PLANT DOMESTICATION AND THE ORIGINS OF AGRICULTURE

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Summary

Of the four primary subsistence strategies recognized by anthropologists, agriculture now dominates. In many societies, less than 1% of the population produces sufficient food supplies to support the whole population. Horticulture remains important in some regions, especially the tropics. A few cultures rely entirely on pastoralism. Foraging, the dominant practice 10,000 years ago, is exceedingly rare today. Agriculture relies on a relatively small palette of domesticated plant resources to sustain the world's human population. Of the more than nearly 2750,000 species of flowering plants, less than 1% has been domesticated. Three species (wheat, corn, and rice) provide more than 60% of the world's calories. Domesticated species have been genetically altered through human selection to such an extent that they can not survive on their own. Common traits of cultivars include increased size of edible parts, increased palatability, decreased armament, absence of dormancy, decreased toxicity, abbreviated flowering,

synchronous phenology, non-shattering fruits, and thinner seed coats.

The shift from foraging to agriculture is called the Neolithic Revolution. The question as to where agriculture first began and who were the first farmers has long interested scholars. The Russian plant geneticist Nikolai Vavilov proposed eight centers of origin: China, India and Indochina, Central Asia, Near East, Mediterranean, Ethiopia, Mesoamerica, and northeastern South America. The American botanist Jack Harlan modified the centers concept and introduced the idea of noncenters, which were large diffuse areas where some crops were domesticated. Current evidence indicates that agriculture developed independently in several regions of the world. An unresolved question is why did humans adopt agriculture? Many hypotheses have been proposed to account for the Neolithic Revolution but there is little consensus for a single explanation. Agriculture most likely was adopted for different reasons in different regions.

1. Introduction

Anthropologists recognize four primary subsistence strategies by which humans acquire nutrients and energy: foraging, pastoralism, horticulture, and agriculture. All rely on plants to varying degrees. Foraging, the oldest strategy, prevailed before agriculture was widely adopted. Foragers obtain all of their caloric requirements from the natural environment. Australian Aborigines are often cited as a classic example of a foraging society. The Calusa of southwestern Florida (U.SA.) developed a sophisticated culture based on aquatic foraging in the resource rich mangrove ecosystem. Despite their reliance on fish or game for much of their protein, wild plants contributed 50-75% of their caloric intake.

Pastoralism is based on husbandry of domesticated animals, including cattle, pigs, sheep in the Old World and llamas and alpacas in the New World. Pastoralism is best suited for grasslands, which are too arid for rain-fed agriculture. Domesticate animals convert cellulose, which can not be digested by humans into digestible proteins and fats. Pastoralists migrated, often seasonally, with their herds. Gathering of wild plant resources and, in some cases, limited cultivation supplemented animal resources. Pastoralism spans a broad range of cultures from Mongols to modern ranchers and herders.

Horticulturists practice small-scale farming, often incorporating small-scale animal husbandy into their subsistence activities. The shift from foraging to strategies that relied on domesticated plant and animal resources occurred independently in several parts of the world 11,000 and 5,000 years ago (Smith 2005). Horticulture persists in many parts of the world, particularly in the tropics. Slash and burn (or slash and mulch in areas lacking a dry season) is a common form of horticulture. After clearing, fallen plant material is allowed to dry and then it is burned. Seeds or vegetative propagules are then sown. In some cases, burning occurs shortly after planting and before seeds germinate or vegetative propagules sprout. Horticulture is characterized by a diversity of crops, life forms, and many varieties within species. Multicropping and intercropping produces fields appear to be chaotic when compared with monocropping practices. Nonetheless, the diverse systems can be highly productive and sustainable.

Fields are actively managed for a period ranging from a few to 5-10 years before new fields are cleared from forests or old fallows. Researchers formerly spoke of abandoned fields, but recent research had shown that horticulturists may continue to manage plots for a century or more. This is especially true of tree resources. Reasons for shifting fields to new sites are varied but include declines in productivity due to soil nutrient depletion, increased herbivore pressure, and increased soil pathogens. However, other reasons unrelated to productivity also may be important. For example, the Siona of Ecuador relocated when trees suitable for canoe construction become extirpated. Shifting patterns are a necessary requisite for most horticulturists. When populations increase or relocation becomes impossible, productivity can decline tremendously. A well studied horticultural society is Hanunóo of the Philippines. Harold Conklin, the 2005 Society for Economic Botany Distinguished Economic Botanist, documented detailed plant knowledge both wild and domesticated species used by the Hanunóo.

Agriculture, an intensive subsistence strategy, allows a few farmers to produce high yields that support an entire society. Cultivation of domesticated plant species, especially grasses, permitted development of large, sedentary civilizations. Intensive agriculture was facilitated by high yielding domesticates, fertilization, and in some cases irrigation. Modern use of pesticides, herbicides, and genetically engineered crops have increased yield even further but often with substantial environmental costs. Agricultural societies often are based on a single grass species such as wheat (*Triticum aestivum*) in Europe and Asia, rice (*Oryza sativa)* in southeastern Asia, or corn (*Zea mays*) in Mesoamerica. Animal husbandry contributes additional protein to the diet.

2. Domestication

2.1 Background

Of the more than 275,000 species of flowering plants, less than 1% has been domesticated. Forty percent of the domesticated species belong to four families: Poaceae, Fabaceae, Rosaceae, and Solanaceae. Human reliance on a limited diversity of plant foods is even more pronounced when one considers that three species (wheat, corn, and rice) provide 61% of the world's calories.

Domesticated species are those that have been altered through human selection to such a degree that their existence depends on humans. Earlier breeders selected traits that improved a species' suitability for food. An unintentional consequence was the decreased ability for cultivars to survive in the wild.

2.2 Characteristics of Domesticates

Different traits have been selected for in different taxa, but they commonly include increased size of edible parts (e.g., fruits or tubers), increased palatability, decreased armament, absence of dormancy, decreased toxicity, abbreviated flowering, synchronous phenology, non-shattering fruits (in Poaceae), thinner seed coats.

Domesticated plants generally have fruits or other edible tissues that are larger than their wild relatives. For example, wild papaya (*Carica papaya*) fruits measure a few cm in length, whereas cultivars may exceed 30 cm. Likewise, ancestors of the potato (*Solanum tuberosum*) have smaller, often spindly tubers. Wild relatives of domesticates are often unpalatable due to the presence of defensive alleochemical compounds. *Lactuca serriola,* the likely ancestor of lettuce (*Lactuca sativa*), bears bitter foliage. Wild potato relatives are rich in glycoalkaloids. Chemicals which imparted unpleasant tastes served an important function in deterring herbivory and plant pathogens. Cultivars also have fewer mechanical defenses. Wild *Citrus* species are notoriously spiny. Domesticated *Opuntia ficus-indica* fruits lack the glochidia found on their relatives. The absence of these defenses is one of the reasons that domesticated species depend on humans for their survival.

In many grasses, all or part of the infructescence disarticulates at maturity. This process, known as shattering, aids in the dispersal of grass fruits. However, it is a highly unfavorable trait for a cultivar. When dispersed from the plant, grass grains are difficult to collect. Early einkorn (*Triticum monococcum*) wheat farmers in the Fertile Crescent selected species with non-shattering infructescences. Two other events were important in the domestication of grasses: polyploidy and free-threshing cultivars. Einkorn and other early wheat domesticates were diploid (2N=14). Natural hybrids between *T. monococcum* and another *Triticum* species produced a fertile tetraploid (*T. turgidum*) after a doubling of chromosomes (2N=28). Increased ploidy level is a common feature of many cultivated taxa. In grasses, the grain or caryopsis remains enclosed by a series of bracts. These must be removed before the grains can be used. A mutation in *T. turgidum* subsp. *dicoccon* (emmer) caused bracts to collapse at maturity producing a free-threshing durum wheat (*T. turgidum* var. *durum*). A hybrid between a tetraploid emmer wheat and a diploid species *T. tauschii* gave rise to the hexaploid bread wheat (*T. aestivum*), which is represented by thousands of modern varieties.

Species selected for their edible seeds usually have thinner seed coats than their wild relatives. For example, domesticated *Chenopodium* species in both North and South America have thinner seed coats than their wild relatives. This allows for larger embryos or more endosperm and thus more biomass for human consumers. Thinner seed coats also may facilitate germination

Several reproductive characteristics are valued in domesticated species. Many species of Rosaceae for example are self fertile, increasing fruit yield. Early and synchronous flowering also have been selected as have day-length neutral plants. Strawberry (*Fragaria ananassa)* varieties have been selected for particular climates and to be day-length neutral.

2.3. The First Farmers

The question as to where agriculture first began has long interested scholars. The Swiss botanist Alphonse de Candolle, a Swiss botanist, published *Origin of Cultivated Plants* in 1882. Combining published data from archeology, plant geography, ethnology, history, linguistics, and natural variation, de Candolle's treatises remains valuable though dated. Unlike de Candolle, Russian geneticist, Nikolai Vavilov, was a devoted field collector who traveled widely in his search for domestication loci. His Russian publication of 1940 (*The theory of origins of cultivated plants*) in 1940 was published in

English in 1951. Vavilov argued that centers of the greatest diversity of a crop represented its center of origin. He originally proposed six centers then added two additional ones: China, India and Indochina, Central Asia, Near East, Mediterranean, Ethiopia, Mesoamerica, and northeastern South America.

Vavilov hypothesized location of the origin for most domesticated plants. Some researchers have criticized the "center or diversity" equals "center of origin" presupposition. Early farmers moved plant material, sometimes over considerable distances. When Columbus landed in the New World, Mexican corn was being grown from Canada to Argentina. Some crops, such as beans and bananas, originated in more than location. Vavilov also missed some centers of origin, including North America and the Amazon.

Jack Harlan believed that Vavilov's centers of origin were centers of diversity and centers of long-standing agricultural activity, which may or may not represent centers of crop evolution or domestication. He modified the centers concept and introduced the idea of "noncenters." These were large diffuse areas where some crops were domesticated. He hypothesized that agriculture originated independently in three regions, each associated with a center of origin and a noncenter. The three regions were a Near East center and a noncenter in Africa, a northern China center and a noncenter in southeastern Asia and the South Pacific, and a Mesoamerican center and a South American noncenter. Harlan believed that there was interaction between each center and noncenter pair.

3. Why Farm?

The question as to where agriculture arose and who were the first farmers has been somewhat resolved. The shift from foraging to agriculture is called the Neolithic Revolution. Rather than a single location and single culture, current evidence indicates that agriculture developed independently in several regions of the world. However, an even more fundamental question remains largely unresolved.

Why did humans shift from foraging to agriculture? Many hypotheses have been proposed but a single reason is not agreed upon by researchers. Perhaps this should not be surprising. Since many cultures independently developed agriculture in many parts of the globe, it is likely that there are site specific reasons for doing so. The main hypotheses on the origins of agriculture are reviewed in the following section. Not all are mutually exclusive and more than one may have played a role in the evolution of agriculture in some regions.

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domesticable species.]

Biographical Sketch

Dr. Bennett is Director of the Center for Ethnobiology and Natural Products and a professor in the Department of Biological Sciences at Florida International University in Miami, Florida. He earned a B.A. in Biology and Geology from Bucknell University, and M.S. in Biology from Florida Atlantic University, and a Ph.D. in Botany from the University of North Carolina at Chapel Hill. He was the 2004-2005 president of the Society for Economic Botany and currently is an associate editor of the journal Economic Botany. He also is a member of the American Botanical Council's Advisory Board and the National Institutes of Health's National Center for Complementary and Alternative Medicine Special Emphasis Panel. His main research focus is Neotropical ethnobotany and ethnopharmacology. Dr. Bennett and his graduate students work in Bolivia, Brazil, Cameroon, Cuba, Costa Rica, Ecuador, Guyana, Japan, Mexico, Panama, Peru, and the U.S. Dr. Bennett's book Ethnobotany of the Shuar of Amazonian Ecuador won the 2006 Klinger Award from the Society for Economic Botany. His research has been published in Ambio, BioScience, Brittonia, Economic Botany, Selbyana, Journal of Tropical Ecology, and Journal of Ethnopharmacology.