SECOND EDITION

Principles of Plant Genetics and Breeding

GEORGE ACQUAAH

WILEY-BLACKWELL

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Principles of Plant Genetics and Breeding

Second Edition

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WILEY-BLACKWELL
A John Wiley & Sons, Ltd., Publication

Wiley-Blackwell is an imprint of John Wiley & Sons, formed by the merger of Wiley's global Scientific, Technical and Medical business with Blackwell Publishing.

Registered office: John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial offices: 9600 Garsington Road, Oxford, OX4 2DQ, UK
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Library of Congress Cataloging-in-Publication Data
Acquaah, George.
Principles of plant genetics and breeding / George Acquaah. — 2nd ed.
p. cm.
Includes bibliographical references and index.
ISBN 978-0-470-66476-6 (cloth) — ISBN 978-0-470-66475-9 (pbk.) 1. Plant breeding. 2. Plant genetics. I. Title.
SB123.A334 2012
631.5'2—dc23 2012010941

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover design by Dan Jubb.

Set in 10/12pt, Galliard-Roman by Thomson Digital, Noida, India

First Impression 2012

Dedication

To my wife, Theresa, with love and appreciation for uncommon character.

Contents

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Preface

The second edition of *Principles of Plant Genetics and Breeding* represents a thoroughly overhauled version of the preceding edition, following recommendations and suggestions from users and reviewers. The major changes in the new edition include restructuring and reordering the chapters to follow more closely with how plant breeding is done in practice, and expanding the molecular genetics component. Also, the basic science information has been reduced. Two of the chapters in the first edition have been transferred to the back of the textbook as supplementary material, so it may be referred to by users only as needed. In this way, students and users who already have a background in genetics will not feel obligated to study those chapters before advancing to more plant breeding related topics. A feature of the first edition that is retained and expanded in the second edition is the inclusion of contributions on selected topics by industry professionals. The book is copiously illustrated to facilitate teaching and learning of the topics.

The book is organized into nine sections. Section I is an overview and historical perspective of plant breeding. Chapter 1 provides an introduction to the field of plant breeding, describing its importance to society while Chapter 2 provides historical perspectives, highlighting the contributions by researchers to knowledge in the field. The two chapters in Section II are devoted to discussing pertinent population and quantitative genetic concepts, to assist the reader in better understanding the practices of plant breeders.

Section III, reproductive systems, comprises four chapters. Chapter 5, autogamy, and Chapter 6, allogamy, focus on reproductive and genetic issues as they pertain to self-pollinated and cross-pollinated species, respectively. Chapter 7 is devoted to discussing the genetic issues associated with crossing plants to reorganize the genetic matrix, while Chapter 8 ends the section with a discussion of issues associated with clonal propagation.

Section IV, deals with germplasm for breeding. It is impossible to conduct plant breeding without the proper germplasm. Chapter 9 in this section focuses on variation and its genetic basis, while Chapter 10 focuses on domestication of plant species. The discussion includes the dependence of plant breeding on heritable variation. Finally, Chapter 11 addresses the matter of plant genetic resources used in plant breeding. It includes a discussion of how germplasm is collected and managed for long term use by breeders.

Section V is devoted to discussing common breeding objectives pursued by plant breeders. The discussions include the genetic basis of those traits and the implication in their breeding. Chapter 12 focuses on breeding for increased yield and improving morphological traits that enhance crop productivity. In the ensuing chapter, 13, breeding for selected quality traits is the focus of discussion. Breeding for disease and pest resistance is a major breeding objective in most crops. This is the subject of Chapter 14, while Chapter 15 is devoted to issues pertaining to breeding for resistance or tolerance to selected abiotic factors, such as salt tolerance.

The topics of Section VI focus on selection or breeding methods. In this section, breeding methods for autogamous species is the subject of Chapter 16, while Chapter 17 is devoted to breeding allogamous species. Chapter 18 concerns the selection methods used for breeding hybrid cultivars while the last chapter in the section, 19, is devoted to discussing the breeding methods used for clonally propagated species. The discussions in these chapters provide the advantages and disadvantages of each method, and include alternative approaches.

Molecular breeding is the subject of Section VII, which received the most overhaul. The concept of markers and various commonly used molecular markers in plant breeding are discussed in detail in Chapter 20, including their advantages and disadvantages, as well the cost and ease of application in breeding. Chapter 21 is devoted to discussing the mapping of genes and the importance of such maps in plant breeding. Marker assisted selection (MAS) as a method of facilitating plant breeding is the subject of

Chapter 22. Chapter 23 focuses on the use of mutagenesis for inducing variability for crop improvement. The discussions include the types of mutagens commonly used in crop improvement, and the success of this approach to breeding. Many important crop species are polyploids. The methods used for improving polyploids are discussed in Chapter 24. The last chapter in this section, 25, addresses the subject of molecular genetic modifications, including the role of genetic engineering in plant improvement. Also, in this chapter, the contemporary subject of genome-wide genetics is introduced.

Section VIII is titled marketing and societal issues in plant breeding. In Chapter 26, the reader is exposed to the process of preparing a cultivar for release to farmers for use. Commercial seed producers ensure the quality of their products through the seed certification process, as described in Chapter 27. Plant breeders protect their products through securing legal protection, the subject of Chapter 28. The last two chapters, 29 and 30, end the section with discussions on social concerns that arise from the applications of biotechnological tools, and issues confronting breeders on the international plant breeding scene.

The last section, IX, is devoted to discussion of the breeding of selected crops. This section includes discussions on the genetics of selected crop plants, germplasm used, and breeding methods used for their improvement. Professional highlights are provided for these chapters.

An effort has been made to organize this book such that the sequence of discussion of topics follows closely the sequence in conducting a plant breeding project. A plant breeding course, at the minimum, is usually an upper level course at the undergraduate level. It is assumed that a student taking a plant breeding course would have received prior instruction in the basic biology, including genetics, botany, and physiology. A review of basic genetic principles is helpful to better understanding the material in this book and a plant breeding course in general. Sometimes, some of this basic material is reviewed as appropriate. In addition, some of the underlying science is presented in the supplementary chapters of the book.

Acknowledgements

The author extends special gratitude to Drs Herman van Eck, Rients Niks, Marieke Jeuken, Gerard van der Linden, Yuling Bai, Paul Arens, Luisa Trindade, Chris Maliepaard and Jaap van Tuyl of the academic staff of the Laboratory of Plant Breeding, Wageningen University and Research Center, in The Netherlands, for their outstanding contribution to this edition. Specifically, Drs Van Tuyl and Arens reviewed and edited Chapter 7 (Hybridization), while Dr van der Linden reviewed and edited Chapter 15 (Breeding for resistance to abiotic stress). Dr Jeuken wrote a boxed reading article on lettuce BILs, while Dr Bai contributed two articles, a supplement to Chapter 39 (Breeding tomatoes) as well as a paper on the introgression breeding of tomatoes as part of the industry highlights featured in the book. Chapter 13 (Breeding for quality) was reviewed by Dr Trindale. Dr Miliepaard deserves special mention for reviewing almost the entire first edition of the book and for making suggestions for accuracy and general improvement of the second edition.

Of the Wageningen team members, the author reserves his profound and deepest appreciation for the invaluable contributions of Dr Herman van Eck who made the initial contact with a proposal to assist with reorganizing the second edition, putting the team together and reviewing Chapter 23 (Mutagenesis in plant breeding) as well. Dr van Eck and Dr Niks collaborated with the author to reorder and restructure the chapters of the first edition to make the contents of the second edition flow more meaningfully. They also suggested additional chapters and topics for inclusion in the new edition. Dr van Eck provided the author with a collection of published literature and personal notes to assist with writing new chapters and updating others. Dr. Niks' additional role included critically reviewing and editing several chapters, including 5 (Autogamy), 6 (Allogamy), 7 (Hybridization), 8 (Clonal propagation) 10 (Domestication), 11 (Plant genetic resources) and, especially, chapter 14 (Breeding for disease resistance), which was overhauled according to his recommendations. The second edition is clearer and more accurate because of his thorough review and insightful critique of the chapters he reviewed.

Notwithstanding the tremendous contribution of the Wageningen team, the final content of the book remains entirely the responsibility of the author. The author also acknowledges with deep fondness the support of Dr Theresa Acquaah, his wife, for her moral support during the preparation of this edition. The final and ultimate appreciation is reserved for the author's mentor and source of inspiration, Dr J.C. El Shaddai.

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Section 1

Overview and historical perspectives

It is informative for students of plant breeding to have an historical perspective of the discipline. Understanding the time line of advances in one's discipline is instructive in itself. It helps the student to put current advances in plant breeding in the proper perspective, appreciating the challenges and opportunities along the way as professionals contributed to knowledge in the discipline.

1
Introduction

Purpose and expected outcomes

***Agriculture** is the deliberate planting and harvesting of plants and herding animals. This human invention has and continues to impact society and the environment. **Plant breeding** is a branch of agriculture that focuses on manipulating plant heredity to develop new and improved plant types for use by society. People in society are aware and appreciative of the enormous diversity in plants and plant products. They have preferences for certain varieties of flowers and food crops. They are aware that whereas some of this variation is natural, humans with special expertise (plant breeders) create some of it. Generally, also, there is a perception that such creations derive from crossing different plants. This introductory chapter is devoted to presenting a brief overview of plant breeding, including its benefits to society and some historical perspectives. After completing this chapter, the student should have a general understanding of:*

1. The need and importance of plant breeding to society.
2. The goals of plant breeding.
3. The art and science of plant breeding.
4. Trends in plant breeding as an industry.
5. Selected milestones and accomplishments of plant breeders.
6. The future of plant breeding in society.

1.1 What is plant breeding?

Plant breeding is a deliberate effort by humans to nudge nature, with respect to the heredity of plants, to an advantage. The changes made in plants are permanent and heritable. The professionals who conduct this task are called **plant breeders**. This effort at adjusting the *status quo* is instigated by a desire of humans to improve certain aspects of plants to perform new roles or enhance existing ones. Consequently, the term "plant breeding" is often used synonymously with "plant improvement" in modern society. It needs to be emphasized that the goals of plant breeding are focused and purposeful. Even though the phrase "to breed plants" often connotes the involvement of the sexual process in effecting a desired change, modern plant breeding also includes the manipulation of asexually reproducing

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plants (plants that do not reproduce through the sexual process). Breeding is hence about manipulating plant attributes, structure and composition, to make them more useful to humans. It should be mentioned at the onset that it is not every plant character or trait that is readily amenable to manipulation by breeders. However, as technology advances, plant breeders are increasingly able to accomplish astonishing plant manipulations, needless to say not without controversy, as is the case involving the development and application of **biotechnology** to plant genetic manipulation. One of the most controversial of these modern technologies is **transgenesis**, the technology by which gene transfer is made across natural biological barriers.

Plant breeders specialize in breeding different groups of plants. Some focus on field crops (e.g., soybean, cotton), horticultural food crops (e.g., vegetables), ornamentals (e.g., roses, pine trees), fruit trees (e.g., citrus, apple), forage crops (e.g., alfalfa, grasses), or turf species. (e.g., Bluegrass, fescue) More importantly, breeders tend to specialize in or focus on specific species in these groups (e.g., corn breeder, potato breeder). This way, they develop the expertise that enables them to be most effective in improving the species of their choice. The principles and concepts discussed in this book are generally applicable to breeding all plant species.

1.2 The goals of plant breeding

The plant breeder uses various technologies and methodologies to achieve targeted and directional changes in the nature of plants. As science and technology advance, new tools are developed while old ones are refined for use by breeders. Before initiating a breeding project, clear breeding objectives are defined based on factors such as producer needs, consumer preferences and needs, and environmental impact. Breeders aim to make the crop producer's job easier and more effective in various ways. They may modify plant structure, so it will resist lodging and thereby facilitate mechanical harvesting. They may develop plants that resist pests, so that the farmer does not have to apply pesticides, or applies smaller amounts of these chemicals. Not applying pesticides in crop production means less environmental pollution from agricultural sources. Breeders may also develop high yielding varieties (or **cultivars**), so the farmer can produce more for the market to meet consumer demands while improving his or her income. The term cultivar is reserved for variants deliberately created by plant breeders and will be introduced more formally later in the book. It will be the term of choice in this book.

When breeders think of consumers, they may, for example, develop foods with higher nutritional value and that are more flavorful. Higher nutritional value means reduced illnesses in society (e.g., nutritionally related ones such as blindness, rickettsia) caused by the consumption of nutrient-deficient foods, as pertains in many developing regions where staple foods (e.g., rice, cassava) often lack certain essential amino acids or nutrients. Plant breeders may also target traits of industrial value. For example, fiber characteristics (e.g., strength) of fiber crops such as cotton can be improved, while oil crops can be improved to yield high amounts of specific fatty acids (e.g., high oleic content sunflower seed). The latest advances in technology, specifically genetic engineering technologies, are being applied to enable plants to be used as bioreactors to produce certain pharmaceuticals (called **biopharming** or simply **pharming**).

The technological capabilities and needs of societies in the past restricted plant breeders to achieving modest objectives (e.g., product appeal, adaptation to production environment). It should be pointed out that these "older" breeding objectives are still important today. However, with the availability of sophisticated tools, plant breeders are now able to accomplish these genetic alterations in novel ways that are sometimes the only option, or are more precise and more effective. Furthermore, as previously indicated, plant breeders are able to undertake more dramatic alterations that were impossible to attain in the past (e.g., transferring a desirable gene from a bacterium to a plant!). Some of the reasons why plant breeding is important to society are summarized next.

1.3 The concept of genetic manipulation of plant attributes

The work of Gregor Mendel and further advances in science that followed his discoveries established that plant traits are controlled by hereditary factors or **genes** that consist of DNA (deoxyribose nucleic acid, the hereditary material). These genes are expressed in an environment to produce a trait. It follows, then, that in order to change a trait or its expression, one may change the *nature* or its genotype, and/or modify the *nurture* (environment in which it is expressed). Changing the environment essentially entails modifying the growing or production conditions. This may be achieved through an agronomic approach; for example, the application of production inputs (e.g., fertilizers, irrigation). While this approach is effective in enhancing certain traits, the fact remains that once these supplemental environmental factors are removed, the expression of the plant trait reverts to the *status quo*. On the other hand, plant breeders seek to modify plants with respect to the expression of certain selected attributes by modifying the genotype (in a desired way by targeting specific genes). Such an approach produces an alteration that is permanent (i.e., transferable from one generation to the next).

1.4 Why breed plants?

The reasons for manipulating plant attributes or performance change according to the needs of society. Plants provide food, feed, fiber, pharmaceuticals, and shelter for humans. Furthermore, plants are used for aesthetic and other functional purposes in the landscape and indoors.

1.4.1 Addressing world food and feed quality needs

Food is the most basic of human needs. Plants are the primary producers in the **ecosystem** (a community of living organisms including all the nonliving factors in the environment). Without them, life on earth for higher organisms would be impossible. Most of the crops that feed the world are cereals (Table 1.1).

Table 1.1 Twenty five major food crops of the world.

1	Wheat	11	Sorghum	21	Apples
2	Rice	12	Sugarcane	22	Yam
3	Corn	13	Millets	23	Peanut
4	Potato	14	Banana	24	Watermelon
5	Barley	15	Tomato	25	Cabbage
6	Sweet potato	16	Sugar beet		
7	Cassava	17	Rye		
8	Grapes	18	Oranges		
9	Soybean	19	Coconut		
10	Oats	20	Cottonseed oil		

The ranking is according to total tonnage produced annually. (Source: Harlan, 1976)

Plant breeding is needed to enhance the value of food crops, by improving their yield and the nutritional quality of their products, for healthy living of humans. Certain plant foods are deficient in certain essential nutrients to the extent that where these foods constitute the bulk of a staple diet, diseases associated with nutritional deficiency are often common. Cereals tend to be low in lysine and threonine, while legumes tend to be low in cysteine and methionine (both sulfur-containing amino acids). Breeding is needed to augment the nutritional quality of food crops. Rice, a major world food, lacks pro-vitamin A (the precursor of vitamin A). The Golden Rice project currently underway at the International Rice Research Institute (IRRI) in the Philippines and other parts of the world, is geared towards developing, for the first time ever, a rice cultivar with the capacity to produce pro-vitamin A (Golden rice 2, with a 20-fold increase in pro-vitamin A, has been developed by Syngenta's Jealott's Hill International Research Centre in Berkshire, UK). An estimated 800 million people in the world, including 200 million children, suffer chronic under-nutrition, with its attendant health issues. Malnutrition is especially prevalent in developing countries.

Breeding is also needed to make some plant products more digestible and safer to eat, by reducing their toxic components and improving their texture and other qualities. A high lignin content of the plant material reduces its value for animal feed. Toxic substances occur in major food crops, such as alkaloids in yam, cynogenic glucosides in cassava, trypsin inhibitors in pulses, and steroidal alkaloids in potatoes. Forage breeders are interested, amongst other things, in improving feed quality (high digestibility, high nutritional profile) for livestock.

1.4.2 Addressing food supply needs for a growing world population

In spite of a doubling of the world population in the last three decades, agricultural production rose at an adequate rate to meet world food needs. However, an additional three billion people will be added to the world population in the next three decades, requiring an expansion in world food supplies to meet the projected needs. As the world population increases, there would be a need for an agricultural production system that is aligned with population growth. Unfortunately, land for farming is scarce. Farmers have expanded their enterprise onto new lands. Further expansion is a challenge because land that can be used for farming is now being used for commercial and residential purposes to meet the demands of a growing population. Consequently, more food will have to be produced on less land. This calls for improved and high yielding cultivars to be developed by plant breeders. With the aid of plant breeding, the yields of major crops have dramatically changed over the years. Another major concern is the fact that most of the population growth will occur in developing countries, where food needs are currently most serious and where resources for feeding the people are already most severely strained, because of natural or human-made disasters, or ineffective political systems.

1.4.3 Need to adapt plants to environmental stresses

The phenomenon of global climatic change that is occurring is partly responsible for modifying the crop production environment (e.g., some regions of the world are getting drier and others saltier). This means that new cultivars of crops need to be bred for new production environments. Whereas developed economies may be able to counter the effects of unseasonable weather by supplementing the production environment (e.g., by irrigating crops), poorer countries are easily devastated by even brief episodes of adverse weather conditions. For example, development and use of drought resistant cultivars is beneficial to crop production in areas of marginal or erratic rainfall regimes. Breeders also need to develop new plant types that can resist various biotic (diseases and insect pests) and other abiotic (e.g., salt, drought, heat, cold) stresses in the production environment. Crop distribution can be expanded by adapting crops to new production environments (e.g., adapting tropical plants to temperate regions). Development of photoperiod insensitive crop cultivars would allow an expansion in production of previously photoperiod sensitive species.

1.4.4 Need to adapt crops to specific production systems

Breeders need to produce plant cultivars for different production systems to facilitate crop production and optimize crop productivity. For example, crop cultivars must be developed for rain-fed or irrigated production, and for mechanized or non-mechanized production. In the case of rice, separate sets of cultivars are needed for upland production and for paddy production. In organic production systems where pesticide use is highly restricted, producers need insect and disease resistant cultivars in crop production.

1.4.5 Developing new horticultural plant varieties

The ornamental horticultural production industry thrives on the development of new varieties through plant breeding. Aesthetics is of major importance to horticulture. Periodically, ornamental plant breeders release new varieties that exhibit new colors and other morphological features (e.g., height, size, shape). Also, breeders develop new varieties of vegetables and fruits with superior yield, nutritional qualities, adaptation, and general appeal.

1.4.6 Satisfying industrial and other end-use requirements

Processed foods are a major item in the world food supply system. Quality requirements for fresh produce meant for the table are different from those for the food processing industry. For example, there are table grapes and grapes bred for wine production. One of the reasons why the first **genetically modified** (GM) crop (produced by using genetic engineering tools to incorporate foreign DNA) approved for food, the "FlavrSavr™" tomato, did not succeed was because the product was marketed as table or fresh tomato, when in fact the gene of interest was placed in a genetic background for developing a processing tomato variety. Other factors contributed to the demise of this historic product. Different markets have different needs that plant breeders can address in their undertakings. For example, potato is a versatile crop used for food and industrial products. Different varieties are being developed by breeders for baking, cooking, fries (frozen), chipping, and starch. These cultivars differ in size, specific gravity, and sugar content, among other properties. High sugar content is undesirable for frying or chipping because the sugar caramelizes under high heat to produce undesirable browning of fries and chips.

1.5 Overview of the basic steps in plant breeding

Plant breeding has come a long way, from the cynical view of "crossing the best with best and hoping for the best" to carefully planned and thought-out strategies to develop high performance cultivars. Plant breeding methods and tools keep changing as technology advances. Consequently, plant breeding approaches may be categorized into two general types: **conventional** and **unconventional**. (This categorization is only for convenience.)

- **Conventional approach.** Conventional breeding is also referred to as **traditional** or **classical breeding**. This approach entails the use of tried, proven, and older tools. Crossing two plants (hybridization) is the primary technique for creating variability in flowering species. Various breeding methods are then used to discriminate among the variability (selection) to identify the most desirable recombinant. The selected genotype is increased and evaluated for performance before release to producers. Plant traits controlled by many genes (quantitative traits) are more difficult to breed. Age notwithstanding, the conventional approach remains the workhorse of the plant breeding industry. It is readily accessible to the average breeder and is relatively easy to conduct compared to the unconventional approach.
- **Unconventional approach.** The unconventional approach to breeding entails the use of cutting edge technologies for creating new variability that it is sometimes impossible to achieve with conventional methods. However, this approach is more involved, requiring special technical skills and knowledge. It is also expensive to conduct. The advent of recombinant DNA (rDNA) technology gave breeders a new set of powerful tools for genetic analysis and manipulation. Gene transfer can now be made across natural biological barriers, circumventing the sexual process (e.g., the *Bt* products that consist of bacterial genes transferred into crops to confer resistance to the European corn borer). Molecular markers are available to aid the selection process to make the process more efficient and effective.

  Even though two basic breeding approaches have been described, it should be pointed out that they are best considered as complementary rather than independent approaches. Usually, the molecular tools are used to generate variability for selection, or to facilitate the selection process. After genetically modifying plants using molecular tools, it may be used as a parent in subsequent crosses, using conventional tools, to transfer the desirable genes into adapted and commercially desirable genetic backgrounds. Whether developed by conventional or molecular approaches, the genotypes are evaluated in the field by conventional methods and then advanced through the standard seed certification process before the farmer can have access to it for planting a crop. The unconventional approach to breeding tends to receive more attention from funding agencies than the conventional approach, partly because of its novelty and advertised potential, as well as the glamour of the technologies involved.

  Regardless of the approach, a breeder follows certain general steps in conducting a breeding project. A breeder should have a comprehensive plan for a breeding project that addresses:

- **Objectives.** The breeder should first define a clear objective (or set of objectives) for initiating the breeding program. In selecting breeding objectives, breeders need to consider:
  (a) The producer (grower) from the point of view of growing the cultivar profitably (e.g., need for high yield, disease resistance, early maturity, lodging resistance).
  (b) The processor (industrial user) as it relates to efficiently and economically using the cultivar as raw materials for producing new product (e.g., canning qualities, fiber strength).
  (c) The consumer (household user) preference (e.g., taste, high nutritional quality, shelf life).

  The tomato will be used to show how different breeding objectives can be formulated for a single crop. Tomato is a very popular fruit with a wide array of uses, each calling for certain qualities. For salads, tomato is used whole, and hence the small size is preferred; for hamburgers, tomato is sliced, round large fruits being preferred. Tomato for canning (e.g., puree) requires certain pulp qualities. Being a popular garden species, gardeners prefer a tomato cultivar that ripens over time so harvesting can be spaced. However, for industrial use, as in the case of canning, the fruits on the commercial cultivar must ripen together, so the field can be mechanically harvested. Furthermore, whereas appearance of the fruit is not top priority for a processor who will be making tomato juice, the appearance of fruits is critical in marketing the fruit for table use.

- **Germplasm.** It is impossible to improve plants or develop new cultivars without genetic variability. Once the objectives have been determined, the breeder then assembles the germplasm to be used to initiate the breeding program. Sometimes, new variability is created through crossing of selected parents, inducing mutations, or using biotechnological techniques. Whether used as such or recombined through crossing, the base population used to initiate a breeding program must of necessity include the gene(s) of interest. That is, you cannot breed for disease resistance, if the gene conferring resistance to the disease of interest does not occur in the base population.
- **Selection.** After creating or assembling variability, the next task is to discriminate among the variability to identify and select individuals with the desirable genotype to advance and increase in order to develop potential new cultivars. This calls for using standard selection or breeding methods suitable for the species and the breeding objective(s).
- **Evaluation.** Even though breeders follow basic steps in their work, the product reaches the consumer only after it has been evaluated. Agronomists may participate in this stage of plant breeding. In a way, evaluation is also a selection process, for it entails comparing a set of superior candidate genotypes to select one for release as a cultivar. The potential cultivars are evaluated in the field, sometimes at different locations and over several years, to identify the most promising one for release as a commercial cultivar.
- **Certification and cultivar release.** Before a cultivar is released, it is processed through a series of steps, called the seed certification process, to increase the experimental seed and to obtain approval for release from the designated crop certifying agency in the state or country. These steps in plant breeding are discussed in detail in this book.

1.6 How have plant breeding objectives changed over the years?

In a review of plant breeding over the past 50 years, Baenzinger and colleagues in 2006 revealed that while some aspects of how breeders conduct their operations have dramatically changed, others have stubbornly remained the same, being variations on a theme at best.

Breeding objectives in the 1950s and 1960s, and before, appeared to focus on increasing crop productivity. Breeders concentrated on yield and adapting crops to their production environment. Resistance to diseases and pests was also priority. Quality traits for major field crops, such as improved fiber strength for cotton and milling and baking quality in wheat, were important in the early breeding years. Attention was given to resistance to abiotic stresses such as winter hardiness and traits like lodging resistance, uniform ripening, and seed oil content of some species. Crop yield continued to be important throughout the 1990s. However, as analytical instrumentation that allowed high throughput, low cost, ease of analysis and repeatability of results became more readily available, plant breeders began to include nutritional quality traits into their breeding objectives. These included forage quality traits, such as digestibility and neutral detergent fiber.

More importantly, with advanced technology, quality traits are becoming more narrowly defined in breeding objectives. Rather than high protein or high oil, breeders are breeding for specifics, such as low linolenic acid content, to meet consumer preferences for eating healthful foods (low linolenic acid in oil provides it with stability and enhanced flavor, and reduces the need for partial hydrogenation of the oil and production of trans fatty acids). Also, a specific quality trait such as low phytate phosphorus in grains (e.g., corn, soybean) would increase feed efficiency and reduce phosphorus in animal waste, a major source of the environmental degradation of lakes.

Perhaps no single technology has impacted breeding objectives more in recent times than biotechnology (actually, a collection of biological technologies). The subject is discussed in detail in later chapters. Biotechnology has enabled breeders to develop a new generation of cultivars with genes included from genetically unrelated species (transgenic or GM cultivars). The most successful transgenic input traits to date have been herbicide resistance and insect resistance, which have been incorporated into major crops species like corn, cotton, soybean, and tobacco. According to a 2010 International Service for the Acquisition of Agri-Biotech Crops (ISAAA) report, GM is far from being a global industry, with only six countries (USA, Brazil, Argentina, India, Canada and China) growing about 95% of the total global acreage (use leads with about 50%). Some argue that biotechnology has become the tail that wags the plant breeding industry. Improvement in plant genetic manipulation technology has also encouraged the practice of gene stacking in plant breeding. Another significant contribution of biotechnology to changing breeding objectives is the creation of the "universal gene pool", whereby breeders, in theory, have limitless sources of diversity, and hence can be more creative and audacious in formulating breeding objectives.

In the push to reduce our carbon footprint and reduce environmental pollution, there is a drive towards the discovery and use of alternative fuel sources. Some traditional improvement of some crop species (e.g., corn) for food and feed is being changed to focus some attention on their industrial use, through increasing biomass for biofuel production, and as bioreactors for production of polymers and pharmaceuticals. In terms of reducing adverse environmental impact, one of the goals of modern breeding is to reduce the use of agrochemicals.

1.7 The art and science of plant breeding

The early domesticators relied solely on experience and intuition to select and advance plants they thought had superior qualities. As knowledge abounds and technology advances, modern breeders are increasingly depending on science to take the guesswork out of the selection process, or at least reduce it. At the minimum, a plant breeder should have a good understanding of genetics and the principles and concepts of plant breeding, hence the emphasis of both disciplines in this book. Students taking a course in plant breeding are expected to have taken at least an introductory course in genetics. Nonetheless, two supplementary chapters have been provided in this book; they review some pertinent genetic concepts that will aid the student in understanding plant breeding. By placing these fundamental concepts in the back of the book, users will not feel obligated to study them but can use them on as needed basis.

1.7.1 Art and the concept of the "breeder's eye"

Plant breeding is an applied science. Just like other non-exact science disciplines or fields, art is important to the success achieved by a plant breeder. Early plant breeders depended primarily on intuition, skill, and judgment in their work. These attributes are still desirable in modern day plant breeding. This book discusses the various tools available to plant breeders. Plant breeders may use different tools to tackle the same problem, the results being the arbiter of the wisdom in the choices made. In fact, it is possible for different breeders to use the same set of tools to address the same kind of problem with different results, due in part to the differences in their skill and experience. As is discussed later in the book, some breeding methods depend on phenotypic selection (based on appearance; visible traits). This calls for the proper design of the fieldwork to minimize the misleading effect of a variable environment on the expression of plant traits. Selection may be likened to a process of informed "eye-balling" to discriminate among variability.

A good breeder should have a keen sense of observation. Several outstanding discoveries were made just because the scientists who were responsible for these events were observant enough to spot unique and unexpected events. Luther Burbank selected one of the most successful cultivars of potato, the "Burbank potato", from among a pool of variability. He observed a seed ball on a vine of the "Early Rose" cultivar in his garden. The ball contained 23 seeds, which he planted directly in the field. At harvest time the following fall, he dug up and kept the tubers from the plants separately. Examining them, he found two vines that were unique, bearing large smooth and white potatoes. Still, one was superior to the others. The superior one was sold to a producer who named it Burbank. The Russet Burbank potato is produced on about 50% of all lands devoted to potato production in the United States.

Breeders often have to discriminate among hundreds and even tens of thousands of plants in a segregating population to select only a small fraction of promising plants to advance in the program. Visual selection is an art, but it can be facilitated by selection aids such as **genetic markers** (simply inherited and readily identified traits that are linked to desirable traits that are often difficult to identify). Morphological markers (not biochemical markers) are useful when visual selection is conducted. A keen eye is advantageous even when markers are involved in the selection process. As is emphasized later in this book, the breeder ultimately adopts a holistic approach to selection, evaluating the overall worth or desirability of the genotype, not just the trait targeted in the breeding program.

1.7.2 The scientific disciplines and technologies of plant breeding

The science and technology component of modern plant breeding is rapidly expanding. While a large number of science disciplines directly impact plant breeding, several are closely associated with it. These are plant breeding, genetics, agronomy, cytogenetics, molecular genetics, botany, plant physiology, biochemistry, plant pathology, entomology, statistics, and tissue culture. Knowledge of the first three disciplines is applied in all breeding programs. The technologies used in modern plant breeding are summarized in Table 1.2. These technologies are discussed in varying degrees in this book. The categorization is only approximate and generalized. Some of these tools are used to either generate variability directly or to transfer genes from one genetic background to another to create variability for breeding. Some technologies facilitate the breeding process through, for example, identifying individuals with the gene(s) of interest.

- **Genetics.** Genetics is the principal scientific basis of modern plant breeding. As previously indicated, plant breeding is about targeted genetic modification of plants. The science of genetics enables plant breeders to predict, to varying extents, the outcome of genetic manipulation of plants. The techniques and methods employed in breeding are determined based on the genetics of the trait of interest, regarding, for example, the number of genes coding for it and gene action. For example, the size of the segregating population to generate in order to have a

Table 1.2 An operational classification of technologies of plant breeding.

Classical/traditional tools	**Common use of the technology/tool**
Emasculation	making a completer flower female; preparation for crossing
Hybridization	crossing un-identical plants to transfer genes or achieve recombination
Wide crossing	crossing of distantly related plants
Selection	the primary tool for discriminating among variability
Chromosome counting	determination of ploidy characteristics
Chromosome doubling	manipulating ploidy for fertility
Male sterility	to eliminate need for emasculation in hybridization
Triploidy	to achieve seedlessness
Linkage analysis	for determining association between genes
Statistical tools	for evaluation of germplasm
Relatively advanced tools	
Mutagenesis	to induce mutations to create new variability
Tissue culture	for manipulating plants at the cellular or tissue level
Haploidy	used to create extremely homozygous diploid
Isozyme markers	to facilitate the selection process
In situ hybridization	detect successful interspecific crossing
More sophisticated tools	
DNA markers	
– RFLP	more effective than protein markers (isozymes)
– RAPD	PCR-based molecular marker
Advanced technology	
Molecular markers	SSR, SNPs, etc.
Marker assisted selection	facilitate the selection process
DNA sequencing	ultimate physical map of an organism
Plant genomic analysis	studying the totality of the genes of an organism
Bioinformatics	computer-based technology for prediction of biological function from DNA sequence data
Microarray analysis	to understand gene expression and for sequence identification
Primer design	for molecular analysis of plant genome
Plant transformation	for recombinant DNA work

chance of observing that unique plant with the desired combination of genes, depends on the number of genes involved in the expression of the desired trait.

- **Botany.** Plant breeders need to understand the reproductive biology of their plants as well as their taxonomic attributes. They need to know if the plants to be hybridized are cross-compatible, as well as to know in fine detail about flowering habits, in order to design the most effective crossing program.
- **Plant physiology.** Physiological processes underlie the various phenotypes observed in plants. Genetic manipulation alters plant physiological performance, which in turn impacts the plant performance in terms of the desired economic product. Plant breeders manipulate plants for optimal physiological efficiency, so that dry matter is effectively partitioned in favor of the economic yield. Plants respond to environmental factors, biotic (e.g., pathogens) and abiotic (e.g., temperature, moisture). These factors are sources of physiological stress when they occur at unfavorable levels. Plant breeders need to understand these stress relationships in order to develop cultivars that can resist them for enhanced productivity.
- **Agronomy.** Plant breeders conduct their work in both controlled (greenhouse) and field environments. An understanding of agronomy (the art and science of producing crops and managing soils) will help the breeder to provide the appropriate cultural conditions for optimal plant growth and development for successful hybridization and selection in the field. An improved cultivar is only as good as its cultural environment. Without the proper nurturing, the genetic potential of an improved cultivar would not be realized. Sometimes, breeders need to modify the plant growing environment to identify individuals to advance in a breeding program to achieve an objective (e.g., withholding water in breeding for drought resistance).
- **Pathology and entomology.** Disease resistance breeding is a major plant breeding objective. Plant breeders need to understand the biology of the insect pest or pathogen against which resistance is being sought. The kind of cultivar to breed, the methods to use in breeding and evaluation all depend on the kind of pest or pathogen (e.g., its races or variability, pattern of spread, life cycle, and most suitable environment).
- **Statistics.** Plant breeders need to understand the principles of research design and analysis. This knowledge is essential for effectively designing field and laboratory studies (e.g., for heritability, inheritance of a trait, combining ability) and for evaluating genotypes for cultivar release at the end of the breeding program. Familiarity with computers is important for record keeping and data manipulation. Statistics is indispensable to plant breeding programs. This is because the breeder often encounters situations in which predictions about outcomes, comparison of results, estimation of response to a treatment, and many more, need to be made. Genes are not expressed in a vacuum but in an environment with which they interact. Such interactions may cause certain outcomes to deviate from the expected. Statistics is needed to analyze the variance within a population to separate real genetic effects from environmental effects. Application of statistics in plant breeding can be as simple as finding the mean of a set of data, to complex estimates of variance and multivariate analysis.
- **Biochemistry.** In this era of biotechnology, plant breeders need to be familiar with the molecular basis of heredity. They need to be familiar with the procedures of plant genetic manipulation at the molecular level, including the development and use of molecular markers and gene transfer techniques.

While the training of a modern plant breeder includes these courses and practical experiences in these and other disciplines, it is obvious that the breeder cannot be an expert in all of them. Modern plant breeding is more *team work* than solo effort. A plant breeding team will usually have experts in all these key disciplines, each one contributing to the development and release of a successful cultivar.

1.8 Achievements of modern plant breeders

The achievements of plant breeders are numerous, but may be grouped into several major areas of impact – yield increase, enhancement of compositional traits, crop adaptation, and the impact on crop production systems.

1.8.1 Yield increase

Yield increase in crops has been accomplished in a variety of ways, including targeting yield *per se* or its

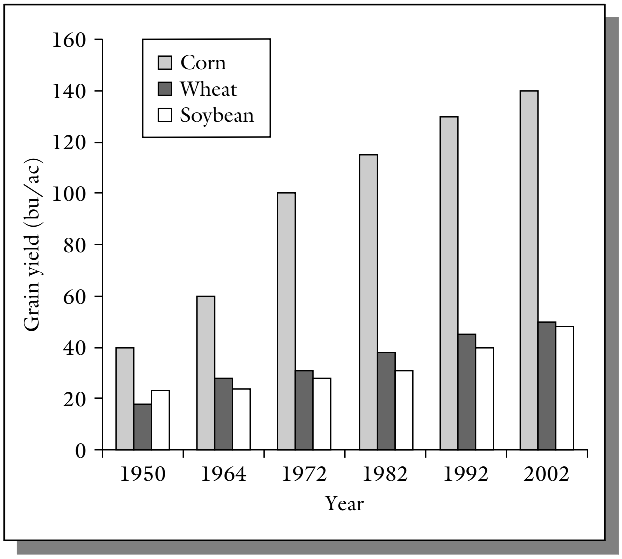

Figure 1.1 The yield of major world food crops is steadily rising, as indicated by the increasing levels of crops produced in the US agricultural system. A significant portion of this rise is attributable to the use of improved crop cultivars by crop producers. (Source: Drawn with data from the USDA.)

components, or making plants resistant to economic diseases and insect pests, and breeding for plants that are responsive to the production environment. Yields of major crops (e.g., corn, rice, sorghum, wheat, and soybean) have significantly increased in the USA over the years (Figure 1.1). For example, the yield of corn rose from about 2000 kg/ha in the 1940s to about 7000 kg/ha in the 1990s. In England, it took only 40 years for wheat yields to rise from 2 metric tons/ ha to 6 metric tons/ha. Food and Agriculture Organization (FAO) data comparing crop yield increases between 1961 and 2000 show dramatic changes for different crops in different regions of the of the world. For example, wheat yield increased by 681% in China, 301% in India, 299% in Europe, 235% in Africa, 209% in South America, and 175% in the USA. These yield increases are not totally due to the genetic potential of the new crop cultivars (about 50% is attributed to plant breeding) but are also due to the improved agronomic practices (e.g., application of fertilizer, irrigation). Crops have been armed with disease resistance to reduce yield loss. Lodging resistance also reduces yield loss resulting from harvest losses.

1.8.2 Enhancement of compositional traits

Breeding for plant compositional traits to enhance nutritional quality or meet an industrial need are major plant breeding goals. High protein crop varieties (e.g., high lysine or quality protein maize) have been produced for use in various parts of the world. Different kinds of wheat are needed for different kinds of products (e.g., bread, pasta, cookies, semolina). Breeders have identified the quality traits associated with these uses and have produced cultivars with enhanced expression of these traits. Genetic engineering technology has been used to produce high oleic sunflower for industrial use; it is also being used to enhance the nutritional value of crops (e.g., pro-vitamin A golden rice). The shelf life of fruits (e.g., tomato) has been extended through the use of genetic engineering techniques to reduce the expression of compounds associated with fruit deterioration.

1.8.3 Crop adaptation

Crop plants are being produced in regions to which they are not native, because breeders have developed cultivars with modified physiology to cope with variations in the duration of day length (photoperiod). Photoperiod insensitive cultivars will flower and produce seed under any day length conditions. The duration of the growing period varies from one region of the world to another. Early maturing cultivars of crop plants enable growers to produce a crop during a short window of opportunity, or even to produce two crops in one season. Furthermore, early maturing cultivars can be used to produce a full season crop in areas where adverse conditions are prevalent towards the end of the normal growing season. Soils formed under arid conditions tend to accumulate large amounts of salts; to use these lands for crop production, salt tolerant (saline and aluminum tolerance) crop cultivars have been developed for certain species. In crops such as barley and tomato there are commercial cultivars in use with drought, cold, and frost tolerance.

1.8.4 Impact on crop production systems

Crop productivity is a function of the genotype (genetic potential of the cultivar) and the cultural environment. The **Green Revolution** is an example