Chapter 1
Tropical Environments, Biodiversity, and the Origin of Crops

Paul Gepts

So long as freedom from hunger is only half achieved, so long as two thirds of the nations have food deficits, no citizen, no nation can afford to be satisfied. We have the ability, as members of the human race, we have the means, we have the capacity to eliminate hunger from the face of the earth in our lifetime. We only need the will.

President J. F. Kennedy, 1963

We believe that it is indeed possible to end world hunger by the year 2000. More than ever before, humanity possesses the resources, capital, technology and knowledge to promote development and to feed all people, both now and in the foreseeable future. . . . Only a modest expenditure is needed each year - a tiny fraction of total expenditure which amounts to $650 billion a year. What is required is the political will to put first things first and to give absolute priority to freedom from hunger.

FAO World Food Colloquium, 1992

Food supplies have also been made more vulnerable by our reliance on a very small number of species: just 30 crop species dominate food production and 90 per cent of our animal food supply comes from just 14 mammal and bird species – species which themselves rely on biodiversity for their productivity and survival. There has been a substantial reduction in crop genetic diversity in the field and many livestock breeds are threatened with extinction . . ..I urge individuals and institutions alike to give greater attention to biodiversity as a key theme in our efforts to fight the twin scourges of hunger and poverty and achieve the Millennium Development Goals.

U.N. Secretary-General K. Annan, 2004

P. Gepts
University of California, Department of Plant Sciences / MS1, Section of Crop and Ecosystem Sciences, Davis, CA 95616-8780, USA.
e-mail: plgepts@ucdavis.edu

Abstract Plants play an important, but often insufficiently recognized. role in human societies, chiefly as providers of food, feed, and fiber, but for other uses as well such as drugs and building materials. In those cases where demand for a particular plant product exceed natural supply, humans initiated cultivation of those plants 10,000 years ago, resulting in the domestication of a limited number of species in several areas of the world, generally located in tropical and subtropical areas. Tropical and subtropical areas consist of several ecozones defined by climate, soil, and vegetation and fauna. One of the major factors distinguishing tropical ecozones is the distribution of rainfall and particularly the length of the dry season, if any. From a biological standpoint, most of biodiversity is concentrated in tropical areas. This may explain in part why the majority of crops discussed in this volume originated in either tropical or subtropical ecozones with summer rains or in the tropical ecozone with year-round rains. The fundamental contribution of genomics to plant breeding is to provide information on the genotypic basis of phenotypic variation. Based on this information, marker-assisted selection systems can be developed that can increase the efficiency at identifying agronomically useful diversity and transferring it into improved cultivars. In turn, marker-assisted selection is expected to increase the efficiency of plant breeding. To achieve this goal, however, genomic resources have to be developed, not only in model species, but especially in target species as illustrated in this volume. Having access to a diverse set of improved crops is a critical element of strategies to alleviate food insecurity and poverty, which affect disproportionately rural populations. Recently, the goal of increasing crop productivity has taken added urgency because of the combined impact of the focus on biofuels and global warming. Genomics is a crucial tool in raising crop productivity for the foreseeable future.

1.1 Introduction

Plants have played and still play an important role in human societies, from traditional, indigenous societies to modern societies with advanced technology. Although the role of plants may not be so readily apparent in our increasingly urbanized societies, examples abound of the lasting impact of plants in human activities (Balick and Cox 1996; Lewington 2003; Marinelli 2005). For example, a survey by Estrada-Lugo (1989) of the citation frequencies of various plant uses in the Códice Florentino, an account of pre-Columbian life by Bernardo de Sahagún in the early 16th century, shows a myriad of uses. These include, but are not limited to, uses as dyes, drugs, fibers, food, forage, fuel, medicines, ornamentals, resins, sleeping aids, spices, and venom. Plants fulfill various roles in ceremonies, construction, rituals, and taxation. In our contemporary societies, the use of plants has not diminished. Either alone, or in conjunction with animal or industrial products, they still play an important role in our daily lives, from building materials for our houses, tires and fuel for transportation, personal care products, an ever-broadening range of vegetables and fruits, paper products, and medical drugs.

Many plant products are derived from wild-growing plants, often at the risk of eventual extinction of the native populations of these plants; some products, however, are harvested from cultivated plants, when the demand has surpassed the production capacity of the original, wild populations. This can be seen as one of the stimuli leading to the origins of agriculture, namely as a response to an imbalance between the local supply and demand of a plant (or animal) product.

The switch from hunting-gathering to agriculture, which took place first some 10,000 years ago more or less simultaneously in several areas of the tropics and semi-tropics (Smith 1995), is one of the most momentous accomplishments of human evolution. Without agriculture, humans would not be able to feed and clothe themselves. The transition to agriculture involved several important changes such as the adoption of a sedentary lifestyle, the development of villages, the acquisition of pottery-making ability, and, not least, the domestication of plants and animals. This transition has, therefore, rightfully been called the Neolithic Revolution because of the all-encompassing changes it induced in human societies.

The specifics of where, when, and why agriculture originated is still the subject of passionate debates, but is beyond the scope of this volume on genomics of tropical crops (Smith 1995; Gepts 2004a; Bellwood 2005; Zeder 2006; Barker 2006). What is of interest, however, are the geographic aspects of crop domestication and cultivation, and particularly their relationship to the tropical environment. I define the tropical environment to include not only those areas that straddle the equator, but also those straddling the Tropics of Cancer (23.5°N) and Capricorn (23.5°S). The Tropic of Cancer runs through Mexico, northern Africa, the Peninsula of Arabia, India, and Indochina. The Tropic of Capricorn runs through southern Brazil, Namibia and South Africa, and Australia. In this introduction, I will present the physical features of the tropical environments, the biogeographical features of the tropical environments, and the geographic distribution of centers of agricultural origins and domestication. I will then proceed discussing – in a general way - the contributions of genomics to plant breeding and the contributions of crop improvement to hunger and poverty alleviation, a context relevant to the tropical focus of this book.

1.2 Tropical Environments

The terrestrial landmasses of Earth are divided into a limited number of ecozones, which are large areas in which physical factors such as climate and soil interact to establish a characteristic environment where an assemblage of plants grow and provide a habitat for animals. Schultz (2005) provides an excellent overview of the nine ecozones that have been recognized. His treatment will be followed in this and the next section. These ecozones form broad, sometimes fragmented, east-west bands between the poles and the equator in the northern and southern hemispheres. In addition to the Polar, Boreal, Temperate Midlatitude, and Dry Midlatitude ecozones, which cover the polar to temperate environments, five additional ecozones are located in subtropical and tropical zones (Table 1.1).

Table 1.1 Semi-tropical and tropical ecozones (modified from Schultz 2005)

Ecozone	Plant formation (climax formations)	Examples of geographic distribution	Proportion of terrestrial distribution (%)
Subtropics with winter rains (Mediterranean)	Sclerophyllous forest and shrub formation	Mediterranean, California, S.W. Australia, S.W. South Africa, Chile	2
Subtropics with year-round rains	Subtropical rain forest	S.E. US, Uruguay and S. Brazil, S. China, E. Australia, E. South Africa	4
Dry subtropics and tropics	Desert and semi-deserts Winter-wet grass & shrub steppes (subtropics) Summer-wet thorn savanna (tropics) and thorn steppe	N. Mexico, N. Argentina, Bolivia, Paraguay, Sahara, Southern Africa, Central Australia	21
Tropics with summer rains	Dry to moist savanna (includes tropical deciduous forest)	S. Mexico and Central America, S. America (N. and S. of Amazon), W. Africa, India, S.E. Asia, N. Australia	16
Tropic with year-round rain	Tropical rainforest	Amazon, C. America, Central Africa, Indonesia, Papua New Guinea	8

Climate is the fundamental factor determining the geographic extent and boundaries of these ecozones and their geomorphological processes, soil formation, plant growth, and land use potential. The most important climatic variables are solar radiation (especially the photosynthetically active radiation between 400 and 700 nm), the mean air temperature, and the length of the growing season, which are the determinants of the annual primary production by vegetation. In addition, the extreme values of these climatic variables and their frequency is also important in determining the distribution of the ecozones. The growing season is defined as the annual total of months with a mean temperature above 5 °C and a precipitation (p, expressed in mm) of double the monthly mean value of temperature (expressed in °C): p (mm) $\geq 2\ t_{mon}$ (°C). In tropical regions, plant growth can be interrupted by drought; in contrast, at middle to high latitudes, plant growth is interrupted by cold.

Climate and vegetation play an important, but not exclusive, role in determining soil type. The chemical fertility of soils refers to the quantity of basic nutrients and how they are bound to soil particles (soluble and exchangeable fractions), which depends on the soil mineral (clay type) and organic matter (humus) composition. The amount of rainfall influences the extent to which certain mineral elements stay

within the soil horizons exploited by plant roots or are leached away. The organic matter content in soils depends on how much and what type of litter is decomposed and under which conditions. The soil structure determines the amount of water available in the root area, which is derived from the difference in water content between the field moisture capacity (maximum of water held in the soil after excess moisture has flowed away) and the permanent wilting point (an equilibrium point between root suction potential and soil water potential).

There is a close correlation between ecozones and major plant formations because of convergent evolution of different plant species as they have become adapted to local conditions. This adaptation process has led to the development of a limited number of life forms (e.g., evergreen broadleaf, dry season deciduous, succulents, and grasses, as proposed by Raunkiaer 1934). In turn, plant formations consist of one or more life forms in characteristic proportions (Table 1.1). The different plant formations show great variation in primary productivity, which is due primarily to the size and structure of the above-ground biomass and climatic and edaphic factors. The larger the biomass, the larger the productivity, with the exception of grasslands in steppes and grassland savannas, which show a higher production capacity from a smaller amount of biomass. The structure of biomass also plays a role in that it determines the size and distribution of leaf surfaces, which play an important role in carbon assimilation.

The leaf area index (total leaf area/total ground surface underneath the leaf cover) is a measure of light interception and varies from 5-6 in deciduous forests to 7-8 in subtropical rainforests and 9-10 in tropical rainforests. Generally, biomass production increases with the leaf area index.

Environmental factors involved in primary productivity include the length of the growing season, solar radiation, temperature, water availability, and soil nutrient availability. In general, biomass productivity is a function of climate latitudinal changes. The highest productivity measures are observed in tropical rainforests because they have year-round rain, high precipitation totals, high temperatures, and intense solar radiation.

1.3 Major Subtropical and Tropical Ecozones (based on Schultz 2005)

1.3.1 Subtropics with Winter Rains

The Subtropic with Winter Rains ecozone (also known as the Mediterranean ecozone) is the smallest (2% of landmass) and most fragmented ecozone. It is present on the five continents, on their western side between 30-40° latitudes between the dry tropics and subtropics (towards the equator) and temperate midlatitudes (on the polar side). Precipitation ranges from 300 to 800 mm, mostly in winter and with a few summer months without rainfall at all. The mean monthly temperature is above 18 °C for at least four months. Plant growth is interrupted mostly in the summer because of drought rather in than in the winter because of cold.

This ecozone is rich in plant diversity with many endemic species. It is dominated by evergreen sclerophyllous forests (now often replaced by sclerophyllous shrubs, because of excessive logging over time). Sclerophylly manifests itself as hardened leaves, with a thickened epidermis, a shiny, waxy surface, and other adaptations to summer drought. In addition to trees and shrubs, the vegetation is also rich in hemicryptophytes (e.g., perennial rosette plants), geophytes (bulbs, rhizomes), and therophytes (seed-propagated plants such as annual legumes or grasses). The primary productivity of this ecozone ranges from 3.5 t biomass dry weight ha^{-1} $year^{-1}$ (in shrub vegetation like the garrigue and chaparral) to 6.5 t ha^{-1} $year^{-1}$ (in oak forest) (Schultz 2005). This ecozone has become a very important player in the global trade of vegetables and fruits.

1.3.2 Subtropics with Year-Round Rain

This ecozone represents 4% of the landmass. It is located between 25° and 35° latitude on the southeastern side of the Americas, Africa, Asia, and Australia. Towards the equator, it borders with the Tropical ecozone with year-round rains and towards the poles with the Temperate Midlatitude ecozone. Extended dry periods are infrequent but growth can be limited by occasional frost spells. Summers are hot because of high insolation and temperatures similar to those in the tropics.

The vegetation in this ecozone is a dense rainforest, which evolves towards the west into a semi-evergreen moist forest and eventually a deciduous forest as precipitation gradually decreases. Productivity ranges from 14 to 23 t biomass dry weight ha^{-1} $year^{-1}$. The natural vegetation has largely been destroyed and replaced by urban areas, industries, agriculture, and forestry.

1.3.3 Dry Subtropics and Tropics

Located in the subtropical high pressure belts in the northern and southern hemispheres, this ecozone consists of three subdivisions, which in total represent 21% of the terrestrial landmass. Deserts and semi-deserts are characterized by grass cover over less than 50% of their surface. In contrast, thorn savannas and steppes (summer rains) and grass and shrub steppes (winter rains) have a grass cover on more than 50% of their surface. Precipitation is low, between 100 and 500 mm per year. There is a high level of solar radiation, but a large proportion is also reflected (albedo of 25–30%).

Vegetation in this ecozone shows adaptation to drought stress. There is an increase in the frequency of woody plants as drought increases. In grass steppes and thorn savannas, hemicryptophytes such as perennial herbaceous plants (e.g., grasses) predominate. The primary productivity is low, ranging from below 0.2 t biomass dry weight ha^{-1} $year^{-1}$ to $2.5 - 3.0$ t ha^{-1} $year^{-1}$.

1.3.4 Tropics with Summer Rains

This ecozone (16% of landmass) is located between the Tropical ecozone with Year-round Rains towards the equator and the Dry Subtropics and Tropics ecozone towards the poles. All months have mean temperatures above 18 °C. The mean temperature is lowest in the winter dry season, which lasts 2.5 to 7.5 months. The annual precipitation ranges from 500 to 1500 mm.

The vegetation of this ecozone is divided into tree, shrub, and grass savannas. Tree density ranges from a near-absence to an almost continuous tree cover, depending on the amount of moisture. The moist savanna shows denser stands of taller trees and taller and denser grasses as well. Soils in the drier savanna have a higher mineral exchange capacity and base saturation. They are also richer in humus. They can support permanent cultivation. Soils in the moister savanna are developed on deeply weathered bedrock. Organic matter decomposes quickly and there is a high level of leaching. Soils are therefore poor in humus and nutrients. Agriculture in moister savannas consists therefore of shifting cultivation with a fallow period of several years. Because of population increases, the length of the fallow period has gradually been reduced with an ensuing reduction in soil fertility.

This ecozone is the most densely settled and agriculturally most intensely used area in the tropics. It has several advantages compared to the Tropics with Year-round Rains. Its soil fertility is higher, the winter dry period allows clearing by fire, extensive grasslands can be used for cattle grazing, and the end of the growing season shows a high intensity of solar radiation. In addition, the duration of the rainy season is sufficient for cultivation of a wide range of crops. The primary productivity of this ecozone ranges from 10 to 21 t biomass dry weight ha^{-1} $year^{-1}$.

1.3.5 Tropics with Year-Round Rain

About 8% of the terrestrial landmass belongs to this ecozone, which extends from the Equator to 10° northern and southern latitudes. The boundary with the Subtropics with Year-round Rains is the 18 °C isotherm for the coldest month and with the Tropics with Summer Rains the 1500 mm precipitation line. It is characterized by year-round rainfall (up to 2000–4000 mm), a strong solar radiation year-round, and a nearly constant temperature (25–27 °C). As a consequence, plant growth continues throughout the year. This ecozone shows many similarities with the Moist Savannas for soil characteristics, vegetation, and land use. The primary productivity is highest, with 20-30 t biomass dry weight ha^{-1} $year^{-1}$, but may require shifting cultivation because of pool soil fertility. Declines in yield are due to loss of nutrients, fixation of phosphates, and increase in aluminum toxicity. Fallows of 15-30 years are required but are increasingly cut short because of population increases. Slash and burn agriculture can be replaced by continuous agriculture with fertilizers and liming.

1.4 Geographic Distribution of Biodiversity

Biodiversity can be defined as the sum total of all living organisms on Earth, including plants and animals, but also fungi, protozoans, bacteria, mycoplasma, and viruses, as individuals, populations, species, communities of organisms, and ecosystems. One way of quantifying biodiversity, but by no means the only one, is to count the number of species. Surprisingly, there is little definitive knowledge about this important data point. Up to 30 million species may exist although only 1.8 million have been described (http://www.earthscape.org/t1/ wie01/new_species.html). In plants, some 250,000 species have been described but by some estimates 300,000 to over 400,000 species may exist (Bramwell 2002; Govaerts 2003).

Biodiversity is unevenly distributed. Generally, many more species are distributed in tropical environments. This gradient has existed since before the time of the dinosaurs and is best documented for animals, including mammals, birds, frogs, and butterflies. For plants, the same general trend holds as well, although other factors may play a role such as aridity. Currie and Paquin (1987) showed that on a global scale plant species richness showed the strongest correlation with climate (evapotranspiration) and net primary productivity (NPP), the two factors being correlated. In turn, areas of high NPP also have a complex vegetation structure. For example, tropical forests shows several layers of vegetation. The tropical rainforest shows four layers at three, six, 30, and 50 m. In contrast, temperate forests only have two layers. Thus, climate (especially temperature and precipitation) is a major determinant of biodiversity (Kleidon and Mooney 2000).

On a more local scale, however, infertile soils can lead to species richness and endemism (e.g., serpentine soils: Brady et al. 2005). In contrast, plant species richness may decrease with increasing productivity presumably because of competition (Mittelbach et al. 2001). Other local attributes attempting to explain the distribution of biodiversity or more detailed analyses of certain variables or processes invoke differences between tropical and temperate areas (Partel et al. 2007), differences in scale of analysis (Sarr et al. 2005), energy flows through different habitats (Clarke and Gaston 2006), or energy–water interactions (Hawkins et al. 2003), differential rates of speciation and extinction in the tropics vs. other areas (Mittelbach et al. 2007), heterogeneity in topography and soils (Nichols et al. 1998), and landscape age and history (Sarr et al. 2005).

The distribution pattern of families of flowering plants reveals an interesting pattern as well. Some 30% of families are widespread, 20% are mainly temperate, and 50% are tropical. This distribution led Crane and Lidgard (1989) to suggest that flowering plants arose first in the tropics. The Ice Age affected species distribution mainly at higher latitudes, but also affected tropical rainforests, which became fragmented. In turn, this fragmentation may have favored speciation as well. Thus, there are many potential factors accounting for the higher diversity in tropical environments.

One consequence of the uneven distribution of biodiversity is the existence of biodiversity "hotspots," areas that are especially rich in species (Myers 1990). Some 25 such hotspots have been identified (Myers et al. 2000). These hotspots contain

44% of all plant species worldwide on 1.4% of the terrestrial surface of Earth. Fifteen hotspots are located in the tropical ecozone with year-round rains, five hotspots in the subtropical ecozone with winter rains (Mediterranean), and nine hotspots are mainly or completely made up of islands. Sixteen hotspots are in the tropics. One of the major threats to these hotspots is human population growth.

A major reason for presenting the different ecozones and the distribution of biodiversity is to examine a possible relationship with centers of agricultural origins and crop domestication.

1.5 Centers of Agricultural Origins and Crop Domestication

It has been known since the 19th century that agriculture originated in specific areas of the world. The current consensus about these areas relies mainly on the three centers (smaller, well-circumscribed areas) and three non-centers (larger, wide-ranging areas) identified by Harlan (1971, 1992), to which a few additional centers are added to account for additional, often more recent results. The three centers are Mesoamerica (southern half of Mexico and northern half of Central America), the Fertile Crescent (an arc of mountainous areas roughly surrounding Mesopotamia and including, from west to east, the Levant [Israel, Palestine, Lebanon, and western Syria], southwestern Turkey, and western Iran), and the north Chinese center (centered around the Huanghe or Yellow river).

The three non-centers include the Andes and areas to the east of this mountain chain, included in the Tropics with Summer Rain and Dry Tropics ecozones (eastern Bolivia, western and central Brazil, Paraguay, Uruguay, and NW Argentina). They also include a broad east-west swath comprising the Sahelian and Sudanian savannas and the Ethiopian highlands. The Asian non-center includes the eastern part of India, the Indochinese Peninsula, the Indonesian and Philippines archipelagos, and New Guinea. These six centers and non-centers are the most important areas of agricultural origins and domestication. There are, however, some areas outside these six centers that have played a role as well. For example, agriculture was initiated independently in the eastern half of the U.S. and gave rise to sunflower, before Mesoamerican crops such as beans, maize, and squash spread to North America. Central Asia witnessed the domestication of the apple and pomegranate.

Crop domestication centers are located disproportionately near or in biodiversity hotspots as defined by Myers et al. (2000) (Table 1.2). About 28% of the surface area of domestication centers lies within these hotspots, whereas the hotspots themselves constitute at most 12% of the subtropical and tropical ecozones (as defined by Schultz 2005), where the major domestication centers are located, or 6% of the total landmass. This non-random location of areas of domestication within the subtropical or tropical ecozones probably reflects the reliance of hunter-gatherers and early farmers on biodiversity for their daily subsistence, which would have been facilitated by an abundance of different species with different life cycles, adaptations, and useful products. Plants that were eventually domesticated were already

Table 1.2 Relative abundance of domestication centers in biodiversity hotspots

	Biodiversity hotspots[1]		Biodiversity non-hotspots	
	Location	Area ($\times 10^3$ km^2)	Location	Area ($\times 10^3$ km^2)
Domestication centers	Tropical Andes	1,258,000	Lowland South America[2]	3,276,145
	Mesoamerica	1,155,000		
	Chocó/Darién/ W. Ecuador	260,600	North America[3]	3,942,627
	Mediterranean Basin (including Levant and S.E. Turkey)	2,362,000	Sahel[4]	3,000,000
			Ethiopia	1,104,300
			China (except South-Central China)	8,840,821
	Caucasus	500,000		
	Indo-Burma	2,060,000	New Guinea	872,840
	South-Central China	800,000		
Total area domestication centers	In biodiversity hotspots	8,395,600	In biodiversity non-hotspots	21,036,733
Non-domestication centers	As listed in Myers et al. 2000	9,048,700	Subtropical and tropical ecozones[5]	76,500,000
	Total biodiversity hotspots	17,444,300	Total landmass	148,939,063

[1] From Myers et al. 2000
[2] Lowland South America: E. Bolivia, Paraguay, western Brazil (Acre, Rondônia, Matto Grosso, Goiás, Tocantins), Uruguay, NW Argentina (Jujuy, Salta, Tucumán)
[3] North America: Eastern half of the 48 contiguous states
[4] Between 100 and 600 mm isohyets; 400–600 km in width over a length of 6000 km
[5] From Schultz (2005)

harvested by hunter-gatherers. Hence, the abundance of species may have allowed the first farmers to choose those species that were most amenable to cultivation.

Harlan (1992) observed that the different ecozones and biomes they harbor had contributed to different extents to our array of crops. In his survey, the two major biomes in this respect were the Subtropics with Winter Rains (Mediterranean) and Tropics with Summer Rains (Savanna) ecozones. Ecozones showing an interruption of vegetation growth, for example due to drought whether in the winter or the summer, are thought to have stimulated transition to a farming economy because seasonal scarcities created a need to establish reserves for storable food such as grains. The majority of crops discussed here originated either in the Tropics with Summer Rains (Savanna to Dry Forest vegetation) or Tropics with Year-round Rains (Table 1.3), reflecting the focus and scope of this volume. It should be kept in mind, however, that while some crops are still cultivated in their original ecozone: e.g., cacao and coffee, other crops have shown an ecological expansion into more temperate ecozones, such as *Phaseolus* beans, maize, and sorghum.

Table 1.3 Taxonomic classification and geographic and ecological origin of crops discussed in this volume

Crop	Order[1]	Family	Main organ harvested	Geographic center(s) of origin	Ecozone origin
Banana/plantain, *Musa* spp.	M	Musaceae	Fruit	Southeast Asia	Tropics with summer rains
Cacao, *Theobroma cacao*	D	Sterculiaceae	Grain	Mesoamerica	Tropics with year-round rains
Chickpea, *Cicer arietinum*	D	Fabaceae	Grain	Southwest Asia	Subtropics with winter rains
Cowpea, *Vigna unguiculata*	D	Fabaceae	Grain	Africa	Tropics with summer rains
Citrus, *Citrus* spp.	D	Rutaceae	Fruit	China	Subtropics with year-round rains
Coffee, *Coffea* spp.	D	Rubiaceae	Grain	Ethiopia	Tropics with summer rains
Eucalyptus, *Eucalyptus* spp.	D	Myrtaceae	Wood	Australia	Widely distributed
Ginger, *Zingiber officinale*, and Turmeric, *Curcuma longa*	M	Zingiberaceae	Rhizome	China and S. Asia, respectively	Tropics with summer rains
Macadamia, *Macadamia* spp.	D	Proteaceae	Nut	Australia	Subtropics with year-round rains
Maize (tropical), *Zea mays*	M	Poaceae	Grain	Mesoamerica	Tropics with summer rains
Oil palm, *Elaeis guineensis*	M	Arecaceae	Fruit	Africa	Tropics with year-round rains
Papaya, *Carica papaya*	D	Caricaceae	Fruit	Mesoamerica	Tropics with year-round rains
Peanut, *Arachis hypogea*	D	Fabaceae	Grain	S.W. Brazil	Tropics with summer rains
Phaseolus beans, *Phaseolus* spp.	D	Fabaceae	Grain	Mesoamerica, Andes	Tropics with summer rains
Pineapple, *Ananas comosus*	M	Bromeliaceae	Fruit	S.W. Brazil	Tropics with summer rains
Sorghum, *Sorghum bicolor*	M	Poaceae	Grain	Africa	Tropics with summer rains
Sugarcane, *Saccharum officinarum*	M	Poaceae	Stem	S.E Asia	Tropics with year-round rains
Yam, *Dioscorea* spp.	M	Dioscoraceae	Root	Africa, S.E. Asia	Tropics with summer rains

[1] D: Dicotyledonae; M: Monocotyledonae

1.6 Genomics of Tropical Crops and Food Security

1.6.1 A Brief Overview of Genomics

The genome of a living organism is the sum total of the information contained in its genetic material, including its biochemical and structural organization, and its expression at the RNA, protein, and metabolite levels. Most genetic material is located in the nucleus but some is also located in cytoplasmic organelles (chloroplast and mitochondria) where they specify functions that are essential for the survival of living organisms. At its most basic, this genetic material is constituted by DNA. The nucleotide sequence of DNA provides the primary level of information responsible for coding enzymatic or structural proteins and ribosomal RNA ("DNA code"). In the nucleus, DNA is packaged with proteins (particularly histones) into chromatin, which, in turn, is the basic constituent of chromosomes. Various reversible chemical modifications, such as acetylations and phosphorylations, affect gene expression and specify chromosomal functional domains. Thus, there is a "histone or epigenetic code," whose effect on gene expression is superimposed onto that of the genetic code specified by the primary DNA sequence (van Driel et al. 2003; Lam et al. 2005). Furthermore, gene expression takes place in several steps, including transcription, splicing, and translation, each of which can have a major effect on trait expression (e.g., Yamaguchi and Mayfield 2005). Additional levels of complexity in gene expression are attributable to epistatic interactions, reflecting the fact that many traits have a complex inheritance. The involvement of more than one gene in a specific trait is the rule rather than the exception. In addition, environmental effects, which are often unpredictable, also play an important role in trait expression. It should, therefore, be clear that the expression of any trait is the outcome of a complex chain of events. Approaches focusing on one gene at a time have limited power to generate a complete picture of biochemical, developmental, and other pathways leading to the expression of economically important traits.

Genomics then is an ensemble of high-throughput analytical methods developed to study the genome of living organisms. Genomics can be further subdivided into areas depending on the target of the inquiry. Structural genomics investigates the DNA sequence of an organism, the distribution of coding sequences within the genome, the features such as centromeres and telomeres responsible for the function of chromosomes, micro- and macro-rearrangements in sequences. The best known examples of investigations in this area are the complete genome sequences of several organisms including plants such as Arabidopsis (Arabidopsis Genome Initiative 2000), rice (Goff et al. 2002; Yu et al. 2002), poplar (Tuskan et al. 2006), and *Medicago truncatula* (http://www.medicago.org/genome/ downloads/Mt1/). Progress has been made, and continues to be made, in the efficiency with which genomes can be sequenced (Hall 2007), suggesting that substantial sequencing will continue and that many more organisms will be sequenced to answer basic scientific questions and understand the molecular basis of economically important traits.

Functional genomics describes the products of genes, including RNA (transcriptomics), proteins (proteomics), and metabolites (metabolomics). Transcriptomics

relies on isolation of mRNA and reverse transcription of these messages into a DNA form to generate either partial- (expressed sequence tags [ESTs]) or full-length sequences of genes expressed in different tissues or in response to different biotic or abiotic external stimuli. In turn, gene indices have been created that list the different genes identified and their redundancies (assemblies) (e.g., plant gene indices at TIGR: http://www.tigr.org/tdb/tgi/plant.shtml). Large collections of ESTs have been established for some species such as Arabidopsis, eucalyptus, rice, soybean, and wheat, and the number for other species is increasing as well (http://plantta.tigr.org/cgi-bin/plantta_release.pl).

The high-throughput nature of genomics generates a large amount of data. To keep up with the data flow and allow its analysis, special software tools have been created, which fall under the label bioinformatics. These tools can, for example, identify similarities in sequence motifs between a query sequence and a database (e.g., BLAST: Altschul and Gish 1996), identify repetitive or microsatellite sequences (e.g., MicrosatDesign: Singan and Colbourne 2005), and align large-scale sequences such as bacterial artificial chromosome (BAC) sequences (ACT or Artemis Comparison Tool: http://www.sanger.ac.uk/Software/ACT).

1.6.2 Contributions of Genomics to the Improvement of Tropical Crops

How can genomics contribute to the genetic improvement of crops, in general, and tropical crops, in particular? This question can be considered both from a short-term perspective (how can the development of improved cultivars benefit from the tools and information provided by genomics?) and a broader view (how does crop improvement fit in the development process of lesser developed countries, particularly in the alleviation of food insecurity and poverty?).

The most fundamental contribution of genomics to plant breeding is to provide information on the genotypic or molecular basis of phenotypic variation for crop biodiversity conservation and genetic improvement (Gepts 2006). Plant breeding has been successful in recombining and deploying new genetic variation based on phenotypic evaluations of suites of genes responsible for the expression of agronomic traits, many of which are under quantitative control. Plant breeders evaluate the expression of suites of genes in the aggregate but, with a few exceptions, cannot select individual loci and allelic variation at these loci. The molecular information provided by genomic approaches consists of the number of loci, the magnitude of the effect of different alleles at these loci, the interactions among loci, the linkage relationships with other genes (coding for the same or other traits) and the environmental effects on gene expression, and, ultimately, the ever-important gene x environment interactions.

A large part of the natural variation of crop plants and their wild relatives has not been used so far in plant breeding (Tanksley and McCouch 1997; Gepts 2000; Gur and Zamir 2004). The high-throughput nature of genomics makes possible an

extensive molecular evaluation of genetic diversity in exotic germplasm, i.e., un-adapted landraces (farmer-improved domesticated lines) and wild relatives. To be applicable to plant breeding, however, these evaluations of molecular variation have to be accompanied with phenotypic evaluation in the field or other locales, a.k.a. phenotyping. These phenotypic evaluations become the rate-limiting factor because multi-year, multi-location trials are required to obtain an accurate estimate of the phenotypic value in the face of a variable climatic and edaphic environment. Further dissection of a trait into component sub-traits can narrow down the genetic control and increase the heritability of the trait (Varshney et al. 2005). Unless plant breeding education is strengthened (Gepts and Hancock 2006), phenotypic evaluations are becoming a lost science as well.

The lack of utilization of exotic germplasm can be attributed to several causes. First, the lack of adaptation of this germplasm prevents its thorough evaluation in local conditions and therefore the discovery of useful variation (e.g., photoperiod sensitivity). Second, certain traits may also prevent evaluations (e.g., seed shatter-ing and viny growth habit of wild legumes make yield evaluations difficult). Third, approaches to characterizing the genetic basis of agronomic traits has emphasized analysis of the progeny of pedigreed crosses between two parents. This reduces the number of germplasm accessions that can be characterized at any one time. Recently, more emphasis has been placed on association mapping (Mackay and Powell 2007), which relies on the analysis of linkage disequilibrium (Flint-Garcia et al. 2003) in existing populations such as germplasm collections. Association mapping by its very nature can lead to a broader analysis of existing genetic diver-sity. Fourth, germplasm banks may have funds for germplasm maintenance but not evaluation because of underfunding. Fifth, the exchange of germplasm is increas-ingly subject to ownership and sovereignty issues arising from international treaties such as the Convention on Biological Diversity and the Trade-Related Intellectual Property Rights (TRIPS) agreement of the World Trade Organization (Gepts 2004b 2006). It is important to note, however, that none of these difficulties is insurmount-able and that genomics allows a more efficient extraction of useful genes from exotic germplasm.

Genomics can assist plant breeding in two major ways. In the short term, it provides a DNA sequence resource that can be used to develop a large number of polymorphic markers, such as microsatellites and single-nucleotide polymorphisms (SNPs). This sequence resource can originate from various sources, including ESTs, BAC-end sequences, BAC sequences, and whole-genome sequences in some cases. Initially, most markers were random markers representing anonymous sequences. Increasingly, however, markers are now also derived from candidate gene sequences. The large number of markers allows for a saturation of the genome and detailed link-age mapping of genes of interest, including quantitative trait loci (QTLs), either by analysis of pedigreed populations (resulting from a cross between known genotypes) or natural populations (association mapping). Once the location of genes and QTLs is determined, further research is generally necessary to identify additional markers near these genes or QTLs to allow application of marker-assisted selection (MAS) (Collard et al. 2005). This contribution of genomics relies on the development of

genomic sequence resources within the target species because polymerase chain reaction (PCR)-based markers such as microsatellites and SNPs depend on precise DNA sequences to develop primers for efficient and unequivocal amplification in the PCR reaction.

The second way in which genomics can contribute to breeding is to identify the specific genes responsible for specific traits. This approach requires a considerably larger investment in genomic resources than the first. It involves the development and utilization of functional genomics tools, such as array technology, map-based cloning, transcript profiling, targeting induced local lesions in genomes (TILLING), and transformation (Sreenivasulu et al. 2007). This identification then allows for the screening of germplasm to discover allelic variants and the development of allele-specific markers for MAS. In contrast with the first approach, model systems such as Arabidopsis, *Medicago truncatula*, tomato, and rice can provide information that helps identify the molecular basis of shared traits with the target species (Morgante and Salamini 2003).

Marker-assisted selection is most suitable in the following selection situations (Xu et al. 2005): to bypass a testcross or progeny test or a laborious field or lab test, to conduct a selection independent of a normal test environment, to test a progeny at an earlier breeding stage or for multiple genes or traits, or to conduct a whole-genome selection. Thus, the main benefit of MAS is to facilitate and accelerate breeding operations in specific situations. It is an additional tool for plant breeders but does not replace regular plant breeding operations, especially field evaluations. It does not replace all types of selection, especially in the case of genetically complex traits, conditioned by a large number of genes with small effects and for which it is difficult to establish a good correlation between markers and phenotypes. Further discussion on the application of MAS is provided by Knapp (1998), Francia et al. (2005), Davies et al. (2006), Ribaut and Ragot (2007), and chapters in this volume. An additional challenge is the existence of gene interactions (epistasis) and epigenetic phenomena (Morgante and Salamini 2003; Varshney et al. 2005; Valliyodan and Nguyen 2006), which, although they have generally been difficult to deal with in genetic analyses (Carlborg and Haley 2004), need to be taken into account to obtain a realistic representation of the genetic control of a trait (e.g., Johnson and Gepts 2002)

In summary, addition of information on variation at individual gene loci and their interactions with other genes and the environment through the use of genomics promises to boost the success of plant breeding to new heights.

1.6.3 Crop Improvement and Food Insecurity and Poverty

Food security has been defined by the Food and Agricultural Organization (FAO) as: "*Food security is a situation that exists when all people, at all times, have physical, social, and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life.*" Some 800 million

people remain currently under-nourished. According to FAO statistics, up to two billion people lack food security intermittently due to varying degrees of poverty (FAO: http://www.fao.org/es/ess/faostat/foodsecurity/index_en.htm). The majority of people undernourished or lacking food security live in southern Asia and sub-Saharan Africa. It has now become clear that food security does not depend only on sufficient production of food, particularly of those providing a dietary energy supply such as carbohydrate crops (e.g., cereal crops, cassava). Actually, the concept of food insecurity is a multi-dimensional problem, as it involves production of a diversified food supply that will supply a wide range of macro- and micro-nutrients based on biodiverse ecosystems, including the harvesting of wild and underutilized species, growing locally adapted varieties, and eating from local ecosystems (Toledo and Burlingame 2006). Most of the crops discussed in this volume are part of a foundation for a nutritious diet because they provide one or more macro-nutrients (Table 1.4) in addition to micronutrients and can complement each other nutritionally (e.g., complementation for essential amino acids between legumes and cereals). In addition, a biodiverse agroecosystem also contributes to productivity and sustainability of agriculture by exploiting different environmental niches and diversifying income sources (Hawtin 2000).

Table 1.4 Macronutrient contributions of crops discussed in this volume (per sample of 100 g[1])

Crop	Water (g)	Energy (Kcal)	Protein (g)	Lipids (g)	Carbohydrates (g)
Banana: Raw	75	89	1	∼ 0	23
Plantain: Raw	65	122	1	∼ 0	32
Cacao: Dry powder	3	229	20	14	54
Chickpea: Mature seeds, raw	12	364	19	6	61
Cowpea: Mature seeds, raw	12	336	24	1	60
Citrus: Orange juice, raw	88	188	1	∼ 0	10
Coffee: Brewed	100	1	∼ 0	∼ 0	0
Eucalyptus	NA	NA	NA	NA	NA
Ginger: Ground spice	9	347	9	6	71
Turmeric: Ground spice	11	354	8	10	65
Macadamia: Raw nut	1	718	8	76	14
Maize: Whole-grain flour	11	361	2	2	77
Oil palm: Oil	0	884	0	100	0
Papaya: Raw	89	39	1	∼ 0	10
Peanut: All types, raw	7	567	26	49	16
Vegetable oil	0	884	0	100	0
Phaseolus beans:					
Snap (green)	90	31	2	∼ 0	7
Dry (kidney)	12	333	24	1	60
Pineapple: Raw	87	48	1	∼ 0	13
Sorghum	9	339	11	3	75
Sugarcane: Granulated sugar	∼ 0	387	0	0	∼ 100
Yam: Raw	70	118	2	∼ 0	28

[1] USDA Nutrient Data Laboratory: http://www.nal.usda.gov/fnic/foodcomp/search/ ; all numbers rounded to nearest integer

Furthermore, there is a strong correlation between agricultural productivity, hunger, and poverty (von Braun et al. 2003). Seventy-five percent of the world's poor live in rural areas and make their living from agriculture. Hunger and child malnutrition are greater in rural than urban areas. The higher the proportion of rural population that obtains its income solely from subsistence farming, the higher the frequency of malnutrition. Malnutrition erodes children's ability to learn and reduces the ability of adults to work and give birth to healthy children. Many of the consequences of childhood malnutrition are seen only much later in adulthood. Thus, malnutrition is part of a self-perpetuating vicious circle that needs to be broken if hunger is to be eliminated.

Rosegrant and Cline (2003) have argued that achieving global food security will require policy and investment reforms on multiple fronts, including human resources and education (for better farming or facilitating careers outside of agriculture), rural infrastructure (e.g., roads, safe drinking water, sewage, health care), water resources, and agricultural research. The latter usually provides a high return on investment. The public sector, charitable organizations, and the civil sector all play important roles in agricultural research, especially in tropical agriculture because of the limited market potential and the capability to develop publicly accessible (i.e., non-proprietary) technologies. Goals of agricultural research include increasing biomass, harvest index, and tolerance to external stresses, most recently drought stress.

One of the main challenges of agricultural research is to address increasing water scarcity. This scarcity is due in part to increasing demand for water from a burgeoning world population but also from agriculture, if increased yields are to become reality. Rockström et al. (2007) have estimated that an additional 1,850 km3/year will be required to produce the food needed to eradicate hunger. Part of the water management solution is to develop new varieties with increased water use efficiency (WUE) and tolerance to drought. Genomics can help obtain such new varieties by identifying drought tolerance or WUE genes that can become targets for selection (e.g., Ribaut and Ragot 2007).

An additional dimension to the contribution of genomics to plant breeding is the changing climatic and economic environment in which agriculture operates (Cassman 2007). Agriculture has until recently been able to keep up with human population growth on Earth as a source of food, feed, and fiber. Currently, however, the balance between food supply and demand is rapidly shifting from surplus to deficit. Due to the rapid rise in prices of petroleum, there is now a global expansion of biofuel production based on maize, oil crops (e.g., oil palm, soybean, Jatropha), and sugar crops (mainly sugarcane). Farmers in some countries will enjoy higher prices for these commodities, but the urban and rural poor will pay much higher prices for basic food staples (as is happening already in Mexico: M. Roig-Franzia: http://www.washingtonpost.com/wp-dyn/content/article/2007/01/26/ AR2007012601896_pf.html). Further uncertainty is caused by global climate change. Increases in production due to higher CO_2 concentration in the atmosphere are more than offset by reductions in yield by increased temperature (Lobell and Field 2007). Alleviating hunger will, therefore, no

longer be a matter of poverty alleviation and more equitable food distribution, but according to Cassman (2007), will depend on accelerating gain in crop yields and overall food production capacity. Plant breeding, aided by genomics, will play an important role in this endeavor.

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