally so overwhelming that, except in the most remote and inhospitable areas, it replaced hunting and gathering as the dominant food procurement type and lifestyle. Hunter-gatherers are found nowadays only in a few regions with extreme conditions, either in rain forests (Indians in the Amazon or Pygmies in central Africa) or steppes (!Kung in southern Africa or Aborigines in Australia). Concurrently, native vegetation has largely been displaced by agricultural ecosystems, not only in areas of dispersal but also in the centers of origin. For example, agriculture accounts for 80% of the annual world deforestation. Some of the most famous landscapes on our planet, such as the golden wheat fields of Montana, the windmill-studded pastures and flower fields of the Low Countries, the rolling hills of Tuscany, and the terraced rice fields of eastern Asia are typical agricultural landscapes in which native species play only a minor role.

The displacement of hunter-gatherer societies by agricultural societies is somewhat paradoxical. Studies of contemporary hunter-gatherer groups have shown that they generally have a desirable lifestyle at least for certain aspects. Food gathering and hunting takes up only part of their time, leaving ample opportunities for leisure time. In addition, their diet is usually quite diverse. Because of the low population density, epidemics of infectious diseases are rare but parasitic diseases are more frequent. In contrast, early agricultural societies are characterized by a heavy labor investment. This includes child labor, which may be one of the reasons for marked increases in population growth following the transition to agriculture. Their diet is much less diverse and subject to variation in availability. Years of abundant harvests can be followed by lean years, hence periodic starvation and malnutrition are frequent. Because of the higher population densities in agricultural societies, infectious diseases may have been more prevalent. It appears that the overall level of well-being was higher in hunter-gather societies than in the agricultural societies that followed them. This observation further raises the question as to why the transition to agriculture took place in the face of a deterioration of living conditions.

The disappearance of natural vegetation is of particular importance in centers of agricultural origins because of the presence of wild relatives of crop species. These wild relatives are sources of genes to improve crops for higher yield and disease and pest resistance, among other traits. Their loss threatens the continued improvement of the crop by plant breeding. This loss is of special concern given the narrow genetic base of most major crops as a consequence of genetic bottlenecks following domestication, dispersal from centers of origin, and twentieth century plant breeding. An additional concern is the loss of wild (i.e. nondomesticated) species altogether, whether related or not to crop plants. Some 250 000 plant species have been described, of which 75 000 are considered to provide edible products. Whether edible or not, at most 2000–3000 have been subject to at least the initial stages of domestication. It is unlikely that most undomesticated species remain so because they proved to be refractory to domestication efforts. This would have required massive efforts to bring each species under cultivation

for a substantial period of time. Rather, for reasons that are not understood, domestication focused on a limited number of species. Whether these species were particularly predisposed for domestication is not known. If they were not, other plant species could be domesticated that would provide useful food or other products to humankind.

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Biographical Sketch

Paul Gepts has been Chair of the Department of Agronomy and Range Science, University of California, Davis, since 1999, having been appointed Professor in 1995. Prior to that he was Associate Professor (1990–1995), and Assistant Professor (1987–1990). His other academic posts and qualifications include Postdoctoral Fellow, Department. of Botany and Plant Science, University of California, Riverside (1985–1987); Ph.D. (Plant Breeding and Genetics) from the University of Wisconsin, Madison (1985); Research Associate, International Center for Tropical Agriculture, Cali, Colombia (1978–1981); and M.S. (Plant Protection), from the Faculté Science Agronomiques, Gembloux, Belgium (1976). He was a Fellow of the Belgian American Educational Foundation (1981–1982), and he serves on the editorial boards of *Genetic Resources and Crop Evolution* and the *Journal of Agricultural Genomics*. His research interests include: genetic diversity, phylogeography, linkage mapping, and structural genomics of tropical food legumes (*Phaseolus*, *Vigna*). His current research focuses on assessing insect-mediated gene flow, the use of wild relatives in breeding, the molecular evolution of domestication, and disease and pest resistance genes.