GENETICS OF FLOWERING PLANTS

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OTHER BOOKS BY THE SAME AUTHOR

Natural History of the Phlox Family (1959)

The Origin of Adaptations (1963)

The Architecture of the Germplasm (1964)

Flower Pollination in the Phlox Family.
With Karen A. Grant (1965)

Hummingbirds and Their Flowers.
With Karen A. Grant (1968)

Plant Speciation (1971)

PREFACE

The primary objective of this book is to present a summary of our knowledge and understanding of the genetics of higher plants. There has been no book-length treatment of basic plant genetics in recent decades. The need for such a treatment has been apparent to many observers of the scene and has led directly to the present work.

The date of publication of Sansome and Philp's *Recent Advances in Plant Genetics* was 1939. This is perhaps the last previous book with the same center of focus as the present work. Yet *Genetics of Flowering Plants* bears little resemblance to *Recent Advances in Plant Genetics,* so greatly has the subject changed during the period since 1939. Basic plant genetics received good coverage in genetics textbooks a generation or two ago, from Baur's classic text (1911–1930) to that of Sirks (1956), but the growth of newer fields of genetics has tended to crowd plant genetics out of the more recent textbooks, and this source of information has also become inadequate.

Let me attempt to place *Genetics of Flowering Plants* in perspective in the current book literature in the same general field. The main emphasis in the present work is on the nature and action of genes, gene systems, linkage systems, and genetic systems in higher plants.

This is not a book on plant breeding (for which see references for Kuckuck and Mudra, 1950; Kappert and Rudorf, 1958–1962; Allard, 1960; and Brewbaker, 1964). Nor is it a book on quantitative genetics (see Falconer, 1960; Hiorth, 1963), or horticultural genetics (see Crane and Lawrence, 1952), although of course it overlaps with all these fields. Similarly this book does not emphasize

plant cytogenetics (for which see John and Lewis, 1965; Brown, 1972) or chromosome evolution in plants (see Darlington, 1963; Stebbins, 1971), though these topics necessarily come into our picture. Certain important topics of plant genetics related to plant evolution were covered recently in a companion volume (Grant, 1971) and require no duplicate treatment here. The valuable monograph of Clausen and Hiesey (1958) contains a wealth of information on many of the topics treated in the present work.

Genetics of Flowering Plants grew out of an earlier book of mine, *The Architecture of the Germplasm* (1964), and bears the marks of its parentage in many places throughout the text. Nevertheless, the center of focus is different in the two books. *The Architecture of the Germplasm* deals with the organization of the diploid genotype, in the light of evidence from several kingdoms of organisms, whereas the present book focuses on the organization and workings of plant genotypes. Many of the examples and stories used in the earlier book are, however, equally relevant to the theme of *Genetics of Flowering Plants,* and have accordingly found a place in it.

The literature of plant genetics is very scattered. It is spread across scores of current journals and through decades of back journal files. The dispersed condition of this literature renders it almost inaccessible to nonspecialists. One of my tasks in writing this book has been to bring together and synthesize a fair sample of the scattered information in plant genetics, with bibliographical references to the original sources. It was not my intention, however, to produce a complete compendium of examples and references on every topic taken up in the book.

Many of the older genetic experiments are as sound and as significant today as they ever were, but are now half forgotten and largely ignored. Another task in covering the subject of the book was to dig out some of these buried studies of earlier periods in genetics. This policy will hopefully give some feeling for the historical depth of our subject.

A minor theme of the book is the presentation of a series of classic experiments in plant genetics, beginning with that of Mendel in Chapter 1, and continuing with others of comparable elegance which are less well known outside specialist circles. It might have

been sufficient for the main purpose of the book to have stated simply the conclusions established by these experiments. But I have described also the methods and logical rationale of the experiments which lead to the stated conclusions. In this way I hope to convey some of the atmosphere of experimental plant genetics, which is quite different from that of other more generally known fields such as microbial genetics and molecular genetics.

Finally, I have tried wherever possible to relate the findings of plant genetics, both old and new, to modern concepts in other branches of genetics.

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CONTENTS

PART I: GENES

PART II: GENE SYSTEMS

CONTENTS

PART III: LINKAGE SYSTEMS

PART IV: GENETIC SYSTEMS

PART I : GENES

CHAPTER ONE

THE MENDELIAN MECHANISM

INTRODUCTION

THE DIPLOID-HAPLOID CYCLE

SEGREGATION IN *PISUM SATIVUM*

INDEPENDENT ASSORTMENT IN *PISUM SATIVUM*

PARTICULATE INHERITANCE

HISTORICAL COMMENTS

THE CHROMOSOME THEORY OF HEREDITY

RECOMBINATION OF LINKED GENES

LINKAGE MAPS

INTRODUCTION   The resemblance between parents and offspring is due to the transmission of a material substance which causes the development of similar characteristics in successive generations. The doctrine of a material basis of heredity was stated by various nineteenth-century biologists: by Mendel (1866), Darwin (1868), Weismann (1883, 1893), de Vries (1889), and others. The nature and mode of organization of this heredity material, however, were to be revealed only gradually and in successive stages, almost entirely in the twentieth century.

The successive revelations have come out of breeding experiments, cytogenetic studies, and biochemical investigations with organisms as diverse as higher animals, flowering plants, fungi, single-celled eukaryotes or protistans, and prokaryotes or monerans. Plants occupied a preeminent position as experimental organisms in the critical early period of modern genetics. The historical trend in genetic work, however, as Mettler and Gregg (1969) point out, has been toward the utilization of ever smaller and shorter-cycled organisms, thus passing from plants to Drosophila to Neurospora to bacteria and viruses.

3

The experimental work on higher plants yielded some of the most important concepts of genetics, from the gene through gene systems to the genotype. These and other concepts originating in plant genetics have entered the mainstream of general genetics. Of course plant genetics has benefited reciprocally as a recipient of basic discoveries such as DNA, made first on members of other kingdoms.

The process of generalizing across two or more kingdoms of organisms, although it has proven fruitful in many cases, is also strewn with pitfalls, and various schools of workers have managed to fall into some of them from time to time. There are universals in genetics; there are generalizations valid within a circumscribed class of organisms; and there are generalizations of intermediate scope which hold for one or more kingdoms but not for all forms of life. One can transfer a basic concept, like that of the gene, from one kingdom to another almost with the stroke of a pen; but the concept, once transplanted, may apply to a different set of phenomena and may come to have an altered meaning in its new kingdom. Herein lies the beginning of confusion.

The present book will attempt to review some of the more important concepts in plant genetics, as regards genes, gene systems, linkage systems, and the unified genotype, in conjunction with the experimental evidence on which these concepts are based. It is desirable to view the gene systems and integrated genotypes in a somewhat broader context. Therefore we will follow the ramifications of our central subject into certain peripheral areas, like gene action and development, but we can only treat these tangential subjects in a very general way here.

THE DIPLOID-HAPLOID CYCLE It is convenient at the outset to recapitulate the normal life cycle of a diploid plant. The individual begins as a single-celled zygote derived from the fusion of two gametes, contributed by its female parent and its male parent. Each gamete carries one set of chromosomes and one set of genes, and is accordingly haploid. The zygote thus receives one set of chromosomes and genes from its mother through the female gamete

and another set from its father through the male gamete, and is therefore diploid in its chromosomal and genetic constitution.

The zygote develops into a mature body by a series of mitotic cell divisions which perpetuate its original chromosomal and genetic constitution. There are some exceptions to this rule which do not concern us here. The individual plant then retains throughout its lifetime the particular combination of maternal and paternal chromosomes and genes which it inherited at zygote formation. When it reaches sexual maturity it produces gametes of its own by the process of meiosis. At meiosis, the homologous maternal and paternal genes and chromosome segments become separated and assorted to different haploid gametes.

Each kind of gene may exist in two or more alternative forms or alleles. If a gene *A* is present in two allelic forms, *A* and *a*, different individuals can exist with the genetic constitutions *AA*, *aa*, and *Aa*. An individual or genotype possessing two identical alleles of the same gene or genes, like the *AA* and *aa* individuals above, is said to be homozygous, whereas an individual or genotype carrying dissimilar alleles (*Aa*) is heterozygous.

An *AA* individual produces gametes all of the constitution *A*. Therefore if *AA* individuals interbreed with other *AA* individuals, or reproduce by self-fertilization, their progeny consist uniformly of *AA* genotypes. Similarly, *aa* genotypes produce all *a* gametes and all *aa* progeny. Homozygotes are true-breeding.

But the heterozygote *Aa*, derived from the union of two types of gametes, *A* and *a*, produces the same two types of gametes at meiosis in equal numbers. The random union of the *A* and *a* male gametes with *A* and *a* female gametes at fertilization then yields daughter genotypes *AA*, *Aa*, and *aa* in regular ratios. If the gene *A* controls some visible characteristic present in alternative states, like round versus wrinkled seeds, the progeny of the heterozygote will differ among themselves, or segregate for this character. A heterozygote or hybrid gives variable or segregating offspring.

SEGREGATION IN *PISUM SATIVUM* Mendel's experiment with the garden pea, *Pisum sativum,* dealt with variation in seven charac-

ters in hybrid progenies. The characters in question and their alternative states were as follows:

Form of seeds: round or wrinkled

Color of cotyledons: yellow or green

Color of seed coat: white vs. grayish-brown; correlated with white vs. violet flowers

Shape of seed pods: inflated or constricted

Color of seed pods: green or yellow

Position of flowers: distributed along length of stem or bunched at top of stem

Length of stem: long or short

Mendel crossed true-breeding pea plants exhibiting the contrasting states for each character, and studied the statistical frequency of the contrasting character conditions in the hybrid progeny in the F_1, F_2, F_3, and subsequent generations. He carried different lines to the F_5, F_6, or F_7 generation (Mendel, 1866, 1965).

From the results of these experiments, Mendel was able to infer the essential facts set forth in the preceding section of this chapter as regards the genetical constitution of the parental plants, the hybrids, and their gametes. The cytological facts were added later, by others.

Let us review Mendel's experimental method and results in regard to the inheritance of seed color. The character in question is actually cotyledon color, but it is seen as seed color, and we will refer to it as the latter. Mendel selected 10 true-breeding plants with either green or yellow seeds as parents. He made the cross of green × yellow in both reciprocal directions. Fifty-eight flowers were cross-pollinated to produce F_1 seeds.

The F_1 seeds, borne in pods on the mother plant, were all yellow, irrespective of the direction of the cross. These F_1 seeds were now sown to produce F_1 plants. The flowers on the F_1 hybrids yielded an F_2 generation of seeds by self-fertilization.

The F_2 generation of seeds showed a segregation into the two parental classes of yellow and green seeds. These alternative types were present in the numbers: 6022 yellow seeds and 2001 green seeds. These numbers correspond to a ratio of 3.01 : 1.

The F_3 generation was derived by self-fertilization of various

plants grown from either green or yellow F_2 seeds. The F_2 plants from green seeds bred true on selfing, giving uniformly green seeds in F_3. Some of the F_2 plants grown from yellow seeds also bred true for the yellow-seeded condition in F_3 and later generations. But other F_2 plants grown from yellow seeds, on self-fertilization, yielded progenies of F_3 seeds which segregated for cotyledon color. Yellow and green seeds reappeared again in the F_3 generation derived from these F_2 parents in a 3 : 1 ratio.

The true-breeding and the segregating yellow-seeded F_2s were found to occur in definite proportions. Out of 519 plants raised from yellow seeds, 353 or about ⅔ produced segregating progenies of F_3 seeds, whereas 166 or about ⅓ of the yellow-seeded F_2 plants were constant for seed color in F_3. This division between segregating and nonsegregating families occurred in subsequent generations from F_4 to F_7.

Mendel obtained similar results for the six other character differences which he studied in the pea. His F_2 data are summarized in Table 1. The average ratio for all segregating characters combined in F_2 is actually 2.98 : 1 or essentially 3 : 1 (Mendel, 1866, 1965).

The 3 : 1 ratio for yellow and green seeds, and the further 1 : 2 ratio for constant or segregating yellow seeds noted above, combine to give a basic 1 : 2 : 1 ratio in the F_2 generation and in the hybrid fractions of subsequent generations. Symbolizing yellow and green seeds by B and b, respectively, Mendel wrote the basic segregation ratio as $B + 2Bb + b$ (we write it $BB + 2Bb + bb$ today).

This formula expresses the hypothesis that the hybrid Bb, though phenotypically yellow-seeded itself, produces two types of pure gametes, B and b, in equal numbers. Mendel tested this deduction by backcrossing the yellow-seeded hybrid Bb reciprocally to the parental type bb, and finding, as expected, a 1 : 1 ratio of yellow and green in the backcross generation. The data supporting this point are included with other similar data in the section of Mendel's paper on "the reproductive cells of the hybrids."

Years later Correns (1900), without prior knowledge of Mendel's work, found the same pattern of segregation for seed color in the pea. His F_2 population of seeds consisted of 1394 yellow and 453 green seeds, which is practically a 3 : 1 proportion. Correns's

TABLE 1·

F₂ SEGREGATION RATIOS OBSERVED BY MENDEL FOR SEVEN PAIRS OF CHARACTER DIFFERENCES IN *PISUM SATIVUM* (MENDEL, 1866, 1965)

Character	No. of each type in F_2	Ratio
Seed form	5474 round 1850 wrinkled	2.96 : 1
Cotyledon color	6022 yellow 2001 green	3.01 : 1
Seed coat color	705 grayish-brown 224 white	3.15 : 1
Pod shape	882 inflated 299 constricted	2.95 : 1
Pod color	428 green 152 yellow	2.82 : 1
Flower position	651 axial 207 terminal	3.14 : 1
Stem length	787 long 277 short	2.84 : 1

F_3 and F_4 generations divided into segregating and constant families in the same manner as had been described by Mendel. Correns thus independently discovered the phenomenon of regular segregation on the basis of parallel experiments with the same plant materials.

Mendel's results with respect to seed color in peas were confirmed at the same time by Tschermak (1900). Shortly thereafter, in the years immediately following the rediscovery of Mendel's laws, these results were confirmed again by Bateson and others.

INDEPENDENT ASSORTMENT IN *PISUM SATIVUM* Mendel next undertook to determine whether the seven pairs of character differences are correlated or independent in inheritance. Is the segregation in one character linked with, or is it separate from, the segregation in other characters?

The analysis of this problem begins with the character combination of seed form and cotyledon color (Mendel, 1866, 1965). The cross was: female parent plants with round yellow seeds × pol-

len parents with wrinkled green seeds. The experimental results can be summarized as follows:

P   round yellow × wrinkled green

F_1 round yellow

F_2 315 round yellow
       101 wrinkled yellow
       108 round green
        32 wrinkled green

F_3 from wrinkled green F_2, nonsegregating
       from round green F_2, segregating for seed form, constant for
          seed color
       from wrinkled yellow F_2, segregating for seed color, constant
          for seed form
       from round yellow F_2, segregating for both characters

Mendel thus observed four classes of phenotypes in the F_2 and F_3 progeny of a dihybrid cross. The phenotypes appeared in a 9 : 3 : 3 : 1 or dihybrid ratio in F_2. The four phenotypic classes could be subdivided further into constant versus hybrid types. Mendel therefore concluded that "the offspring of the hybrids appeared . . . under nine different forms," or in other words, that nine genotypes were present.

The numerical relations between these nine classes of genotypes, moreover, could be resolved into a combination of two separate 1 : 2 : 1 ratios, $AA + 2Aa + aa$ and $BB + 2Bb + bb$ indicating the independence of the two segregating characters. Their independence and separableness were confirmed by the appropriate backcrosses of the hybrid $AaBb$ to the parental types (Mendel, 1866, 1965).

Mendel went on to consider the results of a trihybrid cross involving the characters of seed form, cotyledon color, and seed coat color. The parental character combinations are round, yellow, gray-brown seeds in the female parents, and wrinkled, green, white seeds in the pollen parents. The F_2 generation derived from this cross contained all possible combinations of the three pairs of character differences, both the parental and the various new combinations, or recombinations. Mendel stated in a summary fashion, without presenting data, that the other four characters studied also showed independence, or independent assortment as we call it now.

TABLE 2

GENE SYMBOLS AND LINKAGE GROUPS FOR THE CHARACTERS STUDIED BY MENDEL IN *PISUM SATIVUM* (DATA FROM LAMPRECHT, 1961A, 1961B)

Character	Mendel's symbolism	Modern gene symbols	Linkage groups
Seed form	A	R	VII
Seed color (cotyledon color)	B	I	I
Seed coat color (and flower color)	C	A	I
Pod shape	D *	V	IV
Pod color		Gp	V
Flower position		Fa	IV
Stem length	G *	Le	IV

* Used in letter to Nägeli, 1867.

Modern studies confirm this general conclusion with one exception. The relevant part of Lamprecht's summary of the factorial genetics of *Pisum sativum* is shown in Table 2. Mendel's seven monofactorial characters are determined by genes located in four linkage groups. When two genes occur in the same linkage group they are usually loosely linked, with fairly free recombination. Pod shape and stem length in linkage group IV, however, show definite linkage, with a restricted rate (13%) of recombination between them (Lamprecht, 1961a, 1961b).

PARTICULATE INHERITANCE Mendel's theory of heredity is founded on the phenomena of segregation and independent assortment in statistically precise ratios. From these phenomena he deduced the existence of different kinds of gametes containing the determinants of different pairs of character differences. These determinants are present in the gametes in single form for any given character (*A* or *a*) and in all possible combinations for two or more characters (*AB, Ab, aB, ab*). The different classes of gametes, produced in equal numbers, unite at random in fertilization to give the various classes of phenotypes which appear in regular