ESSENTIALS OF PLANT BREEDING

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Preface

Essentials of Plant Breeding was written as a textbook for a first-semester course in plant breeding. After I wrote my first book, **Breeding for Quantitative Traits in Plants**, in 2002, I told my wife, Chona, that I had written everything I knew in one book and that I was a one-book author. But after teaching my graduate course at the University of Minnesota for several years, I realized it would be useful to have a contemporary textbook that conveys the background knowledge needed for my first book. This second book is therefore a prequel to my first book. My goal was to write a concise book that:

1. Presents the essentials of plant breeding;
2. Explains the science behind the process of plant breeding;
3. Shows how the diversity among plants leads to a diversity of breeding methods; and
4. Leads to an appreciation of the creative power of plant improvement.

The coverage of the subject assumes that the reader has taken a first-semester course in genetics or, at least, has a good grasp of Mendelian genetics from a college biology course. Nevertheless, a review of basic genetics is included (chapter 2). Like other plant breeding textbooks, this book describes how modes of reproduction affect the choice of breeding methods, and outlines the breeding methods appropriate for self-pollinated, cross-pollinated, and asexually propagated species. Chapter 7, which describes the use of DNA markers in plant improvement, has material not found in older textbooks. While other textbooks have opted to include chapters on the breeding of individual crops (e.g., maize, potato, etc.), I thought it would be more informative to examine the general features of breeding for different categories of crops. Chapter 8 therefore describes breeding for field crops, vegetables and fruits, forages, turfgrasses, flowers and ornamentals, and tree and palm species. There is overlap between the material in this book and in my first textbook, particularly on genotype × environment interaction, long-term selection, and several tables and figures.

Research has shown that the textbook learning aids found most useful by undergraduate students are technical terms in bold, chapter summaries, and a glossary (*Weiten et al., 1996, Teach. Psych. 23:105–107*). These learning aids were therefore incorporated in this textbook. This book was written as a no-frills primer, and a class instructor would likely want to use Web media and resources along with this textbook.

I started writing this book in September 2013 while I was on a sabbatical leave at CIRAD in Montpellier, France, and I thank Nour Ahmadi and his colleagues for being very gracious hosts. The following reviewed individual chapters, offered helpful comments and suggestions, and saved me from some embarrassing mistakes: Jim Anderson, Stephen Baenziger, Marcelo Carena, Emily Combs, Natalia de Leon, Nancy Ehlke, Irwin Goldman, Rale Gjuric, Candy Hirsch, Amy Jacobson, Fred Kolb, Lian Lian, Jim Luby, Heather Merk, Jim Orf, Addie Thompson, Josh Sleper, Kevin Smith, Bob Stupar, Todd Wehner, Vance Whitaker, and Jianming Yu. I thank colleagues at the University of Minnesota and scientists at CIRAD for helping me learn more about breeding for horticultural, tropical, and subtropical crops. While my parents, Fernando and Emiliana Bernardo, edited a near-final version of my first book, my eldest daughter, Alyssa, helped edit a near-final version of this book. All the remaining errors in the book, however, are mine.

I thank Chona and our six children—Alyssa, Jessica, Michael, Matthew, Emily, and David—for their love, support, and encouragement. When I count my blessings in this world, they're at the top of my list. Finally, I am indebted to John W. Dudley, who was my Ph.D. major professor at the University of Illinois in 1985–1988. John took a chance on me when I was a 20-year old graduate-student applicant from a modest college in the Philippines, and he taught me well.

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Process of Plant Breeding

1.1 Plants for Human Benefit

Plant breeding is the genetic improvement of plants for human benefit. The expression "*out of thin air*" refers to something that seems to come from nothing, yet it describes what plants do each day. Plants have the amazing ability to capture energy from the sun, draw water from the soil, and use carbon dioxide from the air to synthesize food for us and for the animals that we eat. Humans always have and always will continue to depend on plants and plant-derived products to meet basic needs for food, shelter, clothing, and fuel. An ancient writer of Scripture eloquently described this appreciation for

> "grass [grow] for the cattle, and plants for people to cultivate—bringing forth food from the earth: wine that gladdens human hearts, oil to make their faces shine, and bread that sustains their hearts." – *Psalm 104:14-15*

This book focuses on modern ways to improve modern plants. Yet at the outset we need to recognize the genetic improvement that has already occurred in different plant species, and that today's plant breeders are building upon past genetic improvement. Given the key role of plants in meeting basic needs, it is no surprise that humans have, through the ages, selected and cultivated plant species and plants within a species that best meet such needs.

1.2 Plant Domestication

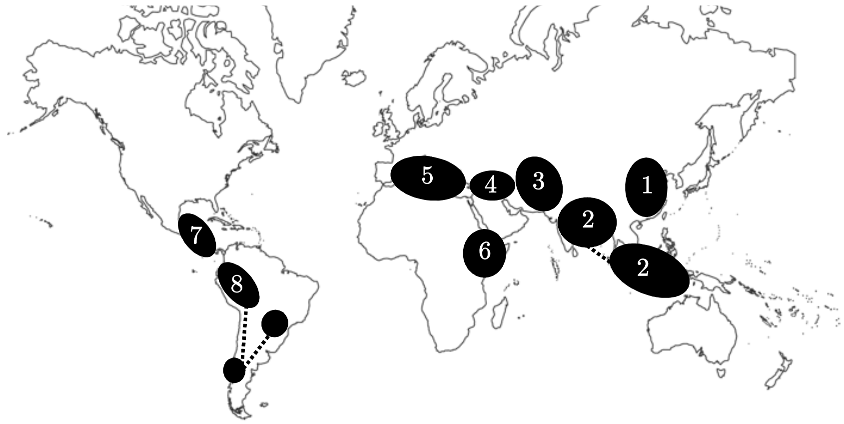
Domestication first occurred when people in ancient times began to discern which plants of a wild species were better than others and to preferentially propagate such plants in subsequent growing seasons. For example, **seed shattering** (i.e., seeds falling from the plant) is advantageous to the plant itself because the phenomenon enhances the dispersal of seeds: the progeny in the next generation have a higher chance of survival due to less competition among themselves for water, nutrients, and sunlight. On the other hand, seed shattering is unfavorable for humans because the seeds become lost or are more difficult to gather. A gatherer who encountered a plant that shattered its seeds easily and a plant that did not shatter its seeds would have tended, by choice or by default, to harvest seeds from the nonshattering type. Nonshattering was therefore a key trait in the domestication of cereals such as rice and wheat, and several genes underlying nonshattering in cereals have since become known.

The **domestication syndrome** refers to a suite of traits that were usually changed when wild species underwent domestication. In addition to nonshattering, other components of the domestication syndrome include early maturity, dwarf stature or compactness of growth habit, photoperiod insensitivity (i.e., ability to flower regardless of daylength), and loss of seed dormancy. Because of these changes in adaptive traits, domesticated species may have difficulty surviving in the wild.

Russian botanist and geneticist **Nicolai Ivanovich Vavilov** proposed in 1926 that regions in the world where many wild relatives of a domesticated species are still found must be the regions where the species was domesticated. Based on his expeditions to collect diverse plant materials, Vavilov identified eight regions in the world that showed a high concentration of diversity for different plant species. These regions, which until today harbor much of the diversity for a given species, have become known as **centers of origin** (Fig. 1.1). It is noteworthy that these centers of origin are largely in warmer climates.

On the other hand, two objections have been raised against Vavilov's proposed centers of origin: (i) later investigations have shown that the proposed centers of origin did not necessarily coincide with the regions of greatest genetic diversity, and (ii) some centers of diversity were too diffuse. An alternative proposal was that plant species were domesticated in three centers and three noncenters, the latter being areas spanning 5000 to 10,000 km. The availability today of technologies for **DNA fingerprinting** has allowed more detailed studies of genetic variation and domestication of cultivated plant species.

Regardless of how centers (and noncenters) of origin are formally demarcated, what is clear is that different species were domesticated in one or more specific regions (Table 1.1). Among staple foods, maize was domesticated in Mexico; common wheat in Turkey; rice in China; potato in Peru;



1: China
2: India and Malaya
3: Central Asia
4. Near East
5. Mediterranean
6. Ethiopia
7. Mexico and Central America
8. South America

FIGURE 1.1. Vavilov centers of origin of plant species.

and grain sorghum in Ethiopia. Among major vegetables, tomato and common bean originated in the Andes and Central America; onion in Central Asia; and the brassicas (e.g., cabbage, broccoli, cauliflower) in southern and western Europe.

The movement of plant species from their centers of origin to different areas around the world is a testament to humans bringing valuable seeds or plant propagules with them when they traveled, and to the resiliency and adaptability of plant species to new areas of cultivation. We take it for granted that non-native species have become widely grown in areas far from their centers of origin. Soybean, for example, originated from China, was introduced to the American colonies in the 1700s and 1800s, and was grown on only 0.6 million hectares in the U.S. in 1924. By the 2010s, more than 31 million hectares in the U.S. were planted each year to soybean and the total amount of production was six times as much in the U.S. as in its native China.

Maize, on the other hand, was introduced twice from the Americas to Europe. Tropical maize was introduced by Columbus to Spain in 1493 whereas temperate maize was introduced, by subsequent explorers, from northeastern America to northern Europe in the 1500s. How and when maize was introduced to Asia and Africa is less clear. What is clear is that this Mexican grass has moved north, south, east, and west. While maize continues to be grown in tropical regions around the world, it has also been bred for adaptation to much cooler climes with the largest area of production in the world being in the temperate U.S. Corn Belt.

TABLE 1.1. Scientific names and likely origins of 25 common domesticated plants.

Plant	Scientific name	Likely place of origin
Alfalfa	*Medicago sativa*	Turkey, Iran
Apple	*Malus × domestica*	Central Asia
Barley	*Hordeum vulgare*	Near East
Bean	*Phaseolus vulgaris*	Central America, Andes
Cassava	*Manihot esculenta*	Brazil
Coconut	*Cocos nucifera*	Southeast Asia, India
Coffee	*Coffea* spp.	Ethiopia, West Africa
Cotton	*Gossypium hirsutum*	Mexico, Andes
Grape	*Vitis vinifera*	Near East
Maize	*Zea mays*	Mexico
Oil palm	*Elaeis guineensis*	West Africa
Onion	*Allium cepa*	Central Asia
Peanut	*Arachis hypogaea*	Paraguay
Petunia	*Petunia × atkinsiana*	South America
Plantain	*Musa* spp.	Southeast Asia
Potato	*Solanum tuberosum*	Peru
Rice	*Oryza sativa*	China
Ryegrass	*Lolium perenne*	Europe
Sorghum	*Sorghum bicolor*	Ethiopia
Soybean	*Glycine max*	China
Sugarcane	*Saccharum* spp.	New Guinea
Sunflower	*Helianthus annuus*	Eastern U.S.
Sweet potato	*Ipomoea batatas*	Central or South America
Tomato	*Solanum lycopersicum*	Andes, Central America
Wheat	*Triticum aestivum*	Turkey

Such movement of plant species has often led to within-species differences across different areas of cultivation. For example, Sir Henry Wickham collected rubber seeds in the Amazon basin in 1875 and smuggled them from Brazil to the Royal Botanic Gardens, Kew near London. Seeds were then sent by the British to their colonies in Ceylon (Sri Lanka) and Singapore, and these introductions eventually led to the establishment of the rubber tree crop in southeast Asia. However, Wickham did not collect seeds from the western Amazon basin. This has led to genetic differences between the more-diverse native Brazilian rubber trees and the less-diverse (but more productive) southeast Asian rubber trees that trace their lineage to the Wickham collection.

Closer to home, the past movement of plant species is easily seen at the dinner table. Some consumers may prefer locally grown foods. But even if food is locally grown, a dinner menu—be it fancy (see below) or simple fare—would likely include foods from plants that originated from distant shores (centers of origin in parenthesis):

SALAD
Red and gold beets (Mediterranean)
Asian pears (China)
Candied walnuts (Near East, Mediterranean)
Goat cheese

GRILLED NEW YORK STEAK
Potato puree (Peru)
Baby carrots (Iran, Afghanistan)
Cipollini onions (Central Asia)

WINE PAIRING
Cabernet Sauvignon (Near East)

DESSERT
Strawberry cheesecake (North and South America)
Arabica coffee (Ethiopia)

1.3 Plant Hybridization and Mendelian Inheritance

Domestication acted upon variation caused by natural **mutations** (i.e., sudden genetic changes) and by natural crossing or **hybridization**. But contemporary knowledge until the 1600s was that plants are asexual entities. After all, it seemed inconceivable that, say, two oak trees could have sex.

The process of sexual reproduction in plants was first demonstrated in 1694 in a series of elegant experiments by German physician and botanist **Rudolf Jakob Camerarius**. He proved the necessity of pollen in forming seeds and noted the role of the female (**pistil**) and male (**stamen**) parts of a plant in fertilization (Fig. 1.2). In 1761–1766, German botanist and natural-history scientist **Joseph Gottlieb Kölreuter** demonstrated that characteristics in a hybrid were intermediate to those in its parents and that the nature of sexual reproduction in plants was fundamentally the same as sexual reproduction in animals. Kölreuter also noted the importance of insects and wind in pollination. In 1849, German botanist **Carl Friedrich von Gärtner** reported the results of nearly 10,000 hybridization experiments in about 700 plant species. These experiments provided irrefutable evidence that plants are sexual entities.

While the pioneering experiments Camerarius, Kölreuter, and von Gärtner confirmed sexual reproduction in plants, the question remained regarding the mechanisms for transmitting a characteristic from the male and female parents to their offspring. Until the 1800s, a prevailing thought was