FUNDAMENTALS FUNDAMENTALS OF PLANT GENETICS AND BREEDING AND BREEDING

James R. Welsh

Fundamentals of Plant Genetics and Breeding

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Preface

This book was written to provide the beginning plant breeding student with a basic set of principles. It can be used by those who only take an introductory course, but it can also serve as the foundation for more advanced study. Most chapters are purposefully brief. Plant breeding courses are traditionally taught in departments with active plant improvement programs and this text is designed so that the instructor can insert his or her own experiences and illustrations throughout the course. I hope this flexibility will show the individuality and creativity of plant breeding. Some of the more recent review articles that can be used to identify detailed readings are included and new science and technology of wide genetic transfers and tissue culture emerging in plant breeding and genetics are briefly discussed in Chapters 18 and 19.

The amount of basic genetics to be included was difficult to resolve. Selection of the topics on Mendelian genetics and related subjects in Chapters 2 to 5 was based on 15 years of experience in teaching plant breeding. Even those students who come into the introductory plant breeding course with a firm grasp of genetics can benefit by having a ready reference for quick review. This material should be especially helpful to students who have difficulty in understanding Mendelian principles. These chapters can be completely ignored or used in whatever manner best suited to the students' needs. The remainder of the book is designed to flow logically from one breeding principle to another and is not based on specific crops or pollination systems. For example, the pure line concepts are extended into inbred line improvement techniques, and the hybrid discussions include both cross- and self-pollinated crops. I hope this will make clear the understanding of principles without stressing traditional (and artificial) divisions of subject matter.

A few simple questions have been included at the end of some chapters. These are problem types that will aid the student in understanding material in the chapter.

Nomenclature and terminology are always troublesome and I have listed scientific names in a glossary at the end of the book to make the material more readable. The use of the terms "corn" versus "maize" and "variety" versus "cultivar" (cultivated variety)

warrants a comment. Corn was chosen since it is a common name frequently used in U.S. literature. Maize is more botanically correct, however, and is used almost exclusively in European publications. The term variety was selected instead of cultivar because of its common usage, especially in the farming community. Cultivar is officially approved for scientific writing.

I gratefully acknowledge the many students and breeder colleagues who provided help and encouragement in the writing of this book. In particular, Dr. S. L. Ladd and Dr. D. D. Stuthman gave many valuable criticisms and suggestions after reviewing the entire manuscript. Dr. T. E. Haus evaluated several chapters and Dr. T. Tsuchiya supplied excellent chromosome photomicrographs. I recognize Colorado State University and my administrators Dr. W. F. Keim, Head of the Agronomy Department, and Dr. D. D. Johnson, Dean of the College of Agricultural Sciences, for making time available to complete this task. Finally, special recognition goes to my wife, Addie, who encouraged and worked with me through the entire manuscript preparation process.

Although many people provided information, any errors or omissions are exclusively my responsibility. This has been a pleasant endeavor—one that I hope will benefit plant breeding students.

JAMES R. WELSH

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INTRODUCTION

People have always been engaged in some form of plant breeding by manipulating genetic systems to design a more desirable product. The definitions of improved characteristics are dictated by the user and lead to a wide potential group of breeding program goals. A producer of dryland grain crops, such as wheat or barley, and a gardener interested only in individual plants produced for aesthetic values will have different requirements and the breeder must respond to them. The array of challenges in plant breeding is extensive, and the number of alternative objectives necessitates establishing goal priorities based on careful study of total production and utilization. Efficient management of financial resources—a limiting factor in any program—is essential for breeding effectiveness.

As a profession, plant breeding offers many opportunities. Breeding programs can range from the work of the backyard hobbyist interested in the personal challenge of plant improvement to multimillion dollar programs designed to generate a financial advantage for a corporation. In competitive agricultural production, economic incentive is the underlying basis for plant breeding. Unproductive plant breeding programs that do not result in improved varieties or hybrids are often short-lived. Conversely, the hobbyist may be interested in developing plants for personal pleasure without particular regard to potential financial opportunities.

The professional breeder in a public or private program is a highly skilled and well-trained scientist. Successful breeders combine educational skills and training with intuition and a certain 2 INTRODUCTION

amount of luck—they are basically gamblers who attempt to improve the odds of a favorable outcome through a knowledge of genetics and breeding manipulations. They must know fundamentals of plant reproduction, function, and culture, and be able to use proper experimental techniques to insure a reasonable probability of making correct breeding decisions. Subject areas include genetics, agronomy, horticulture, botany, plant pathology, plant physiology and biochemistry, statistics, computer science, and economics. Even this partial list indicates that plant breeders cannot be expert in all pertinent subjects; they must recognize their limitations as well as strengths. Breeders often accept responsibility for intergrating and utilizing skills of other professionals in cooperative research efforts. Because of the potential benefit to society from genetic improvement of plant species, scientists in related fields are usually willing to cooperate in breeding and genetic activities.

Mechanical skills and imagination are required for plant breeders to develop equipment and techniques that achieve unique program objectives. The progressive, innovative breeder continually seeks maximum genetic gain with minimum resource input.

By improving food supplies plant breeding has played a major role in helping to reduce massive hunger and starvation on a worldwide basis. The Nobel Peace Prize awarded to Dr. N. E. Borlaug in 1970 is a testimony to the importance of plant breeding to human welfare. Dr. Borlaug's intense efforts in developing improved wheat varieties have led to extensive production increases in many calorie-deficient areas of the world. However, breeding efforts must be coupled with production and marketing improvements and adequate population control, if world food needs are to be properly confronted. As world population continues to increase, food production technology—including plant breeding—will struggle to keep pace with demand.

The advisability of genetically improving yields in crops where apparent surpluses exist is frequently debated. In the United States, for example, "overproduction" of many grain crops has resulted in depressed prices and the need for government subsidies to maintain adequate farm income. On the other hand, esti-

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mates indicate that a significant proportion of the world population experiences some form of hunger or malnutrition every day. In the world marketplace the fine balance between adequate and inadequate supplies of food was demonstrated in 1973. Dramatic price increases followed massive Russian government grain purchases necessitated by weather-related production shortfalls.

Production efficiency is the result of increased output per unit of input. Improved varieties contain built-in production stability factors provided at a minimum financial expenditure for both the producer and the consumer, and aid in insuring a steady food, feed, and fiber supply. Our total environment, including the plant species around us, has a direct effect on our psychological well-being and happiness. In ornamental species, the genetic manipulation of plant characteristics that provide pleasure and enjoyment is an important function of plant breeders.

These brief considerations emphasize that from humanitarian or economic standpoints the breeder has every obligation to continue genetic plant improvement. Plant breeding is the manipulation of a biological system that requires many generations to achieve results; it is also a dynamic, exciting, and challenging profession operating under continually changing conditions. The remainder of this book is devoted to principles and practices related to the art and science of plant breeding.

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MENDELIAN GENETICS

Today's plant breeding utilizes for its basic foundation the genetic principles initiated by the classic investigations of Gregor Mendel. We have advanced significantly in our scientific knowledge of inheritance since his work, but we are still primarily using refinements of Mendelian principles. Mendel, an Austrian monk, was well trained in scientific investigations. His work, reported in 1865 (1), employed simple but effective approaches to the solution of inheritance problems that had troubled scientists for many years. It is important to understand these principles when addressing plant breeding problems and so this chapter is devoted to a detailed description of Mendel's investigations and conclusions. The sound techniques and logic he employed allow his work to stand as a model of methodology in the design of all scientific investigations.

Mendel initially studied a number of different plant species, but two important properties prompted him to choose the garden pea for his major work. First, he recognized several different traits that had repeatable variation between parents. For example, seed shape could be either round or wrinkled, and each variation of the seed-shaped trait was transmitted from generation to generation on a highly repeatable basis. The variations were easily recognizable and could be stabilized into true breeding forms or lines. Secondly, the plants had a flowering mechanism that provided protection, or could be easily protected, against the influence of all foreign pollen. He required that the offspring from a single plant were the result of the union of a male and female from that same

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plant or that they came from specific parental combinations under his control. The garden pea met the requirements for well-defined traits and a closed mating system.

The object of Mendel's experiment was to deduce the rules by which observable inherited variations in certain plant characters were passed from generation to generation. The term "character" means different plant traits or forms, and in his study included seed shape, seed color, flower color, pod shape, pod color, flower position, and stem length. His experiment initially resolved itself into as many separate experiments as there were different characters in which he was interested. Other investigators who had conducted earlier inheritance studies attempted to look at the organisms in their entirety. This approach introduced so much complexity into the system that they were unable to identify specific patterns and mechanisms. Mendel employed the sound scientific principle of reducing a complex question to its component parts for study, and then bringing the parts together for the final conclusions.

Mendel established parents that were true breeding for differing expressions of each character. He did this by selecting specific expressions for several generations until there was no further variation in the progeny. After he had established the true breeding parental lines, he made crosses, or hybridizations, between parents that differed in expression of one character. This was done separately for each of the seven characters. The resulting seeds were harvested and were the beginning of the first generation of the cross (F₁). The seeds were planted and the resulting plants were the F₁ generation. Seeds harvested from these plants were the initiation of the F, generation. In some cases he carried his material through the F₃. In all generations he kept seeds from each plant separate and maintained accurate records. This allowed him to classify and count the number of individuals occurring in each group. With this simple statistical technique, patterns in terms of ratios began to emerge.

We now know that some chance or random deviations will generally occur in any data set, and we use modern statistical techniques to understand the meanings of the deviations. Mendel used no statistical tests because they had not been developed at 6 MENDELIAN GENETICS

that time, and could draw conclusions only from patterns in his data.

MONOHYBRID SEGREGATION

Table 2.1 provides data for each of the seven initial experiments. Mendel used the term "dominant" to describe the expression of the character that appeared in the F_1 generation and "recessive" for the expression that disappeared in the F_1 but reappeared in the F_2 . In each of the seven cases the pattern of 3 dominant: 1 recessive in the F_2 was closely approximated.

He then studied the F_3 generation by evaluating offspring from each F_2 plant. F_1 , F_2 , and F_3 data for the two characters of seed shape and seed color are given in Table 2.2. The F_2 plants that were recessive in appearance produced only recessive individuals in the F_3 . Of the F_2 plants with dominant expression, approximately one-third yielded all dominant progeny, while two-thirds produced progeny that again segregated in a 3 dominant: 1 recessive manner. Combined F_3 information for any population produced an F_2 ratio of 1 pure dominant: 2 mixed dominant-recessive: 1 pure recessive. The term "monohybrid" is now commonly used to refer to the cross between parents with different expressions of a character that will result in a 3:1 ratio or some variation. We now know that this ratio combination is controlled by one inheritance unit called a gene.

Table 2.1 F₁ and F₂ Monohybrid Phenotypic Data For The Seven Characters Studied by Mendel

Character	F ₁	F ₂
Character	<u>* 1</u>	1 2
Seed shape	Round	5474 round: 1850 wrinkled
Seed endosperm		
color	Yellow	6022 yellow: 2001 green
Flower color	Red	705 red : 224 white
Pod shape	Inflated	882 inflated: 299 constricted
Pod color	Green	428 green : 152 yellow
Flower position	Axial	651 axial : 207 terminal
Stem length	Tall	787 tall : 277 short