REVIEW

The evolution of cultivated plant species: classical plant breeding versus genetic engineering

Hakan Ulukan

Abstract Agriculture is the most intensive form of environmental exploitation performed by mankind. It involves replacing the natural ecosystem with an artificial plant community comprising one or more crop species, and weeds can invade the cleared land. Initially, the adoption of agriculture did not necessarily imply an improvement in standard of living (there is, in fact, evidence to the contrary), but as agricultural efficiency improved, surpluses were generated on top of mere subsistence levels. It may take many years of labor in order to obtain a crop that has all of the desired traits. It is not possible to control which genes are transferred from the parents to the offspring, and the results are often uncertain. In comparison, the utilization of genetic engineering to improve crops can be a faster and more precise approach. Unlike traditional breeding, genetic engineering makes it possible to select the specific traits desired and insert the genes that code for them into the plant.

Keywords Agriculture · Classical plant breeding · Domestication · Evaluation · Gene center · Genetic engineering · Cultivation · Heredity

Introduction

The origin of cultivated plants has proven to be a model for the origin of species in some respects, and the process of selection responsible for these differences takes place over time as well as in space (Allard 1960, 1999; Phillips 2006). For thousands of years, farmers have used the genetic variations that occur in wild and cultivated plants to develop their crops (Ellstrand et al. 1999). Genetic diversity gives species the ability to adapt to changing environments, including new pests and diseases (Bull and Wichmann 2001) as well as new climatic conditions and stress factors (Clarkson 1981; Doebley et al. 2006). Plant genetic resources provide the raw material to breed new varieties of crops (Frankel 1977; Ulukan and Özgen 1998; Doebley et al. 2006). These, in turn, provide the basis for more productive and resilient production systems that are better able to cope with stresses such as pest and disease resistance, drought and overgrazing, etc. (Kearns et al. 1998; Ellstrand et al. 1999). Man has made tools for more than a million years, but his crops have evolved under the influence of his powers of observation, selection and imagination for only about 10,000 years (Allard 1960, 1999). Crops and man have evolved together in a kind of symbiosis. Some of these crops, such as maize, would not survive without human intervention, but man's survival is equally dependent on his crops; as well as consuming them as food, plants and their derivatives are used as drugs, oils, pigments, and resins (Phillips 2006), and so an important aim is to increase plant yield and quality through the use of advanced cultivation methods. Among the approximately 250,000–300,000 species of flowering plants that are known (Scotland and Wortley 2003), humankind is fed and clothed by only several dozen major crops (Marshall et al. 2003; Kırda et al. 2007). Interdisciplinary studies combining the tools of evolutionary and molecular biology have provided novel insights into the origins of modern crop species, such as identifying wild progenitors and patterns of genetic diversity (Doebley et al. 2006). The aim of this study is to describe both classical plant breeding and genetic engineering, and to provide an evolutionary critique on and comparison of them.

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Domestication and its possible consequences

Agriculture is one of the most important historical inventions; one that influences settlements and migrations. However, the spread of agricultural plants across Europe and North America has resulted in the fact that crop plants from different geographical regions have some characters in common (Table 1) (Harlan 1992; Poehlman and Sleper 1995; Allard 1999; Gepts 2002). This is due to plant selection (especially unconscious), which can be classified into four substages (Darlington 1973; Willcox 2004): (1) tillage (selection of larger forms, polyploids, earliness); (2) sowing (selection of forms with even and rapid germination); (3) harvesting (selection of nondehiscent forms such as hemp, flax, lettuce, opium poppy); and (4) mode of propagation (cereals, pulses and oil-seed plants which are propagated and grown only for their seeds). Humans started the selection process in order to obtain required characteristics of wild forms (for example germination, earliness, etc.) during domestication (Allard 1999). Most field crops have some in-built protection mechanism against various diseases and wild animal attacks, such as the cyanogenic glucosides found in in cassava and lima beans; the gossypol found in cotton (Kırda et al. 2007); the steroidal alkaloids found in potatoes; the hemagglutinin and trypsin inhibitors found in cereals and pulses; the capsaicinoids and vanillylamines found in chili peppers (Iglesias et al. 1997); the cucurbitacins found in cucurbits; the sulfurous compounds found in brassicas, and the erucic acid found in rapeseed (Hails et al. 1997; Muthukrishnan et al. 2001; Gepts 2002). Similarly, through plant breeding activities, the amounts of poisonous or toxic or semitoxic compounds in some plants have been decreased to insignificant or minimum levels (Bull and Wichmann 2001; Gepts 2002, Şehirali and Özgen 2007). On the other hand, climate change (Parmesan 2006), particularly global warming, could bring about drastic changes in the locations of the world's agro-ecological zones. Because of the limited scope for growth in the world's cultivated areas, each new generation of crop will have to be more productive than its ancestors. To this end, genetic engineering has an enormous potential to help solve problems that have proved intractable using conventional breeding approaches, such as the development of crop varieties with in-built resistance to key pests and diseases and tolerance to stresses such as drought (Clarkson 1981; Tanksley 1993; Park et al. 2004; Doebley et al. 2006; Barnabas et al. 2008). However, the possible impact of these techniques, particularly on human health and the environment, is giving rise to fierce worldwide debate. The improvements obtained in cultivars are hindered by the fact that most of them are sterile, a problem that can be addressed through the use of genetic engineering (Park et al. 2004; Barnabas

et al. 2008). The first transgenic tomato, banana and plantain plants have been produced (Pilson and Prendeville 2004), and most of them are now undergoing testing, marketing and consuming. Many of the staple crops that are important to poor farmers in developing countries, such as cassava, bananas, beans and yams, have received relatively little attention (Allard 1960; Doebley et al. 2006). This situation is likely to continue as plant breeding is becoming increasingly privatized and biotechnology is becoming the fast-growing province of private industry. Thus, for the time being, increasing agriculture's role in the development of the world's poor is likely to continue to depend on the identification, maintenance and use of genetic diversity. Just as the species we depend on comprise a small fraction of all of the species available to us, the genetic diversity of those species comprises a small fraction of the total genetic diversity present in all plants. The species we depend on have become more and more genetically uniform. Plant germplasms can be divided into five classes (advanced and bred varieties; genetic stocks (mutants, euploids, etc.); commercial lines; cytogenetic rearrangements or linkage markers; and bulk populations) as well as composite hybrids developed from crossing a wide variety of cultivars, local varieties and landraces, wild forms, wild relatives or new crops/releases (Allard 1960, Şehirali and Özgen 1987; Harlan 1992, Fowler and Hodgkin 2004; Doebley et al. 2006). The following selection processes operate when wild plants are introduced into cultivation: (1) conscious selection applied deliberately by the growers in order to obtain traits of interest to them; (2) unconscious or automatic selection brought about by the fact that the plants concerned were picked from their original wild habitats and placed in a new (and frequently very different) human-made environment (new traits are automatically selected to fit the new conditions, resulting in a build-up of characteristic domestication syndromes, each fitting the specific agricultural conditions provided by the domesticators). It is now widely accepted that unconscious and conscious selection are closely intertwined and played an important role in shaping many of the domestication traits that characterize crops and distinguish them from their wild ancestors (Willcox 2004). Polyploidy is associated with novel genomic interactions and molecular genetic mechanisms, and is suggested to have opened up new avenues for agronomic improvement (Ramsey and Schemske 2002; Wendel and Cronn 2003; Doebley et al. 2006; Ozias-Akins and Van Dijk 2007). Because many important crops such as wheat (*Triticum* spp.), maize (*Zea mays* L.), and cotton (*Gossypium* spp.) are polyploids, these species provide model organismal frameworks for analyzing the fate of duplicated genes and genomes following polyploid formation (Kırda et al. 2007).

Table 1 Some characters of domesticated plants and examples of plants with these characters

Selection stage	Characters		Example
	General	Special	
Seedling	Increased emergence	Suppressed dormancy	Many plants
Reproduction system	Selfing rate increment		Tomatoes
	Adaptation of vegetation/propagation		Cassava
Harvest or post-harvest	Seed yield increment	Seed shedding prevent	Maize
		More compact growth pattern	Pulses, maize
		Increased number and size of flowers	Wheat, barley maize
		Increased number of seeds per flower	Maize, *Amarathus* spp.
		Sensitivity to and variation with photoperiod	Pulses, rice
		Consumer requirements, dimensions, etc.	Tissues of many plants
		Decreased level(s) of toxic substance(s)	Cassava, lima bean

Agricultural changes for domesticated plants

Conscious classical plant breeding efforts date back to at least 700 BC, when the Assyrians and Babylonians artificially pollinated the palm (Hulse 2004) and native Peruvians domesticated tomatoes in the Andes (Kırda et al. 2007), as well as literally hundreds of other crops. Cereals appear to have usually developed in or near mountainous regions of the subtropics and tropics (Baker 1965; Doebley et al. 2006). Maize was domesticated by native Americans in Mexico and the southwestern US, and, depending on the region and the climate, rice, sorghum, or millet (in tropical areas), and wheat, rye, barley, or oats (in temperate regions) were also domesticated (Willcox 1998, Willcox 2004). While characteristic edible pulses such as beans (*Phaseolus* sp.) and peanuts (*Arachis* sp.) are also native to the Western Hemisphere (Doebley et al. 2006), but there were a poor selection in the leguminous plants, except for certain tropical crops (Baker 1965; Darlington 1973; Allard 1999). In the seventeenth century AD, revolutionary techniques in plant breeding and vegatative propagation were applied to the chief crop plants of temperate regions. Archaeological findings show that some 10,000 years ago, barley, wheat, lentils, pea, flax and vetch were domesticated in the Fertile Crescent region (Harlan 1992; Doebley et al. 2006). The established mix of conscious and unconscious processes that had in a few thousand years yielded vast agricultural improvements began to give way to three types of systematic process. First, there was selection, not casual or unconscious but persistent and unremitting; second, there was propagation, not parochial but national and even international (Allard 1999); third, there was hybridization, based for the first time on the knowledge that pollen as well as ovules contribute something to heredity (Darlington 1973; Rieseberg 1997; Ellstrand et al. 1999). The contemporary geographical distributions of the wild progenitors of these crops

corroborate the archaeological evidence (Allard 1999). Man, in the course of history, has used perhaps 3000 plants as food, and about has domesticated about 200 of these (Phillips 2006). On the other hand, due to the discovery of the effects of heterosis or hybrid vigor and the usage of it commercially (Lippman and Zamir 2007), seed yields of maize, sorghum and pearl millet increased significantly during 1965–1990 (Jauhar 2001); and the cultivation of high-yield wheat (*Triticum* spp.) (Jauhar 2001) and rice cultivars led to the "Green Revolution" during 1960–1970 (Nevo 1998; Cook 2000; Swaminathan 2007). Similarly, the usage of new cytogenetic analytical methods and techniques have caused plant breeding to become an increasingly complex activity; moreover, esp. direct gene transfer attempts to monocotyledons, especially in wheat (Repellin et al. 2001; Reynolds 2007; Rommens et al. 2007). The results of these new cytogenetic analysis methods and techniques in plant breeding can be summarized as follows: an increase in size (gigantism), often accompanied by polyploidy; reduction or loss of natural mechanisms for dissemination; a decrease in the number and an increase in the size of individual propagules (when the seed or fruit is a food source); a disproportionate increase in the size of the part of the plant that humans use; and the loss of delayed seed germination (dormancy) and protective mechanisms such as thorns, toxins, shells and hairiness (Banning 2001) (Table 2).

Genetic variation and development in the cultivated plants

Preserving the genetic diversity at the plant level is the most important and basic aim of the plant breeding, whether by selection, mutation, hybridization, molecular methods, etc. (Allard 1960; Day 1973; Harlan 1992; Poehlman and Sleper 1995; Rieseberg 1997; Allard 1999;

Table 2 General comparison of classical plant breeding and genetic engineering

Classical plant breeding	Genetic engineering
Cultivars are developed much more slowly than when using genetic engineering	Provides a faster and more accurate way of developing new cultivars than classical plant breeding
Studies of the genetic material in species	Aside from mutations, only increases the existing genetic variation
There are some botanical borders	There are no botanical borders
Results can be predicted beforehand	Results cannot be predicted beforehand, so unwanted products can be produced
There are generally no uncertainties or aberrances when backcrossing is utilized	The introduction of genes can lead to somewhat uncertain results and aberrances
Current methods of developing new cultivars are generally genotype-dependent	Often the genotypes used are not suited to genetic engineering in cultivars
Can happen under natural or controlled conditions	Is not "natural!"
Selection is employed	Selection is employed
Does not use a CaMV 35S promoter and various terminators	Usually uses a CaMV 35S promoter and various terminators
Does not employ molecular markers	The process used is usually sped up through the use of molecular markers
Developing a new cultivar takes a long time and a lot of labor, but process difficulties are minor and very simple	Cultivars can be developed in a very short time, but it is an expensive and very complex process
A gene can typically be introduced by backcrossing(s)	
Does not cause wildness in some crops	Can cause wildness in some crops
Does not result in genetic erosion or pollution	If a gene spreads or escapes into another plant, into vegetation or into an ecosystem, genetic erosion or genetic pollution can result
Classical plant breeding has actually introduced deleterious genes from wild relatives into cultivated plants	Transgene silencing could be a major problem

Ulukan and Özgen 1998; Doebley et al. 2006; Shu and Lagoda 2007; Şehirali and Özgen 2007b). Wild relatives of wheat and barley have a fragile rachis (Vavilov 1951) and many other features that equip them to survive in nature, and they are very different from their cultivated relatives. On the other hand, domestication is a very important process conducted by humans to adapt plants and animals to human needs, whether those humans are farmers or consumers. Interestingly, this process of domestication has been conducted for tens of thousands of years (since the last ice age) independently in several regions (Allard 1999; Gepts 2002). The sources of variation, the principles of selection, and the conditions of geographical and genetic isolation all operate equally in wild and in cultivated plants (Doebley et al. 2006). Most artificial selection of cultivated plants is natural to the extent of being unconscious, and most natural selection of wild species that occurs nowadays has an unsuspected artificial component (Darlington 1973; Allard 1999; Bull and Wichmann 2001). Classical plant breeding methods are now widely applied and used to provide food for humanity (Phillips 2006); genetically engineered plants currently produce specialty products. This phenomenon allows scientists to know exactly which genes they are inserting into the genome of the plant. In addition, the genes do not have to be from the same species. *Bt* corn is an example of how a gene from a bacterium can be inserted into a plant (Leniaud et al. 2006). The

development of herbicide-resistant *Bt* plants, virus-resistant maize, soybean and cotton (Jauhar 2001; Wendel and Cronn 2003; Ulukan 2005; Sanderman 2006; Kırda et al. 2007), golden rice (a rice cultivar rich in vitamin A and Fe; Ye et al. 2000; Potrykus 2001; Livermore 2002; Herdt 2006), and the development of varieties that are resistant to European corn borer [*Ostrinia nubilalis* (Hbn.)] (Long et al. 1989) are the best examples of successes of transgenic technology (Bull and Wichmann 2001; Gepts 2002; Doebley et al. 2006). Many of the changes incorporated into plants during the earliest stages of plant domestication were common to several crops, comprising what Vavilov (1951) referred to as "homologous variation." People developed and discovered one of the most basic and important principles of plant breeding, selection (Allard 1960; Gasser and Fraley 1989; Harlan 1992; Losey et al. 1999; Doebley et al. 2006). Selection refers to the (time-consuming) processes of enabling plants and animals to adapt to the changing environmental conditions in a certain region (Allard 1999; Gepts 2002; Doebley et al. 2006; Ulukan 2008). In 1924, the Russian botanist N.I. Vavilov concluded that nearly all of our crop plants are derived from only eight major domestication centers, including Mesoamerica, the Southern Andes, the Near East, Africa, Southeast Asia, and China (Table 3; Vavilov 1951). Archaeological evidence, along with the results of breeding activities, show that new forms of bread wheat that are

hexaploid arose in the seventeenth century BC in Asia Minor due to hybridization between emmer wheat (a tetraploid), which was brought into cultivation in the Fertile Crescent, and a diploid species of *Aegilops* that grows wild in the same region (Vavilov 1951; Willcox 2004). A wide variety of ancestors of the cultivated potato grow wild in Peru, Bolivia and northwestern Argentina (Darlington 1973). The Mediterranean Sea, a barrier to wild plants, has also provided a means of dispersing and bonding established cultivated plants. As a matter of fact, by 1940 it held about 200,000 accessions of wheat, cotton, potato, legumes, vegetables, and other crops. By 5500 BC, cultivation was being practiced over a wider area, and Einkorn wheat (a diploid) was being grown and mixed with emmer (Willcox 2004). A thousand years later, cultivation had reached the swampy plains and irrigated cultivation began (Harlan 1992). Soon agriculture began to appear in Asia Minor and the Fertile Crescent, but cultivation does not appear to have originated until the third millennium BC, in northern China, southern India or Nubia (Darlington 1973; Harlan 1992; Allard 1999). Determining the origin of agriculture is a problematic task, since it predates the invention of writing. The first crops that humans domesticated included barley and wheat (Darlington 1973; Kartha et al. 1993; Ellstrand et al. 1999). It is clear that farming was invented at least twice, and probably more often than this: once in the Fertile Crescent (early sites of settled agriculture have now been excavated in a line around this region, with branches into the Persian and Anatolian table lands), once in East Asia, and probably once in Central and South America. The initial reasons for the introduction of farming may have included climate change (Parmesan 2006). Various characters in cultivated plants are related to their survival in the wild; for example pod cracking in rapeseed, seed dormancy in vetchling (*Lathyrus sativus macrospermus* Zalk.), thorns on roses (*Rosa* spp.), etc. (Liljegren et al. 2000).

Heredity of the agronomic characters in cultivated plants

In 1900, Gregor Mendel, a Moravian monk, was introduced into the scientific mainstream, and modern genetic science was born (Fowler and Hodgkin 2004; Doebley et al. 2006). With the scientific basis of the hereditary pathway of the genes in plant species established, breeders were able to breed plants with required characters with greater precision and efficiency than had previously been possible (Ladizinsky 1985). Initially, the traits were analyzed according to Mendelian genetics, since many of them display quantitative variation and discrete phenotypic segregation classes (Ramsey and Schemske 2002; Willcox

2004; Doebley et al. 2006; Ozias-Akins and Van Dijk 2007). The understanding that crop traits have a genetic basis has encouraged the use of genetics as a means to solve agricultural problems. Thus, there are many examples of genetically determined changes aimed at improving either plant performance in the field or plant-based products. Natural hybridization among certain plant species formed the genetic background of modern bread wheats in Asia Minor. However, bread wheat (*Triticum aestivum* L.) first appeared in European agriculture around 4000–5000 BC and remained relatively unchanged until the eighteenth and nineteenth centuries (Harlan 1992). In the last hundred years, breeding has dramatically altered the wheat we grow. Yields have more than doubled, with at least 50% of this increase in yield being due to genetic changes that have halved the straw length and diverted more resources into ear and grain development. The bread-making quality of the flour has been improved by directed breeding. In the last 30 years, oilseed rape has been modified to increase the suitability of the oil for use in food and the meal for use in animal feed. Wild rapeseed and old varieties cultivated up to the 1970s contain trace amounts of toxic chemicals (for example erucic acid). Natural genetic mutations discovered in particular varieties of oilseed rape have subsequently been bred into most modern oilseed rape varieties in order to eliminate these chemicals. In classical plant breeding, deleterious genes are transmitted to cultivated plants from donors (here wild plants) through linkage (Ulukan and Özgen 1998; Doebley et al. 2006; Şehirali and Özgen 2007b). However, fully domesticated plants may not survive in the wild without human intervention in terms of planting and harvesting (Ellstrand et al. 1999; Gepts 2002). More recently, these same traits have been analyzed by advanced QTL techniques in a limited number of economically important plants, including common bean, tomato, maize, rice and pearl millet (Tanksley 1993; Lee 1995; Gepts 2002; Flint-Garcia et al. 2003; Schmid et al. 2003; Park et al. 2004; Lee et al. 2005; Demuth and Wade 2006; Doebley et al. 2006; Kırda et al. 2007; Lippman and Zamir 2007), and almost all of these characters were found to be quantitative, genetically controlled, and governed by many genes.

Transformation from wild to cultivated forms

We cannot say that there is good agro-ecological evidence for plants derived from hybridization between wild and cultivated forms (Ellstrand et al. 1999). According to information from the Near East and other regions that are the most important plant breeding centers, and many archaeological findings, the transformation of wild cereals to cultivated forms (as measured through morphological

Table 3 Selected agricultural plants and the geographic regions where they were domesticated

| East Asia	Africa	Near East	Europe	North America	Pacific islands	South America
Rice	Sorghum	Wheat	Oats	Corn (maize)	Breadfruit	Quinoa
Millet	Teff	Barley	Rye	Common bean	Sweet potato	Common bean
Buckwheat	Pearl millet	Peas	Beets	Lima bean	Taro	Manioc
Soybean	Foxtail millet	Chickpeas	Hazelnut	Chili pepper	Arrow root	Squash
Adzuki beans	Cow pea	Faba beans	Plum	Sweet potato	Coconut	Tobacco
Turnips	African rice	Lentils	Apple	Sunflower	Yams	Cacao
Chinese radish	Yams	Carrots	Cabbage	Papaya	Lemon	Sweet potato
Canola seed	Oil palm	Beets	Almond	Pumpkin	Grapefruit	Potato
Apricot	Water melon	Safflower	Pear	Tomato	Orange	Cotton
Peach	Okra	Olive	Lettuce	Mango	Mango	Avocado
Water chestnut		Fig	Carrot	Bottle gourd	Banana	Cashews
Cucumber		Fenugreek	Onions	Squash	Clove	Pineapple
Sesame		Dates	Grape		Black pepper	Papaya
Tea					Eggplant	Peanut
					Sugarcane	Chili pepper

variations) happened at least 10,000 years ago (Long et al. 1989, Willcox 1998). From a genetic or breeding standpoint, the limiting factors on progression through the selection process are the phenotypic variation (Allard 1999; Willcox 2004), the number and magnitude of genetic effects (Day 1973; Nevo 1998; Doebley et al. 2006), the heritability, the selection intensity (Falconer 1989; Allard 1999; Doebley et al. 2006), the frequency of mutations (Drake et al. 1998; Doebley et al. 2006), the level of outcrossing, climatic conditions, ecology (Baleé 2006), population size and geography (Rieseberg 1997), migration rate, hereditary pathways of the characters (Doebley et al. 2006), and the degree of recombination linkage (Bull and Wichmann 2001; Baleé 2006) among the genes associated with domestication. During crop migration, the first effect of unconscious selection on mixed crops is to change the species so that different regions come to have widely differing crop species (Allard 1999; Willcox 2004). The second effect, which partly competes with the first, is to change the character of the species (Darlington 1973). Many important results have been obtained in relation to these points at the level of molecular breeding from molecular mapping studies of plants such as maize (in particular), bean, rice, sorghum and tomato, field experiments on rachis brittleness, etc. (Park et al. 2004; Kırda et al. 2007). Using QTL techniques, domesticated characters were found to have simple hereditary pathways (Table 1; Gepts 2002; Flint-Garcia et al. 2003; Lee et al. 2005; Demuth and Wade 2006; Leniaud et al. 2006; Lippman and Zamir 2007). Until the present century, most ideas about the beginnings of agriculture were of European origin. Early sites of settled agriculture have now been excavated, including some around the Fertile Crescent and others that branch into the Anatolian and Persian regions (Allard 1999). These archaeological findings show that the early cultivators were connected. Legume crops such as field bean, lupin and common bean were known before 1550 BC (Gepts 2002). Selection for nonbrittle rachis, coded by a single gene in Einkorn, shows that domestication (as defined by the amount of time needed to achieve a gene frequency of >90–95%) could have taken place within a time span of 200 years (Allard 1999; Gepts 2002; Willcox 2004). The earliest settlements in the region have been dated to the seventeenth century BC, and occur at altitudes of between 120 and 1200 m. They reveal that emmer, two-rowed barley and hexaploid wheat are derived directly from local wild plants (Willcox 2004). Wild barley was widely found in areas from Central Asia to Morocco (Allard 1999), while wild emmer was found only between the upper Dicle river (also known as the Tigris) and Palestine (Willcox 2004). Evidence from prehistory and history is schematized in Fig. 1.

Development and analysis of new cultivars

In both evolution and plant breeding, populations are constantly being sifted for superior types. In this continual sifting, the primary force is selection, where the reproduction of individuals with certain characteristics is favored. Cultivated plants developed from the variations derived through natural hybridization. However, during the last 20 years, sexual propagation methods and genetic engineering techniques have been used at different levels (Nevo 1998; Park et al. 2004; Barnabas et al. 2008). In a molecular breeding sense, premier varieties that have the

Fig. 1 Diagram showing a timetable for the primary expansion of cultivation through the movement of cultivators along with their changing crops across the Old World from the ancient East, and independently across the New World from Mexico and Peru (modified from Darlington 1973)
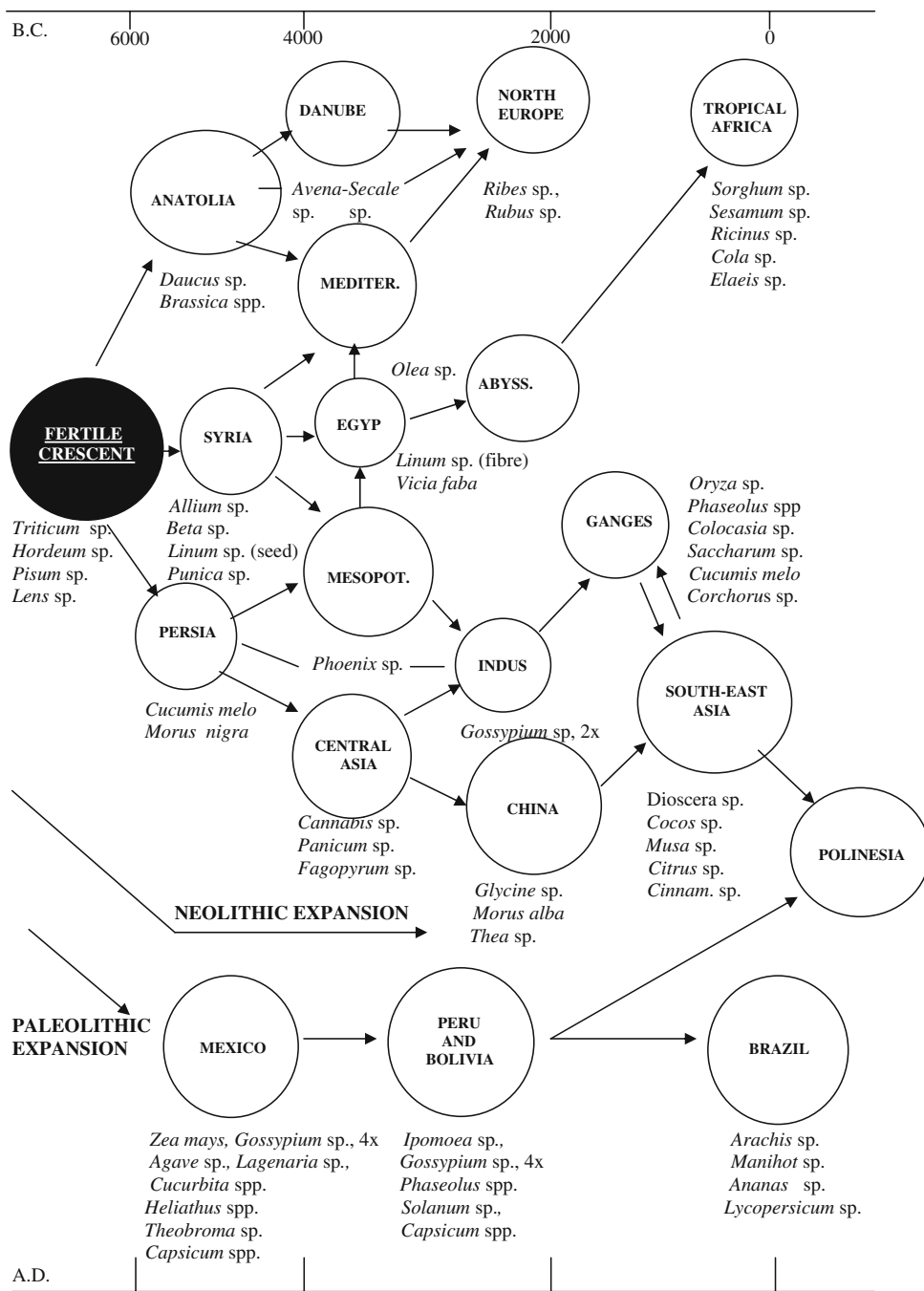
most desirable innate traits are seldom the most amenable to tissue culture (Jain 2001; Doebley et al. 2006). The first plants were transformed in the mid-1980s using *Agrobacterium*-mediated transformation, a method that exploits the natural propensity of the agent that causes the disease crown gall, *Agrobacterium tumefaciens*, to transfer genes into a plant genome (Cook 2000). Many plant species, including tobacco and *Arabidopsis*, can be routinely transformed using this method (Flint-Garcia et al. 2003; Park et al. 2004). Most crop plants, for example transgenic barley (Willcox 2004; Sharma et al. 2006), are not amenable to the application of *Agrobacterium* for routine transformation. The electroporation method, a genetic engineering technique, involves incubating individual plant cells in a solution containing the DNA encoding the gene of interest. While genetic engineering is often said to be the fastest way to develop a new cultivar, some researchers do not believe that this is always true (Gepts 2002), due to the sophisticated processes involved in genetic engineering (involving many different techniques, stages and substages), and the fact that it can produce unexpected physio-morphological results such as gigantism, lethality, etc

(Şehirali and Özgen 2007a). Obtaining a rice cultivar that contains high levels of provitamin A and Fe (namely, golden rice) by incorporating genes from *Erwinia uredovora* bacterium and daffodil is a very good example of plant genetic engineering (Ye et al. 2000; Potrykus 2001; Livermore 2002; Park et al. 2004; Herdt 2006; Barnabas et al. 2008). Plant genetic engineering techniques are providing new possibilities when there is no source of disease resistance in the gene pool (Bull and Wichmann 2001; Fowler and Hodgkin 2004; Barnabas et al. 2008); for example, they can be used to provide papaya with resistance to papaya ring spot virus (PRSV) (Lius et al. 1997; Gepts 2002). These techniques complement classical breeding and genetic variation techniques that are the starting point for any plant-breeding program (Day 1973). Hybrids created using classical plant-breeding techniques have certain agronomic characteristics or characters and are generally genetically stable, while the situation is different when genetic engineering is used (Barnabas et al. 2008). The use of classical plant breeding techniques has resulted in many significant successes in terms of quality and quantity of crop in the last 60 years, especially in hybrid crops (Pilson and Prendeville 2004). Nevertheless, the use of such techniques to improve pest and disease resistance and other agricultural traits did not produce a sufficient degree of improvement, and they resulted in negative effects too. Due to sterility, incompatibility and the limited number of plants used in interspecific hybridization, the successful incorporation of target characters was somewhat diminished. Moreover, it takes a long time to eliminate this negative effect by backcrossing. Using genetic engineering, these negative effects can easily be eliminated, and it is possible to transfer every required character. Applying classical plant breeding methods, it is possible to create new varieties from related species (same genus), but due to botanical borderlines they cannot be crossed. New cultivars of maize, soybean, cotton, papaya, etc. have been developed that carry additional genes that produce traits as diverse as resistance to pests, diseases and herbicides (Wendel and Cronn 2003; Sanderman 2006; Kırda et al. 2007). Some of these cultivars have been readily adopted by farmers, since they greatly facilitate the management of crops (for example herbicide resistance), provide a more effective alternative to current control methods [for instance resistance to European corn borer, *O. nubilalis* (Hübner) in maize and PRSV resistance in papaya (Rimberia et al. 2007)], or offer the only viable route to disease control in the absence of any natural resistance mechanism in the gene pool (Bull and Wichmann 2001; Fowler and Hodgkin 2004; Kırda et al. 2007). The low-toxicity herbicide glyphosate, which prevents the production of 5-enolpyruvylshikimate-3-phosphate synthase, affects wide-leaved weeds and annuals

from the *Poaceae* family. Plants tolerant of glyphosate were created by inserting various mutant genes along with their products into the plants (Sanderman 2006), and plants resistant to sulfonylurea were obtained by inserting mutant acetolactate synthase (ALS) genes. Similarly, the herbicide L-phosphinothricin has been produced by transforming a bar gene from *Streptomyces hygroscopicus* to potatoes and alfalfa, while bromoxynil and 2,4-dichlorophenoxyacetic acid have been produced by transferring bacterial genes (Rommens et al. 2007).

In addition, experiments with *Bt* gene-transformed tomatoes, cotton and maize led to plants resistant to an insect pest; when a trypsin inhibitor (*CpTi*) gene from cowpea was transformed to tobacco plants, the tobacco plant seedlings showed resistance to bugs (*Heliothis virescens*) (Ulukan 2005; Kırda et al. 2007). Similarly, plants transformed with tobacco mosaic virus (TMV) coat protein genes or lettuce mosaic virus (LMV) and tobacco ringspot virus RNA and cDNA displayed a very high degree of resistance to these viruses (Özgen and Özcan 1996; Iglesias et al. 1997). However, wild and cultivated plant forms used in the plant-breeding programs only partially benefitted from this approach, up to certain botanic limits (Day 1973; Ellstrand et al. 1999). The results of classical breeding can be predicted beforehand, and the end products of and production processes used in classical breeding are agronomically more stable and environmentally friendly. In genetic engineering, genes from different families can be combined in one genotype (Park et al. 2004; Barnabas et al. 2008), so it is not possible to predict the results of plant genetic engineering. To put it another way, the results of genetic engineering are not known (Vergragt and Brown 2008). There are no such side effects of classical plant breeding. It is interesting that unexpected results can be seen in a typical model organism used in genetic studies, *Arabidopsis thaliana* (Flint-Garcia et al. 2003; Park et al. 2004). Most plants produced by genetic engineering techniques have a promoter gene (*CaMV 35S*) obtained from the cauliflower mosaic virus (Ulukan 2005; Barnabas et al. 2008), and this situation has resulted in some important and vital biosafety debates. The *CaMV 35S* promoter not only affects transgenes, but also more than a thousand genes located on each chromosome segment and connection site. Moreover, this unit could cause toxin production. Environmental effects on the stability of transgenes appeared in the first year that permission was granted to produce glyphosate herbicide-tolerant and *Bt* cotton, and resulted in the loss of 20,000 acres in Missouri (Sanderman 2006). Extreme climatic conditions may have caused genetic instabilities that resulted in this situation (Fox 1997). Similarly, *Bt* cotton was not found to be resistant to *Helicoverpazea* in Texas (Gore et al. 2000), and many growers have suffered from important agronomic problems

such as insufficient germination in seeds, irregular growth, low crop quality and quantity, and reduced yields.

Conclusion

Plant breeding began ten thousand years ago. Similarly, gene mutations occurred in addition to genetic variations through artificial or natural hybridization, selection, polyploidy, etc. among genera, species and cultivars (Harlan 1992; Poehlman and Sleper 1995; Şehirali and Özgen 1987; Allard 1999; Wendel and Cronn 2003; Doebley et al. 2006; Ozias-Akins and Van Dijk 2007; Şehirali and Özgen 2007a). Very important successes in terms of crop yield and quality, pest and disease resistance and other agronomic aspects have been achieved. Plants were protected against pests and diseases using chemicals for many years, but because of residue effects, organisms gained resistance to the effects of the chemicals. The increasing burden placed on agriculture to feed the world's growing human population also strongly impacts on this issue (Fowler and Hodgkin 2004). Classical plant breeding programs have sometimes failed for genetic reasons, such as sterility, incompatibility, etc., and genetic engineering techniques have proven useful to overcome some of these problems (Oldach et al. 2001; Doebley et al. 2006). While the intensive genetic and cytogenetic work that is being carried out has resulted in more complex plant breeding activities, it has also made it easier to transform foreign/alien genes into cultivated plants. Genetically modified organisms (GMOs) have become a high profile issue for many reasons. Some of these reasons, such as health benefits, harmful effects, consumption, etc., are still being discussed (Pilson and Prendeville 2004; Herdt 2006). In any case, a silent revolution is in progress as GMOs are used as a tool to give scientists and breeders greater insight into the biology and genetics of plants in conventional breeding programs.

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